ABUNDANCE ESTIMATE, SURVIVAL AND SITE FIDELITY PATTERNS OF BLAINVILLE'S (MESOPLODON DENSIROSTRIS) AND CUVIER'S (ZIPHIUS CAVIROSTRIS) BEAKED WHALES OFF EL HIERRO (CANARY ISLANDS)

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Abundance estimate, survival and site fidelity patterns of Blainville's *(Mesoplodon densirostris)* and Cuvier's *(Ziphius cavirostris)* beaked whales off El Hierro (Canary Islands)

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This thesis is submitted in partial fulfilment for the degree of MPhil
at the
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ZcH43 "Anzuelo". Author: CRS.

A mi abuela

¡Atlántico infinito, tú que mi canto ordenas!

Cada vez que mis pasos me llevan a tu parte,

siento que nueva sangre palpita por mis venas

y, a la vez que mi cuerpo, cobra salud mi arte...

El alma temblorosa se anega en tu corriente.

Con ímpetu ferviente,

henchidos los pulmones de tus brisas saladas

y a plenitud de boca,

un luchador te grita

¡Padre!

desde una roca

de estas maravillosas Islas Afortunadas...

Tomás Morales, "Oda al Atlántico"

ABSTRACT

Beaked whales (Fam. Ziphiidae) comprise 22 different species, however due to their cryptic behaviour, information on these species is very limited. Beaked whales appear to be highly sensitive to anthropogenic noise, which can lead to mass strandings. The scarcity of knowledge about the abundance and population dynamics of most beaked whale species impedes the correct assessment of the effects that these impacts have on their populations. Coastal, year round populations of Blainville's and Cuvier's beaked whales were found in El Hierro (Canary Islands) in 2003. Long-term photo-ID studies have been conducted since then using a combination of land and at sea observations. Here I present the first results relating to site fidelity, abundance estimates and apparent survival for Blainville's and Cuvier's beaked whales in the Northeast Atlantic. The number of identifiable adults, i.e. animals with regular to very good photos and recognizable marks in the same area of the body, comprises 69 Blainville´s and 66 Cuvier´s beaked whales. Individuals that were captured in only one year are considered transients (T) while animals seen in multiple years are defined here as recaptured (R). Analysis of site fidelity patterns showed that 35% and 53% of the marked population on Blainville's and Cuvier's, respectively, were recaptured and form island-associated populations with a pattern of residence in the area. In Blainville's, females spend longer periods in coastal waters than males and indeterminate whales (subadults or adult females never observed with calves). Males visit the area during shorter periods and there is an apparent hierarchy in individual male use of the area. Indeterminate individuals seem to emigrate after a 3 year period.

These data coincide with results from Bahamas in showing a higher number of females than males with high site philopatry, and less philopatry in subadults. It has been proposed that these observations in Bahamas could be explained by males fighting for access to the female resident population for polygynous mating, and some subadults leaving the area. In Cuvier’s beaked whales, there is no apparent sexual segregation in the use of the area albeit a low number of calves challenge a robust identification of adult females. More data are needed to define social structure of the Cuvier’s beaked whale population.

Mark-recapture methods were used to calculate abundance estimate and apparent survival in both species. Data was restricted to six years (2010 to 2015) in order to apply open and also closed population models that could account for heterogeneity in the data. Results of closed model estimates (Chapman analysis of two periods pooling data biannually: 2010-2013 and 2012-2015) are robust and provide best estimates corrected by the proportion of marked individuals of 33 (95% CI: 24-46) island associated Blainville´s beaked whales for both periods, and 53 (95% CI: 38-71, for 2010-2013) and 39 (95% CI: 34-44 for 2012-2015) island associated Cuvier´s beaked whales. POPAN open model analyses of the full period provides best estimates of total abundances of 103 (95% CI: 85-125) and 87 (95% CI: 73-103) for Blainville´s and Cuvier´s beaked whales, respectively.

CHAPTER 1

General Introduction

1.1 Beaked whales: generalities

Beaked whales (family *Ziphiidae*) are the second most specious family of cetaceans, with 22 species described to date. Of these, three new species were described in the last two decades (Dalebout et al., 2014, 2002, 1998; Reyes et al., 1991) and a recent finding of genetic divergence in the genus *Berardius* of the North Pacific may raise the number of ziphiid species to 23 (Morin et al., 2017). Regional populations of one studied species, the Cuvier´s beaked whale (*Ziphius cavirostris*), seem to be at least partially genetically isolated (Dalebout et al., 2005). Most beaked whale species can be considered among the least known mammals of the world (Jefferson et al., 2015) and for this reason the majority of ziphiids are classified as "Data Deficient" by the IUCN and in national and international conservation laws. The scarcity of knowledge about beaked whales is due to their distribution in deep waters typically far offshore and to their cryptic behaviour; ziphiids are deep diving animals that spend very little time at the sea-surface (Tyack et al., 2006) and this makes their observation challenging. The diving behaviour of ziphiids has been studied in three species of three different genera using animal borne biologging devices: northern bottlenose whales, *Hyperoodon ampullatus*, (Hooker, 1999), and Cuvier´s and Blainville´s beaked whales, *Mesoplodon densirostris*, (Tyack et al., 2006). These three species have a stereotyped diving pattern formed by a long and deep foraging dive, which can be up to two hours duration and 3 km depth in Cuvier´s beaked whales (Schorr et al., 2014), followed by a series of shorter and shallower recovery dives (Tyack et al., 2006). Blainville´s beaked whales are the smallest of these three species and this probably explains why the dives of Blainville´s beaked whales are shorter and shallower than those of northern bottlenose and Cuvier´s beaked whales. Blainville´s foraging dives are on average 50 min long and 900 m depth, and the mean recovery dives are 15 min long and 150 m depth (Tyack et al., 2006). These three species of beaked whales emerge for short periods of generally 2 to 7 minutes between dives (Hooker & Baird, 1999; Tyack et al., 2006) although they can occasionally stay for up to 15-20 min swimming at or near the surface. This behaviour means that studied beaked whales spend very little of their time at the surface, making it difficult to study the distribution, abundance or behaviour of the species using visual methods. This has led to the use of acoustic methods to study beaked whales. Species studied to date are vocally active during some 20% of the time (Arranz et al., 2011) and their vocal activity is concentrated in waters deeper than 200 m (Johnson et al., 2004). This applies to echolocation clicks and buzzes used mainly for foraging and also for communication signals (Aguilar Soto et al., 2012).

The specialized diving pattern of beaked whales, performing similar depth and duration dives as much larger sperm whales, has led to ziphiids being considered “extreme divers” (Tyack et al., 2006) and may explain their apparent high vulnerability to strand in relation to naval sonar exposure (Cox et al., 2006). The use of military sonar and seismic surveys has coincided with mass strandings of beaked whales in several locations (Castellote & Llorens, 2016; D'Amico et al., 2009), such as the Bahamas (Balcomb & Claridge, 2001), the Mediterranean Sea (Frantzis, 1998) and the Canary Islands. In the latter archipelago, mass strandings from 1985 until 2004 were recorded (Simmonds & Lopez-Jurado, 1991; Martín et al., 2004; Fernández et al., 2005a, 2005b;) until a moratorium on the use of naval sonar was established in 2004. Since then, no more atypical mass strandings of beaked whales have been recorded in the Canary Islands (Fernández et al., 2012).

The scarcity of knowledge about the abundance and population dynamics of beaked whales makes it difficult to assess the level of impact that naval sonar and other human threats may pose for these species at a general level or for their local populations. This underlines the relevance of increasing our knowledge about beaked whale populations to inform conservation management of the species, in addition to contribute to the general knowledge about ziphiids. Line-transect visual surveys have been used to study the distribution and abundance of beaked whales in several parts of the world, e.g. offshore California (Moore & Barlow, 2013), the Alborán sea (Cañadas et al., 2005) and the NE Atlantic (Hammond et al., 2002; Hammond et al., 2013). However, the application of line transect survey methods to study beaked whales is challenged by the low detectability of the species. The resulting abundance estimates are typically imprecise due to the rarity of Ziphiidae sightings. This means that the probability to detect even a dramatic reduction in the abundance of Ziphiidae species is considered very low (Taylor et al., 2007).

The low number of beaked whale sightings during surveys, in addition to the difficulties inherent to the recognition of beaked whales to species level in the wild, may result in surveys pooling sighting data from different beaked whale species gathered during field effort (Barlow et al., 2006). For example, line transect surveys in the Pacific yielded pooled abundance estimates for all beaked whales of genus *Mesoplodon*, *Berardius* and *Ziphius* (Barlow and Forney 2007). In spite of these difficulties, these studies have provided highly valuable information about beaked whales, and even uncovered declining population trends of ziphiids in an area (Moore & Barlow, 2013).

Mark-recapture photo ID methods have been used to study populations of beaked whales in some areas where beaked whales are found in deep waters relatively nearshore, or in identifiable offshore areas of high density, allowing long-term monitoring of beaked whales. These studies have been conducted mainly on three species: northern bottlenose whale in the Gully canyon, Nova Scotia (Whitehead et al., 1997; Gowans et al., 2000); Cuvier's beaked whale in the Ligurian sea, Italy (Rosso, 2010) and California (Falcone et al., 2009) and Cuvier´s and Blainville´s beaked whales in the Bahamas (Claridge, 2006; 2013), in Hawaii, USA, (McSweeney et al., 2007; Baird et al., 2006) and the Canary Islands, Spain (Aguilar 2006; this work).

In the following we describe the study species of this thesis. Morphological descriptions are based on Heyning (1989), Mead (2002) and our own observations.

1.2 Study species

1.2.1 Blainville's beaked whale (*Mesoplodon densirostris,* Blainville 1817)

1.2.1.1 Characteristics and life history

Blainville's beaked whale reach a maximum length of 4.7 metres and 1000 kilograms in weight (e.g., Mead, 1989; Pitman, 2002). Adult females can be slightly larger and heavier than males (MacLeod, 2006) and give birth to calves around 2 metres long weighing 60 kilograms (Pitman, 2002). A striking feature of this species is the massive pair of teeth growing in the middle of the lower jaw of adult males, where the strongly curved lower jaw raises above the upper jaw (Heyning, 1984; Besharse, 1971). Only the tips of the teeth erupt, often getting covered in stalked barnacles (*Conchoderma*). The mouth of the females is less curved and has no erupted teeth (McCann, 1963; Besharse, 1971). The beak is long and usually breaks the water ahead of the body when the whales surface to breath. Adult males have a highly scarred body with linear scars from teeth rakes (McCann, 1963; Heyning, 1984; Heyning, 1989; Mead, 1989) and circular scars produced mainly by cookie cutter shark bites (*Isistius*) (McCann, 1963). There is strong sexual dimorphism and the presence or absence of linear scars, erupted teeth, and an associated young animal, are used in the wild to assess the age and sex of the whales (see section 2.3.3). Blainville´s beaked whales can be grey or brown, with a lighter ventral side and numerous patches of yellowish diatoms on the skin. All or just the tip of the lower jaw can be white, while some adult males have white patches in the top part of the curve of the mouth, where the teeth erupt (Heyning & Mead, 1996). The skin around the small eyes is dark. Newborn calves are grey dorsally and lighter ventrally, with a relatively short beak that can be white in the lower jaw (Ross et al., 1988; Jefferson et al., 2008). There are no data on the age or length of sexual maturity for males. For females, it is thought that they become mature around nine years old (Ross, 1979; Mead, 1984; Claridge, 2013; Reyes et al., 2011)). Calves are 40 to 50% of their mother's size; the length of the largest foetus and of the shortest calf reviewed by Mead (1984) were 190 and 261 cm, respectively. The longevity of this species is unknown. One individual of other Mesoplodon species (*M. europaeus)* can live until 48 years old (Mead, 1989), although this may be an underestimation of the maximum longevity of the species given the small sample size available.

The mating and social structure of Blainville's beaked whale has been defined as polygynous (harem groups) and polyandrous (females associated with different males for successive calves), and fitting a fission-fusion strategy (Claridge, 2006). For mating, they form harem societies in which a single male accompanies a group of two or more adult females, often with their offspring (Claridge, 2006). The same group of females tends to remain together at least during one breeding period to split and re-join with different females for the next calving period (Reyes et al., 2011). During the calving period, females may be associated with different single males (Reyes et al., 2011). Why these males do not remain in the group is unknown but intraspecific scarring on their bodies suggests that the reason could be male-male aggression to gain access to females, in which case the paternity of calves cannot be inferred from accompanying males of females with calves (Hooker et al., 2002). Genetic studies are being carried out by research groups in the Bahamas and the Canary Islands to determine the paternity of calves and other characteristics of the social structure of Blainville´s and Cuvier´s beaked whales, and to assess individual genetic relatedness of whales within and between areas where high site fidelity has been observed for these species.

1.2.1.2 Distribution and abundance

Blainville´s beaked whale is the best known and the widest distributed species of the speciose genus *Mesoplodon*. This is because the species occurs reliably in some areas (Hawaii, Bahamas, Canary Islands), enabling long-term photo-identification studies (Claridge, 2006, 2013; McSweeney et al., 2007; and this study). However, it is still listed as “Data Defficient” in the IUCN Red List (IUCN, 2012). It inhabits the temperate and tropical waters of all the oceans (Mead, 1989), including some enclosed seas with deep waters such as the Gulf of Mexico, the Caribbean Sea and the Sea of Japan. It is, however, defined as “vagrant” in the Mediterranean Sea, with only a few documented sightings (IUCN, 2012). As other ziphiids, Blainville’s beaked whales habitat is defined by deep-water environments (Macleod et al., 2006).

1.2.2 Cuvier’s beaked whale *(Ziphius cavirostris*, Cuvier 1823)

1.2.2.1 Characteristics and life history

Cuvier´s beaked whales are medium sized whales relative to other toothed whales. However, they are among the largest of their family, the ziphiids, with a maximum weight of 3000 kilograms and an average maximum length of 6.3 meters, both for males and females (Mead, 2002). The size of beaked whales makes them larger than all delphinids except the orca (killer whale). A Cuvier's beaked whale's body is torpedo shaped, with a small and falcate (curved) dorsal fin located at the beginning of the last third of the body. The head forms a continuum with the sloping melon and the relatively short beak. The beak is often seen first when the whales break the surface to breathe and can sometimes be deformed. The mouth is slightly curved and in adult males it has a pair of small teeth at the tip, often with parasites visible (*Conchoderma auritum*) (Pringle, 1963; Ross, 1984). There may be up to 18 other vestigial teeth in the lower jaw (Fraser, 1936). There is sexual dimorphism among adults: females and immature males do not have erupted teeth (Heyning, 1989) and photographic records of apparent adult whales without erupted teeth, re-sighted years later with visible teeth, suggest that teeth may erupt late when males have reached adult size, complicating the differentiation of sex in the wild. Cuvier´s beaked whales do not rely on their teeth for foraging but suction-feed, and suction is aided by a V-shaped pair of gular grooves in the lower side of the mouth (Heyning and Mead 1996).

Colouring is very variable, ranging from dark grey or brown to light grey and largely white. Most whales have yellowish brown patches of diatoms, sometimes covering large parts of the body. The colour can be mostly uniform, except for the head, which is often clearer from the blowhole and can be white up to the beak (Heyning & Mead, 1996). However, it is more common to see marked coloration patterns, e.g the white coloration can extend to the dorsal, leaving the sides, fin and caudal peduncle with a darker colour (Heyning & Mead, 1996). Dark patches around the eyes are common. Newborn animals are very dark grey dorsally and lighter grey ventrally but become lighter grey with dark eye patches as juveniles (Leatherwood et al., 1982; Heyning, 1986; Heyning & Mead, 1996). The most evident sign of sexual dimorphism in the coloration is the extended scarring typical of adult males. Linear white scars are consistent with teeth raking, presumably from male-male fights for access to females, and round scars are from cookie cutter sharks (*Isistius*) or lampreys (Heyning, 1986; Heyning & Mead, 1996). White scar tissue in the wounds and the rake scars may function as male advertisement (MacLeod, 1998). Females and immature whales may also have some rake scarring but this is much less common than in males.

Cuvier´s beaked whales tend to occur in small groups (one to six whales) but group sizes as large as 11 individuals have been reported (Scalise et al., 2006). Groups can include females with or without their offspring, immature whales and young, and one or more adult males (McSweeney et al. (2007)). Abundant rake scars suggest that males come together to fight, presumably for access to females (Heyning, 1989). The dense and heavy rostrum in adult males probably serves to strengthen the skull for these fights. There are no data on the age of sexual maturation for this species, although this occurs at an average body length of 5.8 meters in females (as low as 5.13 meters) and 5.50 meters in males (Mead, 1984). The estimated length at birth is 2.70 meters (Mead, 1984). There are no data on inter-calving intervals or seasonality but observations suggest that the reproductive rate may be low. The maximum number of cemented layers found in teeth of Cuvier´s beaked whales (assumed to correspond to annual growth layers) is 62 (reviewed in Heyning, 1989).

1.2.2.2 Distribution and abundance

Cuvier's beaked whale is the most widely distributed of the beaked whale species (Heyning, 1989). It inhabits all oceans from the tropics to subpolar regions between *c.* 60ºN and 55ºS (Jefferson et al., 2015) and it is the only beaked whale recorded regularly in the Mediterranean Sea (Podestà et al., 2006). Molecular genetic analyses have determined that the species forms a monophyletic group globally distributed, with a high degree of differentiation between the North Atlantic and the Mediterranean populations (Dalebout et al., 2005). The Mediterranean cluster shows a lower haplotype diversity suggesting a relatively small and isolated population (Dalebout et al., 2005). The lack of sightings in the Strait of Gibraltar (Cañadas et al. 2005), an area highly surveyed, supports this hypothesis. There are no data on the global abundance of the species but its cosmopolitan distribution and the results from studies in localised areas has led the IUCN to estimate global abundance of Cuvier´s beaked whales as 100,000 or more individuals (IUCN 2017). The IUCN classifies Cuvier´s beaked whales as "Least Concern" and CITES lists this species in its Appendix II.

1.2.2.3 Social structure

Despite being the most cosmopolitan of the ziphiids, little information exists about the social structure of Cuvier's beaked whales. This is partly due to the difficulties in determining sex and age of individuals in this species. The teeth of males are small and their location at the tip of the lower jaw reduces the opportunity to record teeth presence in photographs. Scars from cookie cutter shark bites can be used as indicative of age/sex class in places where these sharks are common (e.g. McSweeney et al. 2007). Consistent association with young is used to identify females, but Cuvier´s beaked whales are born large with respect to the mother, and it is often difficult to assess size during sightings.

McSweeney et al. (2007) analysed 10 years of data from a resident population off Hawaii and observed multiple types of associations, ranging from mother-calf dyads, to male-female pairs, to groups of males and females. Similar variability has been observed off El Hierro, where mother-calf dyads have been observed alone or associated with other mother-calf pairs, sometimes with adult males. Mother-calf pairs and other adults of unknown sex can be found in groups of five or more whales, which sometimes include adult males (C. Reyes unpublished data).

Long-term individual associations have not been reported for Cuvier´s beaked whales except for mother-calf pairs, which have been documented for up to 2 years off Hawaii (McSweeney et al., 2007) and 3.5 years off El Hierro (Reyes et al., 2014). A male-female dyad instrumented with satellite transmitters in Hawaii showed that these animals were associated for eight consecutive days (Schorr et al., 2010). This is consistent with observations off El Hierro, where Cuvier's beaked whales seem to show a fission-fusion social pattern where animals may separate and re-join between dives with others animals in the vicinity (C. Reyes unpublished data).

1.3 Thesis overview

This thesis analyses a long-term photo-ID dataset of Blainville´s and Cuvier´s beaked whales gathered in the coastal deep waters off El Hierro, the most pristine of the Canary Islands. Chapter 2 presents the methods used for data collection and data analysis. Chapter 3 explores patterns of site fidelity of both species, as well as differences in the use of the study area among sex/age classes (types) within each species. Chapter 4 applies mark-recapture analytical models to estimate the number of individuals of each species using the study area and their survival rates (termed local populations hereon). A general discussion is presented in Chapter 5.

CHAPTER 2

General Methods

2.1 Characteristics of the study area

The research area was located off El Hierro island, the westernmost, youngest (1.2 m.a.) and smallest (270 km^2) of the Canary Islands archipelago (Guillou et al., 1996). El Hierro is the summit of a high volcano originating from a “Mercedes star” rift system (Carracedo et al., 2012). Its origin was followed by a number of massive landslides on the rift flanks, which gave the island its characteristic trilobular shape formed by three large bays separated by high points: the bays of El Golfo, at the North; Las Playas, at the East-South East; and Las Calmas, at the South-South West (Figure 2.1). The volcanic raising of El Hierro from the deep oceanic floor created steep slopes (>20º) in the submarine contour of the island, where depths exceeding 1000 m at 1-2 nm from the shore can be found around most of the insular perimeter (Gee et al., 2001a; Gee et al., 2001b;).

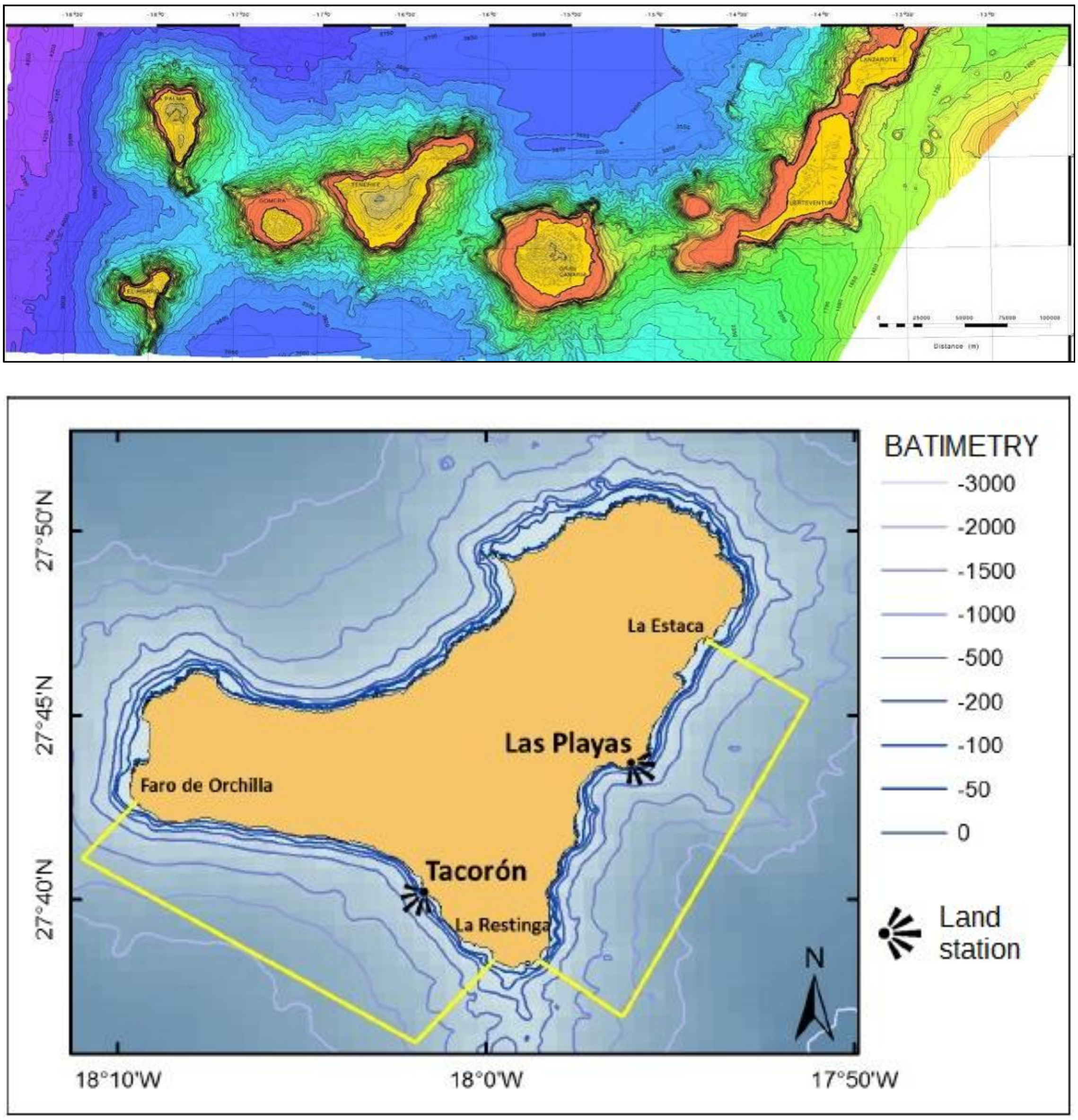

Figure 2.1 Study area: map of the bathymetry in the Canary Islands and map of El Hierro showing the observation points at coastal cliffs used in this study, and the marine area surveyed from each point. Source: J. Acosta (IEO) & Sanchez-Mora, A. 2016.

The altitude of El Hierro (1501 m, Carracedo et al., 2012) acts as a shelter from the South-West flowing Canarian Current and trade winds that dominate the marine and atmospheric circulation of the archipelago. The result is that most of the year there is a lee area at the southwest of El Hierro: the Bay of Las Calmas, delimited by wind lines and relatively isolated from the general oceanographic dynamics. In addition, the “island effect” generates eddies that act at a mesoscale level and enrich the otherwise oligotrophic waters of El Hierro (Braun and Molina, 1984).

The waters of El Hierro can be considered semi-pristine thanks to the near absence of chemical and acoustic pollution and to the maintenance of healthy marine biological communities exploited only by small scale artisanal fisheries. For these reasons, El Hierro has been proposed as a candidate Marine National Park. The bay of Las Calmas holds a Marine Fisheries Reserve and a Special Area of Conservation protected under the Habitats Directive. In addition, El Hierro is included in two important archipelagic marine conservation measures: i) a moratorium on the use of naval sonar within 50 nm of the archipelago, declared in 2004 by the Spanish Government to protect beaked whales and other cetaceans (Fernández et al., 2012; Fernández et al., 2013) ii) the Particularly Sensitive Sea Area of the Canary Islands declared by the International Maritime Organization and limiting the navigation of large ships around El Hierro.

2.2 Field effort

Data were collected between 2003 and 2015 in 45 field seasons conducted off El Hierro. Each field season lasted from 1 to 15 days of daily boat surveys, summing to a total of 436 days of study at sea. Field effort and photo-ID sample sizes were not homogeneous throughout the study period (Figure 2.2.): in 2003, photo-ID data were collected only as ancillary data using analogue photographic cameras. This resulted in a small sample size of photo-identified individuals in spite of a relatively high number of days of field effort (23). In 2006 only 8 days at sea were achieved due to funding limitations. To avoid potential bias resulting from different methodologies used in different years, and large variations in sample size, years 2003 and 2006 were removed from the analysis. The remaining data encompass the period between 2004 and 2015, totalling 405 days of effort at sea with an average of 37 days at sea per year. Data were gathered in short (one week) monthly field seasons in 2004 and 2005, and in longer (>10 days) field seasons from 2007 onwards. All data were analysed according to season of the year and pooled into years for some analyses. Due to weather conditions, the winter season of 2015 was cancelled and the other seasonal field seasons of the year were extended by five days each. In 2011, the eruption of a submarine volcano 1.5 miles off the south of El Hierro

(Fraile-Nuez et al., 2012), reduced the number of total effort days to 18.

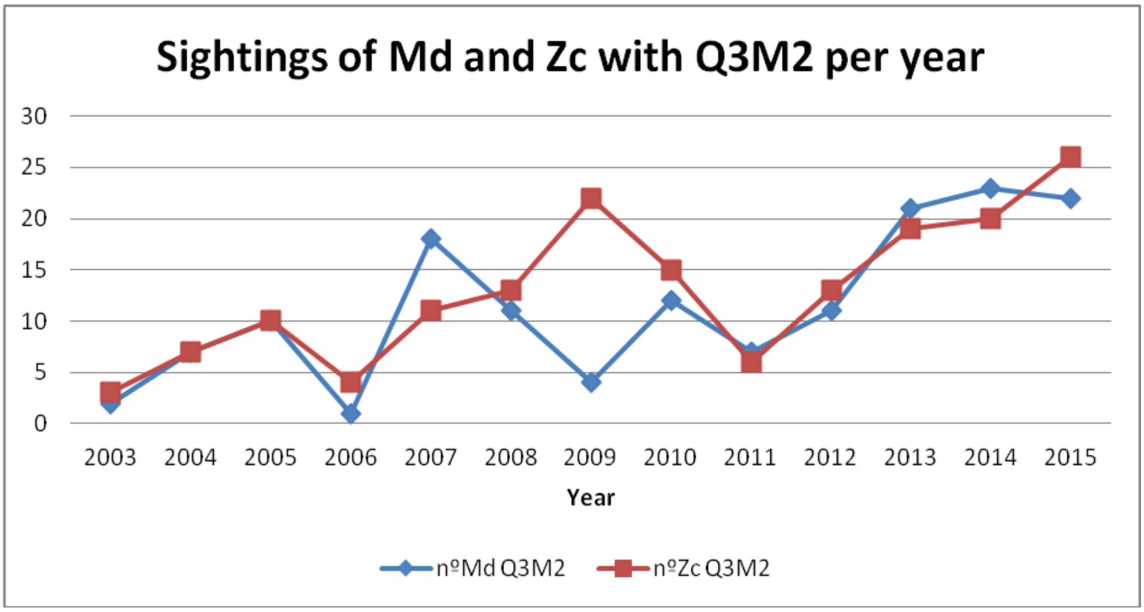

Figure 2.2 Number of individuals of Blainville's and Cuvier's beaked whales with recognizable marks (section 2.4) captured during all the study years (2003 to 2015).

2.3 Data collection

The presence of coastal cliffs and the proximity of deep water close to the shore at El Hierro enabled survey of beaked whales and other cetaceans from land (Arranz et al. 2014), greatly improving the detection rate. Observers on land guided a small boat towards the animals to gather photo-ID, group composition and behavioural data. As far as we know, El Hierro and the Azores archipelago are the only study areas where beaked whales are surveyed from coastal observation stations.

2.3.1 Land stations

Two observation land stations were established on El Hierro to cover two of the three bays of the island: i) Tacorón, located 119 m above sea level in the SW bay of Las Calmas (Figure 2.2); and ii) Las Playas, at 92 m height in the SE bay of Las Playas.

The north bay of the island was discarded due to general bad sea state (Beaufort >4) throughout the year. Sighting effort was performed from one of the observation stations and this station was chosen each day depending on sea state conditions. The bay of Las Playas, which is more affected throughout the year by the trade winds, was prioritised when sea conditions allowed surveying in this bay.

Each observation station was operated by four observers: two used small binoculars (Fujinon 7x50) and each one surveyed half of the field of view of the bay, concentrating effort in waters close to shore (up to some 1.5-2 nm); another observer used long-distance binoculars (Fujinon 15x70), to survey more offshore waters of the bay; the fourth observer took a data-recording/resting position to record data in real time in a computer and guide the boat towards the sightings using VHF radio. Personnel rotated each position every thirty minutes. Binoculars were equipped with compass and reticules to obtain horizontal and vertical angles to the sighting, in order to derive the geographic position of the sightings in real time using software Logtool (M. Johnson, Univ. of St Andrews), programmed in MATLAB and specially designed for this study. Logtool stored data from the sightings (group code, species, nº animals, behaviour, etc), and plotted in real time the locations of the sightings, derived from the reticule and compass data from the binoculars. Also, Logtool plotted in real time the position of the boat, received at the computer from a VHF linked GPS. Tools in Logtool provided course and distance from the boat to the sighting, allowing the observers to guide the boat towards the animals effectively. These tools were especially important to increase the success of the boat to approach beaked whales with short surfacing intervals interspersed by long diving periods.

2.3.2 At-sea sampling

From 2003 to 2008 a 4.5 m inflatable boat was used to approach the whales. From 2008 onwards this was replaced by a 6 m fibre glass boat. The team onboard consisted of four to five researchers: one skipper and observers to survey visually for cetaceans and gather data from each encounter. In 2003, pictures were taken with analogue cameras. From 2004 onwards, these were upgraded to digital cameras: Canon 30D (1) and Canon 60D (2), equipped with 200 and 300 mm lenses. While not collecting data, the boat covered the bay navigating between the 1,000 and 1,500 m isobaths. Researchers onboard scanned 360º for groups combining the use of 7x50 binoculars with naked-eye survey.

Groups were most often located from the land station. Once the boat approached a group, communication was established among photographers and the skipper in order to obtain photos of as many individuals as possible, independently of the degree of identifiability of an animal (i.e. no preference was given to gather photo-ID data of individuals with more conspicuous marks). When possible, photos of both sides of beaked whales were taken. The encounter ended when the whales dove (usually within 3 min of surfacing - Tyack et al., 2006) or the boat left the whales once as good quality photos as possible had been taken of all the individuals. Photos were examined on the boat to obtain tentative identification matches with previously identified individuals. This was performed by expert observers with years of experience of photo-ID studies of beaked whales at El Hierro, aided by a digital Photo-ID catalogue on a tablet.

After each day of at-sea effort, land and boat-based data were checked for consistency. Photos were separated into the different observed groups of the day and analysed to determine group composition, as well as sex and age-class of photographed individuals (Tables 2.4 and 2.5). A preliminary assessment of the identity of the whales and an assessment of photo quality of the photos was undertaken every day. By doing this we were able to decide if more photos of the same whales were needed in potential new encounters with the same group in consecutive days, in order to optimise photo-ID effort and minimise stress on the animals. This did not introduce a bias in effort of photoID on different whales for this study because data were analysed pooling PhotoID data of the full field season, and further pooled in years for most analyses. After each field season, an in-depth analysis of the photos was carried out (see section 2.3.3).

2.3.3 Photo-identification of beaked whales; www.cetabase.info

Body scars are more reliable identifiable characters for individual beaked whales, than nicks on the dorsal fin or the fluke (Claridge, 2006). Body marks have been shown to last (Aparicio, 2008; McSweeney et al., 2007) for 10 years and more in beaked whales (Claridge, 2012; this study). The photo-ID catalogue at El Hierro contains photos of both sides of the animals and of the full body. We divided the body longitudinally into three regions for analysis (Figure 2.3), so that there was a maximum of six identification photographs per individual (Aparicio, 2008).

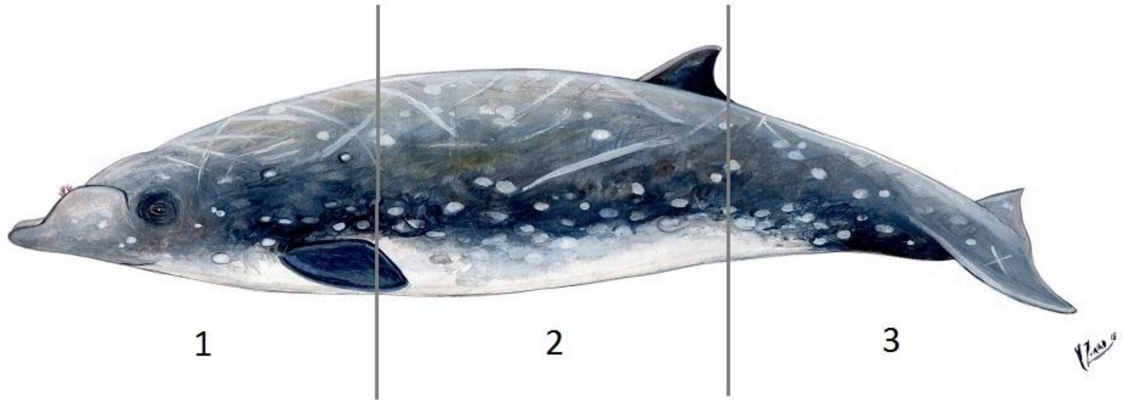

Figure 2.3 Body areas used in this study for photo-ID of beaked whales. 1: anterior zone; 2: medium zone; 3: posterior zone. Drawing courtesy of Chloé Yzoard.

Photos were organised and improved (modifying lighting and exposure) when necessary with software ACDSee. Then, they were categorized based on two different parameters: the quality of the picture "Q" and the marks of the animal "M". The parameter "Q" considered focus, contrast, exposure and angle of the photograph and ranged between 1 and 4, with 1 being the best quality. The parameter "M" was used to classify the type and number of marks, ranging between 1 (no marks) to 4 (animal fully marked). The logic of this classification is that photographs of Q=1 are needed to observe marks M=1 (J. Gordon pers. comm.). Tables 2.1 and 2.2 describe both parameters and provide examples.

Table 2.1 Photo-quality levels (Q)

Q-Level	Description	Example
Q1=excellent	• Sharp image • Close • Good exposure • Focused • Angle parallel	

	• Scars and other marks perfectly distinguishable	
Q2=good	• Less sharp • Might present some gloss/shades • Might be less focused • Angle might be less parallel • Scars and others mark are distinguishable but some details are lost	
Q3=medium	• Not completely focused • And/or bad angle • And/or not sharp • Only conspicuous marks are recognized	
Q4=bad	• Blurry photo • No marks can be differentiated	

Table 2.2 Body marking levels (M)

Level	**Description**	**Example**

M1	• Animal with no marks	
M2	• Animal with few marks	
M3	• Animal with many marks and/or specially distinctive fin notches	
M4	• Animal covered by marks.	

A unique identification code was given to each recognised individual. For individuals with identifiable marks, the code was composed of the initials of the species (“Zc” or “Md”), the location (“H” for El Hierro) and an individual number assigned in order of capture (e.g. ZcH1: first Cuvier’s beaked whale recorded in El Hierro). Individuals with excellent to regular quality photos (Q=1-3), but no identifiable marks (M=1), were classified as “X” (e.g. ZcHX1). Calves and juveniles received a combined code formed by the code of their consistently accompanying whale (presumably their mother), a “C” for calf, and an individual letter. The letter indicated the order of the calf in their mother’s offspring (e.g. MdHC22a: where “a” indicates that this is the first calf (C) recorded for individual MdH22). Individuals that had been followed from first sighting as calves/juveniles until they were independent individuals were assigned a new code that included a "Z" (e.g. MdHZ3: third Blainville's beaked whale followed from calf/juvenile to independent individual). A summary of these codes is presented in Table 2.3.

Table 2.3 Codes used for the photoID catalogue.

TYPE	CODE	EXAMPLE
Marked	General code: spp+locality+number	MdH1
Unmarked	General code + X	MdHX1
Calf/Juvenile	Companion code + C + letter	MdHC1a
Calf/Juvenile to Independent	New general code + Z	MdHZ1

2.3.3.1 Determining sex and age-classes:

Sex and age-class of individuals were assigned following the classification described by Aguilar Soto (2006), Claridge (2006, 2013), Heyning (1989), Mead (2002), and modified by observations made during this study. These characteristics are summarised in Table 2.4 and 2.5 for Blainville's and Cuvier's whales respectively, with personal observations marked as (*):

Table 2.4 Classification of sex and age classes of Blainville´s beaked whales

TYPE	CHARACTERISTICS	PICTURES
Adult male	• Adult size • Heavily arched lower jaw	

	• Pair of erupted teeth • Very numerous linear scars in the rostrum and first third of the back	
Subadult male	• Adult size • Arched lower jaw without erupted teeth • Some linear scars in the rostrum area and first third of the back	 
Adult female	• Adult size • Long arched beak without erupted teeth (and less arched than males) • Seen at least twice in close association with a neonate, calf or juvenile • Some linear scars	 
Indeterminate **/Unknown**	• Adult size • Only slightly arched mandible • Not seen in close association with any neonate, calf or juvenile • May have linear scars	

Juvenile	• ¾ of adult size • Associated to the group of the mother but frequently swimming independently (*) • Few or no scars • Between 1-2 years-old to up to 3-4 years-old (*)	 
Calf	• ½ of adult size • No foetal folds • Shorter beak than adults • Usually no scars • Swimming in close association with a companion adult regularly (assumed mother) (*) • Between neonate to an estimated 1 year old (*)	 
Neonate	• ~1/3 of adult size • With marked foetal folds • Creamy-pinkish lower jaw • Short beak • No scars • Swimming in close association with a companion adult regularly (assumed mother) (*)	 

	• From birth to an estimate of about 6 weeks old • With blaze dorsal fin and dark border	

Table 2.5 Classification of sex and age classes of Cuvier´s beaked whales

TYPE	CHARACTERISTICS	PICTURES
Adult male	• Adult size • Pair of erupted teeth in the tip of the lower jaw • Heavy linear scars along all the body • Light grey or brownish, often with white colouration patches at the head and dorsum	 
Adult female	• Adult size • Seen at least twice in close association with a neonate, calf or juvenile • Usually some scars along all the body • Light grey or brownish	 
Indeterminate/ Unknown	• Adult size or similar Without erupted teeth • Not seen in close association with any neonate, calf or juvenile • Light grey or brownish	

	colouration, it may have a light coloured beak.	
Juvenile	• 3/4 of an adult size • Visible beak and forehead • Associated with its accompanied adult but can swim independently when in a group • Might have few scars or none • Light-grey or brownish coloration	 
Calf	• ½ of an adult size • Small beak and some forehead noticeable • No foetal folds • Usually no scars • Swimming in close association with its accompanied adult • Light grey or brownish colouration	 
Neonate	• ~1/2 of an adult size • With foetal folds • Shorter beak and total lack of forehead • No scars • Swimming in close association with its accompanied adult	 

	• Light grey or brownish colouration	

2.3.3.2 www.cetabase.info:

The best and most up to date photos of each individual were uploaded to the online and open access catalogue www.cetabase.info, run by ULL since 2010 (Reyes et al., 2012). Cetabase was programmed using open software, building a database-intensive web application using */PHP and MySQL/* development technologies. The chosen web server has a Debian GNU/Linux OS to guarantee system stability. Cetabase is based on a logical database structure to store all the information from the sightings and the individual animals. This logic structure allows data to be linked according to defined data-fields and enables further expansion of the structure in an ordered manner. It also enables further expansion of the analytical capabilities of the database, by allowing the programmer to design flexible queries to extract parts of the data and export results in user friendly formats, such as comma separated tables of jpeg images, as they are required by the users. The advantage of using a web application is that the server makes all the programmed analytical tasks once the data are entered in the database. All data are centralized and a periodic back-up in the server guarantees the security of the information, while updates are accessible to users in real time.

Information of all sightings was entered into Cetabase with photo-ID data of the individuals, including the Q and M of each sighting. This enables the user to apply filters to the data in order to select only those animals photo-captured with chosen thresholds of Q and M. Then, Cetabase generates csv files with the results, as well as txt files in program MARK format, ready to use for population abundance estimates (Reyes et al., 2012).

2.4 Population studies

2.4.1 Defining population

In this study we define the populations of Blainville´s and Cuvier´s beaked whales as the whales of these species that use the study area off El Hierro, without implying genetic isolation of these animals with respect to whales in neighbouring areas.

2.4.2 Sighting frequency distributions and re-sighting rates

Site fidelity patterns of the whales were investigated by comparing individual sighting frequencies. This analysis was performed for the full marked populations (see 2.4.3 for the definition of marked individuals) and also separately for different age/sex classes. The results showed a clear distinction between whales observed in one or more of the years of study. Based on these results, in this study we classified individuals as recaptured (R) if they had been observed in two or more of the years of study, and transient (T) for animals observed in only one year. This distinction does not exclude the possibility that animals classified as T may become recaptured if the study continues in time. This source of bias will increase for T individuals observed for first time towards the end of the study period and to examine this bias we quantified the lagged identification rate values for both species.

For recaptured whales, re-sighting rates among seasonal field cruises (short-term site-fidelity) and among calendar years (long-term site-fidelity) were examined throughout the selected 12 years of the study period. The results of these two analyses showed little difference for both species (Tables 3.1. and 3.2). This means that animals observed in only one year were often observed in only one seasonal cruise of that year, while animals observed in different seasonal cruises were nearly always observed in more than one year also. Based on these results, we established the sampling unit as year to increase capture rate. Whales were classified as transients (T) when they were captured in only one of the study years and as recaptured (R) when observed in more than one year.

2.4.3 Marked population

The adult/subadult marked population used for analyses in this study was defined as whales of adult size and body marks in the same area of the body ranging from few marks (M=2) to animals covered by marks (M=4) (see Table 2.2). Poor quality photos (Q=4, see Table 2.1) were excluded from the analysis. The body area with the largest number of individuals fulfilling these filters was selected for further analysis. The application of these filters resulted in 69 individual Blainville's beaked whales for the anterior-left body area (L1) and 66 individual Cuvier´s beaked whales for the medium-right body area (R2). Based on these results, site-fidelity and population abundance analyses were done using body areas L1 for Blainville's and R2 for Cuvier's. Whales with M=1 were classified as unmarked and not used for abundance estimation analyses. Then, abundance estimates were corrected by the proportion of marked whales in the population (see section 2.5.7).

Using individuals with regular marking (M=2) for photo-ID analysis might bias the results if whales with regular marks were not recognised in subsequent sightings and were thus allocated new codes in the catalogue, resulting in an artificial inflation of the number of whales with M=2 classified as transients. To investigate this possibility, we compared the recapture rate of animals with different levels of M, from very good (M=4) to regular (M=2). Data were explored graphically considering the sex-age classes of the individuals. In addition, a binomial Generalised Linear Model (GLM) with a logit link function was used in software R (R Core Team, 2016) to evaluate the influence of marking level and sex/age class on the classification of individual whales as transient or recaptured (T/R ~ Type + Mark level). This analysis was performed independently for Blainville´s and Cuvier´s beaked whales.

2.4.4 Goodness of Fit analysis of heterogeneity in individual capture rates

Previous photo-ID studies of beaked whales show that individuals may use local study areas with very different regularity (Claridge, 2013) and this may introduce heterogeneity in individual capture probabilities. In this study of beaked whales off El Hierro we performed Goodness of Fit (GOF) analyses to evaluate how models fitted capture histories of Blainville´s and Cuvier´s beaked whales considering different sources of heterogeneity of capture probability. GOF analyses were performed with program U-CARE (Choquet et al., 2009) independently for each study species. The models tested in U-CARE can be affected by low sample size and high variability in individual capture histories. For these reasons, this GOF analyses is used just as an indicator of the occurrence of heterogeneity in the data, albeit results showing absence of heterogeneity do not firmly exclude that this source of bias may be affecting the results. In addition, we also used program CAPTURE (within program MARK, White and Burnham 1999) to test further for potential effects of heterogeneity on the results.

2.4.5 Assumptions of mark-recapture models

Basic assumptions of capture-recapture analysis (summarized in Hammond, 1986, Hammond, 2010) are that i) animals are individually identifiable using marks; ii) marks are permanent at least for the duration of the study period; and iii) marks are correctly recorded and reported. Also, the general assumption of simple models is homogeneity in capture probability, although more advanced models are robust to the under-estimation bias in abundance introduced by individual heterogeneity. This is only available in models developed for closed populations (Otis et al., 1978) and not in models developed for open populations. A population is defined as closed for the study period when there are no births or deaths in the marked part of the population, nor permanent immigration of emigration to or from the study area in this period (Schwarz and Seber, 1999). An open population can experience both emigration and immigration, as well as births and deaths. Assumptions of closed populations do not hold for long-term studies, but the bias introduced by using closed population models on open populations can be limited when the study period is short in relation to the generation time of the study species. Applying closed models to open populations overestimates abundance, while applying open models to data series with heterogeneity underestimates abundance (Kendall, 1999). For these reasons, open population models produce a more conservative estimation of abundance. However, open populations are more sensitive to low sample size and often do not converge when applied to small datasets, even when these can be analysed with closed models. In addition, open models tend to provide results with large confidence intervals, and this sometimes reduces the usefulness of the results to inform conservation and management.

To fulfil the assumptions of mark-recapture, only adult/subadult animals with recognisable marks were used for the analysis of this work. Different models were applied to the full dataset to estimate the total abundance of the populations (N_{Tot}), and to the subset of recaptured individuals to estimate the abundance of recaptured animals with higher site-fidelity to El Hierro, which we term "island associated animals" (N_{IA}). The models used in each case are explained below:

2.4.6 Models tested in this study

Open population models (Jolly-Seber -JS-, Cormack Jolly-Seber –CJS- (Cormack, 1964, Jolly, 1965, Seber, 1965) and POPAN) and the Robust Design model -RD- (Pollock, 1982, Kendall et al., 1995, Kendall et al., 1997), which combines open population assumptions among encounter occasions (years) and closed population assumptions among sub-samplings (seasons), were initially applied to attempt to estimate N_{Tot} and N_{IA}. However, many of these models did not converge due to the low sample size of the dataset.

Closed population models (Otis et al., 1978) where used for temporal subsets of the dataset to reduce the bias due to using closed models on long-term data series. To increase sample size when estimating N_{IA} data gathered in pairs of consecutive study years were pooled as a single capture occasion (Tables 4.3 and 4.6).

2.4.7 Proportion of marked individuals (ϑ)

To calculate abundance the estimates obtained using mark-recapture analysis of marked individuals were inflated to account for non-marked individuals. This was done by accounting for the proportion of individuals in the population with identifiable marks (ϑ, theta). Calves and juveniles were considered as unmarked individuals and so included in the calculation of ϑ (Wilson et al., 1999). To calculate ϑ, we selected observations of groups where all the individuals were captured with good quality photos (Q<4) in the body areas used in this study for photo-ID analysis. For each group the number of marked and unmarked whales was determined, and the results averaged to obtain a best mean estimate of the proportion of marked individuals in the populations.

2.4.8 Estimating N_{Total}

The total population size (N_{Total}), which includes marked and unmarked individuals, was calculated as:

$$\hat{N}_{total} = \frac{\hat{N}}{\theta}$$

Where N was the abundance estimate calculated by each model during each sampling period, and ϑ is the proportion of identifiable individuals in the population.

The variance of N_{Total} was calculated using the delta method

$$\text{var}\left(\hat{N}_{total}\right) = \hat{N}_{total}^2 \left(\frac{\text{var}(\hat{N})}{\hat{N}^2} + \frac{\text{var}\left(\hat{\theta}\right)}{\hat{\theta}^2}\right)$$

The confidence intervals were calculated assuming a log-normal distribution for the estimate (Burnham et al., 1987). The lower and upper limits for the 95% confidence interval were calculated as Ntotal/C to Ntotal*C, where C:

$$C = \exp\left(1.96\sqrt{\ln\left(1 + \text{CV}_{\hat{N}_{total}}^2\right)}\right)$$

2.4.9 Apparent survival φ

The study area is restricted to deep waters relatively close to shore, and survey effort concentrates in only one bay of the island each time. Tagging studies of beaked whales in El Hierro show that whales may move among bays of the island and travel up to 12 nm from the coast within periods of less than one day (N. Aguilar and M. Johnson pers. comm.). This, and the low capture probability of beaked whales, means that we cannot solve the ambiguity between survival and emigration, which can be temporary or permanent within the study period. Thus, using program MARK (White and Burnham, 1999), we constructed Cormack-Jolly-Seber models (Cormack 1964; Jolly 1965; Seber 1965) (CJS) to estimate apparent survival (φ*)*. The best model was selected based on the AICc. Models differing in AICc less than 2 units were assumed to be equivalent and the most parsimonious model (the one with fewest parameters) was chosen (Cooch 2009). Even though survival analysis segregated by type (males, females and sub-adults) would have been of interest in case each group made a different use of the area, or had a different survival probability (e.g. adults vs sub-adults) the small dataset for each group prevented us perform age/sex separated analysis of survival.

CHAPTER 3

Site fidelity and residency patterns

3.1 Transient (T) and Recaptured (R) Blainville´s and Cuvier´s beaked whales in El Hierro

The proportion of T and R individuals for each species was calculated separately for different sex-age classes (Table 3.1 and Table 3.2) to investigate if whale type affected site fidelity of beaked whales to the coastal study area of El Hierro.

Table 3.1 Seasonal and yearly captures of Blainville's beaked whales (Md) for seasonal (short-term) and yearly (long-term) transience (T) and recapture (R) rates. nºT season: number of animals seen in only one field season; nºR season: number of animals seen in more than one field season during the same year; nºT years: number of animals seen in only one year; nºR years: number of animals seen in more than one year.

Md	nºT season	nºR season	TOTAL	nºT years	nºR years	TOTAL
Males	15	10	25	15	9	24
Females	5	9	14	5	9	14
Indet.	23	7	30	25	6	31
TOTAL	43	26	69	45	24	69

Table 3.2 Seasonal and yearly capture rates of Cuvier's beaked whales (Zc) for seasonal (short-term) and yearly (long-term) transience (T) and recapture (R) rates. nºT surveys: number of animals seen in only one survey; nºR surveys: number of animals seen in more than one survey during the same year; nºT years: number of animals seen in only one year; nºR years: number of animals seen in more than one year.

Zc	nºT surveys	nºR surveys	TOTAL	nºT years	nºR years	TOTAL
Males	2	13	15	2	13	15
Females	2	7	9	2	7	9
Indet.	27	15	42	27	15	42
TOTAL	31	35	66	31	35	66

3.2 Blainville's beaked whales

The percentage of transient and recaptured individuals in the marked population was 65% (n=45) and 35% (n=24), respectively, but the results varied among different sex/age classes (Figure 3.1.). In males (Figure 3.1.D) more than half of the marked population (62%, n=15 out of 25 whales) is considered transient. In females (Figure 3.1.E) the values are inverted with respect to males, with 64% (9) of 14 females forming the recaptured population. Indeterminates (Figure 3.1.F) show more extreme values, with 81% (25) of the 30 indeterminates in the marked population being transient.

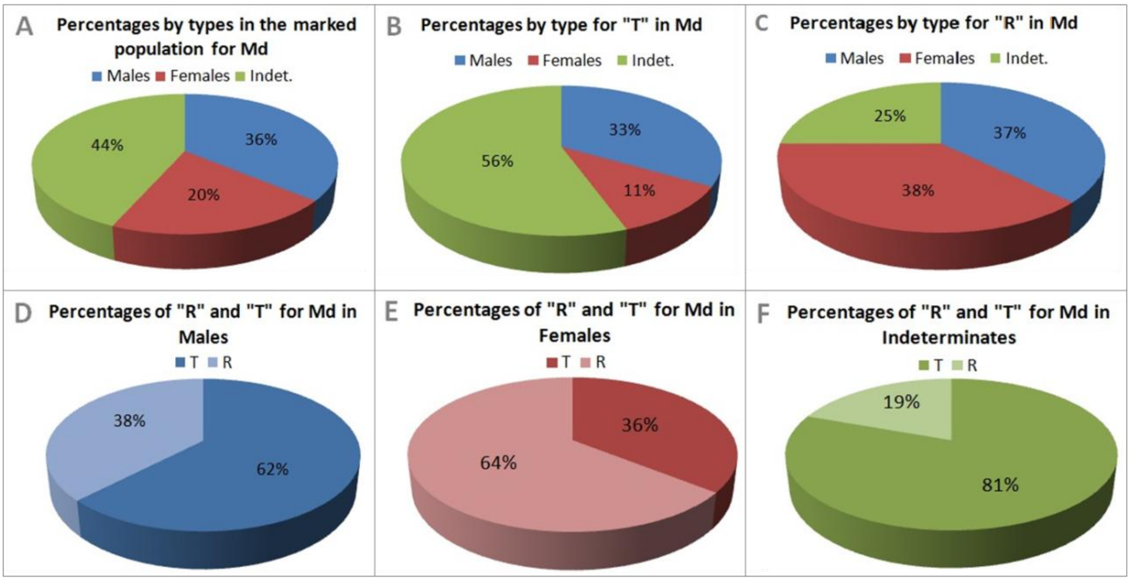

Figure 3.1 Percentage of whales of different types and site fidelity patterns per type of whales for the marked population in *Mesoplodon densirostris* (Md): A) percentages of the marked population divided by whale type; B) proportion of different whale types in the transient population; C) proportion of different whale types in the recaptured population; D), E) and F) percentage of recaptured and transient individuals in male, female and indeterminate whales respectively.

Figure 3.2 provides information on residency patterns. A) Shows the yearly sighting rate, i.e. the number of years that each individual was observed in relation to the total number of years analysed, with a minimum value of 0.18 (animals seen in two of the 11 study years) and a maximum of 0.73 (animals seen in eight different years) ; and B) the ISImax: the maximum inter-sighting interval i.e. maximum number of years between two consecutive sightings of each individual.

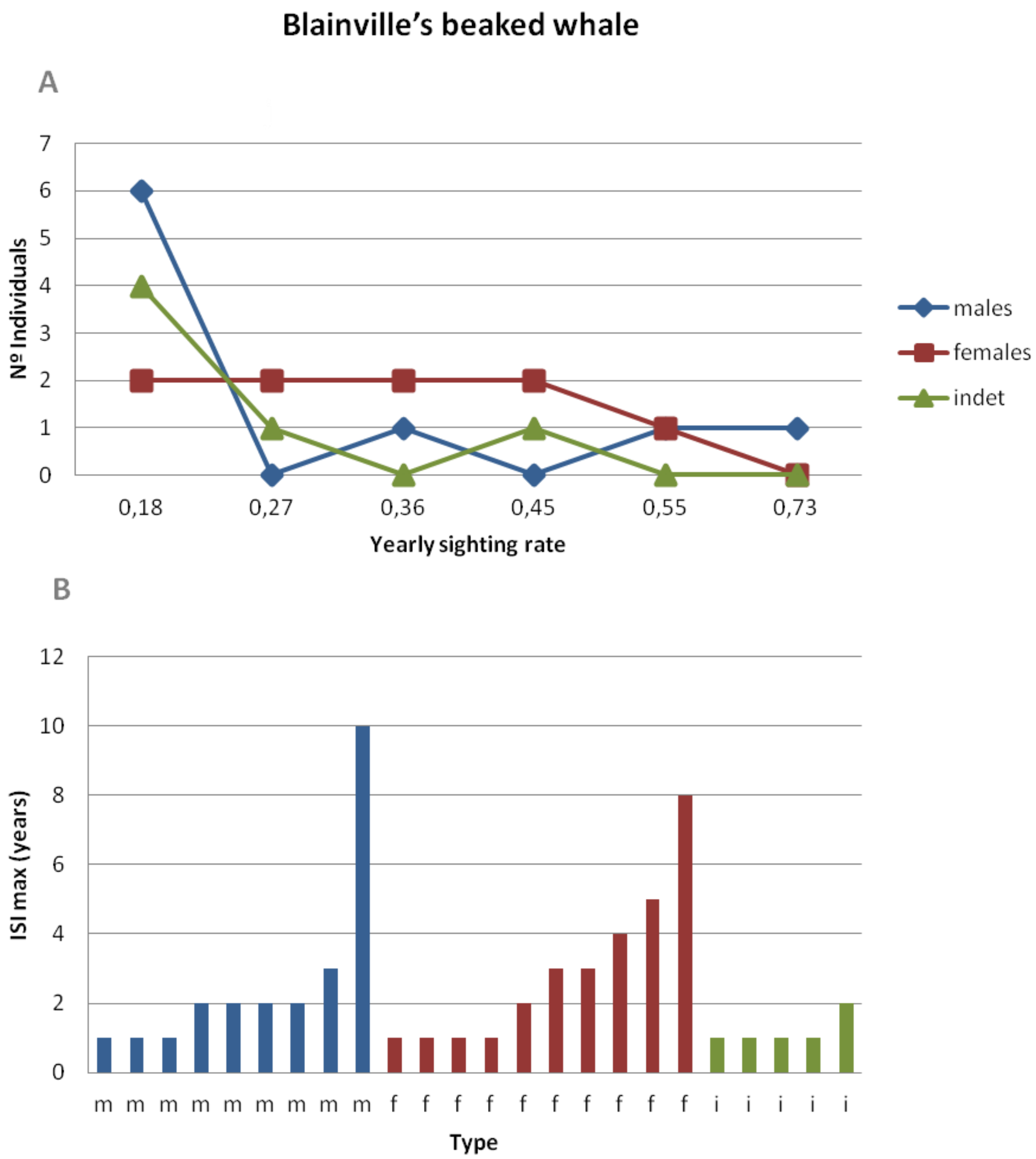

Figure 3.2 Residency pattern of the 24 recaptured Blainville's beaked whales during the 11 years of study: A) Yearly sighting rate: proportion of years an individual was identified divided by the total number of years analysed; B) ISI max: maximum inter-sighting interval an individual was identified between two consecutive sightings grouped by whale sex/age class: "m": males, "f": females, "i": indeterminates.

3.3 Cuvier's beaked whales

Based on numbers from the Table 3.2, the percentage of transients (T) and recaptured (R) Cuvier's beaked whales in the marked population was 47% (31) and

53% (35) respectively, but there was substantial variation among sex/age classes (Figure 3.3).

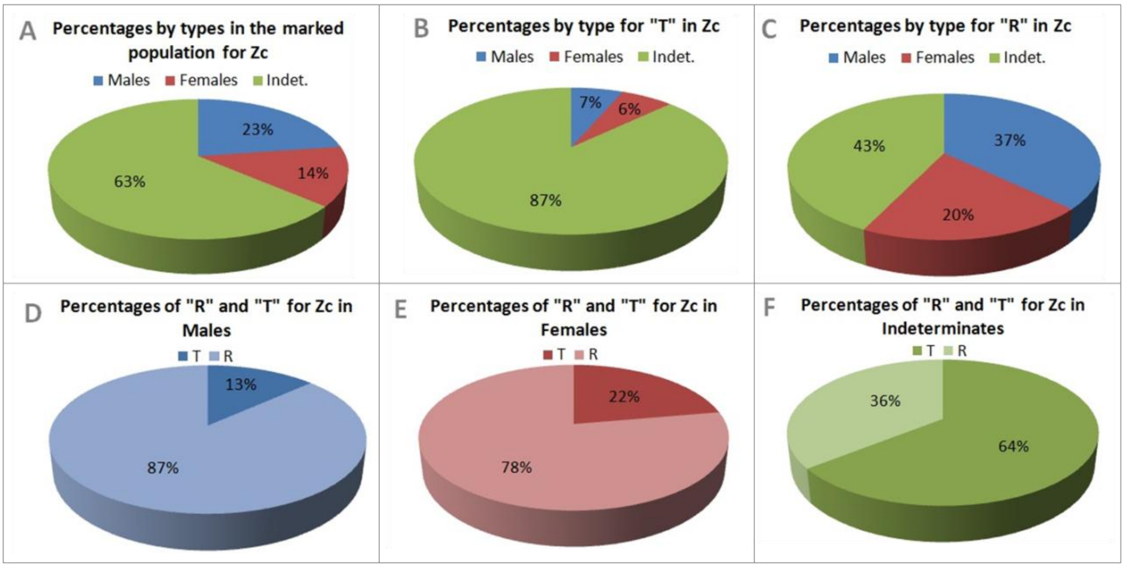

Figure 3.3 Percentage of T and R Cuvier´s beaked whales (Zc) for different sex/age classes): A) percentages of the marked population divided by whale types; B) percentage by types for transients “T”; C) percentage by types for recaptured “R”; D), E) and F) percentage of recaptureds and transients in males, females and indeterminates respectively.

In Cuvier’s beaked whales both sexes presented similar results for the ISI and yearly sighting rates. For indeterminates, more individuals had lower values for the ISI and sighting rates than males/females (Figure 3.4).

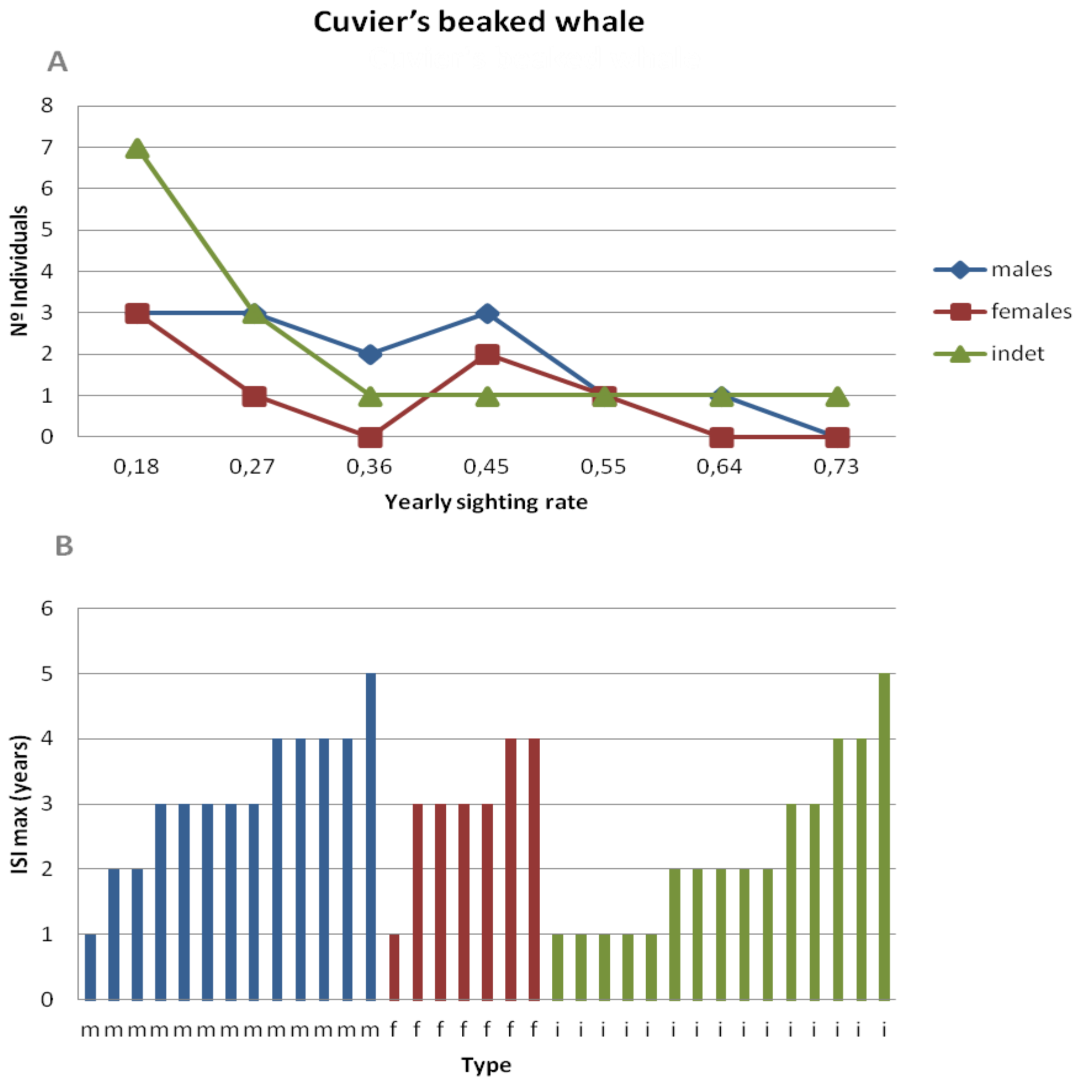

Figure 3.4 . Residency pattern of the 35 recaptured Cuvier's beaked whales during the 11 years of study: **A)** Yearly sighting rate: proportion of years an individual was identified based on the total number of years analysed; **B)** ISI max: maximum inter-sighting interval an individual was indentified between two consecutive years grouped by types: "m": males, "f": females, "i": indeterminates.

3.4 Analysing the effect of the quality of the marks in age/sex structure of the Transient population

When comparing the proportion of transient animals by age/sex structure with regular (M=2) and very recognizable marks (M>2) for each species, results show that a larger proportion of both females and indeterminates, in both species, have more regular (M=2) marks than very distinctive marks (M>2) (Figure 3.5 and 3.6). The binomial GLM assesses if the classification of individuals as R or T was not influenced by a low level of marks (M=2). Results found that age/sex class (and not M level) influenced the probability of an animal being T or R ($p<0.01$) (Tables 3.3 and 3.4).

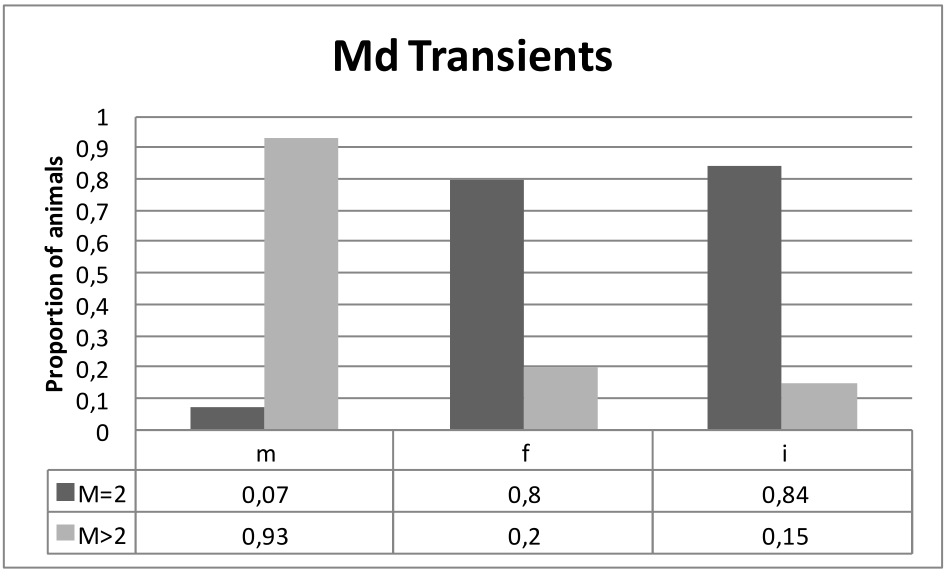

Figure 3.5 Proportion of transient animals with regular marks (M=2) and very recognizable marks (M>2) for each type in Blainville's beaked whales, where "m": males; "f": females and "I": indeterminates.

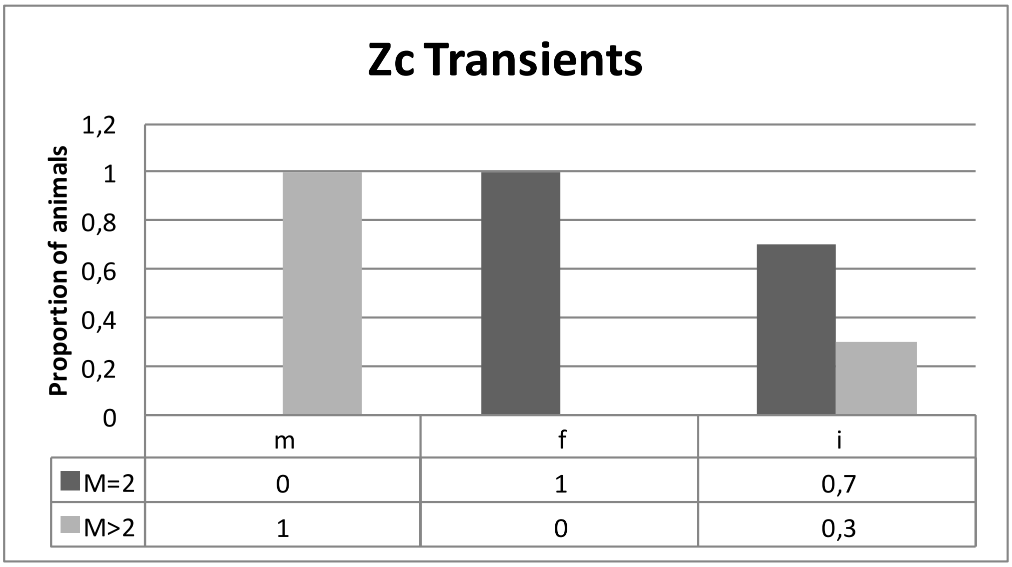

Figure 3.6 Proportion of transient animals with regular marks (M=2) and very recognizable marks (M>2) for each type in Cuvier's beaked whales, where "m": males; "f": females and "I": indeterminates.

Table 3.3 Results of the GLM for Blainville's beaked whale to investigate if the classification of individuals as R or T was influenced by a low level of marks

Md				
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept=F)	16.109	13.531	1.191	0.23384
Type_Indet	-21.251	0.7280	-2.919	0.00351
Type_Males	-0.4720	0.9655	-0.489	0.62497
Mark level (M)	-0.4453	0.5335	-0.835	0.40392

Table 3.4 Results of the GLM for Cuvier's beaked whale whale to investigate if the classification of individuals as R or T was influenced by a low level of marks

Zc				
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept=F)	0.6566	12.158	0.540	0.5892
Type_Indet	-19.508	0.8834	-2.208	0.0272
Type_Male	0.3208	11.912	0.269	0.7877
Mark level (M)	0.2835	0.4359	0.650	0.5156

CHAPTER 4

Abundance estimate and apparent survival

4.1 Data selection

The cumulative numbers of marked Blainville´s and Cuvier´s beaked whales throughout the study period (Figure 4.1. & Figure 4.2) indicates a continuous input of new whales of both species, suggestive of open populations. The pattern is not so clear when the analyses were performed only for recaptured whales in both species the number of new individuals R tends to stabilize with time, suggesting some degree of closure in this part of the population of both Blainville´s and Cuvier´s beaked whales. Both species reached a relatively similar number of recaptured marked whales (24 and 35 individuals for Blainville´s and Cuvier´s beaked whales, respectively). However, the number of whales observed only once during the study period is higher in Blainville´s beaked whales, while the population of Cuvier´s observed at El Hierro is dominated by recaptured whales.

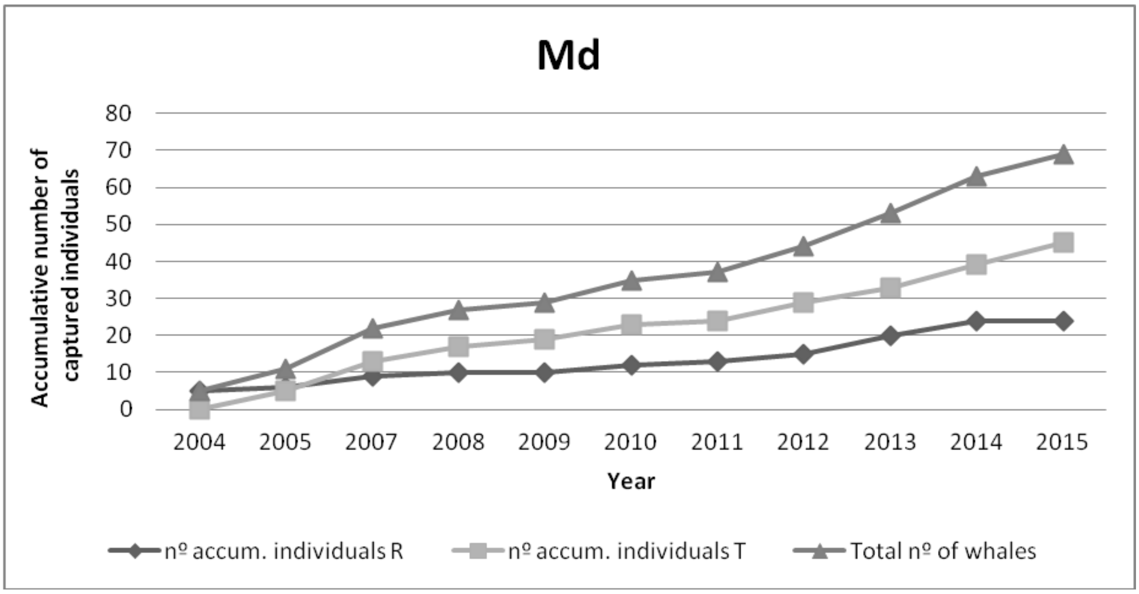

Figure 4.1 Cumulative number of captured Blainville's beaked whales off El Hierro. R: individuals recaptured, i.e. observed more than one year during the study period. T: transient whales observed in only one of the years of study.

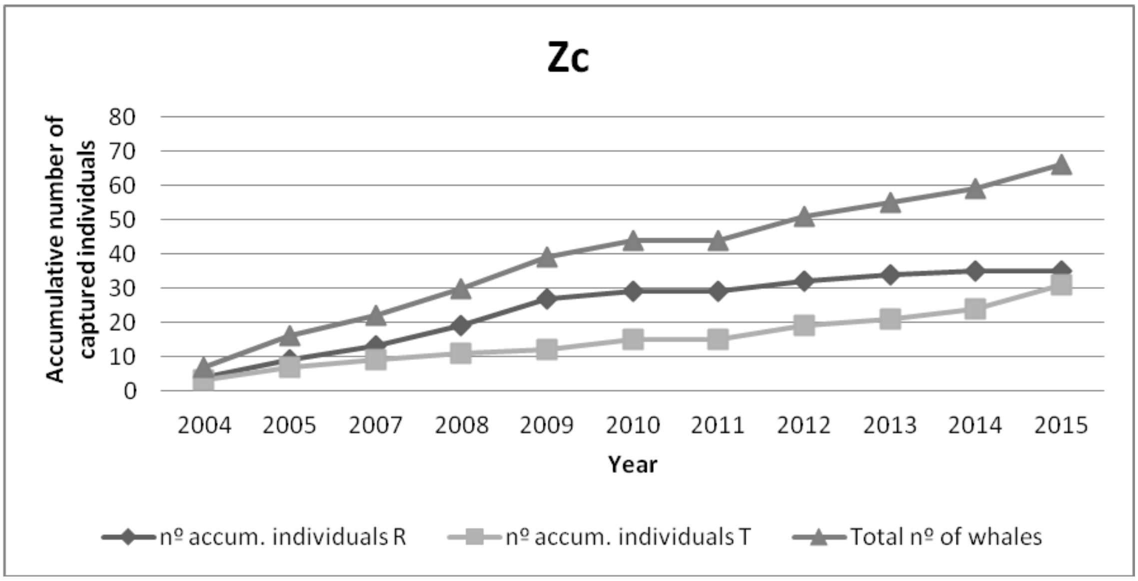

Figure 4.2 Cumulative number of captured Cuvier´s beaked whales off El Hierro. R: individuals recaptured, i.e. observed more than one year during the study period. T: transient whales observed in only one of the years of study.

The sample size of identifiable captured and recaptured individuals varied throughout the study period (2004 to 2015) (Table 4.1.) due to differences in field effort and probably to differences also in sampling methods.

Year	Md		Zc	
	Marked inds	Recaptured inds	Marked inds	Recaptured inds
2004	5	0	7	0
2005	7	2	10	1
2007	13	1	10	4
2008	9	4	13	4
2009	2	0	22	9
2010	10	1	15	5
2011	9	4	6	6
2012	11	4	13	1
2013	15	4	19	4
2014	22	7	20	11
2015	22	12	25	14

Here, to increase the relevance and robustness of the estimate of abundance, we analysed only a subset of the study period including the six most recent years, (2010 to 2015). The period selected for analysis provided a long enough timeline to calculate total abundance throughout the years and to explore potential sources of heterogeneity in the data using closed population models. At the same time, this six years period is short enough to reduce the bias introduced when applying closed population models when needed due to the low sample size resulting in lack of convergence of open population models.

4.2 Proportion of marked individuals (ϑ)

The proportion of marked whales (M≥2) in the populations of the species was estimated from an examination of this proportion in groups where all individuals had been photographed with good quality images (Q≤3). This was achieved for 76 groups of Blainville's and 120 groups of Cuvier's beaked whales, out of 235 and 345 groups observed in total of these species, respectively. The average proportion of marked identifiable individuals in these groups was ϑ=0.694 (SE=0.04) for Blainville's and ϑ=0.690 (SE=0.03) for Cuvier's beaked whales. These results were used to correct the abundance of whales estimated from mark-recapture analysis of marked individuals to obtain estimates of total population size of each species.

4.3 Apparent survival (φ)

Cormack-Jolly-Seber (CJS) model was used to estimate the apparent survival (φ) of both Blainville´s and Cuvier´s beaked whales. This analysis was performed using a long-term dataset of photo-ID data from year 2005 to 2015, excluding 2003 and 2004 for poor quality methodology.

4.3.1 Blainville's beaked whales

The first two models in Table 4.2, with a ΔAIC of less than two, were equivalently supported by the data, implying model selection uncertainty. In this case, we considered both models as valid due to their very similar estimates and associated parameters. However, the lowest AIC value model is also better fitted to the reality of data collection in this study, as it considers variable sampling effort in different years, with a number of years with much higher field effort than others.

Table 4.1 Models tested to estimate the apparent survival of Blainville´s beaked whales off El Hierro. AICw: AICc weight; LK: model likelihood; Deviance: residual deviance; φ: apparent survival; SE: standard error; 95% CI: 95% confidence interval.

Model	AICc	ΔAIC	AICw	LK	Nº Par	Deviance	φ	SE	95% CI
CJS_φ(.)p(2,3)	98.6	0	0.599	1	3	67.48	0.94	0.04	0.78-0.99
CJS_φ(.)p(.)	99.4	0.83	0.396	0.661	2	70.65	0.96	0.04	0.80-0.99
CJS_φ(.)p(t)	108.5	9.91	0.004	0.007	10	56.47	0.94	0.04	0.78-0.99

4.3.2 Cuvier's beaked whales

Model selection information for all fitted models is shown in Table 4.3. The two first models are similarly supported by the data, with a ΔAIC<2. To solve this model selection uncertainty, the most parsimonious (fewer parameters) model was selected (model CJS_φ(.)p(2,3)).

Table 4.2 Models tested to estimate the apparent survival of Cuvier´s beaked whales off El Hierro. AICw: AICc weight; LK: model likelihood; Deviance: residual deviance; φ: apparent survival; SE: standard error; 95% CI: 95% confidence interval.

Model	AICc	ΔAIC	AICw	LK	Nº Par	Deviance	φ	SE	95% CI
CJS_φ(.)p(t)	197.91	0	0.652	1	10	105.75	0.87	0.04	0.78-0.93
CJS_φ(.)p(2,3)	199.48	1.568	0.298	0.46	3	124.37	0.91	0.03	0.82-0.95
CJS_φ(.)p(.)	203.02	5.115	0.051	0.08	2	130.08	0.92	0.03	0.83-0.96

4.4 Investigating sources of heterogeneity with goodness of fit analysis

4.4.1 Blainville's beaked whales

The results of the analysis with program U-CARE showed no signs of heterogeneity in the data due to either transience (Test3.SR p=0.91) or trap-dependency (Test2.CT p=0.84). Results for the global chi-square test also discarded heterogeneity in the data when combining the results of the directional tests (p = 0.98).

4.4.2 Cuvier's beaked whales

The results of the analysis with program U-CARE for Cuvier's whales showed no signs of heterogeneity due to either transience (Test3.SR p=0.12) or trap-dependency (Test2.CT p=0.38). Results for the global chi-square test also discarded source of heterogeneity when combining the results of the directional tests (p=0.87).

However, for both species, these results need to be interpreted with care due to the low sample sizes.

4.5 Abundance estimation

For each species, we estimated total abundance (N_{Tot}) and the size of the population with higher affinity to the coastal waters of El Hierro, or island associated individuals (N_{IA}). The estimation of N_{IA} used only data from recaptured marked individuals. Both for Cuvier´s and Blainville´s beaked whales, the sample size of recaptured individuals was too low to apply open models to estimate abundance. When applied, models JS and POPAN did not converge. To increase sample size, data were pooled in pairs of years (i.e. a capture event pooled data from 2 years) and abundance estimations were performed using the Chapman closed population estimator for pairs of capture events.

4.5.1 Blainville's beaked whales

4.5.1.1 Estimate of N_{IA}

The analysis was performed over pooled data as shown in Table 4.4

Table 4.3 Number of captured marked Blainville´s beaked whales in total (n), per capture event (n1, n2) and recaptured (m2).

Md					
Interval 1	**Interval 2**	**n**	**n1**	**n2**	**m2**
2010+2011	2012+2013	18	10	14	6
2012+2013	2014+2015	22	14	20	12

The best estimates for both analysis periods were the same, resulting in an N_{IA} of 23 recaptured individuals, $N_{IATotal,}$ correcting by ϑ, of 33. There were small differences in the SE and CV of the estimates for the two analysis periods (see Table 4.5)

Table 4.4 Results of the Chapman two-sample estimator for Blainville's beaked whales. (ϑ =0.694, SE=0.52)

			Md				
Period years	**N_{IA}**	**SE**	**CV**	**$N_{IA\ Total}$**	**SE**	**CV**	**95% CI $N_{IA\ Total}$**
2010-2013	23	3.67	0.16	33	18.08	0.55	24-46
2012-2015	23	1.46	0.06	33	17.41	0.52	28-39

4.5.1.2 Estimate of N_{Tot}

Given that the number of transient whales was observed to continually increase during the study period, we first applied open population models to estimate abundance. The only two POPAN models that converged gave the same best estimate of 72 (SE:7.29) individuals (Table 4.6). The best estimate of N_{Tot} corrected by ϑ was 104 (SE: 12.19):.

To explore the presence of bias due to heterogeneity regarding different capture probabilities we applied the two-mixture Pledger closed model (Cooch, 2009). This model estimates total population abundance while considering that there are two main sub-groups of individuals with different capture probabilities. The models only converged when allowed a limited number of variables. Results for the converging models are shown in Table 4.5. Among them we selected the two-mixture Pledger model pi(.)p(t)=c due to its higher AICw (0.98). This provided a best estimate of 82 (SE=24.83, 95%CI:58-172) whales, which corrected by the proportion of marked whales gave a total of 118 individuals (SE:36.42, 95%CI:65-2013), i.e. a similar value that the POPAN analysis. We expect these values to overestimate annual abundance because closed models applied to open populations tend to inflate estimates, and because

POPAN estimates the total number of whales in the study area that were ever alive during the study period, i.e. an overestimate of the number of animals at any one point in time (Cooch 2009).

The above results were compared to multi-sample closed model estimates of the total population using program CAPTURE (run within software MARK, White and Burnham 1999). The estimates of N_{tot} (corrected by the proportion of marked whales) resulting from these closed models were: i) 84 whales, for Mt model (Darroch); ii) 119 whales, for Mh model (Chao); and iii) 123 individuals for model Mth (Chao).

Table 4.5 Model selection diagnostics and estimates of N and N_{Tot} in Blainville's beaked whales ordered by their AIC_c. AIC_c: Akaike information criteria adjusted for small samples; ΔAIC_c: difference in the AIC_c compared to the minimum AIC_c AIC_cw: AIC_c weight; LK: model likelihood; Deviance: residual deviance; SE: standard error; 95% CI: 95% confidence interval.

Md												
POPAN												
Model	**AIC_c**	**ΔAIC_c**	**AIC_cw**	**LK**	**Nº Par**	**Deviance**	**N**	**SE**	**95% CI**	**N_{Tot}**	**SE (N_{Tot})**	**95% CI (N_{Tot})**
φ(.)p(.) pent(.)	14175.55	0	0.99	1	4	13895.93	72	7.29	61-91	103	10.19	83-130
φ(.)p(.) pent(t)	14184.88	9.32	0.01	0.01	8	13895.93	72	7.29	61-91	103	10.19	83-130
PLEDGER TWO-MIXTURE												
Model	**AIC_c**	**Δ AIC**	**AIC_w**	**LK**	**Nº Par**	**Deviance**	**N**	**SE**	**95% CI**	**N_{Tot}**	**SE (N_{Tot})**	**95% CI (N_{Tot})**
pi(.)p(t)=c	56.76	0	0.98	1	14	45.24	82	24.83	58-172	118	36.42	65-213
pi(.)p(2,3)	58.89	2.12	0.25	0.35	4	68.73	66	9.66	55-97	95	4.96	70-129
pi(.)p(.)=c	64.41	7.65	0.02	0.02	2	78.35	59	47.28	53-73	85	68.30	21-339

4.5.2 Cuvier's beaked whales

4.5.2.1 Estimation of N_{IA}

The Chapman analysis of abundance was performed over the sampling intervals shown in Table 4.7.

Table 4.6 Number of captured marked Cuvier's beaked whales (Zc) in total (n), per pair of years (n1, n2) and recaptured (m2)

Zc					
Interval 1	**Interval 2**	**NºIndiv**	**n1**	**n2**	**m2**
2010+2011	2012+2013	28	13	23	8
2012+2013	2014+2015	26	23	21	18

The total population size for the N_{IA} (inflated by theta) was 53 (VAR=388) and 39 (VAR=195) for the first and second period respectively. Results for each pool of years are shown in Table 4.8.

Table 4.7 Results of the Chapman two-sample estimator for Cuvier's beaked whales

Zc							
Period years	**N_{IA}**	**VAR**	**SE**	**CV**	**$N_{IA\ total}$**	**VAR ($N_{IA\ total}$)**	**95% CI**
2010-2013	36	31.11	5.58	0.15	53	388	38-71
2012-2015	27	1.10	1.05	0.04	39	195	35-44

4.5.2.2 Estimation of N_{Tot}

For the POPAN analysis, the model that best fitted was φ(.) p(2,3) pent(.) giving a N estimate of 60 individuals (SE=4.51). This was similar to the results of the best two-mixture Pledger model with a best N estimate of 58 (SE=04.98). The corrected N_{Tot} POPAN and Pledger results are shown in Table 4.9.

The corrected estimates using CAPTURE analysis on Cuvier's beaked whale data gave estimates of 81 (SE=3.25) for the M_t model; 128 (SE=20.23) for the M_h model and 122 (SE=14.69) for the M_{th} model.

Table 4.8 Model selection diagnostics and estimates of N and N_{Tot} in Cuvier's beaked whales ordered by their AIC_c. AIC_c: Akaike information criteria adjusted for small samples; ΔAIC_c: difference in the AIC_c compared to the minimum AIC_c AIC_cw: AIC_c weight; LK: model likelihood; Deviance: residual deviance; SE: standard error; 95% CI: 95% confidence interval.

Zc												
POPAN												
Model	**AIC_c**	**ΔAIC_c**	**AIC_aw**	**LK**	**Nº Par**	**Deviance**	**N**	**SE**	**95% CI**	**N_{Tot}**	**SE (N_{Tot})**	**95% CI (N_{Tot})**
φ(.)p(2,3) pent(.)	199.13	0	0.99	1	5	-89.70	60	4.51	54-73	87	7.55	73-103
φ(.)p(.) pent(.)	207.88	8.73	0.01	0.01	4	-78.75	60	4.69	54-74	87	7.78	73-104
PLEDGER TWO-MIXTURE												
Model	**AIC_c**	**ΔAIC_c**	**AIC_aw**	**LK**	**Nº Par**	**Deviance**	**N**	**SE**	**95% CI**	**N_{Tot}**	**SE (N_{Tot})**	**95% CI (N_{Tot})**
pi(.)p(t)=c	71.62	0	0.96	1	14	60.92	58	4.98	53-75	84	48.09	70-101
pi(.)p(.)=c	78.04	6.42	0.04	0.04	2	92.77	57	3.75	53-69	83	6.51	71-96

CHAPTER 5

GENERAL DISCUSSION AND CONCLUSIONS

All oceans of the world host at least one of the 22 currently recognised species of ziphiids but knowledge about the distribution and use of the area of these species is still poor, while data on their potential movement patterns within or between adjacent ocean basins are still lacking. This scarcity of data limits our understanding about the ecology and biology of beaked whales and impedes assessment of population structure to define conservation management units for ziphiid species. While long range movements have been recorded for individuals in Hawaii (Schorr et al., 2009), a tendency towards site fidelity has been recorded for the same species at the Ligurian Sea (Mediterranean, Rosso, 2010), San Clemente Island (California, Falcone et al. 2009) and El Hierro (Aparicio, 2008 and this study). Also, site fidelity has been found in other concentration areas where Cuvier´s and Blainville´s beaked whales are found year-round, in the three oceanic archipelagos of Bahamas (Claridge, 2006 & 2013), Hawaii (McSweeney et al. 2007) and the Canary Islands (Aguilar de Soto 2006, Arranz et al. 2014, Aparicio 2008). Concentration areas or "hot-spots" might be common for at least some beaked whale species (Barlow et al. 2006) and such locations offer unique opportunities for longitudinal studies to learn about basic life history and population/social structure parameters that are still poorly known for nearly all beaked whale species. The results of this study of site fidelity and local abundance of Cuvier´s and Blainville´s beaked whales off El Hierro are remarkably similar to studies of the same species in other archipelagic concentration areas across the Atlantic (Bahamas) and in the Pacific (Hawaii). This convergence suggests that we are finding robust patterns about the population ecology of the species applicable at least to populations inhabiting waters around oceanic archipelagos.

In spite of the opportunities for research provided by Cuvier´s and Blainville´s beaked whales occurring regularly in deep coastal waters of Bahamas, Hawaii, San Clemente, Ligurian Sea and the Canary Islands, the sample size of captures of distinctive individuals for mark-recapture population analyses is low (Claridge 2006, 2013; McSweeney 2007; this study) and this restricts the application of data-exigent analytical models. Low sample size is probably explained by the difficulties inherent to approaching beaked whales for photoID due to their extreme diving behaviour with typically short surfacing intervals (Tyack et al. 2006). The study off El Hierro is facilitated by the possibility to locate beaked whales from high coastal cliffs increasing detection rates. To our knowledge, land-based observations of beaked whales have been performed only in the Azores (Silva et al. 2014) and off El Hierro (Arranz et al. 2014).

At El Hierro, sample size varied greatly among years throughout the study period. This seems to be better explained by changes in field effort and photoID methods than by changes in population abundance. A similar result was found by Claridge (2013) who observed that in Bahamas the number of captured individuals per year tended to increase with field effort. She obtained a yearly number of captured individuals ranging from 6 to 17, while at El Hierro we captured 2 to 22 (for Blainville's beaked whales) and 4 to 21 (for Cuvier's beaked whales) individuals per year throughout the research period. At the beginning of the study at El Hierro, photoID data were gathered opportunistically during fieldwork directed for tagging studies and using a conventional film camera. Then, there were qualitative and quantitative changes in the capability of researchers to gather good photographic data when a digital camera started to be used in 2004, and then a second and third digital camera started to be used in 2005 and 2014, respectively. Also, the acquisition of a more stable boat in 2008 improved photo quality compared to previous years, when a 4m long inflatable was used for all research. Field effort was very low in 2006 due to funding issues and in 2011 due to an underwater volcanic eruption at the study area (Fraile et al. 2012). Only 8 and 18 days of field effort were performed in 2006 and 2011, respectively, compared to an average of 37 days per year. In spite of these methodological issues, the data gathered off El Hierro has been adequate to extract robust conclusions about site fidelity and population abundance of beaked whales in the area, which are discussed below.

5.1 Site fidelity

Site fidelity/philopatry can occur when animals tend to stay or return to their natal area (natal philopatry) or when they occur regularly at other locations such as breeding or feeding areas (Pearce 2007; Arsenault et al. 2005). In this study, similar to long-term photoID beaked whale studies in Bahamas and Hawaii (Claridge 2006, 2013; McSweeney 2007), we observed that a part of the populations of both Cuvier´s and

Blainville´s beaked whales showed some degree of site fidelity, with observations of some individuals in up to 8 of the 11 study years for both species. In total, 53% of Cuvier´s and 35% of Blainville´s distinctive individuals were observed in two or more years at El Hierro, while the remaining whales were observed only once throughout the study period. We called the first animals “island associated” or “resident” and the second “transients”. Here, the term population refers to the whales that use the coastal waters off El Hierro, without implying genetic isolation. The term “resident” reflects that many island-associated individuals show a pattern of high use of the area that is consistent with some degree of residence. However, sightings of resident individuals in El Hierro may be separated by 1 to 10 years (with a mean of 2.46 years for the overall resident group) in Blainville´s and by 1 to 5 years (with a mean of 2.63 years for the overall resident group) in Cuvier’s beaked whales. Due to this mean yearly inter-sighting interval, it cannot be dismissed that some of the individuals classified as transients may become part of the island associated group in the future, or may be part of this population but were simply never photo-captured more than once by chance.

The population structure of Blainville´s beaked whales off El Hierro is very similar to that observed in Bahamas and Hawaii. In El Hierro, 35% of the 69 distinctive Blainville´s beaked whale individuals were recaptured (observed at least in two years), while in Bahamas this proportion was 34%, out of 44 distinctive individuals found in the non-impacted population at Abaco (Claridge, 2013) and in Hawaii the proportion was 34% (McSweeney et al. 2007). High levels of site fidelity in beaked whales have been also reported in other localised populations: northern bottlenose whales at the

Gully Canyon, in Nova Scotia (Gowans et al. 2000); Cuvier's beaked whale in the Ligurian Sea (Ballardini et al., 2005; Rosso 2010) and Blainville's and Cuvier's beaked whales in Hawaii (Baird et al., 2006; McSweeney et al., 2007).

5.1.1 Blainville's beaked whales

Long-term site fidelity in Blainville's females has been observed in Bahamas (Claridge 2006; 2013), Hawaii (McSweeney et al. 2007) and the Canary Islands (Aparicio 2008, this study). Permanent emigration of adult males and young dispersers from the local populations was also suggested by Claridge (2013). This demographic structure could be associated with their social and mating system, defined as polygyny with harem-like social groups in many cases (Claridge 2006, McSweeney et al. 2007), where females inhabit local areas with high availability of resources, and dominant males would limit the access of other males and subadults to the area, in which adult females would be the resource (Claridge, 2013).

Data on adult females in our population suggest that individuals are resighted in the area during long periods of time, with the same number of individuals (2) seen in 2 to 5 different years, and one individual seen in up to 6 different years. In adult males, 88% of the individuals are resighted in the area with Inter Sighting Intervals (ISI-max) of 1 to 3 years. 66% of the adult males were seen in only two different years while four of them (33%) were seen up to six and seven years. These results are consistent with females inhabiting the area for long periods and males forming hierarchical structures to gain access to the females in the study area.

Although in our study it was not possible to identify the sex of most of the young and subadult individuals due to the lack of recognisable features, two individuals (one adult female and one male) were first observed as calves/juveniles. In these examples, the subadult female remained in the area (or returned to it frequently) up to 2017, i.e. after reaching sexual maturity and calving. In contrast, the subadult male apparently left the area, and was not observed in the study area again until ten years later as an adult. These examples support the hypothesis that at least males disperse as subadults and return once mature to reproduce, while females born in the area seem to stay at or closer to the study area from calves to adult stage.

In El Hierro, the eruption of a submarine volcano in the study area from October 2011 to March 2012 acted as a natural impact that enabled us to study the level of site fidelity and spatial adaptability of the species during a disruptive scenario. Sightings from land and at sea during that period confirmed the presence of individuals from the Blainville's beaked whale resident population (two females, both accompanied of a calf) in the vicinity of the volcano. This high site fidelity and return rates in Blainville's females in resident populations suggests that this behaviour is a key feature in the ecology of this species. The observations during this event seem to support this idea. This is further supported by the observation that 35% of the distinctive Blainville´s identified at the naval range of AUTEC, in Bahamas, were recaptured several times. This site fidelity is in spite of the behavioural reactions of the species to naval sonar measured in the same area, involving foraging disruption and spatial avoidance (Tyack et al. 2012) and the potential implications of these reactions for the lower reproductive success of Blainville´s beaked whale females at AUTEC and in the nearby, but unconnected, population at Abaco (Claridge 2013).

5.1.2 Cuvier's beaked whales

Some studies (Gowans et al. 2000; McSweeney et al. 2007; Claridge 2006, 2013) have found that re-sighting intervals of adult females were significantly longer than for adult males. However, in Cuvier's beaked whales in this study, an analysis of the resident population by sex/age classes shows a similar pattern among all whale types: 80% or more of the individuals spend a maximum of 45% of the study years in the area, indicating similar re-sighting intervals and, therefore, use of the area for all the different types.

In the Cuvier's beaked whale population off Hawaii, the number of identified males and females was very similar (13 and 15, respectively) and the number of indeterminate individuals very small (two) (McSweeney et al. 2007). In San Clemente, adult whales (41 distinctive animals out of 58 identified) were divided in similar number of males and females (16 and 19, respectively), with only 2 subadults and 5 calves (Falcone et al., 2009). In El Hierro, the number of distinctive adult males (13) and indeterminates (15) was approximately double the number of adult females (7). Some of the differences in the results might be explained by the thresholds used to classify whales as adult females, which were more restrictive in the study off El Hierro than off Hawaii and San Clemente. In our study at El Hierro Individuals were only classified as adult females once they had been observed accompanied by their offspring on at least two different occasions, while in Hawaii and San Clemente colouration patterns and presence of scars were used as identification features. This is possible thanks to the correlation found between age and number of cookie-cutter shark scars in those areas, which is not the case in the Canary Islands, where these sharks are not so abundant. Also, off El Hierro, Cuvier’s beaked whale mother-calf pairs tend to appear alone, less often and displaying a much more elusive behaviour than Blainville’s beaked whales (pers. obs.). These two factors could serve to i) decrease the number of positively identified adult females and, ii) decrease the probability of encounter and thus recapture of adult females when accompanied by their calves. Taking this into account, and noting that the observed patters of site fidelity pattern in Cuvier´s beaked whale indeterminate and female individuals are similar at El Hierro, it cannot be discarded that some indeterminates could actually be unidentified adult females.

5.2 Apparent survival

Here we present the first abundance estimate for populations of Blainville’s and Cuvier’s beaked in the eastern North Atlantic.

In live mark-recapture studies, permanent emigration can cause a negative bias in the survival estimates if not taken into account. A way to address that scenario is by calculating the apparent survival (φ).

5.2.1 Blainville's beaked whales

The model that best fitted the data (CJS_φ(.)p(2,3)) was the one accounting for difference in field effort throughout the study period, indicating that this factor could be a source of heterogeneity and needs to be taking into account. The result for the apparent survival in the population in El Hierro was high ($\varphi = 0.96$), similar to the results of Bahamas (Claridge 2013) and consistent with expectations for a long-lived mammal. One source of heterogeneity in our population could be the female-male ratio. This ratio is different in Bahamas (2.41:1; Claridge, 2013) and in El Hierro (1:0.9). At El Hierro, observations have shown that a group of females can be escorted by different males during different moments. That would explain the larger number of adult males here when compared to Bahamas. This larger number of adult males in El Hierro, entering the area after long periods and remaining for variable periods, could be decreasing the apparent survival due to temporal emigration.

Claridge (2013) linked the observed female/male ratio of 2.41:1 in Bahamas to their polygynous harem-like mating system, where the number of females would be double to the number of males. At El Hierro we also observe harems in Blainville´s beaked whales, however, the lower differences in sex ration may be due to temporal emigration and subsequent re-immigration of adult males introducing a source of heterogeneity due to their lower capture probability (no availability in the area). The same would happen if the presence of adult males in the coastal waters (the study area) is ruled by a hierarchical system, where only some of the adult males are available to be captured.

Another source of heterogeneity in survival is probably introduced by indeterminate individuals. Our site fidelity data indicates that this part of the population remains in the area for short periods and then leaves, decreasing the value of the apparent survival. This indeterminates seem to have similar behaviour as the subadults in the hypothesis of Claridge (2013), where subadults would be expelled from the area by dominant adult males or females.

5.2.2 Cuvier's beaked whales

For Cuvier's beaked whales, two models ((CJS_φ(.)p(t) and CJS_φ(.)p(2,3)) resulted comparable due to their ΔAIC (<2). Model CJS_φ(.)p(2,3) was chosen for its lower number of parameters (more parsimonious) and the best estimate was $\varphi=0.96$. As in Blainville's, the model that accounted for different probabilities of capture depending on the level of effort resulted to fit better with the data, suggesting, again, that the level of effort was an important parameter in this study. To our knowledge, there are no previous estimates of apparent survival or survival for any population of Cuvier's beaked whales. In addition to Blainville´s beaked whales, apparent survival in beaked whales has been only estimated for the local population of northern bottlenose whales (*Hyperoodon ampullatus*) inhabiting the Gully canyon off Nova Scotia, resulting on $\varphi\approx0.90$ (Gowans et al., 2000).

Similar to Blainville´s beaked whales, differences in area usage by whales of different age/sex class may need to be considered as a potential source of heterogeneity biasing the estimate of apparent survival.

5.3 Abundance estimate

The fact that both Blainville´s and Cuvier´s beaked whales showed non-homogeneous individual capture probabilities separating “island-associated” (recaptured) whales, and individuals observed only once throughout the study period is consistent with the results of the same two species in Hawaii (MacSweeney et al. 2007) and of Blainville´s beaked whales in Bahamas (Claridge 2013). This suggests a similar pattern with an island-associated part of the populations, and a more oceanic part, in these three archipelagos. Here, estimates of abundance were performed separately on the “resident” or island-associated part of the population. The results for Blainville´s beaked whales were comparable between El Hierro (best estimate of 33 whales) and Bahamas (best estimate of 42 whales). The estimates for the total population in El Hierro were very similar (best estimate of 103 Blainville´s beaked whales) for an open population model (POPAN) and a closed model (Pledger mixture model) suggesting that the underestimation effect of heterogeneity and the overestimation effect of applying closed models to an open population may be compensating each other and are not very strong. Moreover, these values were within the range of results of the analyses performed in CAPTURE to investigate the importance of different sources of heterogeneity on the data (best estimates of 84 to 123 whales for different models). This provides confidence on the robustness of the estimates. The total abundance estimated for the study area off El Hierro was lower than the estimated in Bahamas (mean estimate of 230 whales, with a most precise annual estimate of 155 whales), however, this may be due to a smaller study area off El Hierro, closer to shore due to the use of a land observation platform. Thus, the study at El Hierro may not be capturing as many animals from the “oceanic” part of the population as the boat-based boat surveys performed in Bahamas.

In the case of Cuvier´s beaked whales, this study is to our knowledge the first mark-recapture estimate of abundance of the species. The estimates of abundance for the island-associated part of the population showed a higher temporal variability than for Blainville´s beaked whales, ranging from 53 to 39 whales in the periods 2010-2011 and 2011-2013. The same is found in the case of Blainville´s beaked whales, the estimates of total abundance of Cuvier´s beaked whales off El Hierro using open (POPAN) and closed (Pledger) models were very similar (87 and 84 whales, respectively) and within the range of the estimates using CAPTURE to explore the effects of heterogeneity (estimates of 81 to 128 whales for different models). Again, this provides confidence in the robustness of the results.

The general patterns observed at El Hierro, Hawaii, Bahamas and San Clemente are that Blainville´s and Cuvier´s beaked whales have island-associated populations with high site fidelity to deep coastal waters surrounding these archipelagos. These core inhabitants are not numerous (some 50 whales or less) and can be observed for many years, indicating long term site fidelity for at least some individuals, in spite of natural or anthropogenic sources of disturbance (e.g. volcanic eruptions or naval sonar use). Strong site fidelity reduces the ability of animals to relocate in response to reductions in habitat quality and increases the potential risk of core areas to become attractive sink habitats. These are areas attractive to animals, due to the occurrence of feeding resources, and/or natal/breeding philopatry, but where the mortality exceeds the recruitment. A lower apparent fitness of Blainville´s beaked whales observed at the naval range of AUTEC, when compared to the nearby area off Abaco, in Bahamas, suggests that the possibility of long-term population effects of disturbance cannot be dismissed (Claridge 2013). This possibility is reinforced by the observations of higher site-fidelity in females, which are key for the reproductive rate of populations, mainly in the case of polygynous social systems such as that of Blainville´s beaked whales.

The fact that in all studied areas there are oceanic individuals transiting the area may increase the resilience of the populations. However, it is still unknown if these transient whales reproduce in the areas, thus increasing genetic diversity and potentially connecting local whales with a broader oceanic population.

Conclusions

The main advances to the field made by this thesis are the following:

1. The first results of abundance estimate and survival rates for Blainville's and Cuvier's beaked whales in the Northeast Atlantic waters obtained using mark-recapture methods, and the construction of an open online photoID catalogue www.cetabase.info.

2. A contribution to the understanding of the site fidelity patterns of the two study species, supporting the observations gathered in studies of the same species in Hawaii, Bahamas and San Clemente archipelagos. In these four areas in two different oceans the species show a heterogeneous use of the area, with a part of the populations having high site fidelity while other individuals are apparently transient in the study areas, suggesting that this may be a common pattern in Blainville´s and Cuvier´s beaked whales inhabiting deep water areas around oceanic archipelagos.

3. The data gathered in this thesis have been already applied by the Spanish Ministry MAGRAMA to assess the category of Cuvier´s beaked whale in the National Catalogue of Protected Species

4. The results of this thesis show that El Hierro is an important concentration area for Cuvier´s and Blainville´s beaked whales year round, and that the populations are relatively small. This underlines the importance of maintaining the moratorium to the use of naval sonar within 50 nautical miles off the Canary Islands that was stablished in 2004 after the last atypical mass stranding recorded in the archipelago related to naval manoeuvres.

Future work

This thesis underlines the value of long-term datasets of the study species: two little known and long-lived species of beaked whales. For this reason, it is important to continue the long-term monitoring of the populations off El Hierro to: i) identify population dynamics in a nearly-pristine area and their relation with environmental factors and potential future anthropogenic activities; ii) increase the dataset required to complete the description of natural history parameters of both species, such as age of sex maturation and inter-calving intervals; iii) to genetically characterise the Blainville's and Cuvier' beaked whales populations. The later would enable to better assess the sex of the individuals and the relativeness among them and, therefore, the social structure of both species. In addition, genetic studies are required to assess the connectivity of the whales observed off El Hierro with other study areas within the Canary Islands and in the overall Atlantic. This information would contribute greatly to the understanding of the biology of the species and thus to their conservation.

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