Ecology of Chilean dolphins and Peale's dolphins at Isla Chiloé, southern Chile

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"A quiet day: Chilean dolphins surface in front of the village Yaldad."

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ABSTRACT

Information on the ecology of sympatric species provides important insights into how different animals interact with their environment, with each other, and how they differ in their susceptibility to threats to their survival. In this study habitat use and population ecology of Chilean dolphins (*Cephalorhynchus eutropia*) and sympatric Peale's dolphins (*Lagenorhynchus australis*) were investigated in the Chiloé Archipelago in southern Chile from 2001 to 2004. Distribution data collected during systematic boat-based sighting surveys revealed a distinct pattern of small-scale habitat partitioning, probably reflecting differences in foraging strategies and habitat preference. Chilean dolphins were sighted consistently in the same selected bays and channels in southern Chiloé. Peale's dolphins were distributed over wider areas, and were more frequently encountered in central Chiloé. Spatial overlap between both dolphin species and mariculture farms (for mussels and salmon) was extensive.

Predictive habitat modelling using logistic regression in a model selection framework proved a usefool tool to determine critical habitat from absence-presence data and environmental parameters. Chilean dolphins preferred shallow waters (< 20 m) close to shore (< 500 m) with estuarine influence. Peale's dolphins also occurred predominantly in shallow nearshore waters, but preferred more exposed shores with sandy shoals and were found further from rivers and mussel farms than Chilean dolphins.

Analysis of ranging and movement patterns revealed small-scale site fidelity and small ranging patterns of individually identifiable Chilean dolphins. Individuals differed in their site preference and range overlap suggesting spatial partitioning along environmental and social parameters within the population. Individual Peale's dolphins were resighted less regularly, showed only limited or low site fidelity and seemed to range beyond the boundaries of the chosen study areas.

Mark-recapture methods applied to photo-identification data produced estimates of local population sizes of 59 Chilean dolphins (95% CI= 54 – 64) and 78 Peale's dolphins (95% CI= 65 – 95) in southern Chiloé, and 123 Peale's dolphins (95% CI= 97 - 156) in central Chiloé. An integrated precautionary approach to management is proposed based on scientific monitoring, environmental education in local schools, and public outreach to promote appropriate conservation strategies and ensure the dolphins' continued occupancy of important coastal habitat.

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Chapter 1 Introduction: Setting the scene

1.1. COMPARATIVE ECOLOGY OF SYMPATRIC DOLPHINS

Similar species that co-occur are thought to compete for resources unless they occupy different physical locations and/or use different strategies to exploit these resources (Roughgarden 1976). Co-occurrence of two or more species in the same geographic area, i.e. sympatry, is common in the marine environment where important resources such as prey are clumped and patchily distributed. Studies on the distribution and habitat use of odontocetes (toothed whales) have revealed a range of strategies of co-occurrence based on habitat and resource partitioning (reviewed in Bearzi 2005a). However, only a handful of sympatric populations of dolphins have been well investigated in the field (Baird *et al.* 1992, Ford *et al.* 1998, Hale *et al.* 2000, Herzing *et al.* 2003, Bearzi 2005b).

Inter-specific interactions range from co-occurrence in the same habitat (without direct interactions) to the formation of multi-species groups with coordinated activities. In cetaceans, direct inter-specific interactions are usually short-lived, but notable exceptions of inter-specific long-term associations of the same individuals exist (Baraff and Asmutis-Silvia 1998). The nature of inter-specific interactions is not always clear but interactions can be broadly characterized as:

- a) cooperative, e.g. foraging (Norris and Dohl 1980, Würsig 1986),
- b) competitive, e.g. for food (Shane 1995, Herzing and Johnson 1997),
- c) social-sexual, in the most extreme case resulting in inter-specific mating and hybridization (Reyes 1996, Baird *et al.* 1998),
- d) aggressive-sexual, e.g. lethal inter-specific interactions as misdirected intraspecific infanticide behaviour (Patterson *et al.* 1998),
- e) anti-predatory, e.g. safety in numbers, particularly in oceanic dolphins (Norris and Dohl 1980, Acevedo-Gutiérrez 2002),
- f) predatory, e.g. killer whale (*Orcinus orca*) predation on other cetaceans (Jefferson *et al.* 1991).

The nature of inter-specific interactions is context-specific and depends on many extrinsic (e.g. prey abundance) and intrinsic (e.g. motivational state of the individuals involved) factors. For example, behavioural interactions of the same pod of killer whales with other cetaceans ranges from direct interactions such as predation, harassment, feeding in the same area (e.g. exploitation of the same or associated prey species), play through to non-interactive co-occurrence (Jefferson *et al.* 1991). Bottlenose dolphins were said to "exclude" spinner dolphins (*Stenella sp.*) from their shared daytime habitat when engaged in foraging behaviour (Herzing and Johnson 1997). When not foraging, however, both species were seen socializing together.

In general, sympatric species tend to avoid competition by using behavioural, dietary and physiological habitat specializations (Bearzi 2005a). Habitat use patterns have been investigated by relating dolphin distribution and activity patterns to fixed oceanographic factors (Polacheck 1987, Selzer and Payne 1988, Gowans and Whitehead 1995, Bearzi 2005b), temporally variable physical and/or chemical properties (Reilly 1990, Ballance and Pitman 1998, Reilly *et al.* 1998, Bräger *et al.* 2003) and/or indications of biological productivity (Smith *et al.* 1986, Griffin and Griffin 2003). Correlations between cetacean distribution and environmental variables are unlikely to represent direct causal relationships, but most likely reflect effects of oceanographic features on prey densities (Reilly 1990, Griffin and Griffin 2003, Johnston *et al.* 2005).

Habitat use can vary in relation to the dolphins' life-history requirements and variability in resource availability, such as seasonal or diurnal changes in prey distribution. Such temporal variability is usually reflected in ranging and movement patterns (Irvine *et al.* 1981, Würsig *et al.* 1991, Defran *et al.* 1999, Stevick *et al.* 2002). Thus, investigations of sympatric ecology require information on a variety of ecological aspects at the individual species level.

Insights into sympatric ecology can highlight species-specific differences in exposure to human impacts, such as fisheries bycatch (Hall 1998), and vulnerability of the different populations. Combining information from distribution, ranging and habitat use patterns yields implications for conservation and management. These data can inform decisions about the location and size of conservation areas where

restrictions are to be placed on commercial or industrial activities to protect cetaceans from direct or indirect take (Dawson and Slooten 1993, Hooker *et al.* 1999).

In this thesis, habitat use and population ecology of Chilean dolphins, *Cephalorhynchus eutropia*, and Peale's dolphins, *Lagenorhynchus australis*, two small coastal delphinids sympatric throughout southern Chile, are investigated. Limited data exist on any aspect of the biology of these sympatric species. The relevant information available for each species from published and grey literature is reviewed here to provide the background for the research detailed in the subsequent chapters.

1.2. BIOLOGY OF CHILEAN DOLPHINS

1.2.1. Systematics

Chilean (or black) dolphins belong to the genus *Cephalorhynchus* (Delphinidae, Cetacea), which comprises four strictly coastal species scattered widely in cool temperate latitudes of the Southern Hemisphere. Heaviside's dolphins (*C. heavisidii*) are found around the tip of South Africa and along the west coast to Namibia (Best and Abernethy 1994). Hector's dolphins (*C. hectori*) are endemic to the inshore waters of New Zealand (Baker 1978). Commerson's dolphins (*C. commersonii*) occur along the Argentinean coast, in Tierra del Fuego, around the Falkland Islands, and also have an isolated population at the Kerguelen Islands in the Indian Ocean (Goodall 1988). Chilean dolphins (*C. eutropia*) are endemic to the coastal waters of Chile (Goodall *et al.* 1988).

Pichler *et al.* (2001) suggested monophyly for *Cephalorhynchus* and a pattern of radiation by colonization in a clock-wise direction following the West Wind Drift with origin in South Africa. Chilean and Commerson's dolphins are thought to have speciated along the coasts of South America during one of the many glaciations of Tierra del Fuego (Pichler *et al.* 2001), and are now largely allopatric except for limited geographical overlap in Tierra del Fuego (Goodall *et al.* 1988).

1.2.2. Morphology

Chilean dolphins are small and chunky animals like all members of *Cephalorhynchus*. Maximum length measurements taken for 59 individuals were 165 cm (range 123 - 167 cm) for both males and females (Goodall *et al.* 1988), but

females are known to grow larger than males in the other species of the genus (Baker 1978, Goodall 1988, Best and Abernethy 1994). Body weight ranged from 30 to 62 kg in females (n=15) and from 30 to 63 kg in males (n=32) (Oporto 1987b, Oporto *et al.* 1990).

The colour pattern of Chilean dolphins is complex (Appendix I). It consists of different shades of grey on the dorsal surface with a triangle of dark grey at the jaw tip, dark grey eye patches, a dark semilunate mark behind the blowhole extending to a dark rounded dorsal fin surrounded by a dark cape. The ventral side is white except for a black thoracic shield, a dark caudal peduncle and a dark genital patch with sexspecific pattern. When not surface-active Chilean dolphins can be very hard to see as their greyish colours blend in with the predominantly grey, brown to almost black (tannin-stained) waters in southern Chile (Heinrich, pers. observation, Goodall *et al.* 1988). Their rounded dorsal fins have proven suitable for photo-identification purposes (this study), but the convex shape without a defined tip does not allow a dorsal fin ratio to be calculated as is common practice for delphinids with falcate fins (see Defran *et al.* 1990).

1.2.3. Conservation status

Chilean dolphins are amongst the least known members of the family Delphinidae which includes 32 species worldwide (Jefferson *et al.* 1993). To date there has been no detailed study of their ecology or population dynamics. The existing data on anatomy, population parameters and behaviour have been reviewed comprehensively by Goodall *et al.* (1988) and Goodall (1994).

Abundance estimates are lacking, even over small geographic scales. Some authors have suggested that Chilean dolphins might be locally "abundant" (Goodall *et al.* 1988). Distribution could be patchy throughout the extensive range. Despite the lack of information on past and present population sizes, human impacts could have severely reduced their distribution and abundance (section 1.6). The International Union for the Conservation of Nature (IUCN) lists Chilean dolphins as "data deficient" due to the paucity of available information (IUCN 2000). The current lack of knowledge stems from their distribution (i.e. in remote and/or difficult-to-survey areas), their behavioural characteristics (i.e. unobtrusive and elusive), a lack of qualified observers and a lack of funding for cetacean research in Chile.

1.2.4. Distribution and habitat

Chilean dolphins range along 2,500 km of Chilean coastline from around Valparaíso (33°S) in the North to Seno Grande (55°S) near Cape Horn in the South (Goodall *et al.* 1988, Capella *et al.* 1999) (Figure 1-1). Most sightings have been made between Valdivia (39°S) and Isla Chiloé (41-43°S). Published distribution records are based on a handful of systematic ship-based surveys, opportunistic sightings and beach-cast specimens. The data available to date suggest a close coastal distribution confined to shallow inshore waters, as is true for congeneric Hector's dolphins in New Zealand (Dawson and Slooten 1988). However, in the absence of systematic aerial or ship surveys the distance to which the dolphins range offshore remains unknown.

Within their extensive range Chilean dolphins occur in a variety of habitats. They have been sighted along the open coast with exposure to open ocean swells (Pérez A. and Olavarría 2000), in rivers several kilometres upstream, in sheltered channels and bays, and in the elaborate fjord systems of southern Chile (Goodall *et al.* 1988). In general, Chilean dolphins seem to prefer areas with strong currents, especially with rapid tidal flows, and shallow waters over banks at the entrance to fjords.

Chilean dolphins and congeneric Commerson's dolphins overlap in range only in a small part of the Strait of Magellan and in Tierra del Fuego, at the southern tip of South America. The lack of geographic co-occurrence has been attributed to potentially competitive exclusion and species-specific habitat specialization (Goodall *et al.* 1988). The Pacific and Atlantic coasts of southern South America differ mainly in their physiography. Along the Chilean (Pacific) coast and in south-west Tierra del Fuego where Chilean dolphins roam the predominantly rocky shores have steep profiles deepening abruptly to 30 m or more. Waters are clear but dark and teacoloured and tidal ranges are comparatively small (2-7 m). The east (Atlantic) coast where Commerson's dolphins occur is flat with extensive shallows (e.g. 30 m depth contour more than 2 km offshore), sediment-stirred waters and large tidal ranges (6-13 m). Goodall *et al.* (1988) noted an "excellent" correspondence of the ranges of the two species to these differences in habitat and possibly to differences in prey species.

Chilean dolphins are fully sympatric with Peale's dolphins and Burmeister's porpoises, *Phocoena spinipinnis*. Chilean dolphins and Burmeister's porpoises were captured in the same artisanal gillnet fishery (Reyes and Oporto 1994) suggesting

overlapping use of nearshore waters. Chilean and Peale's dolphins have been seen in the same general area but usually do not seem to associate (Goodall *et al.* 1988, Olivos and Delgado 1990, Lescrauwaet 1997).

1.2.5. Movement patterns

Seasonal or migratory movements have not yet been investigated. Year-round observations at Yaldad (43°08'S), Isla Chiloé (Crovetto and Medina 1991) and Queule (38°23'S) (Oporto 1988) suggested that Chilean dolphins were more abundant in shallow inshore waters (< 20m) during austral spring and summer (October to March). During winter (June-August) fewer or no dolphins were recorded in the same areas. Both studies hypothesized that Chilean dolphins might move offshore in winter following the movements of their inshore prey species or switching to other prey items due to a lack of inshore prey. However, diet of Chilean dolphins has not been investigated systematically. Neither the observations by Crovetto and Medina (1991) nor by Oporto (1988) were corrected for unequal seasonal and spatial sighting effort nor did either study include offshore or alongshore surveys. Opportunistic sightings have reported the year-round presence of Chilean dolphins in various areas throughout their known coastal range (Goodall *et al.* 1988).

Seasonal inshore-offshore movements, possibly related to prey movements, have been suggested for other small cetaceans in southern South America, such as Peale's dolphins (Goodall *et al.* 1997b), Burmeister's porpoises (Goodall *et al.* 1995) and Commerson's dolphins (Goodall 1988). Recent photo-identification work on Commerson's dolphins near Rawson in Argentina indicates seasonal along-shore movements of at least 200 km distance for some individuals of a seemingly resident population (Mora *et al.* 2002, Coscarella 2005). Despite wide-ranging photo-identification surveys there is no evidence of long distance along-shore movements in the well-studied congeneric Hector's dolphins. The most extreme distance between two sightings of the same individual is 106 km (Bräger *et al.* 2002). Hector's dolphins usually have limited ranges extending for about 30 km of coastline and remain in the same area year-round (Bräger *et al.* 2002, Dawson 2002). However, some groups seem to spread further offshore in the winter and there is a general inshore movement of dolphins in the summer, especially into sheltered bays and harbours (Dawson 1991, Bejder and Dawson 2001). Diurnal movements have been suggested for Hector's

dolphins at Banks Peninsula which seemed to be moving inshore into the sheltered harbour in the morning and towards the open sea in the evening (Stone *et al.* 1995).

1.2.6. Prey

The possible diet of Chilean dolphins has been described only from a small sample of dolphins by-caught in a coastal set-net fishery along the open coast (Oporto 1985, Oporto *et al.* 1990). Stomach content analysis revealed the presence of sardines (*Strangomera bentincki*), anchovetas (*Engraulis ringens*), róbalo/Chilean rock cod (*Eleginops maclovinus*), cephalopods (*Loligo gahi*), crustaceans (*Munida subrugosa*) and green algae (*Ulva lactuca*). A dolphin was maintained captive in a tank for several days in Canal Guamblad (southern Chiloé) and consumed róbalo of approx. 20cm length (Oporto 1987a). No quantitative information on prey sizes and diet composition is available.

1.2.7. Predators

Predation is unknown, but potential predators include killer whales (*Orcinus orca*), leopard seals (*Hydrurga leptonyx*) and sharks (Goodall *et al.* 1988). Predatory threats seem to be small, as neither killer whales nor sharks are seen regularly in the known habitat of Chilean dolphins in the southern fjords. Shark predation might be more common along the open coast. White sharks (*Carchraodon cacharias*), Pacific sleeper sharks (*Somniosus pacificus*) and shortfin mako sharks (*Isurus oxyrinchus*) occur in the northern parts of the range of Chilean dolphins and are known to actively predate on other small cetaceans (Crovetto *et al.* 1992, Long and Jones 1996). Leopard seals are only occasional visitors to southern South America and are unlikely to predate on adult dolphins.

1.2.8 Population dynamics

Group sizes are small and seem to vary most commonly between two and 10 dolphins, with most sightings being of only three animals (mean=11, mode=3, range 1-400; n=95; Goodall *et al.*, 1988). The largest aggregations, with many hundreds of dolphins, have been reported along the open coast north of Valdivia (Oporto 1988). For some of those sightings (e.g. from shore), however, species identification is questionable. Nevertheless it has been suggested that group size might vary according to geographic location and habitat type (Goodall *et al.* 1988). The larger aggregations of dolphins observed at the northern limit of their range might represent temporary

associations of smaller groups. This merging and splitting of several small groups into short-term aggregations has been well documented for congeneric Hector's dolphins (Slooten 1994, Slooten and Dawson 1994) and has also been suggested for Heaviside's dolphins (Best and Abernethy 1994) and Commerson's dolphins (Goodall 1988, Coscarella 2005).

At present virtually nothing is known about the life history, population parameters and population genetics of Chilean dolphins. Opportunistic observations indicate potential mating and calving seasons during the austral summer months (Goodall *et al.* 1988), but the undefined terminology used (e.g. "calf", "young", "half-grown animals") for these sightings is inadequate to draw firm conclusions. Periods of gestation and lactation, calving intervals and age at first reproduction are unknown. A maximum age of 19 years was determined by counting the growth layer groups in teeth from 36 stranded and by-caught specimens (Molina and Reyes 1996).

In the absence of data for Chilean dolphins, information on the biology and status of its intensively-studied congener, the Hector's dolphin, might highlight the potential for population impacts to the seemingly similar South American relative. The mating system of Hector's dolphins has been described as multimale-multifemale (promiscuous) (Slooten et al. 1993). Calves are born in the austral spring and summer (November to February) and females produce their first calf at age seven to nine with calving intervals of two to four years (Slooten 1991). Population growth models have shown little potential for population growth under less than the most ideal conditions (i.e. without any human impacts) (Slooten and Lad 1991). Genetic studies of mitochondrial DNA control regions indicate philopatry with a low rate of female dispersal and geographic isolation of Hector's dolphin populations on small geographic scales (Pichler et al. 1998). Overall population size has recently been estimated at less than 8,000 animals, distributed in four discrete and reproductively isolated regions (Pichler et al. 2003, Slooten 2005). Given abundance, population dynamics and genetic information it is obvious that the Hector's dolphin, the bestknown member of Cephalorhynchus, is vulnerable to human impacts and even local extinction (Dawson et al. 2001) and has a poor ability to recover from direct and indirect threats (Martien et al. 1999).

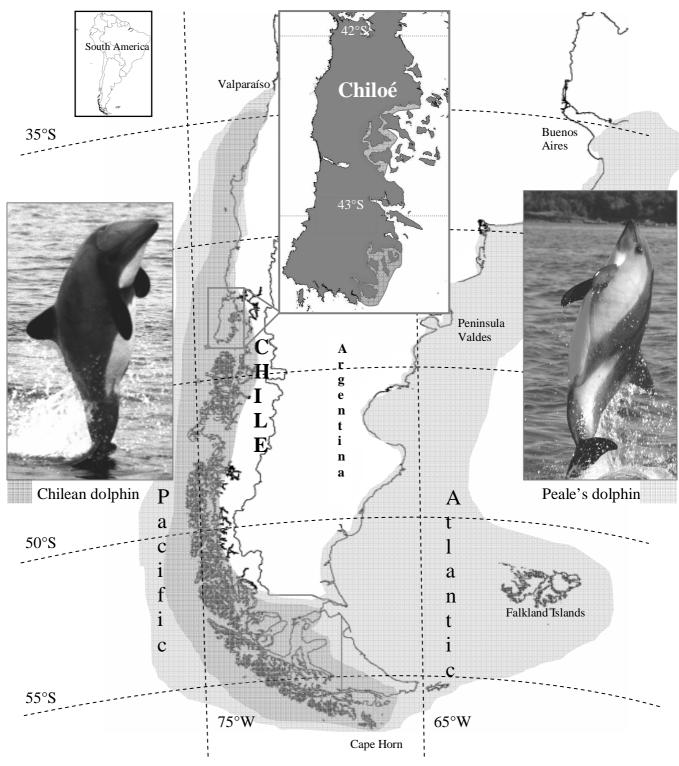


Figure 1-1. Distribution of the Chilean dolphin (*Cephalorhynchus eutropia*) and the Peale's dolphin (*Lagenorhynchus australis*) in southern South America. Note: Offshore distribution is unknown for both species (shading indicates maximum extent of known alongshore range, not continuous distribution). Inset: Overview of Chiloé Archipelago with study areas (shaded).

1.3. BIOLOGY OF PEALE'S DOLPHINS

1.3.1. Systematics

The genus *Lagenorhynchus* (Delphinidae, Cetacea) to which Peale's dolphins belong, comprises six diverse, and probably paraphyletic species (Würsig *et al.* 1997). The taxonomic division is under revision due to findings from recent cytochrome-b sequence analysis (LeDuc *et al.* 1999), but the three Southern Hemisphere species are still considered closely related (new suggested genus *Sagmatias*). Peale's dolphins (*L. australis*) have the most limited range, and are restricted to the coastal waters of southern South America, including the Falkland Islands (Brownell *et al.* 1999)(Figure 1-1). Dusky dolphins (*L. obscurus*) have a discontinuous, largely coastal distribution across the temperate Southern Ocean (including South America, south-western Africa and New Zealand) (Brownell and Cipriano 1999). The oceanic Hourglass dolphins (*L. cruciger*) have a circumpolar distribution in the Southern Ocean, and occur in both Antarctic and Sub-Antarctic waters (Brownell 1999).

1.3.2. Morphology

Peale's dolphins are stocky animals with a pointed but inconspicuous snout. Total length measurements ranged from 130 – 210 cm for females (n=20) and from 138 to 218 cm for males (n=9) (Goodall *et al.* 1997b). The heaviest animal (n=5), a sexually mature female, weighed 115 kg (Goodall *et al.* 1997b).

The general colour pattern is dark grey or black on the dorsal surface, with two areas of lighter pigmentation on the sides (Appendix I). The distinguishing characteristics of Peale's dolphins are: black facial patch covering snout and eyes, simple flank patch without the dorsal and ventral flank blazes found in dusky dolphins, and extension of the white abdominal field into distinctive axillary marks (also seen in *C. eutropia*). The dark and falcate dorsal fin often has a light grey trailing edge and appears well suited for photo-identification studies.

1.3.3. Conservation status

Peale's dolphins are considered the most common cetacean species found around the Falkland Islands (Hamilton 1952) and in the inshore waters of southern Chile (Oporto 1986). However, there is no information on overall or local abundances. The species remains relatively poorly known despite frequent sightings and dedicated research in Tierra del Fuego and the Strait of Magellan (Goodall *et al.* 1997a, Lescrauwaet 1997, Viddi and Lescrauwaet 2005). The IUCN lists Peale's dolphins as "data deficient" (IUCN 2000).

1.3.4. Distribution and habitat

Peale's dolphins inhabit the coastal waters of southern South America, especially the central part of the Strait of Magellan and the fjords of southern Chile, as well as the coastal waters around the Falkland Islands (Webber and Leatherwood 1991, Aguayo-Lobo *et al.* 1998)(Figure 1-1). Maximum range of sightings extends from about 38°S on the Pacific side (Valparaíso, Chile) southward to about 59°S (south of Cape Horn) and up the east coast of South America to about 44°S (Cabo dos Bahias, Argentina) (Crespo *et al.* 1997, Brownell *et al.* 1999), with exceptional sightings recorded at 33°S (Goodall *et al.* 1997a).

Peale's dolphins occupy two major habitats: open coasts over shallow continental shelves to the north and deep, protected bays and channels to the south and west. They appear limited to coastal waters less than 200 m in depth, but some sightings in waters at least 300 m deep have been reported in the northern part of their Atlantic range (Goodall *et al.* 1997a). In the southern and eastern part, Peale's dolphins inhabit waters very near to shore, commonly within or shoreward of *Macrocystis pyrifera* kelp beds (Lescrauwaet 1997, Schiavini *et al.* 1997). In the southern Chilean fjords, the dolphins seem to prefer tide rips over shallow shoals at the entrance of deep bays (Brownell *et al.* 1999), as has been described for Chilean dolphins.

Peale's dolphins and congeneric dusky dolphins overlap widely in their distribution (Brownell *et al.* 1999), but seem to differ in their habitat use: Peale's dolphins are usually coast-hugging while the similarly pigmented dusky dolphins have a wider offshore distribution and appear to prefer areas over or near the continental shelf (Goodall *et al.* 1997a). Peale's dolphins and Commerson's dolphins seem to associate frequently throughout their overlapping ranges (Goodall *et al.* 1988, de Haro and

Iñíguez 1997). Mixed groups have been seen swimming synchronously and engaged in cooperative feeding (de Haro and Iñíguez 1997).

1.3.5. Movement patterns

Nothing is known about the migratory movements of Peale's dolphins, but seasonal movements have been suggested to occur in some areas (Goodall *et al.* 1997a, Lescrauwaet 1997). In the central Strait of Magellan, Peale's dolphins were present year round, but were more abundant in spring and summer when they appeared to move inshore for calving (Lescrauwaet 1997). As suggested for Commerson's dolphins (Goodall 1988), Burmeister's porpoises (Goodall *et al.* 1995), and possibly Chilean dolphins (Goodall *et al.* 1988), inshore (summer) – offshore (winter) movements could be related to the migration of some of the dolphins' prey species (Goodall *et al.* 1997a). As discussed for Chilean dolphins, neither of the published studies had equal sampling effort in winter and summer or included dolphin surveys in adjacent coastal areas or offshore. Hence there is evidence for seasonal changes in abundance and differing use of inshore areas, but the direction of movements remains unknown.

Large scale alongshore movements of up to 780 km have been confirmed for the congeneric dusky dolphins (Crespo et al. 1997, Van Waerebeek and Würsig 2002, Markowitz et al. 2004). In Argentina and New Zealand populations of dusky dolphins exhibit inshore-offshore movements both on a diurnal and on a seasonal scale (Würsig and Würsig 1980, Würsig et al. 1997).

1.3.6. Prey

Peale's dolphins are known for feeding in kelp forests where divers in the Strait of Magellan have observed them take small octopus (Lescrauwaet 1997). They also feed on fish in open waters beyond the kelp, often using cooperative strategies such as circular feeding formations (Lescrauwaet 1997, Schiavini *et al.* 1997). Only a few stomachs have been examined (n=16), and those were collected from dolphins on the southern Atlantic coast and in north-eastern Tierra del Fuego. About 20 prey taxa were identified, mainly consisting of demersal and bottom fish, octopus and squid species which are common over the continental shelf or in kelp beds (Iñíguez and de Haro 1993, Schiavini *et al.* 1997).

1.3.7. Predators

See Chilean dolphins, section 1.2.7.

1.3.8. Population dynamics

Group sizes are usually small and very similar to those reported for Chilean dolphins. Peale's dolphins are most frequently seen in groups of two to 20 dolphins, with average group sizes varying from two to four animals (Goodall *et al.* 1997a, Brownell *et al.* 1999). Aggregations of about 100 dolphins have been observed east of the Falkland Islands (Goodall *et al.* 1997a). As discussed for Chilean dolphins, such large groups most likely represent only short-term aggregations of several smaller groups.

There is little information on reproduction and life history. Calves have been reported from austral spring through to autumn (October to April) (Goodall *et al.* 1997b, Lescrauwaet 1997). The maximum age determined from growth layer groups in the teeth was 13 years for a physically mature female (Goodall 2002).

More information exists for congeneric dusky dolphins which differ from Peale's dolphins in their schooling behaviour (group sizes vary between 40 and 200 animals with aggregations of more than 3,000 dolphins reported) and their distribution (further offshore). Dusky dolphins show marked differences in reproductive behaviours between geographically distinct populations (Würsig *et al.* 1997, Van Waerebeek and Würsig 2002). In Peru and New Zealand, most dusky dolphin calves are born during the winter whereas in Argentina (where dusky and Peale's dolphins overlap) summer is the prime birth season (Van Waerebeek and Würsig 2002). Age at first reproduction for both males and females varies between four and eight years, depending on geographic location and possibly density-dependent effects caused by heavy exploitation and El Niño (Chávez-Lisambart 1998, Van Waerebeek and Würsig 2002).

1.4. CONSERVATION THREATS: PAST AND PRESENT HUMAN IMPACTS

Current understanding of the status and ecology of small cetaceans in Chilean waters is minimal (Aguayo-Lobo *et al.* 1998). Little is known of the nature and extent of the many potential human impacts on their populations. Direct take, incidental bycatch in coastal gillnet fisheries, over-exploitation and destruction of coastal habitat

seem to represent the most pressing conservation concerns (Goodall and Cameron 1980, Oporto and Brieva 1990, Reyes and Oporto 1994, Hucke-Gaete 2000).

Chilean and Peale's dolphins, along with other marine mammal and sea bird species, were taken extensively for bait in commercial fisheries for centolla/southern king crab (*Lithodes santolla*) and centollón/false king crab (*Paralomis granulosa*) in southern Chile (Goodall and Cameron 1980, Cárdenas *et al.* 1986, Lescrauwaet and Gibbons 1994), and to a lesser extent for human consumption (Aguayo-Lobo 1975). The number of dolphins killed for bait purportedly declined from a "guestimated" 4,120 dolphins taken in 1979 (Torres Navarro *et al.* 1979) to 600 dolphins in 1992 (Lescrauwaet and Gibbons 1994). Direct take for bait now seems to have ceased due to more restrictive legislation, changes in fishing methods and target species, and cheap alternative bait sources (Lescrauwaet and Gibbons 1994).

Small cetaceans have officially been protected in Chile since 1977 (Cárdenas *et al.* 1986, Torres 1990). Under the amended "Ley de Caza" (hunting law), which came into force in 1993, all cetaceans are now considered a "manageable resource" and their direct take or targeted killing has been banned for 30 years (Iriarte 1999). However, enforcement of the existing legislation has been notoriously lacking. Incidental take, such as entanglement in fishing gear, is not monitored and fisheries-related mortalities of cetaceans do not have to be reported.

Chilean dolphins, Peale's dolphins and dusky dolphins as well as Burmeister's porpoises are known to have been taken incidentally in coastal gillnet fisheries in Chile (Reyes and Oporto 1994, Aguayo-Lobo 1999). From 1988 to 1990 between 32 and 63 Chilean dolphins, as well as 1-2 Peale's dolphins and around 64 Burmeister's porpoises, were caught annually in a small artisanal gillnet fishery for sciaenids and róbalo operating from one fishing port (39°-40° S) in central Chile (Oporto and Brieva 1990, Reyes and Oporto 1994). By-caught dolphins were often used as bait for conger eel (*Genypterus* spp.) fishing or consumed by fishermen. Carcass retrieval or bycatch reporting programs have not been implemented in Chile. Thus the past and present extent of direct and indirect take cannot be quantified reliably.

Anecdotal evidence suggests that the distribution and abundance of at least Chilean dolphins may have changed during the last decades. The dolphins' present distribution

appears to be relict, at least in part of their known range, as is suggested by their disappearance from the Río Valdivia (Hucke-Gaete 2000). Chilean dolphins had been regularly and reliably sighted in this area in previous years. Causes for the observed "disappearance" of the dolphins are unclear, but it coincided with increased industrial activity (i.e. wood chip processing), salmon farming and shipping traffic in the area.

Mariculture activities, especially the farming of salmon, oysters and mussels, have been increasing in Chile since the early 1990's at a rate unrivalled elsewhere in the world (Hernandez-Rodriguez *et al.* 2000). In 2004, Chile produced around 570,000 metric tons of farmed salmon (*Salmo salar* and *Oncorhynchus* sp.) and approximately 107,000 metric tons of farmed shellfish (SERNAPESCA 2004). Over 80% of all mariculture activities are located in the 10th Región of Chile and most farms are concentrated in the coastal waters of the eastern Chiloé Archipelago (SERNAPESCA 2004).

The ecological effects of salmonid and shellfish farms on the adjacent ecosystem are vast and varied and have been discussed in detail elsewhere (Bushmann *et al.* 1996, Naylor *et al.* 2000, Tovar *et al.* 2000, Kraufvelin *et al.* 2001). Potential impacts on, and interactions with, marine mammals have only recently become the focus of discussion and are mainly deduced from anecdotal evidence and incidental observations (reviewed in Würsig 2001, Kemper *et al.* 2003). Known or potential effects on cetaceans include:

- a) competition for space and displacement from important habitat due to structural components of the farms (e.g. Watson-Capps and Mann 2005),
- b) exclusion from important habitat due to the use of acoustic harassment devices aimed to deter pinnipeds from predating fish farms (e.g. Morton and Symonds 2002, Olesiuk *et al.* 2002),
- harassment from increased boat traffic due to work and maintenance of farms and cultures.
- d) changes in abundance and availability of prey species (both decrease and increase in prey availability, e.g. Bearzi *et al.* 2004),
- e) environmental contamination (with pesticides, fungicides, anti-fouling paint, antibiotics etc.) and increase in marine debris,

f) incidental entanglement in farming gear, such as cage netting, anti-predatory nets, mooring and support lines (Kemper and Gibbs 2001, Kemper *et al.* 2003).

Thus, some evidence for interference of aquaculture farms with habitat use of cetaceans and potentially negative effects exist, but impacts need to be investigated on a case-by-case basis and in more detail. Sound biological background information for the species in question is needed in order to evaluate short-term behavioural changes and possible long-term impacts.

The Chiloé Archipelago appears to be one of the distribution centres of Chilean dolphins (Oporto 1988, Goodall 1994), and possibly also Peale's dolphins in Chile (Goodall *et al.* 1997b). The little scientific information that is available suggests that at least some of the bays represent important habitats for the dolphins during part of their life cycle (Oporto 1986, Crovetto and Medina 1991). The vast, fast and relatively unrestricted mariculture development in this area could be affecting the occurrence and habitat use of both species in yet unknown ways. Thus, the Chiloé Archipelago offered an ideal combination for a comparative and conservation-oriented research project with feasible logistics, known occurrence of Chilean dolphins and Peale's dolphins and an urgent need for population assessment due to existing conservation concerns.

1.5. THE CHILOÉ ARCHIPELAGO

The Chiloé Archipelago (41.8°- 43.4°S) forms the northern boundary of the southern Chilean fjords (Figure 1-1). It consists of one large island (Isla Chiloé Grande) of approximately 180 km length and 70 km width at its widest part, and a multitude of smaller islands. To the west it is bounded by a relatively straight and exposed coastline facing the South Pacific Ocean. To the east, the main island breaks up into a multitude of islands separated from the Chilean mainland and the Andean mountain range by a body of open water, the Golfo Corcovado, of up to 50 km width. To the south, the Golfo Corcovado opens into the South Pacific. To the north, a narrow channel of approximately 3 km width (Canal Chacao) separates Chiloé from mainland Chile.

The climate is cool temperate with annual precipitation exceeding 2,200 mm (Comisión Nacional del Medio Ambiente, Parque Nacional de Chiloé, unpubl. data).

"In winter, the climate is detestable, and in summer, it is only a little better" (quote from Charles Darwin 1860, Chapter on Chiloé, p. 55). Thus, the coastal waters are subject to often intense freshwater input (river run-off and direct precipitation) (Dávila *et al.* 2002). On the sheltered eastern side of Chiloé Grande a brackish freshwater layer of one metre or more often forms at the sea surface, particularly after heavy rainfall. Sea surface temperature ranges from a mean maximum of around 15°C in January (austral summer) to a mean minimum of approximately 10°C in July (austral winter) (Navarro and Jaramillo 1994). Depth rarely exceeds 120 m in the waters surrounding the islands, and shallow bays and inlets of less than 20 m depth are common. Tides are semidiurnal with amplitude ranges of 3 to 5 m (SHOA 2001), and strong tidal currents frequently develop in narrow channels between the islands.

1.6. THESIS STRUCTURE

This thesis presents the first comprehensive and comparative study of the ecology of sympatric Chilean dolphins and Peale's dolphins. The overall aims are to provide information on their distribution (Chapter 2), habitat use (Chapter 3), movement patterns (Chapter 4) and population sizes (Chapter 5) and to compare species-specific ecological requirements. Knowledge of the factors that influence distribution and habitat use is important in ecological as well as in applied contexts, such as the evaluation of existing impacts on populations and the design of appropriate monitoring and management strategies.

Chapters two to four are based on data collected over four field seasons spanning the austral summers and autumns of 2001 to 2004 (January 2001 to April 2004). These chapters are presented as stand-alone investigations addressing specific research questions and using different methodological and analytical techniques. Chapters two and three take a population-level approach using sighting data from dolphin groups collected during systematic boat-based surveys to establish species-specific distribution and habitat use patterns. Chapters four and five use sighting histories of naturally marked and individually identifiable dolphins collected during dedicated photo-identification surveys to determine ranging and site fidelity patterns and population sizes. Chapter six (final discussion) provides a synthesis of the findings, places them into a wider ecological context and lays out a framework for conservation, management and future research avenues.

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Chapter 2 Distribution patterns of small cetaceans and their overlap with mariculture activities in the Chiloé Archipelago

2.1. ABSTRACT

Investigations into the distribution of cetaceans in space and time provide important information on how these animals interact with their environment, with each other and what threats to their survival they might be facing. The study presented here examines the distribution patterns of small cetaceans in the coastal waters of the Chiloé Archipelago (42-43°S) in southern Chile and outlines areas of concern due to spatial overlap with mariculture and other human activities. Boat-based sighting surveys were conducted on 212 days in central and southern Chiloé during consecutive austral summers and autumns from January 2001 to April 2004. Chilean dolphins, Cephalorhynchus eutropia, were sighted consistently in the same selected bays and channels in southern Chiloé, but were only occasionally encountered in central Chiloé. Additional monthly surveys during 2004 confirmed the year-round presence of Chilean dolphins in some areas of high use during summer and suggested seasonal shifts of importance for others. Peale's dolphins, Lagenorhynchus australis, were distributed over a wider area in each study area and were the most frequently encountered species in central Chiloé. Burmeister's porpoises, *Phocoena spinipinnis*, were only sighted in two selected areas with deeper waters in central Chiloé. Habitat partitioning based on depth and behavioural differences could explain the observed patterns of distribution and spatial segregation. Spatial overlap between the dolphins and mariculture farms (for mussels and salmon) was extensive in both study areas. Potential threats to the continued occupancy of important inshore habitat by the three cetacean species are discussed.

2.2. Introduction

Knowledge of the distribution of animals in space and time is fundamental to the understanding of their role in the environment, and allows insights into a species' evolutionary development and behavioural ecology. Information on temporal and spatial patterns of distribution is also crucial to the assessment of threats to the survival of a population and the mitigation of potential or ascertained adverse anthropogenic effects.

The distribution of animals in a population is a complex product of many, often interacting factors. These include the distribution and behaviour of prey (Würsig 1986, Croll *et al.* 2005), predators (Heithaus 2001, Acevedo-Gutiérrez 2002a, Heithaus and Dill 2002), suitable habitats (Carroll *et al.* 1999, Martin and da Silva 2004) and competitors (Ebensperger and Botto-Mahan 1997, Rushton *et al.* 1997, Bearzi 2005a). Current patterns of distribution may also reflect historic legacies left by, now absent, competition or predation (Connel 1980), including human-induced habitat destruction or past reduction in abundance (Whitehead *et al.* 1997, Hill 1999, Bearzi *et al.* 2004a, Gilg and Born 2005).

The distribution of a population may, in turn, impact many aspects of the lives of its members. Limited or clustered distribution of vital resources, such as prey, can attract many competitors. Inter- and intraspecific competition can lead to specialisation in prey selection (Hale *et al.* 2000, Saulitis *et al.* 2000), spatial or temporal segregation of members from the same breeding population (Weilgart *et al.* 1996, Le Boeuf *et al.* 2000) and can affect the patterns of social interactions (Emlen and Oring 1977, Wells *et al.* 1980). Members of similar species that co-occur in the same geographical area are thought to compete for resources, unless they occupy different physical locations and/or feed on different prey (Roughgarden 1976). In open habitats in particular, mixed groups or temporary inter-specific associations might form for protection against predators (Norris and Dohl 1980, Stensland *et al.* 2003). Studies on distribution patterns and co-occurrence of small cetaceans, the group of dolphins and porpoises, have revealed a range of strategies of co-occurrence based on habitat and resource partitioning (reviewed in Bearzi 2005b).

Obtaining detailed information on distribution patterns of cetaceans poses many problems, even for those species in more accessible inshore habitats. Cetaceans can travel quickly over large areas thus requiring repeat surveys to ascertain the temporal duration of their occurrence and to identify trends in distribution. Most species inhabit environments which pose, at least for a large proportion of the time, logistic (and financial) challenges for the researcher, particularly in areas with inclement or unstable weather conditions (i.e. most areas). For surveys conducted from ships, weather and resulting environmental conditions, such as sea state and swell, are crucial factors affecting the probability of detecting cetaceans (Barlow *et al.* 2001, Teilmann 2003). Detectability of animals also varies with body size, group size and behaviour (Barlow *et al.* 2001). Consequently, for many species information on even basic distribution patterns is, at best, patchy (Jefferson *et al.* 1993).

The endemic Chilean dolphin, *Cephalorhynchus eutropia*, is one of eight species of small cetaceans known to inhabit the inshore waters of southern Chile (Aguayo-Lobo *et al.* 1998). Its distributional range encompasses two main habitat types, the open coast and river mouths from 33° to 41°S, and the sheltered bays and channels of the Chiloé Archipelago and the fjords south to 56°S (Goodall *et al.* 1988a). The larger Peale's dolphin, *Lagenorhynchus australis*, is fully sympatric throughout this range. Its distribution, however, extends into the southern South Atlantic where the Peale's dolphin inhabits the exposed coast north to 38°S and reaches across the shallow continental shelf to the Falkland Islands (Goodall *et al.* 1997a).

Information on the distribution of Chilean dolphins is based entirely on anecdotal sightings, strandings and fossil finds (compiled in Goodall *et al.* 1988a). Most published information on Peale's dolphins stems from localized studies in the Strait of Magellan and Tierra del Fuego at the southern tip of South America (Iñíguez and de Haro 1993, de Haro and Iñíguez 1997, Goodall *et al.* 1997b, Lescrauwaet 1997, Schiavini *et al.* 1997, Viddi and Lescrauwaet 2005). The distribution of both species outside the Strait of Magellan (where Chilean dolphins are only seen infrequently (Goodall *et al.* 1988a) and the nature of their sympatric co-existence has not been subject to dedicated study. Anecdotal evidence from limited boat- and shore-based observations (Oporto and Gavilan 1990, Crovetto and Medina 1991, Goodall *et al.*

1997a) suggests that both species co-occur in the sheltered waters of the eastern Chiloé Archipelago in the 10th Region of Chile.

The 10th Region of Chile has experienced a rate of development in mariculture activities (e.g. the marine farming of salmonids and shellfish) unrivalled anywhere else in South America (Hernandez-Rodriguez *et al.* 2000), and contributes over 80% of the national production in Chile (SERNAPESCA 2004). In 2004, this region housed 273 registered salmon farms which produced 477,168 tons of fish (~ 84% of total Chilean production) and 305 shellfish farms which produced 81,741 tons (~ 77% of national production) (SERNAPESCA 2004). These intense and extensive farming activities in shallow nearshore waters undoubtedly have been affecting the local environment (Alvial 1991, Bushmann *et al.* 1996, Claude and Oporto 2000, Soto *et al.* 2001, Miranda and Zemelman 2002, Sepúlveda *et al.* 2004), possibly including the cetacean species inhabiting these waters (Hucke-Gaete 2000, Kemper *et al.* 2003).

In this chapter, the occurrence and distribution patterns of Chilean dolphins and Peale's dolphins in the southern and central Chiloé Archipelago and their overlap with existing and proposed mariculture activities are discussed.

2.3. METHODS

2.3.1. The study areas

This study was conducted in the coastal waters of the eastern Archipiélago de Isla Chiloé (41-43°S, 73-74°W) in southern Chile (10th Region). Most of the 130,000 inhabitants earn their living from peasant agriculture, artisanal fishing, tourism and in the rapidly expanding mariculture industry.

The southern study area was centred around the village of Yaldad (district Quellon) and encompassed the islands from San Pedro to Canal Chiguao (approx. 275 km²). Water depth throughout this area rarely exceeds 50 m (mean depth approx. 26 m). The central study area, located approximately 65 km to the north, was based around the ports of Castro and Dalcahue and spanned the inshore waters from Canal de Yal to Paso Tenaun (approx. 258 km²). Water depth reaches up to 130 m (mean approx. 50 m).

2.3.2. Data collection

The main fieldwork took place over consecutive austral summer and autumn seasons from January 2001 to April 2004 in southern Chiloé, and from December 2001 to April 2004 in central Chiloé. Off-season surveys were carried out from June to December 2004 to provide information on the winter distribution of Chilean dolphins.

Two or three observers conducted systematic boat-based sighting surveys in near-shore waters (≤ 2.5 km from shore) from a 3.8 m outboard powered (20 or 25 hp) inflatable boat travelling at a constant speed of ~ 19 km/h. Locally built wooden boats of 5-7 m length were used for off-season work. Surveys were restricted to calm seas of Beaufort sea state ≤ 3 , periods of no or little precipitation and generally good visibility. Observers continually scanned the area ahead of the boat and out to 90° each side.

In 2001 and during the off-season surveys in 2004, data were collected along predetermined transects paralleling the coast at approximately 400 m from shore. Surveys from December 2001 to April 2004 followed randomized transect lines in a regularly spaced zig-zag pattern with different starting points for each survey (part of a detailed investigation into habitat use, see Chapter three). Small bays and channels were covered completely either during the in- or outbound survey leg. Large bays, such as Bahia Quellon or Bahia Yaldad, were divided into opposite shores where one side to the centre was surveyed during the outbound leg in the morning, and the other during the inbound leg. The order in which adjacent bays or shorelines were surveyed was alternated between survey days (e.g. clockwise or counter-clockwise) to account for potential diurnal patterns in the distribution of the dolphins. A minimum of five to six survey days was required to cover each study area. The southern study area was surveyed completely at least once per month, and the central study area at least three times during a field season.

Locations with extensive coverage by shellfish farms limited access and visibility due to surface structures and floats. Shellfish farms were entered wherever possible and searched between suspended lines to ensure that dolphins were not missed inside the maze of floats.

Effort was logged throughout the survey by recording the position (GPS position and landmarks) at fixed 15-minute intervals, and from 2002 onwards additionally by using the automatic tracking function of the GPS. Sighting conditions were recorded at the start of each survey and thereafter whenever these changed.

When a sighting was made, the following data were recorded: start and end time of sighting, GPS location, landmarks, sighting conditions, species identity, group size (maximum, minimum, best estimates), presence of calves and neonates, a suite of environmental variables (e.g. depth, sea surface temperature), distance to the nearest mariculture structures (determined by laser range finder, < 1000 m) and initial behaviour.

A group was defined as an aggregation of dolphins which were within a radius of 100m of each other, spaced less than 10 body lengths apart. A calf was defined as a dolphin of about $1/3^{\rm rd}$ of the adult size and without foetal fold marks. A neonate was less than $1/3^{\rm rd}$ of the adult size, showed clear foetal fold marks and was seen in constant affiliation with an adult.

Behavioural states of dolphins in the group were assessed via scan sampling all individuals at first sighting (sensu Mann 2000), and before the dolphins were approached closely. Assessing individual, rather than group behaviour helped avoid biases introduced by more conspicuous surface-active behaviours of a few individuals in the group (Mann 2000). To investigate a possible relationship between behaviour and group size, overall group behaviour was later determined as the behaviour exhibited by

- > 50% of the group members (as determined from the scans of individuals). Behaviour was classified into one of six mutually exclusive states:
- ❖ Feed = Direct pursuit or taking of prey, either foraging individually (asynchronous swimming) or cooperatively (synchronous swimming) including long dives; The presence of potential prey was verified either by observing fish scattering away from the dolphins, the dolphins taking prey or the presence of seabirds "plunge diving" or consuming prey in the same location.
- ❖ Plough = Rapid directional surface swimming where dolphins produced splashes and "rooster tails". Individuals surfaced synchronously and moved rapidly in one or several offset lines, usually parallel to the shore. In Chilean dolphins this behaviour was most likely related to foraging as it appears to help aggregate prey (see Crovetto and Medina 1991). Plough differed from feeding because the presence of prey could not be inferred with certainty. In Peale's dolphins, however, plough could not be related to foraging behaviour unambiguously. The same "rooster tailing" was also observed during social interactions when the subject of the apparent "pursuit" was not prey. Other studies have interpreted similar behaviour as feeding (Viddi and Lescrauwaet 2005) or travelling (Goodall et al. 1997a).
- ❖ *Travel* = Moving in one direction and at constant speed with regular surfacings. No splashes or abrupt movements and no prolonged dives.
- ❖ *Mill* = Frequent changes in heading with no net displacement; Regular dives of varying duration. Most likely related to localized foraging, but presence of prey could not be confirmed.
- ❖ Socialize = Interactions between tightly aggregated individuals. Characterized by high levels of surface activity (e.g. leaps). Sexual and aggressive behaviours were included in this category.
- ❖ *Rest* = Stationary or very slow movement, often seen floating at the surface, interspersed with slow rolling surfacings.

2.3.3. Data analysis

The study areas were divided into sectors representing subareas within which effort was uniform (i.e. a subarea was covered completely during a survey day). These sectors provided the basic geographic unit over which spatially and temporally comparable indices for intensity of use, both in terms of occurrence and relative density of dolphins, were calculated. The choice of sector boundaries was guided entirely by practical considerations. Sectors were based on natural geographical units determined by physiogeographical differences (e.g. sheltered bays versus exposed shores) and reflected the survey layout designed to maximise area coverage without repeating routes during one survey day. A measure of occurrence in each sector was calculated as the proportion of positive observations (i.e. presence of dolphins) over the number of full surveys of that sector. Relative density in each sector was determined as the cumulative number of dolphins sighted in a particular sector divided by the distance searched on effort (in km) in this sector.

The spatial and temporal consistency of the observed patterns in occurrence was investigated using multiple logistic regression models built in the software package R, vers. 2.1. (R-DevelopmentCoreTeam 2004). The binary response variable (absence or presence of dolphins) had a binomial error structure and was modelled via a logit link function as a function of spatial (Sector) and temporal (Year) factors. The probability of sighting cetaceans is known to deteriorate with Beaufort sea state (Bft). Mean Bft for each sector (visited during a particular survey) was included as a co-variate and interaction term with Sector to investigate potential biases due to outer sectors being more exposed (i.e. potentially higher mean Bft) than sheltered bays.

Starting from a model with single terms of Sector, Year, mean Bft and two interaction terms (Sector: mean Bft, Sector: Year), the most parsimonious model was selected using a backward stepwise selection procedure based on Akaike's Information Criteria (Akaike 1973) corrected for small sample size, AIC_c (Burnham and Anderson 2002). The model with the lowest AIC_c-value, or if two models had similar AIC_c-values then the most parsimonious one, was chosen for parameter interpretation (Burnham and Anderson 2002) and to calculate predicted sighting probabilities.

Approximately 20 measurements of sea surface temperature (SST) were collected at fixed stations each month during the year-round sighting surveys in 2004 using a digital

conductivity-temperature meter. Months in which the mean (SST) exceeded the yearly average of 11.8°C (SE= 0.36) were termed "summer" (i.e. December to April), and those with lower temperatures "winter" (i.e. June to November). The highest mean monthly SST in 2004 was recorded in February (mean 13.1°C, SE= 0.15) and the lowest in July (mean 9.9°C, SE= 0.04). Temporal patterns of distribution within 2004 were investigated using logistic regression models (see above), but with "Season" (i.e. summer-winter) instead of "Year" as the temporal factor and with an extra interaction term "Season: mean Bft".

Potential annual (or summer-winter) differences in relative density were investigated using the Friedman test. This test is a non-parametric equivalent of a two-way ANOVA based on the consistency of ranks for particular treatments (i.e. sectors) across different blocks (i.e. years). The null-hypothesis that there was no consistent pattern in the ranks of sectors across years was rejected at the conventional $\alpha = 0.05$ level. Friedman tests and all other statistical analyses were performed in Minitab vers.12.23 (Minitab Inc, 1999). Data on species distribution and mariculture locations were plotted with ArcGIS vers.9 (ESRI Inc. 2004).

2.4. RESULTS

Boat-based sighting surveys were conducted on 212 days during summer and autumn spanning a four year period (154 days in southern Chiloé; 58 days in central Chiloé). Survey effort was consistent among years in both study areas (Kruskal Wallis test: southern, W= 5.02, df= 3, p= 0.171; central, W= 3.10, df= 2, p= 0.212), but differed significantly between sectors (Kruskal Wallis test: W= 61.26, df= 20, p< 0.001) (Table 2-1). Analyses of distribution patterns took into account spatial distribution of effort.

2.4.1. Chilean dolphins

2.4.1.1. Patterns of distribution

Chilean dolphins in southern Chiloé showed a spatially restricted distribution with preference for a few selected bays and channels (Figure 2-1). The model that fitted best the occurrence data (based on lowest AIC_c and residual deviance) contained the variables Sector, Year and mean Bft, and the interaction terms of "Sector: mean Bft" (Table 2-2). Fitted probabilities were calculated from the best model using the year 2004 and a mean Bft of 1.4 as standards (Figure 2-2). Chilean dolphins showed a distinct preference for northern Canal Coldita (NCC) and Canales San Pedro/Guamblad (SPE) where the probability of sighting a dolphin during the surveys was predicted at 80% and 95%, respectively. In contrast, Chilean dolphins were never or only rarely seen at western Isla Laitec (WLA), eastern Isla Coldita (ECO), Bahia Quellon (BQU) and Canal Chiguao (CCH). Wide confidence intervals of the fitted sighting probabilities reflected the variability in the sighting data. Beaufort sea state could have affected the detection of dolphins in some areas with lower rates of occurrences (PQU, SCC and BHU), but did not result in a spatial bias in detection of dolphins between sheltered bays and exposed shores. Annual variation in occurrence of dolphins was also low, with only the year 2002 having overall lower sighting probabilities.

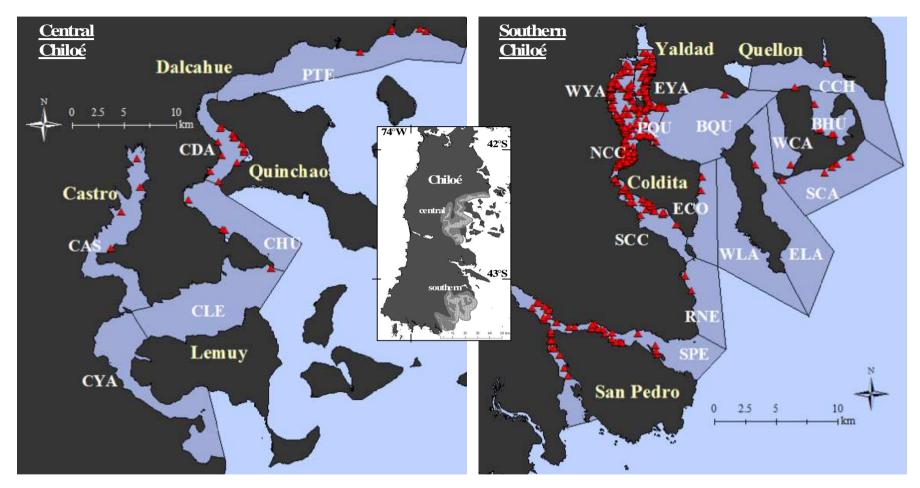


Figure 2-1. Sighting locations of Chilean dolphins (red triangles; n= 378) in the Chiloé Archipelago from 2001 to 2004 (uncorrected for effort). Sectors are shown in dark blue with corresponding three letter labels.

Table 2-1. Summary of survey effort and sightings of Chilean dolphins and Peale's dolphins in different sectors in southern (a) and central (b) Chiloé during austral summers and autumns of 2001-2004. For sizes of sectors see Table 2-8.

a) southern Chiloé (2001-2004)

Sector code	Sector description	Number of surveys	Distance surveyed (km)	Groups of Chilean dolphins	Number of Chilean dolphins	Groups of Peale's dolphins	Number of Peale's dolphins
EYA	East Yaldad Bay	138	1,266	90	547	0	0
WYA	West Yaldad Bay	103	952	72	445	0	0
NCC	northern Canal Coldita	62	496	82	546	0	0
PQU	P. Queupué /Isla Linagua	65	290	14	121	4	6
SCC	southern Canal Coldita	42	584	31	178	4	13
ECO	East Isla Coldita	41	376	2	3	10	27
RNE	Rio Negro/P. Yatac	23	229	2	3	0	0
SPE	C. San Pedro/Guamblad	24	829	47	303	0	0
WLA	West Isla Laitec	29	442	0	0	15	69
BQU	Bahia Quellon	104	1,300	2	12	41	135
ELA	East Isla Laitec	41	520	1	3	16	70
WCA	West Isla Cailin	28	194	1	1	7	14
SCA	South Isla Cailin	18	255	7	32	16	67
BHU	Bahia Huellenquon	18	159	5	15	0	0
CCH	Canal Chiguao	33	452	2	5	11	40
	Total	769	8,346	350	2,072	124	441

b) central Chiloé (2002-2004)

Sector code	Sector description	Number of surveys	Distance surveyed (km)	Groups of Chilean dolphins	Number of Chilean dolphins	Groups of Peale's dolphins	Number of Peale's dolphins
CYA	Canal de Yal	7	483	0	0	0	0
CAS	Estero Castro	27	1,217	4	14	31	165
CHU	Canal Hudson	19	479	3	12	16	69
CLE	Canal Lemuy	16	460	1	6	4	15
CDA	Canal Dalcahue	28	769	14	58	62	316
PTE	Paso Tenaun	7	483	6	32	2	6
	Total	104	3,891	28	122	115	571

Table 2-2. Summary results of the final logistic regression model for Chilean dolphins in southern Chiloé. Sector and Year were considered as factors.

* significant at p= 0.05, ** significant at p= 0.001, \blacklozenge no sighting	* significant at	p = 0.05, *	* significant at	p = 0.001,	no sighting
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Variable	Level	coefficient	SE	z-value	Pr(> z)	
Sector	EYA	0.540	0.3684	1.465	0.143	
	WAY	0.457	0.4490	1.017	0.309	
	NCC	2.047	0.7070	2.896	0.004	*
	PQU	0.822	0.6269	1.311	0.190	
	SCC	1.874	0.7648	2.451	0.014	*
	ECO	-2.217	1.2539	-1.768	0.077	
	RNE	-0.215	1.6528	0.130	0.897	
	SPE	6.412	4.0574	1.580	0.014	*
	WLA	-17.260	2397.3	-0.007	0.994	*
	BHU	-0.493	0.8665	-0.569	0.569	
	ELA	-0.572	2.1462	-0.266	0.790	
	WCA	-4.362	2.9334	-1.487	0.137	
	SCA	0.096	1.3070	0.073	0.942	
	BHU	1.089	1.4855	0.733	0.464	
	CCH	-6.668	3.4428	-1.937	0.053	
Year	2002	-0.823	0.2842	-2.895	0.004	*
	2003	-0.312	0.2954	-1.055	0.292	
	2004	-0.009	0.3454	-0.027	0.978	
Bft		0.162	0.2552	0.636	0.525	
Interaction	WAY: Bft	-0.035	0.3669	-0.096	0.924	
	NCC: Bft	-0.446	0.4911	-0.908	0.364	
	PQU: Bft	-1.600	0.5855	-2.733	0.006	*
	SCC: Bft	-0.980	0.4804	-2.041	0.041	*
	ECO: Bft	-1.256	1.3747	-0.914	0.361	
	RNE: Bft	-1.660	1.2964	-1.281	0.200	
	SPE: Bft	-2.673	2.3575	-1.134	0.257	
	WLA: Bft	-0.145	1427.1	0.000	1.000	*
	BHU: Bft	-2.913	1.2886	-2.260	0.024	*
	ELA: Bft	-1.980	1.8118	-1.093	0.274	
	WCA: Bft	0.792	1.4161	0.559	0.576	
	SCA: Bft	-0.471	0.8536	-0.552	0.581	
	BHU: Bft	-1.251	0.9564	-1.308	0.191	
	CCH: Bft	1.951	1.4242	1.370	0.171	

Null deviance: 838.71 on 605 degrees of freedom Residual deviance: 512.68 on 572 degrees of freedom

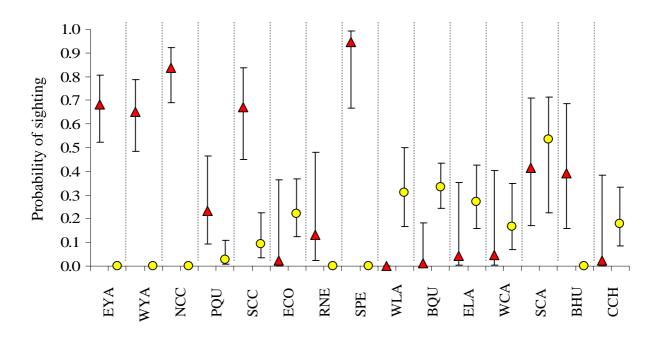


Figure 2-2. Fitted probabilities of sighting Chilean dolphins (red triangles) and Peale's dolphins (yellow circles) in different sectors in southern Chiloé based on the predictions from the best logistic regression models. Error bars denote 95% confidence intervals.

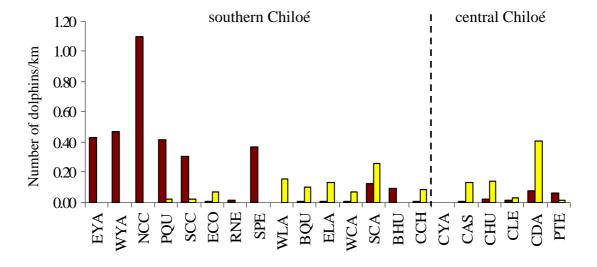


Figure 2-3. Relative density of Chilean dolphins (red bars) and Peale's dolphins (yellow bars) in sectors surveyed in southern (2001-2004) and central (2002-2003) Chiloé.

The relative density of dolphins showed the same pattern as occurrence with relative density being highest in northern Canal Coldita (NCC) and surrounding sectors as well as in Canales San Pedro/Guamblad (SPE) (Figure 2-3, Table 2-1). This pattern was also consistent between years (Friedman test: $\chi^2 = 50.6$, df= 14, p< 0.001).

When comparing year-round sighting data from 2004, the same distributional pattern persisted (Table 2-3). The relative density of dolphins was highest in northern Canal Coldita (NCC) throughout the year (Figure 2-4), followed by the sectors to the northeast (PQU and EYA). This pattern was consistent during summer and winter (Friedman test $\chi^2 = 17.49$, df= 6, p= 0.008).

Table 2-3. Summary of effort and number of Chilean dolphins sighted during the monthly surveys of selected sectors in southern Chiloé during 2004.

Sector Code	Sector description	Numb	er of surv (km sur	Number of Chilean dolphins			
Code		Sun	nmer	W	inter	Summer	Winter
EYA	East Yaldad Bay	35	(264)	11	(157)	140	31
WYA	West Yaldad Bay	20	(136)	9	(120)	88	20
NCC	northern Canal Coldita	19	(115)	10	(101)	145	87
PQU	P. Queupué -Isla Linagua	24	(59)	9	(33)	26	17
SCC	southern Canal Coldita	4	(56)	4	(62)	20	8
ECO	East Isla Coldita	8	(96)	4	(46)	3	1
BQU*	Bahia Quellon*	24	(259)	4	(39)	0	0
	Total	134	(985)	51	(558)	422	164

^{*}Only the western most section was covered each month (approx. $1/3^{rd}$ of BQU).

The model that fitted best the seasonal occurrence data contained the variables Sector, Season and Bft (Table 2-4). The variable Season was retained in the final model (selected based on the lowest AIC_c value) despite not being significant. The limited survey effort in winter could have masked significant seasonal effects. There was evidence that mean Bft influenced presence, or more likely the observer's ability to detect dolphins, but this effect did not differ between sectors or seasons (i.e. the non-significant interaction terms "Sector: mean Bft" and "Season: mean Bft" were not retained in the final model).

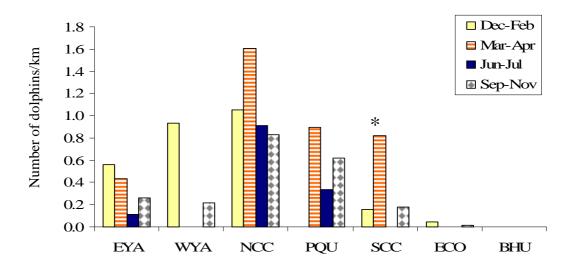


Figure 2-4. Seasonal pattern of relative density of Chilean dolphins in selected sectors in southern Chiloé surveyed at least once during each 3-month period.

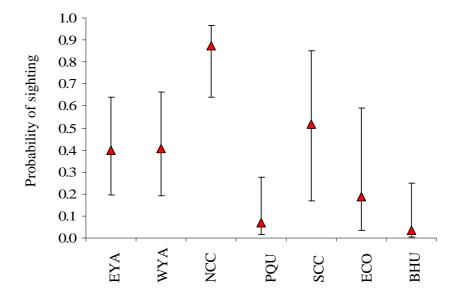


Figure 2-5. Fitted probabilities of sighting Chilean dolphins in different sectors in southern Chiloé throughout the year 2004 based on the predictions from the best logistic regression model, with winter and mean Bft= 1.6 set as standards. Error bars denote 95% confidence intervals.

^{*} is based on one effort day with a single group of 14 dolphins.

Fitted probabilities were calculated from the final model using winter and a mean Bft of 1.6 as standards (Figure 2-5). Sighting probabilities and the pattern of occurrence were similar to those derived from the annual summer/autumn data. Again, northern Canal Coldita (NCC) had by far the highest probability of dolphin occurrence throughout the year. Chilean dolphins were more regularly encountered in Yaldad Bay (EYA, WYA) in the summer than during the winter which was reflected in the large variability in the fitted values. The large variability in the fitted values for SCC most likely stems from the low effort in this sector (Table 2-3).

Table 2-4. Summary results of the final logistic regression model for the year-round occurrence of Chilean dolphins in selected sectors in southern Chiloé during 2004. Sector and Season were considered as factors.

* significant at p= 0.05, ** significant at p= 0.001

Variable	Level	coefficient	SE	z-value	Pr(> z)	
Sector	EYA	1.597	0.5763	2.771	0.006	*
	WAY	1.635	0.6526	2.505	0.012	*
	NCC	3.965	0.935	4.241	0.000	**
	PQU	-0.570	0.9052	-0.63	0.529	
	SCC	2.086	1.0035	2.079	0.038	*
	ECO	0.545	0.9998	0.545	0.586	
	BHU	-1.344	1.1091	-1.212	0.226	
Season	Winter	-0.763	0.4758	-1.604	0.109	
Bft		-0.782	0.2604	-3.005	0.003	*

Null deviance: 188.54 on 136 degrees of freedom Residual deviance: 128.53 on 127 degrees of freedom

Only 28 groups of Chilean dolphins were sighted in central Chiloé (Table 2.1b, Figure 2-1). The model that best fitted the occurrence data contained only the variable Sector (Table 2-5). Chilean dolphins were absent from Canal de Yal (CYA). Canal Dalcahue (CDA) had by far the largest number of sightings (Table 2-1b), and consequently had relatively high, but variable, predicted probabilities of occurrence (Table 2-5, Figure 2-6). Estero Castro (CAS), Canal Hudson (CHU) and Canal Lemuy (CLE) had relatively low predicted probabilities of occurrence (Figure 2-6). Although Chilean dolphins used these sectors, they were sighted less than would be expected given the level of survey effort (Table 2-5). The large variability in the predicted probability of occurrence at Paso Tenaun (PTE) most likely resulted from low survey effort in this area (Table 2-1b, Figure 2-6).

Table 2-5. Summary results of the final logistic regression model for Chilean dolphins in central Chiloé. Sector was considered as a factor.

* significant at	p = 0.05, *	* significant at	p = 0.001.	no sightings
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Variable	Level	coefficient	SE	z-value	Pr(> z)	
Sector	CYA	-17.566	1615.104	-0.011	0.991	*
	CAS	-1.179	0.5718	-2.061	0.039	*
	CHU	-1.792	0.7638	-2.346	0.019	*
	CLE	-2.197	1.0541	-2.084	0.037	*
	CDA	1.099	0.6667	1.648	0.099	
	PTE	0.288	0.7638	0.377	0.706	

Null deviance: 148.33 on 107 degrees of freedom Residual deviance: 90.06 on 101 degrees of freedom

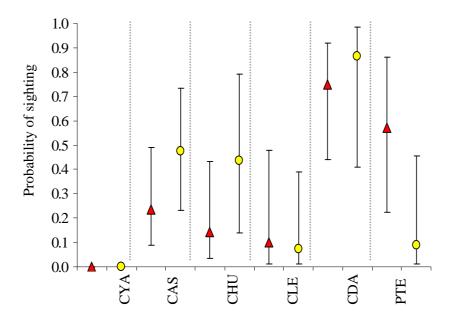


Figure 2-6. Fitted probabilities of sighting Chilean dolphins (red triangles) and Peale's dolphins (yellow circles) in different sectors in central Chiloé based on the predictions from the best logistic regression models. Error bars denote 95% confidence intervals.

2.4.1.2. Group sizes and offspring

Sighting rates were four-fold larger in the southern than in the central study area (Figure 2-7a). Mean group size was also larger in southern than in central Chiloé (t = -2.85, p= 0.007) (Figure 2-7b), but estimates for the central area were based on a small sample size (Table 2-1b). Group size varied significantly with behaviour (ANOVA $F_{5,336}$ = 13.34, p< 0.001), with the largest groups observed feeding (mean= 8.6 ± 0.84 SE) and the smallest travelling (mean= 3.8 ± 0.29 SE) (Figure 2-8a).

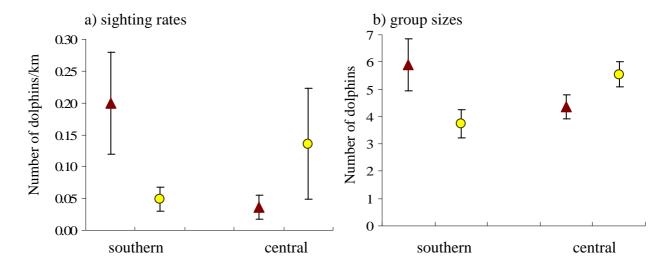


Figure 2-7. Mean sighting rates (a) and mean group sizes (b) of Chilean dolphins (red triangles) and Peale's dolphins (yellow circles) in southern (2001-2004) and central (2002-2003) Chiloé. Error bars denote 95% confidence intervals.

Neonates were sighted from late spring (November) into the autumn (April), but not during winter. In February, up to four neonates and three calves were observed in the same group. Calves were sighted year round, but more regularly so in March and April. By April (early autumn), 75% of all groups (n= 66) contained at least one calf and/or neonate. In contrast, from September to November (spring), only 25% of all groups contained at least one calf. Neonates and calves were sighted in all sectors used regularly by adult Chilean dolphins with no obvious preference for a particular location.

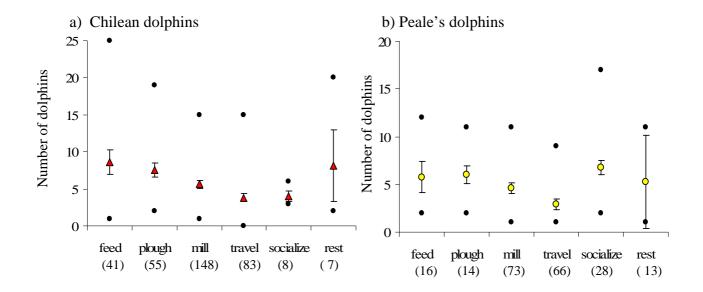


Figure 2-8. Variation in mean group size in relation to behavioural state for Chilean dolphins (a) and Peale's dolphins (b). The number of groups observed is given in brackets. Error bars denote 95% confidence intervals, dots represent range.

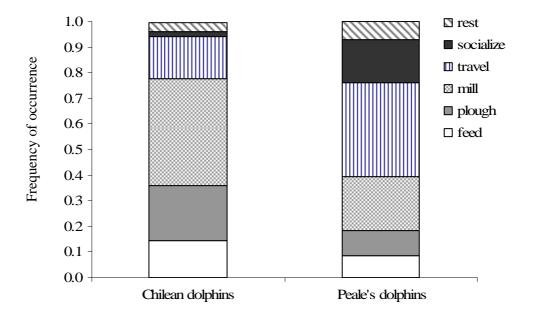


Figure 2-9. Behaviour of Chilean dolphins and Peale's dolphins, calculated as the proportion of dolphins observed in each of the six behavioural states during instantaneous scans at the onset of each sighting.

2.4.1.3. Behavioural patterns

The behaviour of Chilean dolphins at initial sighting was markedly non-uniform (Pearson's χ^2 = 1290.9, df= 5, p-value < 0.001) with milling being the predominant behavioural state (42% of 2,028 dolphins), followed by plough (21%), travelling (17%) and feeding (14%) (Figure 2-9). This pattern in behaviour was consistent across sectors in southern Chiloé (Friedman test, χ^2 = 30.6, df= 5, p < 0.001). In central Chiloé, behaviours differed between sectors (Friedman test, χ^2 = 9.75, df= 5, p = 0.083) with milling being the predominant behavioural state in Canal Dalcahue (CDA, 40%), in contrast to travelling in Paso Tenaun (PTE, 42%) and Canal Hudson (CHU, 38%).

2.4.2. Peale's dolphins

2.4.2.1. Patterns of distribution

Peale's dolphins were encountered in southern and central Chiloé, but did not distribute uniformly in either area (Table 2-1a, Figure 2-10). The final model that best fitted the occurrence data for Peale's dolphins in southern Chiloé contained only the variable Sector (Table 2-6). Peale's dolphins were markedly absent from areas of known high use by Chilean dolphin, i.e. Yaldad Bay (EYA, WYA), northern Canal Coldita (NCC), Canal San Pedro/Guamblad (CSP) and Bahia Huellenquon (BHU). Instead, they seemed to frequent the open shores of east Isla Coldita (ECO), Isla Laitec (WLA, ELA), Bahia Quellon (BQU) and the shoals of southern Cailin (SCA) (Figure 2-10). However, none of these areas were used significantly more often than would be expected from an equal chance of presence or absence during the given level of survey effort (Table 2-6, Figure 2-2).

In central Chiloé, Peale's dolphins were mainly seen in three sectors: Estero Castro (CAS), Canal Hudson (CHU) and Canal Dalcahue (CDA), and were absent from Canal de Yal (CYA) (Table 2-1b, Figure 2-10). The best model to fit the occurrence data contained the variables Sector and Year (Table 2-6). Peale's dolphins had a high predicted probability of occurrence in Canal Dalcahue (CDA) (Figure 2-6), but estimates were quite variable and overall observed occurrence in this sector was not significantly different from chance (Table 2-6). Peale's dolphins were frequently sighted in the Estero Castro (CAS) and Canal Hudson (CHU), but occurrence again was variable and with a tendency to be lower than would be expected given the amount of survey effort in this area (Table 2-6, Figure 2-6). There was also evidence for intra-

annual variability with the year 2003 showing a significantly higher occurrence of dolphins compared to 2002.

Although occurrence did not show a clear pattern of preference by dolphins for any sector in both study areas, relative densities were consistently highest in Canal Dalcahue (CDA) in the central, and off southern Isla Cailin (SCA) in the southern study area (Figure 2-3). The ranking of sectors based on relative densities was consistent between years in both study areas (Friedman tests: southern, $\chi^2 = 44.21$, df= 14, p< 0.001; central, $\chi^2 = 8.38$, df=3, p= 0.039).

2.4.2.2. Group sizes and offspring

For Peale's dolphins, group sizes were significantly smaller in southern compared to central Chiloé (t= 5.1, p< 0.001) (Figure 2-7b). Group size varied significantly with behavioural state (ANOVA $F_{5,204}$ = 12.77, p< 0.001) with the largest groups observed socializing (mean= 6.8 ± 0.60 SE) and the smallest travelling (mean= 2.9 ± 0.23 SE) (Figure 2-8b).

Neonates were seen throughout the summer and autumn (December – April). In March, 42 % of all groups (n= 33) contained at least one calf and/or neonate. Surveys during winter 2004 included few sectors of known regular use by Peale's dolphins. Six groups, including one calf, were recorded off north-eastern Coldita (Sectors PQU, BQU) during early spring (September). Calves were sighted in all sectors where adult Peale's dolphins were seen. Very small neonates (i.e. most likely only a few days old) were sighted mainly at four distinct locations in southern Chiloé (n= 9) consisting of small embayments or rocky outcrops with some kelp (*Macrocystes pyrifera*): Punta White in sector West Laitec (WLA), Trincao to Quellon Viejo in sector Bahia Quellon (BQU), off Punta Queupué (PQU) and along the shores of eastern Isla Coldita (ECO). All mother-neonate pairs were wary and remained within 50 m of the shore and in water less than 3 m deep.

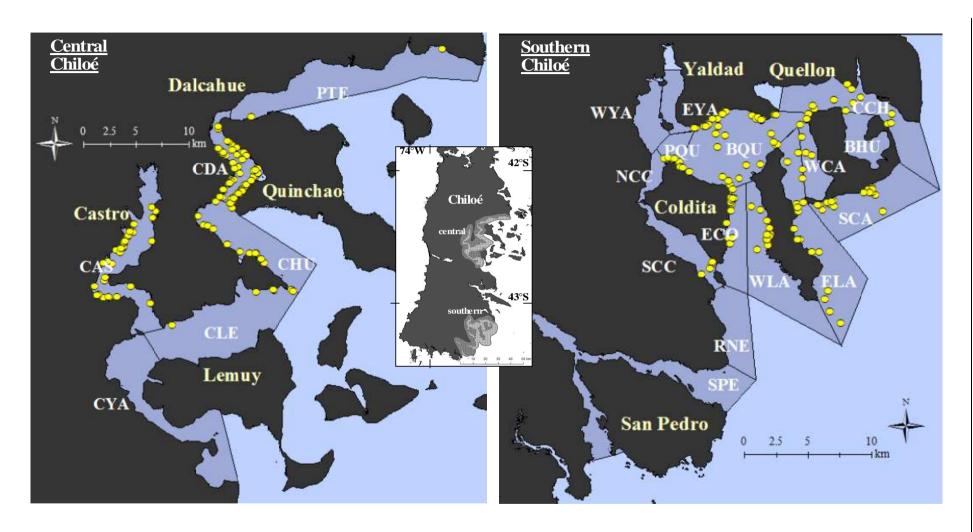


Figure 2-10. Sighting locations of Peale's dolphins (yellow circles; n= 239) in the Chiloé Archipelago from 2001 to 2004 (uncorrected for effort). Sectors are shown in dark blue with corresponding three letter labels.

Table 2-6. Summary results of the final logistic regression models for Peale's dolphins in southern (a) and central (b) Chiloé.

Sector and Year were considered as factors.

a) southern Chiloé

Variable	Level	coefficient	SE	z-value	Pr(> z)	
Sector	EYA	-20.566	1472.4271	-0.014	0.989	*
	WAY	-20.566	1682.8922	-0.012	0.990	*
	NCC	-20.566	2182.4577	-0.009	0.992	*
	PQU	-3.526	0.7174	-4.915	0.000	**
	SCC	-2.277	0.5250	-4.338	0.000	**
	ECO	-1.253	0.3586	-3.494	0.000	**
	RNE	-20.566	3780.1276	-0.005	0.996	*
	SPE	-20.566	4179.0883	-0.005	0.996	*
	WLA	-0.799	0.4014	-1.989	0.047	*
	BHU	-0.693	0.2165	-3.202	0.001	*
	ELA	-0.981	0.3385	-2.898	0.004	*
	WCA	-1.609	0.4899	-3.285	0.001	*
	SCA	0.1335	0.5175	0.258	0.493	
	BHU	-20.566	4179.0883	-0.005	0.996	*
	CCH	-1.520	0.4173	-3.642	0.000	**

Null deviance: 852.57 on 615 degrees of freedom Residual deviance: 333.99 on 600 degrees of freedom

b) central Chiloé

Variable	Level	coefficient	SE	z-value	Pr(> z)	
Sector	CYA	-18.952	1468.02	-0.013	0.990	*
	CAS	-0.095	0.5559	-0.172	0.864	
	CHU	-0.250	0.7878	-0.318	0.751	
	CLE	-2.533	1.0447	-2.424	0.015	*
	CDA	1.870	1.1201	1.670	0.095	
	PTE	-2.330	1.0790	-2.160	0.031	*
Year	2003	2.161	0.7727	2.796	0.005	*
	2004	1.093	0.9663	1.132	0.258	

Null deviance: 108.13 on 78 degrees of freedom Residual deviance: 63.48 on 70 degrees of freedom

^{*} significant at p= 0.05, ** significant at p= 0.001, ♦ no sightings

2.4.2.3. Behavioural patterns

Behaviour states differed significantly in the frequency with which they were observed (in southern Chiloé: $\chi^2 = 190.95$, df = 5, p < 0.001; in central Chiloé: $\chi^2 = 183.91$, df= 5, p < 0.001). Peale's dolphins exhibited the same behaviour patterns in both study areas (Mann Whitney test, W= 35.0, p= 0.809) and data were pooled for comparison with Chilean dolphins (Figure 2-9). Travelling was always the predominant behaviour (37%), followed by milling (21%) and socializing (17%) (Figure 2-9).

2.4.3. Comparing Chilean dolphins and Peale's dolphins

There was very little spatial overlap between Chilean dolphins and Peale's dolphins (Figures 2-2, 2-3, 2-11, Table 2-1). Both species differed markedly in their preference for sectors (Friedman tests; southern: $\chi^2 = 4.96$, df= 14, p= 0.986; central: $\chi^2 = 7.75$, df= 5, p= 0.170). Overall, sighting rates were significantly higher for Chilean dolphins compared to Peale's dolphins in southern, but not in central Chiloé (Mann Whitney tests: W= 4103.5, p= 0.010 and W= 227.0, p= 0.162, respectively) (Figure 2-7a). Group sizes also differed significantly between species and showed a reversed trend in the two study areas (Figure 2-7b).

Occurrence of behavioural states differed significantly between species ($\chi^2 = 1209.9$, df= 5, p< 0.001), with Chilean dolphins seen more frequently engaged in feed/plough/mill (i.e. most likely foraging related) behaviours than Peale's dolphins (Figure 2-9). Only nine incidences of temporal co-occurrence of both species were observed. The nature of the interactions ranged from mixed groups to neutral passes to potentially aggressive encounters (Table 2-7). All observed interactions, even the formation of mixed groups, did not last longer than 10 minutes before the two species appeared spatially separated again or engaged in different behaviours.

Table 2-7. Summary of all incidences of temporal co-occurrence of Chilean dolphin and Peale's dolphin groups observed during this study.

Date	Sector	Chilean dolphin (C.e.)	Peale's dolphins (<i>L.a.</i>)	Type of interaction
19 Feb 2001	SCC	5 + 1 calf: milling	6: travelling	none, within 100 m
23 Mar 2001	BQU	2: travelling	1: travelling	none, within 500 m
15 Apr 2002	SCC	3 + 1 calf: travelling	3 + 1 calf: travelling	none, within 300 m
08 Jan 2003	CDA	4: milling	5: travelling	none, within 100 m
04 Jan 2003	CAS	2: foraging	6: foraging	mixed group
12 Jan 2004	ECO	2 + 1 neonate: travelling	2 + 1 neonate: travelling	mixed for 10 min.
19 Mar 2004	CDA	2: socializing, then foraging	4: foraging	<i>C.e.</i> joined <i>L.a.</i> , foraging as mixed group for 5 min.
21 Mar 2002	CHU	5 + 1 calf: milling	6 + 2 calves: travelling	aggressive? <i>C.e.</i> left area at great speed
09 Feb 2004	PTE	7 + 1 calf: travelling (slow)	4: resting	aggressive? <i>C.e.</i> passed by <i>L.a.</i> ; one <i>L.a.</i> actively pursued <i>C.e.</i> ; <i>C.e.</i> started splashy fast travel (continued for > 4 km)

2.4.4. Sightings of other cetaceans and spatial segregation

One other cetacean species was encountered during this study: the Burmeister's porpoise, *Phocoena spinipinnis* (see photos Appendix I). A total of 18 sightings were made over four years, all of which were restricted to two small areas in central Chiloé (sectors Canal Hudson CHU, Canal Dalcahue CDA, Paso Tenaun PTE) (Figure 2-11). Group sizes ranged from one to five individuals (mean= 3 ± 0.5 SE), with four calves and one neonate seen in separate groups from February to April.

There was evidence for small-scale segregation between dolphins and porpoises (Figure 2-11). Burmeister's porpoises were consistently found in much deeper waters than the dolphins (Figure 2-12). Pairwise-comparisons of median water depth suggest spatial partitioning based on water depth with Burmeister's porpoises using significantly deeper waters than Chilean dolphins (Mann-Whitney test, W = 5650, p< 0.001). Chilean dolphins in turn seemed to prefer a wider range in shallow waters than Peale's dolphins (Mann-Whitney test, W = 101,669, p< 0.001).

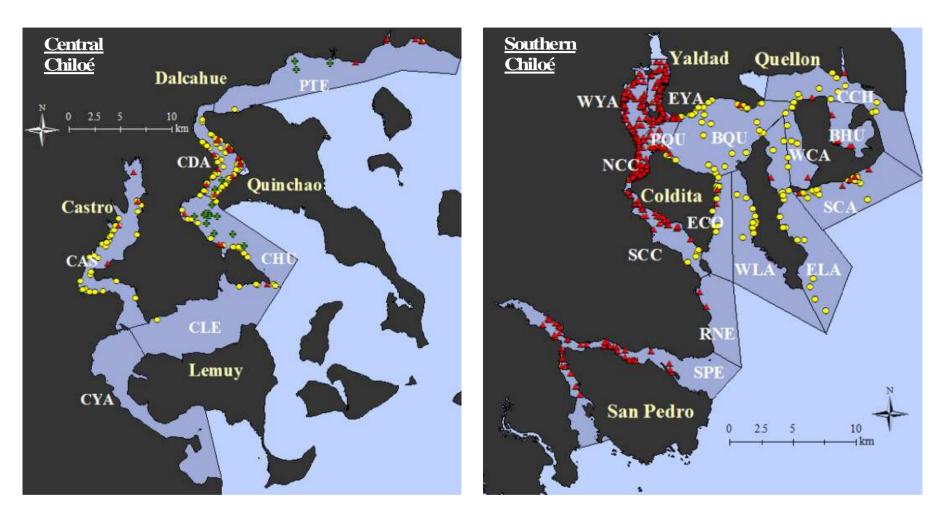


Figure 2-11. Distribution of small cetaceans in the Chiloé Archipelago (42-43° S, 74°W). Chilean dolphins = red triangles; Peale's dolphins = yellow circles; Burmeister's porpoises = green crosses. Sectors are shown in dark blue with corresponding three letter labels.

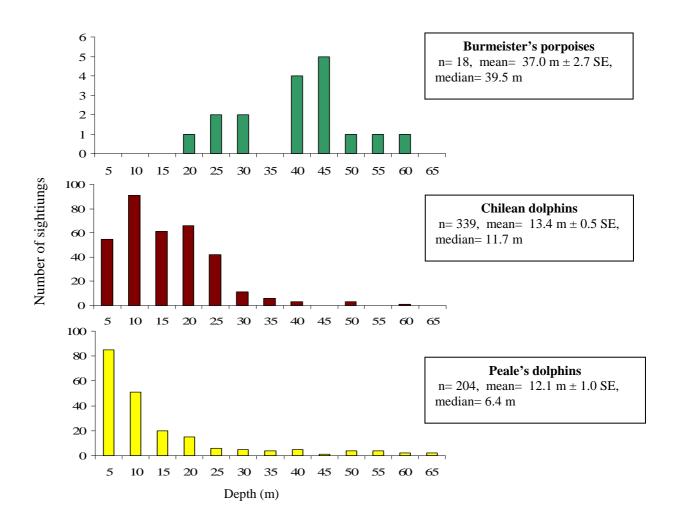


Figure 2-12. Differences in depth range for small cetaceans in the Chiloé Archipelago.

2.4.5. Overlap with mariculture

Mariculture activities were abundant throughout the study areas (Figure 2-13), covering approx. 2 to 5% of coastal waters (Table 2-8). The distribution of Chilean dolphins overlapped extensively with areas used by shellfish farms (sectors EYA, WYA, BHU, CDA) and salmon farms (sectors SPE, SCC, CDA) (Figure 2-14). Other human activities in their range included small-scale artisanal gillnetting (mainly targeting escaped farmed salmonids) with nets placed perpendicular to the shore across the intertidal zone (sectors EYA, NCC, SCC).

The distribution of Peale's dolphins also overlapped with shellfish farms and salmon farms, mostly in central Chiloé (Figure 2-14). Other human activities in their range include shipping traffic and extraction of marine invertebrates from shallow shoals of Islas Laitec (ELA, WLA) and Cailin (SCA) in southern Chiloé (Table 2-8).

Direct interactions with shellfish and salmon farms were not observed for either species, during 140 and 77 hours spent in direct observation of Chilean dolphins and Peale's dolphins, respectively. Only five groups (one Peale's d., four Chilean d.) were seen within 100 m of salmon farm structures, and all appeared to be travelling. Four groups of Peale's dolphins were seen travelling within 100 m of shellfish farms, and one group foraged between the shore and the outer lines of a large shellfish farm. Most observations (80%, n= 37 groups) of Chilean dolphins that were within 100 m of shellfish farms were logged in Yaldad Bay, the area with proportionally the largest coverage by shellfish farms (Figure 2-15, Table 2-8). Chilean dolphins were frequently observed feeding on small schooling fish on the shoreward side outside the shellfish farms (46%, n= 37 groups). Nine groups were observed in open spaces between densely placed sets of growth lines, and in seven instances dolphins appeared to cross under suspended lines and floats. It is not known whether these lines carried vertically suspended growth lines or consisted only of the suspension line held at the surface by polystyrene or make-shift floats (Figure 2-15).

Table 2-8. Extent of mariculture activities in southern (a) and central (b) Chiloé. Information on number and size of concessioned farming areas was adapted from a list compiled by the Chilean Subsecretaria de Pesca (Anon. 2001)¹, updated until October 2001. The list of other anthropogenic activities is based on field observations.

SG = shorebased gillnets;
 SCh = shipping channel (e.g. for ferries);
 AF = artisanal fishing;
 EMI = extraction of marine invertebrates (e.g. boat-based diving for sea urchins and shellfish on natural banks)

a) southern Chiloé

Sector code	Sector description	Sector size (km²)	Number of concessions	Area for shellfish (km²)	Area for salmonidae (km²)	% of sector licensed for mariculture	Other anthropog. activities
EYA	East Yaldad Bay	6.56	13	0.77	-	12	SG
WYA	West Yaldad Bay	9.58	7	0.27	0.07	4	-
NCC	northern Canal Coldita	3.76	-	-	-	0	SG
PQU	P. Queupué –I. Linagua	4.38	1	-	0.04	1	-
SCC	southern Canal Coldita	11.09	2	-	0.30	3	SG?
ECO	East Isla Coldita	13.85	-	-	-	0	SCh
RNE	R. Negro /P. Yatac	15.65	1	-	0.05	0.3	-
SPE	C. S. Pedro + Guamblad	32.67	8	0.31	0.33	2	-
WLA	West Isla Laitec	29.09	2	-	0.29	1	SCh, EMI
BQU	Bahia Quellon	37.54	11	0.80	0.10	2	SCh
ELA	East Isla Laitec	36.18	1	-	0.12	0.3	EMI
WCA	West Isla Cailin	8.86	2	0.02	0.15	2	-
SCA	South Isla Cailin	25.83	-	-	-	0	EMI
BHU	Bahia Huellenquon	9.60	10	0.61	0.22	9	-
ССН	Canal Chiguao	29.40	13	0.15	0.15	12	SCh
	Total	274.04	63	2.92	1.82	2	

b) central Chiloé

Sector code	Sector description	Size (km²)	Number of concessions	Area for shellfish (km²)	Area for salmonidae (km²)	% of sector licensed for mariculture	Other known activities
CYA	Canal de Yal	47.98	42	2.37	2.67	11	-
CAS	Estero Castro	37.15	17	0.12	0.89	3	SCh
CHU	Canal Hudson	35.57	12	0.67	1.99	7	SCh
CLE	Canal Lemuy	58.24	16	0.62	1.09	3	SCh
CDA	Canal Dalcahue	16.62	13	0.12	0.89	6	(SCh)
PTE	Paso Tenaun	62.06	22	0.66	1.08	3	AF
	Total	257.62	122	4.56	8.60	5	

¹ Anon. 2001. Listado de Concesiones de Acuicultura. Subsecretaria de Pesca, Gobierno de Chile. Available from http://www.sernapesca.cl.

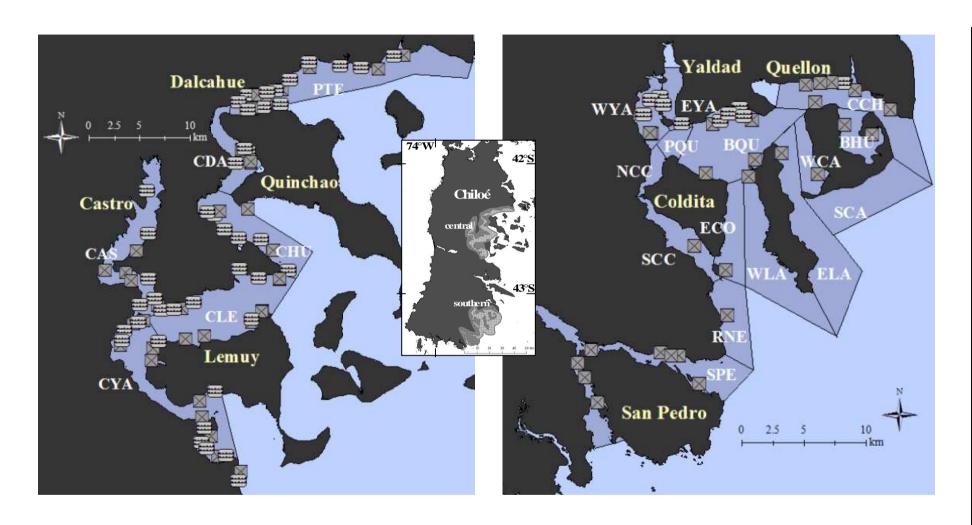


Figure 2-13. Distribution of shellfish farms (> 10 longlines: grey box with lines) and salmonid farms (grey square with cross) in the Chiloé Archipelago. Note: Symbols do not represent individual concessions and are not to scale. Sectors are shown in dark blue with corresponding three letter labels. See Table 2-8 for further details.

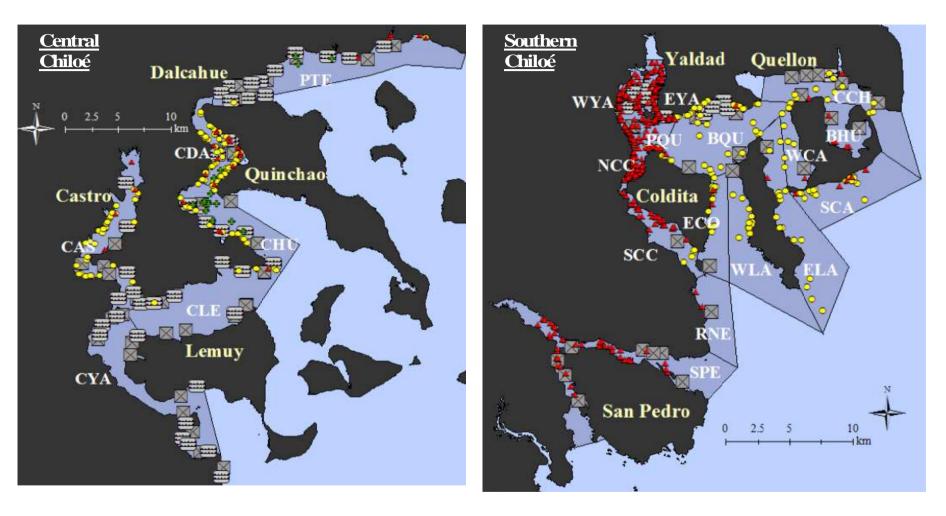


Figure 2-14. Spatial overlap between small cetaceans and mariculture activities in the Chiloé Archipelago (42-43° S, 74°W). Chilean dolphins = red triangles; Peale's dolphins = yellow circles; Burmeister's porpoises = green crosses; Salmonid farm = grey squares with cross; Shellfish farm (> 10 growth lines) = grey boxes with lines. Note: Symbols for salmonid and shellfish farms do not represent individual concessions and are not to scale. Sectors are shown in dark blue with corresponding three letter

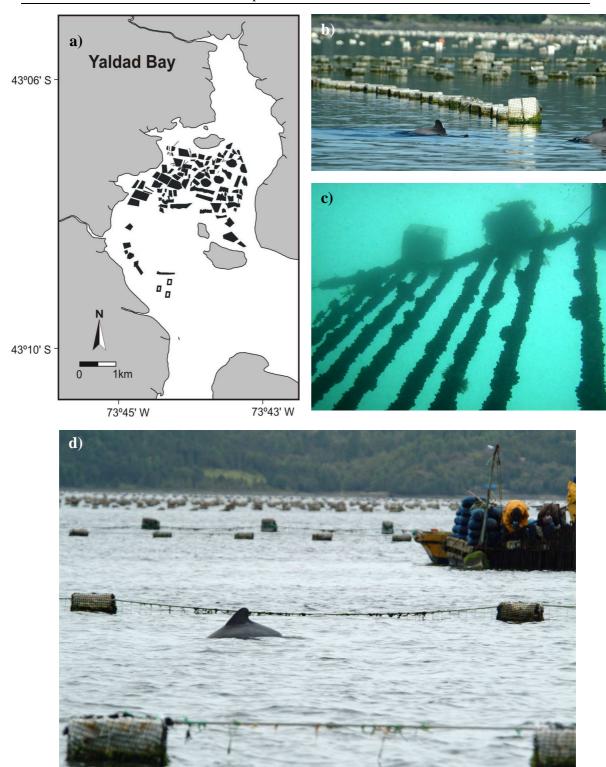


Figure 2-15. Shellfish (*Mytilus chilensis*) farms in Yaldad Bay, southern Chile. **a)** Overview of location and extent of farms (dark blocks) in April 2001 as determined by theodolite readings (adapted with permission from Ribeiro *et al.* 2005):

- **b**) Chilean dolphins in front of capture longlines (photo: S. Heinrich);
- **c**) Underwater view of mussel capture lines suspended from horizontal longlines (photo: D. Schories);
- **d)** Chilean dolphin travelling between empty longlines where horizontal capture lines have recently been harvested (photo: S. Heinrich).

2.5. DISCUSSION

This study presents the first systematic assessment of the distribution and cooccurrence of Chilean dolphins and Peale's dolphins anywhere in their sympatric range. Sightings of both species were not distributed evenly within study areas and differed markedly between central and southern Chiloé. Extensive sighting surveys conducted from a small boat provided an efficient and cost-effective way to cover repeatedly an area of more than 500 km².

2.5.1. Potential methodological biases

Survey effort varied between and within study areas despite all attempts to achieve equal coverage. Logistic restrictions and the rapidly changing, and often adverse, weather conditions favoured surveys in southern Chiloé and in more sheltered inshore bays. These areas coincided with the apparent centre of distribution of Chilean dolphins, whereas Peale's dolphins were mainly encountered in less frequently visited areas. The use of sectors weighted by survey effort should have accounted for spatial biases introduced by unequal survey coverage. Sector delineation was purely based on allocation of survey effort and survey practicalities. Sectors were not designed to reflect biologically meaningful divisions as perceived by the dolphins and were considered spatial units independent of the occurrence of both species.

Data from a sector were only included in the analysis if the sector had been covered completely. In most years, complete coverage consisted of surveying the entire area in a randomized zig-zag pattern. In 2001 and during the winter surveys in 2004, effort concentrated exclusively in a strip of approximately 800-1000 m from the shore. Thus animals further offshore in the larger sectors could have been missed. Over 98% of all sightings of Chilean dolphins and 90% of all sightings of Peale's dolphins occurred within 800 m from the shore, based on data from systematic surveys during the summer covering the entire study area (Chapter 3). Hence results from alongshore surveys can be compared to surveys with effort extending further out from shore. The winter surveys, all of which were crewed by at least one experienced observer from the summer surveys, aimed to document the continued presence of Chilean dolphins in the identified summer habitat, and did not attempt to investigate seasonal offshore movements. The effects of low effort across sectors in winter could not be fully

compensated by pooling data into larger temporal units and winter results should be considered as minimum estimates.

The probability of sighting dolphins in the different sectors did not seem to be biased by differences in Beaufort sea states given the non-significance of this term in most logistic regression models. In fact for safety reasons, outer and more exposed areas, such as the southern shoals of Cailin (SCA) or Paso Tenaun (PTE), were surveyed predominantly in good and calm conditions (Bft 0-2). The use of predicted values of occurrence derived from logistic regression models including all significant terms should have accounted for the remaining potential effects of Bft on sighting probabilities.

The observed pattern should reflect accurately the patchy distribution and spatial segregation of the small cetaceans in the Chiloé Archipelago and did not arise as an artefact of the survey design or analytical techniques.

2.5.2. Chilean dolphins - distribution and behaviour

Sightings of Chilean dolphins were concentrated in three main areas in southern Chiloé where probabilities of occurrence were high, between 60 and 90%. The environmental features that make these selected areas such apparently "attractive" habitat are unknown (but see Chapter 3 for an attempt to determine influential abiotic variables). All areas with high intensity of use by Chilean dolphins are relatively sheltered inshore bays and narrow channels.

The main ecological forces that drive distribution patterns in most mammals, including cetaceans, are protection from predators, availability of prey, suitability for reproduction and competitive interactions (Norris and Dohl 1980, Macdonald 1983, Lima and Dill 1990). Predation on Chilean dolphins has not been observed anywhere throughout their range (Goodall 1994). The most likely potential predators include killer whales (*Orcinus orca*) and sharks, such as Pacific sleeper sharks (*Somniosus pacificus*) or shortfin make sharks (*Isurus oxyrinchus*). None of these potential predators have been reported from the inshore waters of the eastern Chiloé Archipelago. None of the Chilean dolphins observed in this study showed scars or signs of predatory attacks (Heinrich, pers. observation). Prey availability and non-predatory

interactions with other species appear more likely factors underpinning the observed distribution pattern.

When encountered, Chilean dolphins were frequently engaged in foraging-related behaviours, such as feeding (i.e. presence of prey was confirmed), possibly searching for prey in localized patches (i.e. "milling") or cooperatively pursuing and herding potential prey (i.e. "plough"). A systematic behavioural study conducted from a landbased station overlooking Yaldad Bay in southern Chiloé supports the limited boatbased observations from this study. Ribeiro (2003) reported that Chilean dolphins spend more than 50% of their time foraging and feeding in Yaldad bay during summer. The frequency of observed feeding in dolphins has been used as an indicator of prey availability and abundance in particular areas (Würsig and Würsig 1980, Williams et al. 1996, Markowitz et al. 2004). Congeneric Commerson's dolphins (C. commersonii) and similarly sized harbour porpoises (Phocoena phocoena) carry relatively limited energy reserves and usually meet their energetic requirements by regular food intake (Gewalt 1990, McLellan et al. 2002). High quality and abundant prey is particularly important for females during the nursing period when they have to meet the additional energetic costs of lactation (Borjesson and Read 2003). Newborn Chilean dolphin calves were observed from November to April and numbers peaked in February (austral summer). Calves and neonates were seen in all sectors with frequent use by Chilean dolphins. Thus, areas with high intensity of use during the summer might reflect high quality habitat where prey is sufficiently abundant to meet elevated energetic demands of adults and which offers suitably protected habitat for neonates and calves.

A proper assessment of the relationship between foraging activity and distribution requires quantitative information on diet. The only information on potential prey species stems from basic stomach content analysis of a small sample of Chilean dolphins by-caught along the open coast north of Chiloé which identified sardines (*Strangomera benticki*), anchovies (*Engraulis ringens*), róbalo (*Eleginops maclovinus*), cephalopods (*Loligo gahi*), crustaceans (*Munida subrugosa*) and algae (Oporto *et al.* 1990). Anecdotal observations at Chiloé suggest that Chilean dolphins could be feeding on róbalo, pejerrey (*Odontesthes* sp.) and small schooling fish such sardines during the summer (Heinrich, pers. observation, Oporto 1987, Crovetto and Medina 1991).

Prey availability and prey type affect foraging strategies in dolphins which in turn influence group size (Würsig 1986, Acevedo-Gutiérrez 2002b). The largest groups of up to 25 Chilean dolphins were observed in southern Chiloé during foraging behaviour where the dolphins appeared to be corralling fish along the shallow shores (also observed by Crovetto and Medina 1991). Cooperative feeding in large groups has been linked to abundance of schooling prey and has been described for a variety of other delphinids, such as Commerson's dolphins (Goodall *et al.* 1988b, Coscarella 2005), Hector's dolphins, *C. hectori* (Bräger 1998), Peale's dolphins (de Haro and Iñíguez 1997, Schiavini *et al.* 1997 this study) and more pelagic species such as dusky dolphins, *L. obscurus* (Würsig 1986). When prey is patchily distributed or occurs in low abundance dolphins tend to forage individually to reduce intra-specific competition (Irvine *et al.* 1981, Würsig 1986, Coscarella 2005).

Group sizes and encounter rates were significantly smaller in central compared to southern Chiloé, possibly reflecting differences in habitat quality for Chilean dolphins. Although occurrence was predicted to be relatively high in Canal Dalcahue and the outer part of Paso Tenaun, sighting probabilities were very variable due to low survey effort and irregular sighting frequency.

Average group sizes observed during this study were similar to those from incidental sightings, ranging from two to 10 animals with aggregations of several hundred animals reported from the open coast (summarized in Goodall *et al.* 1988a). Variation in group size within the same species is commonly related to differences in habitat type and habitat quality (Wells *et al.* 1980). Variation in group size not only occurs on a larger physiographical scale (e.g. open coast versus sheltered bays) but also appears to reflect much subtler small-scale differences in habitat quality (e.g. central versus southern Chiloé, all sheltered channels).

The confirmed year-round presence of Chilean dolphins in Coldita Channel in southern Chiloé (e.g. Canal Coldita) highlights the importance of this area and suggests that resources were available throughout the year. Dolphins were seen in adjacent Yaldad Bay in all months of the year with the greatest intensity of use from spring to autumn. Anecdotal accounts by local mussel farmers and others suggest that Chilean dolphins re-appear in Yaldad Bay in noticeable numbers in September after a winter low and are then regularly seen until May (G. Burgos and H. Chiguay, pers.

communication, Crovetto and Medina 1991). This temporal pattern of occurrence corresponds well to the seasonal fluctuations in primary production observed in parts of Yaldad Bay (Navarro and Jaramillo 1994). Primary production peaks during the summer most likely with cascading effects across trophic levels potentially leading to a higher abundance of prey for the dolphins.

Anecdotal observations of Chilean dolphins from other parts of their range also indicate year-round presence in the nearshore waters (listed in Goodall *et al.* 1988a, Pérez-Alvarez and Aguayo-Lobo 2002). Seasonal inshore-offshore movements, possibly related to migration patterns of prey, have been suggested for other small cetaceans in southern South America, at least in parts of their range (Würsig and Würsig 1980, Bastida *et al.* 1988, Goodall *et al.* 1995b, Goodall *et al.* 1997a). Offshore distribution, however, has not been investigated systematically in any of these species at any time of the year. No or low observation effort in winter coupled with usually poor sighting conditions hamper conclusions about seasonal inshore presence and offshore movements. Rather than leaving the inshore waters Chilean dolphins could disperse alongshore if prey abundance in the summer habitat does not sustain the same number of individuals during the winter. Seasonal alongshore displacement of several hundred kilometres has recently been recorded for Commerson's dolphins off the Patagonian Atlantic coast (Mora *et al.* 2002, Coscarella 2005).

2.5.3. Peale's dolphins - contrasting distribution and behaviour

Peale's dolphins were spread widely across both study areas. The only noticeable exception was their complete absence from areas of high intensity of use by Chilean dolphins in southern Chiloé and from Canal de Yal in central Chiloé. Predicted sighting probabilities identified the coastline of Isla Laitec and the southern shoals of Isla Cailin in southern Chiloé as important areas but occurrence was generally low and variable. Canal Dalcahue in central Chiloé had the highest predicted probability of occurrence. The large variation in predicted occurrence might reflect temporal variation in usage intensities (e.g. over days or weeks) which was not considered in the analysis.

Despite the inherent limitations of quantifying behaviour during surveys (Mann 2000) behavioural observations made during this study provide some clues for understanding the observed distribution pattern. Peale's dolphins were mainly encountered when "travelling", and to a lesser extend "milling" and "socializing". Feeding behaviour on

small schooling fish, possibly the same type preyed upon by Chilean dolphins, was observed occasionally. Cooperative foraging as observed in Chilean dolphins was less evident and similar "plough" behaviour often appeared to be performed in a social rather than a foraging context. Groups tended to be small (three to five animals), particularly when "travelling". The observed behaviour and distribution patterns were consistent with foraging strategies where dolphins exploit patchily distributed or less abundant resources by travelling between and searching for suitable prey patches (Würsig 1986, Ballance 1992, Karczmarski *et al.* 2000, Bearzi 2005c).

This travel-forage pattern has been well documented for small groups of Peale's dolphins in the Strait of Magellan, southern Chile, where their foraging behaviour and movements are closely linked to the distribution of *Macrocystes pyrifera* kelp forests (Lescrauwaet 1997, Viddi and Lescrauwaet 2005). Similarly dense and widespread kelp forests are rare in the Chiloé Archipelago. In southern Chiloé *M. pyrifera* occurs in small patches along the rocky shores of eastern Isla Coldita, at the fringes of Bahia Quellon and over the shallow sandy shoals of southern Isla Cailin and southern Isla Laitec. In central Chiloé small kelp beds are scattered in Canal Dalcahue and along parts of the western shores of Canal Hudson. These areas are contained in the sectors with the highest predicted probabilities of occurrence of Peale's dolphins. A drawback of using large geographic units like sectors is that the coarse spatial resolution does not allow the separation of important habitat patches from connecting corridors used for transit between patches.

The diet composition of Peale's dolphins has only been investigated for a handful of by-caught and stranded specimens from the southern South Atlantic coast (Iñíguez and de Haro 1993, Schiavini *et al.* 1997). Peale's dolphins appear to specialize on demersal and bottom prey species in areas where kelp is abundant (Schiavini *et al.* 1997). They seem to act more as generalist predators when foraging further offshore over the shallow Argentinian shelf (Iñíguez and de Haro 1993) or in coastal areas where kelp is not abundant (Schiavini *et al.* 1997). In Chiloé, Peale's dolphins could be foraging opportunistically on dispersed prey in the shallow coastal waters by repeatedly visiting areas of previous foraging success (see Würsig 1986).

Neonates were sighted from December to April which is consistent with the summer calving season described for other areas (de Haro and Iñíguez 1997, Lescrauwaet

1997). Peale's dolphins have been observed to move inshore into kelp belts in the Strait of Magellan for breeding (Lescrauwaet 1997). The limited number of observations at Chiloé suggests that females and very small neonates seek out particularly shallow, but not necessarily secluded, areas along the shore.

2.5.4. Burmeister's porpoises – distribution and new sighting records

Burmeister's porpoises inhabit the inshore waters of South America from approximately 05°S on the Pacific to 28°S on the Atlantic coast, possibly with discontinuous distribution (Van Waerebeek *et al.* 2002, Rosa *et al.* 2005). Elusive behaviour, inconspicuous surfacing and long submersion make this species particularly difficult to observe. It is one of the very few small cetaceans for which no photographs of live specimens have been published to date (but see Appendix I). The basic biology of this species is relatively well known (Goodall *et al.* 1995a, Reyes and Van Waerebeek 1995, Brownell and Clapham 1999) due to a large number of carcasses available from incidental catch in gillnet fisheries, directed take and strandings (Van Waerebeek and Reyes 1994, VanWaerebeek *et al.* 1997, Rosa *et al.* 2005).

For Chile, only 13 confirmed sightings of Burmeister's porpoises have been published and several unconfirmed observations are documented in the literature (summarized and reviewed in Goodall *et al.* 1995b, Van Waerebeek *et al.* 2002). Four of these sightings were made in the Chiloé Archipelago during one day (Pitman and Ballance 1994), approximately 20 km from the eastern-most location of the 18 sightings made during this study.

Burmeister's porpoises were seen exclusively but repeatedly at two locations in central Chiloé (Paso Tenaun and Canal Hudson/Dalcahue). As they were sighted regularly in areas with relatively limited effort it is unlikely that they were overlooked in other, more frequently surveyed parts of the study area. Burmeister's porpoises occurred over deeper water compared to both dolphin species and were usually close to small submarine trenches reaching up to 160 m in depth, or in areas with a noticeable slope (based on coarse extrapolation from nautical charts).

During winter 2005, Burmeister's porpoises were observed during numerous occasions close to, but not interacting with, salmon farms in Canal Lemuy and Canal de Yal (P. Fuentes, pers. communication). These sightings are exciting as they were made

by an experienced observer, document the presence of Burmeister's porpoises in the same nearshore waters during the winter, and occurred in areas with relatively deep water where cetaceans had not been observed during this study.

2.5.5. Habitat partitioning

Peale's dolphins and Burmeister's porpoises are able to exploit a wide range of inshore habitats on both sides of the South American continent. In contrast, Chilean dolphins are restricted to the southern South Pacific coast while their allopatric congener Commerson's dolphin overlaps with Peale's dolphins and Burmeister's porpoises along the southern South Atlantic coast. The range separation of the two *Cephalorhynchus* species has been related to the strikingly different coastal habitats on the Pacific and Atlantic sides (e.g. width of continental shelf, water clarity and type of water mass) with a difference in their diets probably reflecting these habitat differences (Goodall *et al.* 1988a).

Intriguingly, Peale's dolphins seem to associate frequently with Commerson's dolphins off the southern South Atlantic coast and both species have been observed foraging in mixed groups (Goodall 1988, de Haro and Iñíguez 1997). Chilean dolphins and Burmeister's porpoises do not seem to interact regularly with any other cetacean species (this study, Goodall *et al.* 1988b, Goodall *et al.* 1995b). However, both species were frequently caught in the same gillnets set 2-13 nautical miles off the open Chilean coast (38°S) (Reyes and Oporto 1994).

In the Chiloé Archipelago, spatial (and/or temporal) segregation of Chilean dolphins, Peale's dolphins and Burmeister's porpoises occurred over small spatial scales (subkilometre range) and was consistent over several years. The driving forces that shape and maintain their co-occurrence are difficult to assess in the absence of dietary information. In well-studied sympatric dolphin species competition for food resources is reduced by dietary divergence (e.g. different prey preference, prey niche) or different habitat use (e.g. different depth range, inshore versus offshore, habitat niche) (summarized in Bearzi 2005b). Habitat partitioning based on selection of different environmental features (e.g. depth) is a likely explanation of the observed distribution patterns in Chiloé. The two dolphin species also seem to differ in foraging strategies. Peale's dolphins show greater flexibility in habitat use than Chilean dolphins which appear to exploit resources in relatively confined area. The three species have recently

been observed in two fjords on the continental side opposite Chiloé (approximately 80 km across the Golfo Corcovado) and showed a very similar pattern of spatial segregation (F. Viddi, pers. communication).

Competitive exclusion of Burmeister's porpoises by large groups of dusky dolphins and bottlenose dolphins (*Tursiops truncatus*) has been suggested based on observations in the Golfo San José, Argentina (Goodall *et al.* 1995b). Burmeister's porpoises were thought to occupy an intermediate niche of approx. 300 - 1000 m from shore and in 5 – 15 m deep water, between inshore bottlenose dolphins occurring in waters of less than 10 m depth, and dusky dolphins with a mean depth of 34 m. Displacement of Chilean dolphins by larger Peale's dolphins as a result of direct interaction has been observed in a few instances (this study, Oporto and Gavilan 1990) but apparently aggressive encounters are an exception. Aggressive (non-predatory) interactions between cetacean species are rare and usually not related to prey (Bearzi 2005b), but rather represent sexual-dominance (Herzing *et al.* 2003, Psarakos *et al.* 2003) or misdirected infanticide (e.g. bottlenose dolphins and harbour porpoises, Patterson *et al.* 1998) behaviours.

2.5.6. Issues of conservation concern

Mariculture activities abound in the central and southern Chiloé Archipelago and most bays and channels are occupied by at least one farm. Locations without mariculture activities are used for shellfish extraction, fishing or constitute shipping routes. Although no direct interactions between cetaceans and any of these activities were observed the multitude and intensity of anthropogenic activities are bound to impact, singly or synergistically, on the local ecosystem and potentially the cetaceans inhabiting these nearshore waters.

2.5.6.1. Mussel farms

Mussel farms have been shown to affect dolphins directly by displacing them from potentially important habitat (Kemper *et al.* 2003, Markowitz *et al.* 2004, Watson-Capps and Mann 2005). Alterations of the local food web due to mussel farms have been documented (Grange and Cole 1997, Mirto *et al.* 2000), but cascading effects reaching apex predators like dolphins have yet to be investigated. Some of the largest mussel farms occur in areas used intensively by Chilean dolphins, at least during part of the year (Figure 2-15). Chilean dolphins were sighted in Yaldad Bay long before mussel farming was initiated there in the mid-1980s (H. Chiguay, pers. communication,

Crovetto and Medina 1991). Recent observations suggest that dolphins could be excluded from large parts of Yaldad bay due to the extensive mussel farm coverage (this study, Ribeiro 2003). Structural components, such as floats and lines, suspended at the surface and extending vertically into the water column (often reaching close to the bottom), could impede dolphin movements and impact on foraging behaviour by acting as visual or acoustic obstructions (Figure 2-15). Field observations of dolphins (this study, Ribeiro 2003, Watson-Capps and Mann 2005) and captive studies of harbour porpoises (Kastelein *et al.* 1995) suggest that small cetaceans are reluctant to swim through ropes. A better understanding of Chilean dolphin movements and habitat use is required before conclusions about exclusion from vital habitat and impacts on foraging efficiency can be drawn.

2.5.6.2. Salmon farms

Ecological effects of fish farming (e.g. salmonids, tuna, and other fin fish) on the surrounding ecosystem are numerous and varied and have received much attention in recent years (Bushmann *et al.* 1996, Naylor *et al.* 2000, Tovar *et al.* 2000, Holmer *et al.* 2001). Cetaceans can be impacted directly by becoming entangled and drowned in the netting from fish cages or anti-predator nets (Kemper and Gibbs 2001, Kemper *et al.* 2003). Predatory attacks on caged fish, as is common for pinnipeds (Nash *et al.* 2000, Kemper *et al.* 2003), have yet to be reported for any cetacean species. Bottlenose dolphins in the Mediterranean have learnt to exploit the abundant wild fish assemblages attracted to the outside of the fish cages by an over-abundance of fish feed (Bearzi *et al.* 2004b). Most fatal entanglements of dolphins appear to occur accidentally when dolphins feed on wild fish associated with the fish cages (Kemper and Gibbs 2001). An unknown number of Peale's dolphins are thought to have died in anti-predator nets at salmon farms around Chiloé (Perrin *et al.* 1994, Claude and Oporto 2000). Foraging behaviour around or direct interactions with salmon farms were not observed during this study, neither for the two dolphin species nor the porpoise.

Dolphins and porpoises alike have been excluded from potentially important habitat by loud aversive sounds intended to deter pinnipeds from predating on caged fish (Johnston and Woodley 1998, Morton and Symonds 2002, Olesiuk *et al.* 2002). These acoustic harassment devices (AHDs) were trialled unsuccessfully by salmon farmers in the Chiloé Archipelago in the 1990s (Sepúlveda and Oliva 2005), and were not used

during this study (M. Sepúlveda, pers. communication; S. Heinrich, unpublished acoustic data).

As for mussel farms, indirect effects on cetaceans via impacts on and alteration of the local food web are difficult to determine. Consequently, relevant information is lacking. The intensity with which salmon and mussel farming occur in the Chiloé Archipelago generate additional, untargeted and yet potentially serious impacts. Boat traffic has increased due to mariculture activities (e.g. for harvest, supply and maintenance of farms) and has increased noise levels that could disrupt or interfere with normal behaviours of cetaceans (Richardson et al. 1995). Chilean dolphins tend to avoid boats and alter their behaviour (at least short-term) in response to passing boats (Crovetto and Medina 1991, Ribeiro et al. 2005). Although such traffic is usually not targeted at the dolphins, effects of boats and behavioural changes might be similar to those caused by whale- and dolphin watching activities (Hastie et al. 2003, Lemon et al. 2005, Lusseau 2005). Salmon farming introduces large quantities of contaminating substances such as antifouling chemicals, antibiotics and solid marine debris into the coastal waters (Haya et al. 2001, Miranda and Zemelman 2002). Millions of farmed salmon have escaped accidentally (or been released intentionally) from salmon farms in southern Chile and constitute a threat to the native fish fauna (Soto et al. 2001).

2.5.6.3. Entanglement in fishing nets

Entanglement in fishing nets or bycatch constitutes the largest and most imminent global threat to small cetaceans (Read *et al.* 2006). Peale's dolphins, Chilean dolphins and particularly Burmeister's porpoises have been subject to bycatch in Chile (Oporto and Brieva 1990) and in other parts of their range (Reyes and Oporto 1994, Goodall *et al.* 1997b, Majluf *et al.* 2002). Information on bycatch of small cetaceans in the fisheries of Chile has never been assessed nationally and has not been documented locally anywhere in the last 20 years.

The ports of Quellon, Dalcahue and Ancud on Isla Chiloé support small artisanal fishing fleets (mainly for hake, silversides, anchovies, conger eel) that fish locally and out into the Golfo Corcovado. An adult male Burmeister's porpoise washed ashore dead in Dalcahue (approximately 400 m from the fishing pier) in December 2002. The carcass was secured by the local maritime authorities and buried to prevent consumption by local villagers (C. Maturina, pers. communication). Photographic

material of the specimen was made available to verify species identification and determine clear net entanglement marks around the snout and head of the animal (photographs courtesy of C. Maturina, Gobernación Maritíma, Castro).

Given that members of the genus *Cephalorhynchus* and the Phocoenoidae (porpoises) are particularly prone to entanglement in fishing gear (Read and Gaskin 1988, Dawson 1991, Reyes and Oporto 1994, Crespo et al. 1997, van Waerebeek *et al.* 1997, d'Agrosa et al. 2000) it is reasonable (but currently unsubstantiated) to assume some ongoing bycatch of Chilean dolphins and Burmeister's porpoises (and possibly Peale's dolphins) off Chiloé.

One of the ecological challenges generated by salmon farming in Chile is the unintended (or intended) release of millions of farmed salmon which act as exotic predators and competitors to the native fish fauna. Soto et al. (2001) suggest that artisanal fishing constitutes the best way of controlling and removing escaped farm fish from the wild. Escaped salmon have become a lucrative alternative target for the struggling artisanal fishing industry (Soto et al. 2001), and are caught in increasing numbers in shorebased gillnets. Shorebased gillnets are the "poor man's ticket" to the salmon bonanza and escaped farmed salmon have become a lucrative product on the larger local markets² (Heinrich, pers. observation). Nets are placed in the shallow intertidal zone perpendicular to shore and are left unattended. They only fish around high tide, which coincides with regular foraging activities of Chilean dolphins in the same area (Heinrich, pers. observation, Ribeiro 2003). Chilean dolphins purportedly have been caught in these nets but were released alive (G. Burgos, pers. communication). Whether entanglement occurs regularly or in substantial numbers is unknown at present. The fact that congeneric Commerson's dolphins are subject to high levels of bycatch in the same type of intertidal gillnet (Iniguez et al. 2003) should be reason for concern.

2.5.7. Concluding remarks

Knowledge of the distribution patterns and occurrence of small cetaceans in the Chiloé Archipelago provides a baseline understanding of how these species interact with each other and their environment. Such information also helps to determine

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² (declared as freshly caught "wild" salmon to unwary tourists)

potential areas of conflict between coastal cetaceans and human activities. The practical challenges of studying cetaceans can make it difficult to detect environmental impacts upon them unless (or until) the effects are very severe. Each individual impact may be sustainable (or too small to detect). For effective management of coastal areas and sustainable use of local resources the cumulative (and potentially synergistic) effects of all potentially impacting activities on a species should be considered. Given the differences in distribution and behaviour, Chilean dolphins, Peale's dolphins and Burmeister's porpoises might be affected to varying degrees by the different types of human activities. Information on the occurrence of small cetaceans in the Chiloé Archipelago helps to raise awareness about these species and introduces them to the regional planning authorities charged with sustainable resource management³ of these coastal waters.

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³ In Chile, all marine mammals are managed as "marine resource" (Iriarte 1999).

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Chapter 3 Habitat selection in Chilean dolphins and Peale's dolphins

3.1. ABSTRACT

Habitat use patterns of mobile animals, such as cetaceans, are linked to the heterogeneous distribution of resources crucial to their survival. Thus, identifying the relationship between the distribution of cetaceans and environmental characteristics provides insights into their ecology and helps identify the location and extent of important habitat. Habitat selection models were developed and tested for two sympatric delphinids, Chilean dolphins and Peale's dolphins, inhabiting the inshore waters of the Chiloé Archipelago (42-43°S) in southern Chile. Occurrence of dolphins (absence-presence) in relation to selected environmental and anthropogenic variables was recorded during systematic boat-based sighting and habitat surveys. Sighting data collected during two austral summers and autumns were used to develop speciesspecific habitat models using logistic regression in a model selection framework. Predictive performance of the derived habitat models was evaluated with crossvalidation and randomisation tests on an independent dataset. Chilean dolphins showed a clumped distribution, occurred mainly within 500 m from shore, in shallow water (< 20 m) and in the vicinity of rivers. Probability of occurrence was highest in sheltered inshore channels and bays in southern Chiloé, and was restricted to isolated patches in central Chiloé. Peale's dolphins occurred in a similar range of depth and distance to shore and showed a positive relationship with distance to mussel farms and salmon farms. Their probability of occurrence was highest in several shallow patches in central Chiloé and shallow shoals along exposed shores in southern Chiloé. Modelling occurrence of both species in relation to each other identified spatial factors, distance to rivers and mussel farms as the most important features explaining their small-scale habitat partitioning. The combination of distance to river and mussel farms reflects the preference of Chilean dolphins for specific environmental characteristics in southern Chiloé and can be interpreted as proxy for nutrient-rich estuarine bays. The predictive models developed in this study have identified important areas for each species in southern and central Chiloé (based on frequency of occurrence) and provide a rigorous framework to test the general ecological importance of the identified habitat characteristics for the distribution of these poorly known species in other areas.

3.2. Introduction

Habitat is defined as the physical and biotic environment in which an organism or community lives (Allaby 1992, p. 209). Cetaceans inhabit a complex three-dimensional environment that is delineated by static geomorphological properties and is characterized by dynamic oceanographic and biotic features. The heterogeneous and fluctuating nature of the marine environment usually leads to a patchy and clumped distribution of suitable habitat which meets species-specific and individual-specific requirements (Stevick *et al.* 2002).

Habitat selection is a behavioural consequence of animals actively selecting where they live (within the constraints of their physiology and life-history strategies), or passively persisting in certain habitats (Boyce and McDonald 1999). Habitat use patterns are a consequence of the influence of selection on survival and reproduction, and the need to optimise the use of resources to maximize fitness (Boyce and McDonald 1999, Stevick *et al.* 2002).

Habitat selection usually reflects a trade-off between the benefit of resource gain (e.g. prey, mates) and the threat of predation (Lima and Dill 1990, Bjørge 2001). Information on the distribution of prey and predators of cetaceans is very difficult to obtain and is lacking for most species. Only a handful of studies have investigated a direct link between habitat use of cetaceans and the distribution of their prey (e.g. Fiedler *et al.* 1998, Macleod *et al.* 2004, Croll *et al.* 2005) and predators directly (Acevedo-Gutiérrez 2002, Heithaus and Dill 2002).

Instead, most studies relate the distribution and activity patterns of cetaceans to more easily determined environmental variables, which are considered to be proxies for the availability of crucial resources. These include fixed physical features (e.g. bathymetry, slope: Reilly 1990, Gowans and Whitehead 1995, Davis *et al.* 1998, Bräger *et al.* 2003, Griffin and Griffin 2003, Hastie *et al.* 2005), temporally variable physical and/or chemical properties (e.g. sea-surface temperature, currents, salinity, water clarity: Reilly 1990, Davis *et al.* 1998, Bräger *et al.* 2003, Griffin and Griffin 2003), and/or indications of biological productivity (Smith *et al.* 1986, Griffin and Griffin 2003, Johnston *et al.* 2005).

Selection of (or preference for) a particular habitat characterized by one or several environmental variables usually is inferred if the target species is seen more frequently or encountered in greater numbers in this habitat type than would be expected by chance alone (Manly *et al.* 1993, Boyce and McDonald 1999). Thus, habitat selection analysis considers the distribution or density of animals in relation to the habitat available to them.

Predictive habitat models go beyond finding explanatory relationships. While understanding where a species occurs is a fundamental ecological requirement, prediction of occurrence is essential for conservation and population management (Boyce and McDonald 1999, Hill 1999, Cabeza et al. 2004, Gibson et al. 2004, Jeganathan et al. 2004). Cetaceans are subject to a wide variety of anthropogenic impacts, including incidental mortality in fishing gear, directed take, competition for prey, contamination from chemical pollution, degradation and loss of important habitat, disturbance, and effects from global climate change (reviewed in Whitehead et al. 2000, Bjørge 2001, Evans 2002). Most commonly, geographically defined mitigation and protective measures are implemented when managing potential (or established) impacts on cetaceans is a legal requirement (e.g. under national law), or is of public concern. Examples include establishment of marine mammal sanctuaries (Dawson and Slooten 1993) or marine conservation areas (Wilson et al. 2004), spatial (and temporal) restrictions of fishing activities (Julian and Beeson 1998, Dawson et al. 2001), exclusion zones for whale/dolphin-watching boats (Lusseau and Higham 2004) or the use of military sonar.

Defining the size and location of protective areas for cetaceans is a challenging task as they are highly mobile, difficult to observe and respond to the dynamics of their environment. Habitat prediction models help to obtain a better understanding of the features that constitute important habitat for the species of concern and to establish testable relationships between the environment and species distribution. Predictive habitat modelling is a well-used tool for defining conservation boundaries in terrestrial animals (Hill 1999, Gibson *et al.* 2004, Jeganathan *et al.* 2004, Rushton *et al.* 2004), but has only recently been applied to cetaceans (Cañadas *et al.* 2005).

In this study, patterns of habitat selection are investigated for two sympatric dolphin species that co-occur in the eastern Chiloé Archipelago in southern Chile. The Chilean dolphin *Cephalorhynchus eutropia*, a small delphinid endemic to Chile, shares the nearshore waters of southern and central Chile with the larger and wider ranging Peale's dolphin, *Lagenorhynchus australis* (Goodall *et al.* 1988a, Goodall *et al.* 1997). Shore-based studies and limited boat-based observations suggest that both species inhabit shallow, often turbid coastal waters and occasionally enter larger rivers (Goodall *et al.* 1988a, Goodall *et al.* 1997). However, Peale's dolphins have been seen in water depth up to 300 m and have also been observed far from shore over the shallow Argentinean continental shelf (Goodall *et al.* 1997). Shore-based habitat studies of Peale's dolphins in the Strait of Magellan have shown a marked preference for coastal kelp beds, *Macrocystis pyrifera*, which appear to constitute important foraging grounds (Lescrauwaet 1997, Viddi and Lescrauwaet 2005).

The spatially exclusive occurrence of Chilean dolphins and Peale's dolphins in the Chiloé Archipelago (Chapter 2) offers the opportunity to investigate whether reliably quantifiable abiotic variables can be used to explain the observed distribution patterns and habitat partitioning. First, habitat selection is investigated for each species separately based on the frequency of use of available habitat. The resulting habitat selection models are tested for fit and generality and the best models are used to generate spatial predictions of occurrence for each species. The distribution of Chilean dolphins in relation to environmental variables is then modelled directly in relation to the occurrence of Peale's dolphins to identify those variables that could drive the observed pattern of habitat partitioning.

Intense mariculture activities (e.g. marine farming of finfish and shellfish) abound throughout the nearshore waters of the Chiloé Archipelago (Chapter 2, SERNAPESCA 2004). Emerging evidence suggests that mariculture farms could influence habitat use patterns of cetaceans (Kemper *et al.* 2003, Markowitz *et al.* 2004, Watson-Capps and Mann 2005). Therefore distance to farms is included in the habitat models as an anthropogenic variable along with a set of potentially influential environmental and spatial factors.

3.3. METHODS

3.3.1. Data collection

Systematic boat-based habitat and sighting surveys for small cetaceans were conducted in the coastal waters of the southern and central Chiloé Archipelago (41-43°S, 73-74°W) in southern Chile (10th Region) over three consecutive austral summer and autumn seasons from December 2001 to April 2004. The two study areas were surveyed completely three to five times during one field season. Surveys were designed to ensure full coverage of the available habitat and followed pre-determined transects with variable start and end points. Transects were placed in regularly spaced zigzag patterns crossing bays and channels from shore to shore and extended up to 2.5 km offshore.

A 3.8 m inflatable boat powered by an outboard (20-25 hp) engine was used to conduct surveys at a constant speed of 10 knots (approx. 19 km/h) and in good weather conditions, i.e. Beaufort sea state \leq 3, no or little precipitation. Two to three observers searched the waters ahead and out to 90° of the transect line for visual cues of dolphins. If dolphins were not sighted the boat was stopped at 15-minute intervals along the transect to collect a variety of environmental measurements and other habitat data, including information on exact location (using GPS), sighting conditions (e.g. Beaufort sea state, swell, precipitation), and a suite of abiotic, biotic and anthropogenic variables) (Table 3-1).

The same set of measurements was obtained whenever dolphins were encountered during transects. Additional information on species identification and the number of dolphins present was also recorded. All measurements were made as close as possible to the location where dolphins were first sighted, usually within a radius of 20 m. Most dolphin groups were approached for photo–identification purposes (see Chapters 4 and 5). Other dolphins sighted while working with a particular group were noted but not included in the analysis presented in this chapter. All surveys were resumed at the initial point of departure from the transect line and continued along the original transect.

Table 3-1. Environmental, spatial and anthropogenic variables recorded during boatbased sighting and habitat surveys in the Chiloé Archipelago.

Variable	Description	Measurement method	Unit
Depth	in situ measurement of water depth	hand-held depth sounder, for > 90 m extrapolated from nautical charts	m
Shore distance	linear distance to nearest coast	Bushnell Pro laser range finder, for > 1,000 m extrapolated from GIS	m
River distance	alongshore distance to nearest river mouth or permanent stream	field observations, extrapolated from GIS	m
SST	in situ measurement of sea surface temperature (at 1m depth)	digital LF 320 conductivity- temperature meter	°C
Salinity	in situ measurement of salinity (at 1 m depth)	digital LF 320 conductivity- temperature meter	ppt
Water clarity	in situ measurement of water clarity	secchi disc depth (30 cm diameter)	m
Mussel farm dist.	linear distance to nearest mussel farm (≤ 1000 m)	Bushnell Pro laser range finder, truncated for distance > 1000m	m
Salmon farm dist.	linear distance to nearest salmon farm (≤ 1000 m)	Bushnell Pro laser range finder, truncated for distance > 1000m	m
Boat distance	linear distance to the nearest moving boat within a 500 m radius; number and type of boat(s) (e.g. fishing, mariculture, ferry)	Bushnell Pro laser range finder	m
Other species	number of individuals and species ID of marine vertebrates within a 300 m radius, e.g. sea lions, sea birds, fish schooling at surface	field observation	
Bft	Beaufort sea state (0-3, categories)	field observation	-
UTM-Easting, UTM-Northing	geographic position expressed in UTM coordinates (-E, -N)	hand-held Garmin GPS 12 XL	-

The choice of environmental variables to be considered for analysis was based on their potential biological importance to the dolphins (e.g. proxies for prey distribution) and availability of reliably measured data. All environmental variables (except "River distance", see below) were collected *in situ* during the surveys. Alternative data, such as information from remote sensing (e.g. satellite derived measurements of sea surface temperature) or nautical charts (e.g. depth) were not available for the study areas, at least not in the fine spatial resolution (i.e. subkilometre range) required to capture the variability of the nearshore habitat. The sampling sites with and without dolphins (i.e. presence and absence) were considered a representative random sample of the habitat available to and used by the dolphins. Sampling sites therefore constituted the spatial unit on which further analysis was based rather than using the more conventional gridor segment-based approach applied in other studies of cetacean habitat use (e.g. Reilly et al. 1998, Gregr and Trites 2001, Hamazaki 2002, Martin and da Silva 2004, Cañadas et al. 2005).

"River distance" was extrapolated from a satellite image (S18-40-2000, NASA Landsat 7 satellite image¹) in a Geographic Information System (GIS). The identification of rivers was based on field observations and visible marks on the satellite image. For this analysis, a river was defined as any permanent body of running freshwater where the mouth of the river was at least 2 m wide. Due to frequent heavy rainfall in the Chiloé Archipelago hundreds of temporary streams and fresh-water run-offs form along the shores abutting larger hills. These non-permanent streams or rivers were not considered.

Distances to mussel farms and salmon farms were determined *in situ* by laser range finder for distances up to 1,000 m and were truncated for distances beyond the measurable range (> 1,000 m). Acoustic harassment devices (AHDs) that could potentially affect the presence of cetaceans over distances of 3,500 m or more (Olesiuk *et al.* 2002) were not used by salmon farms in southern and central Chiloé during this study (Heinrich, unpublished acoustic data; M. Sepulveda, pers. communication, Feb. 2004).

¹ available at https://zulu.ssc.nasa.gov/mrsid/mrsid.pl

3.3.2 Data analysis

Data analysis was carried out in three steps: (1) environmental characterization of the study areas, (2) modelling the distribution of each species in relation to environmental and spatial variables using data collected during the austral summers and autumns of 2002 and 2004 and assessing the predictive power of those species-specific models using data collected during the austral summer and autumn of 2003, (3) direct comparison of spatial distribution and environmental preference between species.

All modelling-related analyses were carried out using the software package R, vers.2.1. with the libraries "mgcv" and "MASS" (R-DevelopmentCoreTeam 2004). Mann-Whitney tests were performed in Minitab vers.12.23 (Minitab Inc, 1999). Data on sampling sites and predicted distributions were processed in ArcGIS vers.9 (ESRI Inc. 2004).

3.3.2.1. Habitat characterization and summary statistics

Pearson product-moment correlation tests were used to examine collinearity between explanatory variables. Mann-Whitney tests were performed to compare the median values for each environmental variable in southern and central Chiloé to highlight environmental differences between study areas. The same non-parametric tests were applied to compare the dataset (2002 and 2004) used for model development and the test dataset (2003) used for cross-validation (see below) to ensure that environmental conditions were comparable between years.

All environmental variables were divided into equally sized bins and plotted to examine the potential relationship (e.g. linear, quadratic, cubic) with the presence of a given dolphin species. The variables "Shore distance," "River distance," "Mussel farm dist," and "Salmon farm dist." were log-transformed as potential influences on the occurrence of dolphins appeared to act over small spatial scales. In the case of "Mussel farm dist." and "Salmon farm dist." log transformation also reduced the effect of artificial heaping at the arbitrarily chosen cut-off point for distances beyond the measured range.

3.3.2.2. Species-specific habitat selection models

a) Model specification

Generalized Linear Models (GLMs) were developed to relate the presence of dolphins to habitat variables. Given that data on dolphin presence behave as a binary variable (i.e. presence versus absence), logistic regression models with a binomial error structure and a logit link function were used (Venables and Dichmont 2004). The logistic regression model was a resource selection probability function of the form (Manly *et al.* 1993):

$$\hat{p}_{i} = \frac{\exp[\beta_{0} + \beta_{1}x_{i1} + \beta_{2}x_{i2} + \dots + \beta_{p}x_{ip}]}{1 - \exp[\beta_{0} + \beta_{1}x_{i1} + \beta_{2}x_{i2} + \dots + \beta_{p}x_{ip}]}$$
1.

where \hat{p}_i is the probability of dolphins being present at site i, β_0 is the intercept and β_I to β_p are the coefficients of the explanatory variables x_I to x_p , respectively. The probability of dolphins being absent at site i was 1- \hat{p}_i .

Modelling the sighting data as binomial rather than Poisson distributed response variable circumvented the problem of overdispersion, which complicates the direct analysis of data on the numbers of social animals observed.

The explanatory variables listed in Table 3-2 constituted the *a priori* biological model and defined the upper limit of the complexity of the species-specific multivariate regression models.

Table 3-2. Candidate variables and their transformations considered during the model building process for Chilean dolphins and Peale's dolphins.

Term		single	quadratic	cubic	ln	interaction
	Depth	X	X	X		
environmental <	SST	X	X	X		
	Shore distance	X			X	
	River distance	X			X	
	Water clarity	X			X	
	Salinity	X				
	Salmon farm dist.				X	
	Mussel farm dist.				X	
_	Bft	factor				
spatial -	UTM-Easting	X				UTMN:
	UTM-Northing	X				UTM-E

b) Model selection

A combination of forward and backward stepwise selection (Venables and Ripley 2002) was used to determine the models that best fitted the data. Forward stepwise selection starts from a simple model and repeatedly adds terms to the model from the pool of specified candidate variables. At each step the effect of including each additional variable or interaction term on the model's fit to the data is evaluated. Thus, the variables with the greatest explanatory power enter the model first. Backward selection does the reverse, by considering the effects of removing one variable or interaction term each time. If a variable no longer contributes significantly to the fit of the model after other terms are added it is removed and placed back into the pool of candidate variables. Conventionally, interaction terms are only included when all the corresponding main effects are present. Here, forward and backward selections were carried out together, simultaneously considering the effects of adding and deleting variables at each step.

The importance of each added term was evaluated using an information-theoretical approach based on Akaike's Information criterion (Akaike 1973), corrected for small sample size (AIC_c). Burnham and Anderson (2002) recommend the use of AIC_c when sample size divided by the number of variables is less than 40, which applied in this case. Models with an AIC_c difference (delta AIC_c) smaller than 2 were considered to have equal support from the data (Burnham and Anderson 2002) and the most parsimonious model was then chosen. Goodness of fit of the final model was investigated using a chi-squared test on model deviance (with H_0 = model correct; H_1 = model not correct). Residuals of the final models were plotted in a GIS to check for spatial patterns in model over- or under-fitting. Spatial correlation in the residuals (i.e. heaping of over-or underdispersed residuals in a certain area) would indicate the lack of an influential predictor variable in the model.

c) Validation of species-specific habitat selection models

Cross-validation is a tool to assess whether the models (selected using AIC_c) reflect not only the pattern in the data from which they were derived but also succeed in capturing a persisting biological relationship between environmental variables and dolphin presence (Burnham and Anderson 2002, Olden *et al.* 2002). The predictive

performance of the species-specific habitat selection models was evaluated using cross-validation on an independently collected dataset (test dataset).

The model to be assessed was fitted to the test dataset using equation 1 and the model coefficients. Its overall predictive performance was determined as:

$$\overline{q} = 1 - \frac{\sum_{i=1}^{n} \left| \left(y_i - \hat{p}_i \right) \right|}{n}$$
 2.

where

 \overline{q} is the mean proportion of all correct predictions,

 y_i is the observation at site *i* (either 0 or 1),

 \hat{p}_i is the probability of observing dolphins at site i,

n is the total number of sites.

For comparison, the simplest model is a random (intercept only) model where the probability that dolphins are present is the same for all sampling sites, i.e. the influence of the environmental variables measured in this study is zero. In this case the probability of dolphins being present at site i in the test dataset is equal to the proportion of occasions on which animals were observed. Based on this intercept model an outcome of either 1 (dolphins are present) or 0 (dolphins are absent) can be generated randomly for every sampling site i according to a binomial process with mean \bar{p} . This procedure was repeated 10,000 times to produce simulated datasets equivalent to the observations but without any relationship between the environmental covariates and the observations. For each simulated dataset, the proportion of simulated observations correctly predicted, using the best model and parameter values chosen from the training dataset, were calculated. The resulting distribution formed the test statistic with which the predictive performance \bar{q} of the more complex model under evaluation was compared. The number of times (out of the 10,000 simulations) where the more complex model predicted better than the intercept model indicated the predictive power of the more complex model.

The same procedure was applied to compare simple models containing only a few parameters with more complex ones. In this case the simpler model was used to generate the test statistics against which the predictive performance of the more complex model was compared. A significantly higher mean predictive power of the complex model supported its use for final interpretation of coefficients and predictions.

The data collected during 2002 and 2004 was used to fit the models (training dataset), and data collected in 2003 constituted the independent test dataset. The division of the data into training and testing datasets was based on the number of absence-presence samples obtained each year. The year 2003 had the biggest sampling effort with the largest number of sightings (presences) of all single years (see section 3.4.), thus providing the most robust test set (i.e. largest number of data points from any single year to be fitted to the model). The model that provided the best predictor for the 2003 test data was identified as the "best prediction" model and was used to derive probability plots for the presence and absence of dolphins in both study areas. Local polynomial interpolation (Bowman and Azzalini 1997) was used to produce smooth surfaces across the probability of occurrence of dolphins predicted by the best model for each sampling site.

3.3.2.3. Inter-specific comparison of habitat selection

The lack of temporal co-occurrence of both species provided a binary response: (1) Chilean dolphins were present at a sampling site (while Peale's dolphins were absent), or (0) Peale's dolphins were present (while Chilean dolphins were absent). The allocation of 1-0 to the two species is interchangeable. A GLM with binomial error structure and with the logit link function was fitted to the data. Model fitting and model selection were conducted using the same approach as described above (*section 3.3.2.2*). The aim here was to test whether environmental and/or spatial variables could explain the observed pattern of spatial segregation between Chilean dolphins and Peale's dolphins (Chapter 2). Therefore there was no need to assess the predictive performance of the model by means of cross validation. Data were pooled for all years (i.e. 2002-2004) to provide a more robust sample size.

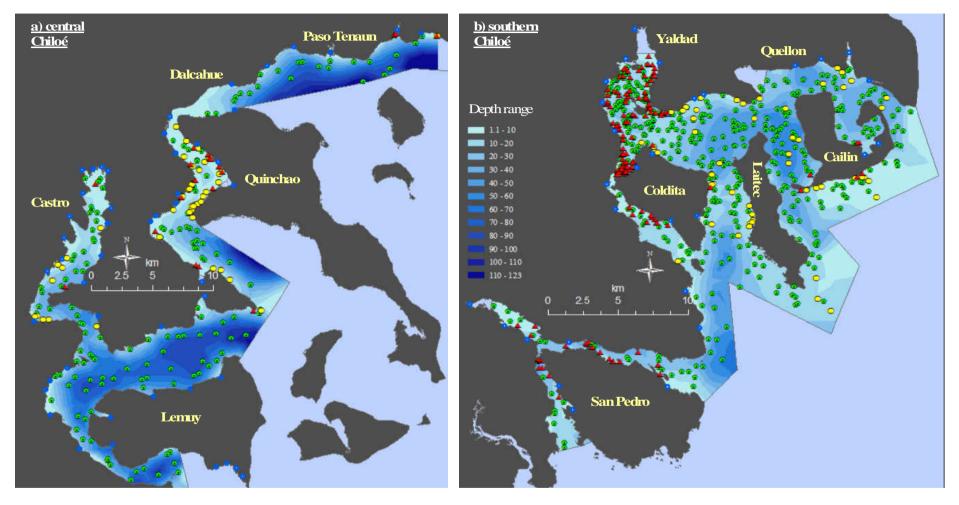


Figure 3-1. Sampling locations with Chilean dolphins (red triangles), with Peale's dolphins (yellow circles) and without dolphins (green circles), in the Chiloé Archipelago in southern Chile during 2002 and 2004 (model fitting data set). Depth (based on *in situ* measurements) is interpolated between sampling locations. River mouths are marked by blue dots.

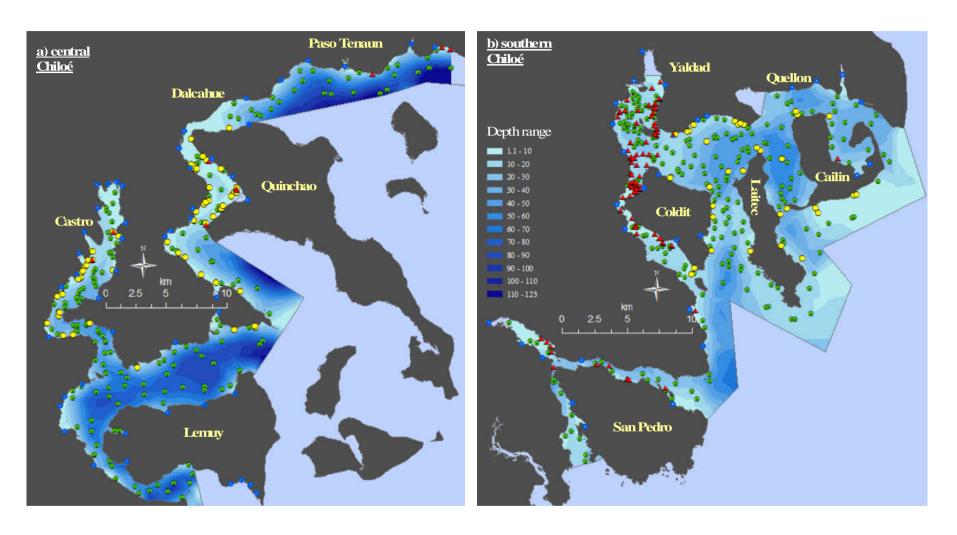


Figure 3-2. Sampling locations with Chilean dolphins (red triangles), with Peale's dolphins (yellow circles) and without dolphins (green circles), in the Chiloé Archipelago in southern Chile during 2003 (testing data set). Depth (based on *in situ* measurements) is interpolated between sampling locations. River mouths are marked by blue dots.

3.4. RESULTS

Systematic habitat surveys were conducted under good sighting conditions on 59, 65 and 42 days during the field seasons of 2002, 2003 and 2004 respectively. Surveys covered a total of 2,443 km, 2,870 km and 2,555 km on effort during these three field seasons respectively.

Data collected during 2002 and 2004 were pooled to form the model fitting dataset. The resulting dataset contained 529 samples collected in the absence of dolphins, 127 samples collected in the presence of Chilean dolphins, and 88 samples collected in the presence of Peale's dolphins (Table 3-2, Figure 3-1). Data collected during the 2003 field season were used for cross-validation and consisted of 398 samples collected in the absence of dolphins, 71 samples collected in the presence of Chilean dolphins, and 77 samples collected in the presence of Peale's dolphins (Figure 3-2). Environmental variables were compared between the model fitting and test dataset using Mann-Whitney tests to ensure that general environmental conditions were comparable between years. Only the variable SST had slightly higher, and the variable Salinity slightly lower, median values in 2003 compared to 2002 and 2004 (Mann-Whitney tests, W= 136,640, p< 0.001, and W= 173326, p= 0.040, respectively).

3.4.1. Habitat characterization

The study areas in central and southern Chiloé differ most markedly in depth. The central study area is, on average, twice as deep as the southern area with depth of over 100 m (Table 3-3) recorded in Canal Lemuy, Canal de Yal and Paso Tenaun (Figure 3-1). In contrast, depth rarely exceeds 50 m in the southern study area. The islands Laitec and Cailin have shallow, and mainly sandy shoals (< 20 m deep) extending southward for more than 2 km offshore (Figure 3-1).

Sampling sites in the southern study area were, on average, located further from rivers than in the central study area (Table 3-3). The central study area extends mainly along the shores of Isla Grande de Chiloé (the main island of Chiloé) where rivers and permanent streams are supplied by a large drainage area consisting of lakes and freshwater run-off from the surrounding hills. In the southern study area, rivers and streams are also common along the shores of Isla Grande de Chiloé.

Table 3-3. Summary of environmental variables used to develop the habitat models for Chilean dolphins and Peale's dolphins based on data collected during 2002 and 2004 in southern and central Chiloé. Mann-Whitney tests were used to compare median values for each variable between study areas at sampling stations without dolphins.

n.s.= not significant; * significant at p= 0.05, ** significant at p< 0.001

	Samples with		Samples without dolphins		
	Chilean dolphins	Peale's dolphins	southern Chiloé	central Chiloé	
Number of samples	127	88	382	147	
Depth (m) mean ± SE; median range	14 ± 0.9; 12 2.5 - 55.8	13 ± 1.7; 6 1.8 - 65.2	$26 \pm 0.9; 21$ $2.4 - 70.6$	44 ± 2.4 ; 42 1.1 – 123	**
Shore distance (m) mean ± SE; median range	253 ± 14; 214 17 - 894	369 ± 40.8; 204 41 - 2,312	636 ± 20.4; 571 78 - 2,450	683 ± 37.0; 586 82 – 2,011	n.s.
River distance (m) mean ± SE; median range	1,288 ± 78.3; 1,185 49 - 5,360	2,250 ± 195.0; 1,764 235 - 9,506	2,648 ± 92.7; 1,975 232 - 9,152	1,914 ± 77.3; 1,637 309 - 4,773	**
SST (°C) mean ± SE; median range	13.8 ± 0.19 ; 12.9 10.8 - 19.6	$13.1 \pm 0.12; 13.1$ $10.4 - 16$	$12.7 \pm 0.08; 12.3$ $10.2 - 21$	$12.9 \pm 0.10; 12.8$ $11.2 - 17.7$	*
Salinity (ppt) mean ± SE; median range	32.1 ± 0.09 ; 32.2 28.8 - 33.8	32.4 ± 0.05 ; 32.3 32.2 - 33.8	32.6 ± 0.05 ; 32.7 27.9 - 34	32.6 ± 0.06 ; 32.6 27.8 - 34	n.s.
Water clarity (m) mean ± SE; median range	5.4 ± 0.17 ; 5 2.5 - 11	$7.3 \pm 0.27; 7$ $1.8 - 15$	$7.2 \pm 0.12; 7$ $2 - 15$	$7.5 \pm 0.32; 7$ 1.1 - 19	n.s.
$\frac{Mussel \ farm \ dist. \ (m)}{mean \ \pm SE}$ $range$	1,073 ± 81.2 15 - (>1,000)	1,823 ± 57.0 31 - (>1,000)	1,621 ± 22.0 22 - (>1,000)	1,506 ± 62.8 8 - (>1,000)	
$\frac{Salmon\ farm\ dist.\ (m)}{mean\ \pm SE}$ $range$	1,756 ± 50.9; 2,000 92 - (>1,000)	1,765 ± 56.9; 2,000 173 - (>1,000)	1,549 ± 33.7; 2,000 68 - (>1,000)	1,531 ± 56.1; 2,000 71 - (>1,000)	
$\frac{Bft}{mean \pm SE; median}$	1.4 ± 0.06; 1 0 - 3	1.4 ± 0.09 ; 1 $0 - 3$	$1.6 \pm 0.04; 2$ 0 - 3	$1.3 \pm 0.07; 1$ $0 - 3$	*

The relatively small islands of Coldita, Laitec and Cailin support no or only a few permanent streams (Figure 3-1). The northernmost part of Bahia Yaldad and the westernmost part of Canal San Pedro form large riverine drainage areas with extensive mud flats and strong estuarine character. Similar bays, albeit smaller in size, exist in central Chiloé in the upper Estuario Castro, Enso Rilan and off Curaco de Velez (near or opposite Isla Qunichao) and to a lesser extent in some of the bays along Paso Tenaun.

Salinity and SST were similar in both study areas but variation was larger in southern compared to central Chiloé (Table 3-3). The lowest salinity values were measured in Yaldad Bay following several days of torrential rainfall, which extended the surface freshwater layer beyond the 1m depth where salinity measurements were taken. The highest SST values were also recorded in Yaldad Bay (during February 2004).

All environmental variables were examined for collinearity using Pearson product-moment correlation tests (Table 3-4). Most correlations were statistically significant but all correlations were weak (all $r_p < 0.3$, except Shore distance- Depth and SST-Salinity: $r_p < 0.5$). Significant correlations most likely resulted from the large sample size (n= 1,242) that made even weak relationships appear statistically significant. Scatter plots of selected environmental variables showed no spurious patterns (Figure 3-3).

Table 3-4. Correlation matrix for the environmental variables (n= 1,242 samples) used in this study obtained form Pearson product moment correlation tests.

" not significant at p= 0.05, * significant at p= 0.05, ** significant at p< 0.001

	Depth	Shore distance	River distance	SST	Salinity	Water clarity	Mussel farm dist.
Shore distance	0.493**	-					_
River distance	0.206**	0.213**	-				
SST	-0.111**	-0.133**	-0.198**	-			
Salinity	0.173**	0.144**	0.125**	-0.451**	-		
Water clarity	0.287**	0.246**	0.174**	-0.295**	0.257**	-	
Mussel farm dist.	0.206**	0.179**	0.200**	-0.241**	0.219**	0.088*	-
Salmon farm dist.	-0.140**	0.023"	-0.030"	0.064*	-0.085*	-0.070*	0.162**

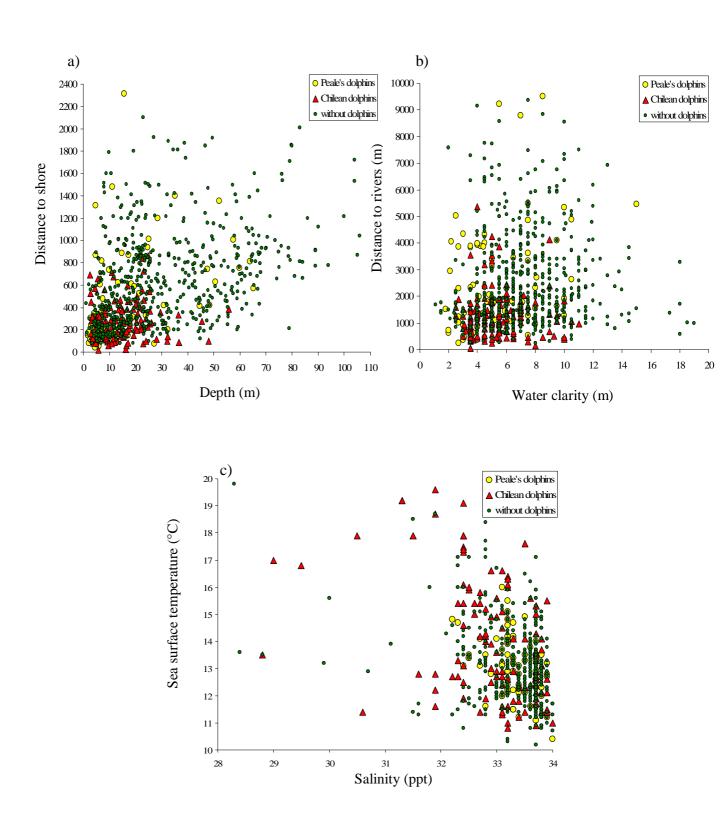


Figure 3-3. Scatter plots depicting the environmental and spatial variables used to develop habitat models for Chilean dolphins and Peale's dolphins (data for 2002 and 2004): Depth and Shore distance (a), Water clarity and River distance (b), Salinity and SST (c).

Distances to mussel farms and salmon farms were similar in both study areas with sampling sites in the central study area being, on average, slightly closer to mussel farms than in the southern area (Table 3-3; see Figure 2-13 in Chapter 2 for a map of farm locations). Boat traffic was observed infrequently within the reliable recording distance of 500 m (6% of sampling sites without dolphins, 10% of sampling sites with Chilean dolphins present, and 18% of sampling sites with Peale's dolphins present) and was not included as a candidate variable in the habitat models.

The presence of other marine vertebrates was not included as a variable due to the variability and uncertainty in the context of co-occurrence and difficulties with consistent recording. Sea birds constituted the most frequently seen taxonomic group (78% of 178 samples with absence and presence of dolphins), followed by small fish scattering at the surface (11%), South American sea lions (Otaria flavescens) (10%) and marine otters (Lontra felina) (1%). The most frequently observed sea birds were magellanic penguins (Spheniscus magellanicus), three cormorant (Phalacrocorax atriceps, P. brasilianus, P. gaimardi), brown pelicans (Pelecanus occidentalis), three gull species (Larus dominicanus, L. pipixcan, L. maculipennis), South American terns (Sterna hirundinacea), seasonally large flocks of sooty shearwaters (Puffinus griseus), black-browed albatrosses (Diomedea melanophris) and giant petrels (*Macronectes sp*).

3.4.2. Habitat selection models

To develop species-specific habitat selection models candidate environmental variables were fitted to two starting models. The first starting model contained only the intercept and only environmental variables were offered as candidates for selection. The second starting model contained the intercept and a spatial component consisting of the single terms UTM-Northing and UTM-Easting (equivalent to latitude and longitude) and the interaction term. Candidate variables and their transformations were the same for both dolphin species (Table 3-2).

3.4.2.1. Chilean dolphins

Ninety percent of all sightings (n= 127) of Chilean dolphins were clustered close to shore (< 500 m) and in relatively shallow waters (< 20 m depth). Chilean dolphins were rarely seen in deeper waters (max. depth 55 m) and were never sighted further than 900 m from shore (Figure 3-3, Table 3-3).

Shore distance was added to the intercept only model first based on its AIC_c score and was deemed to be the most influential variable (Table 3-5). The next variables to be added were the transformed terms for River distance and Depth. During the final steps of model selection the variable Shore distance was exchanged for In Shore Distance. For this exchange to be completed various interim steps were necessary as only one variable could be added/removed from the model at a time. Hence, the variables In Shore distance and SST were added to the model despite their individual contributions having a $\Delta AIC_c < 2$. Their inclusion and the subsequent removal of Shore distance resulted in an overall change in $\Delta AIC_c > 2$ (Table 3-5).

Table 3-5. Model selection based on AIC_c for Chilean dolphins starting from an intercept only model.

Term	Action	Res. Deviance	AIC _c	Δ AIC _c
Intercept	starting	636.06	636.06	
Shore distance	added	483.53	485.71	150.35
ln(River distance)	added	434.53	438.53	47.18
Depth ^ 2	added	417.32	423.34	15.19
Water clarity	added	406.77	414.81	8.53
ln(Salmon farm dist.)	added	401.10	411.16	3.65
ln(Shore distance)	added	397.09	409.18	1.98
SST	added	393.00	407.13	2.05
Shore distance	removed	393.67	405.08	2.05

The final environmental model for Chilean dolphins took the form:

logit(
$$\hat{p}$$
)_{Ce_enviro} = $\beta_0 + \beta_1$ (ln Shore distance) + β_2 (ln River distance) + β_3 (Depth²) + β_4 (Water clarity) + β_5 (ln Salmon farm dist.)

where logit (\hat{p}) is the logistic transformation (the link function) of the probability of Chilean dolphins being present, β_0 is the intercept and β_1 to β_5 are the estimated coefficients of the respective environmental variables (Table 3-6). Model fit was adequate based on a test of goodness of fit (χ^2 , p= 1). The environmental model explained approximately 38% of the variance.

Cross-validation tests using the test dataset from 2003 proved the predictive power of the final model and its generality. The environmental model fitted the test data significantly better than the simulated dataset (p< 0.0001). The mean proportion of correct predictions was 0.82.

Shore distance (or its log-transformation) was confirmed as the most influential single variable. A simple model with only Shore distance (or ln Shore distance) predicted the presence or absence of Chilean dolphins significantly better for the test dataset than for a simulated dataset (p= 0.001). The more complex environmental model, however, performed significantly better than single term models and was marginally better than an interim model containing ln Shore distance, ln River distance and Depth² (p=0.045).

The environmental model showed that Chilean dolphins preferred habitat close to shore and close to permanent rivers and streams, with shallow depth and turbid waters with slightly higher SST (Table 3-6). The probability of sighting Chilean dolphins also increased with distance from salmon farms.

Table 3-6. Results of the "best" habitat model (GLM with binomial error structure and logit link function) relating environmental variables to the presence of Chilean dolphins.

* significant at p= 0.05, ** significant at p< 0.001

Term	logit β	SE	z-value	p-value		Interpretation
Intercept	11.110	2.4470	4.539	0.000	**	
ln(Shore distance)	-1.533	0.2059	-7.448	0.000	**	closer to shore
ln(River distance)	-1.035	0.2077	-4.985	0.000	**	closer to rivers
Depth^2	$-1.3*10^5$	0.0000	-2.132	0.033	*	shallower waters
Water clarity	-0.165	0.0590	-2.790	0.005	*	less clear waters
ln(Salmon farm dist)	0.450	0.2050	2.194	0.028	*	further from salmon farms
SST	0.135	0.0647	2.090	0.037	*	warmer surface waters

Null deviance: 636.06 on 655 degrees of freedom Residual deviance: 393.67 on 650 degrees of freedom

% of explained deviance: 38

When a spatial component was added to the starting model the environmental variables entered the model in the same order of importance (Table 3-7) as with the intercept only model. All variables except SST continued to contribute significantly to the prediction of Chilean dolphin occurrence (Table 3-8). The spatial variables and the interaction term were retained throughout the model selection process and were significant terms in the final model (Table 3-8). Thus, the final environmental-spatial model had the same form as the environmental model above, but with three added terms: $+\beta_6(UTM-Northing) + \beta_7(UTM-Easting) + \beta_8(UTM-E:UTM-N)$.

Table 3-7. Model selection based on AIC_c for Chilean dolphins starting from a spatial model. (:) denotes interaction term.

Term	Action	Res. Deviance	AIC_c	Δ AIC _c
UTM-Easting	starting			
UTM-Northing	starting			
UTM-E: UTM-N	starting	545.08	551.12	
Shore distance	added	446.29	454.33	96.79
ln(River distance)	added	407.18	417.24	37.09
Depth ^ 2	added	393.76	405.42	11.82
Water clarity	added	387.29	401.42	4.00
ln(Salmon farm dist.)	added	380.19	396.36	5.06
ln(Shore distance)	added	377.21	395.96	0.40
SST	added	374.23	394.51	1.45
Shore distance	removed	375.05	393.39	1.12

Table 3-8. Results of the "best" habitat model (GLM with binomial error structure and logit link function) relating spatial and environmental variables to the presence of Chilean dolphins.

	*	significant at $p=0.05$,	** significant at	p < 0.001
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Term	logit β	SE	z-value	p-value		Interpretation
Intercept	-5476.0	1606.0	-3.409	0.001	**	
UTM Easting ◆	0.009	0.0026	3.388	0.001	**	further west
UTM Northing ◆◆	-0.001	0.0003	-3.422	0.001	**	further south
UTM-E: UTM-N	-1.9*10 ⁹	0.0000	3.394	0.001	**	non-uniform spatial distribution
ln(Shore distance)	-1.362	0.2144	-6.352	0.000	**	closer to shore
ln(River distance)	-1.038	0.2121	-4.893	0.000	**	closer to rivers
Depth^2	-0.001	0.0003	-2.133	0.033	*	shallower waters
Water clarity	-0.166	0.0667	-2.491	0.013	*	less clear waters
ln(Salmon farm dist)	0.525	0.2164	2.427	0.015	*	further from salmon farms
SST	0.127	0.0658	1.929	0.054		slightly warmer waters

Null deviance: 636.06 on 655 degrees of freedom Residual deviance: 375.05 on 646 degrees of freedom

% of explained deviance: 41

♦ UTM- Easting refers to longitude in UTM coordinate system. Numbers increase from East to West.

♦♦ UTM- Northing refers to latitude in UTM coordinate system. In the southern hemisphere numbers are negative and decrease from North to South.

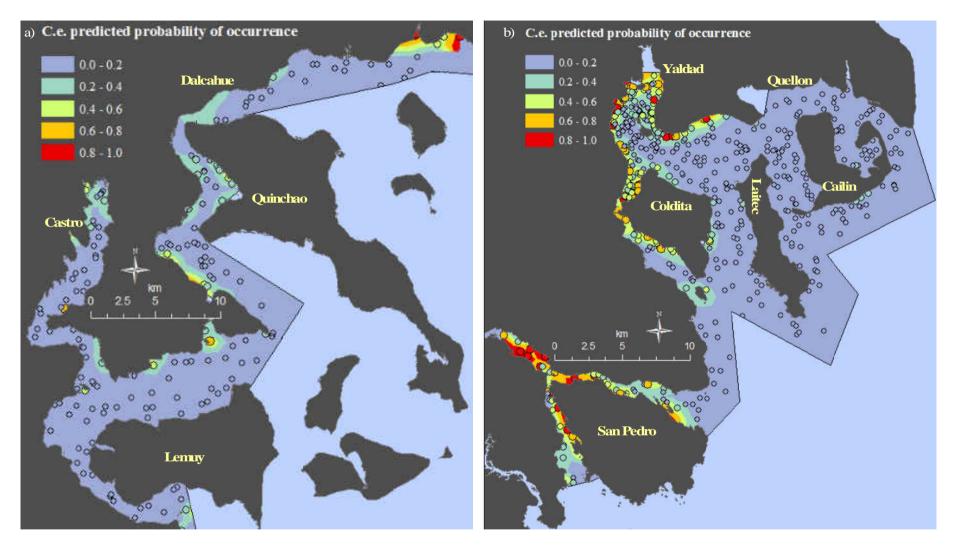


Figure 3-4. Predicted probability of occurrence for Chilean dolphins in central (a) and southern (b) Chiloé from the environmental-spatial model. Predicted values are smoothed across sampling stations (dots) using local polynomial interpolation.

The variable UTM-Northing highlighted the difference between study areas with the probability of dolphin occurrence increasing from North to South (i.e. central versus southern Chiloé). UTM-Easting reflected the distribution pattern of Chilean dolphins in southern Chiloé where the probability of dolphin presence increased from East to West. The environmental-spatial model explained approximately 41% of the variance.

The mean proportion of correct predictions was 0.84 when using cross-validation, which represented a small but statistically not significant improvement in the predictive performance when compared to the environmental model (cross-validation with test dataset, p= 0.169). The environmental-spatial model was selected to calculate the probability values used for plotting predictive surfaces of dolphin occurrence (Figure 3-4) given its lower AIC_c-value, its slightly better predictive performance and its smaller residuals compared to the environmental model.

Visual inspection of the residuals plotted in space showed no spurious patterns. Although residuals tended to be larger at sites with dolphin presence both over- and under-prediction occurred over small spatial scales in Yaldad Bay and Canales San Pedro/Guamblad. Both models tended to under-predict the presence of Chilean dolphins in areas that had only a small number of actual sightings (i.e. Isla Cailin and Canal Dalcahue). Smoothing across single predicted values homogenized this small-scale variation and produced predictive surfaces that reflected the overall pattern apparent from the original data.

3.4.2.2. Peale's dolphins

Sightings of Peale's dolphins were clustered close to the shore and in relatively shallow waters (80% of all sightings < 500 m from shore and < 20 m deep). Peale's dolphins were seen occasionally in waters of up to 65 m depth, but were still within 1,000 m of the shore (Figure 3-3, Table 3-3). The furthest they were seen from shore was 2,300 m in shallow waters less than 20 m depth.

During the model selection process the variables Shore distance and Depth and their transformations were added to the intercept model along with the two anthropogenic variables In Mussel Farm dist. and In Salmon Farm dist. (Table 3-9). The final environmental model for Peale's dolphins had the form:

logit(\hat{p})_{La_enviro} = $\beta_0 + \beta_1$ (ln Shore distance) + β_2 (Depth) + β_3 (ln Mussel farm dist.) + β_4 (ln Salmon farm dist.) + β_5 (Depth²) + β_6 (Depth³) + β_7 (Shore distance).

Table 3-9. Model selection based on AIC_c for Peale's dolphins starting from an intercept model.

Term	Action	Res. Deviance	AIC_c	Δ AIC _c
Intercept		494.69	494.96	<u>.</u>
ln(Shore distance)	added	427.89	429.89	65.07
Depth	added	405.95	409.95	19.94
ln(Mussel farm dist.)	added	383.93	389.95	20.00
ln(Salmon farm dist.)	added	374.54	382.57	7.38
Depth^2	added	368.08	378.14	4.43
Depth ³	added	356.59	368.69	9.45
Shore distance	added	351.66	365.80	2.89

Model fit was adequate based on a test of goodness of fit (χ^2 , p= 1). The environmental model explained approximately 29% of the variance. Cross-validation tests showed that the environmental model fitted the test data significantly better than the simulated dataset (p< 0.0001). The mean proportion of correct predictions was 0.82. A simple model with only ln Shore distance predicted the presence or absence of Chilean dolphins significantly better for the test dataset than for a simulated dataset (p= 0.004). The more complex environmental model, however, performed significantly better than the simple or any of the interim models (p= 0.007).

Table 3-10. Results of the "best" habitat model (GLM with binomial error structure and logit link function) relating only environmental variables to the presence of Peale's dolphins.

* significant at p= 0.05, ** significant at p< 0.001

Term	logit β	SE	z-value	p-value		Interpretation
Intercept	1.442	3.1190	0.462	0.644		
ln(Shore distance)	-1.773	0.4490	-3.949	0.000	**	closer to shore
Depth	-0.279	0.0650	-4.290	0.000	**	shallower waters
ln(Mussel farm dist.)	0.606	0.1711	3.544	0.000	**	further from mussel farms
ln(Salmon farm dist.)	0.571	0.2568	2.224	0.026	*	further from salmon farms
Depth ^ 2	0.007	0.0023	3.202	0.001	**	some flexibility in depth range
Depth ^ 3	$-5.9*10^5$	0.0000	-2.598	0.009	*	shallower waters
Shore distance	0.002	0.0009	2.363	0.018	*	wide range of shore distance

Null deviance: 494.69 on 616 degrees of freedom Residual deviance: 351.66 on 609 degrees of freedom

% explained deviance: 29

[♦] UTM- Easting refers to longitude in UTM coordinate system. Numbers increase from East to West.

^{◆◆} UTM- Northing refers to latitude in UTM coordinate system. In the southern hemisphere numbers are negative and decrease from North to South.

The environmental model showed that Peale's dolphins preferred habitat close to shore and with shallow depth (Table 3-10). The probability of sighting Peale's dolphins also increased with distance from mussel farms and salmon farms.

Adding a spatial component to the starting model resulted in the inclusion of a slightly different set of variables in the final model (Table 3-11). The environmental-spatial model explained approximately 33% of the variance. The environmental-spatial model fitted the test dataset significantly better than the simulated data during cross-validation tests (p< 0.0001). The environmental model and the environmental-spatial model did not differ significantly in predictive performance (mean proportion of correct predictions= 0.81, p= 0.598). Given the amount of variance explained and the smaller AIC_c-value, the environmental-spatial model was chosen to obtain predicted values to plot the probability surfaces (Figure 3-5).

Table 3-11. Model selection based on AIC_c for Peale's dolphins starting from a spatial model. (:) denotes interaction term.

Term	Action	Res. Deviance	AIC_c	Δ AIC _c
UTM-Easting	starting			
UTM-Northing	starting			
UTM-E: UTM-N	starting	475.13	475.13	
ln(Shore distance)	added	391.70	399.74	75.39
Depth	added	368.37	378.44	21.30
ln(Mussel farm dist.)	added	351.74	363.84	14.60
Shore distance	added	343.38	357.52	6.32
Salinity	added	337.21	353.39	4.13
ln(Salmon farm dist.)	added	331.10	349.34	4.05

Visual inspection of the residuals plotted in space showed no systematic spatial pattern. Both models tended to under predict the occurrence of Peale's dolphins for some sampling locations in Canal Dalcahue (central Chiloé) and at southern Isla Cailin, Punta Queupué, Punta Yenecura, Punta Lua (Bahia Quellon), and Canal Chiguao (all southern Chiloé). Probability surfaces smoothed across single predicted values reduced this small-scale variation and seemed to represent the apparent importance of most of these areas.

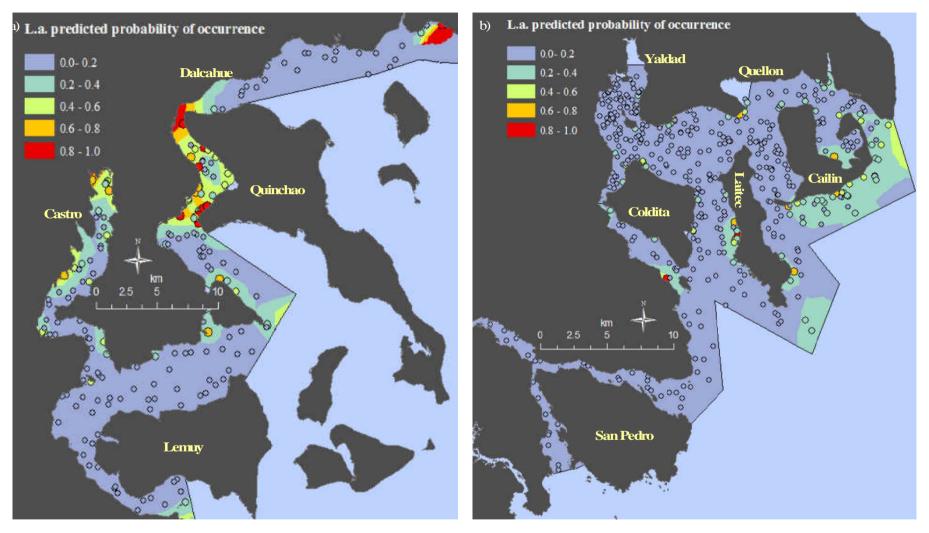


Figure 3-5. Predicted probability of occurrence for Peale's dolphins in central (a) and southern (b) Chiloé from the environmental-spatial model. Predicted values are smoothed across sampling stations (dots) using local polynomial interpolation.

Table 3-12. Results of the "best" habitat model (GLM with binomial error structure and logit link function) relating spatial and environmental variables to the presence of Peale's dolphins.

* significant at p= 0.05, ** significant at p< 0.001

Term	logit β	SE	z-value	p-value		Interpretation
Intercept	4175.00	1682.00	2.483	0.013	*	
UTM Easting ◆	-0.007	0.0027	-2.435	0.015	*	further east
UTM Northing ◆◆	0.001	0.0004	2.506	0.012	*	further north
UTM-E: UTM-N	$-1.4*10^9$	0.0000	-2.465	0.014	*	non-uniform spatial distribution
ln(Shore distance)	-2.366	0.4615	-5.127	0.000	**	closer to shore
Depth	-0.038	0.0098	-3.917	0.000	**	shallower waters
ln(Mussel farm dist)	0.756	0.1932	3.911	0.000	**	further from mussel farms
Shore distance	0.003	0.0008	3.173	0.002	*	wide range of shore distances
Salinity	-0.473	0.1777	-2.661	0.008	*	less saline waters
ln(Salmon farm dist)	0.599	0.2613	2.292	0.022	*	further from salmon farms

Null deviance: 494.69 on 616 degrees of freedom Residual deviance: 331.10 on 607 degrees of freedom

% explained deviance: 33

- ♦ UTM- Easting refers to longitude in UTM coordinate system. Numbers increase from East to West.
- ♦♦ UTM- Northing refers to latitude in UTM coordinate system. In the southern hemisphere numbers are negative and decrease from North to South.

3.4.3. Inter-specific comparison of habitat use

To compare habitat use of Chilean dolphins and Peale's dolphins directly a new set of models was investigated starting from an intercept only model. The candidate set of variables included only those terms that were included in the final habitat models selected for each species. Hence, the candidate variables were the same as in Table 3-2, except that Bft and Salinity were not included.

Table 3-13. Model selection based on AIC_c for inter-specific habitat selection of Chilean dolphins and Peale's dolphins. (:) denotes interaction term.

Term	Action	Res. Deviance	AIC_c	Δ AIC _c
Intercept		489.42	489.42	
UTM-Easting	added	419.52	421.52	67.9
ln(Mussel farm dist.)	added	373.13	377.14	44.38
UTM-Northing	added	332.25	338.29	38.85
UTM-E: UTM-N	added	247.85	255.91	82.38
ln(River distance)	added	242.86	253.03	2.88

Spatial variables (singly and as interactions) made the most significant contribution to explaining the observed occurrence pattern of Chilean dolphins (coded as 1) over Peale's dolphins (coded as 0) (Tables 3-13 and 3-14). Distance to mussel farms was also a highly significant predictor of occurrence of Chilean dolphins over Peale's dolphins and distance to rivers added additional explanatory power to the model. Model fit was adequate based on a test of goodness of fit (χ^2 , p= 1). The final model explained approximately 50% of the variance.

Hence, habitat partitioning between Chilean dolphins and Peale's dolphins was explained mainly by spatial components showing that Chilean dolphins occurred further to the west and south compared to Peale's dolphins. Chilean dolphins also tended to select habitat closer to mussel farms and river mouths than Peale's dolphins.

Table 3-14. Results of the "best" habitat model (GLM with binomial error structure and logit link function) relating the spatial segregation of Chilean dolphins and Peale's dolphins to environmental variables.

*	significant at	p = 0.05	** significant a	t p < 0.001

Term	logit β	SE	z-value	p-value		Interpretation
Intercept	-14260.0	2202.0	-6.474	0.000	**	
UTM-Easting ◆	0.023	0.0036	6.418	0.000	**	C.e. further west than L.a.
ln(Mussel farm dist)	-0.670	0.0000	-4.539	0.000	**	C.e. closer to mussel farms than L.a.
UTM-Northing ◆◆	-0.003	0.1476	-6.495	0.000	**	C.e. further south than L.a.
UTM-E: UTM-N	$4.9*10^9$	0.0005	6.434	0.000	**	spatial segregation
ln(River distance)	-0.552	0.2557	-2.160	0.031	*	C.e. closer to rivers than L.a.

Null deviance: 489.42 on 354 degrees of freedom Residual deviance: 242.86 on 349 degrees of freedom

% explained deviance: 50.4

♦ UTM- Easting refers to longitude in UTM coordinate system. Numbers increase from East to West.

◆◆ UTM- Northing refers to latitude in UTM coordinate system. In the southern hemisphere numbers are negative and decrease from North to South.

3.5. DISCUSSION

Habitat modelling is a powerful analytical tool to investigate where animals are found, why they might occur there and where they could be expected to occur (Boyce and McDonald 1999, Rushton *et al.* 2004). However, the results from habitat models need to be evaluated carefully before conclusions are drawn or generalisations are made. Assumptions and limitations of the models should be considered within their analytical framework and in an ecological context.

3.5.1. Data structure and assumptions

Habitat models are based on the correct classification of sites where animals are present or absent. Cetaceans are inherently difficult to detect as they spend only a small proportion of their time visible at the water's surface. Detectability also varies between species and with sighting conditions (Barlow et al. 2001). In this study, surveys were restricted to good sighting conditions. Sea state was included in the candidate variable set but was not deemed a significant predictor of dolphin occurrence during the model selection process. There was also no apparent spatial bias in the detection of dolphins between sheltered and exposed areas or between the two study areas (Chapter 2). Both dolphin species were detected at similar estimated radial distances from the research boat (Chilean dolphin mean distance= 234 m ± 193.7 SD; Peale's dolphin mean distance= 249 m ± 215.9 SD). As occurrence of dolphins, rather than density was of interest, effective strip width or area searched were not estimated. Dolphins are likely to have been missed while moving along transects between sampling sites. However, absence was recorded at fixed sites where the boat was stopped for the duration of sampling and dolphins at that site could not have been overlooked. Hence, sites with presence of dolphins might have been missed, but presence or absence were classified correctly.

Absence refers to the brief visit to a site during a particular survey. The chance of encountering dolphins at one site compared to another depends on habitat quality but also the number of animals using the area and their group structure (one large versus many small groups). Thus, even good habitats will not always be "used". The strength of model-derived predictions of occurrence is the identification of sites where dolphins could be present given their habitat selection characteristics. Areas of high predicted occurrence indicate preference but do not provide information on behaviour

or density. Areas that are only used occasionally but where dolphins perform crucial behaviours most likely will be under-predicted by occurrence models (see section 3.5.4.).

In this study, discrete points in space and time (i.e. sampling sites) constitute the sampling units and are assumed to be a representative sample of the habitat used and not used by the dolphins. This assumption appears to hold given the extensive spatial coverage and the spread of sampling locations (also a representation of effort) in both study areas. All predictor variables (except River distance) were based on real-time measurements providing snap-shots of the actual environmental conditions compared to extrapolated approximations derived from remotely sensed or other external data sources. Using sampling sites (i.e. species observations) instead of *post hoc* raster classifications (i.e. grid cells or segments) captures the biologically interesting fine-scale variation in the nearshore habitat. It also reduces the scale-dependent biases introduced by choosing a spatial scale to define sampling units (e.g. size of grid cells)(Jaquet and Whitehead 1996, Gregr and Trites 2001).

Other problems of scale, both temporal and spatial, however, require careful consideration. Environmental predictor variables such as SST, salinity and water clarity vary between months (Chapter 2, Navarro and Jaramillo 1994). This study was conducted mainly during austral summer, and during this relatively short time period variation was generally greater between different areas than over time in the same area. Daily fluctuations due to changeable weather conditions were also greater than variation among months. This short-term temporal variation is unlikely to have had a strong effect on dolphin habitat selection. Interannual variation was not significant for most variables except SST and Salinity, but the absolute median differences were small.

It is important to note that conclusions about habitat selection determined in this study only apply to the distribution patterns of dolphins during the summer/autumn. Although Chilean dolphins at least are known to use the same inshore channels year-round (Chapter 2), their preference for certain habitat types as defined by environmental variables might vary. Thus, seasonal changes in habitat selection have yet to be investigated for both species.

A fundamental assumption in statistical analyses is the independence of the underlying data (Sokal and Rohlf 1996). Autocorrelation, the dependence of a particular measurement on its immediate neighbours in space or in time, increases non-independence among the data and cannot easily be addressed in simple regression analyses (Augustin *et al.* 1996, Gregr and Trites 2001). Although methods exist to take account of autocorrelation while exploring the correlation between presence of an organism and environmental variables (i.e. Mantel tests, Legendre 1993), these do not allow predictions to be generated.

In the absence of dolphins, samples were taken at fixed 15-minute intervals which equates to approximately 4.7 km travelled along the transects. The straight-line distance between sampling sites during one survey was usually smaller (approximately 1.2 km) due to the zigzag survey pattern used. During a transect usually only one dolphin group was encountered, or if several groups were seen then these tended to be spaced apart (> 500 m). Dolphin groups that were sighted while already working with a particular group were not used in this analysis.

As surveys were conducted repeatedly in the same areas (over month and years) the cumulative number of sampling sites in areas with higher effort resulted in some sampling sites being located close in space (but not in time) despite transects never being repeated. Many sightings of both species also tended to cluster in certain areas. Although lack of independence is of analytical concern, it is also of biological interest. Clustering of the cumulative sightings of animals in one area across time highlights the importance of that particular habitat. The inclusion of a spatial component in the models should have offset the lack of independence to a certain extent. In addition, cross-validation tests confirmed the fit of the final models for both species and their appropriate complexity. Residuals plotted in space showed no systematic spatial pattern of under- or over-predictions. Thus, autocorrelation most likely is present in the data, the variables included in the models appear to be important predictors of dolphin occurrence. As Gregr and Trites (2001) point out the lack of independence "is more a cause for debating the relative strength and scale of the proposed process rather than a reason for dismissing the hypotheses [about the underlying ecological processes] out of hand."

3.5.2. Model assessment

The fit of a model and the selection of predictor variables deemed to be important often reflect the selection process more than biological relevance (MacNally 2000). In this study, model fit and complexity were evaluated in successive steps to avoid overfitting while obtaining a model with sufficient predictive power. Candidate variables were chosen based on their hypothesized biological importance and the practicality of obtaining reliable measurements. The contribution of each variable to the model fit was evaluated using AIC_c and cross-validation tests on an independent dataset from the same study areas. The combination of these different avenues allowed the derivation of relatively simple but sufficiently complex models with straight-forward biological interpretations. This procedure also highlights the potential lack of some important predictors from the candidate variable set (see section 3.5.3.).

One of the big challenges with regard to habitat models using occurrence data is the lack of easily applicable methods to assess the predictive performance of the models. Model assessment involves comparing derived probabilities with observed categories (i.e. the real absence-presence data). Most studies use thresholds in the predictions above and below which presence and absence are defined (e.g. kappa statistic, classification tables) (Gregr and Trites 2001, Rushton *et al.* 2004, Hastie *et al.* 2005, Jiménez 2005). Threshold methods, however, are highly sensitive to sample size, fail if the number of absence values exceeds that of presence values (as is the case in most studies of habitat selection in cetaceans) and are based on an arbitrarily chosen threshold value. In this study, cross-validation tests using randomisations and comparing the predictive performance of simple and complex models provided a simple and threshold-independent method for model assessment. With this method the predictive performance of any model can be evaluated against that of any other model, not just against a random scenario (e.g. as in Cañadas *et al.* 2005).

Habitat models in this study serve both an explanatory purpose (i.e. to understand what variables are important in habitat selection) and a predictive purpose (i.e. to predict where dolphins are likely to occur given certain habitat types). From an ecological perspective, environmental variables are those of direct interest as they represent proxies for biological features that determine habitat quality. A spatial component can carry importance if it functions as a substitute for an unknown

influential variable that is not included in the candidate set. Thus, inclusion of a spatial component might provide a better fit of the model and enhance its predictive power. However, including spatial components in the model limits general applicability and validity testing to the spatially defined study area.

Models developed for a dataset specific to one area should not be generalized or applied to other areas without careful testing. Cross-validation tests can be used to evaluate how well a model derived for one area predicts the probability of occurrence of dolphins in another area. Thus, the environmental model could be applied to a dataset from a different geographic region where dolphin occurrence and environmental variables have been sampled using the same methods as in this study. Such an approach, if carefully implemented and evaluated, could provide interesting insights into the spatial generality of the observed habitat selection pattern.

3.5.3. Habitat selection in Chilean dolphins

Chilean dolphins show a clumped distribution, centred in Yaldad Bay, Canal Coldita and Canales San Pedro/Guamblad in southern Chiloé and a patchy distribution in central Chiloé (Figure 3-1). The most important predictor variables for their occurrence are distance from shore, distance to rivers and water depth, and to a lesser extent water clarity and SST. Both, the environmental model and the environmental-spatial model performed well during cross-validation tests. The significant spatial components and the amount of variance explained by the final models indicate that other factors not included in the model building and selection process also act upon the distribution and occurrence of Chilean dolphins.

The observed differences in occurrence in central and southern Chiloé seemed to reflect availability of preferred habitat. Preferred habitat was more or less continuous along the shores of Yaldad Bay, Canal Coldita and then again in Canales San Pedro/Guamblad based on predicted probabilities of occurrence (>50%) (Figure 3-4). In contrast, in central Chiloé only isolated stretches of coastline provide the combination of environmental variables predicted to be selected by Chilean dolphins. Encounter rates and group sizes of Chilean dolphins are significantly smaller in central compared to southern Chiloé (Chapter 2). Thus, size and connectedness of preferred habitat appear to influence occurrence and group dynamics, and most likely

density of Chilean dolphins. Density was not considered in the habitat models, but could be incorporated as a next step following the approach by Cañadas *et al.* (2005).

What are the features that make the selected areas in southern Chiloé so attractive to Chilean dolphins? Yaldad Bay and Canal Coldita are bounded by wide intertidal areas of with gently sloping, pebble beaches. In contrast, Canales San Pedro/ Guamblad are lined mainly by steep rocky shores with dense vegetation cover and forests extending to the water's edge. Despite geomorphological differences, these locations are relatively sheltered bays and channels with, at least in parts, strong estuarine character and strong tidal currents (Heinrich, pers. observation, Navarro and Jaramillo 1994). A purported "preference" for areas with estuarine character, river mouths, and close to shore, with strong tidal currents or wave action has been reported for Chilean dolphins throughout their range (Goodall *et al.* 1988a, Pérez-Alvarez and Aguayo-Lobo 2002, Ribeiro 2003), and is also well known for congeneric species (Goodall *et al.* 1988b, Bräger and Schneider 1998, Torlaschi *et al.* 2000, Bejder and Dawson 2001, Coscarella 2005). The observed preference for turbid, and slightly warmer waters most likely reflects oceanographic peculiarities of the selected shallow inshore habitat rather than constituting active selection of these features (Karczmarski *et al.* 2000).

Given that Chilean dolphins seem to spend a large proportion of their time foraging (Chapter 2, Ribeiro 2003), the distribution and occurrence of potential prey could be an important factor underpinning the observed habitat selection patterns. Quantitative information on diet composition and prey sizes of Chilean dolphins is lacking. Three reported prey species, róbalo (Patagonian blenny, *Eleginops maclovinus*), pejerrey (silverside, *Odontesthes* sp.), and possibly sardines (*Clupea* sp. or *Strangomera* sp.), (Oporto *et al.* 1990) inhabit estuaries and sheltered bays during spring and summer (Pequeno and Sáez 2004) and are regularly seen, and caught in shorebased gillnets, in Yaldad Bay (Heinrich, pers. observation). An intense seasonal phytoplankton bloom occurs in Yaldad Bay during the summer fuelled by the estuarine properties of the bay (Navarro and Jaramillo 1994). At the same time, large schools of small fish (< 20 cm in length) and an abundance of piscivorous sea birds congregate in the bays and channels used by Chilean dolphins (this study, Crovetto and Medina 1991), thus supporting the idea of elevated local productivity attracting fish and fish predators.

The importance of estuarine areas as foraging grounds is well documented in the literature for other coastal dolphin species (e.g. Ballance 1992, Gubbins 2002, Flores and Bazzalo 2004, Coscarella 2005).

Although localized abundance of prey related to unique physical-oceanographic features might constitute a strong attractant, social reasons could also be important in habitat selection. Calving (and possibly mating?) mainly takes place during the summer (Chapter 2, Goodall *et al.* 1988a). Thus, the distribution of conspecifics with which to socialize and exploit schooling prey cooperatively (see Chapter 2) is likely to influence an individual's movements and habitat selection (see Chapter 4). The importance of distance to salmon farms is discussed in section 3.5.6.

3.5.4. Habitat selection in Peale's dolphins

Peale's dolphin habitat selection was mainly influenced by distance from shore and depth. Distance to mussel farms and salmon farms were important and potential implications are discussed in section 3.5.6. The spatial components added significantly to the fit of the model but not to its predictive ability. Their inclusion indicates that one or several potentially important variables might not have been considered.

The areas predicted to be important for Peale's dolphins (based on probability of occurrence) are relatively patchily distributed. In southern Chiloé, the shoals and shorelines of south-eastern Islas Laitec and Cailin are predicted to have higher rates of occurrence. In central Chiloé, the central and upper part of the Estero Castro, the south-western shore of Canal Hudson and particularly Canal Dalcahue seem to offer important habitat. In the predictive maps, probability of occurrence is over-predicted at the eastern boundaries of both study areas due to edge effects from smoothing between sampling stations and the lack of data outside the sampling area.

Field observations suggest that one of the potentially unifying features of the selected shallow areas is a relatively soft or sandy bottom sediment with evidence for presence of *Macrocystis pyrifera* kelp in Canal Dalcahue and the southern shoals of Isla Cailin. Shore-based investigations of habitat selection have confirmed the long reported preference by Peale's dolphins for *Macrocystes* kelp beds in the Strait of Magellan in southern Chile (Lescrauwaet 1997, Viddi and Lescrauwaet 2005). Kelp

was not included as a variable in the habitat models in this study as it is generally not very abundant in the Chiloé Archipelago and presence and extent of kelp forests are difficult to determine reliably *in situ*. However, kelp is only one possible feature that was not included in the habitat models and could be important to Peale's dolphins in Chiloé.

Peale's dolphins were mainly seen travelling (see Chapter 2). The patchy distribution of preferred habitat would suggest that they transit between patches, thus potentially traversing most of the study area. Alternatively, individuals might show site fidelity to particular patches of good habitat. Individual ranging patterns are investigated in detail in Chapter 4.

The diet of Peale's dolphins in the Chiloé Archipelago is not known. Based on observations from southern Argentina they could be exploiting demersal prey in shallow waters (Iñíguez and de Haro 1993, Schiavini *et al.* 1997) which in turn shows preference for particular habitat features. They are also known to take the same prey species mentioned for Chilean dolphins above.

As discussed for Chilean dolphins, habitat use based on occurrence does not take into account density or behaviour. Fine-scale observations in the habitat selected by Peale's dolphins (e.g. Canal Dalcahue) could provide insights into the factors underlying its importance and the behaviour displayed there (e.g. as done for *Tursiops truncatus*, Hastie *et al.* 2004, Bailey and Thompson 2006).

In southern Chiloé, the probability of occurrence (i.e. importance of selection) was under-predicted at several sites that field observations suggest are important. These are small isolated sites along the shores of Bahia Quellon (Punta Yenecura, Punta Queupue, and Punta Lua) where single females with very small neonates were observed at several occasions during the summer in different years. These areas might serve as temporary "refuge or nursing areas" for recent newborns (i.e. hours to a few days old) during the most vulnerable period of their life. Habitat models based solely on occurrence will always under-predict areas of short-term importance or of infrequent but important use by a particular part of the population.

3.5.5. Habitat partitioning of Chilean dolphins and Peale's dolphins

Both species showed a marked preference for shallow nearshore waters based on single species-habitat models. There was little spatial overlap when comparing the predicted plots of occurrence. Comparing both species directly in an analytical framework showed a clear pattern of spatially driven habitat partitioning. Only two non-spatial variables were significant and included in the final model. Chilean dolphins selected areas closer to mussel farms and closer to rivers compared to Peale's dolphins.

The proximity to mussel farms in Chilean dolphins should not be interpreted as preference for mussel farms as such. Rather, mussel farms appear to serve as a proxy for some unmeasured characteristics that make this area so attractive to Chilean dolphins. As the majority of sightings of Chilean dolphins close to the mussel farms was made in Yaldad Bay, their occurrence close to mussel farms appears to be driven by the characteristics of this particular location, e.g. estuarine features and high seasonal primary productivity coupled with potentially elevated prey availability (see section 3.5.3.).

It remains unclear whether differences in prey preference and/or feeding strategy could drive the observed pattern of habitat partitioning between Chilean dolphins and Peale's dolphins. Along the southern South Atlantic coast, Peale's dolphins seem to interact, and often forage jointly with Commerson's dolphins, *C. commersonii* (Goodall 1988b, Goodall *et al.* 1997), the allopatric South American congener of Chilean dolphins. Based on detailed diet analysis Commerson's dolphins are thought to be a coastal generalist predator feeding mainly on or near the bottom and exploiting a wide range of fish (up to 30 cm in length), shrimp and squid (Bastida *et al.* 1988). Peale's dolphins are also considered to be generalist predators in the same areas and exploit at least part of a similar prey field (Schiavini *et al.* 1997). Social factors and different life history constraints might also be important aspects influencing the spatial distribution of sympatric species (Bearzi 2005). Although the factors leading to the differences in habitat selection of Chilean dolphins and Peale's dolphins remain unknown, implications for conservation and exposure to potential anthropogenic impacts exist.

3.5.6. Potential impacts on selected habitats

Both species showed a positive relationship with distance from salmon farms, and in the case of Peale's dolphins also from mussel farms. Although Chilean dolphins selected habitat closer to mussel farms than Peale's dolphins, they did not prefer sites close to mussel farms *per se* (i.e. the variable Mussel farm dist. was not significant and not included in the final habitat model for Chilean dolphins).

The observed significant relationship between the dolphins and mussel and salmon farms is best explained by indirect external factors rather than by active selection for, or avoidance of, farms. Mussel farms and salmon farms select specific environmental conditions for proliferation and growth of their farmed stock. Both farm types require space and a minimum water depth due to the height of the underwater structures involved. Vertically suspended mussel growth lines usually extend for 8 m length (Clasing et al. 1998) from the surface. Salmon farm cages are variable in size and extent, but usually are placed in water of more than 15 m depth. Salmon requires clean waters for optimal growth and farms are preferentially placed in areas with some currents to prevent accumulation of biodeposits around the farm complex (Stigebrandt et al. 2004). Mussels, being self-sustaining filter feeders, depend on abundant phytoplankton supply in the water column, as is found in highly productive estuaries with tidal flushing (Navarro and Jaramillo 1994). In addition, there are many technical, practical and legal requirements for placement of mariculture farms (Bushmann et al. 1996), including proximity to settlements, transport and supply routes.

Selection for areas with estuarine character, presumed high primary productivity and some tidal flushing brings Chilean dolphins in direct overlap with prime sites of mussel farming in the sheltered waters of eastern Chiloé. Incidental observations suggest the presence of Chilean dolphins in the three largest estuarine bays of eastern Chiloé, all of which are also used intensively for mussel farming (Heinrich, pers. observation, Goodall *et al.* 1988a). However, as mariculture farms are wide-spread and extensive in the Chiloé Archipelago there are few sheltered areas that are not used by at least one farm type (Anon. 2001).

Displacement of dolphins from critical habitat due to extensive shellfish farms has been observed (Watson-Capps and Mann 2005), and has been suggested for Chilean

dolphins in Yaldad Bay (Kemper *et al.* 2003, Ribeiro 2003). In the absence of information on pre-farming distribution and habitat use patterns of the dolphins, displacement is difficult to establish or refute. A simulation experiment or controlled comparison of used and unused farm sites while accounting for habitat selection criteria of the dolphins might provide a way to gauge the potential for displacement or exclusion from potentially important habitat for the dolphins.

Based on distance to shore, selected depth and requirements for water clarity there seems to be less potential for competition for space between salmon farms and Chilean dolphins or Peale's dolphins. However, salmon farms are numerous in areas of high use by Chilean dolphins (i.e. Canales San Pedro/Guamblad), and by Peale's dolphins (Canales Dalcahue/Hudson). Salmon farms can affect dolphins and their habitat indirectly over an unknown distance due to deleterious changes to the local ecosystem, contamination, disturbance from noise and farm-associated activities (Bushmann *et al.* 1996, Tovar *et al.* 2000, Haya *et al.* 2001, Würsig 2001). Given the lack of understanding of any of the ecosystem components singly, let alone in their cumulative complexity, effects will be difficult to detect, and causal link will be even harder to establish.

Mariculture activities are already widely established in the coastal waters of the 10th Region of Chile (i.e. Chiloé and mainland area) and are expanding rapidly into the remote fjords and bays of the 11th Region to the South (Bushmann *et al.* 1996, Soto *et al.* 2001). Given the vast extent of these areas and the lack of control or enforcement of already existing regulations (Cárdenas *et al.* 2005), potential impacts might be better prevented rather than managed. No-use zones where potentially harmful activities are not allowed to occur might provide a useful approach. A preliminary coastal management plan² has been drafted by the regional authorities suggesting areas for different usage and some rather arbitrarily placed "conservation zones." Identified areas of importance to apex predators like dolphins seem to be important to many other organisms at various trophic levels and could provide at least some biologically founded guidance to the placement of "conservation zones."

² Information available at http://www.goreloslagos.cl/web/webfebr/bordecostero/comunal/

This study provides a rigorous framework to investigate habitat selection in small coastal cetaceans based on careful model selection, evaluation and validation. The derived predictive models could be tested on environmental data from other areas for which similarly collected sighting data of Chilean dolphins and Peale's dolphins are also available. Such a spatially independent validation approach could provide information on the generality of habitat selection patterns. If the model proves robust, it might help target future research efforts to areas of predicted occurrence in the vast expanse of the remote and logistically challenging habitat of Chilean dolphins and Peale's dolphins to the East and South of Chiloé.

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Chapter 4 Site fidelity and ranging patterns of Chilean dolphins and Peale's dolphins: implications for conservation

4.1. ABSTRACT

Movement patterns can reveal much about a species' social dynamics and resource use. They also provide important information on the spatial scales over which monitoring programs and habitat protection measures should be implemented to provide adequate protection for and management of impacted populations. Coastal Chilean dolphins (Cephalorhynchus eutropia) and sympatric Peale's dolphins (Lagenorhynchus australis) are subject to a variety of potential anthropogenic threats, and their population structure, ranges and movements are unknown. Site fidelity, movement and ranging patterns were investigated for individually identifiable Chilean dolphins and Peale's dolphins in the southern and central Chiloé Archipelago, southern Chile in the austral summers of 2001 to 2004. Data were collected during boat-based photo-identification surveys conducted in two predefined study areas, each spanning approx. 270 km². Analysis of sighting histories from 42 regularly seen Chilean dolphins revealed temporary stable small-scale site fidelity and short alongshore movements (mean= 23.1 km, SE= 1.92). Ranges and core areas determined for 11 Chilean dolphins with \geq 20 sightings were small compared to other delphinids and occupied a fraction of the available habitat, possibly reflecting habitat quality and prey distribution. Individual Chilean dolphins differed in their site preference and range overlap suggesting spatial partitioning in relation to environmental and social factors within the population. Individual Peale's dolphins showed only limited or low site fidelity, but observed alongshore movements were similar to those of Chilean dolphins. Low intra-and inter-annual resighting rates suggest that Peale's dolphins ranged beyond the boundaries of the study areas. Implications for population monitoring and spatially explicit habitat protection measures are discussed.

4.2. Introduction

The Chilean dolphin (*Cephalorhynchus eutropia*), a small endemic delphinid, is restricted to the inshore waters of Chile from 33° to 55° S (Goodall 1994). The larger Peale's dolphin (*Lagenorhynchus australis*) occupies the same coastal habitats in Chile, but its distribution extends well into the southern South Atlantic (Brownell *et al.* 1999). Limited information exists on the ecology of both species and ranging and movement patterns have not been investigated to date.

Individual movement patterns can reveal much about a species' social dynamics and resource use and yield implications for most behavioural and life history traits (Rasmussen 1979, Macdonald 1983, Ostfeld 1990). Movements in turn are influenced by the distribution of predators and availability of crucial resources relating to feeding and reproduction (Norris and Dohl 1980, Whitehead 1996, Heithaus 2001, Stevick *et al.* 2002).

Habitat heterogeneity and biological requirements of a species interact to produce diverse patterns in distribution, habitat use and movements between and even within species (McNab 1963, Stevick *et al.* 2002). One of the best-studied small cetaceans, the cosmopolitan bottlenose dolphin, *Tursiops sp.*, provides a good illustration. Some populations are resident staying in a limited area year-round and over several years (Wells 1991, Corkeron 1997); others undertake annual migrations (Shane *et al.* 1986, Kenney 1990). Seemingly resident animals may suddenly extend their usual range by hundreds of kilometres (Wells and Scott 1990, Wilson *et al.* 2004). Such variability in site fidelity and ranging characteristics has been related to habitat differences (Shane *et al.* 1986, Ballance 1992, Defran and Weller 1999), food resources (Scott *et al.* 1990a, Defran *et al.* 1999, Wilson *et al.* 2004) and human impacts (Watson-Capps and Mann 2005, Lusseau *et al.* 2006). Even within one population different strategies of ranging may exist, related to the age, sex or reproductive state of individuals (Wells *et al.* 1980, Owen *et al.* 2002).

Information on the pattern and scale of animal movements is critical to conservation issues. Effective conservation measures and conflict mitigation need to act at appropriate temporal and spatial scales. Efforts to manage adverse human impacts on cetaceans, such as by-catch in fisheries, directed take, whale-watching activities,

habitat degradation, usually focus on discrete locations or groups of animals in defined management areas (Hoyt 2005). Marine Protected Areas need to encompass the movement range, or at least core habitat, of the animals for which protection is sought (Bräger *et al.* 2002, Wilson *et al.* 2004, Hoyt 2005).

Monitoring programmes often target spatially defined populations, i.e. animals that use the designated survey area for the duration of the study. It is important to identify the appropriate size of such areas to base observations and management decisions on a representative sample of the population in question.

Studies of movement patterns allow the investigation of site fidelity, the calculation of home range estimates and the identification of core areas. Site fidelity describes the tendency of an animal to remain in an area over an extended period, or to return to an area previously occupied (White and Garrot 1990). Home range refers to the area that an animal uses to perform normal activities related to foraging, mating, and (in females) nursing (Burt 1943). Within their home range, animals use space disproportionately. Core areas (*sensu* Kaufmann 1962) are areas used more frequently than others, and usually contain important resources (Samuel *et al.* 1985). Core areas can be determined from the intensity of use or the utilization distribution which represents how an individual allocates time within a home range (Samuel *et al.* 1985, Andreassen *et al.* 1993).

Tracking animals in space and time often requires attaching devices that allow regular determination of the animal's location (White and Garrot 1990, Andreassen *et al.* 1993). In cetaceans, non-invasive photo-identification techniques using naturally occurring marks to identify individuals are used widely (Hammond *et al.* 1990, Stevick *et al.* 2002). These have the advantage that animals are not subjected to potentially impacting handling and tagging procedures, a larger sample of marked individuals can be tracked over time, and costs are a fraction of those for attaching tracking devices. Limitations result from restrictions of spatial and temporal resolution of re-sighting data. The probability that an individual is sighted and identified in the study area often depends on its movements and behaviour and on the distribution of survey effort (Turchin 1998). When these limitations are addressed and accounted for, photo-identification has proven to be a powerful tool in identifying

critical areas and establishing conservation zones for cetaceans (Wilson *et al.* 1997, Wimmer and Whitehead 2004).

In this study, systematic photo-identification techniques were used to examine site fidelity and range characteristics of Chilean dolphins and Peale's dolphins in two geographically separated locations in the Chiloé Archipielago, southern Chile. Objectives were to compare movement patterns between locations and between species and to identify key areas and spatial scales for which conservation measures could be implemented.

4.3. METHODS

4.3.1. Data collection

Systematic photo-identification surveys were conducted in the nearshore waters of southern Chiloé from 2001 to 2004, and in central Chiloé from 2002 to 2004 during the austral summer months (spanning December to April). Details on survey design, data collection and data processing are given in Chapter 5.

The size of the study areas (southern Chiloé: approx. 275 km² of water surface; central Chiloé: approx. 260 km²) and the complexity of the coast line precluded full coverage of each area during a single survey day. An attempt was made to survey the southern study area at least twice per month and the central study area at least once per month. A minimum of four to five survey days were required to cover each study area. Survey effort was restricted to good sighting conditions (Beaufort sea state \leq 3, no precipitation). Study areas differed most markedly with regard to water depth (southern Chiloé: median depth = 21 m; central Chiloé: median depth = 42 m) and intensity of use for mariculture (southern Chiloé: approx. 21 fish farm and 41 shellfish farm concessions; central Chiloé: approx. 26 fish farm and 96 shellfish farm concessions).

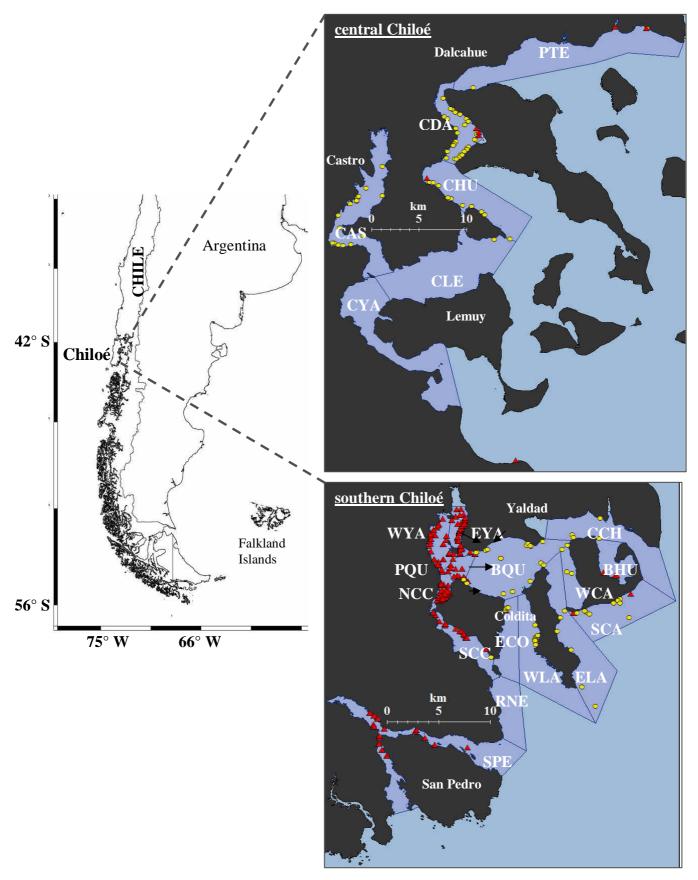


Figure 4-1. Location of study areas and distribution of sightings of individual Chilean dolphins (red triangles) and Peale's dolphins (yellow circles) related to the location of sectors. For sector codes see Table 4-1.

4.3.2. Sighting analyses

Sighting histories and locations for all identifiable individuals (excluding calves) were extracted from species-specific Microsoft Access® databases (*Finbase eutropia* for Chilean dolphins, *Finbase australis* for Peale's dolphins; see Appendix III) where all identification photographs have been archived along with detailed information on each survey and sighting. Gender of individual Chilean dolphins was determined from photographs showing a recognizable dorsal fin and the sex-specific colouration pattern around the genital area (Appendix IV, Goodall *et al.* 1988). Gender could not be determined with certainty for Peale's dolphins as these lack sexual dimorphism in colouration or size. Individuals of both species were classed as "probable female" when they were photographed repeatedly with a calf or neonate by their side.

Individual dolphins with subtle to very distinctive markings (MD 1-3) and photographs of good to excellent quality (PQ3-4) were used in analyses (Chapter 5, Appendix II). If an individual had multiple sightings during one survey (day), only the first sighting was included. Analyses of spatial distribution were based on GPS locations obtained at the beginning of each sighting prior to approaching the dolphins for identification photographs and potentially altering their behaviour due to the presence of the survey boat.

4.3.3. Site fidelity and movements

Logistic restrictions and differences in exposure to swell and weather conditions resulted in unequal distribution of effort within and between study areas, potentially biasing estimation of site fidelity and movement ranges. Subsequently, each study area was divided into sectors (i.e. sub-areas), the size and boundary of which were determined by the survey route, geographic differences (e.g. exposed cliffs versus sheltered bays) and effective survey effort (Figure 4-1, Table 4-1, see also Chapter 2 for more information on sectors). A sector was considered surveyed when it had been covered systematically during a particular survey day.

Observed sighting rates were calculated for each sector and individual by dividing the number of sightings by the number of complete surveys of the sector (maximum one per day) while the individual was known to be alive (i.e. period between first and last sighting) (see Bräger *et al.* 2002). Only sectors known to lie within the species' range were included. To test for site fidelity, observed sighting rates were compared

to expected values using Pearson's chi-squared tests with simulated p-values (1,000 Monte Carlo simulations) recommended for small sample sizes, implemented in the software package R, vers.2.1 (R-DevelopmentCoreTeam 2004). As the same null hypothesis was tested for each individual, Bonferroni's Correction for multiple comparisons (Rice 1989) was applied to adjust the table-wide significance level of $p \le 0.05$.

Only individuals with at least five 5 sightings during three years (two years for animals in central Chiloé) were used to test for site fidelity and to calculate maximum observed alongshore ranges. Alongshore ranges were determined by measuring the shortest linear distances between the two most extreme sightings of one individual without crossing land.

4.3.4. Range and core area use

Distribution probabilities and core area use of individuals were determined using the fixed Kernel home range estimation function in the Animal Movement Analysis Extension (Hooge and Eichenlaub 1997) to ArcView GIS 3.2 (ESRI 1999). The kernel is a non-parametric estimator which provides a probabilistic model of home range and calculates the intensity of area use or utilization distribution (UD) (Worton 1989, Seaman and Powell 1996). The UD represents the probability that an animal spends time at any one place in its range as a function of the distribution of all the positions where it has been observed (Worton 1989). Areas with many sightings will generate a greater kernel UD than areas with few sightings. This study used fixed kernels with least square cross validation to select an appropriate smoothing parameter (Silverman 1986, Hooge and Eichenlaub 1997) as these are considered the least biased home range estimators available (Worton 1995, Seaman and Powell 1996). The 95% UD contour was considered to represent the area that an individual dolphin actually used (i.e. known range), and the 50% UD contour delineated the core area of activity (Hooge and Eichenlaub 1997, Gubbins 2002, Owen *et al.* 2002).

Only individuals with ≥ 20 sightings were included in fixed kernel range estimation. This was considered a trade-off between accuracy of the estimates and number of individuals for comparison. For each individual, only the first sighting location per day was used. Sighting histories spanned at least three years with intervals of several

days to months between individual sightings. Landmass was subtracted from all estimates of range and core areas.

4.3.5. Overlap of individual UDs

The 95% UDs for each dyad (i.e. pair) of dolphins were overlaid and the extent of overlapping areas determined using the Geo-processing Wizard and X-Tool extensions in ArcView 3.2. The degree of overlap for dyads of individuals (O) was calculated (following Lazo (1994)) as:

$$O = \frac{2P_I}{(P_A + P_B)}$$

where P_I is the area of the polygon delimited by the intersection of the individual UDs, P_A is the 95% UD for individual A, and P_B is the 95% UD for individual B.

4.3.6. Association analysis

Coefficients of association (COAs) were calculated for the same dyads of dolphins (i.e. individuals with ≥ 20 sightings) using SOCPROG compiled ver. 2.1. (Whitehead 1995, 2004). The observation period was set to one day and each group formed an association unit. Association was defined by presence in the same group. The "half-weight" index (HWI) was used as individuals were more likely to be scored when separate than when together in the same group (Cairns and Schwager 1987, Slooten *et al.* 1993). The HWI is calculated as:

$$\frac{X}{X + Y_{AB} + \frac{1}{2}(Y_A + Y_B)}$$
 2.

where X is the number of observation periods during which individuals A and B are seen together in the same group, Y_{AB} is the number of observation periods during which individuals A and B are located in separate groups, Y_A is the number of observation periods during which only individual A is observed in a group and Y_B is the number of observations periods during which only individual B is observed in a group (after Cairns and Schwager 1987). Hence COAs ranged from 0 (never seen together) to 1 (always seen together).

Permutation tests were performed in SOCPROG (20,000 permutations) to test whether the observed associations differed from what might be expected at random (Bejder *et al.* 1998, Whitehead and Dufault 1999, Whitehead 2004).

A Mantel test (Mantel 1967) was used to examine whether the extent of spatial overlap between two dolphins was related to the strength of associations between them. The Mantel test estimates the association between two independent dissimilarity matrices describing the same set of entities and tests whether the association is stronger than expected by chance (Sokal and Rohlf 1996, p.814). The first matrix contained the degree of spatial overlap for each dyad of dolphins; the second matrix contained the COAs for the same dyads. The Mantel test was implemented in the Microsoft Excel® Extension Poptools ver. 2.6.9. (Hood 2005) based on the formulae in Manly (1991).

4.4. RESULTS

Survey effort varied within and between study areas, potentially biasing sighting opportunities (Table 4-1). Where possible, unequal survey effort was included in the analyses to account for these spatial biases.

4.4.1. Chilean dolphins

4.4.1.1. Sighting histories

Seventy-two individual Chilean dolphins were identified from 1,995 photographs during 602 individual sightings. In southern Chiloé, 74% of the 57 identified individuals were seen at least five times, with a maximum of 35 sightings for one individual observed during all four years (Figure 4-2). Once identified, Chilean dolphins were resighted regularly and during consecutive years suggesting long-term site fidelity for the majority of individuals (Figure 4-3).

However, in central Chiloé, 60% of the 15 identified Chilean dolphins were sighted only once in three years (Figure 4-3). The most frequently seen individual (ID65, male) had four sightings spread across three years. Given this paucity of sightings in central Chiloé, only Chilean dolphins at southern Chiloé were included in further analyses. Movements of individuals between study areas were not observed.

4.4.1.2. Alongshore ranges and movement patterns

Maximum ranges were determined for 42 Chilean dolphins in southern Chiloé sighted at least five times in three years. Beyond this criterion, alongshore range appeared independent of the number of sightings per individual (Spearman's rank correlation: $r_s = 0.144$, df = 41, p = 0.3622; Figure 4-4). Distances between the most extreme sightings of the same individual ranged from 4 km (only seen in Canales San Pedro/ Guamblad) to 45 km (mean= 23.1 km \pm 1.92 SE). Alongshore ranges did not differ significantly between males (n=3, mean= 25.2 km \pm 6.31 SE) and females (n=7, mean= 23.4 km \pm 4.11 SE) (Mann-Whitney test, W= 17, p > 0.05).

Table 4-1. Annual distribution of survey effort shown as the number of complete surveys of sectors in southern (a) and central (b) Chiloé.

a) southern Chiloé

Sector Code	Sector description	Size (km²)	2001	2002	2003	2004	Total surveys	Median
EYA	East Yaldad Bay	6.56	32	37	38	31	138	34.5
WYA	West Yaldad Bay	9.58	31	31	23	18	103	27
NCC	northern Canal Coldita	3.76	16	13	17	16	62	16
PQU	P. Queupué -Isla Linagua	4.38	13	17	21	14	65	15.5
SCC	southern Canal Coldita	11.09	15	14	9	4	42	11.5
ECO	East Isla Coldita	13.85	10	12	11	8	41	10.5
RNE	Rio Negro - P. Yatac	15.65	6	9	5	3	23	5.5
SPE	C. San Pedro + Guamblad	32.67	6	10	6	2	24	6
WLA	West Isla Laitec	29.09	8	8	8	5	29	8
BQU	Bahia Quellon	37.54	30	28	24	22	104	26
ELA	East Isla Laitec	36.18	10	13	10	8	41	10
WCA	West Isla Cailin	8.86	7	10	6	5	28	6.5
SCA	South Isla Cailin	25.83	5	6	4	3	18	4.5
BHU	Bahia Huellenquon	9.60	7	5	3	3	18	4
CCH	Canal Chiguao	29.40	9	11	7	6	33	8
	Total area	274.04	205	224	192	148	769	

b) central Chiloé

Sector Code	Sector description	Size (km²)	2001	2002	2003	2004	Total surveys	Median
CYA	Canal Yal	47.98	-	4	3	0	7	3
CAS	Estero Castro	37.15	-	12	14	1	27	12
CHU	Canal Hudson	35.57	-	5	6	8	19	6
CLE	Canal Lemuy	58.24	-	7	8	1	16	7
CDA	Canal Dalcahue	16.62	-	7	11	10	28	10
PTE	Paso Tenaun	62.06	-	2	3	2	7	2
	Total area	257.62	-	37	45	22	104	

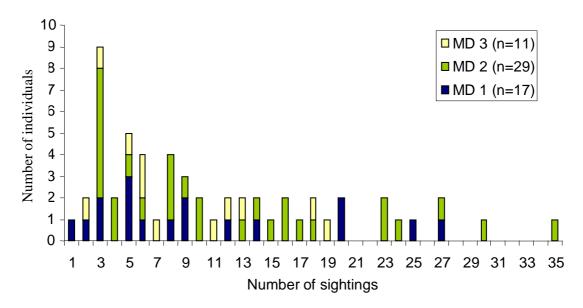


Figure 4-2. Number of sightings of individual Chilean dolphins in southern Chiloé. MD1 – MD3 denote individuals with different distinctiveness of marks (see text).

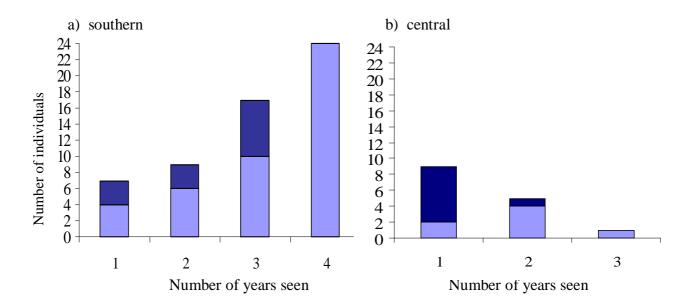


Figure 4-3. Number of years that individual Chilean dolphins were seen in southern (a) and central (b) Chiloé. Light colour denotes individuals seen only in or until the last field season (2004).

The largest alongshore range was recorded incidentally for a male Chilean dolphin (with only four sightings). This individual (ID65) was identified during an exploratory survey at the southern border of the central study area in 2002 and was re-sighted 70 km to the north-east during regular surveys in 2003.

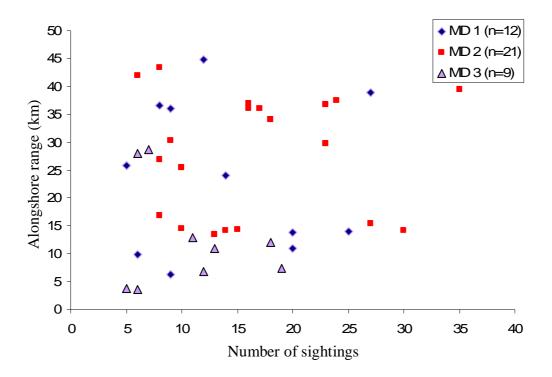


Figure 4-4. Maximum observed alongshore ranges versus number of sightings of individual Chilean dolphins at southern Chiloé. MD1 – MD3 denote individuals with different distinctiveness of marks (see text).

4.4.1.3. Site fidelity

The distribution of sighting locations reflected the limited alongshore ranging pattern and proved largely unaffected by the unequal distribution of survey effort. Sighting rates of Chilean dolphins differed significantly among the 10 sectors in southern Chiloé (Kruskal-Wallis test, H= 304.4, df= 9, p< 0.001) with highest mean rates observed in northern Canal Coldita (NCC) and Canales San Pedro/Guamblad (SPE), and lowest rates in Bahía Quellon (BQU) (Figure 4-5). For most individuals (76%, or 45% after Bonferroni correction was applied), distribution of sightings was not explained by distribution of survey effort (Table 4-2), indicating site fidelity to selected areas within the overall known range.

Table 4-2. Sighting rates of 42 individual Chilean dolphins (with \geq 5 sightings in \geq 3 years) across sectors in southern Chiloé corrected for survey effort. Sex indicated as female (φ), probable female (φ ?), male (\Diamond) and unknown (U). For details on sector codes see Table 4-1.

Dolphin ID	Mark type	Sex	Number of sightings	Number of years seen	EYA	WYA	NCC	PQU	SCC	ECO	SPE	BQU	SCA	BHU	χ² s p-va	Sim. ¶ Ilue
5	M2	9	35	4	0.080	0.049	0.210	0.031	0.048	-	0.083	-	-	-	0.041	
35	M2	8	30	3	0.085	0.069	0.239	0.038	0.111	-	-	-	-	-	0.001	**
13	M2	₽?	27	4	0.109	0.029	0.048	0.015	0.071	-	0.083	-	-	-	0.001	**
19	Ml	₽?	27	4	0.080	0.019	0.065	0.046	0.071	-	0.083	-	-	-	0.001	**
49	Ml	2	25	4	0.075	0.083	0.065	0.077	0.111	-	-	-	-	-	0.004	
9	M2	₽?	24	4	0.043	0.097	0.065	0.031	0.024	-	0.042	-	-	-	0.230	
2	M2	U	23	4	0.051	0.010	0.129	0.031	0.048	-	0.042	-	-	-	0.001	**
38	M2	2	23	4	0.043	0.010	0.129	0.046	0.071	-	0.083	-	-	-	0.004	
7	M3	2	20	4	0.036	0.049	0.081	0.062	-	-	-	-	-	-	0.001	**
39	Ml	₽?	20	3	0.075	-	0.174	0.038	0.037	-	-	-	-	-	0.001	**
46	M1	2	20	3	0.066	0.028	0.196	-	0.074	-	-	-	-	-	0.001	**
1	M2	U	18	4	0.014	0.029	0.081	0.031	0.071	-	0.042	0.010	-	-	0.108	
15	M3	U	18	4	0.051	0.058	-	-	0.071	-	-	-	-	-	0.001	**
16	M2	U	17	4	0.043	0.049	0.065	0.015	-	-	0.042	-	-	-	0.001	**
22	M2	₽?	16	4	0.043	0.049	0.032	0.015	-	-	0.083	-	-	-	0.004	
31	M2	U	16	2	0.029	0.024	0.242	-	0.077	-	0.125	-	-	-	0.001	**
17	M2	2	15	4	0.058	0.039	-	-	0.048	-	-	-	-	-	0.001	**
8	M1	U	14	4	0.036	0.039	0.032	0.015	-	-	-	-	0.111	-	0.080	
53	M2	₽?	14	3	0.028	-	0.196	0.019	0.037	-	-	-	-	-	0.001	**
58	M2	U	13	2	0.043	0.024	0.152	-	0.077	-	-	-	-	-	0.005	
69	MB	₽?	13	2	0.129	0.222	0.188	0.071	0.250	-	-	-	-	-	0.014	
18	MB	2	12	4	0.029	0.039	0.032	0.031	-	-	-	-	-	-	0.014	
48	M1	₽?	12	3	0.047	-	0.130	0.019	-	-	-	-	-	-	0.001	**
27	MB	₽?	11	3	0.047	0.028	0.065	-	0.037	-	-	-	-	-	0.008	
28	M2	3	10	4	-	-	-	-	0.024	-	0.375	-	-	-	0.001	**
12	M2	U	10	3	0.028	0.047	0.043	_	0.026	-	_	-	-	-	0.021	

Table 4-2. Continued, Chilean dolphins, southern Chiloé

Dolphin ID	Mark type	Sex	Number of sightings	Number of years seen	EYA	WYA	NCC	PQU	SCC	ECO	SPE	BQU	SCA	вни	χ²Sim. ¶ p-value
11	M2	9	9	4	0.022	0.010	0.032	-	0.024	-	0.083	-	-	-	0.001 **
29	Ml	\mathbf{U}	9	3	0.028	0.028	0.065	0.019	-	-	-	-	-	-	0.074
37	M1	3	9	3	0.009	0.014	0.065	0.019	0.037	-	0.083	-	-	-	0.463
6	M2	₽?	8	4	0.029	0.019	-	-	-	-	0.042	-	-	0.056	0.001 **
59	M2	\mathbf{U}	8	4	0.036	-	0.032	-	-	-	-	-	0.056	-	0.002
63	M1	\mathbf{U}	8	4	0.022	0.010	0.032	-	0.024	-	0.042	-	-	-	0.292
41	M2	₽?	8	3	-	-	-	-	0.037	-	0.292	-	-	-	0.001 **
14	MB	2	7	4	-	-	-	-	0.048	0.024	0.167	-	-	-	0.015
25	MB	\mathbf{U}	6	4	-	-	-	-	-	-	0.250	-	-	-	0.001 **
30	MB	\mathbf{U}	6	4	-	0.010	0.016	0.015	0.024	-	-	-	-	0.111	0.845
56	M2	\mathbf{U}	6	4	0.014	-	-	-	-	-	0.042	-	-	0.056	0.496
54	Ml	\mathbf{U}	6	2	-	0.049	0.061	0.029	0.077	-	-	-	-	-	0.426
10	M3	\mathbf{U}	5	3	-	-	-	-	-	-	0.208	-	-	-	0.001 **
23	M2	\mathbf{U}	5	3	0.019	0.012	-	-	0.026	-	-	-	-	-	0.524
36	M1	U	5	3	-	-	-	-	0.026	-	0.182	-	-	-	0.007
43	Ml	₽?	5	3	-	-	-	-	0.037	-	0.167	-	-	-	0.004

[¶] tests using simulated p-values were used to test whether the geographical distribution of an individual's sightings was significantly different from expected given the geographical distribution of survey effort; bold = significant at table-wide $p \le 0.05$ level; ** = significant after Bonferroni adjustment.

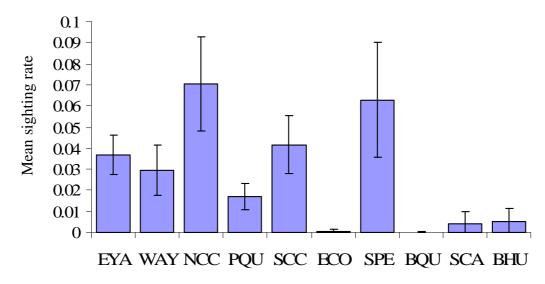


Figure 4-5. Differences in mean sighting rates of individual Chilean dolphins (corrected for effort) across sectors in southern Chiloé. Error bars denote 95% confidence limits.

Individual Chilean dolphins could be grouped together according to two main spatial patterns of site fidelity (Table 4-2). Most individuals (72%) preferred a combination of northern Canal Coldita (NCC, 30 dolphins), East Yaldad (EYA, 33) and West Yaldad (WYA, 30), but also had occasional or regular sightings in southern Canal Coldita (SCC, 25) and Canales San Pedro/Guamblad (SPE, 14). The second group of individuals (19%) showed strong site fidelity only to Canales San Pedro/Guamblad (SPE, 8 dolphins) with occasional sightings in southern Canal Coldita (SCC, 6). In addition, four individuals were only observed in Yaldad and northern Canal Coldita, and one was exclusively seen in Canales San Pedro/Guamblad. Only five dolphins were observed to venture into more easterly sectors of the study area (BHU, SCA, BQU).

4.4.1.4. Ranges and core areas in Chilean dolphins

Fixed Kernel ranges (95% UD) and core areas (50% UD) were calculated for 11 Chilean dolphins, 10 of which had site fidelity and distribution patterns that were independent of the unequal distribution of survey effort (Tables 4-2, 4-3). Ranges based on the 95% UD contour varied from 22 km² to 42 km² (mean= 35.6 km² \pm 8.2 SD). The sizes of individual 95% UDs were not significantly correlated with the number of sightings available for each individual (Spearman rank's correlations: r_s = 0.556, df= 10, p= 0.075).

All dolphins had one to three distinct core areas which, on average, made up 23% of the size of their overall ranges (Table 4-3). These core areas were located at the entrance to East Yaldad Bay, off central West Yaldad Bay and/or in northern Canal Coldita. Maps of ranges and core areas for three individuals representing the different patterns observed between the sample of 11 dolphins are presented in Figure 4-6 (a-c).

As a minimum of 20 sightings was required for inclusion in range estimation, individuals with predominant site fidelity to Canales San Pedro/Guamblad were not considered due to their low number of sightings (Table 4-2). Their lower number of sightings, however, could be attributed mainly to lower survey effort in Canales San Pedro/Guamblad (approx. 60% less effort than northern Canal Coldita), as this area is difficult to access and logistically challenging. In fact individual ID28 (male) showed the highest degree of site fidelity observed (Table 4-2). This dolphin was identified during nearly 40% of all visits to Canales San Pedro/Guamblad. Range and core area were determined for this individual for visual comparison and to highlight the importance of Canales San Pedro/Guamblad for at least some dolphins in the population (Figure 4-6 d).

4.4.1.5. Range overlap and association patterns

Spatial overlap of ranges (based on 95% UDs) was extensive between dyads of dolphins (mean rate of overlap = $80\% \pm 8.4$ SD) ranging from 62% to 97% overlap. Note that the male dolphin (ID 28) was not included in calculation of range overlap. COAs calculated for the same dyads of dolphins varied from 0.05 - 0.64 (mean COA = 0.26 ± 0.04 SD). The standard deviation of the observed dyadic association indices was significantly higher than those from permuted data sets (p= 0.0243), thus rejecting the null hypothesis of individuals associating at random. Dyads of dolphins with a larger range overlap also had significantly higher COAs (Mantel matrix correlation coefficient = 0.287; p= 0.013; 10,000 random permutations).

Table 4-3. Ranges and core area size for Chilean dolphins (with ≥ 20 sightings) determined from 95% and 50% fixed Kernel utilisation distribution (UD) contours. Sex indicated as female (\updownarrow), probable female (\updownarrow ?), male (\circlearrowleft) and unknown (U).

Dolphin ID	Sex	Alongshore range † (km)	95% UD area (km²)	50% UD area (km²)	Number of distinct 50% UD areas	50% / 95% UD ratio
5	94	39.4	41.5	6.83	2	0.16
35	8	14.1	31.5	3.48	2	0.11
13	$\mathop{\supsetneq} ?$	15.3	42.6	9.88	1	0.23
19	$\mathop{\supsetneq} ?$	38.9	46.0	12.43	2	0.27
49	2	13.9	33.3	9.52	2	0.29
9	$\mathop{\supsetneq} ?$	37.5	41.1	16.8	1	0.41
2	U	36.7	40.1	7.52	3	0.19
38	2	29.9	41.1	12.64	1	0.31
7	9	7.3	25.5	7.12	3	0.28
39	♀?	10.9	21.5	2.75	2	0.13
46	2	13.8	26.9	3.67	2	0.14
Mean		23.5	35.6	8.41		0.23
SD		12.89	8.17	4.388		0.092
10*	3	25.5	13.61	3.00	1	0.22

[†] measured as the shortest linear distance between the most distant sightings, not crossing land.

^{*} individual had only 10 sightings (included for comparison, see text).

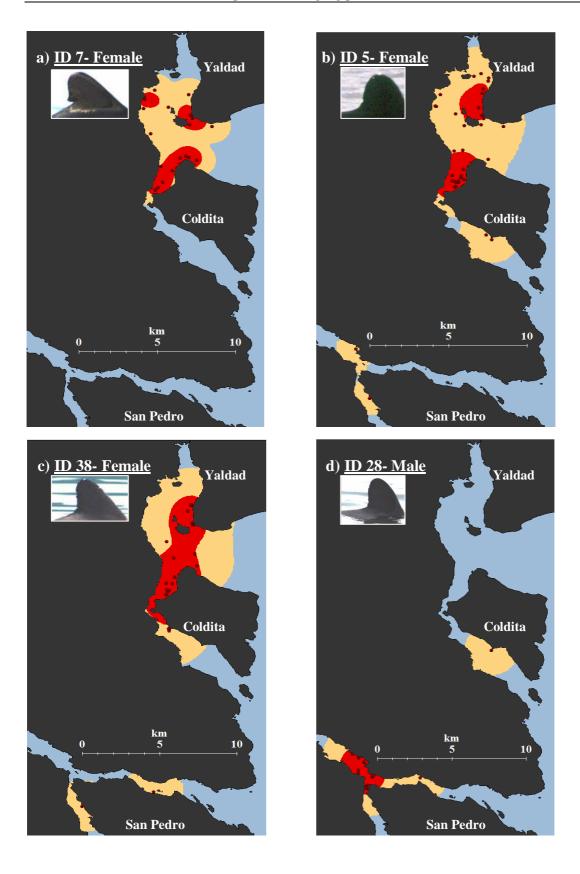


Figure 4-6. Known ranges (yellow = 95% UD contours) and core areas (red = 50% UD contours) of four Chilean dolphins (a-c: females, d: male) in southern Chiloé. Sighting locations are shown as red dots.

4.4.2. Peale's dolphins

4.4.2.1. Sighting histories

A total of 406 photographs were used to identify 79 Peale's dolphins, 34 and 45 individuals at southern and central Chiloé, respectively, during 261 individual encounters. Many individuals were seen only once (40% at southern and 35% at central Chiloé, Figure 4-7). A similar number of individuals, however, were resighted at least once each year after initial identification (Figure 4-8), suggesting intermittent long-term use of either study area. Overall re-sighting rates were low with a maximum of nine sightings for one individual per study area (Figure 4-7)

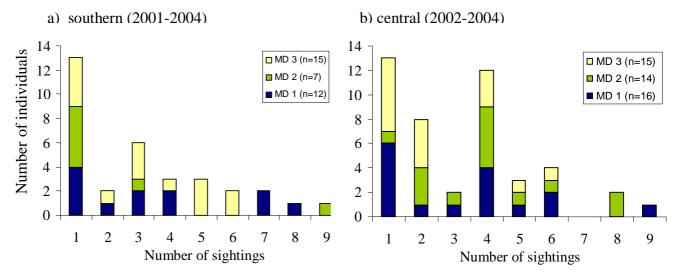


Figure 4-7. Number of sightings of individual Peale's dolphins at southern (a) and central (b) Chiloé. MD1 – MD3 denote individuals with different distinctiveness of marks (see text).

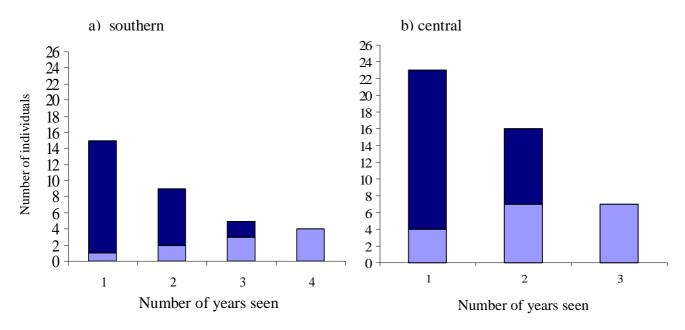


Figure 4-8. Number of years that individual Peale's dolphins were seen in southern (a) and central (b) Chiloé. The lighter colour denotes individuals seen only in or until the last field season (2004).

4.4.2.2. Alongshore ranges and movement patterns

Nine Peale's dolphins in southern, and ten in central Chiloé met the criteria for inclusion in estimates of alongshore ranges. Ranges of Peale's dolphins in southern Chiloé (mean= $15 \text{ km} \pm 1.11 \text{ SE}$, range 10 - 19 km) appeared smaller than those in central Chiloé (mean= $26.8 \text{ km} \pm 5.28 \text{ SE}$, range 4 - 45 km), but the difference was not significant (Mann-Whitney test, W= 80, p> 0.05). Beyond five sightings, maximum ranging distances were not correlated with sighting frequencies, neither in southern nor in central Chiloé (Spearman rank's correlations: $r_s = 0.171$, df =8, p=0.644; and r_s = 0.173, df=9, p=0.665, respectively; Figure 4-9).

As for Chilean dolphins, individual movements between study areas (approx. 65 km in shortest linear distance) were not observed with certainty. Potential but ambiguous matches between medium to good quality photographs were considered for both species, but all were rejected by two of three experienced observers. Observed alongshore ranges did not differ between Chilean dolphins and Peale's dolphins when data were compared across study areas (Mann-Whitney test, W= 1334, p> 0.05).

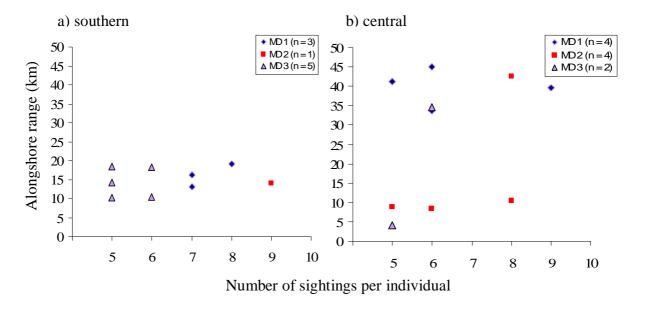


Figure 4-9. Maximum observed alongshore ranges versus number of sightings of individual Peale's dolphins at southern (a) and central (b) Chiloé. MD1 – MD3 denote individuals with different distinctiveness of marks (see text)

4.4.2.3. Site fidelity

Sighting rates of Peale's dolphins, when corrected for effort, also differed significantly between sectors in both study areas (Kruskal-Wallis test for southern Chiloé: H= 20.5, df= 8, p= 0.0086; and central Chiloé: H= 26.8, d.f.= 3, p≤ 0.001). Highest mean sighting rates were observed in southern Chiloé off South Isla Cailin (SCA) and Punta Queupué (PQU), and in central Chiloé in Canal Dalcahue (CDA) (Figure 4-10). Distribution of sightings was explained by distribution of survey effort in all but six cases (Table 4-4), indicating that few individuals exhibited site fidelity. As the number of sightings was low for most Peale's dolphins, sample sizes might have been too small to detect a significant pattern.

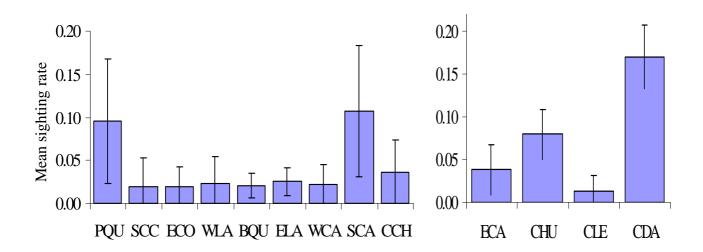


Figure 4-10. Differences in mean sighting rates of individual Peale's dolphins (corrected for effort) across sectors in southern (a) and central (b) Chiloé. Error bars denote 95% confidence limits.

Table 4-4. Sighting rates of 19 individual Peale's dolphins (with ≥ 5 sightings in ≥ 2 years) across sectors in southern (a) and central (b) Chiloé, corrected for survey effort. For details on sector codes see Table 2-1.

a) southern Chiloé

Dolphin ID	Mark type	Number of sightings	Number of years seen	PQU	SCC	ECO	WLA	BQU	ELA	WCA	SCA	ССН	χ² sim. ¶ p-value
4 (♀?)	M2	9	3			0.100	0.143	0.013	0.032		0.071		0.187
13	M 1	8	4	0.200				0.019	0.073	0.071	0.056		0.142
5	M1	7	4	0.077	0.024		0.034	0.029	0.024			0.030	0.368
32	M 1	7	2					0.065		0.091	0.143	0.154	0.192
7	M3	6	4	0.108					0.049	0.036	0.111		0.469
20	M3	6	3	0.308		0.024	0.034	0.019	0.024			0.030	0.894
11	M3	5	4	0.169				0.038	0.024				0.008
1	M3	5	3		0.154	0.053					0.286		0.245
14	M3	5	2								0.300	0.111	0.018

b) central Chiloé

Dolphin ID	Mark type	Number of sightings	Number of years seen	CAS	СНИ	CLE	CDA	X²sin p-val	x²sim. ¶ p-value	
17	M1	9	3	0.154	0.105	0.067	0.071	0.633		
22	M 1	8	3	0.038	0.105		0.179	0.092		
26	M2	8	3		0.105		0.214	0.004	**	
31	M 3	6	3		0.053		0.179	0.024		
64	M3	6	3	0.038	0.105		0.107	0.523		
36	M3	6	2	0.071	0.143		0.143	0.052		
59	M 1	6	2	0.038		0.067	0.143	0.019		
23	M 1	5	2	0.038	0.091		0.167	0.431		
25	M 1	5	2		0.091		0.222	0.056		
30	M2	5	2				0.278	0.002	**	

[¶] z^2 tests using simulated p-values were used to test whether the geographical distribution of an individual's sightings was significantly different from expected given the geographical distribution of survey effort; bold = significant at table-wide p≤ 0.05 level; ** = significant after Bonferroni adjustment.

4.5. DISCUSSION

4.5.1. Biases in movement patterns and site fidelity

Ranging behaviour of individual Chilean dolphins and Peale's dolphins differed markedly and reflected the species-specific distribution patterns (Chapter 2). Chilean dolphins exhibited a high degree of site fidelity within and between summers with individuals differing in small-scale preference for a few selected bays and channels. No such clear patterns were discernible for Peale's dolphins.

Two main possible sources of bias could have affected these results: unequal distribution of sampling effort and heterogeneity in sighting probabilities. Although unequal effort was taken into account in analysis of site fidelity, it potentially introduced bias for those individuals of either species that preferred the lesser surveyed sectors. In the case of Chilean dolphins in San Pedro/Guamblad, their low number of sightings precluded a range comparison with their conspecifics in Yaldad/Coldita. However, comparable small-scale residency and site fidelity patterns were clearly evident in San Pedro/Guamblad. This suggests that site fidelity patterns could have been detected in other areas of low survey effort as well, if they had existed. The general lack of site fidelity in Peale's dolphins within the study areas therefore appears to reflect behavioural differences rather than sampling artefacts.

Tracking movements of identifiable individuals with photo-identification techniques is subject to well-known biases inherent to mark-recapture studies, most notably heterogeneity in sighting probabilities, mark loss or failure to identify marks correctly (Hammond 1986). This study used dolphins with subtle to very distinctive marks to obtain a larger and more representative sample of individuals. Subtle marks are less reliably identified over long time periods which could have produced false positives (i.e. matching individuals when they are different) or false negatives (i.e. rejecting a true match), thus biasing range estimation. However, no differences (or systematic biases) were discernible when comparing the number of sightings, alongshore range or site fidelity of individuals from different mark categories for either species.

Sample size (i.e. the number of positional records per individual) is a crucial factor in the accuracy of home range and core area estimation (Andreassen *et al.* 1993). Kernel-based estimates are less biased than traditional methods (e.g. minimum convex polygon), but tend to over-estimate home range size at small sample sizes (Seaman

and Powell 1996). Urian (2002) suggested that at least 100 sightings per individual dolphin were required to obtain unbiased kernel home ranges. Few studies, however, have access to such detailed long-term data sets. Most studies of dolphin home ranges have therefore used a practical compromise with a minimum of 10 to 30 sightings per individual (Gubbins 2002, Ingram and Rogan 2002, Flores and Bazzalo 2004, Hung and Jefferson 2004). Estimates of range and core area sizes for Chilean dolphins are small compared to most other species (see below), and might be positively biased due to relatively small sample sizes (20-35 sightings per individual). The already emerging pattern of small ranges and core areas should therefore only become more evident as more data become available from ongoing and future photo-identification surveys at Chiloé.

4.5.2. Ranging and movement patterns of Chilean dolphins

Movement ranges of Chilean dolphins are comparable to, or slightly smaller than, those reported for other members of the genus *Cephalorhynchus*. Photo-identified Hector's dolphins, *C. hectori* had alongshore ranges of typically 31 km (2.4 SE) with maximum distance of 106 km between sightings of the same individual (Bräger *et al.* 2002). Three satellite-tagged Hector's dolphins in the same area had a mean home range radius of around 11 km and maximum displacement distances of 50-60 km (Stone *et al.* 2004). Five satellite-tagged Heaviside's dolphins, *C. heavisidii*, off South Africa moved, on average, some 60 km alongshore and up to 22 km offshore (Elwen *et al.* in press). Regular and rapid alongshore movements of at least 250 km have been observed for photo-identified Commerson's dolphins, *C. commersonii*, off Argentina (Coscarella 2005). Such habitual larger-scale movements between more intensely used areas (patches) have been interpreted to reflect locally abundant resources and temporal variability in patch quality (e.g. prey availability) (Hooker *et al.* 2002, Johnston *et al.* 2005).

Habitat characteristics and habitat heterogeneity are known to influence ranging patterns within and between species (Würsig *et al.* 1991, Defran and Weller 1999, Gubbins 2002). In general, animals within a trophic class in habitats of high productivity have smaller home ranges than animals in habitats of lower productivity (Harestad and Bunnel 1979). The long-term site fidelity, small overall ranges (95% UD) and core areas (50% UD) of photo-identified Chilean dolphins at southern

Chiloé suggest that these dolphins find predictable and bountiful resources in this area. Five individuals were sighted within their known summer ranges during winter and spring of 2004 (Heinrich, unpublished data; Christie *et al.*, 2005) providing the first tentative evidence for year-round residency of at least part of the local population.

Small cetaceans in cold water environments, such as Cephalorhynchus (Gewalt 1990) and similarly-sized harbour porpoises, *Phocoena phocoena* (Koopman 1998), have relatively high daily energy requirements, but have a limited ability to carry large energy stores. As a result their movement patterns are likely to be closely related to the distribution of their prey. This appears to be especially true for mature females that must meet the additional costs of pregnancy and lactation through increased energy intake (Read 2001). Coincidentally, most Chilean dolphins included in range estimation were females or presumed females and most calves are born during summer (Chapter 2). Incidental observations suggest that Chilean dolphins could feed on róbalo (Eleginops maclovinus), pejerrey (Odontethes sp.) and schooling sardines (Clupea sp. or Strangomera sp.) (Heinrich, pers. observation, Oporto 1987, Crovetto and Medina 1991) during the summer when large aggregations of small fish occur in the inshore waters of Chiloé and are preyed upon by thousands of sea birds, such as migrating sooty shearwaters (Puffinus griseus) (Chapter 3). Core areas which are thought to contain the most reliable food sources were very small (approx. 8 km²) and were centred in northern Canal Coldita, east and west shores of Yaldad Bay, and possibly the narrows of Canal San Pedro. The core areas in Yaldad Bay match those areas that land-based observations (Ribeiro 2003) had identified as areas of high intensity of use where predominantly foraging behaviour occurred. These areas are characterized by limited depth (< 20 m) and often strong tidal currents and eddies (Heinrich, pers. observation, Winter et al. 1982) which are important features known to congregate prey (Hastie et al. 2003, Johnston et al. 2005).

Occurrence and sighting rates of Chilean dolphins differed markedly between study areas, possibly reflecting differences in habitat quality, even over small spatial scales (see also Chapter 2). The overall distribution of Chilean dolphins extends over some 2,500 km of Chilean coast and includes a variety of very different habitats, such as the sheltered bays and channels of Chiloé, the open coast to the north and a large

oligotrophic fjord system to the south (Goodall 1994). Ranging and movement patterns should be expected to differ between populations in these habitats and comparative (latitudinal) studies are needed.

4.5.3. Comparison with Peale's dolphins

Comparisons between different studies and species are often hampered by methodological differences, for example photo-identification studies (Bräger *et al.* 2002, Coscarella 2005, this study) versus satellite tagging (Stone *et al.* 2004, Elwen *et al.* in press), choice of analytical approaches (i.e. different measures of "range"), sample size effects and different spatial and temporal scales. This study allows for a direct comparison of movement patterns between species and between areas as the same methodological and analytical approaches were used.

In contrast to Chilean dolphins, larger Peale's dolphins had lower re-sighting rates and ranged more widely throughout the study areas (i.e. no clear pattern of site fidelity). Although no unambiguous evidence was found for movements between study areas, measured alongshore ranges probably under-represent movement distances and dolphins might have ranged beyond the boundaries of the chosen study areas. Peale's dolphins in the Strait of Magellan have been reported to travel 70 km in two hours and one individual was observed at locations over 300 km apart (Lescrauwaet 1997). Some individual Peale's dolphins, however, showed preference for a few selected areas (this study, Lescrauwaet 1997). In the Strait of Magellan, preferred areas contain large kelp beds of Macrocystis pyrifera where Peale's dolphins forage for demersal and benthic fish, octopus and squid (Lescrauwaet 1997, Schiavini et al. 1997, Viddi and Lescrauwaet 2005). Comparable kelp forests are rare in the coastal waters of Chiloé, and the diet of Peale's dolphins in the archipelago is unknown. Peale's dolphins could be foraging for patchily distributed or locally less abundant prey, and consequently range over larger areas in search for food. A large proportion of the Peale's dolphins encountered at Chiloé were seen travelling (~ 37%) or milling (~ 20%) (Chapter 2) which could reflect displacement over areas of poor habitat until patches with more suitable resource were reached.

Range and core area sizes could not be determined for Peale's dolphins due to their low number of sightings. Using lack of site fidelity and low re-sighting rates as an indication for possibly larger overall ranges, the general rule that the size of an animal's home range is positively correlated with its body mass (Harestad and Bunnel 1979, Swihart *et al.* 1988) seems to hold true for sympatric Chilean dolphins and Peale's dolphins.

4.5.4. Ranging patterns and population structure

Size and distribution of home ranges are important components of social and mating systems in mammals (Ribble and Stanley 1998). Although ranges overlapped extensively, pairs of Chilean dolphins with the highest range overlap also associated more frequently (i.e. were encountered in the same group) indicating some social influence on ranging patterns. A more detailed analysis of association patterns of all identifiable Chilean dolphins at southern Chiloé suggests a fission-fusion society where most dolphins associate, disassociate and reassociate over time with only some individuals forming strong social bonds (Christie 2005). In small cetaceans with fission-fusion societies, such strong bonds exist in mother-infant pairs (Grellier *et al.* 2003), paired adult males (Owen *et al.* 2002) and some (possibly related) females (Wells *et al.* 1987, Duffield and Wells 1991). Female groupings may function as units within which to rear offspring (Wells *et al.* 1987, Smolker *et al.* 1992).

Most individuals used in range analysis in this study were females or probable females. This sex bias might be coincidence, reflecting biases in gender identification or behavioural differences between the sexes. Given the potential biases in gender determination and the comparable ranging and alongshore movement patterns of the small sample of males, there is currently no evidence for differences in ranging strategies for male and female Chilean dolphins. In species with promiscuous mating systems, males tend to range over larger distances than females as they search for mating opportunities (Wells *et al.* 1987, Scott *et al.* 1990a, Owen *et al.* 2002). Females appear to constitute the limiting resource for males whereas food is considered the limiting resource for females. Female ranges tend to reflect habitat quality and foraging opportunities (Wells *et al.* 1987, Scott *et al.* 1990a).

By limiting potential associates, ranging patterns have been shown to influence social communities in bottlenose dolphins (Wells 1991, Urian 2002, Lusseau *et al.* 2006). Association patterns (Christie. 2005) and small-scale site fidelity (this study) suggest that Chilean dolphins at southern Chiloé might form two distinct "communities", one centred in Canales San Pedro/Guamblad and the other in Yaldad

Bay/northern Canal Coldita. Low survey effort in Canales San Pedro/Guamblad hampered calculation of ranges and direct comparison of range overlap. However, dolphins identified at San Pedro had some of the highest rates of site fidelity (this study), and were never or only rarely observed in Yaldad Bay or Coldita channel despite much greater survey effort in the latter areas. These dolphins also formed a distinct cluster based on their high pairwise associations (Christie 2005).

Extreme site fidelity and limited movements could restrict gene flow between populations. Historic reduction in distribution and contemporary impacts on local populations, such as fisheries related mortality (Pichler and Baker 2000) can lead to gaps in a species' geographical range and give rise to genetically isolated populations, population fragmentation and low genetic diversity (Pichler *et al.* 2001, Parsons *et al.* 2002). Limited dispersal and movements will further restrict opportunities to repopulate depleted areas or compensate losses from locally impacted populations (Taylor 1997). Genetic analysis of the population structure of Chilean dolphins is underway. Preliminary results indicate a low haplotide diversity throughout their range and potential genetic isolation at small-scales (C. Olavarria, pers. comm., 2006). Local reduction in abundance and distribution has been hypothesized for Chilean dolphins and has been attributed to direct take and habitat alterations (Hucke-Gaete 2000), but current information is at best anecdotal.

4.5.5. Ranging patterns and conservation implications

Identifying biologically meaningful units is crucial to the implementation and evaluation of effective conservation actions. Data from this study suggest that Chilean dolphins might not only be highly localized and site-specific, but that populations might divide into even smaller, spatially defined units akin to "communities" in bottlenose dolphins (Connor *et al.* 2000, Gubbins 2002, Urian 2002, Lusseau *et al.* 2006). More data and long-term effort are needed to corroborate these findings.

Several important management implications can be derived, however, especially when taking a precautionary approach (Gray and Bewers 1996) to conservation:

 Chilean dolphins in southern and central Chiloé should be considered as separate populations (or units) for population monitoring (e.g. estimating abundance) and management.

- 2. Potential impacts on, and conservation threats to the dolphins should be evaluated and, if necessary, mitigated on both population (i.e. southern, central Chiloé), and "community" levels (i.e. San Pedro-Coldita/Yaldad). Of particular concern are those core areas identified in Yaldad Bay, Canal Coldita and Canales San Pedro/Guamblad which overlap with intense and spatially extensive mariculture farms for salmon and mussels (Chapter 2). Placement of shellfish farms have been shown to impact on the ranging behaviour of female *Tursiops* (Watson-Capps and Mann 2005) and to exclude them from potentially important habitat. Exclusion effects from mussel growth lines have also been suggested for *Lagenorhynchus obscurus* in New Zealand (Markowitz *et al.* 2004) and for Chilean dolphins at Yaldad Bay (Kemper *et al.* 2003, Ribeiro 2003).
- 3. Habitat conservation measures need to encompass the entire range of the local population. Areas of low or discontinuous use that serve as "corridors" between core areas and between putative "communities" should be included in conservation zones along with appropriate buffer zones around the full ranges.

Information on movement patterns has been used to evaluate the effectiveness of existing spatially explicit habitat protection measures (Bräger *et al.* 2002, Flores and Bazzalo 2004, Wilson *et al.* 2004) and to suggest the boundaries for new sanctuaries (Bräger *et al.* 2002, Hucke-Gaete *et al.* 2004). Apparently stable ranging patterns can change over time in response to environmental changes, such as prey distribution (Wilson *et al.* 2004), and due to directed or non-targeting human activities, such as dolphin-watching (Lusseau *et al.* 2006) and mariculture activities (Watson-Capps and Mann 2005). Continuing to monitor residency and ranging of Chilean dolphins could provide an indirect measure of habitat quality in a rapidly changing coastal environment.

Less frequently sighted Peale's dolphins indicate some typical problems for conservation measures that rely on spatially defined habitat protection. For more mobile species that occupy a large or not well defined range it becomes much harder to determine patterns from individual behaviour based on effort limited re-sighting data. As Peale's dolphins range over larger areas, they are more likely to encounter and overlap with a variety of potentially impacting human activities. In both study areas, Peale's dolphins range over areas which are used extensively by mariculture

(salmon and mussel farming), extraction of shellfish and marine algae from natural banks, artisanal fishing, shipping, and some small-scale tourism ventures (Anon. 2001, SERNAPESCA 2004). Managing interactions and mitigating impacts with possibly synergetic effects at large scales becomes a much more complex issue with many more stakeholders involved. On the other hand Peale's dolphins might be less affected by localized impacts and their movements compensate for local losses.

Although Peale's dolphins exhibited only limited small-scale site fidelity, they used some sites in the study area more regularly than others (see also Chapter 2). The shoals of southern Isla Cailin and north-western Isla Coldita (southern Chiloé) and Canal Dalcahue (central Chiloé) seem to constitute important sites for individual Peale's dolphins within their larger geographical range (see also Chapter 2). Studies of habitat use in relation to environmental characteristics provided insights into the factors that could have influenced these movements and site selection (Chapter 3). Temporal and spatial survey effort should be extended beyond the current study to allow for more detailed information on movement ranges. Thus, monitoring the population of Peale's dolphins and identifying important features for their survival requires use of additional surveys and techniques.

Tracking individual animals with satellite-tags could provide a more detailed spatial and temporal resolution of their movement patterns. Tagging studies have the power to detect diurnal or seasonal movements of individuals or movements over much larger spatial scales (Scott *et al.* 1990b, Würsig *et al.* 1991, Stevick *et al.* 2002), including inshore-offshore movements (Würsig *et al.* 1991, Read and Westgate 1997, Stone *et al.* 2004, Elwen *et al.* in press). Congeners of both Chilean dolphins and Peale's dolphins have been tagged and tracked successfully (Würsig *et al.* 1991, Mate *et al.* 1994, Stone *et al.* 2004, Elwen *et al.* in press). The new generation of Fastloc GPS tags (Bryant *et al.* 2005) promises greater positional accuracy for species inhabiting complex coastal habitat than conventional satellite-tags. Effects of capture, handling and tagging however need to be carefully evaluated with regard to impacts on the local dolphin population and potential biases in the results (Elwen *et al.* in press).

Combining different techniques, such as photo-identification with dedicated habitat use and distribution surveys (Chapters 2 and 3), land-based observations (Ribeiro 2003) and remote tracking (Stone *et al.* 2004, Elwen *et al.* in press) will help to provide a more holistic insight into dolphin conservation ecology.

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Chapter 5 Estimating population sizes of Chilean and Peale's dolphins using mark-recapture techniques: usefulness for future monitoring

5.1. ABSTRACT

Crucial to the evaluation of a species' status are precise estimates of its population size and an analysis of changes over time (i.e. trends in abundance). This study used mark-recapture methods applied to photo-identification data to estimate local population sizes of Chilean dolphins and Peale's dolphins in the nearshore waters of the Chiloé Archipelago in southern Chile during four austral summers from 2001 to 2004. A total of 57 and 15 naturally marked Chilean dolphins, and 34 and 45 naturally marked Peale's dolphins were identified from high quality photographs in southern and central Chiloé, respectively. For Chilean dolphins in southern Chiloé, sufficient data were available to derive annual estimates of abundance by fitting maximum likelihood models for closed populations to the capture histories of marked individuals (implemented in the software program MARK).

The small number of identifiable individuals precluded the use of mark-recapture models for Chilean dolphins in central Chiloé. For Peale's dolphins, two-sample Chapman-modified Petersen estimators were applied to data from consecutive years to produce annual estimates of abundance. Analyses of mark-recapture assumptions suggest that results for Chilean dolphins were robust and that temporary emigration might have affected estimates for Peale's dolphins. All estimates were scaled to account for the proportion of unmarked dolphins in each population. Depending on data sets and mark types used, mean mark rates ranged from 0.38 (SE= 0.05) to 0.63 (SE= 0.5) for Chilean dolphin, and from 0.25 (SE= 0.08) to 0.46 (SE= 0.08) for Peale's dolphin populations. Resulting total estimates of population size were 59 Chilean dolphins (CV= 0.04, 95% CI= 54 – 64) and 78 Peale's dolphins (CV= 0.15, 95% CI= 65 – 95) in southern Chiloé, and 123 Peale's dolphins (CV= 0.19, 95% CI= 97 - 156) in central Chiloé.

Power analysis showed that at least nine years of annual survey data were required for Chilean dolphins to detect a change in abundance of 5% assuming the probability of a Type I error was 0.1. The small and highly localized population of Chilean dolphins in southern Chiloé appears well suited for long-term monitoring and

evaluation of potential impacts of mariculture activities. Monitoring wider ranging Peale's dolphins requires spatial and temporal extension of survey effort and open population models to be used. Albeit of limited geographic scale, these estimates represent the first systematic assessment of abundance for both species throughout their entire ranges.

5.2. Introduction

Knowledge of temporal and spatial variation in the size of animal populations is important in understanding the processes that drive species' population dynamics (Fowler and Baker 1991). Information on the size of a population and its changes over time is also crucial for developing, implementing and evaluating appropriate mangement strategies for exploitation or conservation (Durant *et al.* 1992, Fowler and Siniff 1992). The latter is of particular interest in areas where conflicts arise between human activities and the target species. Throughout the world, coastal environments have increasingly become subject to anthropogenic impact. Human activities can affect cetaceans inhabiting nearshore waters by propagating through the food web (e.g. changes in prey availability, contamination) or by exerting direct pressures on the populations (e.g. harvest, incidental mortality in fishing gear) (Whitehead *et al.* 2000).

The sheltered waters of southern Chile, especially around the Chiloé Archipelago (42-43°S), have seen dramatic increases in the exploitation of the marine environment and changes to the nearshore habitat over the last decades. Mariculture farms (for salmon and mussels) have been expanding rapidly in number, size and sites since the early 1990s (Bushmann *et al.* 1996, SERNAPESCA 1997, Claude and Oporto 2000). In addition, gillnet fisheries and extraction of marine invertebrates are important ongoing activities (SERNAPESCA 2004) along with the increasing development of coastal and marine tourism ventures.

The inshore waters of southern Chile are home to several, mostly poorly known, small cetacean species, including the endemic Chilean dolphin, *Cephalorhynchus eutropia*, and the larger Peale's dolphin, *Lagenorhyhnchus australis* (Aguayo-Lobo *et al.* 1998). Some evidence suggests that past and possibly ongoing human exploitation has impacted both species directly, at least on local scales (Goodall and Cameron

1980, Goodall 2002). During the 1990's, concern was expressed over potentially unsustainable mortality levels of these dolphins hunted for bait in the southern crab fisheries (Cardenas *et al.* 1987, Lescrauwaet and Gibbons 1994) and taken incidentally in coastal gillnet fisheries (Oporto and Brieva 1990, Reyes and Oporto 1994). More recently, habitat alterations and increased mariculture activities have been suspected to be affecting dolphin populations (Claude and Oporto 2000, Hucke-Gaete 2000). Information on pre-exploitation and current population sizes, however, is not available for any part of their distributional ranges (Goodall *et al.* 1988, Brownell *et al.* 1999). Thus, effects of potential impacts on populations of Chilean dolphins and Peale's dolphins cannot be evaluated at present. A systematic assessment of abundance is required to determine population status and develop appropriate management strategies at regional and national levels to ensure continued occupancy of both species (Reeves *et al.* 2003).

The abundance of cetaceans can be estimated using distance sampling techniques, such as line-transect surveys, or mark-recapture methods (e.g. Evans and Hammond 2004). Underlying assumptions, advantages and limitations of both techniques are discussed in detail elsewhere (Hammond 1986, Borchers *et al.* 2002). Choice of technique is driven by financial, logistic, and temporal restrictions, the characteristics of the target species and the research questions to be addressed. Mark-recapture surveys usually require only a fraction of the financial, technical and human resources needed for dedicated line-transect surveys.

Mark-recapture techniques estimate the number of identifiable individuals in a spatially defined population and require repeat surveys to sample individuals representatively. They provide reliable estimates of abundance for populations comprising tens to hundreds of animals of which a high proportion can be individually identified and which occur in readily accessible habitat (Borchers *et al.* 2002), such as coastal populations of dolphins (Wilson *et al.* 1999). Mark-recapture studies are usually limited in spatial extent (but see Stevick *et al.* 2003), and a set of assumptions about the population under investigation needs to be met (Hammond 1986). The concept of population refers to identifiable animals using the designated study area over the length of the study period. Individuals often differ in their availability for identification due to differences in temporal or spatial distribution or behaviour (Otis

et al. 1978). Such heterogeneity of capture probabilities can lead to an underestimation of population size and is often difficult to model (Hammond 1986, Pollock et al. 1990).

Mark-recapture studies rely on the ability to reliably identify individual animals and can often provide ancillary information on movements, life-history and vital population parameters (Hammond *et al.* 1990). Traditionally, they involved capturing and artificially marking animals during encounter occasions. In cetaceans (and across a wide range of taxa spanning terrestrial and marine mammals, amphibians and fishes), natural markings are commonly used to identify individuals (see Hammond *et al.* 1990 for a detailed review for marine mammals). The process of "marking" and "recapturing" entails identifying individuals from suitable photographs taken of the distinctive features during an encounter. These photo-identification techniques and mark-recapture methods have been used extensively to estimate population sizes of coastal dolphins, e.g. *Tursiops sp.* (Williams *et al.* 1993, Wilson *et al.* 1999, Chilvers and Corkeron 2003, Read *et al.* 2003), *C. hectori* (Bräger 1998, Gormley *et al.* 2005), *C. commersonii* (Coscarella 2005).

This study applied photo-identification techniques and mark-recapture methods for the first time to Chilean dolphins and Peale's dolphins. Objectives were to assess the suitability of these techniques to obtain estimates of abundance for the two species, to estimate local population sizes in the central and southern Chiloé Archipelago and to develop recommendations for future monitoring work. The Chiloé Archipelago offered an ideal combination of feasible logistics, known occurrence of both species (Chapter 2, Goodall *et al.* 1998) and urgent needs for population assessment due to existing conservation concerns (Claude and Oporto 2000, Reeves *et al.* 2003). Surveys designed for mark-recapture analysis allowed additional biological information to be obtained (see Chapter 4), could be conducted from a small, inexpensive boat and were most suited to the complex coastline and the shallow coastal waters.

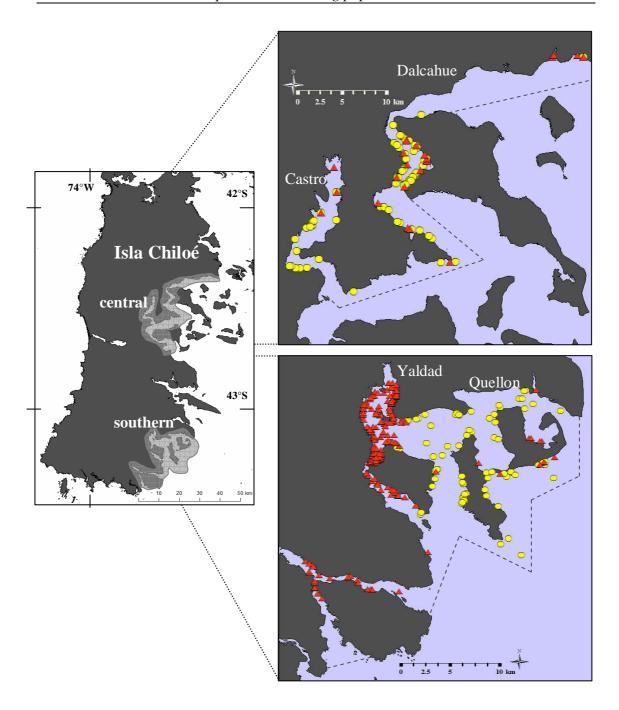


Figure 5-1. The study areas in the central and southern Chiloé Archipelago in southern Chile with distribution of groups of identifiable Chilean dolphins (red triangles) and Peale's dolphins (yellow circles) during photo-ID surveys (2001-2004).

5.3. METHODS

5.3.1. Data collection

Photo-identification surveys were conducted in the nearshore waters of the southern and central Chiloé Archipelago during four to five months each year from January 2001 to April 2004, spanning four austral summers. At least five days were required to complete a full survey of each of the study areas (Figure 5-1). Logistic restrictions limited effort in the central study area to three full surveys per year from 2002 to 2004.

Surveys were restricted to clear and calm conditions (Beaufort sea state three or less). Two to three observers scanned ahead and to 90° of the trackline while travelling at constant speed of approximately 10 knots in a 3.8 m outboard-powered boat. In 2001 transects paralleled the coast at approximately 400 m distance. From 2002 to 2004 alongshore transects as well as randomized zig-zag transects covering the entire study area were used (see Chapter 3). Concurrent investigations into distribution and habitat use patterns showed that both species concentrated within 800 m from shore. Alongshore and zig-zag transect surveys were designed to provide full coverage of this preferred nearshore habitat. Survey methods should not have biased encounter probability or photographic effort.

When dolphins were sighted, time, geographical position (using a handheld Garmin GPS), estimates of group size, presence of calves and neonates, initial behaviour of the dolphins and a suite of environmental conditions were recorded. A neonate showed clear foetal fold marks, was seen in constant association with an adult and was of less than $1/3^{\rm rd}$ of adult length. A calf was slightly larger and no longer had visible fold marks.

The sighted group was approached to obtain photographs of the dorsal fins of as many dolphins as possible, irrespective of their markings. An encounter lasted until all dolphins had been photographed, they moved out of sight or survey conditions precluded further photographic work. A group was defined as an aggregation of dolphins within 100 m of one another, engaged in similar activities and, if moving, heading in the same direction. In 2001 and 2002 photographs were taken using a 35 mm auto-focus camera (Nikon N90) equipped with 80-200 mm or 80-400 mm

vibration-reduced zoom lenses on black and white (Kodak TMAX 400) and slide (Kodak Ectachrome 100 or 200) films. From January 2003 onwards, a digital SLR camera (Fuji Finepix S2) with the same lenses was used. Digital photos were stored as highest quality jpg-files with an output of 4256x2848 pixels (approximately 4.3 MB) per image.

5.3.2. Photo-identification analysis

Photographs were classified into four quality grades (PQ 1-4, poor to excellent) according to focus, angle and visibility of the fin, contrast between fin and background, and size of the fin in relation to the photo-frame. Only photographs of good to excellent quality (PQ 3-4) were included in the analyses presented here.

Distinctiveness of individual marks has been shown to influence individual recognition (Friday *et al.* 2000, Gowans and Whitehead 2001, Read *et al.* 2003). Individuals were assigned a distinctiveness rating (MD 0-3, unmarked to very distinctive) based on the type of marks visible on the fin. Dolphin fins with deep nicks and cuts at the trailing edge (evident even in poor quality photographs) were scored as MD 3. Fins with several smaller but still obvious marks such as distinct notches were scored as MD 2. Subtle or small notches were scored as MD 1. Fins with no distinctive markings were rated MD 0 and were only used to calculate mark rates (see below).

Black and white prints and slides of sufficient quality were scanned at high resolution and stored as tif-files on computer. A custom-written database called FINBASE¹ (based on MS Access 2002 with Visual Basics for Applications) was used to archive and match digitised and digital images along with information from each survey and sighting. The FINBASE identification catalogue was organized by mark types based on user-specified categories. It did not perform automated matching procedures based on shape extracting algorithms (Araabi *et al.* 2000). In FINBASE new candidate images were compared to a selection of fins with similar mark types based on criteria specified by the user. All choices of matches were made by the user

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¹ The FINBASE software used in this study was adapted from a prototype published by J. Adams *et al.* in September 2004, Living Marine Resources Branch of CCEHBR, NOAA, USA; available at: http://www.chbr.noaa.gov/FinBase/.

(in this case the author). If a match was found to an individual already in the catalogue, the new image received a tentative association to the known individual. If no match was made, the individual was given a new identification number and was added to the existing catalogue.

All initial classifications as either matches or new fins were made by the author and were confirmed in independent secondary matching routines. Two to five observers experienced in photo-identification techniques were asked to check matches where identification proved difficult. Separate databases were maintaned for Chilean dolphins (FINBASE *eutropia*) and for Peale's dolphins (FINBASE *australis*).

The photo-identification protocol is described in greater detail in Appendices II+III, including information on sorting, grading, archiving and matching procedures as well as structure and maintenance of the FINBASE databases.

5.3.3. Estimating population size of marked animals

Established mark-recapture estimators that assumed demographic closure between sampling occasions were fitted to the capture histories of marked animals. Each identified dolphin was classed as either seen or not seen during a sampling period irrespective of the number of sightings of this individual. The two-sample Chapman-modified Petersen estimator (Chapman 1951) was applied to sighting data obtained for consecutive years. Population size \hat{N} was estimated as:

$$\widehat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

where

 n_1 = number of animals identified in the first year

 n_2 = number of animals identified in the second year

 m_2 = the number of animals identified in both years.

The variance of this estimate is calculated as

$$\operatorname{var}(\widehat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)^2 (m_2 + 2)}$$
 2.

Sequential Chapman estimates were calculated separately for the two study areas over pairs of years: for Peale's dolphins in central Chiloé from 2002 to 2003, for

Peale's dolphins in southern Chiloé from 2001 to 2004 and for Chilean dolphins in southern Chiloé from 2001 to 2004.

Sufficient data were available to derive independent estimates of population size for Chilean dolphins in southern Chiloé within each year from 2001 to 2004 using model-building procedures. Full closed capture models with heterogeneity were constructed in the program MARK ver.4.2 (White 2004). Models allowed capture probabilities to be constant, vary by time, include heterogeneity and a combination of variation by time and heterogeneity. These models were similar to those implemented in the program CAPTURE as models M0, Mt, Mh and Mth (Otis *et al.* 1978). Unlike CAPTURE, where heterogeneity is modelled for individuals, MARK implements Pledger's (2000) approach to model heterogeneity as a mixture of groups with different capture probabilities. In this study, heterogeneity was included as a mixture of two groups (i.e. low and high capture probabilities).

Choosing the best model required two steps: determining how well the models fitted the data and then selecting the best model. Goodness-of-fit (GOF) tests are commonly used to evaluate model fit but are currently not available for closed capture models with heterogeneity (Stanley and Burnham 1998, White 2004). The program CAPTURE offers GOF tests for the simple term models Mt and Mh and was used to assess how well these models explained the variation in the capture history matrix (Otis *et al.* 1978). Model fit was also evaluated in MARK by calculating the variance inflation factor (c-hat) for the saturated (starting) model, consisting of two mixtures and time dependence of capture probabilities.

The strength of using MARK is that the models from Otis *et al.* (1978) are placed in a likelihood framework allowing model-selection procedures and model averaging to be used (White *et al.* 2001). Akaike's Information Criteria corrected for small sample size (AICc) and, when over-dispersion existed in the data (c-hat > 1), quasi-likelihood adjusted AICc (QAICc) were used to select the most parsimonious model (Hurvich and Tsai 1989, White *et al.* 2001).

5.3.4. Meeting assumptions of mark-recapture analyses

Mark-recapture analyses make explicit assumptions about the nature of the population under investigation and the way it is sampled. Violations of these

assumptions can result in biased estimates. Some sources of biases can be reduced by appropriate sampling design and careful selection of photographic data (Hammond 1986). Mark-recapture analyses commonly assume that 1) marks are recognized with certainty if the animal is re-captured, 2) marks are not lost during the study, 3) animals do not respond to being marked in a way that affects their subsequent probability of re-capture (i.e. behavioural responses), and 4) within a sampling occasion all individuals have the same probability of capture (i.e. no heterogeneity of capture probabilities) (Hammond 1986, Pollock *et al.* 1990).

To reduce biases in *mark recognition*, only data from high-quality photographs (PQ 3-4) were used in analyses. To investigate the influence of mark distinctiveness, estimates were calculated from different subsets of data including individuals with obvious and distinctive marks (MD 2-3) and all mark types (MD 1-3). Subtle marks (MD 1) were more likely to be missed and could positively bias the resulting estimates. Including subtly marked individuals in the analysis, however, increased sample sizes, thus reducing variances and small sample bias.

Mark loss is difficult to measure in the field without double-marking individuals (Gowans and Whitehead 2001, Stevick *et al.* 2001). Most mark-recapture studies with cetaceans have restricted analyses to mark types believed to be permanent, such as dorsal fin nicks, unusual fin shapes and deformities (Lockyer and Morris 1990, Slooten *et al.* 1992, Wilson *et al.* 1999). This study used the same mark criteria (i.e. termed MD 2-3 marks), but also investigated the effects of including subtler marks (MD 1) in some data sets.

Behavioural responses to the process of being marked are unlikely to occur in photo-identification studies where the animals are not physically handled (Wilson et al. 1999). Capture and recapture probabilities therefore were considered equal.

Heterogeneity of capture probabilities is a well-known and potentially serious problem in mark-recapture studies leading to negatively biased estimates (Hammond 1990, Pollock *et al.* 1990). The study areas were surveyed completely during each sampling period to reduce heterogeneity resulting from individual preference for particular sites. The field protocol required an attempt to photograph all dolphins in the group to reduce heterogeneity resulting from some individuals being easier to

photograph than others. It is unlikely, however, that this ideal was achieved with each species during all sampling periods. Where possible, models were investigated that allowed the assumption of equal catchability of individuals to be relaxed. Capture probabilities also depended on the ability to reliably recognise individuals from photographs during the matching process. The use of only high-quality photographs and combinations of mark distinctiveness allowed heterogeneity resulting from some animals being easier to recognise than others to be addressed.

Closed population mark-recapture analyses assume that births, deaths, emigration and immigration do not occur during the study (demographic and geographic closure). Open population models allow these assumptions to be relaxed but invariably provide less precise estimates of abundance and do not allow heterogeneity to be accounted for (Pollock et al. 1990). Estimates of population sizes were obtained separately for each species in the southern and central study areas, assuming geographic closure of populations in each area. Discovery curves (Williams et al. 1993), the cumulative rate of discovery of new individuals, were plotted for each species to evaluate population closure.

Demographic closure can be assumed when the whole set of sampling occasions is sufficiently close in time, e.g. days or weeks apart, as was the case for Chilean dolphins. Neonate and calves were easily recognisable in the field and were not included in the analyses. Some unnoticed recruitment of young animals into the marked population might have occurred between annual sampling periods (e.g. in Peale's dolphins). Crude birth rates were calculated whenever possible as a proxy for recruitment to the marked population to provide a relative magnitude of this potential bias. Crude birth rates were estimated from the minimum count of individual neonates observed each year divided by the estimated total population size.

5.3.5. Estimating total population size

Mark-recapture estimates pertain to the number of marked animals in the population and need to be scaled by mark rate (i.e. proportion of marked animals) to provide an estimate of total population size. Dolphin fins were photographed at random without bias towards marked animals. Assuming that unmarked and marked dolphins had equal probability of photographic capture, the ratio of marked to unmarked fins in each focal group provided an unbiased estimate of mark rate θ :

$$\widehat{\theta} = \frac{\sum_{i=1}^{k} \frac{I_i}{T_i}}{k}$$
3.

with the variance expressed as

$$\operatorname{var}(\widehat{\theta}) = \left(\sum_{i=1}^{k} \frac{\theta_i (1 - \theta_i)}{T_i}\right) / k^2$$

where

 I_i is the number of photographs of dolphin fins with marks in group i,

 T_i is the total number of photographs taken of dolphin fins in group i,

k is the number of groups photographed.

Each mark-recapture estimate of the number of marked animals (\hat{N}) was scaled by the corresponding mark rate $(\hat{\theta})$ of the population to derive total population size (Wilson *et al.* 1999):

$$\widehat{N}_{Total} = \frac{\widehat{N}}{\widehat{\theta}}$$
 5.

with the variance estimated as

$$\operatorname{var}(\widehat{N}_{Total}) = \widehat{N}_{Total}^{2} \left(\frac{\operatorname{var}(\widehat{N})}{\widehat{N}^{2}} + \frac{1 - \widehat{\theta}}{n \widehat{\theta}^{2}} \right)$$
 6.

where *n* is the total number of dolphin fins from which $\hat{\theta}$ was estimated.

The coefficient of variation for the total population size $CV(\hat{N}_{Total})$ can be expressed as CVs of \hat{N} and $\hat{\theta}$:

$$CV(\widehat{N}_{Total}) = \sqrt{(CV(\widehat{N}))^2 + (CV(\widehat{\theta}))^2}$$
7.

Burnham *et al.* (1987) recommend log-normal confidence intervals to be used with abundance estimates, as standard confidence intervals can result in an unrealistic lower limit of zero. Log-normal confidence intervals give a lower limit of $\hat{N}_L = \hat{N}/r$ and an upper limit of $\hat{N}_U = \hat{N} * r$. For 95% confidence intervals, r is given as:

$$r = \exp\left\{1.96\sqrt{\ln(1 + (CV(\hat{N}_{Total}))^2)}\right\}$$
8.

where $(1+(CV(\hat{N}_{Total}))^2)$ is an approximation of var $(\ln \hat{N}_{Total})$.

5.3.6. Monitoring trends in population size

The statistical power to detect changes in population size from annual estimates was investigated using Gerrodette's (1987) general inequality equation:

$$r^2 n^3 \ge 12cv^2 (z_{\alpha/2} + z_{\beta})^2$$
 9.

where r is the annual rate of population change, n is the number of estimates of population size, cv^2 is the squared coefficient of variation of estimated total population size, $z_{\alpha/2}$ is the one-tailed probability of making a Type I error, and z_{β} is the probability of making a Type II error. The probability of making a Type I or II error was set at the 0.10 level (see Wilson *et al.* 1999).

5.4. RESULTS

The number of Chilean dolphins and Peale's dolphins encountered and identified differed markedly between study areas (Tables 5-1. and 5-2.). Overall encounter rates, the number of identifiable individuals and their resighting rates determined the choice of mark-recapture analysis.

5.4.1. Chilean dolphins

In total, 1,995 images of Chilean dolphins were of sufficiently high quality for analyses (31% of total images taken). From these, 57 individual dolphins were identified in southern Chiloé with 17 individuals bearing subtle, 29 bearing obvious and 11 bearing very distinctive marks. In contrast, in central Chiloé, only 15 dolphins were identified, of which eight individuals had subtle, three had obvious and four had very distinctive marks. Due to the low number of recognisable individuals, mark-recapture analysis could not be performed for Chilean dolphins in central Chiloé. A crude minimum estimate of abundance was obtained by scaling the number of dolphins identified each year (Table 5-1) by observed mark rate. Mean mark rate of this population was 0.49 (CV = 0.19) using all mark types (MD 1-3). The resulting minimum estimate suggested that on average at least 13 dolphins (CV = 0.22; 95% CI 10-16) used the waters of central Chiloé in any given survey year.

Survey effort focussed on southern Chiloé and provided a sufficient number of complete surveys each year to estimate population size using a model selection approach. Each year was divided into five to seven encounter occasions based on complete coverage of the study area. Discovery curves levelled off towards the end of each year's sampling period indicating that most marked animals had been identified by then (Figure 5-2).

Models selected for their lowest AIC_c/QAIC_c usually included time-dependence of capture probabilities and heterogeneity (except for the 2004 models; Table 5-3). All estimates were close to the observed number of marked animals. Average capture probabilities for individuals with MD 2-3 marks were high: 0.4 (SE= 0.07) in 2001; 0.35 (SE= 0.10) in 2002; 0.37 (SE= 0.11) in 2003; and 0.48 (SE= 0.05) in 2004.

Table 5-1. Survey effort and number of individual Chilean dolphins with small (MD 1), obvious (MD 2) and very distinctive (MD 3) marks identified in Chiloé.

Year	Study	No. of	No. of	No. of dolphins	Numl	per of ider	ntified indi	viduals
	area	survey days	groups	per survey day	MD 1	MD 2	MD 3	Total
2001	South	44	110	15	8	12	7	27
	Central	-	-	-	-	-	-	-
2002	South	40	67	12	11	15	6	32
	Central	13	10	3	3	2	1	6
2003	South	40	90	13	15	21	7	43
	Central	17	9	3	2	0	3	5
2004	South	31	75	16	17	15	6	38
	Central	11	8	4	6	1	1	8

Table 5-2. Survey effort and number of individual Peale's dolphins with small (MD 1), obvious (MD 2) and very distinctive (MD 3) marks identified in Chiloé.

Year	Study	No. of	No. of	No. of dolphins	Numb	er of ider	ntified indi	viduals
	area	survey days	groups	per survey day	MD 1	MD 2	MD 3	Total
2001	South	44	30	2	3	1	8	12
	Central	-	-	-	-	-	-	-
2002	South	40	33	3	4	2	8	14
	Central	13	23	13	4	7	6	17
2003	South	40	32	3	9	4	13	26
	Central	17	51	16	15	12	10	37
2004	South	31	19	3	5	2	3	10
	Central	11	20	8	7	6	6	19

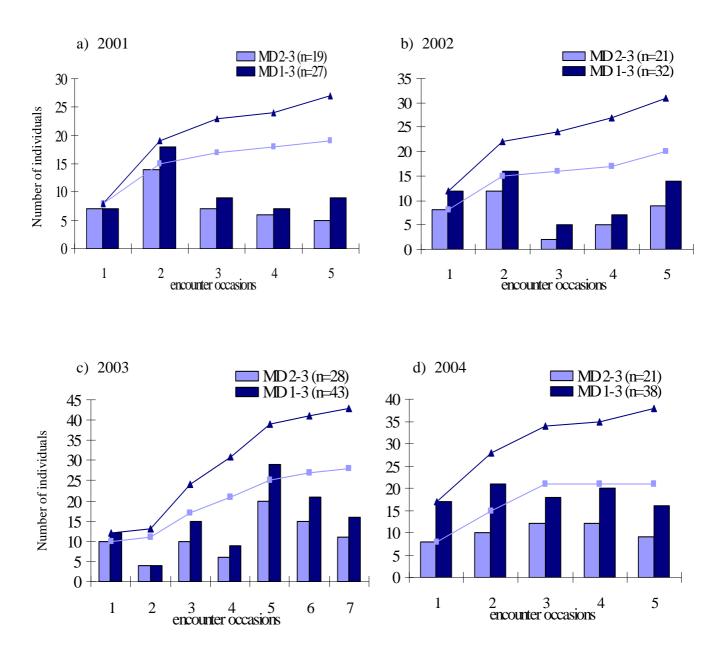


Figure 5-2. Number of individuals identified at each encounter occasion and discovery curves of Chilean dolphins in southern Chiloé from 2001 to 2004. Numbers in brackets give the total number of individuals identified for each subset of mark types.

Estimates from the best models (Table 5-3) were then scaled by corresponding mark rates (Table 5-4). Mark rates differed significantly between years when all mark types (MD 1-3) were included (Kruskal-Wallis test, H= 8.57, df= 3, p= 0.036). Mark rates were not significantly different between years (Kruskal-Wallis test, H= 5.19, df=3, p= 0.158) when only obvious and very distinctive marks (MD 2-3) were considered.

The use of different photographic media might have affected mark classification and recognition, especially of MD 1 type marks. Photographs were taken on black-and-white print film in 2001, colour slide and print film in 2001 and 2002, and occasionally in 2003 and 2004; and predominantly digital photographs in 2003 and 2004. Grading of photographic quality of images did not differ between these media (Kruskal-Wallis Test, H= 1.41, df= 2, p= 0.5). Neither were distinctiveness ratings affected by type of media (Kruskal-Wallis test, H= 2.31, df= 2, p= 0.32).

Estimates of total population size did not differ significantly between data sets (Figure 5-3). Abundance estimates derived from the MD 2-3 data set ranged from a high of 72 dolphins (CV= 0.15) in 2002 to a low of 53 dolphins (CV= 0.06) in 2004 (Table 5-5). The simple mean of the four annual estimates was 63 Chilean dolphins (CV= 0.13; 95% CI= 50 - 82). The inverse CV-squared-weighted mean of the four annual estimates was 59 dolphins (CV= 0.04: 95% CI= 54 - 64).

For comparison, population size in southern Chiloé was also estimated using sequential Chapman-modified Petersen estimators (Table 5-6). Once scaled by mark rates, total population size estimates were slightly, but not significantly, higher than those derived from the MARK models (Figure 5-3). The inverse CV-squared-weighted mean of the three estimates (for MD 2-3 marks) was 73 dolphins (CV = 0.04: 95% CI= 70 - 77).

Table 5-3. Within year estimates of the number of marked Chilean dolphins in southern Chiloé were derived in MARK using full closed capture models.

Notes: p(constant) = model where capture probability is constant; p(time) = model where capture probability varies over time;

p(time)(heterog.)= model where capture probability varies over time and

allows for heterogeneity.

a) Estimates for individuals with obvious and very distinctive marks (MD 2-3)

Year	No. of marked dolphins (MD 2-3)	Encounter occasions	MARK best model	No. of parameters	\widehat{N}	SE (\hat{N})	(\hat{N})	95% CI
2001	19	5	p(time)(heterog.)	7	20	1.4	0.07	19 - 27
2002	21	5	p(time)(heterog.)	9	22	1.7	0.08	21 - 31
2003	28	7	p(time)(heterog.)	14	32	3.8	0.12	28 - 47
2004	21	5	p(constant)	2	21	1.1	0.05	19 - 23

b) Estimates for individuals with all mark types (MD 1-3)

Year	No. of marked dolphins (MD 1-3)	Encounter occasions	MARK best model	No. of parameters	\widehat{N}	$\frac{\text{SE}}{(\hat{N})}$	(\hat{N})	95% CI
2001	27	5	p(time)(heterog.)	9	31	5.4	0.17	28 - 56
2002	32	5	p(time)	6	39	4.1	0.11	34 -52
2003	43	7	p(time)(heterog.)	14	49	4.5	0.09	45 - 65
2004	38	5	p(constant)	2	39	1.5	0.04	38 - 46

Table 5-4. Estimated proportion of Chilean dolphins in southern Chiloé possessing marks. Marks were defined as subtle (MD 1), obvious (MD 2) and very distinctive (MD 3).

 $\widehat{\theta}$ = estimated proportion of dolphins with marks in the population; SE = standard error.

Year	No. of images	$\hat{\theta}$ (MD 1-3)	$SE(\widehat{\theta}) (M 1-3)$	$\hat{\theta}$ (MD 2-3)	$SE(\hat{\theta}) (MD 2-3)$
2001	446	0.55	0.05	0.34	0.05
2002	430	0.54	0.06	0.33	0.06
2003	698	0.69	0.04	0.43	0.04
2004	788	0.74	0.04	0.42	0.04

Table 5-5. Total population size of Chilean dolphins in southern Chiloé (scaled estimates from Tables 5-3 and 5-4) and crude annual birth rates.

a) Estimates for individuals with obvious or very distinctive marks (MD 2-3)

Year	$\widehat{N}_{\scriptscriptstyle Total}$	$\mathrm{CV}(\widehat{N}_{Total})$	95% CI	Minimum number of neonates	Crude annual birth rate
2001	59	0.16	43 - 80	3	5.1 %
2002	67	0.19	46 - 96	6	8.9 %
2003	74	0.16	55 - 101	6	8.1 %
2004	50	0.11	40 - 62	6	12.0%

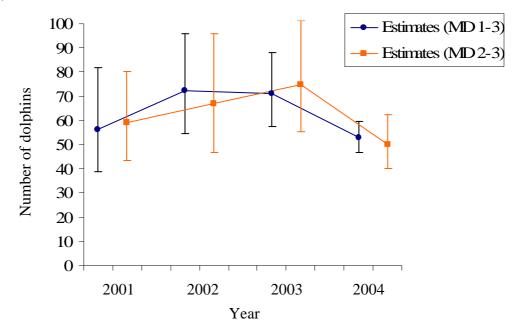
b) Estimates for individuals with all mark types (MD 1-3)

Year	$\widehat{N}_{\scriptscriptstyle Total}$	$\operatorname{CV}(\widehat{N}_{Total})$	95% CI	Minimum number of neonates	Crude annual birth rate
2001	56	0.19	39 - 82	3	5.4 %
2002	72	0.15	54 - 96	6	8.3 %
2003	71	0.11	57 - 88	6	8.5 %
2004	53	0.06	47 - 60	6	11.3 %

Table 5-6. Estimates of the number of marked Chilean dolphins in southern Chiloé with obvious or very distinctive marks (MD 2-3) and with all mark types (MD 1-3) derived from sequential Chapman-modified Petersen estimators.

Mark types	Years	n_1	n_2	m_2	\widehat{N}	$SE(\widehat{N})$	$\mathrm{CV}(\widehat{N})$	95% CI
MD 2-3	2001-02	19	21	15	27	1.6	0.06	25 - 29
MD 2-3	2002-03	21	28	20	29	0.7	0.02	28 - 30
MD 2-3	2003-04	28	21	19	31	1.2	0.04	29 - 32
MD 1-3	2001-02	27	32	20	43	2.8	0.07	40 - 47
MD 1-3	2002-03	32	43	30	46	1.1	0.02	44 - 47
MD 1-3	2003-04	43	38	32	51	1.7	0.03	49 - 53

a) Scaled estimates from best models in MARK



b) Scaled estimates from sequential Chapman estimators

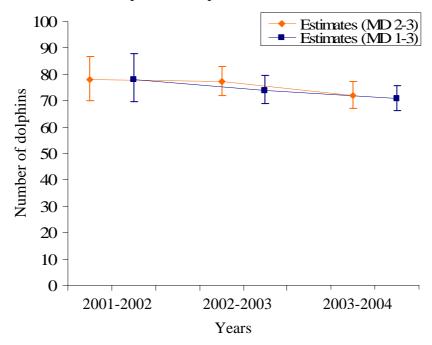


Figure 5-3. Estimates of total population size of Chilean dolphins in southern Chiloé calculated from different subsets of marked individuals. Error bars represent log-normal 95% confidence limits.

5.4.2. Peale's dolphins

For Peale's dolphins, 1,262 images (38% of total images taken) were of sufficiently high quality for analyses. From these, 34 individual Peale's dolphins were identified in southern Chiloé, of which 12 individuals had subtle, seven had obvious and 15 had very distinctive marks. Despite less survey effort, more Peale's dolphins were identified in central Chiloé. A total of 45 individuals were recognized with 16 bearing subtle, 14 bearing obvious and 15 bearing distinctive marks.

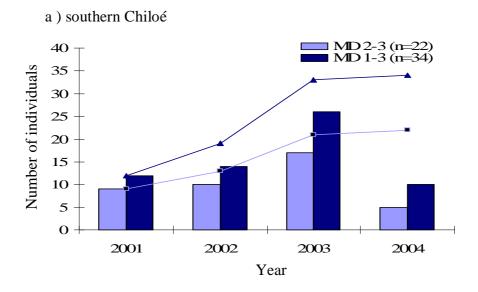
Although identified Peale's dolphins were seen repeatedly within a year, sighting rates of individuals in southern Chiloé were too low to allow the same model building process that was applied to Chilean dolphins. Effort in central Chiloé was limited to three full surveys (i.e. encounter occasions) per year, which also precluded a model-fitting approach (Table 5-2). Sightings of individuals were pooled for each year to provide sufficiently large sample sizes. Sequential Chapman estimators were applied to sighting histories for consecutive pairs of years (Table 5-7). Discovery curves showed that the number of identified individuals increased markedly in 2003 (Figure 5-4).

Estimates were scaled by corresponding mark rates averaged over consecutive years (Table 5-8). Mark rates did not differ significantly between years for the Peale's dolphin population in central Chiloé (Kruskal-Wallis tests: H= 2.37, df= 2, p= 0.305 for MD 2-3; H= 3.33, df= 2, p= 0.19 for MD 1-3). In southern Chiloé, mark rates varied significantly between years only when less marked animals were included (Kruskal-Wallis tests: H= 12.23, df= 3, p= 0.007 for MD 1-3; and H= 4.64, df= 3, p= 0.2 for MD 2-3).

Estimates of the total population size did not differ significantly between years or between data sets incorporating different mark types (Figure 5-5). The total number of Peale's dolphins in southern Chiloé estimated from the MD 2-3 data set ranged from a low of 67 dolphins (CV= 0.22) in 2001-2002 to a high of 91 dolphins (CV= 0.21) in 2002-03 (Figure 5-5, Table 5-9). Estimates for central Chiloé were higher, but not significantly so, given the wide and overlapping 95% confidence intervals for estimates from the two study areas. The total number of Peale's dolphins in central Chiloé estimated from the MD 2-3 data set varied from a low of 122 dolphins (CV= 0.19) in 2002-03 to a high of 149 dolphins (CV= 0.25) in 2003-04 (Figure 5-5). The

inverse CV-squared-weighted mean of these estimates was 78 Peale's dolphins (CV = 0.15; 95% CI= 65 - 95) in southern Chiloé, and 123 Peale's dolphins (CV= 0.19; 95% CI= 97 - 156) in central Chiloé.

Excluding the year 2003 from the data set and calculating the Chapman estimator between the years 2002 and 2004, produced slightly, but not significantly, lower estimates of total population size: 55 dolphins (CV= 0.24; 95% CI= 41 - 75) in southern Chiloé, and 126 dolphins (CV= 0.30; 95% CI= 86 - 185) in central Chiloé.



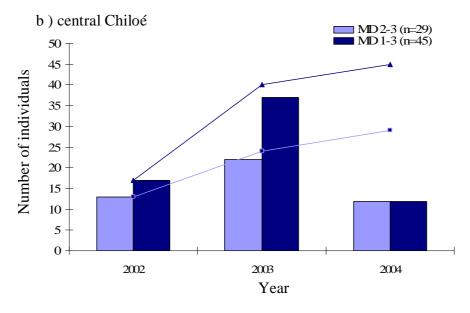


Figure 5-4. Number of individuals identified each year and discovery curves of Peale's dolphins in southern (a) and central (b) Chiloé from 2001 to 2004. Numbers in brackets give the total number of individuals identified for each subset of mark types.

Table 5-7. Estimates of the number of marked Peale's dolphins in southern (a) and central (b) Chiloé with obvious or very distinctive marks (MD 2-3) and with all mark types (MD 1-3) derived from sequential Chapman-modified Petersen estimators.

a) southern Chiloé

Mark types	Years	n_1	n_2	m_2	\hat{N}	$SE(\widehat{N})$	$\mathrm{CV}(\widehat{N})$	95% CI
MD 2-3	2001-02	9	10	6	15	1.8	0.12	13 - 17
MD 2-3	2002-03	10	17	7	24	3.2	0.14	20 - 28
MD 2-3	2003-04	17	5	3	26	6.1	0.24	19 -35
MD 1-3	2001-02	12	14	7	23	3.4	0.15	19 - 28
MD 1-3	2002-03	14	26	9	40	5.6	0.14	33 - 47
MD 1-3	2003-04	26	10	7	36	5.4	0.15	30 - 44

b) central Chiloé

Mark types	Years	$\widehat{N}_{\scriptscriptstyle Total}$	n_2	m_2	\widehat{N}	$SE(\widehat{N})$	$\mathrm{CV}(\widehat{N})$	95% CI
MD 2-3	2002-03	13	22	11	26	1.9	0.08	23 - 28
MD 2-3	2003-04	22	12	6	42	8.6	0.21	32 - 54
MD 1-3	2002-03	17	37	14	45	3.6	0.08	40 - 50
MD 1-3	2003-04	37	12	6	70	15.3	0.22	53 - 92

Table 5-8. Estimated proportion of Peale's dolphins in southern (a) and central (b) Chiloé possessing marks. Marks were defined as subtle (MD 1), obvious (MD 2) and very distinctive (MD 3).

 $\hat{\theta}$ = estimated proportion of dolphins with marks in the population; SE = standard error.

a) southern Chiloé

Year	No. of images	$\hat{\theta}$ (MD 1-3)	$SE(\widehat{\theta}) (M 1-3)$	$\hat{\theta}$ (MD 2-3)	$SE(\hat{\theta}) (MD 2-3)$
2001	97	0.24	0.06	0.13	0.05
2002	121	0.44	0.09	0.32	0.08
2003	257	0.61	0.07	0.26	0.07
2004	79	0.55	0.09	0.33	0.10

b) central Chiloé

Year	No. of images	$\hat{\theta}$ (MD 1-3)	$SE(\hat{\theta}) (M 1-3)$	$\hat{\theta}$ (MD 2-3)	$SE(\hat{\theta}) (MD 2-3)$
2001	-	-	-	-	-
2002	197	0.33	0.07	0.21	0.07
2003	388	0.51	0.05	0.24	0.05
2004	123	0.63	0.14	0.39	0.10

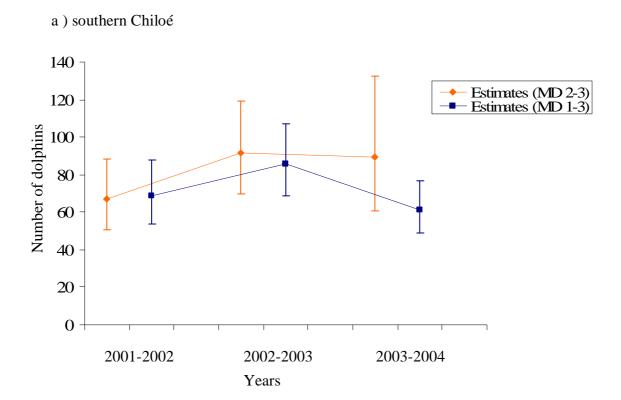
Table 5-9. Total population size of Peale's dolphins (scaled estimates from sequential Chapman-modified Petersen estimators, using mark types MD 2-3) and crude annual birth rates.

a) southern Chiloé

Year	\widehat{N}_{Total}	$\mathrm{CV}(\widehat{N}_{Total})$	95% CI	Minimum number of neonates	Crude annual birth rate
2001				2	
2002	67	0.22	51 - 88	3	4.5 %
2003	91	0.21	70 - 119	2	2.2 %
2004	90	0.31	61 - 133	3	3.3 %

b) central Chiloé

Year	$\widehat{N}_{\scriptscriptstyle Total}$	$\operatorname{CV}(\widehat{N}_{Total})$	95% CI	Minimum number of neonates	Crude annual birth rate
2002				2	
2003	112	0.19	89 - 143	2	1.8 %
2004	149	0.25	108 - 205	1	0.7 %



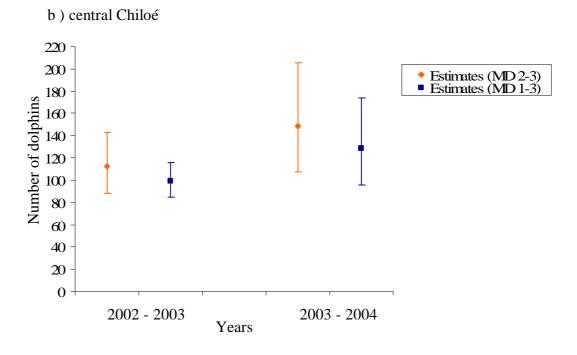


Figure 5-5. Estimates of total population size of Peale's dolphins in southern (a) and central (b) Chiloé calculated from different subsets of marked individuals. Error bars represent log-normal 95% confidence limits.

5.4.3. Monitoring trends

Statistical power was too low (p< 0.3) to detect any biologically plausible trend (<20%) in abundance across the four annual estimates of total population size for Chilean dolphins. The time to detection of a particular trend in abundance is a function of the actual rate of change and the precision of the abundance estimates (Figure 5-6). The length of time required to detect a trend in abundance decreases as the rate of change increases. Time to detection of a trend also decreases as precision of the abundance estimates increases, particularly so when rates of change are small. Assuming annual estimates of abundance with a precision of 13% (CV= 0.13), it would take around 9 years to detect a 5% per annum population decrease with reasonable statistical power (p> 0.9). During that time the population would have declined by about 34% of its original size. If abundance estimates were obtained every two years instead, the time to detection would increase to 11 years, at which time the population would have declined to about 40% of its original size.

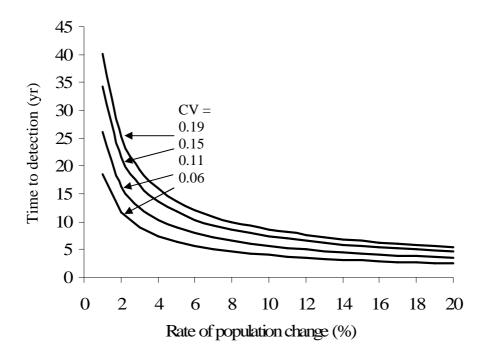


Figure 5-6. Relationship between four observed levels of precision of population estimates for Chilean dolphins, rate of population change and the time until detection of such change. The probability of Type I and II errors was set at 0.10.

5.5. DISCUSSION

Occurrence of Chilean dolphins and Peale's dolphins at Chiloé has been reported in published records since the late 1960s and 1980s respectively (Goodall *et al.* 1988, Oporto and Gavilan 1990). The first estimates of abundance for each species obtained in this study suggest that local populations are very small.

5.5.1. Heterogeneity of capture probabilities

At least for Chilean dolphins, heterogeneity was evident from the models selected in MARK and most likely arose from different behaviour of dolphins towards the research boat. Unlike Peale's dolphins and other delphinids (Goodall *et al.* 1997a, Würsig 2002), Chilean dolphins tend to avoid boats (Crovetto and Medina 1991, Ribeiro *et al.* 2005). Observations in the field suggested that some dolphins were easier to approach, and photograph than others during an encounter. Duration of an encounter was quite variable and consequently affected the probability of photographing all dolphins in the group. An encounter with a group of Chilean dolphins lasted on average 27 minutes (SE= 1.2 min., range= 2 to 95 minutes, n= 239), and with Peale's dolphins on average 29 minutes (SE= 2.0 min, range= 1 to 81 minutes, n= 120). The maximum durations usually arose from lengthy attempts to follow a fast travelling or otherwise uncooperative group. The shortest durations were caused by the dolphins moving out of sight.

This study used high-speed cameras with recording media that allowed for fast shutter speeds as well as image-stabilized high-power zoom lenses. Conventional SLR cameras with print or slide film produced similar results to digital SLR cameras. However, digital photographs were much easier, quicker and cheaper to process and prepare for analysis than conventional print or slide films. Given the predominantly low light conditions and the evasive behaviour of the dolphins, high quality photographic equipment should be considered essential for photo-identification studies of these species.

Although the effects of heterogeneity can best be minimized in the field (Hammond 1986), there seems little additional room to reduce heterogeneity at the data collection stage. Hence, care should be taken to investigate mark-recapture models that allow heterogeneity to be accounted for. Such model-fitting approaches, however, require multi-sample data sets with a sufficiently large number of identified individuals

(White *et al.* 1982, Pollock *et al.* 1990). Model-derived estimates might have suffered from small sample bias due to the small number of encounter occasions and relatively few identified individuals that provided capture histories. Including individuals with subtle marks increased the sample size but did not result in the desired increase in precision. Subtle marks were more prone to be missed or mismatched, potentially leading to inflated estimates. Once corrected for mark rate, however, estimates derived from data sets including or excluding subtle marks did not differ significantly, irrespective of the mark-recapture method used.

For Chilean dolphins, the simple Chapman-modified Petersen estimators provided comparable, consistent and precise estimates across years. However, heterogeneity cannot be accounted for with this method and could have resulted in negatively biased estimates. Estimates for Peale's dolphins were less precise, possibly due heterogeneity and the violation of the assumption of geographic closure (see below).

5.5.2. Mark recognition and mark loss

Mark change and mark loss appeared negligible for both species over the relatively short course of the study. Out of the 62 Chilean dolphins identified, only two known individuals acquired a new feature on their respective dorsal fin. Neither individual changed its mark distinctiveness category. Injuries to the body or dorsal fin that were severe enough to cause existing marks to become unrecognisable were not observed among Chilean dolphins.

Of the 79 Peale's dolphins identified, only one known individual acquired a new feature on its dorsal fin. This new nick changed its mark distinctiveness rating from obvious (MD 2) to very distinctive (MD 3). One Peale's dolphins with very distinctive features at its dorsal fin also bore deep and fresh-looking cuts at its flank and lower dorsal fin when it was first identified. Hence, some mark change might have occurred among some Peale's dolphins.

5.5.3. Geographic population closure

Southern Chiloé had a small, geographically closed population of predominantly resident Chilean dolphins concentrated in three selected bays and channels (Chapter 4). For Peale's dolphins, geographic closure is more difficult to assume, especially across years. A large increase in the number of newly marked individuals (especially

those with subtle marks) was observed in both study areas in 2003, but not in the year before or after. It appears unlikely that this increase was entirely due to mark acquisition in previously unmarked individuals, nor did it result from unequal sampling effort. The average number of dolphins encountered during a survey day was comparable (southern Chiloé), or larger (central Chiloé), than in other years. Of the 16 and 24 new dolphins identified in 2003 in southern and central Chiloé, respectively, only two and three individuals (13%) were seen in the following year.

The observed increase of new identifications in 2003 most likely resulted from temporary immigration into the study areas. Peale's dolphins most likely range beyond the boundaries of the chosen study areas, but individuals have yet to be shown unambiguously to move between southern and central Chiloé (Chapter 4). Rate of individual movements into or out of the study areas remain unknown. However, if a proportion of the population remains unavailable for photographic capture, this would lead to negatively biased population estimates (Hammond 1986).

5.5.4. Demographic population closure

Although neonates and calves were excluded from photographic analysis, some recruitment into the (marked) adult population might have occurred from one year to the next. Minimum estimates of crude birth rates suggest a potential recruitment of up to 8% p.a. in Chilean dolphins and up to 3.3% in Peale's dolphins. The estimate for Chilean dolphins appears rather high for a delphinid (Wells and Scott 1990, Slooten and Lad 1991, Wilson *et al.* 1999), and more comparable to the life history of harbour porpoises (Read 1990). Survival rates are unknown for either species but additions to the population would be counter-balanced by losses (i.e. deaths). Information on mortality rates was not available for either species. Actual recruitment rates into the adult population might be considerably lower.

5.5.5. Comparing population sizes

Local population sizes of Chilean dolphins and Peale's dolphins were small and appeared inversely related to one another in the two study areas. Southern Chiloé was home to a small and resident population of Chilean dolphins that exclusively occupied selected bays and channels (Chapter 4). The Peale's dolphin population in southern Chiloé was comparable in size but individuals ranged over wider areas and were seen less regularly (Chapter 4). In contrast, Peale's dolphins were the dominant species in

central Chiloé in terms of numbers of dolphins and frequency of encounters. Species-specific population structure, prey preference or foraging habitat remain unknown. Nevertheless, the observed pattern in abundance and distribution could represent small-scale habitat segregation to avoid inter-specific competition when resources and carrying capacity of the local environment are limited. Comparably small and seemingly isolated populations have been described for other delphinids, e.g. inshore bottlenose dolphins (*Tursiops* sp.) in New Zealand (Williams *et al.* 1993) or Scotland (Wilson *et al.* 1999). Striking differences in abundance, density and ranging patterns have been related to habitat types and their potential carrying capacity for dolphins as top predators (Chilvers and Corkeron 2003, Read *et al.* 2003). Tentative evidence also exists for congeneric Hector's dolphins (*C. hectori*) where local population sizes ranged from a few dozens to hundreds of individuals (Bräger and Schneider 1998, Gormley *et al.* 2005) depending on location and potential co-occurrence of other species.

Although comparable estimates of abundance are not available for Chilean dolphins or Peale's dolphins, anecdotal information suggests that temporary aggregations of several hundred dolphins could occur along the open coast in the northern part of their range (Goodall *et al.* 1988). If substantiated, such observations could suggest similar differences in numbers in relation to different habitat types. Information on habitat use and population dynamics is needed to place abundance and ranging patterns of each species in an appropriate ecological context.

5.5.6. Conservation implications and population monitoring

A patchy distribution and very small local population sizes make Chilean dolphins particularly vulnerable to anthropogenic impacts. Mariculture farms for salmon (*Salmo salar, Oncorhynchus* sp.) and mussels (*Mytilus chilensis*) abound throughout the range of the small population of Chilean dolphins in southern Chiloé (Chapter 2). Mussel farming activities have been expanding since the late 1980s (Clasing *et al.* 1998), and salmon farming since the mid-1990s (SERNAPESCA 1997, Alvial and Manriquez 1999). Occurrence of both dolphin species has been documented in the area for decades (Goodall *et al.* 1988, Crovetto and Medina 1991, Goodall *et al.* 1997b), but estimates of population size had not been obtained prior to this study. Although much concern has been raised over potential negative impacts of

mariculture on coastal cetaceans (Slooten *et al.* 2000, Würsig and Gailey 2002, Kemper *et al.* 2003, Lloyd 2003), conclusive evidence has been difficult to obtain. Only two studies have systematically assessed impacts of shellfish farms on dolphins (Watson-Capps and Mann 2005, Markowitz *et al.* 2004). Anecdotal evidence suggests that Chilean dolphins might be excluded from parts of potentially important habitat, at least in Yaldad Bay (Kemper *et al.* 2003, Ribeiro 2003).

This study has shown that the population size of Chilean dolphins in and around Yaldad Bay in Southern Chiloé can be estimated by applying photo-identification techniques and mark-recapture methods. Although the current trend of this small population is uncertain, the tools for effective monitoring exist and monitoring efforts have been ongoing since 2001. This population appears well suited to investigate potential long-term effects of intense mariculture activities on a resident coastal dolphin species.

Natural changes in population sizes of small cetaceans are likely to be slow, but unusual mortality (natural or anthropogenic) can cause dramatic declines. Given the precision of estimates obtained in this study, it would take around 9 years of annual mark-recapture estimates to detect a significant (at the 10% probability level) decline in population size of 5%. This time frame would lengthen if abundance estimates were obtained less regularly. Data on important population parameters, such as calving intervals, birth rates and survival rates would be lost if photo-identification surveys were not conducted annually. The length of time to detection would shorten if declines occurred more rapidly or precision of estimates could be increased. The former would have severe consequences for such a small population. The latter is desirable, but requires considerable resources and is often beyond active control due to the behaviour of the target species or logistic restrictions. Hence information on population trends that allow sufficient time to implement effective management strategies cannot be produced over the course of a few years but require dedicated long-term annual monitoring surveys.

The traditional management approach requires that a particular monitoring programme produces empirical evidence for a population decline before mitigating management actions are taken to halt the decline (Thompson *et al.* 2000). As discussed above and as is true for all cetaceans, there are a multitude of factors

hampering the detection of a population decline, such as low statistical power to detect trends due to difficulties with and uncertainties in abundance estimation and failure to identify the cause(s) of the decline (Taylor and Gerrodette 1993, Mayer and Simmonds 1996, Thompson *et al.* 2000). Thus a population decline should not be a necessary criterion for initiating conservation measures (Taylor and Gerrodette 1993). Rather, the precautionary principle (Gray and Bewers 1996) should be applied, especially when a population is small, and might have declined beyond recovery before management actions actually take effect (Thompson *et al.* 2000). Under precautionary management, measures would be implemented to reduce potential threats despite a lack of evidence of causal links. A precautionary management approach should be applied to Chilean dolphin and Peale's dolphin populations at Chiloé given their small current population sizes, unknown historical abundances, patchy distribution and the multitude of existing and expanding human activities suspected to impact cetaceans negatively.

Mark-recapture methods applied to Peale's dolphins highlighted the importance of considering underlying assumptions and explicit survey design. There was evidence for temporary immigration of Peale's dolphins, at least in some years, suggesting that the chosen study areas probably did not encompass the entire range of the local population. Extending survey effort beyond the boundaries of the current study areas could provide important information on movement patterns and help identify more appropriate spatial scales for population monitoring of Peale's dolphins.

Considerable geographic and temporal survey effort is already required to cover the current study areas. This level of effort should be maintained, but it is unlikely that it can be much increased. Geographically extended photo-identification surveys could be limited to one sampling period per year (spanning several days for full repeat coverage). Open population models that allow the assumptions of population closure to be relaxed could be used to monitor population size across a series of years (a minimum of five years is required) (Pollock *et al.* 1990). Hence photo-identification surveys would need to be continued annually to obtain a large enough data set. Open population models tend to produce very imprecise estimates of abundance (Pollock *et al.* 1990). Recently developed open population models that allow temporary emigration/re-immigration and heterogeneity to be taken into account appear to

produce more precise estimates (Whitehead and Wimmer 2005). If assumptions are met, open population models would also provide estimates of survival rates (Pollock *et al.* 1990, Cameron *et al.* 1998, Langtimm *et al.* 1998). A promising new approach that does not require systematically sampling the entire range of the population is the use of multisite mark-recapture estimates in a Bayesian framework (Durban *et al.* 2005). This method can use opportunistically collected sighting data from identifiable individuals when sampling is conducted simultaneously at three or more study sites located throughout the range of the population. Such an approach would benefit from a more detailed knowledge of the range of Peale's dolphins at Chiloé.

This study describes the first comprehensive abundance survey of Chilean dolphins and Peale's dolphins in Chile. It is hoped that the results will lead to the establishment of a long-term monitoring programme of local populations in Chiloé and that appropriate management strategies can be formulated which will ensure the dolphins' continued occupancy of important coastal habitat.

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Chapter 6 General discussion: Insights and outlook

6.1. SYNTHESIS

The endemic Chilean dolphins, *Cephalorhynchus eutropia*, and sympatric Peale's dolphins, *Lagenorhynchus australis*, co-occur in two coastal habitat types in Chile: along the open coast with the northern limit around Valparaíso (33°S), as well as in protected bays and channels of the Chiloé Archipelago (41-43°S) and the southern fjords to the South (55°S) (Goodall 1994, Goodall *et al.* 1997). The Chiloé Archipelago has been considered one of the distribution centres of both species based on compiled anecdotal sighting information (Goodall *et al.* 1988, Goodall *et al.* 1997). The purported importance of this area over the fjords or open coast, however, might simply reflect better sighting opportunities due to accessibility, sighting conditions (e.g. sheltered waters), observer effort (e.g. lay observers, scientific visits) and more detailed record keeping of sightings.

This study was instigated to investigate systematically for the first time the distribution, abundance, site fidelity and habitat use patterns of Chilean dolphins and Peale's dolphins in the Chiloé Archipelago. This region also constitutes the largest, and one of the most intensely used mariculture areas in Chile (SERNAPESCA 2004), thus providing a conservation incentive to the ecological inter-specific comparison. The main goals of this thesis therefore have been centred around three aspects: species-specific ecology, inter-specific or comparative ecology and conservation ecology. In this chapter, the novel results (see also Table 6-1), conservation implications and future research avenues are discussed.

Table 6-1. Comparison of ecological aspects of Chilean dolphins and Peale's dolphins in the Chiloé Archipelago. * Values are median; *range*.

Aspect	Measurement	Chilean dolphins	Peale's dolphins	Source
maximum length (cm)		167	218	Goodall <i>et al</i> . 1997
maximum weight (kg)	MATERIA (1871-1876) (1871-1876) (1871-1876) (1871-1876) (1871-1876) (1871-1876) (1871-1876) (1871-1876) (1871-	63	115	Goodall <i>et al</i> . 1997
CHILOÉ				
group size	mean \pm SE	6 ± 0.2	5 ± 0.2	Chapter 2
	median	5	4	
	range	1 - 26	1 - 17	
reproduction	calving	spring-summer	spring-summer	Chapter 2
	mating	summer?	summer?	
habitat features *	distance to shore (m)	214; 17 - 894	204; 41 - 2,31	Chapter 3
	depth (m)	12; 2.5 - 56	6; 1.8-65	
	water clarity (m)	5; 2.5 - 11	7; 1.8 - 15	
	SST (°C)	12.9; 10.8 - 19.6	13.1; 1 <i>0.4 - 16</i>	
	salinity (ppt)	32.2; 28.8-33.8	32.3; <i>32.2 - 33.8</i>	
	distance to river (m)	1,185; <i>49 - 5,360</i>	1,764; 235 - 9,506	
site fidelity		yes	no	Chapter 4
ranging *	alongshore range (km)	24; 4 - 45	20; 4 - 44	Chapter 4
	"home range" (km²)	40; 22 - 46	?	
abundance	combined MR estimates for central & southern	72 (64 - 80)	201 (162 - 251)	Chapter 5
	Chiloé (95% CI)	(04 - 60)	(102 - 231)	
survival rate	MR estimate (95% CI)	0.90 (0.82 - 0.95)	?	Fuentes 2005
				~
social structure		fission-fusion spatially defined	fission-fusion -	Christie 2005 Chapter 4
		"communities?"		•
anthropogenic effects	distribution of dolphins overlaps with	mussel farms	some mussel farms	Chapters 2 & 3
	1	some salmon farms	some salmon farms	Chapters 2 & 3
		shore-based	shellfish extraction	Chapter 2
		gillnetting		
		boat traffic	boat traffic	Ribeiro <i>et al</i> . 2005, Chapter 2
	dolphins potentially	displacement?,	habitat	Chapter 2
	threatened by	habitat degradation?	degradation?	_
		entanglement?		Chapter 2
		disturbance?	disturbance?	Chapter 2

6.2. DISTRIBUTION AND HABITAT PARTITIONING

Chilean dolphins and Peale's dolphins have a discontinuous patchy distribution in the nearshore waters of central and southern Chiloé (Chapter 2). Both species select shallow coastal waters close to shore (Chapter 3). Chilean dolphins also show a weak preference for turbid and slightly warmer waters that is most likely a by-product of their geographically preferred habitat rather than a clear selection for these environmental conditions. Proximity to rivers, along with geographic location and distance to mussel farms are the most important features explaining the spatial segregation between Chilean dolphins and Peale's dolphins. The preferences for proximity to mussel farms and rivers most likely act as proxies for other features of the coastal environment, such as estuarine character with enhanced primary productivity. The preferred bays seem to attract and aggregate large concentrations of potential prey for Chilean dolphins, at least during the summer. In contrast, the preference of Peale's dolphins for nearshore waters away from mussel and salmon farms seems to reflect a selection of more exposed shores and/or areas with apparently shallow and predominantly sandy bottoms. Thus, the observed spatial habitat partitioning appears to be a result of differences in preferred microhabitat types within the shallow nearshore waters selected by both species.

The direct causal relationships underlying the observed distribution and habitat selection patterns currently remain unknown. As is common in cetacean habitat studies, environmental features are considered proxies for the availability and distribution of critical resources, such as prey, mates, and shelter from predators, all of which are inherently difficult to determine or quantify reliably (Gowans and Whitehead 1995, Fiedler *et al.* 1998, Reilly *et al.* 1998, Griffin and Griffin 2003, Macleod *et al.* 2004, Croll *et al.* 2005). Throughout this thesis prey availability and differences in foraging strategies have been hypothesized to be the primary factors influencing the observed patterns in distribution (Chapter 2), habitat use (Chapter 3), ranging (Chapter 4), and possibly even local abundance (Chapter 5) of Chilean dolphins and Peale's dolphins. Information on prey species and diet composition is lacking for both species in the Chiloé Archipelago, and is scant for the remainder of their ranges. Thus, dietary studies are needed before any firm conclusions about the causal factors underpinning the observed habitat partitioning can be drawn.

The suggested differences in foraging strategies and prey are supported by the findings that Chilean dolphins spend a larger proportion of their time engaged in localized foraging-related behaviours compared to Peale's dolphins (Chapter 2), show a high degree of small-scale site fidelity (requiring a sufficiently large local prey availability to sustain the resident population), and select coastal habitat with estuarine character which seem to function as fish nurseries (Chapter 3). The preference for river mouths and riverine areas, often with strong tidal currents, has been well documented for Chilean dolphins from anecdotal sightings throughout their range (Goodall et al. 1988, Pérez-Alvarez and Aguayo-Lobo 2002). In areas where large and abundant kelp forests, their primary foraging ground in the Strait of Magellan (Viddi and Lescrauwaet 2005), are lacking Peale's dolphins target a wide range of demersal and bottom fish, octopus and squid (Schiavini et al. 1997). The general lack of site fidelity of Peale's dolphins at Chiloé suggests that suitable resources are distributed patchily, with possibly limited local abundance. A greater behavioural flexibility in resource use might explain the larger distributional range of Peale's dolphins compared to Chilean dolphins, spanning different coastal habitat types of the southern South Pacific and South Atlantic (Brownell et al. 1999).

Intriguingly, most reports of co-occurrence of Chilean dolphins and Peale's dolphins describe a lack of direct interaction between them (this study, Goodall et al. 1988, Goodall et al. 1997, Lescrauwaet 1997). Similarly to this study, small-scale spatial segregation between Chilean dolphins and Peale's dolphins has been observed in two continental fjords east of the Chiloé Archipelago (F. Viddi, pers. communication). Thus the observed habitat partitioning could be a general pattern for Chilean dolphins and Peale's dolphins, at least in the islands and fjord region of southern Chile. Such a spatial separation and use of different ecological niches most likely reduces competitive pressure between these two coastal species. Niche selection and the nature of interspecific interactions and habitat partitioning, however, can be expected to vary between habitat types (Ballance 2002, Bearzi 2005). The framework of habitat selection models developed in this study could be used to test the generality of niche selection and habitat partitioning among Chilean dolphins and Peale's dolphins based on habitat characteristics in different areas, such as the continental fjords or the open Chilean coast to the north of Chiloé. This approach requires detailed systematically collected sighting information and accompanying

environmental data on the presence and absence (or density) of both species in different habitat types.

Comparative habitat selection has not been investigated for congeneric species, hence comparisons are limited to incidental observations or largely descriptive studies. Peale's dolphins are fully sympatric with Commerson's dolphins, C. commersonii, in Argentina and the Falkland Islands, and are known to associate in mixed species groups (de Haro and Iñíguez 1997, Goodall et al. 1997). Congeneric dusky dolphins, L. obscurus, co-occur with Heaviside's dolphins, C. heavisidii, in South African/Namibian waters, and with Hector's dolphins, C. hectori, off the South Island of New Zealand. However, dusky dolphins are generally found over the continental shelf and in larger groups compared to Peale's dolphins, and both species are broadly sympatric without direct interaction throughout most of their southern South Atlantic range (Goodall et al. 1997). Given the intra-generic differences in Cephalorhynchus and Lagenorhynchus, generalisations about the nature of intergeneric interactions are difficult. Chilean dolphins differ markedly in some behavioural aspects from all other members of the genus Cephalorhynchus, such as their usually boat-shy and less surface active behaviours, particularly in comparison with their South American congener, the Commerson's dolphin (Heinrich, pers. observation). In all mixed inter-generic associations, the smaller Cephalorhynchus species adapts to the surfacing and behavioural activities of the larger, and usually more boisterous Lagenorhynchus species (de Haro and Iñíguez 1997, Lescrauwaet 1997, Würsig et al. 1997). Chilean dolphins might conform less to the behavioural patterns of Peale's dolphins, and might receive little, if any, benefit from associating with them. Commerson's dolphins and Peale's dolphins on the other hand seem to enhance foraging efficiency by forming mixed groups along the open and exposed Argentinean coast (de Haro and Iñíguez 1997). Commerson's dolphins and Peale's dolphins also co-occur in the sheltered nearshore waters of the Falkland Islands (Brownell et al. 1999) where neither species has been studied in detail to date. The nature of their sympatric co-existence in relation to different habitat characteristics could be investigated in the Falkland Archipelago by applying the same comparative approach used in this thesis for Chilean dolphins and Peale's dolphins.

Niche partitioning has been suggested for sympatric Heaviside's dolphins and dusky dolphins along the open coast of South Africa, where Heaviside's dolphins seem to prefer sandy shores, and shallower cooler waters (Elwen and Best 2003). Spatial habitat partitioning as a result of differences in habitat preference has also been observed in other sympatric inshore cetaceans, such as humpback dolphins (*Sousa chinensis*) and bottlenose dolphins (*Tursiops* sp.) (Chilvers *et al.* 2005), or the *adunctus* and *truncatus* forms of *Tursiops* sp. (Hale *et al.* 2000).

Direct interactions between Hector's dolphins and dusky dolphins were observed at Kaikoura, New Zealand (Würsig *et al.* 1997, Markowitz 2004), where dusky dolphins shelter from killer whale (and possibly shark) predation in or near the inshore surf zone during the day in summer (Würsig *et al.* 1991, Constantine *et al.* 1998), and feed offshore on mesopelagic fish at night (Würsig *et al.* 1997). Mixed groups of Hector's dolphins and dusky dolphins have only been observed in the preferred nearshore habitat of Hector's dolphins, and frequently have involved calves of both species. Enhanced safety from predators (e.g. sharks or killer whales) appears to be the most likely explanation for the observed inter-specific associations (Würsig *et al.* 1997, Markowitz 2004). There is no evidence for predation by killer whales or sharks on Chilean dolphins or Peale's dolphins in the waters around Chiloé (or anywhere throughout their Chilean range), and current predatory pressure does not seem to be a major factor shaping habitat selection of both species.

6.3. RANGING PATTERNS AND LOCAL ABUNDANCE

Movements and site fidelity of individually identifiable dolphins were determined from observations made in daylight hours during four consecutive austral summer/autumn seasons. Diurnal or seasonal movement patterns were not investigated. Thus ranging and residency patterns in this study are temporally limited, and spatially restricted to the two study areas delineated based on practical considerations and logistic restrictions. Despite these caveats clear differences in movements and residency patterns emerged between Chilean dolphins and Peale's dolphins. Individual ranging and site fidelity patterns (Chapter 4) reflected the population-level observations on distribution (Chapter 2) and habitat selection (Chapter 3). Individual Chilean dolphins ranged over short distances (on average less than 25 km), showed a distinct preference for few selected locations (i.e. site fidelity) and concentrated their activities within small home ranges (Table 6-1). In contrast, Peale's dolphins in both study areas exhibited no, or only limited site fidelity, and at least some individuals likely ranged beyond the boundaries of the study areas. However, individuals of both species were not identified unambiguously in both study areas (spaced at least 65 km apart) suggesting limited (if any) interchange among local dolphin populations over small spatial scales, at least during the summer (i.e. peak breeding season).

Documented alongshore ranges of both species were similar to those of photo-identified Hector's dolphins (Bräger *et al.* 2002), and satellite-tagged Heaviside's dolphins (Elwen *et al.* in press). Seasonal alongshore movements of Commerson's dolphins occur over much larger distances (> 200 km) than those of their congeners and might reflect seasonally variable food supply in the study areas along the open coast (Coscarella 2005). Seasonal alongshore movements of similar distances have also been documented for photo-identified dusky dolphins off the South Island of New Zealand (Markowitz 2004). Seasonal alongshore or inshore-offshore movements have not yet been investigated in Chilean dolphins or Peale's dolphins, but have been hypothesized to occur in response to movements of potential prey species (Crovetto and Medina 1991, Goodall *et al.* 1997). Tentative evidence at southern Chiloé suggests that at least Chilean dolphins inhabit the same bays and channels year-round (Chapter 2). The winter distribution of Peale's dolphins off Chiloé (and elsewhere in their range) has not yet been investigated.

In general, ranging and movement patterns in small cetaceans vary in size, usually as a function of various factors, such as body size, physiological requirements, habitat heterogeneity, prey availability and predation pressure (Connor 2000, Stevick et al. 2002). The overall ranging areas (95% utilization distribution (UD) determined via fixed Kernel estimators) of Chilean dolphins with 20 and more sightings were small compared to those of other coastal delphinids, such as inshore bottlenose dolphins (Gubbins 2002, Owen et al. 2002) or humpback dolphins (Hung and Jefferson 2004). Only the marine tucuxi, Sotalia fluviatilis, has an even smaller home range (95% UD), which seem to be linked to an abundant localized food supply in highly productive mangrove forests (Flores and Bazzalo 2004). Estuaries and bays with riverine influence and strong tidal currents, such as the bays and channels preferred by Chilean dolphins, are known for enhanced primary productivity (Navarro et al. 1993, Navarro and Jaramillo 1994) and attract fish and fish predators. Given the small-scale site fidelity and small ranging areas of individuals the local resources seem to satisfy the dolphins' energetic demands and habitat requirements. The temporally stable distribution of individually identifiable Chilean dolphins over four consecutive summers of research at southern Chiloé and the observed habitat selection patterns suggest that the distribution and occurrence of important local resources (e.g. prey) is relatively predictable and dependable across years.

The estimated size of the local population of Chilean dolphins in southern Chiloé is very small with approximately 60 individuals (95% CI 54 – 64, estimated using mark-recapture techniques), excluding calves. Given the temporally stable and spatially restricted distribution and ranging patterns of individuals the local resources might limit the number of resident dolphins using the same area (i.e. density-dependent factors). The low number of sightings of Chilean dolphins in central Chiloé could reflect a lack of suitable or preferred habitat available to them (Chapters 2 and 3). In central Chiloé estuarine areas are patchily distributed and relatively limited in size, and most of the coastal areas are subject to intense mariculture activities (see below).

Social structure and mating strategies are also known to act upon, and in turn be influenced by, ranging and distribution patterns (Wells *et al.* 1980, Owen *et al.* 2002). Chilean dolphins in southern Chiloé appear to live in a fission-fusion society where most dolphins associate, disassociate and reassociate over time with only some

individuals forming strong social bonds (Christie 2005). As the local population is rather small with its distribution centred on several bays and channels, individual dolphins are bound to interact with all members of the local population that exhibit the same ranging patterns. Foraging Chilean dolphins tend to form larger groups than those seen travelling (Chapter 2), probably to benefit from cooperative hunting and an enhanced ability to herd schooling prey. Females and calves appear to aggregate into larger (nursing?) groups towards the end of summer (i.e. calving season). As in other group living mammals (Packer *et al.* 1990, Baird and Dill 1996), there might be an optimal group size and temporally varying incentive for group formation depending on prey type and availability and reproductive benefits.

Tentative evidence has emerged from analysis of association patterns (Christie 2005) and ranging behaviour (Chapter 4) for a subdivision of the local population (defined as all dolphins using the study area) into two geographically separated communities, centred in Bahia Yaldad/ Canal Coldita and in Canales San Pedro/Guamblad, with some overlap of range occurring in southern Canal Coldita. A longer-term data set with a larger sample of individual resightings is needed to corroborate these findings of spatially defined communities, consisting of members of both sexes with relatively high site fidelity and shared habitats (sensu Rossbach and Herzing 1999). Such communities have been observed in coastal bottlenose dolphins (Wells 1991, Gubbins 2002, Urian 2002), and might also exist in Hector's dolphins (Bräger 1999). In the latter species, putative communities have been equated to local populations (Bräger 1999) based on the high degree of site fidelity of individuals, their limited movement ranges (Bräger et al. 2002), and clear mtDNA differences in populations only a few hundred kilometres apart (Pichler et al. 1998). Four regional, genetically different populations of Hector's dolphins are now recognized around the South Island of New Zealand (Pichler et al. 1998), and sub-species status has been proposed for the remnant population of Hector's (Maui's) dolphins off the North Island (Baker et al. 2002).

Given their very similar pattern of site fidelity, small ranges and associations, Chilean dolphins could be expected to exhibit genetic differences over small geographic scales analogous to those found in Hector's dolphins. Variation in habitat features might also contribute to geographic population differences, both behaviourally and genetically. Based on the genetic isolation of North Island and South Island Hector's dolphins (separated by a 30 km stretch of open water), Chilean dolphins along the open coast in the northern part of their range could be expected to be genetically distinct from those in the southern fjords (which are at least several hundred kilometres apart). Genetic studies are needed to define biological boundaries between populations based on genetic interchange and genetic diversity of spatially defined populations. Analysis of a limited number of genetic samples from the fjord region is currently underway, and preliminary results indicate a low haplotide diversity of Chilean dolphins throughout their range and potential genetic isolation at small-scales (C. Olavarria, pers. comm., 2006). Even without ready genetic evidence at hand, the small-scale ranging and habitat selection patterns coupled with very small local population sizes yield important implication for management and conservation of this species (see below).

Analysis of ranging (and association) patterns of Peale's dolphins was limited by the relatively small number of resightings (> 10) of reliably identifiable individuals. Consequently, individual ranging areas could not be determined. The more frequently seen individuals exhibited little or no site fidelity to sectors in the study areas (Chapter 4), but once identified were resighted over several austral summers. Social structure of Peale's dolphins has been described as fission-fusion society with most individuals associating only temporarily (Christie 2005). Limited observations show that at least some individuals in southern Chiloé form long-term associations that have lasted for more than four years (the duration of this study) (Christie 2005). Estimates of local population sizes were much higher for Peale's dolphins compared to Chilean dolphins, particularly in the central study area (123 Peale's dolphins, 95% CI= 97-156 in central Chiloé; 78 Peale's dolphins, 95% CI= 65 – 95 in southern Chiloé; Chapter 5). These data combined with results from habitat analysis and distribution patterns (see above, Chapters 2 + 3) suggest that the coastal waters of the eastern Chiloé Archipelago constitute important habitat for mobile population(s) of Peale's dolphins. The term population is used in the sense of geographically delineated stocks in central and southern Chiloé based on the lack of observed movements of individuals between study areas. Genetic studies have not yet been conducted with Peale's dolphins anywhere throughout their range. Thus, genetic population boundaries and differentiation between geographic regions remain unknown.

Information on genetic diversity and population differentiation is available for congeneric dusky dolphins (Harlin et al. 2003, Cassens et al. 2005) which differ from Peale's dolphins as they occur in much larger groups, often feed on mesopelagic prey over the continental shelf and exhibit large-scale seasonal movements (Würsig and Bastida 1986, Würsig et al. 1997, Markowitz et al. 2004). Genetic and photoidentification studies spanning hundreds of kilometres of the coastal waters of New Zealand have suggested geographic range expansion and a geographically structured population in dusky dolphins probably linked to stratified (sex-specific differences in) seasonal movements (Harlin et al. 2003). No conclusive evidence for genetic subdivisions was found in South American dusky dolphin populations and male-based dispersal has been hypothesized to lead to some limited gene flow between Peruvian and Argentinean populations (Cassens et al. 2005). Whether Peale's dolphins exhibit similar dispersal, movement and genetic differentiation patterns remains currently unknown. It is clear, however, from the findings of this study that Chilean dolphins and Peale's dolphins differ in many ecological and behavioural aspects. Understanding these differences of sympatric species is not only interesting from an ecological point of view but also yields important implications for population viability, management strategies and conservation actions in the nearshore environment of Chiloé, and beyond.

6.4. CONSERVATION IMPLICATIONS: TOWARDS HABITAT PROTECTION MEASURES

The findings detailed above establish important ecological baseline information which has been lacking to date, and provide the background for empirically founded recommendations for the conservation of both species. Several potential threats to the dolphins have been identified based on spatial overlap with and exposure to human activities known (or suspected) to impact cetaceans elsewhere (Chapter 2, see below). It was beyond the scope of this study to evaluate direct causal links or effect size of these potential impacts on the local dolphin populations.

The Chiloé Archipelago and the surrounding waters of the 10th Región Los Lagos have become Chile's most intensely used mariculture area, contributing over 80% of the national production (SERNAPESCA 2004). In 2004, this Region housed 273 registered salmon farms which produced 477,168 tons of farmed salmon (~ 84% of total Chilean production) and 305 shellfish farms which produced 81,741 tons of mussels and oysters (~ 77% of national production) (SERNAPESCA 2004). The intensive production and spatially extensive marine farming activities in the nearshore waters undoubtedly have been affecting the local environment (Alvial 1991, Bushmann *et al.* 1996, Soto *et al.* 2001, Miranda and Zemelman 2002, Sepúlveda *et al.* 2004, Cárdenas *et al.* 2005), including top predators such as marine mammals (Claude and Oporto 2000, Kemper *et al.* 2003, Sepúlveda and Oliva 2005). In addition, incidental entanglement of dolphins most likely occurs in fishing gear used by the artisanal fishing fleet and in shorebased gillnets set for escaped farmed salmon (Chapter 2), but systematic information on bycatch is lacking.

The potential impacts of mariculture activities on cetaceans have only recently become subject to scientific scrutiny (Würsig and Gailey 2002, Kemper *et al.* 2003). Shellfish farms have been shown to affect dolphins directly by displacing them from potentially important habitat (Ribeiro 2003, Watson-Capps and Mann 2005). Structural components, such as floats and lines, suspended at the surface and extending vertically into the water column could impede dolphin movements and impact on foraging behaviour by acting as visual or acoustic obstructions (Markowitz *et al.* 2004). Mussel farms can alter the local food web due to biochemical effects of accumulated faeces and pseudo-faeces, increased nitrogen levels, and depleted chlorophyll *a* levels within and around farms (Grange and Cole 1997, Mirto *et al.*

2000, La Rosa *et al.* 2002). Cascading effects through the food web reaching apex predators like dolphins have yet to be investigated.

Ecological effects of fish farms on the surrounding ecosystem are numerous and varied and have received much attention in recent years (Bushmann *et al.* 1996, Tovar *et al.* 2000, Holmer *et al.* 2001). Cetaceans can be impacted directly by becoming entangled and drowning in the netting from fish cages or anti-predator nets (Kemper and Gibbs 2001, Kemper *et al.* 2003). Indirect effects acting via alterations of the local food web include eutrophication; contamination with antifouling materials, antibiotics and marine debris; changes in composition of benthic assemblages; reduction in species diversity and the introduction of exotic species and diseases to the marine environment (Bushmann *et al.* 1996, Tovar *et al.* 2000). Increased noise levels due to augmented boat traffic associated with mariculture activities could disturb cetaceans (Richardson *et al.* 1995), particularly in areas where important cetacean habitat (e.g. foraging areas) and intense mariculture activities overlap.

In the absence of systematic data on any aspect of the dolphins' biology prior to the onset of intense mariculture farming it is impossible to determine the effects these ongoing and expanding activities might have been exerting on the local dolphin populations. Given the lack of pre-impact data and the uncertainty surrounding the current level of impacts, applying the precautionary principle (sensu Gray and Bewers 1996) to coastal management appears well justified. Unlike a classic management approach where action is only taken when a particular impact has been demonstrated to affect the population (e.g. causing population decline), the precautionary approach entails erring on the side of caution and conservation, without requiring scientific proof of causal effects, before allowing potentially damaging activities (Thompson et al. 2000, Hoyt 2005). Such proof can be particularly challenging to obtain for mobile long-lived animals, such as cetaceans, which per se are difficult to study and where a long-term data set is required to detect any trends in population size with reasonable statistical power (see Chapter 5). In addition, each individual impact may be sustainable or too small to detect, but the cumulative (and potentially synergistic) effects of all impacts could be having deleterious consequences for the population. Thus the potential effects of mariculture should be assessed in context with other potential impacts, such as bycatch and a proposed increase in tourism activities (see

below). For small (i.e. less than 100 animals) and geographically segregated populations like those of Chilean dolphins, the precautionary approach to management appears the best means to safeguard against serious and potentially irreversible population declines, as has been demonstrated for a similarly small and isolated population of bottlenose dolphins (Thompson *et al.* 2000).

As detailed above, Chilean dolphins and Peale's dolphins differ in their habitat use, ranging patterns and estimated local population sizes. Conservation measures need to take these differences into account to provide effective protection. Based on the results from this study the following points should be considered when formulating management strategies:

- a) Chilean dolphins and Peale's dolphins in southern and central Chiloé should be considered geographically defined populations (or units) for population monitoring (e.g. estimating abundance) and management.
- b) Population monitoring of both species should be conducted on an annual basis to ensure timely detection of trends in population size and to build a long-term data set to strengthen analysis of survival rates, movement patterns, social structure and population dynamics.
- c) Larger-scale geographic surveys are needed to better understand ranging and movement patterns of Peale's dolphins and to adjust management boundaries.
- d) Core areas for Chilean dolphins include Bahia Yaldad, northern and southern Canal Coldita, Canales San Pedro/Guamblad in southern Chiloé, and Canal Dalcahue in central Chiloé, and should be considered for the highest level of protection.
- e) Habitat conservation measures for Chilean dolphins need to encompass the entire range of the small local population at southern Chiloé. Areas of low or discontinuous use that serve as "corridors" between core areas and between putative "communities" should be included in conservation zones along with appropriate buffer zones around the full ranges.

- f) Core areas for Peale's dolphins include the south-eastern shores of Isla Coldita, western and southern shores of Isla Laitec and the southern shallow shoals of Isla Cailin (southern Chiloé), and should be considered for the highest level of protection. In central Chiloé important areas are centred in Canal Dalcahue, the shores of Canal Hudson and Estuario Castro.
- g) Additional observations of Burmeister's porpoises (*Phoecena spinipinnis*) suggest that only areas in central Chiloé constitute important habitat for this species. Canal Hudson and the western part of Canal Dalcahue appear to be particularly important to a small group of apparently resident Burmeister's porpoises (Chapter 2).

The development of long-term conservation objectives and management strategies based on the legal framework that is in place in Chile will be one of the most pressing next steps. There are no specific laws targeted at cetaceans in Chile, but most marine mammals are protected from deliberate take by the "Ley de Caza" (hunting law)(Aguayo-Lobo 1999, Iriarte 1999). Aspects of habitat protection can be managed under the "Ley General de Pesca y Acuicultura" (fisheries and aquaculture law) (Aguayo-Lobo 1999, Iriarte 1999). The latter law and its regulatory amendments provide some general criteria for the establishment of marine protected areas and marine parks. Two of the three marine protected areas in place in Chile and two further proposed areas include habitat considered important for cetaceans (Anon. 2003, Hoyt 2005). The latest and largest marine protected area in Chile has been proposed for the waters off southern Chiloé and is mainly targeted at the protection of a recently documented feeding ground of blue whales, Balaenoptera musculus, (Hucke-Gaete et al. 2004, Langman 2005). Outer boundaries and the definition of different usage zones are currently under debate. In addition to the more open water habitat of blue whales, the proposed area is envisaged to encompass coastal waters relevant to small cetaceans such as Chilean dolphins, Peale's dolphins and Burmeister's porpoises (Hoyt 2005). As part of the responsibility of the regional government a coastal management plan for Chiloé has also been under revision for several years. This plan entails, at least on paper, fine-scale definitions of different usage zones, including industrial (e.g. mariculture), tourism, fisheries, marine invertebrate extraction and conservation zones (Anon. 2001). Identifying critical

habitat for cetaceans, i.e. crucial core areas, constitutes important first steps towards good management of marine protected areas aimed at the protection of a wide range of marine taxa with cetaceans as possible indicator¹ species (Hooker and Gerber 2004, Hoyt 2005).

This study is the only one to date to provide systematic information on the critical habitat of small cetaceans in the coastal Chiloé Archipelago. The identified areas are also important to a variety of other marine and estuarine organisms spanning the breadth of taxa from benthic invertebrates to fish, sea birds and other marine mammals (i.e. pinnipeds and otters). Unfortunately only little and localised scientific information is available on the distribution, abundance, or community composition of most other marine organisms. As information about research on other ecosystem components is forthcoming, this should be incorporated in the consideration of conservation zone boundaries. In the interim, dolphins as apex predators might serve as charismatic flagship species (terminology sensu Simberloff 1998) and advocates for urgent conservation actions in an already heavily exploited, impacted and rapidly changing coastal environment. Habitat protection measures should not only provide benefits to the dolphins, but also to the local people whose livelihood largely depends on the use of coastal marine resources and a healthy marine environment. Ultimately, conservation benefits in the coastal waters are likely to depend on the greater vision of policymakers in realizing the benefits of favouring long-term sustainability over short-term economic profit.

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¹ Indicator species (*sensu* Simberloff 1998) are those species whose presence or abundance is used to characterize a particular habitat or biological community or reflect ecosystem health.

6.5. DOLPHIN TOURISM, ENVIRONMENTAL EDUCATION AND CAPACITY BUILDING

Cetaceans have recognized educational, scientific and economic value (Hoyt 2002). Their need for large conservation areas may provide a key to protecting marine habitats and to bringing large new areas under conservation management (Hoyt 2005). Some of the frequently emphasized alternatives to exploitative marine resource use are ecotourism ventures, such as whale-and-dolphin watching tours. Marine tourism operations, particularly those targeting charismatic megafauna such as cetaceans, have transformed many coastal communities world-wide (Hoyt 2002). The well-publicised and high-profile "discovery" of important blue whale habitat south of Chiloé is envisaged to set the scene for responsible whale-watching operations (Hucke-Gaete *et al.* 2004, Langman 2005) in one of the lesser developed regions in Chile.

As a spin-off, tourism interest in other cetacean species, including dolphins, is also increasing in the area. In fact the first ecotourism ventures that target Chilean dolphins and Peale's dolphins along with the rich avifauna, scenic landscape and indigenous cultural experience, are already in preparation by local people in Yaldad (M. Fuentes, pers. communication), and possibly other small coastal villages in southern Chiloé. Given the current absence of tourism infrastructure in southern Chiloé and the unstable, often inclement weather conditions (even in summer), viability of such community-run ecotourism enterprises remains to be seen. Peale's dolphins appear to be a suitable target species for dolphin-watching endeavours due to their generally boat-friendly behaviour. Chilean dolphins, however, hold limited dolphin-watching potential due to their usually boat-shy and rather elusive behaviours (Heinrich, pers. observation, Ribeiro et al. 2005). Given that the local dolphin populations are small, relatively localized and inhabit an already altered environment, additional, and potentially impacting activities should be carefully managed. At present, there are no guidelines or regulations in place for such ecotourism ventures to ensure minimal impact on the target species. Although Chilean waters are visited by 41 species of cetaceans (Aguayo-Lobo et al. 1998), whale-and-dolphin watching tours currently operate at only three sites in Chile, one targeting bottlenose dolphins in the north (Islas Chañaral, Choros and Damas), and two in the southern fjords (Región Magallanes) focussing on humpback whales, Megaptera novaeangliae, Peale's dolphins, Chilean dolphins and Commerson's dolphins.

Most people in the rural communities of Chiloé depend directly or indirectly on marine products for their livelihood, but knowledge of the marine environment is often rather poor. In many world-wide coastal areas where cetaceans are studied environmental education programs are offered to the local communities or wider general public to promote understanding and appreciation of the marine environment. As part of this study educational seminars in rural local schools and public presentations to local communities have been conducted since 2002 to seed environmental awareness among school children, make transparent the ongoing research activities, and stimulate an interest in a better understanding of the local marine ecosystem by using the dolphins as flagship species. At the time of writing of this thesis, over 150 school children and teachers from five schools in rural southern Chiloé have participated in day-long workshops, specially developed environmental games, beach excursions and presentations (Figure 6-1). It is hoped that this community-based work will help to direct changes towards good marine practice and stewardship, and ultimately culminate in more widely supported conservation actions to ensure the continued occupancy of Chilean dolphins and Peale's dolphins in the coastal waters of Chiloé.

The educational programme and field research are ongoing in their 5th and 6th year, respectively. These activities are carried forth by a dedicated team of Chilean biologists and former assistants in this research project. In fact, the field work that was instigated for this PhD thesis has also facilitated one M.Sc. thesis (Ribeiro 2003), has generated data for two Chilean undergraduate theses (Christie 2005, Fuentes 2005) and provided a training opportunity for four students on professional placements and numerous volunteers. It is hoped that the scene has been set, both in terms of establishing a suitable research protocol and capacitating qualified field personnel, for a monitoring programme that could extend into the first dedicated long-term study of the comparative ecology of Chilean dolphins and Peale's dolphins in Chile.



Figure 6-1. Small-group work with school children during an educational visit in the school of Cohaique, southern Chiloé in March 2004.

6.6. FUTURE RESEARCH

Each chapter of this thesis has posed a variety of questions and opened further research avenues. Most of the recommended conservation actions (see above, Table 6-2) require follow-up surveys and extension of the field work, both in space and time. A protocol to monitor local population sizes of Chilean dolphins using photo-identification and mark-recapture techniques is in place. Estimating population size of Peale's dolphins using the same methodology would benefit from larger-scale information on ranging and movement patterns to re-assess the size and location of the survey areas. As a longer time series of systematically collected photo-identification data becomes available, more robust estimates of survival rates (see Fuentes 2005), local abundance (Chapter 5) and ranging patterns (Chapter 4) can be obtained.

Systematic information on distribution or abundance of small cetaceans in the Chiloé Archipelago is not available outside the study areas. The proposed habitat protection measures, particularly the creation and boundary delineation of a marine protected area, require detailed information on distribution, and preferably abundance of all cetacean species in the Chiloé Archipelago, and preferably in the entire 10th Región. Thus larger-scale distribution and abundance surveys are urgently needed to quantify occurrence and distribution patterns of cetaceans using these inshore waters. Visual detection is inherently difficult for elusive and highly cryptic small cetaceans, such as Chilean dolphins or Burmeister's porpoises, as they frequently avoid boats and can only be sighted reliably in good conditions (e.g. Beaufort sea state <3). Combining visual surveys with passive acoustic monitoring techniques can provide better estimates of distribution and relative density (Fristrup and Clark 1997, Gordon and Tyack 2001, Gillespie et al. 2003, Hastie et al. 2003). Existing passive acoustic detection systems and software originally developed for harbour porpoises (*Phocoena* phocoena) (Gillespie and Chappell 2002) could be easily adapted for use with Chilean dolphins (D. Gillespie, pers. communication), the sounds of which have been characterized recently for the first time (Heinrich, unpubl. data, Götz et al. 2005). The sounds of Burmeister's porpoises and Peale's dolphins have yet to be recorded, but could be expected to match those known from their respective congeners. Given the similarity of echolocation sounds of Cephalorhynchus and Phocoena it remains to be seen whether these two species could be distinguished acoustically.

Analysis of movement, ranging and site fidelity patterns have been limited to the study areas and the summer-autumn period. Inclement weather conditions preclude dedicated larger-scale or offshore surveys outside the summer months. However, information on seasonal ranging (and possibly diving) behaviour of Chilean dolphins and Peale's dolphins could provide ecologically important information and would help to ensure that habitat protection efforts encompass the entire range of critical habitat. Although potentially invasive and expensive, transmitters attached to dolphins' dorsal fins constitute the only promising method to track dolphin movements during the winter and over a larger geographic range. A new generation of fast and light GPS Fastloc transmitters are currently being developed at the Sea Mammal Research Unit in Scotland and promise the positional accuracy and spatial fine-scale resolution that satellite transmitters have been lacking (Bryant et al. 2005). Hector's dolphins, C. hectori, and Heaviside's dolphins, C. heavisidii, have been tagged with conventional satellite tags and were tracked successfully over periods of several months with limited or no signs of tagging impacts (Stone et al. 2004, Elwen et al. in press), suggesting that a refined technique might also work for congeneric Chilean dolphins and the more robust Peale's dolphin.

The predictive power of the habitat selection models developed during this study should be tested on environmental data from other areas for which similarly collected sighting data of Chilean dolphins and Peale's dolphins could be obtained. Such a spatially independent validation approach could provide information on the generality of habitat selection patterns. If the model proves robust, it might help target future research efforts to areas of predicted occurrence in the vast expanse of the remote and logistically challenging habitat of Chilean dolphins and Peale's dolphins to the East and South of Chiloé.

Mariculture activities have been identified as potential threats to small coastal cetaceans around Chiloé. No current information on incidental mortality in fishing gear or direct take is available, but both activities are known to have impacted dolphins and porpoises, at least in the late 1980's and early 1990's, in more northerly and southerly parts of their respective ranges in Chile (Lescrauwaet and Gibbons 1994, Reyes and Oporto 1994). Bycatch has been identified as the biggest threat to congeneric species, such as Hector's dolphins in New Zealand (Pichler *et al.* 2003),

Commerson's dolphins in Argentina (Crespo *et al.* 1994, Iñiguez *et al.* 2003), dusky dolphins in Peru (VanWaerebeek *et al.* 1997, Majluf *et al.* 2002) and Argentina (Dans *et al.* 1997), and has been reported for Peale's dolphins (Crespo *et al.* 1994) and Burmeister's porpoises (VanWaerebeek *et al.* 1997, Majluf *et al.* 2002) in other parts of their ranges. Thus, it seems plausible to suspect some unquantified level of fisheries-related mortality to persist in the coastal waters around the Chiloé Archipelago. As first measure and to target further research activities it would be useful to compile information on fishing effort and distribution, gear type, target species as well as known or suspected bycatch to highlight geographic areas of potential concern in the 10th Región. Information on bycatch is not only important to assess mortality rates and population impacts, but could also provide the opportunity to obtain specimens for life history and diet analysis.

Table 6-2. Recommendations for conservation actions to ensure continued occupancy of Chilean dolphins and Peale's dolphins in the Chiloé Archipelago.

Recommendations

- 1 Establish conservation zones in the identified core areas (Canales Coldita, San Pedro, Guamblad for Chilean dolphins; southern Cailin and Laitec, Canal Dalcahue for Peale's dolphins).
- 2 Continue population monitoring in both study areas using the established tools and techniques.
- 3 Conduct larger-scale distribution and photo-identification surveys in the Chiloé Archipelago to better understand movements (especially of Peale's dolphins), and identify areas of intense use outside the study areas (e.g. test habitat preference of Chilean dolphins for other estuarine bays).
- 4 Review fisheries information and interview fishermen and local authorities to evaluate the occurrence and extent of bycatch in artisanal inshore fisheries.
- 5 Continue and expand the recently initiated environmental education programme to increase awareness of and concern for the marine environment at both the political and community level.

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Appendix I "Las toninas de Chiloé"

Morphological characteristcs for field identification of the three small cetacean species sighted in the Chiloé Archipelago. Peale's dolphins (a+b), Chilean dolphins (c+d), Burmeister's porpoises (e+f).



Appendix II – Mark distinctiveness rating

Mark distinctiveness rating:

M0 = no mark, clean fin

M1 = <u>subtle</u> mark; only visible in good photos; e.g. such as small notches, serrated edges, indentations

M2 = <u>obvious</u> mark; visible in medium to good photos; e.g. big notches, scallop cuts (round)

M3 = <u>distinct</u> mars, still visible in poor photos, such as big nicks/ cuts, missing bits of fin

Mark classification used in the descriptions:

Nick: V-shaped cut at the trailing edge (rear part) of the fin, usually classify as M3 type marks

Notch: small indentations along the trailing edge of the fin, can be wavy/long/shallow, or small but deep; usually classify as M1-M2 type marks depending on combination with other features or many notches

Scallop: shallow U-shaped cut at trailing edge (rear part) of the fin, looks like someone has scooped out the mark with a round spoon; usually classify as M2-M3 type marks depending on how deep they are and combination with other marks

Dent: a shallow indentation at the leading edge (front part) of the fin; usually classify as M1-M2 type mark

Tip/top: refers to the upper $1/3^{rd}$ of the fin **Centre**: refers to the middle $1/3^{rd}$ of the fin **Base**: refers to the lower $1/3^{rd}$ of the fin

2) Need to determine Photo Quality (PQ) for all photos!

Size of fin in full frame should be no less than 1 cm as measured on the screen (seen at 100% of original size); When photos are prepared for analysis in Finbase, the PQ evaluation gets included in the file name as last digits_PQ3.jpg

Criteria to be considered are

- fin in focus
- fin obscured by other dolphin or water or other objects
- contrast in photo (fin versus water/ background)
- angle of fin (best is only perpendicular to the boat)
- minimum size of fin (should be around 2 cm at 100% projection size)
- PQ4 = very good photo, in focus (but consider zoom factor/size of fin), at right angle, with no obstructions, and in good contrast
- PQ3 = good photo, three out of four criteria fully met (one criterium a bit compromised but still allowing M1 marks to be recognized)
- PQ2 = poor photo, two out of four criteria met only, only obvious marks can be reliable recognized, this is the poorest quality of photo to still be included in the catalog
- PQ1 = rubbish, only keep this photo if despite its very poor quality there is some obvious information on an individual dolphin in the photo, otherwise do not consider this photo any further.

Appendix II continued – Mark distinctiveness rating

Fins of Chilean dolphins illustrating the three different mark distinctiveness ratings used during the photo-identification study. The same mark type classification was used for Peale's dolphins. Only marks on the dorsal fin were considered during this study.

a) MD 1: subtle mark



b) MD 2: obvious mark



c) MD 3: distinctive mark



Appendix II continued – Photographic quality rating

Fins of the same individual Chilean dolphin (ID13- Juanita, MD2) illustrating different photographic quality ratings used during the photo-identification study. The same classification was used for Peale's dolphins.

a) PQ4: excellent



b) PQ3: good



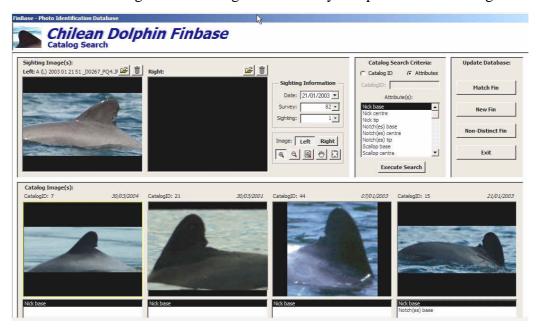
c) PQ2: poor



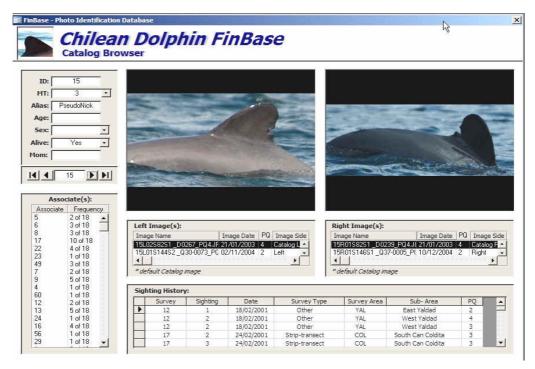
Appendix III FINBASE eutropia (example)

An interactive MS Access® database called FIINBASE was adapted from a prototype created by J. Adams and colleages (2004, available at http://www.chbr.noaa.gov/Finbase/) to match, archive and administrate the identification images. Example shown for Chilean dolphin Finbase.

a) Interface for matching a new image (top left) to potential candidate IDs from the database. Candidate images are presented based on user-selected criteria. Match is made by eye by the user. Note that each candidate image can be enlarged and directly compared with the image to be matched.

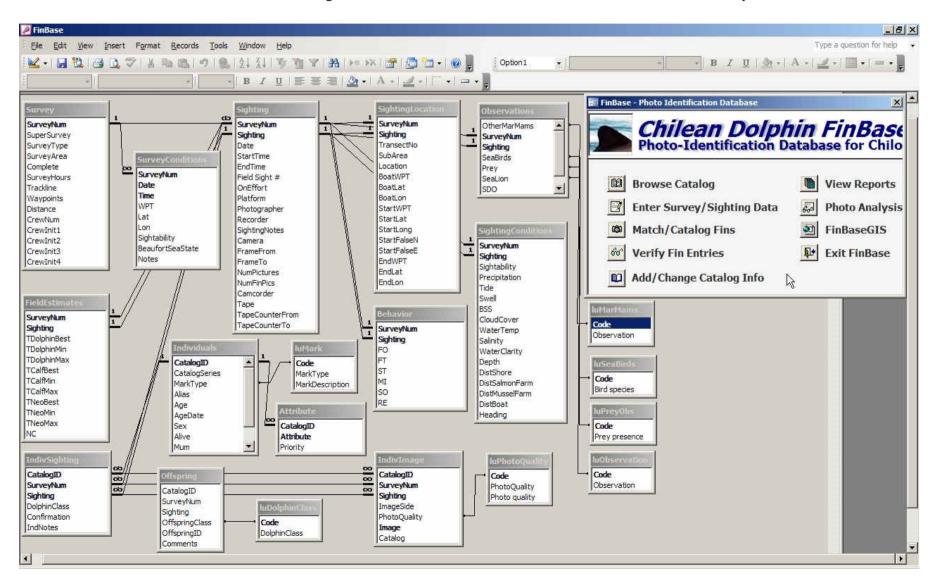


b) Catalogue interface presenting summary sighting information for individual ID15. All images of this particular individual in the catalogue can be viewed in this interface along with the corresponding information about a particular sighting. A separate mask exists for each individual in the database.



Appendix III continued FINBASE eutropia (example)

Internal database structure of FINBASE showing links between tables where data are stored. Inset: Finbase eutropia, main menue.



Appendix IV Gender determination in Chilean dolphins

Sexual dimorphism in the colouration around the genital patch allows to determine gender in Chilean dolphins. Females (a + b) have a small, roughly triangular grey patch around the anterior part of the genital slit. In males (c + d), the genital slit is surrounded by an oval grey patch. Males also have a pronounced dark grey line either side of the vent extending from the dark peduncle into the white abdominal field.



