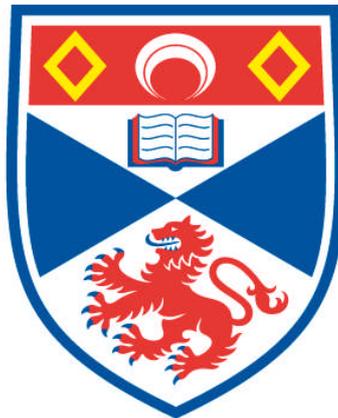


**DISTRIBUTION, SOCIAL STRUCTURE AND HABITAT USE OF
SHORT-FINNED PILOT WHALE, *GLOBICEPHALA*
MACRORHYNCHUS, IN THE CANARY ISLANDS**

Antonella Servidio

**A Thesis Submitted for the Degree of PhD
at the
University of St Andrews**



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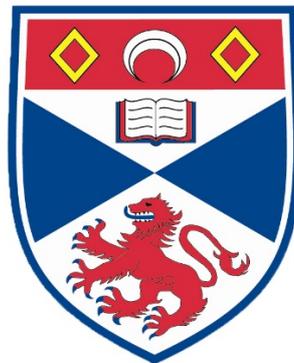
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OF SHORT-FINNED PILOT WHALE, *Globicephala macrorhynchus*,
IN THE CANARY ISLANDS**

Antonella Servidio

**A THESIS SUBMITTED IN PARTIAL FULFILMENT FOR THE DEGREE OF PHD
AT THE
UNIVERSITY OF ST. ANDREWS**



SUBMITTED JULY, 2013

ABSTRACT

The Canary Archipelago is considered one of the planet's biodiversity hotspots and the short-finned pilot whale is a key species in need of conservation measures. To address a lack of knowledge, almost 2,000 day-surveys were conducted (1999-2012) resulting in 1,094 short-finned pilot whale sightings. The species was recorded year-round and distributed non-uniformly around the archipelago, with greater densities concentrated in patchy areas mainly on the leeward side of the main islands. A total of 1,320 well-marked individuals were identified, which exhibited a large degree of variability in site fidelity (from core residents to transients). Evidence of an island-associated sub-population and a transient one was found. Longitudinal data were used to infer population structure and estimate abundance, while a spatial modelling approach was used to study spatio-temporal patterns in habitat use, distribution and abundance.

Spatial modelling revealed habitat preferences in areas between depths of 1000m and 1500m, and higher densities in the south-west of Tenerife and La Gomera (117 short-finned pilot whales recaptured within the two islands). Abundance of 1,980 individuals (CV: 0.33, 95% CI=1,442 – 2,324) was estimated for the entire archipelago, with higher density predicted during the summer months. Mark-recapture analysis estimated 636 resident individuals (CV=0.028, 95%CI=602-671) in the southwest waters of Tenerife between 2007 and 2009.

The social and temporal analyses of the behavioural relationships between pairs of individuals revealed a well-differentiated society with long-lasting and non-random social structure built of constant companions. A hierarchical social system is proposed composed of a population encompassing several clans of pilot whales, each one containing several pods. Nine long-term units were identified with a high degree of association (0.62 - 0.83).

This study, the first to provide combined results on distribution, habitat use, and social structure of the species, provides essential information towards the development of recommendations for much needed conservation measures.

DECLARATIONS

CANDIDATE'S DECLARATIONS:

I, Antonella Servidio, hereby certify that this thesis, which is approximately 125,527 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2007 and as a candidate for the degree of Doctor of Philosophy in September 2007; the higher study for which this is a record was carried out in the University of St Andrews between 2007 and 2013.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy at the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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ACKNOWLEDGEMENTS

This work started a long time ago, when I didn't really know what doing a PhD would mean. It was no always an easy process, but anyhow always challenging and rewarding. It has encompassed fundamental years of my life, different landscapes, and many people who, in a way or in another, contributed to this long delivery.

To my family. Grazie per il vostro appoggio, sempre, e incondizionato. Mi avete trasmesso forza, calore, orgoglio... Grazie a Nayra che mi ha dato la grande emozione di essere la sua mamma e di avermi fatto felice e sorridere anche nei momenti di stanchezza. A Daniele, grazie grazie grazie per essermi stato vicino, per avermi sopportato, capendo quanto fosse importante per me questo lavoro, per avermi spinto a non perdermi d'animo e per essere un ottimo babbo. Grazie ai miei genitori e a mia sorella, senza dei quali non avrei neppure cominciato.

Thank, with the utmost respect, to my supervisors, who made this work possible. To Phil Hammond, who believed in me and with a great patience and professionalism guided my steps. Thanks for the continuous support and, at the same time, for allowing me great freedom to make my own choice. Thanks for leading me to improve my analytics skills. And thank you for being always so positive, transmitting me confidence Because when you said that I could make it, I believed you and I finally did. Thanks to Vidal Martín, por haberme abierto las puertas de este fantástico y emocionante mundo, por haberme enseñado, y por haberme apoyado a lo largo de todo este tiempo. Thanks to Ana Cañadas, amiga y valiosa científica de quien he aprendido mucho, y no solamente de modelización.

Gracias a la Sociedad para el Estudio de los Cetáceos en el Archipiélago Canario (SECAC), que me acogió entre su equipo hace mucho tiempo, y entre proyectos y proyectos, me ofreció la oportunidad de trabajar con los calderones, metiendo a mi disposición experiencia, material, infraestructura, recursos y personal.

Thanks to mis amigos y compañeros de trabajo. Valiosos investigadores, con quien compartí muchos (y largos) momentos de campo y de oficina. Gracias a Silvana Neves, por haber sido presente, ayudándome y apoyándome siempre. Gracias a Mónica y a Kike Pérez-Gil, por todas las risas en los momentos de cansancio, por no haberme dejado tirar la esponja en los momentos difíciles, por su profesionalidad, y por haberme ayudado en la análisis y maquetación de este tesis, y ...gracias a todo el resto de la familia Pérez-Gil, que me acogió en su casa, me alimentó, me hizo sentir parte de ella. Gracias a Nuria

Varo por haber compartido con tanta profesionalidad los largos momentos de zodiac bajo el sol, por haberme siempre transmitido positividad y amistad.

Gracias a Erika Urquiola que por primera creyó en mi, y me ayudo profesionalmente y personalmente durante mis años en Canarias; gracias a Sandra, Leire y Marisa por haber compartidos muchos momentos dentro, pero también más que unos, fuera del trabajo. Gracias a todas las personas que participaron en el trabajo de campo, desde Cristina a Rocío, desde Mercedes a Marimar.

Thanks to Ricardo Antunes for his help in understanding how to approach the short-finned pilot whale social structure. Thanks to Luis Freitas and thanks to Filipe Alves for sharing the same... "interests" and for his advices. Gracias a Dr. Antonio Fernández y Dr. Manuel Arbelo del Instituto de Sanidad Animal y Seguridad Alimentaria de la Universidad de Las Palmas de Gran Canaria, por la colaboración en la información aportada. Gracias a Renaud de Stephanis por sus consejos e ideas que me ayudaron a ver las cosas en un contexto más amplio.

Gracias a Paqui, Iván i Ían por su amistad y calor familiar. Gracias a mis amigos de conferencias. Una pequeña comunidad desperdigada por varios mares de la tierra, que comparten la misma pasión por los cetáceos,... y por una cervecita en compañía después de las charlas.

Y gracias a los calderones de Canarias... volveremos a vernos en vivo, y les reconoceré uno a uno.

TABLE OF CONTENTS

CHAPTER 1 GENERAL INTRODUCTION	1
1.1 INTRODUCTION	2
1.1.1 The Canary Islands archipelago	5
1.2 STUDY AREA.....	6
1.3 BIODIVERSITY AND CONSERVATION IN THE CANARY ISLANDS	9
1.4 PILOT WHALE (<i>Globicephalinae</i>)	11
1.4.1 Phylogeny, Systematic and Distribution	11
1.4.2 Morphology.....	12
1.4.3 Life History	13
1.4.4 Diet and Foraging	15
1.4.5 Social Structure.....	16
1.4.6 World Threats And Conservation Issues	19
1.4.7 Short-Finned Pilot Whales in the Canary Islands	28
1.5 OBJECTIVES AND IMPORTANCE OF THE STUDY.....	31
1.6 LITERATURE CITED	34
CHAPTER 2 SITE FIDELITY AND MOVEMENT PATTERNS OF SHORT-FINNED PILOT WHALES WITHIN THE CANARY ISLANDS.....	56
2.1 INTRODUCTION	57
2.1.1 Range and Distribution Patterns of Short-Finned Pilot Whales in the Canary Islands	60
2.2 GENERAL METHODOLOGY.....	63
2.2.1 General Data Collection Protocol	63
Vessels, Equipment On Board and Crew.....	63
Survey Design	66
Searching Effort and Data Collection	66
Definition	68
2.2.2 Material Available For This Study	70
Archive Data.....	70
Surveys Conducted During the PhD Period	73
2.2.3 Data Organization.....	76
Photographic and Video Footage Material.....	77
Group size.....	80
2.2.4 Data Analysis	80
Occurrence Patterns and Relative Abundance	80
Residency and Site Fidelity	81

<i>Lagged Identification Rate</i>	83
<i>Movement Patterns</i>	84
<i>Match Index</i>	85
<i>Ranging Pattern</i>	86
2.3 RESULTS	88
2.3.1 <i>Occurrence Patterns, Sighting Distribution and Survey Effort</i>	88
2.3.2 <i>Short-Finned Pilot Whale Sightings: Distribution and Relative Abundance</i> .	91
<i>Group dynamics</i>	96
<i>Behaviour</i>	100
<i>Photo-identification analysis</i>	100
<i>Distinctiveness and mark change</i>	101
<i>Discovery curves</i>	101
<i>Lagged Identification Rates (LIR)</i>	102
<i>Recaptures and movement patterns</i>	104
<i>Site fidelity</i>	109
<i>Ranging patterns</i>	111
2.4 DISCUSSION	114
2.5 CONCLUSION	122
2.6 LITERATURE CITED	124
CHAPTER 3 LONG-TERM SOCIAL STRUCTURE, COMPOSITION AND STABILITY OF SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS	137
3.1 INTRODUCTION	138
3.2 METHODOLOGY	143
3.2.1 <i>Study Area and Sampling Methods</i>	143
3.2.2 <i>Data Selection and Organization</i>	144
<i>Sightings</i>	144
<i>Sampling Period</i>	144
3.2.3 <i>Preliminary Analysis</i>	145
3.2.4 <i>Analytical Treatment</i>	145
<i>General Measure of Association</i>	146
<i>Social Differentiation and Precision Analysis</i>	147
<i>Preferred Companionship</i>	147
<i>Community Structure</i>	149
<i>Delineating Stable Groups (Units)</i>	154
3.3 RESULTS	155
3.3.1 <i>Short-Finned Pilot Whale Population in Canary Islands</i>	155
<i>Dyadic Associations</i>	155
<i>Preferred Companionship</i>	157
<i>Temporal Aspects of Social Structure: Lagged Association Index</i>	159
<i>Association Levels: Social Network</i>	160
<i>Association Levels: Cluster Analysis</i>	163
<i>Key Units as Stable Social Groups</i>	168
3.3.2 <i>Short-Finned Pilot Whale Population in Tenerife and La Gomera</i>	172
<i>Preferred Companionship</i>	175
<i>Temporal Aspects of Social Structure: Lagged Association Index</i>	175
<i>Association Levels: Social Network</i>	177
<i>Association Levels: Cluster Analysis</i>	181

<i>Spatial Cluster Segregation</i>	185
3.4 DISCUSSION	189
3.4.1 Methodological Considerations	189
<i>Dataset Selection</i>	189
<i>Sex Differentiation</i>	191
<i>Defining a Group</i>	191
3.4.2 Association Patterns and Gregariousness	192
3.4.3 Short-Finned Pilot Whale Society	194
3.4.4 Future Steps for Conservation	200
3.5 CONCLUSIONS	202
3.6 LITERATURE CITED	204
CHAPTER 4 ABUNDANCE OF THE SHORT-FINNED PILOT WHALE IN SOUTHWESTERN TENERIFE	213
4.1 INTRODUCTION	214
4.2 MATERIALS AND METHODS	219
4.2.1 Data Selection	219
4.2.2 Data Collection	219
4.2.3 Image Selection and Analysis	220
4.2.4 Data Analysis	220
<i>Overview of capture-recapture models</i>	220
<i>General assumptions</i>	221
<i>Open population model</i>	222
<i>Overdispersion</i>	224
<i>Closed population model</i>	225
<i>Data Organization</i>	226
<i>Model selection</i>	227
<i>Correction factor for abundance estimation</i>	229
4.3 RESULTS	231
4.3.1 Surveys and Sightings	231
4.3.2 Photo-Identification and Data Organization	231
4.3.3 Sightings and Resightings	234
4.3.4 Abundance Estimates	239
<i>Open population models</i>	240
<i>Closed population models</i>	241
4.4 DISCUSSION	244
4.4.1 Abundance Estimates	244
<i>Mark loss and mismatching</i>	245
<i>Capture probability</i>	245
<i>Individual heterogeneity of capture probabilities</i>	246
<i>Geographic and demographic closure</i>	248
<i>Models and estimates</i>	249
4.4.2 Biological Relevance	251
4.5 CONCLUSIONS	254
4.6 LITERATURE CITED	255

CHAPTER 5 MODELLING THE HABITAT USE OF SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS	265
5.1 INTRODUCTION	266
5.1.1 Short-Finned Pilot Whales in the Canary Islands	269
5.2 METHODOLOGY.....	270
5.2.1 Study area.....	270
5.2.2 Sighting Data and Survey Effort.....	270
5.2.3 Data Synthesis.....	273
5.2.4 Environmental Data	274
5.2.5 Data Analysis	276
Detection function modelling.....	277
Modelling abundance of groups	278
Modelling group size	279
Abundance estimation.....	279
Uncertainty estimation	279
Habitat usage	280
5.3 RESULTS.....	280
5.3.1 Detection Function.....	281
5.3.2 Habitat Modelling.....	283
Group size and abundance of groups.....	283
Biological factors	300
5.4 DISCUSSION	308
5.4.1 Abundance and Habitat Usage	309
5.4.2 Methodological Issues	318
Movement in response to survey vessels	318
Rounding angles and distances.....	319
Habitat characterization	319
5.5 CONCLUSIONS.....	320
5.6 LITERATURE CITED	321
CHAPTER 6 FINAL DISCUSSION	332
6.1 DISCUSSION	333
6.1.1 Thesis Summary.....	333
6.1.2 Distribution and Habitat Use.....	336
6.1.3 Patterns of Residency and Inter-Island Movements	337
6.1.4 Foraging Behaviour and Multi-Species Competition.....	340
6.1.5 Breeding Behaviour.....	342
6.1.6 Population Structure	343
6.1.7 Implications for Conservation	345
6.1.8 Future Studies	352
6.2 LITERATURE CITED	356

ANNEX 1	364
ANNEX 2	366
ANNEX 3	377
ANNEX 4	397
ANNEX 5	404
ANNEX 6	406
<i>A6.1: PRINCIPAL THREATS ON PILOT WHALES IN CANARY ISLANDS</i>	<i>408</i>
<i>NOISE IMPACT:</i>	<i>408</i>
<i>MARITIME TRAFFIC (FERRIES)</i>	<i>411</i>
<i>WHALE WATCHING</i>	<i>413</i>
<i>ARTISANAL FISHERIES</i>	<i>414</i>
<i>HABITAT DEGRADATION</i>	<i>415</i>
<i>A6.2: FURTHER CONSIDERATIONS</i>	<i>417</i>
<i>A6.3: LITERATURE CITED</i>	<i>422</i>

LIST OF FIGURES

Figure 1.1: Canary Islands (from left to right): El Hierro (south), La Palma (north), La Gomera, Tenerife, Gran Canaria, Fuerteventura, Lanzarote.....	7
Figure 1.2: Canary Islands showing the designated SACs for <i>Tursiops truncatus</i>	11
Figure 2.1: Research platforms: “Chacalote”, “Grampus”, “Oso Ondo”, and “Multiacuatic” (from top left).	64
Figure 2.2: Study area divided in seven different locations: 1) El Hierro; 2) La Palma; 3) La Gomera; 4) Tenerife; 5) Gran Canaria; 6) Lanzarote; 7) Fuerteventura.....	76
Figure 2.3: Track-lines conducted on effort at sea by SECAC since 1999 around the Canary Island on board different vessel types: semi-rigid inflatable boats (red), dedicated motor boats (blue), sailing boats (black), and opportunist vessels such as whale-watching boats and ferries (green). Off-effort track-lines are indicated in grey.	90
Figure 2.4: Total survey effort plotted for grid cells (each two minutes of latitude by two minutes of longitude) conducted at sea by SECAC since 1999 around the Canary Islands waters.....	90
Figure 2.5: Short-finned pilot whale sightings on and off effort, recorded between 1999-2012 in the Canary Islands.....	92
Figure 2.6: Short-finned pilot whale sightings in association with bottlenose and spotted dolphins, recorded between 1999-2012 in the Canary Islands.	93
Figure 2.7: Mean cell encounter rate ER2 in the Canary Islands (sightings/Nm surveyed in each cell).	94
Figure 2.8a-b: Frequency distributions of short-finned pilot whale sightings in the Canary Islands (per 100 h effort), based on (a) water depth; mean=1,077.5 m, SE=16.9), and (b) distance from coast; mean=5.8 km, SE=0.14).	95
Figure 2.9a-b: Distribution of short-finned pilot whale sightings, based on (a) mean water depth and (b) distance from coast. Data are presented using box-and-whisker plots per each island of the archipelago: the middle line shows the median value, the upper and lower lines of the box show 75 th and 25 th percentile, respectively. The ends of the upper and lower vertical lines indicate the minimum and maximum data values, unless outliers are present (*).	96
Figure 2.10: Frequency distribution of short-finned pilot whale group size based on minimum photo-identification and field counts between 1999 and 2012 in the different island of the Canary Archipelago. Groups ranged from one to 80 individuals (mean=16.2; SE=0.5), with most groups (86%) encountered containing between one and 25 whales.	97
Figure 2.11a-b: Mean group size of short-finned pilot whale groups recorded (a) in the islands of La Palma (LP) La Gomera (LG), Tenerife (TN), Gran Canaria (GC), and Lanzarote-Fuerteventura (LZ_FV), and (b) during seasons, between 1999 and 2012. Data are presented using box-and-whisker plots, middle line shows median value, upper and lower lines of box show 75 th and 25 th percentile, respectively. The ends of the upper and lower vertical lines indicate the minimum and maximum data values, unless outliers are present (*, in grey).....	98
Figure 2.12: Group composition for groups of short-finned pilot whales encountered between 2004 and 2010 in Tenerife (TN), Gran Canaria (GC), La Gomera (LG), and Lanzarote-Fuerteventura (LZ_FV): mean proportion of adults, indeterminates, juveniles, calves, and new-borns are presented with respective standard error.....	99

Figure 2.13a-b: (a) Group size differences based on the presence/absence of males (without males, with males and no females, females and males in the same group), (b) group size differences between groups with and without calves.	99
Figure 2.14: Discovery curve showing the number of new well-marked short-finned pilot whales identified each day between 1999 and 2012 in the Canary Islands (a), and of new well-marked in Gran Canaria (b), in Tenerife (c), and La Gomera (d).	102
Figure 2.15: Lagged identification rates (LIRs) for all individual short-finned pilot whales identified in the Canary Islands, between 1999 and 2012; the graph depicts the probability that a whale photographed at time "0" will be identified again at time x within the study area. Data points are represented as circles and the best fitting model (Emigration + Re-immigration) is displayed as a blue line.	103
Figure 2.16: Frequency histogram of the number of times that uniquely marked short-finned pilot whales were captured (A=adults, IND= indeterminate, J= juvenile, C=calves, N=neonates) in the Canary Islands, between 2004 and 2012.....	105
Figure 2.17: Frequency of the number of years between the first and last recapture of individual short-finned pilot whales in the different islands of the archipelago between 1999 and 2012.	106
Figure 2.18: Frequency distribution of Euclidean distance (km) between consecutive sightings of short-finned pilot whales in the Canary Islands.	109
Figure 2.19: Residency categories ("transient", "occasional", "resident", and "core resident") of well-marked, adult and indeterminate short-finned pilot whales sighted in the different Canary Islands, between 1999 and 2012.....	111
Figure 2.20a-b: Ranging patterns of the 193 well-marked, adult and indeterminate short-finned pilot whales sighted at least ten times in the different Canary Islands, between 1999 and 2012, estimated by fixed kernel a) at 95% UD and b) at 50% UD.	113
Figure 2.21: Ranging patterns of the 193 well-marked, adult and indeterminate short-finned pilot whales sighted at least ten times in the different Canary Islands, between 1999 and 2012, estimated by fixed kernel at 50% UD. "Transient" animal sightings are shown in the map as red points.	114
Figure 3.1: Discovery curve showing the cumulative number of short-finned pilot whale individuals identified versus the cumulative number of total identifications recorded (sampling unit set to one day) for well-marked adults and indeterminates. (a) complete dataset of individuals identified in the Canary Islands between 1999 and 2012; (b) only "core residents" and "residents" in good coverage sightings.....	156
Figure 3.2: Distribution of association indices for well-marked core residents and residents identified in the Canary Islands between 1999 and 2012: Distribution of a) half weight association index; b) maximum association index; c) sum of associates for each individual.....	157
Figure 3.3: SLAR for short-finned pilot whales identified since 1999 in Canary Islands. The moving average curve of 10,000 associations (green line) and the curve with no moving average dots are shown in the graph together with approximate standard error bars (produced by jackknife on each sampling period). The best model curve (Model CA - "casual acquaintances" $g'=0.039431*\exp(-0.0001292*td)$) is shown, as well as the null association rate (Full).....	159
Figure 3.4: Social network diagram of all well-marked short-finned pilot whales documented off the Canary Islands, from 2004 through 2012. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Core residents are shown in blue, residents in red, visitors in green, and transients in grey (see Chapter 3 for definitions).	161

- Figure 3.5:** Enlargement of main social network cluster taken from Figure 3.14, showing only core residents (in blue) and residents (in red). 163
- Figure 3.6:** Knot-diagram for well-marked “core resident” and “resident” adult and indeterminate pilot whales identified in Canary Islands between 1999 and 2012. 164
- Figure 3.7:** Modularity-G (Type 1 for gregariousness) and Modularity-P (Type 2 for permutations) for well-marked “core resident” and “resident” adult and indeterminate pilot whales identified in the Canary Islands between 1999 and 2012. Modularity-G suggests 0.658 as best community division value, with an association index of 0.0342. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations)..... 165
- Figure 3.8:** Average-linkage cluster dendrogram (based on half-weight association index) of well-marked “core resident” and “resident” adult and indeterminate pilot whales identified in the Canary Islands since 1999, in good coverage sightings. Cophenetic correlation coefficient=0.95. The 19 cluster numbers are indicated in the boxes. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations), while the blue line represents the cluster division based on knot. 166
- Figure 3.9:** Average-linkage cluster dendrogram (based on the half-weight association index) of well-marked “core resident” and “resident” adult and indeterminate pilot whales identified in the Canary Islands since 1999, in sightings with good photo-identification coverage. Only “key individuals” and their “constant companions” (selected based on their longitudinal sighting histories) are shown in colour, while all the remaining individuals are in grey. 171
- Figure 3.10:** Average linkage cluster analysis based on the half-weight index of key individuals (marked with “*”) and their constant companions selected over the entire Canary Islands short-finned pilot whale population (1999-2012). The CCC of 0.993 indicated a good fit of the hierarchical structure ($Q=0.729$, at $AI=0.552$). 172
- Figure 3.11:** Discovery for new individuals showing the cumulative number of short-finned pilot whales identified versus the cumulative number of identifications recorded (sampling unit set to one day) for well-marked adult and indeterminate whales seen at least once a month for eight months in the islands of La Gomera and Tenerife, between 2004 and 2010 in sightings with good photographic coverage. 173
- Figure 3.12:** Association index distribution for short-finned pilot whales seen at least once a month for eight months, between 2004 and 2010 in Tenerife and La Gomera: a) Half weight association index; b) Maximum association index, c) Sum of associates for each individual. 174
- Figure 3.13:** SLAR for the most frequently seen short-finned pilot whales (seen at least once a month for eight months) identified between 2004 and 2010 in La Gomera and Tenerife, during sightings with good photo-identification coverage. The moving average curve of 1,000 associations (green line) is shown in the graph together with approximate standard error bars (produced by jackknife on each sampling period). The best model curves (Model CC - “Constant Companions”: $g' = 0.097583$ (s.e. 0.010829), and “Model CA - casual acquaintances” $g'=0.098756*\exp(-4.9852e-05*td)$) were also included, as well as the null association rate. 176
- Figure 3.14:** Social network diagram of the 134 individual short-finned pilot whales identified at least once a month for eight months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010). Each different node colour indicates the cluster to which each individual belonged. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Tie strengths of one are indicated by black lines, higher than 0.5 in blue, and

lower than 0.5 in grey. The size of the node increases with the degree. Enlargement of the social network diagram is shown in Annex 3: Figure A3.7..... 179

Figure 3.15: Knot-diagram for the most frequently sighted (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. A knot was suggested at an association index of 0.688, 0.511, 0.120..... 181

Figure 3.16: Modularity-G (Type 1 for gregariousness) and Modularity-P (Type 2 for permutations) diagram for most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Modularity-G suggested 0.68463 as the best community division value, with an association index of 0.049389. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations)..... 182

Figure 3.17: Average-linkage cluster dendrogram (based on the half-weight association index) of the most frequently sighted (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Cophenetic correlation coefficient=0.95. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations), while the blue lines represent the cluster divisions based on knots. 183

Figure 3.18a: Range of clusters 1 - 6, estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) of most frequently seen (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings..... 187

Figure 4.1: Fin distinctiveness profiles and marking categories per each age class of the identified animals represented by Q1 and Q2 quality pictures..... 232

Figure 4.2: Distribution of capture frequencies for poorly marked and well-marked short-finned pilot whales..... 233

Figure 4.3: Recapture frequency of poorly marked and well-marked individuals (A= adults; IND= indeterminates; J= juveniles; C = calves; N = neonates). 234

Figure 4.4: Recapture frequencies of well-marked short-finned pilot whales: data set "-1". 234

Figure 4.5: Recapture frequencies of well-marked short-finned pilot whales: data set "-2". 235

Figure 4.6: Discovery curve of newly identified short-finned pilot whales between April 2007 and March 2009: all identified individuals (blue curve) and well-marked short-finned pilot whales (green curve). 237

Figure 4.7: Dataset without first capture: discovery curve of newly identified short-finned pilot whales between April 2007 and March 2009: all identified individuals (complete data set: blue curve), well-marked short-finned pilot whales (complete data set: green curve), and subset "-1" of well-marked short-finned pilot whales (subset without the first capture: red curve). 238

Figure 4.8: Data set without first capture: discovery curve of newly identified short-finned pilot whales between April 2007 and March 2009: all identified individuals (complete data set: blue curve), well-marked short-finned pilot whales (complete data set: green curve), and subset "-2" of well-marked short-finned pilot whales (subset without the first recapture: orange curve). 239

Figure 4.9: Capture probabilities for the Mtbh model for the Total dataset. Capture probabilities of the two putative populations (Mean $p_1 = 0.018$, $SE = 0.003$; Mean $p_2 = 0.246$, $SE = 0.029$).....	243
Figure 4.10: Capture probabilities for the Mth model for “-2” data set: encounter and recapture probabilities (constrain $p(t) = c(t)$) of the two putative populations (Mean $p_1 = 0.078$, $SE = 0.016$; Mean $p_2 = 0.350$, $SE = 0.036$).....	243
Figure 5.1: Study area in the Canary Islands, divided in the three regions: western islands (El Hierro, La Palma, La Gomera, Area 1); Tenerife (Area 2); eastern islands (Gran Canaria, Fuerteventura, Lanzarote, Area 3).	271
Figure 5.2: Areas covered by sea survey, stratified into different layers based on methodology and platform used: green tracklines A) indicate inflatable boats and small artisanal fishing vessels; black tracklines B) indicate dedicated research vessels, and red tracklines C) indicate ferries.	272
Figure 5.3: Sightings of short-finned pilot whales on effort (black dots) and off effort (red dots), between 1999 and 2012 in the study area in the Canary Islands.	273
Figure 5.4: Frequency distribution of perpendicular distance distribution from the transect line, pooled over the observed covariate. The continuous curves represent the fitted detection functions. a) 0-P.L.: inflatable and fishing boats; b) 1+2-P.L.: sailing boats and research vessels; c) 3-P.L.: ferries.....	282
Figure 5.5a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict (a) abundance of groups and (b) group size of short-finned pilot whales for the whole study area between 1999 and 2012.	284
Figure 5.6: Surface map of predicted short-finned pilot whale abundance for the whole study area between 1999 and 2012. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.	285
Figure 5.7: Surface map of predicted short-finned pilot whale abundance for the whole study area between 1999 and 2012, where dots in red indicate short-finned pilot whales' sightings recorded on effort, and dots in black the ones recorded off effort.	286
Figure 5.8: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of groups during winter (a) and summer (b) seasons of short-finned pilot whales for the whole study area between 1999 and 2012.....	287
Figure 5.9: Shapes of the functional forms of the smoothed covariates used in modelling to predict group sizes during winter (a) and summer (b) seasons of short-finned pilot whales for the whole study area between 1999 and 2012.	287
Figure 5.10a-b: Surface map of predicted seasonal abundance of short-finned pilot whales for the whole study area between 1999 and 2013: a) summer: December-May, b) winter: June-November. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.....	289
Figure 5.11a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict (a) abundance of groups and (b) group sizes of short-finned pilot whales in the western islands of La Palma, El Hierro, and La Gomera, between 2004 and 2012.	290
Figure 5.12: Surface map of predicted short-finned pilot whale abundance for the western islands of El Hierro, La Palma and La Gomera between 2004 and 2012. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red. The black dots indicate short-finned pilot whale sightings recorded on effort.....	290
Figure 5.13a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group (a) and group sizes (b) of short-finned pilot	

whales in the eastern islands of Gran Canaria, Lanzarote, and Fuerteventura between 1999 and 2012.	291
Figure 5.14: Surface map of predicted short-finned pilot whale abundance for the eastern islands of Gran Canaria, Lanzarote, and Fuerteventura between 1999 and 2012. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red. The black dots indicate short-finned pilot whale sightings recorded on effort. ..	292
Figure 5.15: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whales in Tenerife between 2002 and 2010.	293
Figure 5.16: Surface map of predicted short-finned pilot whale abundance for Tenerife between 2001 and 2010. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red. The black dots indicate short-finned pilot whale sightings recorded on effort.....	293
Figure 5.17: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whales in Tenerife in 2002-2006 (a), 2007 (b), 2008 (d), and 2009-2010.	295
Figure 5.18a-d: Surface map of predicted short-finned pilot whale abundance in Tenerife a) 2002-2006; b) 2007; c) 2008; d) 2009-2010. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.	296
Figure 5.19a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group during winter (a) and summer (b) seasons of short-finned pilot whales in the island of Tenerife between 2002 and 2010.	297
Figure 5.20: Shapes of the functional forms of the smoothed covariates used in modelling to predict group sizes during winter season of short-finned pilot whales in the island of Tenerife between 2001 and 2010.	297
Figure 5.21a-b: Surface map of predicted seasonal abundance of short-finned pilot whales for the island of Tenerife between 2002 and 2010: a) summer: December-May, b) winter: June-November. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.....	299
Figure 5.22a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whale abundance in the Canary Islands between 1999 and 2012 during a) feeding; b) resting; c) travelling; d) socialising.	301
Figure 5.23: Shapes of the functional forms of the smoothed covariates used in modelling to predict group size of short-finned pilot whale abundance in the Canary Islands between 1999 and 2012 during travelling behaviour.	301
Figure 5.24a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whale in the island of Tenerife, between 2002 and 2010 during a) feeding; b) resting; c) travelling; d) socialising.	302
Figure 5.25a-d: Surface map of predicted short-finned pilot whale abundance in the island of Tenerife between 2002 and 2010 during a) feeding; b) resting; c) travelling; d) socialising. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.....	303
Figure 5.26a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whales in the Canary Islands (top) and in Tenerife (bottom), between 2002 and 2010: with (a and c) and without (b and d) bottlenose dolphins.	304

Figure 5.27a-c: Shapes of the functional forms of the smoothed covariates used in modelling to predict group size of short-finned pilot whales in the Canary Islands (top) and in Tenerife (bottom), between 2002 and 2010: with (a) and without (b and c) bottlenose dolphins. 304

Figure 5.28a-d: Surface map of predicted abundance of short-finned pilot whales in the Canary Islands (top) and in Tenerife (bottom): with (b and d) and without (a and c) bottlenose dolphins. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red. 305

Figure 5.29a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whale in Canary Islands (top) and in the island of Tenerife (bottom), between 2002 and 2010 with (a, c) and without (b, d) calves. 306

Figure 5.30: Shapes of the functional forms of the smoothed covariates used in modelling to predict group size of short-finned pilot whale in Canary Islands with calves. 306

Figure 5.31a-d: Surface map of predicted short-finned pilot whale abundance in the Canary Islands (top) and in Tenerife (bottom) between 2002 and 2010: groups with calves (a and c) and groups without calves (b and d). The colour gradient indicates the density of animals from 0 in blue to the highest value in red. 307

LIST OF TABLES

Table 2.1. Research surveys conducted by SECAC between 1999 and 2012 in Canary Islands. The name of each project is presented with the number of day-surveys conducted at sea.

Table 2.2: Exponential models available in SOCPROG 2.4 that can be fitted to the lagged identification rates (LIRs) using maximum likelihood and binomial loss. Models describe movements of individuals in and out the study area. Model equations come from the SOCPROG 2.4 manual (Whitehead 2009). N refers to population size in the study area; td = time lag (τ); a_1, a_2, a_3 = parameters of the models.

Table 2.3: Survey effort per year (day, nautical miles, and hours) conducted at sea by SECAC since 1999 around the Canary Island, with sightings on and off effort, encounter rate ER1 (total number of encounters divided by the total number of nm surveyed each year) and ER2 (annual mean of cell encounter rates).

Table 2.4: Total nm travelled and survey effort per island (day, Nautical Miles, and hours) conducted at sea by SECAC since 1999 around the Canary Islands, with on and off effort sightings.

Table 2.5: Encounter rate ER1 (total number of encounters divided by the total number of Nm surveyed each year), and ER2 (range, mean and quartiles of cell encounter rates per island).

Table 2.6: Group size of short-finned pilot whales encountered between 1999 and 2012 in the different islands of the Canary Islands, and by season. Mean values, range, standard error and standard deviation are also shown.

Table 2.7: Photo-identified short-finned pilot whales in the different Canary Islands, between 1999 and 2012: complete photo-identification catalogue, datasets based on picture quality and animal distinctiveness (Q3= good picture quality, Q4= optimum picture quality; D3= distinctive individual, D4= very distinctive individual). Age classes (A= adults, Indet= indeterminates, J=juveniles, C=calves; and N=newborns) are given for the data set Q3 Q4, D3 D4.

Table 2.8: Diagnostics and estimated parameters for models of lagged identification rates (LIRs) applied to all individual short-finned pilot whales identified in the Canary Islands, between 1999 and 2012, and in southwestern Tenerife between 2004 and 2009. Models were also applied to Tenerife and La Gomera to test how pilot whales move between these two islands. td = time lag (τ); a_1, a_2, a_3 = parameters of the models. Values inside the brackets indicate the standard errors of the parameters calculated using bootstrap replications.

Table 2.9: Short-finned pilot whales with a time span of 10 and 11 years between the first and last recapture, within Canary Archipelago: Tenerife (TenS =south-west and TenN =north east areas), Gran Canaria (GC), La Gomera (LG), and Lanzarote-Fuerteventura (LZ_FV) (1999 and 2012). Indicative age and sex class are also detailed (A= adult; Indet= indeterminates; F= female; M= male).

Table 2.10: Number of well-marked short-finned pilot whales of all ages identified in each area and recaptured within the Canary Archipelago (moving individuals): Tenerife South and Tenerife North, Gran Canaria, La Gomera, and La, and Lanzarote-Fuerteventura (1999 and 2012). The number of individuals recaptured at least twice in each island is highlighted in grey.

Table 2.11: Match indices of short-finned pilot whales for different combination of islands and years: return and interchange rates.

Table 2.12: Number of animals in different residency categories ("core resident", "resident", "occasional", and "transient") of short-finned pilot whales in the Canary Islands.

Table 2.13: Range statistics of all 193 animals, "core-residents" and "residents", females and males: mean, standard deviation, minimum and maximum value of the MCP and fixed Kernel (overall ranging at 95%UD and core area at 50%UD). Detailed results of each of the 193 short-finned pilot whales are presented in the Annex 2: Table A.2.2.

Table 2.14: Centres of activity for 95% and 50% UD ranges calculated for the 193 short-finned pilot whales by fixed kernel methods, across the different islands of the archipelago (TNs= Tenerife south, TNn=Tenerife north, LG= La Gomera, GC= Gran Canaria).

Table 3.1: Test for preferred companionship among core resident and resident short-finned pilot whales in the Canary Islands (2004-2012, dataset filtered by good quality pictures, well-marked fins, and adults and indeterminate age classes). Permutations using SOCPROG 2.4. for associations within samples and groups within samples were tested for non-random short and long-term associations (preferred or avoided) and for gregariousness. Results for both tests are from 60,000 permutations using HWI. *P*-values greater than 0.95 are considered significant.

Table 3.2: Models of long term associations fitted to the complete dataset of well-marked adults and indeterminates in the Canary Islands. The standardised association rate is indicated by g' , the time lag is represented by "td" and the parameters of the models by "a1", "a2", "a3", and "a4".

Table 3.3: Division into 19 individual clusters using community division. The original average-linkage cluster dendrogram was built using well-marked "core resident" and "resident" adult and indeterminate pilot whales (Gma) identified in the Canary Islands (1999-2012), in good coverage sightings. The cluster indices are listed for each cluster: mean, sum and maximum values of the association indexes (HWI).

Table 3.4: Key units selected are presented with their correspondent clusters division, and their composition: key and casual companions (CC), males (M), females (F), indeterminate (IND). The mean, standard deviation and range of the association index (HWI) for each unit are also reported.

Table 3.5: Test for preferred companionship among short-finned pilot whales recaptured at least once a month for eight months in the islands of La Gomera and Tenerife, between 2004 and 2010. The dataset was filtered by good quality pictures, well-marked fins, and adults and indeterminate age class, seen in sightings with good photo-identification coverage. Permutations using SOCPROG 2.4. for associations within samples and groups within samples were tested for non-random short and long-term associations (preferred or avoided) and for gregariousness. Results for both tests come from 60,000 permutations using HWI. *P*-values greater than 0.95 are considered significant.

Table 3.6: Models fitted to the most frequently seen short-finned pilot whales (seen at least once a month for eight months) identified between 2004 and 2010 in La Gomera and Tenerife, during sightings with good photo-identification coverage. Maximum likelihood and binomial loss were used for selection and to describe long-term associations (SLAR) of well-marked adults and indeterminates.

Table 3.7: Mean Network Measures for Half-Weight Association Indices among the 134 individual short-finned pilot whales identified at least once a month for eight months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010).

Table 3.8: Division into 11 individual clusters using community division. The original average-linkage cluster dendrogram was built using the most frequently sighted (at least

once a month for eight months) well-marked adult and indeterminate pilot whales identified in Tenerife and La Gomera (2004-2010), in good coverage sightings. The cluster indices are listed for each cluster: mean, sum and maximum values of the association indexes (HWI). Results from SLAR analysis are also reported, with indications of the selected best-model and the estimated group size at stabilization. The corresponding Unit is also presented.

Table 3.9: Range of the 11 clusters estimated by MCP (overall ranging at 100% and 95% UD) and fixed kernel (overall ranging at 50% and 95% UD) of most frequently seen (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. No fixed kernel among-cluster overlapping is reported for each cluster. Mean, SE, maximum, minimum area extensions are also presented. Areas are expressed in km².

Table 4.1: Capture-recapture dataset used for abundance estimation analysis. Number of short-finned pilot whales identified in southwestern Tenerife, between April 2007 and March 2009, grouped in 24 survey sampling units: total dataset, total well-marked individuals, and well-marked adults and indeterminates.

Table 4.2: Filtered datasets, obtained by excluding the first capture (-1) and the first recapture (-2) from the complete dataset of well-marked short-finned pilot whales identified in southwestern Tenerife, between April 2007 and March 2009. Total age-class and only adults and indeterminates are also shown.

Table 4.3: U-CARE results for the three datasets used in the analysis to test for behavioural response (TEST2.CT), for transience (TEST3SR), and to calculate the c-hat for overdispersion.

Table 4.4: Best fitting POPAN models chosen by their QAICc-values, for the three data sets: Total (A), "-1" (B), "-2" (C). Three parameters are estimated in the models: p=capture probability phi=apparent survival, PENT=probability of entry into the population at each occasion, and these can vary by time (t) or remain constant (.). For each model, the table also presents the Δ QAICc, QAICc Weights, likelihood, number of parameters, and model deviance.

Table 4.5: Capture-recapture abundance estimates of short-finned pilot whales in southwestern Tenerife. N_{total} =abundance estimate of the total super-population; N =abundance of well-marked individuals estimated by POPAN open model, for the three datasets. θ = averaged proportion factor of identifiable animals in a school; CV=coefficient of variation; CI= 95% confidence interval.

Table 4.6: Subset of closed population candidate models. Models are presented in decreasing order of AICc. For each model the table presents the Δ AICc, AICc Weights, likelihood, number of parameters, and model deviance.

Table 4.7: Averaged estimates of population size (N) of adult and indeterminate short-finned pilot whales, from closed population models and total population size (N_{total}) after adjusting for the proportion factors of well-marked individuals (θ). The coefficient of variation (CV) and log normal 95% confidence intervals are also presented for N_{total} .

Table 5.1: Variables and groups of variables used in the models.

Table 5.2: Covariates incorporated in detection function modelling. Indications of whether treated as a continuous variable or as a factor, and the levels used when treated as a factor are also reported. Group size, observer experience, cue conspicuousness, and sightability (from optimum "0", to no feasible sighting conditions "4").

Table 5.3: Results of the three detection functions, based on type of platform used: 0-P.L.: inflatable and fishing boats, 1+2-P.L.: sailing boats and research vessels, 3-P.L.: ferries. The following information is presented for each function: type of model; truncation distance, number of observations used for the analysis; probability of

detection (p , SE); effective strip width (ESW, SE); coefficient of variation of p and ESW (%CV); variables selected in the models, with coefficient and SE. Variable "Sightability": type of effort based on sea state and wind strength.

Table 5.4: Model results for the complete dataset of the Canary Islands (1999-2012), for all periods and seasonally (winter: December-May; summer: June-November). The two best fitting models, one for group abundance (group) and one for group size (g.size) are shown in the table, with the selected variables, the estimated degree of freedom (edf; 1 means a linear relationship), and the corresponding percentage deviance explained.

Table 5.5: Model results for the Canary Islands: estimated group abundance, group size,, density and total abundance (with CV and 95% CI) of the species in the studied area.

Table 5.6: Model results for the complete dataset of the whole Canary Islands (1999-2012) and for the three areas: western islands (La Palma, El Hierro, La Gomera; Area 1), Tenerife (Area 2), and eastern islands (Gran Canaria, and Lanzarote-Fuerteventura, Area 3). Seasonal estimation (winter: December-May; summer: June-November) and temporal trend (years: 2002-2006, 2007, 2008, 2009-2010) are also shown for the island of Tenerife. The two best fitting models, one for group abundance (group) and one for group size (g.size) are shown in the table, with the selected variables, the estimated degree of freedom (edf; 1 means a linear relationship), and the corresponding percentage of explained deviance. Seasonal results (winter: December-May; summer: June-November) are also shown.

Table 5.7: Estimated group abundance (with CV and CI), density, and group size (estimated and calculated mean) for the western islands (La Palma, El Hierro, La Gomera; Area 1), Tenerife (Area 2), and eastern islands (Gran Canaria, and Lanzarote-Fuerteventura, Area 3). Seasonal estimation (winter: December-May; summer: June-November) and temporal trend (years: 2002-2006, 2007, 2008, 2009-2010) are also shown for the island of Tenerife.

Table 5.8: Model results for short-finned pilot whale habitat preference related to biological intrinsic factors, in the Canary Islands and in the island of Tenerife: behavioural categories (travelling, socialising, resting, feeding), single or mixed species group with bottlenose dolphins, presence/absence of calves in the groups. The two best fitting models, one for group abundance (group) and one for group size are shown in the table with the selected variables and the corresponding percentage of deviance explained.

LIST OF ANNEXES CONTENTS

Annex 1

Table A1.1: List of the 30 cetacean species cited in the Canary Islands (review in Martín et al., 2009*). Indication of sighting frequency is also presented: species seen all year-round, seasonally, occasionally, and extralimital.

Annex 2

Figure A2.1: Sighting sheet: 1999-2007 front.

Figure A2.2: Sighting sheet: 1999-2007 back

Figure A2.3: Sighting sheet: 2009 -2011 (Oso Ondo).

Table A2.1a: Survey effort per island (Nautical Miles and hours) conducted at sea by SECAC between 1999 and 2012 along Canary Islands waters, Tenerife, Gran Canaria, La Gomera, with sightings on and off effort, and encounter rate ER1 (total number of encounters divided by the total number of Nm surveyed each year).

Table A2.1b: Survey effort per island (Nautical Miles and hours) conducted at sea by SECAC between 1999 and 2012, along Fuerteventura Lanzarote, La Palma, El Hierro, with sightings on and off effort, and encounter rate ER1 (total number of encounters divided by the total number of Nm surveyed each year).

Figure A2.c: Survey effort conducted at sea by SECAC between 1999 and 2012 in the Canary Islands

Table A2.2: Home range estimates of the 193 short-finned pilot whales calculated by MCP and fixed kernel (overall ranging at 95% UD and core area at 50% UD) methods. The Schoener's ratio is also presented as a measure of autocorrelation. Sex differentiations (F=female, M=male, u= unknown) are based only on qualitative observations, and therefore have to be considered with caution.

Annex 3

Figure A3.1: Distribution of association indices for females (top two) and males (middle two) and females-males/males-females (bottom two), well-marked short-finned pilot whales recaptured at least once per months for 8 months in the islands of La Gomera and Tenerife, between 2004 and 2012, in sightings with good photo-identification coverage: a) sum of associates for each individuals, b) maximum associations index.

Figure A3.2: Enlargement of main social network cluster taken from figure 3.4, showing only core residents and residents and the key units selected within all well-marked short-finned pilot whales documented off the Canary Island, from 2004 through 2012. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Residents are shown in grey triangle, and core residents in grey circle. Key unit A is coloured pink, C in yellow, D in green, F in orange, and M in violet.

Figure A3.3: Network showing the key units selected within all well-marked short-finned pilot whales documented off the Canary Island, from 2004 through 2012. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals.

Figure A3.4a: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Units A, B, C. The maximum-likelihood best fit model for each unit and their null association rate are also represented.

Figure A3.4b: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Units D, E, F. The maximum-likelihood best fit model for each unit and their null association rate are also represented.

Figure A3.4c: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Units H, M,N. The maximum-likelihood best fit model for each unit and their null association rate are also represented.

Figure A.3.4d: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Unit O. The maximum-likelihood best fit model for each unit and their null association rate are also represented.

Figure A3.5d: SLAR for female vs female (a), male vs male (b), female vs male (c), male vs female (d) most frequently seen short-finned pilot whales (seen at least once a month during 8 months) identified between 2004 and 2010 in La Gomera and Tenerife, during sightings with good photo-identification coverage. Moving average curves of 1,000 associations for both are plotted with approximate standard error bars (produced by jackknife on each sampling period), over the null association rate. Best model "constant companions": (a) $a_1 = 0.097583$ (s.e. 0.010829); (b) $a_1 = 0.26211$ (s.e. 0.031973); (c) $a_1 = 0.37002$ (s.e. 0.06375); (d) $a_1 = 0.090234$ (s.e. 0.015344). Model selection was made based on QAIC values, and compared to the null association rate. Error bars were obtained by jackknifing.

Figure A3.6: Graphs for mean Network Measures for Half-Weight association Indices between the 134 individual short-finned pilot whales identified at least during 8 months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010). Strength, reach, clustering coefficient, and affinity with standard error are presented for each cluster.

Figure A3..7a-b: Enlargement of the social network diagram of Figure 3.14, representing the different clusters obtained by using "sightings" as unit for association(a= clusters 1,2,3,5; b= clusters 4,6,7,10). Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Tie strengths of one are indicated by black lines, higher than 0.5 in blue, and lower than 0.5 in grey. The size of the node increases with the degree.

Figure A3..7c: Enlargement of the social network diagram of Figure 3.14, representing the different clusters obtained by using "sightings" as unit for association(c= clusters 8,9,10). Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Tie strengths of one are indicated by black lines, higher than 0.5 in blue, and lower than 0.5 in grey. The size of the node increases with the degree.

Figure A3.8a: SLAR curves calculated for the clusters 1-6 of most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales of the southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Moving average curve of 1,000 associations. The best fit-models were selected using the QAIC. Error bars were obtained by jackknifing.

Figure A3.8b: SLAR curves calculated for the clusters 7-11 of most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales of the southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Moving average curve of 1,000 associations. The best fit-models were selected using the QAIC. Error bars were obtained by jackknifing.

Table A3.1: SLAR results calculated for the clusters of most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales of the southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Moving average curve of 1,000 associations. The best fit-models were selected using the QAIC. Error bars were obtained by jackknifing.

Table A3.2: Ranges estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) of short-finned pilot whale key-units identified in Canary Islands between 1999 and 2010.

Figure A3.9a: Ranges estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) for short-finned pilot whale key-units (A,B,C,D,E,F) identified in Canary Islands between 1999 and 2010.

Figure A3.9b: Ranges estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) for short-finned pilot whale key-units (H,M,N,O) identified in Canary Islands between 1999 and 2010.

Annex 4

Figure A4.1: Graphs for binomial correlation with GLM, of the averaged proportion factor of identifiable animals in a school (θ). Deviance residuals: Min=-3.5887; 1Q=-0.8831; Median=-0.0226; SQ= 0.9505; Max= 3.8008. Intercept: estimate=-0.208; SE= 0.03397; Z-value=-6.122; Pr= 9.23e-10. Deviance= 486.63 on 262 degrees of freedom. AIC: 1187.1

Table A.4.1a: Individual captures-recaptures within each sampling unit of the complete dataset: well-marked adult and indeterminate short-finned pilot whales.

Table A4.1b: Individual captures-recaptures within each sampling unit of the dataset without the first captures: well-marked adult and indeterminate short-finned pilot whales.

Table A4.1c: Individual captures-recaptures within each sampling unit of the dataset without the first captures and the first recaptures: well-marked adult and indeterminate short-finned pilot whales.

Figure A4.2a: Recapture frequency of short-finned pilot whales within the islands of Tenerife (blue), La Gomera (green) and Gran Canaria (pink). Total dataset of high quality pictures, well-marked adult and indeterminate animals.

Figure A4.2b: Recapture frequency of short-finned pilot whales within the islands of Tenerife (blue), La Gomera (green) and Gran Canaria (pink). Dataset without the first captures, of high quality pictures, well-marked adult and indeterminate animals.

Figure A4.2c: Recapture frequency of short-finned pilot whales within the islands of Tenerife (blue), La Gomera (green) and Gran Canaria (pink). Dataset without the first recaptures, of high quality pictures, well-marked adult and indeterminate animals.

Annex 5

Table A5.1: Spearman correlation analysis among the main covariates used in habitat use modelling.

Annex 6

Figure A6.1: Particularly Sensitive Sea Areas (PSSAs) in Canary Islands (yellow: circulation routes; blue: coastal navigation area; red: precaution area; grey: separation area; green: restricted area that vessels in transit must avoid). (Image from: Ministry of Agriculture, Food and Environment, 2012).

Figure A6.2: Areas of pressure accumulation that underwater noise can cause (red square: high; violet square: moderate). (Image from: Ministry of Agriculture, Food and Environment, 2012).

Figure A6.3: Pressure accumulation zones caused by the discharges from land (red square: high; violet square: moderate). (Image from: Ministry of Agriculture, Food and Environment, 2012).

Figure A6.4: Pressure accumulation zones caused by the discharges from sea. (Image from: Ministry of Agriculture, Food and Environment, 2012).

Figure A6.5: Submarine emissaries (pink dots). (Image from: Ministry of Agriculture, Food and Environment, 2012).

Table 6.1: Legal framework for cetacean protections in Canary Islands.

Table A6.2: Cetacean species' status in the Canary Islands.

CHAPTER 1
GENERAL INTRODUCTION

1.1 INTRODUCTION

The effectiveness of a conservation management framework is dependent on the ability to effectively detect and evaluate the main factors that might affect the status of a given population. Only if this can be done can the difficult task of setting achievable, measurable, and ecologically meaningful objectives be considered. These factors include distribution habitat use, population size and dynamics, and a wide range of features of the environment (biotic and abiotic, natural and anthropogenic) that might either threaten or enhance species' survival.

The complexity of ecosystems makes understanding the dynamics of a given population difficult task, that is impossible to achieve in the short-term and expensive to accomplish, especially when the target population is a marine top-predator, such as a whale or dolphin species (Fortuna, 2006). Logistically, cetacean research is a challenge. Marine ecosystems are complex and cryptic systems, in which the interactions between species and oceanographic factors can be highly dynamic. Cetaceans are often fast-moving, wide-ranging, elusive and difficult to observe closely at sea because they live primarily beneath the water. These aspects along with the difficulties of working in often hostile marine conditions have led to the development of inventive and sophisticated techniques, as well as more efficient analytical methodologies. The improvements in methodology have also led to more long-term research studies. With advances in technology, and with more effort invested in studying cetaceans, cetology has recently experienced an important turning point. The field has seen a clear shift in methodology from qualitative natural history narratives and a frequent use of terrestrial comparison, to a more focused quantitative analysis and hypothesis testing (Samuel and Tyack, 2000).

Examination of the sighting history of photo-identified individuals has been used to assess movements, fidelity, residency, associations and, therefore, population structure (e.g. Ottensmeyer and Whitehead, 2003; Baird and Whitehead, 2000; Bearzi *et al.*, 2008; Silva *et al.*, 2009; Mahaffy, 2012; de Stephanis, 2008b).

The use of photographic techniques in cetology to identify individuals using their natural markings was first introduced in the early 1980s to study killer whales (Bigg, 1982; Bigg *et al.*, 1987), right whales (Payne *et al.*, 1983) and humpback whales (Jurasz and Palmer, 1981a). This technique was used to study and interpret their social structure by measuring group stability and preferential associations of individuals (Würsig and Würsig, 1977; Würsig, 1978; Defran *et al.*, 1990; Wells and Scott, 1990; Williams *et al.*, 1993).

Only relatively recently have photo-identification techniques been used to improve knowledge of population size, habitat use, social structure, population dynamics, and reproductive and kinship features, which are becoming clearer for a number of cetacean populations (Samuel and Tyack, 2000). By combining methodologies and studying different aspects and features of a species, multidisciplinary studies have been progressively able to provide answers to general biology questions and to provide a more complete and detailed overview that is essential in cases of conservation concern.

Information on changes in population size and life history parameters, such as birth and mortality rate (Seber, 1982; Schwarz and Seber, 1999; Buckland, *et al.*, 1993; Thomas, *et al.*, 2002), is a crucial step towards a better understanding of a species' conservation status. The knowledge of how cetacean density varies spatially as a function of the environment, through research on species' habitat use, including the use of habitat models, can contribute significantly to the conservation of cetacean populations (Guisan *et al.*, 2002; Silva, 2007). Such research can provide information to identify high use areas, assess the effects of habitat change, and address possible protected areas (reviewed in Guisan and Zimmermann, 2000; Redfern *et al.*, 2006; Cañadas *et al.*, 2005; Cañadas and Hammond, 2008).

In general, studies on animal space-use patterns have focused on documenting the range of individuals (Burt, 1943), and how they use space within it. For most species, individuals are not distributed randomly but instead form characteristic patterns of distribution, grouping, ranging, and association (Crook *et al.*, 1976, Boyce and McDonald, 1999). For a number of environment-related reasons, most animals use some parts of their range more frequently than others (e.g. Adams and Davis, 1967; Van Ballenberghe and Peek, 1971; Metzgar, 1973; Georgii, 1980; Springer, 1982; Konecny, 1989; Crawshaw and Quigley, 1989; Macdonald and Courtenay, 1996; Lindzey and Meslow, 1977). The heterogeneity of natural environments results in discontinuities in the distribution of limited resources (e.g. food, mates, and areas for resting, protection from predators, and nursing). If habitats differ in "quality", individuals should be expected to exhibit some degree of habitat selection, in order to obtain maximum advantage from the resources and to reduce levels of resource competition (Wiens, 1976).

It has been proposed that where food resources are abundant, animals tend to use smaller ranges than in areas where resources are limited (Schoener, 1968; Clutton-Brock, 1975; Powers and McKee, 1994; BothandVisser, 2003) or patchy (Schoener, 1968; Clutton-Brock 1975). The interaction between resource availability and space-use patterns is difficult to study, and a good knowledge of the habitat where animals live is

necessary to understand the dynamics of their distribution and how they respond to spatial and temporal environmental variability. The development of spatial statistical tools has improved the capacity not only to understand species-habitat associations but also to predict spatial and temporal patterns of species occurrence (Olden *et al.*, 2002). Information about individual patterns of space use can therefore be an important first step to investigate, providing insights into the relationship between patterns of space use and the spatial and temporal distribution of resources (Brown and Orians, 1970), as well as residency, territoriality, mating system (Clutton-Brock, 1989; Ostfeld, 1990), social organization (Rubenstein and Wrangham, 1986; Ostfeld, 1990), demography (Clutton-Brock and Albon, 1985), evolutionary trajectory and conservation of populations (Krebs, 1994). The ranging patterns and the movement of the individuals can have important effects on the genetic structure of the population (Wiens, 1976) by ensuring opportunities for gene flow to occur between areas. In addition, there is increasing evidence that animal spacing patterns play important roles in determining the spatial distributions of prey and competitors within animal communities (Brown and Orians, 1970; Mech, 1977; Paquet, 1991; Creel and Creel, 1996).

Estimation of population size and life history parameters is also necessary to understand the dynamics of a natural population (Silva *et al.*, 2009); this provides important information for several research areas, such as evolutionary, population and behavioural ecology, management and conservation (Brooks *et al.*, 2004). Identifying dynamic demographic processes, such as fluctuations in survival and recruitment (Hammond *et al.*, 1990), can inform the detection of trends in the status of a population, providing a baseline for future monitoring. Notwithstanding the importance of this information, demographic parameters are not always possible to quantify because specific study designs are required and not always possible, such as long-term data collection of capture histories of individually identified animals (Hammond, 2010).

For most cetacean populations, little is known still about long-term social interactions between individuals and how they change with time. Studying how the interactions between pairs of individuals develop in structured interactions (Hinde, 1976; Whitehead, 1997) could allow the identification of conservation units (e.g. Hoelzel *et al.* 2002, Aschettino *et al.* 2011), and could lead to important inferences being made about environmental influences on social structure and *vice versa*. A wide variety of factors can condition the nature of a specific social system, including environmental variables and phylogeny (Geist, 1974; Emlen and Oring, 1977; Faulkes *et al.*, 1997; Wittemeyer *et al.*, 2005); predator pressure and availability of resources (Myers *et al.*, 1979; Macdonald, 1983; Wrangham and Rubenstein, 1986; Whitehead, 2008); population density (Emlen

and Oring, 1977; Albon *et al.*, 1992); habitat type (Pitelka *et al.*, 1974; Würsig *et al.*, 1989); and species cognitive abilities (Norris and Dohl, 1980; Lott, 1984). In turn, social structure can affect aspects of a species' biology such as habitat use (Baird and Dill, 1996; Ests and Resenbaum, 2003), gene flow (Whitehead, 1998), and the spread of diseases (Lee, 1994; Guimarães *et al.*, 2007).

1.1.1 THE CANARY ISLANDS ARCHIPELAGO

As a result of its geographic location, oceanographic, physical and chemical water parameters, the Canary Archipelago is a unique natural environment, with year-round good climatic conditions, and with one of the planet's highest indices of fauna and flora biodiversity, including up to 30 cetacean species in the archipelago (Martín *et al.*, 1995; López Jurado *et al.*, 2001; Martín *et al.*, 2009). It retains an exceptional potential as a cetacean study ground, with high cetacean density close to the coast due to the narrow continental shelf. Nevertheless, cetacean studies are mainly in their early stages, and have not even covered the principal aspects of the biology of the species most frequently seen.

Parallel concerns for cetacean conservation in the Canary Islands have increased in recent years in relation to progressive habitat degradation. This has been caused by activities threatening local populations such as maritime traffic and whale-watching operations (bottlenose dolphins and pilot whales), anthropogenic noise (beaked whales) and ship-strikes (particularly sperm whales) (Martin *et al.*, 2009; Carrillo and Ritter, 2010). Nevertheless, the lack of basic knowledge of the biology of cetacean populations in the Canary Islands might lead to failures to detect negative impacts resulting from pressures that these cetacean populations are being subjected to. Circumstances that might fail to be detected include changes in abundance or demographic parameters, shifts in overall distribution or core areas of usage, modification of seasonal patterns and changes in social behaviour.

Therefore, from a conservation perspective, it is urgent that studies are set up in the Canary Islands to obtain basic knowledge of the different species, starting with the most frequently seen and resident species, which are those mostly affected by continued and increasing pressure of human activities.

The short-finned pilot whale is one of the most frequent sighted species in the archipelago, one of the few known resident populations in the world and one of the most potentially affected by intense anthropogenic pressure. Current information is scattered

in time and space and mostly descriptive, obtained through different data collection and analysis methodologies, and allows neither an assessment of current status nor a baseline for future comparative studies.

The fundamental goal of this thesis was to gain a better understanding of the biology of short-finned pilot whales in Canary Islands, particularly their distribution, habitat use patterns, abundance and social structure, so that this new information could be used to inform conservation and management of human impacts affecting this species in this area.

1.2 STUDY AREA

The Canary Islands are an archipelago (Figure 1.1) formed by seven independent volcanic islands (Carracedo, 2001) (El Hierro, La Palma, La Gomera, Tenerife, Gran Canaria, Lanzarote and Fuerteventura) and various islets, with a total surface area of 7,273 km² and a coastline of 1,500 km. The archipelago is located in subtropical latitudes, 27° - 30° N, on the continental rise off Cabe Juby, next to the northwest African coast, and belong to the insular arc called Macaronesia, together with Madeira, the Savage Islands, and Cape Verde.

Fuerteventura and Lanzarote at the eastern end of the chain are 100 km from the African coast, and El Hierro and La Palma at its western end are 500 km from the coast. Lanzarote and Fuerteventura are along the crest of the northeast-lying Canary Ridge, on the upper continental rise at a water depth of about 2,000 meters. Its northeast extent is defined by the less than 200 meters deep, flat-topped Conception Bank (Acosta *et al.*, 2005). This ridge is aligned along the contact between the attenuated continental crust to the east and the oceanic crust to the west (Emery and Uchupi, 1984). The other islands of the archipelago, Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro, are surrounded by water 3,000 to 4,000 meters deep, and are on an oceanic crust from the Jurassic (Uchupi *et al.*, 1976). Gran Canaria, Tenerife and La Gomera lie on an east-west line parallel to the oceanic fracture zone in the region, with Tenerife's long axis being oblique to this trend. La Palma and El Hierro, at the western end of the island chain, are offset to the north and south of this line (Acosta *et al.*, 2005). The seafloor of the Canary Islands Basin ranges from 3,000 meters in depth to the east to 4,000 meters to the west. The archipelago's volcanic origin explains the almost absent continental shelf, with a sharp increase in depth at a short distance from shore between the youngest islands of El Hierro, La Gomera and La Palma, and between the main islands,

and depths of 1,500 meters with a more extended shelf between the oldest and eroded islands of Fuerteventura and Lanzarote and the neighbouring African coast (Acosta, 2005).

Gaps between the Canary Islands along the southern side of the basin serve as passageways for the southerly flowing North Atlantic Deep Water at a depth of 2,000-3,800 m and northerly flowing Antarctic Bottom Water below 3,800 m. Volcanism in the Canary Islands region has occurred at various times since the Late Cretaceous, the oldest represented in the east on Fuerteventura and the most recent in the west on La Palma (Le Bas *et al.*, 1986) and El Hierro (2011-2012). Carracedo (1994) has divided the islands into three groups: those that have had eruptions in relatively recent times (less than 500 years ago Tenerife, La Palma, Lanzarote and El Hierro); those with a history of Quaternary volcanism (Fuerteventura and Gran Canaria); and those lacking evidence of Quaternary volcanism (La Gomera). Lanzarote, Fuerteventura and Gran Canaria are in the post-erosional phase, La Gomera is in the repose stage and Tenerife, La Palma and El Hierro are in the shield stage of development (Carracedo, 1999). El Hierro suffered an extensive underwater eruption between October 2011 and November 2012, with the creation of a new sea mount.



Figure 1.1: Canary Islands (from left to right): El Hierro (south), La Palma (north), La Gomera, Tenerife, Gran Canaria, Fuerteventura, Lanzarote.

There are two currents coming from the north-northeast that influence the Archipelago: the trade winds and the descendent eastern branch of the Gulf Current, known as the Canary Islands current or the Canary Islands cold current. The Canary Islands current originates in the Azores, and is one of the main components of the subtropical oceanic eddy of the North Atlantic (Braun and Molina, 1984). It has a length of about 1,500 km, an average speed of 0.1-0.2 m.s⁻¹ (Stramma and Siedler, 1988) and passes the Canary Islands in a southwesterly direction. The trade-winds also circulate from the northeast towards the southwest and, like the current, pass the islands causing an oceanographic mesoscale phenomena of great complexity (Barton *et al.*, 1998) called the "mass effect of the island" (Hernandez-Leon, 1986). Cyclonic and anti-cyclonic cycles arise, as well as calm water areas, warmer filaments along the islands' leeward side, and acceleration of the currents in the channels between islands (Arístegui *et al.*, 1989; Arístegui *et al.*, 1997). These hydrodynamic phenomena are of great importance for the primary production in the waters of the archipelago. By interacting to exchange water properties they favour the transport of organic components, with a consequent localized increase in primary production, contributing to a remarkable increase in the environmental heterogeneity of the Canary Islands waters, which would otherwise be oligotrophic due to their oceanic and subtropical character (low concentrations of nutrients).

The filaments are recurrent features, apparently arising from the interaction of a topographically trapped cyclonic eddy with the outer edge of the coastal upwelling zone. They cause micro outcrops that push the deep chlorophyll towards the surface, whereas the anticyclonic eddies can contribute to the concentration of nutrients and chlorophyll, and to the transport and exchange of biogenic material, including fish larvae (Arístegui *et al.*, 1989; Arístegui *et al.*, 1997, Arístegui *et al.*, 2006). Strong cyclonic eddies, occurring throughout the year, drift slowly southwestwards from Gran Canaria. Only two of the filaments (the Cape Guir and Cape Blanc filaments) remain as major permanent features, even during unfavourable upwelling winds, and thus represent key sites for the export of organic matter to the open ocean waters of the subtropical gyre (Arístegui *et al.*, 2006).

A gradient in the nutrient concentration has been shown that diminishes from the eastern islands towards the western ones, the former being more influenced by rich African waters. In certain areas, some enrichment can occur produced by local upwelling. This can be induced either by winds which blow parallel to the coast for a relatively long distance (e.g. west of Fuerteventura and Lanzarote), or by local topographical features (e.g. north of La Gomera) (Molina *et al.*, 1986).

Water salinity is 36-37‰ (Brauns, 1981; Llinás *et al.*, 1994) and sea surface temperature generally oscillates between 17-19°C in winter and 22-24°C in summer (Mascareño, 1972; Pavón-Salas *et al.*, 2000). Nevertheless, in recent decades a progressive warming of the waters has been observed, also demonstrated by the tropicalization of the ichthyofauna (Brito and Falcón, 1996; Brito *et al.*, 2005). The seasonal thermocline appears from spring to autumn at between 50-120 m depth in the western islands (Braun and Molina, 1984), despite the 800 m depth of the permanent thermocline. Canary Islands waters are colder than expected for its latitude, due to the influence of the cold current and the African upwelling (Hugues and Barton, 1974; Molina and Laatzén, 1986), which mainly affects the eastern and central islands, especially during summer and autumn (Hernández-Guerra *et al.*, 1993). This causes a temperature gradient increase from east to west of the archipelago of about 2 °C, making El Hierro's waters the warmest.

Therefore, like all the major upwelling regions, the Canary current is characterised by an intense mesoscale structure in the transition zone between the cool, nutrient-rich waters of the coastal upwelling regime, and the warmer, oligotrophic waters of the open ocean. The Canary Islands archipelago introduces a second source of variability by perturbing the general southwesterly flow of both ocean currents and trade winds, mainly in the form of vortex streams downstream of the islands (Aristegui *et al.*, 1994).

The combined effects of the flow disturbance and the eddying and meandering of the boundary between upwelled and oceanic waters produce a complex pattern of regional variability. These include a prominent upwelling filament originating near 28°N off the African coast, cyclonic and anti-cyclonic eddies downstream of the archipelago, and warm wake regions protected from the trade winds by the high volcanic peaks of the islands (Baron *et al.*, 1998).

1.3 BIODIVERSITY AND CONSERVATION IN THE CANARY ISLANDS

The great variety of species in the Canary Islands reflects the characteristics of oceanic islands, with the co-existence of tropical and temperate, and coastal and oceanic species. In total, 30 species of cetaceans (Martín *et al.*, 1995; López Jurado *et al.*, 2001; Martín *et al.*, 2009) have been recorded in the archipelago (Martín *et al.*, 2009); the complete list is shown in Annex A1.1.

The presence of the bottlenose dolphin (*Tursiops truncatus*) and the loggerhead turtle (*Caretta caretta*), promoted the creation of designated areas as Special Areas of

Conservation (SAC) within the framework of European Union's (EU) Habitats Directive in 2001 (<http://www.boe.es/boe/dias/2011/09/14/pdfs/BOE-A-2011-14661.pdf>).

The marine strip included between Punta Teno and Punta Rasca (76,648 hectares, SAC ES-7020017), is situated along the southwest coast of Tenerife, the main study area of the present project (Figure 1.2). The submarine topography of the southwest of Tenerife is characterized by a small insular shelf, with a slope that decreases almost parallel to the coast until reaching 1,000 meters depth at 1 nautical mile in front of Punta Rasca and Los Cristianos, 2.5 nautical miles in front of Playa de San Juan, 3.5 nautical miles in front of Los Gigantes and 4.3 nautical miles in front of Punta Teno. In Gran Canaria, five areas were designated as SACs for the bottlenose dolphin: "Franja Marina de Mogán", along the south-west coast (ES7010017, 28,852 hectares), with an extended continental shelf; "La Isleta" (ES7010016, 8,646 hectares), in the north-east of the islands, characterised by deep waters close to the shore, and strong wind and waves most of the year; and three other small areas: "Bahia del Confital" (ES7010037), "Sebadales de Guigui" (ES7011005), and "Sebadales de Playa del Inglés" (ES7010056). In La Gomera, the SAC ES7020123 "Franja Marina Santiago-Valle Gran Rey" comprises 13,139 hectares to the southwest of the island. In El Hierro, the SAC "Mar de Las Calmas" (ES7020057) extends 1.48 nautical miles along the coast for a total of 9,898.4 hectares, and in La Palma, the SAC "Franja Marina de Fuencaliente" (ES7020122) includes 7,055.20 hectares. Two SACs were designated for the island of Fuerteventura, in the northeast the "Sebadales de Corralejo" (ES7010022) and along the southeast coast the SAC "Playas de sotavento de Jandia" (ES7010035), which covered 1,946.69 hectares and 5,461.11 hectares, respectively. In Lanzarote a small area of 1,192 hectares, called "Sebadales de La Graciosa" was designated SAC (ES7010020) downwind of the small island of La Graciosa.

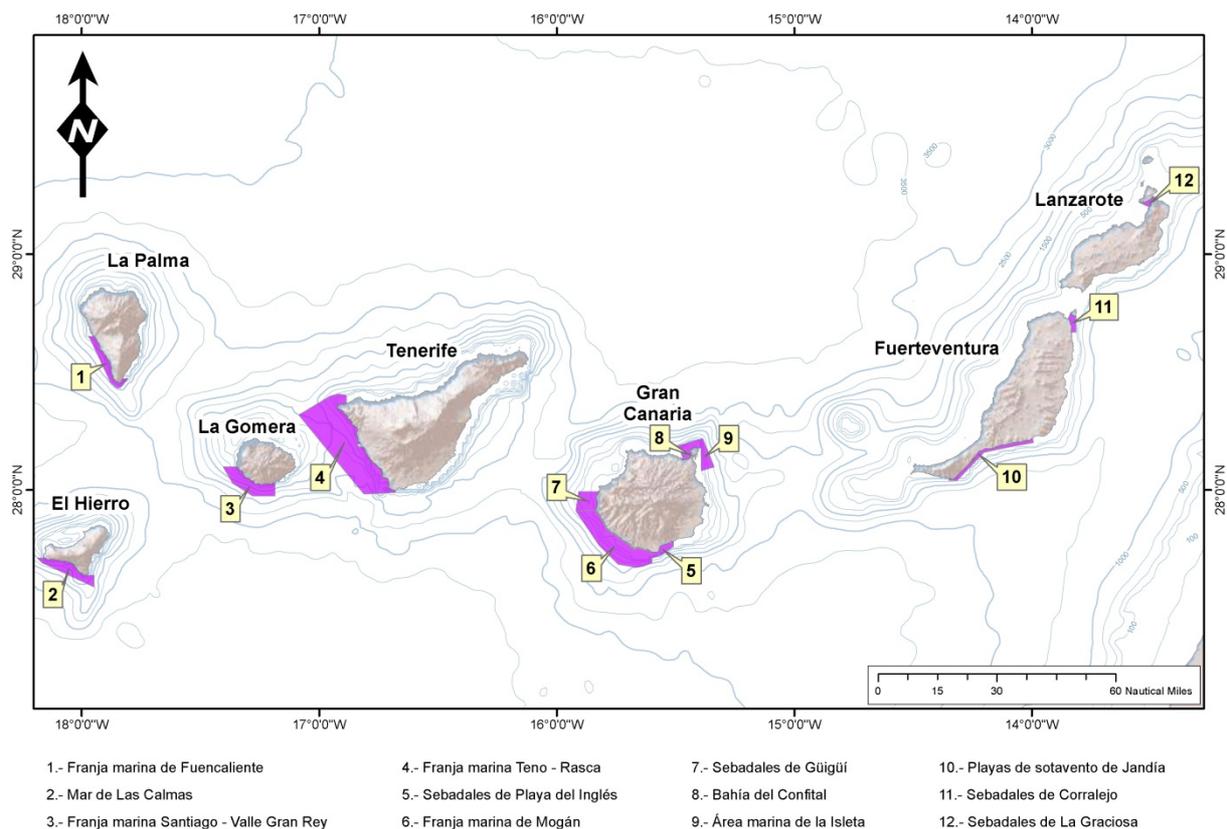


Figure 1.2: Canary Islands showing the designated SACs for *Tursiops truncatus*.

1.4 PILOT WHALE (GLOBICEPHALINAE)

1.4.1 PHYLOGENY, SYSTEMATIC AND DISTRIBUTION

Within the genus *Globicephala* (Lesson, 1828), two species of pilot whales are recognised worldwide: the short-finned pilot whale (*Globicephala macrorhynchus* Gray, 1846) and the long-finned pilot whale (*Globicephala melas*, Traill, 1809), that have three recognised subspecies based on geographic distribution (Bernard and Reilly, 1999). Nevertheless, the taxonomic history of the genus *Globicephala* is complicated (Hershkovitz, 1966), and Oremus (2008), based on shared haplotypes, suggested a revision of long-finned whale sub-species taxonomy.

Although the two species are readily distinguishable using osteological characteristics such as tooth counts and skull morphology (Sergeant, 1962a; Olson and Reilly, 2002) or by genetic analyses (May-Collado and Agnarsson, 2006; Oremus *et al.*, 2009), they are generally considered not to be reliably distinguishable at sea by physical characteristics alone (Olson and Reilly, 2002; Jefferson *et al.*, 2008). However, a recent study carried on

in the northwest Atlantic has shown a simple methodology to identify pilot whales at sea under varying field conditions thanks to a pigmentation contrast and morphometric measures analysis (Rone *et al.*, 2011).

Globicephala macrorhynchus is an oceanic species, distributed in warm and temperate waters of all oceans of the world. Even though this species is mainly pantropical, it has been occasionally observed at high latitudes such as in British Columbia (Baird and Stacey, 1993) in the northwest Atlantic, as well as off the coasts of Galicia (Gonzalez and Lopez, 2000) and France (Olson and Reilly, 2002) in the northeast Atlantic. Long-finned pilot whales are found in cool temperate to subpolar waters with a circumpolar distribution in the Southern Hemisphere and a range in the North Atlantic Ocean, including the Bay of Biscay and the Mediterranean Sea. Even though the distribution of long-finned pilot whales is largely complementary to that of short-finned pilot whales, along the edges of their distributions the two species can overlap and coexist, (e.g., the northwest Atlantic), increasing the difficulty in identifying individuals to species in the field.

The pilot whale appears to be generally nomadic with no fixed migrations. Some north-south as well as seasonal inshore-offshore movements have been described for long-finned pilot whales in different regions related to prey movements or incursions of warm water. The whales off Newfoundland were found, for example, to follow seasonal inshore-offshore movements of shortfin squid (*Illex illecebrosus*), almost disappearing from the area when the squid abundance reduced (Abend and Smith, 1999). Long-finned pilot whales in the Alboran Sea (Cañadas and Sagarminaga, 2000) have shown seasonal preferences for depths occupied by pelagic cephalopods, and demonstrated seasonal preferences for deep water with steep bathymetry in the Strait of Gibraltar during summer months followed by a more even distribution in fall and winter months (de Stephanis *et al.*, 2008a,b).

Only a few populations are known to be present year-round, occurring in Japan (Kasuya and Tai, 1993), California and Hawaii (Olson and Reilly, 2002), Madeira (Alves, 2013), and in the Canary Islands (Carwardine, 1995).

1.4.2 MORPHOLOGY

The pilot whale is a distinctive, medium-sized whale. It has a long slender body, and a thick, keeled tail stock. It is characterized by a bulbous head with a pronounced melon, a small beak and an up-curved mouth-line typical of delphinids that is more marked in young animals and becomes less evident with age. Pigmentation is predominately black,

with three lighter areas that have been found to vary among individuals in short-finned pilot whales (Yonekura *et al.*, 1980): the throat patch; the post-dorsal saddle patch; and the post-ocular patch (Mitchell, 1970). The dorsal fin is broad based, low and falcate, with a rounded tip and a concave trailing edge. It is located one-third of the way along the body (Sergeant, 1962).

The two species differ, as their names suggest, in flipper length (more slender and longer in long-finned pilot whales), and also in skull shape (wider in short-finned pilot whales; Olson and Reilly, 2002), and number of teeth (in both the upper and lower jaws 9-12 pairs of teeth in long- and 7-9 pairs in short-finned pilot whales, Reeves *et al.*, 2002). The tail flukes have sharply pointed tips, a distinct notch, and concave trailing edges.

At birth, long-finned pilot whales measure between 1.6 and 2.0m, slightly longer than the 1.4m of short-finned pilot whales, and weigh around 37 kilograms (Kasuya and Marsh, 1984; Kasuya and Matsui, 1984a). The morphology and dimensions are sexually dimorphic (Kasuya and Matsui, 1984a; Yonekura *et al.*, 1980); males are bigger and more robust than females. Maximum recorded lengths of long-finned pilot whales are 7.2m in males and 6.0m in females (Bannister *et al.*, 1996; Donovan *et al.*, 1993). While short-finned pilot whales can reach 5.8m in length, with a maximum weight of 2,700 kg (even if other sources state 3,600 kg.; Jefferson *et al.*, 1993), females rarely exceed 4 meters and 590 kg (Kasuya and Marsh, 1984). Nevertheless, there are morphologic variations in the species such as in the Pacific waters of Japan, where the northern and southern populations of short-finned pilot whales differ sharply in colour pattern, body size, shape, and in cranial features (Kasuya *et al.*, 1988). However, their taxonomic status remains unsettled (Rice, 1998; Olson and Reilly, 2002). The description of the southern form resembles the pilot whales found in the Canary Islands (Aguilar de Soto, 2006).

1.4.3 LIFE HISTORY

Pilot whales are long-lived mammals. Their life history is quite similar in both species. In short-finned pilot whales, females live longer than males: 63 years versus 46 years (maximum age, Kasuya and Matsui, 1984a). Kasuya and Marsh defined male sexual maturity based on the development of seminiferous tubules of the testes. Fully mature males ranged from 3.94 meters to 5.25 meters in length and were aged from 15.5 to 45.5 years old (mean 17 years; Kasuya and Marsh, 1984). It seems likely that social maturity (when males are successfully breeding within a social group) is attained at older ages than functional maturity (Kasuya and Marsh, 1984). Female sexual maturity was defined as the age of first ovulation, which varied from 7 to 12 years of age (Marsh and

Kasuya, 1984). Body length ranges from 3 m for the smallest mature female to 3.44 m for the largest immature female (Kasuya and Marsh, 1984).

Based on the study conducted in Japan, none of the female short-finned pilot whales over 40 years old had any signs of recent ovulation. Because the oldest female in the sample was 62.5 years of age, there appears to be an extended post-reproductive period in a female pilot whale's life (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; 1986; 1991). The gestation period was estimated at 14.9 months by Kasuya and Marsh (1984) (12 months for long-finned pilot whales). The mean duration of lactation was 2.9 years, and the resting period was estimated to last 2.78 years, with an overall calving interval of 6.92 years (review of Heimlich-Boran of Kasuya and Marsh, 1984) (5 years for long-finned pilot whales). The mean duration of lactation and resting period increases with age. The estimated duration of calf lactation ranged from 0.5 to 3.0 years, with the first ingestion of solid food at the age of tooth eruption (Kasuya and Marsh, 1984). The mean age at weaning was estimated at 3.5 to 5.5 years, with a median of 4 years (Kasuya and Marsh, 1984), even though many animals continue to suckle up to 6 years and the oldest recorded suckling animal was a 14 year old immature male (Kasuya and Marsh, 1984). In all cases, there was a relationship between the duration of lactation and the age of the female. Females who had no recent signs of ovulation (and were assumed to be post-reproductive) were often still lactating and were presumed to be suckling their last calf. The extended duration of lactation in these post-reproductive females represents an increased parental investment when the female's potential for future reproduction has finished (Trivers, 1972; Clutton-Brock, 1984). For short-finned pilot whales in the Northern Hemisphere, seasonal peaks in calving vary in the different populations, while in the Southern Hemisphere peaks occur in spring and autumn (Jefferson *et al.*, 1993).

The maximum recorded age of long-finned pilot whales is 46 years for males, and 59 years for females (Donovan *et al.* 1993). Data from the north-eastern Atlantic suggest that long-finned pilot whale calves are born after a 12 month gestation period, at a length of 1.78 m and weigh between 74 and 79 kg (Donovan *et al.*, 1993). Males reach sexual maturity at between four and five metres at an average age of 17 years, while females reach sexual maturity when smaller and younger, at 3-4 m and 5-15 years (Bloch *et al.* 1993b; Ross 2006). Weaning occurs at between 23 and 27 months, with evidence of prolonged suckling to 7 years in males and 12 years in females (Ross 2006). The calving interval is 3-4 years, but increases with age, such that the average interval is 5.1 years (Donovan *et al.* 1993). Mating occurs primarily in May-June (Desportes *et al.*, 1993; Martin and Rothery, 1993) in long-finned pilot whales. Calving and mating can

apparently occur at any time of the year, but peaks occur in summer in both hemispheres (Jefferson *et al.*, 1993).

1.4.4 DIET AND FORAGING

Pilot whales are known to consume at least 19 neritic and oceanic cephalopod prey species (reviewed in Clarke, 1996). Cephalopods are their principal source of food (Hacker, 1992), complemented by fish and crustaceans (Sergeant, 1962a; Mercer, 1975; Seagars and Henderson, 1985; Overholtz and Waring, 1991; Gales and Pemberton, 1992; Bernard and Reilly, 1999).

Hernandez-García and Martín (1994) described the stomach contents of two short-finned pilot whales found in the Canary Islands as being entirely composed of cephalopods: *Todarodes sagittatus*, *Cranchia* and juveniles of *Megalocranchia*. Nevertheless, in a third stranded specimen the remains of the giant oarfish, *Regalecus glesne* (Martín, personal communication) were also found. These authors made a revision of stomach contents in the species and reported cephalopods of the *Cranchiidae* families, *Histioteuthidae* and *Chiroteuthidae* in specimens in Indonesia, as well as species of *Loliginidae* in South Africa. Studies on long-finned pilot whale stomach contents (Seagars and Henderson, 1985; Gannon *et al.*, 1997; Desportes and Mouritsen, 1993) indicate cephalopods to be their most important prey. Desportes and Mouritsen (1993) reported that 93% of the prey found in 857 stomachs of hunted pilot whales in the Faroe Islands belonged to 12 cephalopod species, and the remaining 7% from fish and crustacean species (*Pandalus montagui* and *Munida tenuimana*).

Aguilar de Soto *et al.* (2008) recorded sound, depth, and orientation from triaxial accelerometers and magnetometers, and suggested prey-chasing behaviour by analysing vertical speed and sound emission during deep dives. Short-finned pilot whales adapt their foraging behaviour to prey types and the circadian cycles in their distribution. Echolocation-mediated foraging during the day is restricted to deep dives (long series of echolocation clicks interspersed with fewer buzzes in contrast to night dives). Some deep dives exceeded 1,000 m with a mean of 15 minutes duration and had an average of only 1.2 prey capture attempts per dive after performing bursts of fast swimming (vertical sprints up to 9 meters/second) (Aguilar de Soto, 2006; Aguilar de Soto, *et al.*, 2008). The high energetic investment and the elevated percentage of dives with no attempts to capture prey seem to be compensated by an elevated calorific value of each prey when captured (Aguilar de Soto, 2006).

Remains of giant squid (*Architeuthis* sp.) found floating near pilot whales off Tenerife (Aguilar de Soto, 2006), and pictures showing squid tentacles in their mouths (Servidio, personal observation), indicate that large deep-dwelling squid could be a target of the bursts of fast swimming. During the night, pilot whales perform both short, shallow (mean of 5 minutes duration and 90 m depth) and deep foraging dives with, in general, more numerous prey-capture attempts per dive using less energetic foraging strategies (Aguilar de Soto, 2006) than dives during the day. This trophic plasticity is probably due to the targeting of large/calorific/fast-moving prey from the deep scattering layer. It reflects a more generalist foraging behaviour during the night, and a more specialist behaviour during the day, adapting to the different prey available (Aguilar de Soto, 2006; Aguilar de Soto, *et al.*, 2008).

Although primarily squid eaters (*Illex illecebrosus* and *Todarodes sagittatus*), long-finned pilot whales will also take small medium-sized fish (herring, *Clupea harengus*; mackerel, *Scomber scombrus*; cod, *Gadus morhua*), when available (Desportes and Mouritsen, 1993; Jefferson *et al.* 1993; Olson and Reilly, 2002). They feed mostly at night, when dives may last for 18 minutes or more and be as deep as 828 m (Carwardine 1995; Heide-Jørgensen *et al.* 2002). Throughout its range, sightings reflect the distribution of the preferred diet (Aguayo *et al.* 1998), with tracking studies showing a preference for the edge of the continental shelf (Bloch *et al.* 1993c; Bloch *et al.* 2003).

1.4.5 SOCIAL STRUCTURE

Little is known about the social structure of either species of *Globicephala* (Ottensmeyer and Whitehead, 2003) but most of the information comes from studies conducted on long-finned pilot whales. A social system similar to the killer whale (*Orcinus orca*) has been hypothesized to characterise the two pilot whale species (Heimlich-Boran, 1993; Connor *et al.*, 1998; Amos *et al.*, 1991a, 1991b, 1993a, 1993b; Fullard, 2000; Fullard *et al.*, 2000). Killer whales spend all of their lives in closed groups (pods), with temporary interactions among them, exhibiting a hierarchical structure (Bigg *et al.*, 1990; Barret-Lennard, 2000) based on matriline, where males never leave the original group except for short moments to join other groups for reproduction (Bigg *et al.*, 1990; Barret-Lennard, 2000).

There have been several genetic studies of North Atlantic long-finned pilot whales (Andersen, 1988; Amos *et al.*, 1993; Caurant *et al.*, 1994; Fullard, 2000; Caurant *et al.*, 1994; Fullard *et al.*, 2000; de Stephanis *et al.*, 2008) which, combined with information

from behavioural studies based on photo-identification, have shown a multigenerational group composition based on matrilineal social structure, with large and stable families, males and females that rarely if ever interbreed (Amos *et al.*, 1993; Fullard, 2000), and apparently without a strong reproductive dominance.

Studies of groups of animals taken in the Faroese drive fishery have examined protein polymorphisms (Andersen, 1988; Amos *et al.*, 1993), organochlorine concentrations (Aguilar *et al.*, 1993), trace metals (Caurant *et al.*, 1994), and intestinal helminth communities (Balbuena and Raga, 1994) and also showed inter-group differences consistent with longitudinally stable behavioural groups. Nevertheless, Amos *et al.* (1993) found that it was not clear whether or not the fathers of each foetus came from one or more different pods. Adult males of the same group, on the other hand, were closely related, based on the excess of heterozygotes in only one allele's loci, which is typical of sibylline twins (Amos *et al.*, 1991a; 1991b). Males from the same group could possibly be brothers who keep associations during adulthood, as happens in chimpanzees (Goodall, 1986) and lions (Packer and Pursey, 1982; Packer *et al.*, 1991). Even though the hypothesis that the adult males of *Globicephala melas* are related to individuals in the same groups in which they were captured is the most supported (Amos *et al.*, 1993), this is not completely conclusive and no information regarding a possible behavioural social system is available. The limitations of using a cross-sectional analysis of group composition to describe longitudinal aspects of pilot whale social structure have raised concerns and the addition of mitochondrial (mtDNA) analysis has been suggested to support these results (Oremus, 2008).

Oremus (2008) conducted a genetic study on long-finned pilot whales stranded in New Zealand in order to investigate whether groups observed at sea represented longitudinally stable "extended matrilineal groups" as suggested in previous studies (Amos *et al.*, 1993; Fullard *et al.*, 2000), or whether they represented ephemeral associations between groups of smaller, stable matrilineal units as suggested by Ottensmeyer and Whitehead (2003). The results showed that stranded groups were composed of multiple unrelated matrilineal units, in contrast to what has been reported in the Faroe Islands studies. Evidence of long-finned pilot whale groups containing multiple unrelated matrilineal units with some degree of natal group philopatry suggests that long-finned pilot whales have a social structure distinct from sperm whales and eastern North Pacific killer whales (Oremus, 2008). De Stephanis *et al.* (2008) proposed that the groups taken in grinds in the Faroe Islands and the "aggregations" recorded in the Alboran Sea (Cañadas and Sagarminaga, 2000) could coincide in structure to "clans" identified in the Strait of Gibraltar and be formed by different pods, similar to killer whale matrilineal units.

Limitations of genetic analysis have been partially complemented by photo-identification studies on free-ranging long-finned pilot whales off Nova Scotia, Canada (Ottensmeyer and Whitehead, 2003). Here, many of the associations found within groups were determined to be ephemeral and degraded over a period of a week with, however, a subset of individuals forming long-term associations; however, the lack of genetic support did not allow any insight into a possible matrilineal structure.

While behavioural studies have been conducted on short-finned pilot whales (Shane and McSweeney, 1990; Heimlich-Boran, 1993, Mahaffy, 2012), detailed genetic individual relationships for this species have not yet been considered in detail (e.g. Shane and McSweeney, 1990; Heimlich-Boran, 1993), so there is no evidence for or against a matrilineal social structure. Genetic studies of short-finned pilot whales killed off the Japanese coast identified two genetically-isolated stocks operating at the inter-population level (Wada, 1988), which were distinctive in phenotypic and morphologic features in body size and pigmentation (Kasuya *et al.*, 1988), but no inferences about social organization were made. A recent study of the social structure of this species in Madeira compared social relationships based on photo-identification data to genetic samples and suggested a social structure based on natal group philopatry, similar to that proposed for long-finned pilot whales. The limited sample for genetic analysis makes this conclusion preliminary and further investigation is needed with a larger sample size (Alves *et al.*, 2013).

Long-term bonds among short-finned pilot whale off the island of Hawaii were studied by Mahaffy (2012), who analysed 267 encounters recorded between 2003 and 2007. A total of 448 distinctive individuals were identified with different degrees of residency suggesting that only some individuals had high site fidelity (154 core residents) with, at the same time, the possibility of multiple populations using the area. Nine longitudinally-stable social units of key individuals (found together more than eight times during the 4 years of the study) and their constant companions (found together more than five times in 3 years) were identified. Some segregation between adult males and female/calf pairs, or adult male dispersion from their natal groups was also suggested as possible. Even though social units represented persistent social entities with some dynamics differing among units, Mahaffy (2012) pointed out that the social and ecological significance of these units remains unclear. The differences found in age and sex-based segregation in the social structure of short-finned pilot whales off Hawaii compared to the study of long-finned pilot whales in the Strait of Gibraltar (de Stephanis *et al.*, 2008b) may indicate differences between the two species, or may simply indicate differences between these two populations (Mahaffy, 2012).

1.4.6 WORLD THREATS AND CONSERVATION ISSUES

Conservation of natural habitats and species is increasingly needed due to the growing negative effects of human activities. Nevertheless, evaluating and quantifying human impacts are generally difficult processes, as is establishing whether management is necessary and at the same time if it will be effective (Gwenith, 2010). The enforcement of the management of human activities is quite challenging, especially in the marine environment where political boundaries are not always clear and the issue of "ownership" can prevent the implementation of protective measures (Pullin, 2002; Reeves, 2003).

In cetaceans, negative impacts on populations are in some cases apparent from commercial whaling, and in the increasing incidence of ship strikes (Jensen and Silber, 2003), entanglement in fishing gear (Johnson *et al.*, 2005) and depleted prey resources (Bearzi *et al.*, 2008). Other factors may also represent serious threats with long term impacts, such as habitat loss and degradation (including environmental and acoustic pollution), climate change, land-based changes (agricultural, industrial and forestry activities), and coastal development (urbanisation, industry, tourism, and construction).

In the increasing effort to conserve cetacean populations, several treaties and conventions have been established (see Reeves 2009) and applied at international, national, regional, and local levels. Some of the most important and also most relevant for the present study are the International Whaling Commission (IWC), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the International Union for the Conservation of Nature (IUCN), the Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention), the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). The Red List, maintained by the IUCN, represents the primary international framework for assessing conservation status (Rodrigues *et al.* 2006). The designation of various forms of marine protected area (specially protected area SPA, special area of conservation SAC, marine conservation zones MCZs, area of special conservation ASC, no take zones NTZs, etc.), is a potentially valuable tool to achieve conservation objectives.

Pilot whales are included in a number of international treaties: Bern Convention (1972, Annex II as "strictly protected"); long-finned pilot whale in the IV protocol of the Barcelona Agreement (Annex II); CEE/CITES regulation (Appendix II), and in Annex IV of the EU directive nº 97/62/CEE on the conservation of Natural Habitats and Wild Fauna and Flora (Habitats Directive) as species of community interest which requires strict protection measures.

In the Red book of Vertebrates, European and Spanish catalogues (<http://www.magrama.gob.es>), long-finned pilot whales are considered as "Data deficient", while in the world catalogue they are considered "Not threatened". Short-finned pilot whales are instead listed in all these catalogues as "Not-threatened". The IUCN Red List of Threatened Species (<http://iucnlist.org>) lists both long- and short-finned pilot whales as "Data deficient". In the Spanish and Canary Islands Catalogue of Endangered Species (<http://www.parcn.es/pub/bop/7l/2010/182/bo182.pdf>) the short-finned pilot whale of the Archipelago is listed as "vulnerable", even though, scientific information, especially at the population level, is lacking to support this designation.

Little is known about the conservation status of pilot whales worldwide, and there is no information on global trends (Taylor *et al.*, 2011). The main threats that could have a negative impact include entanglement in fisheries, noise, and boat collisions. Hunting is localized (long-finned pilot whales in the Faroe Islands, and West Greenland, Taylor *et al.*, 2008; short-finned pilot whales in Japan), and has not had a high impact on the status of the species globally. The combination of these possible threats on this species population has been considered to be sufficient that a 30% global reduction over three generations (71 years for short-finned and 72 years for long-finned pilot whales; Taylor *et al.*, 2008) cannot be excluded.

Direct catch: Due to their highly developed social structure, pilot whales have been traditionally hunted in "drive fisheries", in which pods are generally herded by boats into shallow water and driven to the beach where they are slaughtered. This practice, common during the 19th and 20th centuries, has provided meat, blubber and oil.

In the Faroe Islands, the hunting (*grindadráp*) of the long-finned pilot whale started at least as early as the 16th century (Ridgway, 1998), and continues today. Thousands of whales were killed during the 1970s and '80s (Mitchell, 1975; Hoydal, 1987), with an annual average catch of 850 pilot whales (range: 0-4,480) and cyclic variation, according to North-Atlantic climatic variations (Bloch and Lastein, 1995; Bloch, 1998). After four hundred years of recorded *grindadráp*, over-exploitation does not seem to be a threat and will probably not lead to the abandonment of the *grindadráp* (Fielding, 2010). However, the effects of marine contaminants in pilot whale meat and blubber may threaten continuation of the *grindadráp* (Fielding, 2010).

In other areas of the North Atlantic, such as Norway, West Greenland, Ireland, Iceland (O'Riordan, 1975), and Cape Cod, pilot whales have also been hunted, but less extensively (Kapel, 1975). The fishery at Cape Cod harvested 2,000–3,000 whales per year during the late 19th and early 20th centuries (Mitchell, 1975), while in

Newfoundland it reached its peak in 1956 with 9,794 individuals taken (Pinhorn, 1976), but declined shortly after (Mitchell, 1975) and finally closed. In the Southern Hemisphere, exploitation of long-finned pilot whales has been sporadic and at a low level (Mitchell, 1975). At present, long-finned pilot whales are only hunted at the Faroe Islands and Greenland (Taylor, et al., 2008).

Short-finned pilot whales have been also exploited for centuries in the western North Pacific through both drive and harpoon-gun whaling operations. Between 1948 and 1980, hundreds of short-finned pilot whales were taken annually by small coastal whaling stations and drive fisheries at Hokkaido and Sanriku in the north and Taiji, Izu, and Okinawa in the south (Kasuya and Marsh, 1984), the largest catches of this species (Jefferson *et al.*, 1993). These fisheries were at peak activity in the late 1940s and early 1950s (Kasuya and Marsh, 1984), and in the mid- to late 1980s (Taylor *et al.*, 2008). In 1982, the drive fishery at Taiji expanded, and the harpooning of the northern form was resumed off Sanriku and Hokkaido. Between 1982 and 1985, 519 of the northern form were killed and, during the same period, 1,755 whales of the southern form were also taken. From 1985 to 1989, Japan took a total of 2,326 short-finned pilot whales (Bernard and Reilly 1999). The northern form is now hunted only by small-type coastal whaling, while the southern form is also targeted by drive fisheries, hand harpoon, and cross-bow. In 1993, annual quotas of 50 individuals for the northern form and 500 for the southern form short-finned pilot whale were established (Taylor *et al.*, 2008; National Far Seas Research Institute 1979-2010). In 1997, a catch of 347 short-finned pilot whales was recorded (Olson and Reilly, 2002), reducing to 63 in 2004 (Olson, 2009). After some changes in 1999, when catches increased, in 2012-2013 catches were set at 36 for the northern form and 250 for the southern form (National Far Seas Research Institute 1979-2010). Since the establishment of the quotas, the catches have fluctuated. In 2010, the southern form catches reached only 16% of the quota and, since 2007, no northern form animals have been caught (National Far Seas Research Institute, 1979-2010), possibly due to the recent decline in catch effort or to the suspected decline of the population, or to the combination of the two (Funahashi and Baker, 2011).

The Potential Biological Removal (PBR) method (Wade *et al.*, 2008) has been applied to the populations targeted by Japanese drive hunts to approximate a sustainable catch level (Funahashi and Baker, 2011). Based on this PBR calculation, the 2012-13 catch limit was 1.8 times higher than the PBR threshold (with a recovery factor of 0.5) and the average catches (2006-2010) were 1.9 times higher than the PBR threshold (Funahashi and Baker, 2011). Although the sustainability of the hunt of the northern form has not been evaluated, the 2012-2013 catch limit equates to 0.8% of the estimated abundance

(Baulch and Perry, 2013).

Short-finned pilot whales have also been hunted in harpoon fisheries in the Caribbean and Indonesia. In St Vincent in the Lesser Antilles, a small and intermittently active artisanal fishery killed around 220 pilot whales per year until at least the mid-1970s (Reeves *et al.* 2003). As well, there are indications of a small fishery at St. Lucia Island (Bernard and Reilly, 1999).

Illegal hunting of marine mammals was reported by Dolar *et al.* (1994) in central and southern Visayas, northern Mindanao and Palawan, Philippines, where hunters took dolphins and short-finned pilot whales for bait or human consumption. The whales were taken by hand harpoons or, increasingly, by togglehead harpoon shafts shot from modified, rubber-powered spear guns. Around 800 cetaceans were hunted annually, mostly during the inter-monsoon period of February-May. Although the Department of Agriculture issued Fisheries Administrative Order No. 185 (December 1992) 'banning the taking or catching, selling, purchasing, possessing, transporting and exporting of dolphins', this did not stop dolphin and whale hunting but it did seem to have caused a decrease in the sale of the meat openly in the market.

In the 19th century, whalers took pilot whales off the Azores Archipelagos to compensate for reduced sperm whale catches, and American whalers "practised" hunting for sperm whales on pilot whales (Clarke 1981).

Incidental catch: Pilot whales are taken as incidental catches in various types of fishery, mainly trawls, driftnets, and longlines.

In the Southern Hemisphere very few long-finned pilot whales are reported to be incidentally taken in fisheries (Reyes, 1991). Nevertheless, according to Bernard and Reilly (1999), more pilot whales are probably caught incidentally than are reported. On the east coast of the USA, the non-USA Atlantic mackerel fishery, responsible for taking 141 long-finned pilot whales in 1988, was suspended. Along the Atlantic coast of France, an annual kill of 50-100 *Globicephala melas* was reported in passive nets and traps (Perrin *et al.*, 1994). In British waters, this species is accidentally caught in gillnets, purse seines, and in trawl fisheries (Reyes, 1991). The waters around Cornwall are one of the most heavily fished areas of the United Kingdom. Since the mid-1970s, pilot whale strandings along these coasts increased significantly with seasonal peaks between November and January (Leeney *et al.*, 2008). Sixty-one % of individuals examined were determined to have died due to by-catch in fishing gear.

Pilot whales are also known to be incidentally taken in swordfish driftnets in the Mediterranean (Jefferson *et al.*, 1993). Lopez *et al.* (2003) reported that approximately 200 cetaceans, mainly small dolphins, as well as bottlenose dolphins and long-finned pilot whales, might be caught annually in inshore waters and around 1,500 in offshore waters of Galicia (Spain).

Zerbini and Kotas (1998) reported that in southern Brazilian waters, in 1995 and 1997, the pelagic driftnet fishery for sharks (families *Sphyrnidae* and *Carcharinidae*) incidentally caught various cetacean species, including 15 *Globicephala melas* individuals, making this fishery an important cause of cetacean mortality.

In the North Pacific, by-catches of short-finned pilot whales were mainly linked to driftnet fisheries for swordfish and sharks, and the squid purse seine fishery in California waters, where, in one year, around 30 short-finned pilot whales were taken (Miller *et al.*, 1983). Between 1993 and 1995, in California's drift gill net fishery the mean annual catch reached 20 short-finned pilot whales (Ridgway, 1998; Bernard and Reilly, 1999). Most recently, the pelagic longline fishery has become the major cause of by-catch in this species. In US Atlantic waters, by-catch of pilot whales was mainly in coastal gillnets, bottom and mid-water trawl fisheries, with the highest mortality rate linked to the pelagic longline fishery (Waring *et al.*, 2002); these catches did not exceeded the allowable annual take under US law (Olson and Reilly, 2002). Between 2003 and 2007, the annual estimated mortality or serious injury of both species of pilot whales in this fishery reached a total of 110 whales (Waring *et al.*, 2009). As a result of the exceeded allowable limit, a take reduction plan was implemented, and pilot whale by-catch was addressed by the Atlantic Pelagic Longline Take Reduction Team, with the result that the annual take declined to be lower than the allowable limit (Olson, 2009).

In the Hawaiian longline fishery, about one to two animals per year were reported by Forney and Kobayashi (2007), corresponding to two short-finned pilot whale catches in 24,542 observed sets. In the western Pacific ocean, an estimated 350-750 whales died annually in passive nets and traps set in Japanese fisheries (Bernard and Reilly, 1999). Using molecular monitoring, systematic surveys of 'whalemeat' markets in the Republic of Korea (Baker *et al.*, 2006) revealed the presence of products containing short-finned pilot whale. As Korea has no programme of commercial or scientific whaling, and dolphin and porpoise hunting is not allowed, the only legal source of these products was assumed to be by-catch, as the government reported to the International Whaling Commission. In the Caribbean, off Puerto Rico and the US and British Virgin Islands, entanglement and accidental captures, together with animals being shot or speared, represented the most

common human-related cause of death for short-finned pilot whales (Mignucci *et al.*, 1999).

Chemical pollution: Pilot whales are susceptible to the accumulation in their muscle and blubber tissue of high levels of heavy metals, persistent organic pollutants (POPs), and DDT, which may have an important impact on these long-lived high trophic-level predators (Dam and Bloch 2000).

In the mid-70s, high quantities of DDT and PCB were found in short-finned pilot whales along the western US coast. In contrast, low levels were found in whales from the Antilles and Japan (Bernard and Reilly, 1999; Ridgway, 1998). This was also confirmed by Bustamante *et al.* (2003), who found in the liver, muscle and blubber tissues of two short-finned pilot whales from New Caledonia, levels of Al, Cd, Co, Cr, Cu, Fe, organic and total Hg, Mn, Ni, Se, V, and Zn that were far below levels of concern.

Low levels of DDT were found in long-finned pilot whales from Newfoundland and Tasmania (Ridgway, 1998). In contrast, high levels of DDT and PCB were encountered in pilot whale tissues in the waters of the Faroes, France, UK and eastern US (Ridgway, 1998). However, whales from the Faroes were also contaminated with cadmium and mercury (Simmonds *et al.*, 1994). The frequent and prolonged ingestion of meat contaminated with mercury and cadmium, could cause a health risk especially in children and pregnant women (Haslam, 2003).

Weisbrod *et al.* (2000) reported organochlorine bioaccumulation in long-finned pilot whales stranded and caught in nets in Massachusetts. Reflecting pod-fidelity, whales that stranded together had more similar tissue-levels than individuals of the same sex or age class. The similarity in tissue concentrations within a stranding group, and the high variation among individuals and pods suggested that pilot whale pods are exposed to a large range of pollutant sources, such as through different prey and feeding locations (Desportes *et al.* 1994).

Noise pollution: The increasing level of man-made noise in the marine environment (Nowacek *et al.*, 2007; Weilgart, 2007; Tyack, 2008) during the last half a century (Ross 1976, Urick 1983) is considered one of the factors affecting habitat quality in the oceans (NRC 2003, Tyack 2008), and may have an effect on acoustically sensitive species of cetacean (Rendell and Gordon, 1999; Cox *et al.*, 2006). Underwater noise can cause behavioural changes in cetaceans, impede the process of conveying or acquiring information acoustically (Richardson *et al.*, 1995), and may lead the animals to be displaced from areas important for their survival (Lusseau, 2003; Bejder, 2005; Lusseau *et al.*, 2009). Since the detection of an acoustic signal is ultimately limited by the level of

the ambient noise emitting in the same frequency band as the signal, the introduction of broadband anthropogenic noise into the environment decreases the capability of detecting a signal and may mask sounds that a whale would use for acoustic communication or prey detection (Richardson *et al.*, 1995; Gelfand, 2004). In general, the effective space in which cetaceans are able to detect the signal of a conspecific (Marten and Marler, 1977) decreases with the increasing of the masking noise. In extreme cases, man-made noise may also cause acoustic trauma, i.e. physical damage to the ears, and severe stress to the animal (Rendell and Gordon, 1999; Cox *et al.*, 2006).

One of the most widespread noise sources in the marine environment is shipping and boat traffic (Ross, 1976; Urick, 1983), including recreational and whale-watching vessels (NRC 1994, 2003, McCarthy, 2004). Other noise sources that may impact cetaceans include air guns used during oil and gas exploration, predator deterrent devices used in fish farms, offshore windfarms, and military activity.

Behavioural changes in cetaceans associated with vessel noise have been reported in short-term studies (Richardson *et al.*, 1995; Nowacek *et al.*, 2001; Bejder and Samuels, 2003). However, interpretation and quantification of the impacts of vessel noise on cetaceans is difficult because of the complexity of cetacean behavioural patterns, the lack of baseline data, correlations between fitness and the ability to react (Stillman and Goss-Custard, 2002; Beale and Monaghan, 2004), prior displacement of the most sensitive animals (Bejder *et al.*, 2006a), and also biases that the observation platform itself may introduce (Bejder and Samuels 2003).

Bejder (2005) and Bejder *et al.* (2006b) linked long-term declines in dolphin abundance to increasing vessel activity. The studies demonstrated the need for long-term studies because short-term studies may lead to erroneous conclusions about the actual impact on cetaceans (Bejder, 2005; Bejder *et al.*, 2006b).

Jensen *et al.* (2009) conducted a study on the effect of vessel noise on delphinid communication and concluded that noise from small vessels can significantly mask acoustically mediated communication in these animals. Short-finned pilot whales had a 58% reduction in their communication range due to the presence of a vessel travelling at five knots within 50 m (Jensen *et al.*, 2009).

In the Mediterranean, long-finned pilot whale vocalisations were investigated during active military sonar exercises. Vocalisations changed in response to the noise that dominated the acoustic environment over a significant range, indicating short-term vocal responses of whales to the sound source, but this is of unknown significance (Rendell and

Gordon, 1999).

While conclusive evidence of cause and effect are often lacking, mass stranding events have been spatially and temporally associated with high levels of anthropogenic sound (Hohn *et al.*, 2006). Approximately 145 long-finned pilot whales were involved in three mass stranding events in Tasmania, in 2005. The first two stranding events coincided with the use of high frequency (50-200 kHz) sonar by two Australian naval vessels; one stranding occurred 6 hours before the vessels arrived, and the other just over an hour after the vessels began using the sonar in the vicinity of the stranding. A behavioural reaction to the sonar causing the second and third strandings could not be ruled out (Parsons *et al.*, 2008).

Whale-watching: Whale-watching vessels represent a particular form of vessel traffic that not only contributes to underwater noise in cetacean habitat, but also actively approaches and congregates around specific target cetacean populations (Jensen *et al.*, 2009).

Whale-watching is a growing industry with important socio-economic implications for coastal communities in many countries (O'Connor *et al.*, 2009), and in excess of 700 to 1000 cetacean populations routinely interact with tour boats (Hoyt, 2001). Even though whale-watching has often been considered as a benign activity not directly harming the targeted cetaceans (Hoyt, 1993), concern about the potential disturbance that this industry may have on several cetacean species has increased.

The International Whaling Commission (IWC) has stated that there is "compelling evidence that the fitness of individual odontocetes repeatedly exposed to whale-watching vessel traffic can be compromised and that this can lead to population level effects" (IWC 2006, p. 47).

The potential impact of interactions between tourist vessels and cetaceans has been the subject of several studies for more than 20 years (Baker and Herman, 1989; Corkeron, 2004). Over this period a wide range of short-term effects has been identified and described for many species (Au & Green, 2000; Bejder, *et al.*, 1999; Blane and Jaakson, 1995; Hastie *et al.*, 2003; Lusseau, 2006; Nowacek *et al.*, 2001; Williams *et al.*, 2002). These include modifications in respiration patterns, changes in path directedness and other forms of short-term behavioural alterations as a consequence of apparent horizontal and vertical avoidance tactics (Frid and Dill, 2002).

Moving from the description of short-term changes, which are sometimes contradictory and uninformative (Beale and Monaghan, 2004; Bejder *et al.*, 2006a; Gill *et al.*, 2001), to a more complete understanding of the biological significance of these impacts is challenging (Corkeron, 2004). Nevertheless, recent studies show that short-term behavioural responses could lead to biologically relevant effects which could have long-term consequences for individuals and their populations (Bejder, 2005; Bejder *et al.*, 2006a; Bejder *et al.*, 2006b; Foote *et al.*, 2004; Lusseau, 2005; Lusseau *et al.*, 2006b; Williams *et al.*, 2006).

Repetitive short-term behavioural changes can influence life functions by imposing additional costs to the energetic budget of individuals (Lusseau and Bejder, 2007), influencing the evolutionary dynamics of populations and affecting their vital rates. As has been shown for other anthropogenic impacts (Slooten *et al.*, 2000), alteration of vital rates might affect the viability of populations, especially in small, closed populations with low carrying capacity (Lusseau and Bejder, 2007).

In many areas, the pilot whale is one of the main species targeted by the whale-watching industries, especially where they occur year-round. Among others places, long-finned pilot whales are easily seen in Chile, Nova Scotia/New Brunswick, Faroes, Norway, France, Monaco, southern Spain, Italy, and short-finned pilot whales are the focus of whale-watching in Japan (Hokkaido, Shikoku), Maldives, Philippines, Indonesia, Papua New Guinea, Micronesia, Hawaii, Bermuda, Caribbean (Bahamas, Dominican Republic, US Virgin Islands, Guadeloupe and islands, S. Lucia), Panama, Ecuador, Tenerife, and Azores (Wilson and Wilson, 2006; O'Connor *et al.*, 2009).

Ship strikes: Collisions between cetaceans and vessels are a global issue of growing concern, especially since the 1950s, when the worldwide number of collisions increased markedly on the introduction of ships capable of speeds up to 35–40 knots (IWC, 2008; Laist *et al.*, 2001; Ritter, 2010; Weinrich, 2004).

In 2005, the International Whaling Commission created the Ship Strike Working Group (SSWG) under its Conservation Committee to assess the problem on a global scale, starting with the identification of 'high risk areas' (IWC, 2006). During recent decades, the development of shipping traffic in some parts of the world has become so critical that the issue has been also introduced in the Agenda of the International Maritime Organisation (IMO, 2009).

Until now, only a small number of high risk areas have been identified and described, mainly because the real number of collisions in a given area is rarely known, even when collisions are regularly reported (ACCOBAMS, 2005; Laist *et al.*, 2001; Panigada *et al.*,

2006). It is not possible to account for the number of animals that are lost at sea, especially those that are unlikely to float, and, furthermore, determining the real cause of death in the case of a ship strike, when a necropsy cannot be performed is unlikely. Therefore, quantifying the risk of collision is difficult, as long as the volume of ship traffic (e.g. expressed as the number of transects of certain types of vessels, travel distances and the frequency of transects) and/or cetacean abundance and distribution are not known (ACCOBAMS, 2005; IWC, 2006).

Nevertheless, a number of "hot spots" have been identified as areas where the risk of ship strikes may affect the status of cetacean populations (ACCOBAMS, 2005; Pesante *et al.*, 2002). These include the east coast of the USA (Douglas *et al.*, 2008; Knowlton and Kraus, 2001), the northern Mediterranean Sea (Panigada *et al.*, 2006), the Strait of Gibraltar (de Stephanis and Urquiola, 2006), the Western Pacific (IMO, 2007) and the Canary Islands (de Stephanis and Urquiola, 2006; Ritter, 2010). These areas are characterised by an extensive overlap between high levels of vessel traffic and a known high density of cetaceans (Carrillo and Ritter, 2010).

Where known, vessel strikes have been reported to involve a large variety of vessels, including tankers, cargo or cruise ships, ferries, whale-watching boats, military vessels yachts, and hydrofoils (Jensen and Silber, 2004; Laist *et al.*, 2001; Van Waerebeek *et al.*, 2007; Ritter, 2009), and a wide range of cetaceans species, including large whales (baleen whales, sperm whales; Laist *et al.* 2001), but also smaller cetaceans, like pilot whales, beaked whales, bottlenose dolphins, striped dolphins, killer whales, river dolphins and harbour porpoises (review by Van Waerebeek *et al.*, 2007; Dolman *et al.*, 2006).

Captivity: Short-finned pilot whales have been kept in aquaria and oceanaria. During the 1960s and early 1970s several pilot whales from Japan, southern California and Hawaii were taken into captivity, two of which were at SeaWorld in San Diego (Reeves and Leatherwood, 1984; Walker, 1975). During the 1970s and early 1980s, six pilot whales were captured alive by drive hunts and taken for public display (Ridgway, 1998). Since 1973, some long-finned pilot whales from New England waters were also taken and temporarily kept in captivity (Reeves and Leatherwood, 1984; Walker, 1975). In general, pilot whales have a low survival rates in captivity, with the average annual survival being 0.51 (based on data from the mid-1960s to the early 1970s; Walker, 1975).

1.4.7 SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS

The presence of the short-finned pilot whale around Tenerife has long been known by navigators and local fishermen. Its presence was not officially recorded until Richard

(1936) observed this species between Tenerife and La Gomera during an expedition of the Monaco Oceanographic Museum, and it was only in 1989 that Hervé-Gruyer (1989) recorded its regular occurrence in front of the bay of Los Cristianos in the southwest of Tenerife. Since then, short-term research projects developed in the Canary Islands have analysed different aspects of its biology (Richard, 1936; Heimlich-Boran, 1993; Martín and Montero, 1993; Montero and Arechavaleta, 1997; Martín *et al.*, 2000).

Short-finned pilot whales have been recorded around almost all the islands of the archipelago: Lanzarote (Politi *et al.*, 1996), La Gomera (Ritter, 1996; Ritter *et al.*, 2011), La Palma (Pérez-Vallaza *et al.*, 2008), as well as in the southwest of Tenerife (Escorza *et al.*, 1992; Heimlich-Boran and Heimlich-Boran, 1992; Heimlich-Boran, 1993; Montero and Arechavaleta, 1997). This latter area is where the only systematic research on the species in the Canary Archipelago has been conducted, focusing on the social structure of the population off the southwest of Tenerife (Heimlich-Boran, 1993; Heimlich-Boran *et al.*, 1995). Between October 1989 and July 1991, Heimlich-Boran analysed the different levels of social organization and association patterns among individuals to test the hypothesis that mating occurs outside the social group they belong to. A resident population of 388 individuals inhabiting the area year-round was described, indicating a high level of site fidelity and social bonding, which distinguished these animals from the 107 whales seen only once and classified as visitors (Heimlich-Boran, 1993). The comparison between the images in the catalogue compiled by Heimlich-Boran (1993) and those obtained during 1999-2000 in the island of Gran Canaria (Servidio, *et al.*, 2002) revealed the recapture of six animals that had clear and identifiable marks with almost no modifications. Of these six whales, all except one were classified as residents and two, belonging to the same group "pod T" (Heimlich-Boran, 1993), were recaptured together in Gran Canaria.

The only estimate of abundance for this species is from a line transect study conducted in 2002 in the southwest of Tenerife by Carrillo and Peña (2002), which estimated a total of 362 individuals (95% CI = 241-544). Different usages of this area were identified, mostly localised around the 1.000m isobaths, with a small core area (27 km²) located in front of the main harbours of southwest Tenerife (Carrillo *et al.*, 2010). The encounter rate was highest during the months of September and December (Carrillo *et al.*, 2010).

Some other studies have been conducted on this species in the area, including stomach contents (Hernández-García and Martín, 1994; Fernández *et al.*, 2009), and acoustic behaviour (Martín and Santiago-Medina, 1997). In 2003, two cruises deployed acoustic and movement recording DTags on 23 short-finned pilot whales off Tenerife (Johnson

and Tyack 2003). As previously described (section 1.4.4) combining sound and motion data, it has been shown that while the acoustic behaviour of deep foraging pilot whales is similar to that of other echolocating deep-divers, the tactics apparently used to capture prey at depth differ widely and include a surprisingly energetic behaviour for a breath-holding deep diving animal (Aguilar de Soto *et al.*, 2008).

The conservation of short-finned pilot whales has been discussed in relation to the effects of whale-watching (Martín and Montero, 1993; Montero and Arechavaleta, 1997; Scheer *et al.*, 1998) and ship strike events (de Stephanis and Urquiola, 2006; Carrillo and Ritter, 2010), which are considered among the major threats affecting this species in at least some areas of the archipelago.

The whale-watching industry is an important part of the wide choice of maritime and coastal tourist services offered in the Canary Islands, mainly concentrated in southwestern Tenerife, with a total of 37 vessels licensed and an estimated 625,000 visitors in 2008 generating around 19.8 million euro of direct gross income alone.

The whale-watching activity was legislated in the archipelago via regional decree in 1995 (Decree 320/1995) and last brought up to date in the year 2000 (Decree 178/2000), with the aim to minimize the risk to cetacean populations through a strict code of conduct and minimum quality standards. Nevertheless, there is no active inspection and there is a serious problem of illegal activity conducted by unauthorised boats and more recently also by jet-skis.

Avoidance behaviour to whale-watching vessels has been described for short-finned pilot whales in the southwestern Tenerife (Glen, 2003). In the presence of one or two boats, 28% of sightings involved avoidance reactions, while in the presence of three or more vessels, this percentage arose to 62% of sightings. The author concluded that any impacts from whale-watching vessels should be minimised until it is shown that they are not detrimental to the status of the population.

Several types of ferries operate between the islands, including fast ferries (travelling at approx. 25 knots) and numerous high speed crafts (HSC, reaching maximum speeds of 40 knots; Ritter, 2010) that cover around 29,000 transects and almost 1.5 million kilometres (data from 2007; Ritter, 2010), for several million people (tourists and locals) every year (Rodríguez *et al.*, 2005). The areas of high density ferry traffic in the Canaries, especially between the islands of Tenerife and Gran Canaria and between La Gomera and Tenerife, overlap considerably with important cetacean habitats (Ritter, 2010) as well as with Special Areas of Conservation under the EU Habitat Directive.

Between 1991 and 2010, among the 70 cetacean carcasses found to have died because of anthropogenic interaction, 43 were considered to be involved in vessel-whale collisions (Carrillo and Taverna, 2010). These numbers are considered to be underestimates, not only because collisions may go unnoticed, but also because animals that have been hit may sink to the seafloor or simply drift away (ACCOBAMS, 2005; Laist *et al.*, 2001). Six short-finned pilot whales stranded in Tenerife showed injuries that could be attributed to ship strikes, including large dorsal cuts, multiple traumas on the skull, jaws, ribs, and vertebrae, head or tail cut off (Arbelo, 2007).

During the IWC workshop (IWC 2010), ship strikes were recognised as a definite risk for cetaceans. In the Canary Islands, deep diving species, including sperm whales, pygmy sperm whales, pilot whales and beaked whales have been described as the principal species affected by ship strikes, (Carrillo and Ritter, 2008; Ritter, 2007). The IWC workshop recommended that these populations should be considered as candidates for the development of a conservation management plan or plans to address the risk of ship strikes, following the guidance provided in Donovan *et al.* (2008) and IWC (2010). Furthermore, considering the limited information on the population dynamics of cetaceans in the islands, the Workshop considered it to be urgent to obtain accurate estimates of abundance and distribution for these populations, especially in those area identified as hot spot for ship strikes: the channel between Tenerife and La Gomera, the channel between Tenerife and Gran Canaria, the strait between Lanzarote and Fuerteventura (see Ritter, 2007). A model of risk for the high shipping traffic areas in Tenerife was developed (Tregenza *et al.* 2000, 2002).

1.5 OBJECTIVES AND IMPORTANCE OF THE STUDY

The climatic and oceanographic characteristics of the Canary Islands and the high sighting predictability of short-finned pilot whales in the southwestern Tenerife (Urquiola *et al.*, 1998) have led to this species becoming the main target species of a prospering whale watching industry and it has arguably become the species most affected by anthropogenic activity in the archipelago.

Systematic studies carried on this species in the Canary Archipelago are relatively recent. Beginning in the early eighties, they focused almost exclusively on the social structure of populations to the south of Tenerife and the study of stranded specimens (TRAGSATEC, 2013). No systematic research has been carried out in any of the other islands of the Archipelago. Very little is known about the distribution, seasonality, abundance, population structure, and habitat use of the Canary Islands by the short-finned pilot

whale population. Information on this species is patchy and mostly limited to the island of Tenerife. The majority of the data are included in unpublished symposium proceedings, internal reports presented to the Canary Government or to funding organizations (Martín *et al.*, 1998; Vonk and Martín, 1988; Martín *et al.*, 1992; Carrillo, 1996; Servidio *et al.* 2001, 2002, 2006, 2010; Arbelo, 2007). Moreover, methodological differences in both data collection and analysis prevent comparisons between the results presented by most of these studies. As a result, the current conservation status and the impacts of increasing human activities remain unknown.

The importance of the present project is that it is the first study of this species throughout the coastal-oceanic habitats of the whole archipelago and that it investigates simultaneously the behaviour, social structure, abundance and habitat use of short-finned pilot whales over multiple years. The information from this study represents a first step towards the development of recommendations for proper conservation measures for this species in the Canary Islands.

The thesis is organised in six chapters. Following this introductory chapter are four data chapters, each aimed at investigating specific aspects of the ecology of this species in Canary Islands and to highlight for conservation purposes the basic knowledge needed to develop proposals for management actions. Starting from questions about where and when the whales are, spatio-temporal distribution was investigated in relation to factors that might explain their presence and abundance patterns throughout the area. Identification of individuals enabled studies of how they move among areas, their site fidelity, and if and how they are linked in a structured society. The implication of these findings were investigated in order to understand if each island of the archipelago should be considered a separate conservation environment, or as a combined unit, and to detect the areas where more urgent and important conservation action should be addressed.

Through the analysis of photo-identification data collected since 1993, Chapter 2 investigates short-finned pilot whale residency in the Canary Islands, including their movement patterns within the islands, and the ranging behaviour of individually recognizable animals. Site fidelity for the Canary Islands population is examined and a first distinction between resident and transient populations is made.

Although behavioural studies carried out on the short-finned pilot whale in Tenerife have shown possible philopatry in natal groups and matrilineal structures (Heimlich-Boran, 1993), no studies have jointly taken into account both short and long-term associations in order to study the stability and composition of pilot whale groups. For a better understanding of social structure, association patterns, composition and stability of the

groups of the southwest Tenerife population, visual observation, video footage, and photo-identification techniques have been combined in a detailed analysis, the results of which are presented in Chapter 3.

Chapter 4 tackles the next logical step in the study of population ecology: the population demographic parameters. Especially for island-associated whales, knowledge of the abundance of short-finned pilot whales in the southwest of Tenerife is crucial to define conservation strategies for these cetaceans. The aim of the chapter is thus to provide the first abundance estimate of these whales in Tenerife, by applying mark-recapture statistical models to two years of photo-identification data. Both open and closed population models are investigated.

In Chapter 5, data collected during surveys conducted among the different islands of the Archipelago since 1999 are used to examine spatial patterns in short-finned pilot whale distribution in the Canary Islands. Spatio-temporal trends in cetacean distribution and abundance, their habitat preferences in relation to several physiographical, physical variables, and biological factors are investigated using generalised additive models (GAMs). Models for the prediction of habitat use are developed to improve understanding of the resources and habitats that are used most frequently by this species. Quantitative spatial predictions of density throughout the study area are mapped to inform spatial aspects of conservation and management.

The final discussion chapter presents an overview of the thesis findings, and discusses the challenges encountered and those likely to be faced in future studies. Crucial aspects needed to develop sustainable conservation measures are also presented.

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CHAPTER 2

SITE FIDELITY AND MOVEMENT PATTERNS OF SHORT-FINNED PILOT WHALES WITHIN THE CANARY ISLANDS

2.1 INTRODUCTION

The analysis and description of space-use patterns have been crucial in understanding the ecology of many mammalian populations (Adams and Davis, 1967; Inglis *et al.*, 1979; Inglis *et al.*, 1979). For most species, individuals are not distributed randomly and do not use all areas of their range with the same intensity. Instead, for a number of environment-related reasons, some portions of their range can be more frequently used than others (Adams and Davis, 1967; Van Ballenberghe and Peek, 1971; Metzgar, 1973; Inglis *et al.* 1979; Dixon and Chapman, 1980; Georgii, 1980; Springer, 1982; Konecny, 1989; Crawshaw and Quigley, 1989; Macdonald and Courtenay, 1996) or used differently (feeding, calving, etc.; Burt, 1943), forming characteristic patterns of distribution, grouping, ranging, and association (Crook *et al.*, 1976) with a high degree of variability in range characteristics (Shane *et al.*, 1986; Ballance, 1992). Therefore, animal space-use is the result of physiological and behavioural adaptations to particular environmental features. Various factors that affect space-use have been described: the tendency to remain in a particular area due to site fidelity (Smith, 1976; Shields, 1983; White and Garrott, 1990; Wauters *et al.*, 2001; Selonen and Hanski, 2003) or territorial behaviour (Burt, 1943; Ostfeld, 1990; Newton, 1992; Adams, 2001); the distribution of required or selected resources (Bergerud, 1974); and the location of other animals (e.g., mates, competitors, predators and prey; Wauters *et al.*, 2000).

These behavioural patterns are shaped not only by spatial and temporal changes in the environment, but also by internal biological constraints of individuals, such as age, sex and reproductive condition (Crook *et al.*, 1976). In this context, behavioural strategies evolve to optimize the conditions under which individuals can perform vital functions to maximize fitness, given the specific structure of the habitat in which they live (Crook *et al.*, 1976). Survival depends on the ability to obtain sufficient energy from resources within the environment and, at the same time, on the capacity to avoid predation. Reproduction involves finding receptive individuals with whom to mate and the necessary energy to raise offspring (Crook *et al.*, 1976).

Pressures of avoidance and attraction are usually related to mating opportunities (Emlen, 1973), predator-prey relationships (Mech, 1977; Murray *et al.*, 1994) or competition (Pimm and Rosenzweig, 1981; Maurer, 1984). Access to mates, and therefore the opportunity to reproduce, and predation pressure affect not only where an animal can feed but also how it feeds, and strategies to increase access to mates are often integrated with strategies to exploit food resources (Powell, 2000). Abundance, distribution, and predictability of food resources influence both the size of the area

needed and the way space within that area is used (Davies and Houston 1984). At the most basic level, the range of an animal must be large enough to provide adequate food resources to satisfy energetic requirements (McNab, 1963). Territory shifts are considered to be a behavioural response to the instability of the environment, when food resources fluctuate rapidly and unpredictably (Doncaster and MacDonald, 1991).

In addition, the scale of space-use and movements of individuals can have important effects on the genetic structure of a population (Wiens, 1976) by ensuring or restricting the opportunities for gene flow to occur between areas. While space-use strategies used to satisfy metabolic demands or avoid being killed by predators may increase the chances of survival, maximizing fitness also entails passing genes on to the next generation.

Temporal distribution patterns for individual have been presented in many studies assessing their site fidelity (Defran and Weller, 1999) or residency (Ballance, 1990). Information on site fidelity improves the evaluation of habitat use for particular individuals by recording their recurrence in previously occupied zones. For most species, site fidelity and movement are essential components of these vital functions because foraging, predator avoidance or mate finding depends on them. Therefore, information about individual patterns of space-use within their environment can provide important insights into the factors that affect how animals use resources in space and time (Brown and Orians, 1970), as well as residency, territoriality, mating systems (Clutton-Brock, 1989, Ostfeld, 1990), social organization (Rubenstein and Wrangham, 1986, Ostfeld, 1990), and demography (Clutton-Brock and Albon 1985). Traditionally, studies of terrestrial animal space-use patterns have focused on documenting the home range of individuals. First introduced by Burt (1943), the term home range indicates a region where animals live and perform biologically important activities, such as food gathering, mating and caring for young, often throughout their lifetime (Burt, 1943; Jewell, 1966). Despite criticisms mainly because of its lack of a temporal component (Kernnohan *et al.*, 2001), this definition is still widely used and accepted.

Nevertheless, for highly mobile marine predators, such as cetaceans, which generally live in an environment with no obvious physical boundaries, the traditional concept of home range may not be applicable, or at least should be used with caution. Moreover, home ranges defined over different time scales are not directly comparable (Börger *et al.*, 2008); an animal might show unbounded movement at a small spatiotemporal scale, but still have a well-defined and stable home range at a larger scale (Powell *et al.*, 1997; Weimerskirch 2007). In addition, the timing of the sampling period over which site data

are collected can have a strong effect on the ability to identify temporal patterns (Börger *et al.*, 2006b). Therefore, the concept of an area of more intensive use seems to be more appropriate for marine mammals than the use of home range, and it has been conceived as the "core area" (Hodder *et al.*, 1998; that replaced Hayne's, 1949, original "centre of activity" terminology) of the animal range.

Even though data on geographical range are scarce for most cetacean species, several studies have reported a strong correlation between cetacean movement patterns and the distribution and abundance patterns of their prey (Bowen *et al.*, 2002; Stevick *et al.*, 2002). Generalisations about the interaction between resource availability and space-use patterns have been made, starting from the theory that an individual will maximise food intake while minimising the amount of energy used to obtain food (Krebs and McCleery 1989). In an environment where food resources are abundant, and no aggressive, territorial neighbours are present, animals tend to use only as much space as they need (King, 2002), and to stay in familiar areas rather than risk moving to other areas, even if they are more productive (Switzer, 1993). If resources are uniformly spread throughout the environment, animals are also usually distributed uniformly, and if those resources are defensible, territoriality is often the consequence (Emlen and Oring, 1977). In unpredictable environments, if all areas are equivalently unpredictable, modelling has shown fidelity to be a more beneficial strategy than changing sites (Switzer, 1993). Moreover, it has been proposed that animals have a larger and overlapping geographical ranges in less productive habitats (Harestad and Bunnell, 1979) and in areas with patchily distributed or limited resources because, in both cases, they must travel farther to obtain enough food (Schoener, 1968; Clutton-Brock 1975).

Patterns in the heterogeneity of natural environments and of limited resources (Burt, 1943; Kaufmann, 1962; Samuel *et al.*, 1985; Samuel and Garton, 1987) produce a patchwork system of environmental characteristics, with structures differing in time and space, which influence the distribution of organisms as a response to this variability (Wiens, 1976; Stevick *et al.*, 2002). Patchy distribution and resource abundance may favour the development of territorial strategies: an individual can survive in one patch expending less energy in defending that patch than travelling between patches. Individual or species competition for the same resources in the same ecological niche may further modify the abundance and spatio-temporal distribution of resources and possibly affect strategies in space-use. As more individuals exploit an area of initially abundant resources, the resource value of the area declines until it becomes more beneficial for an individual to move to another area (Milinski and Parker, 1991). Studying core areas and movements within the whole distributional range of a species/population

is an important part of understanding the factors determining space-use and in helping to understand interactions with other individuals and the environment (Samuel *et al.*, 1985).

Cetacean distribution can also be strongly influenced by a diverse range of human activities which can either result in a degree of attraction (Pryor *et al.*, 1990; Fertl and Leatherwood, 1997; Fortuna *et al.*, 1998; Bearzi *et al.*, 1999; Chilvers *et al.*, 2003; Read *et al.*, 2003b; Sini *et al.*, 2005) or, more often, avoidance (Irvine *et al.*, 1981; Janik and Thompson, 1996; Allen and Read, 2000; Nowacek *et al.*, 2001; Morton and Symonds, 2002; Williams *et al.*, 2002a and 2002b; Leung Ng and Leung, 2003; Lemon *et al.*, 2005; Sini *et al.*, 2005; Bejder *et al.*, 2006a,b).

Animals with small ranges and high site fidelity are likely to be more vulnerable to localised impacts because at an individual level they are likely to be exposed to risk more often, while at a population level the impact is likely to be higher because it focuses on a single discrete group with a more limited ability for repopulation than if animals were ranging widely (Elwen, 2008). Localised population impacts can be further intensified if social communities of individuals within a population are not properly recognised and treated (Lusseau *et al.*, 2005). In a species showing high site fidelity, even short distances between groups of animals can result in a separation of communities (Heinrich, 2006). Large numbers, high density and fluid social structure of animals and their near-continuous distribution throughout their range would, to some extent, mitigate any localized impacts on a population, but a better understanding of the levels and effects of human activities affecting a population is always recommended and a cautionary approach to management is strongly suggested (Elwen, 2008).

Studies to increase our understanding of the drivers and scale of animal movement are integral components of the information needed to manage human impacts on wild cetaceans (Hooker *et al.*, 1999; Wilson *et al.*, 1997; Ingram and Rogan, 2002; Hastie *et al.*, 2003b), and have a strong applied value because such movements influence the size and efficacy of marine reserves and management areas (Hyrenbach *et al.*, 2006) and even the level of interaction between different populations of a species (Serrano and Tella, 2003; Belliure *et al.*, 2000).

2.1.1 RANGE AND DISTRIBUTION PATTERNS OF SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS

The Canary Islands lie in a transition zone between the Northwest African coastal upwelling area and the open ocean of the subtropical gyre (Arístegui *et al.*, 1997). The typical aspects of an oceanic archipelago, such as upwelling filaments, cyclonic and

anticyclonic eddies, localised tides and “island mass effect” (La Violette, 1974; Hernández-León, 1986; Arístegui *et al.*, 1994), render the Canary Islands a complex and dynamic ecosystem with highly variable oceanographic patterns and patchy accumulation of nutrients and trophic chain developments, calmer and more stable waters. Although the relationships between these areas and short-finned pilot whale sighting concentration have not been established, these could explain this species' preference for this area as a suitable habitat for resident populations (Montero and Arechavaleta, 1997; Ritter, 2001).

In southwest Tenerife, studies focused on short-finned pilot whales have shown the stable presence of this species (Escorza *et al.*, 1992; Heimlich-Boran and Heimlich-Boran, 1992; Heimlich-Boran, 1993; Montero and Arechavaleta, 1996). Nevertheless, very little is still known about their spatial and temporal distribution patterns along these coasts or about their occurrence in other areas of the archipelago. The study conducted between 1989 and 1991 in southwest Tenerife by Heimlich-Boran (1993) reported the daily presence of pilot whales with 0.77 sightings per day of effort, while in a later study between 1992 and 1993, the encounter rate was 0.92 sightings per day of effort (Martín and Montero, 1993). Another study conducted in the same area confirmed the presence of pilot whales year round (Montero and Arechavaleta, 1997; Montero, 1997; Carrillo and Martín, 1993), with more sightings during the months of April, May and June (Montero, 1997). In Carrillo *et al.* (2002), the encounter rate was 3.57 sightings per day of effort, without significant temporal variation through the year. In the most recent study of the species in the area, Carrillo *et al.* (2010) reported an encounter rate of 1.10 sightings per day of effort, with higher frequency during the months of September (1.85 sightings/day) and December (2.40 sightings/day). Heimlich-Boran (1993) found that the greatest concentration of this species was limited to 25% of the study area, which extended over 50 km². Martín and Montero (1993) reported the high use area to be 180 km², 47% of southwest Tenerife. Montero and Arechavaleta (1997) reported an area of 156 km², while Carrillo *et al.* (2002) identified the most frequently used area to be 27 km², 11% of the entire studied region. All these authors reported a non-homogeneous distribution throughout the study area, with areas of low, medium and high use, based on frequency of occurrence.

However, the results on area usage proposed by all these studies cannot be directly compared because of differences in the way in which they were carried out, including different survey methodology and different ways of processing and analysing the data.

Nevertheless, all studies found that short-finned pilot whales favoured particular water depths in southwest Tenerife. Heimlich-Boran reported an average depth of 1,386

(SE=70m). (Heimlich-Boran, 1993), Martín and Montero obtained a mean depth of 1,101.8 m (Martín and Montero, 1993), Carrillo and Martín (2000) reported a mean depth of 894.5m (SD=240.6), while Carrillo *et al.*, (2002) found a mean depth of 1,000 m.

This species has also been found off northeast Tenerife (Carrillo *et al.*, 2010). The first references of short-finned pilot whale occurrence in the eastern islands originate from a survey around the island of Lanzarote conducted during a 58 day survey between December 1994 and April 1995 (Politi *et al.*, 1996). In La Gomera, one of the western islands, during 1,104 whale-watching trips between 1995 and 2000, sighting data showed the short-finned pilot whales along the southwest coast of the island to be the second most frequent species (15%) in the area, with an average distance from shore of 4.05 nm and average water depth of 932 m (Ritter, 1996). Further studies in the same area detected an increase in pilot whale sighting frequency, especially after 2002, attributed to be a consequence of climate change, including changes in sea surface temperature and overall habitat quality and suitability (Ritter *et al.*, 2011).

Along the west coast of the island of La Palma, data collected between 2003 and 2005 from a whale-watching vessel during 346 days at sea (Pérez-Vallaza *et al.*, 2008) reported the presence of pilot whales in these waters constantly throughout the year (0.214 sightings per day). Pilot whale sightings represented 13% of the total sightings recorded. Seventy-eight per cent of the pilot whale encounters were in waters greater than 1,000m deep, mainly greater than 4nm from the coast.

In preliminary studies, some movements of animals among the different Canary Islands were recorded by Servidio *et al.*, (2001, 2002, 2006, 2007), with recaptures of the same individuals at different islands up to 16 years apart, especially between Gran Canaria, Tenerife and La Gomera. Since 2004, a comparative study of the social structure, distribution, movements and habitat use of the short-finned pilot whale has been conducted in Madeira and the Canary Islands. Comparison of the two photo-identification catalogues has revealed movement of individuals between Madeira and the Canary Islands, with the recapture of 11 animals between the two archipelagos demonstrating, therefore, that short-finned pilot whales range more widely than around each island group (Servidio *et al.*, 2007).

Coastal areas are among the marine habitats most at risk from human activities (McIntyre, 1999; Moore, 1999). Consequently, coastal cetaceans are among the most threatened species of cetaceans and most in need of management intervention to reduce anthropogenic threats (Thompson *et al.*, 2000; DeMaster *et al.*, 2001). Short-finned pilot

whale spatio-temporal distribution and ranging patterns are not yet well understood in the archipelago. This deficiency hampers the ability to assess the impact of human activities on local populations of this species in the area and, therefore, conservation and management efforts.

This study was specifically designed to investigate the occurrence and dispersion of short-finned pilot whales over 13 years in the Canary Islands, with the principal aim of analysing their spatial-temporal distribution and measuring the alongshore range of individuals as a proxy for their range, in order to inform and improve the design of conservation and management interventions for towards this species in Canary Islands. Description of about their occurrence patterns, individual sighting frequencies, distribution and ranging behaviour over time, and information about their residency and group dynamics were considered in order to investigate the existence of resident populations and possibly to distinguish them from an oceanic transient population. Information about residency and group dynamics is also presented.

2.2 GENERAL METHODOLOGY

2.2.1 GENERAL DATA COLLECTION PROTOCOL

Between 1999 and 2012, the Society for Cetacean Study in the Canary Archipelago (SECAC) carried out surveys off the different islands of the Canary Archipelago. Focusing mainly on the islands of Tenerife, Gran Canaria, La Gomera and, since 2005, Lanzarote and Fuerteventura, the survey effort was not uniform in terms of time, sampling areas or platforms used for investigation. Nevertheless, the sampling methodology can be considered comparable and all the data collected could be pooled together and equally treated during the various steps of the different analysis undertaken in this study. Basic sampling that was always conducted included the collection of oceanographic, environmental and survey effort data, and the collection of data relating to observations and encounters with cetaceans including photographs, video footage, and skin and fat tissue samples. Biological, morphometric and stomach contents data have also been collected from stranded animals.

VESSELS, EQUIPMENT ON BOARD AND CREW

A wide variety of vessels was used by SECAC for its research activity since 1999: small semi-rigid inflatable boats, whale-watching vessels, sailing boats, and high powered motor vessels (**Figure 2.1**). Nevertheless, each research platform always had a full set of research equipment and a minimum of two trained researchers, as well as observers.



Figure 2.1: Research platforms: "Chacalote", "Grampus", "Oso Ondo", and "Multiacuatic" (from top left).

During the PhD fieldwork period, the main vessels used were:

- "*Chacalote*": a 5.5m semi-rigid inflatable boat (rib), with a 50 horsepower outboard engine. The boat was used for the surveys off the island of Tenerife and as an auxiliary platform for the surveys around the islands of Lanzarote and Fuerteventura.
- "*Grampus*": a 6m semi-rigid inflatable boat, with a 70 horsepower outboard engine. This boat was used for the surveys around the island of Gran Canaria.
- "*Oso Ondo*": a 17m motor vessel used for surveys around Lanzarote-Fuerteventura.
- "*Multiacuatic*": a 16.5m catamaran dedicated to commercial whale-watching activity in the southwest of Gran Canaria.
- "*Viena*": a 7m wooden fishing boat used for surveys off La Gomera.
- "*Naviera Armas*": a fleet of eight ferry boats from 120m (2x4.624hp), to 175m (4x12,000hp) used as opportunistic platform between the islands of La Gomera and Tenerife, Tenerife and Gran Canaria, Gran Canaria and Fuerteventura.

The research equipment on board the motor boat "Oso Hondo" included: radar, echosounder, GPS, HDV digital video cameras, underwater digital camera, three digital photographic cameras (Canon 10D, 30D and 40D) with zoom lenses Canon EF up to 500 mm, Hi-Tech and Magec hydrophones both with a Magec HP27S amplifier and with a

Fostex FR2 recorder, four 7x50 binoculars, three laptop computers, and a 125 lb power crossbow (Panzer III, Barnett International, Ltd.), with modified arrows (provided by Finn Larsen) for skin sample collection. During the survey, the software LOGGER 2000/2010 (provided by International Fund for Animal Welfare, available at <http://www.ifaw.org>) was used to record GPS positions and time every 60 seconds, through an NMEA cable, environmental variables, cetacean, sea turtle and bird sighting information, as well as anthropogenic activities.

Two observation platforms, when sea conditions allowed, were used simultaneously at 3.60m and 1.73m above sea level. The ribs "Senderismo Acuatico" and "Chacalote" were used as auxiliary inflatable boats for tasks such as photo-identification, video filming, biopsy sampling and TDR tagging. "Oso Ondo" could accommodate up to 12 researchers and volunteers. The survey was conducted with a minimum number of eight trained observers, which took turns at the different tasks of observation (single or double platform) and data recording.

The research equipment on board the inflatable boat "Chacalote" included: two GPS recorders, 7x50 binoculars, two digital cameras (Canon Eos 10D and 30D equipped with a Canon EF 70-200 mm zoom lens), high definition video camera (SONY HDR-HC3 1080i), a Hi-tech hydrophone with a Magec HP27s amplifier and a Fostex FR2 recorder, and a 125 lb power crossbow (Panzer III, Barnett International, Ltd.), with modified arrows (provided by Finn Larsen) for skin sample collection. The two experienced researchers were often assisted by one or more field assistants and volunteers.

The inflatable boat "Grampus" was equipped with: two GPS recorders, 7x50 binoculars, two digital cameras (Canon Eos 10D and 30D equipped with a Canon EF 100-400 mm zoom lens), high definition video camera (SONY HDR-HC3 1080i), and one array with four hydrophones (three at 2m depth and one at 10 m depth). There was always one experienced researcher and one or two field assistants on board.

On the whale-watching vessel "Multiacuatic", the principal researcher was equipped with a digital camera (Canon Eos 30D with a Canon EF 100-400 mm zoom lens), high definition video camera (SONY HDR-HC3 1080i), a GPS recorder, and a laptop computer.

The two experienced observers on Naviera Armas ferries had two 7x50 binoculars, a GPS recorder, and a laptop computer, on which all the relevant data were recorded directly using the software LOGGER 2000/2010 (GPS positions and time every 60 seconds, environmental variables, cetacean, sea turtle and bird sighting information, as well as anthropogenic activities).

SURVEY DESIGN

Survey transects were designed to cross depth contours covering the whole bathymetric range from 50 to 2,000 m up to 20 nautical miles from the coast on board “Oso Ondo” or to 6 nautical miles on the rest of the research vessels, following, in general, a zigzag pattern approximately perpendicular to the coastline, and covering as much of the area as possible at an average speed of 5-7 knots, depending on the vessel. Transects were not systematically designed due to the logistical constraints of the vessels used (relative small vessels, dependent on weather conditions and on the need to return to port every night) and because of the different activities undertaken during cetacean encounters (e.g. photo-identification sessions, biopsy samplings, acoustic listenings and recordings). Nevertheless, the first course outside the harbour was selected randomly, and variations in course due to changes in sea conditions were always made based on external factors and were never dependent on cetacean density. The sampling strategy was identical on all the surveys conducted by SECAC.

SEARCHING EFFORT AND DATA COLLECTION

Searching was conducted only under adequate sighting conditions: sea state Douglas 0 to 2, good visibility (greater than 3 nautical miles), Beaufort wind force scale up to 3, swell less than 2m, and dry weather. For conditions worse than these, searching effort was suspended. An average of 8 hours of surveying was conducted per day.

During the surveying effort, trained researchers rotated every 60 minutes through the different duties of observation and data recording. From different platform heights, depending on the vessels used, two observers simultaneously scanned the horizon, covering 180 degrees in front of the boat (90° each).

The geographic position of the vessel was recorded every minute on a handheld GPS or, during surveys conducted on board “Oso Ondo”, directly on the vessel’s computer from a GPS navigation system logger using LOGGER 2000/2010. During the survey, environmental characteristics were recorded every 15 minutes and every time something changed or happened, such as a new transect, changes in environmental conditions, presence of human activities (nets, fishing boats, sailing and motor boats, ferries, military vessels, whale-watching boats, others), sightings of birds and sea turtles, and floating debris and residue.

When a cetacean or a group of cetaceans was detected, searching effort was suspended and data collection for the sighting began (Sighting sheet, Annex 2: Figure A2.1-A2.3).

The standardized protocols of the Spanish Cetacean Society were followed (Sociedad Española de Cetáceos, 1999). The basic and primary data taken were: time, GPS position, type of effort (if the animal/group of animals was sighted on effort, off effort, or if it was a secondary sightings), species, and estimated radial distance to the detected group (distance estimated by eye, specially designed distance sticks, or binocular reticules). Since 2004, data collected also included: name of the observer making the sighting, angle to the group with respect to the survey track-line, cue (blow, splash, body, jump, birds, presence of whale-watching boat, other), initial behaviour, and the heading (swimming direction) of the animals. Behavioural observations and group composition were also recorded, and photo-identification and biopsy sample collection conducted.

After initial observations of animal behaviour, the boat slowly approached the cetacean(s) to a distance of 60 m or less, and the "contact data" were taken: time, position, confirmation of the species, minimum, maximum and best estimate of the number of animals (group size assessed several times during the sighting), reaction to the boat, presumed-sex and age composition of the group (male, female, new born, calf, juvenile, indeterminate, and adult). Complementary information recorded included: initial behavioural activities (feeding-foraging: chasing or eating fish, long synchronized and repeated dives; resting: stationary in one place, almost without any kind of other activities; socialising: clear and constant interaction among the animals in the group; travelling: directed movements, swimming slowly, moderately or fast), initial swimming speed (slow: < 3 knots; medium: between 3 and 5 knots, fast: > 5 knots), animal course and group cohesion-formation (one compact group, more groups in the area, dispersed individuals). Other data were also collected whenever possible: photo-identification, video recording, biopsy sampling for genetic analysis, and acoustic recordings.

During the photo-identification sessions, pictures were taken of both sides of the dorsal fin as well as of the complete animal in order to record morphologic details and particular coloration patterns. To guarantee equal probability of being photographically captured, pictures were taken, when possible, of all the individuals of the observed group, independently of the presumed age- and sex-class, or the fin recognisability. Any changes in group composition were recorded and when groups/subgroups joined or left, a new photo-identification session was started in order to be sure that all individuals present were captured. The photographs were taken trying to include in the frame the entire exposed dorsal fin with the best possible magnification, with minimal glare, and as perpendicular as possible to the camera's focal axis.

The cameras used during the photographic-sessions changed from single-lens reflex Canon EOS 1 and EOS 5 to digital models in 2004.

On leaving the animals, time, GPS position, final behaviour, course and speed, wind and sea state were recorded and searching effort started again.

Effort and sightings data were recorded in field notebooks and, whenever possible, were also entered directly into the on-board computer using the program Logger 2000 (vessel “Oso Ondo”).

Therefore, all the data collected were stored in the database following the structure of the previous SECAC databases but updated to incorporate new methodology and new data that were considered to be important. The effort databases always included at least: date, time, location, sea conditions, start and end of sightings, and on- off- searching effort status. The sighting database included: date, time, and location of sightings, as well as estimated school size and sex/age composition if pertinent, reaction to the presence of the survey vessel, group cohesion, and a list of sample material collected during the sighting. All the data collected since 1999 were combined into one complete database.

DEFINITION

SIGHTING:

A sighting was used to indicate an encounter of a school of cetaceans seen at the same time, and showing similar behavioural characteristics and at distances of less than 1,000 meters from each other (Sociedad Española de Cetáceos, 1999).

All pilot-whale sightings started when they were first spotted (Ottensmeyer and Whitehead, 2003), and ended when it was considered that all the animals had been photographed and the data collection protocol had been completed. All sightings lasted a minimum of 30 minutes to ensure the inclusion of individuals not initially visible because they were in deep dives (mean deep dive length: 15 minutes (SD=2); maximum deep dive length: 21 minutes; Aguilar de Soto, 2006), or when the vessel had to return to port, or when the school was lost for at least 30 minutes, or finally when the vessel moved from one school of pilot whales to another with at least 1,000 meters separating the nearest individuals of the two schools (Sociedad Española de Cetáceos, 1999). For each sighting, and based on field observations, the approximate percentage of animals photographed was recorded.

GROUP:

During a sighting, a "group" was the basic spatio-temporal unit that defined group membership. It was defined as a spatial aggregation of animals, within 1,000-m of each other, that showed similar behavioural activity and interacted with one another over timescales sufficiently short that there were few (or no) changes in group membership (Karczmarski *et al.*, 2005).

All pilot whales photographed during the same sighting were considered to be members of the same group and thus associated at some level rather than merely being concentrated in the same area ("gambit of group") (Whitehead and Dufault, 1999).

In cases of low photographic coverage (approximately less than 90% of individuals photographed in the sighting), or when animals were widely spread out or when it was impossible to determine the end of one group and the beginning of another, with group boundaries somewhat ambiguous (e. g. Smolker *et al.*, 1992), all the animals were pooled together and considered to belong to the same group in the same sighting event, but the group (and therefore the corresponding sighting) was marked as unsuitable for social structure analysis.

AGE/SEX CLASSIFICATION:

Without the aid of genetic analysis, it was not possible to confirm the sexes of any of the individuals observed (Augusto *et al.*, 2011); however, inferences about the age and sex of certain individuals were made at sea, based on several factors. Following the data provided by Kasuya and Matsui (1984), Yonekura *et al.* (1980), Kasuya and Marsh (1984) and following Heimlich-Boran's interpretations (1993), age/sex classes were here differentiated as:

Adult male: animals never found in association with a calf, with a minimum length of 4 m and a maximum length of 5.8 m. The length of the dorsal fin base was greater than 60% of the length from the blow-hole to the end of the ridge. Prominent dorsal muscles and a convex melon were observed.

Indeterminates: (adult female or sub-adult male): full-sized animals that did not have characteristics of adult males and which did not have a consistent association with a specific immature animal. This category potentially encompassed adult females and adolescent males. Females reach sexual maturity at about 3.2 m and a maximum length of 4 m, which superposes the immature and sub-adult male size (estimated at 10 years

old to reach 3.43m; Yonekura *et al.*, 1980). The dorsal fin was smaller than that of adult males and less curved.

Female with calf (mother): individuals with the physical characteristics of an indeterminate whale but in association with a calf for the entire duration of a sighting.

Juvenile: individuals with little developed dorsal muscles, between 2.5 and 3 m in length, weakly convex melon and generally lighter build than indeterminate animals.

Calf: pilot whales with a length between one third and half of an indeterminate animal (length from 1.4 meters and 37 kilograms up to 2.30 meters at 1.25 years of age; Kasuya and Marsh, 1984).

Newborn: calves for which it was possible to distinguish foetal marks on the body (which last for approximately a month) and which had an incompletely developed melon.

Multiple photographs of the identified individuals were examined to confirm the final age-sex classification.

2.2.2 MATERIAL AVAILABLE FOR THIS STUDY

The data available and included in this thesis combined data from previous surveys conducted by SECAC, between 1993 and 2007, with more recent surveys specifically designed for pilot whales as well as with more general surveys where pilot whales were not the primary target of the study. Since 1999, I was personally involved in most of the surveys considered.

ARCHIVE DATA

The data were collected by SECAC around different islands, in the framework of different projects:

1992-1993:

In the framework of the CETOC (Oceanic Cetaceans of Canaries) projects, SECAC conducted 93 day-surveys in southwestern Tenerife.

Available material: environmental and oceanographic data, photographs for the identification of individuals, sighting observations (group size, general behaviour, sex-age composition).

Platform used: semi-rigid inflatable boat.

Survey: Non-systematically pre-designed transects.

1999-2000:

Data collected within the framework of the project "Conservation of the bottlenose dolphin (*Tursiops truncatus*) and the loggerhead turtle (*Caretta caretta*) in the Canary Islands", carried out by the Biology Department of the University of Las Palmas de Gran Canaria and assigned to SECAC for the eastern islands (LIFE/B4-3200/97/247). Surveying was carried out for sixteen months in Gran Canaria over 122 days, 8 days in Lanzarote, 11 days in Fuerteventura, and 1 day in Tenerife.

Available material: GPS positions, environmental and oceanographic data, video footage with photographs for the identification of individuals, sighting observations (group size, general behaviour, sex-age composition), and skin tissue samples.

Platform used: 14m motor vessel with two 165 HP engines (Monachus).

Survey: Non-systematically pre-designed transects.

2002:

Data collected by SECAC in collaboration with the German company "Aldebarán Marine Research and Broadcast" over 7 days of surveying southeast of Tenerife.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition).

Platform used: 14m sailing boat (Aldebarán).

Survey: Non-systematically pre-designed transects.

Within the framework of a SECAC project for the Canary Islands Government, "Applied studies for the conservation of cetacean populations in the province of Las Palmas de Gran Canaria" (CETOC), 6 months of surveying were carried out with 46 days at sea off Gran Canaria and 2 days in the most eastern islands.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition).

Platform used: 12 m sailing boat (Ninu II).

Survey: Non-systematically pre-designed transects.

2003-2004:

Within the framework of a SECAC project for the Canary Islands Government "A study on the members of the family Ziphiidae in the eastern islands", 43 days of surveys took place during the summer months from June to September between the islands of Tenerife, Gran Canaria, Lanzarote and Fuerteventura.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition).

Platform used: 12 m sailing boat (Ninu II).

Survey: Non-systematically pre-designed transects.

2004-2006:

La Gomera: within the framework of the project "The conservation of *Tursiops truncatus* and *Caretta caretta* in La Gomera" (LIFE03/NAT/E/000062), monthly surveys of 6 days

each, during the period August 2004 – August 2006 were undertaken, during which sampling was conducted over 104 days in an area of 2,826.2 nm² off the island of La Gomera (SAC: Franja Marina Santiago-Valle Gran Rey, ES7020123). Twelve surveys were also conducted off the islands of La Palma and El Hierro.

Available material: GPS positions, environmental and oceanographic data, video footage with photographs for the identification of individuals, sighting observations (group size, general behaviour, sex-age composition), and fat and skin tissue samples.

Platform used: "Chacalote".

La Gomera – Tenerife: within the framework of the project "The conservation of *Tursiops truncatus* and *Caretta caretta* in La Gomera" (LIFE03/NAT/E/000062), 42 opportunistic surveys were undertaken on the Ferry Garajonay Express.

Available material: GPS positions, environmental and oceanographic data, group size.

Platform used: "Garajonay Express".

Survey: Fixed transects

2005:

Gran Canaria-Lanzarote-Fuerteventura: In collaboration with the NGO Oceana, SECAC conducted a 19 day survey among the eastern islands.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition), and video footage with photographs for the identification of individuals.

Platform used: "Oso Ondo".

Survey: Non-systematically pre-designed transects

Tenerife: Within the framework of the project MACETUS, "Study of the population structure, distribution, movement and habitat use of the sperm whale (*Physeter macrocephalus*), short-finned pilot whale (*Globicephala macrorhyncus*), bottlenose dolphin (*Tursiops truncatus*) and spotted dolphin (*Stenella frontalis*) in the Canary Islands", the SECAC carried out a campaign off the southeast of the island, with 15 days at sea, resulting in 40 sightings of short-finned pilot whales.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition).

Platform used: 14 m sailing boat (Morganonline).

Survey: Non-systematically pre-designed transects

Tenerife, Gran Canaria, Lanzarote: During the project "Study, monitoring and education for the conservation of cetaceans in Macaronesia" (EMECETUS), in collaboration with the Câmara Municipal de Machico - the Whale Museum and the Department of Environment of the Environment Department. (INTERREG IIIB AMC, project 05/MAC/4.2/M10), 16 day-surveys were conducted along the islands. Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general

behaviour, sex-age composition), and video footage with photographs for the identification of individuals.

Platform used: 14 m sailing boat (Morganonline) and "Oso Hondo".

Survey: Non-systematically pre-designed transects

2006-2007

Gran Canaria-Lanzarote-Fuerteventura: Within the framework of a project for Caja Canarias, the SECAC carried out surveys for *Grampus griseus* among the eastern islands, resulting in four short-finned pilot whale sightings during 15 days of surveys.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition), and video footage with photographs for the identification of individuals.

Platform used: 14 m sailing boat (Morganonline).

Survey: Non-systematically pre-designed transects

SURVEYS CONDUCTED DURING THE PHD PERIOD

2007-2009:

Gran Canaria: 76 opportunistic surveys (Cetoc_WW) from a whale-watching boat were conducted along the southwest coast of the island resulting in five pilot whale sightings.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition), photographs for the identification of individuals.

Platform used: "Multiacuatic".

Survey: Non-systematically pre-designed transects

2007-2012:

Gran Canaria and Tenerife: During 253 days of survey (GC_CETOC) in the southwestern area and in the Marine Area of La Isleta (ES7010016), 10 days of survey in Tenerife (7 in the northeastern and 3 days in the southwestern island), 2 days in El Hierro (EH_Cetoc), 81 days in Lanzarote, and 44 days in Fuerteventura.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition), video footage with photographs for the identification of individuals, and acoustic recordings.

Platform used: "Grampus" (Gran Canaria), Ibero (sailing boat, Tenerife and El Hierro), "Oso Ondo" (Lanzarote and Fuerteventura).

Survey: Non-systematically pre-designed transects

2007-2009:

Tenerife: Within the framework of the project "Conservation status of the short-finned pilot whale population (*Globicephala macrorhynchus*) and bottlenose dolphins (*Tursiops truncatus*) in the southwest coast of Tenerife" (co-funded by FUNDACION LA CAIXA),

monthly surveys of 7-10 days each from April 2007 to March 2009, and June – July 2009 (total of 230 day-surveys), were carried out off the southeast of the island. Six day-surveys were also conducted off southwestern La Gomera.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition), video footage with photographs for the identification of individuals, acoustic recordings, and fat and skin tissue samples.

Platform used: "Chacalote" (Tenerife); "Viena" (La Gomera).

Survey: Non-systematically pre-designed transects

2009-2012:

Tenerife, Gran Canaria, Lanzarote, and Fuerteventura: Within the framework of the project INDEMARES (LIFE07/NAT/E/00732), surveys among the eastern islands were carried out, between 2009 and 2013. The data collected between January 2009 and January 2012, corresponding to 214 day-surveys, were included in this thesis.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition), video footage with photographs for the identification of individuals, acoustic recordings, and fat and skin tissue samples.

Platform used: "Oso Hondo".

Survey: Systematically pre-designed transects

2010-2011

A total of 164 days of survey was carried out and conducted simultaneously in five SACs off the southwest coast of the islands of Tenerife, Gran Canaria, La Gomera, La Palma and El Hierro (project ZEC-TURSIOPS). All the pilot whale sightings from these surveys were included in this thesis, with the exception of photographs of those recorded off the island of Tenerife.

Available material: GPS positions, environmental and oceanographic data, sighting observations (group size, general behaviour, sex-age composition), video footage with photographs for the identification of individuals.

Platform used: "Oso Ondo", "Viena", "Chacalote", "Grampus".

Survey: Non-systematically pre-designed transects

2011-2012

Cetacean observations from passenger ferries in the Canary Islands (CETOCAN) were collected September 2011 to June 2012. Ferries of the Naviera Armas Company were used as observation platforms between the islands of Fuerteventura, Gran Canaria, Tenerife and La Palma. A total of 128 surveys (52 days) were conducted.

Available material: GPS positions, environmental and oceanographic data, sighting observations (species, group size, general behaviour).

Areas: Inter-island channels: Tenerife-Gran Canaria, Gran Canaria-Fuerteventura.

Platform used: Ferry Naviera Armas.

Survey: Opportunistic vessel, fixed transects.

2.2.3 DATA ORGANIZATION

Three different analysis levels were considered in this study: 1) within study area comparisons, 2) between study areas comparisons, and 3) past-to-present comparisons. Within each study area (island), documentation of the occurrence of short-finned pilot whales throughout the year-long study allowed for the comparison of space-use patterns over seasons. Comparing the results from surveys among the different islands allowed for the documentation of possible movements between areas and analysis of space-use patterns of each area by individuals. Patterns of occurrence, distribution, and individual sighting frequencies during 2007-2012 (this study) were compared to past research conducted by SECAC in the Canary Islands to determine the stability of usage patterns over time. Therefore, this analysis included the entire SECAC dataset including sighting information and photographic material since 1993 in different areas of the Canary Islands (Figure 2.2).

All the surveys were reviewed to ensure that the minimum standard in methodology (survey and data collection) was followed in order to allow data comparison through time and islands. The survey data prior to 1999 were considered not completely suitable, and thus excluded from the analysis. However, all past photographic material was used for descriptive comparisons with more recent photographs.

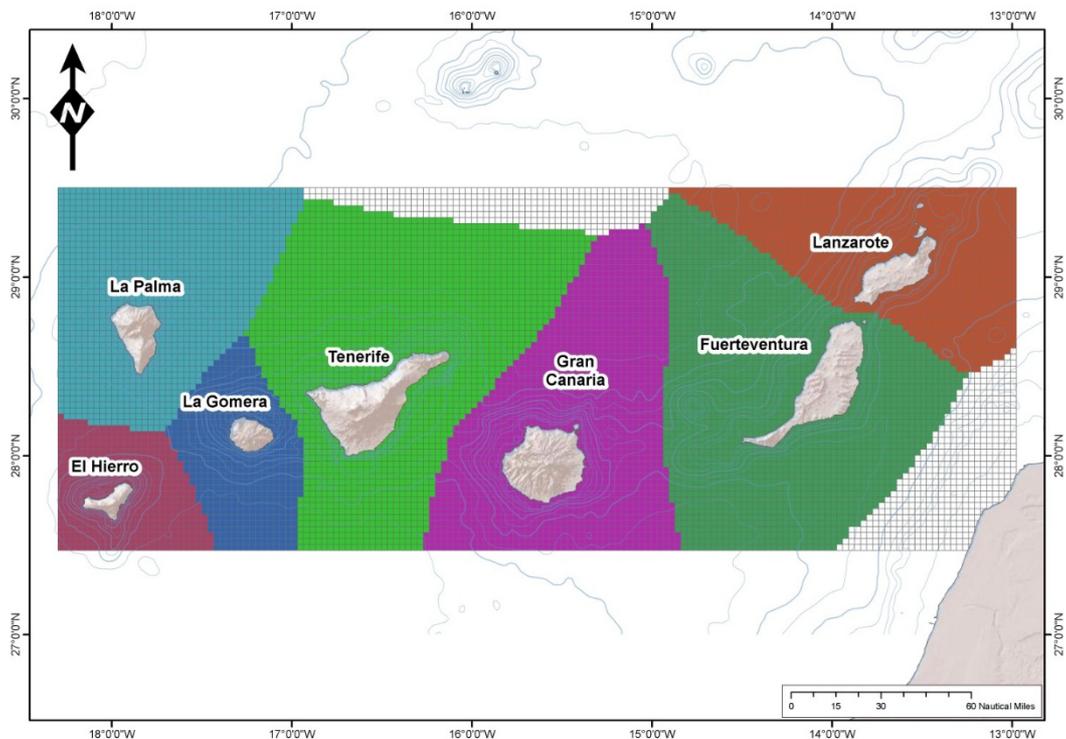


Figure 2.2: Study area divided in seven different locations: 1) El Hierro; 2) La Palma; 3) La Gomera; 4) Tenerife; 5) Gran Canaria; 6) Lanzarote; 7) Fuerteventura.

The survey transects and sighting locations were entered into an ESRI Geodatabase (ArcGIS 10.1), and used in the analysis of occurrence patterns and sighting distribution around each island and within the archipelago. The photographic database was used to construct discovery curves and to examine site fidelity, long-term residency, and movement patterns, possibly confirming between-island movement.

The main analysis was conducted using data around the islands of Tenerife, La Gomera and Gran Canaria, while data from Lanzarote and Fuerteventura were combined due to similarity in the oceanographic and morphologic characteristics of these islands and survey methodology used. Due to the low survey coverage conducted in time and space, data from around El Hierro and La Palma were included only in the preliminary analysis of photo-identification, and for effort calculations.

PHOTOGRAPHIC AND VIDEO FOOTAGE MATERIAL

The study of individual range and distribution patterns in the Canary Islands, the estimation of the abundance of the pilot whale population off the southwest coast of Tenerife (Chapter 4), and the social structure analysis (Chapter 3) all had as a first step the organization and analysis of the photographic and video footage material.

The material included both colour slides on film (Fuji chrome Sensia 100-200 ASA) and digital photographs. All slide images taken between 1999 and 2003 were labelled according to the sighting, roll and picture number. Subsequently, they were studied with an x8-magnifying eyepiece on a light table in order to discard pictures without pilot whales or that were otherwise unusable and the rest were then digitally scanned using Nikon Cool scan IV LS 40 ED. Since 2004, all photographs were digital and labelled according to the sighting number and picture reference number. All the digital images obtained were archived for further analysis.

Photo-identification catalogues with the best picture of each animal and for each island were compiled and compared. Individual short-finned pilot whales were identified from photographs on the basis of their dorsal fin silhouette, and naturally occurring marks and scars on the dorsal fin (Würsig and Würsig, 1977; Würsig and Jefferson, 1990). As many features as possible were used to confirm matches and reduce the possibility of false positives (Scott *et al.*, 1990; Würsig and Jefferson, 1990; Williams *et al.*, 1993). To facilitate the photographic analysis the identification characteristics were classified into 16 categories based on dorsal fin shape, and the number and location of nicks. The latter were classified by location by dividing the dorsal fin into three sections, dents in the leading edge of the fin, and tabs (projections from the trailing edge of the fin) based on

the photo-identification categories used by Heimlich-Boran (1993):

1. CLF=	Clean fin	9. LMN=	Large Multiple Nicks
2. CLS=	Clean fin w/Scallops	10. LNM=	Large Nicks middle Third
3. FDH=	Front Dents or Humps	11. LNT=	Large Nicks Top third
4. FFT=	Flap Finger Tips	12. NNT=	Nicks Near Tip
5. HND=	Handles	13. SBN=	Small Base Nicks
6. HOO=	Hooks	14. SNM=	Small Nicks Middle third
7. IND=	Individuals	15. SNT=	Small Nicks Top third
8. LBN=	Large Base Nicks	16. SQT=	Square-Tips

Although the permanence of injuries has been questioned (Lockyer and Morris 1990), major wounds were considered to be long-lasting, with the caveat that any new marks may obscure identification, unless a good record of the fin evolution of identified animals is kept (Wursig and Jefferson 1990).

Only long-lasting marks (e.g. nicks, cuts and deformities) that were slow to change and believed to be unique so that they could be recognized in subsequent sightings were used in the photo-identification process (Würsig and Jefferson, 1990) to avoid the problem of missing matches due to mark loss or falsely matching different animals.

Through photo-identification comparisons of data on short-finned pilot whales from Tenerife, the long-lasting marks, which included not only nicks and notches but also deep scratches, seemed to last at least 10 years (Servidio *et al.*, 2002). Nonetheless individuals belonging to the clean-fin category, with no identifying marks on their dorsal fins, were not necessarily unidentifiable. Ephemeral scarring such as cookie cutter shark (*Isistius* sp.) bites and tooth-rake marks, as well as overall dorsal fin shape, were occasionally used for the photo-identification matching, to assist in the distinction of individuals without long-lasting marks, and to re-sight individuals between encounters on a short temporal scale. Juveniles, calves and neonates were also matched between sightings based on this secondary scarring and by close, constant association with a conspecific, usually thought to be the mother based on repeated observed associations (Mahaffy, 2012). Clean individuals were eliminated from the majority of analyses but were necessary to determine the proportion of marked animals in a given encounter.

Each image filename included the date and the relevant sighting code. Individual animals identified in encounters were visually sorted into folders and each identified animal received a temporary identification number (GmaID). The best photographs of each pilot whale, regardless of the dorsal fin side pictured, were then compared with the best photograph of all previously identified individuals, and included in the catalogue as either a new identification or as a re-sighting of a known pilot whale. New individuals received a new permanent sequential alphanumeric ID in the catalogue and those that were re-

sightings were incorporated under their existing permanent ID. All photographic sorting/matching was done visually using Adobe Bridge CS5 software. All the images used for the analysis were sorted in folders organised both by sightings and by individual ID. The final result was the creation of a general photo-identification "master catalogue" containing the best pictures (when it was possible from both fin sides) of each identified animals during each capture/recapture and integrating the catalogues built for each island of the archipelago.

Parameters including focus, contrast, parallax, and relative size of fin in the picture were used to grade picture quality (Arnbom, 1987; Dufault and Whitehead, 1993, 1995) as: 1="poor", 2="fair", 3="good", and 4="excellent" (Baird *et al.*, 2008a; Baird *et al.*, 2008b; and McSweeney *et al.*, 2009). Excellent quality images required the following elements: (1) dorsal fin clearly visible and large enough to detect any irregularities present on either the leading or trailing edge of the fin, (2) the focal individual was surfacing approximately perpendicular to the camera focal axis, and (3) the fin was not obstructed by objects such as water droplets, sections of the boat, glare or other individuals, (4) photographs were well exposed, without water droplets, in sharp focus (Hammond *et al.*, 1990).

Each identified individual was classified based on its overall distinctiveness, that is, the ability to recognise it based on its dorsal fin characteristics: number, size and shape of nicks, notches and scars on the leading and the trailing edge of the dorsal fin. The rating followed the ranking scale of 1 to 4: 1= not distinctive, 2= slightly distinctive, 3= distinctive, and 4= very distinctive (Mahaffy, 2012).

The photo quality and individual distinctiveness rating processes were undertaken independently. This was done to minimize any bias created from images of highly distinctive animals that artificially increased photo quality ratings and, *vice versa*, by images of individuals of lower distinctiveness artificially lowering photo quality. Changes to the leading and trailing edge of the dorsal fin (such as the addition of new nicks or notches) were recorded for an individual each time they were observed and the individual was assigned, if necessary, a different level of distinctiveness.

Once the photo-identification process was finished, a database was created, including metadata about each picture and each identified animal: species and sighting code, animal id number, date, island where it was photographed, picture quality and distinctiveness ranks, sex/age class.

Only good quality photographs (categories 3 and 4) and well-marked animals (distinctiveness 3 and 4) were used in the residency analyses because an assumption of equal capture probability was required when the entire database was analysed as a whole. However, these restrictions were relaxed somewhat to conduct some specific analyses on individual movements in order to obtain as much detailed information as possible; in some cases, images that did not meet these strict selection criteria were used if there was confidence in matching.

Although some animals were identified more than once during the same day, the first sighting of the day was used in the analysis of site fidelity and residence patterns to minimise the possibility of dependence in the data.

GROUP SIZE

In each encounter, the group size was estimated by visual observation, with a minimum, maximum, and best value. A photographic coverage index was also assigned in the field, based on the estimation of the approximate percentage of animals photographed. Only sightings where the data collection protocol was considered completed at sea were included in the group size estimation. Moreover, in encounters for which the group size estimate at sea was found to be smaller than the number of individuals identified, the sample size obtained by photo-analyses was used as the approximate encounter group size.

The coverage rating protocol developed by Ottensmeyer and Whitehead (2003), based on the between the number of photographs taken during each sighting and the number of individuals estimated in the field, was not used in this study. In this work, the ratio obtained was not considered to be a good indicator of coverage because in many cases a single picture could be used for identifying more than one animal, thus providing a better coverage indicator than the simple ratio. Moreover, the use of the digital camera has considerably increased the number of photos taken during each sighting, which often has no relation to the number of identified animals in the pictures.

2.2.4 DATA ANALYSIS

OCCURRENCE PATTERNS AND RELATIVE ABUNDANCE

Occurrence patterns and distribution were described for all the study areas by considering the number of pilot whale sightings observed and their distribution in relation to the survey location and frequency.

ENCOUNTER RATE

To account for the uneven geographical distribution of the survey effort, sighting distribution was examined in detail and encounter rates were calculated in two ways:

General encounter rate per island (ER1) was calculated as the ratio of the total number of sightings around each island divided by the corresponding sum of nautical miles covered annually around each island.

The study area was divided into a grid of 160 x 61 cells in the range 27° 28' N to 29° 30' N in latitude and 12° 58' W to 18° 18' W in longitude. Cell area ranged from 11.89 to 12.14 square kilometres. For each grid cell, the annual average encounter rate (ER2) was calculated by dividing the total number of sightings made on effort (including all sightings whether the animals were approached or not) by the sum of the distance in nautical miles covered on effort in each cell. This method allowed for the standardisation of the data used in the analysis in the presence of non-systematic effort surveys.

The location where whales were first sighted was used in order to avoid potential influences on whale behaviour by boat interaction. Reviewing the length of the different segments and the number of sightings in each of them, to avoid problems caused by low effort, it was decided, as the best balance between precision and quantity of data, to exclude from the analysis of encounter rates the cells with a total survey effort less than one nautical mile in any given year, resulting in a set of 1,713 grid cells used for the analyses.

For those grid cells that included land, the encounter rates were weighed by the relative proportion of land within the cell (Bearzi *et al.*, 2008):

The study area was then classified into levels of usage by considering the values of the encounter rate (ER2) in each grid cell, as follows: (1) low usage, if the encounter rate was less than the first quartile, (2) high usage, if the encounter rate was greater than the upper quartile, and (3) moderate usage, for encounter rates within the interquartile range. This simple categorisation was used to provide a rough comparison of usage among areas.

RESIDENCY AND SITE FIDELITY

To provide an overall measure of short-finned pilot whale residency and fidelity to particular areas/sites, data on the sighting frequency, mean monthly sighting rate and extent of movement of individually identified animals were used. Residency patterns in

the Canary archipelago were considered by pooling together all the individuals seen among all the islands but, for finer analysis, only the datasets from Tenerife and La Gomera were used to study individual fidelity to these specific islands, where most of the recaptures occurred. Only good and optimum quality pictures of well-marked adults and indeterminates were used.

Four different residency categories were identified based on individual re-sighting rates, with sampling intervals defined by month and year. For analyses at the level of the whole Canary Islands archipelago, “Core resident” was used to categorise pilot whales sighted at least once in four different years, during each of the four different seasons; the term “resident” was applied to individuals seen over three years and two seasons, and over four years and two seasons. “Transient” was used to categorise whales sighted once or twice in only one season in only one year, while all other frequency combinations were used to define the “occasional” category.

To detect residency patterns related to the islands of Tenerife and La Gomera, where more data were available, a different categorisation methodology was used. Monthly sighting rates were calculated for each identified whale, by computing the proportion of the total number of months in which an individual was recorded relative to the total number of months in which at least one survey was conducted (Parra *et al.* 2006). The seasonal sighting rate was also considered, calculating the total number of seasons in which an individual was recorded as a proportion of the total number of seasons in which at least one survey was conducted.

Sighting rates were then assigned to three categories: 1) whales with low sighting rates (LSR) were sighted in less than 10% of the surveys, 2) whales with moderate sighting rates (MSR) were sighted in 10–30% of the surveys, and 3) whales with high sighting rates (HSR) were sighted in more than 30% of the surveys. Animals with MSR and HSR were considered island related “resident” and “core residents”, respectively, and were present in multiple seasons. Animals with LSR were labelled as “occasional” but present in multiple seasons. Finally, “transient” whales were those with LSR, but observed only in one season (Fury and Harrison 2008).

Even though the criteria used to set the limits to the residency categories were somewhat arbitrary, they allowed, at archipelago and island level, individuals that exhibited multi-season and year site fidelity to the area (“core residents”) to be distinguished from individuals with multiple sightings over a short temporal scale (“residents”) and also animals with some degree of site fidelity to the area (“occasional”)

to be distinguished from individuals seen only once or twice (and in only one season) and therefore considered “transient”.

LAGGED IDENTIFICATION RATE

The lagged identification rate (LIR) was calculated to analyse residency patterns by estimating the amount of time that identified individuals resided in the waters of one of the study areas (Whitehead, 2001). The LIR for any time lag (τ) is defined as the probability that an individual sighted in the study areas at any particular time, is re-identified during any single identification made in the area some time lag later (t) (Whitehead, 2001), and is shown by the equation:

$$LIR(\tau) = \frac{\sum_{j,k \setminus (t_k - t_j) = \tau} m_{jk}}{\sum_{j,k \setminus (t_k - t_j) = \tau} n_j * n_k}$$

where n_j is the number of individuals identified in sampling period j and m_{jk} is the number of individuals identified in sampling periods j and k .

LIRs were calculated at spatial and temporal scales including all sightings for all the islands of the archipelago. LIRs were calculated for the entire duration of the study (no maximum lag was set), including in the analysis all sighting histories of all animals, even those only seen once.

Three models of residency were fitted to the residency rate: 1) closed (no changes in the individuals present in the islands); 2) emigration (individuals could leave the area, and never return); 3) emigration and re-immigration (individuals could enter and leave the area, then re-enter) (Table 2.2).

Plots of lagged identification rates against time were produced for all identified whales to provide indications of the temporal use of the area by individual animals. If the population is closed, the lagged identification rate would be the inverse of the population size. In the case of emigration or mortality, the lagged identification rates would typically decrease at lags greater than about $(\tau) = T$ time units (Whitehead, 1999a, 2001). Therefore, a plot of lagged identification rates that drops sharply after a certain time and then levels off above zero after a longer time would indicate that: (1) many animals leave the study area after residing in the area for a certain time, (2) some animals remain resident, and/or (3) other animals re-immigrate into the study area (Whitehead, 2001).

Computation of lagged identification rates and model fitting were carried out using the computer software SOCPROG 2.4. (Whitehead, 2009) in MATLAB. The model generated to aid in the interpretation of lagged identification rates were fitted to the data using maximum likelihood and binomial loss for the full data set (Whitehead, 2001) () and the quasi Akaike Information Criterion (QAIC) was used to select the best-fitting model (Burnham and Anderson, 1998). Differences in QAIC of 0-2 indicated strong support for both models, 3-10 denoted some support for the model with the higher QAIC, and differences greater than 10 indicated no support for the model with the higher QAIC (Whitehead, 2009). The analysis was conducted using a sampling period of 1 day, and the jack-knife techniques, with 1,000 bootstrap replications, were used to calculate confidence intervals and SEs for each model parameter. The interpretation of the possible models of the different scenarios is presented in Table 2.2. Three models of residency were fitted to the residency rate data: “closed” (no changes in the individuals present in the area), “emigration” (individuals could leave the area, but never return), “emigration and re-immigration” (individuals could enter and leave the area, then re-enter the area; Whitehead, 1990). The terminology used for the fitted models should not be considered literally, and must be placed into context. “Emigration”, for example, refers to emigration from the database not necessarily the study area, and there are no ways of knowing whether animals actually died, left the area or were simply not seen again due to chance.

MOVEMENT PATTERNS

Movements represented by re-sightings of identified whales within the archipelago were documented and the number of whales sighted around different islands was calculated. The data base was re-arranged by pooling each sighting/re-sighting of all identified individuals in chronological order, together with information on the date and first identified location (initial sighting), re-sightings, metadata on age and sex class, and general information about the sighting.

The mean, range, and standard deviation of the minimum travel speed between areas were calculated from the distance travelled in nautical miles during the intervals (in days) between sightings in different areas. The distance between re-sightings of photo-identified individuals was measured in the GIS using the “shortest straight swim” distance (i.e. across bays but around headlands). Distances between sightings were calculated between all subsequent re-sightings of an identified animal.

Table 2.2: Exponential models available in SOCPROG 2.4 that can be fitted to the lagged identification rates (LIRs) using maximum likelihood and binomial loss. Models describe movements of individuals in and out the study area. Model equations come from the SOCPROG 2.4 manual (Whitehead 2009). N refers to population size in the study area; td= time lag (τ); a1,a2,a3 = parameters of the models.

MODEL	MODEL EQUATION	Possible Model Interpretation
A	$R=a1$	Closed population $1/a1=N$
B	$R=1/a1$	Closed population $a1=N$
C	$R=a2*e^{(-a1*td)}$	Emigration/mortality $a1=emigration\ rate; 1/a2=N$
D	$R=(1/a1)*e^{(-td/a2)}$	Emigration/mortality $a1=N;$ $a2=Mean\ residence\ time$
E	$R=a2+a3*e^{(-a1*td)}$	Emigration + reimmigration at any time $a1=emigration\ rate;$ $a2/(a2+a3)=proportion\ of\ population\ in\ study\ area$
F	$R=(1/a1)*((1/a3)+(1/a2)*e^{-(1/a3+1/a2)*td})/(1/a3+1/a2)$	Emigration + reimmigration $a1=N;$ $a2=Mean\ time\ in\ study\ area;$ $a3=Mean\ time\ out\ of\ study\ area$
G	$R=a3*e^{(-a1*td)}+a4*e^{(-a2*td)}$	Emigration + reimmigration + mortality
H	$R=(e^{(-a4*td)/a1})*((1/a3)+(1/a2)*e^{-(1/a3+1/a2)*td})/(1/a3+1/a2)$	Emigration + reimmigration + mortality $a1=N;$ $a2=Mean\ time\ in\ study\ area;$ $a3=Mean\ time\ out\ of\ study\ area;$ $a4=Mortality\ rate$
WITH TWO STUDY AREAS: AREA 1 TO AREA 2		
J	a1	Fully mixed $1/a1=N$
K	$1/a1$	Fully mixed $a1=N$ Migration--full interchange $a1=diffusion$
L	$a2*(1-e^{(-a1*td)})$	Rate from area 1 to area 2; $a2=1/N$
M	$(1/a1)*(1-e^{(-td/a2)})$	Migration--full interchange $a1=N;$ $a2=Mean\ residence\ time\ in\ area\ 1$

MATCH INDEX

The match index was calculated to provide a relative measure of the amount of movement among islands. It is the inverse of the Petersen capture-recapture estimator (Baker *et al.*, 1986; Calambokidis *et al.*, 2001), and it is expressed by the following formula:

$$I_{i \rightarrow j} = \frac{m_{i \rightarrow j}}{a_i \times n_j} \times 1000$$

where a_i and n_j represent the number of individuals marked, respectively, at time 1 in region i and at time 2 in region j ; $m_{i \rightarrow j}$ is the number of recaptures in region j originally marked in region i . The expected number of recaptures is the number originally marked in region i that moves to region j and that are captured there. Since the probability of capture is $p_j = n_j/N_j$ (N_j : population abundance in region j), the expected value of the index is:

$$E(I_{i \rightarrow j}) = \frac{\theta_{i \rightarrow j}}{N_j} \times 1000$$

where p_j is the probability of capture in region j , and $\theta_{i \rightarrow j}$ is the probability that an animal marked in region i moves to region j .

The expected value of the index is directly proportional to the movement probability between regions and inversely proportional to the abundance of the population in the second stratum. Therefore, a low value of this index indicates a small population or small movement probability between areas, while high values suggest a large population or an unlikely interchange of animals (Calambokidis *et al.*, 2001). When $i=j$, the movement probability represents the probability of remaining in the same region, and the index is a relative measure of return. Well-marked adult and indeterminate short-finned pilot whales identified in the different islands of the archipelago were included in this analysis, and the probability of individuals to stay in and return to the same area in consecutive years (return rate) as well as the probability of moving to a different area within the same year and between years (interchange rate) were calculated.

RANGING PATTERN

GIS ArcView 3.2 with the Animal Movement extension (Hooge and Eichenlaub, 1997) was used to determine the size of individual ranges and to examine individual ranging patterns, where "range" indicates the area where the individual was sighted during the study period, which might be somewhat different from the definition of "home range". The size of individual range was calculated by the Minimum Convex Polygon (MCP) method (Mohr, 1947), which is commonly used to estimate range size (Anderson, 1982). The MCP is the smallest convex polygon containing all the observed positions including the outermost sighting locations, and the area within this polygon is an estimate of the area used by an individual whale during the study period, which was calculated by GIS (excluding land mass). Despite its wide use and simplicity, MCP often includes large

areas never used by the animal and ignores patterns of selection within the range (Powell, 2000; Taulman and Seaman, 2000). Due to its sensitivity to sample size (number of locations) (Seaman *et al.*, 1999; Bekoff and Mech, 1984; Laundré and Keller, 1984; Harris *et al.*, 1990; White and Garrott, 1990; Kernohan *et al.*, 2001) and the fact that it defines the entire area used by the animal, the MCP method was only used in this study for comparative purposes and always with caution.

Bootstrap tests were run in order to inspect how the MCP range size grew with increasing number of locations used for each whale. The number of sightings that allowed the area-observation curve to reach the asymptote (where each individual displays a constant centre of activity throughout the study period; Gaustestad and Mysterud, 1995) was used as the minimum number of sightings required to estimate range size; this was then used in the MCP and kernel analysis.

The more informative kernel estimator (Worton, 1989) was applied in ArcView, again using the Animal Movement extension. This estimator is a probabilistic non-parametric method that quantifies the likelihood of finding the animal at any particular location within its range (Worton, 1989), and therefore attempts to assess the animal's use distribution (UD) within an area (Kernohan *et al.*, 2001). Instead of just reporting the size of the area used by the individual during its daily activities, by considering each point of isolation the kernel method provides a more robust analysis (Kernohan *et al.*, 2001; Seaman *et al.*, 1999; Seaman and Powell, 1996; Worton, 1989) that acknowledges the importance of distribution as a whole. It assesses the individual's probability of occurrence within its range at each point, which is evaluated based on the points that surround it (a point that is surrounded by many other points has a high density value).

Even though Kernel estimators may identify ranges including areas never used by the animal, they are still the most widely used method for quantifying the intensity of use because they are the most consistent and accurate of the methods available (Worton, 1989; Seaman and Powell, 1996). They allow for the identification of multiple core areas (centres of activity), revealing internal structures within the range, with the advantage of being robust to autocorrelation and outliers, and stabilising at a sample size less than 50 data points (Kernohan *et al.*, 2001). The fixed kernel was selected as the least biased (Seaman and Powell, 1996) and most efficient method of determining centres of activity. Least-squares cross-validation (LSCV) was used to calculate the bandwidth value (which controls the width of individual kernels, determining the amount of smoothing applied to the data). Despite being considered the most reliable and objective method (Seaman *et al.*, 1999), LSCV has been evaluated as having poor performance in cases of high

autocorrelation as the distance between consecutive positions decreases (i.e. when animals use the same location multiple times) (Worton, 1987; Seaman and Powell, 1996) leading to the underestimation of the size of the ranging area (Kernohan *et al.*, 2001). As suggested in the literature (Swihart and Slade, 1985; Worton, 1987), the data were sub-sampled to eliminate autocorrelation: multiple sightings from the same individual in the same date and location were eliminated from the datasets.

Considering that some degree of autocorrelation was still expected to occur, Schoener's ratio (computed as the ratio of the mean squared distance between successive observations divided by the mean squared distance from the centre of activity; Schoener, 1981) was calculated for each individual and used to assess the amount of autocorrelation in the data and the potential effect on the estimates.

Prior to these calculations, using the harmonic mean outlier removal method (White and Garrott, 1990), individuals found far from the main body of the data were identified as outliers and removed.

The Wilcoxon matched pairs test was applied to both methods to assess for possible differences between their results. Moreover, the overall ranging area (MCP and kernel 95% UD) and core area (kernel 50% UD) were compared using the Mann-Whitney U test.

2.3 RESULTS

2.3.1 OCCURRENCE PATTERNS, SIGHTING DISTRIBUTION AND SURVEY EFFORT

Between January 1999 and October 2012, SECAC conducted 1,782 photo-identification day-surveys at sea around the different islands of the archipelago. A total of 59,230.86 nm were covered (10,307:06 hours), within which 38,131 nm were spent on effort (5,436 hours) (Table 2.3, Table 2.4 and Figure 2.3). Even though the overall effort in the Canary Islands did not vary significantly over years (Kruskal-Wallis rank test, $H_2=15.985$, $df=12$; $p=0.192$) or seasons (Kruskal-Wallis rank test, $H_2=6.093$, $df=3$; $p=0.107$), the effort conducted around each island was homogeneous neither in time nor space (Kruskal-Wallis rank test with $p<0.05$). The number of days spent at sea each year and the number of nautical miles surveyed under favourable sighting conditions varied among years and islands; these data are summarised in Table 2.3, Figure 2.4, and Annex 2: Table A2.2, Figure A2.2). Effort varied seasonally only in the eastern islands (Kruskal-

Wallis rank test, $H_2=18.676$, $df=3$; $p<0.001$, in Fuerteventura; $H_2=12.924$, $df=3$; $p=0.005$, in Lanzarote), with more effort in autumn.

Effort covered mainly the area around the island of Gran Canaria (42% of the total, Table 2.4). Similar overall effort in hours and nautical miles was conducted in the islands of Fuerteventura, Lanzarote, Tenerife and La Gomera, although distributed differently over years and seasons (Annex 2: Table A2.2). Around El Hierro, only 454 nautical miles were covered in 18 day-surveys, 1% of the total effort in the archipelago (Table 2.4). Moreover, especially due to sea conditions, only localised areas of each island were considered and mainly surveyed: southwestern waters off Gran Canaria and the western islands, and southeastern waters off Lanzarote and Fuerteventura. Some surveys were conducted also in waters northeast of Tenerife and Gran Canaria.

Sightings were made in waters that ranged in depth from 140m to 3150m, from 1.38km to 43.8km offshore, where the greater distances corresponded to sightings recorded in the channels between islands. In Gran Canaria, La Gomera, and Tenerife the majority (80%) of effort was concentrated 10km, 8km, and 6km, respectively, from the coast (at depths of 1,050m, 1,043m, and 1,666m, respectively) and at greater depths for the remaining 20% of effort, especially in the channels between the islands. For Lanzarote and Fuerteventura, the wider continental shelf, resulted in surveys that extended farther offshore and 80% of effort was conducted in areas up to 21 km from the coast.

During the study period, different vessels were used as research platforms: dedicated semi-rigid inflatable boats (45%), dedicated motor boats (35%), sailing boats (6%), and opportunistic vessels such as whale-watching boats and ferries (9%) (Figure 2.3).

“CHAPTER 2: SITE FIDELITY AND MOVEMENT PATTERNS OF SHORT-FINNED PILOT WHALES WITHIN THE CANARY ISLANDS”

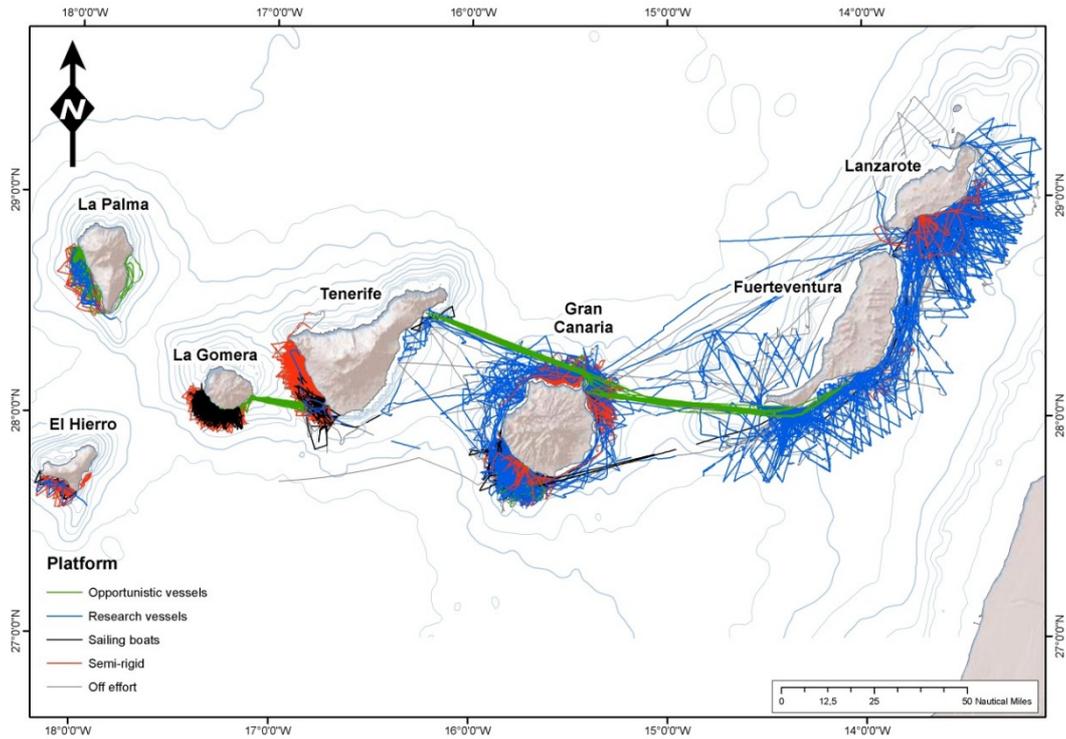


Figure 2.3: Track-lines conducted on effort at sea by SECAC since 1999 around the Canary Island on board different vessel types: semi-rigid inflatable boats (red), dedicated motor boats (blue), sailing boats (black), and opportunist vessels such as whale-watching boats and ferries (green). Off-effort track-lines are indicated in grey.

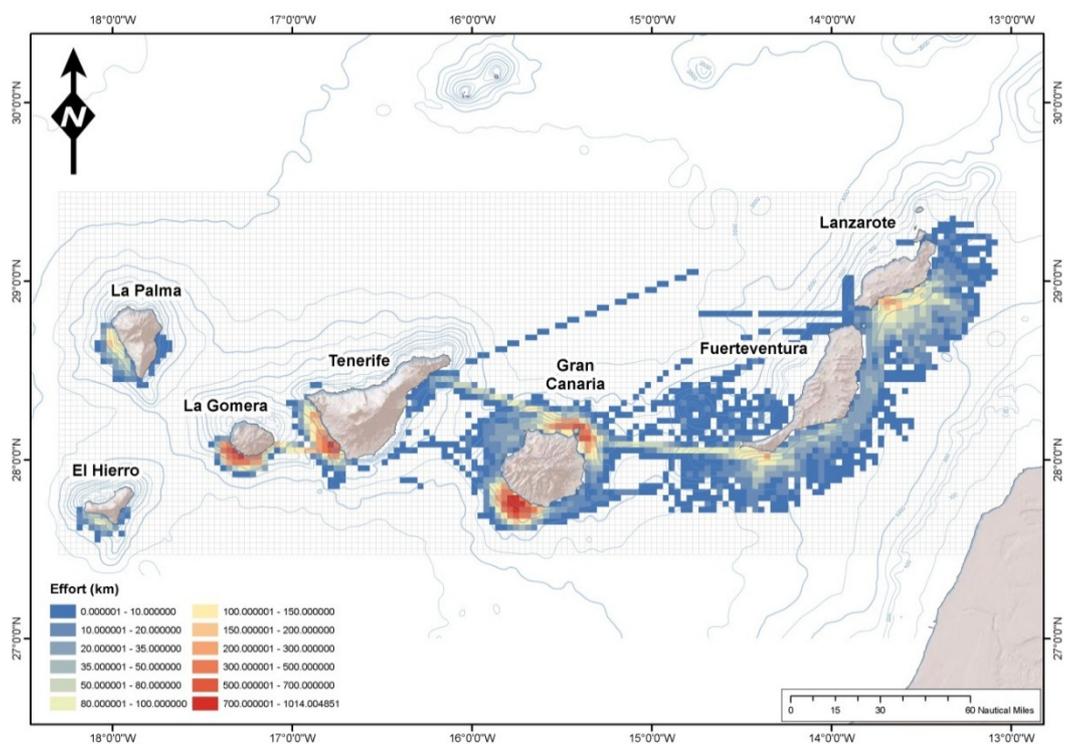


Figure 2.4: Total survey effort plotted for grid cells (each two minutes of latitude by two minutes of longitude) conducted at sea by SECAC since 1999 around the Canary Islands waters.

2.3.2 SHORT-FINNED PILOT WHALE SIGHTINGS: DISTRIBUTION AND RELATIVE ABUNDANCE

During the study period, 4,242 sightings of 23 identified cetacean species were recorded. Short-finned pilot whales were the most frequently seen species, with 1,081 sightings (25.5% of the total), distributed differently over the years and islands (Table 2.3, Table 2.4, and Annex 2: Table A2.2, Figure A2.2). In total, 757 pilot whale sightings were recorded on effort and 324 off effort (163 were secondary sightings) (Table 2.3, Table 2.4, Figure 2.5).

Pilot whales were recorded on 177 occasions associating with different delphinid species: bottlenose dolphins (in 147 sightings), Atlantic spotted dolphins (15 sightings), rough-toothed dolphins, common dolphins, striped dolphins and Fraser's dolphins (all in one sighting each) (Figure 2.6).

Table 2.3: Survey effort per year (day, nautical miles, and hours) conducted at sea by SECAC since 1999 around the Canary Island, with sightings on and off effort, encounter rate ER1 (total number of encounters divided by the total number of nm surveyed each year) and ER2 (annual mean of cell encounter rates).

CANARY ISLANDS							
YEAR	EFFORT			SIGHTINGS		ER	
	Day	nm	h	on EFFORT	off EFFORT	1	2
1999	176	2,297.46	306:44:00	6	4	0.26	0.08 (0.06)
2000	131	1,607.93	205:34:00	4	4	0.25	0.13 (0.07)
2001	-	-	-	-	-		
2002	67	1,380.69	224:42:00	22	12	1.59	0.69 (0.22)
2003	25	758.13	133:40:00	2	0	0.26	0.17 (0.12)
2004	43	1,865.23	258:07:00	17	5	0.91	0.91 (0.32)
2005	84	2,395.48	388:13:00	40	32	1.67	0.94 (0.25)
2006	61	2,786.78	254:32:00	43	8	1.54	1.01 (0.32)
2007	231	3,088.62	458:14:00	243	76	7.87	1.83 (0.46)
2008	206	3,044.24	485:13:00	196	110	6.44	1.26 (0.32)
2009	266	5,591.29	901:36:00	52	35	0.93	0.99 (0.23)
2010	150	7,252.54	1,155:35	86	29	1.19	0.89 (0.22)
2011	128	3,466.49	352:06:00	31	3	0.89	0.62 (0.17)
2012	214	2,597.09	312:40:00	15	6	0.58	0.53 (0.20)
TOTAL	1,782	38,131.95	5,436:55	757	324	1.99	0.72 (0.10)

**"CHAPTER 2: SITE FIDELITY AND MOVEMENT PATTERNS
OF SHORT-FINNED PILOT WHALES WITHIN THE CANARY ISLANDS"**

Table 2.4: Total nm travelled and survey effort per island (day, Nautical Miles, and hours) conducted at sea by SECAC since 1999 around the Canary Islands, with on and off effort sightings.

ISLAND	EFFORT				SIGHTINGS	
	TOTAL nm	Day	nm	h	on effort	off effort
GRAN CANARIA	22,881.04	1,113	15,944.85	2,278:41	27	25
FUERTEVENTURA	9,542.39	145	5,478.23	694:11:00	14	12
TENERIFE	10,079.60	317	5,386.62	819:40:00	621	238
LA GOMERA	6,908.13	162	5,320.28	776:40:00	69	38
LANZAROTE	7,686.97	146	4,422.53	648:46:00	23	10
LA PALMA	1,552.75	45	1,125.28	146:10:00	3	1
EL HIERRO	579.62	18	454.16	72:47:00	0	0
TOTAL	59,230.50	1,655	38,131.95	5,436:55	757	324

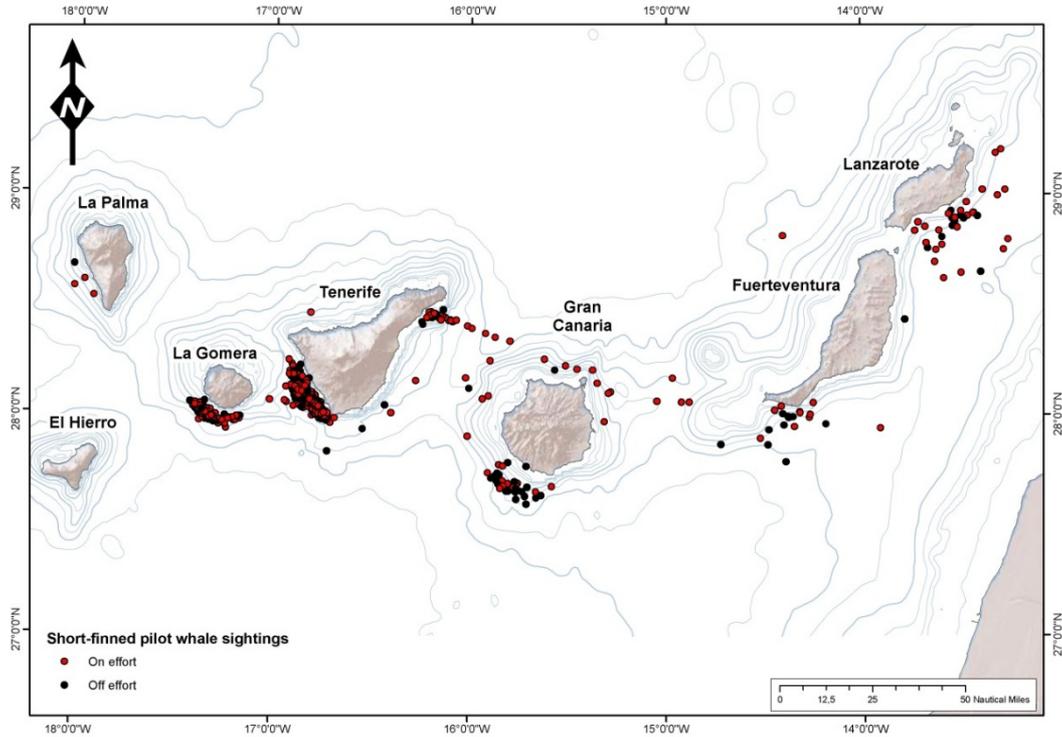


Figure 2.5: Short-finned pilot whale sightings on and off effort, recorded between 1999-2012 in the Canary Islands.

“CHAPTER 2: SITE FIDELITY AND MOVEMENT PATTERNS
OF SHORT-FINNED PILOT WHALES WITHIN THE CANARY ISLANDS”

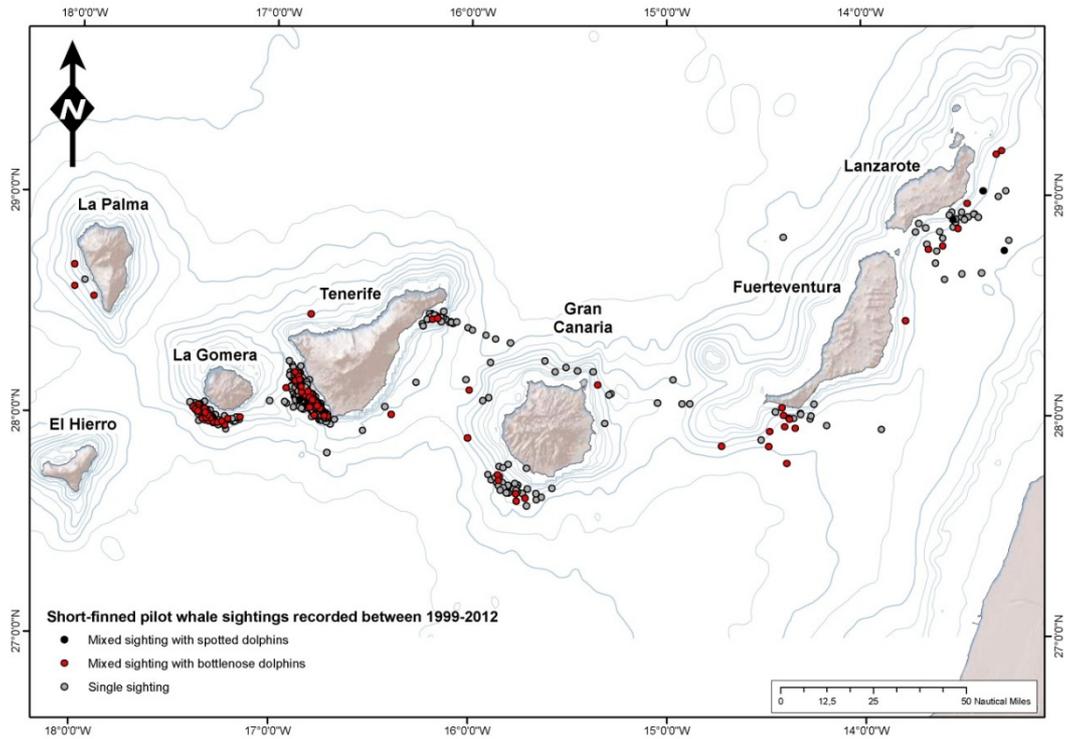


Figure 2.6: Short-finned pilot whale sightings in association with bottlenose and spotted dolphins, recorded between 1999-2012 in the Canary Islands.

Encounter rates were computed for short-finned pilot whale sightings and effort data between 1999 and 2012 in the entire Canary Islands. Limiting the calculation of the encounter rate (ER1 and ER2) to the cells with effort higher than 1 nm, 0.5% of the total effort and eight short-finned pilot whale sightings (four on effort and four off) were discarded. Ninety-two per cent of the cells with survey effort had no associated short-finned pilot whales sightings, while the rest of the cells were characterised by different level of usage, with high usage localised in restricted areas in the southwest of Tenerife and La Gomera (Table 2.5, Figure 2.7).

The overall mean encounter rate ER2 for cells with total effort higher than 1 nm was 0.72 sightings/nm surveyed in each cell (SE=0.10; quartiles=0.0; 0.0; 0.0; range= 0-112.87) and, as expected, lower but more homogeneous than the ER1 (1.99 sightings/nm surveyed in each cell) (Table 2.5). The means were quite variable, with a peak in 2007 and 2008 coinciding with the intensive surveys conducted in Tenerife, where 58% of the total pilot whale sightings were recorded. The peak in effort in 2010 corresponds to the surveys conducted along the coast of Lanzarote and Fuerteventura, a wide area with quite a low encounter rate (Table 2.5). Encounter rates (ER2) were higher during summer and autumn compared to the other seasons (Kruskal-Wallis rank test, $H=9.713$, $df=3$; $p<0.021$).

Short-finned pilot whales were encountered during every day-survey conducted across the waters of Tenerife, with an annual encounter rate of 3.62 sightings/nm surveyed in each cell (SE=0.66; median=0.0; range=0-48.9; n=152) (Table 2.5). Significantly fewer sightings were recorded in the other islands (Kruskal-Wallis rank test, H=172.044, df=6; p<0.001), from a mean of 1.14 sightings/nm (SE=0.34; median:0.0; range: 0-17.07; n=59) in La Gomera to 0 in El Hierro.

Table 2.5: Encounter rate ER1 (total number of encounters divided by the total number of Nm surveyed each year), and ER2 (range, mean and quartiles of cell encounter rates per island).

ISLAND	n	ER 1	ER 2		
		mean	mean	range	median
GRAN CANARIA	406	0.17	0.27 (0.12)	0-44.97	0
FUERTEVENTURA	639	0.26	0.2 (0.11)	0-60.07	0
TENERIFE	152	11.53	3.62 (0.66)	0-48.90	0
LA GOMERA	59	1.3	1.14 (0.34)	0-17.07	0
LANZAROTE	259	0.52	0.49 (0.14)	0-22.70	0
LA PALMA	62	0.27	0.15 (0.09)	0-4.47	0
EL HIERRO	30	0	0	0-0	0

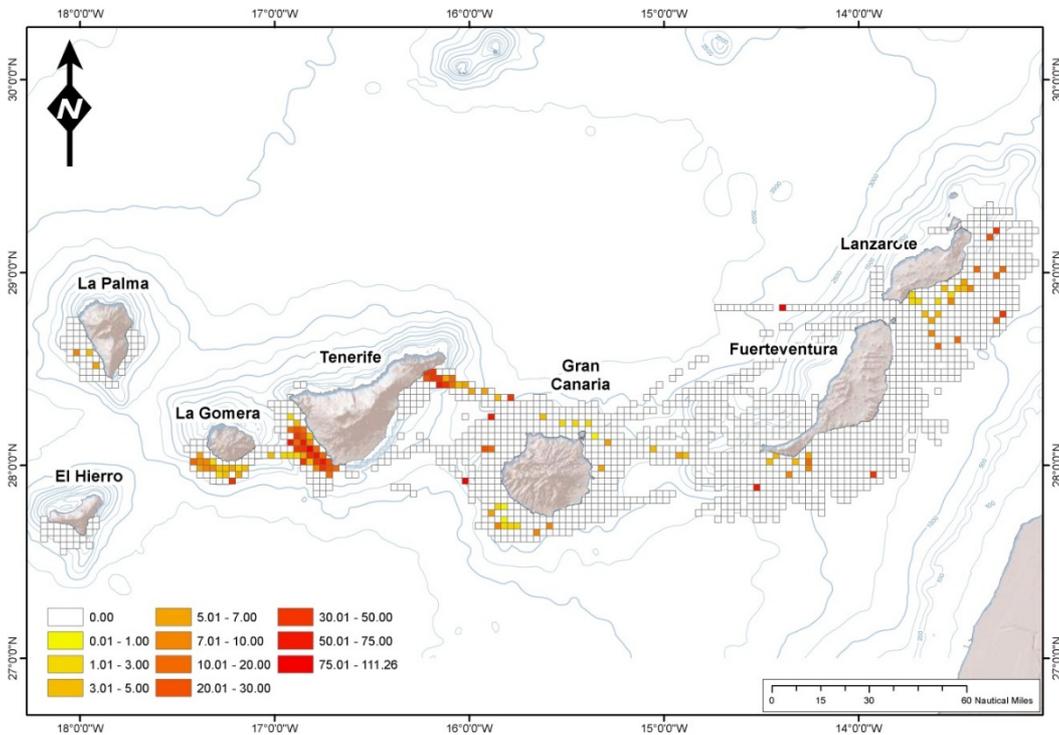


Figure 2.7: Mean cell encounter rate ER2 in the Canary Islands (sightings/Nm surveyed in each cell).

Short-finned pilot whales were sighted in a wide range of depths, with the highest sighting rates mainly occurring between the 900m and 1200m isobaths (mean depth=1077.5m, SD=421.1, SE=16.9), and were found in shallower waters in La Gomera compared to Tenerife (Mann-Whitney, $U=7,162$, $p=0.006$) and Lanzarote-Fuerteventura (Mann-Whitney, $U=90$, $p<0.001$) (Figure 2.8a, Figure 2.9a).

The distance from the coast (mean=5.76km, SD=3.5, SE=0.14) varied over the islands, with higher distances in the eastern islands of Lanzarote-Fuerteventura and Gran Canaria, compared to Tenerife (Mann-Whitney, $U=1,572$, $p<0.001$; $U=1,432$, $p<0.001$, respectively) and to La Gomera and La Palma (Mann-Whitney, $U=114$, $p<0.001$; $U=111$, $p=0.002$, respectively) (Figure 2.8b, Figure 2.9b).

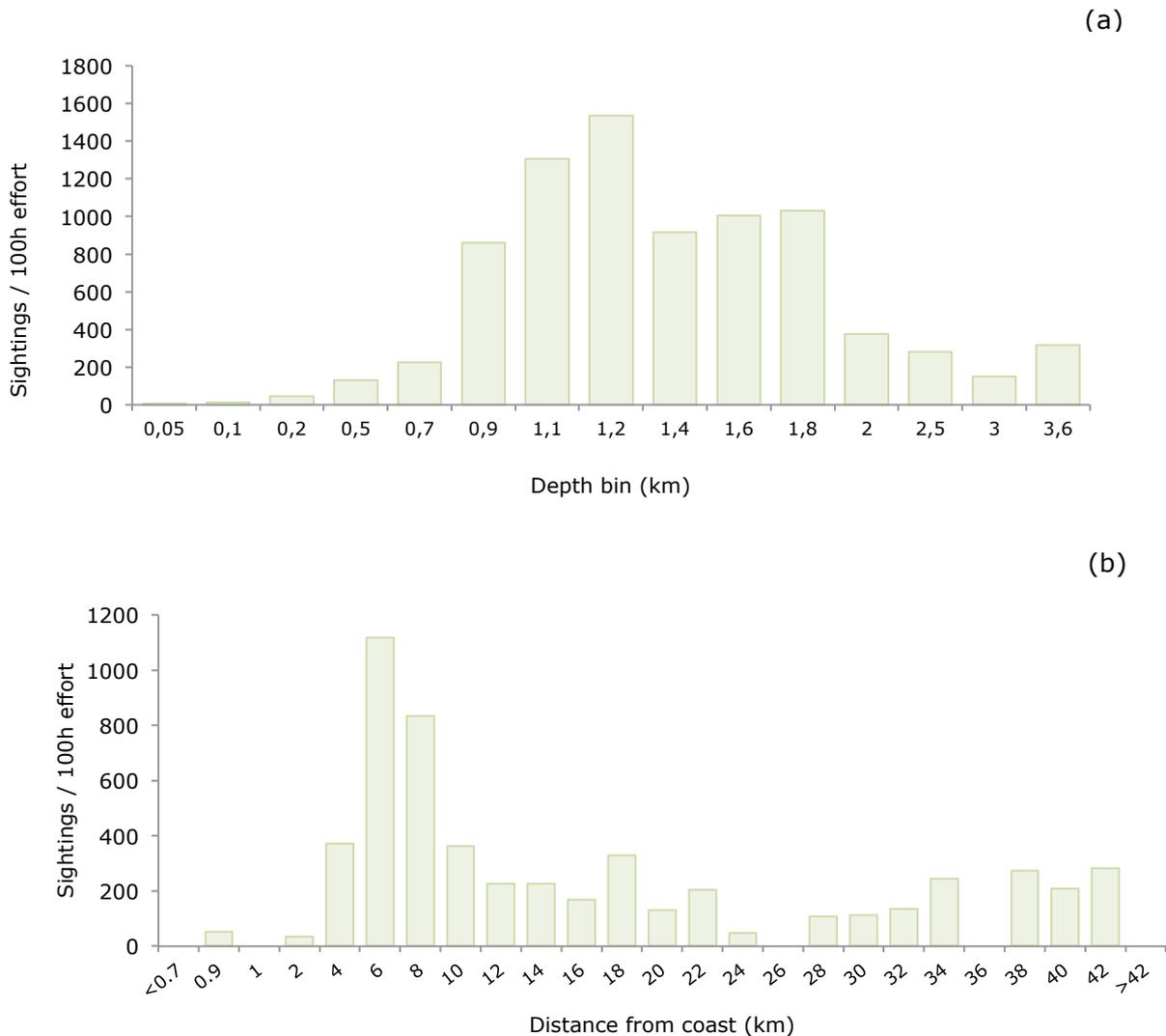


Figure 2.8a-b: Frequency distributions of short-finned pilot whale sightings in the Canary Islands (per 100 h effort), based on (a) water depth; mean=1,077.5 m, SE=16.9), and (b) distance from coast; mean=5.8 km, SE=0.14).

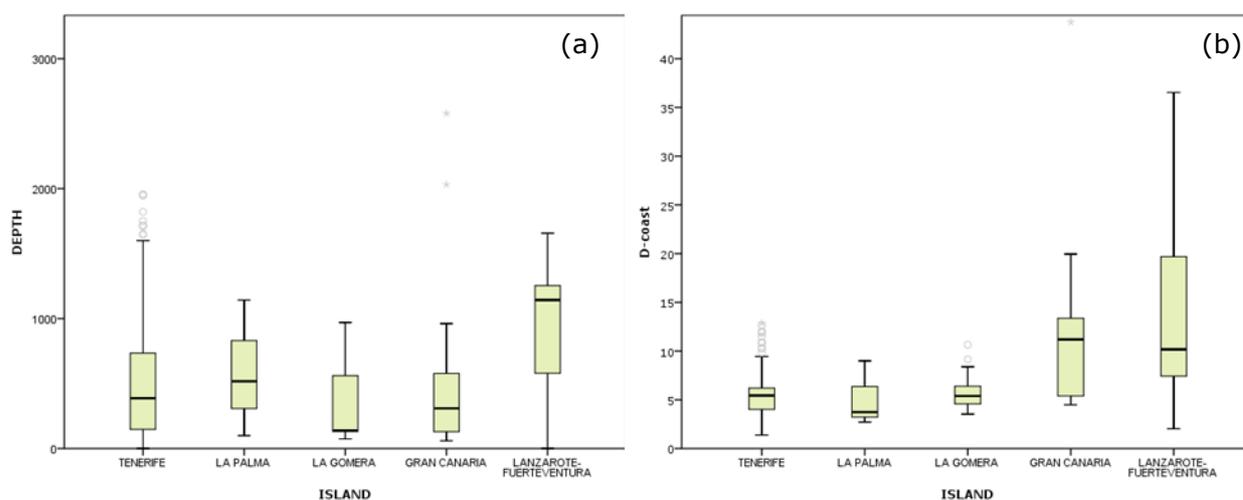


Figure 2.9a-b: Distribution of short-finned pilot whale sightings, based on (a) mean water depth and (b) distance from coast. Data are presented using box-and-whisker plots per each island of the archipelago: the middle line shows the median value, the upper and lower lines of the box show 75th and 25th percentile, respectively. The ends of the upper and lower vertical lines indicate the minimum and maximum data values, unless outliers are present (*).

GROUP DYNAMICS

Group size and composition were calculated per island, and examined for 772 independent groups encountered between 1999 and 2012, including only the sightings that were considered reliable and representative. Group size ranged from one to 80 individuals, with an overall mean group size of 16 individuals (SE=0.5), with most of the groups (86%) encountered containing between one and 25 animals (Table 2.6, Figure 2.10).

Significantly larger group sizes were observed in La Gomera than Tenerife (Mann-Whitney, $U=21861.5$, $p=0.015$), and Gran Canaria (Mann-Whitney, $U=1022.5$, $p=0.013$), and smaller group sizes were seen in Gran Canaria compared to Lanzarote-Fuerteventura (Mann-Whitney, $U=443.5$, $p=0.033$) (Table 2.6.; Figure 2.11a). Statistically significant seasonal differences in group sizes ($H=12.635$, $df=3$, $p=0.005$) were detected, with larger group sizes during summer than spring (Mann-Whitney: $U=18458.5$, $p=0.004$) and autumn. The analysis by island detected seasonal differences in Tenerife, where larger group sizes were found in summer (mean= 16.84, SE=0.84; median=14; range= 1-71; $n= 290$) and autumn (mean= 16.71, SE=0.89; median=14; range= 1-80; $n= 187$), than spring (mean=14.0; SE= 0.8; median=11; range=1-70; $n=153$; Mann-Whitney, $U=11535$, $p=0.015$; $U=11631.5$, $p=0.003$, respectively). No seasonal differences were found in La Gomera, Gran Canaria and Lanzarote-

Fuerteventura (Kruskal-Wallis rank test: $H=4.827$, $df=3$, $p=0.185$; $H=2.075$, $df=3$, $p=0.557$; $H=0.724$; $df=1$, $p=0.868$, respectively) (Figure 2.11b).

Table 2.6: Group size of short-finned pilot whales encountered between 1999 and 2012 in the different islands of the Canary Islands, and by season. Mean values, range, standard error and standard deviation are also shown.

ISLAND	N	Min	Max	Mean	SE	SD	Median
TOTAL	772	1	80	16.2	0.5	11.6	14
TENERIFE	612	1	71	15.8	0.4	11.2	13
LA GOMERA	84	3	80	19.1	1.5	13.7	18
LANZAROTE FUERTEVENTURA	37	1	70	19.8	2.4	14.4	18
GRAN CANARIA	35	1	36	12.6	1.3	7.8	11.50
LA PALMA	4	2	25	13.5	4.7	9.5	13.5
SEASONS							
WINTER	144	1	70	15.1	0.9	11.1	12.5
SPRING	153	1	70	14.0	0.8	10.1	11
SUMMER	290	1	71	17.2	0.7	12.2	14
AUTUMN	187	1	80	17.2	0.9	11.8	14

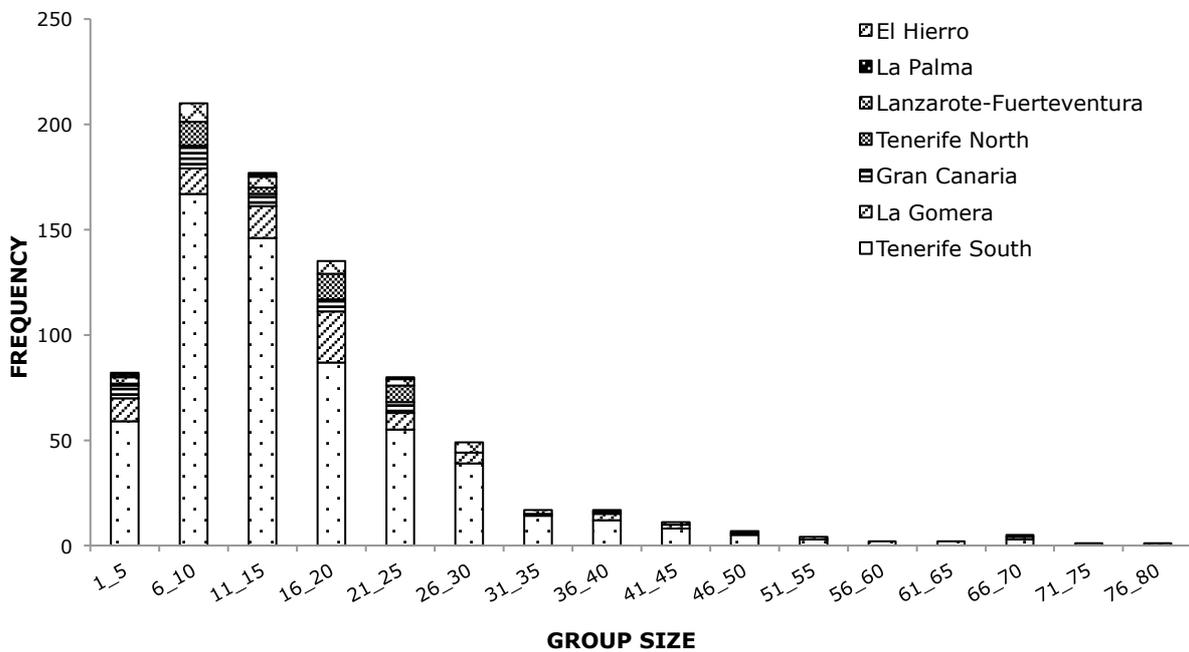


Figure 2.10: Frequency distribution of short-finned pilot whale group size based on minimum photo-identification and field counts between 1999 and 2012 in the different island of the Canary Archipelago. Groups ranged from one to 80 individuals (mean=16.2; SE=0.5), with most groups (86%) encountered containing between one and 25 whales.

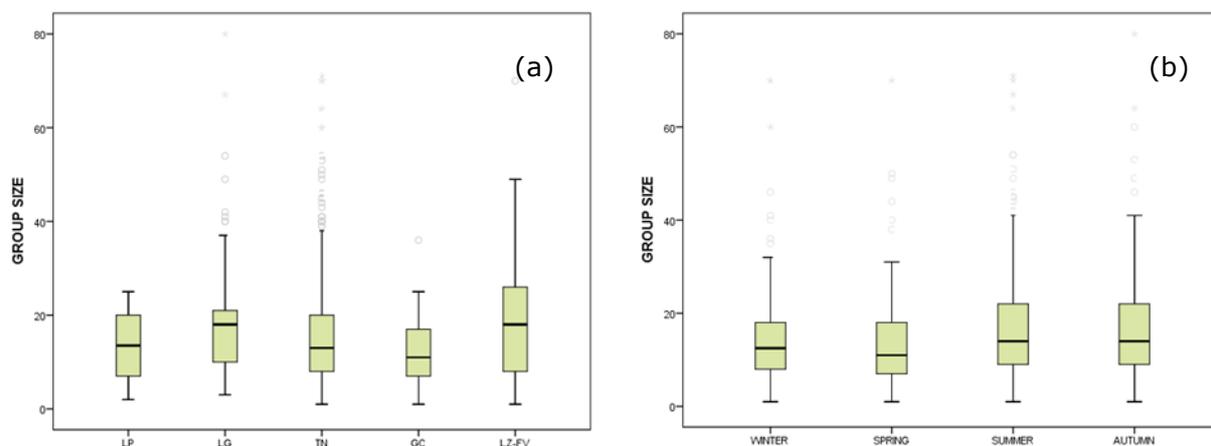


Figure 2.11a-b: Mean group size of short-finned pilot whale groups recorded (a) in the islands of La Palma (LP) La Gomera (LG), Tenerife (TN), Gran Canaria (GC), and Lanzarote-Fuerteventura (LZ_FV), and (b) during seasons, between 1999 and 2012. Data are presented using box-and-whisker plots, middle line shows median value, upper and lower lines of box show 75th and 25th percentile, respectively. The ends of the upper and lower vertical lines indicate the minimum and maximum data values, unless outliers are present (*, in grey).

Analysis of group composition revealed that 64.0% (SE=0.73%) of the individuals encountered in groups were classified as adults, 15.7% (SE=0.55%) as indeterminates, with the remaining 20.3% classified as either juveniles (11.7%, SE=0.38%) or calves/newborns (8.62%, SE=0.46%). Group composition did not differ within the islands (Kruskal-Wallis rank test, $H = 7.174$, $DF=3$, $p = 0.67$) (Figure 2.12, Figure 2.13).

A high frequency of sightings with calves and/or neonates was recorded throughout the archipelago; 53% in La Gomera and Tenerife, 60% in Gran Canaria, and 81% in Lanzarote-Fuerteventura, with a mean per sighting of 1.3 neonates/calves (SD=1.7). 82% of the groups encountered had immature animals (neonates, calves and juveniles). The frequency of sightings with only adults and indeterminate individuals ranged from 14% in the eastern islands to 21% in La Gomera (Figure 2.12, Figure 2.13).

For Tenerife, where the majority of sighting data were collected, group composition was: 67.1% adults (SE=0.77%), 12.6% indeterminates (SE= 0.52%), 11.8% juveniles (SE=0.43%), 7.31% calves (SE=0.39%), 0.93% new-borns (SE=0.11%) (Figure 2.12, Figure 2.13). The presence of neonates was highest during the summer months (52%) followed by autumn (31%) and neonates were present in the same groups as the presumed adult males on 43 occasions (58.9% of sightings that included neonates), suggesting that short-finned pilot whales commonly travel in groups of mixed sex and age, although with some segregation between adult males and neonates.

“CHAPTER 2: SITE FIDELITY AND MOVEMENT PATTERNS OF SHORT-FINNED PILOT WHALES WITHIN THE CANARY ISLANDS”

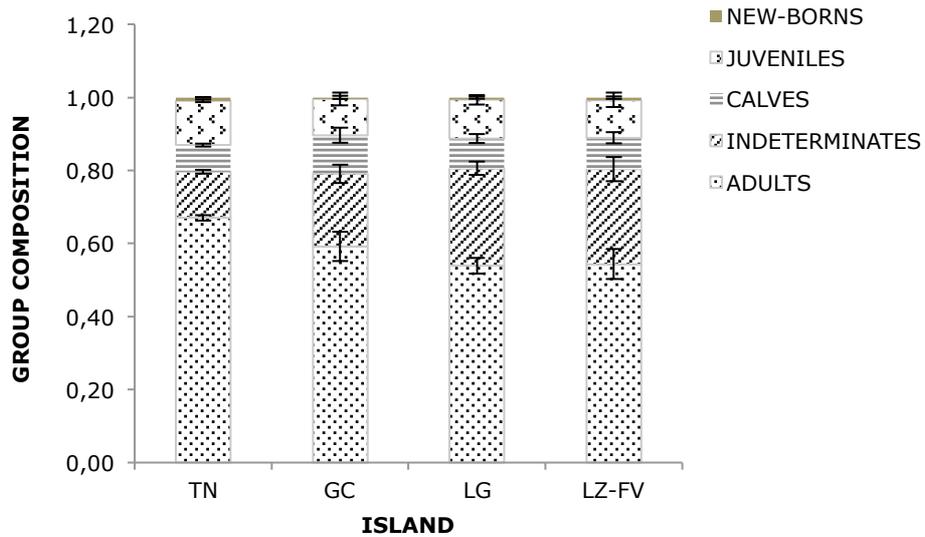


Figure 2.12: Group composition for groups of short-finned pilot whales encountered between 2004 and 2010 in Tenerife (TN), Gran Canaria (GC), La Gomera (LG), and Lanzarote-Fuerteventura (LZ_FV): mean proportion of adults, indeterminates, juveniles, calves, and new-borns are presented with respective standard error.

Group sizes of sightings with males (mean=7, SD=5) were significantly smaller than sightings with no males (mean= 19, SD=12; U=774.500, $p < 0.001$), and when they were in sightings with females present (mean=17, SD=12; U=7,118, $p < 0.001$). The presence of immature animals (juveniles, calves, neonates) resulted in significantly larger groups (mean=19, SD=12) than groups where only mature whales (mean=9, SD=7) were present (U=26675.5, $p < 0.001$) (Figure 2.13).

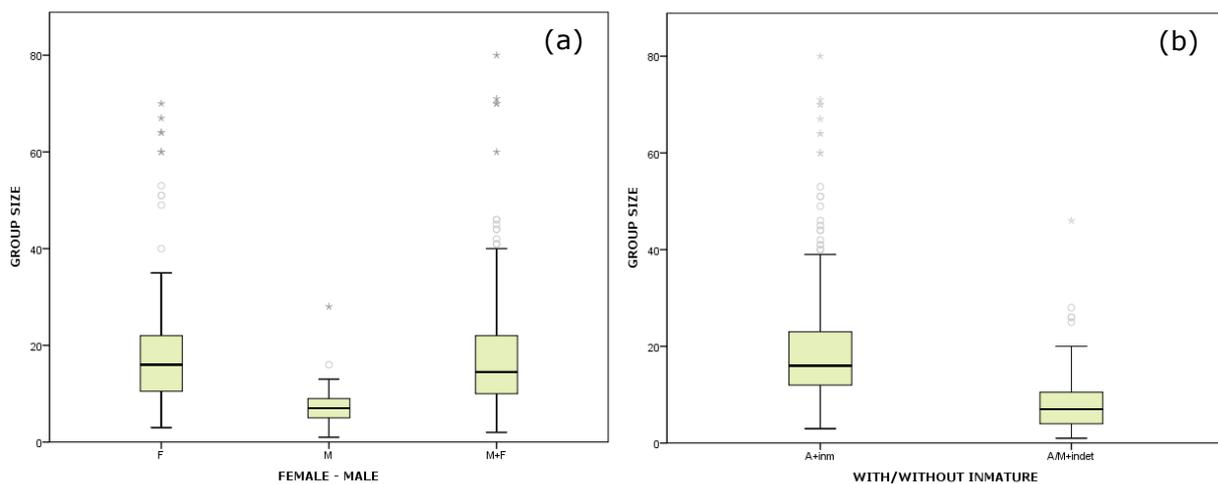


Figure 2.13a-b: (a) Group size differences based on the presence/absence of males (without males, with males and no females, females and males in the same group), (b) group size differences between groups with and without calves.

BEHAVIOUR

Initial behaviour recorded during the study period included all behavioural categories, where travelling (61%) and resting (24%) were the most frequent, while socialising (12%) and feeding (3%) were observed on only a few occasions. All were observed year-round with no substantial differences in frequency, except for socialising which was observed for 77% of the time from June to October. Moreover, off the island of Tenerife, the remains of giant squid (*Architeuthis* sp.) floating near pilot whales were repeatedly observed, as well as a long tentacle in the mouth and marks left on the dorsal fins of some individuals.

PHOTO-IDENTIFICATION ANALYSIS

A total of 234,350 photographs were obtained from 629 sightings, and 190,340 were considered suitable for photo-identification analysis, based on the photographic quality criteria. The overall catalogue of all the identified individuals in all the Canary Islands contained 14,469 dorsal fin photographs belonging to 3,275 unique short-finned pilot whales, within which 1,310 were well-marked individuals (952 adults, 289 indeterminate, 57 juveniles, nine calves, three neonates) with good and excellent quality pictures (Table 2.7).

Table 2.7: Photo-identified short-finned pilot whales in the different Canary Islands, between 1999 and 2012: complete photo-identification catalogue, datasets based on picture quality and animal distinctiveness (Q3= good picture quality, Q4= optimum picture quality; D3= distinctive individual, D4= very distinctive individual). Age classes (A= adults, Indet= indeterminates, J=juveniles, C=calves; and N=newborns) are given for the data set Q3 Q4, D3 D4.

ISLAND	ALL	Q3,Q4 D3,D4					
		TOTAL	A	INDET	J	C	N
TOTAL	3,275	1,310	952	289	57	9	3
TENERIFE	1,842	760	588	123	35	12	2
LA GOMERA	621	271	212	46	11	2	0
LANZAROTE-FUERTEVENTURA	674	282	161	112	7	2	0
GRAN CANARIA	404	190	146	31	9	3	1
LA PALMA	13	10	9	1	0	0	0

DISTINCTIVENESS AND MARK CHANGE

Considering only the mature population (excluding calves and juveniles) of short-finned pilot whales in the Canary Islands, 72% were categorised as well-marked (D3 and D4) and 22% slightly distinctive (D2). The proportion of re-captured individuals increased as distinctiveness increased: 10% of non-distinctive, 28% of slightly distinctive, 36% of distinctive, and 47% of very distinctive whales were re-sighted over the course of the study. The mean number of times an individual was re-captured also increased with distinctiveness: 1.5 for non-distinctive, 2.7 for slightly distinctive, 3.1 for distinctive and 3.8 for very distinctive pilot-whales.

The rate of mark change and mark acquisition was assessed by examining all re-sightings of individuals, looking for new notches or changes in notch shape. A total of 82 acquisition events or mark-changes were recorded on 64 individuals, but only in seven cases did the acquisition of new marks result in a change in distinctiveness category: four animals went from slightly distinctive to very distinctive, and three from distinctive to very distinctive. Considering only the well-marked animals seen off Tenerife (2004-2009), the mark-change rate was estimated to be once every 3.4 to 4.2 years. The low mark-change rate, along with the long lasting presence of scars persisting over ten years (Servidio, *et. al.* 2006), allowed the effect of mark-change to be considered negligible.

DISCOVERY CURVES

Discovery curves constructed from the overall database, and specifically for Tenerife, La Gomera, and Gran Canaria (Figure 2.14), suggested continual recruitment of new individuals to the population throughout the study period (1999-2012). Some levelling off was present in the discovery curve of well-marked individuals in La Gomera, although new well-marked individuals were sighted until the end of the study period. Newly identified whales in the population may correspond to births, immigration into the population, mark change or captures of previously unphotographed short-finned pilot whales.

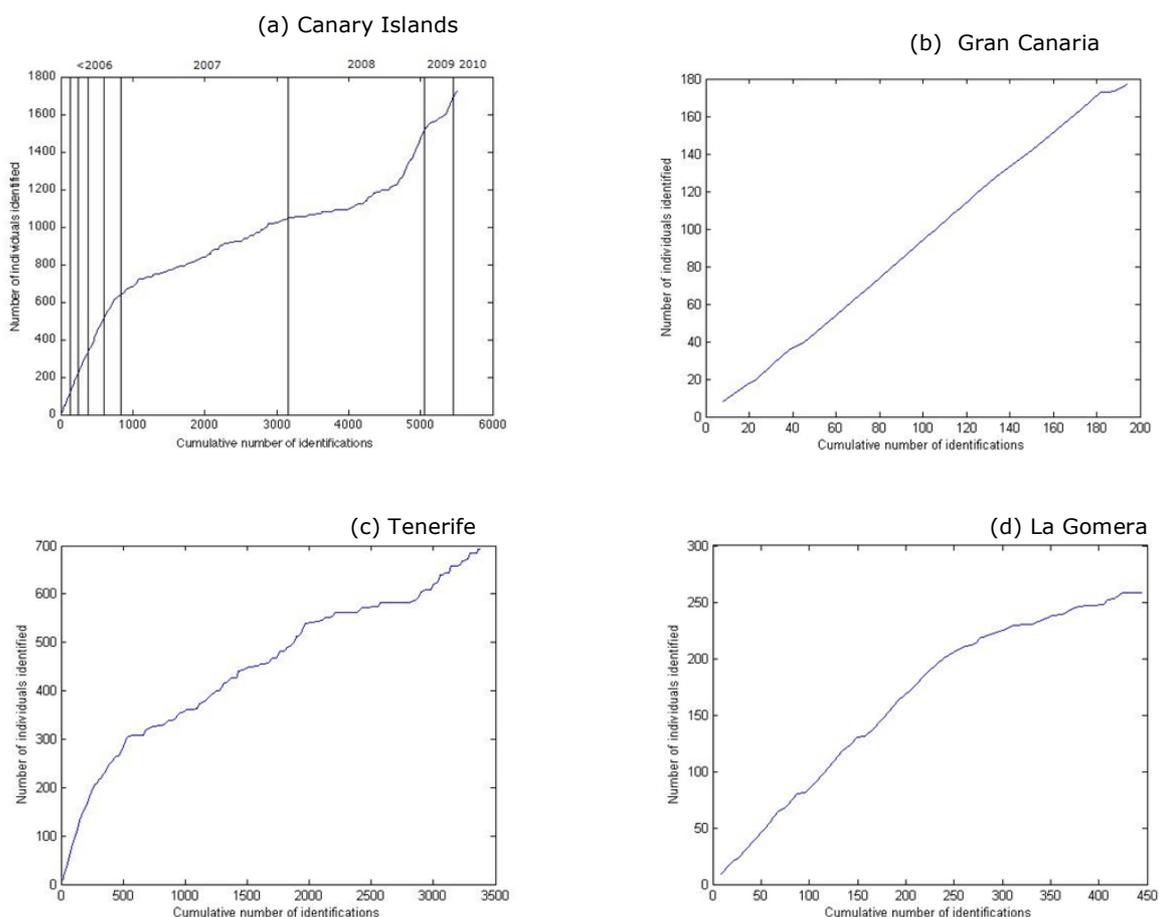


Figure 2.14: Discovery curve showing the number of new well-marked short-finned pilot whales identified each day between 1999 and 2012 in the Canary Islands (a), and of new well-marked in Gran Canaria (b), in Tenerife (c), and La Gomera (d).

LAGGED IDENTIFICATION RATES (LIR)

Residency was first analysed at a large spatial and temporal scale by considering the entire archipelago throughout the whole study period. The best fitting model for the LIR within the study area was the “Emigration + Reimmigration” model (Table 2.8; Figure 2.15). An estimated 254 (SE=10) of the 1,241 identified whales used in this analysis spent an average of 531 (SE=24) days in the Canary Islands before leaving for an average of 4,087 (SE=941) days. Nevertheless, analyses indicated a rather strong overdispersion of the data (variance inflation factor= 4.82), so that results should be interpreted with caution including that the variances of the parameter estimates were likely underestimated.

Data from southwest Tenerife were further analysed because this was the area with the highest number of animals sighted and recaptured. The best-fitting models were “Emigration/mortality” and “Emigration + Reimmigration”, with an estimated 279 animals (Table 3.5) of the 717 identified staying in the area for an estimated average of 2,049 days, a time that was beyond the 4.5 years of the dataset used for the analysis.

These data were also overdispersed (variance inflation factor= 3.67).

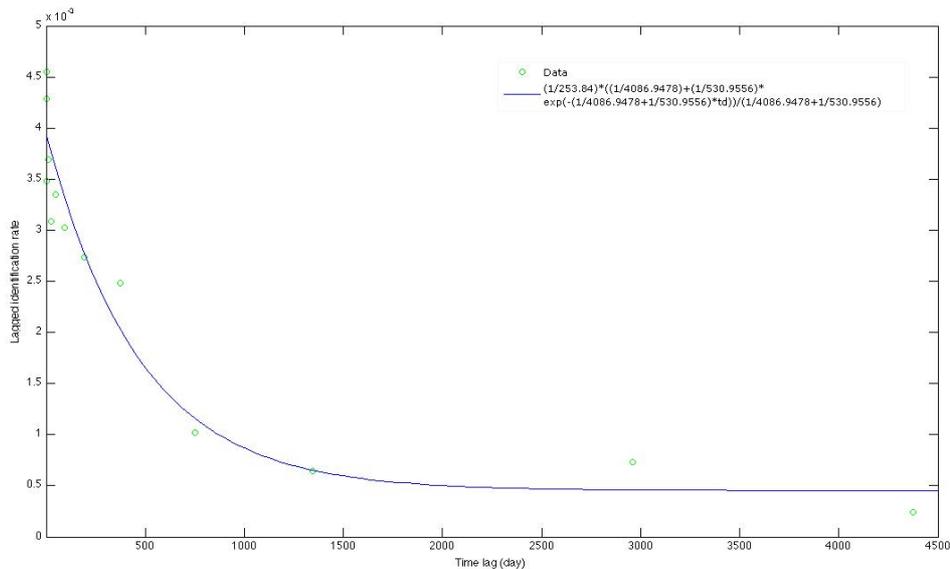


Figure 2.15: Lagged identification rates (LIRs) for all individual short-finned pilot whales identified in the Canary Islands, between 1999 and 2012; the graph depicts the probability that a whale photographed at time “0” will be identified again at time x within the study area. Data points are represented as circles and the best fitting model (Emigration + Re-immigration) is displayed as a blue line.

The LIR calculated for pilot whale movements from the island of Tenerife to La Gomera identified “fully mixed” to be the best fitting model, and estimated a population of 2,718 (SE=361) individuals between the two islands (Table 2.8). These data were very strongly overdispersed (variance inflation factor= 7.82). Calculating the LIR for movement in the opposite direction, from La Gomera to Tenerife, the model that best fitted the data was also “fully mixed”, estimating a population of 1,686 (SE=221). Migration with full interchange (Full mixed) was therefore the best description for the population of La Gomera and Tenerife, supported by the high number of recaptures recorded between the two areas (Table 2.10).

Table 2.8: Diagnostics and estimated parameters for models of lagged identification rates (LIRs) applied to all individual short-finned pilot whales identified in the Canary Islands, between 1999 and 2012, and in southwestern Tenerife between 2004 and 2009. Models were also applied to Tenerife and La Gomera to test how pilot whales move between these two islands. td = time lag (τ); a_1, a_2, a_3 = parameters of the models. Values inside the brackets indicate the standard errors of the parameters calculated using bootstrap replications.

DATASET	MODEL	MEAN RESIDENT			
		a1	a2	a3	
CANARY ISLANDS	Emigration+ Re-immigration	$(1/a_1) * ((1/a_3) + (1/a_2) * \exp((1/a_3 + 1/a_2) * td)) / (1/a_3 + 1/a_2)$	253.84 (9.93)	530.96 (23.82)	4086.95 (941.43)
	Emigration/ Mortality	$a_2 * \exp(-a_1 * td)$	0.000488 (7.1123e-005)	0.00358 (0.00019)	
SOUTHWEST TENERIFE		$(1/a_1) * \exp(-td/a_2)$	279.45 (14.47)	2048.60 (268.28)	
	Emigration+ Re-immigration	$(1/a_1) * ((1/a_3) + (1/a_2) * \exp((1/a_3 + 1/a_2) * td)) / (1/a_3 + 1/a_2)$	279.4567 (84.561)	2048.7279 (1048.901)	354522778 (2400931451)
from Tenerife to La Gomera	Fully Mixed	$1/a_1$	2718.52 (361.05)		
from La Gomera to Tenerife	Fully Mixed	$1/a_1$	1686.18 (221.54)		

RECAPTURES AND MOVEMENT PATTERNS

A total of 617 (50%) of the well-marked individuals were seen only once, 191 (15%) twice, and 433 (35%) whales three to 36 (one animal) times. Recaptures within islands and between islands are summarised in Table 2.9 and presented in Figure 2.16y Figure 2.17, which show the recapture frequency of well-marked adults and indeterminate individuals with good quality pictures.

An additional 180 photo-identification images came from surveys in 1993, which were included only for qualitative descriptions and not for analysis because the effort data were not considered complete and suitable for this study. These photographs were compared to the catalogue and, of the 139 pilot whales identified, 44 satisfied the required standard of photographic quality and fin distinctiveness to be used for comparison. Thirteen of these whales were recaptured, all frequently (up to 22 times) seen in Tenerife between 2004 and 2010, with two animals seen also in La Gomera and Gran Canaria, with recaptures of 16-19 years apart.

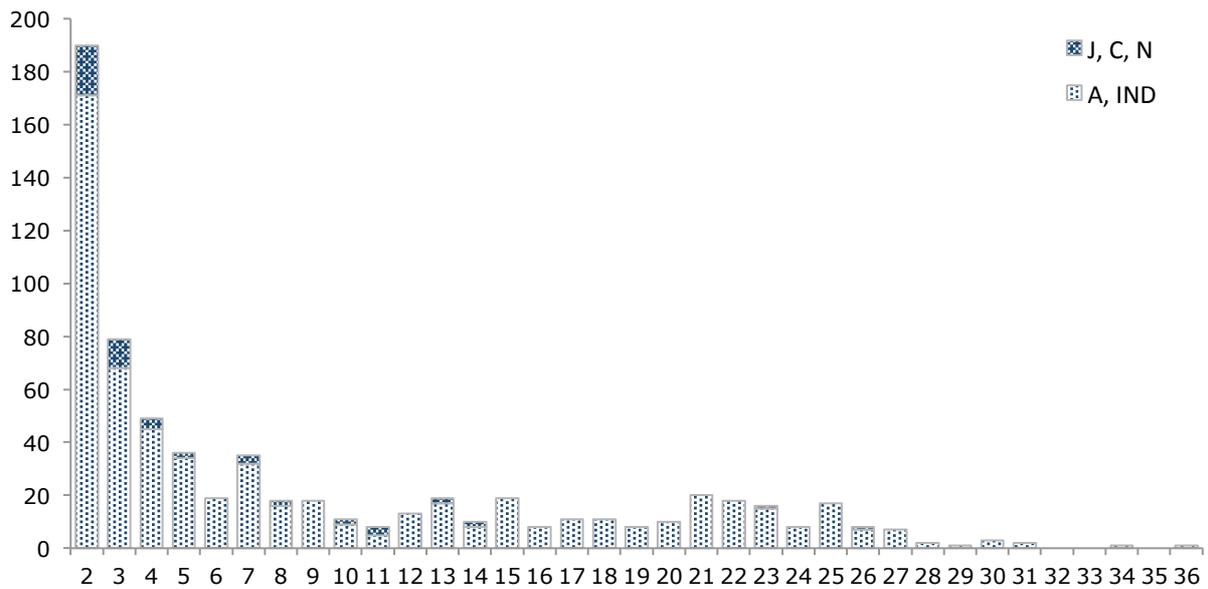


Figure 2.16: Frequency histogram of the number of times that uniquely marked short-finned pilot whales were captured (A=adults, IND= indeterminate, J= juvenile, C=calves, N=neonates) in the Canary Islands, between 2004 and 2012.

The catalogue created by Heimlich-Boran (1993) for Tenerife during surveys from 1991 to 1993 was also reviewed and compared, looking for matches. The difference in picture quality (black and white prints, approximately 80% of the pictures of poor and fair quality, and with low and slight distinctiveness) and the long-time gap resulted in the recapture of only 17 animals, but indicate a residency in the archipelago of two decades. Fourteen animals were re-sighted between 2004 and 2009 in the same area of southwest Tenerife, of which two were also seen in north Tenerife (2012), two in La Gomera (2006) and five in Gran Canaria (in 1999). The remaining three pilot whales were re-sighted only in Gran Canaria in 1999.

For data from the current study, re-sighting intervals (Figure 2.17) ranged from one day to 11.26 years (median = 1.55 year; SE= 0.07): 37.7% of the individuals were recaptured within one year (between two and 14 times), 25.3% in the following year, and 7.3% during a longer time span (four animals seen in ten years, and five in 11 years between two and seven times). Animal “Gma98” was seen 27 times in the islands between 1999 and 2010 (Table 2.9).

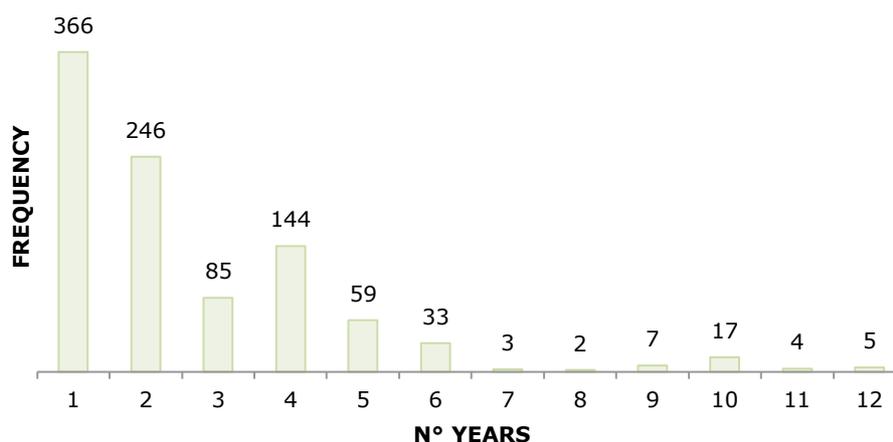


Figure 2.17: Frequency of the number of years between the first and last recapture of individual short-finned pilot whales in the different islands of the archipelago between 1999 and 2012.

Table 2.9: Short-finned pilot whales with a time span of 10 and 11 years between the first and last recapture, within Canary Archipelago: Tenerife (TenS =south-west and TenN =north east areas), Gran Canaria (GC), La Gomera (LG), and Lanzarote-Fuerteventura (LZ_FV) (1999 and 2012). Indicative age and sex class are also detailed (A= adult; Indet= indeterminates; F= female; M= male).

Gma	AGE SEX	99	00	04	05	06	07	08		09	10		11	
		GC	GC	LG	LG	LG	TenS	TenN	TenS	TenS	GC	LG	LZ_FV	
1445	A	1		1						2			2	
1463	A	1								2			3	
511	A/F		1		1	2	1						1	
98	A/F	2			2		10	1	18	7	2			
781	Indet		1				2						4	
790	A/M		2		2	2	1						4	
1702	A		1											2
1837	Indet		1											2

The number of individuals captured in each island and recaptured in different areas is presented in Table 2.10. The within-area rate of re-sightings of adults and indeterminates photographically identified in each island (measured by the match index, Table 2.11) varied, with the highest re-sighting rates in the two sub-areas off southwest Tenerife and La Gomera. Whales identified off Lanzarote and Fuerteventura had low re-sighting rates, with 640 animals seen only once, 34 individuals seen twice, and only two animals also recaptured in Gran Canaria (interchange value of 0.014).

Among the total identified animals during the study period, 237 were detected in more than one island (218 adults and indeterminates), of which 29 (27 adults and indeterminates) were identified in three islands (Tenerife, La Gomera and Gran Canaria). Only two animals were recaptured between the western islands and the rest of the archipelago (Gran Canaria), eleven years apart. Some animals (23) were documented as moving back and forth between Tenerife and La Gomera, with six animals showing such movements up to four times. Two pilot whales moved twice between Tenerife and Gran Canaria, and five moved twice between La Gomera and Gran Canaria. Most of the recaptures of the animals moving between Tenerife and La Gomera (96%) and between Tenerife and Gran Canaria (60%) occurred during the warmer months of the year.

Table 2.10: Number of well-marked short-finned pilot whales of all ages identified in each area and recaptured within the Canary Archipelago (moving individuals): Tenerife South and Tenerife North, Gran Canaria, La Gomera, and La, and Lanzarote-Fuerteventura (1999 and 2012). The number of individuals recaptured at least twice in each island is highlighted in grey.

ISLAND	Gma IDENTIFIED	MOVING Gma	TENERIFE SOUTH	TENERIFE NORTH	GRAN CANARIA	LA GOMERA	LANZAROTE-FUERTEVENTURA
TENERIFE SOUTH	741	169	410	34	35	117	0
TENERIFE NORTH	50	34		3	1	1	0
GRAN CANARIA	190	39			18	16	2
LA GOMERA	271	121				98	0
LANZAROTE-FUERTEVENTURA	282	2					30

Return rates (re-sightings within the same area) were calculated for Tenerife and La Gomera, but it was not possible to calculate them for all the islands and for every year because of the non-homogeneity of the effort conducted across the different islands during the study period.

The same whales were seen in multiple islands both in the same year and in different years. Interchange among islands was most common between Tenerife and La Gomera, both for the same year and among years: match indices of 0.80 and 1.09 for the years 2005 and 2008, and 0.751 between 2004 and 2010. The mean match index for pilot whales in Tenerife and La Gomera in different years (1.53 and 0.95, respectively) was higher than the index calculated by comparing the two areas in the same years (0.632). Nevertheless, the differences were small and values were of the same order of magnitude. Therefore, even though pilot whales were more likely to remain in the same area or move and return to the same area, important interchange movements were

present between Tenerife and La Gomera. The interchange rates within the rest of the archipelago in different years were relatively low, ranging between 0.323 for the central islands and 0.041 for the eastern islands (Table 2.11).

Table 2.11: Match indices of short-finned pilot whales for different combination of islands and years: return and interchange rates.

MATCH INDEX			
RETURN RATE:			
TENERIFE south		LA GOMERA	
2005-2007	1.587	2004-2005	1.536
2007-2008	1.376	2005-2006	1.018
2008-2009	1.615	2006-2008	0.818
		2008-2010	0.423
INTERCHANGE RATE:			
LA GOMERA-TENERIFE SOUTH (different islands in same year)			
2005	0.802		
2008	1.095		
INTERCHANGE RATE:			
LA GOMERA-TENERIFE SOUTH-GRAN CANARIA (different islands and years)			
2004-2010	0.751	LA GOMERA-TENERIFE	
1999-2010	0.323	TENERIFE-GRAN CANARIA	
1999-2010	0.368	LA GOMERA-GRAN CANARIA	
1999-2012	0.041	LANZAROTE_FUERTEVENTURA-GRAN CANARIA	

The average Euclidean distance between consecutive sightings of photo-identified pilot whales was 7.97 km (SE=0.24), ranging varying between 0.11 km and 168.7 km. Even though 84% of the distances were less than 10 km (Figure 2.18), extensive movements of between 100 and 170km were also detected, even if in only a small percentage of cases (1%, n=38). Time intervals between consecutive sightings were quite variable, from one day to 2,930 days (mean=70.6 days, SE=3.7). The mean interval between consecutive sightings of the same individual was similar between winter (96.2, SE=8.50) and spring (168.2, SE=17.8), and between summer (50.0, SE=4.53) and autumn (32.4, SE=2.93), but statistically different between winter-spring and summer-autumn (Kruskal-Wallis rank test: H=342,171, df=3, p<0.001). Moreover, distances were found to be significantly greater in spring compared to the other seasons (Kruskal-Wallis rank test: H=66,371, df=3, p<0.001).

Wide-scale movements were investigated as a function of different sexes: no significant differences were found in the distribution of distances travelled by males and females (Mann-Whitney, $U=537,187$, $p=0.725$).

Three indeterminate short-finned pilot whales, photo-identified in the days following the same sightings (where only nine adults and indeterminates were observed) travelled from southwestern Tenerife to southwestern La Gomera in a maximum of 26:46 hours, across 51.1 km, at an average minimum speed of 1.9 km/h.

Eleven pilot whales, in a group of mixed age class with at least five calves, were photo-identified together in Tenerife over a period of 27:57 hours, travelling along the southwestern coast heading north at an average speed of 0.9 km/h.

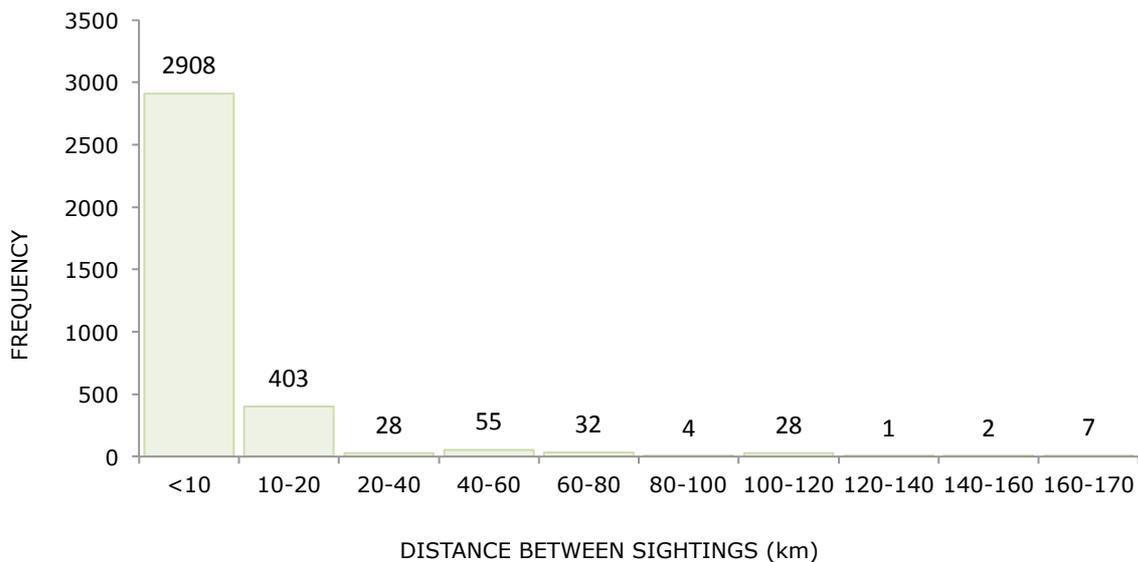


Figure 2.18: Frequency distribution of Euclidean distance (km) between consecutive sightings of short-finned pilot whales in the Canary Islands.

SITE FIDELITY

Of the 3,275 pilot whales identified, 1,241 were used for residency pattern analysis, excluding images of poor and fair quality, indistinctive and slightly distinctive fins, neonates, calves and juveniles (Table 2.12, Figure 2.20). Following the criteria established, in the Canary Archipelago 780 (63%) were classified as “transients”, 156 (13%) as “occasional visitors”, while 255 whales (21%) were considered “residents”, and 50 (4%) “core residents”. Of the latter, 35 were seen between eight and 28 times only in

Tenerife, one in both Tenerife and Gran Canaria, 12 in both Tenerife and La Gomera, and two in all three islands. Lanzarote and Fuerteventura had only "transients" and ten pilot whales recaptured between two and three times in different years in the area ("occasionals"). The "resident" and "core resident" pilot whales in La Gomera (n= 102) and Gran Canaria (n= 35) were all, except for three animals, also seen in Tenerife, a reflection of the high number of recaptures among these three islands.

Table 2.12: Number of animals in different residency categories ("core resident", "resident", "occasional", and "transient") of short-finned pilot whales in the Canary Islands.

ISLAND	CORE RESIDENT	RESIDENT	OCCASIONAL	TRANSIENT	TOT IND
CANARY ARCHIPELAGO	50	255	156	780	1,241
TENERIFE	50	246	128	287	711
LA GOMERA	14	88	56	100	258
LANZAROTE FUERTEVENTURA	0	0	10	263	273
GRAN CANARIA	3	22	14	138	177

All residency categories were observed throughout the year, during all months. Except for the eastern islands of Lanzarote and Fuerteventura, where no "resident individuals" were identified (only a few animals were recaptured up to two times, and only two pilot whales were previously seen in Gran Canaria), "core resident" and "resident" frequencies were, as expected, quite constant over time, while "transient" frequencies were double during warmer months than in the rest of the year. Groups with a mixed composition of residency patterns were also encountered mostly (75%) during summer and autumn.

Group sizes formed only by "core residents" and "residents" were significantly smaller (mean=16, SD=10) than group sizes of mixed residency pattern sightings (mean=23, SD=17; U=17469.5, p=0.01). In contrast, no differences were found between "core residents"-"residents and occasionals"-"transients", and between those and "mixed" groups (U=9031.5, p=0.38,; U=1852, p=0.13).

To better identify residency patterns related to a specific island, residency rates were also calculated using the filtered datasets for Tenerife and La Gomera. For Tenerife, the data collected between 2007 and 2009, when most of the effort was made and most of the recaptures were recorded, included a total of 134 island-related "core residents", 125 "residents", 59 "occasionals", and 453 "transients", with a mean monthly sighting rate of

0.138 (SE=0.005). No “core residents” were found to be exclusively linked to the island of La Gomera, but 37 “residents” and 46 “occasionals” were identified based on the monthly and seasonal rates applied to identify pilot whales between 2004 and 2010 in the island.

“Core residents” were found to cover greater distances between consecutive sightings than “resident” pilot whales, while no significant differences were recorded for the other residency categories (Kruskal-Wallis rank test: $H=1370,627$, $df=3$, $p=0.006$).

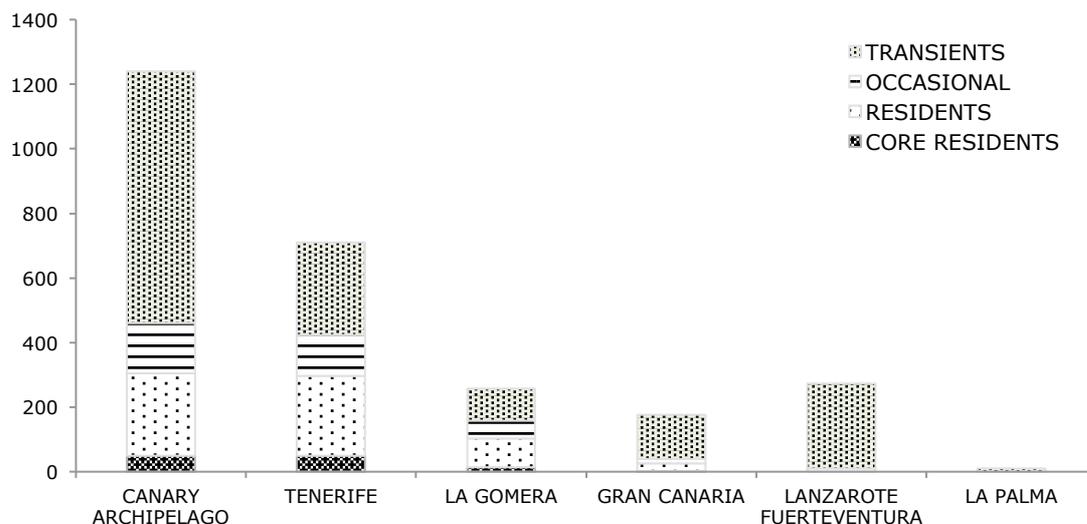


Figure 2.19: Residency categories (“transient”, “occasional”, “resident”, and “core resident”) of well-marked, adult and indeterminate short-finned pilot whales sighted in the different Canary Islands, between 1999 and 2012.

RANGING PATTERNS

Based on the asymptote of the area observation curve, a minimum number of 10 sightings was determined to be an adequate sample size to estimate the size of an individual’s range, leading to a total of 193 animals being selected for this analysis. The small recapture sample size did not allow temporal changes in range size and location to be examined, and some autocorrelation in the data may also have biased the results. The mean Schoener’s ratio (a measure of the degree of autocorrelation in the data for each animal) was 1.54 (SD=0.46) for the kernel data, which can be considered acceptable in accordance with Kenward (2001). For approximately 17% of the individuals used for this analysis, the values of Schoener’s ratio were above 2.0, indicating that data were independent. Some negative bias in range estimates (Swihart and Slade, 1997) was estimated for the rest of the animals, from moderate bias (negative bias of 5%) in 41% of the individuals, to high (negative bias higher than 5%) in 42% of the whales.

Mean MCP range size of the selected whales was 280.9 (SD=593.8) km², varying from 16.2 to 6,562.7 km². The kernel method gave a mean 95% UD area of 355.9 (SD=553.8) km², ranging from 46.1 to 3,673.8, and a 50% UD core area of 77.0 (SD=119.8) km² (Table 2.13, Annex 2: Table A2.2). Correlation between the two estimators was significant (Spearman's rank correlation, $r=0.897$, $p<0.001$, $n=193$). Significant differences (Wilcoxon matched pairs test, $Z=6.589$, $p<0.001$, $n=193$) were found between the estimates obtained by the MCP and 95% UD fixed kernel methods, with larger areas estimated by the latter. These results were not unexpected, because kernel methods tend to overestimate range sizes for small sample sizes (Seaman *et al.*, 1999; Seaman and Powell, 1996; Urian, 2002), whereas MCP significantly underestimates range size (Urian, 2002).

There were no significant differences in the ranges (Kernel 50% and 95% UD) between "core resident" or "resident" whales (Kruskal-Wallis: $H=1.597$, $df=2$, $p=0.450$; $H=3.023$, $df=2$, $p=0.221$, respectively) or when these categories were considered for males and females separately (Mann-Whitney: $U=1334$, $p=0.551$, $N=120$; $U=1.276$, $p=0.349$, $N=120$, respectively).

Table 2.13: Range statistics of all 193 animals, "core-residents" and "residents", females and males: mean, standard deviation, minimum and maximum value of the MCP and fixed Kernel (overall ranging at 95%UD and core area at 50%UD). Detailed results of each of the 193 short-finned pilot whales are presented in the Annex 2: Table A.2.2.

	RANGE	MEAN	SD	MIN	MAX
Total	MCP	280.94	593.76	16.20	6562.71
	Kernel 95% UD	355.90	553.80	46.13	3673.79
	Kernel 50% UD	76.95	119.75	6.77	790.87
	Schoener's ratio	1.53	0.46	0.45	2.65
Core Residents	MCP	201.23	280.57	16.20	977.40
	Kernel 95% UD	1.60	0.43	0.62	2.65
	Kernel 50% UD	331.69	508.76	46.13	3673.79
	Schoener's ratio	72.53	115.30	6.77	790.87
Residents	MCP	612.36	1298.20	16.20	6562.71
	Kernel 95% UD	1.38	0.49	0.45	2.65
	Kernel 50% UD	484.06	782.91	46.13	3673.79
	Schoener's ratio	102.49	159.78	6.77	790.87
Females	MCP	375.40	816.70	16.20	6562.71
	Kernel 95% UD	1.49	0.45	0.62	2.60
	Kernel 50% UD	425.59	649.56	46.13	3673.79
	Schoener's ratio	92.28	141.97	7.26	790.87
Males	MCP	122.90	189.52	22.80	836.69
	Kernel 95% UD	1.64	0.48	0.69	2.65
	Kernel 50% UD	158.70	113.81	58.25	651.08
	Schoener's ratio	35.81	36.22	7.24	198.57

Even though great variability was found in the estimated core areas (50% UD) among animals, as shown by the high standard deviation, 71% of all core areas overlapped in a limited area of 57.7 km² in southwest Tenerife and La Gomera. Overall ranging (95%UD) occupied an area of 417.9 km², encompassing the waters of Tenerife but also in some cases of La Gomera, Gran Canaria, or both. While most of the individual ranges were limited to southwest Tenerife, the kernel method produced multiple centres of activity especially for the 95% UD areas, including also the southwest areas of La Gomera (26 whales) and Gran Canaria (six whales), northeast Tenerife (13 whales), or even three different areas (Table 2.14, Figure 2.19).

The most frequently seen animals seemed to share their range with “transient” animals, which were seen not only when associated with residents in sightings but also when in isolated groups (Figure 2.21).

Table 2.14: Centres of activity for 95% and 50% UD ranges calculated for the 193 short-finned pilot whales by fixed kernel methods, across the different islands of the archipelago (TNs= Tenerife south, TNn=Tenerife north, LG= La Gomera, GC= Gran Canaria).

ISLANDS	50% UD	95% UD
LG	1	1
TNs	191	144
TNs-LG	1	26
TNs-GC	-	6
TNs -TNn	-	13
GC-TFs-LG	-	2
LG-TFs -TNn	-	1

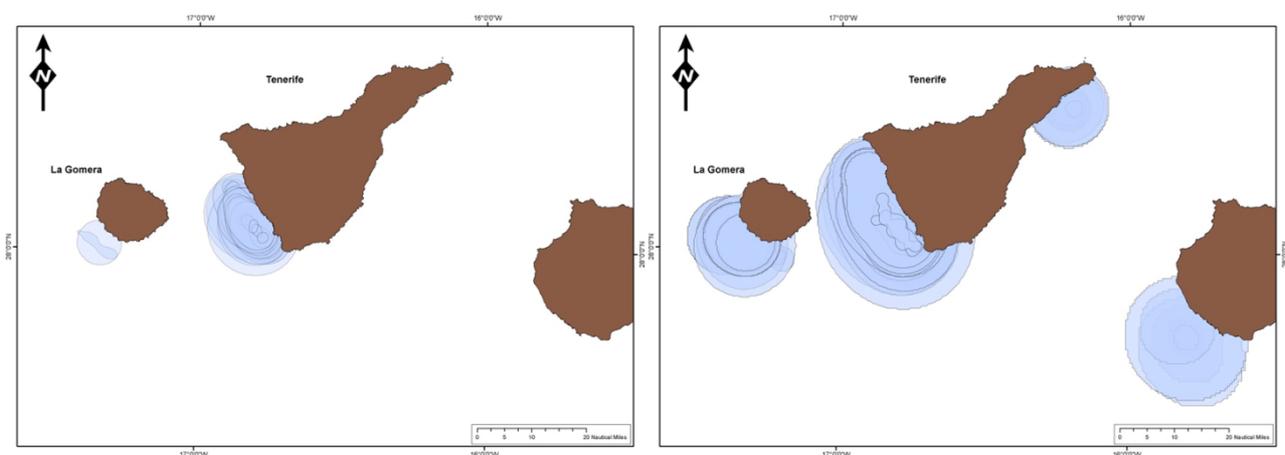


Figure 2.20a-b: Ranging patterns of the 193 well-marked, adult and indeterminate short-finned pilot whales sighted at least ten times in the different Canary Islands, between 1999 and 2012, estimated by fixed kernel a) at 95% UD and b) at 50% UD.

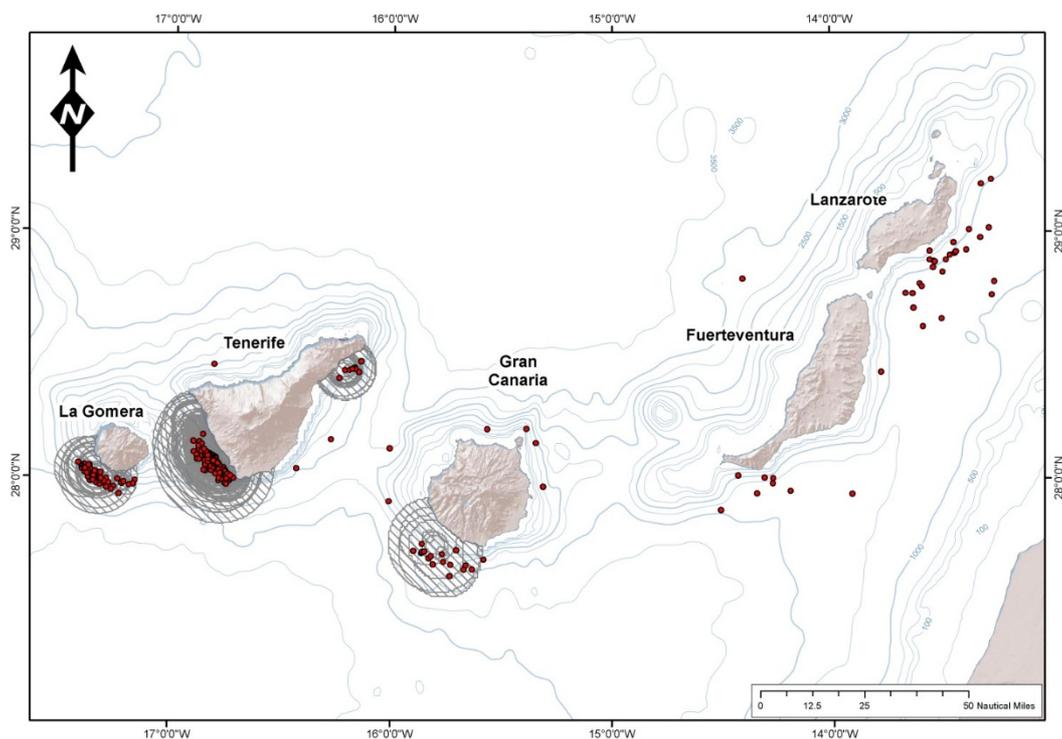


Figure 2.21: Ranging patterns of the 193 well-marked, adult and indeterminate short-finned pilot whales sighted at least ten times in the different Canary Islands, between 1999 and 2012, estimated by fixed kernel at 50% UD. “Transient” animal sightings are shown in the map as red points.

2.4 DISCUSSION

The short-finned pilot whale in the Canary Islands was the most frequently observed species during the study period 1999-2012, but it was not homogeneously distributed in the archipelago, as shown by the high variation in encounter rates calculated for the islands that ranged from 0 to 3.62 individuals per nm in El Hierro and Tenerife, respectively. Seen year-round, with higher encounter rates recorded during the warmer months, pilot whales were largely concentrated within 8 km of the shore, at a mean water depth of 1,077.5m, (SE=16.91), in agreement with previous observations off the island of Tenerife (Heimlich-Boran, 1993; Montero and Martín, 1993; Carrillo and Martín, 2000). However, sightings at much greater depths (2000m) in offshore areas coinciding with inter-island channels were also recorded.

As previously described in Heimlich-Boran (1993) for the island of Tenerife, where individuals were distinguished as *residents* and *visitors*, different residency patterns were observed during the study period in the Canary Islands. “Core residents”, “residents”, “occasional” and “transient” individuals were identified based on their sighting history

frequencies. Long-term site fidelity to the archipelago detected in some short-finned pilot whales is supported by the presence off Tenerife of a rather extensive resident group of whales, with individuals repeatedly sighted over at least three years and up to eleven years. Recaptures up to nineteen years apart between the catalogue created by Heimlich-Boran (1993) and that created in this study further support this and the concept of residency can be extended from the single island of Tenerife to the rest of the archipelago through the long-term recaptures encompassing different islands. Re-sighting data suggest an apparently limited range of pilot whales seen more than ten times, with a core area of 81.6 km² mostly located in southwest Tenerife, which is only a small portion of the overall geographic range of the population in the Canary Islands.

The threshold of a minimum of ten sightings for each recaptured animal was considered to be an adequate sample size for home range estimation in the Canary Islands, based on the asymptote of the area-observation curve ensuring that each individual displayed a constant centre of activity throughout the study period (Gaustestad and Myrsterud, 1995). There is no consensus regarding the minimum number of observations to estimate home range size accurately, which depends on the biology of the animal being investigated, the duration of the study, the estimator chosen and the distribution of the data. Home range estimates with a minimum of 30 observations and preferably more than 50 are recommended (Seaman *et al*, 1999). One hundred and fifty sightings were used to obtain accurate estimates of bottlenose dolphin home ranges in Sarasota; similar results of MCP and kernel estimators were obtained using more than 100 sightings to estimate home ranges (Urian, 2002).

Due to the limited sample size for pilot whales in this study, temporal changes in home range size and location could not be investigated. Nevertheless, it is likely that some changes in ranging patterns might have occurred over the 12 years of the study period as a result, for example, of variation in prey distribution, resource competition within and between cetacean species, social factors and/or anthropogenic pressure.

While the overall range (95% UD) of all individuals occupied an area of approximately 418 km² that encompassed the waters of Tenerife, La Gomera, Gran Canaria, the core area (50% UD) of all these individuals was limited to a restricted area of 82 km² along southwest Tenerife and, for one animal, also a narrow area downwind of La Gomera. The core areas of all these animals were all located in the downwind coastal areas of the islands, coinciding with the calmest waters that are richest in nutrients, mostly with a depth range of 800-1,200m. The large amount of overlap of the individual ranges (82% of the total 95%UD area) and their core areas (71% of the total 50% UD area) left only

four and seven animals (at 95% UD and 50% UD, respectively) that did not share their entire range with other pilot whales; these animals had a slightly more northerly distribution along the southwest coast of Tenerife, and in one case included the island of La Gomera.

Range distribution and size for this species in the Canary Islands has not been studied extensively. Only descriptive results on this species space-use have been reported (Heimlich-Boran, 1993; Montero and Martín, 1993; Carrillo and Martín, 2000). A narrow area of 27 km² was identified as the area with the highest sighting frequency (Montero and Martín, 1993), while Carrillo and Tejedor (2003) identified areas of different pilot whale density levels in southwest Tenerife, with high density areas limited to 46.8 km², and medium density extended to 64.7 km². The large differences in range size between these studies and those (both overall and core range) found in the present study are mostly due to the different survey and analytical methods, the sample sizes, and the lack of comparability between surveys. Despite the fact that the range estimates in the Canary Islands encompass a much larger area than previously described, extending up to three different islands of the archipelago, it is unlikely that the whole area used by these individuals is included in these estimates. There is likely a negative bias as a result of the limited coverage of some areas, especially of the upwind waters.

Different levels of site fidelity notwithstanding, a large resident group of 305 short-finned pilot whales inhabits the Canary Islands, across Tenerife, La Gomera, and Gran Canaria. However, many movements of these “core resident” and “resident” animals were observed outside their estimated core ranges, with a lot of inter-island movements between Tenerife and La Gomera (117 recaptured animals) and, in some cases, also to Gran Canaria. Therefore, these resident whales exhibited considerable temporal and spatial fidelity, especially linked to Tenerife but also more widely across the archipelago.

Considerable variability in residency patterns has been described for the short-finned pilot whale populations in the Hawaii (Mahaffy, 2012) and Madeira (Alves *et al.*, 2013) archipelagos, where three site fidelity levels were described: animals found repeatedly that exhibited long-term fidelity to the main islands, whales that showed some degree of site fidelity by regularly visiting the islands, and transients/visitors recorded year-round (Mahaffy, 2012; Alves *et al.*, 2013).

Though the terms “core resident” and “resident” were used to refer to animals with a high degree of fidelity to the Canary Islands, where they spent the majority of their time, the continuous presence of these animals in the area was not implied. Based on the estimates obtained by the lagged identification rate, 254 (SE=10) animals (a number

similar to the 305 archipelago "core residents" and selected "residents" determined from their capture histories) were estimated to spend about 500 days in the study area and about 4,000 days outside the area. This suggests a high level of residency along with movements over large ranges not covered by the surveys, and/or some form of emigration with a return rate to the islands at intervals greater than the length of the study (as suggested by Heimlich-Boran, 1993).

The low recapture rate of pilot whales in Gran Canaria and in Lanzarote-Fuerteventura, and the almost complete absence (except for two individuals) of inter-island recaptures recorded between the eastern islands and the rest of the archipelago introduced the hypothesis to be further investigated of a different use of the islands by different sub-populations of pilot whales. A high percentage (62%) of whales was seen no more than twice and in only one season ("transients"). New individuals were recorded throughout the entire course of the study year-round, as shown by the continuously increasing discovery curve.

It is not known whether some individuals occurring in the study area are part of a population that use or move through it only at certain times. Animals sighted only once could be: transients passing through; have ranges that barely overlap the study area; be behaviourally less likely to be captured; have died, emigrated or simply have not been re-sighted during the study period in the area (Elwen, 2008). The high percentage of transients recorded might be a result of the large size of the study site (109,000 km² total area, Figure 2.2), that did not allow the whole area to be completely and homogeneously covered. Only 17% of the entire region was surveyed, with different levels of effort.

Most of the northern upwind areas of the islands were excluded, and most of the effort was instead concentrated in the coastal areas of the southern downwind waters of the islands. La Palma, where short-finned pilot whales were described as the third most frequent species (Pérez-Vallazza *et al.*, 2008), was almost unsurveyed during the present study. Therefore, insufficient photo-identification material was collected, and data coverage was unsatisfactory to ensure the detection of possible island-related whales or to identify possible re-captures between this island and the rest of the archipelago. In addition, in El Hierro, only 18 day-surveys were conducted during the study period, and no pilot whale sightings were recorded. Nevertheless, this species is known to visit these waters frequently, especially in the last few years (Aguilar de Soto, pers. comm.). Therefore, a large proportion of the archipelago remains uninvestigated and some areas have been surveyed only recently; this might have resulted in the failure to detect potential new preferred habitats or at least might have limited the ability to show

extensions to those that have been established.

Thus, individuals seen only a few times and labelled as transient might simply have a low level of residency linked to that specific island and, at the same time, be resident animals in other as of yet unsurveyed areas of the same island, or from different regions of the archipelago. Increasing the study area far beyond the range estimated for the identified resident groups might include previously uncaptured whales, possibly lower the number of whales classified as transients, and extend the resident distribution area that is, at the moment, mostly delimited to southwest Tenerife.

The 11 short-finned pilot whales recaptured between the archipelago of Madeira and the island of La Gomera (Servidio *et al.*, 2007) revealed the existence of movement between the two archipelagos and documented the presence in the Canary Islands of transient animals showing high mobility and, therefore, with a possibly wider range extending beyond the single archipelago. Nevertheless, additional collaborative studies including not only photographic material but also genetic samples are needed to investigate the nature of these movements further, identify the level of genetic differentiation between the Canary Islands and Madeira and test whether more than one population is present in these two archipelagos. In the event, the inclusion of areas like the neighbouring archipelagos of Azores, Madeira and Cape Verde, and the Moroccan coast might reveal further information about this species.

Even though southwest Tenerife represents the area of greatest usage for all the most frequently seen pilot whales in the Canary Islands, the resident pilot whales were often observed (32% of the sightings) interacting with occasional and transient individuals, sharing extensive areas of their home ranges, in accordance with results found in Hawaii (Mahaffy, 2012) and Madeira (Alves *et al.*, 2013). Although it is impossible to determine if breeding actually takes place during these encounters, resident pilot whales do not seem to constitute a closed and isolated unit. Rather, it seems more likely that whales from different group residency patterns are not isolated and that there is genetic interchange preventing genetic divergence of geographic-based communities.

Seasonal fluctuation of group size has been described for both short- and long-finned pilot whales, all coinciding with the occurrence of larger groups during a specific season of the year (Felleman *et al.*, 199; Cañadas and Sagarminaga, 2000; de Stephanis *et al.*, 2008b). In Madeira, larger groups were recorded between May and October (Alves *et al.*, 2013), similar to previous studies on short-finned pilot whales in southwest Tenerife (Heimlich-Boran 1993, Carrillo *et al.*, 2010), where larger groups were found during the summer months. In the Canary Islands, during the present study, temporal analysis of

group size confirmed these findings, with larger groups found during summer and autumn.

This difference in group size has been proposed to be related to breeding behaviour, with sub-groups regrouping to mate (de Stephanis *et al.*, 2008b). Similarly, in Madeira, the observation of larger groups coincided with the warmer months, when more visitors and mixed groups were observed in this archipelago (Alves *et al.*, 2013), making it possible for whales of different residency patterns to breed.

In long-finned pilot whales, mating occurs primarily in May-June in the North Atlantic (Desportes *et al.*, 1993). More generally, breeding apparently occurs at any time of the year but with peaks in summer in both hemispheres (Jefferson *et al.*, 1993). In short-finned pilot whales, instead, calving peaks vary in different populations of the Northern Hemisphere, (Jefferson, *et al.*, 1993). Carrillo *et al.* (2010) defined Tenerife as an important calving ground for the short-finned pilot whale, based on the year-round presence of neonates in the area, with a higher frequency between June and October. The seasons when larger group sizes were detected correspond to mating seasons observed in Tenerife by Heimlich-Boran (1993). During this study in the Canary Islands, larger groups mostly occurred when there was a higher presence of neonates in the groups (83%), a higher proportion of “transients” and when there were mixed groups based on sex and residency composition. Therefore, in accordance with the gestation period estimated for this species lasting 14.9 months (Kasuya and Marsh, 1984a), breeding might occur mostly during warmer months when a high proportion of transient and occasional whales enter the archipelago and mix with the resident population, forming larger groups of adults of both sexes.

Nevertheless, only paternity tests would confirm whether the fathers all belong to the resident individuals identified in the Canary Islands or are unknown. The 345 biopsy samples collected during this study, 293 from known photo-identified animals, could help to characterise and distinguish resident from transient animals, including running paternity tests on tissues from groups where all members (calves included, using the scrubbing method) were sampled.

An alternative, but non-exclusive, hypothesis is that larger groups form for foraging. Pilot whales are considered to move following their prey, as recently proposed for long-finned pilot whales in the Strait of Gibraltar (de Stephanis *et al.*, 2008a), where changes in spatial distribution of pilot whales between seasons could be explained by a shift in foraging behaviour, and for short-finned pilot whales in Madeira (Alves *et al.*, 2013). Seasonal inshore and offshore movements of known short-finned pilot whale groups

were, for example, observed off Australia apparently in response to the abundance and spawning of prey (Bernard and Reilly 1999).

The great productivity of the waters around the Canary Islands, compared to oceanic waters, might be responsible for attracting several cetacean species that use the area as a foraging ground. Patchy resources are known to cause an increase in the overall ranging area as well as in the mostly used area. As resource availability decreases, the intensity of use throughout the area becomes even and therefore more patches are visited and more distance moved. In contrast, as resource availability increases, usage is increasingly concentrated in a relatively small region (Ford, 1983). Oceanic islands can be considered generators of biological patchiness (Barton *et al.*, 2000) that, along with the highly dynamic oceanic ecosystem in contrast to the more productive coastal and inshore areas, might justify between-island movements and the arrival of transient whales to the Canary Islands. Prey availability might force animals to explore larger areas and to travel further in search of adequate food patches, as has been increasingly observed in the peripheral islands, such as El Hierro (Aguilar de Soto, pers. comm.).

Therefore, it can be speculated that the archipelago represents an important feeding ground for the short-finned pilot whales that reach the archipelago from the neighbouring ocean regions. Nevertheless, more information on prey distribution and availability is needed before this hypothesis can be tested.

As previously mentioned, the extension of searching effort towards previously unsurveyed areas might lead to a better understanding of the ranging behaviour of this species. Comparative studies between the Canary Islands, Madeira and the Moroccan Atlantic would help detect any seasonality in movements within the areas. Moreover, different methodologies, such as satellite tracking and focal animal observation of the same individuals would allow more insights in this species' ranging patterns.

Some indications of directionality in movements were noticed within the archipelago, mainly towards the island of Tenerife where the highest interchange rate with all the other areas, both within and over years, was found. The transition probabilities for movements detected a higher likelihood of whale displacement from La Gomera towards Tenerife, suggesting that most of Tenerife's core residents tend to spend most of their time in the same limited area. It also suggests that only a small proportion extended their movements toward the neighbouring island of La Gomera, from where, instead, pilot whales had about half the probability to stay or return to Tenerife, as confirmed by recapture data with 23 whales that travelled between Tenerife and La Gomera from two to four times: two between Tenerife and Gran Canaria twice, and five between La

Gomera and Gran Canaria twice.

Data were, in any case, insufficient to test possible changes over years and across all areas because effort in time and space was non-homogeneous across the Canary Islands, without simultaneous surveys in the different areas. Such surveys are recommended to better understand the movement dynamic within the archipelago.

The average distance between consecutive sightings of individual whales was about 8 km (SE=0.22), and most of the documented movements (84%) were less than 10 km. Nevertheless, whales also travelled long distances between the islands: some animals were observed to move 169 km between Gran Canaria and La Gomera (3 years apart), and 97 km between Gran Canaria and Tenerife (8 years apart). Daily movement patterns of resident animals were documented between La Gomera and Tenerife (three indeterminate whales moving at an average speed of at least 1.9 km/h). While "core resident" and "resident" animals had restricted movements (mostly island-related to Tenerife), the distances were not significantly different from what was found for "occasional" individuals.

In promiscuous mating systems, males are expected to range more widely than females in search of receptive mates (MacDonald, 1983; Wells *et al.*, 1987; Wauters and Dhondt, 1992; Owen *et al.*, 2002), which may lead to an appearance of different ranging strategies, unless males and females are differentiated (Elwen, 2008). However, these considerations must be applied to this study with caution because sex differentiation was based only on qualitative assessment and not supported by genetic studies. Both sexes showed similar ranging and core area sizes; there was no evidence that sex influenced movement patterns or home range size of pilot whales in the Canary Islands. Long distance movements were not restricted to a single sex and, in most cases, mixed groups travelled the greatest distances between the islands, including groups with calves.

Nevertheless, the degree of movement detected might be biased by the lower effort in some islands, with some probable underestimation. Because not all the individuals exhibited the same degree of mobility, these longer trips may also reflect some social differentiation that only further studies based on genetic analysis might reveal.

In any case, long distance movements for this species are not unexpected, considering the fact that short-finned pilot whales are capable of wide-ranging movement. Animals have been tagged off southwest Tenerife (Aguilar de Soto *et al.*, 2008; Jensen *et al.* 2011) but with a focus on diving and acoustic behaviour, not on horizontal ranging. Aguilar de Soto *et al.*, (2008) measured vertical swim speeds during deep dives of up to 9m per second. However, whether or not these highly energetic swim speeds can be

extrapolated to horizontal and long-range movements is questionable (Scheer, 2012). Sakai *et al* (2011) analysed swim speed and acceleration of tagged short-finned pilot whales off Hawai'i. During horizontal and shallow ranging with intermediate surfacing bouts (which might rather be the swimming style during long-range travelling) the whales swam at speeds ranging from 0.1 to 2.5 metres per second. At such speeds, and assuming that the whales do not rest, they would travel a maximum distance of approximately 9km per hour. Again, these swim speeds might be inaccurate for the calculation of long-range movements (e.g. measured whales might be observed during phases of recovery after deep dives) because the authors measured time windows with relatively short durations. Andrews *et al.*, (2011) tagged eight short-finned pilot whales off Hawai'i with tag attachments lasting five to 47 days. The authors demonstrated movements for a single whale surrounding the whole island (the Hawaiian archipelago has a perimeter of approximately 350 miles) over less than 40 days. Furthermore, rehabilitated long-finned pilot whales were shown to travel hundreds of kilometres after release over 61-94.5 day tracks (Nawojchik *et al* 2003; Mate *et al* 2005). The 11 short-finned pilot whales recaptured between Madeira and La Gomera covered around 320 km of oceanic waters in a maximum of 20 days (Servidio *et al.*, 2007).

Therefore, short-finned pilot whales were shown to swim at high speeds and have the potential for long-distance movements, supporting evidence that transient short-finned pilot whales come from outside the Canary Islands.

2.5 CONCLUSION

A first overview of short-finned pilot whale in Canary Islands was generated in this thirteen-years (1999-2012) longitudinal study, encompassing information on its distribution and frequency, generalities on group dynamics, estimation of recapture rates, movements, and ranging behaviour of the recaptured animals among the islands. The detection of important areas for this species and the understanding of its spatio-temporal movement dynamic among the islands provide a wide range of significant information, useful for a better comprehension of its status in the archipelago, and for the development of conservation strategies.

The short-finned pilot whale is a regularly present species in Canary Islands, documented throughout the year even if with different temporal and spatial distributions along the coasts of the archipelago. The different residency patterns indicate the simultaneous presence of transient animals that may simply be crossing the archipelago and a more

stable population closely linked to the islands, mainly to Tenerife and La Gomera. The southwestern waters of these islands, identified as important areas where most of the resident individuals range and develop their different vital activities (e.g. feeding and calving), also represent areas of conservation interest, as a consequence of possible habitat degradation due to the increasing anthropogenic impact. Therefore, monitoring this species on a long-term basis to allow the detection of possible changes in its dynamics is of vital importance.

The wide range of individual mobility among the main islands that might extend to neighbouring waters beyond the Canary Islands archipelago, suggests the possibility of different use of the area and the presence, to be further investigated, of multiple sub-populations between whales of markedly different resident patterns. Nevertheless, only genetic studies will be able to verify the nature of any differentiation among the populations of the Canary Islands, as well as genetic variation among individuals with different residency patterns.

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CHAPTER 3

**LONG-TERM SOCIAL STRUCTURE, COMPOSITION AND
STABILITY OF SHORT-FINNED PILOT WHALES IN THE
CANARY ISLANDS**

3.1 INTRODUCTION

Social structure (or social organization) normally refers to the sum of the social behaviour of an individual or to the relationship patterns between individuals (Gosling and Petrie, 1981; Hinde, 1976; Whitehead and Dufault, 1999; Kappeler and van Schaik, 2002) across all relevant spatio-temporal scales. Following the framework proposed by Hinde (1976), the study of the social structure of a population is based on identifying individual animals and recoding their day-to-day interactions, through the analytical challenge of obtaining measures of nature, quality, and patterning of the relationships among its members (e.g. Hinde, 1976; Symington, 1990; Connor *et al.*, 1992; Whitehead, 1997, 1999, 2008b; Baird and Whitehead, 2000; Wronski and Apio, 2006). When interactions cannot be directly observed to infer relationships, studies on association patterns between individuals may also allow inference about the social organisation of the target animal populations (Whitehead, 1995), and provide an important opportunity to investigate the relationships between social structure and environmental factors (Baird and Whitehead, 2000). Therefore, links between individual behaviour and population biology (Sutherland, 1996) should be investigated considering local interactions among individuals and their environment at both group-level and population-level scales (de Stephanis, 2007).

Non-randomness in social interaction patterns (i.e. individuals have a greater affinity to interact with some than with others) and individual variation in social contact patterns (i.e. some individuals have many while others have few contacts; Krause and Ruxton, 2002) has important consequences for population level processes. Who interacts with whom and the local and global population social structures have implications for central issues in ecology and evolution (Krause and Ruxton, 2002; Croft *et al.*, 2008). It can shape the way disease and parasites are spread within and among populations (Newman, 2002b; Corner *et al.*, 2003; Altizer *et al.*, 2003; Cross *et al.*, 2004; Keeling and Eames, 2005, Guimarães *et al.*, 2007; Böhm *et al.*, 2008; Godfrey *et al.*, 2009; Drewe, 2010), how they transmit information is transmitted in a population (e.g. Whiten 2000; Rendell and Whitehead 2001; Hoppitt *et al.*, 2010), and how behaviours are learned (Giraldeau *et al.* 1994; Krause *et al.*, 2007). It can also shape the way a population exploits its environment (Hoelzel, 1993; Baird and Dill, 1996; Connor *et al.*, 1998) and mould patterns of gene flow (Pusey and Wolf, 1996; Sugg *et al.*, 1996; Krutzen *et al.*, 2003), competition for resources (including mating opportunities), cooperative behaviour and reciprocity (Alexander, 1974; Whitehead, 1997). Therefore, social organization can influence the ecology, genetics and population biology of a species (Wilson *et al.*, 1975;

Whitehead, 2008b), and thus understanding its social organization may also lead to important implications for management and conservation.

Quantification of interaction require long-term observational data and the analysis of group size and composition through the identification of individual animals over extended periods of time using persistent natural or artificial markings (Lusseau *et al.*, 2006). Long-term observational studies allow unique insight into the social structure of groups and have proved important in evaluating conservation priorities (e.g. Vucetich *et al.*, 1997), for several large mammal populations (e.g. Packer *et al.*, 1990; Baird and Whitehead, 2000; Fernando and Lande, 2000; Durant *et al.*, 2004; Sinha *et al.*, 2005; Wittemyer *et al.*, 2005; Sundaresan *et al.*, 2007; Lusseau, *et al.*, 2006). Moreover, quantifying the social structure of a specific population and evaluating its social dynamics through a long term study provide the basis towards a better understanding of how extrinsic factors shape social patterns and the consequences of past and future changes in social dynamics. In addition, because changes in the stability of social units can often represent real-time responses to the effect of extrinsic factors, studying the social structure history of a population may provide a useful benchmark for monitoring its health and sustainability (Parsons *et al.*, 2009).

Time spent together has been largely used to delineate the relationship between pairs of individuals (dyads) by employing association indexes (Whitehead and Dufault 1999). Various studies have found that animals spending more time together than would be expected by chance tend to be socially associated (e.g. bottlenose dolphins: Connor *et al.*, 1999, 2001; chimpanzees: Mitani and Amstler, 2003; elephant: Wittemyer *et al.*, 2005), and therefore, measuring how much time individuals spend together appears to be a behaviourally meaningful way of quantifying their social association (Hinde 1976). For the majority of social species, group composition is dynamic and individuals are part of a network of individual associations that vary in strength, type and dynamics and can move between social groups leading to a highly interconnected social network.

The networks approach (Wilson, 1975) helps to define the architecture of networks of animal social relationships, and provides details for a better understanding of the implications of social structure for fitness at the individual and the population level: examples include the influence of individuals on a network (Darden *et al.* 2009; Jacoby *et al.* 2010), the role individuals play within the network (Lusseau and Newman, 2004; Lusseau, 2007), finding and choosing a sexual partner, developing and maintaining cooperative relationships (Croft *et al.* 2006, 2009), and engaging in foraging and anti-predator behaviour.

Marine mammals have evolved a variety of social systems. The social organisation and group stability of wild-ranging cetaceans have been studied intensively in several odontocete species, including sperm whale (e.g., Lettevall *et al.*, 2002; Whitehead, 2003), bottlenose dolphin (e.g., Wells, 1991; Connor *et al.*, 2001; Chilvers and Corkeron, 2002; Gero *et al.*, 2005), killer whale (e.g., Baird and Whitehead, 2000), and pilot whale (e.g. Heimlich-Boran, 1993; Ottensmeyer and Whitehead, 2003; Mahaffy, 2012).

Within stable social groups, a great variety of mutualisms can occur (Connor, 1995), based upon kin selection (Hamilton, 1964), reciprocity (Trivers, 1971), by-product mutualism or pseudo-reciprocity (Connor, 1986). Since most of these forms of mutualism require repeated interactions between a given pair of individuals, social structure studies should focus at the individual level in order to understand the selective mechanisms behind the formation and maintenance of stable groups. Different association patterns among individuals within a unit are expected to depend on which specific evolutionary mechanism is acting and on the nature of the benefits incurred by the individuals (Gero *et al.*, 2008).

Three types of preferred associations or avoidances might occur: (1) mutualistic, in which both parties show similar tendencies (e.g. in cooperative foraging, defence of calves); (2) unidirectional, in which only one party shows a preference or avoidance while the other shows indifference or the opposite tendency (i.e. certain animals show an attraction to a class of animals or to a given social role) or when an individual incurs by-product benefits when foraging; and (3) obligate, in which the association is necessary (dependent calf and its mother) (Gero *et al.*, 2008). These delineations may lead to different levels of group segregation, separated in communities or defined into social clusters within one community (Gero *et al.*, 2008).

Therefore, in any social structure study, the target population should be investigated to determine whether more than one community coexists, to identify the number and composition of social groupings in order to reveal individual association preferences, and to determine the social structure of the population (Whitehead, 1997).

Some species, like most of bottlenose dolphin communities, have been shown to exhibit a fusion-fission social structure where the associations among individuals show a defined pattern that can vary depending on the animal age and gender (Connor *et al.*, 2000; 2001). Other odontocete species form long-term associations within stable social groups. For example, social structure of the resident ecotype of the Pacific Northeast killer whale is composed of related matrilineal social units, with no dispersion from the original group except for reproduction purposes when they briefly join other groups (Bigg *et al.*, 1990;

Weilgart and Whitehead, 1990; Amos *et al.*, 1993b; Barrett-Lennard, 2000). A similar type of social structure has been proposed for other species, such as the two pilot whale species (Amos *et al.*, 1991b; 1991a; Amos *et al.*, 1993a; 1993b; Heimlich-Boran, 1993; Connor *et al.*, 1998; Fullard *et al.*, 2000; de Stephanis, 2007; Mahaffy, 2012).

In general, mammal species are characterised by a geographical or social dispersion of males, females or both (Greenwood, 1980). Generally, female distribution is mostly related to resources, while male distribution depends on female availability (Trivers, 1972; Bradbury and Vehrencamp, 1977; Wrangham, 1980; Clutton-Brock *et al.*, 1982; Connor *et al.*, 2000). In many polygenic mammals, males avoid endogamy by dispersing from their natal group in search of mating opportunities once they have reached maturity. On the other hand, females often remain in their natal groups and raise their offspring in association with their parental females (Greenwood, 1980; Pusey, 1980; Pusey and Packer, 1997).

The social structure of short-finned pilot whale has been described in Heimlich-Boran's (1993) study conducted over 22 months between 1991 and 1992 in southwestern Tenerife. The author identified a total number of 495 individuals, grouped in 46 different "pods" using a cluster distance coefficient to measure co-occurrence. The associations among pods were significantly greater from April to September than from October to March, which corresponds to the peak of births as well as conceptions. Pod structure was analysed for both age and sex composition: they were composed of an average of 2.5 (SD=0.2) males, 2.2 (SD=0.4) mothers, 4.7 (SD=0.5) unknown animals, and 3.0 (SD=0.5) immature. The pods with immature individuals (70%) were defined "reproductive", and were significantly larger than the remaining (30%) "non-reproductive". The association analysis for pod composition showed that pilot whales from different pods occasionally travelled together, and associations between age and sex classes showed significant differences depending on the pod membership of the individuals. Overall, associations involving adult males were stronger than associations involving mothers. Since the highest ranked associations within a pod were found to be among mothers, and with other pods between mothers and adult males, Heimlich-Boran (1993) proposed that male pilot whales are not the fathers of the calves present in their pods, suggesting that copulations might occur between members of different pods when they are joined in bigger groups, or when males leave momentarily their original pod.

Genetic studies on *G.melas* support this hypothesis, indicating that males do not breed within their own pods (Amos *et al.*, 1991b; 1991a). If mating occurred within the pod, associations would be expected to occur most often between the reproductive females

and adult males of the same pod. Moreover, if copulations do not take place between individuals of the same pod, but rather when pods meet, the strong cohesive nature of short-finned pilot whales would be based on non-reproductive benefits. Foraging and predator defence were suggested to be the main benefits of group living in this species (Heimlich-Boran, 1993).

Heimlich-Boran (1993) suggested that babysitting behaviour (while the mother dives, other individuals stay at the surface with the offspring) would also occur in short-finned pilot whales. This hypothesis has been supported by the study conducted on diving behaviour of *Globicephala macrorhynchus* off Tenerife, where individuals were instrumented with multisensor and acoustic recording Dtags, used to monitor the acoustic behaviour of individuals, as well as the sounds of nearby co-specifics (Aguilar de Soto, 2006): since deep diving leads to an important loss of energy, calves and juveniles might not be able to follow the adults, and therefore stay at the surface under the care of other females to facilitate reuniting after dives.

The social unity generated by a lack of dispersal from the natal group, as described for this species (Heimlich-Boran, 1993), might lead to a population that is especially vulnerable to both demographic and environmental stochasticity (Guimaraes *et al.*, 2007). Testing the existence of structured social bonds, and examining their temporal patterns within the short-finned pilot whale population in Canary Islands would provide key baseline data to evaluate socioecological interactions and to model the potential impact of future events.

Different aspects of the social and population structure of short-finned pilot whales in the Canary Islands were investigated in the present study using photographic identifications of individuals. The principal goal was to gain insight into their association patterns and long-term social system, assessing the extent to which associations among individuals are persistent with time, and determining the temporal and spatial structure of social interactions in this population.

Knowing if short-finned pilot whales in Canary Islands waters belong to a single large oceanic population and should therefore be considered a single conservation unit, or if they are separated into multiple populations could contribute greatly to the establishment of effective conservation measures, as part of a long-term management plan.

3.2 METHODOLOGY

In order to understand the selective mechanisms behind the creation and maintenance of stable group social structures, analysis must focus on the individual level (Gero *et al.*, 2008). A prerequisite for determining the social organization of a population is analysing individual association preferences by firstly documenting the occurrence, number and composition of social groupings (Whitehead, 1997).

The general procedure to convert long-term photographic identification databases into social structure models is to define and calculate association indices between all pairs of identified individuals that together form an association matrix (Cairns and Schwager, 1987; Ginsberg and Young, 1992). Association matrices are difficult to interpret directly, especially when derived for a large number of individuals. Their interpretation can be improved by using techniques such as cluster analyses or sociograms. Permutation tests can be used to test for preferred/avoided associations (Whitehead, 1999b).

These methodologies were applied to investigate social structure of the short-finned pilot whale population off the Canary Islands, following a parallel approach used for this species by Mahaffy (2012) in Hawaii and, when possible, the approach used by Heimlich-Boran (2003) in Tenerife, to allow for a direct comparison between studies.

3.2.1 STUDY AREA AND SAMPLING METHODS

For the detailed social structure study, only short-finned pilot whale data collected during the years in Tenerife (2007- 2009) and La Gomera (2004 - 2010) were used. The choice of only selecting animals seen off these two islands was to narrow the analysis to animals with high residency in the archipelago, and that probably belong to the same population as indicated by the high number of recaptures recorded between photo-identified individuals from these two locations, as shown in Chapter 2. By considering the temporal and spatial distribution of the effort and the similarity of methodological aspects (same vessel, researchers, and survey protocol) of the surveys conducted, a more detailed and reliable analysis was possible.

Additional analyses of long term bonds between individuals and of the broader social network structure of this population were conducted including observations from surveys in northeastern and southwestern Gran Canaria (since 2004), in southwestern Tenerife between 2004-2006, in northern Tenerife (2010-2012), and Lanzarote-Fuerteventura (2004-2012). Data from earlier studies in Tenerife were not included because of insufficient photographic coverage of individuals in each sighting.

For the specific purposes of this analysis, photo-identification sessions and sampling methods at sea followed a strict protocol of data collection (Chapter 2), including general sighting data collection, photographic sessions, continuous digital camera recording, gender determination, kinship analysis, relative cohesion/dispersion, and general behavioural states.

3.2.2 DATA SELECTION AND ORGANIZATION

SIGHTINGS

Only groups that were considered to have high photographic coverage were selected and used for analysis. In order to reduce the probability that an individual present during a sighting was not photographed, Ottensmeyer and Whitehead (2003) established a protocol assigning a coverage index based on the ratio between the number of pictures taken during a sighting and the group size. With the introduction of digital cameras, the images obtained during photo-identification sessions at sea have increased in number and quality. In this study, with the exception of one, all the groups sighted were characterized by a number of pictures much greater than twice the group size (corresponding to the higher and most representative coverage index in Ottensmeyer and Whitehead, 2003). A different method of selection was therefore necessary used.

Each sighting was evaluated at sea and marked as usable or not usable for social structure analysis. Sightings with animals in very dispersed groups, where differentiation from other possible groups was not possible with confidence and where it was also not possible to estimate group size reliably, were excluded from analysis. Cases where groups were lost (or research efforts were stopped due to external factors) before finishing the photographic session were also excluded. Moreover, after the photo-identification process, sightings in which the number of photo-identified individuals was fewer than 90% of the group size estimated by direct observations at sea, and sightings where the difference between photo-identified individuals and the number of animals counted at sea was greater than 20 individuals (excluding the possibility of two or more groups together) were also excluded. This resulted in 444 sightings included in the analysis and 164 rejected.

SAMPLING PERIOD

The sampling period for social structure studies must be chosen carefully. It must be long enough to include a period that allows interactions among individuals but at the same time not so long as to allow the majority of the study population to interact (Whitehead,

2008b). As in other studies that investigated association patterns in odontocete species, including short-finned pilot whales (Mahaffy, 2012), long-finned pilot whales (Ottensmeyer and Whitehead, 2003; de Stephanis *et al.*, 2008b), and killer whales (Ivkovich *et al.*, 2010), the sampling period was set at one day. This period was chosen to avoid replicate associations within the same day and to remove demographic effects occurring during the study period, such as birth, death, immigration, and emigration (Whitehead, 1999b). Therefore, to ensure independence of sampling and to minimize possible autocorrelation of sightings, re-sightings of identified individuals needed to be separated by at least one day to be included in the analysis, and only the first sighting of an individual animal was used if an individual whale was sighted more than once in a day (Bejder *et al.*, 1998; Chilvers and Corkeron, 2002). In cases where individuals were re-sighted twice or more in the same day, the corresponding sightings were included in the analysis only if there was at least a 50% difference in group composition of individuals, and if these sightings did not occur at the same time, or with some time overlapping (Elliser and Herzing, 2012).

3.2.3 PRELIMINARY ANALYSIS

The photo-identification analysis followed the general methodological protocol explained in Chapter 2. Only good quality images (quality rated as 3 and 4) of well-marked individuals (distinctiveness rated as 3 and 4) were used.

Important information for social structure analysis, such as recapture frequency, recapture distribution in the different distinctiveness categories, and potential changes in category due to mark addition were considered and presented in Chapter 3. Discovery curves of all individuals and only well-marked individuals were also calculated. In addition, in Chapter 3, residency patterns were also analysed, underlining different degrees of site fidelity in the islands (core residents, residents, visitors and transients) and further investigated through the lagged identification rate.

The association pattern analyses were conducted in MATLAB 7.0., using SOCPROG statistical modules developed by Hal Whitehead to analyse the social organisation of animal communities (Whitehead, 1999a, 2008b).

3.2.4 ANALYTICAL TREATMENT

In many studies, where quantification of direct social interaction is difficult, the presence of two individuals within the same social grouping is used as a measurable expression of social linkage (Sailer and Gaulin, 1984; Cairns and Schwager, 1987). Occurrence in the same group is considered a measure of association, as it is likely that most interactions

take place within groups (Bräger, 1999). The underlying assumptions are that physical co-occurrence signifies social affiliation, and the amount of time together correlates with the strength of the affiliation (Bejder *et al.*, 1998). Therefore, this study adopted the assumption that animals that were spatio-temporally clustered were interacting with one another, and considered to be associated with every other individual in that group ("gambit of the group" rule; Whitehead and Dufault, 1999). The use of the photo-identification technique implies that individuals were considered to be associated if they were photographed within the same group during a sighting.

GENERAL MEASURE OF ASSOCIATION

In order to calculate the strength of the behavioural relationship between the dyads (pairs of individuals) in the population, two indices of co-occurrence frequency are typically used: "simple ratio association index" (SRI) and "half weight association index" (HWI) (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Whitehead, 2008b). The value of these association indices ranges from 0, for animals that are never seen together, to 1, for animals that are always seen together.

The SRI assumes that all individuals during any sampling period are recognised and equally identifiable, and that the ratio is an unbiased estimate compared to the dyadic association (Ginsberg and Young, 1992; Whitehead, 2008b). In cetacean studies based on photo-identification, it is quite common for some individuals to be more likely to be identified and recorded separately than when together, or for some interactions not to be recorded or identified. The HWI better accounts for these biases, and therefore it is considered a more precise indicator of association, and is generally preferred (Ginsberg and Young, 1992; Whitehead, 2008b). To minimise bias (Cairns and Schwager, 1987) and to enhance comparability within studies (e.g. Wells *et al.*, 1987; Smolker *et al.*, 1992) the half-weight association index was therefore used in this analysis.

The dataset used in the calculation of association indices included photo quality 3 and 4 (good and very good), distinctiveness 3 and 4 (distinctive, and well distinctive fins), for adults and indeterminates encountered in the Canary Islands in sightings with good coverage. Moreover, only animals selected as "core residents" and "residents", following criteria explained and calculated in Chapter 3, were included. This truncation of the dataset restricted the analysis to animals known to be present over most of the study period in the area, removing individuals considered to be occasional and transient in Tenerife (Chapter 2).

SOCIAL DIFFERENTIATION AND PRECISION ANALYSIS

In order to determine the power and precision of how well matrices of association indices modelled social structure, a correlation coefficient (r) between the true associations indices (proportion of sampling period that a pair actually spent associating) and their estimated association indices were calculated and used. A correlation coefficient of $r = 0.8$ was considered sufficiently strong to be representative of the described social structure, while individual association values between 0.40–0.79 were categorised as moderate and somewhat representative, and values of 0.39 or less were considered low and not representative (Rogers *et al.*, 2004; Whitehead, 2008b). This information revealed how reliable the results were, and whether there were sufficient data for the results of the analysis to be representative of the true social structure of the population. Values of social differentiation between 0–0.3 would indicate a relative homogeneity of association indices, a value greater than 0.5 would reflect a differentiated society, while values above 2.0 would suggest a strong differentiated society (Whitehead, 2008a, b).

The HWI of association was implemented to estimate the correlation coefficient and social differentiation, and the likelihood method was used running 1,000 bootstrap replicates, with a resolution of integration equal to 0.001 (default in SOCPROG).

By making the assumption that the observations of associations are Poisson distributed and that effort is equally concentrated on all dyads, it is possible to predict the accuracy of social representations (Whitehead, 2008a).

The values obtained were then compared to Table 3.15 in Whitehead (2008b), where the quantity of data required for different levels of social differentiations are summarised, in order to estimate the number of observations per dyad needed to form a somewhat representative view (at $r=0.4$) and a highly representative view (at $r=0.8$) of social structure. Even though pilot whales are expected to violate the assumption that effort is equally concentrated on all dyads, this last equation may still provide a useful approximation of the amount of data required (Mahaffy, 2012).

PREFERRED COMPANIONSHIP

Permutation tests (Bejder *et al.*, 1998; Whitehead, 1999b) were used to test whether the observed association patterns were significantly different from what might be expected if associations were random, given a population size and residency patterns identical to the study population. Therefore, dyad occurrences were defined using the Manly and Bejder permutation technique (Manly, 1995; Bejder *et al.*, 1998), with modifications introduced

in Whitehead (1999a, 2008b) and Whitehead *et al.* (2005). A potentially observed standard deviation of the significantly higher pairwise association indices than those obtained from permuted datasets would be considered evidence that individuals avoided or preferred companions (Whitehead, 1999b).

To test the null hypothesis that there are no preferred or avoided companions, "permuting groups within samples" and "permuting associations within samples" methods were employed. Even though the latter has been indicated as the most useful method due to its fewer assumptions, and because it takes into account that not all the individuals are present in each sampling interval (due to birth, death, migration, *etc.*), it does not test for short-term companionships. Therefore, both methods were considered and applied in this study. Significantly high standard deviation (SD) and high coefficient of variation (CV) of the real association indices compared with the values obtained by the randomly permuted data indicate the presence of long-term preferred companions in the population. In contrast, short-term preferred associations are indicated by a significantly smaller CV (Whitehead *et al.*, 2005; Whitehead, 2008b). Moreover, a significantly smaller proportion of non-zero HWIs in the observed versus random data (Whitehead, 2008b) would indicate avoided companions.

All selected sightings with good coverage were included, and permutations using the simple ratio and half-weight association indices were generated for each test (Whitehead, 2009), starting from 1,000 permutations until the p values stabilised (Bejder *et al.*, 1998; Whitehead, 2008b) and with 1,000 flips per permutation.

After each permutation, the HWI for each pair was calculated, and the observed HWI was compared with expected values of the HWI. If >95% of observed HWI estimates were higher than the expected HWI, then it can be concluded that there are non-random associations.

Following Durrell *et al.* (2004) and Gero *et al.* (2005), preferred associations among dyads were detected by examining dyadic association indices in relation to the mean association index of the population. Strong dyadic association ("friends") was defined when greater than twice the mean index of all coefficients of association (individuals that are associated at least twice as much as the expected value of a dyad chosen randomly in the community; Whitehead, 2008a), weak dyadic association ("acquaintances") when less than this threshold, and, finally, avoidance association when less than half of the mean (Durrell *et al.*, 2004; Gero *et al.*, 2005; Whitehead, 2008a).

COMMUNITY STRUCTURE

Three analysis levels were conducted to examine potential differences in association patterns and to detect possible trends in community structure of short-finned pilot whales in the Canary Islands: 1) association level; 2) networking, and 3) temporal stability of associations.

1) ASSOCIATION LEVEL: SOCIAL NETWORK ANALYSIS

Social network analysis visually inspects and mathematically evaluates long-standing conceptual frameworks of social organisation and structure (e.g. Wilson *et al.*, 1975; Hinde, 1976), and provides a single conceptual framework within which it is possible to study the social organisation of animals at all levels (individual, dyad, group, population) and for all types of interaction (aggressive, cooperative, sexual, etc.) (Krause *et al.*, 2009).

Social networks create clusters using a divisive method: starting from one large cluster, the population is divided into smaller clusters until the desired stopping point (e.g. maximum modularity) is reached. A good cluster division provides many edges within clusters and few between (Newman and Girvan, 2004). The eigenvector method was used to maximize modularity (modularity-G and modularity-P) in weighted networks following Newman (2006a).

Different measures were estimated for the overall network as well as for each whale in the network: "degree" (number of direct ties an animal has), "strength" (sum of association indices of any individuals with all others, as a measure of individual's gregariousness; (Barthelemy *et al.*, 2005); "eigenvector centrality" (a measure of how well an individual is associated to other individuals but also how well its close associates are themselves associated; Newman, 2004; Whitehead, 2009); "reach" (a measure of how well an individual is indirectly connected to others in the population), "cluster coefficient" (the degree to which an individual's immediate neighbours are connected, describing how densely or sparsely the network is clustered around the focal individual, as a measure of individual sociality), and "affinity" (weighted average strength of individuals' associates, that determines whether individuals strongly connect to individuals which also have strong connections; Barthelemy *et al.*, 2005).

The population of well-marked adult and indeterminate pilot whales recorded in the Canary Islands in good coverage sightings was first considered to give a general overview of the network distribution, especially looking for associations between "transient", "occasional", "resident", and "core resident" individuals. For a more detailed

examination of social structure, and to find a balance between too few individuals that may give a truncated picture of the network, and too many animals that may result in an unwieldy or highly fragmented network, a second network was built using only the most frequently sighted animals from La Gomera and Tenerife. Special attention was given to the role of potential inter-connecting individuals between the different networks, trying to understand the possible reasons that could have made them different from others in the network (Lusseau and Newman, 2004). Moreover, experimental tests were conducted by removing these key individuals to investigate better the effect on the social system that the network analysis would predict.

The significance of the groups identified by the clusters and, therefore, whether associations of all possible dyads within clusters were significantly different than associations among clusters, was evaluated by performing Mantel test with 1,000 permutations (Manly, 1995; Bejder *et al.*, 1998; Whitehead, 1999b). Large p-value, positive t-value, and positive matrix correlation indicate higher association within clusters than among them.

Network analysis was run in SOCPROG 2.3 (Whitehead, 2008a) and NetDraw 2.123.

2) ASSOCIATION LEVEL: CLUSTER ANALYSIS

The possible existence of particular social groups within the short-finned pilot whale population and its long-term presence were tested via hierarchical agglomerative cluster analysis, using average-weight linkage with SOCPROG 2.4.

Association patterns among the most frequently sighted whales were also graphically represented. The result of this clustering was a tree-like hierarchy showing the clustering structure from all individuals as separate clusters to all individuals as members of one large cluster (Digby and Kempton, 1987).

Cluster analysis was created using "core resident" animals (Chapter 2) sighted in the Canary Islands, including only sightings with sufficient photographic coverage in order to have a general insight in the general social structure of this population. Only pilot whales identified in the southwest of Tenerife (2007-2009) and in La Gomera (2004-2010) were used for a finer analysis. For this, the selected pilot whales were only well-marked adult and indeterminate individuals from good coverage sightings, seen at least once a month for eight months, with a high monthly sighting rate (the individual seen in at least 30% of the months with research effort) combined with a high seasonal sighting rate (seen in

at least 60% of the seasons during all the seasons in which the study was conducted; Chapter 2).

Based on the definition of "group" used in the field (Chapter 2), each sighting defined in this study as usable for social structure analysis complied with strict spatial (associated animals within 1,000 m area) and temporal (membership composition stable during the duration of the sighting with no mixing with other group of animals in the area) boundaries and ensured a high photographic coverage of all the animals in that group. Therefore, the individuals identified in these sightings would form a social group close to a "pod" structure, a closely related matriline structure where the animals are typically seen together at least 50% of the time, and that are stable over many generations (Bigg *et al.*, 1990).

Associations were calculated using the average-linkage method, which works directly on similarity matrices and is favoured over other methods as it is less affected by sampling error and extreme values (Whitehead and Dufault, 1999). The average-linkage method averages all similarities between individuals and neighbouring clusters rather than relying solely on the most similar (single-linkage) or least similar (complete linkage) individual.

Despite being considered marginally useful when dealing with large, sparse populations (Whitehead, 2008b), cluster analysis can be a useful way to classify and visually display relationships between individuals using association indices. However, as pointed out by Whitehead (2008b), a dendrogram can also prove visually deceptive, suggesting complex social structures when none actually exist.

To indicate whether cluster analysis can be used to model social structure, the cophenetic correlation coefficient (CCC) was used to determine how well the dendrogram matches the association matrix, by measuring the correlation strength between the dyadic association values in the similarity matrix and their position within the dendrogram. A CCC of >0.80 indicates the dendrogram is a good match to the association matrix and well represents the population (Whitehead, 2008a). If separate units were detected, Mantel permutation tests (Schnell *et al.*, 1985) were performed to investigate correlations between two association matrices under the null hypothesis that associations/interaction rates between and within clusters were similar.

An empirical method proposed by Ottensmeyer and Whitehead (2003) examines the structure of the dendrogram r along the plot of cumulative bifurcations looking for sudden changes ("knots") that would define the population division.

The modularity coefficient Q was calculated with Newman's (2006a) eigenvector method to measure social differentiation and to detect meaningful clusters along the dendrogram, by distinguishing the more parsimonious clustering step as the one that provides the higher average association index within clusters, and at the same time the lower average association index between clusters (Lusseau, 2007; Whitehead, 2008a).

Values with a range from 0.0 (randomly formed clusters) to 1.0 (clusters with no shared associations and a highly compartmentalised population) were expected by implementing two modified versions in SOCPROG 2.4: termed Modularity-G, to investigate gregariousness by focusing on association preference, and termed Modularity-P, to examine gregariousness and data structure by focusing solely on preferred/avoided associates. A Q value of about 0.3 was indicated by Newman (2004) as the threshold to consider the cluster division acceptable. The potential presence of meaningful substructure within clusters was therefore explored for each cluster using community division, looking for clusters with Q value higher than 0.3.

The clusters obtained were further investigated by considering their spatial distribution in the area, looking for spatial overlapping or segregation. The size of each cluster range was calculated through the Minimum Convex Polygon (MCP) and Kernel methods (detailed methodology explained in Chapter 2).

3) TEMPORAL STABILITY OF ASSOCIATIONS

An important aspect of social structure is represented by the temporal patterning of relationships (in Hinde's conceptual framework, 1986), which gives insight into the longitudinal nature of these relationships. The "lagged association rate" (LAR), introduced by Whitehead (1995), allows for the tracing of changes in association between dyads along time lags after a sampling period where they were together, by estimating the probability still to be associated at a later given time (Whitehead, 2001).

Differently from the LAR, the Standardised Lagged Association Rate (SLAR) has been suggested in cases of uncertainty whether all true associates of an individual are accurately recorded within each sampling period (Whitehead, 1995). In photo-identification studies it is likely that all associations are not recorded, so lagged and null association rates were standardised (divided by the number of recorded associates, Whitehead, 1999a).

Lagged association rates are displayed graphically with time lag (τ) along the x-axis and are plotted using a moving average that can be adjusted by modifying the range of time over which $g(\tau)$ is calculated to exclude random noise and create a smoother graph.

Precision of estimated lagged association rates was estimated by jackknifing, by sequentially eliminating data from each date from the dataset (Sokal and Rohlf, 1995; Whitehead, 2009).

Lagged association rates were then compared to the null association rate (Whitehead, 1995) to determine whether preferred associations were present in the population. The null association rate, calculated by the LAR, indicates a non-preferred association among pairs of individuals (Whitehead, 2009): the probability that two individuals associate is independent from whether they have associated before. The standardized null association rate was simply calculated as the inverse of the number of individuals documented (i.e. population size) minus that individual.

Mathematical models proposed and used by Whitehead (1995) describing different rates of exponential decay, that is, models of temporal stability, were then fitted to the population temporal pattern of association, to assess the probability of two animals remaining associated after various time lags.

Two types of associates were taken into consideration by the four models available in SOCPROG 2.4.: "constant companions", permanent associations with stable companions that stay associated until death (possible indicator of closed non-interacting units) and "casual acquaintances", non-permanent relationships that decay over various time lags but may re-associate at a later time point. Each model possesses a combination of different associated levels. The models were fitted to the SLAR curve using maximum likelihood estimation (Whitehead, 1995, 1999a), and the model best describing the temporal dynamics of association patterns was indicated by the smallest value of the quasi-Akaike Information Criterion (QAIC; Whitehead, 2007). Jackknifing was used to calculate the SE for each model parameter, as a measure of estimate precision (Whitehead, 2007).

Because the lagged association rate is intended to describe the entire population, complete capture histories, independently from the sighting coverage, of all well-marked adults and indeterminates (with good and optimum quality photos) identified since 1999 in the Canary Islands were considered for this analysis, and not only the most frequently encountered, in order not to positively bias the estimated rates (Baird and Whitehead, 2000).

The analysis was conducted in SOCPROG 2.3 (Whitehead, 2008b), applying an appropriate moving average, setting a day as sample unit, with a sighting as grouping factor, and represented using a log x-axis.

DELINEATING STABLE GROUPS (UNITS)

The procedure described in Christal *et al.* (1998), Christal and Whitehead (2001), with modifications following Ottensmeyer and Whitehead (2003), and de Stephanis *et al.* (2008b), and Mahaffy (2012) was used to detect the presence of long-term social bonds between individuals, by exploring whether the identified structures are persistent in time or whether fluidity within these structures exists. Individuals sighted at least five times during at least four different years with each observation of the individual separated from the previous one by a gap of at least 180 days, were identified as "key individuals". The choice of this specific time span was made to ensure that calendar years did not artificially inflate sighting records and also to allow for comparison with other studies of the social structure of pilot whales (long-finned pilot whales in the Strait of Gibraltar by de Stephanis *et al.* (2008b), and short-finned pilot whales off Hawaii islands by Mahaffy (2012). Key individuals with overlapping sighting histories belonged to the same unit. In order to discard the possibility that allocation to the same unit would simply depend on the extensive sighting histories and not truly represent the longitudinal association preference, a minimum dyadic association index of 0.50 was required to place a key individual in the same unit. When this condition was not met, and the association index was below 0.50 for one or more dyads, a key individual was kept in the unit only if the majority (>50%) of dyadic associations were above the 0.50 criterion. Analogously, key individuals that did not meet the minimum criteria for inclusion in a given unit but that had multiple dyadic associations above 0.50 with other key individuals were also considered on an individual basis (Mahaffy, 2012).

Following a similar procedure, individuals sighted in the same group as the key individual for at least three years, at least four times, with each observation of the group separated from the preceding one by a gap of at least 180 days, were selected as constant companions of the key individual. As with key individuals, for both key individuals and other constant companions to be assigned to the same unit, the criterion that the majority (>50%) of dyadic associations were above the 0.50 criterion was applied. In cases where constant companions were assigned to more than one unit, association indices were examined to determine the most appropriate unit for allocation (Mahaffy, 2012).

Once units (a key individual and all of its constant companions) were defined, each of them was examined quantitatively and qualitatively to ensure unit membership was an accurate representation of the social structure, and to eventually detect the presence of further division in smaller units (line units, de Stephanis *et al.*, 2008b): dendrograms and SLAR were calculated for units with more than three individuals.

3.3 RESULTS

The analysis was conducted at two levels, using two different subsets of the data: overall analysis of association strength and temporal pattern for the entire Canary Islands population (1999-2012), and a finer analysis of social structure using only the most frequently seen whales off the islands of La Gomera and Tenerife (2004-2010).

3.3.1 SHORT-FINNED PILOT WHALE POPULATION IN CANARY ISLANDS

DYADIC ASSOCIATIONS

Both simple ratio and half-weight indices were calculated for "resident" and "core-resident" short-finned pilot whales identified in the Canary Islands between 1999 and 2012 (Chapter 2). Notwithstanding that the inferences drawn were very similar for the two association indices, in order to minimise biases and to allow comparability within studies, only the results using half-weight association index are presented here.

Using only good and very good quality pictures of well-marked adult and indeterminate animals that were identified only during good coverage sightings, 291 whales seen between June 1999 and March 2012 were selected and included in this analysis.

While the cumulative number of all photographically identified individuals in the Canary Islands (638 well-marked adult and indeterminate whales belonging to all residency classes) shows a continuous addition of new whales (**Figure 3.1a**), the discovery curve built for "core residents" and "residents" (**Figure 3.1b**) shows that the number of new individuals increased little after about 1000 total identifications.

The social differentiation of the study populations was estimated at $S=4.059$ ($SE=0.204$) indicating a strongly differentiated society. The correlation coefficient was estimated at $r=0.880$ ($SE=0.008$), with a mean association value per dyad (0.21), indicating a "somewhat representative" picture of the social system (0.03, threshold indicated by

Whitehead, 2008a), but with a value not very far from that indicated for "good" representation of social structure (0.28).

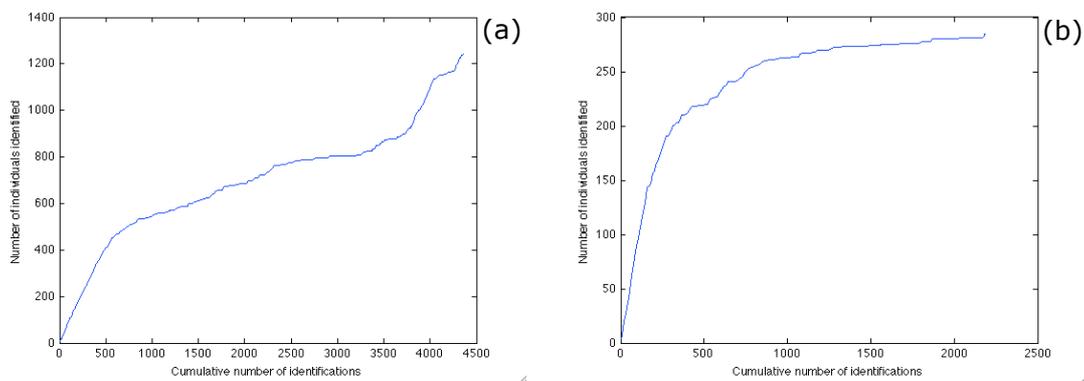


Figure 3.1: Discovery curve showing the cumulative number of short-finned pilot whale individuals identified versus the cumulative number of total identifications recorded (sampling unit set to one day) for well-marked adults and indeterminates. (a) complete dataset of individuals identified in the Canary Islands between 1999 and 2012; (b) only "core residents" and "residents" in good coverage sightings.

Overall association indices within the study population were low, with a mean association index of 0.02 (SD=0.01; range=0.00–0.05; Figure 3.2a). Nevertheless, an average maximum association index (Figure 3.2b) for each individual of 0.77 (SD=0.15; range=0.36–1.00) suggested that some whales formed strong dyadic bonds, in association with the same individuals at least 40% of the time (Figure 3.2b), and that they also differed in the number of individuals with whom they were associated (mean=8.00, SD=3.18) (Figure 3.2c). Membership ranged from 2 to 14.58, indicating differences in individual gregariousness (Figure 3.2c).

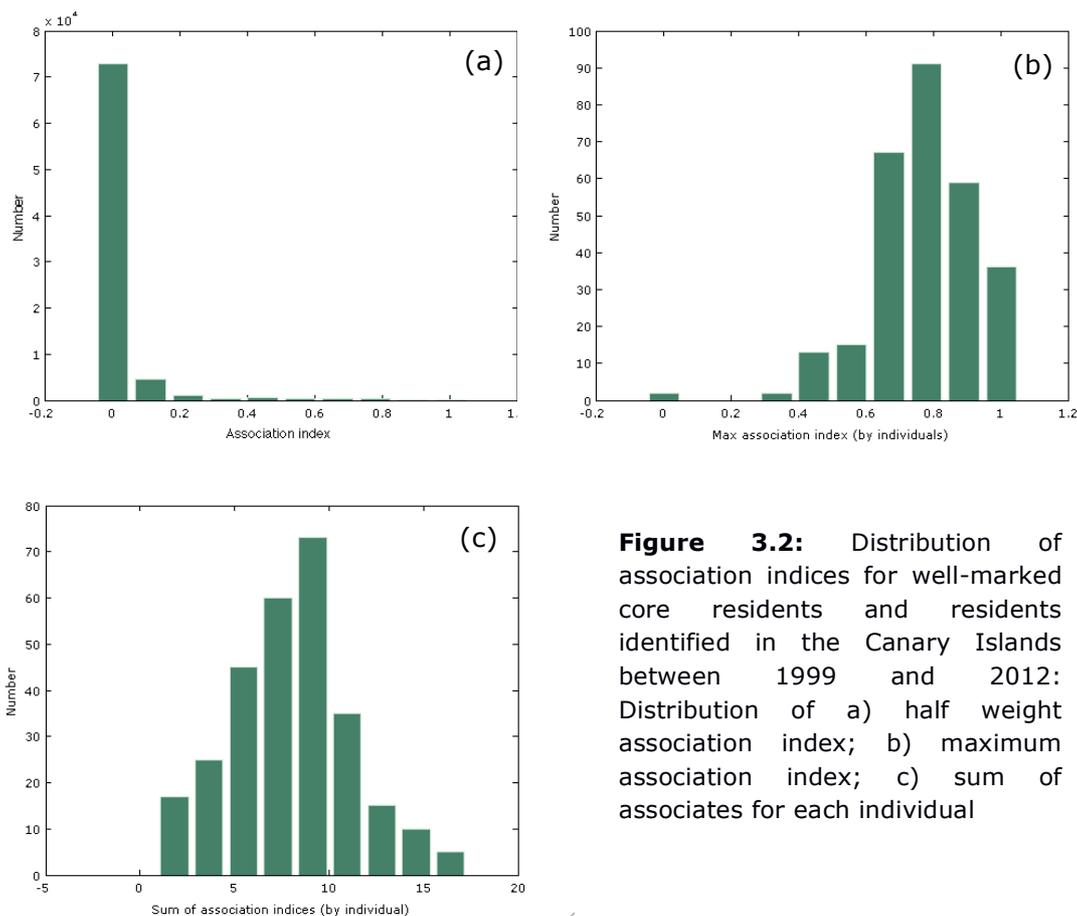


Figure 3.2: Distribution of association indices for well-marked core residents and residents identified in the Canary Islands between 1999 and 2012: Distribution of a) half weight association index; b) maximum association index; c) sum of associates for each individual

PREFERRED COMPANIONSHIP

For each test runs were repeated with 1,000 trials per permutation. Starting from 10,000 permutations, and progressively increasing the number, the p -values stabilised at 60,000 permutations for both association indices and groups. Once the p -value had stabilised, each test was then repeated three times.

The observed association pattern tested with permutations was found to be significantly different from what would be expected if they were randomly distributed, for both short-term and long-term companionship (Table 3.1).

Significantly higher SD and CV values of the observed association indices compared to those estimated for both permutation tests indicated a wider range of associations than expected if whales were associated at random and the preference of long-term preferred companions in the selected population. No short-term effects were noticed (real mean

higher than the estimate in "permute groups within samples" test). Moreover, the smaller proportion of non-zero association indices in the observed data versus the permuted ones for both tests indicated the presence of some long-term avoidance of the same individuals (Table 3.1).

Table 3.1: Test for preferred companionship among core resident and resident short-finned pilot whales in the Canary Islands (2004-2012, dataset filtered by good quality pictures, well-marked fins, and adults and indeterminate age classes). Permutations using SOCPROG 2.4. for associations within samples and groups within samples were tested for non-random short and long-term associations (preferred or avoided) and for gregariousness. Results for both tests are from 60,000 permutations using HWI. *P*-values greater than 0.95 are considered significant.

	PERMUTE GROUPS WITHIN SAMPLES		PERMUTE ASSOCIATIONS WITHIN SAMPLES	
	Observed	Permuted	Observed	Permuted
Mean association index HWI	0.025 p=1.000	0.024		
Standard deviation of HWI	0.101 p=1.000	0.074	0.102 p=1.000	0.079
Coefficient of variation of HWI	4.103 p=1.000	3.115	4.103 p=1.000	3.304
Proportion of non-zero of HWI	0.100 p=0.001	0.144	0.100 p=0.000	0.135
Standard deviation of typical group size	6.278 p=1.000	5.296		

A total of 40,470 possible dyadic associations were counted in the selected "resident" and "core resident" dataset: 90% of the dyads (36,429) were never recorded in association, while the remaining dyads did not show associations with values below 0.04 (threshold value for preferential associations: two times the mean association index). The absence of casual "acquaintance" as well as "avoided" associations (values below half of the mean), and the presence of 4,041 "preferred association" dyads (10%) with an association index equal to or greater than 0.04 indicated the presence of a selected proportion of individuals in dyadic association sharply separated from the remaining individuals (Figure 3.2a).

TEMPORAL ASPECTS OF SOCIAL STRUCTURE: LAGGED ASSOCIATION INDEX

Possible temporal patterns in social structure were investigated using the lagged association index on the complete dataset of the 638 short-finned pilot whales identified (all well-marked adults and indeterminates and all sightings irrespective of their coverage,) in the archipelago (1999-2012).

The Standardised Lagged Association Rate (SLAR) analysis (Figure 3.3) indicated that non-random associations persisted over the entire study among individuals, and that the observed curve stabilised at a level that was always higher than expected if pilot whales were associated at random (null association rate = 0.001). The model that best fitted the temporal distribution was "casual acquaintances" (Whitehead, 1995) (Figure 3.3; Table 3.2).

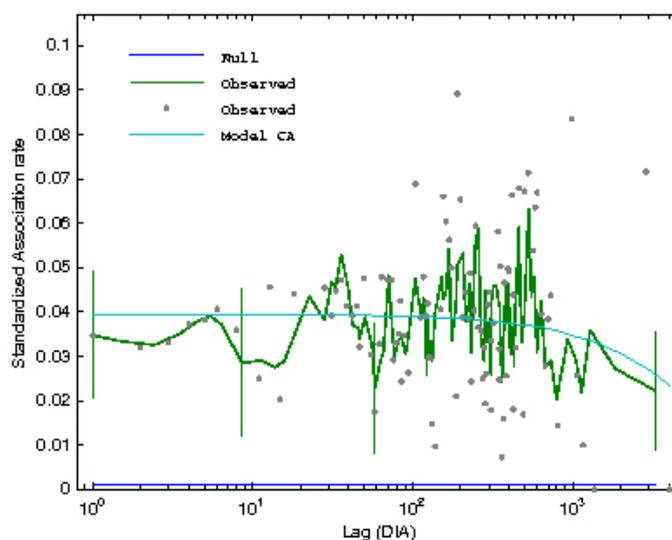


Figure 3.3: SLAR for short-finned pilot whales identified since 1999 in Canary Islands. The moving average curve of 10,000 associations (green line) and the curve with no moving average dots are shown in the graph together with approximate standard error bars (produced by jackknife on each sampling period). The best model curve (Model CA - "casual acquaintances" $g'=0.039431 \cdot \exp(-0.0001292 \cdot td)$) is shown, as well as the null association rate (Full).

By visual inspection of the curve, it can be seen that associations between pilot whales seem to remain constant for a long time, never reaching the null association rate, over a time scale ranging from one to approximately 3,430 days. There is a slight fall of the lagged association curve, indicative of some disassociation, starting after 620 days that might be due to the loss of resolution in the data collection after that time, and/or demographic events (Whitehead, 2008a). Based on the results of the Casual

Acquaintances model, the typical group size (gregariousness) of the population in the Canary Islands was estimated at 25 individuals ($1/a_2$, $a_2=0.039431$) with associations estimated to persist for 7,752 days (21.2 years; $1/a_1$, $a_1=0.000129$), which is beyond the scope of the study. This indicates that some individuals were not casual acquaintances but maintained strong dyadic association at least throughout the study period.

Table 3.2: Models of long term associations fitted to the complete dataset of well-marked adults and indeterminates in the Canary Islands. The standardised association rate is indicated by g' , the time lag is represented by "td" and the parameters of the models by "a1", "a2", "a3", and "a4".

MODEL	BEST FIT	PARAM	QAIC	ΔQAIC	MODEL SUPPORT
CASUAL ACQUAINTANCES	$g' = a_2 \cdot \exp(-a_1 \cdot td)$ $a_1 = 0.000129$ (s.e. $9.9489e-05$) $a_2 = 0.039431$ (s.e. 0.0049059)	2	39453.78	0	BEST 1
TWO LEVELS OF CASUAL ACQUAINTANCES	$g' = a_3 \cdot \exp(-a_1 \cdot td) + a_4 \cdot \exp(-a_2 \cdot td)$ $a_1 = 33.1833$ (s.e. 202.5039) $a_2 = 0.0001292$ (s.e. 0.0004444) $a_3 = 8.5974$ (s.e. 27.5389) $a_4 = 0.039431$ (s.e. 0.015912)	4	39457.78	4.00	SOME SUPPORT
CONSTANT COMPANIONS	$g' = a_1$ $a_1 = 0.037973$ (s.e. 0.0041756)	1	39463.57	9.79	NO SUPPORT
CONSTANT COMPANIONS AND CASUAL ACQUAINTANCES	$g' = a_2 + a_3 \cdot \exp(-a_1 \cdot td)$ $a_1 = 1.2819$ (s.e. 0.085822) $a_2 = 0.038056$ (s.e. 0.0040768) $a_3 = -0.017176$ (s.e. 0.038376)	3	39466.44	12.66	NO SUPPORT

ASSOCIATION LEVELS: SOCIAL NETWORK

Based on the different residency patterns shown using the criteria established for pilot whale populations in the Canary Islands (Chapter 2), and using only sightings with good coverage, 50 "core residents", 241 "residents", 136 "occasional", and 450 "transients" were identified. A social network diagram was built using a spring-embedding algorithm to depict closeness between the four different resident categories (Figure 3.4).

The association strengths calculated within clusters were significantly higher than those among clusters (Mantel permutation test with $p=1$; t-value=137.95; matrix

correlation=0.68). The mean, the maximum, and the sum of the association index values were higher for within clusters than for between clusters (means: 0.39, SD=0.17 vs. 0.01, SD=0.01; maximum: 0.89, SD=0.12 vs. 0.16, SD=0.10; sum: 7.65, SD=2.71 vs. 2.53, SD=1.72), supporting the division into 52 clusters based on the selected modularity ($Q=0.646$).

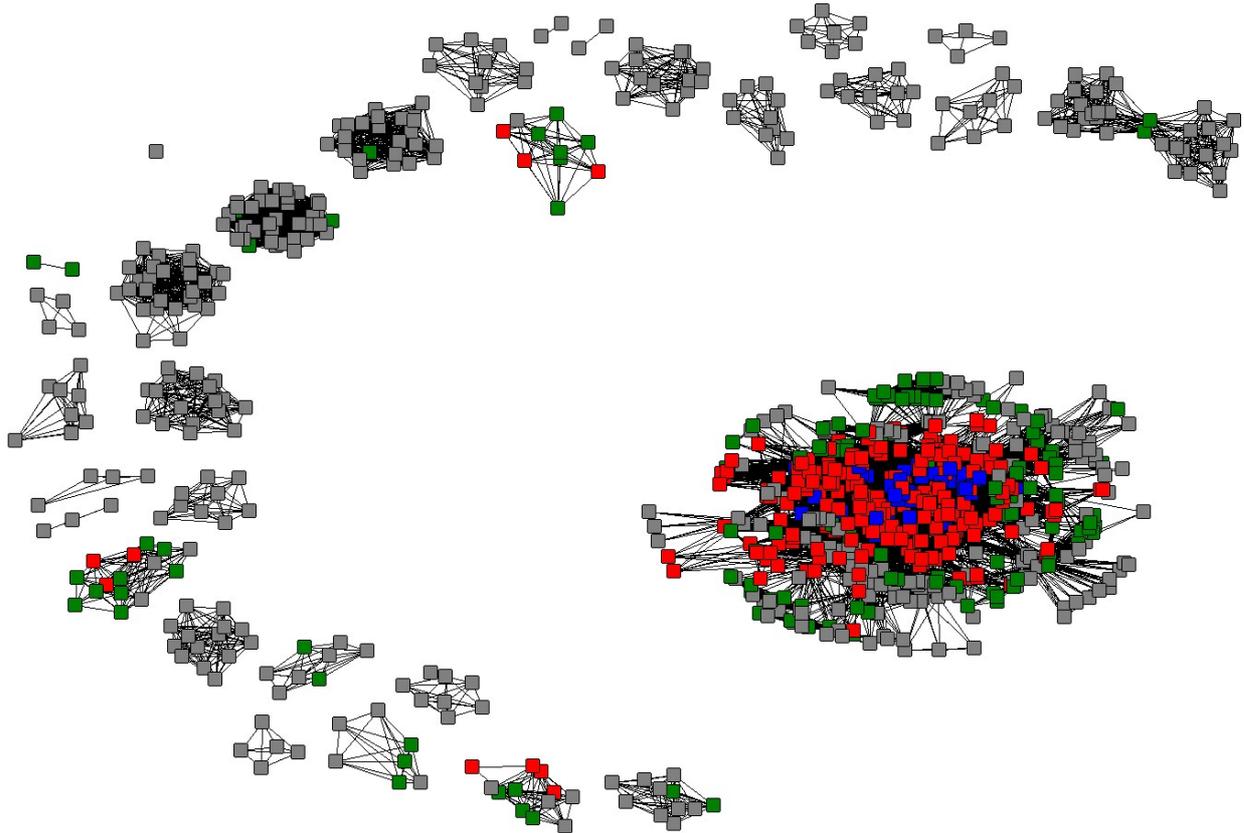


Figure 3.4: Social network diagram of all well-marked short-finned pilot whales documented off the Canary Islands, from 2004 through 2012. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Core residents are shown in blue, residents in red, visitors in green, and transients in grey (see Chapter 3 for definitions).

The network diagram showed a core social network of 549 animals (62.6% of the total population analysed), where all the core residents were concentrated, and 30 satellite clusters of 328 animals (membership range 1-39; mean=10.93, SE=9.12) not linked to the main component (Figure 3.4). Three satellite networks were composed of a mix of transient, occasional and resident whales seen in Tenerife and La Gomera. Six satellite

networks, three from Tenerife and three from Lanzarote-Fuerteventura, were composed of some occasionals mixed with transients, while all the remaining satellite networks contained only transient animals (from Tenerife or Lanzarote-Fuerteventura). One cluster was formed by a solitary node; a transient individual sighted in Tenerife in a group with five other animals was excluded from the analysis as it did not satisfy the distinctiveness requirements.

The core social network contained all four residency types, with 166 transients connected to individuals belonging to each of all the other categories, core residents included, and with animals seen in southern Tenerife, La Gomera and Gran Canaria. While transients were mainly confined to the satellite clusters (63%) and to the outer fringes of the main component along with the occasionals (75%), residents were clustered in the interior portions of the graph (96%), clustered together with the core residents (Figure 3.4). Removal of transients and occasionals showed that the principal component remained almost unchanged in its structure, with great interconnections and similarity (vertex similarity mean= 0.44, SE=0.11) among individuals, and either between or within the 19 different clusters detected (see detailed Mantel test results in the following paragraph Association levels: cluster analysis; Figure 3.5).

The overall eigenvector centrality mean was 0.3 (SE=0.01), ranging from 0 to 0.23, and the overall reach mean was 96.46 (SE=11.95). The strength found within-clusters was higher than that observed for between-clusters (within-cluster strength mean was 7.70 (SE=0.93) and ranged from 1.25 (SE=0.16) to 11.76 (SE=1.31); among-cluster strength was 0.13 (SE=0.08) and ranged from 0 to 1.7 (SE=0.72), indicating a highly assortative society. In this highly segmented society, the mean affinity values of the different clusters are very similar to their mean strength, and strong correlations are present over individuals between measures, suggesting that important individuals are preferentially linked with each other (Whitehead 2008a). In this selected population of short-finned pilot whales, while the correlation coefficient between strength and affinity was quite high at $r=0.86$, the correlation between strength and the clustering coefficient was unusually (Newman, 2003b) negative ($r=-0.389$).

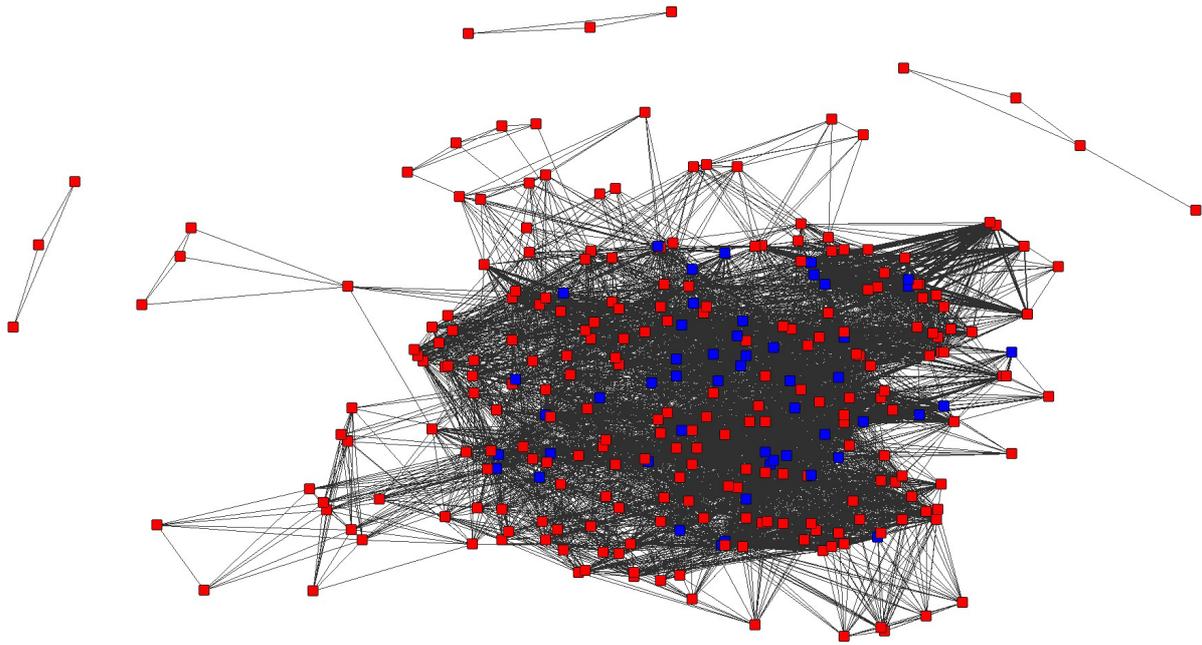


Figure 3.5: Enlargement of main social network cluster taken from Figure 3.14, showing only core residents (in blue) and residents (in red).

ASSOCIATION LEVELS: CLUSTER ANALYSIS

For an overall view of short-finned pilot whale social structure in Canary Islands, the hierarchical cluster analysis was performed using HWI on individual whales identified as "core residents" and "residents" in Canary Islands (dataset 1999-2012).

The knot-diagram did not allow a clear assessment of division into social entities, offering only a dubious and subjective interpretation of the knot distribution, apparently addressing a value of 0.596 (Figure 3.4). Maximum modularity-G suggested that the best division was at 0.658 of modularity, corresponding to the association index of 0.0342. In contrast, the Modularity-P gave a Q value lower than the 0.3 threshold to support the cluster analysis created; the Q value was 0.221 and corresponded to an association index 0.0951 (Figure 3.7). Therefore, only modularity-G was considered reliable as an appropriate cluster division and used for the analysis.

Newman's eigenvector method, combined with Modularity-G, gave a final modularity value of 0.643, and divided the Canary Islands population into 19 clusters of variable size and association strength (Figure 3.8). All the eigenvector values were different from 0,

excluding further uncertainty in the formation of this cluster. Given a CCC value of 0.95825, the dendrogram produced was highly representative of the study population association structure.

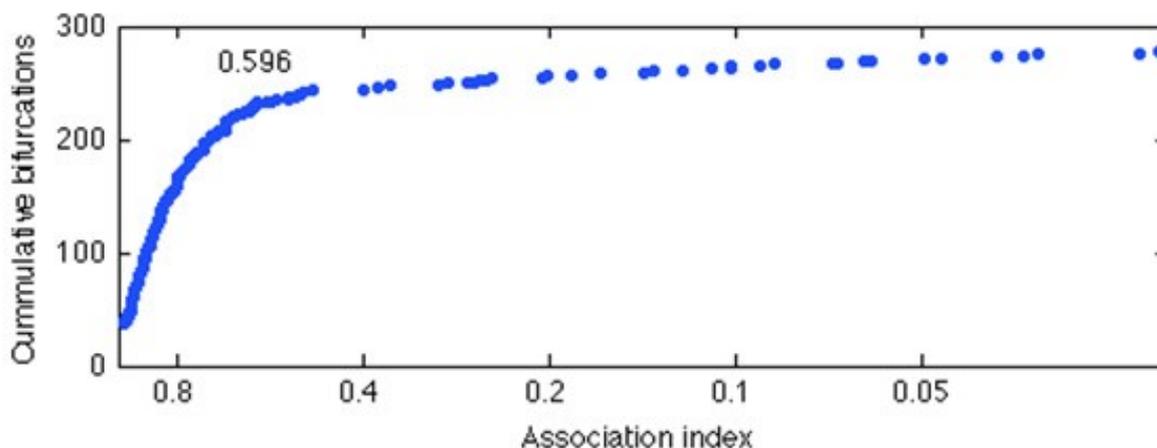


Figure 3.6: Knot-diagram for well-marked "core resident" and "resident" adult and indeterminate pilot whales identified in Canary Islands between 1999 and 2012.

The large positive matrix correlation coefficient of 0.633 supported the existence of significant differences in association strength within or between clusters (rejection of the null hypothesis). The association levels calculated for the pilot whales within clusters were significantly higher than those among clusters (Mantel permutation test with $p=1.00$). The mean association index within clusters was higher than between clusters (mean=0.79, SD=0.09 vs. mean=0.15, SD=0.09); the maximum association index values were also higher within clusters than between them (mean=0.82, SD=0.10 vs. mean=0.49, SD=0.25), further supporting the cluster division based on selected modularity. On the other hand, the sum of the associations showed within cluster values to be lower than between clusters (mean=2.65, SD=0.93 vs. mean=3.91, SD=2.21). This indicates that even though the divisions within the study population created by maximizing modularity were supported (high CCC value, and Mantel test results), there might also be strong dyad associations between individuals from different clusters.

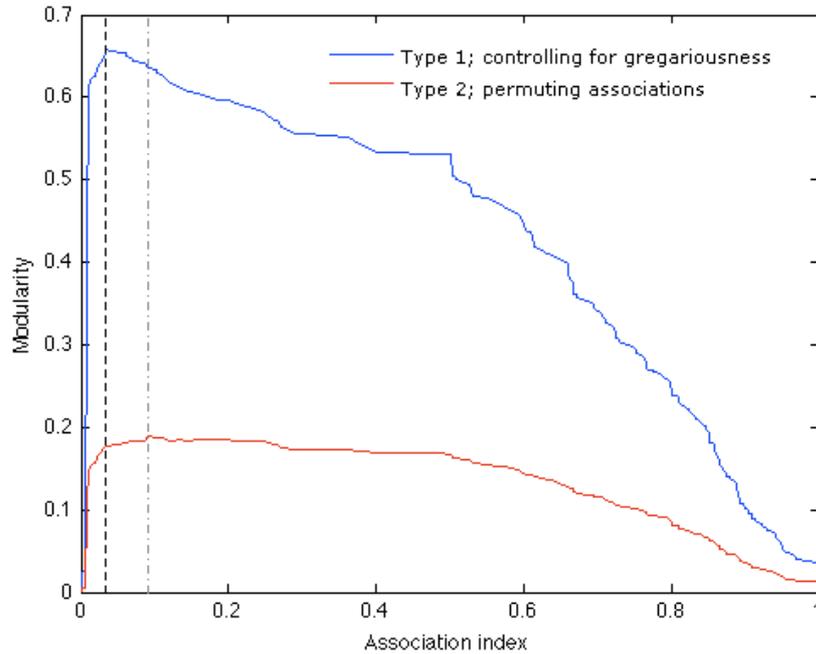


Figure 3.7: Modularity-G (Type 1 for gregariousness) and Modularity-P (Type 2 for permutations) for well-marked "core resident" and "resident" adult and indeterminate pilot whales identified in the Canary Islands between 1999 and 2012. Modularity-G suggests 0.658 as best community division value, with an association index of 0.0342. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations)

Further comparisons were conducted on the association index distribution pattern of individual clusters: eight of the nineteen clusters had quite a low overall mean association index, ranging between 0.24 to 0.36 (Clusters 5, 6, 8, 9, 10, 12, 15, and 16; Table 3.3) but with high maximum association index values between 0.80 and 0.87. Moreover, different levels of association were also evident, and some animals that were highly associated with an individual in their own cluster simultaneously had high index values with animals of other clusters, which might explain the result for the sum of association values within and between clusters.

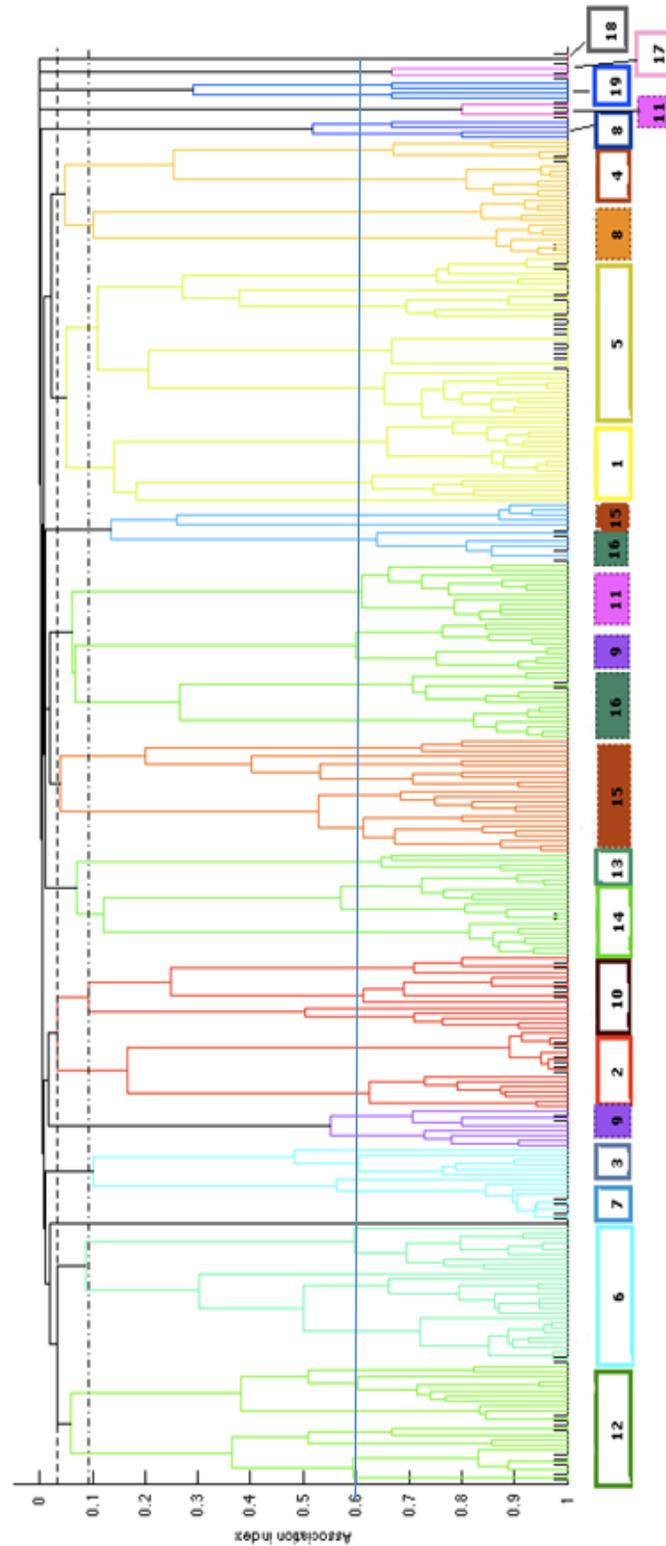


Figure 3.8: Average-linkage cluster dendrogram (based on half-weight association index) of well-marked "core resident" and "resident" adult and indeterminate pilot whales identified in the Canary Islands since 1999, in good coverage sightings. Cophenetic correlation coefficient=0.95. The 19 cluster numbers are indicated in the boxes. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations), while the blue line represents the cluster division based on knot.

In general, the larger clusters had also the lower mean association index, suggesting that these cluster division might partially be an artefact of size rather than only of social partitioning. Nevertheless, looking at the association index distribution in the three larger clusters, different patterns are apparent. Cluster 5 showed quite a separated division into three association groups, based on different levels of association index values: the overall association mean was 0.25 (never higher than 0.30 ± 0.03) but with a maximum association index of 0.89 ± 0.07 . Cluster 6 combines individuals with a high maximum association index value (0.87 ± 0.16), but with a mean always lower than 0.5, indicating the presence of three different trends of association. In Cluster 15, the 27 pilot whales showed a very low overall association index (0.23 ± 0.08) but again with a high maximum association index (0.84 ± 0.06) and differentiation into three different association patterns. Smaller more cohesive groupings for each of Clusters 8, 9, and 16 were also present, reflecting the differences in association index distribution.

Cluster membership varied in number and ranged from three to 33 individuals (mean 15, $SD=9$). Applying the averaged proportion of well-marked individuals in the population calculated for the Canary Islands (0.446, $CV=0.0191$), following the methodology explained in Chapter 4 for marked-individual in Tenerife, the total estimated group size is almost twice the group size measured in the field (33, $CV=0.59$ vs. 16, $CV=0.7$).

Considering the sex composition of each cluster through observation, males, females, and adults/indeterminates were recorded in 14 of the 19 clusters, with a greater proportion of females (38%) over males. Cluster 7 comprised seven individuals identified as males and one adult and indeterminate, seen between 16 and 25 times over a two year period (five times seen all together). Identified females were not present in Clusters 17 and 19, where only males and/or adults were found, while males were absent in Clusters 11 and 13. Eight clusters contained individuals seen in the islands of both Tenerife and La Gomera, and eight other clusters had individuals also seen in the island of Gran Canaria, three of them with whales recorded over a period of 11 and 12 years (Clusters 8-10-14 and 16 respectively). Only Cluster 4 contained whales sighted only in southwestern Tenerife. In Cluster 2, 12 of the 16 pilot whales were classified as "core residents".

Table 3.3: : Division into 19 individual clusters using community division. The original average-linkage cluster dendrogram was built using well-marked "core resident" and "resident" adult and indeterminate pilot whales (Gma) identified in the Canary Islands (1999-2012), in good coverage sightings. The cluster indices are listed for each cluster: mean, sum and maximum values of the association indexes (HWI).

CLUSTER	N° Gma Tot	Mean Assoc. HWI (sd)	Sum of Assocs (sd)	Max. Assoc (sd)
1	16	0.43 (0.13)	7.38 (1.93)	0.84 (0.20)
2	16	0.49 (0.08)	8.37 (1.19)	0.91 (0.07)
3	6	0.63 (0.08)	4.15 (0.42)	0.75 (0.10)
4	12	0.54 (0.08)	6.90 (0.85)	0.92 (0.07)
5	33	0.25 (0.03)	8.97 (1.07)	0.89 (0.07)
6	29	0.36 (0.11)	10.99 (3.04)	0.87 (0.16)
7	9	0.78 (0.11)	7.22 (0.87)	0.89 (0.13)
8	16	0.29 (0.10)	5.31 (1.44)	0.89 (0.07)
9	18	0.36 (0.05)	7.06 (0.89)	0.89 (0.07)
10	15	0.24 (0.03)	4.36 (0.47)	0.80 (0.09)
11	17	0.40 (0.15)	7.40 (2.48)	0.81 (0.11)
12	24	0.33 (0.06)	8.49 (1.32)	0.88 (0.09)
13	4	0.60 (0.05)	2.81 (0.15)	0.71 (0.11)
14	17	0.40 (0.03)	7.40 (0.53)	0.87 (0.05)
15	27	0.23 (0.08)	6.91 (2.16)	0.84 (0.06)
16	22	0.26 (0.07)	6.56 (1.41)	0.87 (0.16)
17	3	0.87 (0.03)	2.73 (0.06)	0.90 (0.01)
18	3	1.00 (0.00)	3.00 (0.00)	1.00 (0.00)
19	4	0.75 (0.07)	3.24 (0.22)	0.85 (0.08)

KEY UNITS AS STABLE SOCIAL GROUPS

Following the selected criteria, based on their longitudinally stable distribution, 13 social units were selected. One key individual was found with no constant companions (key-unit "G"). Only units with more than three individuals were analysed, resulting in ten key units.

Each unit was examined using pair-wise association indices (HWI); only a few dyadic associations had a value lower than 0.5, while all the rest were greater than this threshold (in some cases reaching values of 1). Constant companions with dyadic association values less than the 0.50 criterion (0.07-0.19) were removed from the units (one in Unit A, two in Unit C and one in Unit H). Two individuals could have initially been assigned to two different units, but different association index values allowed them to be allocated to a specific one. Final unit delineation is shown in Table 3.4: the ten units identified 67 animals, 14 key individuals, and 53 constant companions. Unit membership

ranged between three and 12 individuals and, with the exception of units A and B that were composed of three key individuals, the remaining units included only one key whale. The mean association index rate ranged from 0.64 to 0.83 (Table 3.4).

All short-finned pilot whales included in the key units were previously identified as "core resident" and "resident" animals. Unit D comprised all "core resident" individuals, except for one animal that was nevertheless seen 20 times between 2007 and 2008 in Tenerife (but six sightings were excluded from the analysis due to insufficient picture quality). Individuals with ID 98, 100 and 115 (Key unit A) persisted together in the islands of Tenerife, La Gomera and Gran Canaria between 1999 and 2012, when they were seen more than 20 times each and 15 times together. Pilot whales 111, 122, 126 and 634 (Key unit M), seen 31, 33, 24, and 25 times, respectively, were also documented together at least 19 times in the island of Tenerife and Gran Canaria over a period of 10 years since 1999, with association indices of 0.79-0.95. They were all included together in the dendrogram (Figure 3.8) in the same clusters.

More than half of the key individuals were females, only one was male, and the rest were adults and indeterminate individuals.

The network representation of the key units is shown in Annex 3: Figure A3.2 and A3.3.

Table 3.4: Key units selected are presented with their correspondent clusters division, and their composition: key and casual companions (CC), males (M), females (F), indeterminate (IND). The mean, standard deviation and range of the association index (HWI) for each unit are also reported.

UNIT	IND	KEY IND	CC	M	F	MEAN HWI	SD	RANGE	CLUSTER
A	7	3	4		6	0.81	0.02	0.71-0.89	14
B	8	3	5	1	5	0.64	0.03	0.50-0.92	-
C	7	1	6		2	0.81	0.02	0.64-0.96	16
D	7	1	6	1	4	0.71	0.03	0.54-0.94	2
E	5	1	4			0.83	0.04	0.78-1.00	5
F	3	1	2			0.67	0.12	0.56-0.80	13
H	12	1	11		6	0.66	0.04	0.45-0.94	11
M	10	1	9	1	7	0.66	0.04	0.46-0.95	14
N	4	1	3	1		0.80	0.09	0.67-0.91	17
O	4	1	3		1	0.73	0.07	0.67-0.83	8

A dendrogram was built using only key individuals and constant companions (Figure 3.9). The nine social units built with the longitudinal sighting histories were maintained and

exactly correspond to the cluster division applying the eigenvector-based method for community division, which also identified nine clusters.

The Mantel test revealed that individuals belonging to a specific unit had significantly higher association index levels than among units ($p=1$); the mean association index within units was 0.90 (SD=0.05, much higher than the mean between clusters (0.08, SD=0.03). Maximum association indices were still greater, even if only slightly, within units than among units (0.90, SD=0.05 vs. 0.82, SD=0.06) supporting the unit divisions and at the same time also indicating the presence of individuals highly associated with individuals of other units. On the other hand, the overall sum of the association index for within unit associations was much lower than between units (1.54, SD=0.04 vs. 5.01, SD=1.94) showing that the key units identified were not isolated, but instead formed by individuals that showed some associations outside their own cluster. The positive value of the matrix correlation (0.358) supported the rejection of the null hypothesis that no significant difference in association strength within or among clusters (units) existed.

Single dendrograms and their corresponding SLAR were plotted for each key unit and are shown in Annex 3: Figure A3.4. The dyadic association within clusters never fell below 0.5 and reached 1.0 as a maximum value. In eight clusters, the social system model that best fit the curve was the constant companion model. Only the cluster corresponding to unit M had casual acquaintances as the best fit model. The cluster analysis applied to each of the key units detected in the Canary Islands population, identified a further differentiation in the key units F, B, H and M (association index lower than 0.67, SD=0.12), even if only the first was supported by modularity, each in possible smaller units (line units), (Annex 3: Figure A3.4).

These results were compared to the membership profiles obtained from hierarchical clusters of selected populations of the Canary Islands in order to highlight the finer details of their social organization. Therefore, the original dendrogram was modified and the individuals not contained in the key units were greyed-out, while key individuals and their corresponding constant companions were kept in colour (Figure 3.9). Moreover, a new cluster was built using the restricted dataset which contained only those individuals that met the minimum criteria selected for key individuals/constant companions (Figure 3.10). Of the 19 clusters originally present in the dendrogram, 11 disappeared completely and six partially. The remaining two persisted completely intact: Cluster 17 coincided exactly with key unit N, while Cluster 14 was formed by the two key units A, E and M combined. Key units D, O, H, and C matched with part of Cluster 2, 5, 8, 11, and 16. The members of key unit B were not included in the clustering analysis because their sightings did not have sufficient photographic coverage.

The community division supported the division of these pilot whales in the same division obtained by their longitudinal sighting. Association within clusters (and therefore within units) was significantly higher than between ($p=1$; $r=0.35766$; 0.90 , $SD=0.05$ vs. 0.09 , $SD=0.03$).

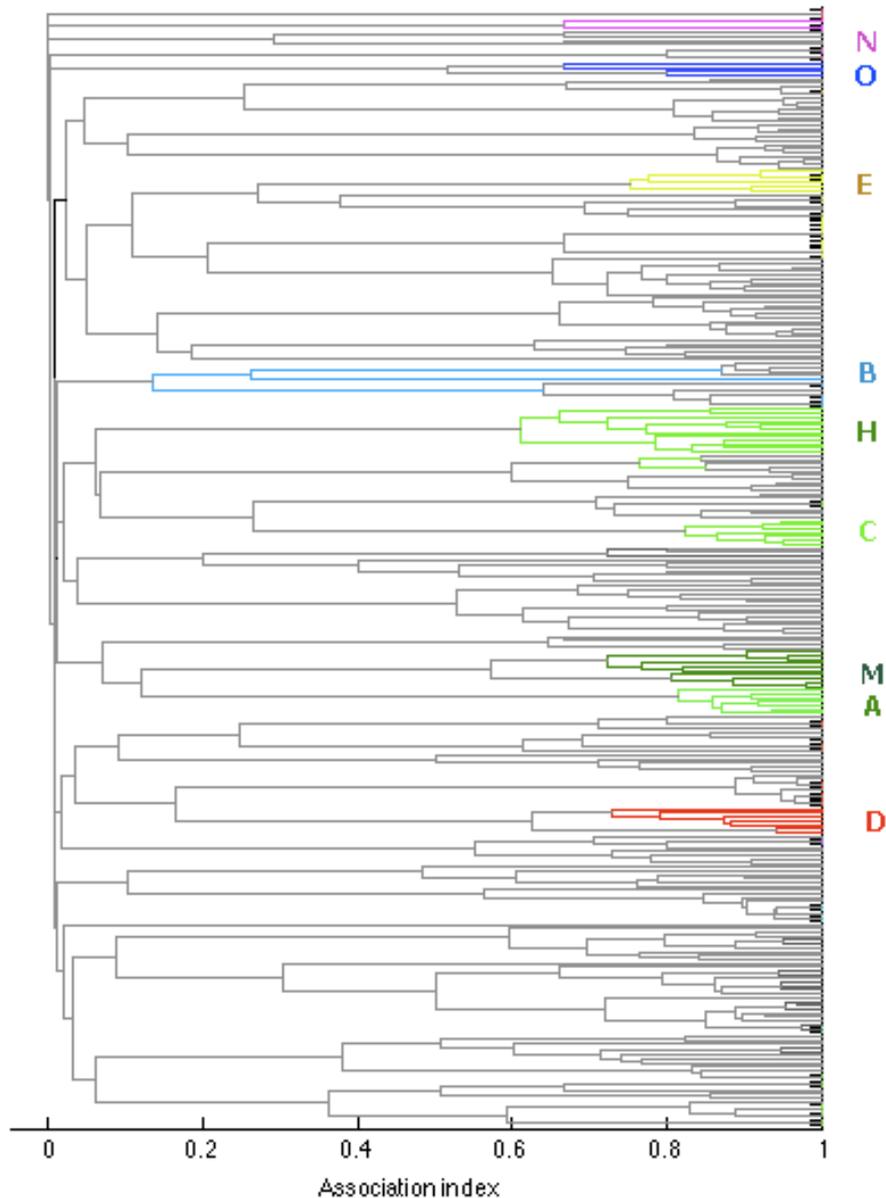


Figure 3.9: Average-linkage cluster dendrogram (based on the half-weight association index) of well-marked "core resident" and "resident" adult and indeterminate pilot whales identified in the Canary Islands since 1999, in sightings with good photo-identification coverage. Only "key individuals" and their "constant companions" (selected based on their longitudinal sighting histories) are shown in colour, while all the remaining individuals are in grey.

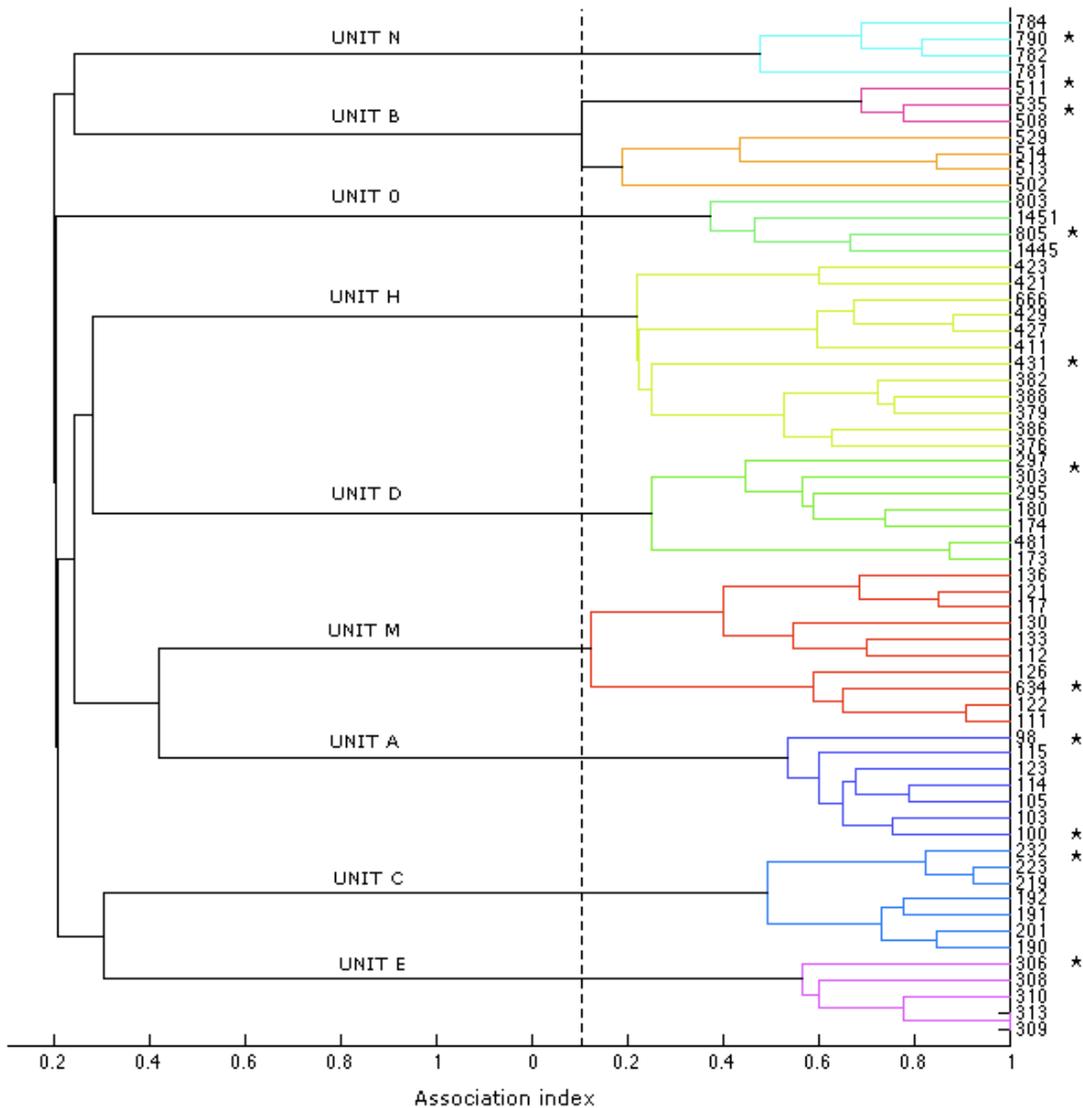


Figure 3.10: Average linkage cluster analysis based on the half-weight index of key individuals (marked with “*”) and their constant companions selected over the entire Canary Islands short-finned pilot whale population (1999-2012). The CCC of 0.993 indicated a good fit of the hierarchical structure ($Q=0.729$, at $AI=0.552$).

3.3.2 SHORT-FINNED PILOT WHALE POPULATION IN TENERIFE AND LA GOMERA

Further analysis of the social structure of this species was conducted with a more restricted database. A total of 134 short-finned pilot whales recorded in the two islands of Tenerife and La Gomera during 351 sightings between 2004 and 2010 was selected by including only the most frequently sighted whales (at least once a month for eight months, with high monthly and seasonal rates; see Chapter 2). All the selected groups

met the photo-identification standards (only good quality images of distinctive fins) and filtered by good photo-identification sighting coverage.

For the selected individual subset used for this analysis, after an initial steady increase in the number of newly identified whales, the discovery curve rapidly levelled off and remained almost constant (Figure 3.9).

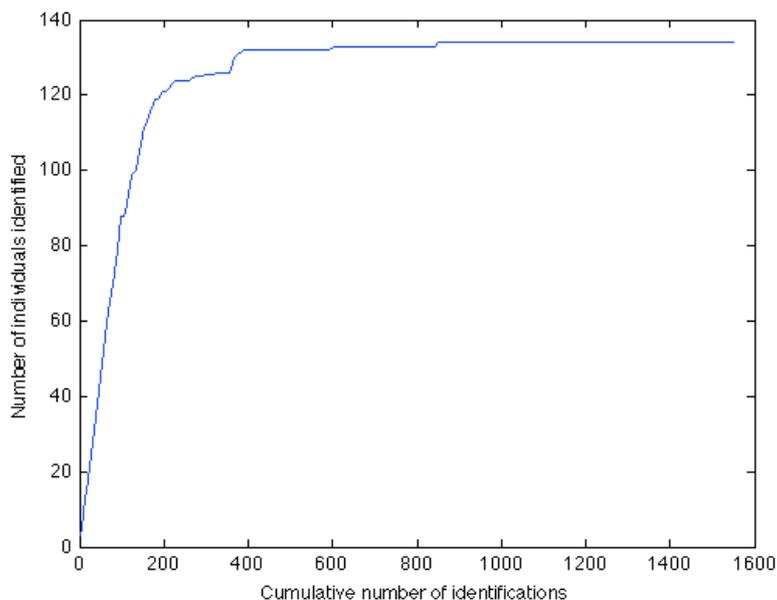


Figure 3.11: Discovery for new individuals showing the cumulative number of short-finned pilot whales identified versus the cumulative number of identifications recorded (sampling unit set to one day) for well-marked adult and indeterminate whales seen at least once a month for eight months in the islands of La Gomera and Tenerife, between 2004 and 2010 in sightings with good photographic coverage.

The social differentiation of the selected pilot whales was estimated at $S=2.9$ ($SE=0.134$) indicating a strongly differentiated society. The correlation coefficient was estimated at $r=0.942$ ($SE=0.005$), with a mean association per dyad of 0.93 and a mean association per individual of 124.33, indicative of an excellent representation of social structure and probable rejection of the null hypothesis of non-preferred/avoided companionship (Whitehead, 2008a).

Overall mean association indices within this selected population were still quite low, with a value of 0.04 ($SD=0.01$, range=0.00–0.07). However, the average maximum association index (Figure 3.12b) for each individual was high 0.76 ($SD=0.11$, range=0.47–1.00). While the great majority of dyadic associations were 0 indicating no

association (Figure 3.12a), a small proportion of individuals formed strong dyadic bonds with the same individuals almost 50% of the time.

Looking for patterns, the association indices (half-weighted index) were investigated based on qualitative assessments of sex differentiation (Annex 3: Figure A3.1).

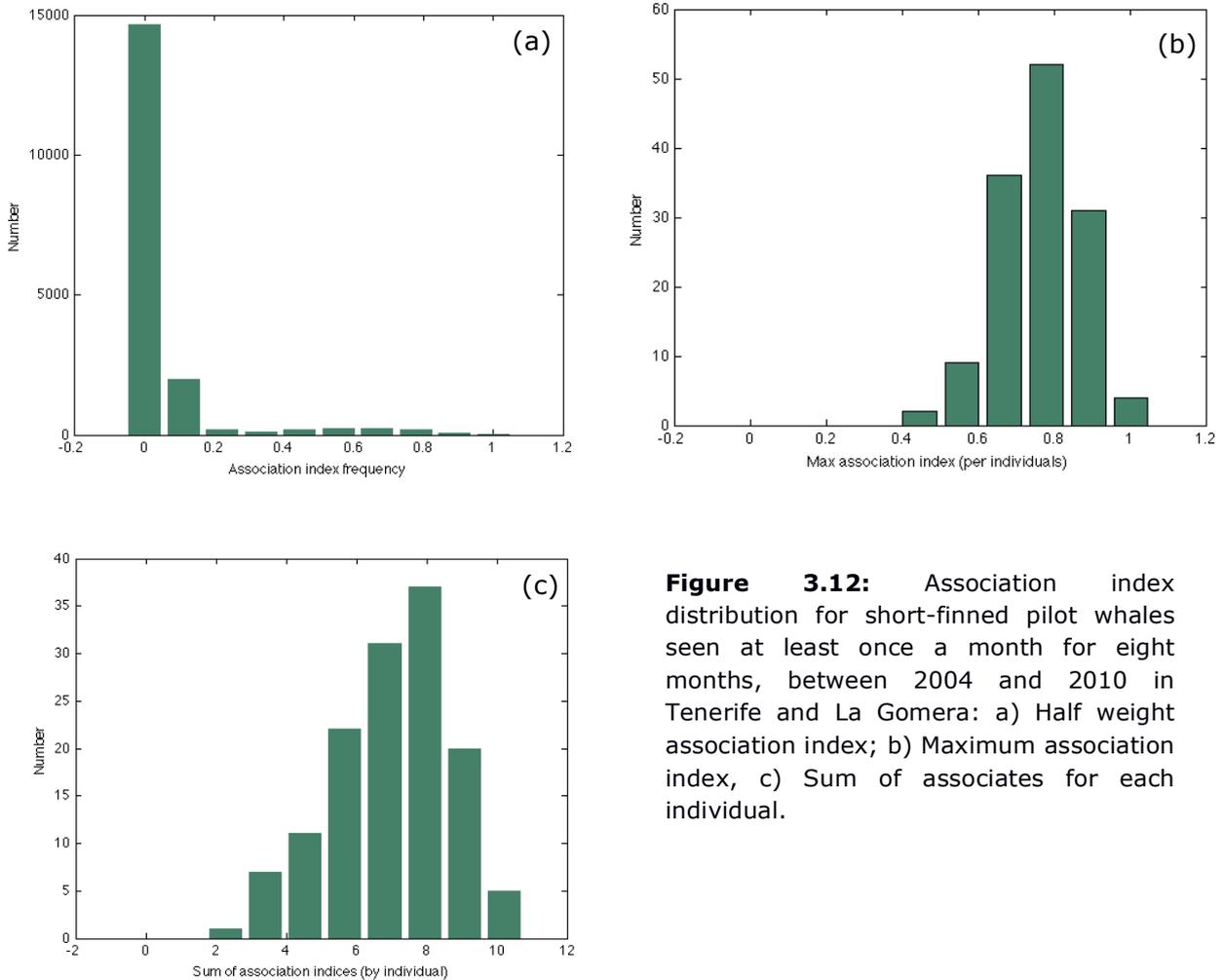


Figure 3.12: Association index distribution for short-finned pilot whales seen at least once a month for eight months, between 2004 and 2010 in Tenerife and La Gomera: a) Half weight association index; b) Maximum association index, c) Sum of associates for each individual.

Of the 8,911 possible dyadic associations among the selected individuals, the majority of dyads (82%) were never documented in association; 1,312 showed a value more than double the overall mean association index (0.08) indicating "preferred associations", while only 310 showed some level of association below the index threshold, indicating few "casual acquaintances". No avoidance was found.

The observed association pattern, tested with permutations, was found to be significantly different from what would be expected if they were randomly distributed.

PREFERRED COMPANIONSHIP

Permutation tests for preferential companionship were randomly run 60,000 times, after which the p value stabilised. The SD and CV of the observed mean association index were significantly higher than the randomly permuted data (Table 3.5), indicating that individuals were associating significantly more often (by grouping together or avoiding one another) than expected by chance, and preferred long-term companionships that span across sampling periods. The smaller proportion of non-zero association indices in the observed data in both tests indicated the presence of some long-term avoidance of the same individuals (Table 6.5). Mean association index for the observed data was not significantly different from the randomly permuted data (observed mean=0.0595, random mean=0.0597, $p=0.006$; Table 3.5).

Table 3.5: Test for preferred companionship among short-finned pilot whales recaptured at least once a month for eight months in the islands of La Gomera and Tenerife, between 2004 and 2010. The dataset was filtered by good quality pictures, well-marked fins, and adults and indeterminate age class, seen in sightings with good photo-identification coverage. Permutations using SOCPROG 2.4. for associations within samples and groups within samples were tested for non-random short and long-term associations (preferred or avoided) and for gregariousness. Results for both tests come from 60,000 permutations using HWI. P -values greater than 0.95 are considered significant.

	PERMUTE GROUPS WITHIN SAMPLES		PERMUTE ASSOCIATIONS WITHIN SAMPLES	
	Observed	Permuted	Observed	Permuted
Mean association index	0.060 $p= 0.006$	0.060		
Standard deviation	0.176 $p= 1.000$	0.111	0.1758 $p=1.000$	0.120
Coefficient of variation	2.955 $p= 1.000$	1.862	2.955 $p=1.000$	2.031
Proportion of non-zero	0.265 $p= 0.000$	0.450	0.265 $p=0.000$	0.425
Standard deviation of typical group size	3.189 $p= 1.000$	2.368		

TEMPORAL ASPECTS OF SOCIAL STRUCTURE: LAGGED ASSOCIATION INDEX

The most frequently seen short-finned pilot whales in Tenerife and La Gomera (2004-2010) were also investigated for temporal patterns in their social structure using the lagged association index on the reduced data set containing only sightings with good photo-identification coverage.

The SLAR analyses were stable over time, higher than expected by chance alone, and never approached the random association rate, providing further evidence for preferential companionship (Figure 3.13).

Associations were quite stable over time and were best described by both "constant companions" and "casual acquaintances" models (Whitehead, 1995) (Figure 3.13; Table 3.6). On the other hand, the "constant companions and casual acquaintances" and "two levels of casual acquaintances" models also have some support (Table 3.6).

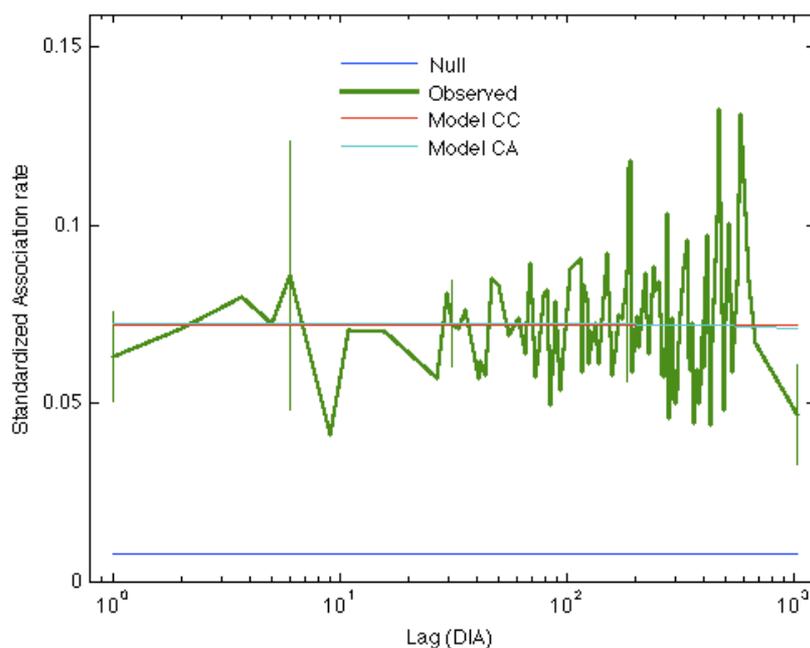


Figure 3.13: SLAR for the most frequently seen short-finned pilot whales (seen at least once a month for eight months) identified between 2004 and 2010 in La Gomera and Tenerife, during sightings with good photo-identification coverage. The moving average curve of 1,000 associations (green line) is shown in the graph together with approximate standard error bars (produced by jackknife on each sampling period). The best model curves (Model CC - "Constant Companions": $g' = 0.097583$ (s.e. 0.010829), and "Model CA - casual acquaintances" $g'=0.098756 \cdot \exp(-4.9852e-05 \cdot td)$) were also included, as well as the null association rate.

Associations between pilot-whales seem to persist constantly for a time scale ranging from one to approximately 670 days, with a final fall of the lagged association curve perhaps due to the loss of resolution in data collection after that time, and/or demographic events such as emigration and mortality (Whitehead, 2008a). Typical group size (gregariousness) of this sub-population was estimated based on the results of the Casual Acquaintances model: 10.13 individuals ($1/a_2$, $a_2 = 0.098756$) with associations estimated to persist for 20,059 days (54.96 years; $1/a_1$, $a_1 = 4.9852e-05$), again beyond the scope of the study.

SLARs were also built looking for sex associations through time: males-males, males-females, females-females/females-males, and results presented in Annex 3: Figure A3.5.

Table 3.6: Models fitted to the most frequently seen short-finned pilot whales (seen at least once a month for eight months) identified between 2004 and 2010 in La Gomera and Tenerife, during sightings with good photo-identification coverage. Maximum likelihood and binomial loss were used for selection and to describe long-term associations (SLAR) of well-marked adults and indeterminates.

MODEL	BEST FIT	PARAM	QAIC	ΔQAIC	MODEL SUPPORT
CONSTANT COMPANIONS	$g'=0.038126$ $a1 = 0.07207$ (s.e. 0.00599)	1	31869.6369	0	BEST 1
CASUAL ACQUAINTANCES	$g'=0.072412*e^{-2.0977e-05*td}$ $a1=2.0977e-05$ (s.e.0.00017708) $a2 = 0.072412$ (s.e. 0.0069293)	2	31871.5716	1.9347	BEST 2
CONSTANT COMPANIONS AND CASUAL ACQUAINTANCES	$g'=0.07215+-0.15752*e^{-2.8584*td}$ $a1= 2.8584$ (s.e. 96.9604) $a2= 0.07215$ (s.e. 0.0060147) $a3= -0.15752$ (s.e. 211.8759)	3	31872.9995	3.3626	SOME SUPPORT
TWO LEVELS OF CASUAL ACQUAINTANCES	$g'=-0.12478*e^{-2.5702*td}+0.072645*e^{-3e-05*td}$ $a1 = 2.5702$ (s.e. 164.036) $a2=3e-05$ (s.e. 0.00018995) $a3 = 0.12478$ (s.e. 83.9008) $a4 = 0.072645$ (s.e. 0.0071636)	4	31874.8719	5.235	SOME SUPPORT

ASSOCIATION LEVELS: SOCIAL NETWORK

A social network diagram was also generated for the 134 individual pilot whales identified at least once a month for eight months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010). The 11 clusters detected using a final modularity index value of 0.669 are represented in Figure 3.14.

Table 3.7 summarises the network statistics for this population. The standard errors of the network measures, calculated by performing 1,000 bootstrap replicates, showed differences among clusters: only for some clusters and some measures, the difference between clusters was less than twice the sum of the standard error for the clusters (Table 3.7, Annex 3: Figure A3.6). Within-cluster strengths were much higher than between-cluster strengths (the smaller strength value within-cluster was 3.72, SE=0.34, much higher than the higher among-cluster values of 0.81, SE=0.57), suggesting a

highly assortative society. This was confirmed by the matrix correlation coefficient of 0.761 between the association indices and the 1:0 matrix of the same/different cluster (Mantel permutation test, $p=1$). The eigenvector centrality was 0 or close to 0 for most of the clusters and heavily loaded on cluster 2 (0.25, SE=0.01), the most strongly connected cluster. Reach shows a pronounced variance among clusters, with range values from 32.59 (cluster 4, SE=5.95) to 119.05 (cluster 2, SE= 7.87). The mean affinity values of the different clusters are almost identical to their respective mean strength, and strong correlations are present over individuals between measures (correlation coefficient between strength and affinity at $r=0.88$ and between strength and clustering coefficient at $r=0.399$), suggesting a highly segmented society. Nevertheless, the overall mean of the clustering coefficient of 0.41 (SE=0.02) indicates the existence of tight and quite closed social units (cluster 2 with clustering coefficient of 0.63, SE=0.05) but, at the same time, individuals associate with their neighbours which may not associate with each other (cluster 7, clustering coefficient of 0.24, SE=0.03).

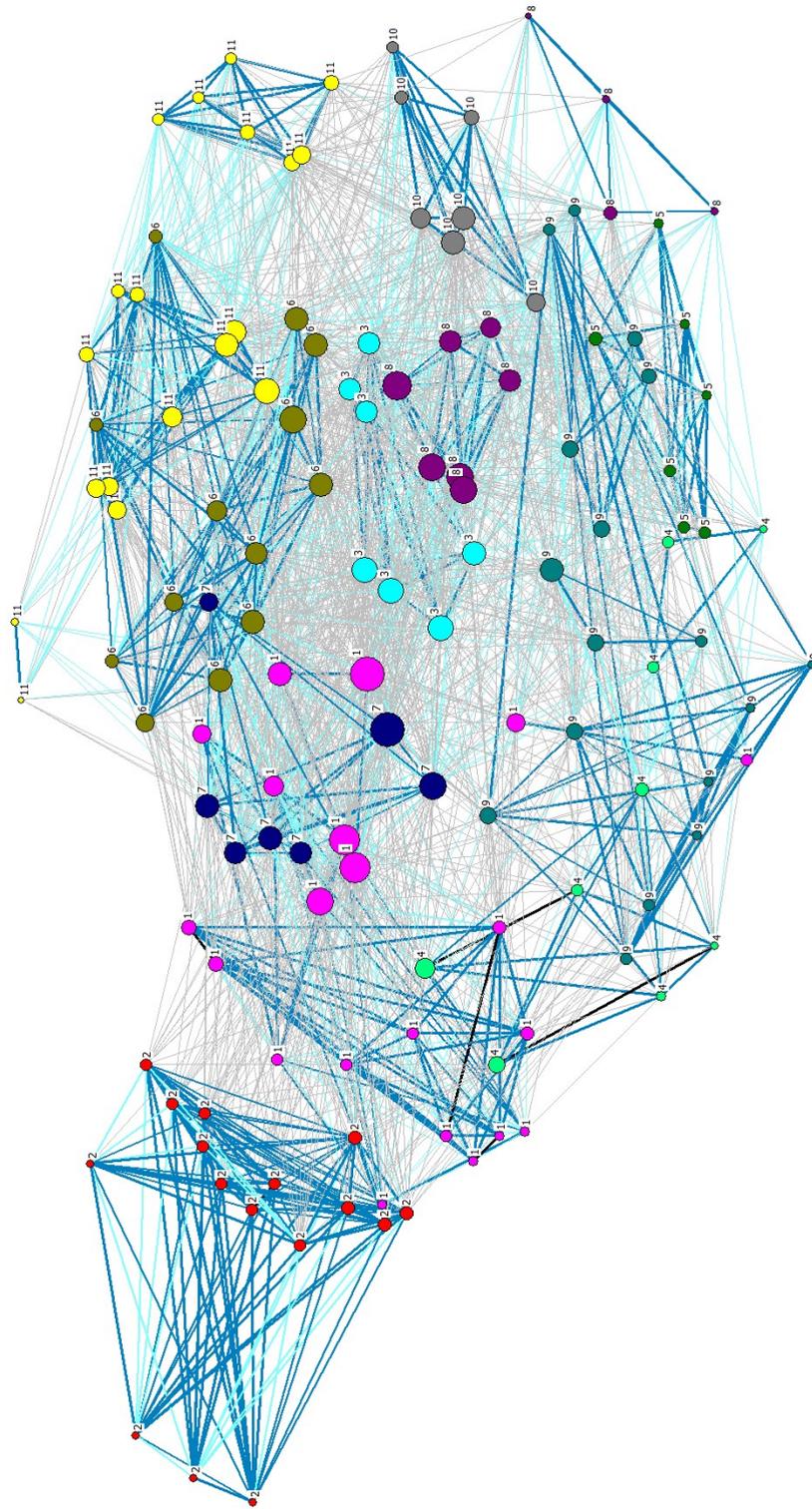


Figure 3.14: Social network diagram of the 134 individual short-finned pilot whales identified at least once a month for eight months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010). Each different node colour indicates the cluster to which each individual belonged. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Tie strengths of one are indicated by black lines, higher than 0.5 in blue, and lower than 0.5 in grey. The size of the node increases with the degree. Enlargement of the social network diagram is shown in Annex 3: Figure A3.7.

Table 3.7: Mean Network Measures for Half-Weight Association Indices among the 134 individual short-finned pilot whales identified at least once a month for eight months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010).

	STRENGTH	EIGENVECTOR CENTRALITY	REACH	CLUSTERING COEFFICIENT	AFFINITY
Overall	7.91 (2.18) SE=0.36	0.04 (0.08) SE=0.01	67.37 (28.4) SE=6.51	0.41 (0.14) SE=0.02	8.16 (1.46) SE=0.39
ID Range	2.04-11.85	0-0.27	13.06-128.7	0.11-0.7	5.31-11.8
Among clusters					
1 (n=21) SE	8.13 (1.95) 0.83	0.01 (0.01) 0.02	69.64 (19.96) 12.88	0.41 (0.19) 0.05	8.41 (0.79) 0.71
2 (n=16) SE	10.96 (0.75) 0.99	0.25 (0.02) 0.05	119.05 (7.87) 20.83	0.63 (0.05) 0.07	10.86 (0.15) 0.94
3 (n=7) SE	8.53 (0.3) 0.92	0.01 (0) 0.02	70.25 (2.14) 13.2	0.38 (0.02) 0.06	8.23 (0.05) 0.7
4 (n=9) SE	5.22 (1.24) 0.48	0.01 (0.01) 0.01	32.59 (10.1) 5.95	0.34 (0.14) 0.06	6.15 (0.48) 0.61
5 (n=7) SE	6.28 (0.46) 1.14	0 (0) 0.01	42.41 (2.48) 16.85	0.49 (0.03) 0.13	6.76 (0.15) 1.37
6 (n=13) SE	9.71 (1.05) 1.01	0.01 (0) 0.04	91.31 (8.82) 17.5	0.4 (0.07) 0.07	9.41 (0.14) 0.86
7 (n=7) SE	8.59 (0.95) 1.6	0.04 (0.01) 0.04	76.34 (7.26) 24.66	0.24 (0.03) 0.05	8.9 (0.18) 1.29
8 (n=11) SE	7.24 (2.8) 0.94	0.01 (0) 0.02	56.90 (28.97) 13.1	0.29 (0.05) 0.05	7.38 (1.48) 0.77
9 (n=17) SE	6.16 (1.01) 0.49	0 (0) 0	41.27 (7.94) 5.84	0.38 (0.14) 0.05	6.67 (0.28) 0.45
10 (n=7) SE	7.48 (0.87) 0.8	0 (0) 0.01	57.41 (6.65) 11.29	0.42 (0.08) 0.09	7.67 (0.07) 0.72
11 (n=19) SE	7.41 (1.99) 0.59	0 (0) 0.01	59.34 (17.83) 9.24	0.4 (0.08) 0.04	7.88 (0.6) 0.6

Pairwise comparisons show the existence of differences in centrality measures between some individuals, indicating differences in contribution to the structure of the network. Strength ranged from 2.04 to 11.85, the clustering coefficient from 13.06 to 128.7, and affinity from 5.31 to 11.8. Twenty-one individuals seem to play a central role in the association patterns by being the individuals that contribute most significantly to the social network: with strength values above 10, eigenvector centrality different from zero, reach above 80, clustering coefficient above 0.26, and affinity above 8.4. No cutpoints (nodes or relation) were detected that were able, if removed, to disconnecting the component into different blocks.

ASSOCIATION LEVELS: CLUSTER ANALYSIS

Hierarchical cluster analysis was performed using HWI on the 134 individual pilot whales identified at least once a month for eight months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010). Again, only results from HWI are reported here, having found no substantial differences in cluster composition. Stabilisation was already reached after 1,000 permutations.

The cluster produced had a CCC value of 0.983, and was therefore highly representative of the study population association structure. The knot-diagram does not show evidence of a multi-level breaking point that could suggest separation into multi-tiered social organization; instead there is a possible knot in coincidence of an association index of 0.606 (Figure 3.12; Wittemyer *et al.*, 2005). Nevertheless, due to the difficult and often subjective lecture of the knot-diagram, the Newman's eigenvector method combined with Modularity-G was preferred and eleven clusters were identified ($Q=0.685$, $AI=0.0494$), which suggested a final modularity index value of 0.669 (Figures 3.15, 3.16, 3.17). No individuals with eigenvector values close to 0 were found, excluding further uncertainty in the formation of this cluster.

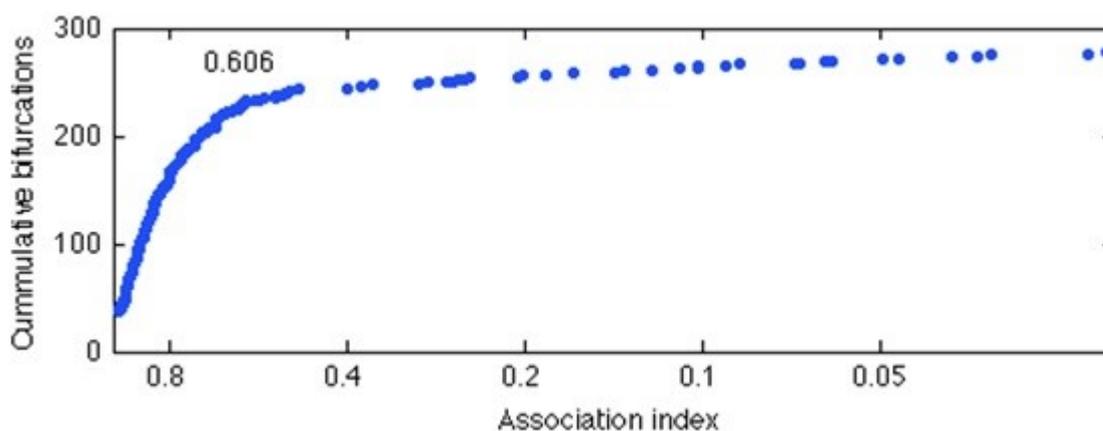


Figure 3.15: Knot-diagram for the most frequently sighted (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. A knot was suggested at an association index of 0.688, 0.511, 0.120.

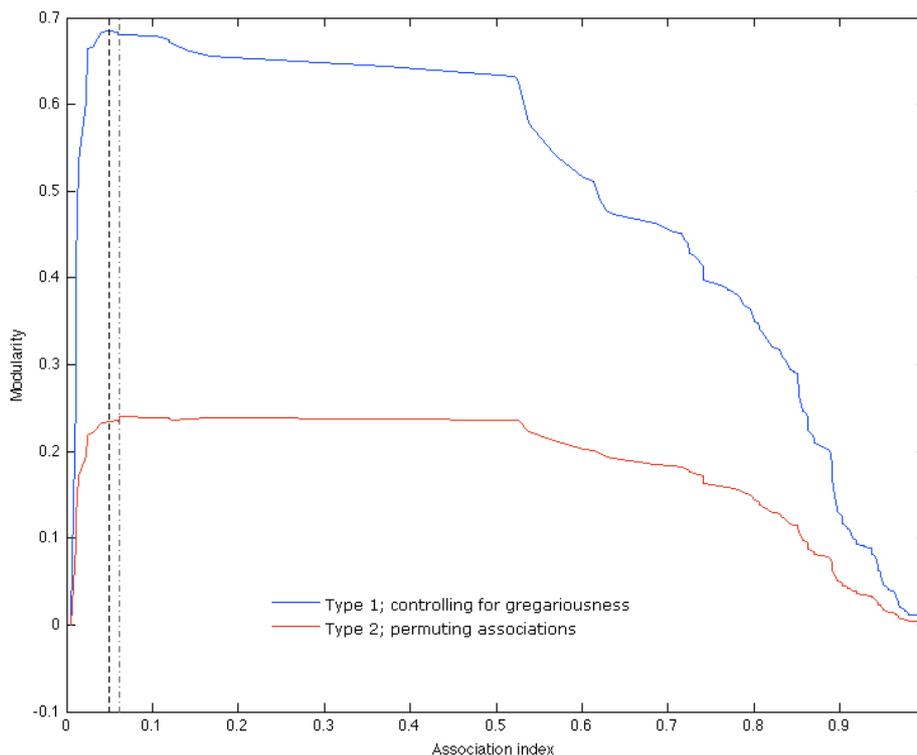


Figure 3.16: Modularity-G (Type 1 for gregariousness) and Modularity-P (Type 2 for permutations) diagram for most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Modularity-G suggested 0.68463 as the best community division value, with an association index of 0.049389. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations)

Individuals within clusters had significantly higher levels of association than those among clusters (Mantel permutation test, $p=1.00$); the mean association index within clusters was 0.52 ($SD=0.22$) while the mean association index among clusters was 0.01 ($SD=0.01$). A large, positive matrix correlation coefficient of 0.761 further supported the rejection of the null hypothesis of no significant differences in association strength within or among clusters.

Both maximum association indices and association sums were substantially greater within clusters than among clusters (0.90, $SD=0.08$ vs. 0.14, $SD=0.10$; 7.13, $SD=2.36$ vs. 1.79, $SD=1.41$, respectively). This indicates that the divisions within the study population created by maximizing modularity was supported (based on a high CCC value, and Mantel test results), but at the same time might suggest the existence of different patterns in association index distribution within clusters, which might explain the quite low value of the overall association mean. In five clusters, the mean association index was lower than 0.5, with some dyadic associations equal to 0 (Table 3.8.7).

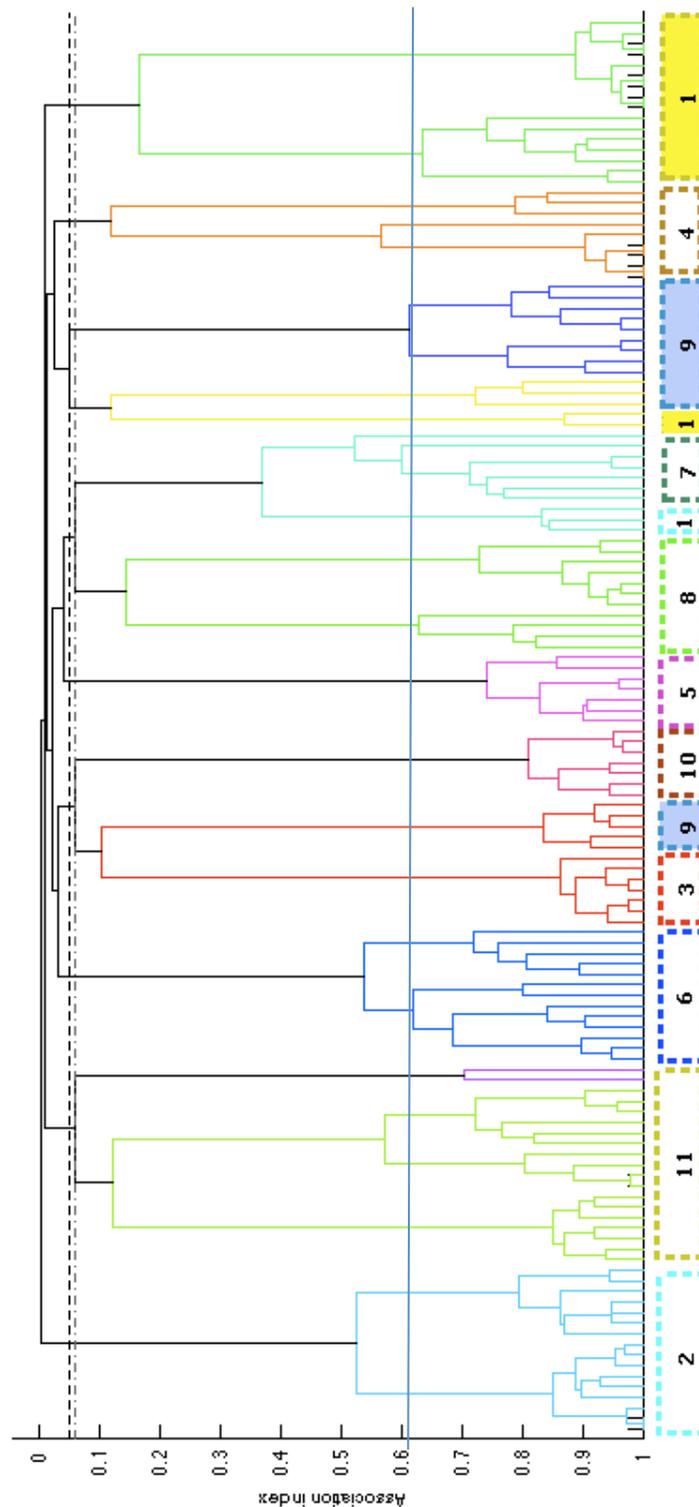


Figure 3.17: Average-linkage cluster dendrogram (based on the half-weight association index) of the most frequently sighted (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Cophenetic correlation coefficient=0.95. The dashed lines indicate the cluster division based on Modularity-G (Type 1 for gregariousness), Modularity-P (Type 2 for permutations), while the blue lines represent the cluster divisions based on knots.

Cluster membership varied in number and ranged from seven to 21 individuals (mean 13, SD=4.7) (Table 3.8.).

Applying the average proportion of well-marked individuals in the population calculated for Tenerife and La Gomera (0.5218, CV=0.0109), the total estimated group size is still statistically larger than the group size measured in the field (23, CV=0.4 vs. 16, CV=0.74; one-way Anova, $F=6.337$, $p=0.12$).

Males, females and adults/indeterminates were recorded in eight of the 11 clusters, with a greater proportion of females (54%) over males (13%). Clusters 10 and 4 comprised only males and adults/indeterminates, while cluster 3 did not include males.

Key unit C and D were included in Cluster 1, while key unit A, F, and M together coincided almost completely with Cluster 11 (Table 3.8).

SLAR analysis was performed to investigate the temporal pattern of each cluster identified by clustering the dataset (Table 3.7; Annex 3: Table A3.1., Figure A3.8a-b). Clusters 2 to 8, and cluster 10 showed preferential companionships and associations stable over time, higher than expected by chance alone, and almost never approaching the random association rate: constant companion was the best-fit model selected. The gregariousness estimated by SLAR almost exactly matched with the number of animals counted in the corresponding cluster. Clusters 1, 9, and 11, characterised by the lowest mean association indexes (Table 3.8) were instead better described by "casual acquaintances" (the first two) and "constant companions and casual acquaintances" models (the last one). In cluster 1 and 9 the final gregariousnesses stabilised at a lower numbers of the original cluster sizes, to the group size of 10, and 8 individuals, respectively. Cluster 11 showed some dissociation after 137 days, with a stabilised group size of 10 individuals, coinciding to one of the three key units that contained (key-unit M).

Again, the larger clusters (Cluster 1, 9, and 11) had the lowest mean association index, and had a casual acquaintances component, suggesting that in these cases the cluster division might partially be an artefact of size rather than only of social partitioning.

By calculating the mean cluster sizes for clusters 1, 9, and 11, described by "CA" and "CC+CA" models (the last one), the size membership at the stabilization level of their SLAR, and after applying the correction factor for well-marked individuals, the total estimated cluster size was not significantly different from the one measured in the field (18, CV=0.30 vs. 16, CV=0.74; one-way Anova, $F=0.901$, $p=0.343$). By using instead

only the point at which the SLAR curve of all the identified clusters stabilised (Ottensmayer and Whitehead 2003), the number of individuals present in a group that are actually long-term companions was of 16 whales (CV=0.35; no significantly different from the one measured in the field: one-way Anova, $F=0.120$; $p=0.729$).

Table 3.8: Division into 11 individual clusters using community division. The original average-linkage cluster dendrogram was built using the most frequently sighted (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in Tenerife and La Gomera (2004-2010), in good coverage sightings. The cluster indices are listed for each cluster: mean, sum and maximum values of the association indexes (HWI). Results from SLAR analysis are also reported, with indications of the selected best-model and the estimated group size at stabilization. The corresponding Unit is also presented.

N°	CLUSTER				SLAR		UNIT
	N° Gma Tot	Mean Assoc. HWI (sd)	Sum of Assocs (sd)	Max. Assoc (sd)	Model	N° Gma est.	
1	21	0.32 (0.13)	7.33 (2.64)	0.89 (0.07)	CA	10	C, D
2	16	0.66 (0.04)	10.92 (0.54)	0.94 (0.04)	CC	15	
3	7	0.87 (0.01)	6.25 (0.08)	0.94 (0.03)	CC	6	
4	9	0.42 (0.14)	4.37 (1.15)	0.84 (0.14)	CC	6	
5	7	0.73 (0.03)	5.37 (0.19)	0.86 (0.03)	CC	6	
6	13	0.61 (0.04)	8.27 (0.48)	0.86 (0.05)	CC	12	
7	7	0.66 (0.07)	4.98 (0.40)	0.80 (0.09)	CC	6	
8	11	0.45 (0.12)	5.45 (1.15)	0.82 (0.12)	CC	9	
9	17	0.30 (0.10)	5.72 (1.59)	0.88 (0.05)	CA	8	
10	7	0.84 (0.02)	6.07 (0.14)	0.94 (0.03)	CC	6	
11	19	0.33 (0.09)	6.97 (1.70)	0.84 (0.12)	CC+CA	10	A, F, M

SPATIAL CLUSTER SEGREGATION

The ranges for each of the 11 clusters obtained are presented in Figure 3.18 and 3.19. The areas of the MCP were determined without excluding the outliers in order to show the maximum extent of the total area possible used by these animals: the recaptures recorded in Tenerife, La Gomera and Gran Canaria were therefore included, although further analysis is required to establish whether use of the last two islands is habitual and they are not outliers for the clusters. The mean MCP (95%) range size of the 11 clusters was 198.2 km² (SE=86.1), cluster no. 5 being the smallest with 29.8 km², and no. 8 the largest with 740.6 km². The kernel method produced a mean 95% animal's use distribution (UD) area of 302.6 km² and a much smaller 50% UD core area of 77.5 km² (Table 3.9).

Table 3.9: Range of the 11 clusters estimated by MCP (overall ranging at 100% and 95% UD) and fixed kernel (overall ranging at 50% and 95% UD) of most frequently seen (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. No fixed kernel among-cluster overlapping is reported for each cluster. Mean, SE, maximum, minimum area extensions are also presented. Areas are expressed in km².

CLUSTER	KERNEL 95%		KERNEL 50%		MCP	
	TOT	No Overlap	TOT	100%	95%	
1	472	36.5	122	893	140	
2	103	0	19	63	51	
3	471	37.5	107	781	90	
4	386	2.15	110	181	63	
5	64	0	17	38	30	
6	299	0	86	448	88	
7	63	0	12	49	41	
8	492	5.55	137	864	803	
9	148	0	35	219	63	
10	138	0	29	78	72	
11	692	120	178	5481	741	
<i>Mean</i>	303	18.3	78	827	198	
<i>SE</i>	64	11	17	476	86	
<i>Minimum</i>	63	0	12	38	30	
<i>Maximum</i>	692	120	178	5481	803	

Even though the range areas differed in extension, a considerable overlap was observed in the area used by these animals, and this was especially evident in the core areas. Therefore, even if separated in different social groups, these pilot whales seem to share the same restricted area of southwestern Tenerife, with almost no segregation (Figure 3.18a-c). In fact, only a small proportion of each range (mean=3%) did not overlap with the range of another cluster, and the surface shared by all clusters was 16% of the total area they used (Table 3.9).

Range (MCP and Kernel) was also calculated for the each of the key units identified in (Annex 3: Table A3.2, Figure A3.9).

CHAPTER 3: "LONG-TERM SOCIAL STRUCTURE, COMPOSITION AND STABILITY OF SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS"

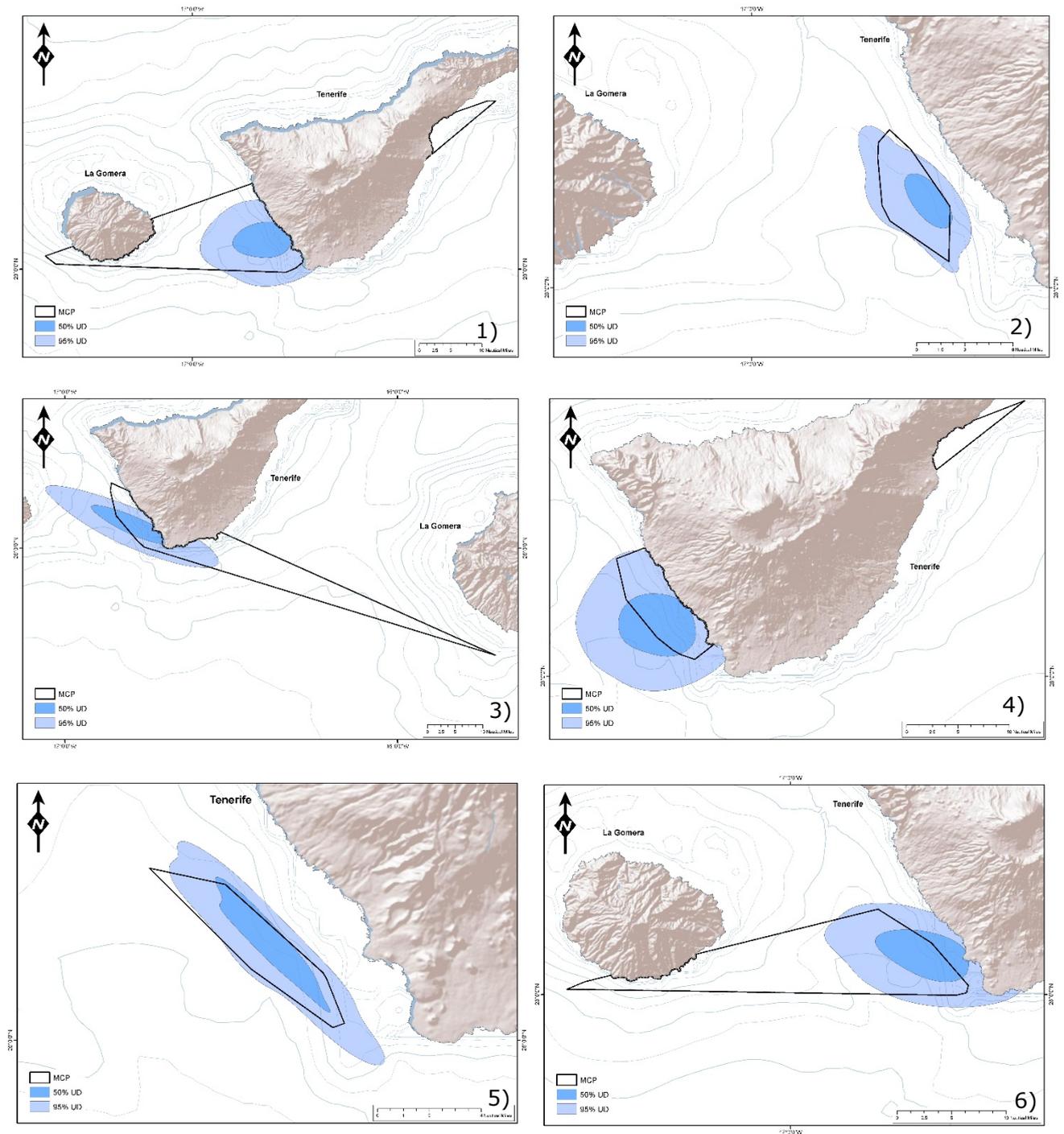


Figure 3.18: Range of clusters 1 - 6, estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) of most frequently seen (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings.

CHAPTER 3: "LONG-TERM SOCIAL STRUCTURE, COMPOSITION AND STABILITY OF SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS"

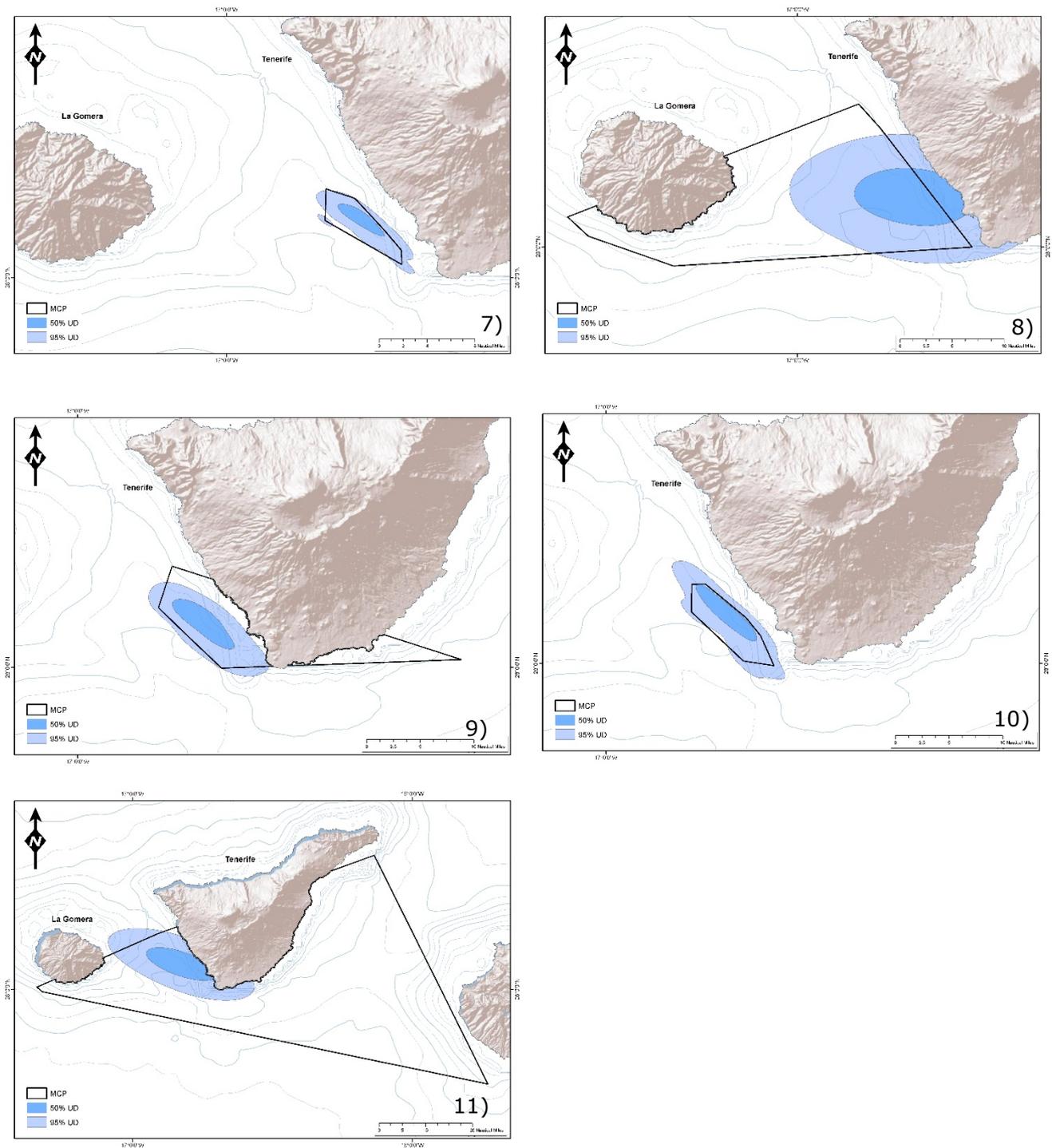


Figure 3.19: Range of clusters 7 - 11, estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) of most frequently seen (at least once a month for eight months) well-marked adult and indeterminate pilot whales identified in southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings.

3.4 DISCUSSION

3.4.1 METHODOLOGICAL CONSIDERATIONS

DATASET SELECTION

The difficulties in studying deep-diving cetacean species have slowed the process of advancing knowledge of how individuals interact with each other. In contrast to socio-ecologically similar terrestrial animals (Weilgart *et al.*, 1996), marine mammal social behaviour is still poorly understood and there is only basic knowledge for many species and much to learn.

In the attempt to fill this gap, the long-term multi-year datasets on short-finned pilot whales collected over the principal islands of the Canary Archipelago were analysed. With some adaptations based on the specific data available and on the population studied, this work was structured to facilitate comparisons with the studies conducted on this species by Heimlich-Boran in Tenerife (1993), more recently by Alves *et al.* (2013) and Mahaffy in Hawaii (2012), and for long-finned pilot whales by Ottensmeyer and Whitehead (2003) in Nova Scotia and de Stephanis *et al.* (2010) in the Strait of Gibraltar.

The first challenge of this study was how to handle the large dataset in order to balance the quantity and quality of information that best suited each general or detailed analysis of pilot whale social structure in the Canary Islands. The choice of a dataset for each analysis was therefore a crucial initial set-up that required particular attention in order to focus on finding the right answer to the specific question addressed. For instance, while the initial social structure analysis database was thought to be limited only to the population off southwest Tenerife recorded during 2007 and 2009, where most effort was made and most recaptures were documented, the finding on range extension and the great number of recaptures recorded within the islands forced me to consider also including data from the other islands in the general social organization analysis, and of a subset of the data from La Gomera and Tenerife for finer scale analysis.

Considering that association patterns based upon the amount of time that animals spend together are influenced both by individual ranging patterns or habitat preference, and by genuine social affiliations, the choice of this specific dataset was based on consideration of the estimated low variation in these whales' ranging patterns. Therefore, even though some individuals might range widely and visit the estimated core area only occasionally, the majority of the selected individuals have only been observed within the two study

areas of Tenerife and La Gomera. Consequently, estimates of association patterns were considered not to be biased by the fact that individuals with similar ranging patterns are more likely to be sighted together.

A common issue in social association studies is defining the minimum number of sightings required to include an individual in the analysis. There is no a general consensus in literature on the appropriate threshold of sightings required, ranging from two (Slooten *et al.*, 1993) or three (Rogers *et al.*, 2004) sightings per individual to ten (Quintana-Rizzo and Wells, 2001) or 30 (Gero *et al.*, 2005). Chilvers and Corkeron (2002) discussed the trade-off between ensuring that data are representative of the population (i.e. by including the maximum number of individuals) while also making sure that data are reliable of the individuals (e.g. by including individuals with maximum sighting frequency). If the methodology applied in Alves *et al.* (2013), Mahaffy (2012) and de Stephanis (2007) of selecting individual pilot whales sighted at least four times for finer social structure analysis (cluster, network analysis, and key units selection) had been followed, a high number of animals (almost 300) would have been selected with the risk of losing detection capability of association patterns. In addition, in southwestern Tenerife, many repeated recaptures in subsequent days might have biased the effective fidelity of individuals to the area.

Therefore, instead of selecting a defined number of sightings, this study considered residency categorisation the best choice to filter animals, depending on the analysis to be conducted. Network analysis was applied to the entire population of well-marked individuals to generate a general social structure image, while for more detailed analyses (association index distribution, SLAR, preferred companionship, and identification of key units) only "core residents" and "residents" were selected, following the criteria described in Chapter 2. The core and resident differentiation was therefore considered a way to reduce the number of individuals and to narrow the search of possible social organization patterns to a more suitable set of individuals.

Besides the great confidence in considering the cluster division (CCC values) to be representative of the study population association structure, the number of animals was still quite high (182) and with a wide range of association indices, and therefore difficult to interpret. The cluster dendrogram was only marginally useful for such a large population (Whitehead, 2008b), but was helpful in visually displaying general relationships among individuals using association indices and comparisons with other association methods, such as networks and key units based on sighting histories. Cluster and network analysis were therefore undertaken using similar criteria to those used by

Mahaffy (2012) and de Stephanis (2007), by narrowing the selected data to the islands of La Gomera and Tenerife, raising the sighting frequency selection level by only considering animals with a high monthly sighting rate combined with a high seasonal sighting rate. The restriction applied also allowed for more confidence in the detailed social structure analysis, because the areas considered were characterised by a high encounter rate (0.7 whales per square kilometres in La Gomera, and in 4.6 in Tenerife; Chapter 2), and because the surveys conducted here had this species as the specific target with a purpose designed methodology.

SEX DIFFERENTIATION

Differentiation between males and females was based only on field observations, and was not supported by genetic analysis. Even though an animal was assigned to one of the two classes only if some specific morphological and behavioural characteristics were met, there may still be some uncertainty in this classification until genetic analysis is conducted. This has been done for long-finned pilot whales, where no significant differences between sexes were found in dorsal fin shape, saddle patch density and number of mark points (Augusto *et al.*, 2013). Analysis requiring sex determination was undertaken only using individuals for which multiple observations were available to confirm sex ("residents" and "core residents" in the Canary Islands, and the most frequently sighted animals in Tenerife and La Gomera). A pilot whale was considered a female if it was seen associated with a calf for the entire duration of a sighting and in all the observations, and an adult male if it showed specific morphological features (bigger size and particular fin shape) and was never found in association with a calf. Nevertheless, these results were not further investigated, nor were they included in detail in the present study, pending confirmation from genetic analysis.

DEFINING A GROUP

How to define a group, and the method used at sea to differentiate it from other possible groups is one of the critical factors in social structure studies that conditions both the analytic steps to follow and the final results obtained.

As previously defined, the "gambit of group" rule was used to identify a set of animals that were associated as a group: spatio-temporally clustered animals, with the majority of interactions occurring with other members within rather than outside, were considered to be associated with every other individual in that group (Whitehead and Dufault, 1999; Whitehead, 2008b). Nevertheless, some reflections must be reported here considering the great difficulty sometimes met in distinguishing the correct limit of different and

simultaneous groups of pilot whales in the area during the surveys conducted in southern Tenerife. While in the rest of the archipelago no more than one group was met at a time, in Tenerife, on multiple occasions, different groups were observed to mix and then separate again, with doubtful interactions. Alternatively, different groups were also found in a restricted area at the same time and not always separated by the established 1,000 m threshold, but showing apparently different behaviour. Also, an approaching boat could affect the general behaviour of the animals, which could react to the vessel in different ways, from attraction to evasion, and from increasing cohesion to separation and dispersal. Moreover, the presence of numerous and frequent whale-watching vessels along with private boats often limited data collection, preventing good sighting coverage and the general view of the entire group or groups present in the area. Consequently, in order to be conservative and use only reliable data, many sightings that did not meet the established criteria were discarded from the subset of data for Tenerife, probably losing important details that could enrich those available on social associations and patterns in structure.

Therefore, the protocol followed at sea in this study established strict limits and narrowed the identification of a group to a social group of strongly related individuals, in a restricted space that, during the sighting, followed the same general behaviour and did not mix with other group(s) even if in the area.

A great limitation of this analysis was the use of only well-marked individuals, thereby excluding immature animals (neonates, calves and juveniles), and all the individuals with indistinctive or slightly distinctive fins. The social units and the clusters formed included only a limited percentage of individuals and of all the possible individual interactions and associations possible within and between them that could limit the general inferences made about social structure from the results of the analysis. The group sizes obtained from cluster analysis and social unit differentiation were therefore adjusted by the estimated proportion of well-marked individuals in the population (Chapter 4), making them comparable to the size of the groups observed at sea.

3.4.2 ASSOCIATION PATTERNS AND GREGARIOUSNESS

The association patterns of short-finned pilot whales in the Canary Islands indicate a well-differentiated society, with long-term preferential associations. Despite repetitive encounters in the same area, individuals were recorded in association only in a small fraction of all possible associations, characterised by strong inter-individual bonds. A

similar pattern was found in Hawaii (Mahaffy, 2012), with short-finned pilot whales in a quite well differentiated society ($S=1.311$; $SE=0.014$; $r=0.428$) with heterogeneous levels of associations, characterised by strong bonds with "preferred companions", and by a small portion of the all possible associates sharing the same area. Long-lasting relationships defined the social structure of short-finned pilot whales in the archipelago of Madeira, where most of the whales captured at least four times were grouped in the dendrogram with preferred companions (Alves *et al.*, 2013).

Even though "casual acquaintances" was the best-fitting model for the Canary Islands population, the temporal analysis indicated the existence of non-random long-lasting relationships between dyads with stable companions that persisted over the entire study. Some gradual disassociation started after 630 days (slight fall in the lagged association curve), which might be due to the loss of resolution in data collection after that time, and/or demographic events (Whitehead, 2008a). The arrival of newborns has also been suggested to decrease the relationship between a mother and its previous calf, with a subsequent destabilization of the general group structure (Alves *et al.*, 2013; de Stephanis, pers.comm).

Social network analysis for the Canary Islands population supported a division into 31 clusters, different in size and association strength (overall mean strength 7.91 ± 2.18). Satellite clusters, mostly formed by transient animals, were pilot whales sighted in the waters of Lanzarote and Fuerteventura (52%), and animals sighted in Tenerife and La Gomera waters, linked in 14 separated networks. Therefore, parallel to transient clusters that reached these areas without interacting with the "local" population, a proportion of transient (37%) and occasional (75%) individuals were observed as belonging to the main network, directly linked also to high site fidelity whales. A general assortative society was thus indicated by the networking analysis, with the principal network composed of all the different highly interconnected residency patterns, but at the same time also with important animals preferentially linked to each other.

The cluster analysis based on "core resident" and "resident" whales in Canary Islands was a highly representative characterization of the association structure of this population ($CCC=0.97661$), with 19 clusters identified and differentiated by mean association indices, in which within-cluster associations were significantly higher than those between clusters.

The most frequently sighted animals in Tenerife and La Gomera were also examined using the different analytical techniques of cluster analysis, network analysis and temporal analysis, but were also further investigated for range calculation. This pilot

whale subset showed a strongly differentiated society characterised by no random preferential associations that remained stable over both short and long-term sampling periods. The cluster analysis identified 11 clusters, with much higher within-cluster associations than those between clusters, and with mean affinity values of the different clusters that were almost identical to their mean strength, suggesting a high assortative and segmented society. Temporal analysis showed an overall stability in association patterns over the long-term with some casual acquaintances or mixed association levels found especially in the clusters with low mean association indices.

Differences in gregariousness (cluster size ranged from seven to 21) might be related to differences in individual sociality associated with age/sex classes or indicative of relative social standing within the population. Association based on sex and age class could not be deeply investigated in this study because no genetic analysis was available to support the field observations. Nevertheless, general behavioural tendencies were assessed showing, as previously described by Heimlich Boran (1993) and by Mahaffy (2012), evidence of persistent social groups of mixed age and sex, with some segregation between adult males and female/calf pairs or male dispersal from the original natal group observed in the field (Chapter 2). The cluster analysis identified similar patterns in cluster composition: one cluster was composed of only females and indeterminates, two clusters of only males or adults, while the remaining eight clusters were characterised by associations between the two sexes, in variable proportions.

Therefore, a high proportion of sightings/clusters contained both males and females, as similarly described by Alves *et al.* (2013) and de Stephanis *et al.* (2008b), where between-sex associations were found to be more common, but different from that observed in Hawaii, where age and sex-based segregation was more defined and frequent, with more than half of the social units without calves or juveniles in association with an adult. Based on this sex-based segregation, the hypothesis of the existence of different social structures between long-finned and short-finned pilot whales might not be applicable to the population in the Canary Islands, instead favouring the other more likely hypothesis of differences among populations (Mahaffy, 2012).

3.4.3 SHORT-FINNED PILOT WHALE SOCIETY

Natal group philopatry in a stable matrilineal social structure, similar to that described in killer whales in the eastern North Pacific (Bigg *et al.*, 1990; Barrett-Lennard, 2000), was first suggested for short-finned pilot whales by Heimlich-Boran (1993) based on visual observations and extrapolation from the genetic analysis of long-finned pilot whales (Amos *et al.*, 1991a; 1991b; Amos *et al.*, 1993a; 1993b). Since then, new studies on

long-finned pilot whales have supported the matrilineal system, implying relatedness between members of both sexes within the natal group (Fullard *et al.*, 2000; Ottensmeyer and Whitehead, 2003; de Stephanis *et al.*, 2008b). Fullard *et al.* (2000) proposed that long-finned pilot whales in the Faroe Islands form multi-generational matrilineal groups, the group size of which would likely increase with the identification of shared ancestors. Based on this, Ottensmeyer and Whitehead (2003) suggested that related matrilineal groups of long-finned pilot whales in Nova Scotia join into extended matrilineal groups.

Nevertheless, this proposed similarity between the killer whale pods and the extended matrilineal groups of long-finned pilot whales in the Faroes has been questioned (Connor, 2000; Ottensmeyer and Whitehead, 2003; Oremus, 2008). Genetic analysis of a stranded group of short-finned pilot whales in New Zealand identified multiple unrelated matrilineal groups, and suggested that while natal group philopatry has been demonstrated within matrilineal groups, multiple matrilineal groups in association do not necessarily indicate relatedness (Oremus, 2008). This finding offered an important distinction between pilot whale social structure and killer whales of the coastal eastern North Pacific, and may indicate an intermediate social structure between sperm whales and killer whales (Mahaffy, 2012).

Recent studies on short-finned pilot whales, albeit with no or limited genetic samples included in the analysis, have both suggested a similar social structure based on a stable matrilineal society composed of a hierarchy of social units (Mahaffy, 2012; Alves *et al.*, 2013).

The social structure identified in short-finned pilot whales of the Canary Islands is in direct agreement to the previously proposed beliefs of a natal group philopatry within the resident populations (Heimlich-Boran, 1993; Mahaffy, 2012; Alves *et al.*, 2013). The use of association indices for the analysis of pilot whales in the Canary Islands allowed the relative strength of affiliation among individuals to be examined both within and between the identified social entities, and the null hypothesis that the resident population of pilot whales associate randomly with one another to be tested. A strong degree of social cohesion of the eleven recognized pods in Tenerife and La Gomera within the studied population was assessed. The results clearly showed non-random patterns of association and significant preference for associating within persistent social groupings, in a social hierarchy structure with overall average rate of intracluster association consistently higher than intercluster associations.

The generally high connectedness of the resident pilot whales in Tenerife-La Gomera (and in the Canary Islands overall), also identified a network where social groupings are

not only distinctive cohesive entities, but also not isolated structures highly interconnected to each other, with a great proportion of individuals of a cluster interacting with individuals of other clusters. The resulting picture appears quite complex and without a clear distinction in multi-level social grouping and in few cases also in distinctive clustering with some dissociation with time and casual acquaintance component. In fact, given the wide range in membership and association strengths among some of the identified clusters, it is likely that the larger social clusters represent aggregations of multiple smaller cohesive social units in temporary association. Four identified key units, longitudinally stable for at least a decade, were in fact included in the two largest clusters, characterised by low mean association index, by the presence of two different trends in the capture histories of the whales, and by a casual acquaintance component in membership, with some dissociation over time. Therefore, the apparent discrepancy found between the mean group size observed at sea and the significantly higher mean cluster size might be a consequence of the temporary persistence of the larger clusters. Mean group sizes estimated in the field for Tenerife-La Gomera (16, SD=11.8, CV=0.75) were similar to the values obtained by hierarchical cluster analysis if the estimated sizes were calculated by combining the stable clusters (constant companion in the SLAR analysis) and the three clusters with casual acquaintance component, at their curve stabilization level (18, CV=0.30). This might indicate that clusters formed by constant companions and where no temporal dissociation was estimated could be considered reasonable proxies for determining cohesive social groups, closely approximating to the social unit observed at sea, indicated as "pods" under the definition used by Bigg *et al.* (1990). With this term, Bigg *et al.* (1990) described groups of closely related matrilineal killer whales that are typically seen together, travelling, foraging, socializing together at least 50% of the time, and that are stable over many generations. However, the use of this term has been questioned by Ford and Ellis (2002), who instead defined it as a transitional grouping that reflects the relatedness of recently diverged matrilineal groups.

The mean group sizes estimated at sea in this study were found to be similar to those observed at sea by Alves *et al.* (2013) in Madeira (mean=18, SE=1.17, CV=0.08), but smaller than those observed by Mahaffy (2012) in the main Hawaiian Islands (mean=20.4, SE=0.73, CV=0.04). Due to the different methodology followed by Heimlich-Boran (1993), who defined a group as all whales within 250 m of each other exhibiting similar behavioural characteristics, the mean group size is not directly comparable to more recent studies on the species. Nevertheless, based on the assumption that 85% of the study population was considered distinctive and that clustering methods produced similar results, Ottensmeyer and Whitehead (2003)

estimated that the majority of Heimlich-Boran's social groups contained 11 or fewer individuals, which is a smaller group size than in the present study and the studies conducted in Hawaii and Madeira.

On the other hand, the mean pod size estimated by clustering analysis for pilot whales in the Canary Islands showed an opposite tendency to that obtained in Hawaii, where the larger group size observed at sea was considered to refer to social grouping in temporal association (Mahaffy, 2012). Mahaffy, in fact, explained the discrepancy of smaller group size values obtained by cluster/sub-cluster and unit size analysis. In this way, the mean group size estimated at sea, once corrected for the overall distinctiveness proportion of individuals in the study population, would be similar to the mean group size of 12.5 (SD=0.94, CV=0.08) obtained by cluster/sub-cluster divisions. Alves *et al.* (2013) identified eight short-finned pilot whale social entities in Madeira, interpreted as meaningful pods (Bigg *et al.*, 1990), with a mean size higher, but not significantly, than estimated at sea (mean cluster size= 15, SD=9 animals).

The long-finned pilot whales in the Strait of Gibraltar were described by de Stephanis *et al.* (2008a) to exhibit several large temporary aggregations of individuals, pods, with an estimated mean group size of 14 (SD=18 whales), similar to the social system proposed for the fish-eating "resident" killer whales from the eastern North Pacific (Bigg *et al.*, 1990). Each pod encompassed several line units (detected by longitudinal sighting history analysis), similar to the killer whale system based on matrilineal units. The key units with high mean association indices (units with association index ≥ 0.76) were identified as single "line units", while those with lower mean association indices (with association index ≤ 0.63) as pods formed by multiple line units (de Stephanis *et al.*, 2008a).

Following the nomenclature of Bigg *et al.* (1990), the existence of clan social structure in long-finned pilot whales was documented by genetic analysis, which found parallel variation in allele frequencies among separate pods (Amos *et al.*, 1991b), but less variation in older animals. This suggested that linked pods shared common ancestors, but that the pods did split and younger animals were more distantly related (Amos *et al.*, 1991b). De Stephanis (2007) and Alves *et al.* (2013) recently suggested that the social structure of pilot whales is based on clans. Long-finned pilot whale social structure has been compared to the fish eating killer whale social structure (de Stephanis, 2008a), with pods forming clans. Similar structure was described in short-finned pilot whales in Madeira (Alves *et al.*, 2013) with the existence of at least three clans of island-associated whales, each of them combining two to three pods. Relatedness was found to be higher

within groups than between groups, and highly related individuals tended to be over-represented within groups rather than between groups. Large groups were suggested to represent temporary aggregations of smaller unrelated groups, and a hierarchical matrilineal system that also included pods and clans. Even though this latter study and the present one clearly showed social structure similarities between the two areas, reinforced by being based on the same analytical methodology, and by the already reported existence of whale movements between the two archipelagos (Servidio *et al.*, 2007), there was insufficient evidence to apply the social structure characterised by the presence of multi-tiers social division described in Madeira to the Canary Island population in the present study.

Therefore, since it would not be surprising if social structure varied between species, but also within a species, no pre-conceived social structure findings previously described for both long- and short-finned pilot whales in other areas should be applied here without direct analysis. Unfortunately, since the methodologies used by Heimlich-Boran (2003) to study the same pilot whale population in Canary Islands are quite different from the ones here applied, it is difficult to discern whether the apparent difference/similarities are real or a product of the biases of each method. Nevertheless, in this study no evident social structure similar to killer whale clans was clearly identified, as it was firstly introduced by Heimlich-Boran (1993), who also did not find evidence of discrete clans because the relationships between specific individuals were considered to be responsible for forming the links between linked pods.

Differences in fine social structure level might be geographically based, or linked to genetic differences. However, without a genetic comparison, this is not possible to determine. In fact, to determine what the identified clusters/units really represent biologically, the best clues would likely come from extensive genetic studies, as were conducted on the long-finned pilot whales hunted in the Faroese drive fishery (Amos *et al.* 1991a, 1991b, 1993a, 1993b; Fullard, 2000; Oremus, 2008). Therefore, despite the temptation to apply the social system of the eastern Northern Pacific killer whales to pilot whales, based on similarities in group composition (i.e., groups of mixed age and sex) and association strength (i.e., in association more than 50% of the time), genetic relatedness of the social units identified in the Canary Islands can only cautiously be assumed and their social and ecological significance remains unclear.

The term "community", generally used to indicate a social grouping of individuals, lacks specific definition and often leads to ambiguous interpretations. "Community" can be used for individuals with long-term site fidelity or as specifically and behaviourally isolated individuals, nearly all in association with each other (Whitehead, 2008a; Urian *et*

al., 2009). Instead, the definition offered by Bigg for fish-eating "resident" killer whales (Bigg *et al.*, 1990) identifies a community as a group of individuals in occasional association that share the same area. Similar to Hawaiian "core individuals" (Mahaffy, 2012), core resident pilot whales in the Canary Islands that were spatially concentrated mostly in Tenerife and La Gomera could be considered a "community" under Bigg's definition due to the presence of differentiated sub-groups and the small proportion of dyadic associations estimated, but would not fit the "community" pattern proposed by Whitehead (2008a). The term community was also used by de Stephanis *et al.* (2008b) to address the long-finned pilot whale population in the Strait of Gibraltar, consisting of repeatedly-sighted individuals, most of which (88%) were in strong association with another individual (HWI index of at least 0.5).

Preliminary evidence of different site fidelity levels for a single island, extended to neighbouring islands, or extended further to the Madeira and Canary archipelagos (Chapter 2) might suggest the co-existence of multiple sub-populations in the archipelago: resident/island-associated ones and a transient/oceanic one. The existence of multiple populations in a relatively restricted area has already been described in different regions and for different species, such as the inshore and offshore populations of false killer whales in Hawaii (Baird *et al.*, 2009). The possible existence of multiple populations or sub-populations of short-finned pilot whales has also been proposed in Hawaii (Mahaffy, 2012), where a demographically-independent island-associated population, characterised by a high level of site fidelity only for the island of Hawai'i (core residents with no inter-island re-sightings) and a pelagic or offshore population were identified. Also, short-finned pilot whales in Madeira exhibited a large degree of variability in site fidelity, including residents with long-term island fidelity of up to 14 years, regular visitors that might use the archipelago either for mating and/or feeding, and transients that might belong to an open pelagic population (Alves *et al.*, 2013).

Even though short-finned pilot whales are known to have very low mtDNA diversity, likely due to their matrilineal social structure (Whitehead, 1998), an unexpected lack of genetic diversity was found between large resident and transient groups in Madeira (Alves *et al.*, 2013). The presence of at least one community of short-finned pilot whales in Madeira, and another moving seasonally and breeding when they met, would lead to potential gene flow that would prevent genetic divergence of island-associated communities and, therefore, to the existence of a single population in the warm-temperate oceanic waters of the north-east Atlantic (Alves *et al.*, 2013) that would likely extend to the Canary Islands.

As it has yet to be supported by genetic analysis, the nature of short-finned pilot whale population structure in the Canary Islands cannot be definitively assessed, and the ecological significance of the different social structure levels of this species in Canary Island remains unclear.

3.4.4 FUTURE STEPS FOR CONSERVATION

Short-finned pilot whales in the Canary Islands have been subjected to strong and growing anthropogenic pressure in some restricted areas of the islands of Tenerife and Gran Canaria. General opinion and conservation proposals, without any further specific management implications, have treated this species as a single "stock", based only on the information available for the southwestern population of Tenerife, without including the rest of the archipelago. Appropriate conservation measures should consider not only information regarding distribution, movement, and general life history parameters but also population structure, in order to target conservation measures at populations that require them. The existence of different residency patterns, with island-associated core residents mainly localized in the islands of Tenerife and La Gomera, along with transient whales that characterize the most peripheral islands of the archipelago, requires specific consideration. Even though they should not be considered demographically independent populations, conservation measures should be adapted to populations of whales around the different islands and to the different anthropogenic pressures faced in these different places.

The presence of non-random associations within the resident population presented in this study has both positive and negative conservation implications. Their social interactions give the opportunity for cultural transmission and social learning (Giraldeau *et al.*, 1994; Deecke *et al.* 2000; Rendell & Whitehead 2001; Yurk *et al.* 2002), but also could affect the population in terms of disease transmission (Altizer *et al.* 2003; Cross *et al.* 2004). In fact, as a consequence of their complex social structure, pilot whales may be particularly vulnerable to infectious diseases, since disease risk increases with the close proximity of individuals and high frequency of interindividual interactions and contacts (Altizer *et al.* 2003; Caillaud *et al.* 2006; Guimaraes *et al.* 2007). Moreover, as a strongly matrifocal species, the loss of key individuals within the social units (e.g. as a result of anthropogenic pressure, like fishery interaction) could weaken unit stability (Williams and Lusseau, 2006). Since the resident population demonstrated strong group cohesiveness, short-finned pilot whales off the islands of Tenerife-La Gomera may warrant special management considerations.

Comparative studies of short-finned pilot whales around the oceanic archipelagos of Madeira, Azores, and Cape Verde, as well as the Atlantic waters of Morocco would allow for more comprehensive conservation management plans to be defined. With more information, plans could be adapted to a single limited archipelago-related population, or to multiple sub-populations characterized by different residency patterns: a resident/island related ones showing high site fidelity to Canary Islands, and a transient/ocean one, with a wide range extended at least to the Madeira archipelago. The suggestions made by Alves *et al.* (2013) of the existence of a single meta-population that would encompass the warm-temperate oceanic waters of the north-east Atlantic should be considered, even though with cautions based on that not all the central tenet of the meta-population theory (Levins, 1969, 1970; Hanski and Simberloff, 1997) may be met in these macaronesian archipelagos (i.e. the relative probability of extinction and recolonization). Even though the two population were found not to be geographic isolated (Servidio *et al.*, 2007), the low level of genetic variability found in Madeira by comparing resident and transient individuals, and the great similarity found in the general structure of pilot whales in the two areas, means that further analysis could be informative. Extending the longitudinal study of individuals, and conducting genetic sampling of the behaviourally studied populations would allow evaluation of the proposed presence of only one meta-population (Alves, *et al.*, 2013) extending between the two archipelagos.

The natural next step of this study will be to analyse the biopsy samples collected since 1999 from 345 short-finned pilot whales in the Canary Islands. No studies have jointly taken into account both short and long-term associations in order to study the stability and composition of the pilot whale social groupings by combining such extensive genetic data with visual observation, video footage and photo-identification techniques. The samples collected in Tenerife and La Gomera (293) during 2007-2009 derive from photo-identified individuals, and on many occasions, all mature members of the group were sampled, as well as the calves on the same occasions, using the scrubbing method.

This would allow for the real nature of the social associations described in this study to be defined with more confidence, comparing cluster-social networks based on observation to those built on genetic relationships, and offering a deeper insight into the social structures and culture of short-finned pilot whales. The mechanisms involved in the evolution of social structure over longer and shorter time spans should be studied through the application of molecular markers, both nuclear and mitochondrial. MtDNA sequences would investigate the population structure of short-finned pilot whales in the Canary Islands and the phylogenetic relationships within Macaronesian archipelagos. Micro-satellite markers would provide information about pilot whale genetic variability,

determination of gender, kinship within and between social groups, social structure and reproductive success, patterns of dispersal and individual recognition.

Moreover, a more detailed analysis of the photo-identification material and field notes collected during the surveys in Tenerife between 2007 and 2009, in which neighbouring animals, cluster composition of small units, relative distances and movements from one to another were also documented at sea, may lead to new insights if compared to individual genetic analysis of pod associations and segregations.

Additional surveys extended to all the islands of the archipelago would also be important to evaluate the stability of associations and to detect potential changes and trends. Changes in the degree of social cohesion and the number of social clusters within the population could in fact have important effects on mating patterns and population growth rates. Further study in southwestern Tenerife and La Gomera, would allow seasonal trends in social structure to be quantified, which would represent the first step towards a better understanding of the factors that shape this species social dynamics and the effects of changing patterns of social structure. Moreover, further analyses exploring potential explanatory covariates and seasonal effects would help to resolve significant intrinsic and extrinsic factors shaping pilot whale populations' sociality. Considering the longevity of pilot whales (Chapter 1), a long-term observational study would, therefore, provide important insights for understanding both the social and population dynamics of short-finned pilot whales.

3.5 CONCLUSIONS

Examining community structure in the Canary Islands population and subsequently examining group dynamics, association rates, and network statistics has provided novel insights into the complex nature of social interactions and offers basic information for further investigation in the area. Strong evidence of well-differentiated societies, with long-term preferential associations and stable companions that persisted over the entire study, were found to characterise the short-finned pilot whales of the archipelago. A hierarchical social system composed of pods has been suggested, showing stability in structure and localised distribution with almost no differences in range and habitat preferences.

Even though short finned pilot whales in the Canary Islands show a social structure that might be described as natal group philopatry, very similar to that found for long-finned (Amos *et al.*, 1993a; Fullard *et al.*, 2000; Ottensmeyer and Whitehead, 2003; de

Stephanis *et al.*, 2008b) and short-finned pilot whales (Heimlich-Boran, 1993; Mahaffy, 2012, Alves *et al.*, 2013), the lack of genetic analysis that could confirm this description did not allow further comparisons. Similarity to the social structure of killer whale matriline structure and extrapolations from the other oceanic archipelagos of Hawaii and Madeira, therefore, can only be cautiously proposed for this population.

For conservation purposes, the evaluation of potential threats differently affecting pilot whales in the different islands should be carried out, under consideration of the suggested co-existence of multiple sub-populations in the archipelago (resident/island-associated or transient/oceanic).

Moreover, collaborative studies between the neighbouring Atlantic archipelagos, through comparisons of photo-identification catalogues and population genetics analysis are encouraged.

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CHAPTER 4

**ABUNDANCE OF THE SHORT-FINNED PILOT WHALE IN
SOUTHWESTERN TENERIFE**

4.1 INTRODUCTION

A thorough understanding of population processes and ecosystem functioning should be the basis of any ecological theory and wildlife management (Smallwood and Schonewald 1998, Thompson et al. 1998, Evans and Hammond 2004). This is increasingly important in a world where biodiversity is threatened by climate change, habitat loss, overexploitation or impacts from introduced species (e. g. Caughley, 1994; Roberts and Hawkins, 1999). Decisions on how to best conserve a wild population should, therefore, be based on a good understanding of that population's demography (Coulson *et al.*, 2001; Boyce *et al.*, 2005) and the links between its key fitness components and its environment (Oosthuizen *et al.*, 2012). Biases in the demography estimates could lead to inaccurate predictions of the future status of a population, which may result in the application of inadequate conservation policies and the failure to achieve management objectives (Brook *et al.*, 1997). Instead, accurate estimates of population size and demographic parameters are needed to identify the main intrinsic and extrinsic factors influencing population dynamics, including processes that would not be obvious from abundance data alone (Lebreton *et al.*, 1992; de Little *et al.*, 2007). They can be combined into a population model that can be used to assess the viability of the population over time, evaluate the relative impacts of different threats, provide information on the processes and mechanisms influencing changes in the observed parameters (Brooks *et al.*, 2004), set performance targets against which responses to management can be measured, highlight areas where further research is necessary, and predict how the population will respond to different management strategies (Lettink and Armstrong, 2003).

One widely used method to estimate abundance and demographic parameters (survivorship, recruitment and population growth) is mark-recapture analysis (Lebreton *et al.*, 1992), which uses individual-based information in a probabilistic framework to interpret rates of addition and loss to the marked population over time. This method represents a powerful statistical tool in conservation management and can be used in any situation where animals that inhabit the study area during the study period are sequentially marked or identified and later detected by recapture or resighting (Jolly, 1965; Seber, 1965; Pradel, 1996). Initial marking is, therefore, followed by one or more subsequent capture occasions. The combination of these multiple recapture occasions allows for a compilation of the capture history of sighted individuals: a record of whether each individual was observed or not in each sampling occasion (White and Burnham, 1999), usually indicated by a series of 1s or 0s (1=captured or 0=not captured) in discrete periods of data collection. The basic method uses data on marked individuals

and their proportion in subsequent samples to estimate population size and other population parameters (Seber, 1982).

Mark-recapture models have routinely been used to estimate population parameters of several taxa of avian, amphibian, fish, terrestrial and marine mammal species (e.g., Otis *et al.*, 1978; Wilson *et al.*, 1999; Akçakaya, 2000; Schaub *et al.*, 2001; Bjørndal *et al.*, 2003; Bradshaw *et al.*, 2003; Bailey *et al.*, 2004; Converse *et al.*, 2006; Bradshaw *et al.*, 2007; Silva *et al.*, 2009; Verborgh *et al.*, 2009).

In cetacean research, photo-identification has been widely used to estimate population sizes (see e.g., Hammond, 1986a, 1990; Williams *et al.*, 1993a; Read *et al.*, 2003). Mark-recapture data can come from photographic individual recognition (Hammond, 1986a; Wilson *et al.*, 1999; Williams *et al.*, 2002), by recording animals' naturally occurring markings (Würsig and Würsig, 1977; Defran *et al.*, 1990; Wells and Scott, 1990; Williams *et al.*, 1993b; Wilson *et al.*, 1999) in a catalogue. The natural markings used as the basis of individual photo-identification recognition for capture-recapture analysis are usually long-lasting, slow changing and unique nicks and notches on dorsal fins (Würsig and Würsig, 1977; Wells, 1991), saddle patch patterns (Baird and Stacey, 1988; Olesiuk *et al.*, 1990), pigmentation and markings on the tail flukes and flanks (Agler *et al.*, 1990; Whitehead and Waters, 1990), and callosity patterns on the rostrum (Bannister, 1990; Payne *et al.*, 1990). There are many cetacean species where photo-identification of natural markings can be applied to "mark" the animals for mark-recapture analysis. The list includes humpback (*Megaptera novaeangliae*), right (*Eubalaena glacialis*), fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), sperm (*Physeter macrocephalus*), northern bottlenose (*Hyperoodon ampullatus*), killer (*Orcinus orca*), and pilot whales (*Globicephala macrorhynchus*, *Globicephala melas*), and several species of dolphins, particularly bottlenose dolphins (*Tursiops truncatus*) (Hammond, 2009).

Despite the importance of long-term life history data of top predators, such as whales and dolphins, given the increasing role that top predators are playing in the monitoring and management of marine ecosystems particularly as indicators of environmental change (e. g., Weimerskirch *et al.*, 2003; Boyd *et al.*, 2006; Costa *et al.*, 2010), detailed knowledge of the dynamics of most marine mammal populations is incomplete (Cantor *et al.*, 2012). The natural behaviour of these animals and their complex life history (Hammond, 1986a, 1990) along with logistical constraints, make studying free-ranging cetaceans challenging, expensive, and time-consuming (see Taylor and Gerrodette, 1993). Understanding the causal factors responsible for changes in the status of these

long-lived and slow-reproducing species requires long-term data series, which are difficult to obtain and maintain (logistically and financially). Cetaceans are highly mobile, generally have wide geographical ranges, and spend their entire life cycle at sea, mainly underwater. They are rarely isolated from neighbouring populations and there are frequently individuals with varying degrees of residency in the study area (Connor *et al.*, 2000). Additionally, within a population, individual animals often differ in their patterns and in the extent of their movements depending on gender, age-class, reproductive status or strategies (Wells *et al.*, 1980; Stevick *et al.*, 2002). This means that setting the limits of the study area to include their entire distribution range is not usually possible, even when populations appear to inhabit well-defined geographic areas.

As a consequence, assessments of population size and demographic parameters have concentrated on populations of large migratory baleen whales (e. g., Buckland, 1990; Barlow and Clapham, 1997; Caswell *et al.*, 1999; Chaloupka *et al.*, 1999; Fujiwara and Caswell, 2001; Gabriele *et al.*, 2001; Zeh *et al.*, 2002; Calambokidis and Barlow, 2004; Mizroch *et al.*, 2004; Bradford *et al.*, 2006; Ramp *et al.*, 2006; Ramp *et al.*, 2010), or cetaceans that inhabit coastal areas (e.g., long-finned pilot whales, Verborgh *et al.*, 2009)). For the same reason, much of the available information has low precision, which leads to low capacity to detect trends in populations (see Taylor *et al.*, 2007). Coastal dolphin populations have been the subject of some of these studies (e.g., Hersh *et al.*, 1990; Cameron *et al.*, 1999; Gaspar, 2003; Stolen and Barlow, 2003; Parra *et al.*, 2006; Lukoschek and Chilvers, 2008; Reisinger and Karczmarski, 2010).

Moreover, short finned-pilot whales have been considered to be abundant throughout their range (Olsen, 2009), and although estimates of abundance exist for several areas, there is no information on global trends in the abundance of this species (Taylor *et al.*, 2011) and only few and localized data are available. The limited literature available reports estimates of mortality, growth and reproductive rates based on stranded and hunted whales in Japan (Kasuya and March 1984), and presents abundance estimates obtained only from line-transect surveys (reviewed by Olson, 2009).

In the eastern tropical Pacific, abundance estimates of short-finned pilot whales significantly increased from 1986–1990 to 1998–2000 (Gerrodette and Forcada, 2002) going from 136,448 (%CV= 39.1) in 1996 to 589,315 (%CV=25.5). In the Pacific waters of northern Japan, a long-term study (1985-1997, and 2006) on the northern form of the short-finned pilot whale showed a declining trend in abundance, with higher values in 1985 (6,287-8,646; CV=0.53-0.55), followed by a severe decline in 1986–1988, and then a slight recovery in 1991–2006 (2,431-3,879; CV=0.60-0.50) (Kanaji *et al.*, 2011).

The southern form had an estimated sub-population of about 14,000 in coastal waters (Miyashita, 1993). Dolar *et al.* (2006) estimated abundances in the Philippines of 7,492 (CV = 29%) in the eastern Sulu Sea, and 179 (CV = 96%) in the Tañon Strait. The Gulf of Mexico contains at least 2,388 (CV=48%) animals (Mullin and Fulling, 2004), and 31,139 (CV=27%) both long- and short-finned pilot whales were estimated to exist in the Exclusive Economic Zone of the western North Atlantic (Waring *et al.*, 2009). In the entire Exclusive Economic Zone (EEZ) surrounding the main Hawaiian Islands, 8,846 (%CV=0.49) short-finned pilot whales were estimated (Barlow, 2006). This species was also reported as the most commonly sighted species during a shipboard survey of the Hawaiian Islands EEZ and were estimated to be among the most abundant delphinid species in these waters. Short-finned pilot whales were also among the most frequently sighted delphinids during a small-vessel survey conducted off the island of Hawaii (Baird *et al.*, 2008), but were less frequently seen in similar surveys off Kauai and Niihau (Baird *et al.*, 2006).

Only in Japan (Kasuya and Tai, 1993), off Santa Catalina Island (California, Shane and McSweeney, 1990), Hawaii (Olson and Reilly, 2002), and the Canary Islands (Carwardine, 1995) is this species known to be present year-round, with individuals belonging to resident populations.

Although the presence of short-finned pilot whales in southwestern Tenerife has been known for a long time by local fishermen, it was only in the early 1980s that their residency was demonstrated in the first scientific studies carried out in the island (Hervé-Gruyer, 1989). To date, almost no systematic studies were conducted on the population that inhabits these waters, and none in the other islands of the archipelago. Moreover, those studies that have been conducted were generally scattered over time and space, and the surveys were conducted with major differences in methodology, not allowing for a conservation of the present study with the earlier ones.

Heimlich-Boran (1993) estimated the population in Tenerife in 1992 to have reached 388 residents (well-marked animals seen more than once, or only once but in association with other animals seen more than once) and 107 visitors (animals seen only once in discrete groups and not in the company of any animals seen more than once). Nevertheless, this study was a simple cumulative analysis, with values obtained by counting photo-identified individuals during the survey period, and without taking into account the proportion of poorly marked individuals. A more recent study, based on line transect sampling, estimated a population of 362 individuals (CI= 241-544) in southwestern Tenerife (Carrillo and Peña, 2002).

The general gaps in knowledge of the natural history of short-finned pilot whales in the Canary Islands has equally led to the lack of any direct conservation measures implemented to help protect this most frequently seen species of the archipelago. For the local government, conservationists, general public, whale-watching operators and users, the major concern has always been about the size of the resident pilot whale population in these waters and it has become increasingly important to address this concern. Therefore, there is a recognised and urgent need and urgency for basic information on its population parameters, such as population size, distribution, behaviour and survival to allow assessment of status and the implementation of a correct management strategy.

Restricting the capture-recapture analysis described in this chapter only to the subset data collected during the intensive survey effort in 2007-2009 in this area should lead to more reliable results on the population that encompasses most of the resident pilot whales in the archipelago, and in the area that embraces nearly the entire range of the most frequently seen whales in the archipelago, and that, at the same time, is subjected to the highest anthropogenic pressure of all Canary Island waters (Chapter 2). These coastal waters off the southwestern Tenerife correspond to the areas where human impacts are likely to be especially severe because of the increasing environmental pollution, prey depletion by fisheries, maritime traffic together with the lack of monitoring these activities. The growth of whale watching industries (Elejabeitia and Urquiola, 2009), the high density of ferry lines and of recreational vessels that visit these waters every day year-round, combined with the increasing number of harbours and growing tourist infrastructures along these coasts make southwestern Tenerife a potential high risk area that may eventually cause changes in abundance, demographic trends and distribution of pilot whales in the area.

In this framework, the major goals of the photo-identification study presented here are: (1) to obtain the first reliable abundance estimate of short-finned pilot whales off the southwest coast of Tenerife, with special focus on the resident population; (2) to establish a basis for future work to estimate short-finned pilot whale life history parameters, such as birth and mortality rates, to investigate decreases or increases in their population size; and (3) to discuss the conservation implications of the results.

The study was designed as a mark-recapture experiment. Spatial and temporal distribution of surveys, the photographic effort at sea, the matching of photographs, and the choice of the most appropriate data sets and models were made to minimise violation of mark-recapture assumptions.

4.2 MATERIALS AND METHODS

4.2.1 DATA SELECTION

Data analysis was restricted only to the monthly surveys carried out between April 2007 and March 2009 along the southwest coast of Tenerife, in the Special Area of Conservation Punta Teno-Rasca (SAC ES-7020017). The surveys conducted prior to 2007 and after 2009 in the northern area around Los Gigantes coast were excluded from this analysis because of the potential effect of the lower sampling effort and lack of homogeneity of coverage in space and time. Moreover, the camera equipment upgrade in 2004 to use digital cameras led to a significant increase in photographic quality.

4.2.2 DATA COLLECTION

Surveys were conducted in an area of approximately 550 km². All the surveys started from Las America harbour and extended south to Punta Rasca and north to Playa Santiago (SAC ES-7020017, Figure 1.2.). Random zig-zag transects were run throughout the area on board the 5,5 meter inflatable boat "Chacalote". In all surveys, the same photographer and at least one of the two field assistants were present. Usually the surveys extended from early mornings to late afternoons and, only occasionally, were halted when weather conditions deteriorated due to rain, strong wind, very high swell, or low visibility ("calima").

Whenever pilot whales were sighted, the survey route was interrupted, the boat speed decreased and the individual(s) were approached carefully to a distance suitable for image capture given the prevailing conditions, and in a position to have the identifying marks available for image capture. In each encounter, the general methodology protocol was followed: location, time, environmental data were collected, as well as group behavioural observations, and group composition. Then, when possible, photo-identification and genetic data collection sessions were performed. Photographs of individual short-finned pilot whales were taken using Canon Eos 10D or 30D, autofocus digital cameras equipped with a Canon AF 80-300 zoom lens. Surveys details, photo-identification methodology, photograph analysis, and general procedures are described in detail in Chapter 2. Estimation of group size was repeated several times during the sighting and subsequently confirmed with the photographic material (Ballance, 1990). After ensuring that a sufficient number of good quality pictures had been taken, the group was abandoned and the survey started again.

To try to ensure equal sighting rates for each individual, the survey protocol was geographically randomized, and the surveys were conducted to avoid confounding of

location and time of day. Specifically, certain locations were not consistently surveyed during similar times or in a predictable sequence or, in the event, were considered off effort (e.g. in the vicinity of fish farms).

4.2.3 IMAGE SELECTION AND ANALYSIS

For capture-recapture analysis based on photo-identification techniques, after the process of individual recognition and matching, and before further analysis, two important issues were considered: the level of photographic quality needed for accurate identification, and the level of natural markings in an individual to be considered sufficiently identifiable. Only in this way could the capture-recapture estimates obtained be considered reliable.

The selection of the best thresholds is complex, especially to attempt to minimize the potential error that can occur during the photo-identification process. Photo-quality and individual distinctiveness have been shown to affect capture-recapture estimates (Friday *et al.*, 2008). When an individual is incorrectly identified, the record of sighting histories obviously becomes inaccurate. Therefore, all marks must be noted and correctly recorded, in order to avoid matching errors, and the matching process accurate in order to avoid abundance bias (e.g. Slooten *et al.*, 1992; Jacobson *et al.*, 1997; Cerchio, 1998; Karanth and Nichols, 1998; Smith *et al.*, 1999; Da Silva *et al.*, 2000; Garrigue *et al.*, 2004; Durban *et al.*, 2005), which could lead to false-negatives (missing matches) with a consequent overestimation of population size, or to false-positives (two or more different individuals considered the same) with a consequent underestimation of population size (Hammond, 2010).

. Therefore, according to the general methodology protocol set for this study (Chapter 2), each photograph in the photo-identification catalogue was graded according to its quality: poor (1), fair (2), good (3), excellent (4). Each individual was then evaluated and classified based on its overall distinctiveness, grading the level of its recognisability thanks to its dorsal fin characteristics from non-distinctive (1), slightly distinctive (2), distinctive (3), or very distinctive (4) fins, respectively.

4.2.4 DATA ANALYSIS

OVERVIEW OF CAPTURE-RECAPTURE MODELS

Application of mark-recapture statistical theory and models can be used on individual sighting histories to estimate population parameters. The population under study and the

characteristics of the survey methodology employed are the factors that most affect the selection of a particular mark-recapture model.

Classically, abundance has been estimated through closed population modelling (Otis *et al.*, 1978), which assumes a static population, where animals are neither lost from or added to the population during the study. The more realistic open population models account for temporal changes in population size as a balance between additions (births or immigration) and deletions (deaths or emigration) (Lebreton *et al.*, 1992), chiefly to estimate survival rates. By using a combination of both approaches, it is possible to estimate abundance from closed models and survival rate from open models (Pollock, 1982). Recent developments in mark-recapture models permit the use of the robust design and an integrated approach to estimate survival and transition rates between observable and unobservable states, as well as allowing for individual heterogeneity in sightability (McClintock *et al.*, 2006; McClintock and White, 2009).

The encounter histories of the identified individuals were used to estimate short-finned pilot whale abundance in southwestern Tenerife using the software MARK (White and Burnham, 1999).

GENERAL ASSUMPTIONS

In mark-recapture methods, the number of animals that have never been captured is estimated using the capture-histories of the animals that have been captured (Hammond, 2010). Therefore, these population size estimates are especially sensitive to violation of model assumptions. Survey design plays an important role in the level of potential bias that result from mark-recapture analysis. It is not uncommon that data collected during surveys not specifically design for this propose are used to estimate mark-recapture abundance; such estimates may be especially prone to violation of assumptions, which cannot always be recovered through analysis (Hammond, 2010).

Because assumption violation can lead to biased estimates, it is important that assumptions are explored, validated and carefully described (Williams *et al.*, 1993a; Wilson *et al.*, 1999; Read *et al.*, 2003), based on the specific requirements of the models used for the analysis (Otis *et al.*, 1978 and Seber, 1992, reviewed in Hammond, 1986, 1990 and in Evans and Hammond, 2004).

OPEN POPULATION MODEL

If a population is subject to animals leaving and entering the population through births, deaths, emigration and immigration during a study, then population is considered open, and open population models in mark-recapture methods should be used.

The basis of open population models is estimating survival probability (ϕ) and capture probability (p). Once capture probability is known, population sizes for each capture occasion (denoted as i) can be estimated. The probability of capturing an animal depends on the probability it is alive and available to be seen, and the probability that it is seen conditional on it being alive and available.

Open population mark-recapture models require the following assumptions to be met:

- 1- All animals (of an identifiable class or group) have the same survival probability
- 2- Within a sampling occasion, all animals (of an identifiable class or group) have the same capture probability;
- 3- Marks are unique, do not change and are not lost during the experiment and are accurately identified on each sighting occasion;
- 4- The duration of each capture occasion is instantaneous in relation to the intervals between sessions. Sampling events, capturing and marking, are carried out within discrete time intervals and the duration of each sampling event must be short in relation to the total duration of the sampling program;
- 5- All emigration from the study area is permanent;
- 6- Observations are independent events.

The Jolly-Seber model (JS) is often considered the starting point model for further open capture-recapture models (White, 1982). It provides year-specific estimates of apparent survival and capture probability, but also of population size, and recruitment ("births") (Pollock *et al.*, 1990), of both marked and unmarked animals. While population size can be estimated, it is often very difficult to avoid substantial bias in the estimation of this parameter, mainly because of individual heterogeneity, which cannot be accounted for.

The Cormack-Jolly-Seber model (CJS), which is a variant of JS model, only uses marked animals and allows for variability in survival and capture probabilities among sampling occasions (time-dependent variation). This model cannot estimate population size or recruitment, because only marked animals are followed over time.

The assumptions of equal survival and capture probability required in the basic JS and CJS models are often unrealistic in biological populations. The study area might not

include all of the species' range, and might also be used by migratory animals or by animals with different degrees of residency. Moreover, there may be behavioural differences. Modifications to models allow assumptions to be relaxed so that survival and capture probability can be estimated for groups of animals of an identifiable class (Lettink and Armstrong, 2003).

Schwarz *et al.* (1993) and Schwarz and Arnason (1996) developed a modification of the classic Jolly-Seber model. Because this model was first implemented in the software POPAN (<http://www.cs.umanitoba.ca/~popan/>), it is commonly called the "POPAN model". This new parameterisation, known as the "super-population" approach (Schwarz and Arnason, 1996; Williams *et al.*, 2011), first estimates the number of individuals present during the first capture occasion, and then estimates the number of individuals that enter the population between the first and the second capture occasions (and then the number of new entries in all subsequent capture occasions). This model allows for temporary movement to and from a larger superpopulation, and provides estimates of apparent survival (ϕ), probability of resighting (p), probability of entry into the population ($Pent$) and the total super-population size (N).

Therefore, the model aims to estimate the number of animals present at any capture occasion and additionally the total or cumulative number of individuals that use the site during the study period (\hat{N}^*), by adding the number of individuals present during the first capture occasion (\hat{N}_1) and the sum of the new entrants (\hat{B}_i) at subsequent k capture occasions:

$$\hat{N}^* = \hat{N}_1 + \sum_{i=1}^{k-1} \hat{B}_i^*$$

Unless specifically associated with static group covariates (e.g., sex, age, body weight), heterogeneity in capture probabilities among individuals cannot be modelled using open models (Pradel *et al.*, 1997) and estimates of population size and recruitment rates may suffer from serious bias (Carothers, 1973), while survival estimates are relatively unaffected.

The following parameters were estimated from POPAN models: ϕ (apparent survival), p (recapture probability), $Pent$ (probability of entry into the population at each occasion) and N (size of super-population, i.e., the number of individuals within the population using the study area during the entire study period). All the data sets were tested to determine whether models with constant or time-varying parameters provided a better fit to the data: a model where all parameters were constant, and one where all were time-

varying, a model with time-varying or time invariance for survival and recapture estimates. *PENT* always varied with sampling occasion (time), and *N* was a single estimate for each data set (Schwarz and Arnason, 1996). For the full time variation model (x sampling occasions), POPAN generated $x - 1$ estimates of ϕ , x estimates of p , $x - 1$ estimates of *PENT* (corresponding to the probability of entry into the population for occasions 2, 3, etc.) and one estimated of *N*.

The multinomial logit function was used as a link function for survival (ϕ), for detection probabilities (p), and for the probability of entry (*PENT*); the log-link function was used as a link function for *N* (as recommended by Schwarz and Arnason, 2007).

OVERDISPERSION

The goodness-of-fit test (GOF) diagnostic procedure, available in program U-CARE was used to test whether the starting general model was a reasonable fit to the mark-recapture data. When lack of fit was suspected based on the results of the GOF tests, some indications of how much extra binomial 'noise' (variation) was present were first needed in order to accommodate it.

The magnitude of this overdispersion cannot be derived directly from the various significance tests that are available for GOF testing; instead a way to quantify the amount of overdispersion is by using the variance inflation factor (\hat{c} : 'c-hat') (Lebreton *et al.*, 1992).

Estimates of \hat{c} equal to 1 indicate no overdispersion or heterogeneity in the data, at which point the use of AICc values is reliable; \hat{c} between 1 and 3 indicates minor overdispersion; \hat{c} between 3 and 10 indicates high overdispersion, with consequent suspect model estimates; \hat{c} greater than 10 denotes major departures from assumptions in the dataset, and the need to change to a better global model.

In the JS model, the only available method to calculate \hat{c} is to use the chi-square statistic obtained by programs RELEASE (Burnham *et al.*, 1987) and U-CARE (version 2.2.5, Choquet *et al.*, 2005), and divide it by the number of degrees of freedom. The program U-CARE allows for the calculation of the chi-square statistics of several tests (TEST2 and TEST3), and was also used to detect and diagnose eventual unexpected heterogeneity in apparent survival and re-sighting probabilities.

Program MARK also uses \hat{c} to adjust the confidence intervals of the estimated parameters.

CLOSED POPULATION MODEL

In a closed model, the population is assumed to remain constant, with no change in size and in composition within the temporal and spatial scale of the study. This requires both biological (births and deaths) and geographical (immigration and emigration) closure (Thompson *et al.*, 1998). The simplest closed model has two capture sessions. In the first capture session, a group of animals is caught, marked and released. The population is then re-sampled on one subsequent occasion. The proportion of marked animals in the second sample should reflect the proportion of animals marked in the entire population if model assumptions are met.

Closed models assume that:

- 1- There is no birth, death, immigration or emigration during the study;
- 2- Marks are unique, do not change and are not lost during the experiment and are accurately identified on each sighting occasion;

Following Otis *et al.* (1978), multi-sample closed population models can incorporate up to three broad sources of capture probability variation:

- 1- temporal variation in capture probability (t) from occasion to occasion;
- 2- behavioural responses to capture (b) where animals respond to initial capture so that recapture probabilities are either greater (trap happy) or less (trap shy) than initial capture probabilities;
- 3- encounter probabilities of individual animals may differ because of inherent differences of individuals, leading to individual heterogeneity (h).

The full range of models available was applied to all three selected datasets. By applying one or more constraints of the different parameters, the resulting closed-population models were: null model with all capture and recapture probabilities equal (M_0); time varying capture probabilities (M_t); behavioural response in capture probabilities (M_b); individual heterogeneity in capture probabilities (M_h); and their combinations (M_{th} , M_{tb} , M_{bh} , and M_{tbh}) (Otis *et al.*, 1978; Huggins, 1989).

Pledger's (2000) mixture models were implemented in program MARK, in which the population is assumed to be composed by a mixture of groups, each formed by individuals with instead the same capture probabilities (Norris and Pollock, 1996; Pledger, 2000). Considering that models with three or more mixtures would likely lead to the unidentifiability of parameters, only two groups of individuals were modelled.

Despite the fact that the photo-identification method should not lead to changes in capture probabilities, models with behavioural response were also included within the possible models.

All the models tested were fitted using the sine link function, which is the default in program MARK. Confidence intervals of the parameters were calculated using profile likelihood intervals.

DATA ORGANIZATION

An important step to consider when analysing a mark-recapture population study is the initial data organization: selecting the right data set/s and combining the capture occasions in appropriate sampling units, considering their timing and contents.

A preliminary overview of the data collected between 2007 and 2009 in the southwestern of Tenerife allowed important assessments and choices on the number, frequency and duration of sampling occasions.

For the available data, the objective for determining the sampling occasions was to find the best balance between maximising capture probability and minimising heterogeneity. It was obtained by choosing a sufficient number of sampling occasions with sufficient recaptures while maintaining an adequate time separation between sampling occasions that was long enough to allow the population to mix, and recapture occasions of negligible length relative to the interval between them, to prevent mortality with sampling occasions. In particular, sampling occasions were designed to meet the assumptions that capture probability was similar for individuals of a given type, and that capture sessions were effectively instantaneous in comparison to the intervals between sessions. This means that each sampling occasion was considered to have covered the entire study area (or at least the habitat suitable for the species, in this case approximately the extensions of the estimated ranges for the pilot whales seen at least 9 times, Chapter 2 and 6), that the search efforts was consistent over this area, and that it is reasonable to assume that individuals do not differ in capture probability due to geographical survey locations.

In order to obtain robust estimates, the general biology of the target species, the number of animals in the data set, the average capture probability, and its geographical distribution were also considered to establish the best number of required capture occasions and their arrangement into the different sampling units.

After the preliminary review of the available dataset, and based on these considerations, all the possible analysis models were considered and evaluated in order to find the most appropriate given the available data, to minimize bias and increase the accuracy of the population size estimations (Hammond, 2010). The aim was to find a parsimonious model, i.e. a model that included useful factors to explain the data but excluded irrelevant ones (Burnham and Anderson, 2002).

These considerations resulted in the data collected during the two year surveys being pooled into 24 sampling occasions, using the monthly survey as the sample unit, with the exception of October 2008, which was divided into two different sampling periods (Table 4.1.).

Once the sighting database was organised into these sampling occasions, the capture histories were developed for all the identified and selected animals of the target population by sequentially noting their presence (1) or absence (0). The frequency of occurrence of each capture history was used to calculate the probability of the various possible encounter histories, using maximum likelihood estimation methods implemented in MARK. MLE parameter estimation was used to determine the population parameters that maximize the probability (likelihood) of a particular capture dataset (Lebreton *et al.*, 1992; White and Burnham, 1999).

As shown in Chapter 2 and later in Chapter 6, southwestern Tenerife represented the area where most of the ranges of the "resident" short-finned pilot whales are concentrated. At the same time, a high percentage of "transients" animals still occurred in these waters all year-round between 2007 and 2009. By excluding from the analysis the animals that were seen one and two times, abundance estimations of the most frequent animals inhabiting this areas could be calculated. Therefore, the total data set was analysed as well as the two filtered data sets, obtained by excluding from the analysis:

- 1- the first capture of all the well-marked animals, thus assuming the capture probability of seeing them again during the two-year study was 0.
- 2- the first capture and first recapture of all the well-marked animals, thus assuming the capture probability of seeing them again during the two-year study was 0.

MODEL SELECTION

WITHIN CANDIDATE MODEL SELECTION

The set of candidate models produced for each analysis was developed based on the knowledge of the ecology of the population under study and on the specific survey

design, and always included the general model containing all potentially important effects. This was used to evaluate how well the model fitted the data, using GOF tests available in program U-CARE (version 2.2.5, Choquet *et al.*, 2005). This program examined the departure of the data from the assumption of independence between individuals and within the capture history of each of them (Burnham, 1991). It calculated the chi-square statistics of several tests and the goodness of fit of the general model is given by the sum of the statistics and by the degrees of freedom of the appropriate components of these tests (Lebreton *et al.*, 1992). Moreover, U-CARE Test 2 components were used to detect and diagnose heterogeneity in re-sighting probabilities for individuals known to have survived (trap-dependence: trap- happy or trap-shy; Sandland and Kirkwood, 1981; Pradel, 1993) and to test for directional transience (null hypothesis H0: there is no difference in the probability of being later reencountered between "new" and "old" individuals encountered simultaneously) (Pradel *et al.*, 1997).

Any statistical analysis involves model selection. The aim is to find the most parsimonious model, i.e. a model that includes factors that are useful to explain the data but excludes irrelevant factors (Burnham and Anderson, 2002).

One way to select the best model is by using the information-theoretic method, which comes from merging information theory and likelihood theory (Burnham and Anderson, 2002). The Akaike Information Criterion (AIC) computes the model likelihood (the probability of getting the observed data if the model is correct) penalised by the number of estimable parameters in the model. The plausibility of alternative models can be weighted based on their AIC values. This means that parameter coefficients can be estimated either from the best model alone, or by a model averaging process, taking the AIC values of the models into account.

The AICc is a transformation of the maximized log-likelihood that has been adjusted for the relatively small ratio of estimated parameters to sample size (Akaike, 1973; Hurvich and Tsai, 1989). In the open population model, the AICc values and standard errors of parameter estimates were adjusted for overdispersion by calculating a dispersion factor from the goodness-of-fit statistics to give a quasi-AIC (QAICc). The model with the lowest QAICc value was considered to be the model with the most support from the data, and selected as the most parsimonious. All other models were evaluated based on their QAICc relative to the best fitting model (Δ QAICc).

Models with Δ (Q)AICc less than or equal to two were considered equally likely, models with Δ (Q)AICc between two and 10 have some but decreasing support, whereas models

that differed by 10 units or more were inferred to have no support from the data (Burnham and Anderson, 2002).

Instead of using a single best model to make inferences, in cases of uncertainty as to which model was considered the best, model averaging was performed based on the normalized Akaike weight to obtain more precise parameter estimates and unconditional standard errors (SE) (Burnham and Anderson, 2002).

FINAL MODEL CHOICE

The discovery curve representing the cumulative number of identified individuals during the study period was created to visualize the identified proportion of the target population plotting for the cumulative number of all the animals and for the well-marked individuals.

The robust design model requires time intervals between consecutive primary periods long enough to allow the population to change through birth/death and immigration/emigration, and secondary sampling occasions close enough in time and sufficiently short to allow the assumption of a closed population. In the present study, the surveys were conducted almost continuously for at least six days up to thirteen days, every month throughout the two-year study. Although the robust design model was investigated and applied to the data, it was excluded from the final analysis because it was considered inappropriate for the present data.

The program RELEASE goodness of fit test (Burnham *et al.*, 1987) and U-CARE were performed on the most parameterised POPAN model (fully time-dependent $p(t)$ $\phi(t)$ $\psi(t)$) and the variance inflation factor, $c\text{-hat}$ (\hat{c}), calculated. The open population model (POPAN formulation) was utilised first, because it was considered the model for which the assumptions were most likely to be met. Nevertheless, closed population models were also applied and evaluated, because the duration of the study (two years) in comparison to the lifespan of the target animals of this study, this population may be reasonable approximated to be closed.

CORRECTION FACTOR FOR ABUNDANCE ESTIMATION

Population estimates obtained from mark-recapture models refer only to the population of identifiable individuals. Therefore, the proportion of unidentifiable animals was also considered and estimated.

Total population size (N_{total}) was calculated by dividing the population estimate taken from the mark-recapture models (N) by the proportion of identifiable individuals. Using only good and excellent photos, the number of individuals with long-lasting marks was averaged over all individuals observed in each encounter where all individuals in the school were determined, regardless of their degree of distinctiveness (including calves) (Wilson *et al.*, 1999). This method relies on (1) an extensive photo-identification effort, making it likely that most, if not all, animals are photographed (Ballance, 1990); and (2) a consistent attempt to photograph as many animals as possible in a group, regardless of their dorsal fin markings and body size (or age class).

Within all datasets, only 557 sightings that met specific conditions were used for this calculation, excluding those in which:

- 1- sightings of photo-identified individuals were less than the number of individuals estimated by direct observations at sea;
- 2- sightings with group sizes (by photos or by field observations) greater than 40 individuals;
- 3- sightings where the difference between photo-identified individuals and the number of animals counted at sea was greater than 20 individuals;
- 4- sightings marked in the original database as unsuitable because the photo-identification session did not ensure enough coverage or did not provide reliable group size estimates at sea;

In order to estimate the proportion of individuals with long-lasting marks in high quality-photos, binomial regression analysis in R 2.15.2 (R Development Core Team, 2006) software was used to predict the average proportion ($\hat{\theta}$).

Total population size was obtained as:

$$N_{total} = \frac{\hat{N}}{\hat{\theta}}$$

where:

\hat{N} = mark-recapture estimate of the number of animals with long-lasting marks

N_{total} = estimated total population size

Variance of N_{Total} was estimated using the delta method (Seber, 1982) as follows:

$$CV^2(N_{total}) = CV^2(\hat{N}) + CV^2(\hat{\theta})$$

Where CV is the ratio of the SE to the estimate.

As recommended by Burnham *et al.* (1987) the 95% confidence interval for the total population size was constructed assuming a lognormal approximation and calculated by the formulae:

$$\hat{N}_{total}^L = \hat{N}_{total} / C \text{ for the lower limit}$$

$$\hat{N}_{total}^U = \hat{N}_{total} * C \text{ for the upper limit}$$

where:

$$C = \exp\left(1.96 \sqrt{\ln\left(1 + \left(\frac{SE(\hat{N}_{total})}{\hat{N}_{total}}\right)^2\right)}\right)$$

4.3 RESULTS

4.3.1 SURVEYS AND SIGHTINGS

Along the southwestern coast of Tenerife, between April 2007 and March 2009, 218 photo-identification surveys were made, totalling 2,830.6 nautical miles conducted on effort. Short-finned pilot whales were seen on all surveys in the study area, and of the total of 1,098 sightings of all species recorded, 675 were pilot whale sightings. The photographs used for the analysis derive from 601 sightings.

4.3.2 PHOTO-IDENTIFICATION AND DATA ORGANIZATION

The poor quality pictures graded as 1 and 2, having a higher probability of failing to be matched, were excluded from the analysis, and only pilot whales with distinctive dorsal fin marks (grades 3 and 4) were considered. Only data from adult and indeterminate individuals were used in abundance estimate calculation. Unmarked animals, become marked over time, normally after the first four to five years of life, and the severity increases over time (Würsig and Jefferson, 1990). The acquisition of markings is cumulative, especially in adult males or non-reproductive females, while younger individuals tend to be more likely unmarked or poorly marked. Therefore, juveniles, calves and neonates were eliminated from the analyses, but were used to determine the

proportion of well-marked animals in each encounter and a correction factor to modify the abundance of well-marked animals.

About 146,000 fin photographs of short-finned pilot whales were taken during the selected sighting sessions at sea in southwestern Tenerife. After a more stringent quality selection, 103,800 were considered suitable for inclusion in the photo-identification analysis. Following the selected methodology (Chapter 2), the final catalogue included 11,133 dorsal fin photos (5,806 right, 5,327 left) for a total of 1,666 pilot whales identified, regardless of fin-side, age-class, photo-quality and fin distinctiveness. From these, 1,180 were individuals identified by high quality pictures, and 713 animals were also categorised as "well marked" ("very distinctive" and "distinctive"): 547 were adults, 118 indeterminates, 34 juveniles, 12 calves, and 2 new-borns.

Figure 4.1 summarises the proportion of individuals in each age category subdivided into different fin distinctiveness categories (for good and very good quality pictures), showing an increase in distinctiveness with age.

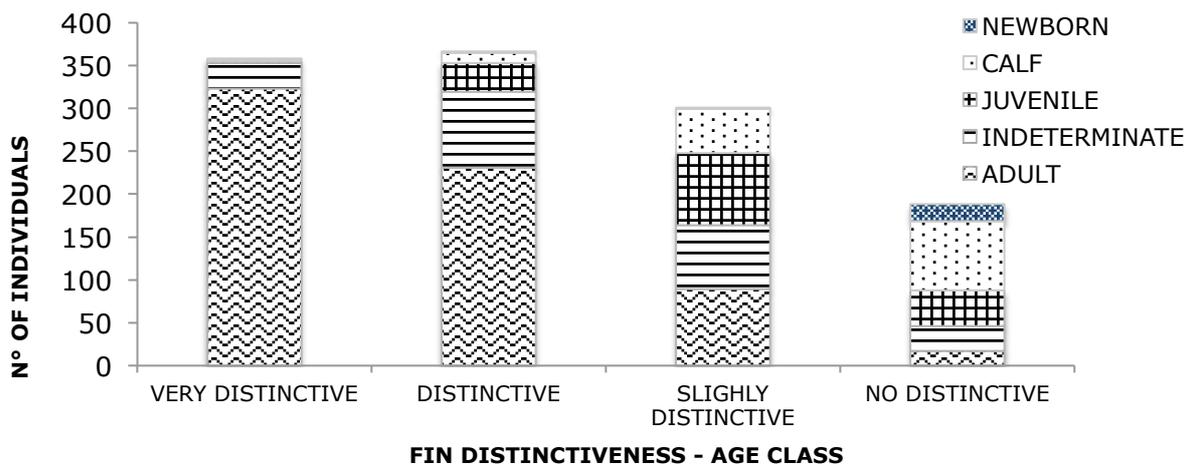


Figure 4.1: Fin distinctiveness profiles and marking categories per each age class of the identified animals represented by Q1 and Q2 quality pictures.

After all the adjustments, the final dataset for abundance estimation analysis contained 665 well-marked animals identified by high quality (good and very good quality) pictures: 547 adult and 118 indeterminate animals (Table 4.1.).

Capture occasions were then pooled into 24 sampling units, as a balance between achieving reasonable sample size and sufficient recaptures between sampling occasions, and to ensure a sufficient number of occasions (Figure 4.2, Annex 4: Table A.3.1).

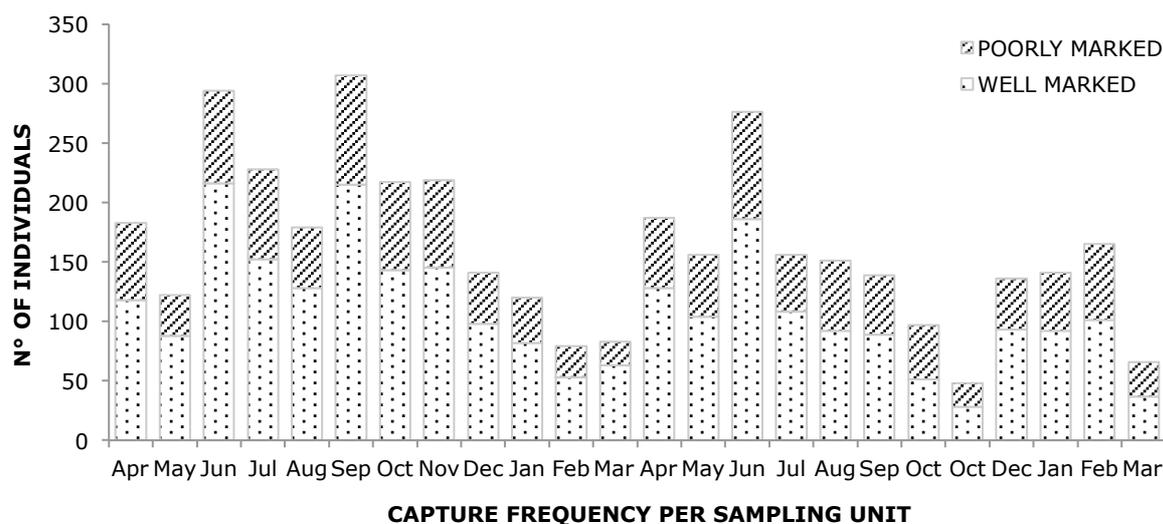


Figure 4.2: Distribution of capture frequencies for poorly marked and well-marked short-finned pilot whales.

Table 4.1: Capture-recapture dataset used for abundance estimation analysis. Number of short-finned pilot whales identified in southwestern Tenerife, between April 2007 and March 2009, grouped in 24 survey sampling units: total dataset, total well-marked individuals, and well-marked adults and indeterminates.

SAMPLING OCCASION	DATE	N° SIGHTING	IDENTIFIED ANIMALS	WELL MARKED TOTAL	WELL MARKED A, IND
1	04/2007	24	183	118	115
2	05/2007	22	122	88	84
3	06/2007	35	291	215	202
4	07/2007	34	228	152	147
5	08/2007	35	179	128	123
6	09/2007	42	307	215	198
7	10/2007	30	217	143	137
8	11/2007	37	218	145	139
9	12/2007	19	141	98	93
10	01/2008	16	120	82	80
11	02/2008	14	79	53	51
12	03/2008	14	83	63	62
13	04/2008	27	186	127	121
14	05/2008	30	156	104	97
15	06/2008	41	276	186	176
16	07/2008	34	156	108	105
17	08/2008	28	151	92	85
18	09/2008	13	137	88	82
19	10/2008	17	93	51	48
20	10/2008	6	48	28	26
21	12/2008	29	136	93	91
22	01/2009	18	141	92	84
23	02/2009	26	164	101	96
24	03/2009	10	66	37	33
		601	1180	713	665

4.3.3 SIGHTINGS AND RESIGHTINGS

The number of times a specific individual was seen was plotted to investigate whether there was evidence of some individuals having a high capture probability, which could be indicative of capture probability heterogeneity, and be indicative of concentrated use of the study area by certain individuals ("core residents" and "residents", Chapter 3). The distribution of the recapture frequencies (Figure 4.3), including or even excluding the poorly marked individuals, suggests the presence of at least two different "populations" characterised by their capture probabilities: many pilot whales seen only once/twice (329, 77 respectively); and animals encountered many times (259, from 3 to 16 times). Recaptures per sampling unit are shown in Annex 4: Table A.3.1.

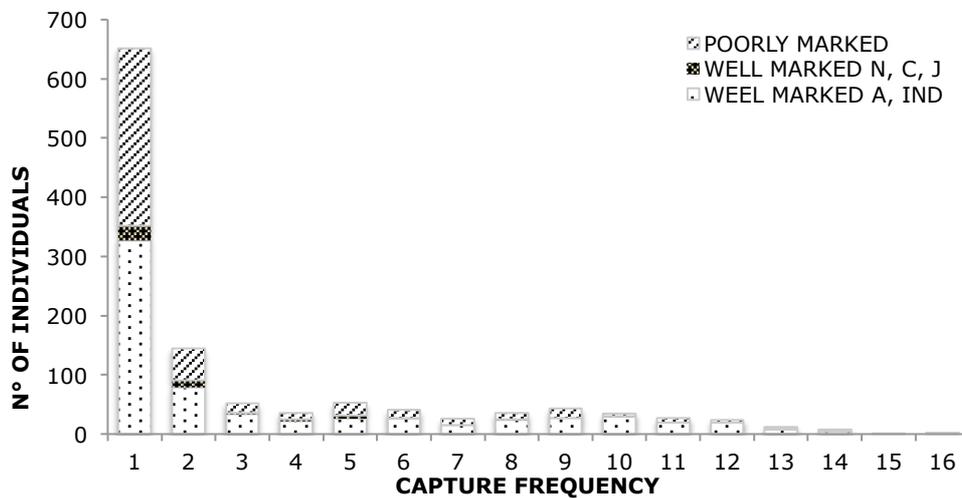


Figure 4.3: Recapture frequency of poorly marked and well-marked individuals (A= adults; IND= indeterminates; J= juveniles; C = calves; N = neonates).

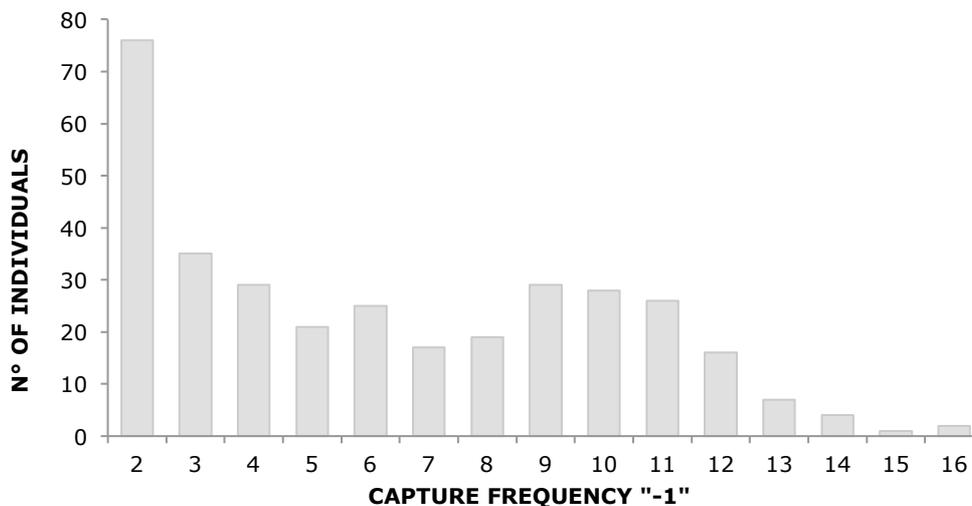


Figure 4.4: Recapture frequencies of well-marked short-finned pilot whales: data set "-1".

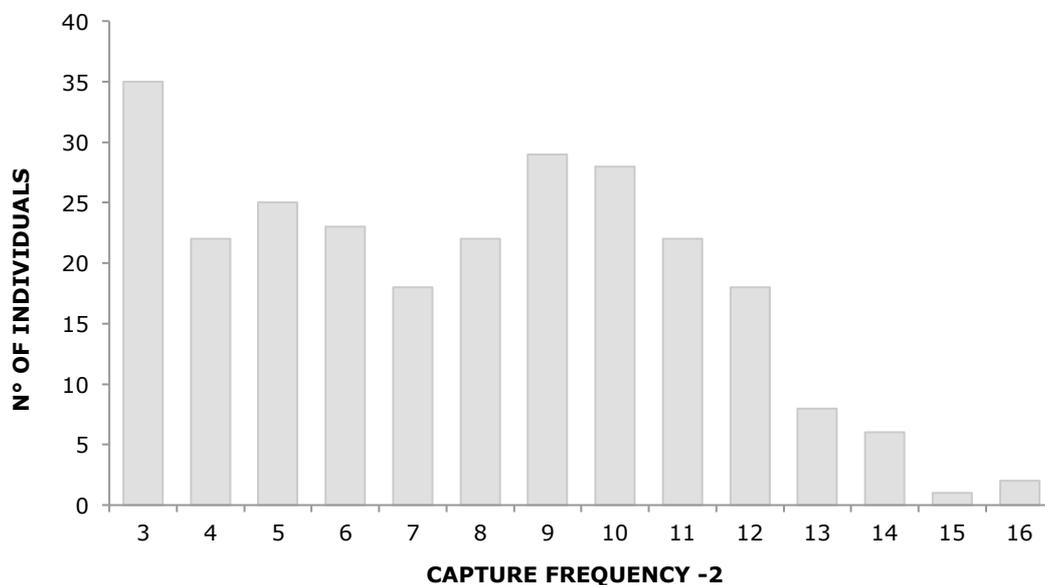


Figure 4.5: Recapture frequencies of well-marked short-finned pilot whales: data set "-2".

Following these adjustments, the dataset without the first capture contained 421 well-marked animals, with 394 adults and indeterminates, while the dataset without the first and second recapture contained 324 well-marked individuals, with 302 adults and indeterminates (Table 4.2). Corrected recapture frequencies are shown in Figure 4.4. and Figure 4.5. Dataset "-1" still contains many (31%) individuals seen only once, while in dataset "-2", the frequency of animals seen only once decreases markedly, although still corresponds to 18% of the total individuals photo-identified. Recaptured individuals within each sampling units are shown in Annex 4 Table A.4.1a-c.

The discovery curve of new individuals (Figure 4.6) showed little decrease in rate of discovery over time for either the complete dataset or only well-marked animals), indicating that new individuals continued to be recruited to the population throughout the study period, especially if individuals with unreliable marks were included. The discovery rate was slightly lower during the second year of the study, especially for well-marked individuals. Nevertheless, it did not reach an asymptote, indicating that the number of individuals identified was not the total number of individuals in the population, suggesting that new individuals would have been found with additional surveys.

Table 4.2: Filtered datasets, obtained by excluding the first capture (-1) and the first recapture (-2) from the complete dataset of well-marked short-finned pilot whales identified in southwestern Tenerife, between April 2007 and March 2009. Total age-class and only adults and indeterminates are also shown.

SAMPLING OCCASION	DATE	TOTAL DATA SET -1	A, IND DATA SET -1	TOTAL DATA SET -2	A, IND DATA SET -2
1	04/2007	21	21	3	3
2	05/2007	59	57	30	30
3	06/2007	140	133	98	94
4	07/2007	135	130	110	106
5	08/2007	108	104	96	92
6	09/2007	168	157	134	125
7	10/2007	109	105	103	100
8	11/2007	126	122	114	110
9	12/2007	77	74	72	69
10	01/2008	50	49	33	33
11	02/2008	50	48	48	46
12	03/2008	48	47	48	47
13	04/2008	119	114	114	109
14	05/2008	98	91	90	84
15	06/2008	177	170	166	160
16	07/2008	107	104	103	100
17	08/2008	92	85	92	85
18	09/2008	68	65	62	59
19	10/2008	47	44	46	44
20	10/2008	19	19	19	19
21	12/2008	65	63	61	59
22	01/2009	83	76	74	68
23	02/2009	74	70	72	69
24	03/2009	37	33	37	33
		421	394	325	303

During the first six months, the mean number of new and well-marked individual recruitment was 7.52 (SD=8.33), which dropped to 3.35 (SD=5.68) in the following six months, while for the second year the mean was 1.64 (SD=3.27). During the first six months, 46.5% (329 individuals) of the total well-marked animals had already been encountered; during the following six months 216 more animals were identified (30.4%). In the first half of the second year the curve shows a clear decrease in the discovery rate (only 7.36% of new recruitment) with an increase again in the second half (15.6% of new individuals).

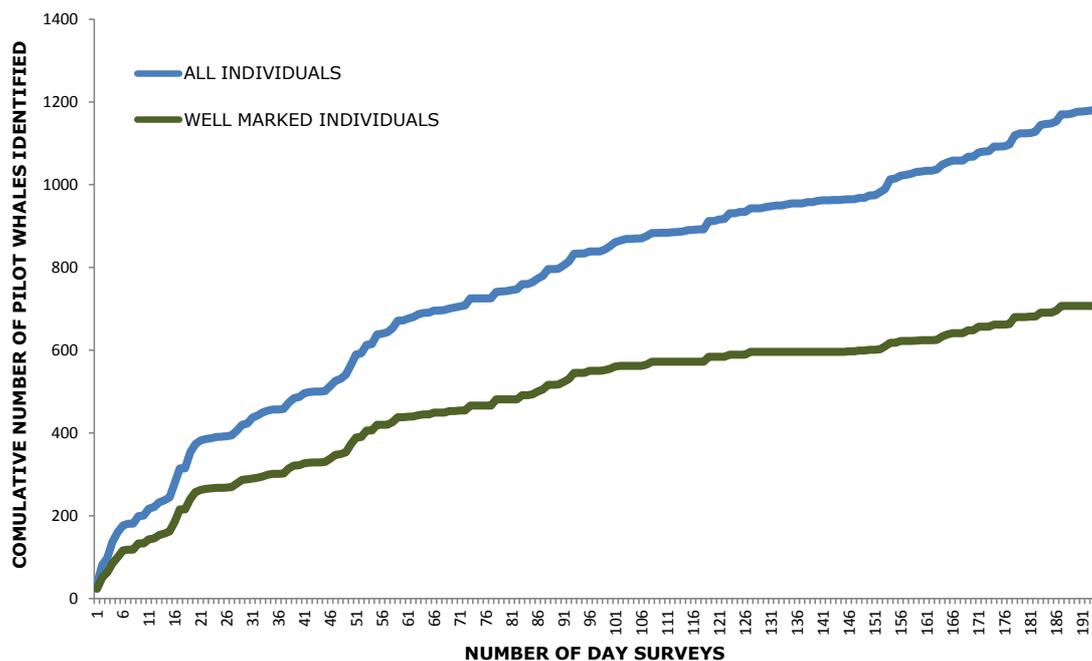


Figure 4.6: Discovery curve of newly identified short-finned pilot whales between April 2007 and March 2009: all identified individuals (blue curve) and well-marked short-finned pilot whales (green curve).

Discovery curves were also graphed for the datasets obtained by excluding the first capture and first recaptures, in order to show the recruitment trend without the assumed transient animals, leaving only the individuals encountered in at least two (or three) sampling occasions.

The discovery curve without first captures showed a recruitment of 62.8% of the total animals during the first six months of the study (mean value for new and well-marked individual recruitment = 5.83 (SD=7.30)), and of 24.7% individuals during the following six months. In the first and second half of the second year only 30 and 25 animals, respectively, were added to the curve (individual recruitment rate mean = 0.007; SD= 1.393) (Figure 4.7).

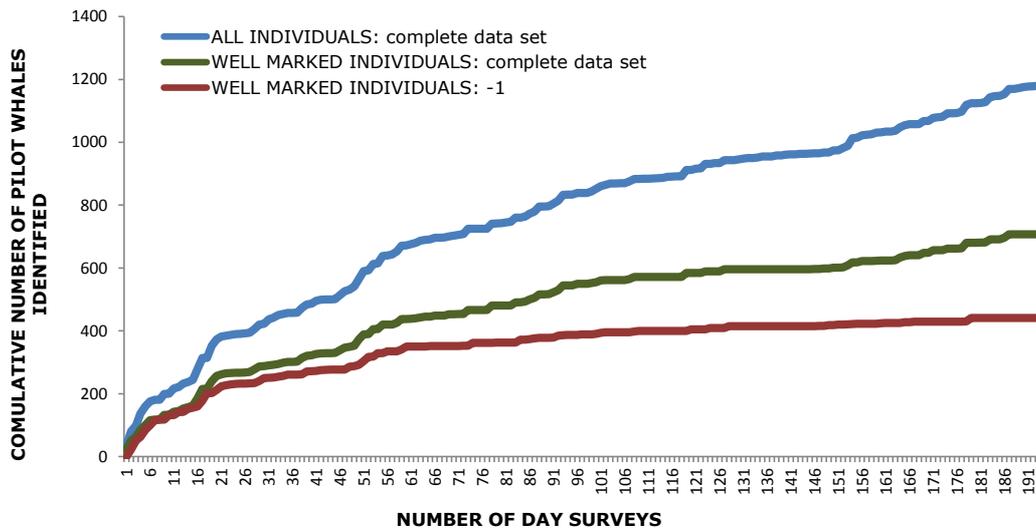


Figure 4.7: Dataset without first capture: discovery curve of newly identified short-finned pilot whales between April 2007 and March 2009: all identified individuals (complete data set: blue curve), well-marked short-finned pilot whales (complete data set: green curve), and subset "-1" of well-marked short-finned pilot whales (subset without the first capture: red curve).

Considering the dataset obtained by eliminating the first two capture occasions, during the first six months of the study 72.8% of the total animals had already been identified (mean individual recruitment rate of 0.026, SD=0.021), and during the following six months only 71 individuals were added. During the first half of the second year the new recruitment corresponded to 3.70% of the entire set of well-marked animals, and finally, during the 13th month, the curve reached 95% of the photo-identified pilot whales. During the 20th month, there were 324 animals until the end of the discovery curve, indicating that almost or all marked resident individuals in the population were captured during the study period, and thus suggesting closure of this population subset (Figure 4.8).

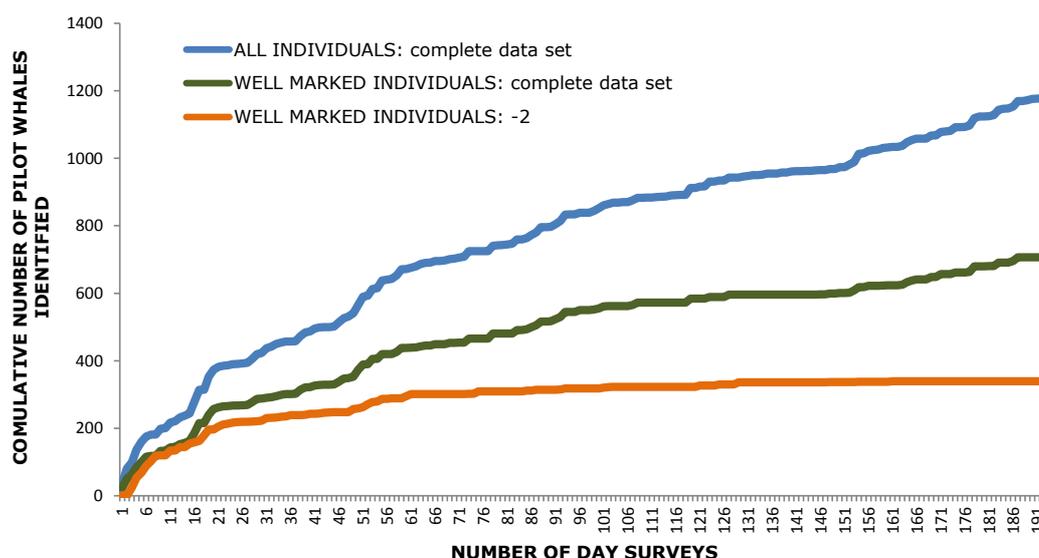


Figure 4.8: Data set without first capture: discovery curve of newly identified short-finned pilot whales between April 2007 and March 2009: all identified individuals (complete data set: blue curve), well-marked short-finned pilot whales (complete data set: green curve), and subset "-2" of well-marked short-finned pilot whales (subset without the first recapture: orange curve).

4.3.4 ABUNDANCE ESTIMATES

Despite the general expectations in photo-identification techniques, U-CARE showed a highly significant result for a behavioural response for adults and indeterminates, showing evidence of trap-happiness (TEST2.CT) (Table 4.3).

The directional test for transience (TEST 3SR) was also highly significant, indicating that newly marked individuals had a lower probability of being re-sighted on subsequent occasions than previously marked animals (Table 4.3).

Table 4.3: U-CARE results for the three datasets used in the analysis to test for behavioural response (TEST2.CT), for transience (TEST3SR), and to calculate the c-hat for overdispersion.

DATA INPUT	TEST3.SR		TEST2.CT		GLOBAL TEST			U-CARE \hat{c}	RELEASE \hat{c}
	N	p	N	p	χ^2	df	p		
TOTAL	21.856	0	-6.695	<0,001	988.869	134	0	7.380	6.171
-1	14.341	0	-4.922	<0,001	611.994	117	0	5.231	4.357
-2	8.339	<0.001	-4.999	<0,001	404.500	111	0	3.644	2.980

OPEN POPULATION MODELS

In the POPAN open population model analysis, for all three datasets, the model that best explained the data, with a significantly smaller QAICc, was for constant apparent survival probability, and time varying capture probability and recruitment (ϕ (.) p(t) pent(t)) (Table 4.4).

Results indicated that goodness of fit, and therefore model structure, was unsatisfactory ($\hat{c} = 7.3796$ by U-CARE, or 6.1707 by RELEASE) with a significant deviation from the assumption. The same result was also obtained for the -1 and -2 data sets: $\hat{c} = 5.2307$ U-CARE and $\hat{c} = 4.3567$ RELEASE, $\hat{c} = 3.6441$ U-CARE and $\hat{c} = 2.9803$ RELEASE, respectively, still showing some overdispersion.

Corrections were applied to adjust the model estimates, and the highest c-hat estimates were used, before averaging the models. The estimates of the parameters obtained for all three data sets are presented in Table 4.5.

Table 4.4: Best fitting POPAN models chosen by their QAICc-values, for the three data sets: Total (A), "-1" (B), "-2" (C). Three parameters are estimated in the models: p=capture probability phi=apparent survival, PENT=probability of entry into the population at each occasion, and these can vary by time (t) or remain constant (.). For each model, the table also presents the Δ QAICc, QAICc Weights, likelihood, number of parameters, and model deviance.

A) TOTAL

Model	QAICc	Δ QAICc	QAICc Weights	Model Likelihood	N° Par	Q Deviance
p(t) phi(.) pent(t)	1,267.8559	0	0.9984	1.0000	38	320.0316
p(t) phi(t) pent(t)	1,280.7229	12.8670	0.0016	0.0016	47	313.8735
p(.) phi(.) pent(t)	1,313.5949	45.7390	0.0000	0.0000	12	419.5005

B) -1

Model	QAICc	Δ QAICc	QAICc Weights	Model Likelihood	N° Par	Q Deviance
p(t) phi(.) pent(t)	1,416.5113	0.0000	0.9997	1.0000	36	538.3496
p(t) phi(t) pent(t)	1,432.7327	16.2214	0.0003	0.0003	45	535.7114
p(.) phi(.) pent(t)	1,492.1867	75.6754	0.0000	0.0000	9	669.4525

C) -2

Model	QAICc	Δ QAICc	QAICc Weights	Model Likelihood	N° Par	Q Deviance
p(t) phi(.) pent(t)	1,752.2426	0.0000	0.9987	1.0000	36	745.9756
p(t) phi(t) pent(t)	1,765.4749	13.2323	0.0013	0.0013	42	746.5824
p(.) phi(.) pent(t)	1,866.0038	113.7612	0.0000	0.0000	10	913.3283

In order to estimate the total super-population (N_{total}), the number of animals with long-lasting marks (adults and indeterminates) in the population estimated by POPAN open model (\hat{N}) was corrected by the averaged proportion of identifiable animals in the population (θ). The estimated θ using 263 sightings was: 0.448 (CV= 0.0187) (Annex 4: Figure A4.1).

Estimated N_{total} was: 1,424 (CV_{total}=0.0622), 794 (CV_{total}=0.0340), and 611 (CV_{total}=0.0428) for the total, -1 and -2 datasets, respectively (Table 4.5). For all three datasets, the apparent survival estimate was very high: 0.955 (SE= 0.008); 0.979 (SE=0.006) for the -1 dataset; 0.995 (SE=0.003) for the -2 dataset.

Table 4.5: Capture-recapture abundance estimates of short-finned pilot whales in southwestern Tenerife. N_{total} =abundance estimate of the total super-population; \hat{N} = abundance of well-marked individuals estimated by POPAN open model, for the three datasets. θ = averaged proportion factor of identifiable animals in a school; CV= coefficient of variation; CI= 95% confidence interval.

DATA INPUT	N	CV	95% CI		θ	θ CV	N	CV	95% CI	
									total	total
TOTAL	638	0.0593	564	712	0.448	0.0187	1,423	0.0622	1,260	1,608
-1	356	0.0284	336	376	0.448	0.0187	794	0.0340	743	849
-2	274	0.0384	254	295	0.448	0.0187	611	0.0428	562	665

CLOSED POPULATION MODELS

The diagnostics for the closed population models, for the full range of models and each dataset, are given in Table 4.6.

Time and then heterogeneity seem to be the key factors in model selection (Mtbh, Mth, Mbt). The best models for the "Total" and "-1" datasets was Mtbh, the most general model incorporating heterogeneity, behaviour, and time variation in capture probability. In dataset "-2", by excluding individuals seen only twice and the first two captures of the rest of the animals, at least part of the variation in capture probability is excluded. This is shown by the best model being Mth, with no behavioural effect but still allowing capture

probability to vary from one sampling occasion to the next and between the two putative populations characterised by different capture probabilities.

Table 4.6: Subset of closed population candidate models. Models are presented in decreasing order of AICc. For each model the table presents the ΔAIC_c , AICc Weights, likelihood, number of parameters, and model deviance.

A) TOTAL

Model	AICc	ΔAIC_c	AICc Weights	Model Likelihood	N° Par	Deviance
Mt bh	3,748.2960	0.0000	0.84969	1.0000	51	4,126.6931
Mt b	3,751.7703	3.4743	0.14956	0.1760	72	4,087.3488
Mt h	3,762.3860	14.0900	0.00074	0.0009	50	4,142.8151
M b	4,398.1066	649.8106	0.00000	0.0000	5	4,869.3227
M bh	4,399.7478	651.4518	0.00000	0.0000	6	4,868.9602
M h	4,409.9256	661.6296	0.00000	0.0000	4	4,883.1448
M t	5,474.3335	1,726.0375	0.00000	0.0000	25	5,905.3566

B) -1

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	N° Par	Deviance
Mt bh	3,932.9315	0.0000	0.9998	1.0000	49	3,631.6064
Mt h	3,949.9645	17.0330	0.00020	0.0002	48	3,650.6701
Mt b	3,973.8769	40.9454	0.00000	0.0000	68	3,633.8475
M b	4,579.4402	646.5087	0.00000	0.0000	5	4,366.8707
M bh	4,581.2324	648.3009	0.00000	0.0000	6	4,366.6592
M h	4,586.7749	653.8434	0.00000	0.0000	4	4,376.2085
M t	4,764.2737	831.3422	0.00000	0.0000	25	4,511.5113

C) -2

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	N° Par	Deviance
Mt h	3,694.7938	0.0000	1.00000	1.0000	47	3,300.2721
Mt bh	3,723.1032	28.3094	0.00000	0.0000	36	3,350.8705
Mt b	3,749.7981	55.0043	0.00000	0.0000	64	3,320.6787
M t	4,151.9875	457.1937	0.00000	0.0000	24	3,803.9832
M bh	4,298.3532	603.5594	0.00000	0.0000	6	3,986.5225
M b	4,298.9091	604.1153	0.00000	0.0000	5	3,989.0821
M h	4,347.8420	653.0482	0.00000	0.0000	4	4,040.0181

Despite these attempts, the heterogeneity of capture probabilities was unlikely to have been completely overcome. For the total dataset, but also for the most restricted one (dataset without the first capture and recapture), the results for close population models still show two quite distinctive encounter and capture probabilities trends (Figure. 4.9. and 4.10), distinguishing between two different groups of pilot whales, one with significantly higher values compared to the other.

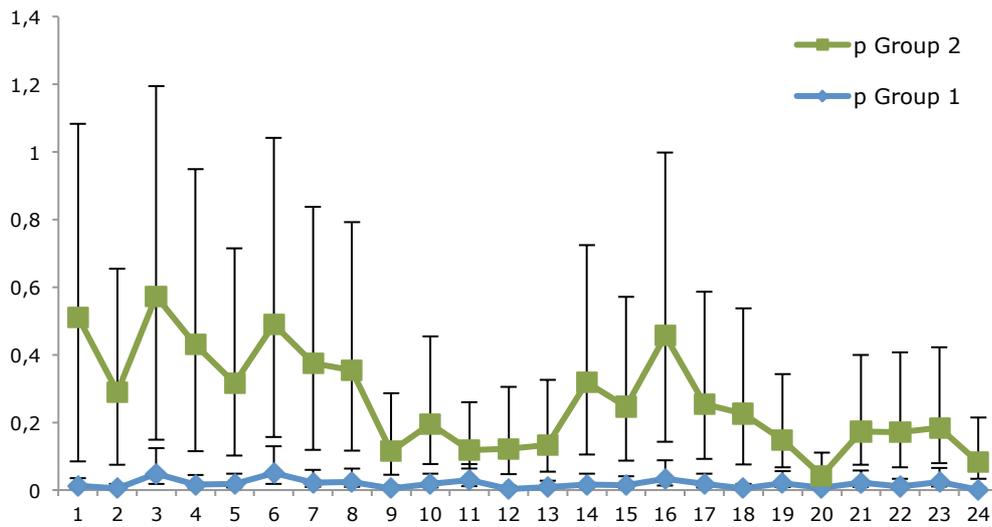


Figure 4.9: Capture probabilities for the Mtbh model for the Total dataset. Capture probabilities of the two putative populations (Mean $p_1 = 0.018$, $SE = 0.003$; Mean $p_2 = 0.246$, $SE = 0.029$).

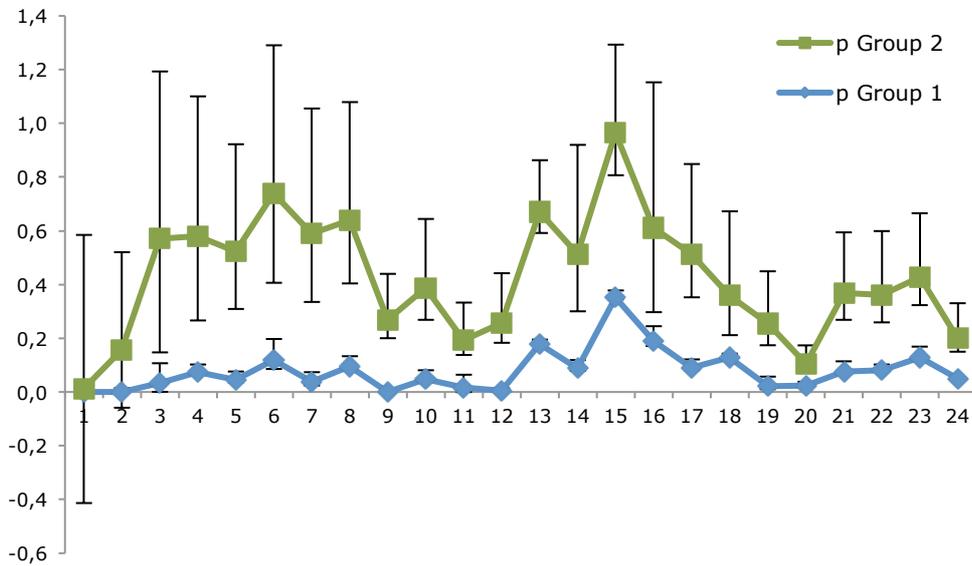


Figure 4.10: Capture probabilities for the Mth model for "-2" data set: encounter and recapture probabilities (constrain $p(t) = c(t)$) of the two putative populations (Mean $p_1 = 0.078$, $SE = 0.016$; Mean $p_2 = 0.350$, $SE = 0.036$).

Estimates of the total abundance of short-finned pilot whales in southwestern Tenerife, corrected for the proportion of identifiable animals, are summarized in Table 4.7 for the total, -1 and -2 datasets, respectively (Table 4.7).

Table 4.7: Averaged estimates of population size (N) of adult and indeterminate short-finned pilot whales, from closed population models and total population size (N_{total}) after adjusting for the proportion factors of well-marked individuals (θ). The coefficient of variation (CV) and log normal 95% confidence intervals are also presented for N_{total} .

DATA SET	N	CV	95% CI		θ	θ CV	N_{total}	CV_{total}	95% CI	
TOTAL	1,209	0.1377	560	1,661	0.4482	0.0187	2,698	0.139	2,057	3,538
-1	559	0.1549	444	803	0.4482	0.0187	1,247	0.156	920	1,690
-2	285	0.0204	277	301	0.4482	0.0187	636	0.028	602	671

The estimated number of animals of the two putative populations (two-mixture closed model) was calculated multiplying the averaged estimates of population size (N) by the value of π for the estimated abundance in the first group and multiplying by $(1-\pi)$ for the second group. For the total population with no restrictions, 1,019 and 190 were the whales with the lower and the ones with higher values of capture probability, respectively. For the dataset "-2", 160 animals and 125 were the ones with higher and lower values of capture probability, respectively.

Models that accounted for heterogeneity of capture probabilities were a better fit compared to others and gave higher estimates, confirming the presence of capture probability heterogeneity within the data (Williams *et al.*, 1993; Wilson *et al.*, 1999).

4.4 DISCUSSION

4.4.1 ABUNDANCE ESTIMATES

A crucial concern in employing any type of mark-recapture model is the initial evaluation of whether the population can be considered open or closed. There is no definitive test and several researchers (e.g., Otis *et al.*, 1978; Begon, 1979) have suggested that prior experience and knowledge are the best guidelines for this determination. *A priori* information often aids in assessing a general core area of usage by confirming consistent re-sightings of individuals within a survey region. Therefore, the choice of the best capture-recapture analysis methodology for this study was based on considerations which combined previous knowledge, as well as assessments on how and which basic model

assumptions could be considered to be met or not. In the attempt to alleviate the bias due to assumption violations, model selection for this study was thus made based on the following considerations.

MARK LOSS AND MISMATCHING

Changes in distinctiveness categories via the progressive addition of new dorsal fin nicks and notches over time, with consequent increased difficulty in matching different pictures of the same dorsal fins, are a relatively infrequent occurrence over short periods of time (Wilson *et al.*, 1999), such as the sampling intervals used in this study. It is therefore considered that mark loss or gain were negligible over the duration of this analysis (as described in Chapter 2). Violation of this assumption can be considered extremely unlikely and any bias should tend towards zero.

Despite great effort during the photo-identification analysis, the assumption that each individual is accurately recognized on each sighting occasion might not be met completely. The very large number of photographs and the large number of pilot whales identified made the photo-identification process quite tedious and difficult, with an increasing chance of committing identification errors and bias in abundance estimates (Gould and Pollock, 2002). In this study, only high-quality photographs and unambiguous markings were used during the photo-identification process, minimising the likelihood of violating this assumption.

CAPTURE PROBABILITY

The most difficult assumption to satisfy in this kind of analysis is the equal probability of capture among individuals. The sources of these differences may arise from a great variety of factors.

As with other studies of this nature based on photo-identification, violation of the assumption that marking does not affect future catchability is considered unlikely (Hammond, 1990; Wilson *et al.*, 1999; Read *et al.*, 2003). Nevertheless, once an individual has been encountered, it may simply ignore the vessel or react in a manner that reduces the probability of image capture. If an individual consistently avoids researchers, it may never be captured. Alternatively, individuals may intentionally approach the research vessel. Response behaviour may be due to a previous experience, wariness or curiosity. Behaviour may also be correlated with the distinctiveness of markings. A positive response to boat presence may also result in more frequent interactions and greater probability of acquiring natural markings as a result of

interactions with vessels and gear. Additionally, the age and experience of a calf may directly affect its response to capture efforts.

The test for a behavioural response showed that short-finned pilot whales in southwestern Tenerife had significant trap-happiness (increase in recapture probability after first capture). In these coastal waters, the population lives in an area where encounters with boats are relatively common and the animals do not normally avoid the whale-watching boats and small recreational vessels that approach them at slow speed and manoeuvre carefully to minimise disturbance. Also considering the general protocol followed in this study during fieldwork, it seems quite improbable that the benign process of being photographically 'captured' could lead to changes in response behaviour. Nevertheless, a certain familiarisation and even a curious attitude could be present in this population, especially in the resident individuals and especially towards the research vessel used to conduct this study. The inflatable boat Chacalote, which was used for the first time in the area during this study, had some physical features (length and coloration) that might superficially resemble an adult pilot whale. These aspects might, at least partially, explain the trap-happiness estimated for these animals. The presence of animals with different residency patterns in the same groups (see Chapter 2) made evaluation of the first reaction (25% of the time described as mixed behaviour) to the vessel approach useless for further investigations as to whether the differences in reactions were linked to different residency pattern.

INDIVIDUAL HETEROGENEITY OF CAPTURE PROBABILITIES

It was assumed that all individuals could occur in the study area at any time during the sampling period. Nevertheless, the assumption of equal capture probability of all individuals within a sample is often violated in cetacean mark-recapture studies (Hammond, 2001), which would lead to an underestimation of the population size.

Differences in capture probability may be a result of individual characteristics and group associations. Factors such as individual preferences for certain areas, differences in surface activity, surfacing patterns or boat-response behaviour (Hammond, 1986; Wilson *et al.*, 1999), but also age, gender, and group size may influence detectability and affect the probability of obtaining usable photographs. In this study, the selection of only a subset of individuals (in this study "adults" and "indeterminates") for parameter estimates was used to decrease heterogeneity and bias in capture probabilities, even though it may make the determination of how demographic estimates can be extended to the entire population more difficult.

The strong bond that characterizes this species' social structure indicates that the probability of seeing one individual may be highly related to the observance of other individuals. However, some associations may be transitory (Connor and Smolker, 1995) or related to behaviour, for example, feeding (Smith *et al.*, 1981; Fertl and Würsig, 1995; Rossbach and Herzog, 1999). Consequently, sightings and missed observations may be clustered (Cowan and Malec, 1986). It is possible that either entire groups or individuals within a group may be missed. Whitehead (2001) found both evidence and lack of support for heterogeneity when investigating within-group probability of sperm whales sightings.

Capture probability may be also influenced by variation in residency patterns; "transient" pilot whales have a high probability of being unavailable for capture (Pradel *et al.*, 1997) by having no chance of returning (permanent emigration), or by being part of the population but not always present in the study area (temporary emigration). Therefore, the documented differences in residency frequency within the pilot whales included in this study, with some individuals seen only once or twice during only a season ("transients", Chapter 2) would result in a lower capture probability. The effect of this on the estimates, and the way the different models could handle it, was investigated by applying the analysis also to the two data sets obtained by excluding the first capture and the first capture and recapture, respectively.

Heterogeneity might also be caused by survey design if survey effort is not representative. During each monthly sampling unit, an attempt was made to cover the whole study area homogeneously. The northern area in front of Los Gigantes was excluded by the analysis because it was insufficiently surveyed, and truly equal probabilities of encountering each individual were unlikely. To minimise heterogeneity, a great effort was also made to photograph every individual in a group and avoid preferentially photographing any particular individual. Pictures containing several individuals at once, up to entire groups, were also analysed during the photo-identification session of each sighting, looking for animals that could have been missed in order to decrease any possible effect of animals with more distinctive marks having higher catchability. More accurate final group sizes were therefore obtained. Despite these attempts, heterogeneity of capture probabilities was unlikely to have been completely overcome, most notably owing to individual preferences for particular areas combined with the fact that the departure harbour was always the same. Although the first course of the boat was randomly chosen, some areas might have been surveyed more intensively than others during the same daytime hours.

GEOGRAPHIC AND DEMOGRAPHIC CLOSURE

For a population to be geographically closed, each member of the population must be within the limits of the study area during surveys. Nevertheless, study areas are almost always smaller than the area inhabited by the target population: some aggregations of animals may have a lower probability of being seen and therefore the whole population does not have an equal chance of being captured (Hammond, 2010); this capture heterogeneity tends to produce negatively biased estimates of population size. As described in Chapter 2, the surveyed area in this study has been shown to mostly coincide with the range of the most frequently seen animals in the archipelago, but it is only a portion of the entire range of these animals. The comparison of the pilot whales identified in all the Canary Islands showed varying degrees of residency, as at any given time there was a mixture of residents, temporary migrants and transient individuals in the main study area and there were movements around the different islands of the archipelago, especially between Tenerife and La Gomera. One hundred and sixty nine individuals, 27% of the total well-marked pilot whales used for abundance estimation photographed in Tenerife, had also been sighted in other areas of the archipelago: 117 in La Gomera and 35 in Gran Canaria (23 in all three islands). Among these, the animals sighted more frequently in La Gomera had only been encountered once in Tenerife. Therefore, by removing from the complete dataset first (-1 dataset) and first and second (-2 dataset) captures, the analysis would exclude the greater percentage of moving whales (Chapter 2), and instead be focused in the "resident" animals in southwestern Tenerife.

The length of the study also implies that the study population cannot be demographically closed. Therefore, the assumption of demographic closure within the chosen sampling period was considered to be initially violated, and the open population methods were initially considered the most appropriate. On the other hand, demographic closure depends on the study length relative to the population dynamics of the study species. Closure can be approximately met if the study is short enough that births and deaths are likely to occur only at low rates (Hammond *et al.*, 1990). Short-finned pilot whales are large mammals with low reproductive rates and long life spans: births and deaths might have occurred during the two-year study, but the rates are low enough that bias in population estimates is likely to be small (Hammond, 1986). In addition, an advantage of closed population models is that they allow heterogeneity of capture probabilities to be modelled.

MODELS AND ESTIMATES

In an attempt to alleviate bias due to the violation of equal capture probability, and to account for the heterogeneity present in the data (overdispersion, a behavioural response and the presence of transient animals, as shown from U-CARE test results), open and closed population model options were investigated, as well as the possibility of restricting the dataset by excluding transient individuals, with the assumption that animals seen only once or twice were not going to be seen again in the area.

The Jolly-Seber open population model allows for variation in survival/emigration and births/immigration to obtain abundance estimates (Jolly, 1965; Seber, 1965; Thompson *et al.*, 1998). However, abundance estimation is not as robust in an open model as in a closed model for two reasons: 1) by having fewer assumptions, the abundance estimates are less precise (Thompson *et al.* 1998); 2) the open population model relies solely on Model Mt for abundance estimation, and does not include capture heterogeneity (Thompson *et al.* 1998). The assumption that marked and unmarked individuals have the same probability of capture must then be made (Hammond, 2010). On the other hand, closed population models can allow for heterogeneity in capture probability and are useful in providing abundance estimates.

After all these considerations, the chance of obtaining a more reliable abundance estimate of the resident population abundance without underestimation due to heterogeneity was investigated by excluding the first capture from the original data and, in addition, also the first recapture. By eliminating the first encounter from the total dataset (Annex 4: Figure A4.2a.), the resulting data subset still contained 86 individuals that were photo-identified in Tenerife but also sighted in La Gomera, and 31 in Gran Canaria (17 in all three islands) (Annex 4: Figure A4.2b). After also removing the first recapture from the total dataset, there were still 65 animals initially identified in Tenerife that had also been encountered in La Gomera and 25 in Gran Canaria (15 seen in all three islands) (Annex 4: Figure A4.2c).

The differences in residency patterns found in the Canary Islands population, as described in Chapter 2, with strong presence in southwestern Tenerife but also with individuals apparently just passing through, led to considering the POPAN open population model. The high number of animals seen only in one sampling occasion (49% of the animals considered in the analysis) and the continuous addition of new pilot whales to the catalogue, as shown in the discovery curve, could not have been solely attributed to births within the population, to the acquisitions of new scars, or to random capture probability. It must also have been due to movement of animals among the

islands (especially coming from La Gomera), and of temporary immigration of new animals into this area from neighbouring waters (Chapter 2).

The POPAN model, when applied to the total dataset, produced final abundance estimates that were approximately half those obtained by the Pledger two-mixture closed models (638, CV=0.0593 vs 1209, CV=0.1377). Such a difference is indicative of heterogeneity in the data that could not be accounted for by the open population model. However, the use of the closed population model probably introduced some positive bias in the abundance estimates (Hammond, 2010).

When excluding animals seen only on one sampling occasion, the abundance estimates produced by the open and closed models were still quite different (356, CV= 0.0284 vs 559, CV=0.155, respectively). The still increasing discovery curve from this dataset (Figure 4.7), as well as the quite high number of animals seen on only two sample occasions (12% of the total number of animals available for the analysis) (Figure 4.5), and the 117 animals detected in other islands, highlighted the continued heterogeneity of capture probability in the dataset.

When, instead, the dataset was further reduced by eliminating the first capture and the first recapture, the discovery curve levelled off (Figure 4.8), and the abundance estimate became quite similar for open and closed models: 274 (CV=0.038) and 285 (CV=0.020), respectively. In Chapter 3, by simply counting the capture frequencies of the different individuals, 241 animals were considered residents. The abundance estimates from the open and closed models applied to the dataset reduced by removing animals seen once and twice are thus consistent with the number of identified animals and a high capture probability, producing a robust abundance estimate for the most frequently seen pilot whales in the area.

Nevertheless, some heterogeneity in the data was still evident as shown by the different capture probabilities estimated for two mixtures (groups) in the closed model (mean= 0.078, SE=0.016; mean= 0.350, SE=0.036; Figure 4.10). This is probably due to the presence of two levels of site fidelity (with 125 whales with low and 160 with high capture probability) as seen in the sighting histories in the main area of southwestern Tenerife (Chapter 3): 134 individuals belonging to the "core resident" group and 125 defined as "residents" in the area, with 90 animals also seen in the neighbouring islands of La Gomera and/or Gran Canaria.

Considering that the database selected for this analysis was limited to only two years of study, a short time compared to the long lives of short-finned pilot whales (Chapter 1),

the estimate from the closed population model with two groups applied to the dataset excluding animals seen once or twice is considered the best estimate of the resident population in southwestern Tenerife: 636 (CV=0.028; 95%CI=602-671).

The best estimate of the total population in the Canary Islands during the study period is considered to be 2,697 animals (CV=0.139, 95%CI=2,057-3,538) from the closed population model with two groups applied to the total dataset that best accounts for heterogeneity.

Nevertheless, the estimate for the total population must be considered an underestimate. Even though heterogeneity of capture probabilities was addressed and taking into account the possibility of a slight overestimate from using a closed population model, it is clear that not all animals in the study area had a chance to be captured.

4.4.2 BIOLOGICAL RELEVANCE

The absence of direct conservation measures applied to short-finned pilot whales in the Canary Islands is rooted in the general lack of knowledge on even basic information about short-finned pilot whale population parameters. Moreover, the uneven character of the literature available for this species complicates understanding of their ecology and further delays the already slow process of implementation and enforcement of general conservation actions. Although the Canary Islands represent a perfect area to develop intensive long-term studies with relatively few resources (time and money) because of the easy and year-round accessibility of the species (Urquiola et al., 1998), the research studies conducted prior to the present work did not give a homogeneous picture of basic aspects of their natural history. The information was scattered in time and space, mostly limited to the island of Tenerife, and provided only descriptive details about their distribution or abundance obtained through studies carried out as a by-product of general purpose photo-identification surveys, quite likely to suffer from violation of the methodological assumptions. Moreover, differences in survey design and methodology do not allow for comparisons between them that would provide information about possible trends in the population.

Despite this, the abundance estimates from previous studies were widely accepted and used for general assessment. For the local authority, press and general public, the resident population of short-finned pilot whales in the southwest of Tenerife was 362 (Carrillo and Peña, 2002) - 388 (Heimlich-Boran, 1993) whales, with no major changes in abundance over almost a decade. Ignoring the differences in methodology in these estimates, the results apparently suggested the constant presence of this species with no

differences in abundance. The general threats, especially the growing anthropogenic pressure in the area, were, therefore, not seriously considered and the population in the area was considered sustainable. Despite the species being listed as "Vulnerable" in the National Catalogue of Threatened Species and these waters being part of a Special Area of Conservation (SAC) under the European Union's Habitats Directive for the presence of bottlenose dolphin, no specific monitoring programmes or conservation strategies have ever been implemented.

The estimates presented here for 2007-2009 were obtained using mark-recapture analysis of photo-identification data, similarly to studies on many other species (Evans and Hammond, 2004; Taylor et al., 2007; Parra *et al.*, 2006; Lukoschek and Chilvers, 2008; Reisinger and Karczmarski, 2010; Ramp *et al.*, 2010), but never previously applied to short-finned pilot whales. The estimated 636 (CI: 602-671) island-related whales that live in an approximate 550 km² area equate to a mean density of 1.16 animals km⁻², much greater than for long-finned pilot whales in the Strait of Gibraltar (Verborgh, et al., 2009), where survey methods and analytical approaches were consistent with those used in this study. Results suggest that pilot whale density in the area is greater than in most other areas where mark-recapture (for long-finned pilot whales) or line-transect studies have been conducted (reviewed by Olson 2009). Nevertheless, comparisons with abundance estimates obtained in other waters should be made cautiously because of the different methods used.

This study's results indicate that the southwest of Tenerife supports one of the world's highest densities of resident short-finned pilot whales, and thus demonstrate the significance of this aquatic habitat, which also supports high cetacean biodiversity with 24 species recorded (Martin et al., 2009). Besides some inter-island movements between Tenerife and the neighbours islands of La Gomera and Gran Canaria, regular photographic recapture showed that a large proportion of whales sighted in Tenerife had high levels of site fidelity, with individuals seen almost monthly in this area (Chapter 2). These aspects make this area an important "natural laboratory" for cetacean research, and further highlight the need for protecting this unique and vulnerable area through the adoption of substantial management measures informed by scientific evidence and for promoting environmentally conscious development.

As a result of the particular oceanographic conditions, with localised areas rich in nutrients in generally oligotrophic water, a high density of whales within the area might be related to prey availability (Chapter 2). The calm waters due to the mass effect of the island and the deep water very close to the coast (Chapter 1) would also make this area

also especially suitable for reproduction. Predation by sharks is also quite unlikely because large sharks are not present in the region and there is no evidence of shark attacks on pilot whales. Cookiecutter shark marks were observed but these do not represent a serious and direct threat to the population in the area. On the other hand, the waters of Tenerife have been submitted to continuous and growing anthropogenic pressure: coastal development with modifications of the habitat, the inter-island ferry network, tourism, whale-watching operations, and fisheries. Water quality in the area has worsened due to pollutants carried by the wastewaters from coastal cities and the increase in tourist infrastructure. Agriculture and fish farming have affected nutrient flow into the area, which might result in increased eutrophication (European Communities, 2002).

Changes in the environment (natural or anthropogenic) might directly affect population size (Gerrodette, 1987; Gerrodette and DeMaster, 1990; Kasuya, 1991; Sibly and Hone, 2002; Branch *et al.*, 2004), either by increasing mortality or inducing a shift in habitat use. However, in long-lived, adaptable and highly social marine mammals, such as short-finned pilot whales, rapid and direct reactions to environmental changes would not be expected. In fact, population size might remain stable or even decrease when well below carrying capacity (Pitcher, 1990; Gerber *et al.*, 2000; Waring *et al.*, 2002; Estes *et al.*, 2005).

Even though the assessment of on-going threats was not the aim of this study, some general actions would be important to consider in order to benefit water quality and marine biodiversity: (1) curtailment of anthropogenic pollutants and nutrients from city waste waters; (2) efforts to prevent illegal fishing; (3) monitoring and management of fish farming to limit eutrophication and other kinds of damage; (4) assessing the environmental impact of activities that may alter (or may have altered) the area's natural hydrology; (5) monitoring of whale watching activities, as established by existing regulation, to ensure compliance with the code of conduct, and also of recreational vessels and jet skis that illegally conduct whale-watching; (6) regulating the activities of ferries and pleasure boating, peaking in the summer, to reduce disturbance to cetaceans and collision risk.

At present, southwestern Tenerife is the only area within the archipelago with enough data to provide robust abundance estimates based on photo-identification techniques. Despite the copious amount of data processed in this study, the two year survey period is a very short time for a long-lived mammal and insufficient to investigate survival rates and other population parameters, and certainly not trends in such parameters over time.

Future studies should take into account the possibility of conducting simultaneous surveys in the different islands of the archipelago (especially Gran Canaria, La Gomera and Tenerife) in order to apply, for example, multi-site mark-recapture methods of analysis (Durban *et al.*, 2005). Cross-matching of individuals between areas would improve knowledge of their spatial and temporal use of their range, and enable more accurate estimates of population parameters for the whole population. In addition, the surveys should be designed using a consistent protocol. Application of a Robust Design model framework would be desirable so that abundance estimates could be determined during multiple short periods with closed populations and survival rates estimated from multiple years of data, taking into account any temporary emigration (reviewed in Pine *et al.*, 2003; Pollock, 1982).

4.5 CONCLUSIONS

The results of this study provide the first robust and reliable estimate of population size for the resident population of short-finned pilot whales in southwestern Tenerife, demonstrating the importance of this area. The results also represent an important first step towards understanding the population dynamics and are hence a necessary foundation for informed decision-making and improved conservation of this population. The study is also an important step towards evaluation of the conservation status of the species in the Canary Islands, so that the impact on the resident pilot whales of the growing pressure of human activities along these coastal habitats can be assessed and managed.

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CHAPTER 5

**MODELLING THE HABITAT USE OF SHORT-FINNED
PILOT WHALES IN THE CANARY ISLANDS**

5.1 INTRODUCTION

The description and quantification of patterns in the distribution and abundance of species and the processes that determine them represent fundamental aspects of ecology. Therefore, knowing where the animals are, what environmental characteristics influence their use of habitat, understanding how cetacean density varies spatially as a function of these factors and knowledge of their inter-relationships provide insight into the characteristics that define cetacean habitat and can contribute significantly to the management and conservation of cetacean populations (Cañadas and Hammond, 2008). Spatial models can provide crucial information to assess the effects of habitat change, to establish protected areas, and for decision-makers who must act to reduce, minimize, or eliminate the harmful effects of human activities on a specific cetacean species (Guisan and Zimmermann, 2000; Redfern *et al.*, 2006).

While many studies have revealed cetacean association with specific physical and biological features at distinct spatial and temporal scales (e.g. Evans, 1987; Baumgartner *et al.*, 2001; Murase *et al.*, 2002; Tynan *et al.*, 2005; Marubini *et al.*, 2009; Scott *et al.*, 2010), the predictability of species-habitat associations and the underlying biophysical mechanisms are still poorly understood (Yen *et al.*, 2004). This may be partly explained by the fact that cetacean-habitat relationships are usually indirect, and cetacean distribution likely reflects the way prey species respond to physical and oceanographic features (Ballance *et al.*, 2006), representing the main determinant of marine mammal distribution (e.g. Benoit-Bird and Au, 2003; Hastie *et al.*, 2004; Frederiksen *et al.*, 2006; Friedlaender *et al.*, 2006).

Because prey abundance is often hard to measure directly (Guisan and Zimmermann, 2000; Jaquet and Gendron, 2002), other more easily obtained environmental variables are instead typically used as proxies, even if they are not always directly and causally related with animal presence (Redfern *et al.*, 2006). Several physiographic (e.g. depth, slope, aspect), oceanographic (e.g. sea surface temperature) and biological variables (e.g. chlorophyll a surface concentration) have been successfully used to describe cetacean habitat preference (e.g. Cañadas *et al.*, 2002; Davis *et al.*, 2002; Hamazaki 2002; Yen *et al.*, 2004; Cañadas *et al.*, 2005; Ferguson *et al.*, 2006; Panigada *et al.*, 2008; Praca and Gannier, 2008).

Environmental variability can cause marked shifts in the distribution of many cetacean species, which have the ability to respond to the dynamic nature of the marine ecosystem by changing their distribution patterns to follow favourable habitats as they

move through time and space (Forney, 2000). Nevertheless, it may be difficult to discriminate distribution patterns caused by cetacean-habitat associations from those linked to other aspects of the species' biology (e.g., migrations, movements related to reproduction) (Ballance *et al.*, 2006). Nevertheless, for species characterised by complex ecology, social structure and behaviour, the study of their distribution and habitat use should consider not only "extrinsic" factors (i.e. abiotic and biotic environmental), but also biological factors (Cañadas and Hammond, 2008). Other potentially important factors affecting habitat use could also include factors such as feeding strategies, behavioural state, presence of calves, inter-specific relationships (Cañadas and Hammond, 2008), predation risk (e.g. Heithaus and Dill, 2002), competition (e.g. Shane, 1995) and reproductive needs (e.g. Ersts and Rosenbaum, 2003).

Cetacean biologists commonly use line-transect sighting surveys in order to provide information on abundance and distribution (e. g., Hammond, 1984; Sigurjónsson *et al.*, 1989; Wade and Gerrodette, 1993; Barlow, 1995; Forney *et al.*, 1995; Branch and Butterworth, 2001; Waite *et al.*, 2002; Hammond, 2010). However, classical line-transect surveys require equal probability of sampling the study area (e.g. Buckland *et al.*, 2001), with transects selected randomly and independently from animal distribution. In surveys not designed in this way, other analysis methods are necessary (Buckland *et al.*, 2004; Hedley and Buckland, 2004; Gomez de Segura *et al.*, 2007). Spatial modelling methods using line-transect survey data offer a viable technique to model the distribution of cetaceans using data from line-transect surveys without the need for equal coverage survey designs (Hedley *et al.*, 1999; Hedley and Buckland, 2004; Hedley *et al.*, 2004).

This method combines line transect sampling with spatial analysis to predict density distribution based on the relationship between observed animals and spatial and environmental covariates, as well as taking into account the probability of detecting them. Therefore, it is an appropriate method for analysing data collected from dedicated surveys without a systematic design or from "platforms of opportunity" (Buckland *et al.*, 2004). Another advantage is that density surface modelling allows the abundance estimation in any subset of the study area (Gómez de Segura *et al.*, 2007). Moreover, in spatial distance sampling models, the abundance estimate precision may increase by including environmental features if variability in density along the trackline is a result of variation that can be explained by these features rather than sampling error (Hedley *et al.*, 1999; Forney, 2000; Williams, 2003).

Statistical methods in the form of generalized linear models (GLMs) or generalized additive models (GAMs) provide powerful tools for constructing habitat models that have been widely used to improve ecological understanding and to aid conservation and management initiatives (Guisan, *et al.*, 2002; Silva, 2007). Animal density is modelled along the trackline as a function of spatial or environmental covariates, and then that relationship is used to predict density over the entire study area (Williams *et al.*, 2006).

GLMs are mathematical extensions of linear models that are not restricted to normally distributed data and thereby allow for non-linearity and non-constant variance structures in the data (Hastie and Tibshirani, 1990). They are based on an assumed relationship between the mean of the response variable and the linear combination of the explanatory variables through a link function. Data may be assumed to be from several families of probability distributions, including the normal, binomial, Poisson, negative binomial, or gamma distribution, many of which better fit the non-normal error structures of most ecological data, e.g. counts or presence/absence data.

GAMs, described by Hastie and Tibshirani (1990), are non-parametric extensions of GLMs that allow the incorporation of additive smooth functions determined by the data. They also allow non-normally distributed data and use a link function to relate the mean of the response variable to smooth functions of the explanatory variable(s). The strength of GAMs is their ability to deal with non-monotonic, non-linear relationships between an independent variable and multiple predictors, which are more common in nature than linear relationships; Oksanen and Minchin, 2002). They allow quantitative exploration of species-habitat relationships, when little is known about the underlying mechanisms responsible for generating the observations (Guisan *et al.*, 2002; Olivier and Wotherspoon, 2005). They are ecological models of continuous relationships, producing spatial predictions that are functions of the environment. These characteristics are therefore different from techniques such as classification and regression trees, which are based on a series of binary decisions derived by dichotomizing the data (Olivier and Wotherspoon, 2005), or geostatistical methods that produce spatial predictions based only upon location (Lehmann *et al.*, 2002).

Comparing the different modelling techniques, Moisen and Frescino (2002) found that GAMs built on real data performed marginally better than other techniques (classification and regression trees, artificial neural networks, and linear models) when predicting data from test samples. GAMs have regularly been used to analyse the distribution and density of marine species in relation to geographical and environmental variables (e.g.,

Swartzman *et al.*, 1992; Daskalov, 1999; Forney, 1999; Hedley *et al.*, 1999; Forney, 2000; Bellido *et al.*, 2001; Maravelias and Papaconstantinou, 2003; Ferguson *et al.*, 2005; Cañadas and Hammond, 2008; Valavanis *et al.*, 2008) and to provide valuable information for conservation purposes (Redfern *et al.*, 2006).

5.1.1 SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS

To date, no studies conducted on short-finned pilot whales in the Canary Islands have considered species-habitat association by quantifying its density as a function of the environment.

The studies conducted so far in the south west of Tenerife have only considered their presence-absence distribution, and have shown a non-homogeneous distribution throughout the study area, with areas of low, medium and high use. Heimlich-Boran found higher concentrations limited to 25% of the 50 km² study area in the south-west of Tenerife (Heimlich-Boran, 1993). Subsequent work restricted the most frequently used area to 27 km², 11% of the studied region at a mean depth of 1,066 m (Carrillo and Tejedor, 2003). Nevertheless, the differences in these studies, especially in the survey methodology, do not allow useful comparisons of the results to be made.

Given the patchy distribution of short-finned pilot whales in the archipelago, and differences in site-fidelity (Chapter 2), information on their species-habitat relationships would allow identification and quantification of the importance of a specific habitat and therefore areas where the implementation of conservation actions would be more urgent for this species. Therefore, understanding where, and why, this species occurs within the range of the potential habitats, should be accompanied by information on the scale and relative importance of actual or potential anthropogenic threats to them and priorities of possible mitigation measures.

The habitat use of short-finned pilot whales in the Canary Islands was investigated here through a spatial modelling approach using physiographic (depth, slope, distance from the coast), remotely sensed variables (Sea Surface Temperature SST, Chlorophyll-a concentration Chl-a), and biological factors (i.e. reproductive status, behaviour, inter-specific relationships). An extensive data set on this species in the whole archipelago was used for the analysis to model regional and seasonal variation in habitat use, and to map model predictions. The primary goal of the study was to analyse short-finned pilot whale distribution. The average number of whales that use the area was estimated to evaluate and quantify the importance of the study area to the population by testing whether pilot

whales show preferences for specific areas, conditioned by specific factors, and then to assess the vulnerability to the increasing threats due to the growing anthropogenic pressure.

Specific aims of this study were:

- 1) to examine spatio-temporal (geographical, seasonal, between-year) patterns and trends in short-finned pilot whale distribution and abundance in the Canary Islands;
- 2) to explore the influence of "extrinsic" (i.e. abiotic and biotic environmental) and "biological" factors (i.e. reproductive status, behaviour, inter-specific relationships) on the distribution patterns of the species.
- 3) to use relationships between short-finned pilot whale distribution and "extrinsic" and "biological" factors to derive quantitative spatial predictions of the density of individuals throughout the study area.

The results of this study constitute the first step in the development of conservation and management actions in Canary Islands and also serve as a baseline for future work, which is especially important in light of the increasing anthropogenic pressure on the species, and the progressive change of habitat.

5.2 METHODOLOGY

5.2.1 STUDY AREA

Transects were not systematically designed, but the resulting route covered an extensive range of habitat types over the entire archipelago (Figure 5.1): shallow regions near the shore, steep slope areas, sea mounts and canyons, and deep oceanic areas, affected by different current systems; high anthropogenic impact areas, with intense boat and ferry traffic, and close to important inhabited centres, as well as the oceanic corridors between the islands generally covered only by occasional fisheries and cargo boats. Figure 5.1 shows the area considered in the analysis, which encompasses 22,447 square kilometres.

5.2.2 SIGHTING DATA AND SURVEY EFFORT

The dataset used for the analysis came from the different SECAC surveys conducted in the archipelago between 1999 and 2012 (Chapter 2). The data previously collected, between 1993 and 1998, were not included in this analysis as they were too limited.

The studies were conducted on board a variety of platforms, following slightly different protocols at sea, depending on the target species (Figure 5.2; Chapter 2). Therefore, basic information was always collected and data reliability was assured by the presence of experienced observers. Because of this, and because data collection was spatially and

temporally broad enough to incorporate a range of habitat variability for cetacean-habitat modelling purposes, dedicated studies and surveys on platforms of opportunity (whale-watching boats and ferries) collected data that could be considered equivalent (e.g. Cañadas *et al.*, 2005; Redfern *et al.*, 2006) and then included in the analysis. In this way, better area coverage was achieved and the study was conducted on a broader geographic scale, especially considering the importance of including areas of high and low cetacean densities to differentiate species habitat from non-habitat (Redfern *et al.*, 2006).

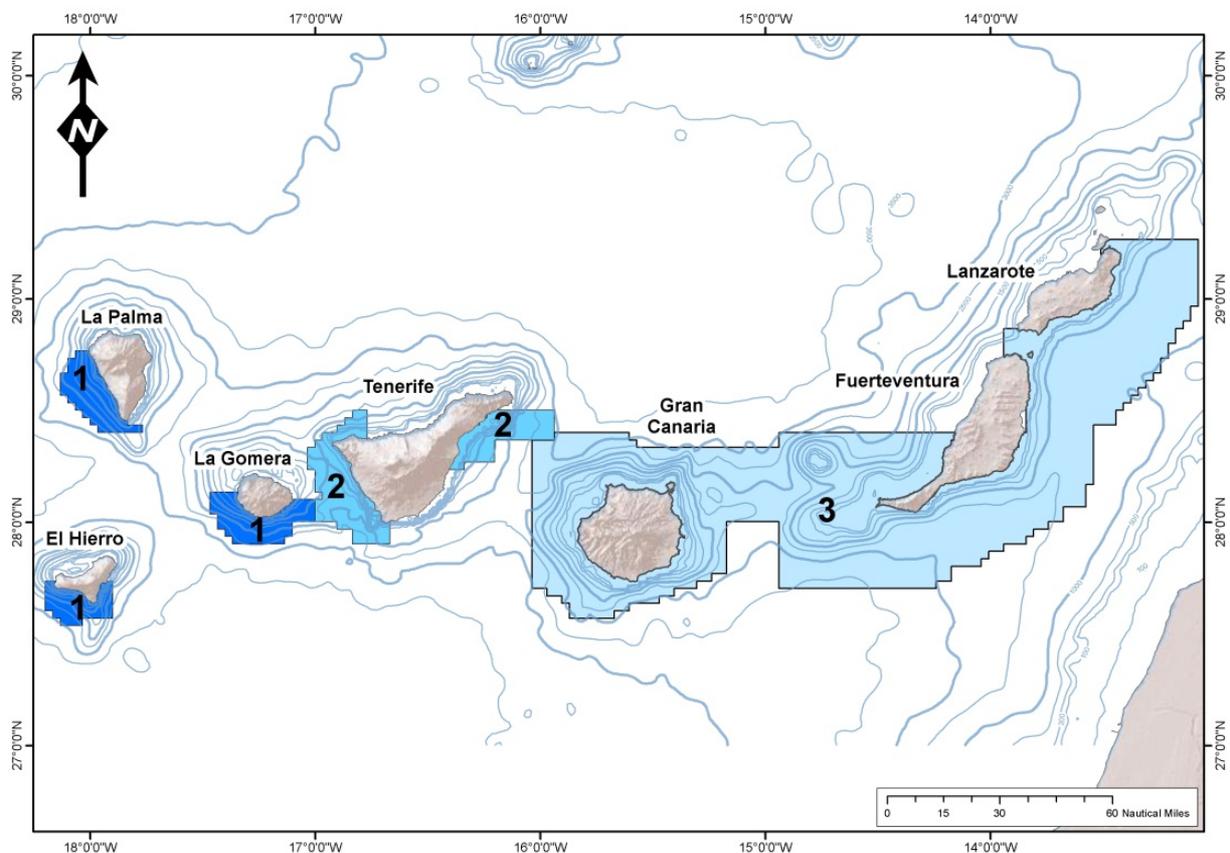


Figure 5.1: Study area in the Canary Islands, divided in the three regions: western islands (El Hierro, La Palma, La Gomera, Area 1); Tenerife (Area 2); eastern islands (Gran Canaria, Fuerteventura, Lanzarote, Area 3).

The area covered over the years was stratified into different layers based on the different survey methodologies and platforms used (see the general methodology description in Chapter 2). Inflatable boats and small artisanal fishing vessels were pooled together based on similar protocol and boat features (Figure 5.2). Surveys conducted on sailing boats were separated from surveys on dedicated research vessels, and from surveys on board ferries between the islands (Figure 5.2).

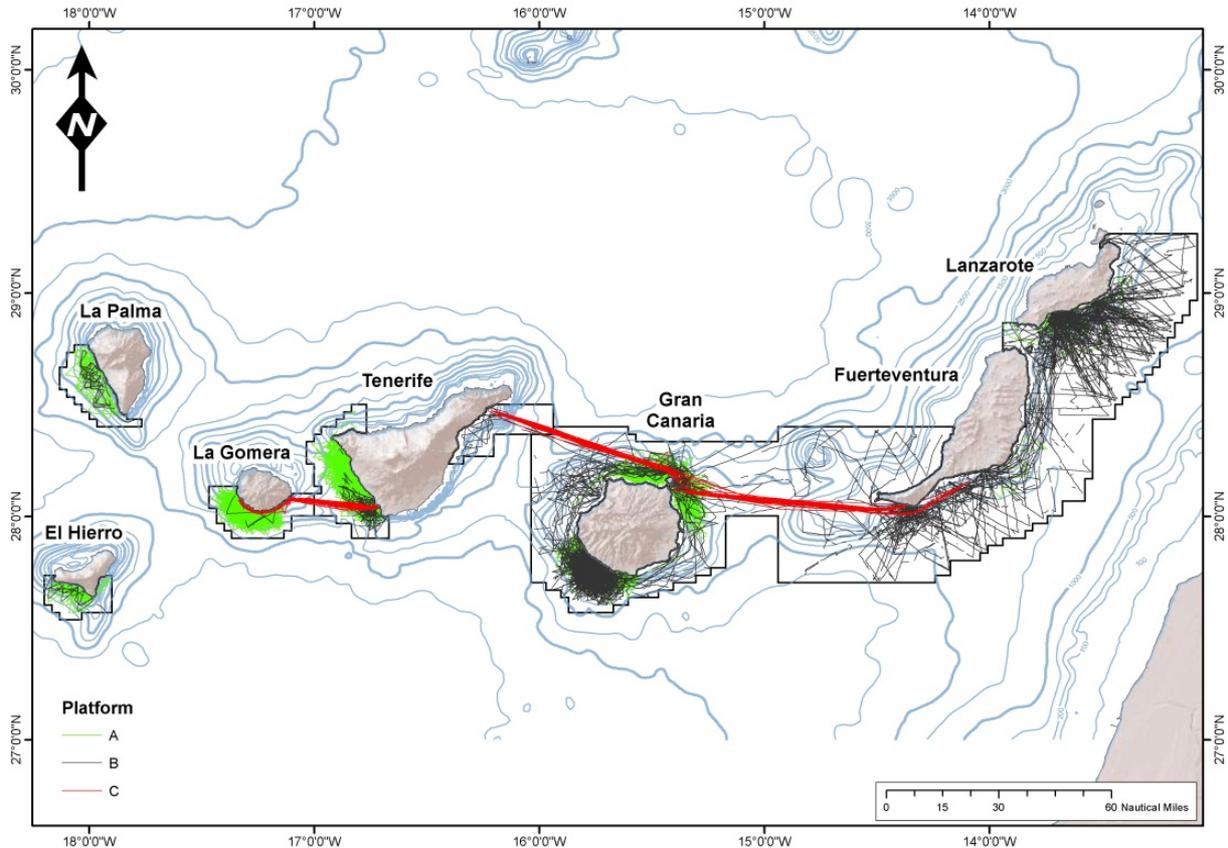


Figure 5.2: Areas covered by sea survey, stratified into different layers based on methodology and platform used: green tracklines A) indicate inflatable boats and small artisanal fishing vessels; black tracklines B) indicate dedicated research vessels, and red tracklines C) indicate ferries.

To facilitate data analysis and for comparative analysis in addition to considering it as a whole, the archipelago was divided into different regions, based on the oceanographic, and physiographic features of the water of the different islands, the different vessels used (Figure 5.2), and sighting distribution in relation to effort (encounter rate, Chapter 3; Figure 5.3): 1) El Hierro, La Palma and La Gomera, 2) Tenerife, and 3) the eastern islands of Gran Canaria, Lanzarote and Fuerteventura. The island of Tenerife, where most pilot whale sightings are concentrated, was considered individually and also explored for spatial and temporal trends.

None of the surveys was conducted using a strict protocol of systematically designed equal coverage probability transects because of the logistic limitations of the different vessels (relatively slow cruising speed, high dependence on weather conditions and the necessity to return to port every night), and the specific objectives of the different projects with protocols that were incompatible with such a survey design.

The survey protocol followed, as well as the protocols for data collected during surveys and sightings, is extensively presented in Chapter 2.

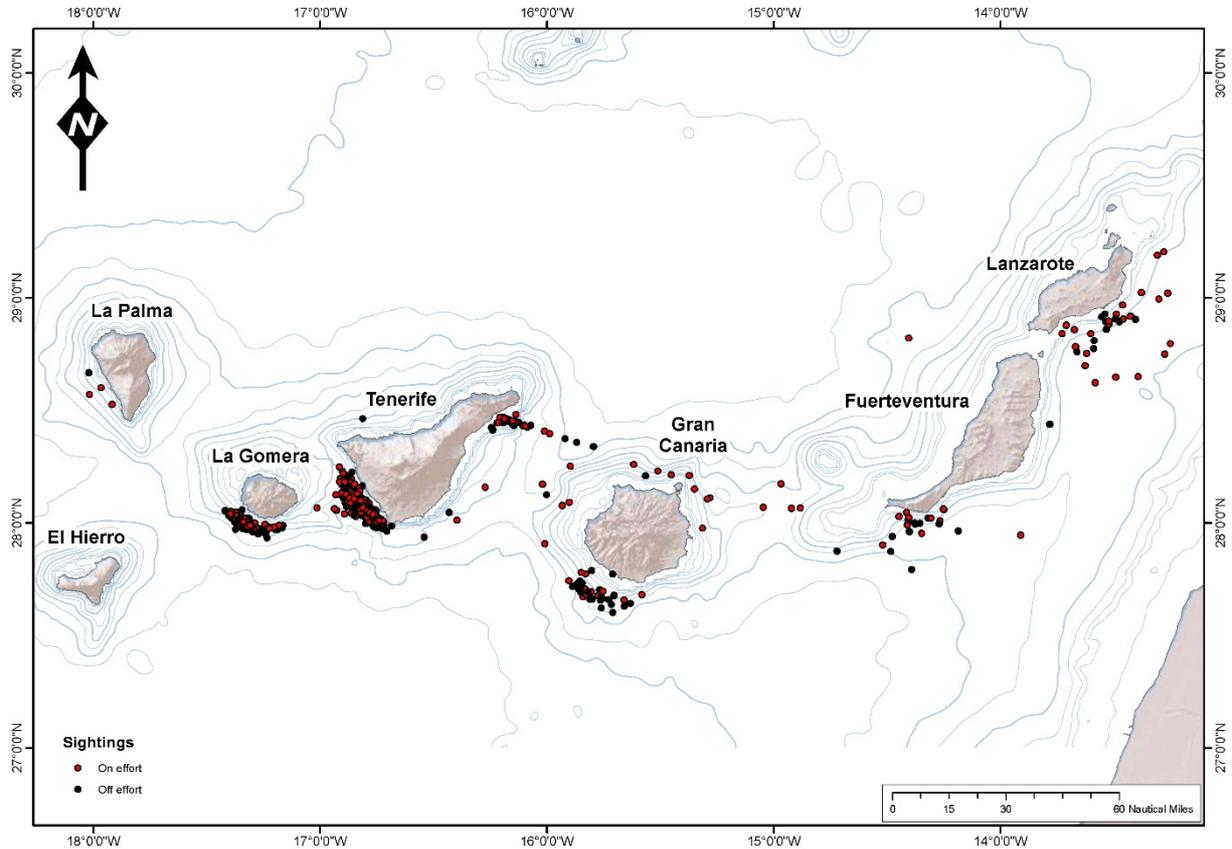


Figure 5.3: Sightings of short-finned pilot whales on effort (black dots) and off effort (red dots), between 1999 and 2012 in the study area in the Canary Islands.

5.2.3 DATA SYNTHESIS

The data collected were reorganized and eventually pooled in joint categories specifically for this analysis. The fields "sea state" (Douglas:0-3), "wind force" (Beaufort:0-3) and "swell" (categories of a half metre each, and less than 2m) were treated separately but also were combined in a single field "Sightability", with categories from 0 to 4, from optimum to inadequate sighting conditions (the data in category 4 were not used for the analysis). Vessel type was combined with platform height (e.g. two platforms at different levels above the sea in "Oso Ondo") and aggregated into four categories (P.L.= platform-sea level): 0-P.L. for the inflatable and fishing boats; 1-P.L. for sailing boats and for the main deck of research boats; 2-P.L. for high platforms in research boats, and 3-P.L. in the case of ferries.

Survey tracks, effort and species sighting data were plotted using Geographic Information System software (ArcGIS 10.1): locations, time, information on school size, group composition and activity, environmental parameters and all other considered variables. Using ArcGIS 10.1, the study area was divided into a grid of cells with a resolution of two minutes of latitude by two minutes of longitude (approximately 3.5 km by 3.5 km), resulting in 1,950 cells covering the entire area: 168 for the western area, 1,613 for the eastern area, and 169 for the island of Tenerife. This grid size was a compromise between the resolution of the environmental data available, the aim of determining environmental relationships and the need to avoid the large majority of cells having no sightings. Each grid was populated by values of the geographical and environmental covariates (Table 5.1). This grid polygon vector layer overlapped the GIS layers containing pilot whale sightings, and observation effort data.

All on-effort transects were divided into segments of homogeneous effort type (minimum 0.1 km, maximum 3.7 km, average 1.5 km), assuming little variability in physical and environmental features within each segment. By intersecting the grid polygon layer with the sightings and segments layers, each segment was assigned a number of sightings and a value for each environmental covariate corresponding to the average of the relevant grid cell.

5.2.4 ENVIRONMENTAL DATA

Specific data on physical and environmental features for habitat use analysis were not collected *in situ* for the entire study area. The following environmental variables were available for use to model short-finned pilot whale density (Table 5.1).

1. Latitude and longitude.
2. Data on seabed depth were extracted from nautical charts of the Hydrographic Institute of the Spanish Navy and for each cell of the grid the mean, the standard deviation, and the logarithm of the depth were calculated. Distances from the 200 m and 1000 m isobaths were also calculated.
3. Data on the gradient of the seabed slope (maximum rate of change in depth in a given grid cell expressed as a percentage slope) were calculated from nautical charts of the Hydrographic Institute of the Spanish Navy. The contour index (CI) was also calculated as (maximum depth-minimum depth)/distance between them.
4. Satellite-derived sea surface temperature (SST) and chlorophyll concentration (Chl) data were sourced from the climatological average value of a time series of Level 3 Standard Mapped Image (SMI) products, published by the NASA GSFC

Ocean Color Group. Daily images of 1/24 degree resolution were used, with a pixel resolution of 4 km². Averages for both SST and Chl were calculated monthly and seasonally (winter: December-May and summer: June-November) (Fieldman and McClain, 2012, <http://oceancolor.gsfc.nasa.gov>).

Table 5.1: Variables and groups of variables used in the models.

VARIABLES AND GROUPS	DEFINITION
GEOGRAPHIC	
Lat	Latitude
Lon	Longitude
UW/DW	Upwind/Downwind
PHYSIOGRAPHIC (depth, with resolution of 100 m)	
Depth	Depth (mean)
DepthMax	Max value of depth
DepthMin	Minimum value of depth
DepthRange	Range of depth
Logdepth	Logarithm of depth
DistCoast	Distance from coast
LogDistCoast	Logarithm of distance from coast
Dist200	Distance from the 200 m isobaths
Dist1000	Distance from the 1000 m isobaths
PHYSIOGRAPHIC (bottom, with resolution of 100 m)	
DepthCV	Coefficient of variation of depth
DepthSTD	SD of depth
Slope	Slope (m/Km ²)
Slope aspect	From -180° to +180° with respect to true north
CI	Contour index ((max. depth-min.depth) x100/max.depth)
OCEANOGRAPHIC (satellite image, with resolution of 4 km²)	
ChIAWi	Mean winter chlorophyll concentration (December-May)
ChIASu	Mean summer chlorophyll concentration (June-November)
ChIA	Mean annual chlorophyll concentration
SSTWi	Mean winter SST (December-May)
SSTSu	Mean summer SST (June-November)
SST	mean annual SST
SSTstdWi	SD of winter SST (December-May)
SSTstdSu	SD of summer SST (June-November)
SSTstd	SD of annual SST

Additionally, other variables considered important for pilot whale distribution were taken into account and calculated for each grid cell: slope aspect (compass orientation of the slope, ranging from -180° to $+180^{\circ}$ with respect to true north), distances (from the midpoint of each grid cell) from shore, upwind and downwind water (based on exposure towards the main sea currents coming from the northeast). Other factors were also considered in order to investigate possible differences in habitat preferences based on the presence/absence of calves in the groups, the presence/absence of mixed sightings with bottlenose dolphins, and on different behavioural categories (travelling, resting, feeding, socialising).

Examining the mean values per month of the different variables calculated for the entire study period, the data were stratified and combined into pooled time periods; the sea surface temperatures and the chlorophyll values were combined in two "seasons" (June-November; December-May) as well as being pooled in an annual mean.

Prior to modelling, the variables were tested for correlation using Spearman's rank correlation coefficient. In the case of significant ($p < 0.05$) high correlation ($r > 0.5$) between variables, the first of the variables selected by the stepwise model selection was retained and any variables with which it was correlated were discarded.

5.2.5 DATA ANALYSIS

Model-based abundance estimation was done following Cañadas and Hammond (2006, 2008) and can be summarised in the following steps:

- 1- estimation of the detection function for each platform category, and of the covariates that could have affected it;
- 2- modelling of the number of groups as a function of geographical and environmental covariates, using the effective searched area (from the effective strip half-width, ESW, obtained from the detection function) as an offset;
- 3- modelling group size as a function of covariates – if no model was appropriate, mean group size was calculated;
- 4- estimation of pilot whale abundance for each grid cell based on model prediction obtained in steps 2 and 3, by multiplying the predicted group abundance by the mean or predicted group size;
- 5- mapping the results to show the total short-finned pilot whale abundance in Canary Islands, and for each selected sub-area.

DETECTION FUNCTION MODELLING

The detection function gives the probability of detection of short-finned pilot whale groups as a function of perpendicular distance from the line transect and any additional covariates that are found to affect detection probability. Different functions were calculated for each of the four different platform type/height categories (PL. 0-3). For effort type 0-PL. a total of 428 sightings were used, 19 sightings for 1-P.L., 38 sightings for 2-P.L., and 61 sightings for 3-P.L. To reduce the number of different combinations, 1-PL. was combined with 2-PL.

The complete data set was visually inspected for evidence of rounding in distance and angle measurements. Consequently, a smearing procedure was applied to the data by selecting a random angle ($\pm 3\%$ of the value), within a "smearing sector" centred on the recorded position (Buckland *et al.*, 2002). For the sighting distances recorded as "0", a random value was chosen between 0m and 20m for 0-P.L, and between 0m and 50m for the rest of the platforms. All non-zero distances were smeared by $\pm 30\%$ of the value, independent of the survey platform used.

The software DISTANCE 6.0 release 2 (Thomas *et al.*, 2009) was used to estimate the detection function using the multiple covariate distance sampling (MCDS) method (Marques 2001, Thomas *et al.*, 2002). After a preliminary inspection of the distribution of the perpendicular distances, they were right truncated prior to analysis.

In order to find the best fitting function to the data, the covariates in Table 5.2 were included in the analysis singly and progressively in combination. The best detection functions were selected using Akaike's Information Criterion (AIC).

Table 5.2: Covariates incorporated in detection function modelling. Indications of whether treated as a continuous variable or as a factor, and the levels used when treated as a factor are also reported. Group size, observer experience, cue conspicuousness, and sightability (from optimum "0", to no feasible sighting conditions "4").

COVARIATE	TYPE	LEVELS
Observer	Factor	2 levels: expert, and not expert
Sea state: Douglas	Factor	4 levels: 0, 1, 2, 3
Wind force: Beaufort	Factor	4 levels: 0, 1, 2, 3
Swell	Factor	4 levels: 0, 1, 2, 3
Sightability	Factor	4 levels: 0, 1, 2, 3

The effective strip half-width was extracted for each level of the covariates in those detection functions where covariates were selected using software R (R 2.4.1, R Development Core Team, 2006).

MODELLING ABUNDANCE OF GROUPS

A Generalized Additive Modelling (GAM) framework was used to model the abundance of groups (N_i), based on the relationship of animals sighted with environmental variables. The observed number of groups was used as the response variable, and the Tweedie error distribution (Tweedie, 1984; Jorgensen, 1987) was used to account for any over-dispersion.

Applying a logarithmic link function (to appropriately relate the data to the linear model and to ensure positive values of the mean response), the general structure of the model was:

$$\hat{N}_i = \exp \left[\ln(a_i) + \theta_0 + \sum_k f_k(Z_{ik}) \right]$$

where the offset variable a_i is the effective search area for the i^{th} segment (calculated as the length of the segment multiplied by twice the effective strip half width), θ_0 is the intercept to be estimated, f_k are smoothed functions of the explanatory covariates to be estimated, and z_{ik} is the value of the k^{th} explanatory covariate in the i^{th} segment.

For fitting GAMs, the package "mgcv" (Wood, 2000; Wood, 2006) was used in R version 2.15.2 (R Development Core Team, 2012, <http://cran.r-project.org>) to fit the models. As described by Cañadas and Hammond (2006), three indicators were used to select the best-fitting models: 1) the General Cross Validation (GCV) score, an approximation to AIC (Wood, 2000, 2001) in which smoothing parameters are chosen by the software to minimise the GCV score of the models; 2) the percentage deviance explained; and 3) the probability that each variable is included in the model by chance.

The default maximum number of knots, equivalent to degrees of freedom and an indication of the complexity of the fitted smooth curves) is 10 for single covariate smooth functions, and 30 for covariates in interaction. To reduce potential overfitting, the maximum number of knots for the smooth functions for each explanatory covariate were

limited according to the dataset being analysed (never exceeding 25% of the total number of positive observations).

The number of groups was then predicted for each cell of the study area using the values of the environmental variables in each cell and the selected best-fitting model.

MODELLING GROUP SIZE

Group size was expected to vary spatially and as a function of environmental covariates so group size was also modelled using GAMs (Borchers and Burt, 2002; Hedley and Buckland, 2004; Cañadas and Hammond, 2006). The number of pilot whales sighted in each group (s_j) was the response variable. A logarithmic link function was used, with a quasi-Poisson error distribution.

The general structure of the model was:

$$E(s_j) = \exp \left[\hat{g}_j(y, v) + \theta_0 + \sum_k f_k(Z_{jk}) \right]$$

where θ_0 is the intercept to be estimated, f_k are smoothed functions of the explanatory covariates to be estimated, and z_{jk} is the value of the k^{th} explanatory covariate in the j^{th} group. The models were selected manually, following the same criteria described for the group abundance models.

ABUNDANCE ESTIMATION

The estimated abundance of pilot whales for each grid cell was calculated by multiplying the predicted abundance of groups and the predicted group size. The total abundance of whales was obtained by summing the abundance of all grid cells over the study area, and the density was calculated by dividing this abundance by the total area.

UNCERTAINTY ESTIMATION

Group abundance uncertainty was estimated using a non-parametric bootstrap of the data (400 replicates with replacement; Cañadas and Hammond, 2008), using R software,

using day as the re-sampling unit, to obtain the coefficient of variation (CV) and percentile based 95% confidence intervals (Cañadas and Hammond, 2008). It was not possible to calculate a single CV for the abundance estimate for each dataset, as there were three different detection functions (one for each of the three platform classes: 0-PL., 1/2-PL., and 3-PL) applied to the data within a single model. Instead, a range of final CVs was obtained using the delta method (Seber, 1982), combining the CV from the bootstrap with the CV from each detection function used.

HABITAT USAGE

The non-homogeneous effort conducted along the different islands during the study period, and the great concentration of short-finned pilot whale sightings in the southwest of Tenerife lead to the decision to perform the analysis at different levels, through stratifications in terms of area and time. Habitat usage was explored in the archipelago as a whole, and also dividing the entire area into three sub-regions corresponding to: the most western islands (El Hierro, La Palma, and La Gomera); the central island (Tenerife); and the most eastern islands (Gran Canaria, Lanzarote, and Fuerteventura) to enable differences in pilot whale densities in these three areas to be highlighted better than when the data were analysed together. The modelling analysis also produced seasonal and annual estimates by using the complete dataset for the entire archipelago and for Tenerife (discarding the other two islands because of the lack of uniform effort over time). In addition, the biological factors, behavioural categories, groups with or without calves, and presence of groups mixed with bottlenose dolphins, were investigated for evidence of differences in habitat usage in the Canary Islands and Tenerife.

The predicted abundance surfaces were plotted in prediction maps, where colour gradation helped to locate the areas of higher predicted probability of encountering the whales. Animal densities were inferred from visual inspection of the maps.

5.3 RESULTS

A total of 68,302.5 km were searched on effort between 1999 and 2012, during which 706 sightings (plus 292 off effort sightings) of short-finned pilot whales were observed (see Chapter 3). Effort and sightings were distributed non-homogeneously around the different islands of the archipelago and varied annually (Chapter 3), and by research platform used (Figure 5.2).

5.3.1 DETECTION FUNCTION

Detection functions were estimated (Table 5.3, Figure 5.4) for each platform type:

0-P.L.: inflatable and fishing boats. Perpendicular distance data were truncated at 1,400 m, discarding five sightings and leaving 423 sightings for analysis. The hazard rate function was selected as the best fitting model with cosine as the series expansion and two adjustment terms. Type of effort ("sightability") was the only covariate retained in the model (Table 5.3, Figure 5.4a)

1/2-P.L.: sailing boats and research vessels. Perpendicular distance was truncated at 1,500m, discarding three of the total 59 sightings. The best fitting model selected was the half normal key function with cosine series expansion, with two adjustment terms. No additional covariates were selected (Table 5.3, Figure 5.4b).

3-P.L.: ferries. Perpendicular distance was truncated at 600m, after which 46 of the total 61 sightings were included in analysis. The hazard rate function was the best model selected with cosine series expansion and no adjustment terms (Table 5.3, Figure 5.4c). No additional covariates were selected.

Table 5.3: Results of the three detection functions, based on type of platform used: 0-P.L.: inflatable and fishing boats, 1+2-P.L.: sailing boats and research vessels, 3-P.L.: ferries. The following information is presented for each function: type of model; truncation distance, number of observations used for the analysis; probability of detection (p, SE); effective strip width (ESW, SE); coefficient of variation of p and ESW (%CV); variables selected in the models, with coefficient and SE. Variable "Sightability": type of effort based on sea state and wind strength.

DATA SET	MODEL	TRUNCATION DISTANCE	Nº SIGH	p	ESW	% CV	VARIABLES	COEFF.	SE
0-P.L.	HAZARD-RATE	1400	423	0.304	425.58	4.16	Intercept of the scale parameter	245.30	3.47
							Power parameter	2.33	1.53
							Covariate "Sightability"	0.38	0.11
1/2-P.L.	HALF-NORMAL	1500	56	0.454	680.54	14.93	Intercept of the scale parameter	760.10	108.50
							Power parameter	0.33	0.18
3-P.L.	HAZARD-RATE	600	46	0.247	147.97	30.17	Intercept of the scale parameter	62.83	37.04
							Power parameter	1.23	0.36

CHAPTER 5: "MODELLING THE HABITAT USE OF SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS"

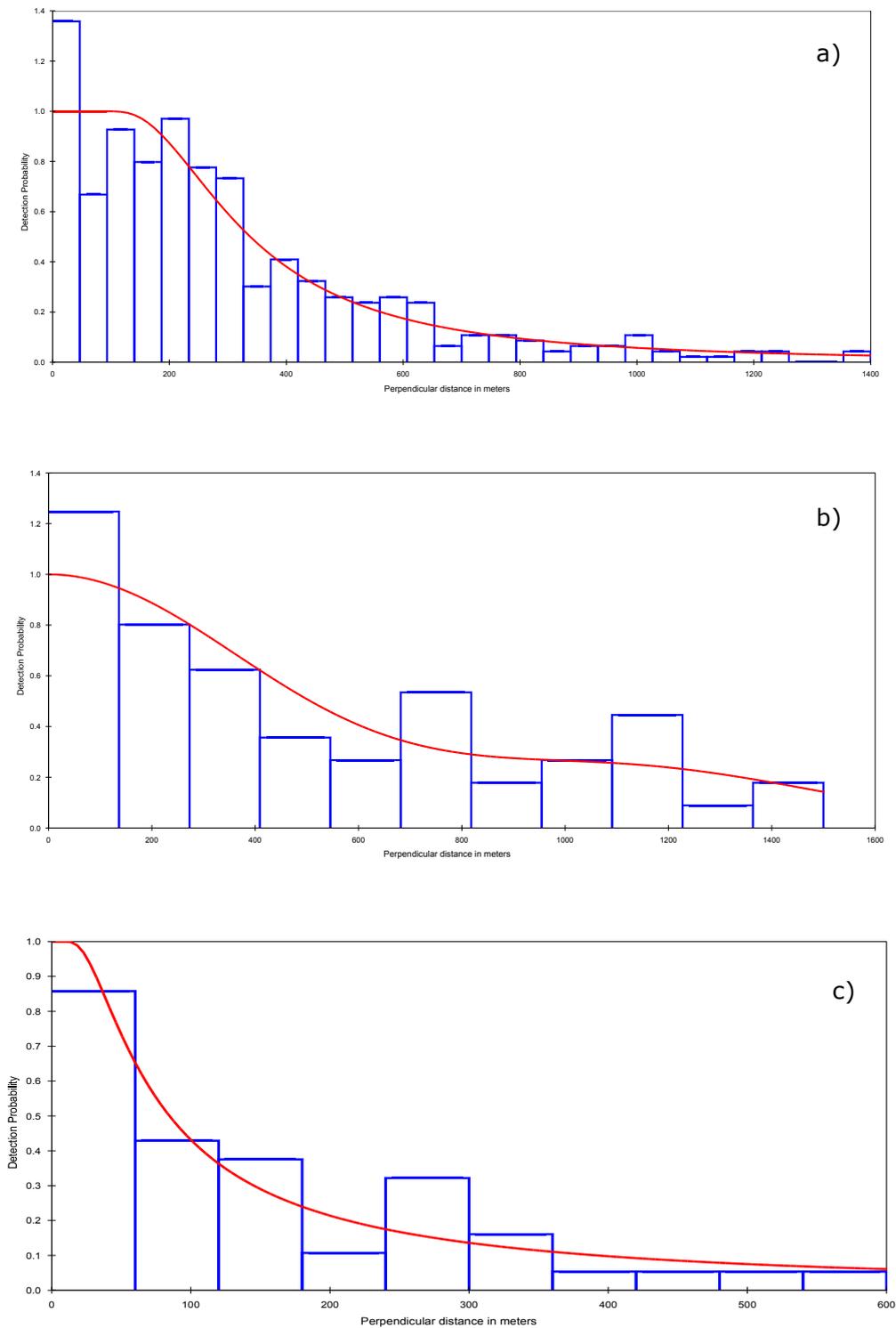


Figure 5.4: Frequency distribution of perpendicular distance distribution from the transect line, pooled over the observed covariate. The continuous curves represent the fitted detection functions. a) 0-P.L.: inflatable and fishing boats; b) 1+2-P.L.: sailing boats and research vessels; c) 3-P.L.: ferries.

5.3.2 HABITAT MODELLING

As shown in Table A5.1 (Annex 5), significant strong correlations ($r > 0.5$) were observed between longitude and slope, longitude and chlorophyll and sea surface temperature, and between slope and temperature.

As already described for the Archipelago (Chapter 1), sea surface temperatures decrease with longitude, with colder waters in the eastern islands of Lanzarote and Fuerteventura under the effects of upwelling from deep and cold waters that are rich in nutrients next to the coast of Morocco. Temperatures also increase (with greater correlation during winter) in areas of the central and western islands with greater variability in depth range/bottom contour, these areas being less affected by the influence of upwellings, and at the same time more conditioned by anthropogenic factors such as discharges. In addition, oceanic and therefore deeper waters are less rich in chlorophyll, as typical for oligotrophic waters. Moreover, reflecting the general topography of the archipelago, slopes decrease with longitude, with a larger continental shelf in the eastern islands.

GROUP SIZE AND ABUNDANCE OF GROUPS

The combination of visual inspection of the fitted smooth relationships and evaluation of the values obtained from the likelihood tests for the significance of the models (mostly with very low values: $p < 0.00001$), the GCV score and the percentage deviance explained showed that all the selected models fitted adequately.

Correlated covariates, generally not used in the same models, were nevertheless tested and, in some cases, incorporated in the selected models when they significantly improved the model fit.

In some cases, group size modelling found no significant explanatory covariates to fit, and therefore the mean group size of the specific dataset was multiplied by predicted group abundance to predict animal abundance.

Details of the models fitted to the Canary Islands dataset are detailed in Table 5.4, with their corresponding list of selected variables and percentages of explained deviance.

For the whole Canary Islands dataset between 1999 and 2012, abundance of groups was best predicted by the interaction of latitude and longitude, and depth (highest predicted

abundance of groups at approximately 1000–1500m) (Figure 5.5a). Estimated group abundance for the entire archipelago was 120 groups of short-finned pilot whales (Table 5.5).

Although with low values of explained deviance, group size was mainly explained by depth, showing decreasing values with depth, and by longitude (Figure 5.5b), with similar group size in the western and central islands but with larger group sizes predicted toward the eastern islands of Lanzarote and Fuerteventura (Figure 5.5b). The overall mean group size was estimated at 16.4 pilot whales (Table 5.5).

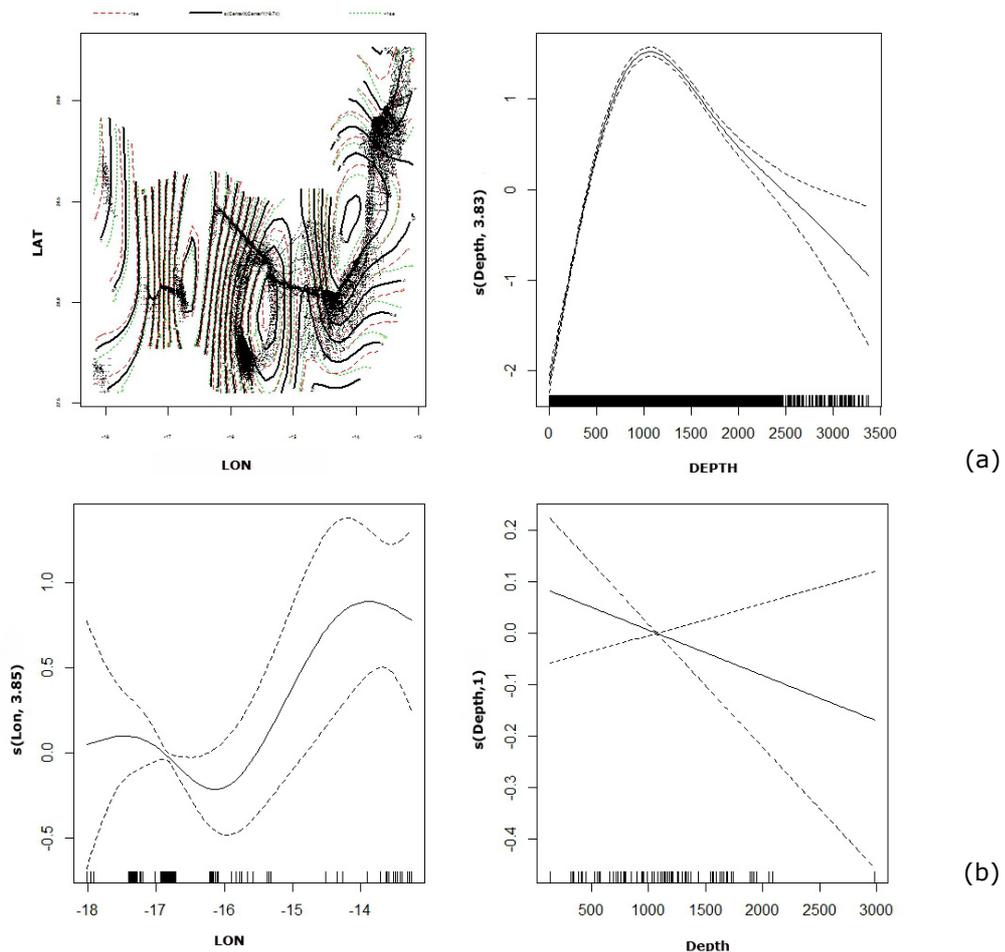


Figure 5.5a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict (a) abundance of groups and (b) group size of short-finned pilot whales for the whole study area between 1999 and 2012.

Table 5.4: Model results for the complete dataset of the Canary Islands (1999-2012), for all periods and seasonally (winter: December-May; summer: June-November). The two best fitting models, one for group abundance (group) and one for group size (g.size) are shown in the table, with the selected variables, the estimated degree of freedom (edf; 1 means a linear relationship), and the corresponding percentage deviance explained.

SUBSET	MODEL	VARIABLES	% DEV EXP
CANARY ISLANDS	GROUP	(Lon,Lat,edf=17) +s(Depth,edf=4)	43.20%
	G.SIZE	(Lon,edf=4)+s(Depth,edf=1)	5.55%
WINTER	GROUP	(Lon,Lat,edf=17)+s(Depth,edf=8)	45.40%
	G.SIZE	(Lon, edf=1)	8.17%
SUMMER	GROUP	(Depth,edf=6)+s(Lon,edf=6)	42.40%
	G.SIZE	(Lon,edf=5)+s(Depth,edf=1)	5.96%

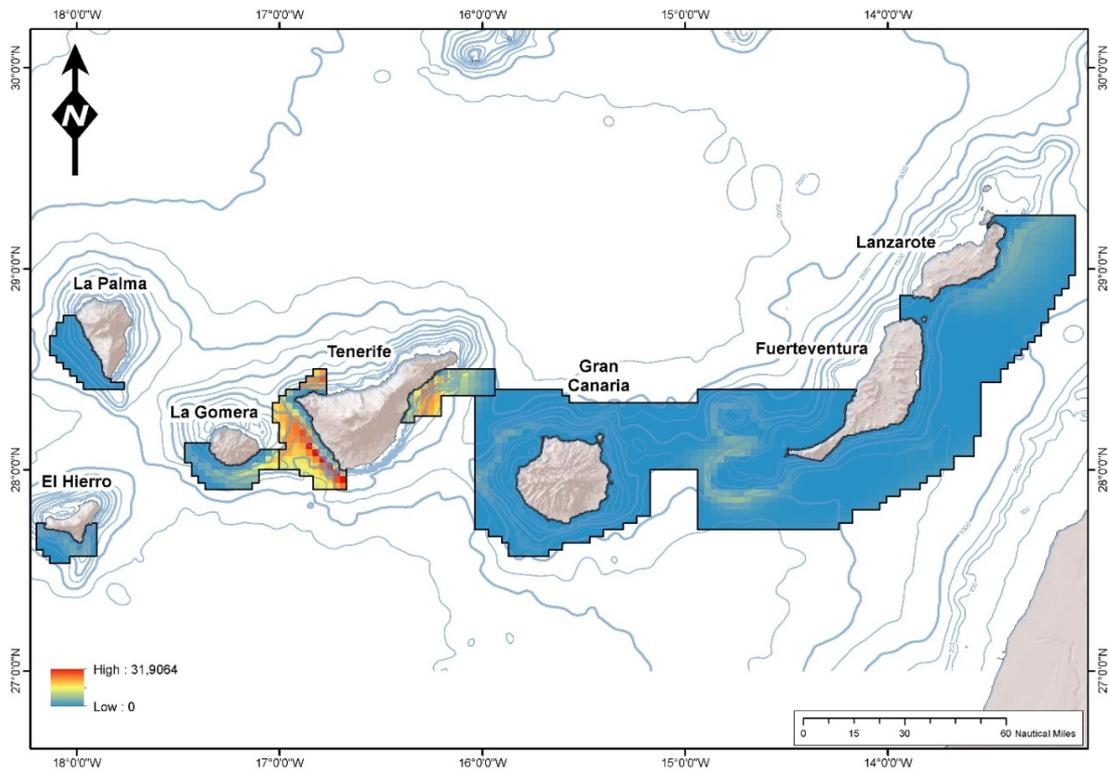


Figure 5.6: Surface map of predicted short-finned pilot whale abundance for the whole study area between 1999 and 2012. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.

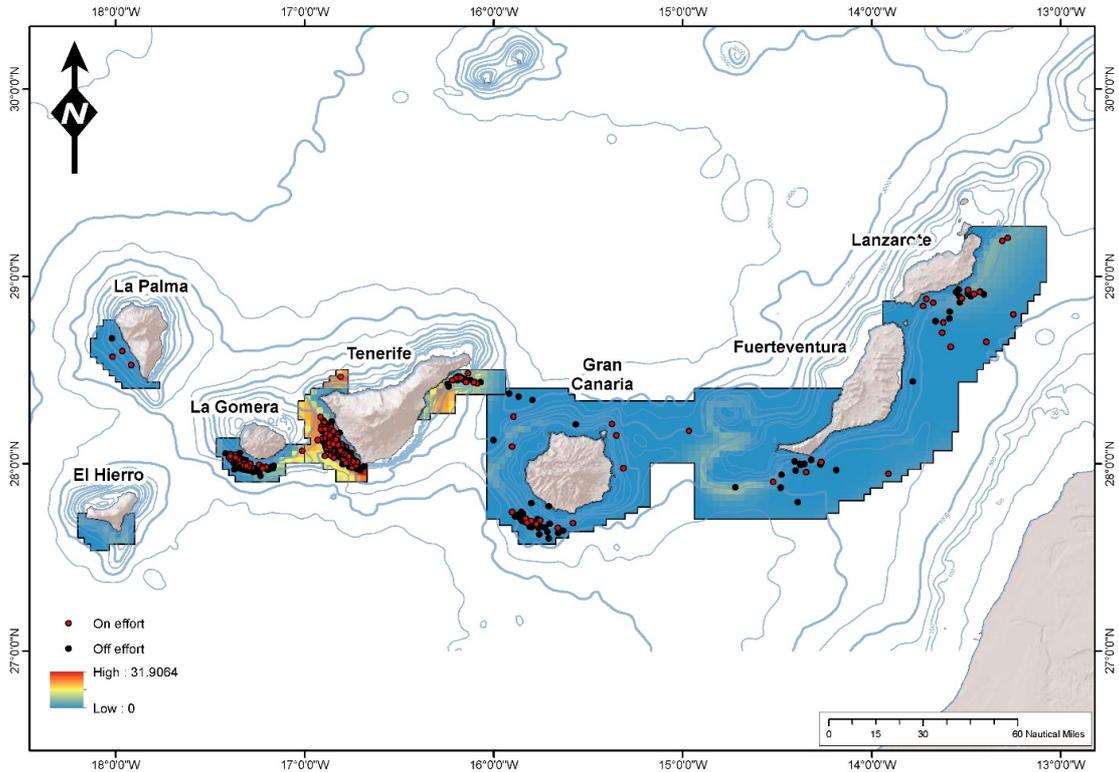


Figure 5.7: Surface map of predicted short-finned pilot whale abundance for the whole study area between 1999 and 2012, where dots in red indicate short-finned pilot whales' sightings recorded on effort, and dots in black the ones recorded off effort.

The point estimate of abundance for the entire archipelago was estimated at 1,980 animals (% CV= 32.8; 95% CI= 1,442 to 2,324), with an overall estimated density of 0.088 whales km⁻² (95% CI= 0.064 to 0.103) (Table 5.5, Figure 5.6, 5.7).

Pilot whale abundance during the winter and summer seasons (December-May, June-November, respectively) was again mostly explained by mean depth and geographical coordinates, which explained 45.4% and 42.4% of the deviance, respectively (Table 5.5.). Higher abundance of groups was predicted in both seasons up to 2,000 m, with a bimodality during winter with a higher peak around 3,000 m (Figure 5.8.). Group size predictions, with larger groups towards the eastern islands, were significantly larger during winter ($Z=22.114$, $p<0.001$).

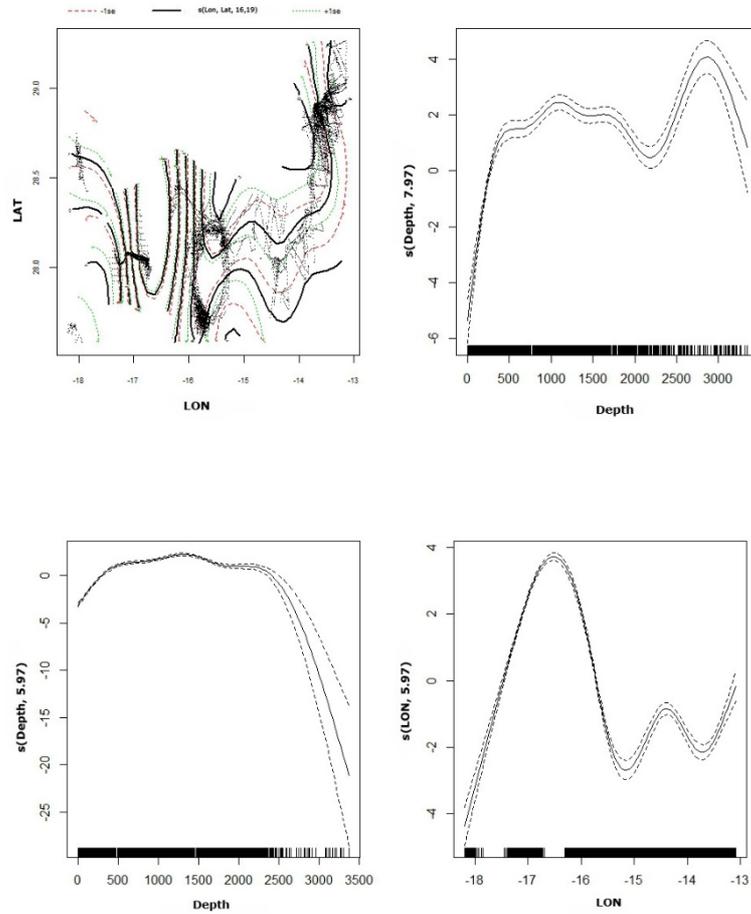


Figure 5.8: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of groups during winter (a) and summer (b) seasons of short-finned pilot whales for the whole study area between 1999 and 2012.

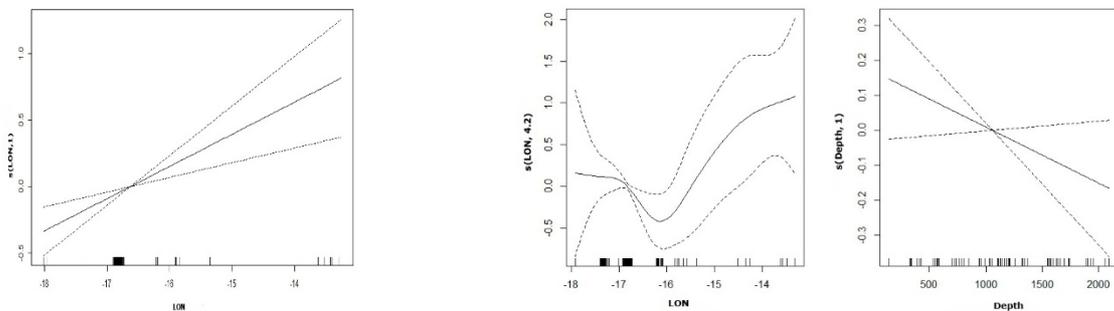


Figure 5.9: Shapes of the functional forms of the smoothed covariates used in modelling to predict group sizes during winter (a) and summer (b) seasons of short-finned pilot whales for the whole study area between 1999 and 2012.

Significantly higher density was estimated during the summer months (summer density: 0.112 whales km⁻², %CV=32.4, 95%CI = 0.091 to 0.138; winter density: 0.086 whales km⁻², %CV=35.2, 95%CI = 0.057 to 0.125; Z=4.861, p<0.001). The high number of sightings around the island of Tenerife was likely the cause of latitude and longitude explaining the majority of the deviance.

Table 5.5: Model results for the Canary Islands: estimated group abundance, group size, density and total abundance (with CV and 95% CI) of the species in the studied area.

SUBSET	GROUP ABUNDANCE	GROUP SIZE	ABUNDANCE			DENS
			TOT	CV	95% CI	
CANARY ISLANDS	120	16.4	1980	0.33	1442-2324	0.088
WINTER	111	17.3	1926	0.35	1270 - 2799	0.086
SUMMER	163	15.4	2510	0.32	2046 - 3094	0.112

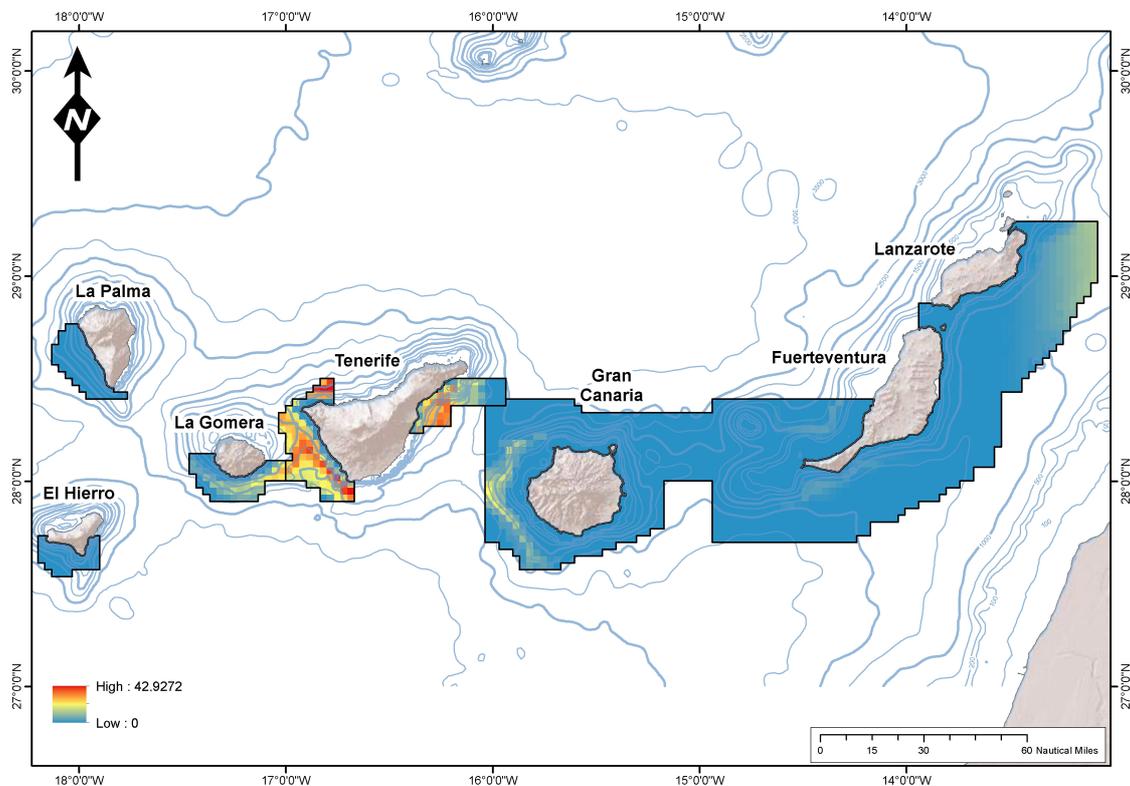


Figure 5.10a: Surface map of predicted seasonal abundance of short-finned pilot whales for the whole study area between 1999 and 2013: summer: December-May. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.

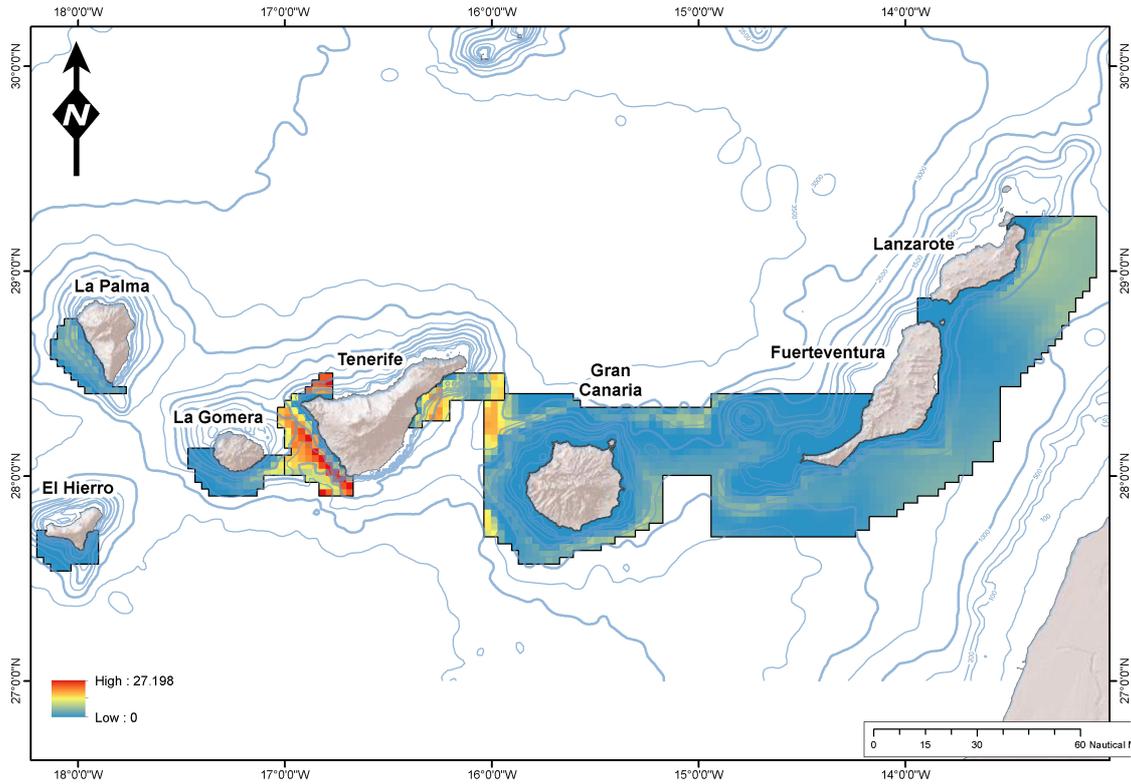


Figure 5.11b: Surface map of predicted seasonal abundance of short-finned pilot whales for the whole study area between 1999 and 2013: winter: June-November. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.

The large heterogeneity in distribution and density predicted by the models reflects the differences in abundance and encounter rates among the different islands, as presented in Chapter 3. The high number of sightings and high predicted density in the southwest of Tenerife could have masked patterns of predicted distribution in other parts of the archipelago. Therefore, models were fitted to data from the three different areas into which the archipelago was divided separately, to investigate more details on habitat use and abundance in these areas.

Western islands: La Palma, El Hierro, La Gomera

In the western islands, the covariates that best explained group abundance were related to the seabed physiography (slope), with a clear preference for steeper surfaces (14.6% explained deviance) (Figure 5.11a.; Table 5.6.). For group size the model retained contour index (CI) (18.8% of explained deviance), with larger groups where there was a more highly variable sea bed (Figure 5.11b). Abundance for this area was estimated at 103 pilot whales (%CV=36.9; 95%CI= 52 to 129), with a density of 0.057 whales km⁻² (95%CI=0.029 to 0.071) (Table 5.7., Figure 5.12).

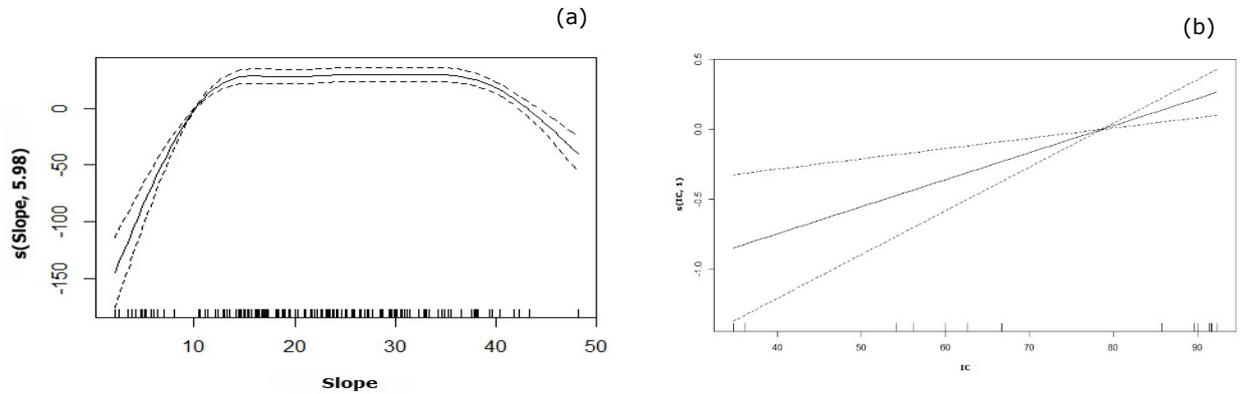


Figure 5.12a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict (a) abundance of groups and (b) group sizes of short-finned pilot whales in the western islands of La Palma, El Hierro, and La Gomera, between 2004 and 2012.

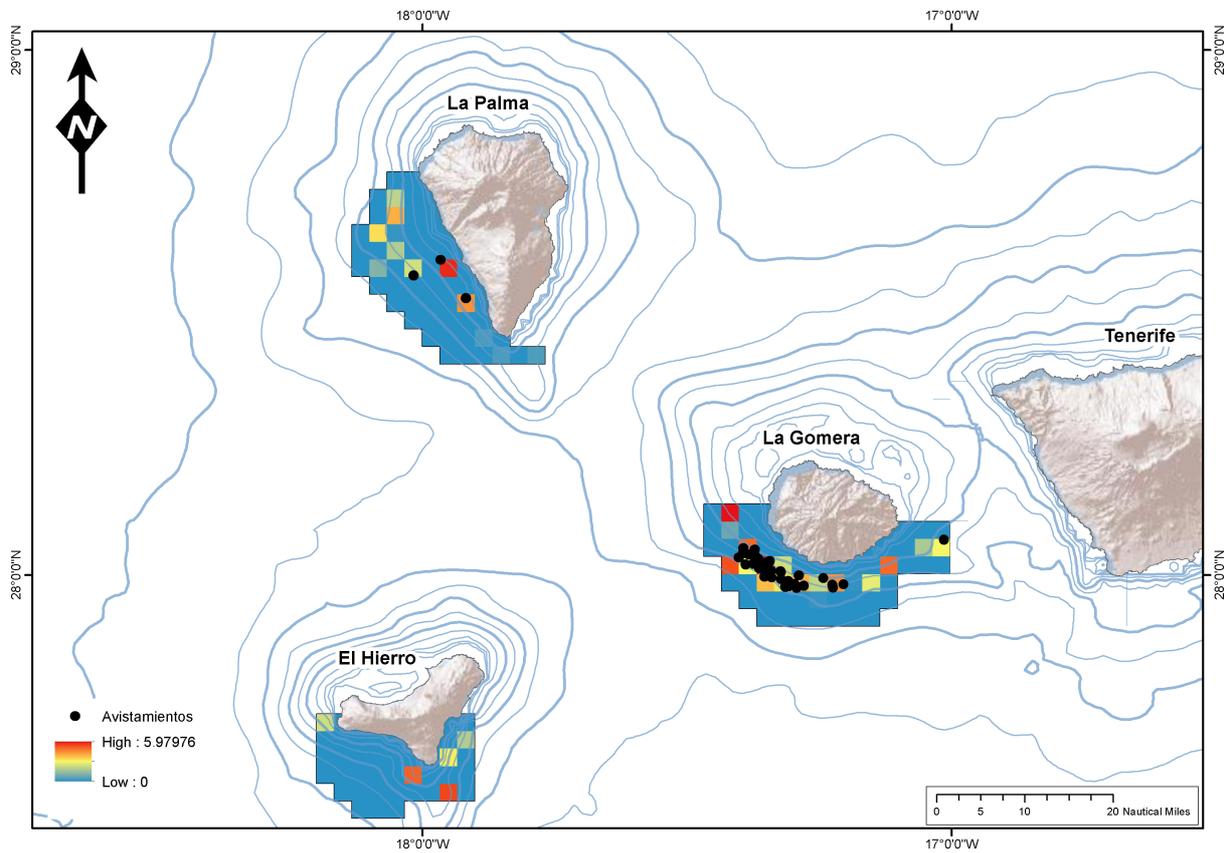


Figure 5.13: Surface map of predicted short-finned pilot whale abundance for the western islands of El Hierro, La Palma and La Gomera between 2004 and 2012. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red. The black dots indicate short-finned pilot whale sightings recorded on effort.

Eastern islands: Gran Canaria, Lanzarote, Fuerteventura

Mean depth and sea surface temperature explained 20.4% of the deviance, with higher density of up to 2,000 m depth, with a peak at 21.3°C (Figure 5.13a.). Longitude was retained for predicting group size (18.5% of explained deviance, Table 5.6), which increased towards the easternmost areas of the archipelago (Figure 5.13b). Abundance was estimated at 375 (%CV=41.9; 95%CI=181 to 542) with a density of 0.020 whales km⁻² (95%CI=0.010 to 0.029; Figure 5.14., Table 5.7).

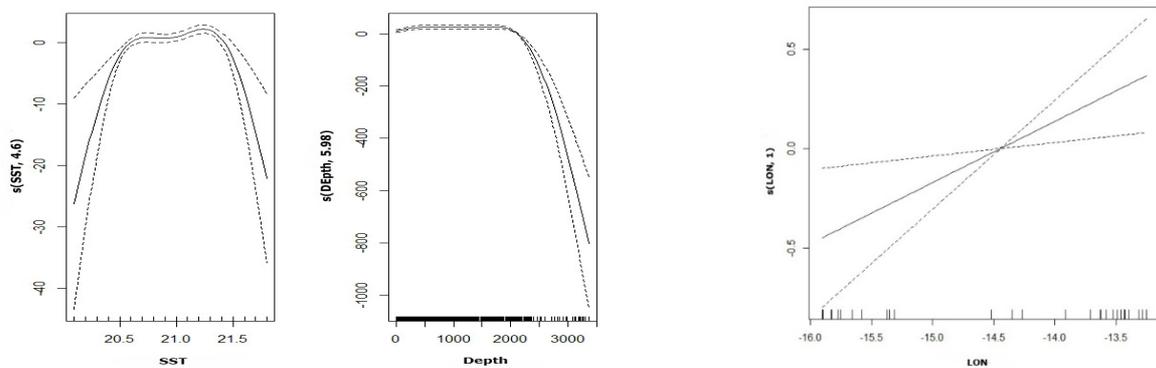


Figure 5.14a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group (a) and group sizes (b) of short-finned pilot whales in the eastern islands of Gran Canaria, Lanzarote, and Fuerteventura between 1999 and 2012.

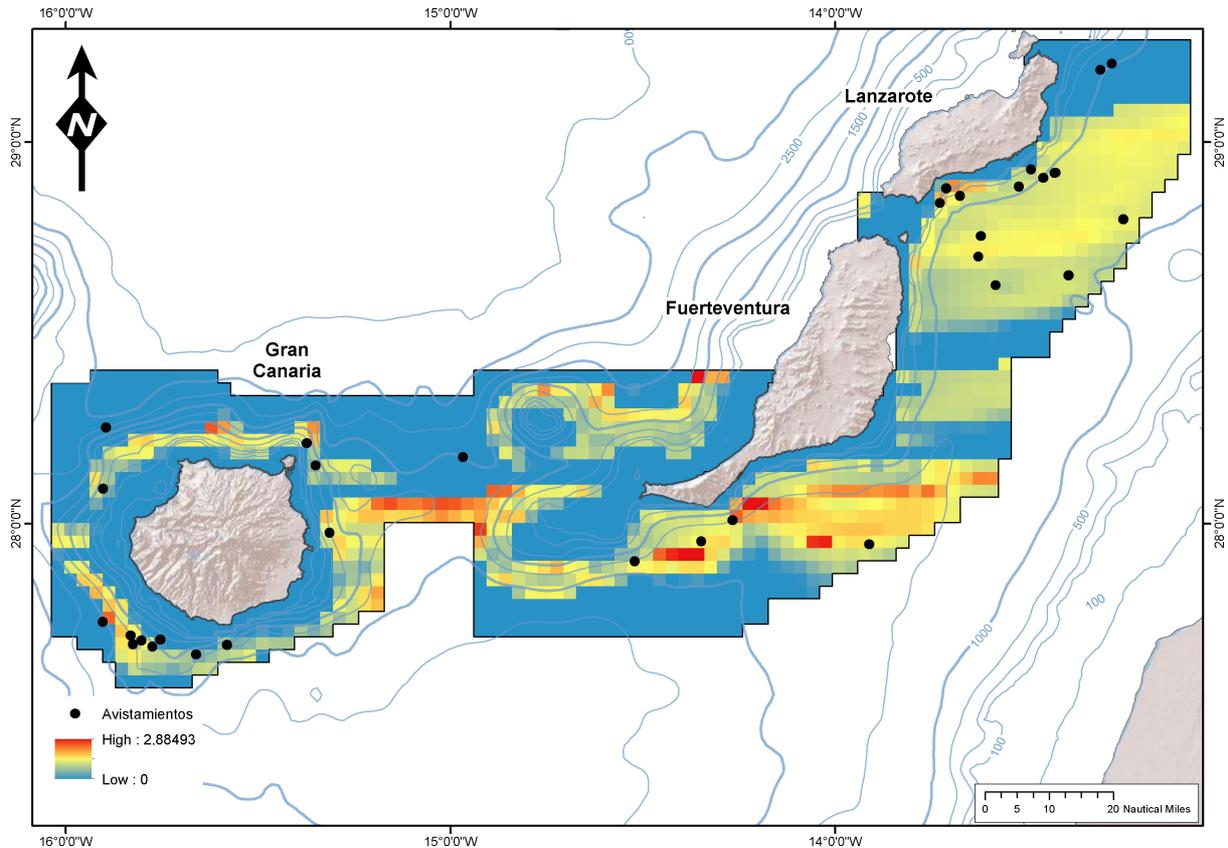


Figure 5.15: Surface map of predicted short-finned pilot whale abundance for the eastern islands of Gran Canaria, Lanzarote, and Fuerteventura between 1999 and 2012. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red. The black dots indicate short-finned pilot whale sightings recorded on effort.

Tenerife

In the island of Tenerife, the group abundance of pilot whales was again predicted by depth and slope, which explained 17.9% of total deviance (Table 5.6.). Greater group abundance was found in depths around 1,800 m, and a bimodal preference distribution of seabed slope was predicted, with two peaks around 15 m/Km⁻² and 30 m/Km⁻² (Figure 5.15). Mean depth was the covariate that best predicted group size, but because it explained little of the deviance (2.08%), it was not used in the prediction. Total abundance of animals was estimated at 1,223 (%CV=30.8; 95%CI= 1,046 to 1,267), with a density of 0.657 whales km⁻², mainly distributed to the southwest of the island (95%CI= 0.562 to 0.681; Figure 5.16, Table 5.7.).

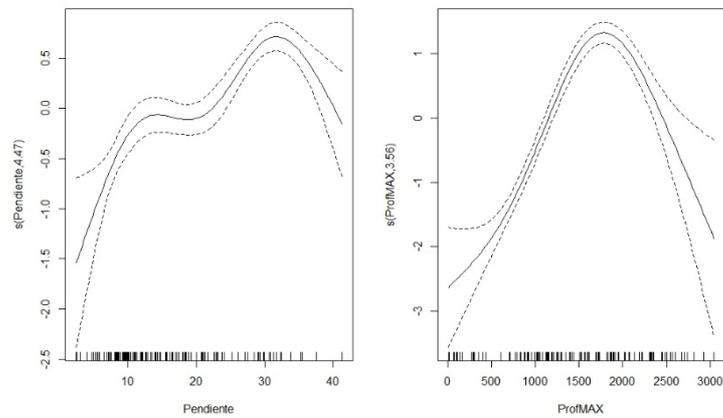


Figure 5.16: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whales in Tenerife between 2002 and 2010.

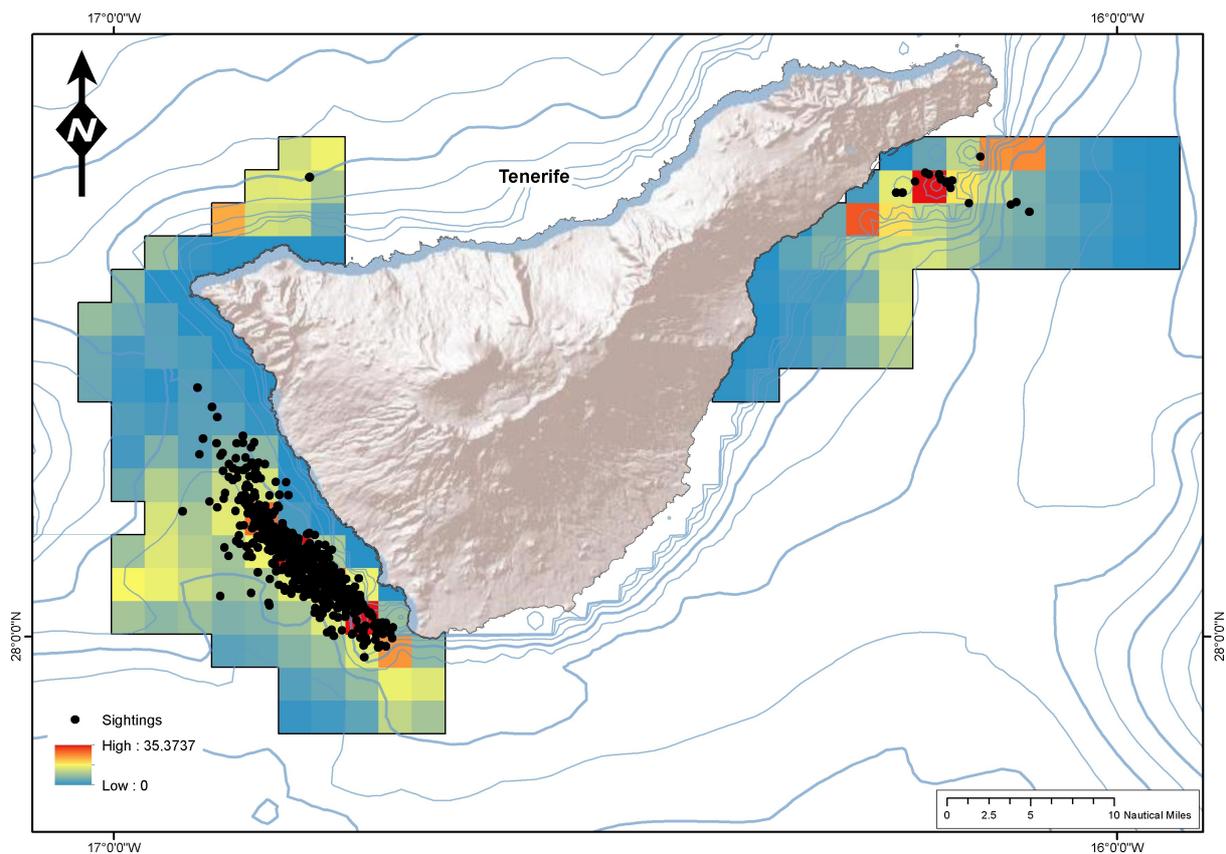


Figure 5.17: Surface map of predicted short-finned pilot whale abundance for Tenerife between 2001 and 2010. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red. The black dots indicate short-finned pilot whale sightings recorded on effort.

Examining the predictions obtained for each region for the different islands, the areas with the highest abundance mostly coincide with the southwest and north east of the island of Tenerife, with some areas identified also in the south of Fuerteventura, east of Lanzarote and west of La Gomera and Gran Canaria (Figure 5.12, 5.14, 5.16), mostly supported by pilot whale sightings recorded in the archipelago (Figure 5.7.). Nevertheless, the estimates for the islands of La Palma, El Hierro and Gran Canaria must be interpreted with caution, since it was not possible for them to calculate the CVs and CIs through bootstrap for the small sample size of sightings recorded on effort in each of these islands.

Estimated abundance and density were significantly higher in Tenerife (1,223 animals, 95% CI=1,046 to 1,267, and 0.66 whales per Km^{-2} , 95% CI=0.562 to 0.681) compared to the rest of the archipelago (density: $H=515.85$, $df=5$, $p<0.001$). La Gomera had the second highest density (0.096 whales km^{-2} , 95% CI= 23 to 121). Surprisingly, the island of El Hierro, with no recorded sightings during the study period, had the second highest predicted density among the remaining islands (0.053 whales km^{-2}). Due to the significantly higher value of group size (group size: $H=401.8$, $df=2$, $p<0.001$) estimated in the waters of Lanzarote and Fuerteventura, the estimated abundance was the second highest in the archipelago (290, 95% CI= 125 to 487).

The island of Tenerife was the only area that had sufficient number of sightings for investigation by season and year.

Examining temporal trends in abundance and distribution, depth was the covariate that best explained the deviance, in association or interaction with slope and latitude, depending on the year considered (Figure 5.17). Whales were found, for all years, to be mainly distributed between 800 and 1,800m depth with a slight bimodality, and lower values at 1,300m (Figure 5.17a-d). Explained deviance ranged between 13.7% and 25.2% (Table 5.6.). Only in 2007 was a model for group size useful (using geographical references), but this explained only a low percentage of the deviance. Therefore, for all the years, mean group size was used to produce the final abundance surface map (Table 5.7.).

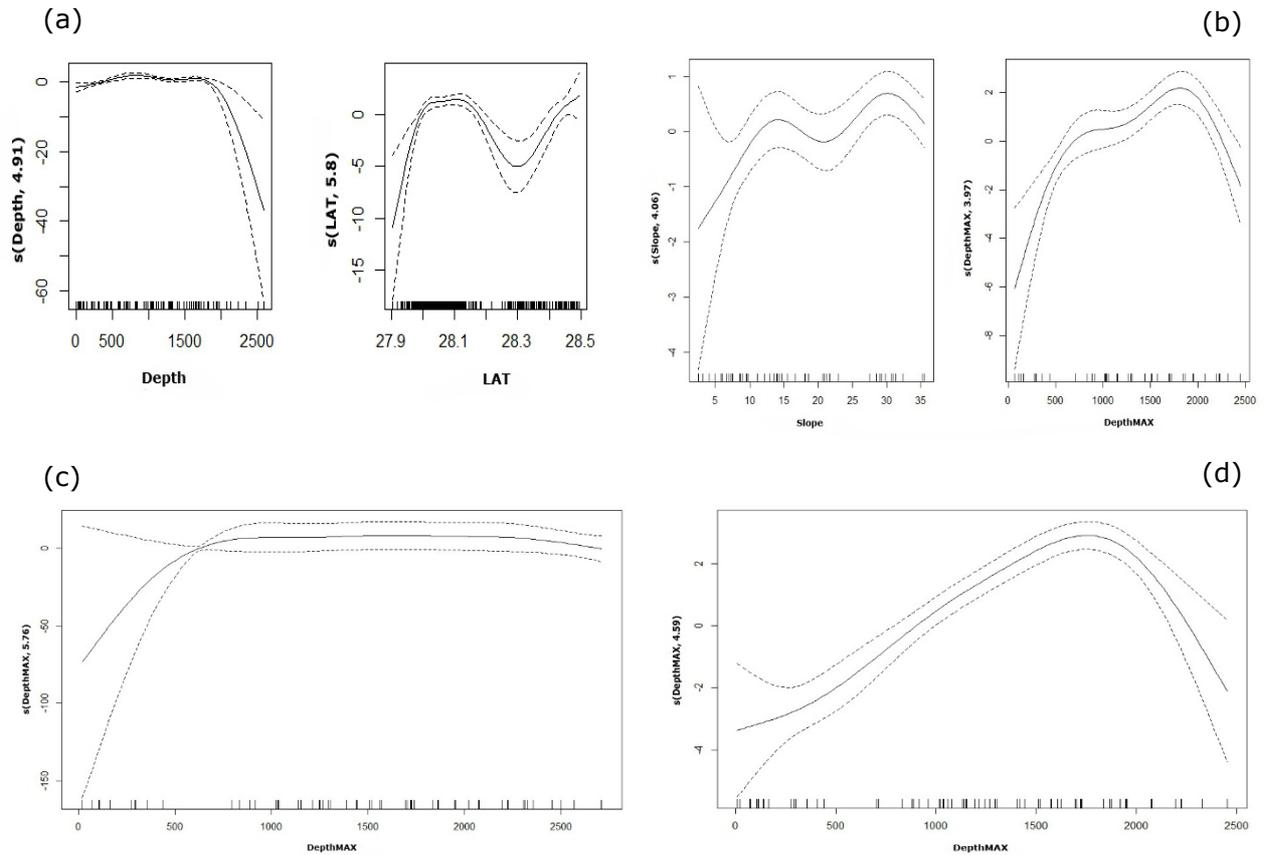


Figure 5.18: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whales in Tenerife in 2002-2006 (a), 2007 (b), 2008 (d), and 2009-2010 (c).

Density increased from the first years of the study (0.260 whales km^{-2} , 95%CI=0.187 to 0.296) to 2007 (0.899 whales km^{-2} , 95%CI= 0.659 to 1.013; $Z=-9.415$, $p<0.001$), and 2008 (0.892 whales km^{-2} , 95%CI=0.735 to 0.973; $Z=-11.275$), but there was a significant decline in the following years 2009-2010 (0.693 whales km^{-2} , 95%CI= 0.533 to 0.709; $Z=-6.778$, $p<0.001$). Total abundance was estimated for the years 2002-2006 at 485 (%CV=33.0; 95%CI= 348 to 551), for 2007 at 1,672 (%CV=32.5; 95%CI= 1,227 to 1,885), for 2008 at 1,661 (%CV=31.3; 95%CI= 1,367 to 1,811), and 2009-2010 at 1,289 (%CV=31.4; 95%CI= 991 to 1,319) short-finned pilot whales (Figure 5.18; Table 5.7.).

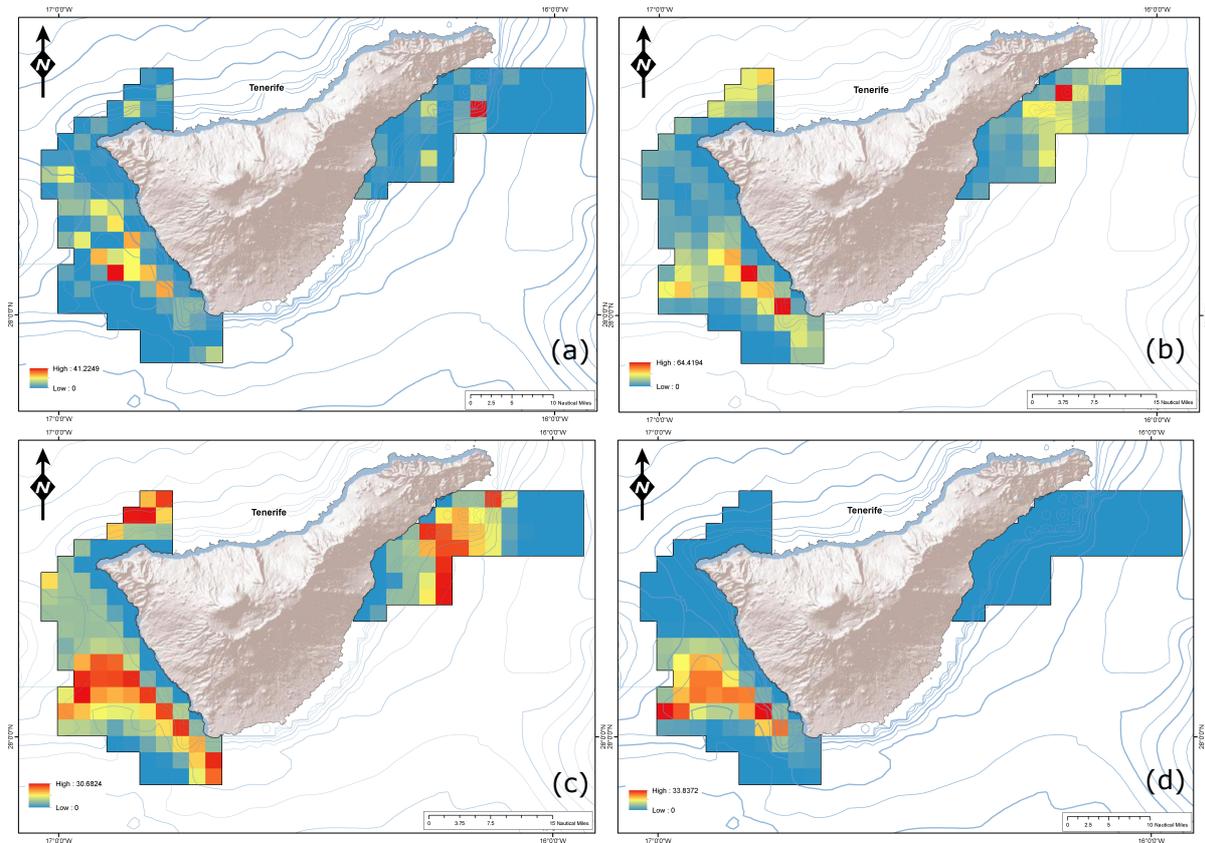


Figure 5.19a-d: Surface map of predicted short-finned pilot whale abundance in Tenerife a) 2002-2006; b) 2007; c) 2008; d) 2009-2010. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.

During summer the predicted abundance of groups was higher in deeper water around 1,500m with two peaks at medium and high slopes (22% of the deviance explained; Table 5.6., Figure 5.19.). During winter, abundance of groups was higher on flatter slopes when distant from the 1,000 m isobaths, with a progressive increase towards shallower water around 1,000m at both high and low slopes (Figure 5.19a-b).

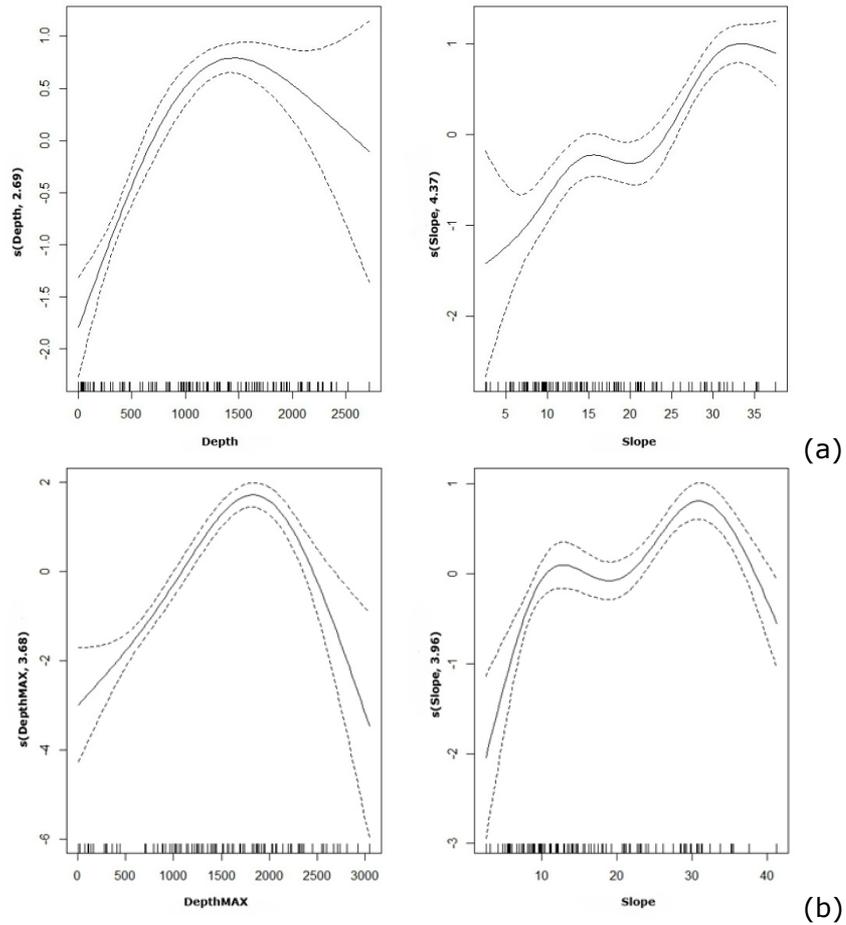


Figure 5.20a-b: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group during winter (a) and summer (b) seasons of short-finned pilot whales in the island of Tenerife between 2002 and 2010.

While during summer no significant covariates were found for group sizes, during the winter season, group sizes were found to be related to depth, and predicted to be larger in areas with flat or steep bottom surface (Figure 5.20).

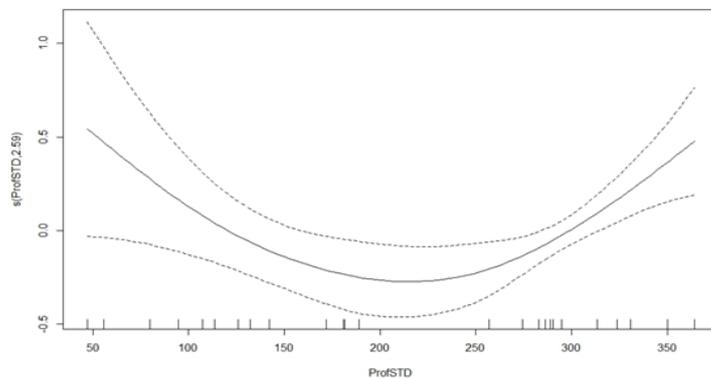


Figure 5.21: Shapes of the functional forms of the smoothed covariates used in modelling to predict group sizes during winter season of short-finned pilot whales in the island of Tenerife between 2001 and 2010.

The point estimate of abundance and density for Tenerife show no statistical differences between seasons, in contrast to what was found for the entire archipelago where higher group abundances were estimated during summer months (Figure 5.20).

After variable selection, the final models selected slope and depth as the strongest predictors of pilot whale group abundance (Table 5.6, Figure 5.21a-b.). There were significant differences between the areas ($H=376.175$, $df=2$, $p<0.0001$), higher in Tenerife compared to the eastern islands ($Z=9.210$, $p<0.001$) and the western islands ($Z=6.886$, $p<0.001$).

Table 5.6: Model results for the complete dataset of the whole Canary Islands (1999-2012) and for the three areas: western islands (La Palma, El Hierro, La Gomera; Area 1), Tenerife (Area 2), and eastern islands (Gran Canaria, and Lanzarote-Fuerteventura, Area 3). Seasonal estimation (winter: December-May; summer: June-November) and temporal trend (years: 2002-2006, 2007, 2008, 2009-2010) are also shown for the island of Tenerife. The two best fitting models, one for group abundance (group) and one for group size (g.size) are shown in the table, with the selected variables, the estimated degree of freedom (edf; 1 means a linear relationship), and the corresponding percentage of explained deviance. Seasonal results (winter: December-May; summer: June-November) are also shown.

SUBSET	MODEL	VARIABLES	% DEV EXP
LP_EH_LG (Area 1)	GROUP	(Slope,edf=6)	14.60%
	G.SIZE	(CI,edf=1)	18.80%
GC_LZ_FV (Area 2)	GROUP	(SST,edf=4)+(Depth,edf=4)	20.40%
	G.SIZE	(Lon,edf=1)	18.50%
TN (Area 3)	GROUP	(Slope,edf=5)+(DepthMAX,edf=4)	17.90%
	G.SIZE	-	
TN YEAR			
TN 2002-2006	GROUP	(Depth, edf=5) + (Lat,edf=6)	17.30%
	G.SIZE	-	
TN 2007	GROUP	(Slope, edf=5)+(DepthMAX,edf=4)	21.40%
	G.SIZE	-	
TN 2008	GROUP	(DepthMAX,edf=6)	13.70%
	G.SIZE	-	
TN 2009-2010	GROUP	(DepthMAX,edf=5)	25.20%
	G.SIZE	-	
TN SEASONS			
SUMMER	GROUP	(DepthMAX,edf=4)+(Slope,edf=4)	21.2%
	G.SIZE	-	
WINTER	GROUP	(Depth, edf=3)+(Slope,edf=5)	13.70%
	G.SIZE	(DepthSTD,edf=3)	11.20%

Table 5.7: Estimated group abundance (with CV and CI), density, and group size (estimated and calculated mean) for the western islands (La Palma, El Hierro, La Gomera; Area 1), Tenerife (Area 2), and eastern islands (Gran Canaria, and Lanzarote-Fuerteventura, Area 3). Seasonal estimation (winter: December-May; summer: June-November) and temporal trend (years: 2002-2006, 2007, 2008, 2009-2010) are also shown for the island of Tenerife.

SUBSET	GROUP ABUNDANCE	GROUP SIZE	ABUNDANCE			DENS
			TOT	CV	95% CI	
LP_EH_LG (Area 1)	7	14.0	103	0.37	52 - 129	0.057
LP		12.6	11	-	-	0.017
EH		15	24	-	-	0.053
LG		15.3	68	0.58	23 - 121	0.096
GC_LZ_FV (Area 2)	14	27.3	375	0.42	181 - 542	0.020
GC		19.4	85	-	-	0.014
LZ_FV		21.23	290	0.74	125 - 487	0.024
TN (Area 3)	83	14.8	1223	0.31	1046 - 1267	0.657
TN YEAR						
TN 2002-2006	31	14.2	485	0.33	348 - 551	0.261
TN 2007	96	17.4	1672	0.33	1227 - 1885	0.899
TN 2008	112	14.8	1661	0.31	1367 - 1811	0.893
TN 2009-2010	99	13.0	1289	0.31	991 - 1319	0.693
TN SEASONS						
SUMMER	99	15.1	1369	0.31	1122.7 - 1427.0	0.736
WINTER	81	15.1	1229	0.34	924.7 - 1650.9	0.661

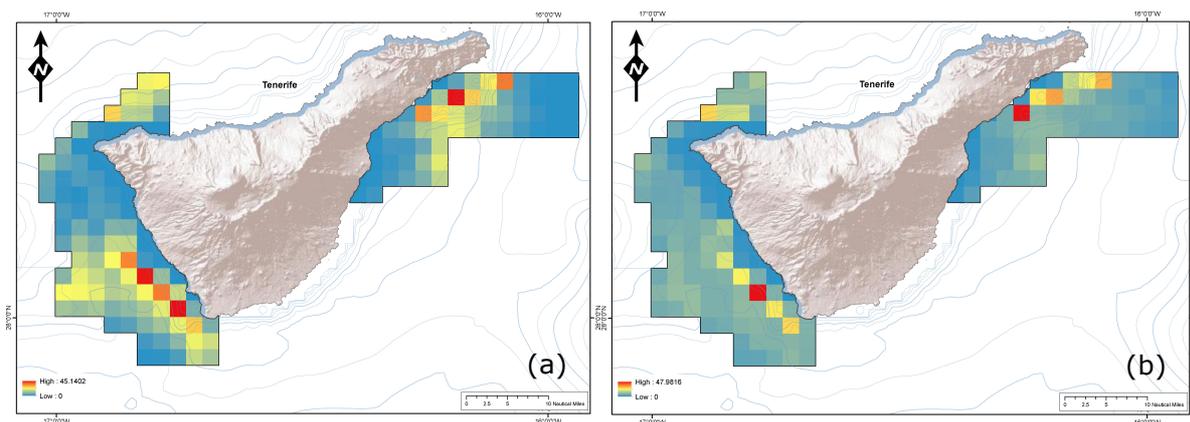


Figure 5.22a-b: Surface map of predicted seasonal abundance of short-finned pilot whales for the island of Tenerife between 2002 and 2010: a) summer: December-May, b) winter: June-November. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.

BIOLOGICAL FACTORS

Three biological factors were investigated: behavioural categories (feeding, travelling, socialising, and resting), whether or not calves were present, and single and mixed species groups with *Tursiops truncatus*. They were explored using both the database of the entire archipelago, and Tenerife alone.

Behaviour categories

In the majority of cases, pilot whales were encountered while they were travelling (61%) and resting (24%); only on a few occasions were they found socialising (12%) and feeding (3%). This was the case in the Canary Islands in general, and in Tenerife specifically.

The predicted group abundance based on the different behaviours was mostly influenced by geographic variables, due to the strong effect that the island of Tenerife has over the rest of the archipelago, and by depth group covariates (Table 5.8.). Apart from the feeding category, predicted abundance of groups engaged in the other behaviours was higher for depths around 1,600 m, with a wider depth range (800-2,000 m) when socialising, localised in the study area as far as 15°W longitude (excluding the islands of Lanzarote and Fuerteventura). Groups in feeding activity were found more abundant in areas characterised by mean annual surface temperatures higher than 21°C (17.60 of explained deviance) (Figure 5.22a-d).

Explained deviance for the group size model was low (7.29%). Group size for travelling groups was best explained by geographical covariates (larger groups towards Lanzarote) (Figure 5.23, Table 5.8.).

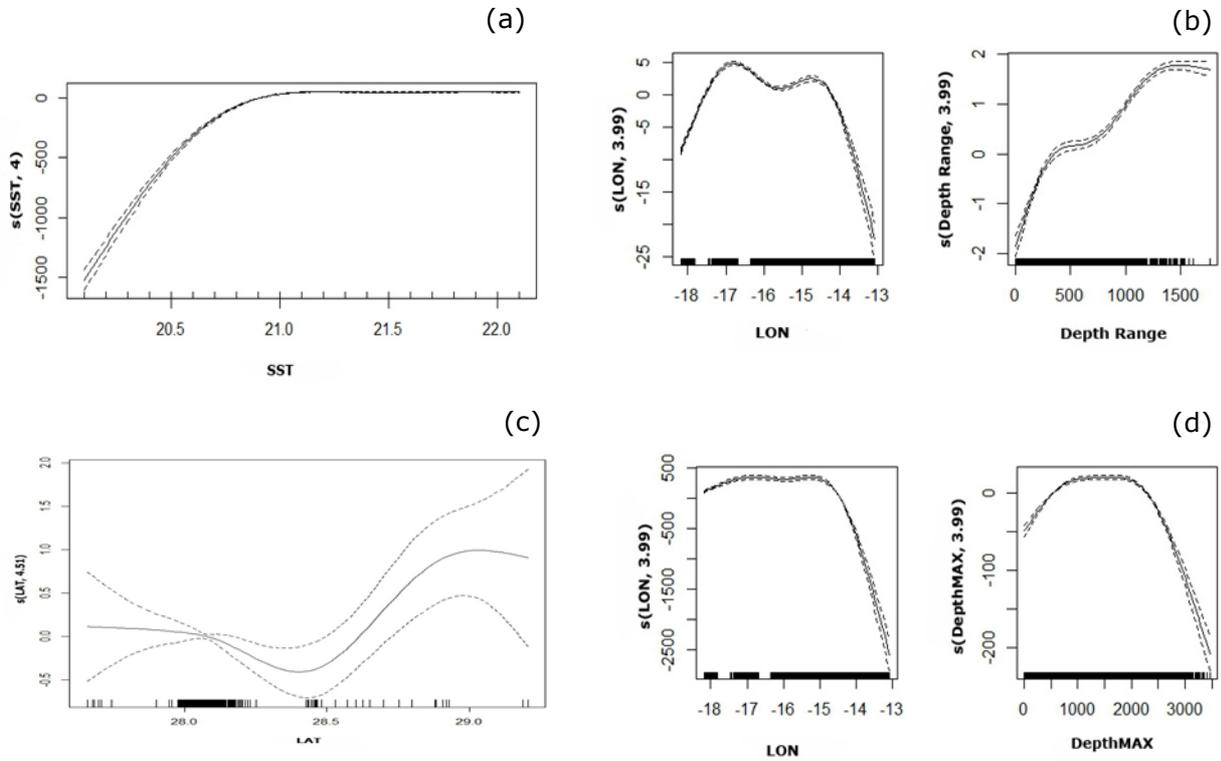


Figure 5.23a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whale abundance in the Canary Islands between 1999 and 2012 during a) feeding; b) resting; c) travelling; d) socialising.

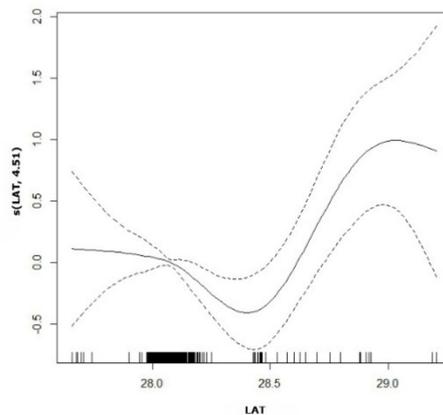


Figure 5.24: Shapes of the functional forms of the smoothed covariates used in modelling to predict group size of short-finned pilot whale abundance in the Canary Islands between 1999 and 2012 during travelling behaviour.

When the same categories were investigated for the island of Tenerife alone, the geographical covariates were less important for group abundance estimation; depth explained between 10.3% and 14.2% of the deviance (Table 5.8.). The majority of behavioural activities were predicted to be conducted in mostly overlapping areas (Figure 5.25). Higher group abundance was predicted at distances from the coast of 8 km (at approximately 1,400 of depth, range between 766 m and 1,458 m) when travelling; resting and socialising were mostly associated with the 1600 m isobaths (which correspond to distances from the southwestern coast of Tenerife of between 4.82 and 9.25 km). Feeding behaviour was associated with sea surface temperature; groups were predicted to be more abundant in water around 1,000 m (mean distance from the coast of 5.5 km) at 21 C° (Figure 5.24, Figure 5.25, Table 5.8).

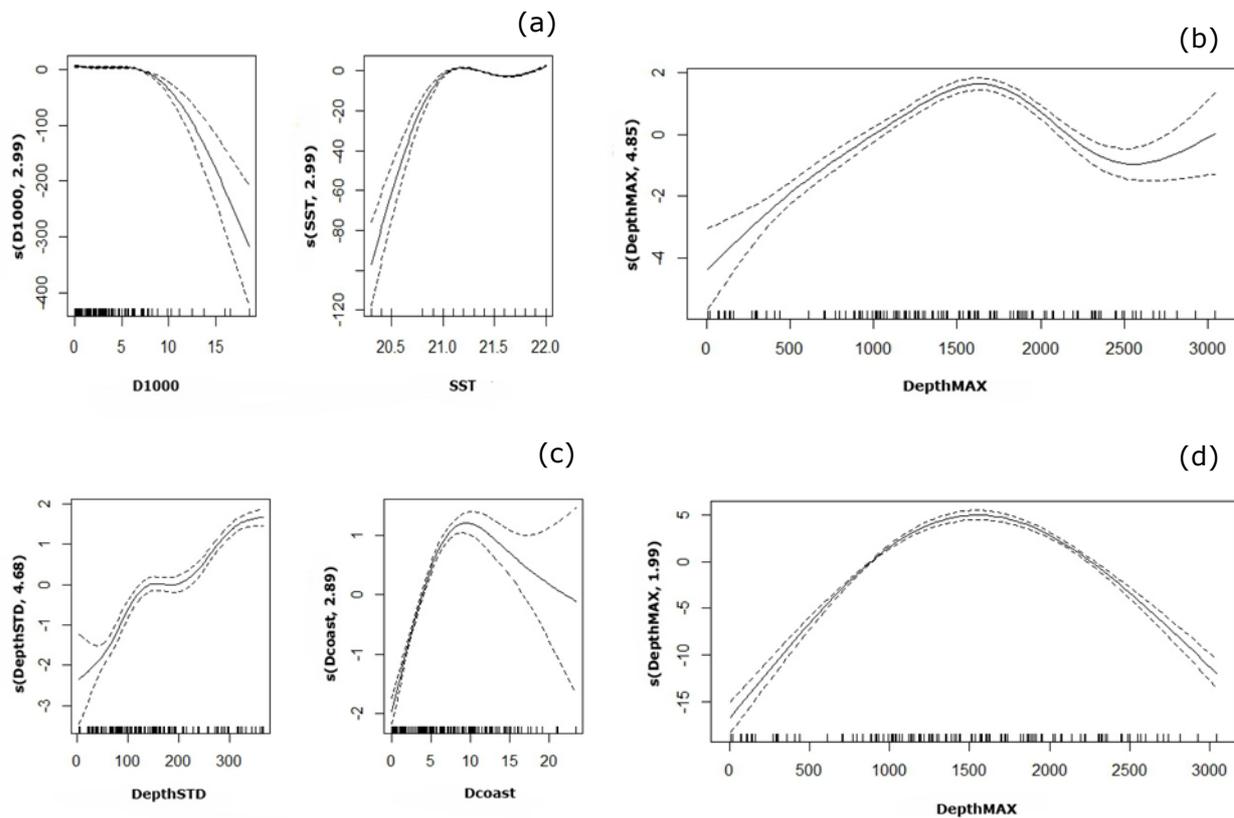


Figure 5.25a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whale in the island of Tenerife, between 2002 and 2010 during a) feeding; b) resting; c) travelling; d) socialising.

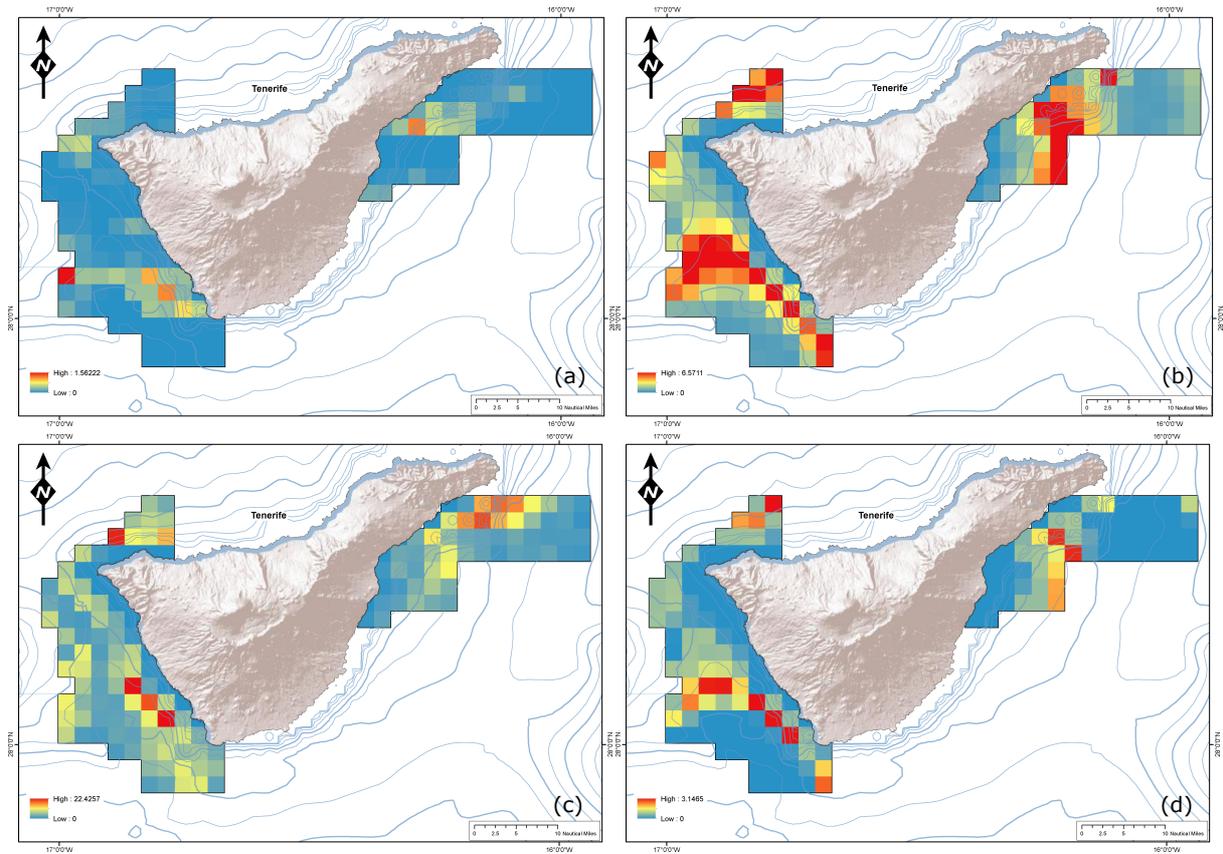


Figure 5.26a-d: Surface map of predicted short-finned pilot whale abundance in the island of Tenerife between 2002 and 2010 during a) feeding; b) resting; c) travelling; d) socialising. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.

Single and mixed groups

In Tenerife, pilot whales were found in mixed association groups with bottlenose dolphins in 104 sightings but only 24 of them were on effort, mostly during summer months (80% between June and October). The covariates that best explained the distribution in the presence of this second species were distance from the coast and slope (low deviance explained of 6.2%), with smaller group sizes at increasing distances from the 200 m isobaths. The sightings in association with *Tursiops* were distributed in a wider distance range closer to the coast, with decreasing density beyond 15 km from the coast than when pilot whales were found alone, with higher density in coincidence with the peak at 8 km from the coast, and at medium high values of slope (bimodality at 15 and 30m/Km⁻²) (Figure 5.26., Table 5.8.).

No marked differences in habitat use were found between groups with and without bottlenose dolphins, when the Canary Islands, as a whole, was modelled (Figure 5.27).

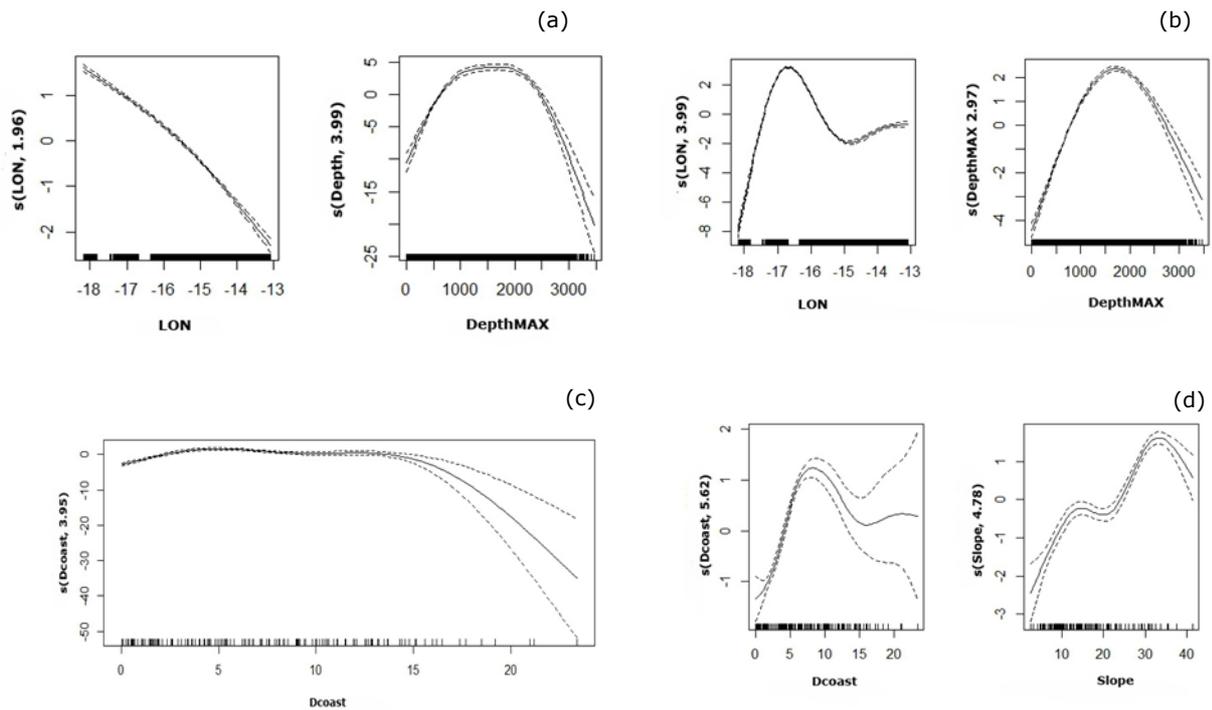


Figure 5.27a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whales in the Canary Islands (top) and in Tenerife (bottom), between 2002 and 2010: with (a and c) and without (b and d) bottlenose dolphins.

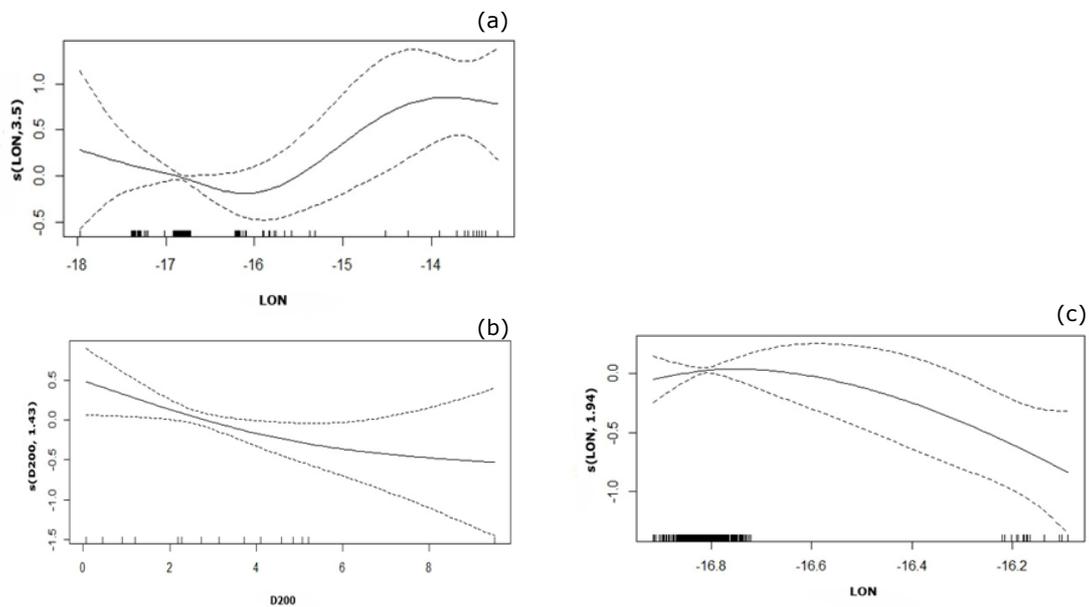


Figure 5.28a-c: Shapes of the functional forms of the smoothed covariates used in modelling to predict group size of short-finned pilot whales in the Canary Islands (top) and in Tenerife (bottom), between 2002 and 2010: with (a) and without (b and c) bottlenose dolphins.

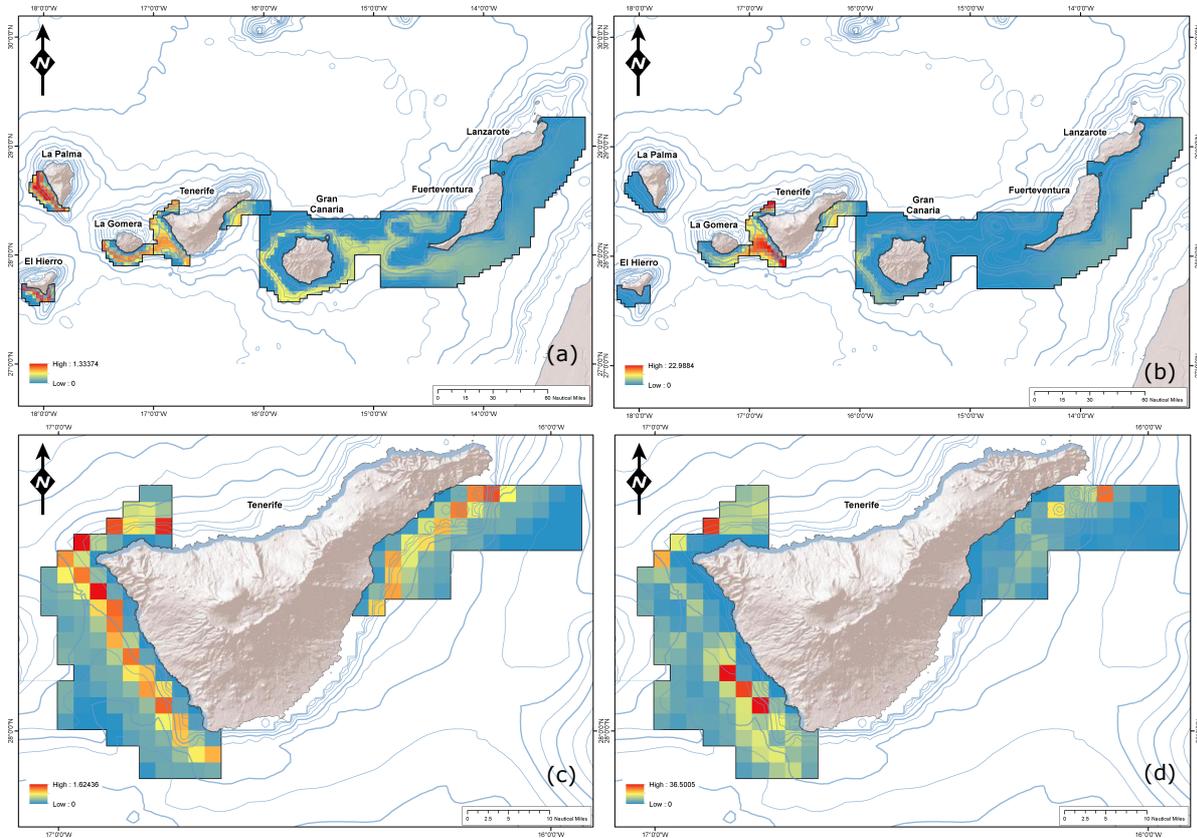


Figure 5.29a-d: Surface map of predicted abundance of short-finned pilot whales in the Canary Islands (top) and in Tenerife (bottom): with (a and c) and without (b and d) bottlenose dolphins. The colour gradient indicates the density of animals from 0 in blue, to the highest value, in red.

Presence of calves

Calves were observed in approximately 60% of the recorded groups (sightings on effort), significantly more frequently during summer months (Chapter 3) in both the Canary Islands as a whole and around Tenerife. The predicted abundance of pilot whales was similarly explained by depth and contour features, the only difference being that when calves were present in the groups the predicted area used extended much closer to the coast (Figure 5.29, Figure 5.30). Nevertheless, significant differences in density were estimated when calves were present or absent for both datasets analysed (Canary Islands: $Z=-15.868$, $p<0.001$; Tenerife: $Z=-5.297$, $p<0.001$) (Figure 5.31, Table 5.8.).

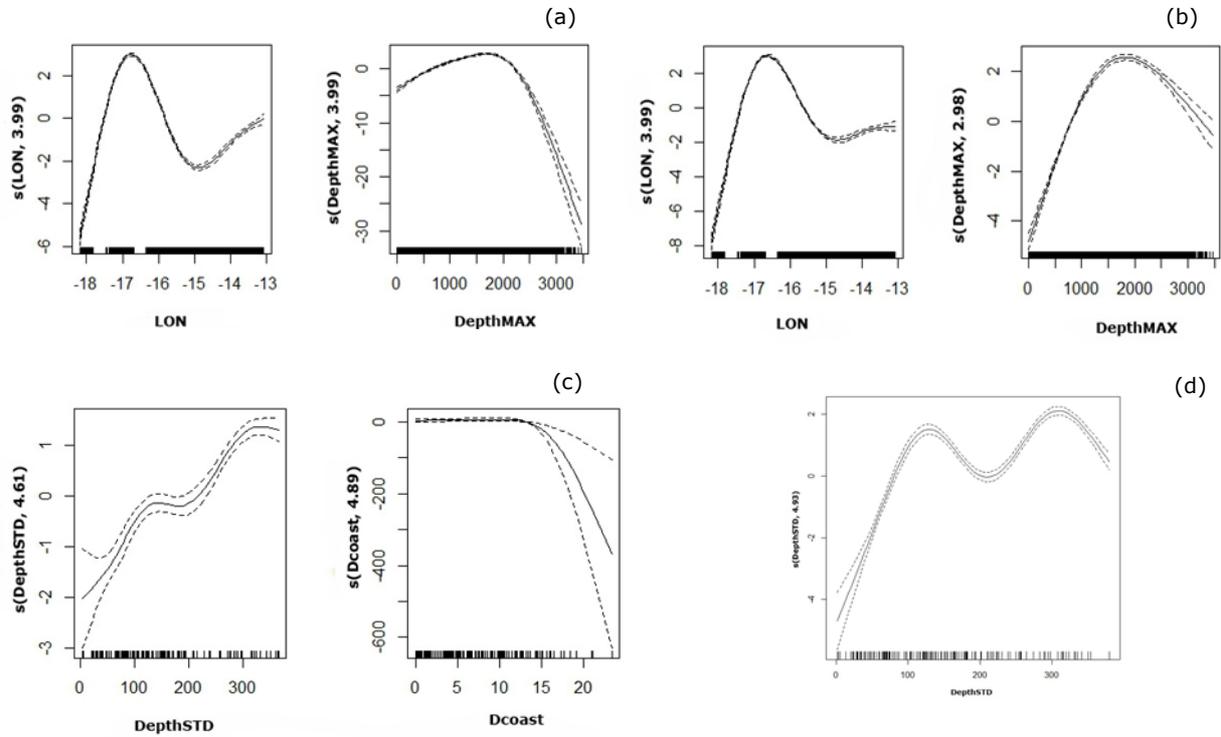


Figure 5.30a-d: Shapes of the functional forms of the smoothed covariates used in modelling to predict abundance of group of short-finned pilot whale in Canary Islands (top) and in the island of Tenerife (bottom), between 2002 and 2010 with (a, c) and without (b, d) calves.

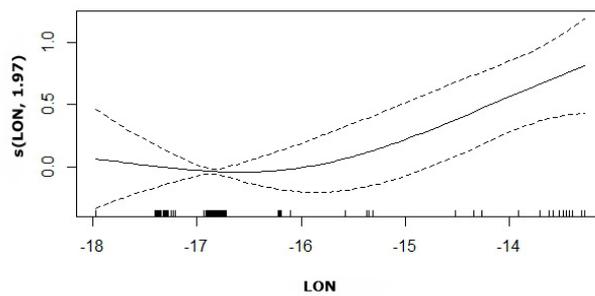


Figure 5.31: Shapes of the functional forms of the smoothed covariates used in modelling to predict group size of short-finned pilot whale in Canary Islands with calves.

CHAPTER 5: "MODELLING THE HABITAT USE OF SHORT-FINNED PILOT WHALES IN THE CANARY ISLANDS"

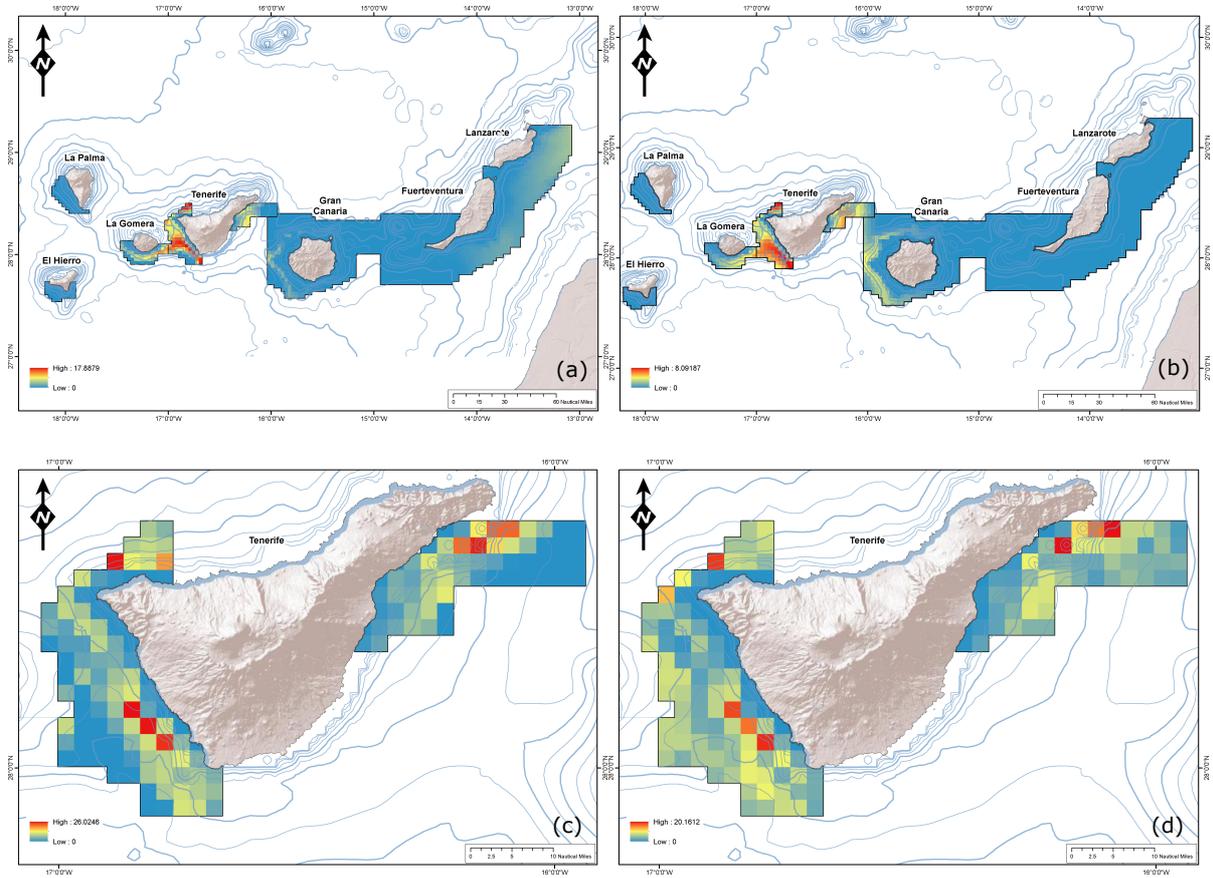


Figure 5.32a-d: Surface map of predicted short-finned pilot whale abundance in the Canary Islands (top) and in Tenerife (bottom) between 2002 and 2010: groups with calves (a and c) and groups without calves (b and d). The colour gradient indicates the density of animals from 0 in blue to the highest value in red.

Table 5.8: Model results for short-finned pilot whale habitat preference related to biological intrinsic factors, in the Canary Islands and in the island of Tenerife: behavioural categories (travelling, socialising, resting, feeding), single or mixed species group with bottlenose dolphins, presence/absence of calves in the groups. The two best fitting models, one for group abundance (group) and one for group size are shown in the table with the selected variables and the corresponding percentage of deviance explained.

SUBSET	MODEL	CANARY ISLANDS		TENERIFE	
		VARIABLES	% DEV EXP	VARIABLES	% DEV EXP
BEHAVIOUR					
TRAVELLING	GROUP	(Lon,edf=4)+s(DepthMAX,edf=4)	39.60%	(DepthSTD,edf=5)+s(D_costa,edf=3)	14.20%
	G.SIZE	(Lat,edf=5)	7.29%		
SOCIALISING	GROUP	(Lon,edf=3)+s(DepthMAX,edf=3)	44.90%	(DepthMAX, edf=3)	14.2%
	G.SIZE	–	–		
RESTING	GROUP	(Lon,edf=4)+s(DepthRange,edf=4)	34.80%	(DepthMAX, edf=5)	10.30%
	G.SIZE	–	–		
FEEDING	GROUP	(SST, edf=4)	17.60%	(D_1000,edf=3)+s(SST_anual,edf=3)	13.30%
	G.SIZE	–	–		
SINGLE/MIXED GROUP					
With Ttr	GROUP	(Lon,edf=2)+s(DepthMAX,edf=4)	18.20%	(D_costa,edf=4)	6.2%
	G.SIZE			(D_200, edf=2)	21.70%
Without Ttr	GROUP	(Lon,edf=4)+s(DepthMAX,edf=3)	43.30%	(D_coast,edf=5)+s(Slope,edf=5)	16.60%
	G.SIZE	(Lon, edf=5)	4.57%	(Lon, edf=5)	2.18%
WITH CALVES/WITHOUT CALVES					
With calves	GROUP	(Lon,edf=4)+s(DepthMAX,edf=4)	39.40%	(DepthSTD,edf=5)+s(D_coast, edf=5)	15%
	G.SIZE	(Lon,edf=5)	7.53%		
Without calves	GROUP	(Lon,edf=4)+s(DepthMAX,edf=3)	34.10%	(DepthSTD,edf=5)	13.40%
	G.SIZE	–	–		

5.4 DISCUSSION

The relationship between cetacean distribution patterns and oceanographic and physiographic data has been the subject of several studies, with different analytical techniques applied to a variety of species, but only a few have been on pilot whales (Cañadas *et al.*, 2005; Barlow *et al.*, 2009), and none on short-finned pilot whales in the eastern Atlantic Ocean. The only studies carried out in the Canary Islands focused on descriptive relationships between this species' distribution and environmental variables in the area (e.g. Aguilar and Brito, 1999; Arranz *et al.*, 2008; Pérez-Vallazza *et al.*, 2008b), various reports and symposium proceedings (e.g. Vonk and Martin, 1988; Martín *et al.*, 1992; Carrillo, 1996; Arbelo, 2007; Carrillo *et al.*, 2010), with no inference on spatial and temporal variation in this species distribution and abundance among the different islands

of the archipelago. This study presents the first insights into the habitat uses of one of the commonest cetacean species in the Canary Islands.

5.4.1 ABUNDANCE AND HABITAT USAGE

The predicted abundance surfaces for short-finned pilot whales in the study area based on the spatial model results were well supported by the observed data, indicating that the models provided a reliable description of the spatial variation in pilot whale abundance in the Canary Islands, even though they explained only 12.9% to 45.7% of the deviance for group abundance and 3.1% to 16.7% for group size, depending on the dataset used for the modelling. Moreover, the estimates obtained from models with similar GCV and deviance explained were quite similar, indicating that the predictions achieved were quite robust to model uncertainty.

However, despite the generally good results obtained in the present study, the predictions obtained through the GAMs should be considered with caution. The flexibility in model selection in GAMs can sometimes cause model overfitting and lead to "edge effects" in prediction. This, in turn, can lead to unrealistic densities and surface maps as well as to overestimation of the correlation between animal distribution and environmental variables (Ferguson and Bester, 2002) and could be a cause of unexpectedly high predicted density.

The small number of sighting in some subset data, did not always allow the use of the best fitting model in the bootstrap simulations. Even though they could explain a higher percentage of deviance, the more complex models, caused in some cases the bootstrap to fail, indicating a possible overfitting of the data. In order to limit this effect, in these occasions simpler models were chosen, both for the point estimate and for the bootstrap simulation, mostly by not including covariates interaction and by lowering the degrees of freedom allowed in model fitting, which was therefore set to not exceed 25% of the total number of positive observations included in the specific analysis. Nevertheless, this method had the disadvantage of selecting covariates with a reduced percentage of the deviance explained. Especially when modelling group abundance, some sub-datasets gave predictions with some "edge effect", mainly in the northwest of Tenerife. Whether in some cases the visual inspection of the predicted maps (and residuals plots) showed that this effect was reduced by forcing the covariate to use a lower degree of freedom or by replacing it with a more suitable one, in a few cases this problem seemed to persist.

Modelling the short-finned pilot whale data by exploring this species habitat usage at different spatial levels, from the archipelago as whole to the single island, allowed more detail in the spatial distribution of densities to be seen and, at the same time, allowed overall and seasonal estimates for the whole of the Canary Islands to be obtained.

Predictions at small scales (by island) were produced using models fitted to the eastern and western areas of the archipelago with the associated assumption that factors that determine abundance at a small scale are the same as those at large scales.

The predicted density patterns from the models were very similar to the observed data, but also highlighted new areas that might be important for this species and, therefore, valuable to be explored in future studies. Short-finned pilot whales did not use the study area uniformly but showed higher densities in patchy areas mainly localised downwind of the main islands coming from the northeast (Aristegui *et al.*, 1994), off the southeastern or southwestern coasts of the islands, depending on the island coast contour. Nevertheless, 3% of the total sightings were found in waters north of the islands, especially off the island of Gran Canaria (17 sightings), the only island where intensive surveys were also conducted in the upwind waters. This suggests that further effort along northern coasts should be conducted and might reveal higher pilot whale densities than those found to date, as well as potentially detecting new areas of usage. While the physiographic variables are similar between up- and down-wind coasts, the oceanographic characteristics show large differences in surface temperature, chlorophyll distribution, and general direction and strength of the currents and eddies which may lead to a different usage (distribution and abundance but also biological aspects) of the areas.

The general area preference seems to be quite stable across time, with abundance prediction significantly higher off the island of Tenerife, especially along the southwestern coasts, already a well-known area for easy accessibility to this species. Higher abundance estimates in Tenerife were obtained for 2007 and 2008, but in the absence of a clear long-term trend, the annual differences may simply reflect the natural variability in the occurrence of the species in the area. Alternatively, there may be an underlying trend that only further years of survey might detect. Furthermore, the southwest of La Gomera was highlighted as the second most important area for pilot whale density, confirming recent studies (Peña *et al.*, 2006; Smit *et al.*, 2010). Moreover, some underestimation in abundance may have affected the final abundance estimation, due to the high number of sightings (30% of the total) recorded off effort in this area resulting

from information from other boats. Their presence was also confirmed for the island of Lanzarote (Politi *et al.*, 1996), and Gran Canaria (Servidio *et al.*, 2002), thus including these areas together with Fuerteventura, as the area used by this population, albeit at a different level of density.

While groups were distributed throughout the areas identified by the overall model, a different pattern was found for the westernmost islands. The low density predicted for the island of La Palma in the present study was likely due to the limited survey effort conducted during the present study in this area. This is in contrast with the literature (Pérez-Vallazza *et al.*, 2008a) that describes this species as the third most common in the area with a constant pattern of presence throughout the year and 0.214 sightings per day along the southwest of the island. Surprisingly the models identified the southwest of the island of El Hierro as the third most important island for pilot whale density, after Tenerife and La Gomera. No sightings were recorded during the study period in this island, nor were strandings ever documented (Canary Islands Stranding Network, 2012). Nevertheless, transient pilot whales have been recorded in these waters more frequently in recent years (Aguilar de Soto, pers. comm.), partially reflecting the model prediction.

On the other hand, the presence or absence of whales in an area might be unrelated to the modelled environmental covariates and on the contrary be a consequence of other biological factors, such as the social behaviour of the animals. El Hierro has been described as a high density area for beaked whales, especially Blainville's beaked whales, which have been recorded year-round off the southern coast of El Hierro (Aguilar de Soto, 2006). Aguilar de Soto *et al.* (2011) described the two different feeding behaviours of pilot whales and Blainville's beaked whales, with overlapping foraging depths, around 600 m – 700 m (Aguilar de Soto, 2006; Aguilar de Soto *et al.*, 2011). The spatial segregation of the two resident populations (short-finned pilot whales in Tenerife and Blainville's beaked whales in El Hierro) was pointed out, hypothesising differences in foraging tactics and therefore in the targeted resources at depth. The real nature of this separation is unknown, but different ecological requirements may represent one potential explanation: pilot whales seem to feed on prey with more muscle mass than on less mobile prey with lower individual caloric value, as suggested for beaked whales (Aguilar de Soto *et al.*, 2011). Even though the geography and oceanic features might justify the predicted density of the species in this area, niche segregation between pilot whales and Blainville's beaked whales might be the cause of the scarce presence of pilot whales off the island of El Hierro.

In this study, topography was found to be the driving environmental factor affecting pilot whale distribution in the entire area. The final models retained covariates from the depth group (maximum, mean, and standard deviation of the depth, slope, contour index, and distance from the 1000 m isobaths) as the best predictors of whale abundance in most of the datasets used in analysis. Sea surface temperature and distance from the coast were also sometimes retained by the models. Although physiographic variables were competing with spatial covariates in model selection (latitude and longitude, when the entire archipelago was considered as a whole), the present analysis provides compelling evidence that bottom depth and slope are significantly influencing the presence of pilot whales in the Canary Islands. Similar to a previous study on this species in the Canary Islands (Heimlich-Boran, 1993; Carrillo *et al.*, 2010) the 1,000-1500m depth range was identified as that where most of the sightings were concentrated, moving towards deeper waters during winter, especially within the eastern islands (2500m). Similar observations were reported in the Hawaiian Archipelago (Mahaffy, 2012), with preferences for 1000-2000m depths.

When the three areas were modelled separately, the covariates retained by the best fitting models were different from those retained by the models for the whole archipelago, with the addition of slope and contour index as important covariates and with preference for medium and high seabed gradients, especially within the eastern islands and, during summer, the island of Tenerife.

Similarly, long-finned pilot whales in the Strait of Gibraltar showed seasonal preference for deep waters with steep bathymetry during summer months and more even slopes during fall and winter months (de Stephanis, 2008; de Stephanis *et al.*, 2008a). As explained for bottlenose dolphins (Lusseau and Higham, 2004), the usage of different habitat might also be a consequence of different social activities in which the animals are involved. Feeding behaviour in Tenerife seemed to be mainly related to a narrow area around the 1000 m isobaths, characterised by medium and high slope gradients, and a sea surface temperature of 21 °C, greater than the annual mean value.

Temperature may have direct and indirect effects on cetacean distribution, for example through its effects on the energetic costs of thermoregulation (MacLeod *et al.*, 2009) and on prey distribution (Rubín, 1994; Baumgartner, 1997; Davis *et al.*, 1998; Murase *et al.*, 2002; Tynan *et al.*, 2005). In contrast to the findings in the Pacific, where populations of short-finned pilot whales showed genetic, morphometric and life history differences related to SST (Kasuya *et al.*, 1988; Wada, 1988), in the present study the sea surface

temperature was not found to influence distribution. This might be due to the small temperature range of only five degrees between the maximum and minimum mean values found during the study period, with little differences within the eastern and western islands of the archipelago (Mascareño, 1972; Pavón-Salas *et al.*, 2000).

Pilot whale movements do not follow strict or regular migration patterns. Some north-south as well as inshore-offshore movements have been described in different regions (e.g. Newfoundland, Abend and Smith, 1999), related to the distribution, density and movement of their prey or incursions of warm water. In contrast, marked seasonality in the distribution of short-finned pilot whales has been observed off southern California, where their seasonal abundance appears to be correlated with the seasonal abundance of spawning squid and mainly associated with high relief topography. In both coastal and pelagic waters of the eastern tropical Pacific the density of population centres appears to change seasonally in response to major changes in the current structure of the area. Moreover, there seems to be a seasonal distribution related to depth; pilot whales were found in significantly shallower water during winter (depth 375m) than summer (800m) (Bernard and Reilly, 1999).

In the Canary Islands, the pilot whale population has been recorded year-round (e.g. Carwardine, 1994), with no evidence of regular emigration. Nevertheless, abundance differences were predicted here between seasons, with higher density during the summer months. This might coincide with the potential incursions into the Canary Islands of new pilot whales from neighbouring areas, as supported by the fact that there were twice as many animals photo-identified only once or twice during summer than during winter. The exception was in Lanzarote and Fuerteventura where the opposite tendency was noticed and where no resident individuals have been identified so far (with only a few animals recaptured up to two times, and with just two pilot whales previously seen in other islands of the Archipelago). Moreover, eleven recaptures were recorded between Madeira and the Canary Islands, ten of them during summer, with one animal moving between the two archipelagos at least three times between 2004 and 2006 (Servidio *et al.*, 2007). In Tenerife, where no significant seasonal differences were observed in density, the appearance of new individuals during summer (transients) might be compensated by the temporary departure of resident individuals to other waters; 96% and 60% of the individuals recaptured between Tenerife and the islands of La Gomera and Gran Canaria, respectively, were recorded here during the summer months (Chapter 3).

School sizes estimated by the models for the Canary Islands as a whole and for the different islands were similar to those based on direct field observations, with an overall value of 16.4 animals per group. Groups were larger in the eastern islands and smaller in the island of Gran Canaria. Nevertheless, in most analyses the available covariates explained a small amount of deviance that did not exceed 8% (except for the eastern and western areas, with 18.8% and 18.5%, respectively). Seasonal estimates for the entire archipelago showed larger group sizes in winter than in summer, and no significant differences between the two seasons for the island of Tenerife. These results seem to contradict field observations, and previous studies for the south west of Tenerife (i.e. Heimlich-Boran, 1993), where larger groups were described in summer. The reasons of these apparent discrepancies might lie in not having identified the covariates on which group size depends, such as social structure and behaviour.

As found in the Hawaiian Islands (Barlow, 2006), in the Canary Islands cetacean densities are higher closer to shore than in offshore waters, because of the narrow continental shelf that leads to the presence of both oceanic and inshore cetacean species close to the coast (Martín *et al.*, 1992). This probably also reflects the increased productivity or spatial and temporal predictability of prey associated with island effects (Baird *et al.*, 2008). Fish and cephalopod (pilot whale prey) distributions, have been found to be related to numerous oceanographic and environmental features, including depth (Gil de Sola, 1993), upwelling (Guerra, 1992; Rubin, 1997) and fronts, which create hotspots of primary and secondary production (Rubín, 1994).

Therefore, depth and slope steepness might be associated and crucial factors in describing cephalopod vertical distribution (e.g. Praca *et al.*, 2009) by also interacting with water circulation to determine the downwelling / upwelling movements that create a complex system of eddies that are considered to act directly on the availability and concentration of prey in the area (Davis *et al.*, 1998; Cañadas *et al.*, 2005). A number of high trophic level pelagic species have been shown to concentrate around and/or use mesoscale eddies as foraging habitat (e.g. Davis *et al.*, 2002; Seki *et al.*, 2002; Bakun, 2006; Polovina *et al.*, 2006; Yen *et al.*, 2006). Oceanographic and topographic features combined are likely to promote vertical and horizontal water movements that enhance primary productivity and thus sustain a richer biomass in the entire trophic web (Tynan *et al.*, 2005).

Although they also feed on fish, pilot whales are thought to be primarily adapted to feeding on both neritic and oceanic cephalopods (Hacker, 1992), ommastrephids being

the main prey in most areas (Clarke, 1996). Mintzer *et al.* (2008) examined the stomach contents of short-finned pilot whales from the North Carolina coast; *Brachioteuthis riisei* (numerical abundance 28%), an oceanic species, was the most important cephalopod prey, but *Taonius pavo* (12%) and *Histioteuthis reversa* (9%) also represented a substantial part of the diet. A large number of otoliths belonging to the fish *Scopelogadus beanii* were present (25%), indicating that these whales fed primarily off the continental shelf prior to stranding. This stomach content composition differed from those of short-finned pilot whales from the Pacific coast in which neritic species dominate the diet (Hacker, 1992). These findings also suggested that there is a considerable difference between the diet of short- and long-finned pilot whales in the western North Atlantic (Fullard *et al.*, 2000). The latter feed predominantly on the long-finned squid (*Loligopealei*), whereas the former feed on deep-water species.

Stomach contents of short-finned pilot whales in the Canary Islands indicate that their diet is mostly based on cephalopods. Contents of stomachs from short-finned pilot whales stranded in Tenerife and Lanzarote were found to contain entirely cephalopods: *Todarodes sagittatus*, *Cranchia* and juveniles of *Megalocranchia* (Hernández-García and Martín, 1996; Fernández *et al.*, 2009). Recurrent observations at sea off the island of Tenerife of the remains of giant squid (*Architeuthis* sp.) floating near pilot whales, as well as photographic footage of a long tentacle in the mouth and marks left on the dorsal fins of some individuals indicated that this deep sea squid represents at least part of the diet of pilot whales, as suggested previously by Aguilar de Soto *et al.* (2008). This is in accordance with their high-cost feeding strategy focussed on large and calorific prey capable of moving fast (Aguilar de Soto *et al.*, 2008).

These species of cephalopods principally occur at depths between 200 and 800 m (Quetglas *et al.*, 2000), but their spatial distribution in the whole study area is unknown, making the linking of pilot whale habitat to the distribution of their different prey quite difficult. However, the modelled habitats revealed preferences in depths of 1000-1500 m, which correspond to areas of step bathymetric relief influenced by environmental features favourable to high concentrations of cephalopods (O'Dor and Coelho, 1993; Quetglas *et al.*, 2000; Boyle and Rodhouse, 2005).

The reasons for different cetacean species living in the same area and/or habitat are not well understood. Different species may use the same habitat in different ways, e.g. with spatial segregation on a fine scale, hunting at different times of the day, by pursuit of different prey organisms, the dietary divergence being considered the dominant factor

(Herzing *et al.*, 2003; Bearzi, 2005; Qu  rouil *et al.*, 2008). Short-finned pilot whales have been frequently recorded in multispecies groups. In the eastern tropical Pacific, approximately 15% of pilot whale sightings include other cetaceans: bottlenose dolphins, striped dolphins, and tuna-dolphin aggregations (*Thunnus albacares* and *Stenella* spp.). Pilot whales have also been sighted with short-beaked common dolphins, Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), gray whales (*Eschrichtius robustus*), fin and sperm whales, and killer whales (Bernard and Reilly, 1999).

In Tenerife, bottlenose dolphin and short-finned pilot whale distribution remains quite separate, with bottlenose dolphins concentrated in coastal areas, especially close to Punta de Teno, and pilot whales clearly distributed around the 1000 m depth contour, slightly south (Carrillo *et al.*, 2010). Nevertheless, short-finned pilot whales have been recorded during the study period in the Canary Islands about 10% of the time in association with bottlenose dolphins, especially off the island of La Gomera, as already described by Ritter *et al.* (2011). Both species, when together, have been recorded at a different depth than those preferred when alone: pilot whale sightings in association with *Tursiops* were distributed over a wider distance range closer to the coast, and in general bottlenose dolphins were found at a greater depth than when alone. It is not very likely that feeding on common prey causes these aggregations due to the different foraging strategies of deep diving pilot whales compared to bottlenose dolphins, which predominantly feed in coastal waters close to the surface. On the contrary, protection from predators in an open deep water habitat might play a role in bottlenose dolphin strategy to favour one-sided association with pilot whales (Martin, pers. comm.; Ritter *et al.*, 2011).

The high frequency of sightings with calves and/or neonates has not only been reported in the southwest of Tenerife (Carrillo *et al.*, 2010), but has also been recorded during almost every month of the year in the rest of the archipelago, with only 17.8% of pilot whale sightings composed only of juveniles and/or mature individuals. Therefore, not only the island of Tenerife (Carrillo, *et al.* 2010) but also the rest of the archipelago can be considered as an important calving ground for this species (Chapter 3). While for other species (e.g. common dolphins, Ca  adas and Hammond, 2008) the presence of calves in the groups marked a different use of the habitat with preference toward more coastal waters, in the Canary Islands only slight differences were observed in the general distribution. In both cases, group abundance was higher at a depth of 1500 m, although groups with calves/neonates also seemed to extend their habitat toward more coastal waters. As previously described by Heimlich-Boran (1993), this species was observed on

multiple occasions during the study period performing a "babysitting" strategy (Gordon, 1987), in which calves remained at the surface with an adult or sub-adult animal while the group was foraging at depth, increasing protection for the calf and an easier subsequent location (Aguilar de Soto, 2006), as well as permitting mothers greater foraging freedom (Whitehead, 1996). This might explain why the group would prefer deeper waters regardless, being more favourable for foraging, with no necessity to move towards more coastal waters looking for protection for the calves. At the same time, the calm waters that usually characterise the preferred southern areas, the deep water close to shore, and the island mass effect which leads to the concentration of nutrient-rich waters on the lee side of islands might allow the whale to develop different behavioural activities in the same habitat range, at depths of 1400m -1600 m.

In this study, the analytical approach used most likely oversimplifies the complex relationships that exist between pilot whales and their environment, not least by the unavailability of relevant covariates. Direct and detailed information about the abundance and distribution of pilot whale prey would be of great benefit for better understanding of the relationship of this species with its environment.

Modelling the distribution of cetacean species is a difficult task especially due to their complex ecology and behaviour, because they live in a highly dynamic environment and because they can move rapidly over large distances (Redfern *et al.*, 2006). There might be more factors affecting their distribution in the study area, which were not used in the analysis, either because they were not available, or because they were not identified as important covariates. Feeding ecology is likely to be the prime factor influencing cetacean distribution (Gaskin, 1976), but information on prey distribution and abundance is usually difficult to obtain and often unavailable, as was the case in this study.

The horizontal and vertical mobility of prey, combined with temporal variability, make habitat use difficult to predict over small spatial and temporal scales, and environmental parameters are more available and are measured more accurately than fine-scale prey distribution. According to Torres *et al.* (2008), environmental parameters can generate better models of cetacean habitat preferences than models derived from prey distribution data, due to the difficulty of accurately measuring the latter at an appropriate scale.

On the other hand, there are some disadvantages to using such proxy measures that have to be taken into consideration. Typically, they only explain a small proportion of the observed variability in animal occurrence, and their use limits the ability to extrapolate to other areas because they represent unknown combinations of direct predictors; the same

proxy measure might be caused by a different combination of predictors in different geographical contexts, resulting in a different relationship with animal occurrence (Guisan and Zimmermann, 2000).

Future research is needed to detect possible variation in abundance and distribution of the short-finned pilot whale in the Canary Islands and to evaluate the stability of the species habitat use in time and space, especially with the increasing anthropogenic impact on its environment. Searching effort was mostly limited to the south coasts of the islands and additional evidence is required by including in further studies areas that are as yet unsurveyed or insufficiently surveyed. Extrapolation of predictions outside the survey region is not advisable until further validation of the predicted habitat use is rigorously tested with independent data (Ferguson *et al.*, 2006; Panigada *et al.*, 2008). Similar habitats or processes might be conditioned elsewhere by different indirect variables (Hamazaki, 2002), and the effect of the identified predictors could also differ outside the sampled area (Panigada *et al.*, 2008).

Moreover, more covariates should be included in the analysis, such as spatio-temporal variation in water currents and eddies, and how the seafloor may affect the current flow and water circulation, to better understand the complex relationships between environmental proxies and whale presence. Anthropogenic factors may also be interesting to include, such as distance from the main cities and from the ferry lines. The role of other ecologically relevant processes in shaping habitat use also remains to be tested, such as interspecific competition with other squid-eating cetaceans (Waring *et al.*, 2001). Further investigations into pilot whale diet using more recent techniques, such as stable isotopes or fatty acid analyses (Ackman and Eaton, 1966; Michener and Schell, 1994), would provide more precise information on this part of their ecological niche.

5.4.2 METHODOLOGICAL ISSUES

MOVEMENT IN RESPONSE TO SURVEY VESSELS

The impact on abundance estimates of possible responsive behaviour to survey vessels was not taken into account. This was considered to be a negligible factor because the general initial behaviour recorded for the most recent surveys was of indifference to the approach of the vessel. Moreover, the partial inconsistency of the database for the first survey years didn't allow for further analysis. In future surveys, a stricter initial data recording on the initial aspect of the animals and their behaviour is recommended,

allowing further analysis to explore whether or not there is a response to the survey vessels (e.g. Palka and Hammond, 2001).

The absence of a second platform on the research vessels precluded the estimation of the probability of detection of the transect line ($g(0)$). However, $g(0)$ is considered likely to be close to 1. Pilot whales are quite visible at sea because of their wide dark dorsal fin and because they form groups of 14 animals on average. The sighting conditions during the surveys ensured high visibility and detectability and the low speed of the vessels during the search guaranteed a long period of time available for detection (Cañadas and Hammond, 2008).

ROUNDING ANGLES AND DISTANCES

All distances were estimated by naked eye so long distances were likely to have been estimated with less accuracy, and generally all distance were rounded to convenient values. Therefore, the data were smeared to minimise possible bias in density estimates, positive in case of underestimation or negative if overestimated. No calibration tests were conducted for each observer, survey, and vessels used. The only exceptions were the surveys conducted between 2004 and 2009 in La Gomera and Tenerife on board the inflatable boat Chacalote, where the same experienced observers followed the same methodology for collecting data. Here distances estimated by eye to an object were compared to distances measured by GPS, and no under or over-estimation was detected. These surveys covered 80% of the total number of short-finned pilot whale sightings recorded between 1999 and 2012, so some under or over-estimation in distance measurement in the other 20% cannot be excluded. However, even if some bias did occur, it is unlikely that this would strongly affect the final estimates because only a smaller portion of the data could have been affected. On the other hand, the variability that arises by recording angles and distances with the naked eye was not taken into consideration in this study, and therefore the CVs of the estimated abundance are likely underestimated.

HABITAT CHARACTERIZATION

Following similar methodology in the literature, the study area was divided into a grid of cells with a resolution of two minutes of latitude by two minutes of longitude, obtaining 1,950 cells for the entire area. Even though each grid cell was assumed to incorporate little variability in physical and environmental features, 8% of the grid included large differences in water depth (greater than 1000m difference) in the first six-seven miles

from the coast, and especially around the islands of Lanzarote and Fuerteventura. Considering also that these cells mostly correspond to the area with the highest pilot whale density, and that the covariates mostly selected by the models were depth-related, this could cause the loss of some resolution in the fitted relationships. This might have the effect of spreading the effect of these covariates to a wider area, or even leading to otherwise misleading results.

Future analysis should consider methods of finding a better compromise between the number of grid cells and the precision and variability of the features contained in each. The resolution of the available variables can define areas as small as 4 km, much smaller than the area used for this analysis. On the other hand, the number of cells would increase along with the number of cells with no sightings resulting in greater overdispersion in the data. For future analysis, it is recommended that grid cells of different sizes are constructed to explore the impact on results.

5.5 CONCLUSIONS

Knowledge about the distribution patterns of short-finned pilot whales in Canary Islands has improved substantially as a result of the present work. The new information on habitat use of this species represents a first step in developing specific conservation measures in the archipelago. Further work is needed to improve the still limited understanding of the species' ecology in the Canary Islands, to assess the current status of this population and to provide effective conservation and management efforts.

The new information on population abundance, distribution and preferred habitats for short-finned pilot whales, especially with respect to their different needs such as feeding or reproduction, represents a baseline to put any identified threats to this species into context and to establish priority conservation and mitigation measures, specific for each area. Closely related to the topography of the seabed, the predicted density distribution in the archipelago around the shelf edge downwind of the main islands indicate patchy areas of high usage, where pilot whales also concentrate to feed and where the large majority of the calves are encountered. These areas, identified as important to the species, unfortunately also correspond to the strongest exposure to the impact from human activities: pollution from land sources, overfishing, and disturbance by the intense

maritime traffic of recreational and whale watching vessels as well as ferries. Therefore, the continental shelf and shelf edge areas identified in the Canary Islands, especially in southwestern Tenerife where the short-finned pilot whales seem to be more vulnerable (feeding and calving grounds), is also where the marine environment appears to be more vulnerable (stronger anthropogenic impact). Notwithstanding that attempts to develop management strategies for pilot whale conservation should be extended to the whole archipelago, priority should be given to the conservation or restoration of the marine environment in these downwind areas especially off Tenerife, La Gomera and Gran Canaria, where they appear to encompass the majority of the resident population and where the anthropogenic impacts are concentrated.

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CHAPTER 6
FINAL DISCUSSION

6.1 DISCUSSION

6.1.1 THESIS SUMMARY

The present study originated from a need to increase knowledge of short-finned pilot whales in the Canary Islands. Apart from a few studies conducted off the island of Tenerife, which were limited to a restricted area and scattered over time, no information on their biology and ecology has been collected to encompass the entire archipelago or combine general aspects of their distribution, habitat use and social structure. The lack of basic information on the dynamics of this population in the Canary Islands has hindered assessments of its current conservation status, which is nevertheless classified in the Spanish and Canary Islands Catalogues of Endangered Species as "vulnerable".

Effective conservation measures for a species with such complex ecology and social structure requires information on population size, residence and ranging patterns, social structure and the influence of environmental features on their distribution and habitat use that can only come from an in-depth and long-term investigation. The relevance of the present project therefore is that it pulled together all this information on short-finned pilot whales in the entire archipelago, in order to provide the basis to develop targeted and effective mitigation and conservation measures.

Based on this purpose, the general study protocols were assessed to ensure the collection of complete data coverage of the different aspects of the biology of this species in the Canary Islands. Nevertheless, surveys specifically designed for pilot whales were limited to the islands of La Gomera and Tenerife, and to a small part of the entire study period (three and two years, respectively). The asynchronous nature of the data collected, with no simultaneous surveys around the different islands, meant that general aspects of their population biology could not be assessed at the scale of the archipelago, so that it was not always possible to identify patterns in the entire Canary Islands. In addition, comparisons among areas of the archipelago could not always include all the islands and, in some cases, important questions were left open to future investigations. This was the case, for example, for seasonal and annual movement patterns in the archipelago, demographic parameter estimates (survival and recruitment rates), and abundance trends.

Nevertheless, detailed and focused analysis was conducted in some restricted areas, especially in southwestern Tenerife and La Gomera. Detailed analysis of social structure, abundance and movements were possible here, thanks to the large amount of data collected in these areas where most of the short-finned pilot whale sightings were

recorded. These analyses revealed important aspects of this species' ecology that were previously unknown; important not only for this population in the Canary Islands but also useful for other areas because new inferences on residency, ranging patterns, and habitat use are now available for further comparative studies. Nevertheless, the general lack of literature on short-finned pilot whales in contrast to some more studied cetaceans (e.g. bottlenose dolphins, reviews in Connor, 2000) limited comparative assessments here mostly to the recent studies conducted in the two archipelagos of Hawaii (Mahaffy, 2012) and Madeira (Alves *et al.*, 2013), where the social structure of the short-finned pilot whale populations were studied.

The overall predefined objectives of the study were considered to be successfully achieved:

- General overview of short-finned pilot whale occurrence, distribution and movements in the Canary Islands;
- First photo-identification catalogue of this species in the main islands;
- Differentiation among whales of different residency patterns at archipelago and island level;
- First abundance estimation of the resident population of southwestern Tenerife;
- Identification of the most important environmental and biological factors affecting the occurrence, distribution, and abundance of this species in the archipelago;
- Characterisation of the social structure of short-finned pilot whales in the Canary Islands.

Site fidelity and movement patterns within the Canary Islands (chapter 2)

Surveys conducted between 1999 and 2012 in the Canary Islands allowed the year-round presence of short-finned pilot whales in the archipelago to be assessed, with the exception of the island of el Hierro where direct visual observations have so far not reported their presence.

The extensive photo-identification material analysed allowed the creation of the first photo-identification catalogue for this species in the Canary Islands, with 3,275 individuals identified, of which 1,310 were well-marked whales.

Based on the recapture histories, with whales seen up to 36 times over a time range from one day to 11 years, different levels of residency patterns were identified for the first time: 50 "core residents", 150 "residents", 156 "occasionals", and 780 "transients". Island-related individuals were also identified for the islands of Tenerife and La Gomera.

The sighting encounter rate varied greatly among the islands, with a range of 0-0.49 sightings/nm in the most peripheral islands, and 3.62 and 1.14 sightings/nm in Tenerife and La Gomera, respectively. Group size, with an overall mean of 16 whales (SE=0.5, median=13), also varied among the islands with larger groups found in Lanzarote-Fuerteventura and La Gomera (mean=20, SE=2.4, median=18; and mean=19, SE=1.5, median=18, respectively). In Tenerife, seasonal changes in group size showed larger groups during summer and autumn. Group composition was similar among the islands, with sightings generally of mixed age and sex classes. Neonates were mainly present between summer and early autumn (83% of the total sightings), more than half in groups where males were also identified.

Movements within and among islands were detected and quantified over the study period. However, short-finned pilot whales were also shown to be capable of long distance movements up to 169 km (mean=8 km, SE=0.22), encompassing different islands of the archipelago (especially La Gomera).

While the overall ranges (mean=355.9 km², SD=553.8) of the most frequently sighted individuals combined areas of the islands of La Gomera, Tenerife, and Gran Canaria over a total area of 417.9 km², the core areas of usage (mean=76.9, SD=119.7) extended for a much smaller total area of 81.6 km², with overlapping ranges in 71% of this area, localised in the southwestern Tenerife.

Long distance movements were undertaken by both sexes and most of the time it was mixed groups that travelled the greatest distances between the islands, including groups with calves.

Social structure, composition and stability in the Canary Islands (chapter 3)

The social structure of short-finned whales in the Canary Islands was assessed for the first time. A general assortative society was indicated by the network analysis, supporting division into 31 clusters, showing that animals were preferentially linked to each other but, at the same time, that individuals of different residency patterns were also highly interconnected. A well-differentiated society with long-term preferential associations and strong inter-individual bonds which persisted over the entire study period was identified in the archipelago. For the population of Tenerife and La Gomera, a hierarchical social system based on 11 pods, with a mean of 18 (CV=0.3) individuals, was identified, showing stability in structure with almost no differences in range.

Abundance estimation in southwestern Tenerife (chapter 4)

An accurate and precise population estimate was generated for all short-finned pilot whales using the area southwest of Tenerife between 2007 and 2009 and, for the first time, for the resident population (island-related "core resident" and "resident individuals") inhabiting these waters. Mark-recapture open and closed population models were explored and the final estimates were 636 (CV=0.028; 95%CI=602-671) resident animals, and a total of 2,698 individuals (CV=0.139; 95%CI=2,057-3,538).

Habitat use in the Canary Islands (chapter 5)

Short-finned pilot whale abundance and distribution were modelled using Generalized Additive Models (GAMs), and the covariates (environmental variables, fixed geographic variables, biological and extrinsic factors) that best explained spatiotemporal patterns in their distribution and density in the archipelago were identified. Variables related to depth best explained group abundance, predicting areas of high usage especially in areas downwind of the islands at depths of 800-1,500m, deeper waters around 1,500m during summer and shallower depths closer to the coast (1,000m) during winter. The overall population was estimated using density surface modelling at 1,980 individuals (CV=0.32, 95%CI=1,441-2,324), higher during warmer than during colder months.

Special attention was given to the island of Tenerife where differences in abundance and habitat use were investigated annually and seasonally: an overall total of 1,223 whales (CV=30.8; 95%CI= 1,046-1,267) were estimated, with peaks during 2007 and 2008, and an overall density of 0.657 whales km⁻², mainly distributed between depths of 800 and 1,800m. Groups engaged in feeding activities were mainly predicted to occur in surface temperatures higher than 21° while, for the remaining behavioural categories group abundance was predicted to be higher at depths around 1,600 m. In Tenerife, sightings in association with bottlenose dolphins were predicted to be made at greater distance from the coast than when pilot whales were found alone. Higher densities were predicted at 8 km from the coast at medium-high values of seabed slope. No differences were found in density between groups with or without calves.

6.1.2 DISTRIBUTION AND HABITAT USE

The complex and dynamic ecosystem of the Canary Islands is typical of an oceanic archipelago, including upwelling filaments, cyclonic and anticyclonic eddies, localised tides, and "island mass effect" (La Violette, 1974; Hernández-León, 1986; Arístegui *et al.*, 1994). These mostly originate from the Canary Currents to which the islands are an important obstacle that generates massive mesoscale perturbations (Aristegui *et al.*, 1997).

Compared to oceanic waters, the waters around the Canary Islands are extremely productive, and are characterised by highly variable oceanographic patterns, patchy accumulation of nutrients and trophic chain developments, with warmer, calmer and more stable waters in the downwind areas (Barton *et al.*, 2000). These important factors contribute to this archipelago being a "hot-spot" for cetacean biodiversity (Martin *et al.*, 2009), whilst also influencing the distribution of the species among the different islands.

Recorded year-round, short-finned pilot whales were distributed non-uniformly around the archipelago, with greater densities concentrated in patchy areas mainly on the leeward side of the main islands. Distribution was mainly associated with specific physical and biological features that characterise the archipelago, areas with depths around 1,000-1,500m with medium-high seabed gradients were where most of the animals were seen (Chapter 3) and predicted (Chapter 5). These results confirm that this species is mostly linked to continental shelf breaks, slopes, and areas of high physiographic relief (Carwardine, 1995; Bernard and Reilly, 1999; Olso, 2009), as previously reported for this species in studies conducted off Tenerife (Heimlich Boran, 1993; Martín and Montero, 1993; Montero and Arechavaleta, 1997; Martín *et al.*, 2000, 2009; Carrillo *et al.*, 2010) and more recently in the archipelagos of Madeira (Alves *et al.*, 2013) and Hawaii (Mahaffy, 2012).

Population abundance in the archipelago was predicted to be around 2,000 animals, with higher density predicted during the summer months, and movements towards deeper waters (2,500 m) during the winter season, especially within the eastern islands (Chapter 5), which coincides with seasonal changes in oceanographic phenomena (Arístegui *et al.*, 1994; Hernández-León, 2001a; Hernández-León *et al.*, 2002a). Highest density was predicted (Chapter 5) supported by observations at sea (Chapter 3) in southwestern Tenerife, followed by the island of La Gomera.

6.1.3 PATTERNS OF RESIDENCY AND INTER-ISLAND MOVEMENTS

As described for the short-finned pilot whale in Hawaii (Mahaffy, 2012) and in Madeira (Alves *et al.*, 2013), and by Heimlich-Boran (1993) for the population in the southwestern waters of Tenerife, this species showed a marked variability in residency patterns in the Canary Islands. Temporal analysis of the resident pilot whales (lagged identification rate, Chapter 2) suggested a high level of residency along with wide ranging movements outside the surveyed area, and/or some form of emigration with a return rate to the archipelago after a time interval greater than the length of the study (as previously suggested by Heimlich-Boran, 1993). While a high proportion of animals (63%) were seen only once or twice during the study period, a small group of pilot

whales (4%) was repeatedly sighted during all seasons and throughout the study, up to eleven years. "Core resident", "resident", "occasional" and "transient" whales (adult and indeterminate well-marked animals) were distinguished based on their capture history built using photo-identification data collected between 1999 and 2012.

While site fidelity is generally defined based on the amount of time animals spend in a specific area (Wells and Scott 1990), the parameters used to define cetacean residency patterns vary widely and are often influenced by the topography of the study area and access to the study population (Mahaffy, 2012). The criteria used in the Canary Islands to distinguish the different residency categories were, in fact, subject to the geography of the islands and to the survey design, favouring downwind areas, and, depending on the research platform used, more coastal waters or further offshore. Nevertheless, limiting the survey areas to restricted regions was not only a consequence of these constraints, but it was also based on previous studies conducted in the archipelago that identified the downwind regions as the areas with the highest cetacean biodiversity (e.g. Richard, 1936; Escorza *et al.*, 1992; Heimlich-Boran, 1993; Martín and Montero, 1993; Politi *et al.*, 1996; Montero and Arechavaleta, 1997; Martín *et al.*, 2000, 2009; Pérez-Vallaza *et al.*, 2008; Carrillo *et al.*, 2010). Therefore, even though these distinctions were quite arbitrary, they allowed, at archipelago and island level, whales with high site fidelity, especially in the downwind areas, to be distinguished from those that showed more nomadic behaviour, or at least a wider range that could encompass different coastal and offshore regions.

Understanding of the characteristics of transient animals is limited and somewhat confused. Transient whales might represent animals that were not recaptured simply because they were missed during the photo-identification survey studies, or were not available to be photographed because they were not in the area being surveyed at that moment. A large proportion of the Canary Islands area is still unsurveyed. Therefore, transient whales might instead have stronger site fidelity linked to another area of the archipelago that has received little or no survey effort. On the other hand, the 11 pilot whales recaptured between the archipelagos of Madeira and the Canary Islands (Servidio *et al.*, 2007) showed that there are transient animals in these waters, that are not limited to coastal waters, as are the resident whales of southwestern Tenerife (Chapter 2).

Pilot whales are not known to make regular long-range movements; only north-south or inshore-offshore movements have been described (e.g. Newfoundland, Abend and Smith, 1999), mostly following prey distribution changes or in response to changes in the current structure of the area (Leatherwood *et al.*, 1988). Nevertheless, tagging studies

have reported extensive ranging movements (Andrews *et al.*, 2008; Nawojchik *et al.* 2003; Mate *et al.* 2005), and extrapolation from studies of diving behaviour (Aguilar de Soto *et al.* 2008; Jensen *et al.*, 2011, Sakaii *et al.*, 2011) has demonstrated that these animals have the physical potential to undertake long-distance movements. Therefore, it appears reasonable to expect that the recaptures recorded between the Canary Islands and Madeira are not isolated events. Rather they are likely to be indicative of more frequent long-range movements among these groups of islands that are separated by large areas of deep open waters.

Lanzarote and Fuerteventura had the highest percentage of transient individuals; 89% of the individuals seen in these waters. No resident whales were identified and only a few animals were recaptured up to two times during the study period. There was almost no interchange of animals with the rest of the archipelago (except for two pilot whales previously identified in Gran Canaria), as confirmed by the low value of 0.041 for the match index calculated for these islands in different years (Chapter 3). The opposite situation was recorded for the islands of Tenerife and La Gomera, where pilot whales identified as transients represented only 40% of all the identified animals. The rest of the animals showed high site fidelity to these islands, with animals recaptured repetitively over the study period. The 50 pilot whales identified as "core residents" and the 255 "residents" in the Canary Islands were almost all seen also in Tenerife, and 33% of them in La Gomera.

In the Canary Islands, the higher abundance of short-finned pilot whales predicted during warmer seasons (Chapter 5) might coincide with the potential incursions into the archipelago of transient whales from neighbouring areas, as supported by the fact that twice as many whales photo-identified only once or twice (in the same season) were recorded during summer than during winter.

There were no seasonal differences in predicted abundance in Tenerife (Chapter 5). The movement of transient animals into these waters may be compensated by the temporary movements of resident individuals from this island towards neighbouring areas. This seems to be confirmed by the higher number of recaptures between Tenerife and La Gomera, and Tenerife and Gran Canaria; 96% and 80% of the recaptures, respectively, were recorded during the summer months (Chapter 2).

The distances among the islands of the archipelago do not prevent inter-island movements, given the ranging ability of this species. In Tenerife, whales recaptured in different islands were mostly recaptured again in Tenerife (return rate of 1.5) but in Gran Canaria and La Gomera animals recaptured in different islands were more numerous than

those recaptured more than twice in the same island. Although there were individuals that were strongly associated with either Tenerife or La Gomera, quite a high interchange rate (0.6) was found between the two islands, with 117 individuals recaptured and some whales repeatedly sighted in both islands up to four times, back and forth, with a clear directionality of animals moving from La Gomera to Tenerife. Moreover, animals leaving the island of La Gomera had a lower tendency to return to the island in the same year than animals returning to Tenerife (Chapter 2).

6.1.4 FORAGING BEHAVIOUR AND MULTI-SPECIES COMPETITION

The factors that influence residency patterns of pilot whales among the islands are poorly understood. Movements of upper trophic level predators in an open ocean environment are determined at least partly by the distribution, density, and movements of their prey (Whoodworth *et al.*, 2012). As also shown in Hawaii (Barlow, 2006), cetacean densities in the Canary Islands were higher closer to the coast around the main islands of the archipelago than in offshore areas, because of the narrow continental shelf that allows deep diving and also the presence of coastal species relatively close to the coast. This apparently reflects an increase in productivity or spatial and temporal predictability of prey associated with island effects (Baird *et al.*, 2008a). The islands and their interaction with winds and currents create a complex system of eddies, which act as retention zones, trapping nutrients in the core of the anticyclonic eddies and in the boundary of cyclonic structures near the islands (Hernández-León, 2001a; Hernández-León *et al.*, 2002a). Mesoscale eddies have been described as foraging habitats for a number of high trophic level pelagic species (e.g., Davis *et al.*, 2002; Seki *et al.*, 2002; Bakun, 2006; Polovina *et al.*, 2006; Yen *et al.*, 2006). They have been frequently proposed to enhance nutrient retention along continental shelf systems and near islands (Sponaugle *et al.*, 2002; Queiroga and Blanton, 2005). Great concentrations of mesopelagic organisms were found to be related to the anticyclonic eddies in the southern waters of Tenerife and Gran Canaria (Bordes *et al.*, 1999; Wienerroither *et al.*, 2009), and to concentrations of pelagic decapods south of Fuerteventura where another anticyclonic eddy formed (Foxton, 1970a, b).

Foraging decisions need to take into account travel time to each prey patch, the type of food in each patch, and the density of that food (Krebs and Cowie, 1976; Cowie, 1977; Werner and Hall, 1974). When resources are not evenly distributed across environments but instead occur in patches, as is typical of oceanic islands (Barton *et al.*, 2000), the ranging areas of higher trophic level predators are generally extended to encompass larger areas. Cetaceans in the Canary Islands might therefore be expected to travel throughout the archipelago searching for adequate prey patches.

The eastern islands, visited almost exclusively by transient pilot whales, are characterised by wider continental shelves, with greatest depths of 1,400m far offshore, by waters generally open to the effects of the main northerly currents, and by several mesoscale physical features. These latter features include: the effect of eddies in the accumulation of zooplankton and fish larvae, the role of the deep scattering layers (located between 400 and 600m depth) in the structure of the pelagic ecosystem, and cold upwelling filaments from the Northwest African shelf to the islands which transport waters rich in chlorophyll (Hernández-León *et al.* 2007). In the western islands, the effect of the anticyclonic gyre brings an important contribution of nutrients to these areas quite close to coast and the mass effect ensure shelter from the main currents (Hernández-León *et al.* 2007). These areas are characterised by transients but also a high concentration of resident pilot whales. Deep waters close to the coast make these waters areas especially suitable for raising calves and other vital activities.

Competition for resources, including habitat, might be an important factor affecting residency pattern distributions among the islands. In the eastern islands, short-finned pilot whales may have to compete for resources with other deep-diving species whose presence has been recorded year-round (Pérez-Gil *et al.*, 2011, Martin, personal comm.). Eight (40%) of the 20 cetacean species detected during SECAC surveys between 2007 and 2010 in these waters were teuthofagous and deep-diving whales of the families Ziphiidae (Cuvier's, Blainville's and Gervais' beaked whale), Physeteridae, Kogiidae (pygmy and dwarf sperm whale) and Delphinidae (short-finned pilot whale and Risso's dolphin) (Pérez-Gil *et al.*, 2011, Pérez-Gil *et al.*, 2011).

Diet data available for these species show a preference for cephalopods, which are recognised as one of the most important food resources worldwide (Clarke, 1977; Whitehead, 2003). Stomach contents of beaked whales in the Canary Islands contained mostly oceanic cephalopods: *Taonius pavo*, *Histioteuthis* sp, *Mastigoteuthis schmidti* and *Octopoteuthis sicula* (Santos *et al.*, 2007). Studies on sperm whale prey remains have indicated that their diet is mostly based on oceanic cephalopod (mainly *Gonatus* sp., *Histioteuthis bonnellii*, *Architeuthis* sp.), even though some fish species (*Pollachius virens*, *Lophius* sp.) were also found (Santos *et al.*, 2002). Oceanic cephalopods have been described also as the most common prey in the diet of pilot whales (*Todarodes sagittatus*, *Cranchia* and *Megalocranchia*; Hernández-García and Martin, 1994; Fernández *et al.*, 2009). In Tenerife, remains of giant squid (*Architeuthis* sp.) found floating near pilot whales off Tenerife (Aguilar de Soto, 2006), and observations of animals with squid tentacles in their mouths (Servidio, personal observation) indicate that large deep-dwelling squid could also be part of the diet of pilot whales.

The coexistence of several deep-diving cetacean species in a relative small area could lead to direct competition for food resources. Species that are members of the same ecological guild with similar diet might use particular resources in different proportions, or more generally, employ more or fewer resource types, by having a wide and narrow niche range, respectively (generalists or specialists) (Whitehead, 2003). Dietary niche separation and geographic segregation have been proposed, for example, in beaked whale's species with similar dietary preferences (MacLeod *et al.*, 2003). Therefore, different ecological requirements may be responsible for differences in habitat use as well as the development of different diving and feeding strategies (Baird *et al.*, 2002, 2006; Zimmer *et al.*, 2003; Johnson *et al.*, 2004; Tyack *et al.*, 2005, Watwood *et al.* 2006; Aguilar de Soto *et al.* 2008). Pilot whales seem to feed on prey with more muscle mass than on less mobile prey with lower individual caloric value, as described for beaked whales (Aguilar de Soto *et al.*, 2011). Different pilot whale site fidelity with respect to the other deep-diving species found in these waters year-round might represent, therefore, a feeding strategy response whereby Lanzarote and Fuerteventura are excluded from their core range.

In Tenerife and La Gomera, although there is high cetacean biodiversity in terms of the number of species found, species other than pilot whales occur only occasionally (Carrillo *et al.*, 2010; SECAC, unpublished) or in confined areas with almost no overlap with the core range of pilot whales, therefore limiting direct competition for space and resources. Even though pilot whales and bottlenose dolphins are repeatedly observed together in Tenerife, their distributions remain largely separated, with bottlenose dolphins concentrated mostly along the coast further north than the more offshore and southern distribution of short-finned pilot whales.

6.1.5 BREEDING BEHAVIOUR

An alternative, but not exclusive, hypothesis to explain the presence of transient pilot whales in the Canary Islands, especially those sighted in Tenerife and La Gomera, could be related to breeding behaviour. The high productivity that characterises the waters of the Canary Islands compared to the oceanic waters that surround them and the unusual and fairly predictable concentrations of nutrients quite close to the coast are important factors to enable a population to exist in a limited area year-round, and also to attract and support the requirements of transient animals.

Seasonal changes in group size have been observed in short-finned (Tenerife, Madeira, and Hawaii) and long-finned pilot whale populations (Cañadas and Sagarminaga, 2000; de Stephanis *et al.*, 2008b). In the Canary Islands, larger groups were observed during

the summer and autumn. Differences in group sizes have been proposed to be associated with breeding behaviour, with sub-groups combining to mate (de Stephanis *et al.*, 2008b). In the Canary Islands, larger groups occurred when more transient animals were recorded and mixed groups in residency patterns were more numerous and therefore had the chance to breed, a pattern also seen in Madeira (Alves *et al.*, 2013). Neonate and calf records were more concentrated during summer-early autumn and, considering the gestation period of this species (Kasuya and Marsh, 1994a), breeding might occur mostly during the warmer months.

Even though it is not possible to assess whether the arrival of transients is related to breeding or whether breeding actually takes place during these encounters, resident groups do not seem to be closed, isolated structures and it seems likely that these temporal associations might also involve interactions. Movements among the islands and between the Canary Islands and neighbouring waters could present opportunities for breeding and lead to gene flow in the population. This seems to be the case for short-finned pilot whales in Madeira, where an unexpected lack of genetic diversity was found between residents and transient short-finned pilot whales (Alves *et al.*, 2013), probably as a consequence of breeding behaviour in these two groups of animals.

6.1.6 POPULATION STRUCTURE

Studies of killer whale populations in the northeast Pacific have shown the existence of at least two ecotypes of killer whales inhabiting the same area, with different general residency patterns associated with dissimilarities in morphology, genetics, feeding and traveling behaviour, acoustic behaviour, and social structure: fish-eating resident and mammal-eating transient killer whales (Baird and Stacey, 1988; Ford, 1991; Ford *et al.* 1998, 2000; Ford & Ellis, 2006; Yurk *et al.*, 2002; Foote *et al.*, 2010). The social structure found in the resident population of killer whales (Bigg *et al.*, 1990; Barrett-Lennard, 2000) has been extended to long-finned pilot whales (Amos *et al.*, 1993; Fullard *et al.*, 2000; Ottensmeyer and Whitehead, 2003; de Stephanis *et al.*, 2008b) and has been proposed for short-finned pilot whales (Heimlich-Boran, 1993; Mahaffy, 2012, Alves *et al.*, 2013); a natal group philopatry in a stable matrilineal social structure encompassing several clans, each one containing several pods.

The social structure and composition of Canary Islands resident pilot whales (Chapter 6) shows similarities to that proposed for the population in Madeira (Alves *et al.*, 2013); a social structure composed of pods combined in clans. However, the lack of genetic analysis that could confirm the natal group philopatry with multiple extended matrilineal structures, mean that comparisons to the social structure of killer whale matriline structure and

extrapolations from the other oceanic archipelagos of Hawaii and Madeira should be considered cautiously.

Analysis of association patterns between individuals showed that short-finned pilot whales in the Canary Islands form a well-differentiated society, with long-term preferential associations and stable companions. The temporal analysis identified the existence of at least ten longitudinally social units, with highly associated members within each unit, and stable over at least 11 years (1999-2011).

Selecting the most frequently seen well-marked adults and indeterminates identified in Tenerife and La Gomera in good coverage sightings, 11 pods were identified (Chapters 2, 3), showing stability in structure and localised distribution with almost no differences in their core ranges. The cluster analysis built on this dataset identified animals in strong association stable over time, and with a social network where all the animals belonging to the same core-cluster, with no cut-points, no satellite clusters, and an overall strength of 7.91 (SE=0.36) (Chapter 3). These whales coincided with the whales identified as "core residents" linked to the island of Tenerife. This suggests that the most frequently sighted pilot whales in La Gomera likely belong to the same sub-population of animals found in Tenerife or at least share the same area. The ranging distribution of animals seems to confirm this because even pilot whales that were recaptured repeatedly in La Gomera had centres of activity located in a limited area in southwestern Tenerife, where their ranges overlap (Chapter 2). Only 26 animals (well-marked adults and indeterminates) extended their ranging area to both islands (Chapter 2).

The resident pilot whales in southwestern Tenerife, the population size of which was estimated at 636 (CV=0.28, 95%CI= 602-671) (Chapter 4), were found in association with individuals (pods) with an estimated mean group size of 18 whales (CV=0.30, considering the stable clusters and the three clusters with casual acquaintance component, at their curve stabilization level), similar to those found for this species in Madeira (18, CV=0.08; Alves *et al.*, 2013).

While both resident and transient populations have been extensively studied in killer whales, there is no information about the social structure of transient pilot whales. In the Canary Islands, the available information did not allow comparative analysis between pilot whales with differences in social structure and residency patterns. Transients were observed in mixed groups of age and sex, and also found in association in larger groups (larger than when seen by themselves) with animals of different residency patterns, core residents included. This is different to what is observed in killer whales, which usually

travel in small groups (Ford and Ellis, 2000) with no mixing or breeding recorded between residents and transients (Baird and Dill, 1995; Barrett-Lennard and Ellis, 2001).

Odontocetes display high plasticity in behaviour which allows them to adapt to different environmental conditions and to use resources effectively. A given species can display a variety of feeding strategies, different area usage and association patterns, as described for bottlenose dolphins (Connor, 2000). Differences in their habitats, such as geomorphological features, area and predictability of resources, might lead to the development of different social strategies in delphinids (Gowans *et al.*, 2008). Although more information is needed to explore this further, the differences in the ecology between the resident and transient short-finned pilot whales in the Canary Islands could result from the geomorphological characteristics of the habitat, which may have an effect on their distribution, ranging extension, habitat use and on social organization, as described for the Russian killer whale (Burdin *et al.*, 2007).

The co-existence of different levels of residency patterns in the Canary Islands and in more offshore areas suggests the existence of multiple sub-populations in the archipelago, where at least a resident/island-associated population (mainly linked to Tenerife) seems to co-exist and interact with transient/oceanic whales (Chapter 2, 3). The presence of multiple populations within a restricted geographic region has already been described for this species in the archipelago of Madeira (Alves *et al.*, 2013) and of Hawaii (Mahaffy, 2012), where high levels of site fidelity were observed for some island-related whales, with almost no inter-island movements, interacting with a more pelagic population.

6.1.7 IMPLICATIONS FOR CONSERVATION

Cetacean populations are affected worldwide by a wide range of different human activities, including the direct impacts of hunting, by-catch in fishing gear and ship-strikes, and the indirect impacts of habitat degradation by fishing or construction, chemical and noise pollution, the overexploitation of prey resources and the effects of warming oceans (Harwood, 2001).

The necessity to identify and quantify the severity of these threats and to take action to mitigate them when needed is widely reflected in the national legislation of many countries, and in a number of international organisations: European Union, International Council for the Exploration of the Sea (<http://www.ices.dk/>), International Whaling Commission (<http://www.iwcoffice.org/>), Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR) (<http://www.ospar.org/>) and United

Nations Environment Programme Convention on Migratory Species (<http://www.cms.int/>).

The marine protected area (MPA) is a common tool used by many international regulatory bodies (e.g. OSPAR Convention 1992; EU Habitats Directive 1992; ACCOBAMS 1996; ASCOBANS 2006) to conserve marine habitats and species, including cetaceans (e.g. Agardy, 1994; Agardy, 2000; Faucher and Weilgart, 1992; Hooker *et al.*, 1999; Hoyt, 2005; Hyrenbach *et al.*, 2000; Notarbartolo-Di-Sciara *et al.*, 2008, Alves *et al.*, 2013). However, questions have been raised as to whether this is the most suitable method for protecting species (Boersma and Parrish, 1999; Hoyt, 2005; Kelleher and Kenchington, 1992). In many cases, the designation of an area for protection may not be necessary or the most appropriate solution to minimise a threat or pressure on a species (Cañadas *et al.*, 2005; Notarbartolo di Sciara, 2008), and to balance aspects of sociology and biology (Jentoft and Chuenpagdee, 2009). This is especially the case for cetaceans which may be distributed across large areas, and for which the dimensions and limits of any protected areas might not make any ecological sense to ensure the achievement of the conservation objectives (Cañadas, 2006). Therefore, a suite of measures should be considered including direct action to address identified threats through specific and targeted measures to ensure the most effective conservation strategy for the species.

The rapid development in tourism in recent years, especially in southwestern Tenerife, has caused an increase in the demand for recreational activities. This has led to the growth of numerous companies that supply marine excursions, including short-finned pilot whale watching, and the building of new marinas. Habitat degradation, direct and accidental contamination of the sea and coastal deterioration, acoustic pollution, fishing activity, and intensification of maritime traffic (Ritter, 2010; Carrillo and Ritter, 2011) together represent an increasingly worrying suite of threats to the conservation of this species and the rest of the cetaceans that inhabit these waters year-round. Moreover, the future possible development of oil platforms in the waters between Lanzarote-Fuerteventura and Morocco might have a strong impact on cetacean populations, including short-finned pilot whales. Considering these threats, it is essential to obtain a better understanding of the different cetacean populations and their habitats in the archipelago to understand the extent to which they are impacted by a particular threat, and therefore to inform conservation action.

Although this study did not directly address specific conservation issues in the Canary Islands (a qualitative identification and evaluation of the main anthropogenic threats to pilot whales is detailed in Annex 6), the new and additional information here presented

can be put towards a more complete assessment of the status of short-finned pilot whale population(s) off the Canary Islands.

The results provided by the present study establish the necessary baseline information as a scientific reference for conservation actions. This information can then be used to help the development and appropriate implementation of conservation actions on this species in the archipelago. Although the vulnerability of this species has not been assessed, the continuous anthropogenic pressure is sufficient for it to be considered vulnerable in the Spanish and Canary Islands Catalogue of Threatened Species. Therefore, it seems well justified to propose the inclusion of short-finned pilot whales among the species in need of strict protection through the development of a detailed conservation plan specific to this species.

The information that this study provides on the ecology of short-finned pilot whales in the Canary Islands illustrates the heterogeneity in distribution and residency patterns among the different islands (Chapter 2). This species is capable of large movements, as demonstrated by the frequent inter-island movements, and by the resightings between the Canary Islands and Madeira Archipelago (Chapter 2). The general tendency in past conservation proposals was to extrapolate information obtained from the only studied population of southwestern Tenerife to the rest of the archipelago, including treating this species as a single "stock". Moreover, the absence of genetic analysis undertaken to investigate the effective existence of demographically independent populations of pilot whales in Canary Islands based on their different residency patterns (Chapter 2), would lead to treating this species in the archipelago as a single management unit. This should be revised to consider as populations the stable island-associated social entities of core resident whales, mainly located in Tenerife and La Gomera, as well as transient whales that are characteristic of the more peripheral islands of the archipelago (Chapters 2 and 3). This would allow the designation of conservation measures for highly mobile individuals crossing more oceanic waters, as well as specific evaluations of the impact that the different threats might have in each island, characterised by different levels and features of anthropogenic pressure.

Therefore, considering the wide range of this species, its habitat is represented by an extraordinarily dynamic environment, combining different areas characterised by different environments and different combinations of threats. In this case, limiting management to areas with rigid limits would be insufficient for this species' conservation in the Canary Islands. Moreover, the human activities that might represent a threat are in general not restricted to a particular area, nor with equal intensity everywhere, and the management of these activities within an area could not handle external pressures

coming into the areas as a result of the three-dimensional nature of the marine environment (Allison *et al.*, 1998; Zacharias and Ruff, 2000; Jamieson and Livings, 2001).

As a first step, an impact assessment should be carried out to evaluate and quantify the main threats that affect or could potentially affect short-finned pilot whales in the Canary Islands. This assessment should also quantify the pressure of each threat in each island of the archipelago and, considering that some human activities may act cumulatively and that some threats may be caused by several human activities.

As well as long-range movements, this study also shows how the ranges of the core resident pilot whales, and of their social groups, coincide with their high density area predicted by spatial modelling analysis. The population was present routinely all year long, in a very small fraction of its range located in southwestern Tenerife around the 800-1600m depth range, quite stable across time, with no major fluctuations during the years and seasons of the study period (Chapter 5).

Therefore, the southwestern area of Tenerife can be address not only as an important hotspot for cetacean biodiversity, with 24 species recorded (Chapter 1; Martin *et al.*, 2009), but also as a critical habitat for at least short-finned pilot whales, performing an important function in the ecosystem of short-finned pilot whales. It represents one of the world's highest-density and year-round core area (Chapter 2, 3, 5), where the highly bonded, persistent and highly structured core network of the resident Canary Islands population (Chapter 3), especially delimited in the waters of Tenerife and La Gomera (Chapter 2 and 3), undertake most of their life activities of rearing young (a shown by the regular presence of offspring including newborns), feeding, socialising and resting (based on behavioural observations during the study; Chapter 2 and 5). Southwestern Tenerife, where the short-finned pilot whales seem to be more vulnerable (feeding and calving grounds), is also where the marine environment appears to be more vulnerable (stronger anthropogenic impact). In addition to being important to whales, this area also has the strongest exposure to high-use and high-risk human activities. The fact that intensity of movements of large ships in Canary Islands is among the highest observed anywhere, suggests that these waters warrant closer inspection to assess and mitigate other conservation threats associated with shipping, such as ship strikes, chronic exposure to oil, and acoustic habitat degradation from shipping noise. Thus, these habitats, which constitute essential areas for the daily routine of a large portion of the resident population, offer the whales a mixed blessing of sorts.

These aspects make this area in agreement with the criteria used for determining a critical habitat of cetaceans, intended as intensively used habitats, important for day-to-day well-being and survival of the population, regularly used for feeding, resting and reproduction, but also where animals suffer some sort of impact that could be alleviated through protection measures (Reeves, 2010; Hoyt, 2005 and 2011; ACCOBAMS, 2009).

Moreover, reinforcing the importance of the waters off southwestern Tenerife, the areas used for the development of activities associated with feeding, breeding, and calving may also be critical to protect: critical habitats to cetacean preys, to productive upwellings or ocean fronts, and to topographic features favourable for providing foraging opportunities for cetaceans (Reeves, 2010; Hoyt, 2005 and 2011).

The delimitation of the critical area for pilot whales in Canary Islands therefore results relatively straightforward towards the southwestern Tenerife. The decisions on which represents the most appropriate mechanism for the conservation of a critical area involve a series of considerations: the ranging area of the species, how it is used and for how much of the year; the type and level of anthropogenic threats impacting the population; the ecology and life history of the target population; practical concerns such as management capacity in the area; and alternative mechanisms that might be employed (e.g. marine spatial planning, vessel restrictions) (Clarke and Dolman, 2010). Besides the *ecological* criteria, there are several other economic and pragmatic criteria (Salm *et al.*, 2000; Reeves, 2010) that these areas should also represent: importance to local fisheries, economic value for fishing and whale watching, recreational and scientific research value, and urgency of protection.

In this context, the presence of an MPA, supported by an area-based management plan, where management priorities commence from the habitat rather than from the target species (Pikitch *et al.*, 2004; Harwood, 2010) seems to represent a valuable option. In fact, it seems to represent a highly effective conservation tool for the resident population of Canary Islands, by providing the target island-associated population with the space necessary for critical life processes to take place; establishing specific mechanisms to assess, manage and limit the range of human activities occurring in this area; and providing science with a reference point against which to assess other managed sites.

Excluding Lanzarote and Fuerteventura, where on-going projects have been developing proposals for SACs under Natura 2000 (i.e. LIFE07/NAT/E/00732), another 12 SACs have already been established in the other islands since 2011 (Chapter 1) for the presence of bottlenose dolphin, and 12 based on other protected features (habitat or species) of special interest under the Habitat Directive. Management plans specific for each area

have been developed and presented in the "Orden 14661" (http://www.boe.es/diario_boe/txt.php?id=BOE-A-2011-14661).

This document includes a summary of the biology and conservation status of the target species and an overview of the principal threats in the area, the general conservation objectives and actions for managing each of the areas.

Nevertheless, as also pointed out by this document, the information so far collected about bottlenose dolphins in the Canary Islands, used to justify the creation of the SACs and to develop the conservation plans, is limited and only provides data about their distribution in the Archipelago and qualitative insights in their sociality, with no abundance estimates of evaluation of demographic trends, movement patterns, social structure, and habitat use. Therefore, the previous lack of basic information about this species' ecology allowed only generalizations about the impact of the threats and about the conservation actions to be undertaken, which are likely to be insufficient or inadequate. Suggestions to compensate the lack of knowledge through further studies on this species distribution and population dynamics were therefore proposed in the BOE-A-2011-14661, for the planned update of the management plan document.

Some of the established areas have been identified to be of insufficient size for including the main distribution areas of bottlenose dolphins (BOE-A-2011-14661; Ritter, 2012; Castrillón *et al.*, 2011). Numerous studies conducted by SECAC among the islands (i.e. MACETUS, E-MECETUS, LIFE/03/NAT/E/000062, ZEC-Tursiops, INDEMARES LIFE07/NAT/E/00732; see Chapter 2) have provided important collection of data and developed internal or official reports for the various administrations showing that the boundaries of the SACs in La Gomera, Gran Canaria (Franja Marina de Mogán), and La Palma included only a portion of the recorded sightings of this species, and therefore of the ranging area of use year-round. From here, it was suggested to extend these areas to at least 5 nm from the coast (SECAC, LIFE03/NAT/E/000062; Ritter, 2012; Castrillón *et al.*, 2011). On the contrary, the SAC Franja Marina de Teno-Rasca did represent the bottlenose dolphin distribution in the area. These results were reflected in the BOE-A-2011-14661, where further research studies were suggested to accommodate bottlenose distribution better by extending to the adjacent areas of the SACs of Mogán in Gran Canaria, La Graciosa, La Gomera, and La Palma. When bottlenose dolphins are sighted together with pilot whales they are at greater depth and distance from the coast than when seen alone, and mostly along the border or outside the SACs of La Gomera and Gran Canaria. Therefore, an extension of the areas of these existing SACs further offshore would provide additional protection for pilot whales.

Short-finned pilot whales were listed together with other species as important species (Annex V of the law 42/2007) in only four (Franja Marina de Teno-Rasca and Sebadales de Anteguera, in Tenerife; Franja Marina de La Isleta, in Gran Canaria; Franja Marina de Santiago-Valle Gran Rey, in La Gomera) of the 24 SACs declared in Canary Islands. However, the management actions established in these SACs to regulate fishing activities, maritime traffic, aquaculture and recreational activities, and for encouraging stakeholder integration, coordination and cooperation between public administration, research, and education also provides an important "umbrella" effect for the conservation of all the cetacean species present in the areas (Zacharias and Roff, 2001; Cañadas, 2006; Fortuna, 2006; Alves *et al.*, 2013).

Based on these considerations, when the next revision of the conservation plan of the SACs for bottlenose dolphins occurs, at least the external limit of the SACs ES7010017 in Gran Canaria, ES7020123 in La Gomera, and ES7020122 in La Palma should be extended, as proposed in the management plan BOE-A-2011-14661, as well as the SAC ES7020120 of the "Sebadales of San Andres" by including the waters in front of Santa Cruz de Tenerife. In parallel, SACs for bottlenose dolphins, with their corresponding management plans, should be established for the islands of Lanzarote and Fuerteventura. The fact that 14% of pilot whale sightings had been observed associated with bottlenose dolphins in the Canary Islands (Chapter 2) may reinforce the importance of including pilot whales among the species listed as important in Annex V of the law 42/2007 at least in Franja Marina de Mogán and Fuencaliente (based on the data of Pérez-Vallazza *et al.*, 2008). On the other hand, in the SACs of Franja Marina de Teno-Rasca, that includes the identified critical area for the resident population in the Canary Islands, more urgent and strict management actions should be undertaken, as suggested by its official management plan.

In view of the many inter-island movements between Tenerife and La Gomera of the 117 recaptured pilot whales (Chapter 2), many considered belonging to the core resident network linked also to the island of Tenerife, and the many similar aspects that these two islands share (in terms of the proportion of the resident population found there year-round, the tendency for animals to develop all the important behaviour life in this area, and the increasing anthropogenic pressure mostly due to increasing maritime traffic and whale-watching activity), La Gomera and the channel between these two islands represent also further important components of the critical habitat for pilot whales. This movement corridor is vital to ensure that animal hotspots do not become islands of biodiversity and is crucial to long-term population viability (Reeves, 2009). The importance of connections between individual SACs creating a MPA network rather than

individual areas essentially isolated from one another has been considered especially appropriate for cetaceans, whose critical habitats may be separated by large distances (Reeves, 2009; Hoyt, 2005a; Hoyt, 2009; Commission on Geosciences, Environment and Resources, 2001), like the islands of an archipelago. The presence of inter-islands movements of bottlenose dolphins among the islands of El Hierro, La Gomera, La Palma and Tenerife (Tobeña *et al.*, in press) may reinforce this consideration. As suggested in the management plan BOE-2011-14661, after the intermediate evaluation of the management plan the possibility of zonation of the areas will be evaluated, with the identification of highly-protected, 'core' areas corresponding to critical habitat, mixed zones (including the water channels between the islands), surrounded by 'buffer' zones where non-conflicting activities are allowed to take place (e.g. Hoyt, 2005a; Hoyt, 2009; Hyrenbach *et al.*, 2000; Kelleher, 1999; Reeves, 2009).

These measures would ensure a more effective protection of the larger part of the main habitat for bottlenose dolphin but at the same time also include those areas identified as most important for the pilot whales and with the greatest anthropogenic pressure: southwest of Tenerife and La Gomera. Therefore, the actions and recommendation provided by the management plans proposed for bottlenose dolphins in the increased network of SACs would also represent a first useful conservation tool for pilot whales.

From here, further monitoring of the species, as well as the anthropogenic threats, and the viability and effectiveness of any implemented mitigation measures, should be considered as an essential part of management (e.g. Donovan, 2005). Moreover, continuous monitoring through long term research studies should be promote in order to detect possible trends in pilot whales abundance and distribution, to evaluate the conservation status of their habitat facing an increasing anthropogenic pressure, and therefore, to periodically review the efficiency of the management actions and, if necessary adjust them to any changes (Habitat Directive, Annex IV, Article 12-4).

6.1.8 FUTURE STUDIES

This study has provided most of the basic information on this species in the Canary Islands. This sets the baseline for future studies that can, for the first time, build on this strong foundation, by making comparisons that were not possible during this study (e.g. survival rates, abundance changes, etc.) because of a lack of continuity in comparable long term effort in the same areas.

From a conservation point of view, the most urgent aspect to consider in further studies is estimation of the population life history parameters, to allow assessment of trends in

survival and reproductive rate of this species and evaluate its conservation status in the Archipelago.

Moreover, assessment of the impacts of the main potential threats outlined in this work is highly recommended including: short and long-term impact of the whale-watching activity on the major species targets, with special attention given to their behavioural responses, habituation or possible changes in range; acoustic and physical impact of marine traffic; and habitat degradation.

A number of new, more complex and more ambitious questions arise.

At a first step, all the material collected during the study period of this thesis should be analysed. Genetic analysis of the 365 biopsy samples collected between 1999 and 2010 (293 photo-identified animals) would allow many of the questions left open after this study to be investigated, as well as allowing testing of some of the proposed hypotheses.

The existence in the Canary Islands of different populations could be tested with the aim of differentiating and quantifying resident and transient whales.

The nature of social clustering, and the presence of a multi-level society could be investigated, by testing whether these can be defined purely based on genetics or whether behavioural and cultural factors might also be involved in their determination.

The sex of sampled animals could be determined to test the existence of any sex-related differences in group composition, principal aspects of movement, and range.

Sex differentiation conducted at sea during this study could be tested using genetic analysis and, in case of discrepancy, the results based on the differentiation in this study could be reviewed. The literature produced on this species in the archipelago (e.g. Heimlich-Boran, 1993) could be re-examined, and eventually re-interpreted. Moreover, the methodology used by Augusto *et al.*, (2013) for sex recognition at sea of long-finned pilot whales could be applied to short-finned pilot whales.

Mating systems, relatedness between and within sexes, and the role of males within the groups could be investigated through paternity tests in those groups where all members were biopsied (calves included, via scrubbing technique).

Based on a wide sample size, and the combination of observational data and genetic analysis, whether or not short-finned pilot whale social structure is based on matrilineal phylopatry could be investigated.

Genetic and behavioural comparisons between short- and long-finned pilot whales could be explored to investigate differences and similarities in social structure and habitat preference between the two species.

Polygenetic relationships among short-finned pilot whales could be investigated among the Macaronesian archipelagos of the Canary Islands, Madeira, Azores, Cape Verde, and possibly also including the Atlantic coast of Morocco.

Photo-identification analysis conducted in more detail by considering additional data recorded and documented at sea on neighbouring animals, small unit composition, relative distances and movements from one group to another could offer new insight into this species' social structure if compared to individual genetic analysis of pod association and segregation.

Stable isotope and fatty acid analysis may be useful in improving the scarce knowledge of the diet and feeding habits of this species.

Analysis of acoustic records (133 acoustic recordings associated with pilot whale sightings and identified individuals) could allow investigation of any differentiation among individuals identified as members of different pods, clans (or possibly sub-populations or populations), or among different individuals with different residency patterns.

In addition, further studies should include the following:

General protocols of survey methodology and data collection should be specifically designed for this species, requiring longer photo-identification sessions in order to ensure sufficient coverage of the sightings.

Satellite tracking could be useful to study the ranging movements of individuals, especially through the deployment of tags on identified resident and transient individuals, as well as on whales of different identified pods/clans.

Simultaneous surveys conducted around the different islands could improve knowledge of spatial and temporal habitat use and movement patterns.

Extending the surveys to previously unsurveyed areas, especially in the upwind areas of islands could eventually detect new important areas for pilot whales, as well as identify new individuals, and possibly review site fidelity differentiation.

Multi-disciplinary co-operative studies to collect data on oceanographic and biological parameters, such as plankton and nutrient composition, together with regular cetacean

surveys in the archipelago could allow further investigation of how cetaceans use the habitat of the Canary Islands archipelago.

Co-operative and comparative studies among Macaronesian archipelagos could provide a wider perspective of the ecology of this species in eastern Atlantic waters.

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CHAPTER 6: "FINAL DISCUSSION"

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ANNEX 1

Table A1. 1: List of the 30 cetacean species cited in the Canary Islands (review in Martín et al., 2009*). Indication of sighting frequency is also presented: species seen all year-round, seasonally, occasionally, and extralimital.

Family: **Balaenopteridae**

Blue whale	<i>Balaenoptera musculus</i>	Extralimital
Fin whale	<i>Balaenoptera physalus</i>	Seasonal
Sei whale	<i>Balaenoptera borealis</i>	Extralimital
Bryde's whale	<i>Balaenoptera edeni</i>	Seasonal
Minke whale	<i>Balaenoptera acutorostrata</i>	Extralimital
Humpback whale	<i>Megaptera novaeangliae</i>	Occasional

Family: **Balaenidae**

Right whale	<i>Eubalaena glacialis</i>	Extralimital
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Family: **Physeteridae**

Sperm whale	<i>Physeter macrocephalus</i>	Year-round
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Family: **Kogiidae**

Pigmy sperm whale	<i>Kogia breviceps</i>	Year-round
Dwarf sperm whale	<i>Kogia sima</i>	Extralimital

Family: **Ziphiidae**

Northern bogglenose whale	<i>Hyperoodon ampullatus</i>	Extralimital
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	Year-round
Gervais beaked whale	<i>Mesoplodon europaeus</i>	Year-round
Blainville's beaked whale	<i>Mesoplodon densirostris</i>	Year-round
Sowerby's beaked whales	<i>Mesoplodon bidens</i>	Extralimital
True's beaked whale	<i>Mesoplodon mirus</i>	Extralimital

Family: **Phocoenidae**

Harbour porpoise	<i>Phocoena phocoena</i>	Extralimital
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Family: **Delphinidae**

Killer whale	<i>Orcinus orca</i>	Occasional
False killer whale	<i>Pseudorca crassidens</i>	Occasional
Pygmy killer whale	<i>Feresa attenuate</i>	Extralimital
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	Year-round
Long-finned pilot whale	<i>Globicephala melas</i>	Extralimital
Rough toothed dolphin	<i>Steno bredanensis</i>	Seasonal
Pantropical spotted dolphin	<i>Stenella frontalis</i>	Seasonal
Striped dolphin	<i>Stenella coeruleoalba</i>	Year-round
Spinner dolphin	<i>Stenella longirostris</i>	Extralimital
Fraser's dolphin	<i>Lagenodelphis hosei</i>	Extralimital
Common dolphin	<i>Delphinus delphis</i>	Seasonal
Bottlenose dolphin	<i>Tursiops truncates</i>	Year-round
Risso's dolphin	<i>Grampus griseus</i>	Year-round

*MARTÍN, V., SERVIDIO, A., TEJEDOR, M., ARBELO, M., BREDERLAU, B., NEVES, S., PÉREZ-GIL, M., URQUIOLA, E., PÉREZ, E. and FERNÁNDEZ, A. (2009). Cetaceans and conservation in the Canary Islands. *The 18th Biennial Conference on the Biology of Marine Mammals*. Quebec, Canada.

ANNEX 2



FICHA # _____

FICHA DE AVISTAMIENTO GENERAL

Fecha	Hora Det Ac (Pma)	Hora Det	Hora Cto	Hora Fin	Avistamiento #
Especie²		Esfuerzo³		E/NE Razón	
Ángulo	Reticula	Prismáticos	Distancia	Cue ⁵	Observador
					Posición ⁶
					Anota
					Razón Fin ⁷
MINI	MAXI	MEJOR	Rango ⁸		
Extensión ⁹ (m x m)		En un grupo	En subgrupos ¹⁰ - (Nº)	Sueños	
Adultos	Crías	Animales blancos (<i>Ziphius/Ggr</i>) ¹¹			
Juveniles	Neonatos	% moteados (<i>Sfr</i>) ¹²			
		Machos maduros (<i>Gma/Oor</i>) ¹³			
Rum ini ⁴	Actividad ini ⁵		Reacción ¹⁶		
Rum fin	Actividad fin		% contact ¹⁷		
Comportamientos de superficie ¹⁸					
Sp área #1	Dist	Sp área #2	Dist	Sp área #3	Dist
Basura		Esperas		Nº	
AVES	Sp	Formación	BARCOS	Tipo ¹⁹	Reticula
#1			#1		Dist (m)
#2			#2		Actividad ²⁰
#3			#3		
DATOS					
Foto-ID:	nº animales	Foto-ID ²¹	Fotógrafo #1	Tarjetas	
Vídeo:	Contador ²²		Fotógrafo #2	Tarjetas	
Acústica:	Contador		Fotógrafo #3	Tarjetas	
Heces:	Piel suelta	Otras muestras			
BIOPSIAS	si	no	Intentos	Fallos	
Código	Hora	Tira	Clase Edad	Sexo	Gen
1					
2					
3					
Subgr	Hora cto	Hora fin	Dist a Sg1	Min	Max
1					
2					
3					
Responsible Científico:					
FIRMA					
Observaciones:					
Patrones inmersión (Zifios/Orcales)					
	H _↑	R _↑	H _↓	R _↓	Hpto _↑
1					
2					
3					
4					
5					
6					
7					
8					

Sociedad para el Estudio de los Cetáceos en el Archipiélago Canario (SECAC), Edif. Antiguo Varadero 1ª planta Local 8 B - Urb. Puerto Calero - 35371 Yaiza, Isla de Lanzarote.
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PROGRAMA DE INVESTIGACIÓN DE LOS ZIFIOS DE CANARIAS
 CANARY ISLAND BEAVER WHALE RESEARCH PROGRAM



Figure A2. 3: Sighting sheet: 2009 -2011 (Oso Ondo).

TABLE-FIGURE A.2.1.

Table A2.1a: Survey effort per island (Nautical Miles and hours) conducted at sea by SECAC between 1999 and 2012 along Canary Islands waters, Tenerife, Gran Canaria, La Gomera, with sightings on and off effort, and encounter rate ER1 (total number of encounters divided by the total number of Nm surveyed each year).

YEAR	CANARY ISLANDS					TENERIFE				
	EFFORT		SIGHTINGS			EFFORT		SIGHTINGS		ER1
	Nm	H	on EFF	off EFF		Nm	H	on EFF	off EFF	
1999	2297.46	306:44	6	4		16.27	1:46	1	0	6.15
2000	1607.93	205:34	4	4						
2001										
2002	1380.69	224:42	22	12		148.96	25:07	17	11	11.41
2003	758.13	133:40	2	0						
2004	1865.23	258:07	17	5		128.72	16:38	6	2	4.66
2005	2395.48	388:13	40	32		225.7	53:57	19	17	8.42
2006	2786.78	254:32	43	8		552.29	21:38	30	0	5.43
2007	3088.62	458:14	243	76		1432.88	233:47	243	67	16.96
2008	3044.24	485:13	196	110		1212.22	213:30	196	103	16.17
2009	5591.29	901:36	52	35		456.01	80:40	40	27	8.77
2010	7252.54	1155:35	86	29		834.82	146:47	47	8	5.63
2011	3466.49	352:06	31	3		164.84	6:36	17	1	10.31
2012	2597.09	312:40	15	6		213.89	19:15	5	2	2.34
TOTAL	38,131.90	5,436:55	757	324		5,386.62	819:40	621	238	11.53

YEAR	GRAN CANARIA				ER1	LA GOMERA				
	EFFORT		SIGHTINGS			EFFORT		SIGHTINGS		ER1
	Nm	H	on EFF	off EFF		Nm	H	on EFF	off EFF	
1999	2001.63	268:48	5	4	0.25					
2000	1455.09	187:27	4	4	0.27					
2001										
2002	1156.95	186:51	5	1	0.43					
2003	489.03	86:06			0					
2004						557.66	96:10	5	2	0.9
2005	670.11	90:51	0	1	0	1007.53	177:47	17	14	1.69
2006						2151.97	216:46	13	8	0.6
2007	1181.3	164:30	0	8	0					
2008	742.52	108:55	0	2	0	91.68	16:55	0	4	0
2009	3498.76	562:05	4	2	0.11	340.8	62:10	1	2	0.29
2010	3002.5	470:47	1	3	0.03	1170.65	206:53	33	8	2.82
2011	936.51	55:17	6	0	0.64					
2012	810.45	97:04	2	0	0.25					
TOTAL	15,944.85	2,278:41	27	25	0.17	5,320.28	776:40	69	38	1.3

ANNEX 2

Table A2.1b: Survey effort per island (Nautical Miles and hours) conducted at sea by SECAC between 1999 and 2012, along Fuerteventura Lanzarote, La Palma, El Hierro, with sightings on and off effort, and encounter rate ER1 (total number of encounters divided by the total number of Nm surveyed each year).

YEAR	FUERTEVENTURA					LANZAROTE				
	EFFORT		SIGHTINGS		ER1	EFFORT		SIGHTINGS		ER1
	Nm	H	on EFF	off EFF		Nm	H	on EFF	off EFF	
1999	228.8	29:06	0	0	0	50.76	7:05	0	0	0
2000	94.06	10:41	0	0	0	58.78	7:26	0	0	0
2001										
2002	68.95	11:47	0	0	0	5.83	0:57	0	0	0
2003	87.8	15:52	0	0	0	181.3	31:42	2	0	1.1
2004	536.4	63:22	3	1	0.56	320.44	33:51	1	0	0.31
2005	457.75	60:08	2	0	0.44	34.38	5:31	2	0	5.82
2006	1.85	0:32	0	0	0	80.67	15:36	0	0	0
2007	441.67	55:49	0	1	0	32.77	4:08	0	0	0
2008	197.85	29:19	0	1	0	753.29	108:17	0	0	0
2009	374.15	58:37	0	0	0	921.56	138:04	7	4	0.76
2010	805.94	121:50	1	7	0.12	709.05	107:03	3	2	0.42
2011	1129.29	118:05	6	0	0.53	754.66	111:49	2	2	0.27
2012	1053.72	119:03	2	2	0.19	519.03	77:18	6	2	1.16
TOTAL	5478.23	694:11	14	12	0.26	4422.53	648:46	23	10	0.52

YEAR	LA PALMA					EL HIERRO				
	EFFORT		SIGHTINGS		ER1	EFFORT		SIGHTINGS		ER1
	Nm	H	on EFF	off EFF		Nm	H	on EFF	off EFF	
1999										
2000										
2001										
2002										
2003										
2004	175.43	22:08	2	0	1.14	146.58	25:58	0	0	0
2005										
2006										
2007										
2008						46.69	8:17	0	0	0
2009										
2010	468.68	63:43	1	1	0.21	260.89	38:31	0	0	0
2011	481.18	60:19			0					
2012										
TOTAL	1125.28	146:10	3	1	0.27	454.16	72:47			0

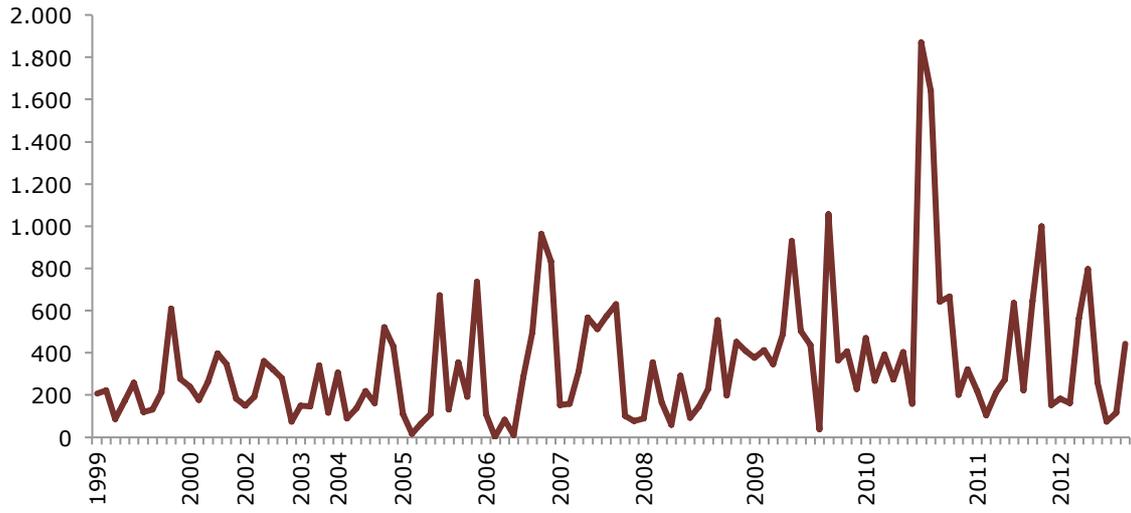


Figure A2c: Survey effort conducted at sea by SECAC between 1999 and 2012 in the Canary Islands

Table A.2.2.

Table A.2.2: Range estimates of the 193 short-finned pilot whales calculated by MCP and fixed kernel (overall ranging at 95% UD and core area at 50% UD) methods. The Schoener's ratio is also presented as a measure of autocorrelation. Sex differentiations (F=female, M=male, u= unknown) are based only on qualitative observations, and therefore have to be considered with caution.

ID_N	SEX	RESIDENCY	MCP	Kernel 95% UD	Kernel 50% UD	Schoener's ratio
130	F	CR	31.325	84.188	10.900	1.8
133	F	R	36.986	97.469	22.478	1.7
136	F	CR	52.764	113.694	19.687	1.6
879	M	R	55.860	162.652	37.596	1.9
880	F	R	36.803	157.738	53.283	1.7
881	M	R	44.363	138.147	37.497	1.9
882	F	R	68.531	170.696	49.019	1.9
900	F	R	226.299	660.035	148.860	2.4
140	u	R	18.825	55.645	11.695	1.5
143	F	R	16.202	46.132	11.003	1.0
145	u	R	25.627	73.591	19.340	0.8
146	u	CR	36.170	76.731	12.285	1.4
150	F	CR	32.889	90.002	14.140	1.0
153	F	R	28.675	64.967	7.746	1.6
17	F	CR	341.928	252.996	56.028	1.2
156	F	CR	36.170	86.971	20.750	1.9
157	M	R	27.448	70.251	15.956	1.1
158	F	R	21.255	73.947	22.379	2.0
161	F	R	974.164	560.659	165.899	1.3
1020	F	R	925.021	1403.070	292.682	0.7
1022	F	R	51.431	148.448	18.903	1.8
163	F	R	676.811	598.312	182.407	0.9
164	F	R	65.781	98.037	15.113	1.8
165	F	R	969.228	553.018	149.171	1.3
167	F	R	977.401	566.030	152.185	1.3
169	u	R	899.219	603.917	166.356	1.2
171	u	R	72.835	113.758	16.227	1.8
173	M	CR	51.261	93.654	18.831	1.4
174	F	CR	56.792	100.316	18.432	1.2
180	F	CR	68.277	115.076	18.976	1.5
187	F	R	91.014	116.310	10.677	1.7
188	M	R	46.317	85.829	15.611	2.1
189	M	CR	48.091	88.808	16.296	2.0
190	u	CR	711.287	675.952	156.792	1.2
191	u	R	711.287	842.896	193.892	1.2
192	u	CR	711.287	647.808	157.518	1.2
201	u	R	711.287	917.264	207.937	1.2
23	M	R	59.578	153.675	36.269	1.3
219	F	CR	721.369	752.056	169.029	1.2
223	F	R	721.369	831.505	184.146	1.2
24	M	R	58.250	139.003	35.561	1.7
232	u	CR	721.369	677.870	152.551	1.2
235	M	R	740.777	430.046	103.506	2.0
236	M	R	35.719	105.763	12.628	1.5
237	u	R	671.890	704.122	169.125	2.1
238	u	R	399.880	363.349	98.966	1.5
25	M	R	59.578	148.027	36.268	1.3

ANNEX 2

ID_N	SEX	RESIDENCY	MCP	Kernel 95% UD	Kernel 50% UD	Schoener's ratio
241	u	R	679.183	513.696	123.951	2.1
244	M	R	46.610	146.475	21.667	2.4
245	F	CR	556.868	366.904	99.599	1.3
247	F	CR	507.616	332.102	76.014	1.2
249	F	CR	71.984	157.090	45.664	2.6
252	u	CR	556.868	326.209	83.563	1.2
26	M	CR	439.828	282.041	75.241	1.1
253	u	CR	869.341	870.038	176.968	0.9
255	u	R	46.038	140.103	18.562	1.7
258	u	R	31.287	96.886	36.313	1.9
259	u	CR	22.213	83.517	20.285	2.3
260	u	R	24.992	71.339	9.349	2.2
261	u	R	20.059	81.094	17.431	1.9
264	u	R	19.391	68.355	13.065	2.0
265	F	R	25.394	73.427	14.021	2.3
266	u	R	75.471	127.058	21.989	1.5
267	u	R	72.111	120.239	23.393	1.5
268	M	R	77.891	136.237	18.135	1.7
269	M	R	77.990	147.761	32.435	1.4
270	M	R	72.247	132.120	26.731	1.3
271	u	R	72.111	118.787	22.183	1.6
272	M	R	74.413	132.761	23.480	1.4
30	M	R	54.976	164.985	41.797	1.3
31	u	R	55.037	142.560	23.304	1.7
288	F	CR	283.448	293.406	90.349	1.2
32	M	R	55.511	126.055	33.658	1.5
294	u	R	40.323	68.726	13.626	1.8
295	F	CR	53.710	86.407	11.784	1.1
297	u	R	65.614	134.742	29.492	1.3
298	F	R	35.848	62.156	13.006	2.0
33	M	R	55.511	122.730	31.171	1.6
303	F	CR	326.047	302.558	68.168	2.0
309	u	R	411.431	1581.329	316.780	1.8
34	M	R	233.526	256.065	78.002	1.4
313	u	R	411.431	1581.329	316.780	1.8
319	F	R	25.547	59.160	11.766	1.6
35	F	R	41.606	109.479	26.348	1.3
36	F	CR	308.819	272.064	63.893	1.2
323	F	R	38.224	100.294	20.596	1.8
324	u	R	47.647	117.361	23.933	1.9
37	F	R	55.879	124.803	18.280	2.0
326	F	R	44.278	120.139	19.818	2.6
332	F	R	581.980	349.969	76.412	1.3
336	M	R	30.448	76.342	21.370	2.6
340	M	R	22.800	58.252	12.952	2.1
341	u	CR	346.767	270.972	64.175	2.1
342	u	R	39.731	78.851	9.608	2.0
348	F	R	37.274	74.213	7.319	1.6
349	F	R	36.107	88.628	16.129	2.4
39	F	R	38.230	119.090	33.479	1.9
42	u	R	34.134	108.307	30.869	1.5
363	u	R	30.765	62.035	15.238	2.4
364	u	R	19.479	52.998	10.949	2.4
365	u	R	28.859	74.747	13.773	2.5
367	u	R	28.099	64.248	12.102	1.9
368	u	R	41.628	70.538	10.774	1.8
43	M	R	233.526	246.369	63.608	1.4
371	u	R	58.733	93.366	11.236	1.2

ANNEX 2

ID_N	SEX	RESIDENCY	MCP	Kernel 95% UD	Kernel 50% UD	Schoener's ratio
44	F	R	50.057	127.732	21.886	1.8
372	F	CR	384.813	291.501	61.573	1.1
373	M	R	88.929	117.366	10.462	1.4
375	u	R	405.830	320.045	58.633	2.0
376	u	R	598.857	1088.124	254.972	1.2
379	F	R	731.138	1327.294	249.047	1.3
382	F	R	731.138	1557.318	266.107	1.0
386	u	CR	590.507	1099.784	224.381	1.1
388	F	R	702.239	1497.074	261.979	1.0
46	u	R	34.857	95.239	16.351	2.0
389	F	R	80.233	105.868	9.157	1.8
391	M	R	91.624	155.527	13.505	1.1
49	F	R	254.359	318.776	62.542	1.3
411	F	R	619.638	1168.538	213.468	0.9
413	u	R	24.661	59.246	10.299	1.6
414	F	R	547.244	1685.706	347.051	1.2
4	F	CR	59.361	69.949	7.747	2.0
421	u	CR	1619.406	3187.409	487.709	0.9
422	M	R	44.777	116.710	25.627	2.4
423	u	R	831.411	2056.581	608.951	0.9
50	u	R	62.802	93.734	11.099	1.5
431	u	R	709.829	1252.153	233.459	1.3
51	F	CR	62.802	98.799	12.706	1.5
52	u	R	62.802	97.962	12.476	1.7
53	u	R	51.067	86.146	6.772	1.7
442	F	R	28.456	108.691	47.222	1.3
54	F	R	50.405	88.432	8.193	1.5
451	u	R	45.702	101.918	19.256	1.1
460	u	R	28.456	108.691	47.222	1.3
58	F	R	50.405	103.396	8.415	1.5
470	M	R	82.212	159.597	26.932	1.4
59	M	R	50.405	93.312	7.239	1.5
60	u	R	50.405	98.336	10.098	1.5
480	F	R	58.726	137.581	18.180	1.5
481	u	CR	51.261	90.997	19.113	1.5
61	F	R	57.880	103.980	10.647	1.5
486	u	CR	668.527	394.107	105.510	1.0
488	u	CR	43.574	86.910	10.522	1.1
489	u	CR	47.492	95.222	9.901	1.0
490	M	R	60.664	103.764	17.064	1.1
491	F	R	60.567	89.305	12.755	1.2
494	F	CR	47.492	92.734	10.656	1.0
497	u	R	69.570	115.570	11.772	1.9
64	F	CR	62.039	101.991	11.698	0.9
499	u	CR	60.664	94.105	10.594	0.8
500	F	CR	53.803	88.018	8.967	0.9
509	F	R	804.893	3673.788	790.873	0.6
515	F	R	664.299	2002.754	484.605	1.0
67	F	CR	88.631	141.471	19.124	1.1
69	u	R	72.771	141.898	18.146	1.2
555	F	R	53.808	79.463	9.891	1.4
556	u	O	32.745	79.782	12.837	2.4
73	u	R	56.622	91.832	9.940	1.4
76	F	R	37.104	67.182	7.261	2.1
596	u	R	24.066	57.561	13.458	1.9
80	F	R	62.853	113.396	13.328	1.1
81	u	CR	88.631	137.916	18.179	1.2
83	F	R	88.631	192.240	39.303	1.3

ANNEX 2

ID_N	SEX	RESIDENCY	MCP	Kernel 95% UD	Kernel 50% UD	Schoener's ratio
84	F	CR	93.034	156.995	16.730	1.1
9	F	R	53.808	77.936	8.338	2.0
634	F	CR	826.515	807.090	236.817	1.1
91	u	R	103.828	279.655	63.626	1.6
658	F	R	100.208	272.299	64.016	1.6
659	u	R	75.703	259.815	82.124	1.6
674	u	R	32.662	167.390	34.623	1.4
96	F	R	128.275	260.464	51.235	1.5
98	F	CR	6562.707	3053.166	635.344	1.1
11	F	CR	60.835	73.966	8.423	2.1
100	F	CR	2949.990	2182.767	491.691	1.5
103	F	CR	583.046	449.640	103.690	1.1
105	F	R	99.826	243.907	54.174	1.5
111	u	R	558.871	408.315	116.077	1.2
711	M	R	53.468	112.348	25.323	2.5
712	u	R	48.349	88.572	22.058	1.4
713	M	R	44.355	83.376	10.795	2.5
112	F	R	39.291	88.692	11.017	1.8
714	u	R	49.436	181.869	40.649	1.5
114	F	R	792.724	720.049	199.482	1.3
115	F	CR	2262.985	933.004	253.900	2.5
117	F	R	60.689	98.116	15.103	1.5
13	F	CR	320.466	181.808	42.812	2.1
750	u	R	345.354	717.300	148.690	2.6
121	F	CR	60.689	100.721	14.514	1.4
122	M	R	836.691	651.077	198.572	0.7
123	u	R	91.833	182.658	17.073	1.1
126	F	R	826.515	954.612	264.618	0.7
821	F	R	47.828	104.455	15.209	1.8
2148	u	R	27.428	136.504	42.893	1.7
		MEAN	280.94	355.90	76.95	1.54
		SD	593.76	553.80	119.75	0.45
		MIN	16.20	46.13	6.77	0.62
		MAX	6562.71	3673.79	790.87	2.65

ANNEX 3

FIGURE A3.1

Based on qualitative observation on morphology, behaviour and presence of calf in association, the most frequently seen short-finned pilot whales off Tenerife and La Gomera (recaptured at least once per months for 8 months, between 2004 and 2012) were sexed, and 63 females and 26 males were identified. Looking for patterns, their association indices (half-weighted index) were investigated (Figure A3.1). Lacking of genetic analysis the results have to be taken with caution.

Association rates differ significantly between and within sex classes (Mantel tests: $t=6.33082$, $p=1$, $r=0.101$). The null hypothesis that associations between classes and within classes are similar could be rejected since the p value obtained ($p=1$) did not fall between 0.025 and 0.975 (Whitehead, 2003). Inter-class associations (0.04, SD=0.02) were not as strong as intra-class association (0.08, SD=0.03), with a significant tendency for same sex associations to be strongest. However, average association levels were still quite low (0.07, SD=0.02 for females and 0.07, SD=0.02 for males). Female – female class association showed the presence of strong bonds between some females (0.86, SD=0.15) which, at the same time, differs in the number of females with whom they were associated (sum of association means=5.85, SD=1.57; max mean=0.86, SD=0.15). Male-male association was somehow slightly lower (mean=0.07, SD=0.05, sum of association means =2.73, SD=1.19; maximum mean=0.69, SD=0.30). In contrast, maximum interclass association values were lower (0.53, SD=0.28 for female-male, and 0.45, SD=0.36 for male-female) with a sum of association indices even lower (1.06, SD=0.49 for female-male, and 2.58, SD=2.14 for male-female).

ANNEX 4

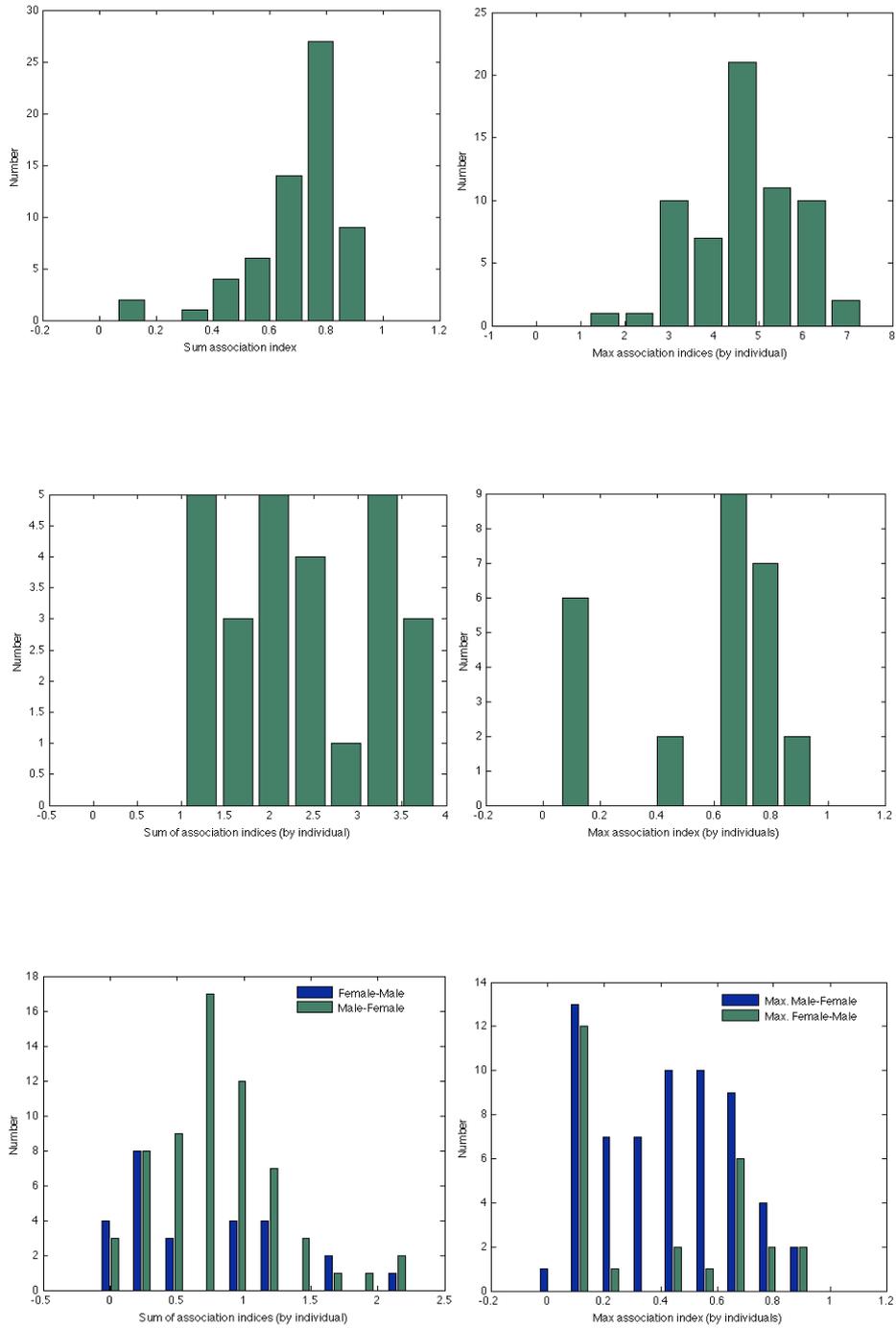


Figure A3.1: Distribution of association indices for females (top two) and males (middle two) and females-males/males-females (bottom two), well-marked short-finned pilot whales recaptured at least once per months for 8 months in the islands of La Gomera and Tenerife, between 2004 and 2012, in sightings with good photo-identification coverage: a) sum of associates for each individuals, b) maximum sum associations index.

Figure A3.2

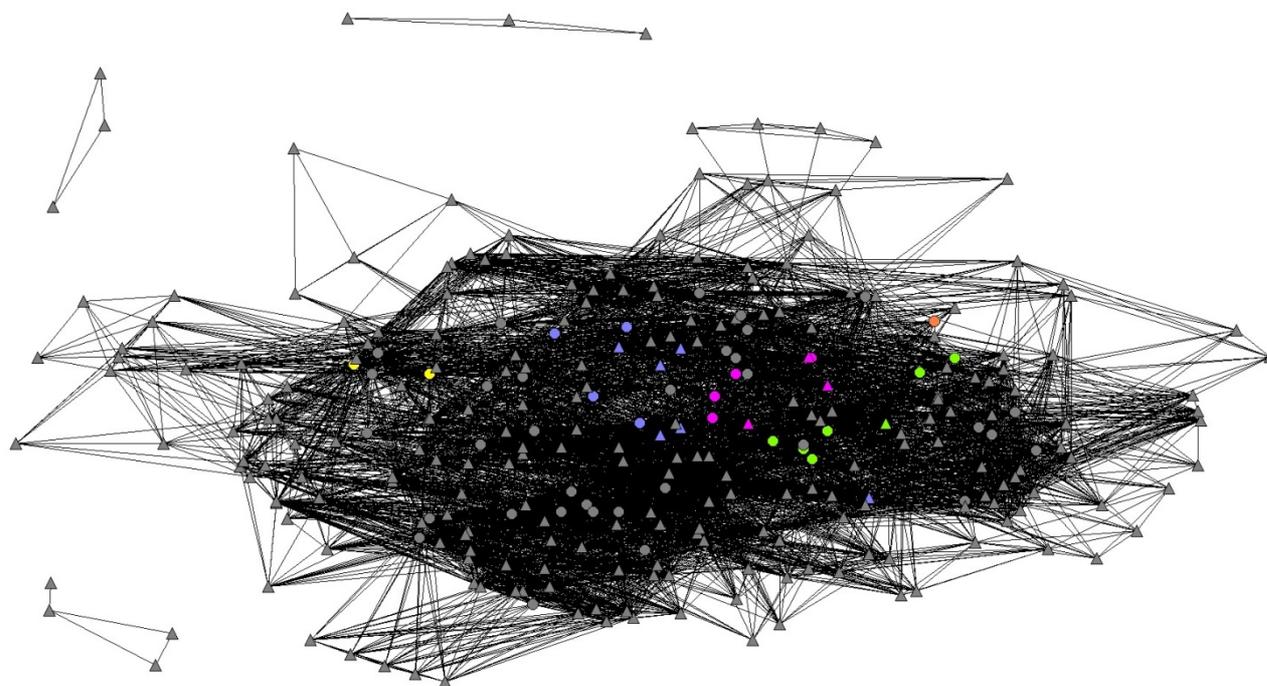


Figure A3.2: Enlargement of main social network cluster taken from figure 3.4, showing only core residents and residents and the key units selected within all well-marked short-finned pilot whales documented off the Canary Island, from 2004 through 2012. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Residents are shown in grey triangle, and core residents in grey circle. Key unit A is coloured pink, C in yellow, D in green, F in orange, and M in violet.

Figure A3.3

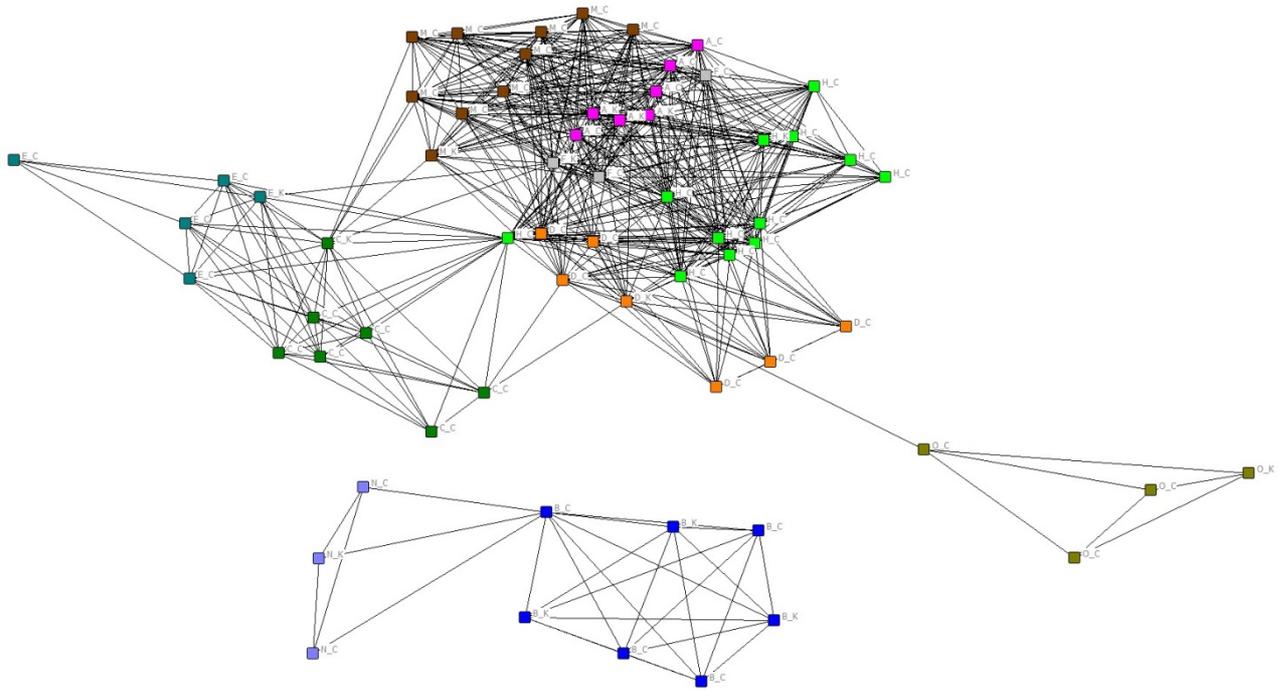
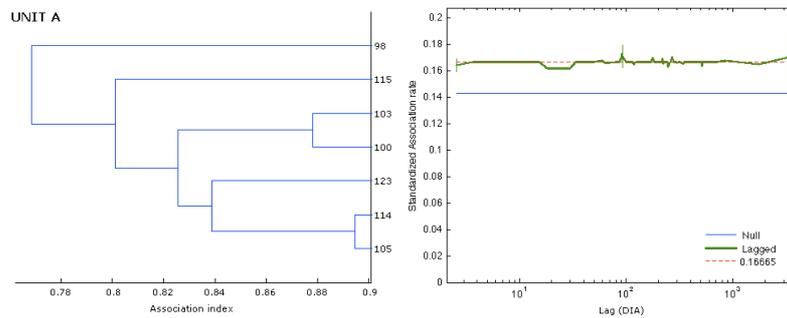
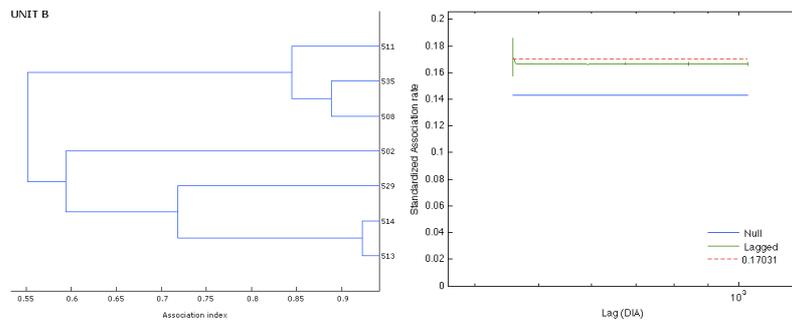


Figure A3.3: Network showing the key units selected within all well-marked short-finned pilot whales documented off the Canary Island, from 2004 through 2012. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals.

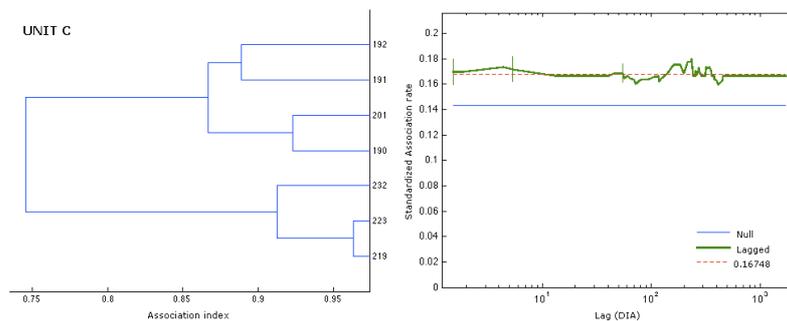
FIGURE A3.4



Moving average of 400 associations; best model fit=const. comps.; CCC= 0.77155. Q=0.14296 at AI=0.7684. Group size estimated:6.



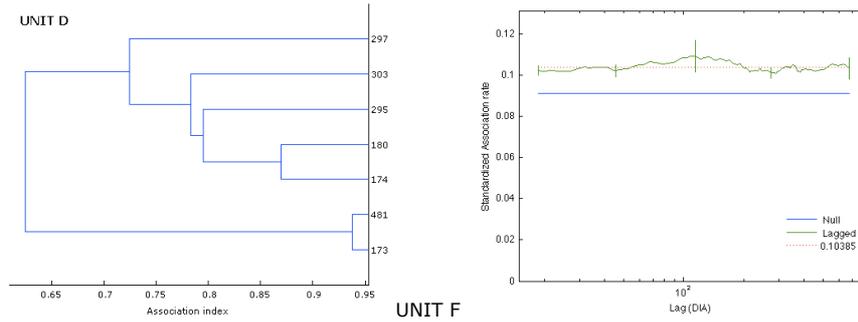
Moving average of 800 associations; best model fit=const. comps.; CCC = 0.95009. Q=0.14296 at AI=0.7684. Group size estimated:6



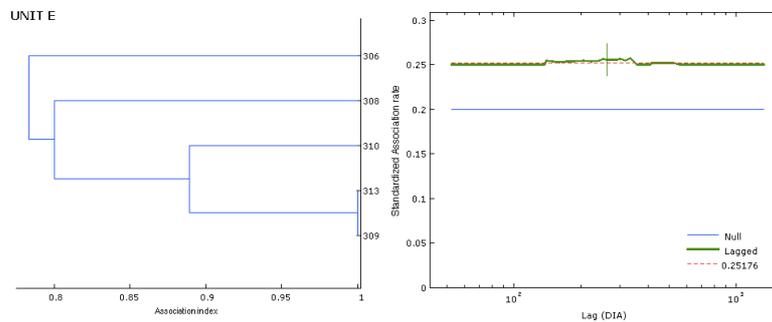
Moving average of 400 associations; best model fit=const. comps.; CCC = 0.84682. Q=0.14576 at AI=0.74594. Group size estimated:6.

Figure A3.4a: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Units A, B, C. The maximum-likelihood best fit model for each unit and their null association rate are also represented.

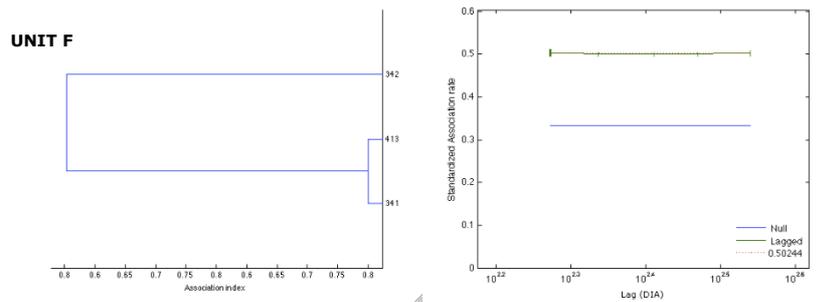
ANNEX 4



Moving average of 800 associations; best model fit=const. comps.; CCC = 0.90551. Q= 0.12521 at AI=0.62449. Group size estimated:10.



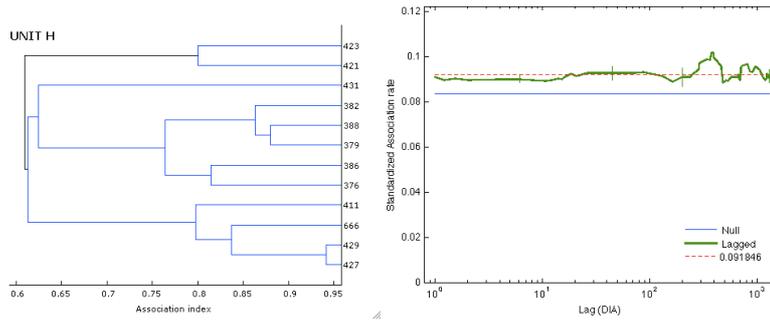
Moving average of 200 associations; best model fit=const. comps.; CCC = 0.9961. Q=0.20034 at AI=0.78333. Group size estimated:4.



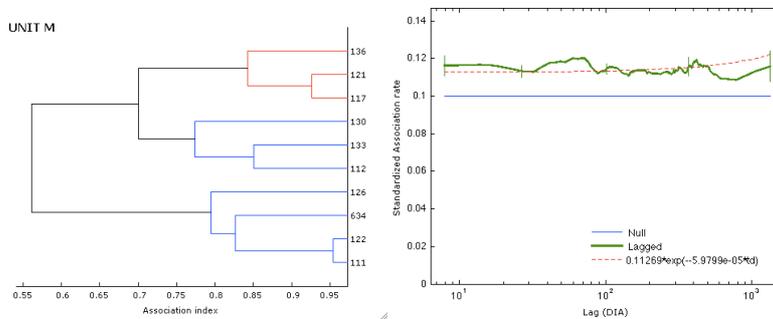
Moving average of 100 associations; best model fit=const. comps.; CCC = 0.94048. Q=0.33519 at AI=0.60143. Group size estimated:2.

Figure A3.4b: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Units D, E, F. The maximum-likelihood best fit model for each unit and their null association rate are also represented.

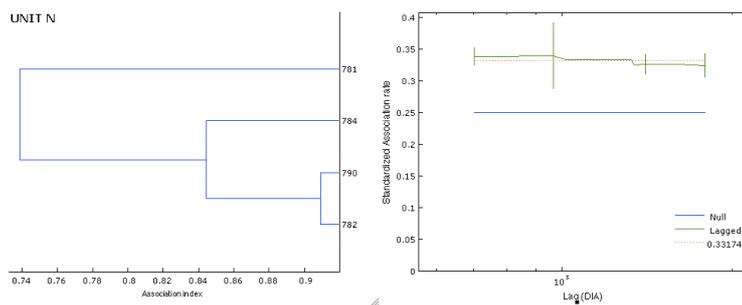
ANNEX 4



Moving average of 200 associations; best model fit=const. comps.; CCC = 0.85265. Q= 0.077308 at AI=0.62039. Group size estimated:11.

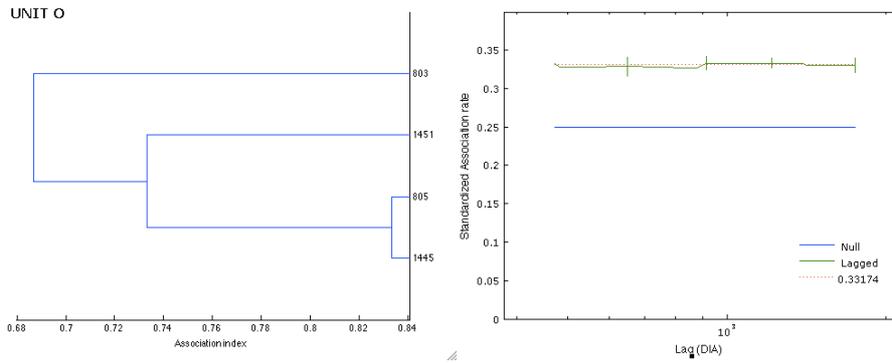


Moving average of 10000 associations; best model fit=casual acqu.; CCC = 0.90119. Q=0.12538 at AI=0.7009. Group size estimated:9.



Moving average of 100 associations; best model fit=const. comps.; CCC = 0.82143. Q= 0.25055 at AI=0.73889. Group size estimated:3.

Figure A3.4c: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Units H, M,N. The maximum-likelihood best fit model for each unit and their null association rate are also represented.



Moving average of 100 associations; best model fit=const. comps.; CCC = 0.76718. Q= 0.25043 at AI=0.68687. Group size estimated:3.

Figure A3.4d: Average-linkage cluster analyses of association (half-weight association index) between individuals included in the identified Key Unit O. The maximum-likelihood best fit model for each unit and their null association rate are also represented.

FIGURE A3.5

The short-finned pilot whales in Tenerife and La Gomera (2004-2010) were also investigated for temporal patterns in their social structure using lagged association index on the reduced data set containing only sightings with good photo-identification coverage.

SLARs were also built looking for sex associations through time: males-males, males-females, females-females/females-males. Associations within animals of the same sex (male-male and female-female) show a constant distribution along the time at least for 440 days, with no decline at the end: "constant companions" was in both cases the best-fitted model (Figure A62a-b). The association rate between the two sexes had again "constant companions" as the best-fitted model (Figure A62c-d), nevertheless the combinations female-male (Figure A62c) show a peculiar and increase curve steeper starting around day 115, reaching a standard association index of 0.4 after 400 days (starting at association index of 0.3).

The typical group size (gregariousness) for association within sexes of the population in Canary Islands was estimated for female-female at 10.2 individuals ($1/a$), and for male-male at 3.8 individuals.

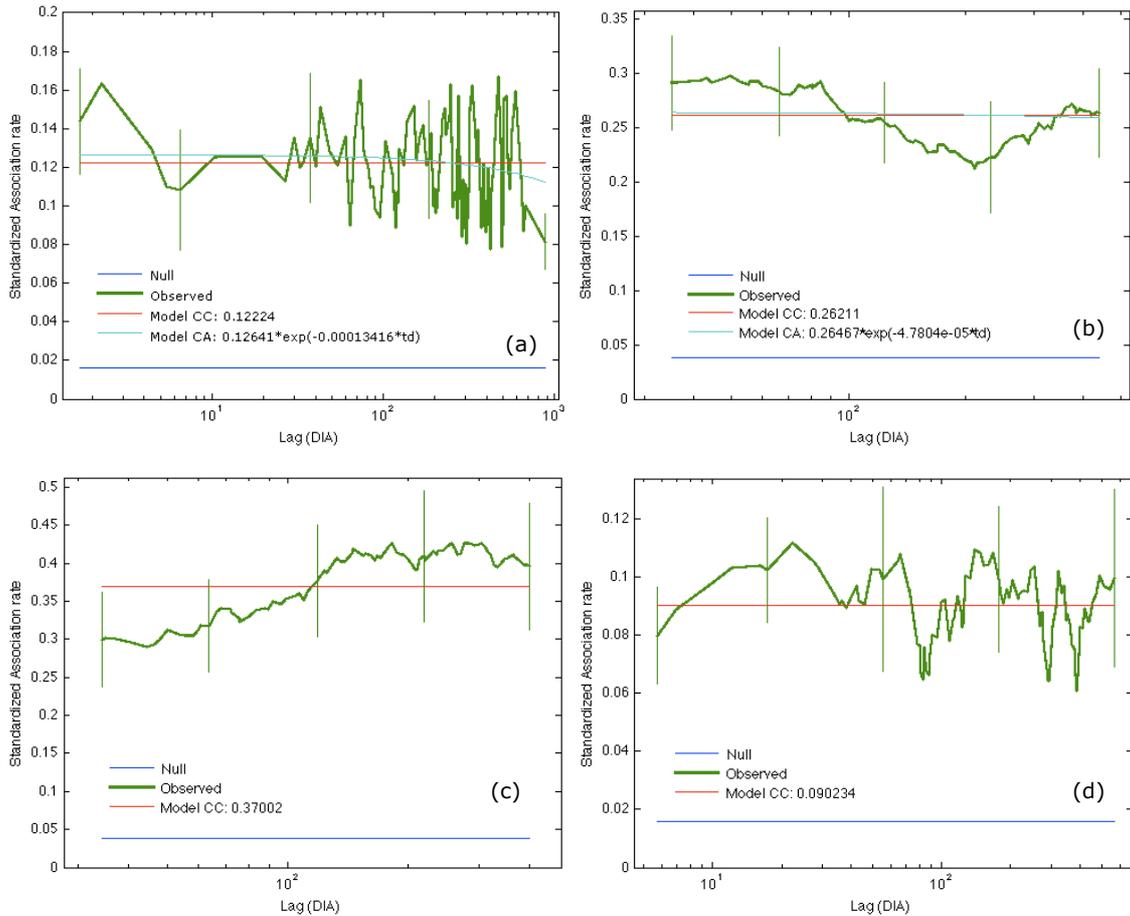


Figure A3.5a-d: SLAR for female vs female (a), male vs male (b), female vs male (c), male vs female (d) most frequently seen short-finned pilot whales (seen at least once a month during 8 months) identified between 2004 and 2010 in La Gomera and Tenerife, during sightings with good photo-identification coverage. Moving average curves of 1,000 associations for both are plotted with approximate standard error bars (produced by jackknife on each sampling period), over the null association rate. Best model “constant companions”: (a) $a_1 = 0.097583$ (s.e. 0.010829); (b) $a_1 = 0.26211$ (s.e. 0.031973); (c) $a_1 = 0.37002$ (s.e. 0.06375); (d) $a_1 = 0.090234$ (s.e. 0.015344). Model selection was made based on QAIC values, and compared to the null association rate. Error bars were obtained by jackknifing.

Figure A3.6

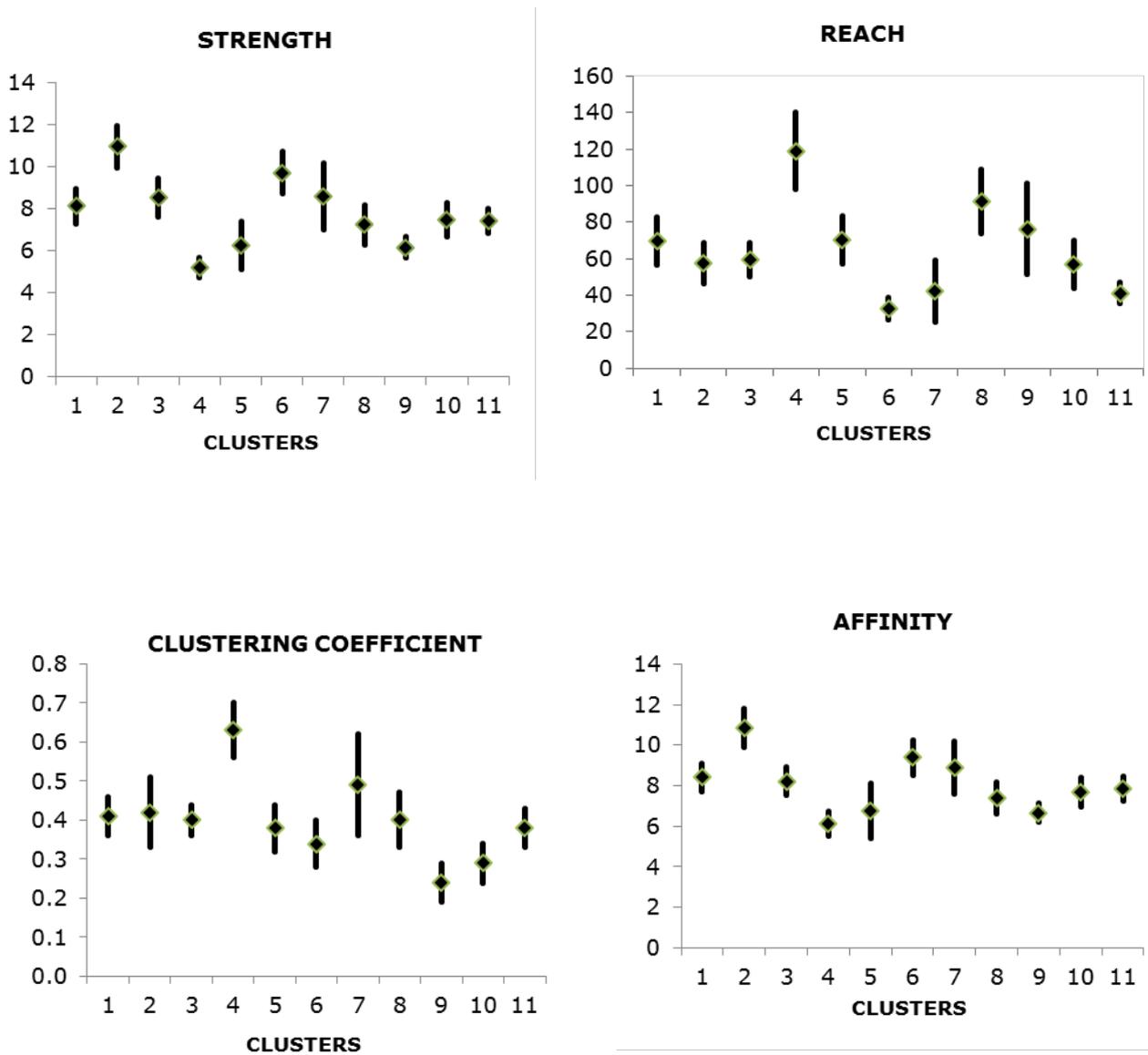


Figure A3.6: Graphs for mean Network Measures for Half-Weight association Indices between the 134 individual short-finned pilot whales identified at least during 8 months in La Gomera and Tenerife during sightings with good photo-identification coverage (dataset 2004-2010). Strength, reach, clustering coefficient, and affinity with standard error are presented for each cluster.

Figure A3.7

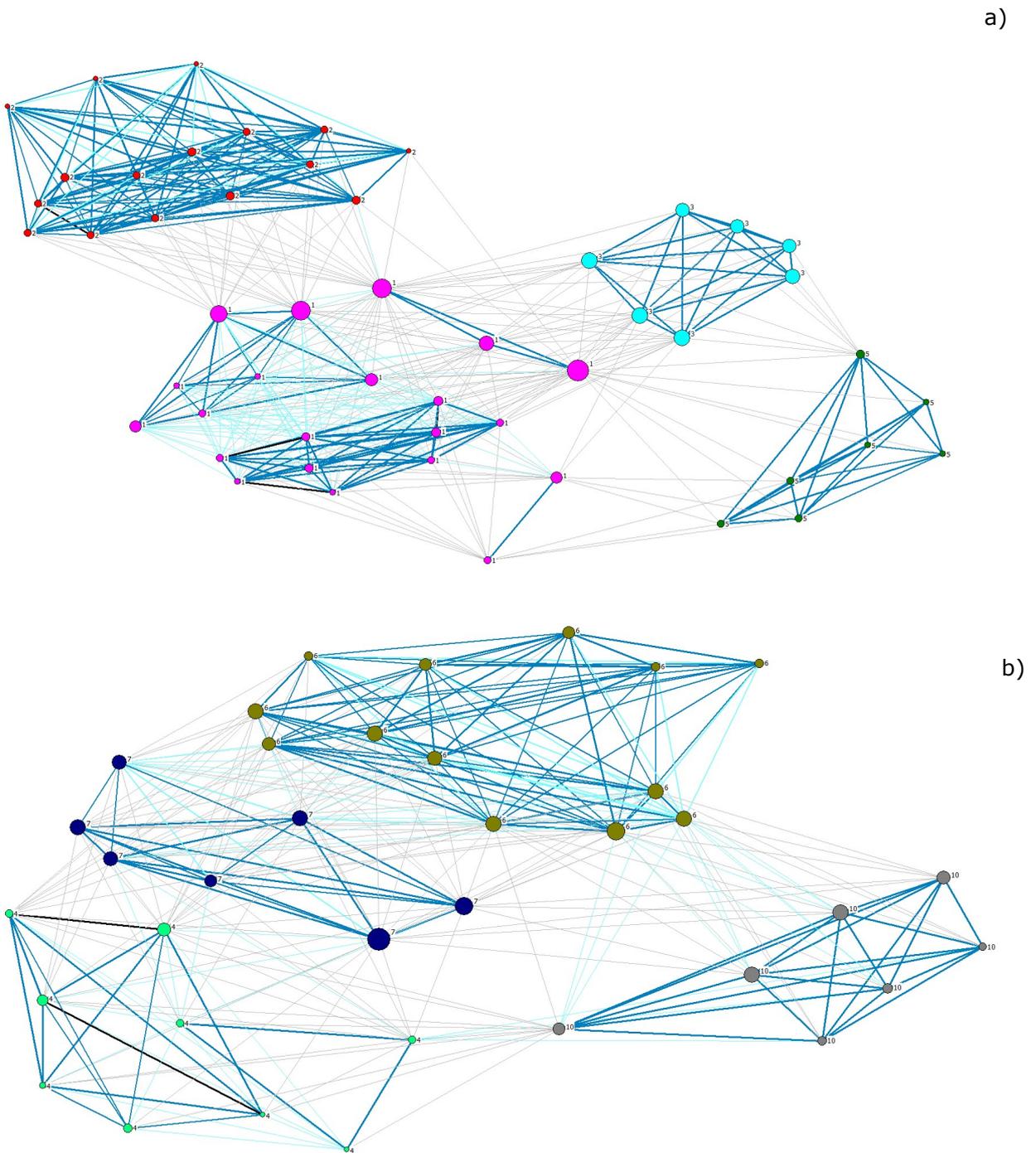


Figure A3.7a-b: Enlargement of the social network diagram of Figure 3.14, representing the different clusters obtained by using "sightings" as unit for association (a= clusters 1,2,3,5; b= clusters 4,6,7,10). Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Tie strengths of one are indicated by black lines, higher than 0.5 in blue, and lower than 0.5 in grey. The size of the node increases with the degree.

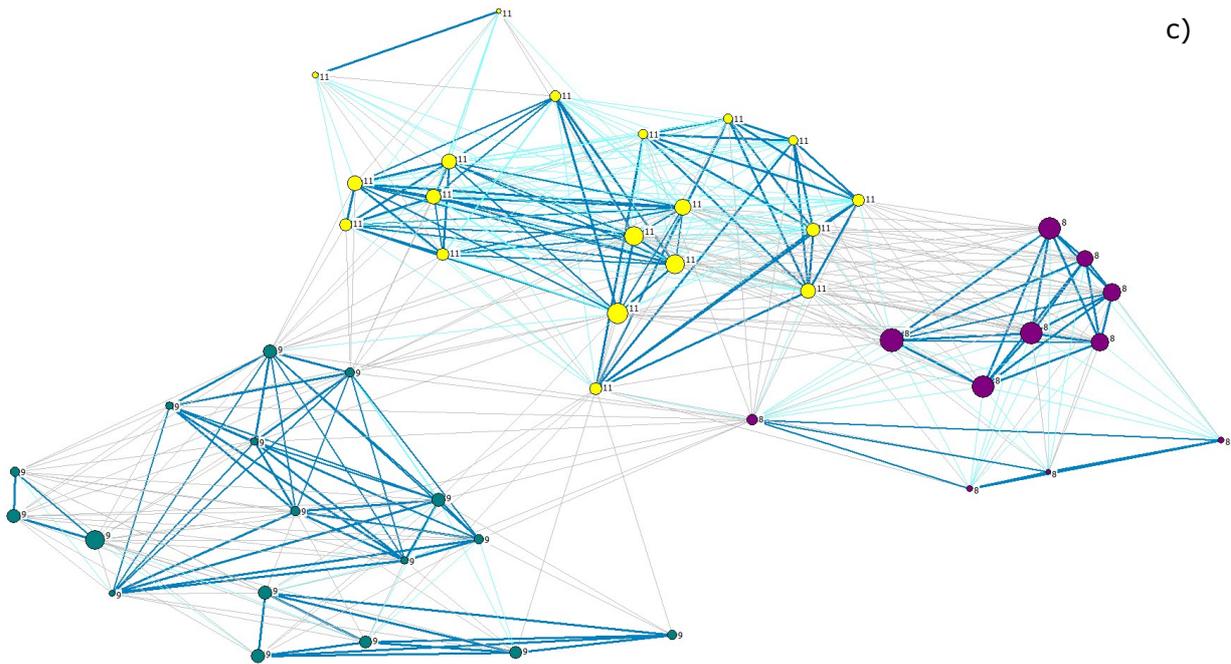


Figure A3.7.c: Enlargement of the social network diagram of Figure 3.14, representing the different clusters obtained by using “sightings” as unit for association ($c =$ clusters 8,9,10). Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals. Tie strengths of one are indicated by black lines, higher than 0.5 in blue, and lower than 0.5 in grey. The size of the node increases with the degree.

FIGURE A3.8

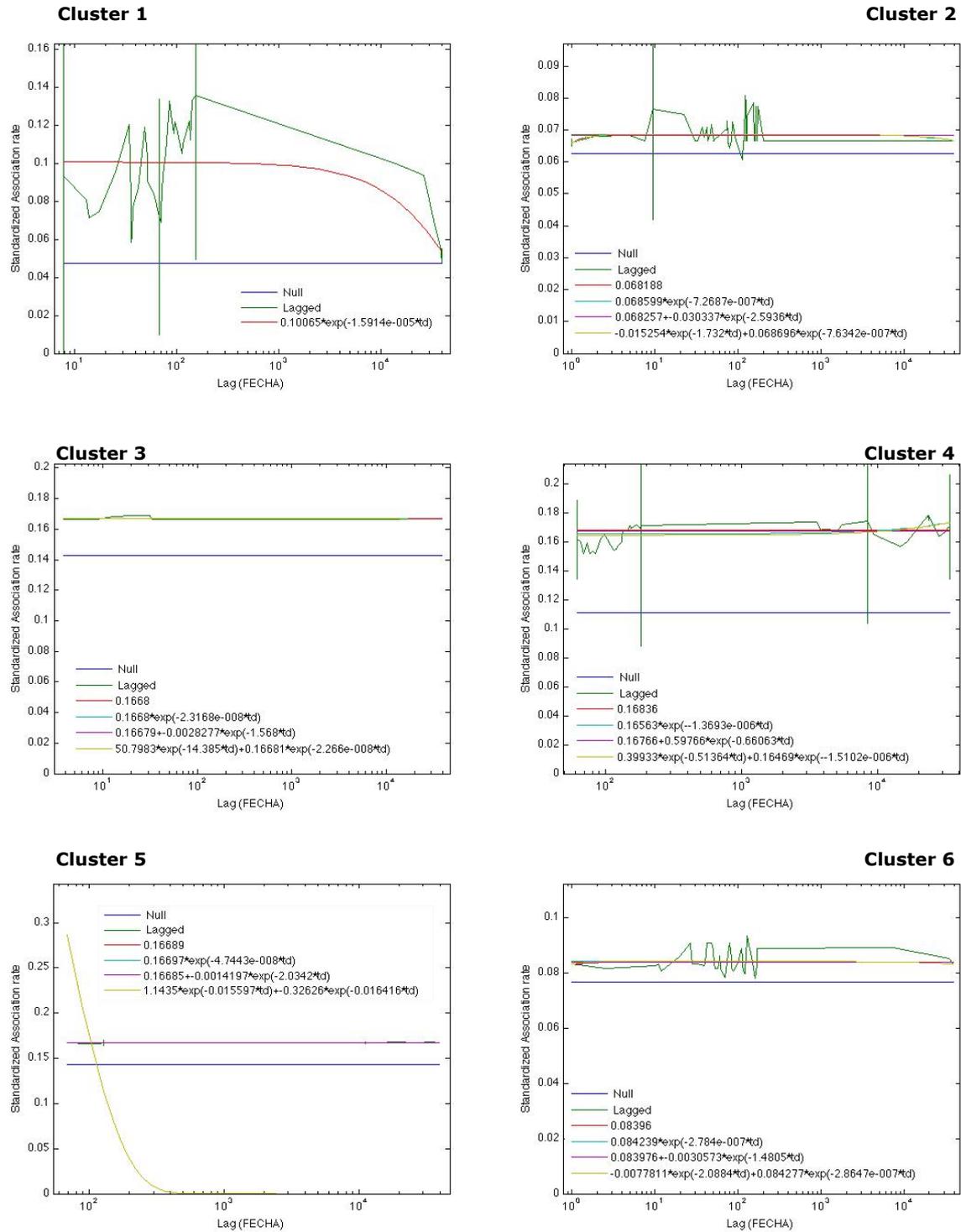


Figure A3.8a: SLAR curves calculated for the clusters 1-6 of most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales of the southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Moving average curve of 1,000 associations. The best fit-models were selected using the QAIC. Error bars were obtained by jackknifing.

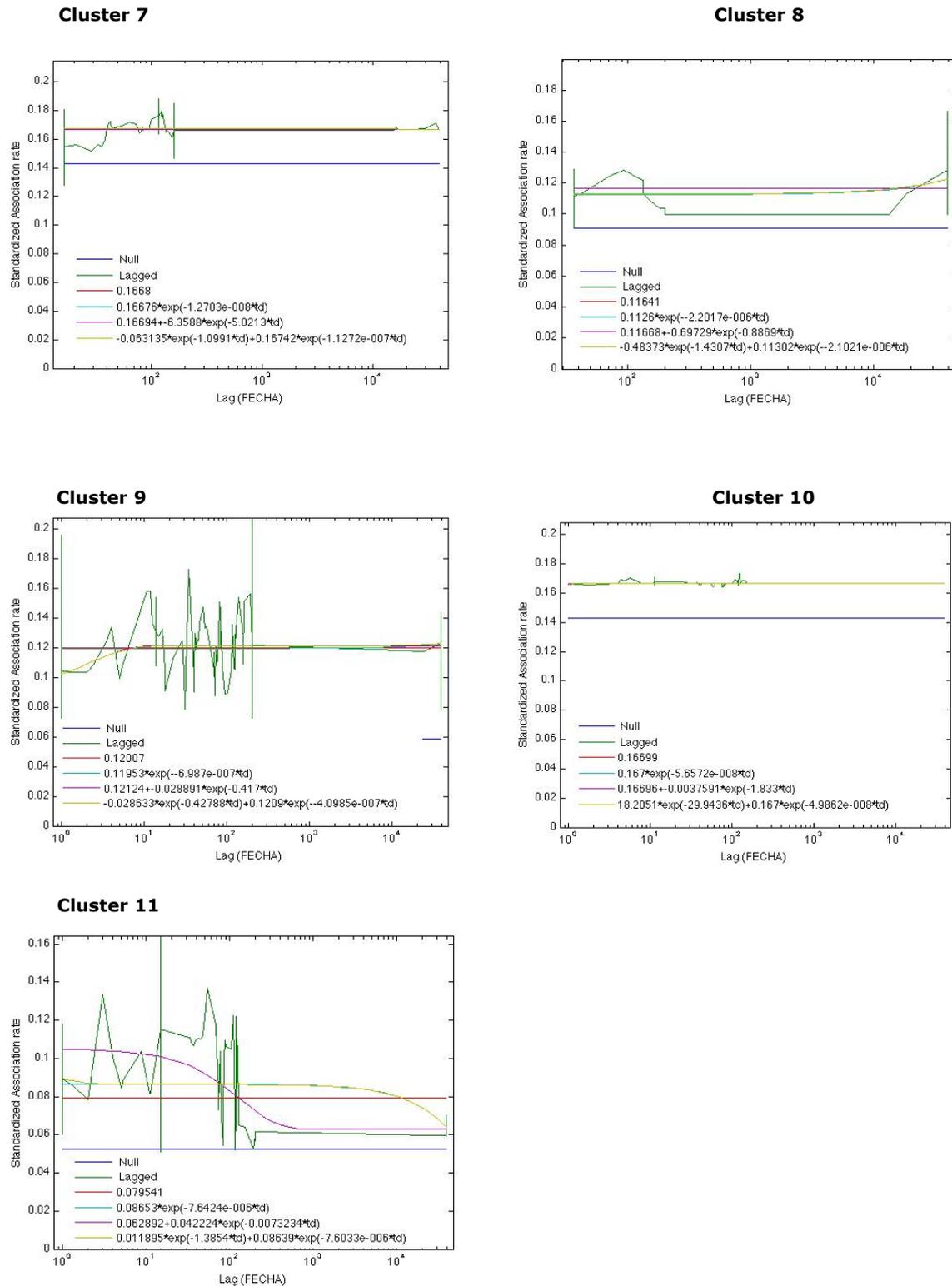


Figure A3.8b: SLAR curves calculated for the clusters 7-11 of most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales of the southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Moving average curve of 1,000 associations. The best fit-models were selected using the QAIC. Error bars were obtained by jackknifing.

TABLE A3.1

Table A3.1: SLAR results calculated for the clusters of most frequent (at least once a month for eight months) well-marked adult and indeterminate pilot whales of the southwestern Tenerife and La Gomera, between 2004 and 2010, in good coverage sightings. Moving average curve of 1,000 associations. The best fit-models were selected using the QAIC. Error bars were obtained by jackknifing.

CLUSTER	MODEL	BEST FIT			Q/AIC	PARAM.
		g'	a1	a2		
1	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = 1.5914e-005 (s.e. 0.003181)	a2 = 0.051438	2956.15	2
		g' = a1	a1 = 0.068188 (s.e. 0.001414)		72297.70	1
2	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = 7.2687e-007 (s.e. 2.5815e-005)	a2 = 0.068599 (s.e. 0.0018615)	72298.30	2
		g' = a1	a1 = 0.1668 (s.e. 0.00018308)		10185.37	1
3	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = 2.3168e-008 (s.e. 1.3987e-005)	a2 = 0.1668 (s.e. 0.00029169)	10187.37	2
		g' = a1	a1 = 0.16836 (s.e. 0.035629)		1530.60	1
4	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = -1.3693e-006 (s.e. 0.000489)	a2 = 0.16563 (s.e. 0.041902)	1532.40	2
		g' = a1	a1 = 0.16689 (s.e. 0.00063196)		5.28	1
5	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = 4.7443e-008 (s.e. 0.71258)	a2 = 0.16697 (s.e. 0.16639)	7.28	2
		g' = a1	a1 = 0.08396 (s.e. 0.00057211)		18231.25	1
6	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = 2.784e-007 (s.e. 0.00016318)	a2 = 0.084239 (s.e. 0.0012346)	18233.18	2
		g' = a1	a1 = 0.1668 (s.e. 0.0043157)		3439.95	1
7	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = 1.2703e-008 (s.e. 0.00064811)	a2 = 0.16676 (s.e. 0.011155)	3441.95	2
		g' = a1	a1 = 0.11641 (s.e. 0.023561)		1395.54	1
8	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = -2.2017e-006 (s.e. 0.0013912)	a2 = 0.1126 (s.e. 0.027463)	1397.09	2
		g' = a1	a1 = -6.987e-007 (s.e. 0.00065645)	a2 = 0.11953 (s.e. 0.01507)	8861.65	2
9	CASUAL ACQUAINTANCES CONSTANT COMPANIONS	g' = a2*exp(-a1*td)	a1 = 0.12007 (s.e. 0.013095)		8863.48	1
		g' = a1	a1 = 0.16699 (s.e. 0.00064277)		16794.82	1
10	CASUAL ACQUAINTANCES CONSTANT COMPANIONS AND CASUAL ACQUAINTANCES	g' = a2*exp(-a1*td)	a1 = 5.6572e-008 (s.e. 4.3393e-005)	a2 = 0.167 (s.e. 0.0009123)	16796.81	2
		g' = a2+a3*exp(-a1*td)	a1 = 0.0073234 (s.e. 11.5255)	a2 = 0.062892 (s.e. 0.039312)	a3 = 0.042224 (s.e. 69.5406)	8363.49

Table A3.2

Table A3.2: Ranges estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) of short-finned pilot whale key-units identified in Canary Islands between 1999 and 2010.

KEY-UNIT	MCP 95%	Schoener	Kernel 95%	Kernel 50%
A	5178.28	0.43	1094.27	239.26
B	1135.55	1.59	-	-
C	55.60	1.90	661.63	180.72
D	69.61	1.99	313.92	87.84
E	649.17	2.31	1565.02	266.14
F	34.51	1.14	297.33	71.54
H	716.55	1.37	1548.68	297.98
M	69.61	0.40	276.11	62.06
N	453.95	0.75	-	-
O	1697.77	1.42	-	-

Figure A3.9

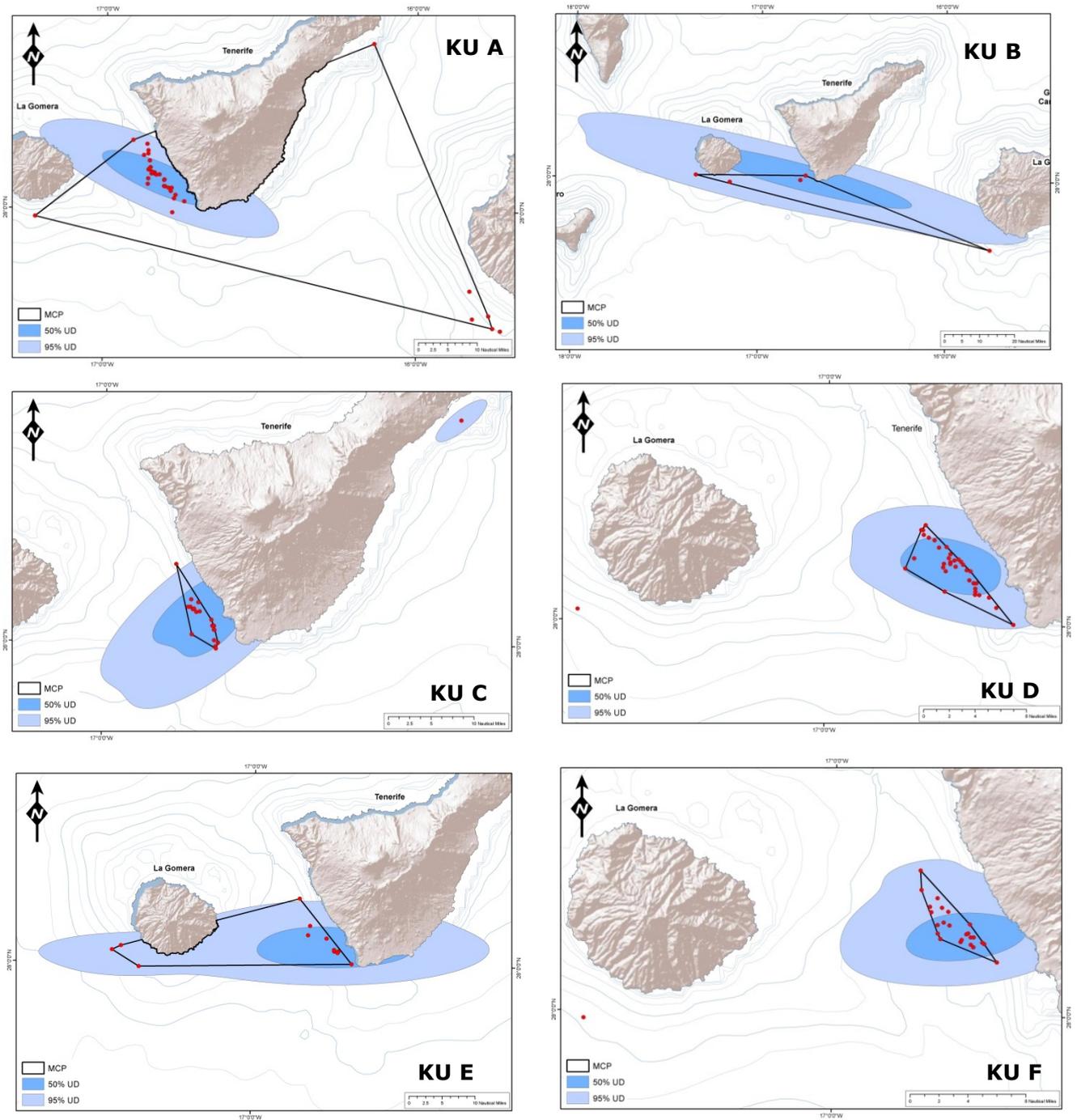


Figure A3.9a: Ranges estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) for short-finned pilot whale key-units (A,B,C,D,E,F) identified in Canary Islands between 1999 and 2010.

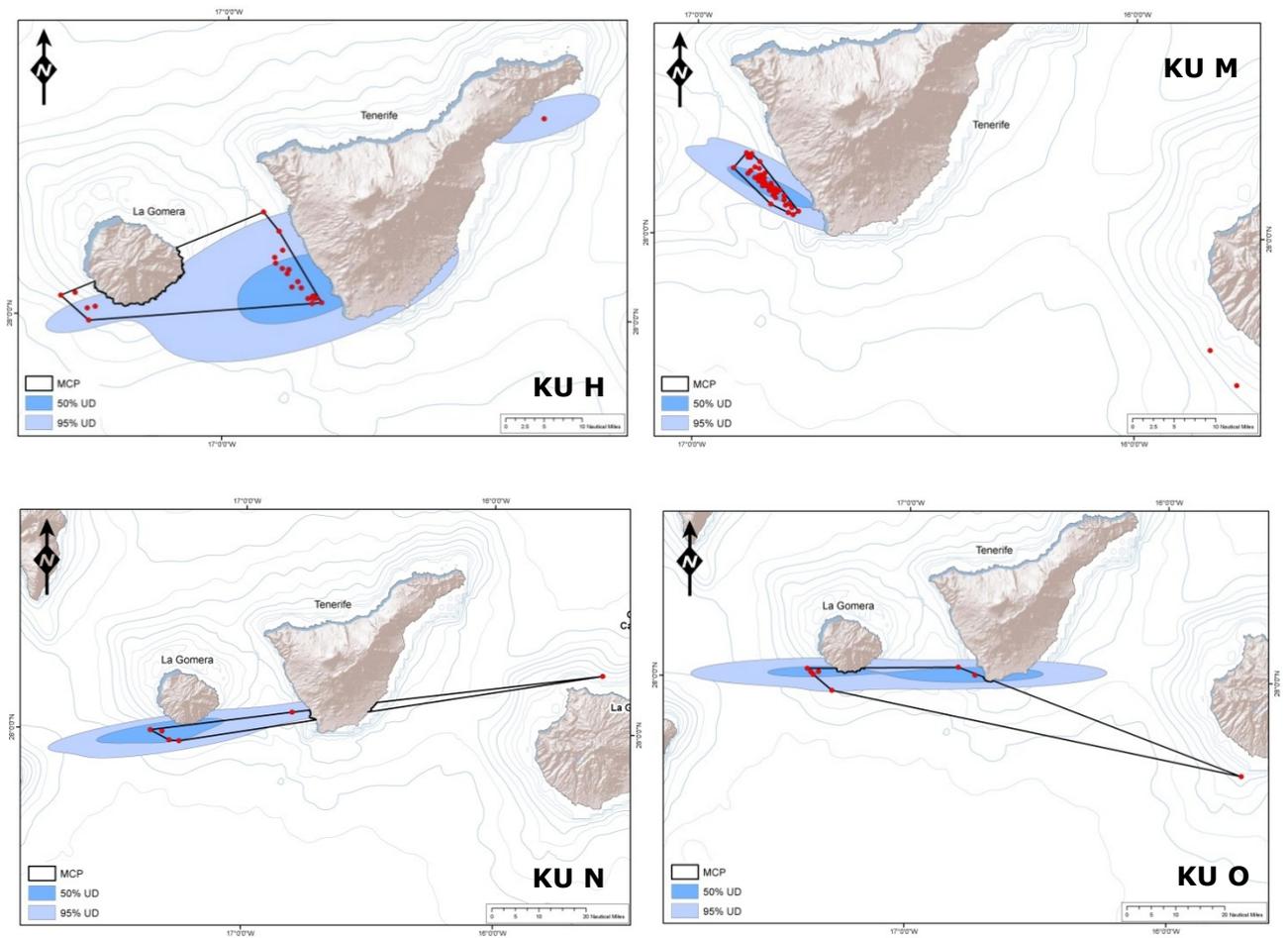
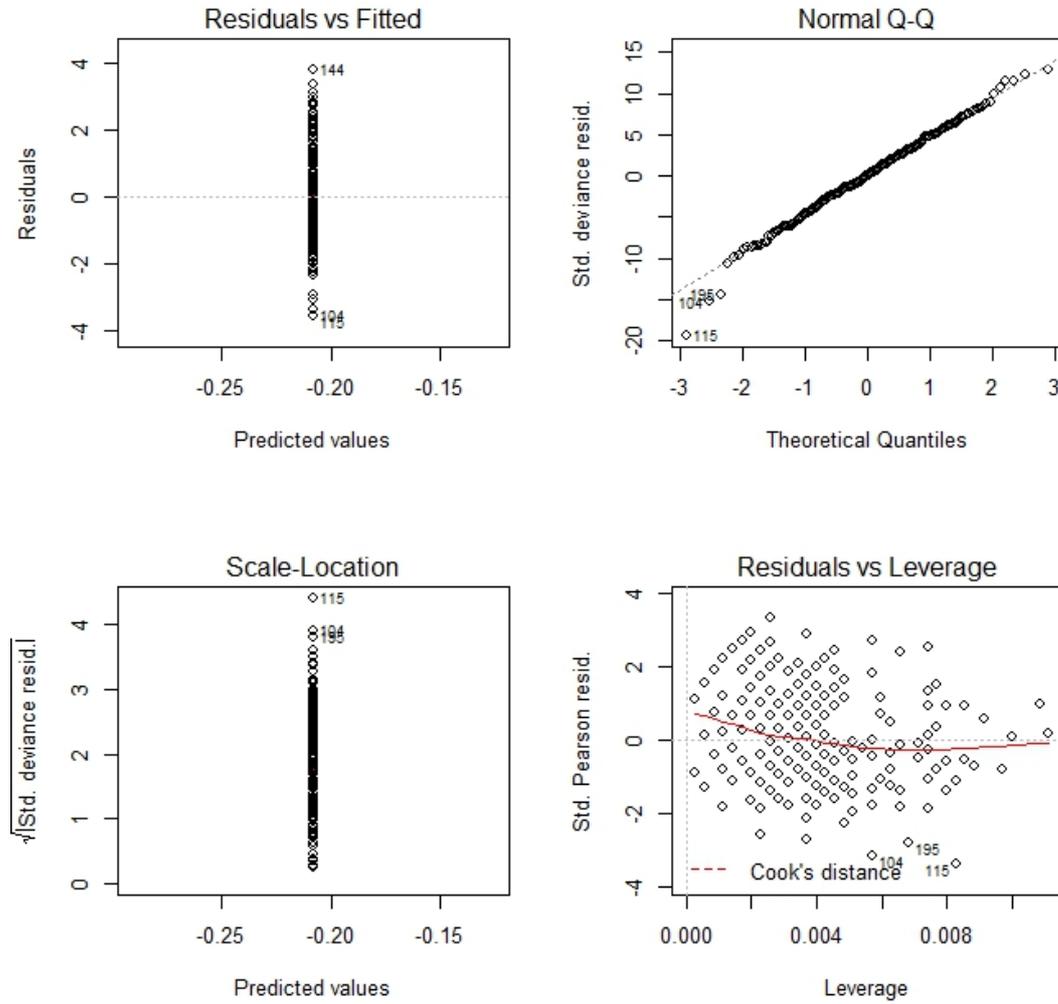


Figure A3.9b: Ranges estimated by MCP and fixed kernel (overall ranging at 95% UD and 50% UD) for short-finned pilot whale key-units (H,M,N,O) identified in Canary Islands between 1999 and 2010.

ANNEX 4

Figure A4.1: Graphs for binomial correlation with GLM, of the averaged proportion factor of identifiable animals in a school (θ). Deviance residuals: Min=-3.5887; 1Q=-0.8831; Median=-0.0226; SQ= 0.9505; Max= 3.8008. Intercept: estimate=-0.208; SE= 0.03397; Z-value=-6.122; Pr= 9.23e-10. Deviance= 486.63 on 262 degrees of freedom. AIC: 1187.1



ANNEX 4

Table A.4.1a.: Individual captures-recaptures within each sampling unit of the complete dataset: well-marked adult and indeterminate short-finned pilot whales.

	N° RECAPTURES PER SAMPLE UNIT																								TOTAL RECAPTURES				
	N RECAPTURES	2007												2008												2009			
		04	05	06	07	08	09	10	11	12	01	02	03	04	05	06	07	08	09	10	10	12	1	2		3			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24				
1	115	-	40	78	64	49	63	55	57	30	16	19	19	55	44	66	38	47	16	24	12	25	27	40	16	900			
2	84		-	58	46	38	62	39	41	22	19	19	21	34	30	55	33	21	22	14	2	21	36	16	6	655			
3	202			-	87	73	96	66	65	42	21	29	32	59	56	96	58	54	38	25	14	41	49	38	13	1052			
4	147				-	60	72	65	68	41	23	36	25	61	53	77	46	49	30	30	10	28	47	34	14	869			
5	123					-	67	52	46	37	36	9	26	41	44	62	45	31	21	13	9	27	39	34	5	644			
6	198						-	66	66	50	21	32	33	50	46	88	64	36	37	15	2	31	34	26	17	714			
7	137							-	83	30	26	19	30	48	44	62	46	44	22	32	8	26	23	31	14	588			
8	139								-	33	18	13	18	47	48	70	39	44	17	27	7	29	30	23	25	488			
9	93									-	10	24	24	30	15	50	28	32	20	4	6	16	22	13	9	303			
10	80										-	10	3	21	10	25	19	16	10	16	4	2	7	13	8	164			
11	51											-	18	25	20	29	22	19	9	3	0	10	12	17	3	187			
12	62												-	21	10	29	22	21	23	6	3	8	9	11	2	165			
13	121													-	37	67	36	50	26	27	11	26	30	39	14	363			
14	97														-	53	35	24	6	12	3	20	35	36	15	239			
15	176															-	59	45	27	21	12	42	51	35	24	316			
16	105																-	31	18	15	2	27	24	25	15	157			
17	85																	-	22	25	13	26	19	26	13	144			
18	82																		-	9	3	13	17	14	1	57			
19	48																			-	10	9	7	14	9	49			
20	26																				-	5	6	8	1	20			
21	91																					-	16	15	4	35			
22	84																						-	20	8	28			
23	96																							-	10	10			
24	33																								-	0			

ANNEX 4

Table A4.1b.: Individual captures-recaptures within each sampling unit of the dataset without the first captures: well-marked adult and indeterminate short-finned pilot whales.

	N° RECAPTURES PER SAMPLE UNIT																								TOTAL RECAPTURES				
	N RECAPTURES	2007												2008												2009			
		04	05	06	07	08	09	10	11	12	01	02	03	04	05	06	07	08	09	10	10	12	1	2		3			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24				
1	21	-	8	18	12	10	14	9	11	3	1	5	3	12	11	12	3	8	5	3	2	6	0	9	2	167			
2	57		-	44	35	28	44	26	29	17	14	14	12	25	21	40	25	15	15	10	2	17	23	13	5	474			
3	133			-	72	64	84	65	64	31	21	22	25	51	54	77	47	46	26	24	12	35	42	35	12	909			
4	130				-	54	68	62	67	37	23	33	21	60	53	76	43	48	27	30	10	27	47	31	13	830			
5	104					-	62	50	45	37	9	24	26	41	44	62	45	30	21	13	9	27	39	34	5	623			
6	157						-	65	65	46	18	31	32	47	46	87	51	33	31	15	2	31	34	25	16	675			
7	105							-	69	26	19	22	30	45	44	56	43	44	22	32	8	22	23	31	10	546			
8	122								-	33	18	13	18	40	48	70	39	44	17	27	7	29	30	23	25	481			
9	74									-	3	24	24	28	13	46	28	32	20	4	6	16	22	13	9	288			
10	49										-	10	2	21	10	25	18	16	10	16	4	2	7	13	8	162			
11	48											-	18	25	20	29	22	19	9	3	0	10	12	17	3	187			
12	47												-	21	9	21	22	21	23	6	3	8	9	11	2	156			
13	114													-	37	65	36	50	26	27	11	26	30	39	14	361			
14	91														-	53	35	24	6	12	3	20	35	36	15	239			
15	170															-	59	45	27	21	12	42	51	35	24	316			
16	104																-	31	18	15	2	27	24	25	15	157			
17	85																	-	22	25	13	26	19	26	13	144			
18	65																		-	9	3	13	17	13	1	56			
19	44																			-	10	9	7	14	9	49			
20	19																				-	2	6	8	1	17			
21	63																					-	16	15	4	35			
22	76																						-	20	8	28			
23	70																							-	10	10			
24	33																								-	0			

ANNEX 4

Table A4.1c.: Individual captures-recaptures within each sampling unit of the dataset without the first captures and the first recaptures: well-marked adult and indeterminate short-finned pilot whales.

	N° RECAPTURES PER SAMPLE UNIT																								TOTAL RECAPTURES				
	N RECAPTURES	2007												2008												2009			
		04	05	06	07	08	09	10	11	12	01	02	03	04	05	06	07	08	09	10	10	12	1	2		3			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24				
1	3	-	2	3	1	0	3	1	1	1	1	1	2	0	2	1	2	2	2	0	0	3	0	1	0	29			
2	30		-	30	23	19	24	9	19	8	8	7	3	9	14	22	16	7	4	3	0	11	16	9	4	265			
3	94			-	55	48	71	50	49	26	18	22	23	40	39	64	38	35	17	15	7	26	25	24	11	703			
4	106				-	50	59	54	60	27	20	27	16	47	47	64	31	33	20	24	10	23	44	22	6	684			
5	92					-	59	49	45	35	9	24	25	39	43	56	44	30	20	13	7	25	36	30	5	594			
6	125						-	63	63	44	18	31	31	46	45	78	51	33	29	15	2	31	33	25	14	652			
7	100							-	66	25	19	20	29	45	44	54	43	42	22	32	8	20	23	31	10	533			
8	110								-	33	18	13	18	40	48	68	39	44	17	27	7	28	30	23	25	478			
9	69									-	3	24	24	28	13	46	28	32	20	4	6	16	22	13	9	288			
10	33										-	10	2	17	10	22	14	13	7	16	4	2	7	12	8	144			
11	46											-	18	25	20	29	22	19	9	3	0	10	12	17	3	187			
12	47												-	21	10	21	22	21	23	6	3	8	9	11	2	157			
13	109													-	37	65	36	50	26	27	11	26	30	39	14	361			
14	84														-	51	35	24	6	12	3	20	35	36	15	237			
15	160															-	57	44	27	21	12	42	51	35	24	313			
16	100																-	31	16	15	2	27	24	25	15	155			
17	85																	-	22	25	13	26	19	26	13	144			
18	59																		-	9	3	13	17	13	1	56			
19	44																			-	10	9	7	14	9	49			
20	19																				-	2	6	8	1	17			
21	59																					-	16	15	4	35			
22	68																						-	20	8	28			
23	69																							-	10	10			
24	33																								-	0			

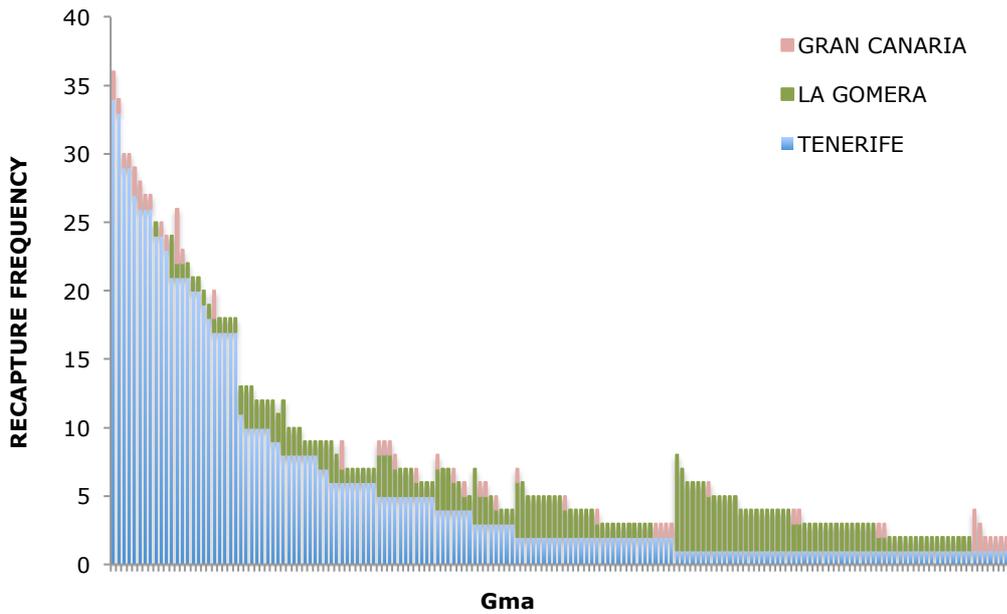


Figure A4.2a.: Recapture frequency of short-finned pilot whales within the islands of Tenerife (blue), La Gomera (green) and Gran Canaria (pink). Total dataset of high quality pictures, well-marked adult and indeterminate animals.

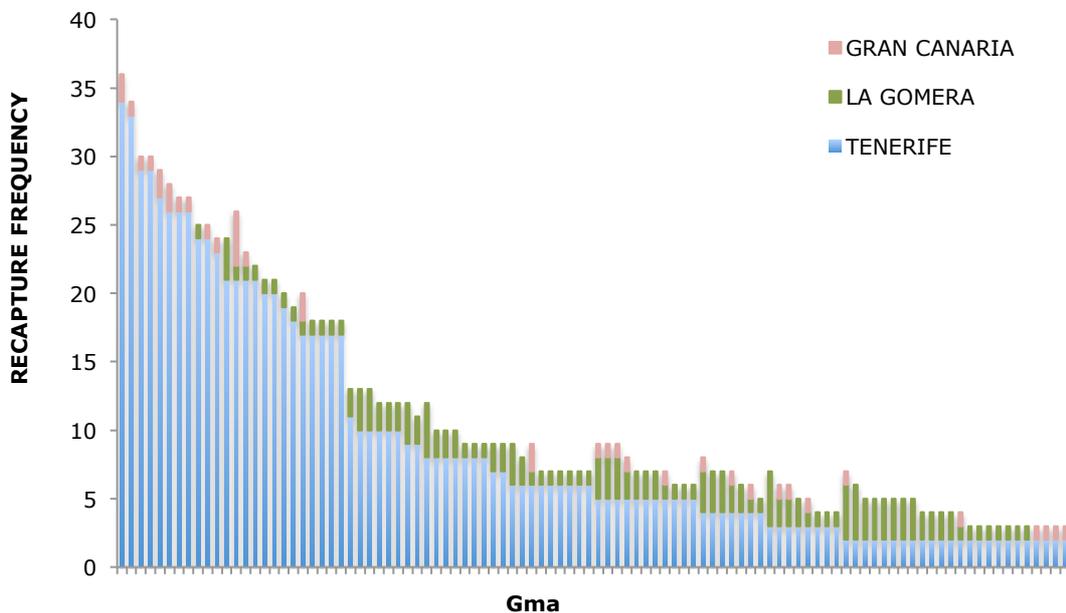


Figure A4.2b: Recapture frequency of short-finned pilot whales within the islands of Tenerife (blue), La Gomera (green) and Gran Canaria (pink). Dataset without the first captures, of high quality pictures, well-marked adult and indeterminate animals.

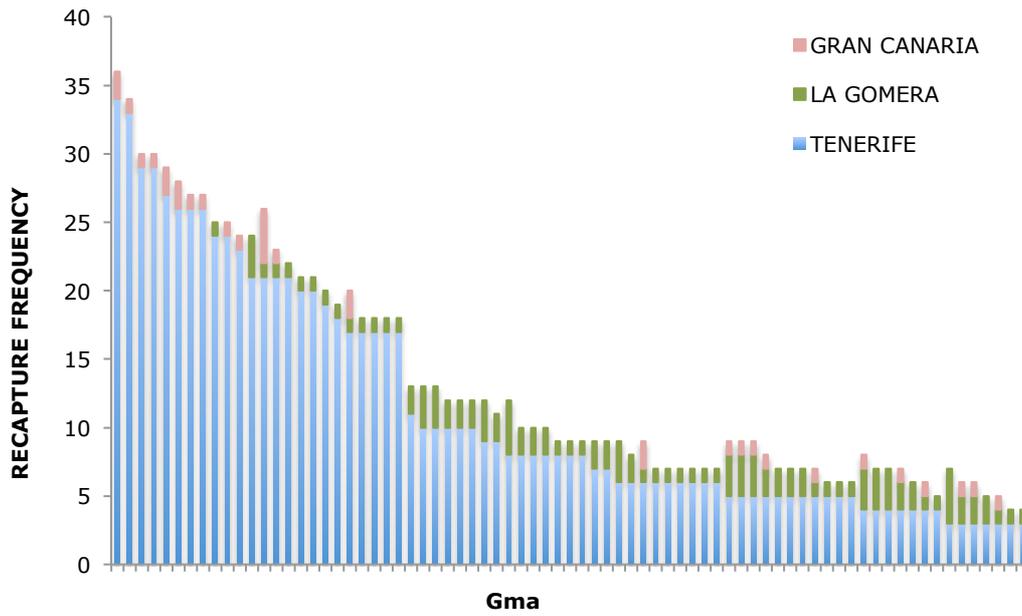


Figure A4.2c: Recapture frequency of short-finned pilot whales within the islands of Tenerife (blue), La Gomera (green) and Gran Canaria (pink). Dataset without the first recaptures, of high quality pictures, well-marked adult and indeterminate animals.

ANNEX 5

Table A5.1.: Spearman correlation analysis among the main covariates used in habitat use modelling.

	Lon	Lat	Depth	Depth min	Depth Max	Depth SD	Depth Range	Depth Log	Depth CV	IC	Slope	Distance from Coast	Distance from 200m Depth	Distance from 1000m Depth	SST (winter)	SST (summer)	Chl (winter)	Chl (summer)
Spearman Correlation																		
Lon																		
Correlation Coeff																		
Sig. (2-code) Coeff																		
Lat	.451**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Depth	-.084**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Depth min	.000																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Depth Max	-.213**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Depth SD	.000																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Depth Range	-.506**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Depth Log	.000																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Depth CV	-.413**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
IC	-.419**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Slope	-.544**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Distance from Coast	.300**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Distance from Coast Log	.300**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Distance from 200m	.350**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Distance from 1000m	.256**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
SST	-.544**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
SST (winter)	-.977**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
SST (summer)	.157**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Chl (winter)	-.561**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		
Chl (summer)	.616**																	
Correlation Coeff																		
Sig. (2-code) Coeff																		

ANNEX 6

A6.1: PRINCIPAL THREATS ON PILOT WHALES IN CANARY ISLANDS

During the study period (1999-2012) in Canary Islands, short-finned pilot whales have been found to be affected by various threats and risk factors, whose incidence and degree of impact vary considerably by island. The strong synergistic component of the anthropogenic threats cause that some of the factors or actions which may not represent a threat to cause the decline of the population if isolated, once linked to other threats or risks may have a decisive influence for the conservation of the species, their habitat, and the marine biocoenosis in the archipelago. This situation, which generally affects all species in the archipelago, is for some species more threatening due to their coastal ecology or greater residency, like for pilot whales, and happens both within SACs and outside them.

The main threats affecting or that could affect short-finned pilot whales in the islands include: habitat degradation, anthropogenic noise and physical disturbance caused by the presence of whale-watching and recreational boats, and transit of commercial fishing vessels, cruise liners and freighters.

NOISE IMPACT:

In Canary Islands, anthropogenic noise can proceed from a wide variety of sources, with different intensity depending on islands and the vicinity to the major urban centers and harbors. They include specific and limited in time and space actions, such as the placement of submarine cables and pipelines, the mooring of any element on the seabed, discharge of harbor dredges, creation of port and coastal defense infrastructures (e.g. Granadilla harbor in the southeastern Tenerife), but also continuous and widespread activities such the maritime traffic, that represent the most extent noise source in the archipelago.

Moraleda and Pantoja (2012) provided in their technical report extensive information about the underwater noise emitted by marine traffic in Spanish territories, and suggested mitigation measures of marine noise pollution.

Representing a crucial passage center for large oceanic routes between Europe, Africa and Asia and between port in the Mediterranean Sea and Central America and South America, Canary Islands have to bear intense maritime traffic. Given this, and because the high ecological value of the archipelago and its consequent vulnerability to episodes of accidental pollution, in 2005 the Marine Environment Protection Committee of the International Maritime Organization (IMO) designated the Canary Islands as a Particularly Sensitive Sea Area (PSSA), admitting the proposal that Spain made under the Part XII of the United Nations Convention on the Sea Law of 1982. In 2006, the Maritime Safety Committee of IMO adopted the final protection measures for the area, which entered into force on December 1, 2006.

The PSSA includes the waters externally limited by a polygonal line joining the ends of the outer limit of the territorial sea (12 nautical miles) around the Canary Islands, comprising approximately 30,000 km², and over 1,500km of shoreline (Figure A6.1). It was anyhow recognized that the sensitive area should reality cover a larger area, thus allowing a future extension up to 60,000 km² (Ministry of Agriculture, Food and Environment, 2012).

The protective measures associated with PSSA include (Figure A6.1):

- Restricted areas to Navigation: used exclusively by artisanal fisheries and interisland shipping to and from the harbors within this area, prohibiting the navigation of ships in transit.
- Mandatory navigation routes in the PSSA along two preset routes for the ships in transit whose origin is not an harbor of the Canary Islands: western route (halfway between Tenerife and Gran Canaria), and eastern route (halfway between Gran Canaria and Fuerteventura).

Notification system for entering and exiting from the PSSA for all ships dedicated to the transport of heavy hydrocarbon in transit or destined to a Canary Islands harbor. These notifications are made through the Rescue Coordination Centers of Las Palmas and Tenerife of the Ministry of Development.

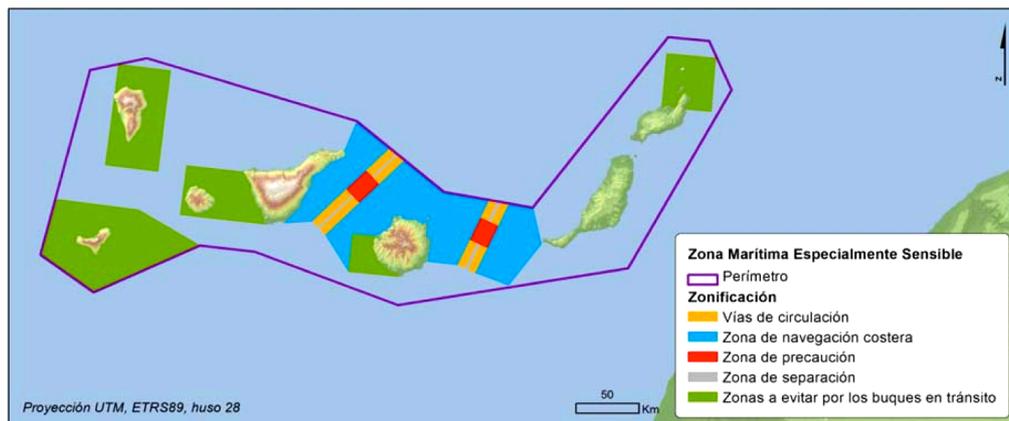


Figure A6.1: Particularly Sensitive Sea Areas (PSSAs) in Canary Islands (yellow: circulation routes; blue: coastal navigation area; red: precaution area; grey: separation area; green: restricted area that vessels in transit must avoid). (Image from: Ministry of Agriculture, Food and Environment, 2012).

In the Canary Islands there are 38 ports (from 15 in Tenerife to one in El Hierro) and 6 docks for sports with a total of 8,108 berths. The highest vessel density is registered along the main routes, between Tenerife, Gran Canaria and Fuerteventura as well as in areas surrounding the harbors, mainly in Gran Canaria (La Luz) and in Santa Cruz de Tenerife (Ministry of Agriculture, Food and Environment, 2012).

The noise generated by large fast ships, such as tankers or merchant, is quite intense and concentrated in the low frequency range (5-500 Hz). These noise sources are the most common near the major harbors and along the mostly used shipping routes and can spread over long distances due to their low frequency increasing background noise even far away from the emission hot spots. Similarly, small boats, recreational fishing vessels, whale watching boats, modern freighters and passenger ships, such as ferries / high speed ferries,

generally generate noise at high frequencies, whose characteristics depend on the type of engine, the size of the vessel and its speed, with also considerable individual variation among comparable vessel classes. This would lead that in some areas of intense traffic of recreational vessels the underwater noise level may be also high, likely to interfere with the vocalizations of many odontocetes species (Morisaka et al. 2005; Tejedor *et al.*, 2012).

In the Canary Demarcation, three areas have identified with potentially high levels (southwestern Tenerife-La Gomera, around the Santa Cruz de Tenerife and Las Palmas de Gran Canaria harbors) and two with potentially moderate levels of underwater noise (south of Fuerteventura and southeastern Lanzarote) (Figure A6.2) (Ministry of Agriculture, Food and Environment, 2012). The localized areas are linked to the main commercial harbors and the main navigation routes between Los Cristianos and La Gomera, and areas with fishing activity, such as the west of Tenerife and the southern coasts of Fuerteventura, Lanzarote and La Gomera (Ministry of Agriculture, Food and Environment, 2012).

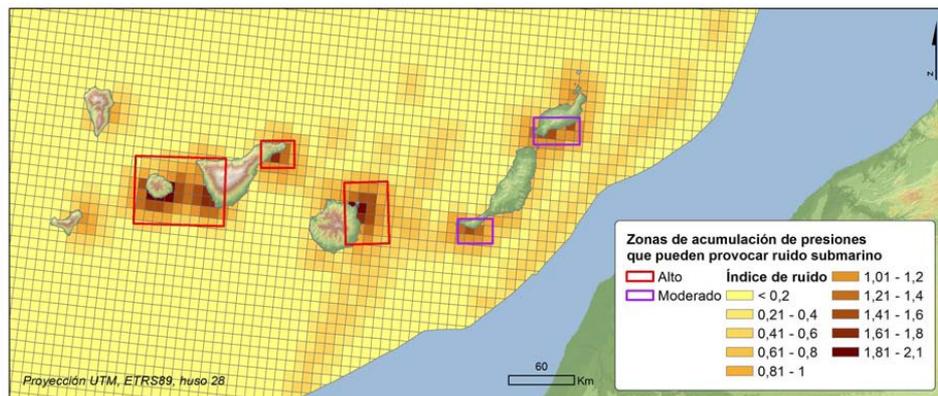


Figure A6.2: Areas of pressure accumulation that underwater noise can cause (red square: high; violet square: moderate). (Image from: Ministry of Agriculture, Food and Environment, 2012).

Hydrocarbon prospections: Several studies have related mass mortalities of cetaceans with seismic exploration during hydrocarbons prospection (Malakoff, 2002; Peterson, 2003; Palacios *et al.*, 2004). The research phase previous to hydrocarbon explorations generally contemplates the use of seismic techniques in order to map the seabed structure. Conducting bathymetry and seismic study on the substrate lead to the emission of pulses of compressed air or ultrasounds at different frequencies depending on the method used, but mostly comprised between 235 and 246 dB. Considering that the demarcation area is of 486,195 km², the marine surface affected by activities related to hydrocarbon exploration, where it could be developed seismic work, would be 6311.38 km², representing about 1.3% of thereof (Ministry of Agriculture, Food and Environment, 2012).

On 16th March 2012, The Spanish Government Ministers Council, approved the Royal Decree 547/2012, which grants the companies Repsol Investigaciones Petrolíferas, S.A., Woodside

Energy Iberia, S.A. and RWE Dea AG licenses to explore for hydrocarbons in the Atlantic Ocean off the coasts of the islands of Fuerteventura and Lanzarote (Canary Islands, Spain). The project has authorized nine prospecting areas with a total area of 6,160km² located at a distance of between 10 and 60km off the coast, and includes the drilling of at least two exploratory wells in a true vertical depth (TVD) between 2.500 m to 4.000 m below mean sea level (maximum water depth of 1500 m).

Military and scientific activities that use sound: In Canary Islands, several atypical mass strandings in the last 20 years (Fernández *et al.*, 2005; Santos *et al.*, 2007; Jepson *et al.*, 2003; Martin *et al.*, 2004), temporally and geographically correlated with naval exercises using antisubmarine medium frequency active (MFA) sonars (Cox *et al.*, 2006), indicates the presence of species sensitive to noise exposure. Necropsy on beaked whales stranded between 2002 and 2004 showed severe tissue damage with systemic gas-fat embolic disease, comparable to severe decompression syndrome (Fernández *et al.*, 2003; Jepson *et al.*, 2003; Fernández *et al.*, 2004; Fernández *et al.*, 2005). A moratorium signed in 2004 by the Ministry of Defense and the Canary Government, prohibited further execution of military maneuvers associated with sonars within the waters of Canary Islands. Even though no official documents have extended the veto after 2010, the local authorities have ensured that the moratorium remains in place, and that together with the Ministry of Defense and Marine Affairs are defining critical areas for cetaceans in Canary Islands.

MARITIME TRAFFIC (FERRIES)

The Canary Islands have experienced rapid economic development in the last 30 years, increasing demands for inter-island transport of passengers and goods. The result has been a dramatic increase in the inter-island traffic, with the emergence in recent years of medium and high speed craft, fast-ferries, which are gradually replacing conventional ferries. The archipelago supports one of the highest densities in the world of maritime traffic (Ritter, 2010). The length of between islands annual tracks of the regular ferries (15-20 knots), of medium speed fast ferries (21-29 knots) and high speed fast-ferries (30 knots or more) summed 66,000km, 570,000km and 845,000km, respectively (Ritter, 2010). Most of these fast lines crosses areas known for their high cetacean density, and parallel to the development of this maritime traffic there has been an increase in the number of stranded cetaceans with signs of having been overwhelmed by such crafts (de Stephanis and Urquiola, 2006; Ritter, 2010).

The stranding network (Canary Islands Government, Institute of Animal Health of the Faculty of Veterinary Medicine, Tenerife Conservation and SECAC; Reports to the IWC) has recorded over the last 20 years all the cetacean deaths caused by collisions occurred in Canarias. From 1985 to 2010, 62 cetaceans deaths have been documented due to vessel collision (Arbelo, 2007; Carrillo and Ritter, 2010; Canary Government, 2009; SECAC unpublished data), of which 60 (96.77%) has been recorded since the introduction of fast ferries in 1991. The most frequently encountered species is the sperm whale with 36 cases (58.06%), although in recent years there have been several examples of whale (fin whale, sei whales, and indeterminate), pygmy sperm whales, dwarf sperm whales, Cuvier's beaked whales, Gervais beaked whale and pilot whales (Carrillo and Tejedor, 2006; de Stefanis and Urquiola 2006; Arbelo, 2007; Carrillo, 2007; Carrillo and Ritter 2008; Carrillo and Ritter, 2010). Therefore, it seems that collisions mainly affect deep diving species, slow and difficult to detect on the surface (Carrillo and Ritter, 2010; Ritter, 2010).

In 2000, with the aim of assessing the potential risk that the high-speed vessels may represent, a study conducted by the Institute of Marine Studies of the University of Plymouth, the University of La Laguna, and Tenerife Conservation Society, developed a risk model for areas of high maritime traffic, like Tenerife (Tregenza *et al.*, 2000, 2002). The authors described a mathematical model that determines the risk of collision and examined the implications on cetacean population in the protected area that are crossed by the high-speed lines. The model estimated the possibility that a total number of 467 short-finned pilot whales collisions happen per year in the channel between Tenerife and La Gomera and 8 collisions per year in the channel between Tenerife and Gran Canaria. Although, these results warned about the actual risk posed by high speed vessels for cetaceans in the Canary Islands (Tregenza *et al.*, 2000), they should be interpreted with caution due to a potential overestimation of the collision probability, since not enough information about this species distribution, density and diving patterns was then available, and since for the model calculation these animals were considered to react with a general "indifferent behaviour" when high-speed ferries were present.

At present, it is likely that the majority of collisions between whales and ferries/fast ferries crews goes unnoticed due to the size and speed of these vessels. Moreover, the mortality associated to collisions tends to be underestimated because the collided bodies might not reach the coast, because preyed, sunk, or washed away by oceanic currents (Carrillo and Ritter, 2010; Ritter, 2010). Even though the real extent of this mortality is unknown as well as the effect of this mortality on cetacean population, it has been indicated as a potential elevate and dangerous issue for the conservation of cetaceans in the archipelago. This situation is exacerbated by the limited general knowledge on basic aspects of cetaceans in the area.

Speed limits appear to offer an effective way to mitigate this problem (IWC, 2010). It was recommended to introduce a maximum speed limit of 13 knots for the MPA in La Gomera to be applied to all ferries and other craft in transit (Carrillo and Ritter, 2010; Ritter, 2010).

WHALE WATCHING

The activity of whale watching in the Canary Islands began in the southwestern coast of Tenerife in the late eighties, after the discovery of a population of short-finned pilot whales. Since then, this activity experienced a rapid development, with a not equal growth for all the islands. While most operators are extensively located in the southwestern regions of the islands of Tenerife, Gran Canaria and La Gomera (28, 8, and 7 vessels, respectively), in the island of La Palma the activity is confined only to three boats. In 2008, the number of licensed vessels and passengers capacity estimated by Elejabeitia and Urquiola (2009) was respectively of 26 ships and 2,356 passengers in Tenerife, and of one vessel and 53 passengers in La Palma. Gran Canaria counted with a fleet of seven ships with a total capacity of 668 passengers, while La Gomera totaled three boats with a total capacity of 124 passengers. Therefore, of the 37 vessels licensed in the archipelago in 2008, the island of Tenerife owned the 70% of the total vessels, the 65% of retailers and the 70% of the passenger carrying capacity (Elejabeitia and Urquiola, 2009), with slight fluctuations in the number of vessels and the passenger capacity recorded from one year to another and among the islands. The direct income generated by this activity was calculated to reach in 2008 a total of 19.8 million Euro. Likewise, there is a marked difference in the type of vessels used for this tourist activity among the different islands: while in Tenerife and Gran Canaria the fleet mostly consists of catamarans with large passenger capacity, in La Gomera old wooden boats and artisanal fisheries are used once adapted for the whale-watching activity.

Whale watching in the Canary Islands, as well as nautical infrastructure, are based inside the Special Areas of Conservation (SACs), where various human activities are concentrated, especially in the south of Tenerife and Gran Canaria, and La Gomera at lesser extent. Target species vary from island to island: short-finned pilot whale and bottlenose dolphin in the southwestern coast of Tenerife and La Gomera; bottlenose dolphin and rough-toothed dolphin in Gran Canaria and La Palma (Elejabeitia and Urquiola, 2009).

In the recent years there has been a growing concern about the potential effect of this activity on cetacean populations in Canary Islands, highlighting the continued presence with the animals of these vessels over several hours, every day of the year. Parallel to the activity of whale-watching recreational boats, transport and fishing vessels operate in these same areas. In marine SACs of Franja Marina Teno-Rasca and of Mogán, are not rare cases of bullying, harassment and agglomeration of boats around dolphins or whales, a situation that could last for several hours. Moreover, because of the desired high speed, activities such as jet skis,

para-gliders towed by boats, water-skiing also have the potential to come into conflict with cetaceans and other animals frequenting coastal waters (e.g. breeding sea birds).

In the effort to ensure cetaceans conservation and protection, the responsible Canary Government for Conservation of Nature and Environment approved a regulatory Decree to regulate whale-watching in the islands. In 1995, the Decree 320/1995 was adopted (BOC 148, November 20). The increased pressure in the sector forced the Canary Islands Government to draft a new decree in 2000 (178/2000) to resolve issues insufficiently addressed in the previous Decree, introducing the development of an ecological impact study and the need to obtain the consequent authorization statements. The code of conduct was implemented and the presence of a specialized cetacean tourist guide, officially titled by the Canary Islands Government, was required on board. Moreover, the grant of a distinctive flag called "Blue Boat" was also used to distinguish the boat with all the qualifications set by the corresponding regulations. Nevertheless, neither patrolling service has been functioning, nor adequate awareness campaigns were conducted.

The only study realised in the attempt to evaluate possible disturbance in Canary Islands was undertaken in 2000 on the population of bottlenose dolphins and pilot whales off the southwestern coast of Tenerife (Aguilar de Soto *et al.*, 2000). Short term behavioural reactions of these two species in response to different strategies of boat approach were evaluated recording changes of course, speed and group spacing, taking into account also the presence/absence of calves and mature males when possible. In pilot whales, the results showed significant trends in behavioural changes of the animals in relation to the social composition of the groups and the approach strategy used by the vessels: mature male seemed to play a major role in causing the group to react, especially in case of chasing boat approach (Aguilar de Soto *et al.*, 2001). This suggest that habituation to the presence of boats may happened only until the extent that they don't chase the animals (Aguilar de Soto *et al.*, 2001). No specific studies have been conducted so far in Canary Islands to quantify the impact that whale-watching activity may have combining observation on short and long term response behaviour. As well, since it was not the aim of the present work specific data were nor provided in this thesis.

ARTISANAL FISHERIES

The fishery fleet in Canary Islands is mostly limited to small-medium size handmade vessels. In general, the Canary fishing fleet can be classified based on their main fishing activity: sardinal fleet (trawls engaged in the extraction of coastal pelagic resources); tuna fleet (boats with an average length of 15m that work in the archipelago as well as close to Africa, saving the catch in ice); small-scale coastal feet (small units with an average length of 10m with

enough tank capacity to hold live baits for tuna or to storage small pelagic catches), and coastline fleet (small boats, never spending the night out at sea).

Interactions between cetacean and artisanal fisheries occur in all SACs studied, but are quite limited to bottlenose dolphins and especially intense in the island of El Hierro, where there is a serious conflict between this species and the longline fishing gears, and in La Gomera mostly while fishing for tuna. No strandings or interaction with fisheries have been officially reported so far for short-finned pilot whales.

HABITAT DEGRADATION

In Canary Islands there are several (direct or indirect) factors that can favor the habitat degradation of cetacean species, as the loss of the optimal characteristics for the presence of the same: increasing of coastal infrastructure, water and seabed pollution, shipping, fisheries and aquaculture industry, noise pollution, etc. These factors may represent an important impact on cetaceans and even affect the patterns of temporary or permanent emigration to adjacent areas especially in a highly structured society (Alcook, 1989), such as pilot whale.

The activities that introduce waste into the marine waters can be developed at the sea, as for example navigation and fishing, and associated to the coastal area, such as beach tourism, or come from activities conducted on land. Marine waste can cause significant impacts on the marine environment in general and on the biota in particular, especially on certain species, such as mammals, birds, turtles and fish through ingestion. Although it is produced by human activities, with the help of winds and currents it can spread to the most remote places, far from the original sources.

In the Canary Demarcation, one area has been identified with high potential contribution of land-based waste (northeastern Gran Canaria) and three areas with moderate potential (Santa Cruz de Tenerife, Tenerife south and Arrecife area). The introduction of waste into the marine environment may also result from the discharge of sewage into the sea from land, without these having been previously subjected to a purification process. In some areas of the Demarcation, the General Direction of the Coast and Sea Sustainability reported accumulation of waste in front of the Roques de Anaga (waste dumped by visitors), in Puntallana Reserve of La Gomera (garbage accumulations on the platform and on the cliffs), and eastern Fuerteventura (floating debris; Figure A6.3). The garbage of marine origin comes mainly from fishing and boating activities, mostly concentrated along the water channels between Tenerife-La Gomera, Gran Canaria-Tenerife, Fuerteventura-Gran Canaria and Lanzarote-Fuerteventura (Figure A6.4) (Ministry of Agriculture, Food and Environment, 2012).

The presence of plastic debris in stomachs of cetaceans is becoming an increasingly common circumstance (Santos *et al.*, 2001), in fact, there are several records of stranded cetaceans

with plastic or other solid waste in their stomach, directly responsible of their deaths, mainly for intestinal occlusion.

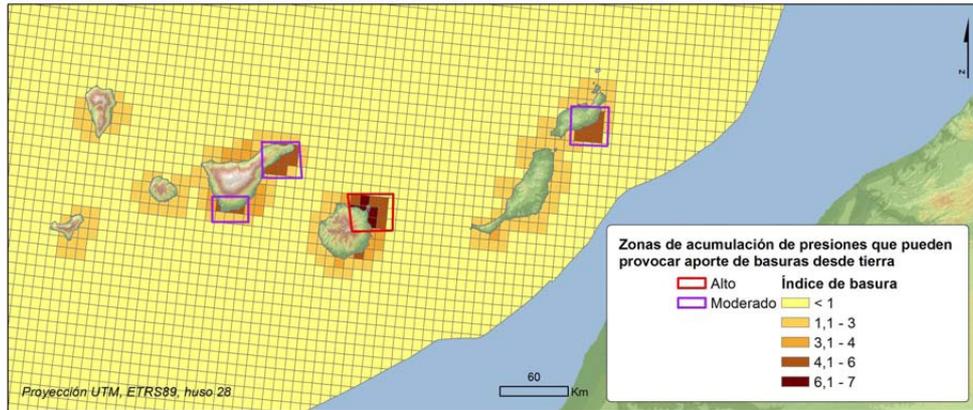


Figure A6.3: Pressure accumulation zones caused by the discharges from land (red square: high; violet square: moderate). (Image from: Ministry of Agriculture, Food and Environment, 2012).

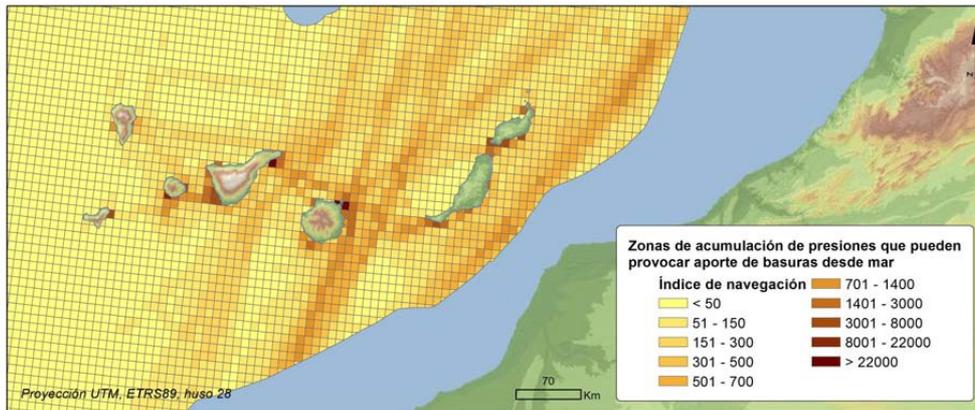


Figure A6.4: Pressure accumulation zones caused by the discharges from sea. (Image from: Ministry of Agriculture, Food and Environment, 2012).

According to the information provided by the Canary Islands Government, in the archipelago there are a total of 46 urban agglomerations (only 26 with wastewater treatment plants) of more than 10,000 population discharging water of different nature (e.g. discharges from wastewater treatment plants, facilities for sewage pumping, industrial facilities, seawater desalination). Moreover, a total of 51 emissaries have been registered throughout the archipelago (Figure A6.3), with a length between 5 and 135m, four of them discharging untreated sewage and 10 in poor condition v.

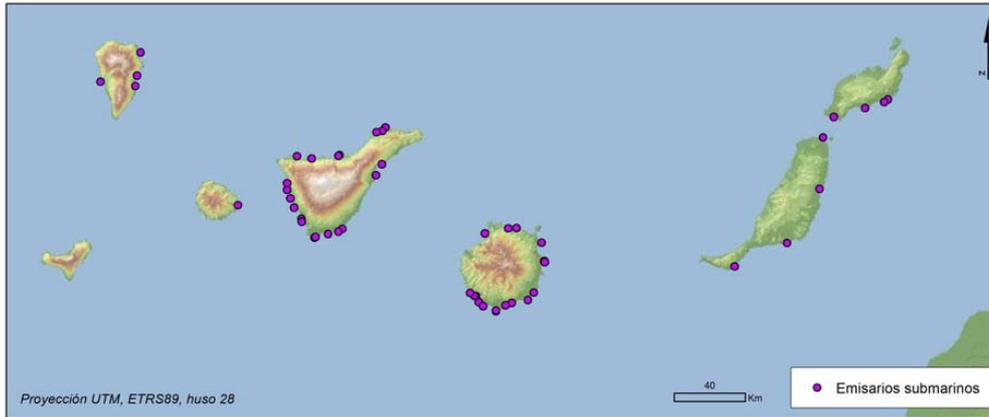


Figure A6.5: Submarine emissaries (pink dots). (Image from: Ministry of Agriculture, Food and Environment, 2012).

Most cetaceans occupy the last link in the marine food chain, making these long-living animals especially sensitive in their tissues to the accumulation of high concentrations of heavy metals, organochlorines and hydrocarbons. A toxicology study conducted on 11 bottlenose dolphins stranded in the Canary Islands (1997-2005) found levels of PCBs and DDTs in liver and subcutaneous fat (blubber) similar to those found in Northern Europe (Carballo *et al.*, 2008). No further studies have been conducted on other species in the archipelago.

A6.2: FURTHER CONSIDERATIONS

Measures to monitor and reduce impacts on the marine environment have been established on a national and European level and developed in a “sector by sector approach”, which has resulted in a not always functional patchwork of policies, legislation, programmes and actions plans at national, regional, and international level. The legal frameworks available that would support further cetacean protection in the Canary Islands are listed in Table A6.1, which shows that the combining of different level of actions within different administrative entities has resulted in a slowing down of their combined functioning. Therefore, harmonising Spanish/Canary Islands efforts should be encouraged to ensure a more effective and agile implementation of the conservation measures established.

In addition, it is necessary to review the effectiveness and the correct application of the existing legislation in Canary Islands, and the reinforcement of some of the established measures.

The presence of a detailed code of conduct, first established in 1995 (Decree 320/1995), for the regulation of the whale-watching activities should have minimised some of the potential negative effects on this population (see for example Bejder *et al.* 2006a, 2006b; Lusseau and

Bejder, 2007). Nevertheless, in recent years the Canary Islands have witnessed a general relaxation of some important aspects:

- the environmental impact study required to start the activity is no longer requested since it was repealed by the Tourism Law of the Canary Islands;
- even though the licence for whale-watching should be renewed every year, the “blue flag” delivered by the Canary Islands Government to identify the licensed operators has not been renewed in recent years;
- Qualified guides are not present on board and are no longer considered a factor for obtaining the licence because there are insufficient personnel available, especially because the last official course offered by the Canary Islands Government to obtain the qualification was in 2007. Moreover, since the educational programme is also no longer requested (even though it is mentioned in the Decree), no standard information presented to whale watching tourists has been required, with a consequent high number of trips offered with relatively low information content (Ritter, 2012).

Therefore, the original legislation should be strictly restored, with some reinforcement of the educational aspects of the trips (presence of a guide), of reduction of the negative impacts of the vessel through more technical and specific craft design (associated with an ecological impact study), of the decrease of whale-watching pressure by limiting the number of active vessels based on time scale (time of day, days per week, etc.). The patrolling service, active only until 2000 in southwestern Tenerife, should be implemented in all the archipelago, through direct monitoring by boat or flights, incognito observers and/or land based observation platforms to monitor the whale-watching vessels but also the recreational private boats, and the increasing jet ski, divers, para-gliders towed by boats, etc., that illegally develop the activity. Moreover, increasing the quality of the whale watching experience is strongly recommended, through more informative narrative during or prior to the trips, and through further collaboration with research and educational entities.

The Canary Islands have experienced an increase in inter-island marine traffic, including medium, fast and high-speed ferries, which may represent an important threat to the well-being of cetaceans and other marine life. In parallel, an increasing number of collisions have been documented in the archipelago (Carrillo and Ritter, 2010). Speed limits have been proposed for all ferries and other sea-going crafts to not exceed 13 knots inside the MPA in La Gomera (Carrillo and Ritter, 2010). This limitation should be extended to all the areas characterised by a high density of cetacean and other anthropogenic activities (fishing, whale-watching, etc.). The underwater noise from shipping traffic would be also reduced by the introduction of this speed limit.

The Sensitive Sea Areas established for the Canary Islands (PSSA), with the identification of zones with different level of vessel usage provide a strict regulation of boat traffic in these waters. The application of this zonation, and the introduction in 2010 of the automatic identification system for vessels and their route characteristics, made the application of this regulation easy to monitor. Nevertheless, the construction of new harbours (as in Granadilla, in the southeast of Tenerife), will introduce new inter-island routes of medium-large sized

vessels, leading to a need to review the general transit dynamics and the delineation of the restricted areas.

Based on Law 37/2003 (Table A6.1), and the growing concern due to the increasing sources of underwater noise (vessels of all kinds, general construction works, hydrocarbon exploration, military activities, acoustic harassment devices, etc.; Law 21/2013), continuous updating and detailed acoustic mapping of the Canary Islands waters is highly advisable, to detect the most sensitive areas in the archipelago.

Table 6.1: Legal framework for cetacean protections in Canary Islands.

LEGAL FRAMEWORK	DESCRIPTION
Annex IV, Habitats Directive	All species of cetacean are designated as being in need of protection
National Catalogue of Threatened Species	(Short-finned pilot whales is listed as "Vulnerable")(Table A6.2)
Canary Islands Catalogue of Threatened Species	(Short-finned pilot whales is listed as "Vulnerable")(Table A6.2)
Royal Decree 178/2000	on the regulation of the whale-watching activity in the Canary Islands
Royal Decree 1727/2007	about the establishment of measures for cetacean protection
Law 42/2007	Natural Heritage and Biodiversity, on the prohibition of developing any action with the objective of killing or harassing the species included in the LESRPE list (Table A6.2), as well as destroying or damaging feeding or resting areas
Law 4/2010	on the Canary Islands Catalogue of Protected Species (without contradicting the national law), where the sperm whale is included in the category of vulnerable species while the other species refer to the category included in the national catalogue
Royal Decree 139/2011	to develop the List of Wildlife Species with the corresponding conservation measures and the Spanish Catalogue of Endangered Species
Real Decree 1274/2011	which proposed the establishment of MPAs and RN2000 areas in the marine environment and ensured consistent management of marine species and habitats especially in relation to underwater noise as a threat to biodiversity
Law 37/2003 (Royal Decree 1367/2007)	with the objective of reducing the acoustic contamination that might cause significant effect on humans, properties, and environment
Law 41/2010	on the Protection of the Marine Environment
Law 21/2013	to evaluate the impact that public or private projects might have on the environment

The compliance of all the actions legally established by the Public Administration relating to the management of the activities affecting the Canary Islands waters should be revised and implemented effectively where not applied, starting with the urban and vessel discharges and waste into the waters. Moreover, further monitoring should be considered to prevent and

control water pollution and to promote the maintenance and updating the Specific Plan for Marine Pollution Contingency of the Canary Islands Government on the potential impacts on cetaceans.

Education, public awareness, and further implication of the different stakeholders should be also undertaken: intergovernmental and national authorities, scientists from several disciplines, representatives from industry, local communities, and interested NGOs.

On the other hand, all stakeholders (Canary Islands Government, general public, schools, etc.) should take advantage of this species, using it as a 'flagship' to the protection of the entire ecosystem, either throughout educational events or specific legislation. Increasing public awareness would also lead to a direct deeper involvement in the conservation activities, and in the respect of the present legislation.

Table A6.2: Cetacean species' status in the Canary Islands.

SPECIES	CATEGORY 2001 a	CATEGORY 2010 a	IUCN RED LIST STATUS (2008) b	LESRPE
Blue whale <i>Balaenoptera musculus</i>	in danger of extinction	vulnerable / special protection*	endangered	
Sei whale <i>Balaenoptera borealis</i>	in danger of extinction	vulnerable / special protection*	endangered	
Fin whale <i>Balaenoptera physalus</i>	in danger of extinction	vulnerable / special protection*	endangered	
Common minke whale <i>Balaenoptera acutorostrata</i>	vulnerable	vulnerable / special protection*	least concern	
North-Atlantic right whale <i>Eubalaena glacialis</i>	in danger of extinction	in danger of extinction	endangered	
Humpback whale <i>Megaptera novaeangliae</i>	of special interest	of special interest	least concern	
Sperm whale <i>Physeter macrocephalus</i>	vulnerable	vulnerable	vulnerable	
Short-finned pilot whale <i>Globicephala macrorhynchus</i>	vulnerable	vulnerable / special protection	data deficient	
Common bottlenose dolphin <i>Tursiops truncatus</i>	vulnerable	vulnerable / special protection	least concern	
Risso's dolphin <i>Grampus griseus</i>	vulnerable	of special interest	least concern	LESRPE
Short-beaked common dolphin <i>Delphinus delphis</i>	of special interest	of special interest	least concern	
Striped dolphin <i>Stenella coeruleoalba</i>	of special interest	of special interest	least concern	
Pygmy sperm whale <i>Kogia breviceps</i>	of special interest	of special interest	data deficient	LESRPE
Long-finned pilot whale <i>Globicephala melas</i>	of special interest	of special interest	data deficient	LESRPE
Orca <i>Orcinus orca</i>	of special interest	--	data deficient	
Kogia sima <i>Dwarf sperm whale</i>				LESRPE
Hyperoodon ampullatus <i>Northern bottlenose whale</i>				LESRPE
Mesoplodon densirostris <i>Blainville's beaked whale</i>				LESRPE
Mesoplodon europaeus <i>Gervais' beaked whale</i>				LESRPE
Mesoplodon mirus <i>True's beaked whale</i>				LESRPE
Ziphius cavirostris <i>Cuvier's Beaked Whale</i>				LESRPE

a) Source: Gobierno de Canarias, 2001; 2010.

b) IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded on 20 January 2012.

* The category "special protection" was newly introduced to the 2010 catalogue, which states that it become effective in the case of a downlisting of a species within the National Spanish Species Catalogue (the according national category is given in the first place here)

LESRPE: List of Wildlife Species under Special Protection

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