Spatial ecology of delphinids in Queen Charlotte Sound, New Zealand: Implications for conservation management

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This thesis is dedicated to my parents. Without you, I would not exist. You have supported me during every major decision I have made without judgement. I am eternally grateful for you, your love and your support. I could not have done this without you.

I also dedicate this to the memory of my Grandma Cross. I have felt your strength along this challenging path. I miss you.

> “It is not the mountain ahead of you that wears you down, it’s the pebble in your shoe”
>
> –*Muhammad Ali (and Robert W. Service)*

Frontispiece

–Robert Frost

Abstract

Understanding species' ecological interactions and area usage depends on clear insight into their temporal and spatial patterns. Such information combined with recognition of regional human-invested interests, is crucial for developing conservation management efforts. Queen Charlotte Sound (QCS), South Island, New Zealand is a unique environment inhabited by diverse marine life, including several cetacean species. The area is subject to rising levels of anthropogenic activity inclusive of marine farming, tourism and vessel traffic. With conservation management in mind, this thesis focused on three key delphinid species: Hector's (*Cephalorhynchus hectori*), bottlenose (*Tursiops truncatus*) and dusky dolphins (*Lagenorhynchus obscurus*). Specifically, this study sought to: 1) explore long-term historical temporal and spatial trends in delphinid occurrence 2) identify recent patterns in delphinid distribution, density and range 3) investigate delphinid species' habitat use 4) initiate research of regional swim-with-dolphin tourism.

Dolphin sighting data were: 1) collated from tour vessel logbooks spanning 1995–2011 and 2) collected during dedicated surveys aboard opportunistic platforms from 2011–2014. Dynamic and static environmental variables were sourced from local government agency databases to use in analyses with both datasets. Historical delphinid presence (from logbook data) was correlated with dynamic environmental variables during two separate time frames (1995–2002; 2003–2011), using Generalized Additive Models (GAMs) and Generalized Linear Models (GLMs). Spatial patterns of these sightings were explored across temporal periods (*i.e.,* seasons; blocks of year). Dedicated survey data were used to generate kernel density estimates and to determine species' range and central range. These dolphin density estimates were correlated with static and dynamic habitat parameters using (GAMs). Spatial predictions were then generated from the resultant significant variables. Bottlenose dolphin engagement in swim-with-dolphin encounters was assessed according to several proxies using Linear Models (LMs) and GLMs.

A total of 5,295 historical records consisting of 6,055 delphinid sightings were compiled, demonstrating a long-term presence of the focal species. Of these, Hector's dolphins consistently had the highest trip encounter rate. Seasonal patterns indicated peaks in occurrence for Hector's during summer/autumn, bottlenose during autumn/winter and dusky dolphins during winter/spring. Further investigation with GAMs suggested that each species' presence was associated with a unique set or range of dynamic variables. Annual variation occurred amongst all species. During both historical time frames (1995–2002 and 2003–2011), Hector's dolphin occurrence was associated with higher SST values. Bottlenose dolphins displayed an association with mid-low SST (during 1995–2002) and with high turbidity (during 2003–2011). Dusky dolphins were influenced by low SST (during both time frames) and from 2003–2011 were also influenced by low turbidity and mid-value tidal range. Spatial patterns illustrated that Hector's and dusky dolphins have become more restricted in their use of QCS over time. Finally, logbook data indicated an increased prevalence of swim-with-dolphin encounters, suggesting an expansion of local tourism from 2004–2011.

A total of 677 dedicated opportunistic surveys were completed. These equalled 1,613 hrs of search effort spanning 263 km^2. Sighting rate calculations indicated that Hector's and bottlenose dolphins occurred more frequently than dusky dolphins. Seasonality was particularly notable amongst Hector's dolphins, whereas the sighting and encounter rates were higher during summer and autumn. The collective range of all species suggests that delphinids utilized most of QCS. However, both the range and central range of Hector's dolphins were more limited. Notable spatial patterns included peaks in Hector's dolphin density mid-Sound, during summer/autumn and peaks in bottlenose dolphin density toward the outer Sound during summer/autumn. Temporal overlap was relatively high for bottlenose and Hector's dolphins (0.67) and low for Hector's and dusky dolphins (0.22), while spatial overlap was quite low for all species combinations. The patterns explored here offer evidence of temporal and spatial multi-species habitat partitioning within QCS. This may be due to the broader ecological trends within New Zealand and is likely attributed to the availability and movement of prey.

Habitat models (GAMs) indicated a unique set of significant drivers associated with dolphin density for each species. Hector's dolphins displayed an association with dynamic and static variables (SST, fluorescence, depth, slope and distance to the closest marine farm). Dusky dolphins were influenced by the same variables, as well as year. Consistency with the earlier models in the association with SST for Hector's (higher values) and dusky dolphins (lower values) was detected. Bottlenose dolphins were only influenced by static variables (depth, slope and distance to the closest marine farm) and year. The habitat differences suggested by these models offer further insight to the ecological meaning of dolphin spatial patterns in QCS. In particular, these findings offer additional evidence of delphinid resource partitioning, specifically on a trophic scale. This likely occurred because all three species exhibit both dietary and foraging plasticity. While similarities were observed between comparable studies in other areas, the presence of some variation is likely due to unique physical and hydrographic regional characteristics. Spatial predictions that were generated from significant model variables were valuable in estimating potential locations of dolphin density beyond sighting locations, including areas that they previously occupied.

Data representing animal area usage, like those presented here, are integral to conservation management, especially amidst growing anthropogenic influences, like tourism. This first ever tourism-based study in QCS indicated bottlenose dolphins as the main target species for swim-with-dolphin activity. A total of 190 bottlenose dolphin swim encounters were assessed according to several proxies. Interactions were very short ($\bar{x}$=4.2 min), with most dolphin reactions neutral (82.9 %), suggesting animal disinterest. Swim encounters occurred regularly, irrespective of group composition or behavioural state. Furthermore, tour operators travelled great distances ($\bar{x}$=11.7 km) amongst dolphin groups to complete swim encounters, demonstrating pursuit of interaction. Collectively, these proxies suggest a lack of dolphin engagement in swim activity.

This thesis encompassed the first multi-species comprehensive assessment of delphinid density, range, habitat use and swim-with-dolphin tourism in QCS. It established a baseline of data, contributing to regional ecological knowledge. Detailed evidence of when and where three sympatric dolphin species utilized QCS was provided. Moreover, this work established an understanding of delphinid inter-specific interactions and associations with habitat variables. Applications of the findings presented here include contributions to developing comprehensive conservation management and further research. Periods and regions of high density and predicted density may be considered in regional management decisions regarding anthropogenic use of the Sound and during the design of future surveys.

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Along the way that you discover that, a PhD is much more than a research project and a written document. It is an opportunity for intellectual, emotional and personal growth that will test your limits. It is a journey; the road less travelled. The assistance and insight of supportive and generous people lend to its fruition. As such, I gratefully acknowledge those people in my life that have supported me throughout my journey, without whom, this project would not have been a reality.

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"They always say that time changes things, but you actually have to change them yourself."

–Andy Warhol

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List of Abbreviations

AIC	Akaike information criteria
ANOVA	Analysis of variance
BSS	Beaufort sea state
CI	Confidence interval
CTD	Conductivity temperature depth
df	Degrees of freedom
DOC	Department of Conservation
e.g.	*exampli gratia*, for example
ER	Encounter rate
et al.	*et alii*, and others
GAM	Generalized additive model
GIS	Geographic information system
GLM	Generalized linear model
GME	Geospatial modelling environment
GPS	Global positioning system
hp	horsepower
i.e.	*id est*, in other words
IDW	Inverse distance weighted
IUCN	International Union for Conservation of Nature
IWC	International Whaling Commission
KDE	Kernel density estimate
km	Kilometres
LM	Linear model
LINZ	Land Information New Zealand
m	Metre
MDC	Marlborough District Council
min	Minute
mm	Millimetres
MPAs	Marine protected areas
MSIMT	Marlborough Sounds Integrated Management Trust
MSRMP	Marlborough Sounds Resource Management Plan
MODIS	Moderate resolution imaging spectroradiometer

NIWA	National Institute of Water and Atmospheric Research
NOAA	National Oceanographic and Atmospheric Administration
NZ	New Zealand
NZTM	New Zealand transverse mercator
OISST	Optimum interpolation sea surface temperature
pers. comm.	Personal communication
pers. obs.	Personal observation
PoPs	Platform of opportunity
QCS	Queen Charlotte Sound, New Zealand
SCUFA	Self-contained underwater fluorescence apparatus
SD	Standard deviation
SE	Standard error
sp.	Unspecified species within a certain genus
SR	Sighting rate
SST	Sea surface temperature
subsp.	Subspecies
TER	Trip encounter rate
VIFs	Variation inflation factors
°	Degrees
°C	Degrees Celsius

Publications and presentations

The following presentations and report were produced during this PhD, based on the findings presented in this thesis.

Conferences

Cross, C.L., Clement, D., and K. A. Stockin. 2013. Queen Charlotte Sound, NZ: A region of high species diversity and significance for nationally endangered cetacea. *20th Biennial conference of the Society for Marine Mammalogy, Dunedin, NZ* (poster).

Cross, C.L., M. D. M. Pawley, R. Summers and K. A. Stockin. 2017. Characterizing the distribution and habitat of Hector's dolphins using GIS. *20th Annual conference of the Society for Conservation GIS, Monterey, CA, USA* (oral).

Cross, C.L., M. D. M. Pawley, D. Clement and K. A. Stockin. 2017. The first quantitative investigation of Hector's dolphin density and habitat use in Queen Charlotte Sound, New Zealand. *22nd Biennial conference of the Society of Marine Mammalogy, Halifax, Nova Scotia, Canada* (oral).

Administrative report to the Department of Conservation

Cross, C.L. 2013. Queen Charlotte Sound: A habitat for marine mammals. *Interim report to the Department of Conservation, Picton, New Zealand*. 36 p.

Chapter 1

General Introduction

A foggy winter day in Queen Charlotte Sound, New Zealand.

1.1 Introduction

Cetacean conservation management efforts are vital when threatened, endangered and/or endemic species are present in a region. Effective management can be very complicated, as it involves the consideration of a number of complex biological interactions. Insight into species' interactions can be accomplished by establishing an understanding of their temporal (MacLeod *et al.*, 2004) and spatial (Parra, 2006) patterns. Moreover, management efforts can benefit from understanding species' ecological drivers, which can be accomplished through the use of analytical techniques such as habitat modelling (Bailey & Thompson, 2009). In addition to patterns of animal area usage, management must consider social, economic and anthropogenic factors (Higham *et al.*, 2008). These include cetacean tourism, which has an expanding global presence with potentially adverse consequences (Christiansen *et al.*, 2014; O'Connor *et al.*, 2009).

The research presented in this thesis involved collating historical records and collecting opportunistic data in order to explore long-term spatial and temporal patterns of three delphinid species: Hector's *(Cephalorhynchus hectori hectori*), bottlenose (*Tursiops truncatus*) and dusky (*Lagenorhynchus obscurus*) dolphins, in Queen Charlotte Sound (QCS), New Zealand (NZ). Sighting data were related to environmental covariates to examine species' occurrence and habitat use. Furthermore, elements of swim-with-dolphin tourism were investigated due to interest for regional expansion of this industry.

This introductory chapter provides background literature on the focal species, animal ecological interactions and some applicable analytical techniques. Sources for cetacean data, the history of cetacean tourism and local management are also investigated. The thesis structure and rationale are provided at the end of this chapter. The goal of this thesis was to contribute to the growing base of scientific knowledge for these three dolphin species, while benefitting regional conservation management.

1.2 Focal species' biology, habitat and range

Several marine mammal species occur in QCS. These include Hector's, bottlenose, dusky and common (*Delphinus* spp.) dolphins; killer (*Orcinus orca*) and humpback (*Megaptera* *novaeangliae*) whales, as well as New Zealand fur seals (*Artocephalus forsteri*). Background on the biology and habitat of this study's focal species are explored here.

1.2.1 Hector's dolphins

Hector's dolphins are small, blunt-headed dolphins with a low, rounded dorsal fin. They are mostly grey, with distinct markings that include a white belly, black, masked appearance, black flippers, tail and dorsal fin. Life span is 19–20 years with sexual maturity at 6–9 years (Slooten, 1991). They reach 1.4 m in length and exhibit sexual dimorphism, whereas females are larger than males at all ages (Slooten, 1991). Hector's dolphins are endemic to NZ with a very limited distribution (Brager *et al.*, 2002). Their range is restricted to coastal regions of the west (Rayment *et al.*, 2011), east (Weir & Sagnol, 2015) and southern tip of the South Island (Bejder & Dawson, 2001), as well as the Marlborough Sounds (Davidson *et al.*, 2011). The subspecies Maui dolphin (*C.h.maui*) is mainly distributed along the west coast of the North Island (Derville *et al.*, 2016; Oremus *et al.*, 2012; Figure 1.1).

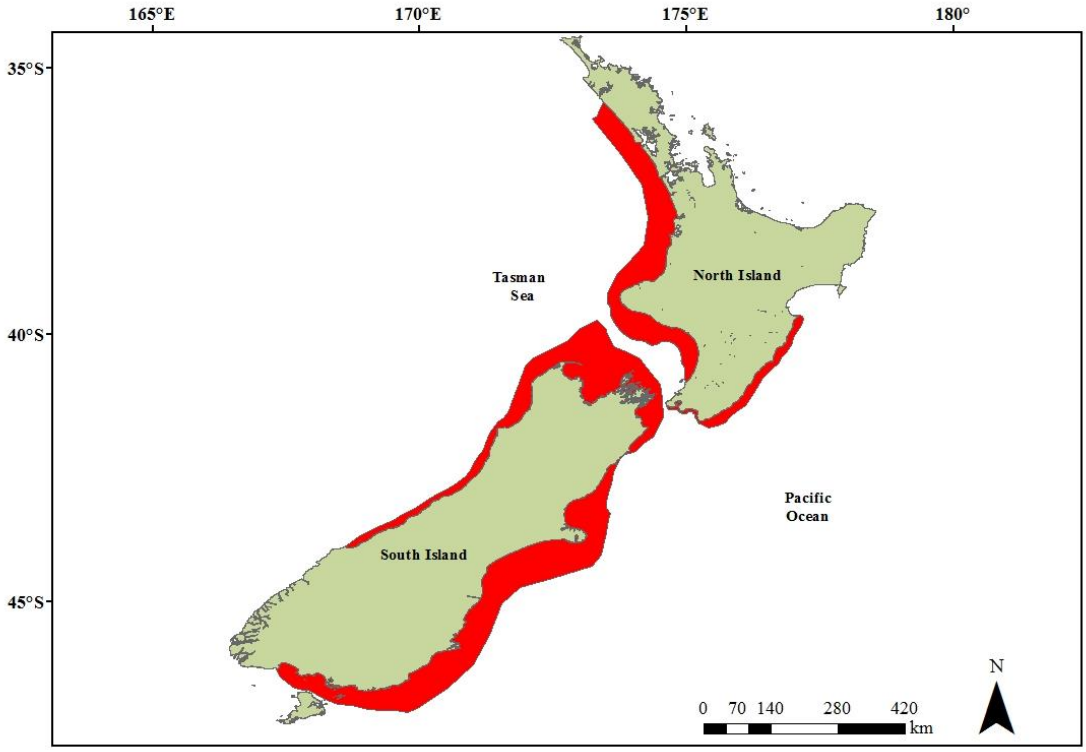


Figure 1.1. Distribution and range of Hector's (*Cephalorhynchus hectori hectori*) and Maui (*C. hectori maui*) dolphins around NZ, represented in red. The map was created from spatial data sourced from www.iucnredlist.org.

Recent surveys indicate a South Island population estimate of 14,849 (CV:11%, 05% CI 11,923 –18,492; Mackenzie & Clement, 2016).While this updated value is roughly twice that of earlier estimates (7,270; CV = 16.2%; Slooten *et al.*, 2004), the 1970 population was projected to be 29,316 (CV = 0.16; Slooten, 2007). Hector's dolphins are classified as endangered according to global and NZ threat classification systems (Baker *et al.*, 2016; Reeves *et al.*, 2013).

1.2.2 Bottlenose dolphins

Bottlenose dolphins are characterized by a robust body, curved dorsal fin, distinctively prominent melon and a short rostrum. Adult size varies geographically and ranges from 2.0–3.8 m (Wells & Scott, 2002). In general, they have a life span of 48–57 years (Wells & Scott, 1999) and reach sexual maturity between 5–14 years (Wells, 2003).

This species has a cosmopolitan distribution occupying tropical and temperate latitudes extending from 45°N to 45°S (Figure 1.2). They are considered one of the most adaptable delphinid species, inhabiting pelagic and coastal oceanic waters, as well as bays, estuaries and the lower reaches of rivers (Kenney, 1990; Reeves *et al.*, 2002). Within NZ waters, bottlenose dolphins exist as three separate geographic populations (Baker *et al.*, 2010). They range along the northeast coast of the North Island (Constantine, 2002; Dwyer *et al.*, 2016), the Marlborough Sounds (Merriman *et al.*, 2009) and Fiordland (Williams *et al.*, 1993). Gene flow between these populations is limited (Tezanos-Pinto *et al.*, 2009).

Globally, bottlenose dolphins are classified as least concern (Hammond *et al.*, 2012) due to their widespread distribution and lack of immediate threat for global decline. However, under the NZ threat classification system, this species has recently been uplisted to a Nationally Endangered status (Baker *et al.*, 2016; Baker *et al.*, 2010). Population estimates conclude 205 individuals in the Fiordland population (Currey *et al.*, 2009a), 211 (95% CI = 1995–232) in the Marlborough Sounds (Merriman *et al.*, 2009) and 424 (95% CI = 417–487) in the Northeast population (Constantine, 2002). Rationale for the Endangered status is based on evidence that indicates decline in two of the populations (Currey *et al.*, 2009b; Tezanos-Pinto *et al.*, 2013). Due to its isolation and risk of extinction, the Fiordland population meets criteria for a Critically Endangered status (Currey *et al.*, 2009a, 2011).

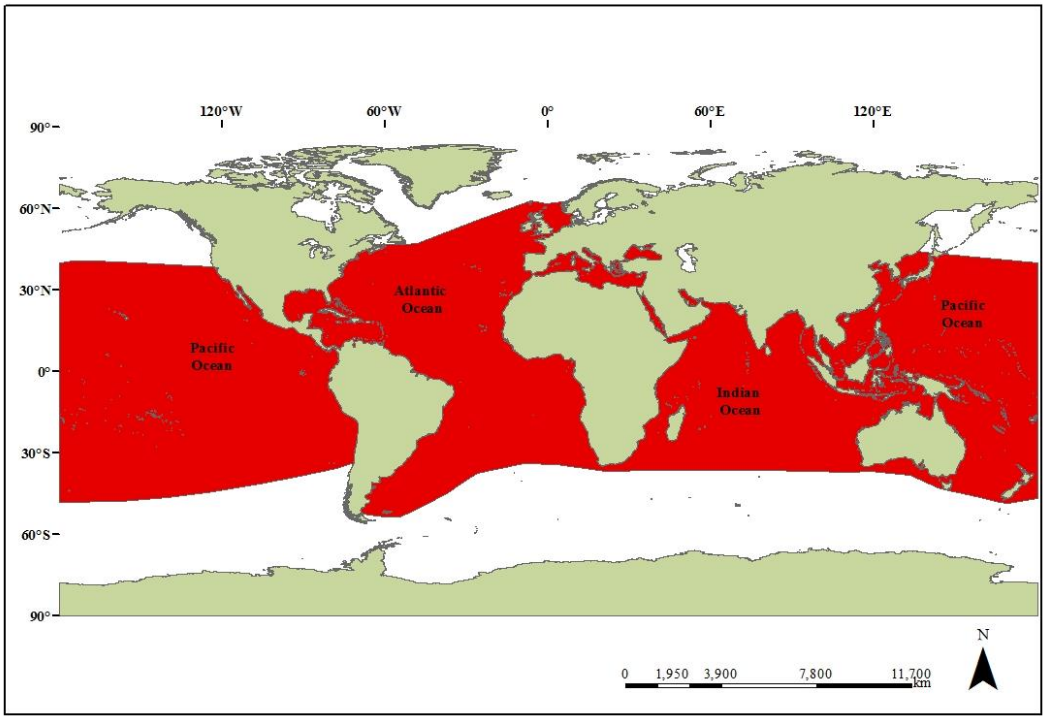


Figure 1.2. Global distribution of bottlenose dolphins (*Tursiops truncatus*) displayed in red. The map was generated from spatial data sourced from www.iucnredlist.org.

1.2.3 Dusky dolphins

Dusky dolphins are identified by distinct markings that include a dark diagonal band and two diagonal white streaks along the flank. They lack a distinct beak and have a blunt, triangular dorsal fin. Dusky dolphins are small, sexually dimorphic delphinids. In NZ, they reach lengths of about 1.8 m, have a life span of 30–36 years and become sexually mature at 7–8 years (Cipriano, 1992).

The range of dusky dolphins is restricted to the southern hemisphere including southern South America (Garaffo *et al.*, 2010), southern Africa (Elwen *et al.*, 2010) and NZ (Würsig *et al.*, 2007; Figure 1.3). In NZ, they are best understood from studies of populations located off Kaikoura and in Admiralty Bay within the Marlborough Sounds (Markowitz, 2004; Würsig *et al.*, 1997; Würsig *et al.*, 2007). Estimates indicate that up to 2,000 individuals at a time inhabit Kaikoura and the total NZ population is around 12,000–20,000 (Markowitz, 2004). On a global scale, dusky dolphins are classified as data deficient due to limited information to assess abundance and present decline (Hammond *et al.*, 2008). They were classified in the same manner within the NZ threat classification system (Baker *et al.*, 2010). However, a recent assessment has indicated that dusky dolphins in NZ are an endemic subspecies with an uncertain taxonomic status (Baker *et al.*, 2016).

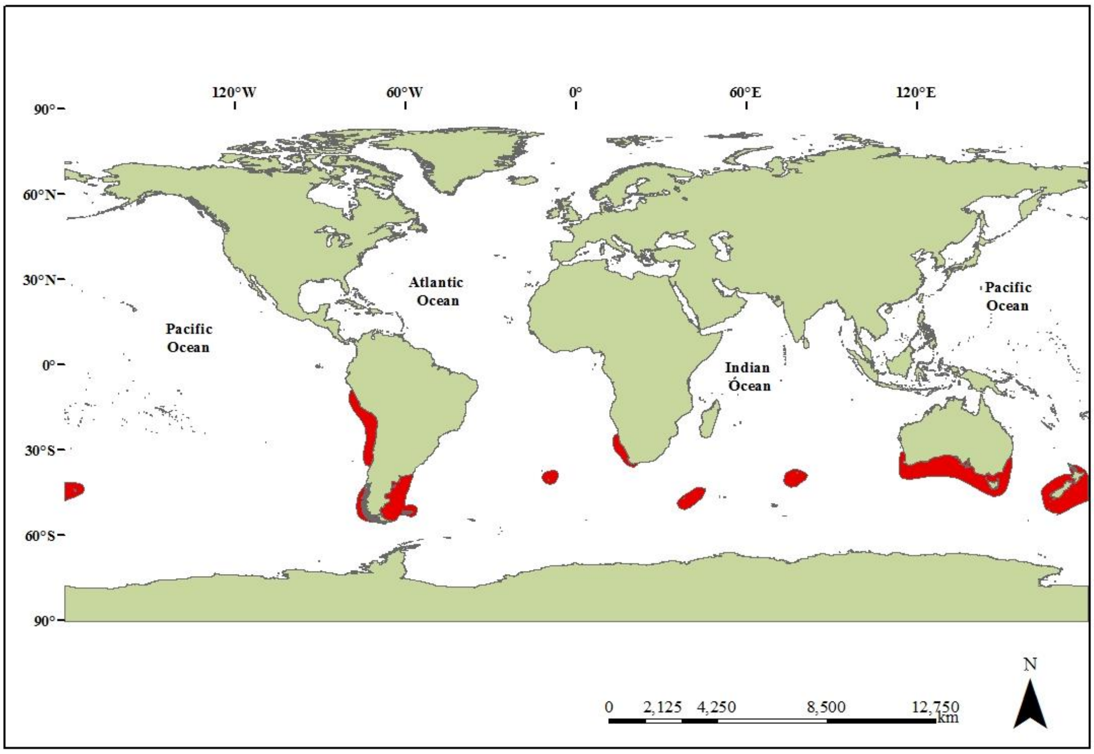


Figure 1.3. Global distribution of dusky dolphins represented in red. The map was based on spatial data sourced from www.iucnredlist.org.

An overall goal was that this thesis would provide beneficial information to conservation managers. Given the conservation status of Hector's, bottlenose and dusky dolphins, the justification to focus the present study on these three species described here, was that they were most likely subject to potential impact from growing anthropogenic influences such as tourism, vessel traffic and aquaculture (refer to section 1.6 for details). Furthermore, while other species of marine mammals do occur, Hector's, bottlenose and dusky dolphins were the most commonly observed species in the study. The fundamental objective of this thesis was to investigate the ecology of these three species in QCS. From an ecological perspective, when multiple species inhabit the same area, it is particularly interesting to explore the ways in which they utilize their shared space.

1.3 Animal interactions, sympatry and resource partitioning

Community structure and function are determined by the interactions amongst organisms (Lawlor, 1979) and take place according to one of four general categories. Mutualism occurs when both organisms benefit. Commensalism takes place when one organism benefits at no loss to the other. Predation arises when one organism benefits at a cost to the other. Finally, competition results in a cost to one or both organisms. These relationships can be complex and emerge in a variety of forms.

Examples of each interaction can be found in the terrestrial realm. Mutualism occurs through animal dispersal of seeds and pollination of plants. Commensalism is evident amongst tiny Microhylid tree frogs that take refuge inside miniature pitcher plants (*Nepenthes ampullaria*). Predator-prey interactions occur amongst the Canadian lynx (*Lynx canadensis*) in North American forests that depends on its prey, the snowshoe hare (*Lepus americanus*; Stenseth *et al.*, 1997). Lastly, spotted hyenas (*Crocuta crocuta*) struggle to compete with lions (*Panthera leo*) for food in Namibia (Trinkel & Kastberger, 2005).

These interactions similarly occur in the marine environment. Mutualistic relationships are present amongst Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins that occur in mixed groups and benefit from protection and cooperative foraging efforts (Herzing & Johnson, 1997). Moreover, mutually beneficial interspecific social behaviour takes place amongst groups of tucuxis (*Sotalia fluviatilis*) and bottlenose dolphins (Acevedo-Guitierrez *et al.*, 2005). Pilot fish (*Naucrates doctor*) benefit by following elasmobranchs including the oceanic whitetip shark (*Pterolamiops longimanus*) for protection (Backus *et al.*, 1956). Seabirds similarly profit from coordinated foraging behaviour amongst Guiana dolphins (*Sotalia guianensis*; Rossi-Santos& Flores, 2009). Predation is apparent amongst tiger sharks (*Galacerdo cuvier*) that specialize on large green sea turtles (*Chelonia mydas*; Witzell, 1987) and bottlenose dolphins that prey upon smaller harbour porpoise (*Phocoena phocoena*; Wilson *et al*., 2004). Lastly, mating *Tursiops sp*. exhibit sexual aggression/scarring (Scott *et al.*, 2005) as a result of competition, while multiple Gobiodon fishes (Munday *et al.*, 2001) and numerous delphinid species (Bearzi, 2005c) display the use of shared space and/or resources.

While interspecific interactions can vary according to the aforementioned categories, competition is common (Bearzi, 2005c; Henkel, 2009; Munday *et al.*, 2001; Scott *et al.*, 2005;

Spitz *et al.*, 2006). Competition amongst sympatric (two or more species occupying the same region) species can lead to competitive exclusion (Hardin, 1960). Therefore, organisms often develop strategies to reduce competition in order to share resources, so that co-existence can occur (Roughgarden, 1976). This is accomplished by niche partitioning, which involves the division of aspects that define an organism's ecological role, or niche (Hutchinson, 1957; Pianka, 1974). Niche partitioning can take place along temporal, (the alternating use of an area), spatial (the use of different regions within an area) and/or trophic (the utilization of different prey resources) scales. The division of resources can arise in a variety of forms and are specific to each region.

Examples of division along all of these aspects can be found in the terrestrial realm. For instance, several species of *Myotis* bats in Colorado, USA, occupy the same watering hole at different times on a fine-scale basis to share a resource that could not concurrently accommodate them (Adams & Thibault, 2006). Meanwhile, spatial separation occurs amongst grizzly (*Ursus arctos*) and black (*U. americanus*) bears that associate with different landscape features (*i.e.*, terrain, vegetation and land cover) in response to competition and growing human influence (Apps *et al.*, 2006) in Golden, British Columbia, Canada. Finally, in South Africa it is observed that dietary specialization allows for the co-existence of sympatric bat-eared foxes (*Otocyon megalotis*) and black-backed jackals (*Canis mesomelas*), while the jackals and cape foxes (*Vulpes chama*) display spatial, temporal and dietary partitioning in order to co-exist (Kamler *et al.*, 2012).

Niche partitioning similarly arises in a number of interesting forms in the marine environment. For example, young juvenile elephant seals (*Mirounga leonina*) on Macquarie Island, Tasmania, Australia, spend more time in some regions than older ones, allowing for temporal (as well as spatial) segregation amongst different age groups (Field *et al.*, 2005). Additionally, in the U.S. Virgin Islands, two shark species utilize varying regions of a particular bay. Blacktip sharks (*Carcharhinus limbatus*) use a wide extent, while lemon sharks (*Negaprion brevirostris*) remain more confined to the mangrove-lined seagrass habitat (DeAngelis *et al.*, 2008). Lastly, sympatric New Zealand (*Arctocephalus forsteri*) and Australian (*A. pusilus*) fur seals along the south coast of Kangaroo Island, Australia display prey specialization amongst sex and age groups to maximize co-existence and ultimately, their survival in this shared space (Page *et al.*, 2005).

1.3.1 Why investigate these interactions?

The research in the aforementioned examples provide evidence that organisms interact in a number of different ways. Species have developed a diverse range of adaptations as strategies to support co-existence amongst other organisms in dynamic surroundings. Knowledge of such interesting ecological adaptations can be applied toward spatial planning (Opdam *et al.*, 2001) and marine spatial planning (Agardy *et al.*, 2011) in efforts to improve conservation efforts and mitigate growing human influences amongst shared space (Halpern *et al.*, 2008b). For example, amidst a number of anthropogenic influences including offshore activities and vessel traffic, about 1/3 of the Great Barrier Reef has been allocated as no-take zones. This was part of the plan to conserve natural resources within the reef, while considering human needs (Fernandes *et al.*, 2005). Likewise, an evolving plan within Belgian waters exists. This involves the identification of areas inhabited by rare species and the future establishment of legal zoning to protect biodiversity levels amongst expanding human usage, such as shipping and fisheries (Douvere *et al.*, 2007).

Accordingly, by exploring Hector’s, bottlenose and dusky dolphin spatial and temporal patterns in QCS, insight may be gained into their ecological adaptations to this particular region of NZ. These investigations are critical since limited regional research has been conducted collectively on these three delphinid species, despite growing anthropogenic use. Knowledge of their patterns and habitat utilization may be incorporated into area management within QCS and ultimately benefit species’ conservation efforts.

1.4 Survey and data sources

To detect the presence of niche partitioning and better understand animal usage of a region, animal temporal and spatial patterns can be quantified upon the collection of distribution data. Such studies are traditionally conducted via dedicated systematic line transect surveys (Buckland *et al.*, 2001). For cetaceans specifically, these often take place on ships (Forney *et al.*, 2015), smaller boats (Pitchford *et al.*, 2016) or via aerial surveys (Hammond *et al.*, 2013). However, the design and implementation of unbiased, dedicated surveys are expensive, particularly in the marine environment; therefore, it is not always feasible to assess the distribution or density of all populations (Williams *et al.*, 2006a). Alternatively, the comparison of opportunistic data collected over an extended period from the same platform or platform type (*i.e.*, allowing for similar search methodologies) can be very useful for these purposes (Evans & Hammond, 2004). Such Platforms of Opportunity (PoPs) include ferries (Kiszka *et al.*, 2007), survey vessels designed for an alternate purpose (Palacios *et al.*, 2012) and tour boats (Hupman *et al.*, 2015). PoPs are being increasingly utilised for cetacean investigations on a broad range of topics including distribution patterns (Viddi *et al.*, 2010). They prove to be particularly advantageous in under-studied or rather inaccessible regions (Williams & Crosbie, 2007).

In addition to opportunistic surveys, more non-traditional data sources are becoming popular and have proven informative and beneficial. These include the use of citizen science and historical records. Citizen science involves the engagement of members of the public in scientific research. This can take place amongst local communities on a small scale basis like the collaborative efforts of students and professionals to enumerate and measure trees in a wildlife region of Washington State, USA (Galloway *et al.*, 2006). Citizen science can be applicable in larger areas as well. For instance, a standardized database on the distribution and abundance of native and invasive crab species along the Northeast coast of the United States has been established from the efforts over 1,000 volunteers (Delaney *et al.*, 2008). Moreover, expansive global networks can be developed through citizen science efforts. For example, eBird has initiated a world-wide community of bird watchers to collect bird occurrence data that is stored in a unified database accessible to scientists and conservationists alike (Sullivan *et al.*, 2009). This web-enabled program has evolved its capacities via user feedback and is an important source for bird distribution and biodiversity data (Sullivan *et al.*, 2014). The capacity for such research has been facilitated by the widespread use of technologies including GPS, sensors, smartphones and mobile applications (Newman *et al.*, 2012).

Similar to the broad capacities of citizen science effort, historical records can be accessed from a number of sources. These include natural history and museum collections (Hill *et al.*, 2012; Hoeksema *et al.*, 2011), tourism logbooks (Dahood *et al.*, 2008), amateur nature organization archives (Butler, 2003), as well as hunting (Virgos *et al.*, 2007) and professional/recreational fishing records (Last *et al.*, 2011). The use of such records includes research on animal distribution, *e.g.*, Iberian lynx (*Lynx pardinus*) in Portugal, habitat suitability, *e.g.*, jaguar (*Panthera onca*) in the southwestern United States (Hatten *et al.*, 2005), the occurrence of species decline, *e.g.*, decrease of large predatory sharks in the Mediterranean Sea (Ferretti *et al.*, 2008) and species status, *e.g.*, inferred extinction of Christmas Island pipistrelle (*Pipistrellus murrayi*) and Baiji (*Lipotes vexillifer*). Moreover, sources of ecological/environmental change such as anthropogenic influences from overfishing (Jackson *et al.*, 2001), shipping traffic (Tournadre, 2014), population growth and associated land development have been explored (Fitzpatrick & Kleegan, 2007).

In essence, data sources accessed from a range of platforms contribute to understanding patterns in animal distribution, intra/interspecific interactions and ultimately, the development of broader ecological insight. Moreover, the exploration and characterization of animal habitat can be accomplished with analytical tools such as habitat modelling.

1.5 Habitat use and habitat modelling

Fundamental ecological research questions are shaped around how an animal may share space with other organisms and its interconnectedness to the environment, or what constitutes its habitat. Habitat use is defined as the way an animal utilises the collective physical and biological components in their habitat, while habitat preference refers to a disproportional use of some resources over others (Hall *et al.*, 1997). An animal's habitat may be influenced by numerous factors including the availability of prey, predator avoidance, offspring survival and anthropogenic influences (Boyd *et al.*, 2015; Heithaus & Dill, 2002; Lusseau, 2005; Mann & Watson-Capps, 2005). In the terrestrial realm, several species of land mammals in Colorado, USA, display decreased activity and occupancy levels in the presence of higher urban development (Goad *et al.*, 2014). Wading birds in the Florida Everglades, USA, demonstrate preference for shallow depth and sparse vegetation, likely linked to foraging efficiency (Lantz *et al.*, 2011).

In the marine environment, tiger shark (*Galeocerdo cuvier*) preference for a shallow seagrass habitat in Shark Bay, Western Australia, is associated with a high abundance of available prey (Heithaus *et al.*, 2002). Similarly, as top predators, marine mammals rely primarily on prey availability and foraging success, despite the influence of the other factors mentioned *e.g.*, predator avoidance, offspring survival and anthropogenic influences (Benoit-Bird *et al.*, 2013; Heithaus & Dill, 2002; Lambert *et al.*, 2014a; Mannocci *et al.*, 2014b). Since prey sampling, particularly in the marine environment is often logistically challenging, a number of obtainable and interpretable variables including sea surface temperature (SST), turbidity and bottom gradient are used as proxies to explore habitat use (Gannier & Petiau, 2006; Macleod *et al.*, 2008; Redfern *et al.*, 2006; Tepsich *et al.*, 2014; Zerbini *et al.*, 2016).

Habitat modelling is a research tool (Guisan & Zimmermann, 2000) which, in essence, numerically represents habitat preference (Wintle *et al.*, 2005). Modelling techniques have been widely used to investigate the habitat of plants (Gogol-Prokurat, 2011), terrestrial birds and mammals (Brotons *et al.*, 2004; Wintle *et al.*, 2005), as well as marine birds and mammals (Azzellino *et al.*, 2012; Bailey & Thompson, 2009; Davoren *et al.*, 2003). Models can be descriptive, whereas they define habitat associations and identify important areas (Azzellino *et al.*, 2008a; Baumgartner *et al.*, 2001; Dellabianca *et al.*, 2016; Scott *et al.*, 2010). This may contribute to the understanding of a region's biodiversity and benefit conservation planning efforts (Wintle *et al.*, 2005). Meanwhile, predictive models forecast animal abundance, density or probability of occupying a location (Boveng *et al.*, 2003; Mannocci *et al.*, 2014b; Redfern *et al.*, 2017).

A range of modelling techniques has been developed. Data availability will determine which methods are appropriate. Categories of data include presence-only or presence-absence data (Brotons *et al.*, 2004; Gormley *et al.*, 2011). Furthermore, models can take into account not only the presence of animals or plants (Garaffo *et al.*, 2010), but also the count of individuals at a specific location (Mannocci *et al.*, 2014a). Moreover, techniques and adaptations have been developed to address regions with sparse data (Cunningham & Lindenmayer, 2005). Presence-only techniques include Ecological-Niche Factor Analysis which calculates suitability based on how the species mean and variance differ from the global mean and variance, respectively (Hirzel *et al.*, 2002). More recently, Maximum Entropy models have been developed to determine the probability of suitable habitat in a region by combining layers of environmental and animal occurrence data according to pixel or grid (Phillips *et al.*, 2006).

While presence only methods are useful, when presence and absence data are collected, other options of data analysis are more suitable. A range of approaches have been utilised to explore habitat relationships including Analysis of Variance (ANOVA; Baumgartner *et al.*, 2001), canonical correspondence analysis (Reilly & Fiedler, 1994), classification trees (Turgeon & Rodriguez, 2005) and environmental envelope modelling (Kaschner *et al.*, 2006). Regression analysis is amongst the most common technique used for habitat modelling. This can include Linear Models (LMs), a straight-forward and commonly used technique to analyse the relationship between a response and one or more predictor variables, following a normal distribution (McCullagh & Nelder, 1989; *e.g.* Hooker *et al.*,). Generalized Linear Models (GLMs), are an extension of LMs, and also model a response variable as a function of one or more predictors (McCullagh & Nelder, 1989). However, the response can account for different types of data such as binomial or presence/absence data (Azzellino *et al.*, 2012), and Poisson or count data, *e.g.*, number of animals or sightings (Bailey & Thompson, 2009). These relationships are expressed through the use of various link functions (McCullagh & Nelder, 1989). GLMs assume a parametric, *i.e.*, linear relationship. In contrast, Generalized Additive Models (GAMs) are non-parametric extensions of GLMs, so instead of assuming linearity, a sum of smooth functions summarize the trend of the response (Hastie & Tibshirani, 1986; Hastie & Tibshirani, 1990). While GLMs may be easier and more straightforward to interpret, GAMs allow for flexibility to capture complicated ecological associations, so these may be preferred for habitat modelling (Elith & Leathwick, 2009; Redfern *et al.*, 2006). GAMs may be selected when one or more of the variables exhibit non-linearity (Guisan *et al.*, 2002; Redfern *et al.*, 2006).

This thesis utilised GAMs and GLMs to model dolphin presence (using data from historical records; refer to Ch. 2) and GAMs to model the number of dolphins (*i.e.*, dolphin count from current data; refer to Ch. 4) in response to several explanatory variables. For both of these chapters, presence and absence data were available, so regression analysis was appropriate (as opposed to various presence-only techniques). GLMs were selected for modelling the linear, binomial data used in Ch. 2. GAMs were applied (in both Ch. 2 and Ch. 4) when non-linearity was detected. Thus, the selected techniques were appropriate and applicable to investigate delphinid habitat in QCS; the first regional study of its kind. Moreover, similar modelling techniques (specifically, LMs and GLMs) were utilized elsewhere in this thesis to investigate aspects of swim with dolphin tourism (refer to Ch. 5).

1.6 Threats and anthropogenic influences

Spatial data analyses, including habitat modelling can be informative and beneficial to conservation management. This may be particularly useful in under-studied areas and for endangered species exposed to potentially harmful anthropogenic influences.

1.6.1 Threats to focal species

Cetaceans share their habitat with a growing number of human activities. As a result, in general, they face a diversity of threats including directed and incidental takes, entanglement, pollution (*e.g.*, chemical, noise and marine litter), ship/vessel strikes, military sonar, oil spills, climate change (with subsequent changes in habitat) and prey depletion (Parsons *et al.*, 2010a; Parsons *et al.*, 2010b). New Zealand delphinids, in particular, are subject to several influences that threaten their survival.

The major source of decline in Hector's dolphin population is due to interaction and entanglement with fisheries gear (Dawson & Slooten, 2005; Dawson, 1991a, 1991b; Slooten, 2007; Slooten *et al.*, 2000). Hector's dolphin distribution throughout NZ waters overlaps with gillnet fisheries (Dawson, 1991a; Slooten, 2007). Nets are made of monofilament and hang in the water. They are likely difficult for delphinids to detect, thus, entanglement can ensue, resulting in drowning and death (Dawson, 1991b; Ohsumi, 1975). The population decline has compounding threats including limited gene flow (Hamner *et al.*, 2012; Pichler, 2002; Pichler & Baker, 2000). This can affect genetic diversity and problems such as inbreeding, thus, threatening healthy reproduction and long-term survival of the species (Hamner *et al.*, 2012; Pichler, 2002). Moreover, Hector's dolphins are subject to chemical pollutants (Dawson & Slooten, 1993), namely the accumulation of polychlorinated biphenyls (PCBs) and organochlorine (OC) pesticide levels (Stockin *et al.*, 2010). While the consequences of these levels in Hector's dolphins is not fully understood, these pollutants are known to affect reproduction (Bowman *et al.*, 1989; Fry, 1995).

The three populations of bottlenose dolphins around NZ (Northland, Marlborough Sounds and Fiordland) demonstrate little gene flow (Tezanos-Pinto *et al.*, 2009). This high degree of genetic isolation is a risk for this species in NZ. Low genetic diversity can lead to complications such as inbreeding, which affects birth rate, reproduction, resistance to disease and can lead to reduced growth and high extinction rates (Keller & Waller, 2002). Moreover, the decline in these separate populations could influence regional community structure (Currey *et al.*, 2009a). A concern for dusky dolphins in NZ is the marine farming industry. Admiralty Bay in the Marlborough Sounds is the focal region of NZ's green-lipped mussel (*Perna canaliculus*) farm industry. Dusky dolphins occur regularly in this region (Markowitz, 2004) and display avoidance of actual mussel farms within the bay, relative to the surrounding habitat (Markowitz *et al.*, 2004; Pearson *et al.*, 2012). This may affect movement, coordinated feeding behaviour and lead to a decline in the occurrence of this species in the region (Markowitz *et al.*, 2004; Pearson *et al.*, 2012). Furthermore, dolphin interaction with farms occur (López & Shirai, 2007) may pose the risk of physical entanglement for dusky dolphins and other delphinids.

Additional influences including vessel traffic and tourism pose potential threats common to Hector's, dusky and bottlenose dolphins within New Zealand waters. Vessel interaction can lead to death (Stone & Yoshinaga, 2000) or direct physical harm (Dwyer *et al.*, 2014). Moreover, changes to residency patterns (Lusseau, 2005) and behavioural alterations can ensue (*e.g.,* decreases in resting and socializing; increased erratic movement/aerial displays; Lusseau 2003, 2004, 2006). Such changes may affect social interaction and infer energetic costs (Lundquist *et al.*, 2012). Swim-with-dolphin tourism, specifically, has led to dolphin behavioural changes such as decreased resting behaviour (Constantine *et al.*, 2004; Markowitz *et al.*, 2009), tightening of dolphin groups (Bejder & Dawson, 1999; Markowitz *et al.*, 2009), dolphin avoidance of swimmers/vessels (Bejder & Dawson, 1999; Constantine, 2001) and closer approaches/dolphin tolerance to the use of auditory stimulants (Martinez *et al.*, 2012).

1.6.2 Anthropogenic influences in QCS

A number of the aforementioned anthropogenic influences occur within the study site in QCS. Marine farming of King salmon (*Oncorhynchus tshawytscha*) and green-lipped mussels has been in operation since the 1980s and late 1960s, respectively (Haworth, 2010). Salmon and mussel farms were operating at several sites within the Sound as of 2014 (pers. comm., P. Johnson, MDC, January 2014; Figure 1.4 indicates locations). Vessel traffic is also present within QCS. Ferry service between NZ's North and South Islands operates frequently. Two ferries pass through QCS and the Tory Channel for the arrival/departure in/out of Picton Harbour (refer to Figure 1.4) and collectively offer up to nine crossings daily, in each direction (Bluebridge, 2019; Interislander, 2019). Moreover, passenger and cargo ships traverse QCS and dock in the adjacent Shakespeare Bay (MDC, 2014; refer to Figure 1.4). Additionally, QCS experiences vessel traffic from recreational (Marlborough Marine Radio Association Inc., 2014) and several commercial operators (*i.e.*, water taxies; tour boats; Arrow, 2019; Beachcomber, 2019; Cougarline, 2019; Picton Water Taxis, 2019). Furthermore, slips occur along Queen Charlotte Drive that runs along the edge of QCS (refer to Figure 1.4), introducing sediment and a source of pollutants to the water (Miller, 2016). Further details regarding these influences are discussed in section 2.4.3.

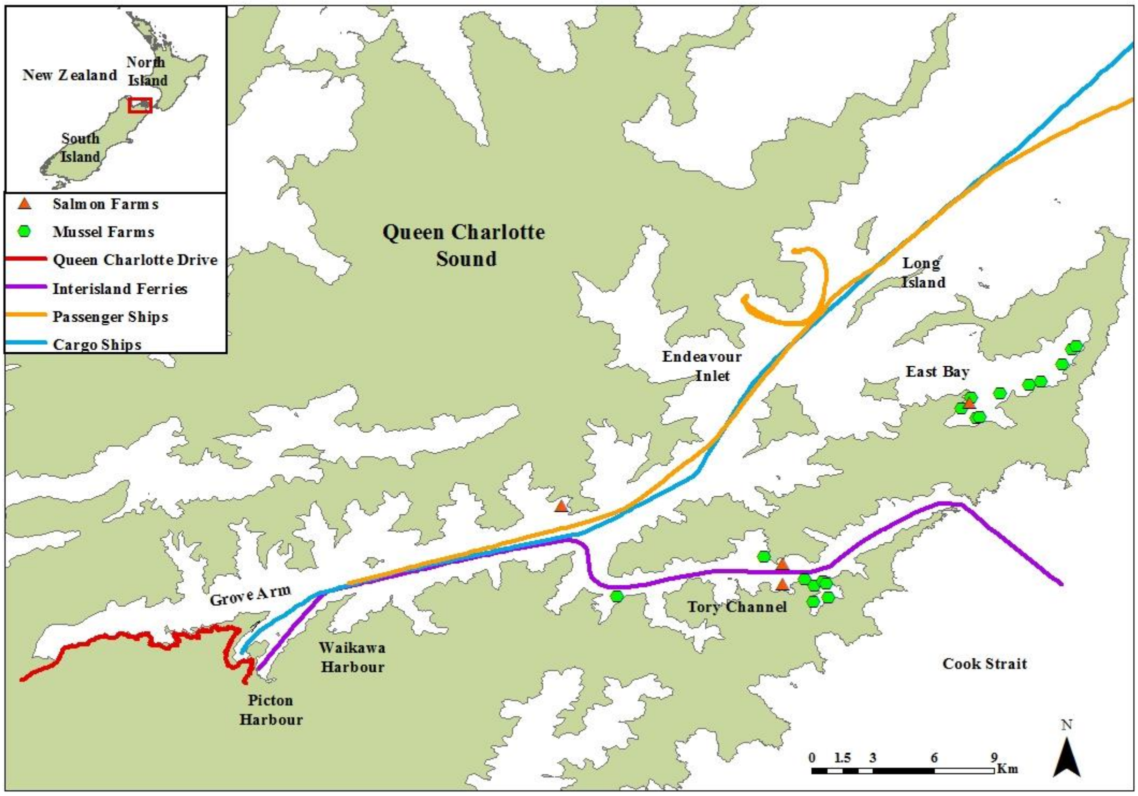


Figure 1.4. Anthropogenic influences within the study area in QCS and Tory Channel. These include King (Chinook) Salmon (*Oncorhynchus tshawytscha*) and green-lipped mussel (*Perna canaliculus*) farms; the typical pathways of commercial vessels including the interisland ferries, cargo and passenger (cruise) ships; and the location of Queen Charlotte Drive running along the Inner Sound.

1.7 Management

Growing anthropogenic influences and their associated threats dictate the need for appropriate management measures globally and locally. Species conservation is reliant upon effective management and therefore, the tactics that are employed. These can vary greatly in approach, ranging from inaction to extensive involvement (Cook *et al.*, 2010). On land, nature reserves are common; however, conservation may require additional considerations (Lindenmayer *et al.*, 2006; Scott *et al.*, 2001). Land management can include a focal species approach, which supports the conservation of a sensitive species or group of species (Lambeck, 1997). Alternatively, management can follow a holistic ecosystem approach (Tallis & Polasky, 2009). Specifically, a spatial approach involves the conservation of natural processes and landscape features through the recognition of their spatial patterns (Forman & Collinge, 1997). For example, landscape patches can be scored according to economic and biological use to maximize land use efficiency and protect biodiversity (Polasky *et al.*, 2008).

Similar to the terrestrial realm, management of the marine environment varies greatly (Day, 2002; Klein *et al.*, 2010). Management approaches include increased education efforts, the proposal of marine zoning (Day, 2002), the creation of marine protected areas (MPAs) or marine reserves (Hooker & Gerber, 2004) and the implementation of management or action plans (Bannister *et al.*, 1996; Hoyt, 2005). Ideally, management schemes will be specific to a region, maintain early and continuous involvement of all stakeholders and consider any potential future developments or known changes (Ehler, 2008; Higham *et al.*, 2008). Ecosystem-based Marine Spatial Planning (MSP) is a comprehensive step-by-step approach that considers the social, economic and ecological elements that influence a region (Foley *et al.*, 2010). This process relies on understanding and mapping the spatial and temporal diversity of the marine environment (Ehler & Douvere, 2009). MSP can overcome deficiencies (*e.g.*, poor planning/design) that may be present in some management measures (Agardy *et al.*, 2011).

Emerging efforts are being made to incorporate spatial planning into comprehensive marine and coastal management measures (Halpern *et al.*, 2012). Zoning proposals, management plans and regulations have been drafted and instituted based on MSP worldwide, including Europe, the U.S., Australia (Douvere & Ehler, 2009; Osmond *et al.*, 2010) and the high seas (Ardron *et al.*, 2008). Such efforts begin with research focused on species spatial distribution and habitat preference (Azzellino *et al.*, 2012; Bailey & Thompson, 2009; Corkeron *et al.*, 2011).

1.7.1 Marine mammal management in New Zealand

In New Zealand, the Department of Conservation (DOC) holds the legal mandate for the management of marine mammals as per the Marine Mammals Protection Regulations, which provide for the "conservation, protection and management of marine mammals" (Marine Mammals Protection Regulations, 1978, 1992). These regulations also dictate that the Minister of Conservation is responsible for management and delineation of marine mammal sanctuaries (Marine Mammals Protection Regulations, 1978). There are currently five sanctuaries within New Zealand established for the protection of Hector's dolphins. These were created by DOC based on relevant distribution, incidental catch and biological data (Dawson & Slooten, 1993). Other management measures have been taken in NZ in response to some of the current threats facing marine mammal species. For example, DOC and local operators collaborated to establish a voluntary rest period in order to limit exposure of dusky dolphins to tour vessels in Kaikoura, NZ (Duprey *et al.*, 2008). Likewise, a voluntary code of conduct was established in Doubtful Sound, NZ, that stipulates dolphin protection zones and regulates the vessel approach of dolphins (Department of Conservation, 2008).

In addition to the aforementioned conservation measures, spatially explicit cetacean research has taken place in NZ providing information to conservation managers, often with practical applications. For example, spatio-temporal mapping (which is essential for MSP) was completed for several cetacean species in the Hauraki Gulf (Dwyer *et al.*, 2016). The spatial and temporal trends of Hector's dolphins in the Banks Peninsula contributed to the design of a protected area to restrict gillnet fisheries (Rayment *et al.*, 2011; Rayment *et al.*, 2010). Moreover, habitat modelling of Maui dolphins may benefit conservation measures in the North Island west coast based on dolphin habitat use, not solely distribution (Derville *et al.*, 2016). Finally, spatial/behavioural patterns of bottlenose dolphins in Doubtful Sound led to the establishment of critical and important areas, suggesting the need for a multi-zoned sanctuary (Lusseau & Higham, 2004).

1.7.2 Local management

Important advances in marine mammal management have been made in NZ as a whole. Likewise, in QCS (and the broader Marlborough Sounds) specifically, the management scheme is evolving. A comprehensive management approach in this region has recently been developed. In 2012, the Marlborough Sounds Integrated Management Trust was established to facilitate sustainable management of QCS and the surrounding Marlborough Sounds. This integrated approach to management considers all stakeholders including industry, agency and natural resources. The trust seeks involvement from invested parties as well as specialists. Furthermore, they support research, particularly where gaps in knowledge exist (Jorgensen *et al.*, 2012; refer to section 6.2.1 for further detail). The best conservation management decisions are based on scientific evidence (Cook *et al.*, 2010), thus, the scope of this thesis will inform managers and facilitate holistic decision making. As part of this, it is critical to consider anthropogenic influences, including, but not limited to tourism.

1.8 Cetacean tourism

Worldwide, cetacean tourism has experienced considerable growth with widespread implications. Locally (in QCS), previous research has not been focused on this industry. It is critical to investigate regional tourism to begin to understand its potential influence on species' ecology.

1.8.1 History and trends

1.8.1.1 Global

Cetacean watching involves some commercial aspect to see, swim with or listen to any species of wild whale, dolphin or porpoise in its natural environment. The origins of this industry started on a small scale as a one man, one boat operation to view grey whales (*Eschrichtius robustus*) off San Diego, California, USA (Hoyt, 1984). However, whale watching has experienced extensive growth. In the early 1970s shore-based whale watching was popular and the number of vessel-based excursions began to increase (Hoyt & Parsons, 2013). By the 1980s, activities expanded beyond the U.S. to several countries including Argentina, the U.K. and NZ (Hoyt & Parsons, 2013). The most recent account indicates that a total of 119 countries worldwide are involved in some form of whale watching (O'Connor *et al.*, 2009; Figure 1.5).

Figure 1.5. Map of countries displayed in black, as of 2008 involved in marine mammal tourism. Source: O’Connor *et al*., 2009.

Cetacean tourism has experienced a 3.7% average annual growth rate from 1998–2008, which is equivalent to an estimated 12.9 million global whale watchers (O'Connor *et al.*, 2009). Not only has this industry expanded in size and distribution, but it has evolved in scope. Platforms include a wide variety of vessels including kayaks, dinghies, ferries and cruise ships; as well as aircraft (Hoyt & Parsons, 2013). Furthermore, attempts at closer interactions with cetaceans involve activities such as dolphin provisioning and swimming with dolphins and whales (Samuels *et al.*, 2000). Food provisioning emerged in Brazil, several regions of Australia and in Florida, USA, albeit illegally. Swim-with-dolphin programs have appeared in various regions globally, including Australia, NZ, the Canary Islands and Hawaii, USA (Samuels *et al.*, 2000). In Australia, the Dominican Republic and Tonga the industry has expanded to include swimming with large whales (Hoyt & Parsons, 2013).

1.8.1.2 New Zealand

Amidst rapid global growth in cetacean tourism, NZ has been the forerunner in the development of this industry (Orams, 2004). Whale watching originated in NZ in 1987 in Kaikoura, while the locations with dolphin watching and swimming quickly spread throughout the 1990s (Hoyt, 2001; Orams, 2004). The Marine Mammals Protection regulations were updated in 1992 to include the regulation of human contact and the behaviour of commercial operators around marine mammals (Marine Mammals Protection Regulations, 1992).

Regional offices of the Department of Conservation are responsible for issuing permits for commercial activity with marine mammals (Marine Mammals Protection Regulations, 1992). Full permits allow operators to approach, view and swim with dolphins. Opportunistic dolphin viewing permits allow a maximum viewing time of 10 minutes for dolphins and seals and prohibits the deviation off course for marine mammal viewing (Marine Mammals Protection Regulations, 1992). By the year 2001, a total of 75 permits had been issued at various locations throughout NZ (Neumann, 2001). Whale watching continues to grow and remains an integral aspect of NZ tourism. The estimated 546,445 whale watchers have more than doubled since 1998, with an average annual growth rate of 9%. Operators at 10 locations around the country in both the North and South Islands are currently permitted for whale watching activities, many of which conduct swim-with dolphin tours (Figure 1.6). In QCS, a permit was first issued in 1992 and tours started in 1995. Two operators in the area currently hold permits; however, further requests for permits have been submitted (pers. comm., R. Grose, November 2011).

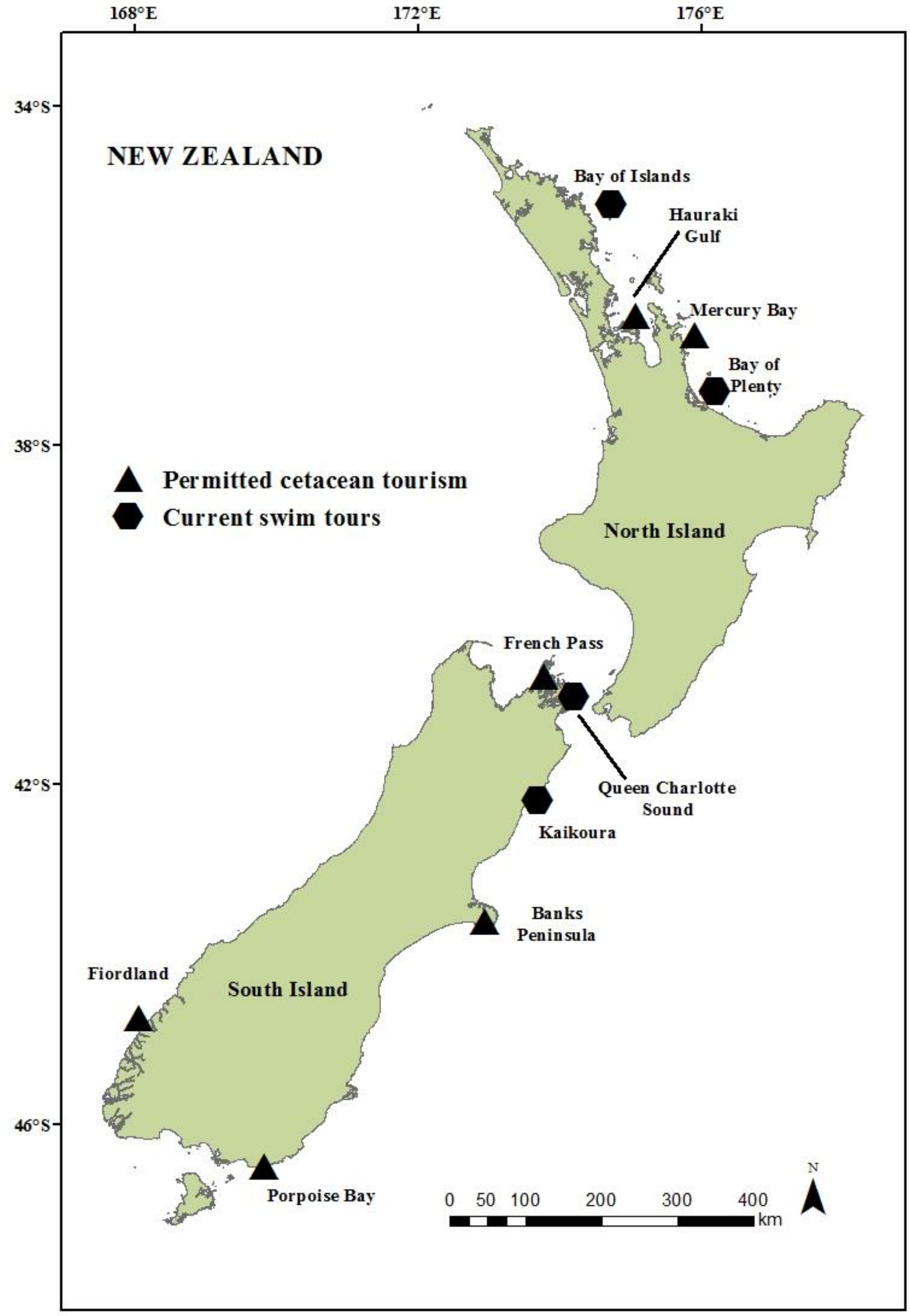


Figure 1.6. Current locations in NZ where permits to conduct cetacean tours are maintained, represented by the triangle. The hexagon represents those locations where dolphin swimming is currently taking place.

1.8.2 Cetacean tourism research

A number of advantages accompany the growth of this industry. The economic expansion has led to the creation of jobs and income, which has been particularly beneficial in developing nations (O'Connor *et al.*, 2009). An estimated 3,000 whale watch companies worldwide employ approximately 13,200 people. Globally, these operations generated $2.1 billion of income in 2008 (O'Connor *et al.*, 2009). Specifically, NZ whale watching constituted 4% of the worldwide total and generated over $80,000 of total expenditures (O'Connor *et al.*, 2009). Furthermore, operators are increasingly adding educational value to tours (Andersen & Miller, 2005; Chen, 2011). Whale watch tours have shown to encourage environmentally sustainable actions and the intention to support marine conservation (Ballantyne *et al.*, 2011; Zeppel, 2008).

In spite of its advantages, this industry is accompanied by a number of disadvantages. In fact, attention was first given to whale watching by the International Whaling Commission (IWC) in 1975 when it was deemed potentially detrimental that boats were manoeuvring amongst whales in their breeding grounds off Mexico (O'Connor *et al.*, 2009). In the early 1990s, the IWC took on the role of overseeing whale watching on an international basis and were consulted for scientific advice on matters regarding whale watching (Hoyt & Parsons, 2013). Concerns about the impacts on the target species' welfare and behaviour are also expanding as the whale watching industry grows (Orams, 2004; Steckenreuter *et al.* 2011; Steckenreuter *et al.* 2012; Stockin *et al.* 2008). As such, a number of recent studies worldwide have investigated this developing industry.

1.8.2.1 Global

Worldwide, numerous studies have shown that whale watching results in behavioural alterations amongst target species. For example, behavioural budget studies indicate decreases in foraging and resting behaviour/patterns amongst tucuxis (*Sotalia fluviatilis*) and Risso's dolphins (*Grampus griseus*) off Brazil and the Azores, respectively (Carrera *et al.*, 2008; Visser *et al.*, 2011). The close proximity of tour boats is associated with increased surface active behaviours amongst killer whales (*Orcinus orca*) around the San Juan Islands, USA and humpback whales (*Megaptera novaeangliae*) off Southeastern Australia (Noren *et al.*, 2009; Stamation *et al.*, 2010). Additionally, tour boats influence the swimming speed (Matsuda *et al.*, 2011) and direction (Mattson *et al.*, 2005) of bottlenose dolphins (*T. aduncus* and *T. truncatus*), around Japan and South Carolina, USA, respectively. Changes to vocalizations have also been observed. Bottlenose dolphin whistles occur more frequently and at a higher rate when vessels approach, off Sarasota, FL, USA (Buckstaff, 2004). Likewise, killer whales off Washington State, USA, display longer call duration when tour boats are nearby (Foote *et al.*, 2004). Behavioural changes can even have biological implications, such as changes to respiration rate and the capacity to utilise energy (Christiansen *et al.*, 2014).

1.8.2.2 New Zealand

In NZ, a growing number of tourism-based studies have been undertaken on several species. Findings of tourism-based research in NZ on the focal species of this study in Milford and Doubtful Sounds and Kaikoura indicate consequences including changes in behaviour/social interactions and residency patterns (discussed in section 1.6.1). Likewise, studies on common dolphins in the Hauraki Gulf and the Bay of Plenty show that periods of foraging/resting and foraging, respectively, are impacted by the presence of tour boats (Meissner *et al.*, 2015; Stockin *et al.*, 2008). Small groups of this species, in particular, in Mercury Bay avoid vessels (Neumann & Orams, 2006).

1.8.2.3 Swim-with-cetacean research

Studies focused specifically on cetacean swimming activities reveal similar negative consequences including behavioural changes. Threats to focal species in the Bay of Islands, Kaikoura, Porpoise Bay and Akaroa, NZ, include changes in behavioural budget, group composition and vessel/swimmer avoidance (discussed in section 1.6.1). Likewise, in Australia, bottlenose dolphins exposed to swim-with-dolphin tourism exhibit changes to their behavioural budget (Peters *et al.*, 2013) and humpback whales in Tonga display increased activity when vessels approach closely during swims (Kessler *et al.*, 2013).

1.8.3 Implications of cetacean tourism

The aforementioned research related to cetacean tourism has a number of associated implications for the target species. Displays of increased surface activities are indicative of animal disturbance (Markowitz *et al.*, 2009; Noren *et al.*, 2009; Stamation *et al.*, 2010). Avoidance (of swimmers or vessels) represents a behavioural modification suggesting animal disinterest or sensitization (Constantine, 2001). Likewise, displacement from an area suggests avoidance and animal disinterest (Lusseau, 2005). Meanwhile, neutral responses suggest habituation, which could be associated with decreased stress response. Although this may allow animals to avoid the adverse physiological effects of stress, it may also mean that animals cannot access energy stores when needed (Romero & Wikelski, 2002; Walker *et al.*, 2006).

Changes to the behavioural budget resulting in decreases in vital behaviours such as foraging and resting can have biological implications such as changes to respiration and energy utilization; ultimately affecting long-term fitness (Christiansen *et al.*, 2014; Williams *et al.*, 2006b). Lastly, acoustic changes are likely compensation to allow for communication in a noisy environment (Buckstaff, 2004; Foote *et al.*, 2004).

In light of all these potential risks, ongoing research and efficient management are crucial. Despite the history of tourism in QCS, there has been no previous dedicated research on this topic. As such, this thesis explored aspects and implications of swim-with-dolphin tourism with bottlenose dolphins in QCS to form a baseline of data. Meanwhile, the broader patterns of distribution and habitat use contributed to the ecological understanding of three delphinid species. Ultimately, the findings in this study can serve as the basis for future research and benefit the efforts of comprehensive conservation management.

1.9 Thesis structure and rationale

Comprehensive management measures in the Marlborough Sounds region are currently being initiated (refer to section 1.7.2). All-inclusive area management requires the consideration of complementary information regarding all invested parties and natural resources (Foley *et al.*, 2010). In QCS, this includes the recognition of three main delphinid species, of which two are Nationally Endangered and the third has an uncertain taxonomic status (Baker *et al.*, 2016). The region is exposed to a number of anthropogenic influences including vessel traffic, marine farming and tourism. Specifically, investigations into dolphin tourism worldwide have indicated a number of proven negative consequences for cetacean species (Christiansen *et al.*, 2014; Meissner *et al.*, 2015; Steckenreuter *et al.*, 2011). This industry is on the rise globally (O'Connor *et al.*, 2009), while local interest has been expressed by operators to obtain additional permits (pers. comm., R. Grose, November 2011).

These collective conditions in QCS create the urgent need for delphinid research. Conservation management will benefit from understanding delphinid species' temporal and spatial trends (*e.g.,* for MSP). These data are particularly important considering the lack of previous quantitative multi-species delphinid data in QCS. Likewise, current trends of swim-with-dolphin tourism are a crucial component in evolving regional management measures. Previous tourism-based studies in QCS have been non-existent despite the presence of regional dolphin tourism for nearly 20 years. This research aims to establish baseline trends in delphinid distribution, density and habitat use. Likewise, swim tourism is investigated for the first time to explore local industry characteristics and dolphin engagement in swim activities. The scope of this work strives to contribute to integrative management goals.

This thesis is comprised of four research chapters (Chapters 2–5). It is prefaced by this general introduction (Chapter 1) and concludes with an overall discussion (Chapter 6). The chapters have been written in a format as preparation for publication. As a result, some repetition exists; however, reference was made within the thesis to other sections to avoid reiteration as much as possible. Each chapter is summarised as follows:

Chapter 1 provides background information on the major themes presented in the thesis. These include a literature review focused on focal species biology and habitat; animal interactions amongst sympatric species and habitat use. Sources of cetacean data, data collection and some analytical techniques are explored. Current threats, anthropogenic influences and local management issues including cetacean tourism are also discussed. This chapter was written by C.L. Cross and improved by edits from K.A. Stockin.

Chapter 2 explores the advantages of employing historical sighting records through the investigation of patterns of Hector’s, bottlenose and dusky dolphin occurrence, distribution and swim tourism in QCS. Data were collated from a collection of historical tour vessel logbooks that were regularly maintained from 1995–2011. Delphinid temporal and spatial data were standardised by the number of vessel trips. Temporal trends were correlated with associated environmental data. The frequency of occurrence of dolphin swim events during tours was assessed. Sighting location data were explored using a geographic information system (GIS). C.L. Cross collated the data provided by E-Ko Tours (formerly known as Dolphinwatch & Nature Tours), with generous help from D. Pook, S. Kerr and R. White. Environmental data were generously provided by NOAA and LINZ. Suggestions on aspects of modelling provided by A.M. Meissner were incorporated. C.L. Cross analysed the data and wrote the chapter with statistical advice from M.D.M. Pawley. Edits were provided by K.A. Stockin, D.M. Clement and M.D.M. Pawley.

Chapter 3 describes and compares patterns in distribution, density and range of Hector’s, bottlenose and dusky dolphins in QCS. Data were collected year-round via opportunistic, non-systematic boat-based surveys from 2011–2014. Seasonal relative densities were assessed via comparison of dolphin encounter and sighting rates. Techniques in GIS were utilised to calculate kernel density estimates and species' range. Furthermore, species overlap was calculated. The study was designed by C.L. Cross with input from K.A. Stockin and D.M. Clement. Data collection and analyses were conducted by C.L. Cross. Advice with statistical analyses was provided by M.D. Pawley and D.M. Clement and guidance with GIS was provided by R. Summers. The chapter was written by C.L. Cross and improved by edits from M.D.M. Pawley, D.M. Clement and K.A. Stockin.

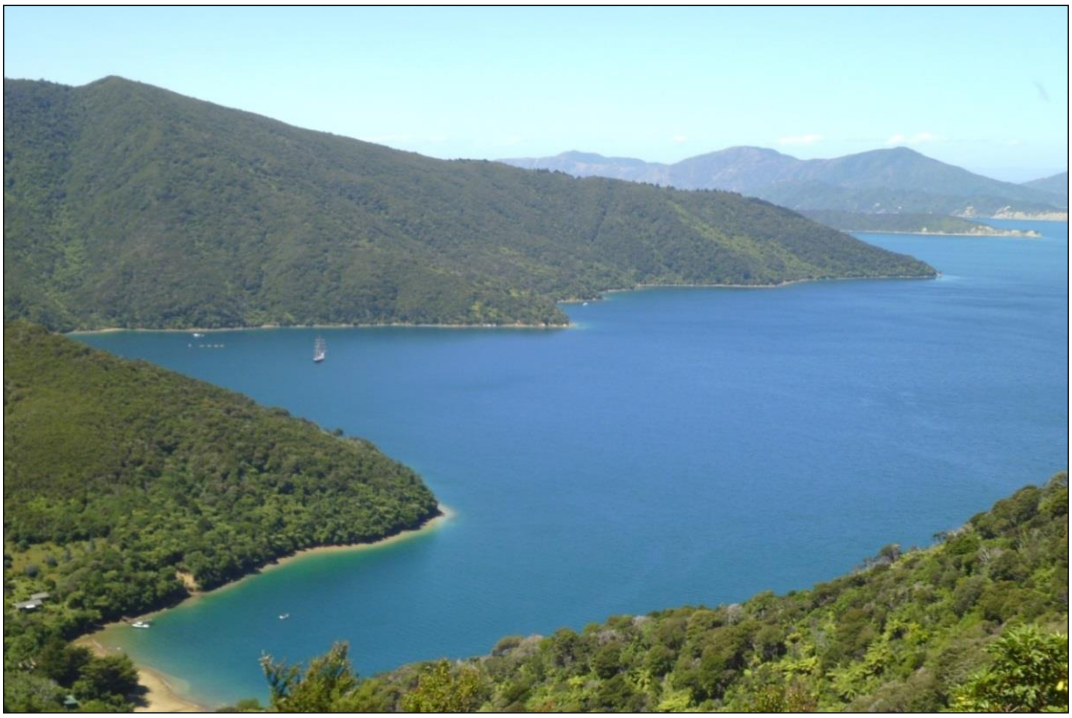
Chapter 4 explores habitat use of Hector's, bottlenose and dusky dolphins in QCS. Dynamic and static covariates associated with delphinid density were investigated using GAMs. The significant model variables were used to generate spatial predictions indicating where dolphins may occur. Environmental data were generously provided by MDC and NIWA. Data were collected and modelled by C.L. Cross. M.D.M. Pawley and L.P. Garrison were consulted for statistical advice on aspects of modelling. The chapter was written by C.L. Cross and improved by edits from M.D.M. Pawley, D.M. Clement and K.A. Stockin.

Chapter 5 examines bottlenose dolphin swim-with-dolphin tourism in QCS. As a first assessment of swim tourism in the region, the characteristics of target groups and operator techniques were explored. Furthermore, bottlenose dolphin engagement during swim-with-dolphin encounters was assessed via several proxies. C.L. Cross designed the study with help from K.A. Stockin. Statistical advice was provided by M.P.M. Pawley. Data were collected and analysed by C.L. Cross. Improvements were made as suggested by M.D.M. Pawley and K.A. Stockin.

Chapter 6 concludes by synthesising the findings of the data chapters in respect to one another and highlights the important scientific contributions of this work. Moreover, the applications of these findings to conservation management were explored. A number of explicit recommendations were outlined.

Chapter 2

The value of long-term historical records: Assessing delphinid trends in Queen Charlotte Sound, New Zealand



Panoramic view of Queen Charlotte Sound, New Zealand. Photo: Liam Wright

2.1 Introduction

The use of extended datasets can be beneficial in order to address a number of important ecological questions (Clutton-Brock & Sheldon, 2010). Through the use of long-term monitoring, complex inter-specific and ecosystem level interactions can be detected (Brown *et al.*, 2001). Long-term distribution information can be used to detect spatial patterns and larger-scale changes in area usage over time, such as the introduction or loss of populations (Bruno & Selig, 2007; Condit *et al.*, 2000). Animal abundance and population trends can be calculated, whereby the potential decline of key species can be identified (Conrad *et al.*, 2004; McPherson & Myers, 2009; Moreno *et al.*, 2007). Furthermore, it may be possible to identify anthropogenic changes and their potential impacts (Gardner *et al.*, 2003; Keating *et al.*, 2000). Despite its value, scientific monitoring on a prolonged basis is often not feasible because of a lack of resources. Opportunistic historical data, however, may be available from various sources including archives from environmental/wildlife organizations (Duffy *et al.*, 2009; Kiszka *et al.*, 2010), museum collections (Bartomeus *et al.*, 2013), sighting logs from naturalists and members of the public (Cheney *et al.*, 2013), stranding and whaling records (Torres *et al.*, 2013), fishermen's accounts (Maynou *et al.*, 2011) and vessel logbooks (Dahood *et al.*, 2008). These types of resources may help to determine trends in relative occurrence, distribution and abundance of terrestrial flora and fauna (Duffy, 2011; Palma *et al.*, 1999), as well as marine animals such as fish, turtles and cetaceans (Brito & Sousa, 2011; McClenachan *et al.*, 2012).

Data collection for cetaceans, in particular, is challenging, due to the limited time that dolphins and whales spend at the surface in often remote or inaccessible locations. Thus, if sighting records are available, they may be particularly worthwhile within this field of research. However, historical records have often been overlooked for cetacean research, due to a number of possible constraints or limitations. Firstly, historical literature may only be available as documents or archives and thus, pertinent information may be challenging and time consuming to compile. This may be compounded by barriers such as language, hand writing or unclear information (McClenachan *et al.*, 2012). Furthermore, records may be missing detailed information such as species identification, group size, vessel track data or the distinction between an absence of sightings and simply the lack of survey effort. If all sightings are not documented, due to observer or reporter bias, for example (Van Strien *et al.*, 2013), records will be incomplete and may falsely represent trends. Likewise, if sighting data is not standardized by survey effort, the ability to compare trends and perform quantitative analyses may be limited, thereby yielding results with relatively ambiguous conclusions (McPherson & Myers, 2009).

Despite some inherent disadvantages, information originating from sources other than dedicated scientific studies has proven to be valuable, particularly in under-studied regions (Maynou *et al.*, 2011). In many instances, they may be the only source of data for a region and sole ecological baseline (McPherson & Myers, 2009), offering insight into species' stock structure (McLellan *et al.*, 2002), diversity, distribution and range patterns (Fertl *et al.*, 2003; Kiszka *et al.*, 2010; Palmer *et al.*, 2014). Furthermore, such data can often be correlated with abiotic factors (Cotton *et al.*, 2005; Dahood *et al.*, 2008; Srinivasan *et al.*, 2015). These may aid in the recognition of complex ecological interactions such as resource partitioning and predator/prey dynamics that link an animal to a region (Correia *et al.*, 2015). Such information may be particularly valuable regarding the occurrence of rarely encountered and/or endangered species (Palmer *et al.*, 2014; Wang & Yang, 2010). Moreover, historical records can shed light on the presence of human influence, including evidence of vessel collision with marine mammals (Laist *et al.*, 2001) and changes in cetacean reactions to ships (Watkins, 1986). Data such as these are critical considering the recent increases in vessel traffic (Tournadre, 2014), the speed and size of ships (Kaukiainen, 2014; Laist *et al.*, 2014) and their overlapping shared space with marine mammals (Monnahan *et al.*, 2015).

It is important to recognize opportunistic data for their value and potential numerous scientific contributions (Jefferson & Schiro, 1997), since biases (*e.g.*, reporter, observer or detection) can often be identified and even accounted for (Kery *et al.*, 2010; Szabo *et al.*, 2010), so that the restrictions of the data are understood (Evans & Hammond, 2004; Pikesley *et al.*, 2012). Scientists can benefit from using the outcomes of studies based on historic literature when designing future dedicated surveys (Palmer *et al.*, 2014). As an additional benefit, such crucial information can be acquired at a minimal or zero cost, which is often one of the most challenging hurdles of undertaking scientific studies (Kiszka *et al.*, 2004), particularly in pelagic or isolated locations. Above all, these types of data may serve an integral role in the conservation management of under-studied, multi-species regions explicitly when populations are declining or status is uncertain, threatened or endangered (Azzellino *et al.*, 2008b; Esteban *et al.*, 2014; Torres *et al.*, 2013).

One such area that has a documented presence of several delphinid species (Clement *et al.*, 2001; Duffy & Brown, 1994; Markowitz, 2004; Merriman *et al.*, 2009; Webb, 1973) is Queen Charlotte Sound (QCS), located on the South Island of New Zealand (NZ). Hector's dolphins (*Cephalorhynchus hectori hectori*) are endemic to NZ, as well as globally and nationally endangered (Baker *et al.*, 2016; Reeves *et al.*, 2013). Bottlenose dolphins (*Tursiops truncatus*), a globally cosmopolitan species, are deemed endangered within NZ, while dusky dolphins (*Lagenorhynchus obscurus* subsp.) have recently been considered an endemic subspecies in NZ, despite an International Union for Conservation of Nature (IUCN) data deficient status (Baker *et al.*, 2016; refer to section 1.2 for more details on individual species). Previous investigations of Hector's, bottlenose and dusky dolphins in QCS have been limited in number and scope and have been part of research that extended beyond QCS (*i.e.,* the broader Sounds region, or coastal New Zealand). For example, Merriman *et al.*, (2009) assessed the social structure and movement patterns of bottlenose dolphins within the Marlborough Sounds. Abundance estimates were calculated for Hector's dolphins (Clement *et al.*, 2001) and exploratory surveys for dusky dolphins were conducted (Markowitz, 2004).

The Marlborough District Council (MDC) and the Department of Conservation (DOC) have since deemed QCS an "important habitat for dolphins and whales" (Council, 2016). However, spatial and temporal patterns have not been investigated over an extended time frame. Data of this nature are central in the establishment of a regional baseline. Future studies can be compared against this to gauge how delphinid use of QCS may change temporally and in response to human influences. As the access point to the South Island, QCS is frequented by inter-island ferries, as well as commercial and recreational vessels (refer to section 1.5 and Figure 1.4). Waikawa and Picton Harbours have steadily expanded in size and capacity (Newcombe & Johnston, 2016), while the number of marine farms has increased (Baines, 2012; Haworth, 2010; New Zealand King Salmon, 2016).

In light of this steady anthropogenic expansion, limited marine mammal research has been initiated in QCS. However, historical records of vessel trips and dolphin sightings were consistently maintained by tour vessel operators from 1995–2011. Access to these records allowed for the rare opportunity to investigate historical delphinid use within QCS. The specific aim of this chapter was to assess these long-term historical sighting records as a potential baseline for delphinids in QCS by exploring:

- Temporal trends of key delphinid species' occurrence and associated environmental correlates
- Spatial patterns in delphinid distribution and density
- Trends in swim-with-dolphin tourism

2.2 Methods

2.2.1 Study site

To offer a general understanding of the workings of the environmental correlates that were considered in this chapter, a basic description of the QCS catchment and influential physical oceanographic features (*i.e.,* currents and tides) are outlined here. QCS is a semi-enclosed body of water that is located along the northern tip of NZ's South Island (41°11 S, 174°11 E; Figure 2.1). Cook Strait, the body of water that separates NZ's North and South Islands, adjoins QCS at its northern entrance and via Tory Channel.

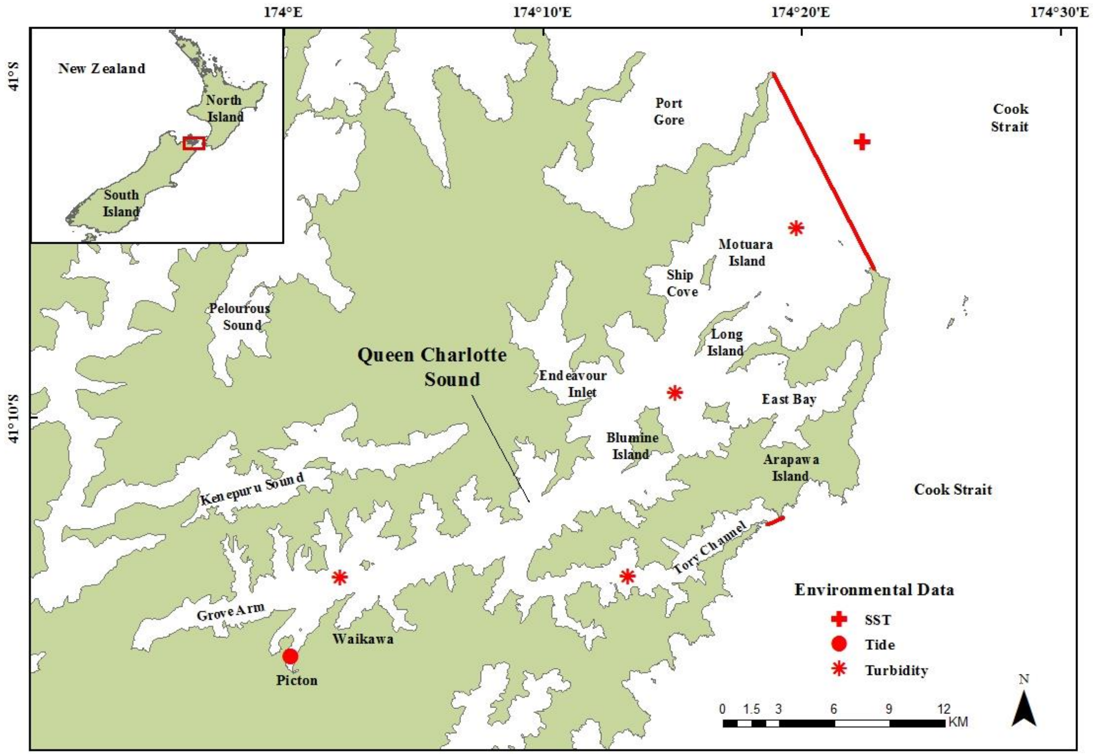


Figure 2.1. Study area within QCS and Tory Channel. The study area is delineated from the adjoining Cook Strait by the red lines at the Northern entrance of QCS and the end of Tory Channel. Sea surface temperature (SST) data were collected in Cook Strait, outside the Sound indicated by "+" and the tide data were collected inside Picton Harbour indicated by a circle. Turbidity data were sourced from up to four locations, specified by an "*"and then averaged to represent the value for the Sound as a whole.

The region is comprised of numerous bays, which are all connected by a rugged, convoluted shoreline. QCS spans ~50 km in length and ~14 km at its widest point, while Tory Channel is ~16 km long and a maximum of about 3 km. Collectively, QCS and Tory Channel cover an area of around 290 km^2. Numerous small streams, not exceeding 1 m^3s^{-1} (Hadfield *et al.*, 2014), from the surrounding 243 km^2 catchment area (Heath, 1974) feed into QCS (Heath, 1974). Since heavy rains can occur (Davidson *et al.*, 2011), erosion of sediment can take place (Fahey & Coker, 1992). An estimated 200 tons of fine sediment, derived from greywackie, argillite and schist, may enter the Sound on an annual basis, subsequently increasing the concentrations of suspended sediment (Fahey & Coker, 1992).

Three currents (the D'Urville, the East Cape and Southland currents) circulate and mix in Cook Strait, which feed into the Sound. The D'Urville Current, derived from the Westland Current is characterised by warm, saline subtropical water and moves into Cook Strait from the northwest. The East Cape and Southland Currents travel along the east coast of NZ from the north and south, respectively (Heath, 1985). Sea surface temperatures (SST) range from approximately 12°C during austral winter to approximately 18°C during austral summer (Hadfield *et al.*, 2014). The tidal cycles in NZ are unique because there are two (semi-diurnal) high and low tides and the tidal range (explained by the synchronicity between lunar and solar cycles) varies around the coast (Heath, 1985). The tides in Cook Strait are notable since they are 150° out of phase. Tidal flow in Cook Strait is highly variable and influenced by weather conditions (Heath, 1985). The tidal current in Tory Channel and the entrance of QCS are strong and taper off further within the Sound (Davidson *et al.*, 2011). Tidal current within QCS is determined by a tidal range with a maximum mean difference of about 1.5 m during spring tide (Davidson *et al.*, 2011). The unique environment within QCS supports biological diversity including a variety of macroalgae, invertebrates, finfish, as well as the aforementioned cetaceans (Davidson *et al.*, 2011).

2.2.2 Data collection and processing

A database of surveys and cetacean sightings was collated from logbooks that were recorded by three operators of one eco-tourism company from January 1995–November 2011. Trips were conducted year-round from 1995–2002 and only sporadically during winter from 2003 onwards. Data collected from trip records includes date, time of day (*i.e.,* morning = trips departing before 1200 hrs; afternoon = trips departing after 1200 hrs), weather conditions, the presence (or absence) of dolphin sighting(s), sighting location(s), species, the intention to undertake a dolphin swim encounter (2004–2011) and the occurrence of dolphin swim encounters. Weather was classified to account for poor sighting conditions characterized by rough seas and poor visibility. These were defined by phrasing which included *rain*, *bad weather*, *rough conditions* and *wind*. Furthermore, any trips that served an alternate purpose as a water taxi to transport passengers or gear within the Sound were noted. It is probable that dolphin sightings were missed during such trips as search effort likely differed from that of the eco-tours. Confidence in species identification was deemed high since tour operators were considered to have reliable familiarity with local species, as a consequence of regular encounters during daily activities (as in Meissner, 2015).

Sighting location data consisted of either Global Positioning System (GPS) coordinates or the names of the bays or regions of the Sound. In some cases, locations were referred to by local names not listed on a chart and local residents were consulted to determine their meaning. Bay names and regions were compiled and ascribed GPS coordinates by selecting the coordinates of the location associated with the centroid of the named area. Records lacking mention of *rain*, *bad weather*, *rough conditions* and *wind* assumed clear weather and therefore suitable sighting conditions. Any records missing relevant information regarding species ID or date were not considered and if swim encounters were not mentioned, they were assumed to be absent from the associated trips.

2.2.2.1 Environmental Data

Environmental variables (SST, tide and turbidity) were accessed and utilized to explore the potential ecological connections of several delphinid species to the QCS region.

2.2.2.1.1 SST

Daily SST values were sourced from National Oceanographic and Atmospheric Administration (NOAA) 1/4° optimum interpolation sea surface temperature (OISST; NOAA, 2015), which combines values derived from satellite, ship and buoy platforms on a 0.25° resolution regular grid (NOAA, 2015; Reynolds *et al.*, 2007; Appendix 2.1a). Values for the analysis were extracted daily from a grid in Cook Strait, located just outside of QCS (Figure 2.1). This was used as a proxy for SST within the Sound, as it was the closest long-term dataset to QCS available that corresponded with the sighting records.

2.2.2.1.2 Turbidity

Turbidity data were sourced from Moderate Resolution Imaging Spectroradiometer (MODIS) satellites, which collect data in 36 spectral bands every two days (Maccherone, 2016). Two variables that were available as far back as 2002 were extracted from this source, to consider for use in further analysis. The first was backscatter (a measure of total suspended matter in the water) detected at 555 nanometres m^{-1} and calibrated using a quasi-analytic algorithm (NASA, 2015; Nechad *et al.*, 2010). The second was remote sensing reflectance detected at 555 nm $steradian^{-1}$, indicative of particulate matter in the water column (NASA, 2015; Appendix 2.1b). The spatial resolution of the data is 500m x 500m, often making data collection within 1km from land inaccurate. Data were accessed from this dataset at up to four spatial locations within QCS and Tory Channel for each sampling period (Figure 2.1). For each measure of turbidity, the values from all locations were averaged to represent the mean value for QCS as a whole. Monthly averages were then calculated since data were not available each day. Initially, scatterplots were used to examine the relationship between both measures of turbidity (backscatter and reflectance data). Since these were highly correlated ($R^2 = 0.73$), reflectance data were retained as the proxy for turbidity, as it resulted in more available data points than the backscatter data.

2.2.2.1.3 Tide

Tidal predictions compiled for standard barometric pressure and adjusted for NZDT, were sourced from Land Information New Zealand (LINZ) for Picton Harbour (41°17'S 174°00'E; Figure 2.1). Tidal range is the difference between high and low tide. To calculate daily range, values (m) for low tide were subtracted from high tide (Appendix 2.1c). Since tidal current is driven by the difference in tides, or tidal range (Heath, 1974), this represents a measure of potential tidal current.

2.2.3 Data analysis

2.2.3.1 Temporal trends

One trip was considered a standard unit of effort. Survey records that indicated poor sighting conditions or a water taxi trip (previously defined) that may have biased sighting ability (Forney, 2000) were excluded from subsequent analyses. Annual and seasonal patterns were examined by calculating a trip encounter rate (TER) for each year and austral season separately for each species. These were calculated as follows:

$$\text{TER} = \frac{\text{total number of surveys each species were present}}{\text{total number of surveys}}$$

Records in which no sightings occurred were included. Calculations were separated according to time frames to account for the consistent presence of winter data from 1995–2002 and its absence thereafter, when trips did not run. Data from morning and afternoon trips were pooled together. To avoid pseudo-replication, only the initial sighting for the first trip per day represented that species' daily presence (Cooper, 2008). Surveys with no sightings (or only with sightings of other species) were used as a proxy for species' absence. Austral seasons were defined as follows: summer: December–February, autumn: March–May, winter: June–August and spring: September–November. Years were coded from December to the following November so that data in the month of December was averaged with the subsequent austral summer months, but categorised as the following calendar year.

2.2.3.2 Association with environmental correlates

Delphinid presence-absence in QCS according to daily trip (derived as explained in 2.2.3.1) was investigated in reference to the aforementioned environmental variables (refer to 2.2.2.1). Regression analyses (*e.g.,* Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) were explored because these are commonly applied to test cetacean presence in reference to one or more explanatory variables (Arcangeli *et al.*, 2016; Azzellino *et al.*, 2012; Goetz *et al.*, 2015; Marini *et al.*, 2015). GLMs model a response variable as a function of one or more predictors, assuming a parametric relationship (McCullagh & Nelder, 1989). In comparison, GAMs are data-driven, non-parametric extensions of GLMs, relying on a sum of smooth functions to summarize the response, instead of assuming linearity (Hastie & Tibshirani, 1986; Hastie & Tibshirani, 1990; Yee & Mitchell, 1991). These are appropriate when the model includes non-linear effects and are more flexible than GLMs and other model forms (Guisan *et al.*, 2002; Redfern *et al.*, 2006). Therefore, GAMs allow for the capture of complicated ecological relationships (Elith & Leathwick, 2009).

Here, the response variables (delphinid species' daily presence in QCS) were examined for linearity and homogeneity of variance, to determine the appropriate model form. Evidence of non-linearity was detected amongst at least one of the continuous explanatory variables in each model, with the exception of the Hector's dolphin model for 2003–2011. For this case, GLMs were used, whereas GAMs were used in all other cases. Errors followed a binomial distribution.

SST and tide were integrated into the database on a daily basis and turbidity was summarized monthly, as was consistently available. Sightings were sorted and coded separately by species. Variation Inflation factors (VIFs) were used to detect multicollinearity amongst the variables. Although the limit for these is not definitive (Zuur *et al.*, 2007), a cut-off value of three was chosen (Zuur *et al.*, 2009a) to exclude collinear variables for further analysis. SST and season were collinear, but SST was retained over season to explore its potential contribution to delphinid ecological understanding (Dellabianca *et al.*, 2016; Svendsen *et al.*, 2015).

Separate models were run for each species. To retain all possible variables that could be useful in explaining delphinid species' presence in QCS, the full models (Figure 2.2) were fit with a backward selection process estimating all parameters and excluding non-significant explanatory variables at each step (Goetz *et al.*, 2015). Following standard practice (Zuur *et al.*, 2007), habitat variables that were smooth terms were limited to four degrees of freedom to allow for clear biological interpretation. Results were compared using Akaike's Information Criterion (AIC) and those with the lowest AIC values were accepted. For consistency and comparability across the entire time period, only data from complete years and months available during each year were used. Separate time frames were used due to the availability of data for the parameter turbidity (and the winter season, as mentioned). Models were initially run with data year-round from 1995–2002, but without the parameter turbidity, because it was not available for a full year until 2003. Subsequent models were then re-run to include turbidity from 2003–2011, but these lacked data during the winter season (for a summary of data availability, refer to Figure 2.2). Year was treated as a continuous variable. Analyses were conducted in R version 3.2.1 (R Core Team, 2015).

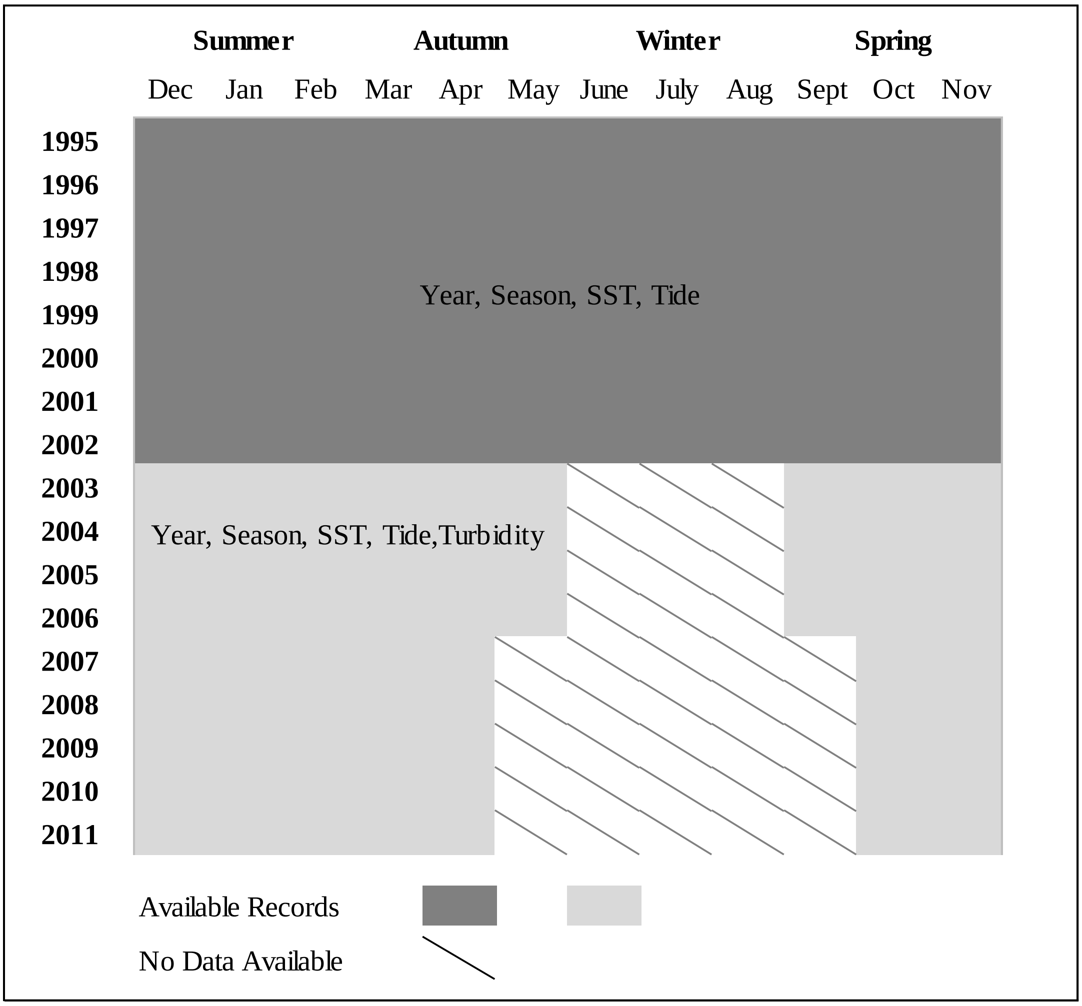


Figure 2.2. A summary of the data available from tour vessel log books and initial model variables tested for delphinid occurrence in QCS, NZ, during 1995–2011. The dark grey represents the data available from 1995–2002, including winter months and the variables year, season, SST and tide. The light grey represents the data available from 2003–2011, excluding winter months and including the variables year, season, SST, tide and turbidity. The diagonal lines represent a lack of data.

2.2.3.3 Spatial trends: distribution and density

Delphinid distribution patterns could not be explored in association with the environmental data, since it was not available at the appropriate spatial scale (*i.e.,* data represented one point or an average of the entire Sound). However, delphinid distribution and density patterns in isolation could be explored. All records including delphinid spatial location were plotted in ArcMap 10.0. Sightings were standardized in 3x3 km grid cells (refer to Figures 2.12–2.17) that spanned the collective extent of sightings within QCS. The grid cell size offered consistency with data analysis in subsequent Chapters 3 and 4. Sightings were standardized by the number of trips per time frame (*i.e*., season; block of years), so that trip encounter rates per grid cell were calculated. These calculations are based on the assumption that trips passed through all grid cells during each trip, meaning that the same number of trips was assigned to each grid cell for each time frame. This assumption was based on information regarding trip paths obtained from previous owners (pers. comm., Zoe Battersby, July, 2014). Additionally, recent GPS data collected aboard tour vessels indicated vessel pathways with similar coverage of QCS (refer to Figure 3.2) Such data standardization allowed for the consistent comparison of trip encounter rates across temporal periods. For Hector's and dusky dolphins, group size was incorporated into calculations to represent the number of animals per trip per grid cell. For bottlenose dolphin sightings that were plotted, 30% (n = 403) were missing group size estimates, prior to the year 2000. This may have been due to the operators becoming accustomed to counting larger groups of dolphins in the early years of running trips. Since this may bias comparisons, group size data were not used for these calculations and the number of sightings per trip per grid cell was calculated instead for bottlenose dolphins. Maps of trip encounter rate (animals per trip or sightings per trip) for each species were produced across the whole time period, during blocks of years (1995–1999; 2000–2005 and 2006–2011) and across seasons.

2.2.3.4 Trends in swim-with-dolphin tourism

To explore historical trends in dolphin swim tourism in QCS, several aspects of the records were examined. Firstly, to assess if there was growth within the industry, the percentage of tours with swim encounters was calculated by as follows:

$$\%\text{ tours with swims} = \frac{\text{total number of annual dolphin swim encounters}}{\text{total number of annual swim tours}}$$

Records from 2004 onwards began to indicate if a trip was an intended or dedicated “swim trip” and additionally if a swim encounter indeed took place during these trips. Therefore, to determine the likelihood that intended swim trips during this period resulted in actual swim encounters, the following equation was applied (as shown).

$$\text{success of tours} = \frac{\text{total number of actual annual dolphin swim encounters}}{\text{total number of intended annual swim tours}}$$

Finally, the dolphin species with which swim encounters took place were totalled overall and on an annual basis.

2.3 Results

Data spanned January 1995–November 2011 and included a total of 5,295 surveys (3,154 morning and 2,141 afternoon trips). A total of 6,028 delphinid sightings including species were recorded (refer to Figure 2.3). The most commonly observed species were Hector’s (n = 2,703), dusky (n = 1,676) and bottlenose (n = 1,488) dolphins. The other three species included killer whales (*Orcinus orca*), common dolphins (*Delphinus* spp.) and pilot whales (*Globicephala* spp.). Collectively these comprised less than 3% of all sightings, so data regarding these species were not further considered here.

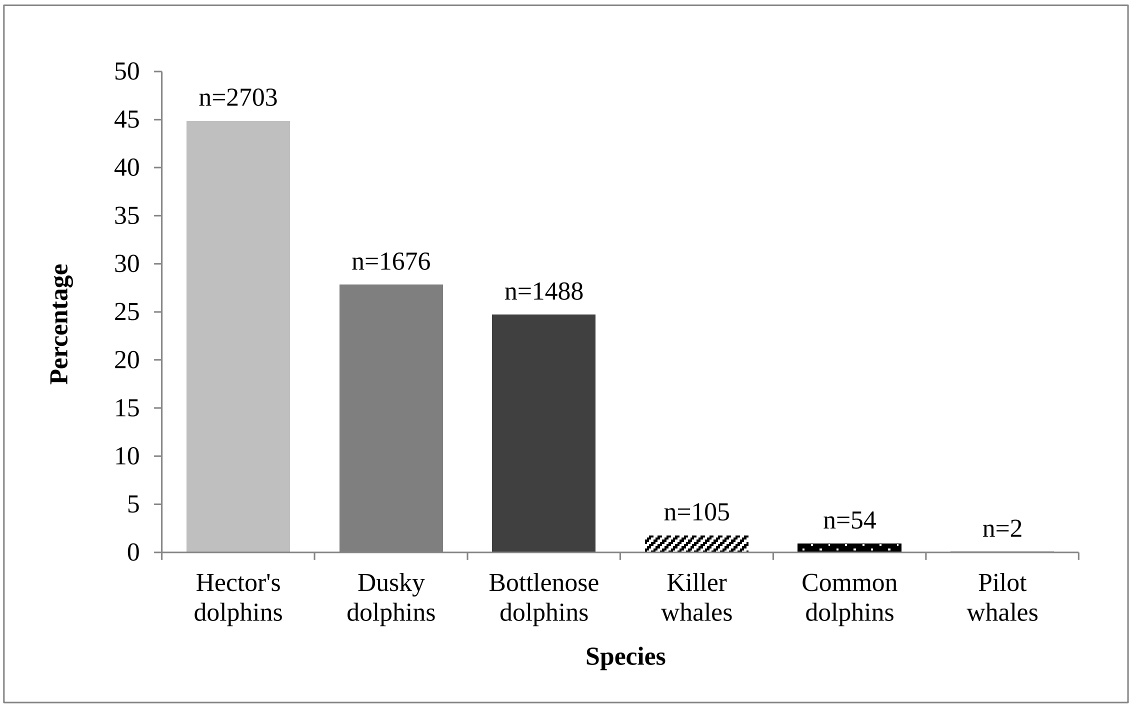


Figure 2.3. Delphinid sightings recorded in dolphin tour vessel logbooks in QCS, NZ, from 1995–2011.

2.3.1 Temporal trends

A total of 4,336 surveys remained for data analysis after surveys with poor sighting conditions or water taxi trips (both previously defined in section 2.2.2) were excluded. All three species were present during each survey year. The mean TER for each species across all years was greatest for Hector's dolphins (n = 0.42) and significantly lower for bottlenose and dusky dolphins (Table 2.1). Hector's dolphin occurrence fluctuated, with notable peaks in 1998, 2003, 2005 and 2007; while a gentle decline was observed from 2007–2011 (Figure 2.4). Bottlenose dolphin occurrence also fluctuated. A decline occurred from 1999–2005, despite a slight peak in 2004, while a steady increase from 2008 onwards took place (Figure 2.4). Dusky dolphin occurrence increased until 2002, fluctuated until a peak in 2008 and exhibited a steady decline thereafter, until 2011 (Figure 2.4). The TER calculations for the two time frames (1995–2002; 2003–2011) followed similar trends (Table 2.1). The patterns suggest that increased bottlenose dolphin occurrence was mirrored by decreased occurrence of Hector's dolphins and to a lesser degree, dusky dolphins (2003–2011). Likewise, drops in bottlenose dolphins were accompanied by peaks in the occurrence of both Hector's and dusky dolphins. Data from 1995–2002 revealed that the three species were present during all seasons. Distinct seasonality and similar patterns were observed during both time frames (Figure 2.5). The patterns suggest opposing seasonal peaks amongst the species. Peaks in bottlenose dolphin occurrence were present in autumn and winter. Occurrence increased for Hector's dolphins during summer and for dusky dolphins during spring (Figure 2.5).

Table 2.1. Trip encounter rate (TER) of delphinids in QCS, NZ, during the time frames 1995–2011, 1995–2002 and 2003–2011. Data were collected from historical tour vessel logbooks. Note that different times were due to the availability of data as displayed in Figure 2.2*.

Time Frame	Species	TER Range	Overall TER
1995 – 2011	Hector's	0.29 – 0.60	0.42
	Bottlenose	0.08 – 0.62	0.27
	Dusky	0.06 – 0.52	0.24
1995 – 2002	Hector's	0.04 – 0.58	0.34
	Bottlenose	0.14 – 0.44	0.23
	Dusky	0.06 – 0.48	0.20
2003 – 2011	Hector's	0.17 – 0.65	0.51
	Bottlenose	0.23 – 0.41	0.28
	Dusky	0.06 – 0.73	0.28

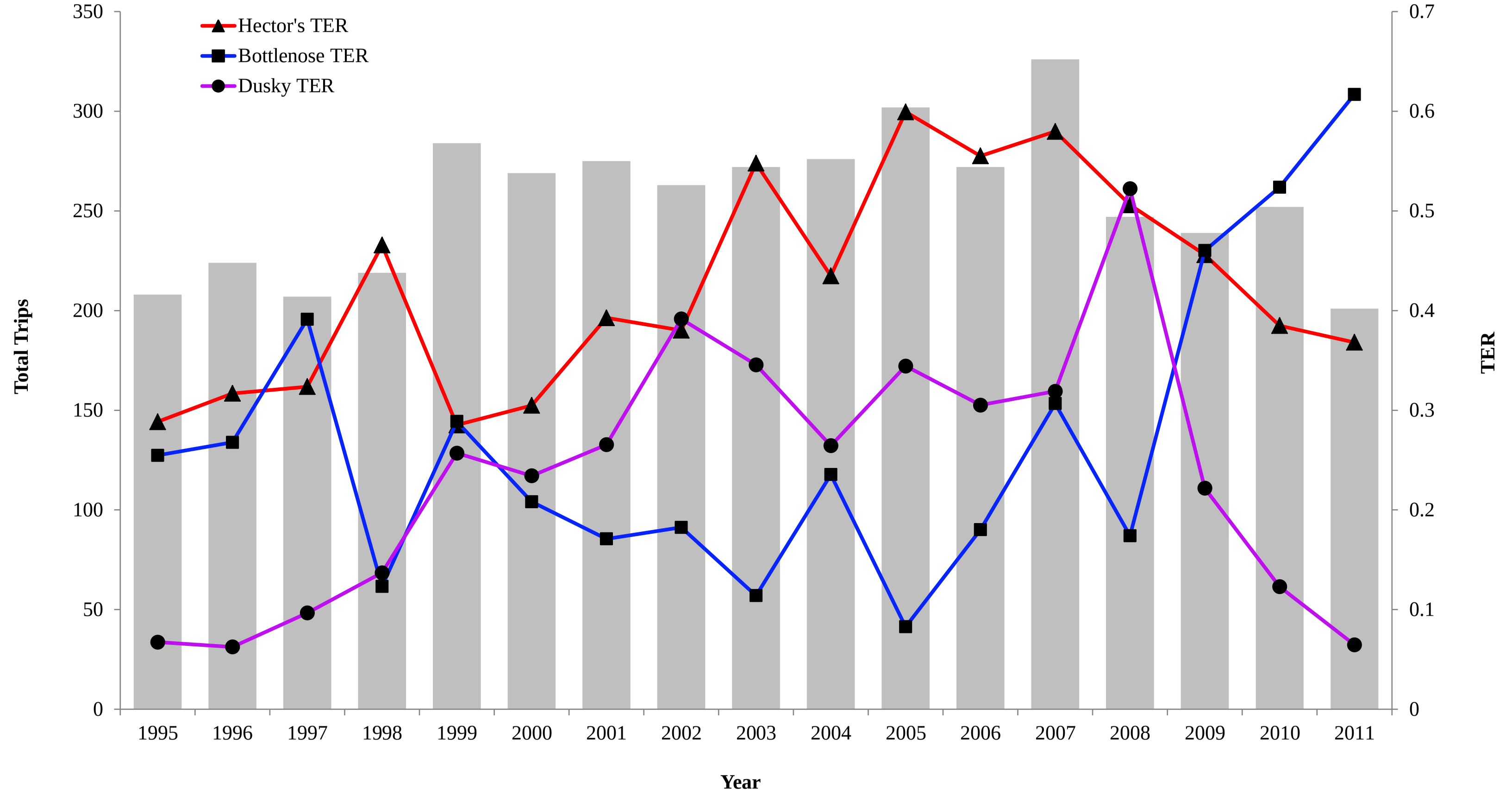
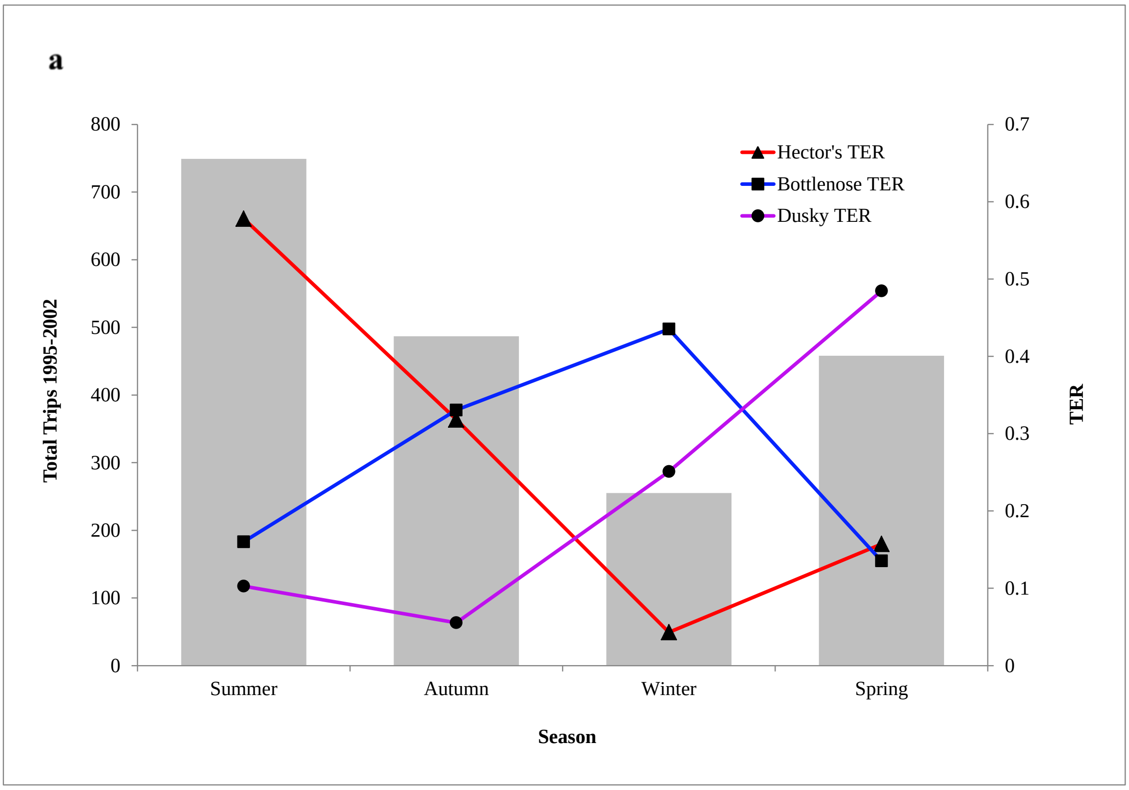


Figure 2.4. Annual trip encounter rate (TER) for Hector’s, bottlenose and dusky dolphins displayed (colored lines) overlaying total number of annual trips (represented by the light grey columns) collated from dolphin tour operator vessel logbooks in QCS, NZ, from 1995–2011.



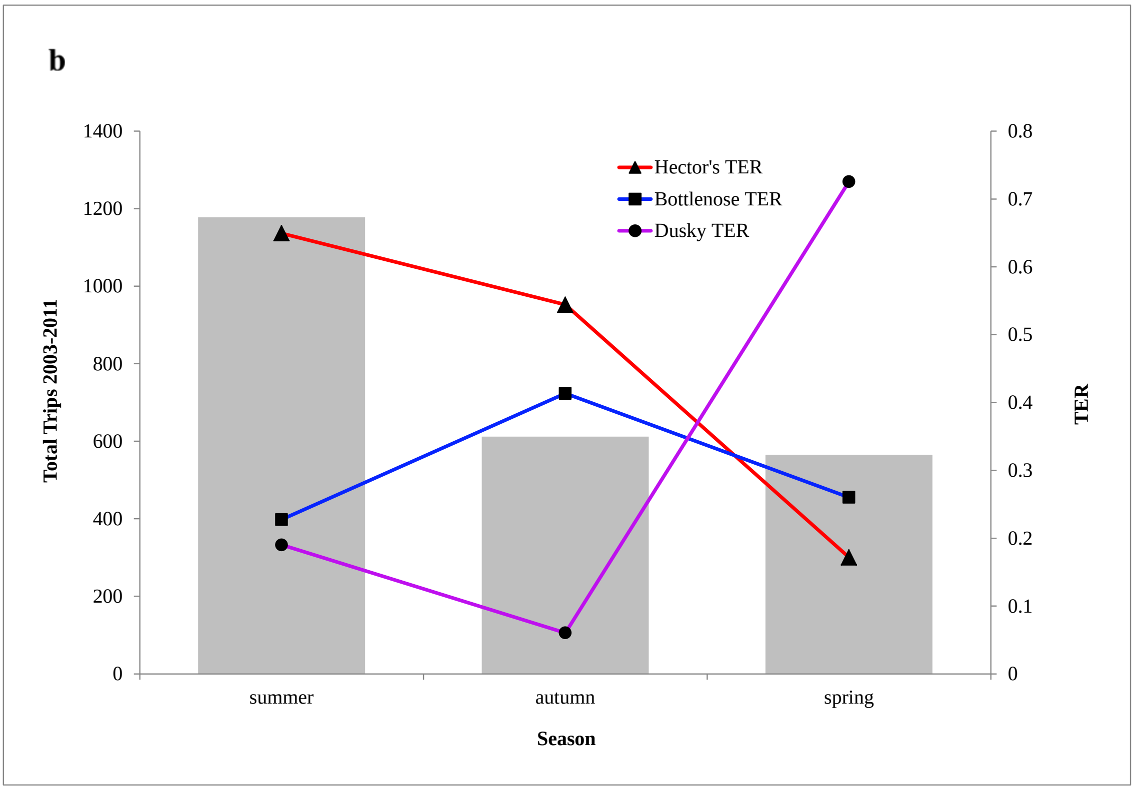


Figure 2.5. Seasonal trip encounter rate (TER) for Hector’s, bottlenose and dusky dolphins displayed (colored lines) overlaying total number of seasonal trips (represented by the light grey columns) during a. 1995–2002 and b. 2003–2011 (excluding winter data). Data were collated from tour operator vessel logbooks in QCS, NZ, from 1995–2011.

Table 2.2. Environmental correlates associated with Hector’s, bottlenose and dusky dolphin presence in QCS from 1995–2011.

	Habitat Values								
Variables	**Hector's Dolphins**			**Bottlenose Dolphins**			**Dusky Dolphins**		
	Mean	*Range*	*SD*	*Mean*	*Range*	*SD*	*Mean*	*Range*	*SD*
1995–2002									
SST (°C)	16.17	11.80 – 19.52	1.38	15.00	10.9 – 19.6	2.12	14.20	10.9 – 18.5	0.64
Tide (m)	1.08	0.4 – 1.7	0.33	1.11	0.4 – 1.7	0.32	1.12	0.5 – 1.7	0.32
2003–2011									
SST (°C)	16.06	12.3 – 18.7	1.23	15.30	11.6 – 18.7	1.40	14.40	11.30 – 18.71	1.19
Tide (m)	1.08	0.3 – 1.7	0.34	1.09	0.3 – 1.7	0.33	1.08	0.3 – 1.7	0.33
Turbidity (sr^{-1})	0.003963	0.001937– 0.006471	0.0086	0.004099	0.001937– 0.006753	0.00813	0.004244	0.001937– 0.006753	0.00097

2.3.2 Summary of environmental correlates and model selection

The various environmental correlates associated with Hector's, bottlenose and dusky dolphin presence in QCS spanning 1995–2011 are summarized in Table 2.2.

2.3.2.1 Hector's dolphins

2.3.2.1.1 1995–2002 model

The best fit GAM for Hector's dolphin presence in QCS was as follows: presence ~ s (year) + s (SST). The inclusion of tidal range did not improve the model (Appendix 2.2b). Hector's dolphins were present across all years with some cyclic fluctuations (p = 0.0001; Figure 2.6). A higher likelihood of presence was associated with higher SST, up to 16°C where it then tended to plateau ($p < 0.0001$; Figure 2.6). The model explained 16.8% of the deviance (Appendix 2.2). For a summary table of all final models and their output values refer to Table 2.3.

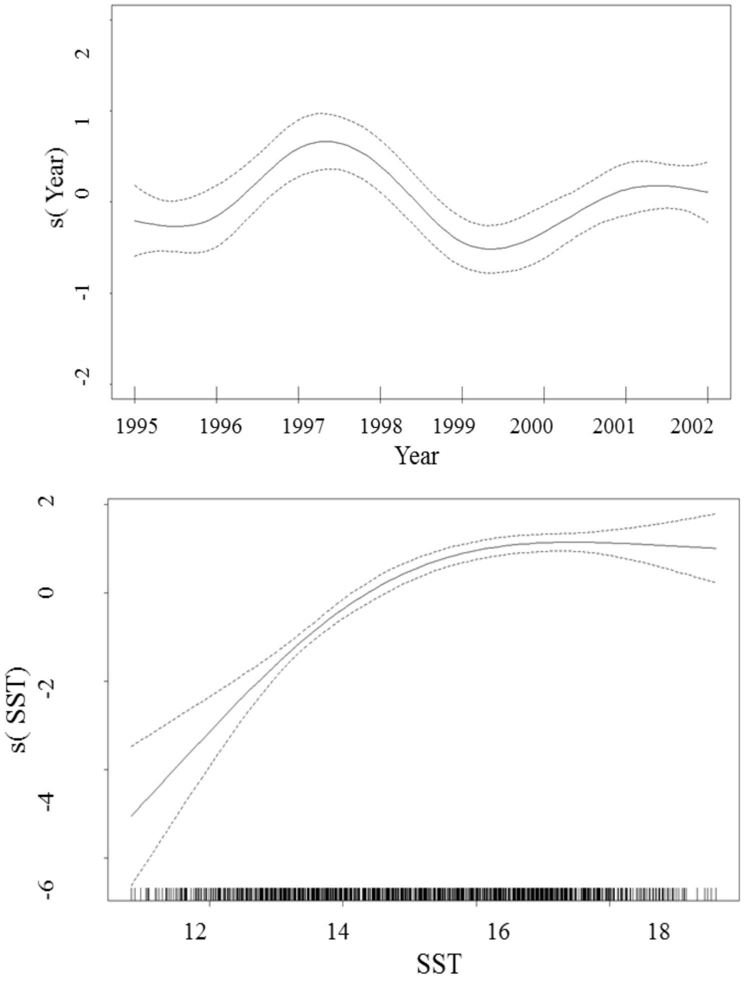


Figure 2.6. Partial residual plots from the best fit GAM of Hector's dolphin presence in QCS, NZ, from 1995–2002. Dotted lines represent ± one SE and the vertical mark on the x-axes represent the distribution of data in the model.

Table 2.3. Summary of final model forms and output for delphinid daily presence in QCS, NZ, from time frames 1995–2002 and 2003–2011.

Species	Time Frame	Final Model	Deviance Explained	R^2
Hector's	1995 – 2002	s (year) + s (SST)	16.8%	0.18
	2003 – 2011	year + SST	15.7%	0.22
Bottlenose	1995 – 2002	(year) + s (SST)	2.5%	0.024
	2003 – 2011	s (year) + (turbidity)	20.0%	0.24
Dusky	1995 – 2002	(year) + s (SST)	23.5%	0.25
	2003 – 2011	s (year) + s (SST) + s (turbidity)+ s (tide)	43.3%	0.46

Table 2.4. Linear model term output values and associated calculation allowing for a meaningful interpretation of the model results.

Species	Time Frame	Parameter	Estimate	Backtransformed value	((100 x exp beta) -1) %
Hector's	2003–2011	Year	–0.17789	0.8361	–16.4
Hector's	2003–2011	SST	0.69518	2.0041	100.4
Bottlenose	1995–2002	Year	–0.07042	0.0932	6.8
Bottlenose	2003–2011	Turbidity	0.026	1.0263	2.6
Dusky	1995–2002	Year	0.324	1.3830	38.3

2.3.2.1.2 2003–2011 model

The best fit GLM for Hector's dolphin presence in QCS during this time frame was: presence ~ (year) + (SST). The effect of year indicated that Hector's dolphin presence in QCS decreased, on average, by 16.4% per year during this time frame ($p < 0.0001$; Table 2.4; Appendix 2.3). The linear effect of SST indicated that Hector's dolphins were 2.00 times as likely to occur as SST increased by 1°C ($p < 0.0001$; Table 2.4). There was no obvious plateauing, as indicated during the previous time frame. The model explained 15.7% of the deviance (Appendix 2.3). While the deviance explained was slightly lower and the AIC value slightly higher, this was deemed the best model since tidal range was not significant ($p > 0.05$) and no clear preference was detected for the variable turbidity.

2.3.2.2 Bottlenose dolphins

2.3.2.2.1 1995–2002 model

The best fit GAM for bottlenose dolphin daily presence in QCS was: presence ~ (year) + s (SST). The inclusion of tidal range did not improve the model (Appendix 2.4b). The linear effect of year indicated that bottlenose dolphin presence decreased during this time frame as they were generally 6.8% less likely to occur from one year to the next ($p = 0.01$; Table 2.4; Appendix 2.4). A higher likelihood of bottlenose dolphin presence was associated with mid-low temperatures ($p < 0.001$; Figure 2.7, Appendix 2.4). The model only explained 2.5% of the deviance (Appendix 2.4).

2.3.2.2.2 2003–2011 model

The best fit GAM during this time frame was presence ~ s (year) + turbidity. The inclusion of SST and tidal range with data from 2003–2011 did not improve the model (Appendix 2.5b). The effect of year indicates a significant change in bottlenose dolphin presence, with some inter-annual fluctuation ($p < 0.0001$; Figure 2.8, Appendix 2.5). The linear effect of turbidity indicates that bottlenose dolphins were 2.6% more likely to occur in QCS when turbidity increased by 0.0001 sr^{-1} ($p = 0.01$; Table 2.4, Appendix 2.5). The model explained 20.0% of the deviance (Appendix 2.5).

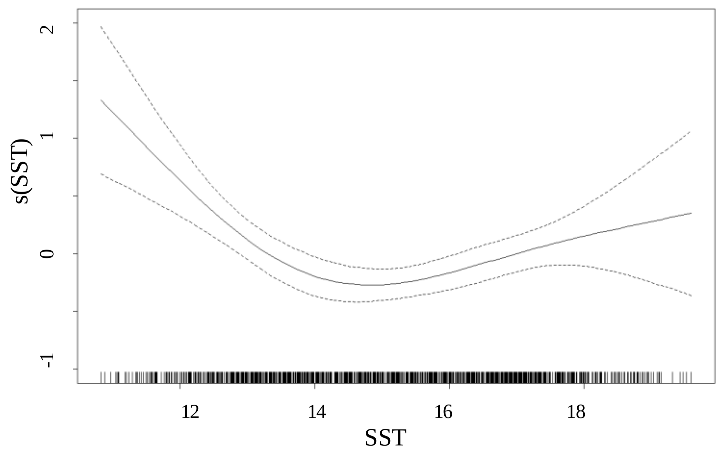


Figure 2.7. Partial residual plot from the best fit GAM of bottlenose dolphin presence in QCS, NZ, from 1995–2002. Dotted lines represent ± one SE and the vertical marks on the x-axes represent the distribution of data in the model.

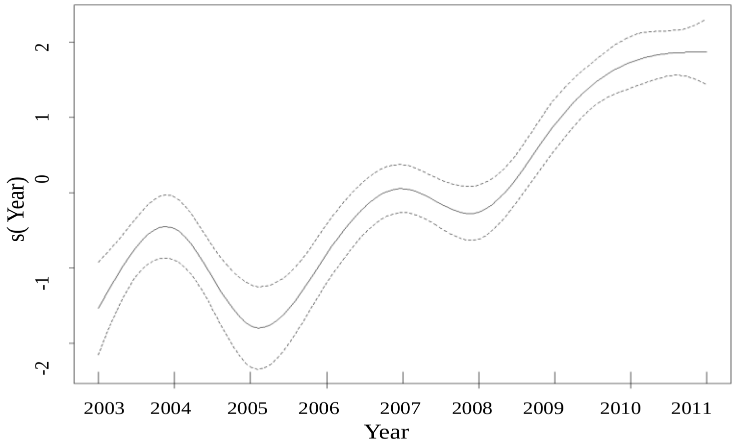


Figure 2.8. Partial residual plot from the best fit GAM of bottlenose dolphin presence in QCS, NZ, from 2003–2011. Dotted lines represent ± one SE and the vertical marks on the x-axes represent the distribution of data in the model.

2.3.2.3 Dusky dolphins

2.3.2.3.1 1995–2002 model

The best fit GAM for dusky dolphin daily presence was as follows: presence ~ (year) + s (SST). The variable tidal range was not significant ($p > 0.5$) and did not improve the model (Appendix 2.6b). A higher likelihood of presence was associated with lower temperatures ($p < 0.0001$; Figure 2.9; Appendix 2.6). The model suggests that dusky dolphin presence increased, on average by 38.3% per year during this period ($p < 0.0001$; Table 2.4; Appendix 2.6). The model explains 23.5% of the deviance (Appendix 2.6).

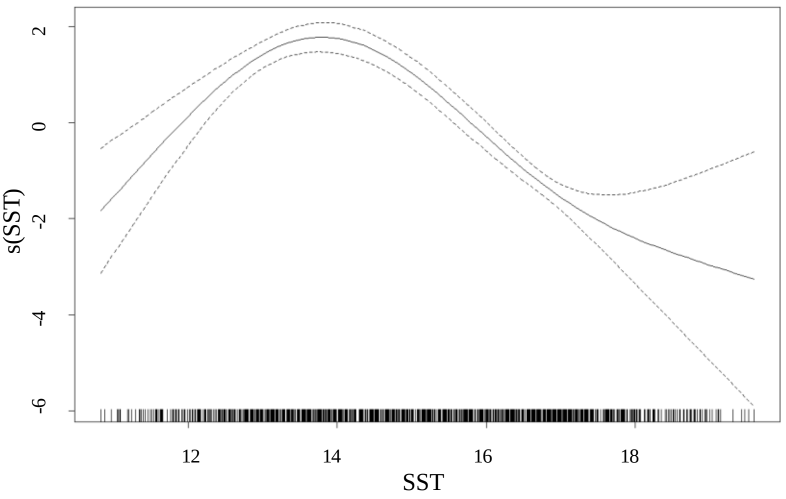


Figure 2.9. Partial residual plot from the best fit GAM of dusky dolphin presence in QCS, NZ, from 1995–2002. Sighting data were sourced from tour vessel log books. Dotted lines represent ± one SE and the vertical marks on the x-axes represent the distribution of data in the model.

2.3.2.3.2 2003–2011 model

The best fit GAM for dusky dolphin daily presence during this time frame was: presence ~ s (year) + s (SST) + s (tidal range) + s (turbidity; Appendix 2.7). The likelihood of dusky dolphin presence indicated variation until 2008, where a visible decline occurred ($p < 0.0001$; Figure 2.10; Appendix 2.7). The non-linear effect of SST indicates a higher likelihood with low range SST values ($p < 0.0001$; Figure 2.10; Appendix 2.7). The non-linear effect of tidal range indicated slight evidence of an increase in presence with mid-range values ($p < 0.01$; Figure 2.10; Appendix 2.7). The effect of turbidity indicated a slight decrease in presence that plateaued, as values increased ($p < 0.0001$; Figure 2.10; Appendix 2.7). The model explained 43.3% of the deviance (Appendix 2.7).

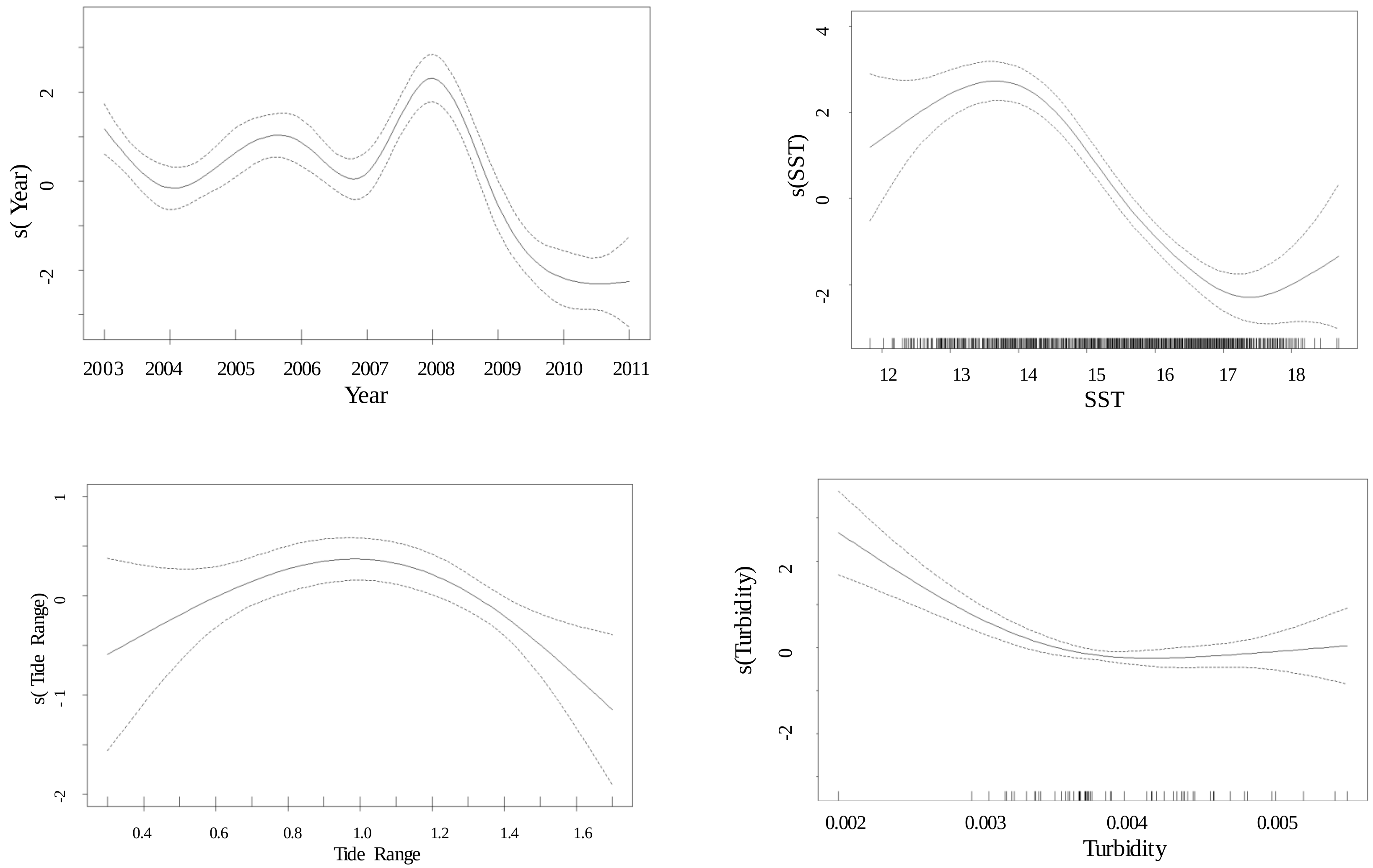


Figure 2.10. Partial residual plots from the best fit GAM of dusky dolphin presence in QCS, NZ, during 2003–2011. Dotted lines represent ± one SE and the vertical marks on the x-axes represent the distribution of data in the model.

2.3.3 Spatial trends: Distribution and density

A total of 5,782 sightings included location data. Of these records, 44.9% (n = 2,598) Hector's, 23.3% (n = 1,350) bottlenose and 28.6% (n = 1,651) dusky dolphin sightings were plotted. Mean group size for Hector's dolphins was 5.1 (SD = 3.44; SE = 0.007; n = 2,557) and for dusky dolphins was 9.5 (SD = 6.33; SE = 0.16; n = 1,541). Bottlenose dolphin group size was not further considered here (see explanation in section 2.2.3.3).

2.3.3.1 Hector's dolphins

Hector's dolphins were distributed throughout the entire Sound, while greater concentrations generally occurred in the middle and inner Sound over the study period (1995–2011; Figure 2.11). Over time, the distribution became more concentrated around the middle Sound (Figure 2.11). Seasonal variation in distribution of animals was observed. The distribution was widespread during summer, autumn and spring, but higher density regions were more apparent during summer and autumn around the middle Sound (Figure 2.12). Distribution was restricted to more central regions during winter and in much lower densities (Figure 2.12).

2.3.3.2 Bottlenose dolphins

As explained in section 2.2.3.3, calculations for this species were represented by the number of sightings per trip, whereas the other species were represented by the number of animals per trip. Bottlenose dolphin sightings were distributed throughout the Sound, with high concentrations scattered throughout (Figures 2.13; 2.14). No major density shifts were observed across the years (Figure 2.14) while seasonal density was only slightly greater during winter and lowest during spring (Figure 2.14).

2.3.3.3 Dusky dolphins

Dusky dolphins used the extent of the study area (Figures 2.15; 2.16). Dusky dolphin densities were generally greater within the inner Sound waters during the 1990s and have slowly restricted back to the mid/outer Sound during the later 2000s (Figure 2.15). Dusky dolphin densities in QCS exhibited seasonal shifts with peaks during winter and spring (Figure 2.16). Animals were mainly concentrated within the inner Sound during winter and spread more evenly throughout the Sound by spring (Figure 2.16).

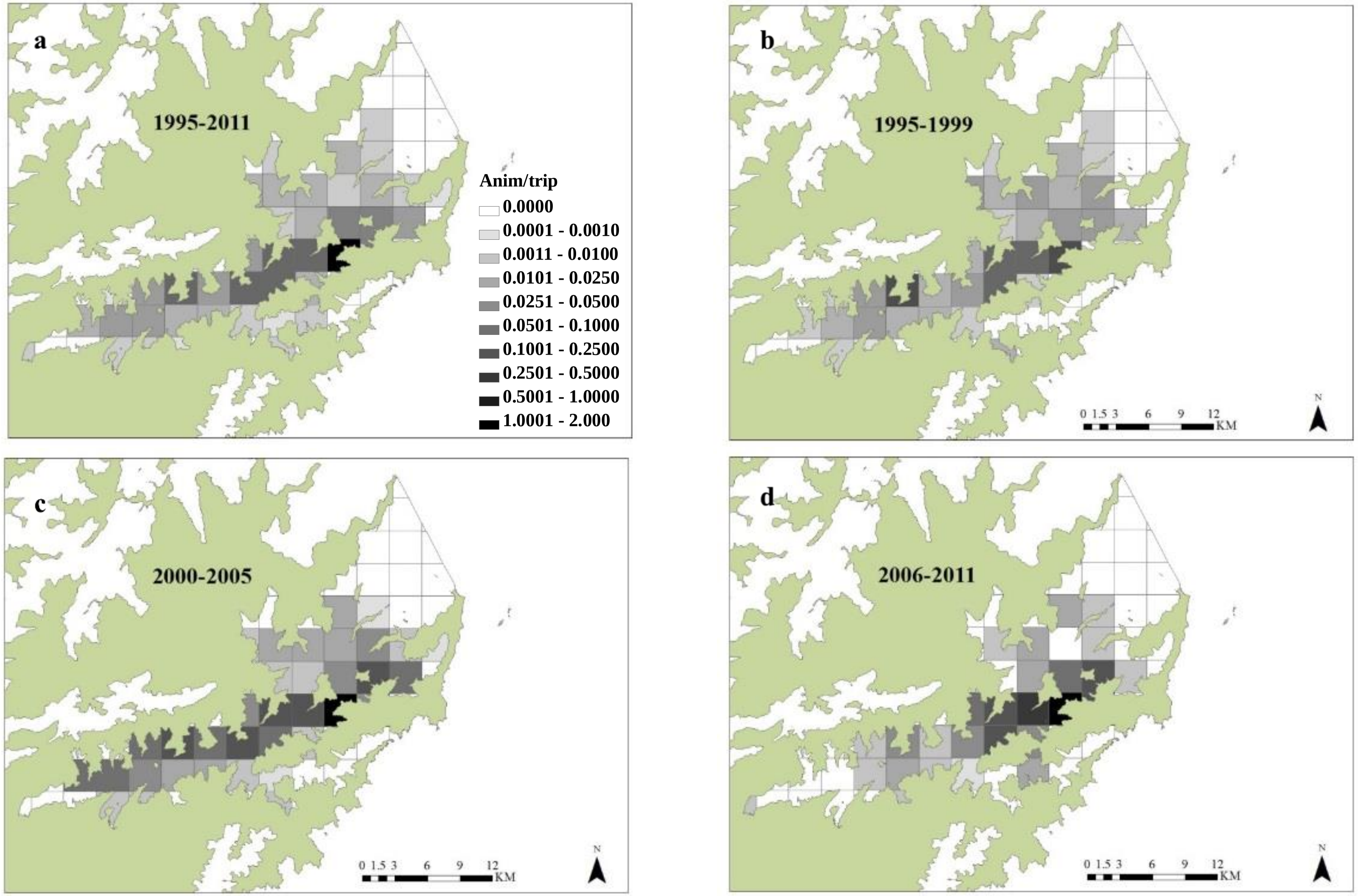


Figure 2.11. Distribution of Hector’s dolphins in QCS. Animals per group were standardized per 3x3 km grid cell by number of trips during a. 1995–2011, b.1995–1999, c. 2000–2005 and d. 2006–2011. Data were collated from tour operator vessel logbooks from 1995–2011.

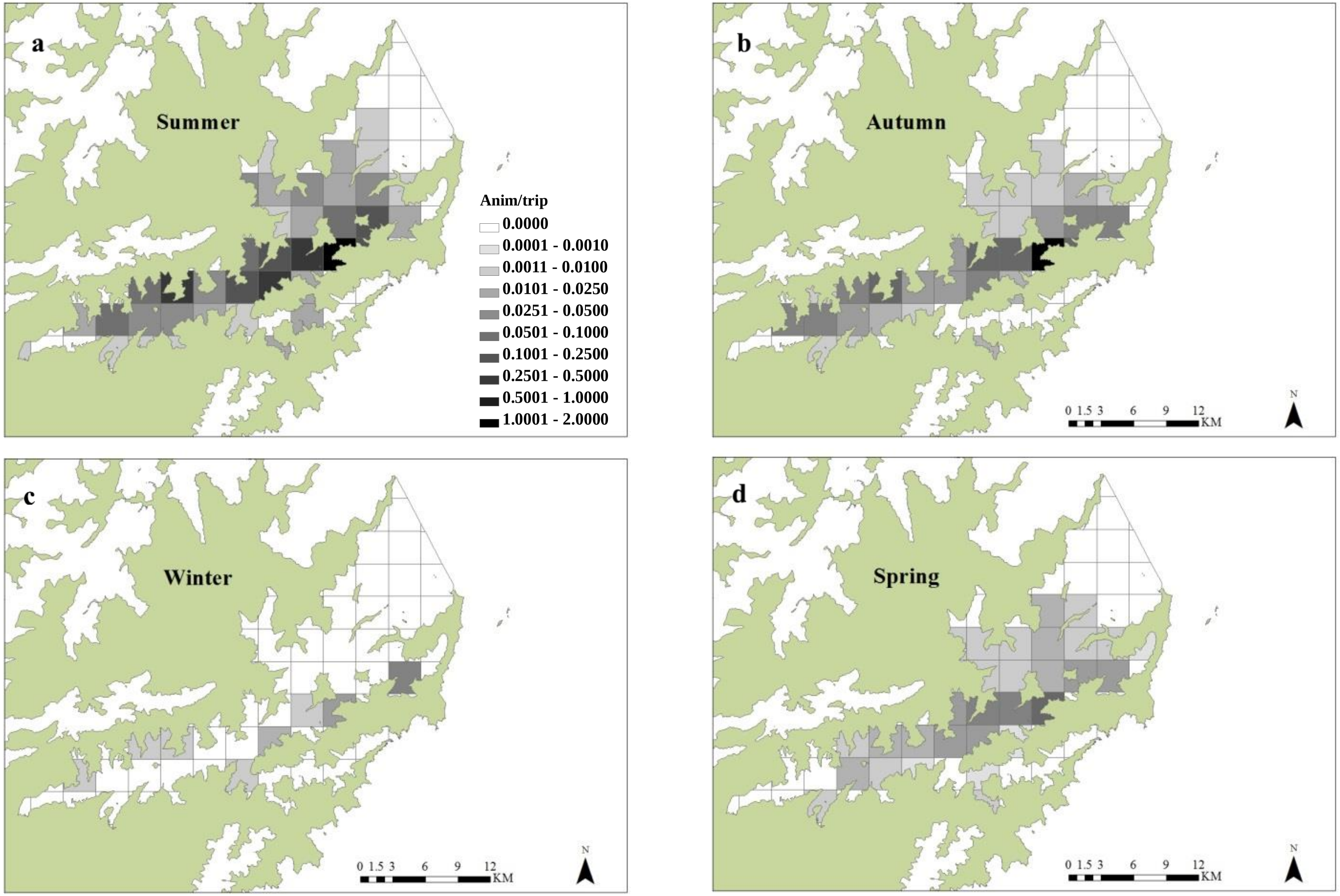


Figure 2.12. Distribution of Hector’s dolphins in QCS. Animals per group were standardized per 3x3 km grid cell by number of trips during a. summer, b. autumn, c. winter and d. spring. Data were collated from tour operator vessel logbooks from 1995–2011.

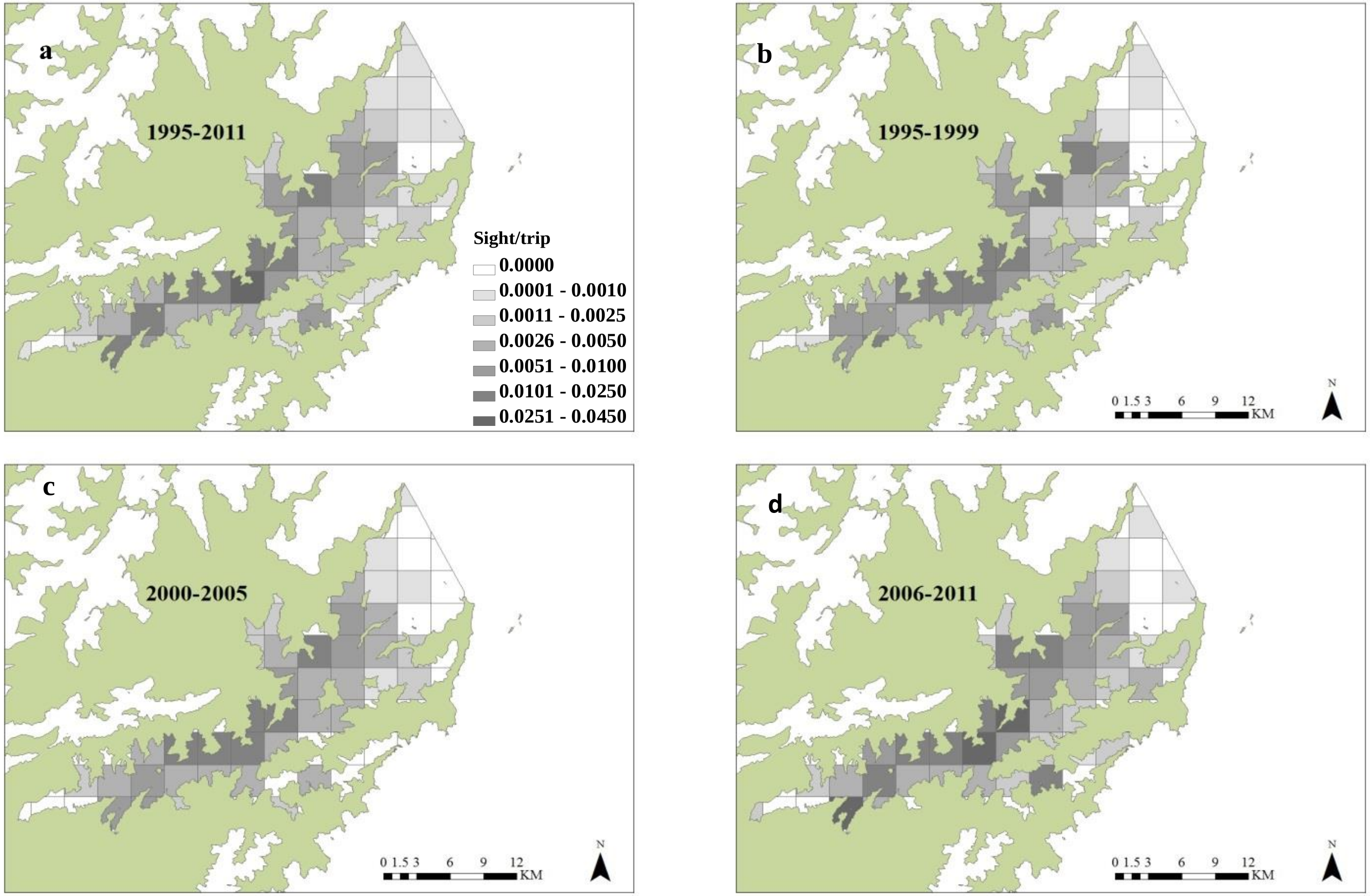


Figure 2.13. Distribution of bottlenose dolphins in QCS, NZ. Sightings were standardized per 3x3 km grid cell by number of trips during a. 1995–2011, b.1995–1999, c. 2000–2005 and d. 2006–2011. Data were collated from tour operator vessel logbooks from 1995–2011.

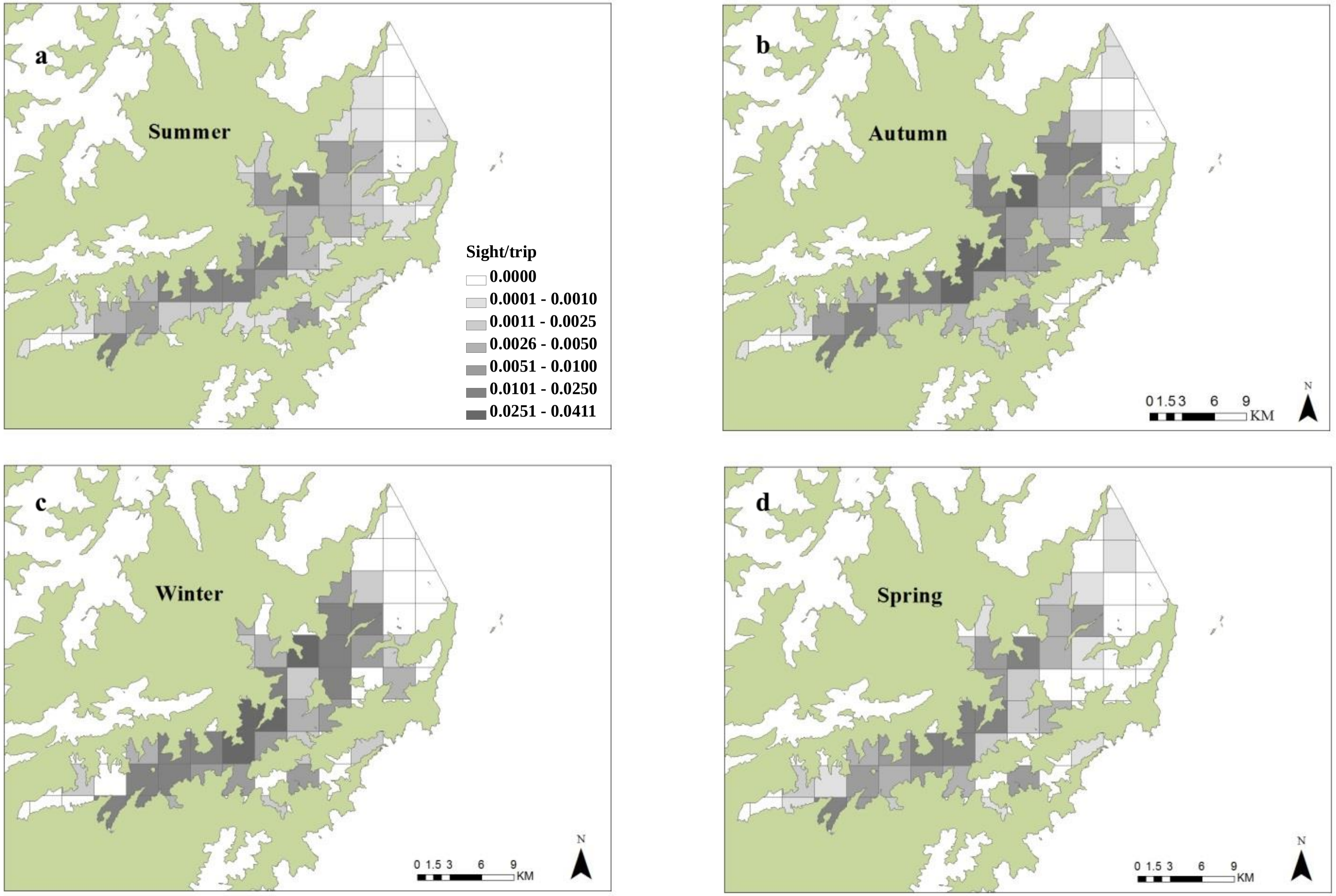


Figure 2.14. Distribution of bottlenose dolphins in QCS, NZ. Sightings were standardized per 3x3 km grid cell by number of trips during a. summer, b. autumn, c. winter and d. spring. Data were collated from dolphin tour operator vessel logbooks from 1995–2011.

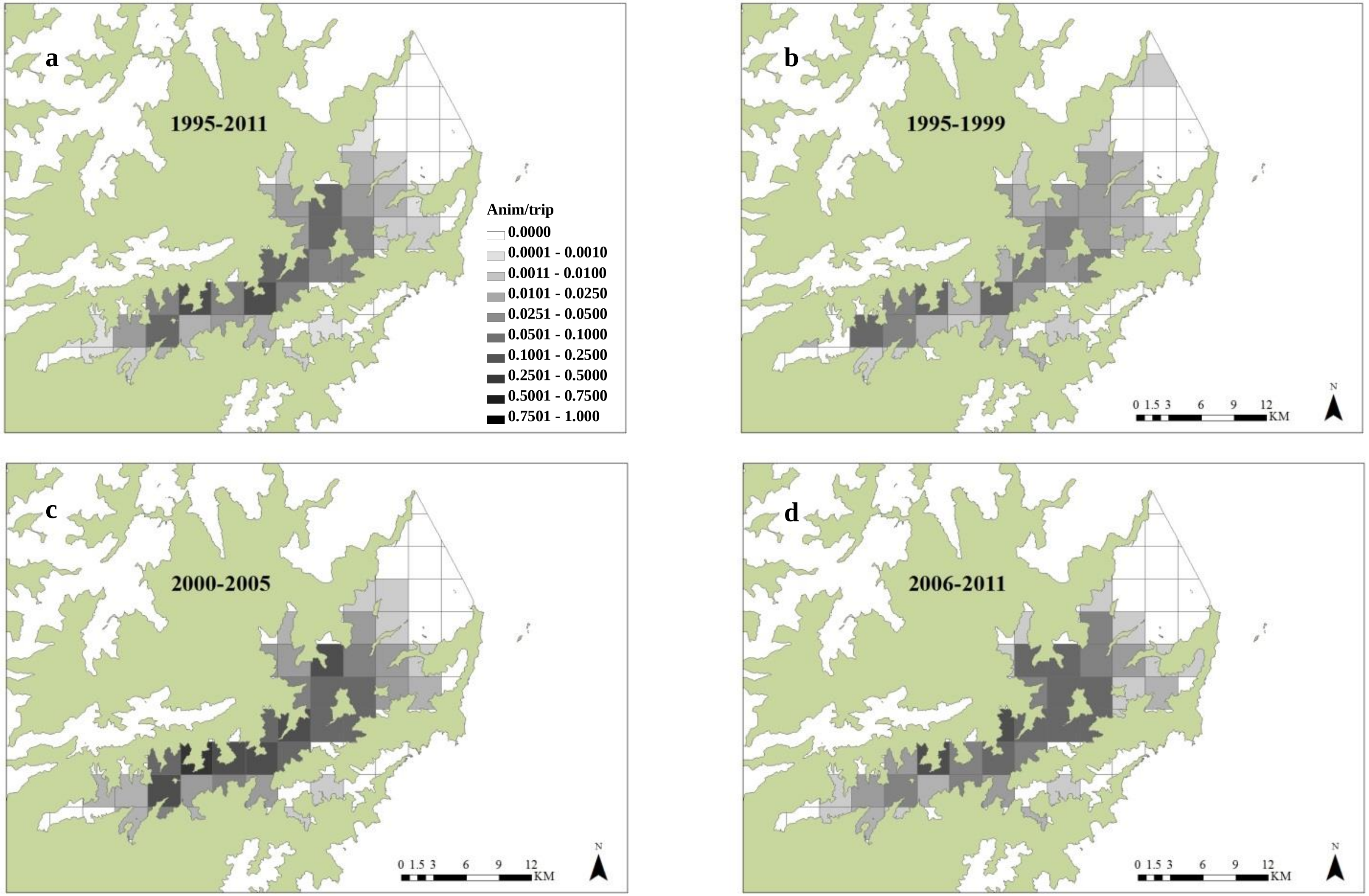


Figure 2.15. Distribution of dusky dolphins in QCS, NZ. Animals per group were standardized per 3x3 km grid cell by number of trips during a. 1995–2011, b.1995–1999, c. 2000–2005 and d. 2006–2011. Data were collated from dolphin tour operator vessel logbooks.

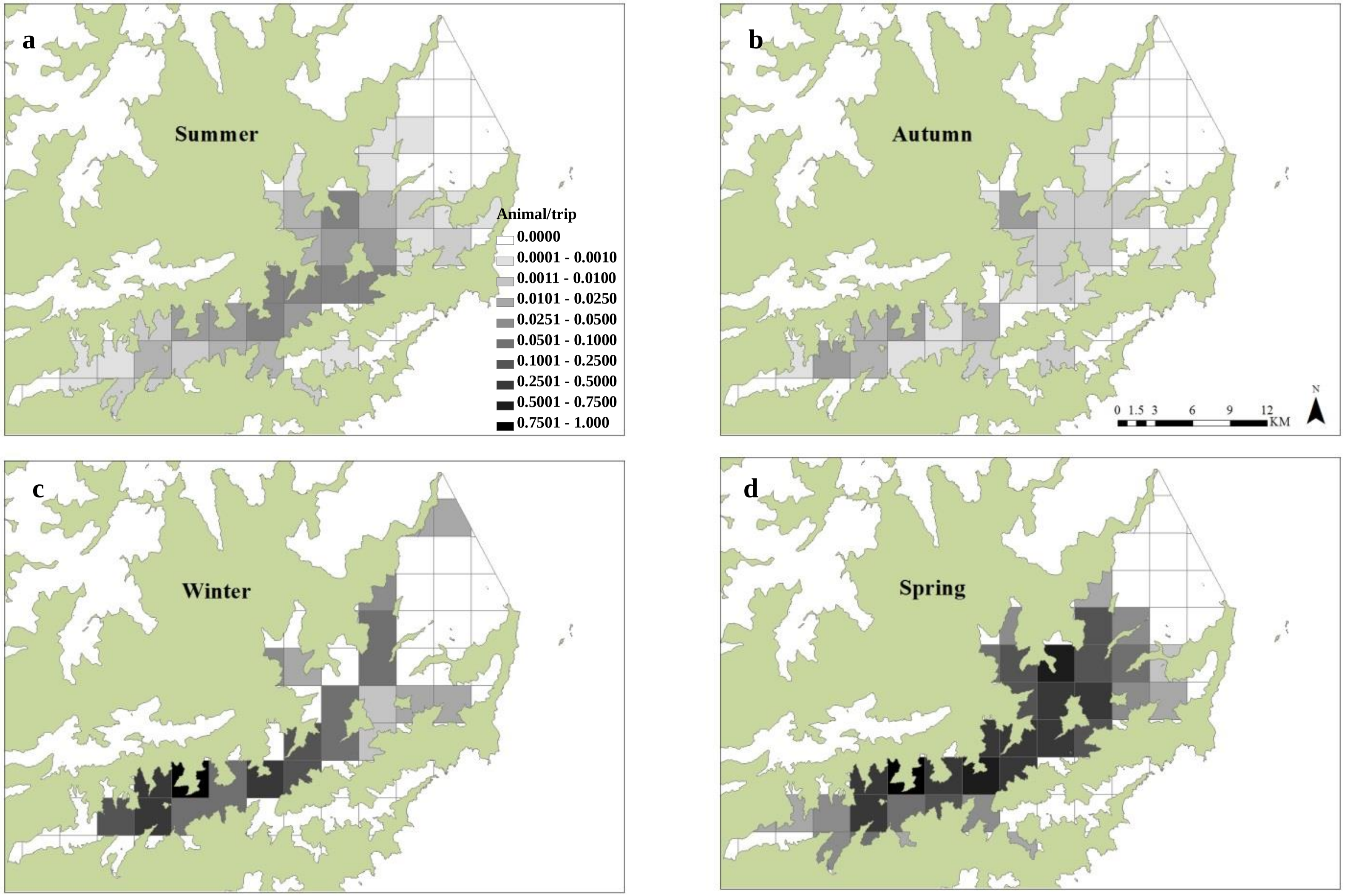


Figure 2.16. Distribution of dusky dolphins in QCS, NZ. Animals per group were standardized per 3x3 km grid cell by number of trips during a. summer, b. autumn, c. winter and d. spring. Data were collated from dolphin tour operator vessel logbooks from 1995–2011.

2.3.4 Trends in swim-with-dolphin tourism

As indicated by the historical logbooks, swim-with-dolphin tourism in QCS expanded during the study period. Swim encounters occurred sporadically when tourism was initiated in the late 1990s, with 5.4% (n = 18) in 1995 and only one swim trip in both 1997 and 2001 (0.3%). From 2004 onwards, swim encounters increased steadily with more than a third of the trips (n = 73, 35%) including a dolphin swim encounter by 2011 (Figure 2.17).

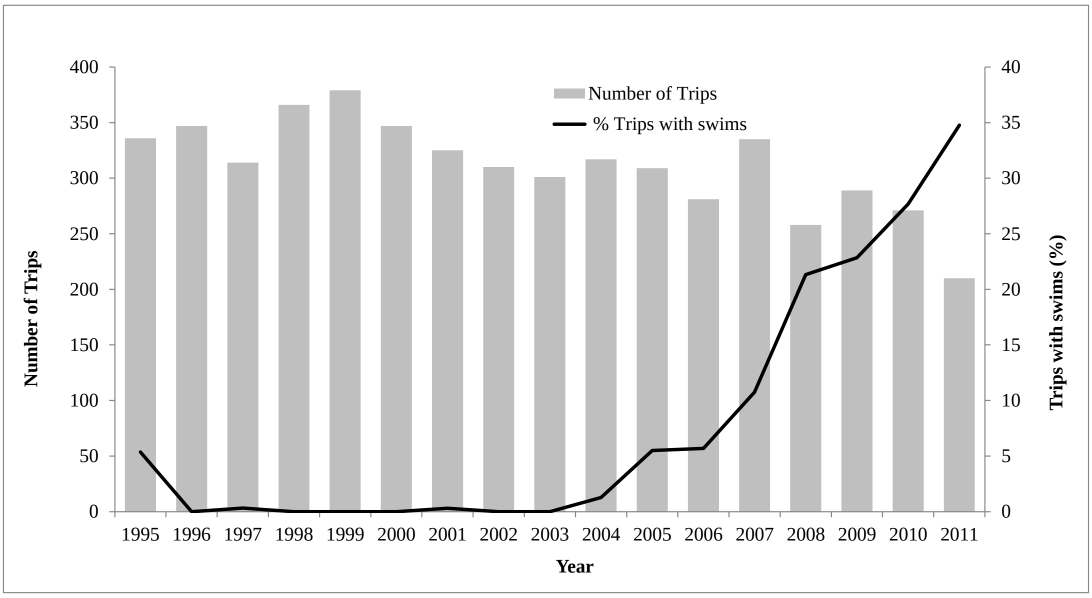


Figure 2.17. Records from dolphin tour operator vessel logbooks in QCS from 1995–2011, indicating the total number of annual trips as well as the percentage of trips that included dolphin swim encounters.

The number of intended swim trips during 2004–2006 was low (n ≤ 31) and most of these resulted in an actual swim encounter. From 2007–2011, the number of intended swim trips increased, but so did the percentage of trips with an actual swim encounter relative to intended swim trips. In 2007, 44% of intended swim trips resulted in a swim encounter, which increased quite steadily to 73% in 2011 (Figure 2.18). Overall, swim encounters occurred most frequently with bottlenose dolphins (n = 201, 56%), followed by dusky dolphins (n = 120, 33%) and to a lesser degree, Hector's dolphins (n = 23, 6%). Swim encounters with dusky dolphins decreased from 2004 onwards, while swim encounters with Hector's dolphins only occurred between 2007 and 2010 (Figure 2.19).

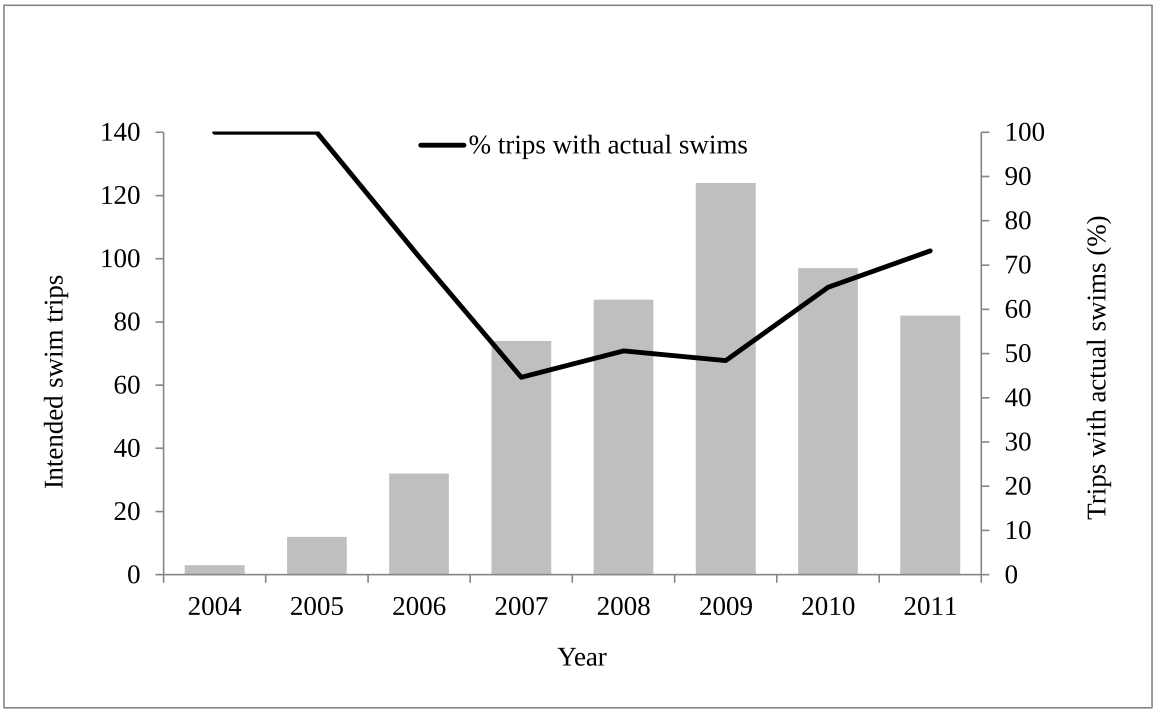


Figure 2.18. The total number of intended dolphin swim trips and the percentage of trips with an actual dolphin swim encounter, that took place during dolphin tours in QCS, NZ, from 2004–2011.

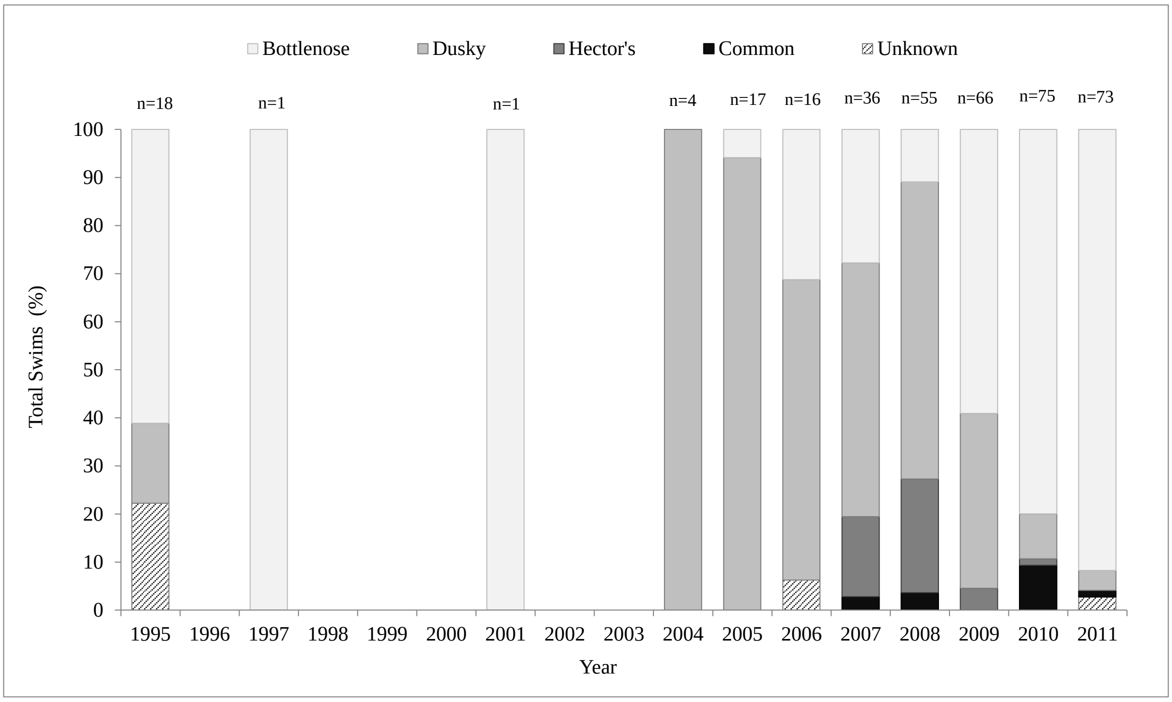


Figure 2.19. The percentage of swim encounters according to species that occurred during dolphin tours in QCS, NZ, from 1995–2011. Note that no swim encounters were recorded during 1996, 1998–2000; 2002–2003.

2.4 Discussion

Historical animal sighting records can be used to explore temporal and spatial patterns, make correlations with natural and anthropogenic influences and benefit species conservation efforts. For example, the identification of shifts in land/habitat use associated with climate change and/or anthropogenic expansion may be possible (Rowe *et al.*, 2010). Moreover, historical records can serve as baseline data that not only allow for comparisons to the current state of the ecosystem, but also for future projections (Lotze & Worm, 2009). Historical baselines are particularly critical in under-studied regions to assess regional diversity and identify the presence of threatened species (Kiszka *et al.*, 2010).

The present study compiled data from historical logbooks spanning 16 years to establish a baseline of delphinid occurrence in QCS. From these data, the presence of six delphinids was recognized, while patterns in occurrence, relative density and spatial distribution were identified for the three main species: a NZ endemic/endangered species (Hector's dolphins), a NZ endangered species (bottlenose dolphins) and an endemic subspecies (dusky dolphins) within QCS (Baker *et al.*, 2016). There has been limited research on marine mammals in QCS (Clement *et al.*, 2001; Duffy & Brown, 1994; Markowitz, 2004; Merriman *et al.*, 2009), with no multi-species examinations. Here, the use of logbooks led to the establishment of invaluable, long-term (> 15 years) baseline data, which would have otherwise been unknown.

2.4.1 Temporal trends

In the present study, the collation of historical records allowed for the elucidation of temporal trends amongst three key delphinid species in QCS, NZ. Overall, Hector's dolphins had the highest TER across the entire time frame. However, all three species displayed temporal fluctuations including strong seasonal signals (*i.e.,* peaks in Hector's dolphins during summer, bottlenose dolphins during autumn and winter; dusky dolphins during spring). Furthermore, the GAMs revealed that the occurrence of each species displayed a significant association with year, while long-term trends suggest opposing occurrence amongst the species. Alternating temporal patterns, on annual or seasonal scales, could be suggestive of niche partitioning to allow for the sharing of resources (Roughgarden, 1976) amongst similar species in QCS. Evidence of this phenomenon similarly occurs amongst several cetacean species in the Bahamas, some of which are permanent while others are only sporadic visitors (MacLeod *et al.*, 2004). Likewise, temporal partitioning is noticeable amongst common (*Delphinus delphis*) and white-sided dolphins (*L. acutus*) that are present in the Gully, on the edge of the Scotian shelf during different seasons (Gowans & Whitehead, 1995). However, interesting patterns such as those detected in QCS (like overseas studies) could be further indicative of life history dynamics around NZ and a number of potential complex ecological interactions such as variations in prey availability (Benoit-Bird *et al.*, 2004), predator avoidance (Heithaus & Dill, 2006), dietary/metabolic requirements (Worthy & Edwards, 1990), anthropogenic influence (Lusseau, 2005), or a combination of these factors (refer to extended discussion in section 3.4).

The detection of long-term temporal trends in delphinid occurrence in QCS is valuable for developing comprehensive Sounds management. This includes the consideration of natural resources as well and human activity (Halpern *et al.*, 2008a). The data presented here may support temporal limitations in use of QCS, if this is deemed necessary for delphinid conservation measures (as in Tyne *et al.* 2015). Moreover, these data can be used to focus monitoring efforts, to design future similar studies, or as a point of reference for comparison with more current data (as in Chapter 3).

2.4.2 Association with environmental correlates

Data from historical records can complement research findings from dedicated surveys. For example, the investigation of long-term tour operator sighting records of dusky dolphins off Kaikoura, NZ, indicate seasonal onshore/offshore movement (Dahood *et al.*, 2008), consistent with previously identified patterns from dedicated surveys (Markowitz, 2004). To further investigate temporal trends and the drivers associated with animal occurrence, the correlation of historical records with suitable corresponding natural and/or anthropogenic data can be useful. In the present study, the temporal occurrence of delphinid species in QCS were tested against commonly used proxies in cetacean studies: SST (MacLeod *et al.*, 2007; Macleod *et al.*, 2008; Tynan *et al.*, 2005), turbidity (Brager *et al.*, 2003; Clement, 2005; Gannier & Petiau, 2006; Smith *et al.*, 2009) and tidal features (de Boer *et al.*, 2014; Fury & Harrison, 2011b; Guilherme-Silveira & Silva, 2009; Ijsseldijk *et al.*, 2015). The GAMs provided some evidence that historical delphinid presence in QCS may have been related to environmental covariates similar to findings from dedicated and opportunistic surveys elsewhere (Correia *et al.*, 2015; Goetz *et al.*, 2015; Marubini *et al.*, 2009; Wiseman *et al.*, 2011)

In general, cetaceans will occur in a region because that area allows for access to the animals' basic needs (*e.g.*, food and protection). Behavioural studies often indicate that dolphins spend a high proportion of time foraging/feeding (Bearzi, 2005a), which direct prey observation can confirm (Acevedo-Gutierrez & Parker, 2000). Moreover, gut content analyses may suggest close agreement between the presence of prey species within known dolphin habitat and their stomach content (Barros & Wells, 1998). Additionally, the analysis of predator data may detect that the distribution of foraging dolphins reflects a balance between available prey and the risk of predation (Heithaus & Dill, 2002). Direct prey and predator data are often not available if cetacean data are accessed through historical records or via citizen science. However, researchers often rely on more readily available environmental variables as proxies, which may provide insight into dolphin ecology (Redfern *et al.*, 2006) and sufficiently predict dolphin habitat (Torres *et al.*, 2008).

2.4.2.1 SST

The association of SST with delphinid occurrence and distribution can often be linked to foraging or prey availability (Garaffo *et al.*, 2011; Macleod *et al.*, 2008; Scott *et al.*, 2010; Weir *et al.*, 2012). In the absence of predator, prey or behavioural data for Hector's or dusky dolphins in QCS, SST may be a logical suitable indictor of prey. Hector's dolphins primary prey, red cod (*Pseudophycis bachus*; Miller *et al.*, 2013) move offshore during colder months (Beentjes *et al.*, 2002; Beentjes & Renwick, 2001). Hector's dolphins likely follow these species at Bank's Peninsula (Brager *et al.*, 2003; Miller, 2014), which may also explain their consistent association with higher SST in QCS (during both time frames), in this study. Similarly, dusky dolphins display a steady correlation with lower SST in QCS, in both time periods. Likewise, previous work indicates the regular occurrence of this species foraging in the Marlborough Sounds during the winter months (Markowitz, 2004; McFadden, 2003).

2.4.2.2 Turbidity

Turbidity may be another informative habitat variable in cetacean studies (Brager *et al.*, 2003; Fury & Harrison, 2011a; Miller & Baltz, 2010). The models for bottlenose and dusky dolphins detect an influence of the variable turbidity associated with animal presence in QCS during 2003–2011. Bottlenose dolphin occurrence, in the present study and elsewhere is associated with slightly increased turbidity (Miller & Baltz, 2010). Some prey species may congregate in turbid waters as a form of protection (Fury & Harrison, 2011a). However, the patterns detected here for bottlenose dolphins may be explained by their improved foraging efficiency in turbid waters since prey that are reliant on vison to detect predators may be at a disadvantage to delphinid echolocation in such conditions (Ballance, 2002; Brager *et al.*, 2003; Miller & Baltz, 2010). Conversely, a higher occurrence of dusky dolphins was detected in QCS with slightly lower turbidity values. Dusky dolphins exhibit a range of foraging tactics on a variety of prey (Duffy & Brown, 1994; McFadden, 2003; Vaughn *et al.*, 2007; Vaughn *et al.*, 2008). It is possible that some of the fish species that they access as prey may occupy foraging grounds only when turbidity is low (Cyrus & Blaber, 1992), which would explain the patterns detected here.

No clear signal was detected for turbidity in the model for Hector's dolphins in QCS. However, elsewhere in New Zealand, Hector's dolphins displayed some preference for turbid waters (Brager *et al.*, 2003) as did the similar Maui dolphin (*Cephalorhynchus hectori maui*; Derville *et al.*, 2016). It may be that this variable is be more informative on a finer scale (as in Bailey and Thompson, 2009) than was available in this study. Water clarity can be affected by natural factors such as flood conditions (Fury & Harrison, 2011a), but also changes in human activity and increases in substances like detergents and fertilizers (de Jonge *et al.*, 2002). A number of anthropogenic changes have occurred in QCS, which may affect congregations of prey, but also the general health of the ecosystem (refer to discussion in section 2.4.3 and associated management recommendations in section 6.2.2.1.

2.4.2.3 Tide

Marine mammal species often associate with tidal features (Bailey & Thompson, 2010; de Boer *et al.*, 2014; Ingram *et al.*, 2007). Cetaceans may occur in tidally active regions (Ingram *et al.*, 2007) or may associate with tidally driven fronts where prey may congregate (Bailey & Thompson, 2010; de Boer *et al.*, 2014). Likewise, dusky dolphins in the present study exhibit an association with mid-value tidal range, which may equate to mid-range tidal current. Tidal current may increase foraging ability by transporting prey, thus increasing its abundance (Simard *et al.*, 2008) as well as the diversity of available species (Benjamins *et al.*, 2015; Vlietstra *et al.*, 2005). Furthermore, prey may be disoriented, or segregated by fast moving water and be more vulnerable to predation (Benjamins *et al.*, 2015; Ferguson *et al.*, 2012). Thus, dusky dolphins may benefit from these features in QCS. They forage for diverse prey using a range of tactics (Koen-Alonso *et al.*, 1998; McFadden, 2003; Vaughn *et al.*, 2007; Vaughn *et al.*, 2008; Viddi & Lescrauwaet, 2005). Animals that utilize various foraging techniques may be heavily affected by dynamic variables, which would explain why the model for dusky dolphins in QCS indicates the combined influence of tidal range, SST and turbidity.

2.4.2.4 Year

For all the models in this study, year was an important correlate and some variation existed amongst the significant model covariates across time frames. While temporal changes in delphinid occurrence were likely associated with a combination of natural dynamic factors, they reinforce the need to repeat studies over time to detect potential fluctuations and their associated meaning. While the models selected several dynamic variables, the deviance explained was low, which may be typical of these types of analyses (Forney *et al.*, 2012; Mannocci *et al.*, 2014b), but could also indicate that additional factors may have been influential. For example, since the consideration of dynamic variables were only possible here, it may be that static features of QCS (and their associated characteristics) also influenced dolphin occurrence. Therefore, the need for more extensive habitat investigations may be warranted and the model outcomes in the present study may illustrate potential proxies to explore further. Moreover, although historical sighting logs were standardized by trip, finer scale standardization may be more informative and comparatively interesting (refer to Chapters 3 and 4). Such data could be correlated with contemporaneously collected environmental variables using spatial habitat models that may offer more information regarding delphinid habitat use within QCS.

2.4.3 Spatial trends: Distribution and density

In addition to temporal trends, historical records can be used to explore patterns in species' distribution and relative density. For example, incidental sighting and stranding records off Cornwall, southwest Britain (1991–2008) indicated defined regions of high cetacean density (Pikesley *et al.*, 2012). Meanwhile, original whaler's logbooks from the North Pacific Ocean revealed a previously broader range of Pacific right whales (*Eubalaena pacifica;* Josephson *et al.*, 2008).

Collectively, in QCS, all species were detected to have widespread use of the study area. The data in this study were standardized to allow for the comparison of spatial patterns across temporal periods. Some distinct spatial patterns were identified. Bottlenose dolphins were distributed extensively throughout the area, with density maximums during winter. Similarly, dusky dolphin density was higher during winter, as well as spring. While dusky dolphins exhibited broad use of the region, peaks shifted away from the inner Sound by the late 2000s. Meanwhile, density estimates of Hector's dolphins were higher during summer and autumn. The data indicate that the mid-Sound has been important for 16 years. However, its value for Hector's dolphins seems to have grown over time, as density estimates increased in this region and notable shifts away from the far reaches of the inner and outer Sounds occurred. The recognition of spatial shifts such as these is a particular advantage of long-term historical data. Shifts in delphinid distribution could be attributed to natural shifts in the environment or compounding effects of anthropogenic expansion (Wang *et al.*, 2017), leading to changes in the ecosystem that affect the overall health of the region, alter prey availability (Smith *et al.*, 2013) and/or the presence of predators (Heithaus *et al.*, 2009).

Coastal development such as road construction and plantation forestry activities has led to erosion, including several substantial slips within the 1990s and 2000s along Queen Charlotte Drive, above Grove Arm in the Inner Sound (refer to Figure 2.21; Miller, 2016; Urlich 2015). Resultant sedimentation of fine deposits (Urlich, 2015) and numerous contaminants (Newcombe & Johnston, 2016) can directly impact water clarity, cover and kill benthic communities and thus, impact and/or displace animals further along on the food chain (Morrison *et al.*, 2009; Thrush *et al.*, 2004; Urlich, 2015). Moreover, ferries have increased in size and speed including the introduction of high-speed (ferries) in the late 1990s (Newcombe & Johnston, 2016; Parnell *et al.*, 2007). Large vessels, like ferries can also lead to erosion and sedimentation (Handley, 2016). Although speed was restricted in late 2000, fast ferries caused the accumulation of sediment and irreparable damage along the shoreline in QCS, specifically, effecting Grove Arm (Parnell *et al.*, 2007).

These anthropogenic influences in QCS may have contributed to shifts in Hector’s and dusky dolphin distribution away from the inner Sound where sedimentation occurred and likely had the biggest effect. In this area, tidal flow is low and not strong enough to prevent the accumulation of sediment (Hadfield *et al.*, 2014; Urlich, 2015). Evidence of the cumulative impacts of sedimentation in QCS include a *Macrocystis* die-off between 1990–2000 (Handley, 2016). Furthermore, it is suggested that a regime shift occurred over several decades in QCS. This led to declines amongst species including pilchard (*Clupeidae*) and rock lobster (*Jasus edwardsii*) that have not recovered and are still under threat (Handley, 2016). Thus, associated implications higher up the food chain may have caused dolphins to move to areas close to the opening of QCS at Cook Strait, where more productive, tidally refreshed waters occur (Hadfield *et al.*, 2014).

In addition to changes associated with coastal development and the ferries, QCS has experienced an increase in recreational boating, as evidenced by the submission of applications to enlarge Waikawa Harbour for additional berths and moorings (Mackenzie, 2008). Since Picton and Waikawa Harbours are located in the inner Sound, it is possible that increased vessel traffic in and out of these harbours associated with additional boats, has contributed to changes in dolphin spatial patterns, particularly the movement of Hector's dolphins away from the inner Sound/harbour area. Intensified boat traffic can lead to a number of changes in the environment including increased ambient noise (Hildebrand, 2009), which could disrupt marine mammals. Previous studies investigating the influence of boat traffic on marine mammals include changes to vocalization patterns/communication abilities (Holt *et al.*, 2009; Jensen *et al.*, 2009) and alterations to biologically vital behaviours like foraging (Meissner *et al.*, 2015; Pirotta *et al.*, 2015), resting (Steckenreuter *et al.*, 2011; Visser *et al.*, 2011) and socializing (Visser *et al.*, 2011). Furthermore, dolphins have been shown to change their temporal and spatial patterns in response to high vessel traffic (Lusseau, 2005; Rako *et al.*, 2013). Therefore, it is logical that over time, dolphins in QCS have moved away from such areas of high use and rising vessel traffic.

Marine farming has also had a growing presence within QCS. Greenshell mussel (*Perna canaliculus*) and King Salmon (*Oncorhynchus tshawytscha*) farms have expanded in capacity, including the construction of one new Salmon farm in East Bay (1990) and two in Tory Channel (during 1992 and 2007; Baines, 2012; Haworth, 2010). Nutrients from mussel farms can lead to biodeposits, fouling organisms and additional inputs of carbon and nitrogen (Christensen *et al.*, 2003; Handley, 2015). Meanwhile finfish farms can form deposits of faeces, excess feed and organic particles, leading to an over-enriched environment (Handley, 2015; Keeley, 2013). Thus, over time, these can have an impact on the balance and general health of the ecosystem, which could influence the distribution patterns of delphinids as well as other marine life. In East Bay, QCS, mussel shell debris accumulated and a number of benthic organisms were affected under growing structures of mussel farms (Davidson & Richards, 2014). The growing presence of these farms may have been a contributing factor to the restricted use by Hector's dolphins, particularly in the far reaches of East Bay, where several mussel farms have been located since the mid-1990s. Mussel farm structures likely impede area usage and foraging amongst the similar Chilean dolphin (*C. eutropia*) off southern Chile (Ribeiro *et al.*, 2007), whereas bottlenose dolphins tend to associate with finfish farms, likely to increase their foraging capacity (Bonizzoni *et al.*, 2014; López, 2012). Although bottlenose dolphins consistently occurred in Tory Channel where two King salmon farms exist, a slight increase in density was detected mid-channel in the late 2000s, around the time when the second farm was constructed.

While anthropogenic growth likely contributed to some of the trends identified within QCS, changes within the ecosystem could have also taken place despite anthropogenic shifts. Natural die-offs or shifts in prey items could directly or indirectly lead to shifts in delphinid distribution. Furthermore, changes amongst predators (*i.e.*, large and small sharks) within QCS could have taken place. In fact, in nearby Pelorous Sound, a possible regime shift was thought to have occurred over time, in which an increased number of small shark species was noted mainly after 2006, coupled with a decrease in larger (shark) species (Handley, 2015; Myers *et al.*, 2007). If the dynamics were similarly impacted in QCS, something comparable may have lended to the restricted use of the Sound over time by Hector's and dusky dolphins.

Most likely it is a combination of all these changes that could have had compounding impacts to the ecosystem and thus, direct and/or indirect affects for delphinid ecology and spatial patterns. Regardless of natural or anthropogenic influences, or a combination, the identification of these patterns detected using historical records are an important resource for conservation managers. In multi-species regions in particular, animal spatial patterns may offer evidence in support of potential protective measures (Douvere, 2008), especially where elevated sighting or encounter rates occur. Thus, regions of high density in QCS identified from this research may be considered for spatial restrictions (*i.e.,* protected areas, zoning; Rayment *et al.*, 2011). Moreover, the findings presented here highlight the importance of long-term monitoring. Shifts in species distribution and area usage can occur (Hartel *et al.*, 2015). Therefore, protected areas should account for animal movement (Hartel *et al.*, 2015; Wilson *et al.*, 2004). Moreover, the designation of protected regions may need to be re-evaluated to account for potential changes in animal distribution, or as additional information becomes available (Rayment *et al.*, 2010). Consistent with a comprehensive management approach, all aspects of the area (*i.e.,* other species, anthropogenic activities) need to be evaluated regularly to account for any changes (Halpern *et al.,* 2008; Martins *et al.,* 2013; refer to further discussion of this topic in sections 1.6 and section 6.2.2.

2.4.4 Trends in swim-with-dolphin tourism

A further benefit of using historical records is that they can be useful in detecting trends of anthropogenic influence. Since the present study represents data collected from vessel logs, it depicts long-term trends in regional dolphin tourism. The data revealed: 1) an increase in the percentage of trips with dolphin swim encounters; 2) an increased number of intended (*i.e.*, dedicated) swim trips resulting in actual swims; and 3) the introduction of dolphin swim encounters with a prohibited species, as time progressed.

The increased percentage of trips with swim encounters in QCS over time is consistent with global trends of expansion within the cetacean tourism industry (Hoyt & Parsons, 2013; O'Connor *et al.*, 2009). Interviews with the original owners revealed that they did in fact have a full permit (allowing viewing and swimming) from the time that the permit was issued in 1994 (pers. comm., Zoe Battersby, July, 2014), precluding any assumptions that these findings were attributed to permitting differences. The original owners casually offered swim encounters to patrons when the company was initially established. They were not fond of people's expectations with dolphin swims and did not find the inclusion of dolphin swims to be necessary (pers. comm., Zoe Battersby, July, 2014).

In Akaroa, NZ, swim activities have expanded to the point where up to 18 dolphin swim trips occur daily (Martinez *et al.*, 2011). While swim-with-dolphin tourism in QCS took place on a comparatively small scale, the historic trends in QCS indeed represent the capacity for continued growth. This presents a management concern, considering the potential implications that tourism and swim tourism research reveal, including alterations to dolphin behavioural budget (Meissner *et al.*, 2015; Stockin *et al.*, 2008) and responses such as vessel (Constantine, 2001) and area avoidance (Lusseau, 2005). Such changes can result in biological implications to energy utilization and overall population fitness (Christiansen *et al.*, 2014; Williams *et al.*, 2006b).

The historical logbooks also indicated that the percentage of intended swim trips resulting in actual swims increased. Different interpretations of these results may be possible. For example, over time with repeated exposure, dolphins may have become more tolerant or habituated (Bejder *et al.*, 2009) to swim activity (*e.g.,* Orams, 1995). However, this is impossible to fully understand without behavioural data. Alternatively, operators may have become more dedicated to deliver their patrons a swim trip, as intended (Whitt & Read, 2006). Both of these explanations of the findings should alert conservation managers to the potential implications of dolphin tourism in QCS, particularly since swim tourism has been operating unstudied for years. Moreover, this study helped formulate further research questions, including the consideration of ways to assess dolphin engagement in swim encounters (refer to Chapter 5).

Lastly, these records demonstrate that swim encounters started to occur with a prohibited species (*i.e.,* Hector's dolphins). The inability to locate alternative species, paired with pressure on the operators (Whitt & Read, 2006) may have played a role in the observed trends. These findings emphasize the importance of frequent monitoring and the regular review of local permitting in order to support sustainable tourism (*i.e.,* tour activities that are in line with management objectives; Miller & Twining-Ward, 2006).

2.5 Limitations and Conclusions

This study established a baseline of temporal and spatial trends of delphinids within QCS through the collation of long-term historical sighting records. This research resulted in a number of important findings, while offering suggestions for further regional investigations. Nonetheless, inherent limitations often accompany historical data; therefore, they need to be acknowledged here. For example, entries in the database were recorded consistently from 1995–2011, representing an uninterrupted archive, however, despite the continuity of the records, the tour company had three owners during that time frame. Thus, it was assumed that the methods for searching and data recording were similar. It was also assumed that species identification was by an experienced crew member or skipper and was thus, accurate. While sighting conditions and search effort (*i.e.,* trips with an alternate purpose) were accounted for (refer to sections 2.2.2 and 2.2.3.1), there may have been occasions when inclement weather or water taxi trips were not recorded, so these trips would have been included in the analyses. This could have equated to under estimations if dolphins were not recorded during these trips, but may have just not been detected.

Moreover, data analyses in this study were limited in scope. Like similar research, the lack of archived GPS tracks was a limitation. In contrast to most historical studies, however, a major advantage here was that trips with and without dolphin sightings were recorded, so the data were able to be standardized by trip number. However, the method of standardization was limited as it allowed for temporal comparison of spatial patterns, but not absolute abundance or density estimates. Additionally, bottlenose dolphin sightings were missing group size data so sightings for this species could not be standardized to the same level of specificity as the others.

This may explain why more noticeable long-term spatial shifts were detected for Hector's and dusky dolphins. Furthermore, the model outcomes in this study were limited in capacity. The deviance explained by the models was generally low, which may have been due to the limited availability of the environmental proxies (*i.e.,* SST sourced just outside the Sound and tide sourced inside Picton Harbour). In addition, the response of the variable turbidity may have been influenced by its relatively limited availability (*i.e.,* it was summed monthly).

Records indicated that swim encounters occurred with Hector's dolphins even though this was a non-permitted species in QCS. As such, it is possible that these data were not always recorded (*i.e.,* reporter bias) and were underrepresented. However, while older records can often be inadequately preserved with portions of the data lost or missing, it is records missing clear location data, or species identification that are impractical (Boshoff & Kerley, 2010). In this collection, while some records may have been missing pertinent information like group size, the essential information (*i.e.,* species and location) were consistently available. Reading through handwritten logbooks for data collection was a tedious and time-consuming endeavour, however, this invaluable investment led to a baseline of data within QCS.

Despite some shortcomings, the database compiled in this study traces the long-term occurrence and distribution of three delphinid species. Exploration of these archived records resulted in the detection of a number of meaningful trends in QCS. In particular, this study indicated that amongst delphinids, Hector's dolphins, an endemic and endangered species, had the highest relative density in QCS across 16 years, suggesting that it is an important region for this species. The investigation of environmental covariates suggests their possible influence on delphinid temporal occurrence in QCS. Furthermore, delphinid spatial data exploration indicated seasonal shifts in all three species and notable long-term shifts amongst Hector's and dusky dolphins. Finally, the growth of regional swim-with-dolphin tourism was recognized. Discounting these historical records would have been a detriment, as the patterns during that time frame would not have otherwise been demonstrated. Thus, the present study provides evidence supporting the value of using historical datasets for cetacean research.

The techniques used here may also be beneficial in other areas where historical records are accessible. Efforts can be made to approximate sighting locations when exact coordinates are not given, similar to the method used here. Likewise, where possible, researchers may standardize sighting data in a comparable manner to investigate temporal trends and/or spatial patterns or shifts over time. Moreover, environmental data can be accessed where available to explore potential ecological contributions. The application of one, or a combination of these methods may add meaning to historical sighting records, lending to scientific contributions elsewhere. Researchers in regions with limited funding, in particular, may find these techniques valuable.

The findings presented here subsequently led to a number of additional questions that influenced the design of further research for this thesis that will be discussed in successive chapters. These include the exploration of more current trends in species' distribution and density (refer to Chapter. 3), factors that contribute to delphinid habitat use (Chapter 4) and characteristics of swim-with-dolphin tourism within QCS (Chapter. 5). This research demonstrates that when considering historical data sources, while it is important to be mindful of potential drawbacks, the focus must remain on the crucial role that these type of data may serve.

Chapter 3

Distribution, relative density and range of sympatric delphinids in Queen Charlotte Sound, New Zealand

Hector’s (*Cephalorhynchus hectori hectori*), bottlenose (*Tursiops truncatus*) and dusky (*Lagenorhynchus obscurus*) dolphins in Queen Charlotte Sound, NZ.

3.1 Introduction

Cetaceans are highly mobile animals that often utilize the marine environment disproportionately, with distribution varying on temporal and spatial scales (Samuel *et al.*, 1985; Viddi *et al.*, 2010). The investigation of these patterns, particularly in multi-species areas allows for an understanding of ecological interactions. These may include the distinct adaptations that sympatric species develop to reduce competition (Roughgarden, 1976). As with all organisms, the specific resources necessary for cetacean survival, categorized in terms of trophic, temporal and spatial aspects (Pianka, 1974) define its niche, or ecological role (Hutchinson, 1957). Competitive exclusion can be avoided and co-existence will occur when similar species partition their niches along at least one of these defining aspects (Pianka, 1974). This can be accomplished as a result of prey specialization (Ballance, 1985) or spatial and/or temporal segregation of the region (Bearzi, 2005b). For example, sympatric striped (*Stenella coeruleoalba*) and short-beaked common dolphins (*Delphinus delphis*) in the Bay of Biscay (Northeast Atlantic, between France/Spain), exhibit slight differences in their diet content (Das *et al.*, 2000). Similarly, stable isotope analysis reveals that rorqual species existing in close proximity in the Gulf of St. Lawrence, Canada, consume dissimilar proportions of shared prey items (Gavrilchuk *et al.*, 2014). Conversely, bottlenose (*Tursiops truncatus*), short-beaked and long-beaked (*D. capensis*) common dolphins in Santa Monica Bay, California, occur throughout the year, but bottlenose dolphin association with shallow water and common dolphin association with deeper water indicate spatial segregation within the bay (Bearzi, 2005c). In the Bahamas, permanent species segregate according to depth, while transient species occur when resources are high and are hypothesized to be otherwise competitively excluded (MacLeod *et al.*, 2004).

While the recognition of trends in cetacean spatial and temporal distribution may be interesting from an ecological perspective, it also has potentially important functional applications. Quantifying species' distribution and aspects of its niche are integral for the development of effective management (Hastie *et al.*, 2003a). Well-designed and comprehensive management plans, which include all aspects of a region, are critical for conservation efforts (Guisan & Thuiller, 2005), particularly when endangered species are involved (Weir & Sagnol, 2015). However, management of the marine environment is complex and involves the consideration of a number of interacting components. Marine Spatial Planning (MSP) is one approach to organize the use of the marine realm, while balancing its competing uses with the protection of resources (Portman, 2016). This concept has expanded from a number of quantitative approaches in the terrestrial domain (Lafortezza *et al.*, 2005) and is an evolving practice in the marine environment.

The incorporation of distribution and density data into spatial management plans can help reduce potential conflict and cumulative impacts related to the expansion of anthropogenic activity (Fulton *et al.*, 2015). Kernel estimation methods are deemed popular and robust for estimating animal range (Kernohan *et al.*, 2001). Meanwhile, animal sighting rates (SR) and encounter rates (ER), respectively, account for the number of sightings (groups) or animals (incorporating sighting group size), per unit of survey effort. These are useful measures to determine the relative density or relative abundance of a population on temporal (monthly or seasonal) scales, as in Dwyer *et al.* (2016) or between two or more species (Kiszka *et al.*, 2007). Such calculations can also be used in replicate studies to monitor populations for changes over extended periods (Bearzi *et al.*, 2005). This can be useful in a dynamic environment, particularly as the rise of human influences and stressors on coastal regions challenge managers (Crowder & Norse, 2008). Anthropogenic growth is being observed in many forms including housing and infrastructure development (Jefferson *et al.*, 2009), the expansion of aquaculture (Tal *et al.*, 2009) and the presence of vessel traffic. Specifically, increased vessel traffic involves direct influences such as pollution and habitat degradation from things like anchor damage and bilge water discharge (Lloret *et al.*, 2008). Likewise, indirect influences include noise pollution that can impact animal communication abilities (Codarin *et al.*, 2009; Jensen *et al.*, 2009) and even lead to displacement (Buckstaff *et al.*, 2013).

In New Zealand (NZ), human related influences such as fishing, aquaculture and tourism are important aspects of the economy (Statistics New Zealand, 2010, 2015). As the gateway between the North and South Islands, Queen Charlotte Sound (QCS) is utilized by the inter-islander ferries, commercial and recreational boaters, and in aquaculture (refer to section 1.6 and Figure 1.4 for details). While the adjoining Waikawa Marina is one of NZ’s largest with over 600 berths, increased vessel traffic has led to pressure for expansion (Mackenzie, 2008). Marine farming of King (Chinook) Salmon (*Oncorhynchus tshawytscha*) has been present in QCS since 1985, but three additional farms were built between 1990–2007 (Baines, 2012; Haworth, 2010) and another new one in 2014 (Monk, 2015). Furthermore, within QCS and Tory Channel there are currently 18 existing greenshell mussel (*Perna canaliculus*) farms, which grew from an experimental venture in the 1960s. Despite anthropogenic expansion in

QCS, limited cetacean research has been conducted (Clement *et al*., 2001; Markowitz 2004; Merriman *et al*., 2009; refer to section 2.1). The investigation of historical records indicated the presence of multiple species, temporal trends in species' occurrence and shifts in long term distribution (refer to Chapter 2). These findings, however, suggest the need for more detailed investigation within QCS in order to understand current patterns. Platforms of opportunity (PoPs; *e.g.,* ferries, tour boats, other survey vessels) can be a convenient, resourceful way to collect cetacean data at a minimum cost (Ingram *et al.*, 2007). In QCS, the opportunity for regular, extended data collection was made possible through existing tour vessels. The goal of this chapter was to determine temporal trends in density and patterns of distribution for three sympatric delphinids and to develop an understanding of how they may be partitioning the region. A secondary goal of this research was to contribute to the comprehensive conservation management of QCS by delineating important regions and periods of time for these focal delphinid species. Specifically, the objectives were to:

- Examine temporal relative densities of dolphin groups and animals
- Explore patterns in spatial distribution by using kernel density estimates to:
    - quantify seasonal spatial use of QCS
    - determine species' overall range within QCS
- Calculate species' temporal and spatial overlap

3.2 Methods

3.2.1 Study site

In this and subsequent chapters, the Sound is segmented into four sections: the outer, middle and inner Sound; and Tory Chanel (Figure 3.1), similar to those determined by Hadfield *et al.* (2014; refer to Figure 2.2.1 for further study area details). The outer Sound meets Cook Strait at Cape Jackson (174°19'E; 40°59'S) and Cape Koamaru (174°22'E; 41°5'S). The middle Sound stretches to Bull Head (174°8'E; 41°12'S) and Kaitapeha Bay (174°10'E; 41°13'S). The inner Sound extends to Okiwa Bay (173°54'E; 41°5'S). Tory Channel reaches from Dieffenbach Point (174°8'E; 41°13'S) and Kaitapeha Bay to the channel entrance at Cook Strait (174°19'E; 41°12'S).

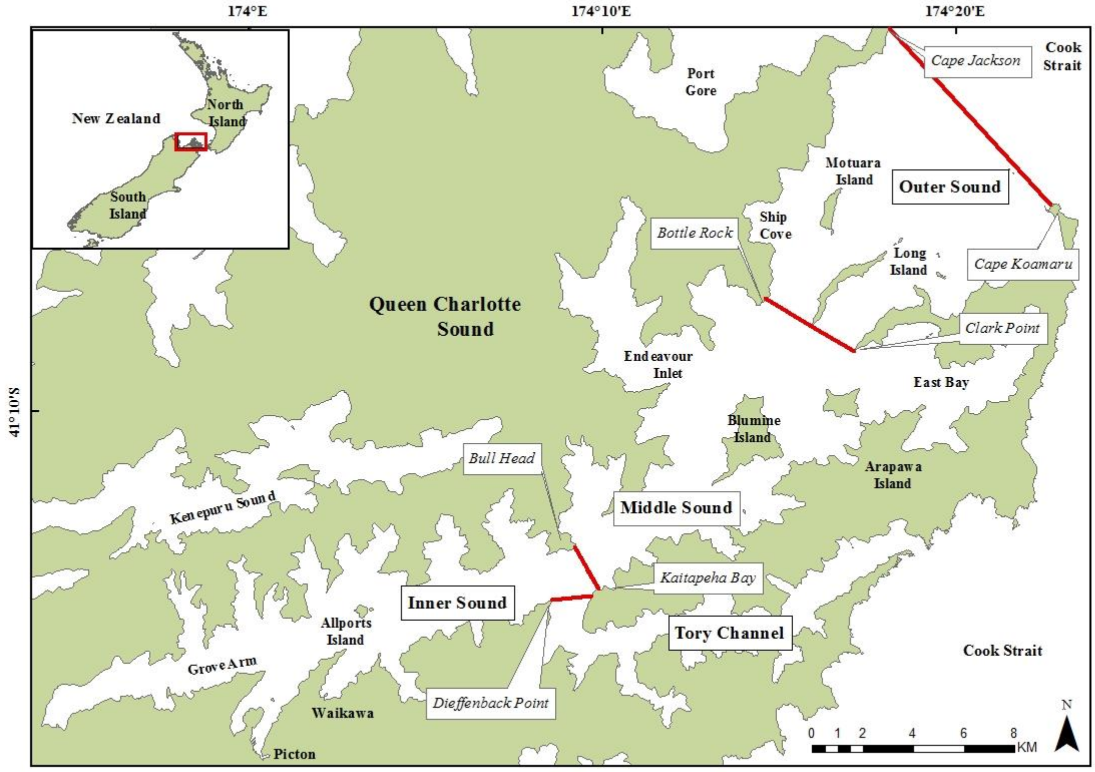


Figure 3.1 Study area in QCS, NZ, indicating major points of interest as well as delineated sections of the Sound (outer, middle, inner and Tory Channel) based on those derived by (Hadfield *et al.*, 2014).

3.2.2 Data collection

Dolphin sighting data were opportunistically collected from December 2011 to April 2014 aboard two catamaran tour vessels with similar specifications (Table 3.1).

Table 3.1. Specifications of tour vessels that were used for data collection in QCS, NZ, from December 2011–April 2014.

Specifications	Vessel A	Vessel B
Length (m)	13	13
Viewing height (m)	2.4	2.5
Engine type	Inboard propeller	Inboard propeller
Engine power (hp)	220	300
Maximum speed (knots)	18	19

Due to the opportunistic nature of the data collection, vessel operators and prevailing weather conditions determined survey tracks and the direction of travel. Trips departed twice daily, during the morning and afternoon from Picton Harbour (Figure 3.1). Morning trips (on vessel A) were dedicated swim-with-dolphin trips operating during the months of October–April. They departed at 0900 hrs and lasted up to four hrs in duration. Afternoon trips took place on both vessels and collectively operated year-round, departed at 1300 hrs and lasted up to five hrs in duration. Surveys were considered non-systematic in design (*e.g.*, Ingram *et al.*, 2007) but followed semi-fixed paths, so most of the Sound was sampled, although coverage in some areas of the study area were more thorough than others (Figure 3.2).

Visual surveys were conducted via naked eye and 10x30 Canon binoculars by the primary observer (CC-author) and at least one other trained observer (Wiseman *et al.*, 2011). A continual scanning protocol in a 180° arc ahead of the vessel was followed (Mann, 1999). “On effort” surveys commenced when the boat arrived at Picton Harbour (*i.e.*, the jetty at the entrance of the port) and continued until re-entry to this location. Sighting conditions (weather, Beaufort Sea State *i.e.,* BSS, visibility and glare) were continually assessed and updated throughout the survey as they changed. Search effort was changed to “off-effort” in periods of rain, BSS > 3, poor visibility (*i.e.,* obstructed by rain or fog) and glare > 50% in the observer’s field of view, since detection ability decreases in lesser conditions (Kiszka *et al.*, 2007). Visual cues such as fins breaking the surface, splashing and blows were used to help detect cetaceans (Berghan & Visser, 2000). When the vessel stopped, observers continued to search for cues with the naked eye or binoculars but in a 360° search area. Vessel location data were collected continually every 10 sec using a GARMIN Etrex 20. When a dolphin group/individual was initially sighted, a Global Positioning System (GPS) waypoint was recorded and the survey was changed to “off effort.” The sighting cue was recorded and bearing (°) and distance (m) to the group/individual was visually estimated (*e.g*., Ingram *et al*., 2007), using the vessel length (13 m) as a scale. Estimates were validated against fixed points (*i.e.,* land, stationary vessels) using reticle binoculars by a trained, experienced observer. The vessels would typically approach the dolphins, whereby an additional GPS waypoint at the closest approach to the group was recorded, if not, the survey took place in “passing mode” (*i.e.*, while in transit; Wall *et al.*, 2006).

Species and group size were assessed via the naked eye, or through binoculars, if from a distance. Search effort recommenced upon departure from a group/individual to search for independent groups. A group was defined as any number of animals in apparent association, moving in the same direction and likely involved in the same behaviour (Shane, 1990; Wells *et al*., 1980). Dolphins may alternate group structure by fission-fusion (breaking into smaller subgroups and then re-coalescing into the larger pod). Small subgroups are considered part of the entire large group from which they originate (Defran & Weller, 1999). Group size was assessed for minimum, maximum and best estimate values at sea, but given the interspecific variation in group size and range, best estimate values were used for analytical consistency (Kiszka *et al.*, 2007).

3.2.3 Data analysis

3.2.3.1 Survey effort

Due to the opportunistic nature of the data collection, the vessel speed was not uniform, and at times the vessel remained stationary. Therefore, surveys were standardised by the amount of time actively searching (on-effort; Wall *et al*., 2006, Elwen *et al.*, 2009). Although distance (*i.e.,* km travelled searching) is a more traditional form of data standardization, time (*i.e.,* hrs searching) was deemed more appropriate in this study since the vessel speed and thus, distance covered could not be controlled (MacLeod *et al.,* 2004). Search effort was quantified by summing the total amount of time spent on effort in 3x3 km grid cells per survey using features in ArcGIS 10.0 (ESRI, 2011). The grid was created using the *Genvecgrid* tool in Geospatial Modelling Environment (GME; Beyer, 2014). Total survey effort coverage (Appendix 3.1) was used to select this cell size (3x3 km) to allow for a minimal coverage of five surveys or 0.5 hrs per grid. Areas with low survey effort can result in over-inflated relative abundance and density estimates (Rayment *et al.*, 2009). Therefore, grid cells that were sampled less than five times or 0.5 hrs during the study period were removed (Ingram *et al.*, 2007) and associated sightings were deemed off-effort.

Austral seasons were defined as: summer (December–February), autumn (March–May), winter (June–August) and spring (September–November) as per Merriman (2007). All analyses in ArcGIS were conducted using the New Zealand Transverse Mercator (NZTM) 2000 projection. Vessel tracks were downloaded from the GPS unit using Garmin Basecamp (Garmin International, 2011). They were examined and off-effort sections were removed according to corresponding waypoints. Files were saved monthly in csv format and subsequently imported into ArcMap.

3.2.3.2 Sightings and group sizes

Sighting data consisted of on-effort sightings and group size best estimates. GPS waypoints that were recorded at the closest approach were used for sighting location data. For those groups that were not approached, sighting locations were estimated by using the measure tool in ArcMap based on the initial sighting waypoints and the recorded bearing and distance measurements. In order to remove potential outliers and prevent inflated density estimates, sighting data were truncated to eliminate the most distant sightings (Becker *et al.,* 2014). This ensured that calculations were performed on sightings within distances that were consistently and confidently observed. Sighting distances were binned, into 200 m (bottlenose dolphins) and 100 m (dusky and Hector’s dolphins) intervals. The larger bins for bottlenose dolphins were due to the farther sighting distances for this larger, more conspicuous species. Limits were determined arbitrarily using cumulative frequency histograms whereas the majority (95%) of sightings consistently occurred. Data normality was explored using a Shapiro-Wilk test. Since data were non-normally distributed, Kruskal-Wallis tests were used to explore interspecific differences in mean group size and seasonal differences in mean group size for each species. Analyses were conducted in SPSS version 21 (IBM, 2012) and ArcMap 10.0 (ESRI, 2011). The significance level was set at 0.05.

3.2.3.3 Temporal relative density

The relative densities of all species were calculated in terms of SR and ER, the respective number of groups or animals encountered per hr of search effort. This proxy has been used in comparable studies as a means of interspecific comparisons and to assess patterns of temporal occurrence or population change (Elwen *et al.*, 2009; Spyrakos *et al.*, 2011; Wall *et al.*, 2006; Weir, 2011). Seasonal SRs and ERs were calculated by adding the total number of sightings or individuals and dividing by the total number of hrs per austral season. Mean seasonal SRs and ERs were selected over annual values (Appendix 3.2) to allow for comparison between species and other studies. One way Analysis of Variance (ANOVA) or Kruskal-Wallis tests were used to test for seasonal differences in SR and ER, depending on data normality, which was explored using a Shapiro-Wilk test. Associated sampling variance was calculated as per the following equation (Buckland *et al.*, 2001):

$$Var\left(\frac{n}{L}\right) = \frac{\sum_{i=1}^{k} \frac{l_i}{L} \left(\frac{n_i}{l_i} - \frac{n}{L}\right)^2}{k-1}$$

The total number of groups or animals was represented by n, while the total number of hrs spent on effort was represented by L. The number of groups or animals in a survey day was represented by n_i while l_i was the number of hours on effort per survey day and k represented the number of days surveyed in a season.

3.2.3.4 Spatial relative density and range

Kernel density estimation (KDE) was calculated using the *Kernel Density* tool, in the *Spatial Analyst* extension of ArcGIS, to explore seasonal patterns of relative density of delphinid species in QCS. Density values were calculated based on dolphin sightings, standardized by the number of individuals in a group and the survey effort (hrs) per 3x3 km grid cell, per season (Dwyer *et al.*, 2016). These weighted values account for the heterogeneity of survey effort amongst grid cells. Selected settings within the KDE tool included search area, which was set to 4,000 m. This was the smallest value that conservatively predicted dolphin densities while limiting the kernel to consider information from only adjacent cells (Chainey, 2013; Rayment *et al.*, 2011). Additionally, the output cell size was set at 500 m, as this was determined to produce a near continuous surface (*e.g.,* Dwyer *et al.,* 2016). This parameter primarily impacts the visual appeal of the output and while its influence on the predictions may vary, they are likely minor (Chainey, 2013). The estimates were confined to a mask that was equivalent to the total area of the grid, so that predictions did not surpass the survey region.

Spatial relative densities were calculated for each species using all sightings and the total survey effort per grid, overall and per season, in the aforementioned manner. These KDE rasters were then used to calculate 95% and 50% isopleths, which represent each species' 95% and 50% utilization distribution or range and central range within QCS, as in (Rayment *et al.*, 2009). Since these calculations were restricted to data from the study area, it is important to highlight that they exclusively represent species' usage within QCS only, as the various species' "true" (home/core) range may extend beyond the study area (*e.g.,* Ingram & Rogan, 2002; Sprogis *et al.*, 2016). Thus, for the purposes of this study and to avoid confusion, the 95% isopleth is referred to as "range" and 50% isopleth is referred to as "central range" within QCS. Using the *Isopleth* tool in GME (Beyer, 2014), isopleths were created and then converted into polygons using tools in ArcMap. The total area of the range and central range were calculated using the geometry calculator in ArcGIS. Since no significant difference in seasonal ERs across years were detected (Hector's: ANOVA $F_2 = 2.74$, p = 0.1; bottlenose: $\chi^2 = 2.35$, df = 2; p = 0.31; dusky: $\chi^2 = 0.31$, df = 2, p = 0.86; Appendix 3.2) seasonal KDE were calculated by season across the whole study period.

3.2.3.5 Species overlap

Measuring overlap amongst the various dimensions of a niche can help identify the degree to which niche segregation is taking place (Schoener, 1968). A number of metrics (*e.g.,* Schoener's *D,* Bray-Curtis, Pianka's *O,* Horn's *R*) have been developed and increasingly used to quantitatively measure niche overlap (Roedder & Engler, 2011). Comparison amongst several techniques indicates that Schoener's *D* performs best (Roedder & Engler, 2011). Here, overall temporal overlap was calculated using Schoener's statistic, which is traditionally used with values representing the relative use of a particular habitat (Schoener, 1968; Warren *et al.*, 2008; Warren *et al.*, 2010). The following formula was utilized, whereas the calculated values for the SR of each species combination *i.e.*, Hectors (x) and bottlenose (y) are represented by *p*x and *p*y, respectively, for each season (of each year), *i*. This results in a value, *D*, ranging from 0 to 1, whereas 0 represents no overlap, and 1 represents complete overlap (Schoener, 1968).

$$D\,(px,py) = 1\text{-}\tfrac{1}{2}\textstyle\sum_{i=1}^{n}\ \left| px,i - py,i \right|$$

For spatial data, Schoener's statistic is recommended to be used with Kernel density functions for an unbiased estimate of *D* (Broennimann *et al.*, 2012). Therefore, in order to quantify interspecific spatial overlap in the same manner as above, the kernel density rasters representing overall and seasonal relative density were converted to centre point values using the *Raster to Point* tool in ArcMap. In this manner, the value at the centroid of each 500 m^2 KDE output grid cell was exported from ArcMap so that Schoener's *D* could be calculated for the spatial data as well, using the same equation. To create depictions of species' spatial overlap, individual species' range were overlaid (*i.e.*, Hectors/bottlenose, Hector's/dusky, bottlenose/dusky and all three species) and transparency settings were adjusted in ArcGIS to allow areas of overlap to be distinctly visible.

3.3 Results

3.3.1 Survey effort

A total of 677 surveys were conducted in QCS from December 2011 to April 2014 that resulted in 1,613 hrs of "on effort" search effort covering a survey area of 263.3 km^2 (refer to Figure 3.2). This was comprised of 301 AM surveys (553 hrs) and 376 PM surveys (1060 hrs). Surveys occurred during each month of the study, but as a result of the opportunistic nature of data collection, survey effort was not equal. It was the highest during the second year of sampling Table 3.2) and almost twice as high during summer and autumn seasons (Figure 3.3). Sampling occurred during three years for summer and autumn and two years during winter and spring.

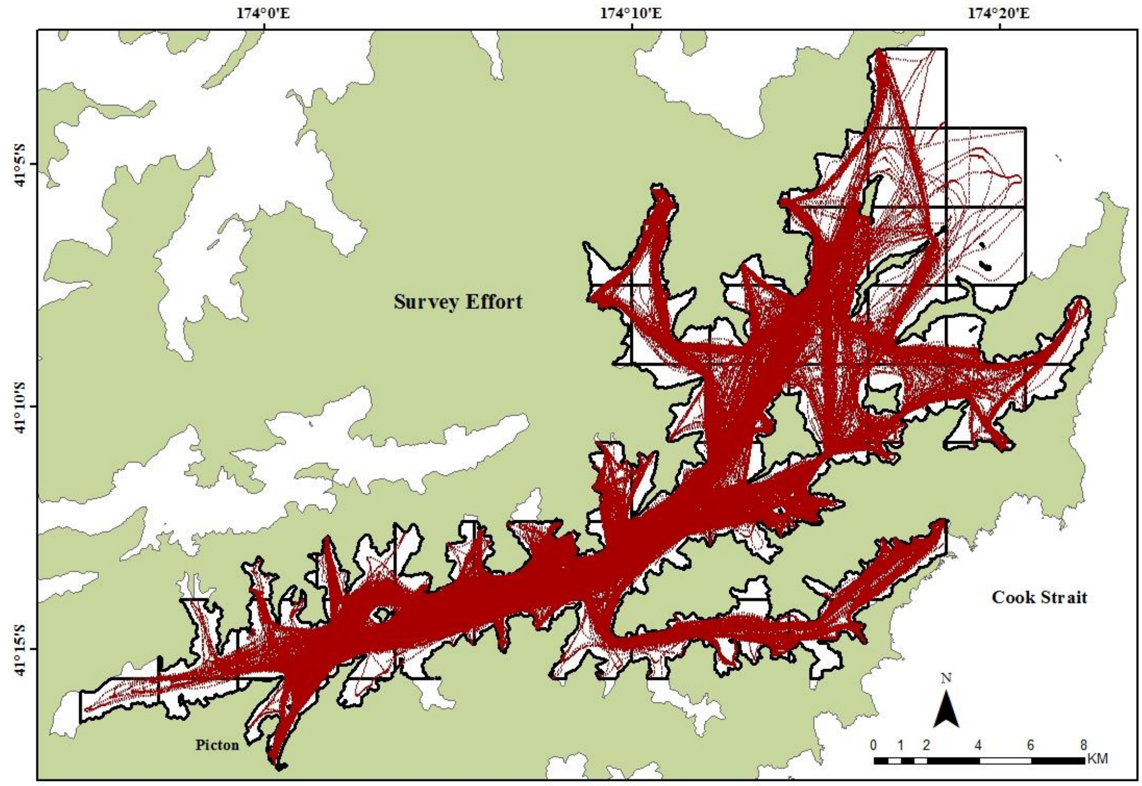


Figure 3.2. Search effort from surveys during December 2011–April 2014 in QCS, NZ.

Table 3.2. Seasonal effort, indicated by the number of surveys and hours, during opportunistic data collection in QCS, NZ, from December 2011–April 2014.

	Summer		Autumn		Winter		Spring		Totals	
	Surveys	Effort (hrs)	Surveys	Effort (hrs)	Surveys	Effort (hrs)	Surveys	Effort (hrs)	Surveys	Effort (hrs)
2012	52	140.7	64	170.7	38	109.4	53	120.9	207	**541.7**
2013	85	206.5	82	220.1	54	165.6	59	134.6	280	**726.8**
2014	113	208.5	77	136.4	–	–	–	–	190	**344.8**
TOTAL	**250**	**555.7**	**223**	**527.1**	**92**	**275.0**	**112**	**255.5**	**677**	**1613.3**

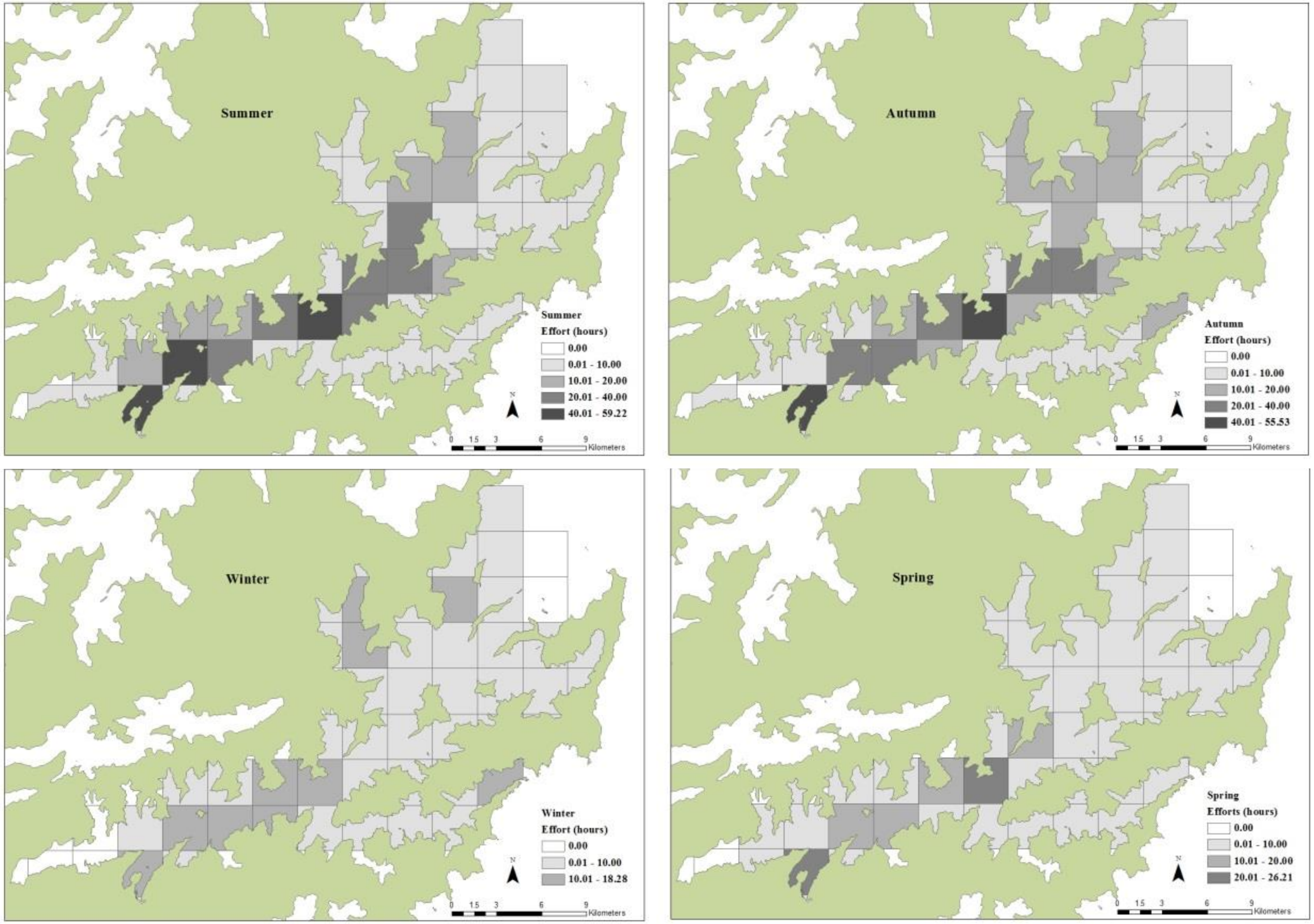


Figure 3.3 Seasonal survey effort standardized within a 3x3 km grid from surveys in QCS, NZ, from December 2011–April 2014.

3.3.2 Sightings

Following data truncation, there was a total of 290 Hector's dolphin, 268 bottlenose dolphin and 71 dusky dolphin sightings. Bottlenose dolphins were sighted up to 4,000 m from the vessels with 50% and 95% detected within ~400 m and 2,000 m, respectively. Data were truncated at 2,000 m since sightings beyond this were sporadic. Hector's dolphins were sighted up to 1,500 m from the vessels with 50% and 95% detected within ~200 m and 500 m, respectively. Dusky dolphins were sighted up to 1,600 m from the vessels with 50% and 95% detected within ~200 m and 500 m, respectively. Thus, for both species, the data were truncated at 500 m (Appendix 3.3).

3.3.3 Group sizes

Kruskal-Wallis tests indicate that mean group size differed significantly between the three dolphin species ($\chi^2 = 314.64$, df = 2, $p < 0.001$). Pairwise comparisons indicated significant differences between all species ($p < 0.001$). There was no evidence of a seasonal effect on Hector's dolphin group size ($\chi^2 = 4.26$, df = 3, p = 0.24; Table 3.3) or dusky dolphin group size ($\chi^2 = 2.36$, df = 3, p = 0.50; Table 3.3). However, there was evidence of a seasonal difference on bottlenose dolphin group size ($\chi^2 = 26.82$, df = 3, $p < 0.001$), whereas values in autumn were greater than spring ($p < 0.001$; Table 3.3).

Table 3.3. Group sizes of sympatric delphinids (Hector’s, bottlenose and dusky dolphins) observed on-effort during opportunistic surveys conducted from December 2011–April 2014 in QCS, NZ.

		Mean	SD	SE	Range	n
Hector's	Summer	4.2	3.5	0.3	1 – 20	168
	Autumn	3.8	2.8	0.3	1 – 14	106
	Winter	1.7	0.6	0.3	1 – 2	3
	Spring	3.6	3.7	1.0	1 – 13	13
	Overall	**4.0**	**3.3**	**0.2**	**1 – 20**	**290**
Bottlenose	Summer	27.6	20.2	2.2	1 – 75	86
	Autumn	36.5	20.9	2.1	2 – 80	97
	Winter	25.2	17.5	2.6	2 – 80	46
	Spring	17.9	18.2	2.7	2 – 70	39
	Overall	**29.1**	**20.7**	**1.3**	**1 – 80**	**268**
Dusky	Summer	7.8	2.1	0.8	5 – 10	8
	Autumn	5.2	4.7	2.1	1 – 13	5
	Winter	10.3	11.5	2.7	3 – 40	18
	Spring	8.4	6.3	1.0	2 – 30	40
	Overall	**8.5**	**7.7**	**0.9**	**1 – 40**	**71**

3.3.4 Temporal patterns: Relative density and temporal overlap

Significant variation was detected in the mean number of groups encountered within the study area (mean SRs; $\chi^2 = 8.38$, df = 2, $p = 0.02$). The values for bottlenose (mean = 0.17, SD = 0.06, n = 10) and Hector's dolphins (mean = 0.16, SD = 0.12, n = 10) were both greater than the value for dusky dolphins (mean = 0.05, SD = 0.075, n = 10; $p = 0.006$ and $p = 0.03$, respectively). Likewise, there was a statistical difference between the mean number of individuals encountered for each species (mean ERs; $\chi^2 = 19.35$, df = 2, $p < 0.001$). The values for bottlenose dolphins (mean = 4.88, SD = 2.63, n = 10) were greater than both Hector's (mean = 0.63, SD = 0.59, n = 10) and dusky (mean = 0.43, SD = 0.67, n = 10; $p < 0.01$ and $p < 0.001$) dolphins, respectively.

A significant seasonal effect was detected amongst SRs (ANOVA $F_3 = 23.39$, $p = 0.01$) for Hector's dolphins (Figure 3.4). Values in summer (mean = 0.29, SD = 0.07, n = 3) were higher than spring (mean = 0.05, SD = 0.01, n = 2, $p = 0.003$) or winter (mean = 0.009, SD = 0.01, n = 2); and values in autumn (mean = 0.2, SD = 0.006, n = 3) were higher than spring ($p = 0.03$) or winter ($p = 0.01$). There is some evidence of higher seasonal ERs (ANOVA $F_3 = 4.62$, $p = 0.053$) in summer (mean = 1.20, SD = 0.65, n = 3) compared to winter (mean = 0.02, SD = 0.02, n = 2; $p = 0.06$; Figure 3.4). There was no evidence of seasonal variation in SRs (ANOVA $F_3 = 0.16$, $p = 0.92$) or ERs ($\chi^2 = 4.66$, df = 3, $p = 0.20$; for bottlenose dolphins (Figure 3.5) or SRs ($\chi^2 = 6.8$, df = 3, $p = 0.078$) or ERs ($\chi^2 = 5.82$, df = 3, $p = 0.12$) for dusky dolphins (Figure 3.6). The calculation of Schoener's *D* for SR of dusky and Hector's dolphins was relatively low (0.22), suggesting little temporal overlap for these species, while the value for bottlenose and Hector's dolphins was much greater (0.67), suggesting higher temporal overlap. The value for dusky and bottlenose dolphins was mid-range between the other groups (0.49; Table 3.4).

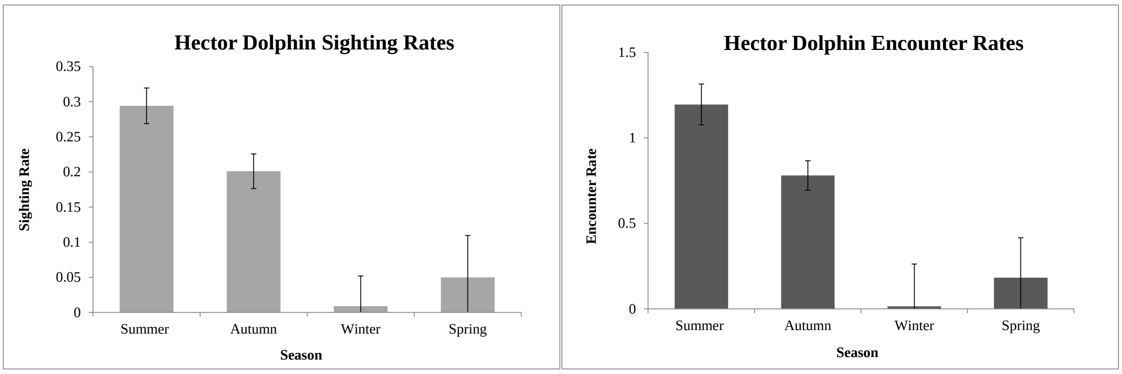


Figure 3.4. Seasonal sighting and encounter rates (± SD) of Hector's dolphins (*Cephalorhynchus hectori*) for surveys in QCS, NZ, during from December 2011–April 2014. *Note that scale differs amongst species.*

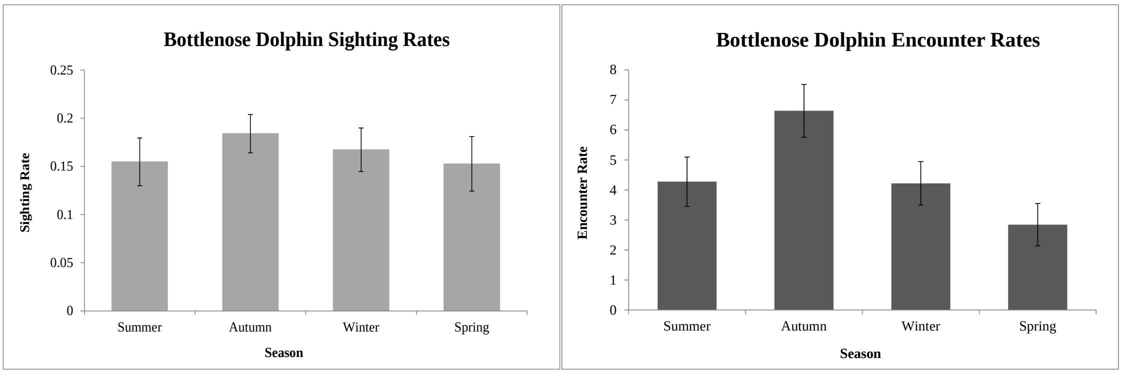


Figure 3.5. Seasonal sighting and encounter rates (± SD) of bottlenose dolphins (*Tursiops truncatus*) during surveys in QCS, NZ, from December 2011–April 2014. *Note that scale differs amongst species.*

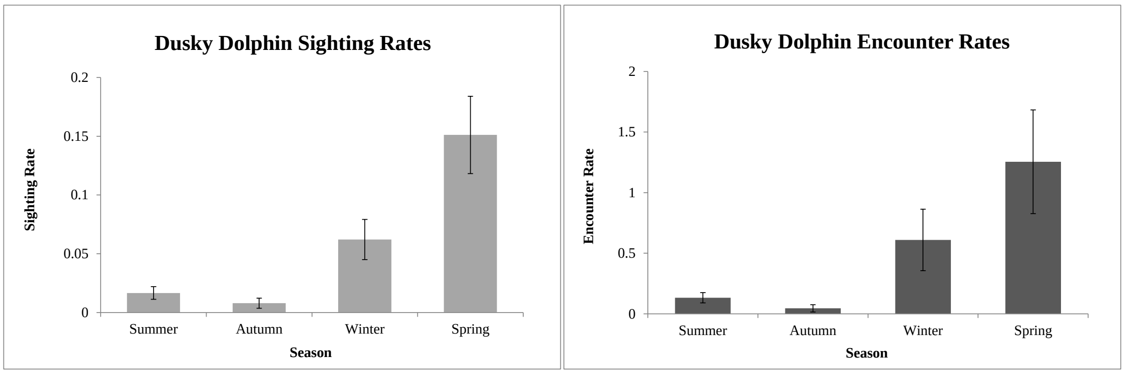


Figure 3.6. Seasonal sighting and encounter rates (± SD) of dusky dolphins (*Lagenorhynchus obscurus*) during surveys in QCS, NZ, during from December 2011–April 2014. *Note that scale differs amongst species.*

Table 3.4. Schoener’s *D* values indicating overall temporal overlap of all delphinid species’ combinations in QCS Sound, NZ, during December 2011–April 2014.

	Bottlenose	Dusky
Hector's	0.67	0.22
Bottlenose		0.49

Table 3.5. Overall range and central range of Hector’s, bottlenose and dusky dolphins within QCS from December 2011–April 2014.

Species	Central range (km^2)	Range (km^2)
Hector's	10.6	58.8
Bottlenose	65.2	187.1
Dusky	8.5	124.8

3.3.5 Spatial patterns: Distribution, spatial relative density and range

3.3.5.1 Hector’s dolphins

Hector’s dolphins were distributed from Allports Island through the central part of the Sound, in Tory Channel as far out as Motuara Island. The central range and overall range covering 10.6 km^2 and 58.8 km^2 (Table 3.5), respectively, were mainly localised to the middle Sound (Figure 3.7). Distribution and density varied seasonally, as dolphins were more widespread and in greater densities during summer and autumn. Hotspots around Pickersgill Island and south of Blumine Island were more concentrated during the summer season (Figure 3.8). The estimates in Tory Channel for Hector’s dolphins during autumn appear over-inflated, likely because of the convoluted shape of QCS.

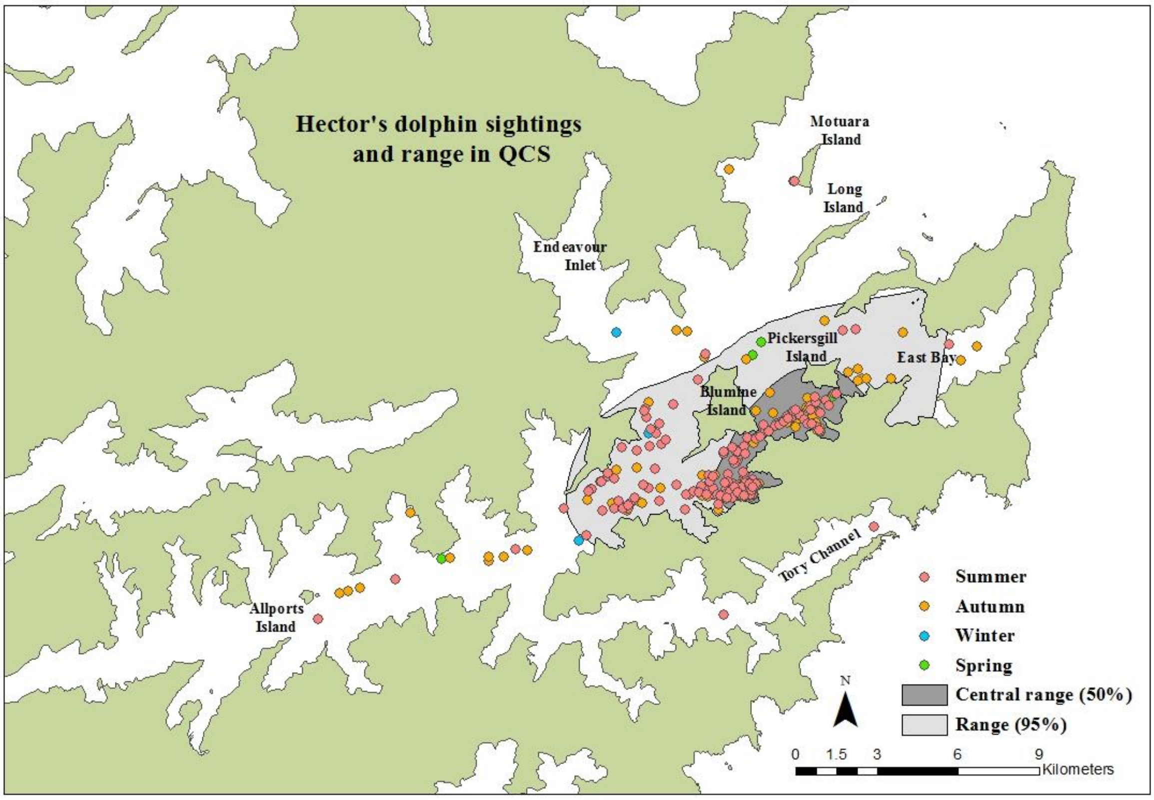


Figure 3.7 Central range and range of Hector’s dolphins (*Cephalorhynchus hectori*) in QCS, NZ, during December 2011–April 2014.

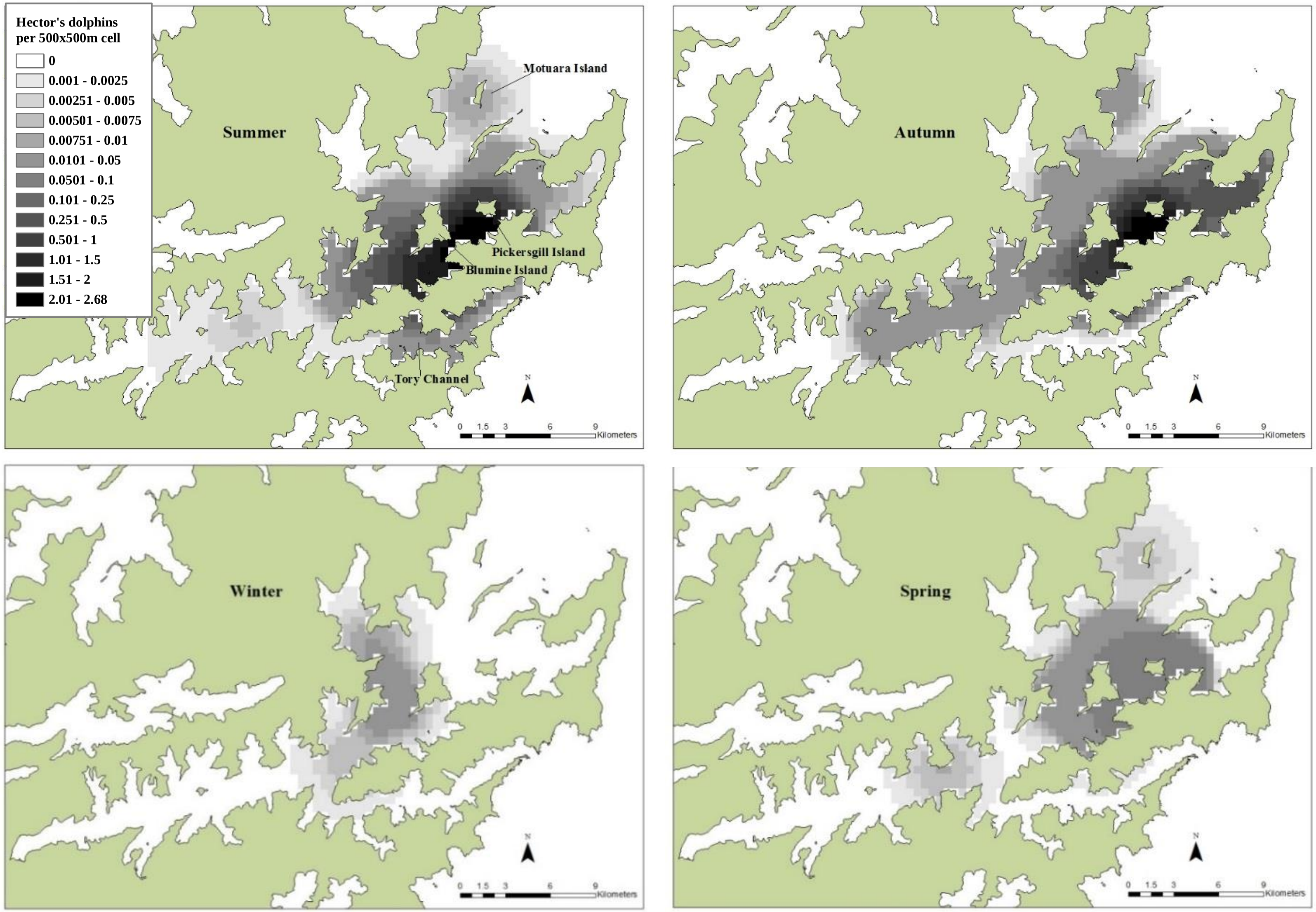


Figure 3.8. Seasonal kernel density estimates of Hector's dolphins (*Cephalorhynchus hectori*) in QCS, NZ, from December 2011–April 2014.

3.3.5.2 Bottlenose dolphins

Bottlenose dolphin range (187.1 km^2) spread throughout the extent of the study area, from Picton Harbour and the start of Grove Arm in the inner Sound, through the middle Sound, Tory Channel, Endeavour Inlet, East Bay and the outer Sound. Their central range, covering 65.2 km^2 (Table 3.5), extended from the middle to outer Sound (Figure 3.9). Distribution was more widespread in summer and autumn, while more of the sightings during winter and spring were situated toward the inner Sound. Density values were quite consistent throughout summer and autumn, but higher values were observed toward the outer parts of the Sound, as fewer, but large groups of animals congregated near the Sound entrance. In contrast, numerous small groups were sighted further in the Sound during summer and winter. Hotspots in winter were observed near Allports Island, as well as toward the Outer Sound. Spring hotspots were observed around Bay of Many Coves, the entrance of Tory Channel, outside Endeavour Inlet and East Bay (Figure 3.10). In East Bay during spring there was one particularly large sighting. To investigate its effect, this sighting was removed and the spring KDE was re-run (Appendix 3.4a). This offers some evidence that the hotspot in East Bay was the result of over-inflation from the large sighting, combined with lower survey effort here.

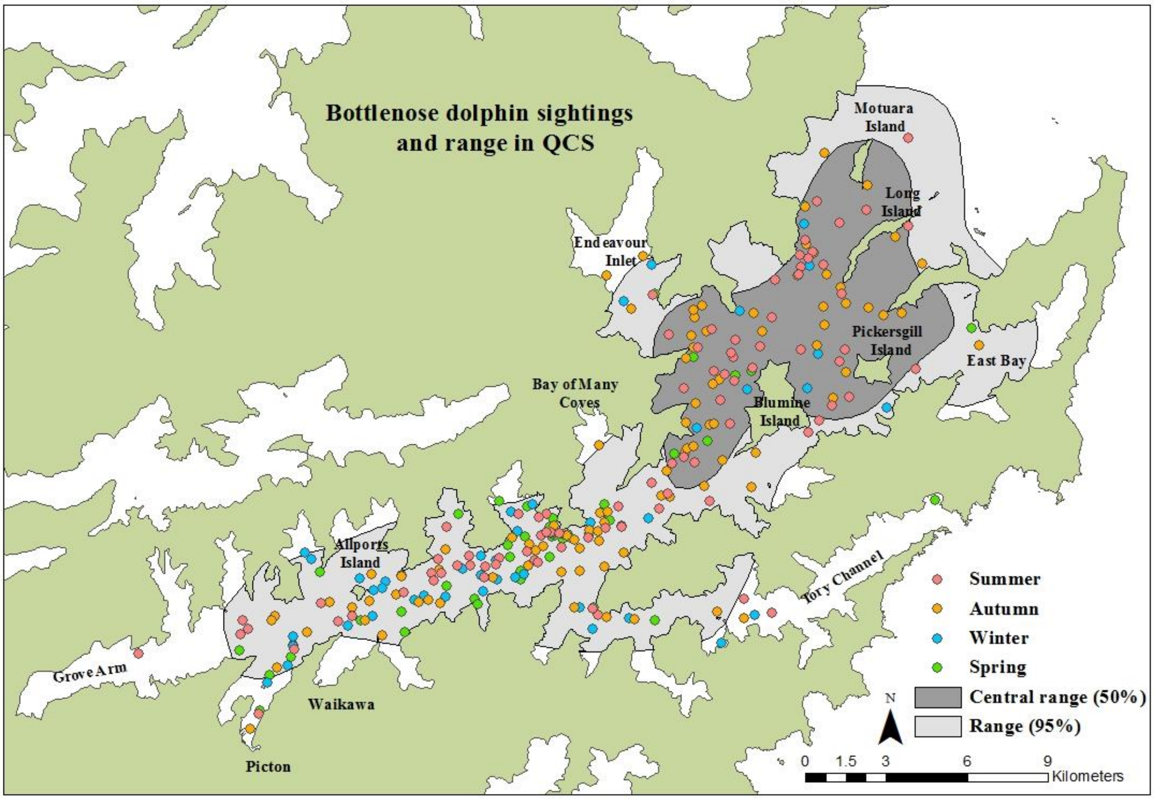


Figure 3.9. Central range and range of bottlenose dolphins (*Tursiops truncatus*) in QCS, NZ, during December 2011–April 2014.

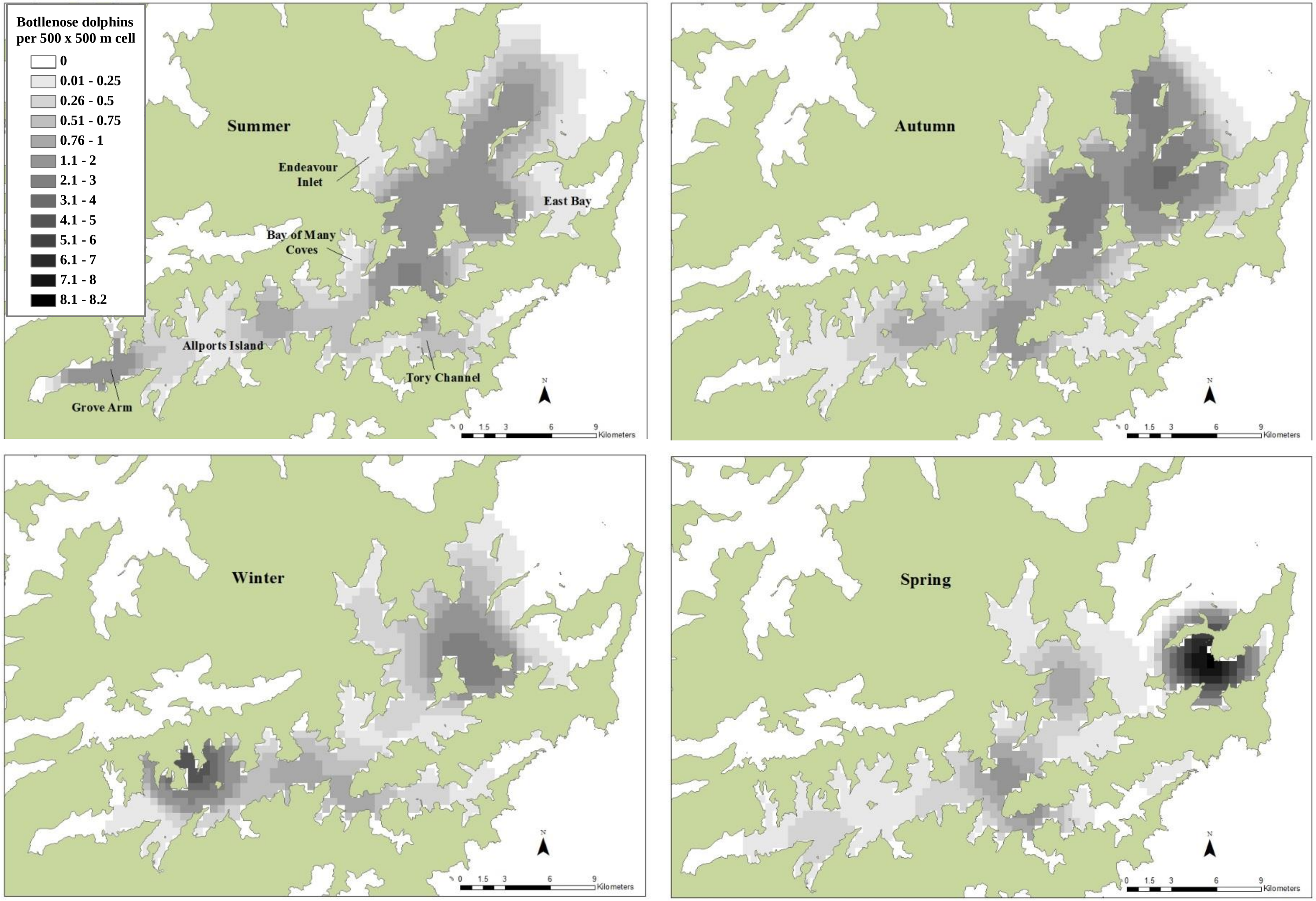


Figure 3.10. Seasonal kernel density estimates of bottlenose dolphins (*Tursiops truncatus*) in QCS, NZ, during December 2011–April 2014.

3.3.5.3 Dusky dolphins

Dusky dolphin distribution extended from Picton Harbour and Grove Arm in the Inner Sound, in Tory Channel, the middle Sound, Endeavour Inlet, East Bay, through to Long Island. The range (124.8 km^2; Table 3.5) mainly spanned the middle Sound, while the central range (8.5 km^2) was concentrated within the inner Sound (Figure 3.11). Distribution and density varied seasonally. Higher value cells were located toward the outer Sound and Allports Island/Blackwood Bay during summer. During autumn, hotspots were situated around Tory Channel, Bay of Many Coves and East Bay. Values were higher in winter and spring. Hotspots were observed during winter from Allports Island to Ruakaka Bay, as well as throughout the middle and outer Sounds. During spring, hotspots occurred in the inner Sound, particularly Grove Arm, as well as throughout the middle Sound (Figure 3.12). There was an exceptionally large group (n = 30) in Grove arm during spring. This was removed and the spring KDE was re-run (Appendix 3.4b), suggesting that some over-inflation occurred here from this sighting and the combined low survey effort. Likewise, these factors may have heavily dictated the patterns of the core range of this species (Appendix 3.4c).

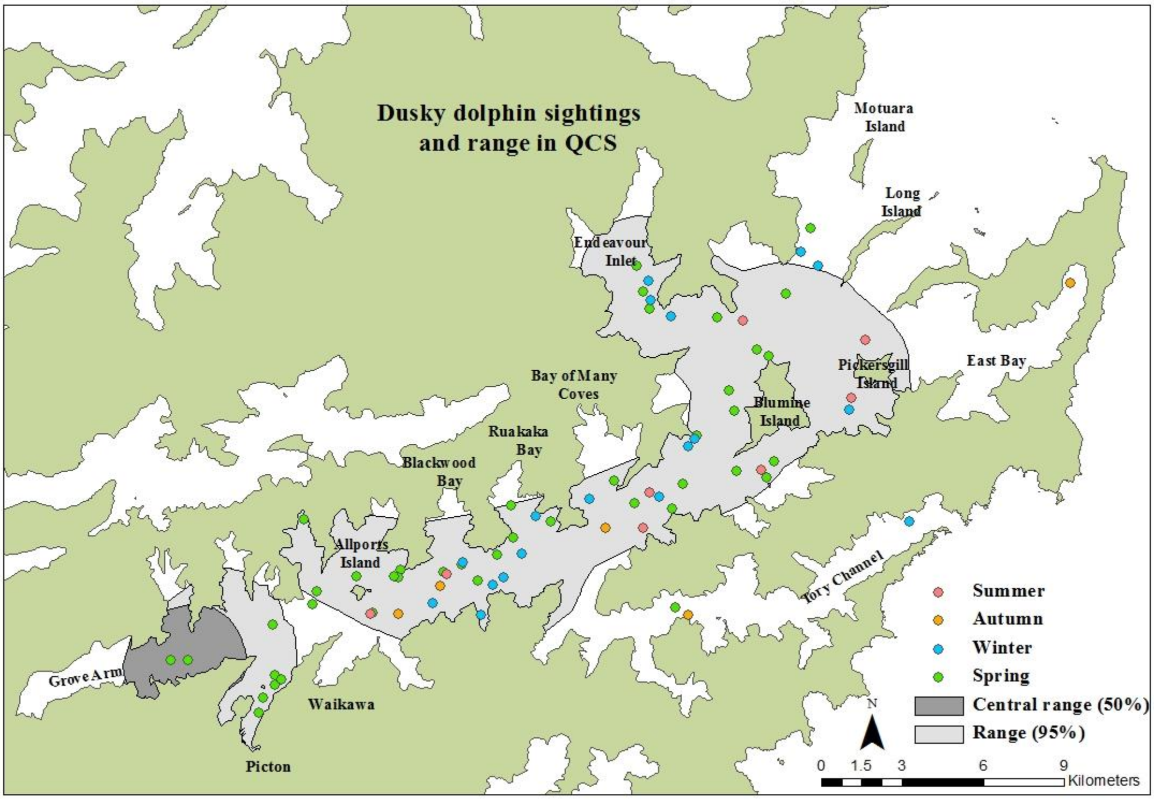


Figure 3.11. Central range and range of dusky dolphins (*Lagenorhynchus obscurus*) in QCS, NZ, during December 2011–April 2014.

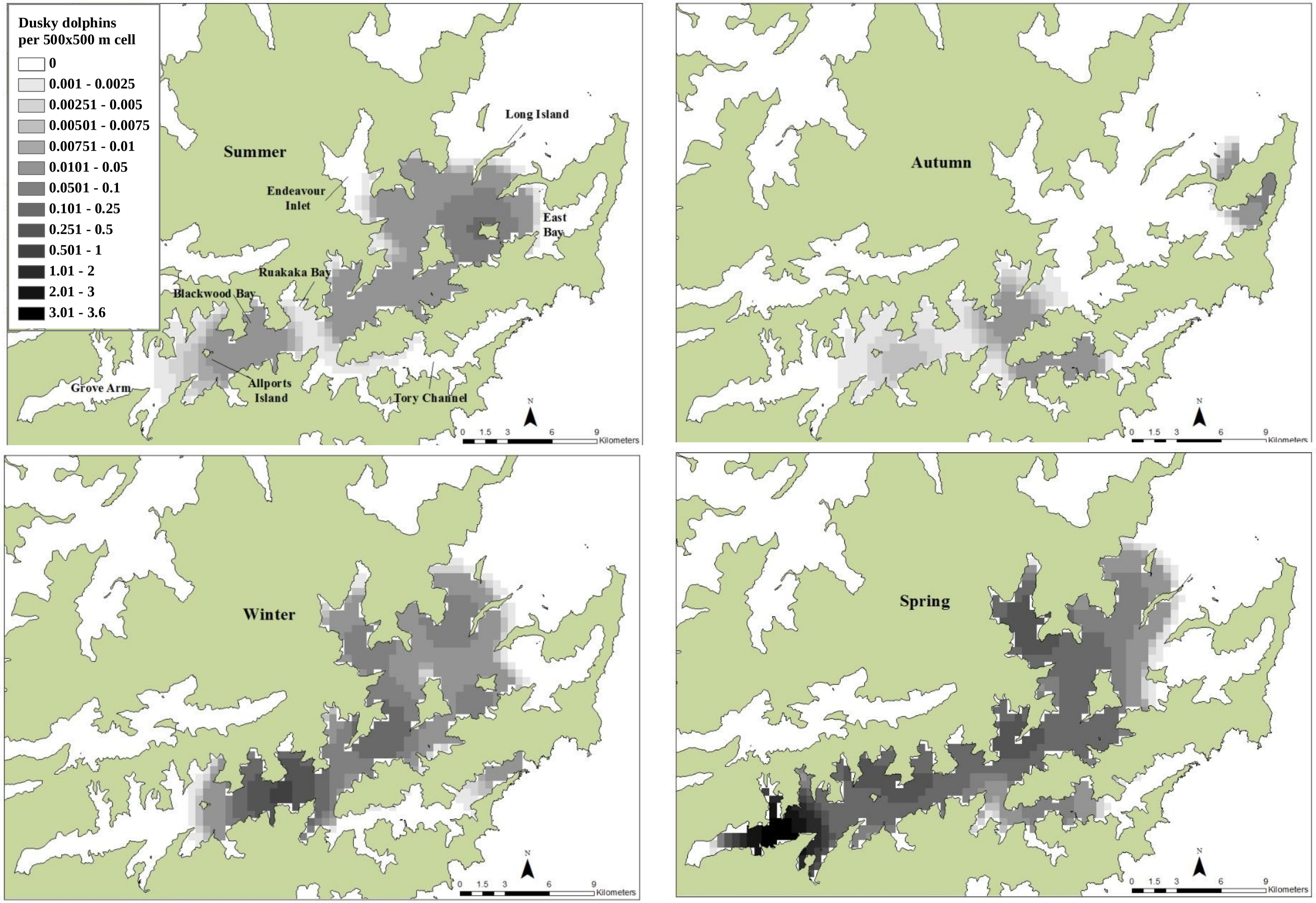


Figure 3.12. Seasonal kernel density estimates of dusky dolphins (*Lagenorhynchus obscurus*) in QCS, NZ, from December 2011–April 2014.

3.3.6 Spatial overlap

3.3.6.1 Overall spatial overlap

The Schoener's *D* value indicated that bottlenose and dusky dolphins exhibited fairly low spatial overlap (0.35; Table 3.6) in the inner and central parts of the Sound (Figure 3.13a). The value for Hector's and bottlenose dolphins was slightly lower (0.31; Table 3.6) and spatial overlap was mainly apparent in the central part of the Sound (Figure 3.13b). The Schoener's *D* value for Hector's and dusky dolphins was the lowest (0.13; Table 3.6) indicating the lowest spatial overlap between these two species. This occurred only within the central part of the Sound (Figure 3.13c). The spatial overlap of all three species was limited to that of Hector's and dusky dolphin overlap (Figure 3.13d).

3.3.6.2 Seasonal spatial overlap

Overall, values of Scheoner's *D* for seasonal spatial overlap between species were all low (less than 0.5). The greatest values were observed during the summer season for all species combinations (Table 3.7), while spatial overlap between bottlenose/dusky dolphins was the greatest with a value of 0.54.

Table 3.6. Scheoner's *D* values indicating overall calculated spatial overlap of all delphinid species' combinations in QCS, NZ, during December 2011–April 2014.

	Bottlenose	Dusky
Hector's	0.31	0.13
Bottlenose		0.35

Table 3.7. Scheoner's *D* values indicating overall seasonal spatial overlap for all delphinid species' combinations in QCS, NZ, during December 2011–April 2014.

Season	Bottlenose/Hector's	Hector's/Dusky	Bottlenose/Dusky
Summer	0.32	0.43	0.54
Autumn	0.26	0.08	0.18
Winter	0.18	0.32	0.38
Spring	0.17	0.09	0.22

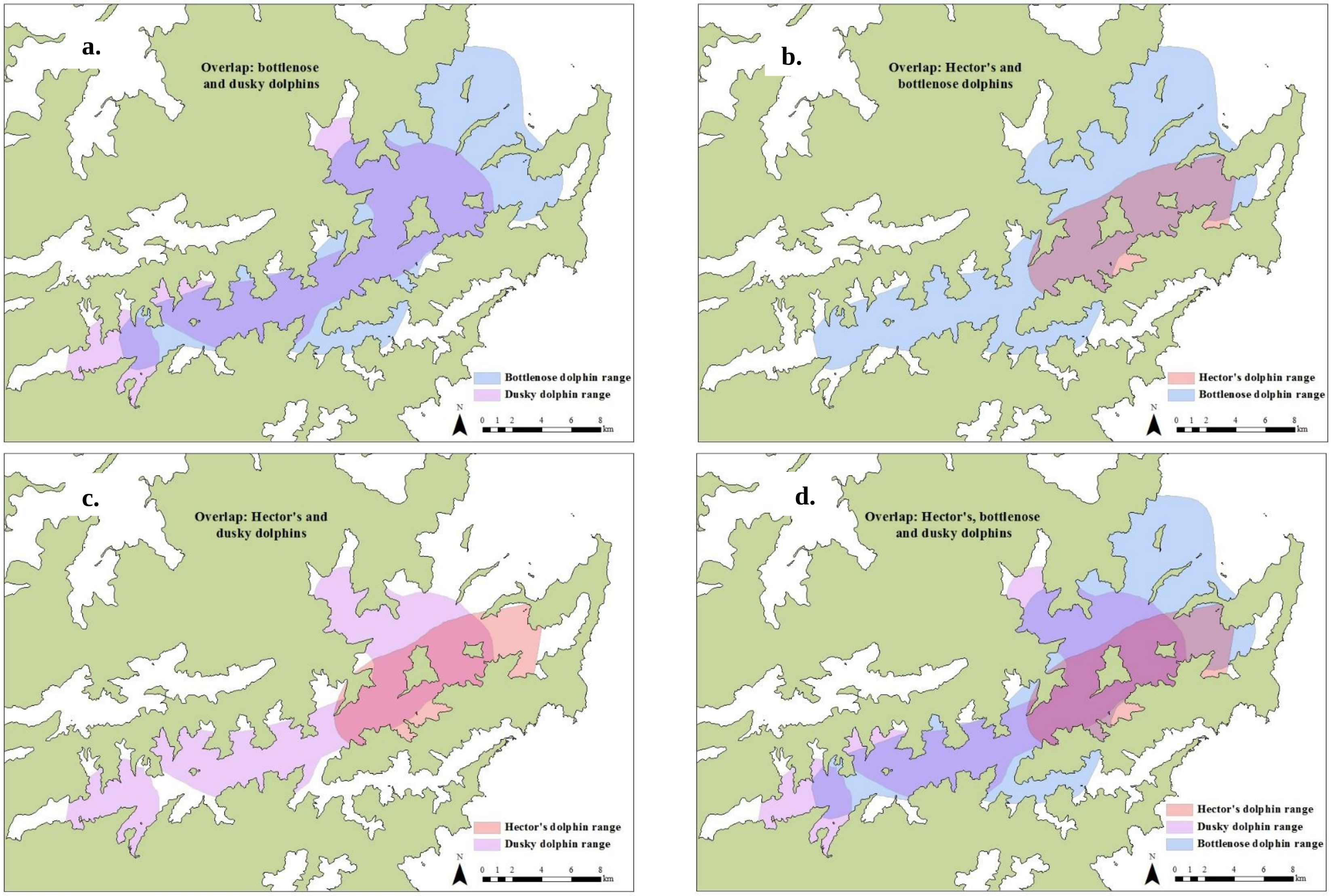


Figure 3.13. Depiction of overall range overlap for species combinations: a. bottlenose/dusky, b. Hector's/bottlenose, c. Hector's/dusky and d. all three species. Individual species ranges are represented by the colours indicated in the legends and the overlap is a blend of these individual colours.

3.4 Discussion

3.4.1 Ecological interpretation of delphinid spatio-temporal trends

In the present study, opportunistically collected data were analysed to establish current temporal and spatial trends of delphinids in QCS. Inferences were drawn about the ecological meaning of these patterns.

It is likely that during winter, Hector's dolphins were moving outside of QCS and offshore, as consistent with trends along the east coast of the South Island (Mackenzie & Clement, 2014). They probably moved along the South Island east coast toward Cloudy or Clifford Bay (Appendix 3.5; DuFresne *et al.*, 2006; Mackenzie & Clement, 2014) or even further South along the coast near Clarence where density during winter is relatively higher (Mackenzie & Clement, 2014). Such movement would explain the significant seasonal trends in SRs and ERs exhibited by Hector's dolphins' inside of QCS. Similarly, in nearby Kaikoura, NZ, dolphin groups during autumn and dolphin numbers during summer and autumn collectively, were the greatest (Weir & Sagnol, 2015). Off Banks Peninsula, nearly the full extent of Hector's dolphins offshore distribution was surveyed. The number of animals or sightings did not change seasonally, but during summer, clumps of sightings were found in inshore waters, while a more evenly spread distribution across the whole range occurred during winter (Rayment *et al*., 2009; 2010). Indeed, alongshore movement of Hector's dolphins from the general eastern Marlborough region to the South Island east coast has been indicated by genetic connectivity between the Cloudy Bay and Kaikoura-North populations (Hamner *et al.*, 2016).

The patterns of Hector's dolphins in QCS are seemingly attributed to the availability of suitable prey items that move in/out of QCS. Indeed, this species follows the movement of red cod (*Pseudophycis bachus*) off Banks Peninsula, NZ (Miller, 2014). Moreover, they feed on a range of prey including other demersal fishes, small schooling fish like sprat (*Sprattus* sp.) and pelagic species such as ahuru (*Auchenoceros punctatus*; Miller *et al.*, 2013). Since these species occupy different aspects of the water column, it suggests that prey selection by Hector's dolphins depends on prey availability and accessibility (Miller *et al.*, 2013).

Similarly, dusky dolphins move between locations amongst NZ waters. They travel from Kaikoura into nearby Admiralty Bay in the western part of the Marlborough Sounds (and likely QCS and the other Marlborough Sounds), as indicated by catalogued individuals identified in both locations (Markowitz *et al.*, 2004). As they travel north during the colder months, dusky dolphins likely congregate in the Sounds for foraging, then travel south again during the rest of year (Benoit-Bird *et al.*, 2004; Markowitz, 2004; McFadden, 2003). Dusky dolphins appear to be adaptable in terms of diet and foraging strategies. For example, in enclosed areas such as Admiralty Bay, they feed diurnally on small schooling fishes oscillating between a range of prey items and various foraging tactics (Duffy & Brown, 1994; McFadden, 2003; Vaughn *et al.*, 2007). Meanwhile, off Kaikoura, large groups of dusky dolphins move offshore to feed nocturnally by following the vertical migration of the deep scattering layer amongst Kaikoura Canyon (Cipriano, 1992). Given the flexibility of diet in both species, Hector's and dusky dolphins in QCS probably relied on different food sources. While the temporal patterns of both species are likely due to broader dynamics within NZ, the low temporal overlap (Hector's ER and SR were significantly lower when dusky dolphin presence increased) may have mutually benefitted both species' foraging efficiency.

Like the other species, bottlenose dolphins pass in and out of QCS. They regularly move throughout the entire Sounds system; most likely as a part of a much larger true home range that incorporates the Marlborough Sounds (Brager & Schneider, 1998; Merriman *et al.*, 2009). They are likely in search of a variety of available resources such as demersal and pelagic fish species and cephalopods (Gibbs *et al.*, 2011; Lusseau, 2003c). Animal sympatry implies (temporal and/or spatial) partitioning of a habitat and its resources, unless species utilize different food sources (Schoener, 1974). Given their rather high temporal and relatively low spatial overlap, bottlenose and dusky dolphins in QCS displayed some degree of spatial segregation and likely shared waters in QCS by relying on different foraging strategies and/or food sources. This may be feasible since both species rely on a broad diet. Furthermore, dusky dolphins in QCS, similar to Admiralty Bay, are typically observed in small coordinated groups (Markowitz, 2004), while bottlenose dolphins are often reported passing through the Sound travelling and foraging in very large groups, particularly during autumn (Merriman, 2007; pers. obs.).

Bottlenose and Hector's dolphins also displayed high temporal and very low spatial overlap indicating that they were also largely using QCS at the same time, but exhibiting extreme spatial partitioning. These patterns could be the result of a number of factors. For example, the small and restricted range of Hector's dolphins within QCS may have served as a form of protection from possibly aggressive bottlenose dolphins. In fact, hostile interactions of bottlenose dolphins with smaller species, resulting in serious injury or death, have been witnessed and concluded from stranded specimens of harbour porpoise and several juvenile delphinids in the U.K. (Barnett *et al.*, 2009; Ross & Wilson, 1996; Wilson *et al.*, 2004). Similar to the present study, a restricted distribution is common for Hector's dolphins and other similar *Cephalorhynchus* species (Dellabianca *et al.*, 2016; Rayment *et al.*, 2009). The need for protection may have been intensified by the relative group sizes of these species, given that bottlenose dolphin groups were comparatively larger than the other species in QCS. A similar group structure was observed amongst bottlenose dolphins within NZ waters off Great Barrier Island (mean = 34.6; range = 1–76; Dwyer *et al.*, 2016) and elsewhere, such as off Chile (mean=25; range=2–100; Olivarria *et al.,* 2010) and around the Azores (mean = 21.3; range = 1–110; Silva *et al.*, 2008). Meanwhile, small group size mean and range is typical for Hector's dolphins (Martinez, 2010; Rayment *et al.,* 2011; Weir & Sagnol, 2015). Moreover, the patterns in QCS were comparable to similar sympatric species including bottlenose, Peale's (*Lagenorhynchus australis*) and Chilean (*C. eutropia*) dolphins amongst the fjords and channels of Chilean waters (Olavarria *et al.,* 2010; Ribeiro *et al.*, 2005; Viddi & Lescrauwaet, 2005).

Ultimately, the specific combination of physical and hydrographic features in QCS influences resource availability, thus, delphinid patterns. QCS is characterized by the presence of numerous bays that provided various habitat options for dolphins. Spatial differences in tidal flow and seasonal temperature variation contribute to fluctuating availability of prey resources (Davidson *et al.*, 2011; Hadfield *et al.*, 2014). Meanwhile, the relatively shallow depth may allow for ease in foraging and prey capture for all species. In comparison, off Bank's peninsula, Hector's dolphins' offshore shift during winter is explained by prey movement, which is influenced by higher productivity, sea surface temperature and salinity (Miller, 2014). While a similar shift occurs off the west coast of the South Island, it is less pronounced (Mackenzie & Clement, 2016), likely due to more subtle temperature variation and/or comparatively steeply sloping bathymetry that could influence the presence of prey (Rayment *et al.*, 2011). Likewise, productivity in Kaikoura Canyon influences dusky dolphin foraging and inshore/offshore movement, which is a vastly different environment to the shallow, semi-enclosed Marlborough Sounds (Benoit-Bird *et al.*, 2004; Markowitz, 2004).

Comparable species to those in QCS were found amongst suitable habitat elsewhere and were likewise influenced by unique regional characteristics. For example, in contrast to dusky and Hector's dolphins in QCS, duskies and Heaviside's (*C. heavisidii*) occurred concurrently off

South Africa, likely due to their association with different habitat characteristics there. Dusky dolphins occurred amongst sandy shores in the area, while Heaviside's dolphins were in regions exposed to swell, providing greater availability of their primary prey (Elwen *et al.*, 2010). Peale's dolphins (*L. australis*) off Patagonia, Chile, occurred more frequently during spring, like dusky dolphins during spring (and winter) in QCS. However, unlike Hector's dolphins in QCS, no seasonal patterns occurred amongst sympatric Chilean dolphins (*C. eutropia*) off Patagonia. Peale's dolphins congregate near regions with coastal complexity, whereas Chilean dolphin movement was possibly limited by depth (Viddi *et al.*, 2010). The habitat associations of delphinids within QCS are further explored in Chapter 4.

In addition to regional characteristics and prey availability, delphinid patterns in QCS may have also been marginally influenced by the presence of other predatory species. Killer whales (*Orcinus orca*) pass in and out of QCS on occasion (Cross *et al.*, 2013) and have been known to attack numerous marine mammal species, including dusky and bottlenose dolphins (Jefferson *et al.*, 1991; Visser, 1999). Furthermore, predatory sharks including threshers (*Alopias* sp.), bronze whalers (*Carcharinus brachyurus*) and blue sharks (*Prionace glauca*; Davidson *et al.*, 2011) occur in QCS, but are likely more abundant in the adjoining Cook Strait (Garrick, 1956). Therefore, it is probable that predation by sharks explains why delphinids were found within QCS as a whole (as opposed to Cook Strait). While foraging and travelling between regions, delphinids may retreat to QCS as a safe haven, providing a particular benefit when calves are present. The small group size of dusky dolphins in QCS was notable, especially since groups are typically larger (< 10 to > 70 and 1–50; Degrati *et al*., 2008; Pearson, 2009) and remarkably sizable off nearby Kaikoura (50 to > 1000; Markowitz, 2004). Larger groups of dusky dolphins may have occurred in the open waters of Cook Strait (as they do off Kaikoura), while small subgroups separated and entered QCS where the risk of predation was lower, thus, eliminating the need for protection from conspecifics.

While the aforementioned factors likely explain delphinid spatial patterns in QCS, the presence of the Long Island-Kokomohua Marine Reserve near QCS northern entrance may have contributed to these patterns. The size and abundance of blue cod is greater within the reserve compared to low reef fish abundance elsewhere in the Sound (Davidson *et al.*, 2011; Davidson *et al.*, 2014). A portion of bottlenose dolphins' central range coincided with the reserve, where foraging efficiency may have been greater. Finally, spatial patterns may be further explained by anthropogenic growth within QCS and the surrounding bays. Coastal development and forestry have led to runoff and sedimentation, as well as a number of chemical and organic pollutants (Miller, 2016; Newcombe & Johnston, 2016; Urlich, 2015). The introduction of invasive species and a notable decline in fisheries have been recognized (Newcombe & Johnston, 2016). Furthermore, recreational and commercial boating has expanded in capacity with potential associated implications (Mackenzie, 2008; Parnell *et al.*, 2007; see sections 1.6 and 2.4.3 for further details).

3.4.2 Conservation management

The valuable ecological interpretation of these data are complemented by their practical applications for conservation management. At present, integrated, comprehensive management of the Marlborough Sounds is evolving (refer to section 6.2.1 for details). Spatial planning is an important component of this process and is dependent on the mapping of temporal and spatial patterns such as those presented here (Ehler & Douvere, 2009). This research highlights delphinid species' hotspots within QCS and their collective use of the entire Sound. Thus, regions of high density, or the Sound as a whole may be considered for further monitoring and the potential establishment of protective measures such as the delineation of zones and/or a MPA (Douvere, 2008; Ehler, 2008). The conservation management applications and associated recommendations of these data are discussed in detail in section 6.2.2.

3.5 Limitations and conclusions

This chapter represents an assessment of current patterns of delphinid temporal and spatial relative density in QCS, where specific periods and regions of species' utilization were identified. Furthermore, the results offered evidence for multi-species habitat partitioning in the region. However, there are some fundamental restrictions to acknowledge about the data and selected analyses. Firstly, it is important to reiterate that these patterns were confined to the study area. All of these species are also found in other regions of NZ (*e.g.*, Brager & Schneider, 1998; Hamner *et al.*, 2016; Markowitz *et al.*, 2004; Merriman *et al.*, 2009) thus, their home ranges extend far beyond QCS. The methods of analyses may have some intrinsic limitations. For example, low sighting numbers combined with high group sizes and low survey effort can result in over-inflated KDE estimates, which occurred in this study a couple times (refer section 3.3.5), likely influencing some of the results (refer to Appendix 3.4). This may be due in part to a lack of control over the survey path (and thus, equal survey effort), which is one of the limitations of opportunistic data collection in general (Isojunno *et al.*, 2012; Kiszka *et al.*, 2007). It is important to note here that a true hotspot may not be present in East Bay during spring for bottlenose dolphins (as observed from the re-analysis exempting one notably large sighting; refer to Appendix 3.4a). Likewise, the hotspot for dusky dolphins during spring may spread further out from the Inner Sound then represented here. Dusky dolphin core range may also extend further out and be greater in area (up to 33.0 km^2; refer to Appendix 3.4c). From a management perspective, it is important to consider the practical applications of these effects. It is recommended that future dedicated studies strive for equal survey coverage, incorporating more effort in regions where it was low in this study (*i.e.,* the Inner Sound, East Bay and the Outer Sound).

In recognition of minor inherent limitations, this research offers valuable insights into the ecology of Hector's, bottlenose and dusky dolphins. The trends presented here can be placed in the context of historical patterns to compare potential changes in delphinid usage of QCS over time. The data standardization method ensures relevance of the findings to any future statistical comparisons. As such, continued monitoring and research can be designed according to these outcomes. Moreover, these research findings serve as a tangible resource for Marine Spatial Planning efforts, as part of comprehensive management of the Marlborough Sounds.

Chapter 4

Habitat use of delphinids in Queen Charlotte Sound, New Zealand

Hector’s (*Cephalorhynchus hectori hectori*), bottlenose (*Tursiops truncatus*) and dusky (*Lagenorhynchus obscurus*) dolphin groups in Queen Charlotte Sound, NZ.

4.1 Introduction

Scientists have long been intrigued by the exploration of patterns in animal distribution (Guisan & Thuiller, 2005). Investigations into the ecological links that dictate these patterns have become widespread (Elith & Leathwick, 2009). Multiple factors likely contribute to suitable cetacean habitat including predator avoidance (Heithaus & Dill, 2002), competition for resources (Friedlaender *et al.*, 2009), offspring survival (Mann & Watson-Capps, 2005), prey availability (Boyd *et al.*, 2015) and an overlap with human activity (Lusseau, 2005). However, despite the contribution of numerous influences, it is likely that the location of suitable prey is the primary driving force of cetacean habitat selection (Lambert, Mannocci, *et. al.*, 2014). As top marine predators, cetaceans must select and utilize their environment and resources in order to maximize foraging efficiency (Estes *et al.*, 2011; Mannocci *et al.*, 2014b).

Although the identification of regions with appropriate prey can be indicative of suitable cetacean habitat, prey data are difficult to directly sample. In comparison, environmental proxies are much more readily available and accessible (Redfern *et al.*, 2006). Commonly utilised static and dynamic environmental variables include depth (Picanco *et al.*, 2009; Tynan *et al.*, 2005), bottom gradient (Tepsich *et al.*, 2014), sea surface temperature (SST) (MacLeod *et al.*, 2007; Macleod *et al.*, 2008; Tynan *et al.*, 2005), tide (Fury & Harrison, 2011b; Guilherme-Silveira & Silva, 2009; Ijsseldijk *et al.*, 2015), turbidity (Brager *et al.*, 2003; Clement, 2005; Gannier & Petiau, 2006; Smith *et al.*, 2009), rainfall (Lusseau, 2005) and primary productivity in the form of chlorophyll (Zerbini *et al.*, 2016). When possible, environmental parameters are collected concurrently with sighting data (McGowan *et al.*, 2013) which can occur from a number of different platform types (refer to section 1.4 for details). However, since *in situ* environmental data are not always feasible, remotely sensed data are often used (*e.g.*, for SST, chlorophyll and depth; Becker *et al.*, 2014; Dellabianca *et al.*, 2016; Garaffo *et al.*, 2011). Other valuable proxies include temporal (year, month or season; Azzellino *et al.*, 2012) and anthropogenic factors including vessel traffic (Lusseau, 2005) and marine farming (López & Shirai, 2007; Markowitz *et al.*, 2004; Watson-Capps & Mann, 2005).

The relationships between cetacean sightings and various proxies can be explored through the development of habitat models (Azzellino *et al.*, 2012; Ferguson *et al.*, 2006a; Marubini *et al.*, 2009). These can be descriptive or highly analytical depending on the number and type of variables and availability of survey effort data (Redfern *et al.*, 2006). A widely used technique for capturing complicated non-linear cetacean habitat relationships involves the utilization of Generalized Additive Models (GAMs; Becker *et al.*; Embling *et al.*, 2010; Marubini *et al.*, 2009; Spyrakos *et al.*, 2011). They are an extension of Generalized Linear Models (GLMs) in which the linear predictors are replaced by a sum of smooth functions (or smoothers; Hastie & Tibshirani, 1986), that summarize and estimate the trend of the response variable (Hastie & Tibshirani, 1990) and provide flexibility for fitting often complex ecological relationships (Elith & Leathwick, 2009).

Habitat modelling allows for a better understanding of the connections cetaceans have with the variability that exists within the marine environment. As a result, scientists hope to recognize the conditions that are ideal for the assemblage of prey, which offers insight into techniques that cetaceans may be using for foraging. For example, the significance of bottom slope could indicate that animals are using the physical features of the region to help them locate and herd prey in specific regions (Hastie *et al.*, 2003b). Associations with dynamic features could indicate that cetaceans are following the movement of productive patches (Benoit-Bird *et al.*, 2013; Benoit-Bird *et al.*, 2011) or, specifically, frontal zones (Doniol-Valcroze *et al.*, 2007; Gill *et al.*, 2011) where prey aggregations may occur. Conditions created by the unique combination of dynamic and static parameters specific to a region allow for elucidation of the ecological complexities that attract animals (Pirotta *et al.*, 2011) and make intraspecific comparisons across different regions particularly interesting (Pirotta *et al.*, 2011).

Knowledge of the environmental factors that are associated with species distribution can lead to the detection of species' tolerable ecological limits (Dellabianca *et al.*, 2016). As a result, managers may be able to anticipate animal response to variation such as global climate change (Harwood, 2001; Lambert, Pierce, *et al.*, 2014). Moreover, spatial predictions based on habitat parameters are able to offer information beyond what distribution and calculated density estimates can provide. The environmental parameters associated with animal locations can be used to predict similar locations where these animals may also be found. This valuable application fundamentally expands surveying capacity, since logistically speaking, it is typically impossible to sample an entire study area. Managers benefit when considering regions where cetaceans will encounter the least impact from the expansion of anthropogenic activities (Becker *et al.*, 2014), which can be particularly important in data poor regions (Redfern *et al.*, 2017). Such studies can lend to the creation of area restrictions (Dransfield *et al.*, 2014) or Marine Protected Areas (MPAs) in regions of high predicted animal occurrence or density

(Embling *et al.*, 2010), or complement existing management schemes. Additionally, habitat predictions point to regions of interest for the design of future studies, specifically the locations where more focused sampling may be necessary (Azzellino *et al.*, 2012).They can also offer information regarding the scale of sampling or analyses (Bailey & Thompson, 2009) and types of data that are needed. Thus, these efforts constitute the stepping stones for conservation efforts of endangered or declining populations (Dawson *et al.*, 2013; Dellabianca *et al.*, 2016; Derville *et al.*, 2016). Growing anthropogenic influence along the coasts (refer to sections 1.6, 2.1 and 3.1) and economic exclusive zones (Srinivasan *et al.*, 2012), coupled with escalating cetacean decline at the population (Tezanos-Pinto *et al.*, 2013) and species levels (Hamner *et al.*, 2014), dictates a rising need for these types of investigations in New Zealand.

Due to NZ's isolation, a number of species are naturally limited (Baker *et al.*, 2010) and both flora and fauna are very sensitive to change (Saunders & Norton, 2001). Several cetacean species found in NZ have a precarious status (Baker *et al.*, 2016). Decline or loss amongst such populations could be a detriment to the country's biodiversity (Baker *et al.*, 2010). Emerging research focused on cetacean distribution (Dwyer *et al.*, 2016), habitat (Derville *et al.*, 2016), ecology (Miller *et al.*, 2013) and rising threats (Slooten & Davies, 2012) have taken place throughout the country. Moreover, resultant management and conservation measures have been explored (Guerra & Dawson, 2016; Slooten, 2013). In Queen Charlotte Sound (QCS) specifically, the historical occurrence of the three main delphinid species has been examined (Chapter 2) and their spatial and temporal patterns have been investigated (Chapters 2 and 3). However, there is a gap in knowledge regarding factors that drive these patterns. Therefore, the aim of this chapter was to explore the spatial habitat use of the delphinids regularly using QCS. The specific objectives were to:

- Model delphinid density in relation to potential variables including environmental, temporal and human-related factors
- Generate spatial predictions of expected delphinid distribution and density in QCS based on the significant covariates indicated by the habitat models

4.2 Methods

4.2.1 Study site

QCS is a semi-enclosed body of water located on the northern edge of NZ's South Island (41°11 S, 174°11 E). It joins the Cook Strait along the Northern Sound entrance and via Tory Channel. The sunken river valley is long and relatively narrow and characterized by a complex shoreline (~50 km long and ~1–14 km wide). The depth throughout is rather shallow, reaching a maximum of ~80 m. The physical oceanographic and geographic features of QCS were described in further detail in section 2.2.1.

4.2.2 Data collection

4.2.2.1 Environmental data

Environmental variables considered in this study were based on parameters that had biological importance to cetaceans in other studies, as well as the availability of high quality data. The Marlborough District Council (MDC) and National Institute of Water and Atmospheric Research (NIWA) have been conducting monthly water quality surveys at 11 set locations throughout QCS and Tory Channel since July 2011 (Figure 4.1). Access to this database was gained for the period spanning December 2011–April 2014.

Oceanographic data were collected using a Seabird SBE19+ Conductivity Temperature Depth (CTD) with a Turner Self-Contained Underwater Fluorescence Apparatus (SCUFA) fluorometer through July 2013 and an ExoSonde CTD instrument from August 2013 onwards. These instruments recorded data in vertical profiles of the water column. Analyses in this study were limited to the use of surface data (0–2 m) to allow for comparability with the data explored in Chapter 2. Environmental sea surface data like SST and fluorescence are commonly used proxies in delphinid distribution and habitat studies (Dransfield *et al.*, 2014; Iwahara *et al.*, 2017; Joiris *et al.*, 2016; Martin Svendsen *et al.*, 2015) representing the dynamic environmental parameters used in modelling. Since chlorophyll has the ability to fluoresce (*i.e.*, emit light at a longer wavelength; Williams & Bridges, 1964), *in situ* measurements of fluorescence is a way to monitor chlorophyll (Lorenzen, 1966). Furthermore, since phytoplankton contain chlorophyll, this measurement is a proxy to assess phytoplankton biomass (Falkowski & Kiefer, 1985; Falkowski & Kolber, 1995).

Additionally, four static or fixed environmental parameters were considered: depth, slope, distance to shore and distance to the closest marine farm. Depth was obtained from a bathymetric grid produced from the NIWA coastal bathymetry database (NIWA, 2014). This grid was then used to calculate bottom gradient (slope). Finally, the distance of dolphin sightings to the closest marine farm was calculated, as a measure of anthropogenic presence and to explore their potential regional influence. The locations of all marine farms existing during the period of data collection were sourced from MDC (Figure 4.1).

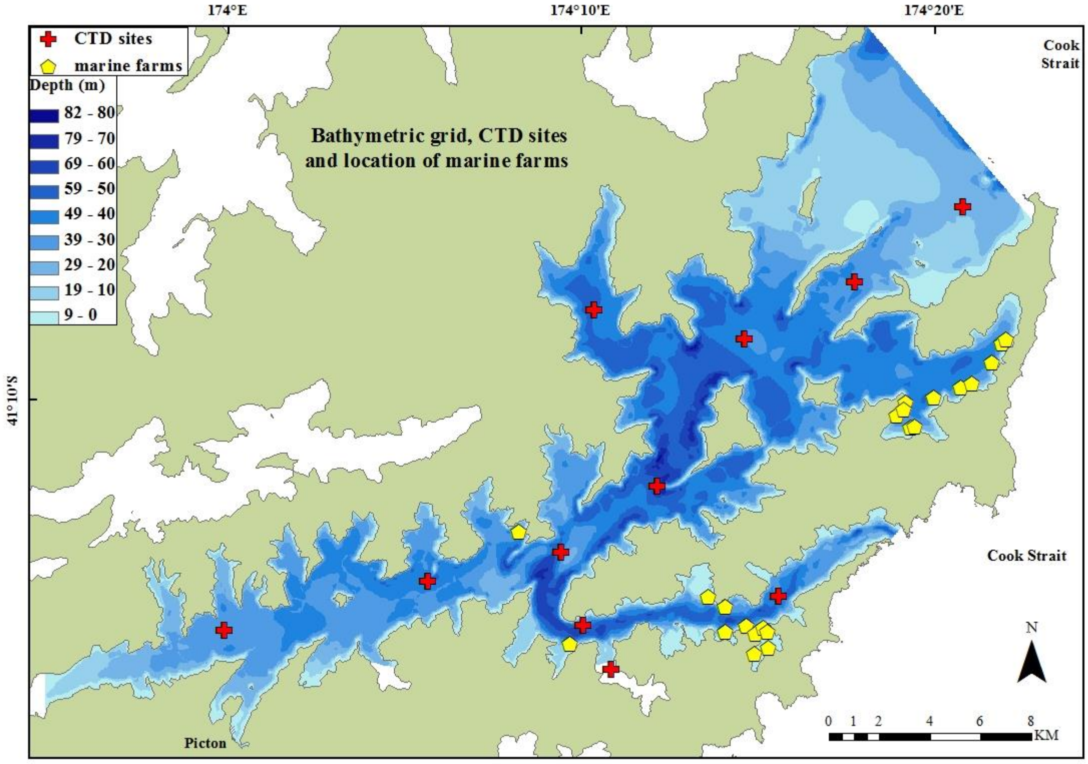


Figure 4.1. The study area in QCS, NZ indicating a depth grid (m) sourced from NIWA, the sites of MDC CTD environmental data collection from December 2011–April 2014 and the locations of marine farms during this time frame.

4.2.2.2 Dolphin sighting and survey effort data

Dolphin sighting and survey effort data were collected opportunistically aboard two tour vessels from December 2011–April 2014. Surveys departed from Picton Harbour twice daily and followed a non-systematic survey design. Time invested in searching for dolphins was classified as “on effort,” and switched to “off effort” when approaching animals, during a sighting or when weather or detection conditions declined (*i.e.*, precipitation, loss of daylight, Beaufort Sea State >3). Further details regarding the survey platforms and data collection are included in section 3.2.2. When dolphins were sighted, visual assessment took place to confirm species and estimate group size. A dolphin group was any number of animals in apparent association, moving in the same direction and likely involved in the same behaviour (Shane, 1990; Wells *et al.*, 1980). Group size was assessed for minimum, maximum and best estimate values at sea to account for variation in gregariousness amongst species. Only best estimate values were used in analysis (Kiszka *et al.*, 2007).

4.2.3 Data analysis

4.2.3.1 Processing

4.2.3.1.1 Environmental data

Since two instruments were used during the study period, values at depth were compared when both instruments were deployed simultaneously. There was a perfect correlation amongst temperature values, while a slight difference was detected between data collected from the fluorescence sensors ($R^2 = 0.91$). Therefore, a correction factor determined from the comparison ($y = 0.3127 x + 0.7882$) was applied to the fluorescence data collected with the second instrument so that the data across the whole time period were comparable.

Water surface values of monthly data for SST and fluorescence were averaged over the top two meters of the water column and according to austral season, defined as follows: Summer = December–February, autumn = March–May, winter = June–August and spring = September–November. Seasonal averages were calculated, because monthly data were not consistently available for all stations. The resulting surface data were used to estimate values at un-sampled areas in the study site with the *Inverse distance weighted* (IDW) tool in the *Spatial Analyst* extension of ArcMap. This method of data interpolation is based on the premise that points closer to the samples are more similar in value, and thus more heavily weighted in the estimation than points that are further away (Li & Heap, 2008). IDW was selected over other methods of data interpolation (*e.g.,* kriging and spline) because it is more computationally simple and can perform optimally with environmental data (Bhowmik & Cabral, 2011).

Final IDW calculations involved the adjustment of several settings. The field “variable search radius” specifies the search distance for each interpolated cell according to a designated number of data points. The value 12 was selected. The “power” field controls the weight of distant points and can affect the smoothness of the resulting surface. For this field, the value 2 was selected. Slight differences were noted amongst generated surfaces when values were adjusted for power and the number of points, whereas adjustments to the output cell size had no influence. Therefore, default settings were selected as these were commonly used values in other studies (Baltas, 2007; Beckler *et al.,* 2005; Zengin *et al.,* 2010).

The seabed gradient (or slope) was calculated from the bathymetric grid by using the *Slope* tool in the surface toolbox within the *Spatial Analyst* extension of ArcMap. Distance of each sighting to the nearest point on shore and distance to the nearest marine farm were calculated using the *Near* tool in the *Analysis Tools* extension in ArcMap. Calculations in ArcMap were conducted in the NZTM 2000 projection.

4.2.3.1.2 Dolphin sighting and survey effort data

For extended details as to how survey effort data were processed and how sighting data were truncated, refer to sections 3.2.3.2 and 3.3.2. In order to integrate environmental data into the associated dolphin sighting database, the values of depth, slope, SST and fluorescence were assigned from the bathymetric gradient and seasonal environmental rasters using the *Extract Values to Points* tool within the *Extraction* toolbox in the *Spatial Analyst* extension of ArcMap. A grid with 3x3 km cells was created using the *Genvecgrid* tool in Geospatial Modelling Environment (GME; Beyer, 2014). The grid cell size affects the amount of survey effort and number of sightings per cell and can influence habitat associations (Bailey & Thompson, 2009). The selected size was determined by the size of the study area and total survey effort coverage (Pennino *et al.*, 2017), allowing for a minimum amount of effort in each grid cell (*i.e*., 5 surveys or 0.5 hrs per grid cell). Spatial gaps in data collection occurred (particularly in the Outer Sound, bays within the Inner Sound, Endeavour Inlet and East Bay; refer to Appendix 3.1), due to the lack of control in sampling associated with the opportunistic surveys. Gaps in survey effort are limiting (Kiszka *et al.*, 2007) and can lead to overinflated density estimates (Rayment *et al.* 2009; refer to sections 3.3.5.2; 3.3.5.3 and Appendix 3.4). While several grid cell sizes were trialled, the 3x3 km grid cell size was appropriate for the analyses since it eliminated these data gaps, while allowing for analytical consistency with the previous chapter (refer to 3.2.3).

All covariate values associated with sightings (SST, surface fluorescence, depth, slope, distance from shore and distance to closest marine farm) were then averaged per grid cell according to season and year, while the number of individual animals for each species (per grid cell according to season and year) was calculated by summing sighting group size estimates. Furthermore, to characterize background data, a uniform, random subset of the survey tracks was generated by selecting a point for every one minute of on-effort survey data, per trip (Phillips *et al.,* 2009). This was a representative sampling of the environmental conditions in the survey area (Phillips *et al.,* 2009), which allowed modelling to incorporate regions where surveys took place but no sightings occurred as per Ferguson *et al.* (2006b). Environmental values were extracted to this subset of points and all associated covariate values were averaged per grid cell according to season each year, as detailed above. Data were aggregated according to austral seasons since season was the finest temporal scale for the dynamic environmental parameters.

When boat speed is consistent during systematic studies, the distance covered is often the common method of data standardization. In this case, data standardization according to time was considered more appropriate due to the opportunistic nature of the data collection and thus, the inability to control vessel speed (Elwen *et al.*, 2009; MacLeod *et al.*, 2004; Wall *et al.*, 2006). Search effort was quantified by summing the total amount of time spent on effort in each 3x3 km grid cell using features in ArcGIS 10.0 (ESRI, 2011). The data were summed per season (per year) and integrated into the database.

4.2.3.2 Habitat preference

The range of habitat variables associated with each species were summarized and compared using one way Analysis of Variance (ANOVA).

4.2.3.3 Modelling framework

Since sufficient sighting data were available for each species, models were fit separately. Modelling data according to species can be much more ecologically meaningful than pooling by higher taxonomic group (Viddi *et al.*, 2010) and it allows for interspecific comparisons within and across study sites. The number of dolphins (per species) within individual grid cells was the response variable modelled in relation to the environmental parameters (*i.e.*, explanatory variables; Table 4.1). The covariates season and year were factors, while all other covariates were continuous variables.

Table 4.1. Summary of initial models representing the factors influencing the number of Hector's, bottlenose and dusky dolphins per grid cell in QCS from 2012–2014.The response variable, all potential explanatory variables included in the initial model and the model form are displayed.

Response Variable	Explanatory Variables	Model Form
Number of dolphins	year, season, SST, fluorescence, depth, slope, distance to shore, distance to closest marine farm, effort (offset)	GAM

Regression analyses (*e.g.,* GLMs and GAMs are frequently used to explore cetacean habitat relationships (Arcangeli *et al.*, 2016; Azzellino *et al.*, 2012; Goetz *et al.*, 2015; Marini *et al.*, 2015). The advantage of GAMs (over GLMs) is their capacity to handle non-linear relationships between the response and explanatory variables, where the relationship is determined by the data and not restricted by the model form (Guisan *et al.*, 2002). Cetacean habitat relationships are often complex and found to be non-linear (Forney, 2000). In this study, evidence of non-linearity was detected amongst at least one of the continuous explanatory variables, so GAMs were utilized.

The GAMs for each species were initially fit with a Poisson error distribution, which is appropriate for count data but assumes that error variance is equal to the mean (Hoef & Boveng, 2007). Over-dispersion (a variance greater than that of the mean) of the response was detected. Therefore, models were re-fit using a negative binomial distribution, a recommended and commonly used approach for over-dispersed count data (e.g. Dransfield *et al.*, 2014; Hoef & Boveng, 2007; McGowan *et al.*, 2013; Spyrakos *et al.*, 2011; Ward *et al.*, 2011). This approach is a logical option for modelling such data, as it includes an (over-dispersion) parameter that allows for aggregations of individuals (Ward *et al.* 2011); a phenomena that occurs frequently amongst marine mammals (Brager, 1999; Louis *et al.*, 2015; Pearson *et al.*, 2017). A Quasi-Poisson distribution was considered as a modelling alternative, but was not appropriate in this case due to the fairly large over-dispersion (Zuur *et al.*, 2009b).

Variance inflation factors (VIFs) were used to assess for multi-collinearity amongst the explanatory variables. While the cut-off level for VIFs is subjective (Zuur *et al.*, 2007), a value of three was selected (*e.g.*, Zuur, 2009) to remove collinear variables prior to analysis. In all models, season and temperature were collinear. Season was removed so that the effect of temperature could be explored. Models were then iteratively run through backwards selection eliminating the variables with the least explanatory power ($p > 0.05$) at each step (Goetz *et al.*, 2015) and comparing Akaike Information Criterion (AIC) to select the best model (Bailey & Thompson, 2009). According to convention, habitat variables that were smooth terms were restricted to four degrees of freedom (Zuur *et al.*, 2007). Survey effort (hrs) was retained as an offset in all models to account for non-uniformity across grid cells (Mannocci *et al.*, 2014a). Encounter rate predictions were then generated based on the optimal combination of covariates in the final models.

4.3 Results

4.3.1 Dolphin sighting and survey effort data

From December 2011–April 2014, a total of 677 surveys were conducted in QCS, which resulted in 1,613.3 hrs of on-effort survey data, spanning a total survey area of 263.3 km^2. This included 301 AM surveys (553.1 hrs) and 376 PM surveys (1060.2 hrs; see Table 3.2). While surveys were conducted during each month of every season during the study period, some variation in spatial coverage took place (refer to Figure. 3.2). A total of 290 Hector's, 268 bottlenose and 71 dusky dolphin groups were observed on effort (refer to Table 4.2). Dolphin groups ranged in size from 1–20 (mean = 3.95, SD = 3.28) for Hector's, 1–80 (mean = 29.13, SD = 20.7) for bottlenose, and 1–40 (mean = 8.54, SD = 7.69) for dusky dolphins (Figure 4.2; refer to section 3.3.3 for more detail). The number of dolphins per 3x3 km grid cell (spanning all seasons/years) ranged from 1–270 for Hector's dolphins (mean = 14.88, SD =35.89), 1–360 for bottlenose dolphins (mean = 54.22, SD = 48.89) and 3–55 for dusky dolphins (mean = 12.62, SD = 13.60; refer to Table 4.3).

Table 4.2. The number of dolphin sightings per species according to year and season in QCS, NZ from December 2011– April 2014.

		Summer	Autumn	Winter	Spring	Totals
Hector's	2012	32	33	0	4	**69**
	2013	59	45	3	9	**116**
	2014	77	28	-	-	**105**
	Total	**168**	**106**	**3**	**13**	**290**
Bottlenose	2012	32	34	17	28	**111**
	2013	18	25	29	11	**83**
	2014	36	38	-	-	**74**
	Total	**86**	**97**	**46**	**39**	**268**
Dusky	2012	5	1	5	6	**17**
	2013	2	4	13	34	**53**
	2014	1	0	-	-	**1**
	Total	**8**	**5**	**18**	**40**	**71**

Table 4.3. Summary statistics of Hector’s, bottlenose and dusky dolphins per grid cell per season and year in QCS, NZ from December 2011– April 2014.

	Dolphins/Grid Cell		
	Mean	*Range*	*SD*
Hector's	14.9	1 – 270	35.9
Bottlenose	54.2	1 – 360	48.9
Dusky	12.6	3 – 55	13.6

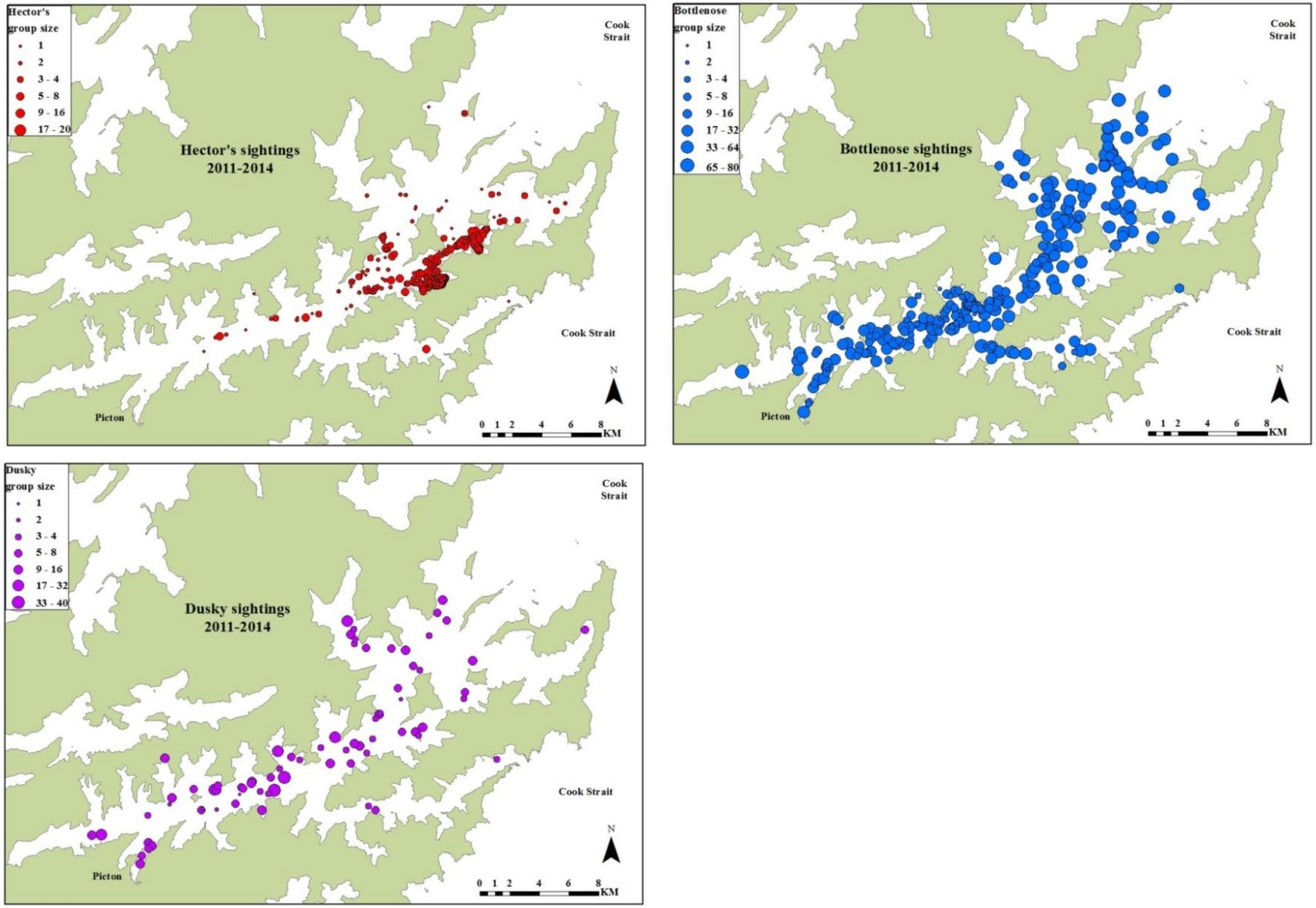


Figure 4.2. All dolphin sightings in QCS, NZ during December 2011–April 2014. Sighting group sizes are represented by graduated symbols.

4.3.2 Environmental Data

The bathymetric grid in QCS indicated values ranging from 0–82 m in depth (Figure 4.1). Bottom gradient ranged from 0–53.5° (Figure 4.3). Overall SST values during the study period ranged from 11.6–18.7°C, while fluorescence ranged from 0.0–2.27 mg/m^3 (Table 4.4).

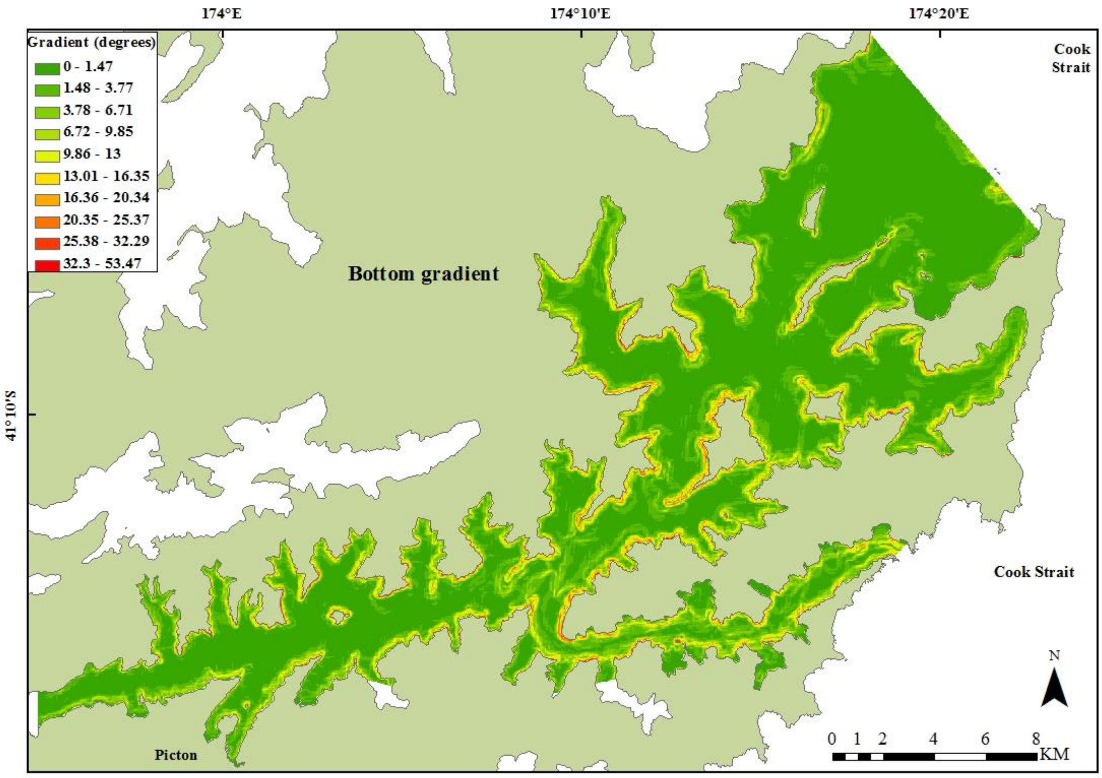


Figure 4.3. Bottom gradient of the study area in QCS, NZ.

Table 4.4. Summary of the dynamic environmental variables a. SST and b. fluorescence according to season and year in QCS, NZ from December 2011– April 2014.

a. Year	Season	SST Range °C	Mean	SD
2012	Summer	14.2 – 17.4	15.9	0.51
	Autumn	13.4 – 14.9	14.4	0.23
	Winter	11.6 – 12.6	12.1	0.15
	Spring	13.7 – 15.0	14.2	0.20
2013	Summer	15.5 – 18.7	17.2	0.62
	Autumn	14.6 – 15.7	15.4	0.25
	Winter	11.8 – 12.5	12.1	0.12
	Spring	13.4 – 15.7	14.1	0.32
2014	Summer	15.2 – 18.4	16.9	0.50
	Autumn	15.1 – 16.8	15.7	0.22

b. Year	Season	Fluorescence Range mg/m^3	Mean	SD
2012	Summer	0.0 – 0.9	0.4	0.14
	Autumn	0.8 – 1.4	1.0	0.10
	Winter	0.8 – 1.6	1.0	0.12
	Spring	0.6 – 0.8	0.7	0.03
2013	Summer	0.6 – 0.9	0.7	0.05
	Autumn	0.8 – 2.2	1.2	0.30
	Winter	0.8 – 1.6	1.1	0.14
	Spring	0.9 – 1.1	1.0	0.05
2014	Summer	0.6 – 0.7	0.6	0.02
	Autumn	0.9 – 1.6	1.1	0.10

4.3.3 Habitat preferences

4.3.3.1 Hector's dolphins

Dynamic variables SST and fluorescence associated with Hector's dolphins ranged from 12.00–18.71°C and 0.6 –1.7 mg/m^3. Depth and slope spanned 7.16–66.51 m; and 0.05 – 13.66°, while distance from shore and the closest marine farm were 48.87–969.88 m and 406–10,477 m, respectively (refer to Table 4.5).

4.3.3.2 Bottlenose dolphins

Dynamic variables SST and fluorescence for bottlenose dolphins ranged from 11.70–19.93°C and 0.01–1.85 mg/m^3. Static variables depth and slope associated with this species were 6.5–68.5 m, and 0.02–24.74°, while distance from shore and the closest marine farm spanned 25.01–1316.93 m and 479.6–16,020.9 m, respectively (refer to Table 4.5).

4.3.3.3 Dusky dolphins

Dynamic variables SST and fluorescence associated with dusky dolphins were 11.9–18.7°C and 0.4–1.5 mg/m^3. Depth and slope spanned 14.1–68.9 m and 0.1–17.6°, while distance from shore and the closest marine farm ranged from 87.60–1077.74 m and 103.1–14,368.6 m, respectively (refer to Table 4.5).

Table 4.5. Habitat preferences for Hector's, bottlenose and dusky dolphins in QCS, NZ from December 2011– April 2014.

	Habitat Values								
Variables	**Hector's Dolphins**			**Bottlenose Dolphins**			**Dusky Dolphins**		
	Mean	*Range*	*SD*	*Mean*	*Range*	*SD*	*Mean*	*Range*	*SD*
SST (°C)	15.52	12.00 – 18.71	2.22	14.96	11.70 – 19.93	3.87	14.07	11.86 – 18.71	3.80
Fluor (mg/m^3)	0.89	0.60 – 1.67	0.23	0.89	0.01 – 1.85	0.35	0.91	0.42 – 1.50	0.31
Depth (m)	43.82	7.16 – 66.51	11.86	39.85	6.50 – 68.54	11.90	41.25	14.05 – 68.87	11.30
Slope (°)	2.76	0.05 – 13.66	2.45	3.77	0.02 – 24.74	4.53	3.38	0.02 – 17.60	3.78
Shore (m)	458.83	48.87 – 969.88	205.18	482.43	25.01 – 1316.93	266.72	484.77	87.60 – 1077.74	248.75
Marine (m)	4258.62	406.00 – 10,477.90	2142.00	5627.71	479.60 – 16,020.90	3344.07	5501.20	103.13 – 14,368.58	3049.25

4.3.3.4 Interspecific comparisons

Interspecific comparisons of habitat parameter values offered some evidence of variability. A significant effect of SST amongst species was detected (ANOVA: F (2) = 10.53; $p < 0.001$). The values for Hector's dolphins (mean = 15.52°C; SD = 2.22) were greater than those associated with bottlenose dolphins (mean = 14.96, SD = 3.87; p = 0.05) or dusky dolphins (mean = 14.07, SD = 3.80; $p < 0.001$) and the values for bottlenose dolphins were greater than dusky dolphins ($p < 0.05$). There was some evidence of a significant effect of depth (ANOVA: F (2) = 2.85; p = 0.05). The values associated with Hector's dolphins (mean = 43.82, SD = 11.86) were higher than those associated with bottlenose dolphins (mean = 39.85, SD = 11.90; $p < 0.05$). Likewise, there was some evidence of the effect of distance to the closest marine farm amongst species (ANOVA: F (2) = 5.00; $p < 0.05$). The values associated with Hector's dolphins (mean = 4,258.62, SD = 2,142) were lower than those associated with bottlenose dolphins (mean = 5,627.71, SD = 3,344.07; $p < 0.05$). There was no evidence of interspecific differences amongst species for the other parameters, fluorescence (ANOVA: F (2) = 0.14; $p > 0.05$), slope (ANOVA: F (2) = 0.187; $p > 0.05$) and distance from shore (ANOVA: F (2) = 2.61; $p > 0.05$).

4.3.4 Habitat model selection and predictions

4.3.4.1 Hector's dolphins

The best fit GAM representing the number of Hector's dolphins per grid cell was as follows: number of dolphins ~ s (SST) + s (fluor) + depth + s (slope) + s (marine) + offset (effort). The model explains 62.1% of the deviance (Table 4.6). The variables year and distance to shore were not retained because they were not significant and did not improve the model (Table 4.7). Hector's dolphin density per grid cell increased with mid-high depth. The number of dolphins per grid cell was higher with slope values less than 2°. Dolphin density increased with increasing SST, until about 16.5°. The number of dolphins increased to mid-high fluorescence values and then declined as uncertainty increased with higher values. Dolphin density slightly increased from around 2,000–6,000 m from the closest marine farm and slight decrease between 9,500 –10,500 m (Figure 4.4). Model predictions for Hector's dolphins indicate peaks during the summer and autumn seasons. Higher density was generally predicted for the central region of the study area, around Blumine Island, Long Island and to a lesser degree toward the inner Sound (Figure 4.5).

Table 4.6. Parameter estimates of the variables selected in the best fit GAM for Hector's dolphin habitat use. Significance codes are "***" 0.001, "**" 0.01, '*" 0.05, "." 0.1.

Variable			
Smooth terms	edf	χ^2	p value
slope	2.66	13.2	0.012 *
SST	2.87	58.86	< 0.001 ***
fluorescence	2.72	21.07	< 0.001 ***
dist marine	2.69	2.92	< 0.001 ***
	df	χ^2	p value
depth	1	6.79	0.009 **
offset effort	1	6.38	0.012 *

Deviance explained = 62.1%; n = 429

Table 4.7. AIC and deviance explained for all candidate GAMs for Hector's dolphins.

Model	Variables Included	AIC	Deviance Explained (%)
1	Year + s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	775.06	63.2
2	Year + s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Marine)+offset	773.00	63.3
3	**s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Marine)+offset**	**773.63**	**62.1**
4	s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	776.13	62.4
5	s(SST) +s(Depth)+s(Slope)+s(Marine)+offset	784.94	57.6
6	s(SST) +s(Depth)+s(Slope)+s(Fluor)+offset	835.94	40.9
7	s(SST) +s(Depth)+s(Fluor)+offset	835.62	39.0
8	s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Shore)+offset	838.10	40.9
9	Year+s(SST) +s(Depth)+s(Slope)+s(Shore)+offset	855.46	33.3
10	Year + s(Depth)+s(Slope)+s(Shore)+offset	889.14	27.0
11	s(Depth)+s(Slope)+s(Shore)+offset	896.40	20.1

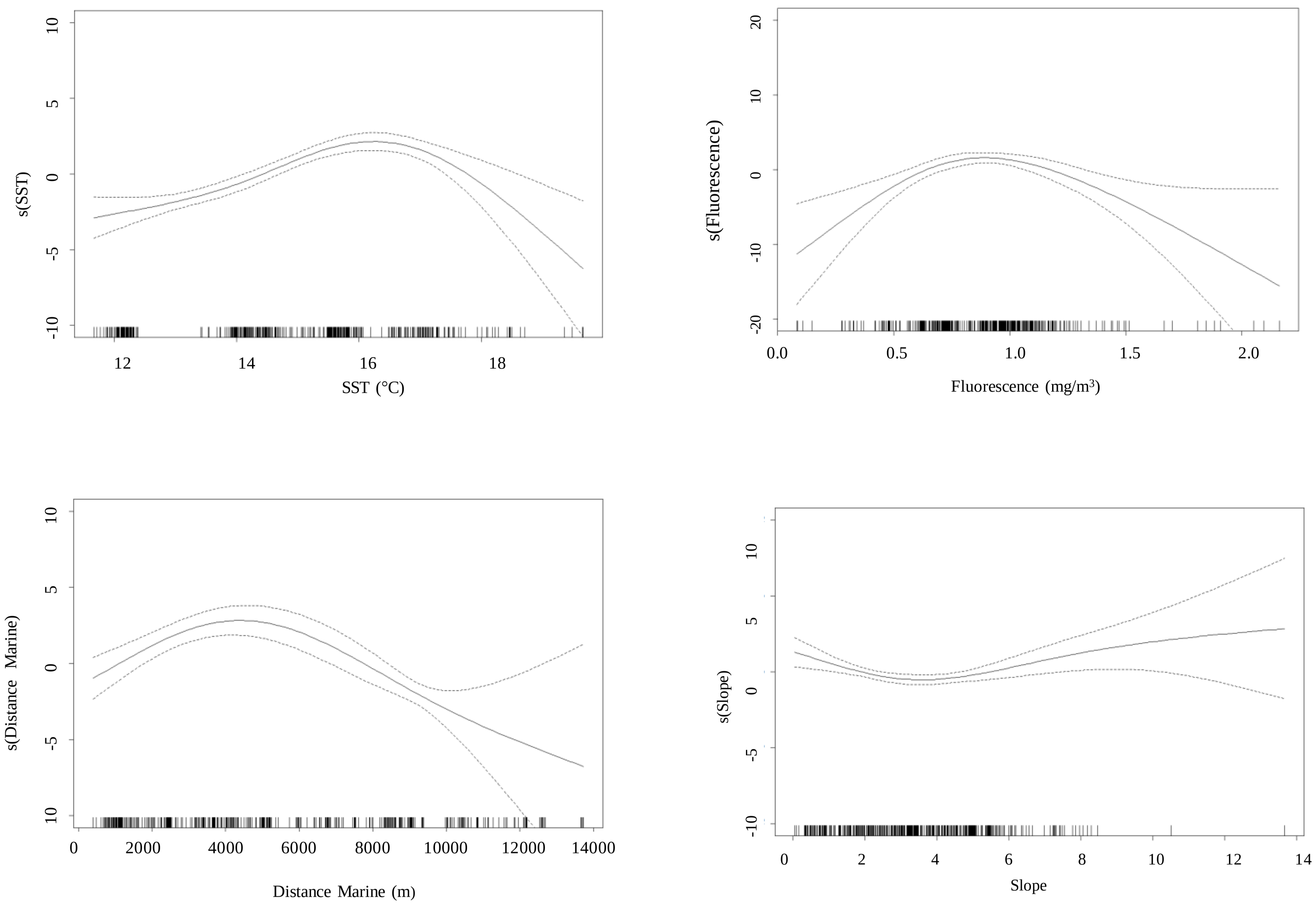


Figure 4.4. Partial residual plots from the best fit GAM of Hector's dolphin habitat use. Dashed lines represent +/- one SE and the vertical marks on the x-axis represent the distribution of points in the model.

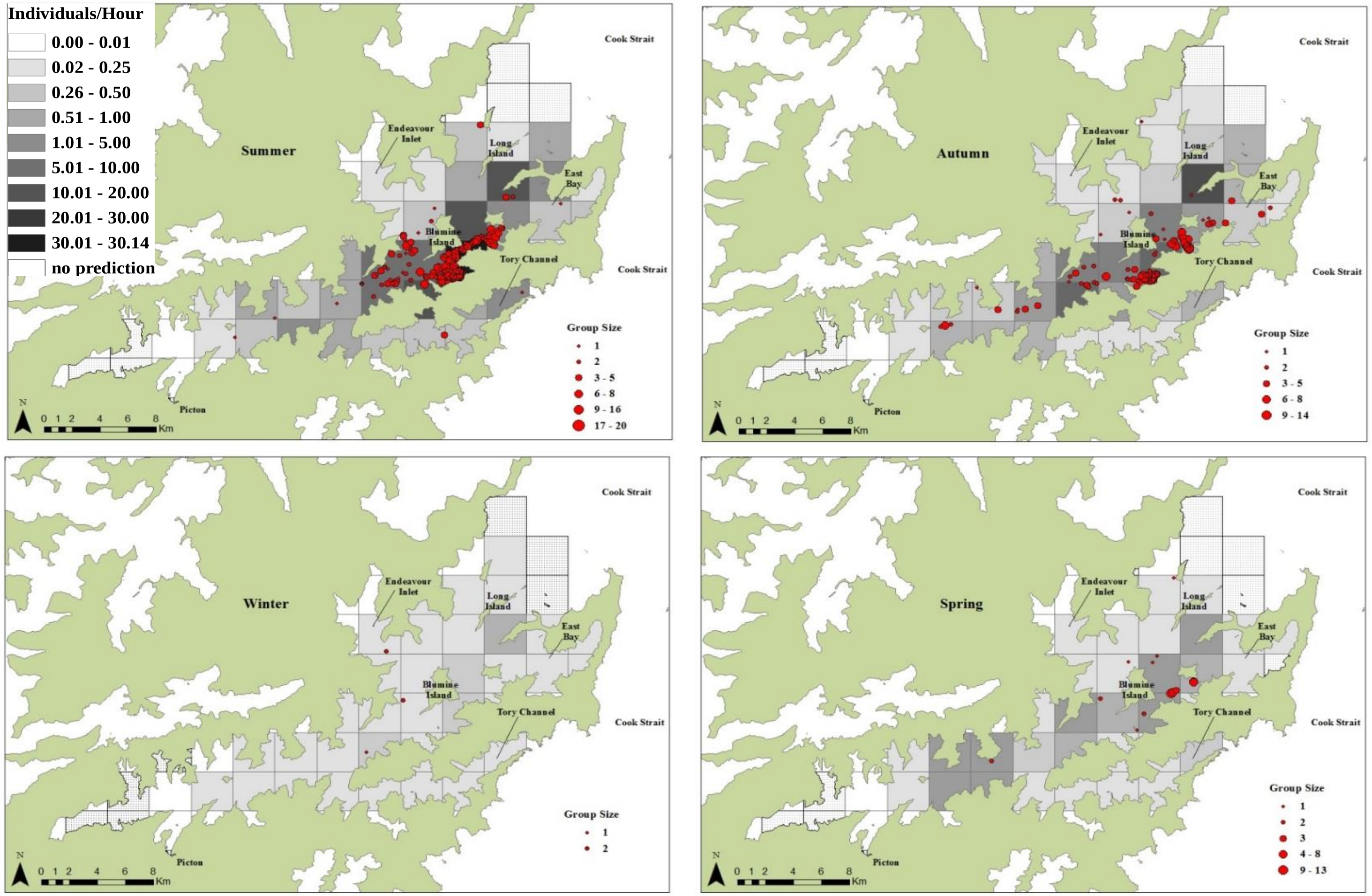


Figure 4.5. Predicted density (count of dolphins/hour) of Hector’s dolphins in QCS, NZ during each season of data collection from 2011–2014. Red dots indicate actual Hector’s dolphin sightings.

4.3.4.2 Bottlenose dolphins

The best fit GAM representing the number of bottlenose dolphins per grid cell was as follows: number of dolphins ~ year + depth + s (slope) + s (marine) + offset (effort). This model explains 28.3% of the deviance (Table 4.8). The variables SST, fluorescence and distance from shore were not included in the model because they were not significant (Table 4.9). The model suggests that the bottlenose dolphin density was on average 5.4 times higher from year one to three ($p < 0.001$). Dolphin density increased with increased depth. The number of dolphins was high with very gentle slope values, decreased until about 3° and increased until slope peaked at about 14°. Density was relatively uniform until about 7,500 m to the closest marine farm and then decreased slightly thereafter (Figure 4.6).

Model predictions for bottlenose dolphins were generated annually since the significant parameters included year as well as the static environmental variables. Although predictions indicate that this species may be using most of the Sound, notable peaks in density shifted from the middle Sound in year one, to the inner Sound in year two and then areas in the middle/inner Sound and Tory Channel during year three. Moreover, the predicted values were much higher for the third year of sampling (Figure 4.7).

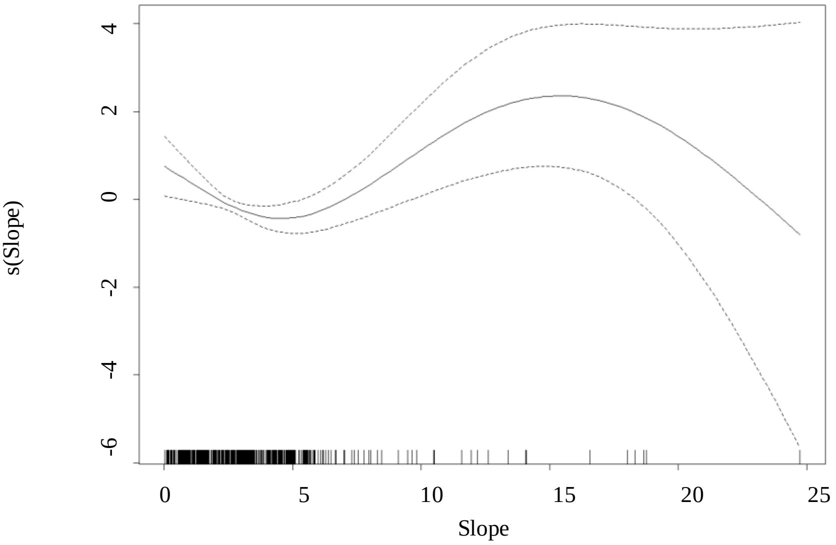
Table 4.8. Parameter estimates of the variables selected in the best fit GAM for bottlenose dolphin habitat use. Significance codes are “***” 0.001, “**” 0.01, ‘*” 0.05, “.” 0.1.

Variable			
Smooth terms	edf	χ^2	p value
slope	2.74	14.13	0.0094 **
dist marine	2.16	6.47	0.048 *
	df	χ^2	p value
depth	1	52.08	< 0.001
year	2	19.89	< 0.001
offset effort	1	42.24	< 0.001

Deviance explained = 28.3%; n = 424

Table 4.9. AIC and deviance explained for all candidate GAMs for bottlenose dolphins.

Model	Variables Included	AIC	Deviance Explained (%)
1	Year + s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	1939.63	29.0
2	Year+s(Fluor)+s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	1938.29	28.8
3	Year+s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	1936.86	28.7
4	**Year+s(Depth)+s(Slope)+s(Marine)+offset**	**1936.04**	**28.3**
5	Year+s(Depth)+s(Slope)+offset	1939.32	26.0
6	Year+s(Depth)+s(Slope)+s(Shore)+offset	1941.04	26.1
7	Year+s(SST)+s(Depth)+s(Slope)+s(Marine)+offset	1937.77	28.4
8	Year+s(Fluor)+s(Depth)+s(Slope)+s(Marine)+offset	1937.93	28.4



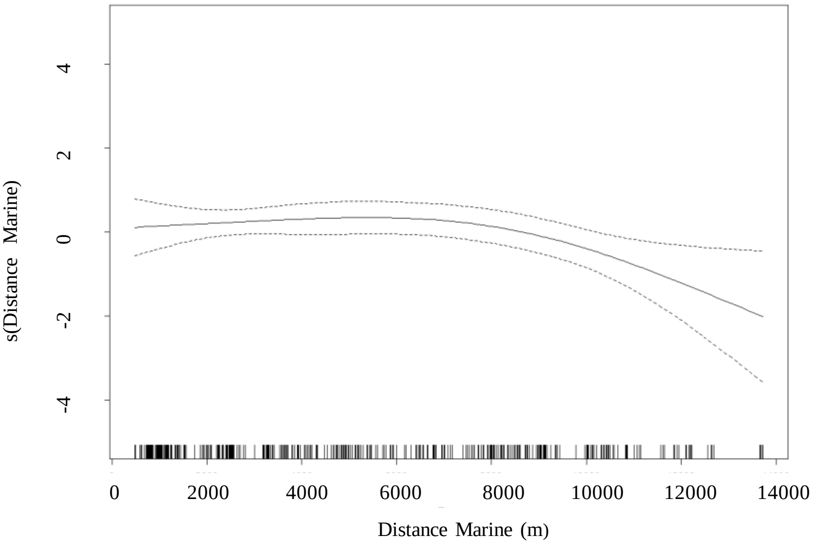


Figure 4.6. Partial residual plots from the best fit GAM of bottlenose dolphin habitat use. Dashed lines represent +/- one SE and the vertical marks on the x-axis represent the distribution of points in the model.

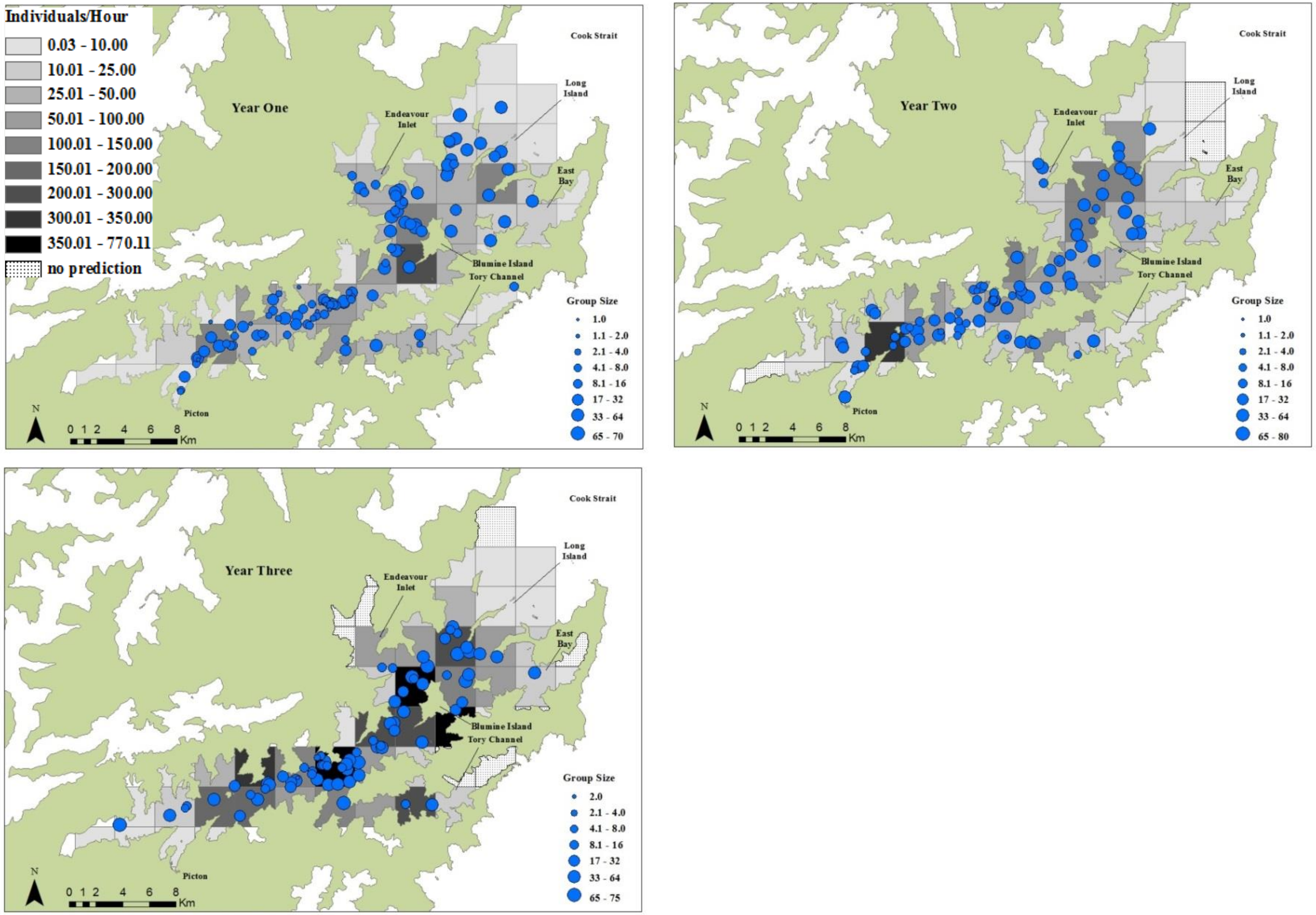


Figure 4.7. Predicted density (count of dolphins/hour) of bottlenose dolphins in QCS, NZ during each year of data collection from 2011–2014. Blue dots indicate actual bottlenose dolphin sightings.

4.3.4.3 Dusky dolphins

The best fit GAM representing the number of dusky dolphins per grid cell was as follows: number of dolphins ~ year + s (SST) + fluor + depth + s (slope) + s (distance to closest marine farm) + offset (effort). The model explains 69.9% of the deviance (Table 4.10). The variable distance from shore was not significant, so was removed (Table 4.11). The model suggests that the dusky dolphin density was on average 3.84 times higher between years one to three ($p < 0.0001$). There was an inverse relationship with density and fluorescence as well as an inverse relationship with depth. The number of dolphins per grid cell was relatively constant until about 15°C and then decreased with increased SST. Dusky dolphin density decreased until a slope of about 4°, and then increased until about 10°. Density increased as distance to the closest marine farm increased until about 3,500 m and then displaced no noticeable preference thereafter (Figure 4.8).

Model predications for dusky dolphins indicate peaks during winter and spring seasons, particularly during year two when more sightings and larger groups were encountered (Figures 4.9; 4.10). The occurrence of sightings was low during summer and autumn, thus, predicted animal density was also very low (Figures 4.9–4.11). No prediction was generated for the autumn season of the third year because no sightings were observed during this period (Figure 4.9).

Table 4.10. Parameter estimates of the variables selected in the best fit GAM for dusky dolphin habitat use. Significance codes are “***” 0.001, “**” 0.01, ‘*” 0.05, “.” 0.1.

Variable			
Smooth terms	edf	χ^2	p value
slope	2.97	78.73	< 0.001 ***
SST	2.53	20.36	< 0.001 ***
dist marine	2.61	14.4	0.0018 **
	df	χ^2	p value
year	2	20.36	< 0.001 ***
depth	1	5.13	0.024 **
fluorescence	1	8.47	0.004 **
offset effort	1	38.97	< 0.001 ***

Deviance explained = 69.9%; n = 428

Table 4.11. AIC and deviance explained for all candidate GAMs for dusky dolphins.

Model	Variables Included	AIC	Deviance Explained (%)
1	Year + s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	524.32	71.89
2	**Year + s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Marine)+offset**	**524.89**	**69.9**
3	Year + s(SST) +s(Fluor)+s(Depth)+s(Slope)+s(Shore)+offset	532.77	67.3
4	Year + s(SST) +s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	531.73	68.9
5	Year + s(SST) +s(Fluor)+s(Slope)+s(Shore)+s(Marine)+offset	529.72	68.3
6	Year +s(Fluor)+s(Depth)+s(Slope)+s(Shore)+s(Marine)+offset	545.42	63.8

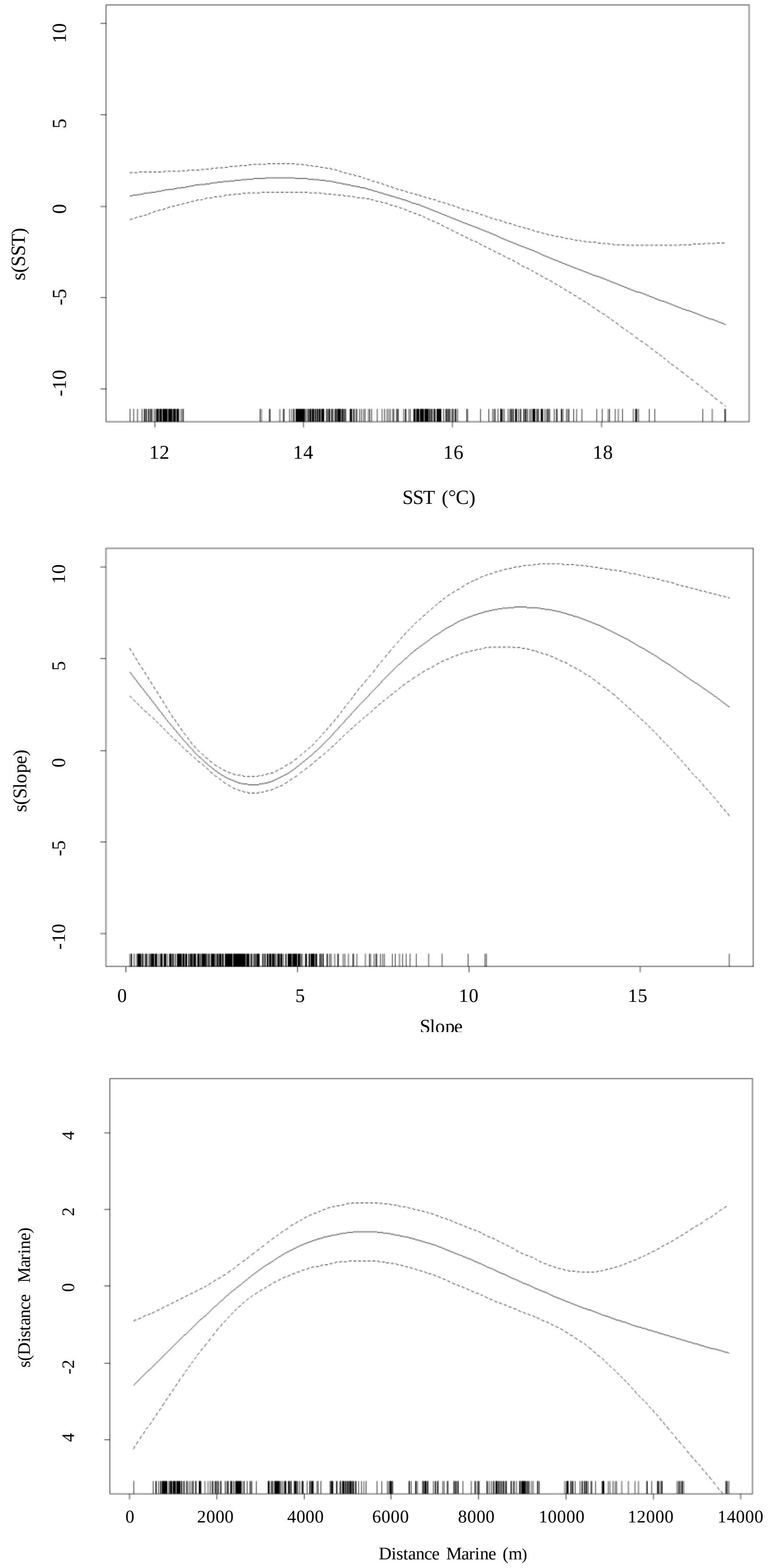


Figure 4.8. Partial residual plots from the best fit GAM of dusky dolphin habitat use. Dashed lines represent +/- one SE and the vertical marks on the x-axis represent the distribution of points in the model.

Figure 4.9. Predicted density (count of dolphins/hour) of dusky dolphins in QCS, NZ during each season of data collection in 2012. Purple dots indicate actual dusky dolphin sightings.

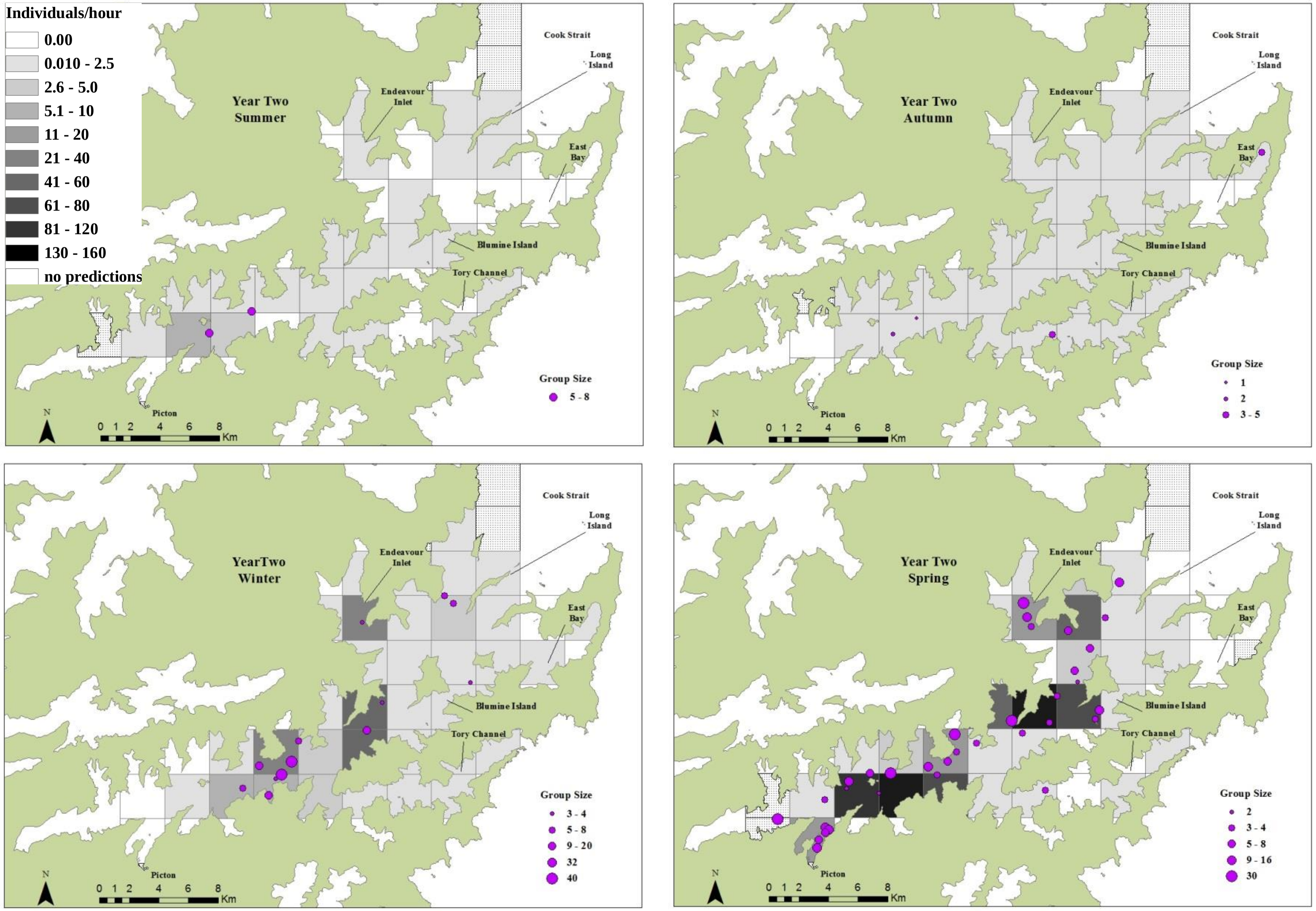


Figure 4.10. Predicted density (count of dolphins/hour) of dusky dolphins in QCS, NZ during each season of data collection in 2013. Purple dots indicate actual dusky dolphin sightings.

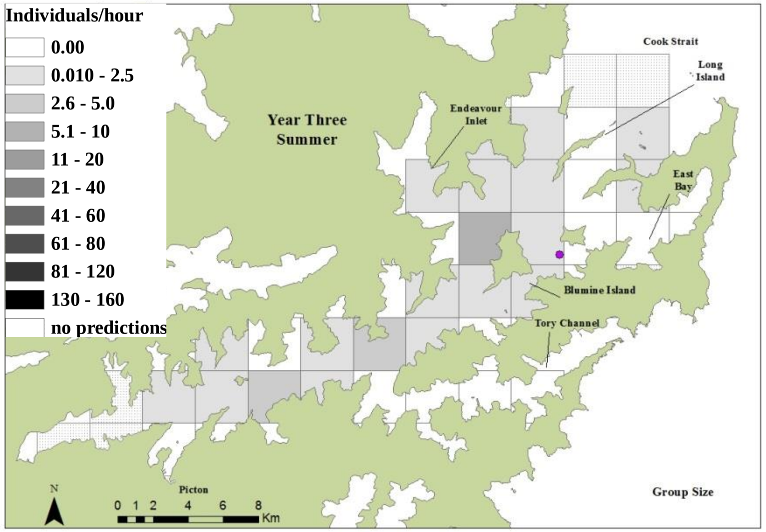


Figure 4.11. Predicted density (count of dolphins/hour) of dusky dolphins in QCS, NZ during summer of 2014. Purple dots indicate actual dusky dolphin sightings.

4.4 Discussion

This study represents the first time that delphinid habitat modelling was undertaken in the Marlborough Sounds and the only time that Hector’s, bottlenose and dusky dolphin habitat were modelled concurrently. The findings offer insight as to variables that may have contributed to these three species’ distribution and density in QCS. All species exhibit some temporal variation as well as an association with other parameters.

4.4.1 Interspecific comparisons

Differences amongst species’ habitat associations were detected. Bottlenose dolphins only displayed an association with static parameters. While Hector’s and dusky dolphins were associated with the same environmental variables (SST, fluorescence, depth, slope and distance to closest marine farm), dusky dolphins also varied annually. Some variation existed amongst the mean values that influenced all three species. The mean value for SST was higher for Hector’s dolphins than bottlenose or dusky dolphins and higher for bottlenose than dusky dolphins. The mean depth associated with Hector’s dolphins was greater than that of bottlenose dolphins, while the mean distance to the closest marine farm was shorter for Hector’s than bottlenose dolphins. The deviance explained by the models was highest for dusky, followed by Hector’s and bottlenose dolphins.

The findings provided in Chapter 3 offered evidence that the three species were spatially and temporally segregating the habitat in QCS to varying degrees and indicated that trophic partitioning may have been occurring as well (section 3.4). In the present chapter, segregation amongst the species according to environmental proxies was apparent, similar to the outcomes of studies elsewhere, with these or comparable species (Becker *et al.*, 2014; Dellabianca *et al.*, 2016; Garaffo *et al.*, 2011). Thus, the findings here offer further evidence to support the presence of resource partitioning in QCS on a trophic level. The flexibility amongst Hector’s, bottlenose and dusky dolphin foraging strategies and diet likely contribute to this (McFadden, 2003; Miller, 2014; Reeves *et al.*, 2002).

4.4.2 Hector’s dolphins

The model results (gentle slope, mid-depth) suggest that Hector’s dolphins were primarily using flatter, mid-depth regions of QCS. This is conceivably a reflection of their foraging habits, which likely include that they prey upon bottom-dwelling and/or benthopelagic species. The region around Patten Passage (east of Blumine Island, refer to Figure 4.5), where a high concentration of Hector's dolphins occur, is exposed to strong tidal currents since water from Cook Strait enters at both the Northern entrance of the Sound and via Tory Channel. The tidally refreshed water here supports various benthic invertebrates such as tubeworms, anemones, sponges and bivalves (Davidson *et al.*, 2011), which may sustain a range of species up the food chain in the surrounding area that serve as Hector's dolphin prey. Species found in QCS include a range of demersal fish, including red cod (*Pseudophycis bachus*), sole (*Peltorhamphus* sp.) stargazer (*Crapatalus* sp.), as well as Bothiid and Pleuronectiid flounder (Davidson *et al.*, 2011). These are amongst the prey items found in the diet of Hector's dolphins off Banks Peninsula, as well as similar *Cephalorhynchus* species elsewhere (Bastida *et al.*, 1988; Caicedo, 2005; Clarke & Goodall, 1994; Heinrich, 2006; Miller *et al.*, 2013; Oporto, 1985; Oporto *et al.*, 1990).

While Hector's dolphins' diet in QCS probably includes a diverse range of benthic and benthopelagic species associated with static features, the inclusion of dynamic factors in the model suggests that Hector's dolphins may also search for productive patches and/or follow prey. The model specified an association of Hector's dolphins with mid-high fluorescence values. Areas of higher fluorescence equate to higher phytoplankton chlorophyll (Lorenzen, 1966) and suggest higher oceanic productivity (Valiela, 1995) that can be an informative proxy for cetacean habitat and foraging habits (Moura *et al.*, 2012; Panigada *et al.*, 2008). Summer surveys of the Greater Cook Strait region indicated peaks in chlorophyll (>0.6–>1.5 mg/m^3) off the Marlborough Sounds, relative to the surrounding areas (Bradford *et al.*, 1986). This may explain Hector's dolphins' use of the region and the seasonal peaks in density (refer to section 3.3.5) and predicted density, as they follow productive regions and thus, prey. Red cod (and possibly other species), move offshore during winter (Beentjes *et al.*, 2002; Beentjes & Renwick, 2001), likely precipitated by SST variation (Beentjes & Renwick, 2001). Therefore, Hector's dolphins' association with higher SST in QCS, as specified by the model, is probably indicative of these seasonal trends in prey movement, as proposed by Brager (2003) and Miller (2014). Moreover, the regions of high Hector's dolphin density and predicted density in QCS may be convenient for easy passage to follow prey in and out of the Sound.

Other similar species associate with higher SST including maui dolphins (*C. hectori maui*), a subspecies of Hector's dolphins (Derville *et al.*, 2016) and the comparable Commerson's dolphins (*Cephalorhynchus commersonii*) off Patagonia (Garaffo *et al.*, 2011). While

Cephalorhynchus species seem to share a positive correlation with SST; they are generally distributed in colder waters of the Southern hemisphere, suggesting biological adaptations for heat loss, such as a high metabolic rate (Kastelein *et al.*, 1993). Thus, the association with higher seasonal SST does not likely serve as a direct metabolic or energetic gain.

Dynamic oceanographic features can vary in significance according to different regions of the study site (Miller, 2014). Comparable studies elsewhere indicate some differences in results. For example, depth was a significant variable in other studies on Hectors's (Brager *et al.*, 2003; Rayment *et al.*, 2011; Weir & Sagnol, 2015), Maui's (*Cephalorhynchus hectori maui*; Derville *et al.*, 2016) and Chilean dolphins (*C. eutropia*; Heinrich, 2006). However, animals elsewhere were associated with shallower water. This is likely explained by variation amongst study sites. QCS is relatively shallow, narrow and enclosed, whereas, studies on the same or similar species spanned much deeper waters where the ocean floor may not be accessible (Rayment *et al.*, 2011). Likewise, in contrast to the present study, Hector's dolphins elsewhere (Rayment *et al.*, 2011; Rayment *et al.*, 2010; Weir & Sagnol, 2015), Commerson's dolphins (*Cephalorhynchus commersonii*) off Patagonia (Garaffo *et al.*, 2011) and Chilean dolphins (Heinrich, 2006) displayed a preference for coastal distribution. These locations were situated with a closer proximity to open ocean influence, unlike the enclosed QCS.

While prey movement likely dictates dolphin movement in these studies, proximity to shore in more exposed areas may also provide protection to small cetaceans, particularly if young animals are present (Garaffo *et al.*, 2007; Wursig & Wursig, 1979). Indeed, as the smallest delphinids, *Cephalorhynchus* species may be quite vulnerable. Known shark attacks on Hector's dolphins are limited (Brager *et al.*, 2003) and while attacks by killer whales have not been documented (Visser, 1999), they have occurred (D. Clement, pers. comm., June, 2017). Similarly, predation on Chilean dolphins is not well known, but killer whales and leopard seals (*Hydrurga leptonyx;*Goodall *et al.*, 1988), as well as a number of shark species including white sharks (*Carcharidon cacharias*), shortfin mako (*Isurus oxyrinchus*) and Pacific sleeper sharks (*Somniosus pacificus*) may be potential threats (Crovetto *et al.*, 1992; Long & Jones, 1996).

4.4.3 Bottlenose dolphins

The parameters of the best fit GAM suggest that temporal and static factors contributed to bottlenose dolphins' distribution and density in QCS. Higher dolphin density was associated with areas of high and low slope as well as increased depth. Bottom slope can affect the mixed layer depth (Armi & Millard, 1976) and subsequently upwelling and oceanic productivity (Marra, 1978). This may provide a barrier against which prey can be herded, thus aiding in prey capture, as observed by Bailey &Thompson (2010). Therefore, bottlenose dolphins in QCS may be using the rises along various bays and the main channel to assist in herding prey while foraging in large groups (refer to section 3.4). This tactic may reduce energetic costs (Bailey & Thompson, 2010), as they pass throughout QCS and the adjacent sounds (Merriman *et al.*, 2009). Furthermore, the association with areas of increased depth and gentler slope may indicate that the dolphins were also using deeper and flatter regions of the Sound, perhaps to access alternate prey by using different feeding tactics (Torres & Read, 2009).

Given the overall adaptability of this species, it is likely that bottlenose dolphins in QCS display flexibility in foraging strategies and diet. Bottlenose dolphins have a cosmopolitan distribution spread amongst a variety of habitat types including oceanic, coastal estuarine and seagrass bed environments (Kenney, 1990; Reeves *et al.*, 2002). Their diet amongst these habitats varies according to availability and consists of an extensive range (species, size and lifestyle) of fishes, cephalopods and crustaceans (Barros & Wells, 1998; Blanco *et al.*, 2001; Gannon & Waples, 2004). In (Doubtful Sound) NZ, specifically, diet studies indicate that bottlenose dolphins feed on indigenous demersal and reef dwelling fishes and to a lesser extent, on ephemeral, pelagic species (Lusseau & Wing, 2006). Similar prey sampling in QCS would complement dolphin distribution data collection providing further insight in this region.

Like the present study, both depth and slope are significant factors in determining bottlenose dolphin distribution/density elsewhere. Variation amongst these results are likely due to differences amongst the type of study sites (*i.e.*, open bay, open ocean, semi-enclosed Sound; see Table 4.12), as with Hector's dolphins (refer to section 4.4.2). For example, the seasonal correlation with depth in the Hauraki Gulf and Bay of Islands was attributed to seasonal on shore/off shore movement of the dolphins (Dwyer, 2014; Hartel *et al.*, 2015). This is likely due in part to predator avoidance (Hartel *et al.*, 2015), which may not be needed for bottlenose dolphins within the relatively shallow, protected QCS (refer to section 3.4).

Table 4.12. Studies from locations within New Zealand and elsewhere investigating an association of bottlenose dolphins with static parameters.

Location	Habitat Type	Parameters	Reference
Hauraki Gulf, NZ	open bay	shallow depth, high slope	Dwyer, 2014
Bay of Islands, NZ	open bay	high depth (summer) shallow (winter)	Hartel *et al.* 2015
Liguarian Sea	open ocean	high depth, slope variability	Azzellino *et al.* 2012
Northwest Atlantic Ocean	open ocean/shelf break	mid-depth	Davis *et al.* 1998
Gulf of Mexico	ocean basin/shelf break	shallow depth	Hamazaki, 2002

While bottlenose dolphin diet is diverse, habitat use may also vary on a regional basis and be affected by differences in local hydrography. For example, Doubtful Sound is influenced by considerable freshwater influx from natural and anthropogenic sources (Rutger & Wing, 2006). This may affect concentrations of nutrients (phosphate and nitrate), chlorophyll and dissolved oxygen in this region (Peake *et al.*, 2001), which subsequently leads to variations in phytoplankton biomass and primary productivity (Peake *et al.*, 2001; Tyrell, 1999) that form the base of the food chain. In this dynamic environment, bottlenose dolphin distribution is consistently influenced by SST (Elliott *et al.*, 2011; Schneider, 1999). Comparatively, QCS has only limited freshwater input from various small streams (Hadfield *et al.*, 2014) and dolphin density was not influenced by the dynamic variables that were tested during the present study. However, year was significant and predictions shifted spatially, suggesting that other dynamic variables not explored here, may have been contributing to density patterns. Moreover, bottlenose dolphins are more likely influenced by the dynamics of the greater Marlborough region (refer to section 2.4) as they move in and out of the neighbouring sounds (Merriman *et al.*, 2009).

4.4.4 Dusky dolphins

The parameters of the best fit GAM indicate that a combination of temporal, dynamic and static factors contributed to dusky dolphin distribution and density in QCS. These results suggest that this species may display flexibility in foraging habits within the region, like they do in Admiralty Bay, NZ (Duffy & Brown, 1994) and elsewhere. While variations amongst the Marlborough Sounds exists, QCS and Admiralty Bay are influenced by similar factors as a result of their shared geographic history and adjacency to Cook Strait (Davidson *et al.*, 2011). Dusky dolphins in Admiralty Bay feed diurnally on schooling fish using a range of feeding tactics including cooperative bait ball feeding (Duffy & Brown, 1994; McFadden, 2003; Vaughn *et al.*, 2007; Vaughn *et al.*, 2008). Strategies are influenced by changes in prey species or behaviour (Vaughn *et al.*, 2007). Likewise, dusky dolphins exhibit notable differences in foraging techniques in other regions. Off Kaikoura, NZ, strategies include nocturnal feeding on fish and squid with seasonal plasticity (Benoit-Bird *et al.*, 2004; Cipriano, 1992; Markowitz *et al.*, 2004). Comparatively, animals found off Argentina are mesopelagic, diurnal feeders, with a diet consisting primarily of anchovies (Koen-Alonso *et al.*, 1998; Würsig *et al.*, 1997). The similar Peale's dolphin (*Lagenorhynchus australis*) off Southern Chile is observed foraging primarily in kelp beds (Viddi & Lescrauwaet, 2005), on octopus and squid (Viddi & Lescrauwaet, 2005) and probably on demersal or benthic fishes (Moreno & Jara, 1984).

While it is likely that dusky dolphins in QCS are very adaptable and access prey based on availability, it may also be that the associations presented in this study may not be as strong for this species since this had the lowest sighting rate (section 3.3.4), thus the least amount of data. While the deviance explained by this model was high (69.9%), this may represent the best fit to the available data. Predictions varied annually and may have been more dependable when sightings were higher. However, dusky dolphin occurrence and density were similarly influenced by static and dynamic factors including depth, slope, distance to shore, chlorophyll and SST along Patagonia, Argentina (Garaffo *et al.*, 2010; Garaffo *et al.*, 2011). Previous work in Golfo Nuevo, showed that while dolphins are typically found in deeper waters of the study area, like the present study, they exhibit obvious interannual variation (Garaffo *et al.*, 2007). The findings here indicate an inverse relationship with dusky dolphin density and surface fluorescence, in contrast to the findings by Garaffo (2010). As described previously (refer to section 4.4.2), fluorescence (chlorophyll) is a measure of productivity; however, it may be that in this case, surface measurements were not the best indicator of the movement of prey below the surface (*i.e.*, in a baitball). Measurements further below the surface or bottom measurements as noted by Miller, 2014 might be more informative in QCS for this species.

The species examined in this study did not display obvious clumping around or total avoidance of the marine farms. However, for both dusky and Hector's dolphins, the models indicated an increase in density as distance increased to approximately 3.5 and 6 km respectively, so some avoidance of the immediate areas around the marine farms may have occurred. Marine farms could influence the general health of the ecosystem (refer to section 2.4.3). Furthermore, their actual structure could potentially limit animal movement and foraging abilities, as suggested of dusky dolphins in Admiralty Bay that rarely use the areas within mussel farms (Markowitz *et al.*, 2004; Pearson *et al.*, 2012). Similarly, Heinrich (2006) observed that the probability of sighting Peale's and Chilean dolphins increased with increased distance from salmon farms, and mussel farms (just for Peale's dolphins). Moreover, bottlenose dolphin occurrence decreased in Shark Bay, Western Australia upon the placement of an aquaculture farm (Watson-Capps & Mann, 2005). In the present study, bottlenose dolphin density was relatively uniform as distance from marine farms increased. However, on numerous occasions they were directly observed foraging in the bays amongst the salmon farms (per. observ.). There may be an attraction to prey congregating around the farms (Bonizzoni *et al.*, 2014). In fact, studies in other areas indicate a positive correlation of bottlenose dolphins with aquaculture farms (Bonizzoni *et al.*, 2014; Piroddi *et al.*, 2011). The conclusions regarding this parameter were quite vague for bottlenose dolphins. However, it is important for future Sound development to be cognizant that some avoidance of the farms by the other species may have occurred. The consideration of the farms separately by individual type as in Heinrich, 2006, may offer further ecological meaning to these findings.

4.5 Limitations and conclusions

The findings in this chapter offer important insights to the ecological links of three dolphin species to their habitat in QCS. They also serve as a practical role for developing regional conservation management efforts. Habitat mapping is crucial to management and conservation endeavours because species and their environments can be more efficiently managed if their distribution and environmental limits or boundaries are understood (Pennino *et al.*, 2017). Species distribution data is informative, but may be limiting since point data may not be completely representative of areas that animals could occupy (Ross & Howell, 2013). Habitat modelling based on environmental parameters expands our knowledge, providing a more complete representation of habitat use to inform management decisions than species distribution data alone (Gormley *et al.*, 2013; Ross & Howell, 2013). Therefore, the findings presented in this chapter are a logical complement to those presented in Chapter 3 and beneficial for the consideration of protective measures (refer to section 6.2.2 for discussion on conservation management applications of these data).

While this study presents original findings applicable to conservation management, the data collection and analysis were associated with some limitations. Like other opportunistic studies, the data collection involved no control over survey design, survey effort and spatial coverage leading to constraints in the sampling methods and subsequent restrictions regarding data standardization and analysis (Viddi *et al.*, 2010). Specifically, limitations in survey effort and the dynamic data collection dictated the resolution of the analysis. Environmental sampling and data analysis at different resolutions may result in different meanings for a species (Bailey & Thompson, 2009; Guisan & Thuiller, 2005). Cetacean habitat relationships can vary according to scale since patterns in environmental parameters also change depending on scale (Ballance *et al.*, 2006). At larger scales, the number of sightings and survey effort are higher (higher SR/ER), but this results in covariates that are averaged over a larger area as well (Hamazaki, 2002; Redfern *et al.*, 2006). Furthermore, the selected method of analysis (GAMs) is accompanied by the challenge of establishing a balance between the number of observations and the number of degrees of freedom in order to select the appropriate level of smoothness, which may influence the meaning of the results (Guisan *et al.*, 2002). Likewise, the deviance explained by GAMs is typically low (< 40%, but mostly ~10%; Forney *et al.*, 2012; Mannocci, Laran *et. al.* 2014), although sometimes much higher (83.4%; Dellabianca *et al.*, 2016). The relatively high values in the present study, particularly for Hector's and dusky dolphins, may have been due in part to the scale at which the data were analysed. Dedicated surveys that allow for control over survey design, survey effort and possibly a smaller grid cell size may lead to the detection of more fine scale environmental variation and habitat associations.

Despite some limitations, there are numerous benefits associated with the collection of cetacean habitat data via opportunistic platforms. Scientific contributions of the present study in particular, include its role as the first regional investigation of delphinid habitat use and the first time that Hector's, bottlenose and dusky dolphin habitat was modelled concurrently. Variables associated with delphinid density in QCS were explored, suggesting that each species' habitat use was characterized by a combination of different parameters or parameter values. This research provided interpretive information on each species' regional ecology and further evidence of the occurrence of resource partitioning in QCS.

Habitat segregation based on environmental parameters has been observed amongst similar species elsewhere (Dellabianca *et al.*, 2016; Garaffo *et al.*, 2011). Moreover, this is a commonly observed phenomenon amongst cetaceans globally (Becker *et al.*, 2014; Roberts *et al.*, 2016;

Svendsen *et al.*, 2015; Tepsich *et al.*, 2014). Interestingly, the consideration of the same species and same parameters in different regions produces some varying results (*i.e.,* Hector's dolphins in shallow water close to shore; bottlenose dolphins in relatively shallower waters and associated with SST; dusky dolphin's direct relationship with chlorophyll). This suggested that the unique combination of regional physical and hydrographic features in QCS (*i.e.,* relatively shallow, enclosed region with limited fresh-water input and influx from Cook Strait in two regions) may have impacted animal distribution or density.

These habitat models were not only descriptive but also allowed for visualization of where the dolphins could be located, given certain conditions in the environment. For all species, spatial predictions generated from the significant model results revealed that dolphins could have been using more of the area than indicated by their sighting locations. For Hector's dolphins specifically, while regions of higher density are generally located around the central part of the Sound, predictions indicate that Hector's dolphins could also be located in regions of the Sound once previously occupied (*i.e.,* further in and further out; refer to Figure 2.11). The models highlight the value and importance of year-round data collection and the inclusion of temporal variables. Oftentimes cetacean data collection is limited to the summer months (Becker *et al.*, 2014), while data that are collected from one season or year cannot always be used to accurately predict distribution or density during other time periods (Azzellino *et al.*, 2012; Becker *et al.*, 2014). Predictions in the present study indicated that regions of high density shifted either across season or subsequent year. It is likely that habitats change temporally (monthly, seasonally or annually), primarily due to variations in prey availability (Azzellino *et al.*, 2012). However, the significance of temporal parameters could also be a reflection of further variables, including other human-related factors that were not tested here.

Through the present research, a better understanding of Hector's, bottlenose and dusky dolphin ecology within QCS has been gained. Varying results with similar studies elsewhere conclude that there may be a unique ecological connectivity of these animals to the area. Further studies can be designed around the results presented here. Moreover, this work can complement management-based decision making. Ultimately, this research contributes to the conservation of three nationally important species within New Zealand waters.

Chapter 5

First insights to swim-with-dolphin tourism in Queen Charlotte Sound, New Zealand

A group of swimmers and bottlenose dolphins (*Tursiops truncatus*) with
a swimmer during a swim encounter in Queen Charlotte Sound, New Zealand.

5.1 Introduction

Effective conservation management is contingent upon the consideration of all aspects of a region, including anthropogenic and natural factors (Douvere, 2008). Thus far, this thesis examined current and long-term delphinid spatial and temporal trends and habitat use. As a complement to these findings and a further critical component in developing species' conservation management efforts, the present chapter focuses on swim-with-dolphin tourism activities in Queen Charlotte Sound (QCS).

Ecotourism is nature-based exploration or travel that ideally promotes environmental education, while being sustainably managed (Blamey, 2001). This concept emerged in the 1970s and has since widely expanded in scope and capacity (Blamey, 2001). As charismatic megafauna, marine mammals *i.e.,* Cetacea (whales and dolphins), Sirenia (sea cows), Pinnipedia (seals, sealions, walruses) and Ursidae (polar bears) are a popular focus of ecotours (Barney, 2005; Hausmann *et al.*, 2017). In particular, during the past two decades, whale watching (tours with some commercial aspect to view, swim with or listen to any species of whale, dolphin or porpoise) has rapidly developed into a global industry (Hoyt, 2001). From its inception in the 1950s, whale watching has grown from an occasional event, to more than 3,000 worldwide companies spanning 119 countries and serving approximately 13 million people (Hoyt, 2001; O'Connor *et al.*, 2009).

The expansion of whale watching has been viewed as an alternative option to regions involved in whaling (Cunningham *et al.*, 2012). The economic benefits of this industry include the creation of jobs and generation of income (Wilson & Tisdell, 2003), which is particularly important in economically developing nations (O'Connor *et al.*, 2009). Furthermore, whale watching has the capacity to promote public awareness about cetaceans (Lopez & Pearson, 2017) and increase patrons' likelihood to contribute to or engage in conservation efforts (Lopez & Pearson, 2017; Wilson & Tisdell, 2003).

Despite the benefits associated with this industry, the expansion of cetacean tourism has precipitated concern over the potential impacts on target species (O'Connor *et al.*, 2009; Spradlin *et al.*, 2001). All tour companies do not operate uniformly and in some cases may be perceived as no less of a detriment than whaling (Neves, 2010). An increasing number of dolphin-based tourism studies have been undertaken, indicating a range of potentially negative implications. Short-term changes associated with tour activities include decreases to the proportion of time cetaceans spent foraging, resting and/or socializing (Carrera *et al.*, 2008; Lundquist *et al.*, 2012; Meissner *et al.*, 2015; Stockin *et al.*, 2008; Visser *et al.*, 2011), increased group cohesion (Markowitz *et al.*, 2009), increased surface behaviour (Markowitz *et al.*, 2009; Stamation *et al.*, 2010), longer dive times (Lusseau, 2003b) and changes to speed (Matsuda *et al.*, 2011) and direction (Mattson *et al.*, 2005). Such behavioural alterations may have biological consequences, including increased respiration rate and energy expenditure (Christiansen *et al.*, 2014). Moreover, the extended presence of tourist activities may influence the mother-calf bond (Mann *et al.*, 2000) and compromise survival (Mann & Watson-Capps, 2005). Tourism can cause shifts in habitat use or complete area avoidance (Bejder & Samuels, 2003; Constantine *et al.*, 2004; Lück, 2007; Lusseau, 2004, 2005) and on a long-term basis can lead to decreased relative abundance (Bejder *et al.*, 2006).

Swim tourism, in particular, has increased as operators attempt to provide people closer interactions with marine mammals (Cowling *et al.*, 2014; Kessler *et al.*, 2013; Lundquist *et al.*, 2012; Samuels & Bejder, 2004). Twenty species of cetaceans are targeted for swim tourism (Samuels *et al.*, 2000) spanning upwards of 14 countries worldwide (O'Connor *et al.*, 2009). This industry has grown to include a total of nine vessels operating up to 18 trips daily that engage in swim-with-dolphin activities (Martinez *et al.*, 2011). As this branch of cetacean tourism has expanded, so has emerging research.

Results from recent studies indicate that in the presence of swim tourism important dolphin behaviours including foraging (Filby *et al.*, 2017), resting (Constantine *et al.*, 2004) and socializing (Peters *et al.*, 2013) decrease. However, increased activity levels occurred during rest periods (Courbis & Timmel, 2009), with the use of auditory stimulants in the water (Martinez *et al.*, 2012) and upon closer vessel approach (Kessler *et al.*, 2013). Furthermore, increased whistle production (Scarpaci *et al.*, 2000) and increased group cohesiveness (Bejder & Dawson, 1999) were observed during swim activities. Short term behavioural modifications may indicate underlying physiological shifts (Walker *et al.*, 2006) and progress into longitudinal behavioural modifications including sensitization and habituation (Bejder *et al.*, 2009; Constantine, 2001; Thompson, 2009). In addition, they could have long-term biological implications (Christiansen *et al.*, 2013; Hastie *et al.*, 2003b; Lusseau & Bejder, 2007). Studies of cetacean swim tourism indicating direct consequences to target species have elicited a heightened awareness regarding management needs within the industry. Guidelines may be absent (Allen *et al.*, 2007), inappropriate or lack enforcement (Constantine & Bejder, 2008). Management efforts vary regionally and may require more active involvement (Filby *et al.*, 2014a). Recommendations include that operators be charged appropriate fees and engage patrons in education (Kessler & Harcourt, 2010). A limit to permitted licenses and zoning regulations are also suggested (Kessler & Harcourt, 2012). In light of the need for management improvements, in addition to varied cetacean responses to tourism at the local, species and even population levels, regional scale studies of this expanding industry are imperative.

In New Zealand (NZ), cetacean watching is an integral aspect of tourism, and has been in existence for more than 20 years. Operators in more than 10 locations in both NZ's North and South Islands offer whale watching, with many including swim-with-dolphin activities (O'Connor *et al.*, 2009). The present study was conducted in Queen Charlotte Sound (QCS), a semi-enclosed sunken valley at the northeastern tip of NZ's South Island (refer to section 2.2.1 for more detail). Bottlenose (*Tursiops truncatus*), common (*Delphinus* spp.), dusky (*Lagenorhynchus obscurus*) and Hector's dolphins (*Cephalorhynchus hectori hectori*) occur here (Davidson *et al.*, 2011; Duffy & Brown, 1994; Merriman *et al.*, 2009; Webb, 1973). Currently, two companies are permitted to interact with marine mammals. One is allowed to view all species and conduct swims with bottlenose, dusky and common dolphins, as well as New Zealand fur seals (*Arctocephalus forsteri*). The second holds a viewing permit that allows the observation of all species that may be opportunistically encountered. However, to date, no investigation of tourism and swimming activities in this or the greater Marlborough Sounds region has been completed. This is despite the fact that permitted dolphin tourism has been in operation in QCS since 1995 (refer to Chapter 2). Similar to trends elsewhere, operations in QCS have grown as the focus of trips has shifted from ecotours with opportunistic dolphin viewing to swim-with-dolphin tours (refer to Chapter 2). In addition, requests for further permits in QCS have been lodged (pers. comm., R. Grose, November, 2011). This proposed regional expansion prompted the need to examine current trends of swim tourism in QCS.

Most recent research has focused on the effects of the industry on the target animals, offering evidence of several potentially unfavourable consequences (described earlier). The current study includes a baseline examination of the target species, animal group dynamics and operator techniques, which were then used as variables to assess multiple measures (proxies) of bottlenose dolphin engagement in swim-with-dolphin tourism in QCS. Specifically, this study aimed to examine:

- Characteristics of swim-with-dolphin tourism in QCS in terms of:
    - target species
    - bottlenose dolphin group dynamics
        - group size
        - group composition
    - bottlenose dolphin behaviour prior to initial vessel approach and first swim attempt
    - origin of swim attempts and the number of other vessels present
    - operator techniques during bottlenose dolphin swim encounters
        - vessel approach method
        - vessel distance from dolphins during swimmer entrance into water
        - number of swim attempts
        - number of swimmers
        - swimmer orientation to the dolphins
- Measures of bottlenose dolphin engagement in swim-with-dolphin tourism in QCS including:
    - likelihood that sightings resulted in swim encounters
    - duration of swim attempts
    - distance operators travelled to track dolphins during swim encounters
    - reactions of dolphins to swim attempts

5.2 Methods

5.2.1 Study site

The study site encompassed QCS and Tory Channel, divided into four sectors, as described in section 3.2.1 and depicted in Figure 3.1. These four sectors were included as categorical explanatory variables to determine if spatial variation in swim tourism existed in the study site.

5.2.2 Data collection

Data were collected for multiple variables, which defined the characteristics of swim-with-dolphin tourism in QCS, and were used as explanatory variables to measure variation in proxies for bottlenose dolphin engagement in swim-with-dolphin tourism in QCS (Table 5.1).

Table 5.1. Data categories and explanatory variables that were collected in QCS, NZ from November 2011–April 2014.

Category	Variables
Temporal	year, season
Spatial	sector of QCS
Anthropogenic	initial vessel number
Operator Techniques	number of attempts, vessel approach, distance from dolphins at swimmer entrance in water, swimmer orientation to dolphins, swimmer number
Dolphin Group Dynamics	species, group size, presence of young, initial behavioural state

A description of the swim-with-dolphin industry is provided here to ensure clarity with the procedures and terminology discussed in this chapter and to provide rationale for similarities and differences amongst methods used in comparable studies. A dolphin encounter was defined as any dolphin group sighted and subsequently approached by the tour vessel to ≤ 300 m. Those including a dolphin swim were referred to as swim encounters hereafter and spanned the time from the start to the end of the sighting including the dolphin swim (Scarpaci *et al.*, 2003). During a dedicated swim-with-dolphin trip, when dolphins were sighted, the tour operator would typically approach the group (if sighted from a distance) and then decide if they were going to proceed with a swim encounter. If so, passengers were briefed on the procedures and instructed to prepare (*i.e.*, get into wetsuits). Swimmers entered the water via steps that were lowered at the back of the boat. Each time this occurred within the same dolphin swim encounter, it was considered a swim attempt. One or multiple swim attempts occurred within a swim encounter.

The operator used a variety of methods to approach the dolphins upon successive swim attempts, so these were categorized according to previously established methods (Scarpaci *et al.*, 2003). Likewise, several methods of swimmer placement in the water, in reference to the dolphins were utilized and based on similar research (Constantine, 2001; Martinez *et al.*, 2011). In the Bay of Islands, NZ, an interaction was defined as at least one dolphin milling for a minimum of 15 sec around at least one swimmer (Constantine, 2001). Similarly, in Akaroa, an interaction was defined as at least one dolphin remaining within 5 m of a swimmer for at least 10 sec (Martinez *et al.*, 2011). These measurements of an interaction were not typically feasible in the present study due to variation in dolphin behaviour and typical operator methods in QCS compared to the other sites.

For example, in the Bay of Islands, NZ, bottlenose dolphins were commonly milling, while in Akaroa, NZ, Hectors dolphins were commonly milling, diving or socialising and engaged with swimmers for extended time periods (Constantine, 2001; Martinez *et al.*, 2011). In comparison, in QCS, large dolphin groups (mean = 36.9) were typically travelling (43.2%) at the start of encounters. Moreover, operator approach methods were usually (66.5%), J-style (vessel travels parallel to the dolphins and then moves ahead) and swimmer placement was primarily in front of the dolphins (66.3%). The combination of dolphin behaviour and operator methods created a situation that was much different than those in other regions (as detailed in 5.3.1 and discussed in 5.4), so those measurements of an interaction were not deemed accurate assessments of dolphin interest in QCS. Therefore, some alternate measures were considered to assess dolphin swim tourism in this study. Several proxies were interpreted in the context of relevant literature in order to comprehensively examine the industry in this region and to gauge bottlenose dolphin engagement in swim activity in QCS. These include:

- *A high likelihood that a dolphin sighting resulted in a dolphin swim encounter (i.e., swimmers were placed in the water with dolphins at least once during a sighting)*
  A high occurrence of swims during dolphin sightings may suggest tour industry success in this region. It may also be interpreted as a commitment by the operator to engage in swim events (Whitt & Read, 2006), despite the situation (*e.g.,* lack of dolphin interest, or unsuitable dolphin behaviour/group dynamics). Therefore, the likelihood of swim encounters was examined in reference to dolphin group dynamics as well as temporal variables.

- *Swim attempt duration*
  Swim attempt duration was a direct measure of animal interest in swimmers (Filby *et al.*, 2014a; Markowitz *et al.*, 2009; Martinez *et al.*, 2011), whereas shorter attempts equated to low dolphin interest/engagement in swim activity.

- *The distance travelled amongst dolphins during swim encounters*
  This was used to gauge operator pursuit of interaction, whereas long distances travelled between swim attempts during a swim encounter represent an increased vessel presence (*e.g.,* leapfrogging; Williams *et al*., 2002).

- *Reactions of dolphins*
  Following Peters *et al*. (2013), attraction was defined as ≥ 50% of the dolphins in a group swimming towards the swimmers. This was a representation of dolphin interest/engagement.

A single permitted operator conducted commercial dedicated swim-with-dolphin trips in QCS during the entire study period (2011–2014). The dates for years one, two and three spanned across 2011–2012, 2012–2013 and 2013–2014, respectively. An individual tourism year spanned three austral seasons. These were defined as austral spring (October–November), summer (December–February), and autumn (March–April), *i.e.,* only when tourist activities were in operation. Tours departed daily at 0900 hrs (subject to passenger minimums) and lasted up to four hours in duration. Although vessel paths followed fixed paths to a certain extent, the survey design was asystematic (refer to section 3.2.2 for details). Data collection was limited to favourable viewing conditions *i.e.*, no precipitation; Beaufort Sea State (BSS) ≤ 3 (Wilson *et* *al.*, 1997) and suspended if conditions deteriorated and compromised observation ability. Dolphins were located via naked eye and 10x30 Cannon binoculars, via continuous scanning methodology (Mann, 1999).

At the start of an encounter (previously defined in this section), a 300 m radius was scanned and the number of vessels (recreational or commercial boats) was recorded. Multiple swim attempts (previously defined) typically occurred within the same swim encounter and were measured from the time that swimmers entered the water until the attempt was terminated. This time was selected because the distance of the boat from the swimmers or prevailing weather conditions sometimes required extra time for swimmers to exit the water. The mean duration of 1) swim attempts, 2) collective, successive swim attempts within the same encounter and 3) swim encounters were compared to determine what fraction of the swim encounters (*i.e.*, the duration that the vessel was in the presence of dolphins) actually represented the presence of swimmers with dolphins. Swim duration, location and vessel track data were collected using a Garmin Etrex 20 Global Positioning System (GPS). Prior to each swim attempt, the different strategies the operator utilized to approach a group of dolphins were recorded and categorized as per Table 5.2. At the initiation of each swim attempt, the distance (m) of the vessel from the dolphins was visually assessed using the vessel length (13 m) for scale. At this point, the orientation of the swimmers in regards to the dolphins was also recorded and categorized as per Table 5.3.

Table 5.2. Vessel approach methods at the initiation of dolphin swim attempts in QCS from 2011–2014. Method definitions modified from (Scarpaci *et al.*, 2003).

Method	Definition
J	travels parallel to dolphins and then moves in front of them
In path	approaches in the direction of the dolphins' travel
Parallel	approaches dolphins along either side
No approach	remains in location from swim previous attempt
Reverse	reverses toward dolphins
Direct	moves directly amongst a group of dolphins

Table 5.3. Swimmer orientation in reference to dolphins in QCS from 2011–2014. Method definitions modified from (Constantine, 2001; Martinez *et al.*, 2011).

Swimmer Orientation	Definition
In path	swimmers placed in (≥50%) of dolphins' path of travel
Side and ahead	swimmers placed to the side and ahead of (≥50%) dolphins
Amongst	swimmer placed in the vicinity (within 300 m) of (≥50%) dolphins travelling in no particular direction

The number of swimmers was recorded as the maximum number present in the water at any time during the swim attempt (Markowitz *et al.*, 2009). Visual assessment of dolphin group dynamics occurred throughout the swim attempt. Groups were assessed across all species, including any multi-species groups and were assessed according to details described in section 3.2.2. Group structure was assessed for the presence of calves, defined as animals < 1/2 the size of adults (Fertl, 1994; Mann & Smuts, 1999) and neonates which were < 1/3 the size of adults, with visible foetal folds and/or uncoordinated behaviour (Mann & Smuts, 1999). It is recognised that visual boat-based assessment of dolphin group dynamics can often be difficult, so data with any uncertainty regarding the presence of calves or neonates were excluded from analysis (Constantine, 2002).

The behaviour of a dolphin group was assessed via scan sample by surveying the entire group from left to right (Mann, 1999) and determined according to the predominant group behaviour (*i.e.,* > 50% of individuals visible at the surface; Mann, 1999). Behavioural states were categorized as per Table 5.4.

Dolphin behaviour was assessed before the vessel initially approached the dolphin group and prior to each swim attempt to compare for changes observed in the presence of tourist activities (*i.e.,* the vessel/swimmers). Upon swimmer entrance in the water, dolphin reactions were measured based on the response of ≥ 50% of the dolphin group (Mann, 1999; Peters *et al.*, 2013) and classified as per Table 5.5.

Table 5.4. Behavioural state of dolphins in QCS from 2011–2014. Method definitions adapted from (Constantine, 2002; Shane *et al.*, 1986).

Behavioural State	Defintion
Travelling	persistent directional movement
Foraging	deep diving/circling; dolphins involved in an effort to capture/pursue prey; prey fequently observed
Socialising	displays of mating, leaping, chasing other dolphins; body contact
Milling	frequent change in direction; no apparent forward motion; animals surfacing in multiple directions
Resting	animals display slow movments in tightly cohesive group (<1 body length); animals often stationary and barely break the surface

Table 5.5. Dolphin reactions to swim tourism in QCS from 2011–2014. Method definitions modified from (Martinez, 2010; Neumann & Orams, 2005).

Reaction	Definition
Attraction	at least 50% of dolphins changed direction and approached swimmers/vessel
Avoidance	at least 50% of dolphins changed direction and moved away from swimmer/vessel
Neutral	at least 50% of dolphins maintained course of travel or behaviour in presence of swimmers/vessel

5.2.3 Data analysis

Variation in swimmer number was assessed using one-way analysis of variance (ANOVA) with Tukey HSD post hoc tests. The frequency of behavioural states prior to the initial vessel approach and prior to the first swim attempt were compared using a Chi-square test of Independence. These tests were performed using SPSS version 21 (IBM, 2012). Spatial data were plotted using ArcMap 10 (ESRI, 2011).

Generalized linear model (GLMs) and linear models (LMs) were conducted in R version 3.2.1 (R Core Team, 2015). All continuous response variables were initially tested for linearity and homogeneity of variance, forming the basis by which the appropriate model form for each response variable was selected. Explanatory variables were categorized when necessary for statistical purposes. Specifically, (1) the presence of at least one calf or neonate was a binary factor, collectively referred to as young. 2) approach methods were categorized as: non-invasive (no approach; parallel), invasive (J; in-path) and unspecified (direct; reverse) according to interpretation of current marine mammal regulations (Marine Mammals Protection Regulations, 1992) and (3) initial vessel number was a binary factor indicating the presence of ≤ 3 or > 3 vessels, reflecting the current limit of vessels within 300 m of a group of dolphins (Marine Mammals Protection Regulations, 1992).

The response variables that were modelled as measures of bottlenose dolphin engagement in swim-with-dolphin tourism included:

- The likelihood that a bottlenose dolphin sighting resulted in a swim encounter
- Swim attempt duration measured in total minutes
- Distance operators travelled to track dolphins during swim encounters; measured as total kilometres: calculated by first converting GPS swim encounter tracks to polylines within Arc Geographic Information System (GIS) 10.0 using Geospatial Modelling Environment (GME) tools (Beyer, 2014). Polyline lengths were measured by calculating the difference between start and end points with the calculate geometry function in ArcMap.
- Dolphin reactions

Models were run testing these response variables in relation to potential explanatory variables as per Table 5.6.

Table 5.6. Summary of initial models representing measures of bottlenose dolphin engagement in swim-with-tourism: the response variables, all potential explanatory variables included in the initial model and model forms that were run on data collected in QCS from 2011–2014.

Response Variable	Explanatory Variables	Model Form
Liklihood sightings resulted in swim encounters	year, season, location, dolphin group size, presence of young, initial behaviour	GLM
Swim attempt duration	year, season, location, dolphin group size, presence of young, initial behaviour, approach method,vessel distance, swim attempt number, swimmer number	LM
Distance operators travelled	year, season, location, dolphin group size, presence of young, initial behaviour, initial vessel number	LM
Dolphin reactions	year, season, location, dolphin group size, presence of young, initial behaviour, swimmer number, approach method, swimmer placement	GLM

Models were fit with a backward selection process eliminating non-significant explanatory variables at each step, determined by a likelihood ratio test (Goetz *et al.*, 2015). Models were compared using Akaike's Information Criterion (AIC) and the simplest models and/or those with the lowest AIC values were accepted. To describe the final models, post hoc tests (Tukey multiple comparison) were run when applicable in order to compare significant model term levels.

Models with binary response variables (likelihood that sightings resulted in swim encounters and dolphin reactions) were examined with GLMs with binomial distribution and logit link function. Continuous variables were examined for evidence of non-linearity and since this was not found, GLMs were selected over Generalized Additive Models (GAMs). The logit link is the default for logistic regression models with binary data and thus, appropriate in all three cases (Zuur *et al.*, 2009b). Dolphin reactions were categorized as neutral or responsive (collectively attraction and avoidance). Models were then run between neutral versus avoidance and neutral versus attraction responses, respectively. Initial models included data from years two and three, as the covariates swimmer entrance and approach method were not recorded during the first year.

The relationship between the response variable swim duration was tested in relation to multiple explanatory variables using a LM. The assumptions normality and independence were validated, making this model form appropriate. To account for heteroscedasticity (unequal variance in the residuals), the response variable was log transformed (Zuur *et al.*, 2009b). The initial model for swim duration included data from years two and three as the explanatory variables approach method and distance of vessel from swim start, were not available during the first year of sampling. The relationship between the response variable distance operators travelled to track dolphins during a swim encounter was also tested in relation to multiple explanatory variables with a LM, which was an appropriate model form given that the data validated the model assumptions (normality, independence and heterogeneity; Zuur *et al.*, 2009).

5.3 Results

5.3.1 Characteristics of swim-with-dolphin tourism

5.3.1.1 Target species, group dynamics and behaviour

In total, 309 dedicated swim-with-dolphin boat trips were assessed from November 2011–April 2014. During this time, 224 swim encounters occurred with bottlenose, common and dusky dolphins; dusky/Hector’s dolphin groups (*i.e.*, mixed groups) and New Zealand fur seals (Figure 5.1). A total of 190 dolphin swim encounters took place, of which 76.3% (n = 145) occurred with bottlenose dolphins. Since bottlenose dolphins were the primary species with which swim encounters occurred, swim data relating only to this species were further explored here. Consecutive dolphin swim attempts occurred with the same group, with the exception of three trips in which swim encounters took place with more than one species or group.

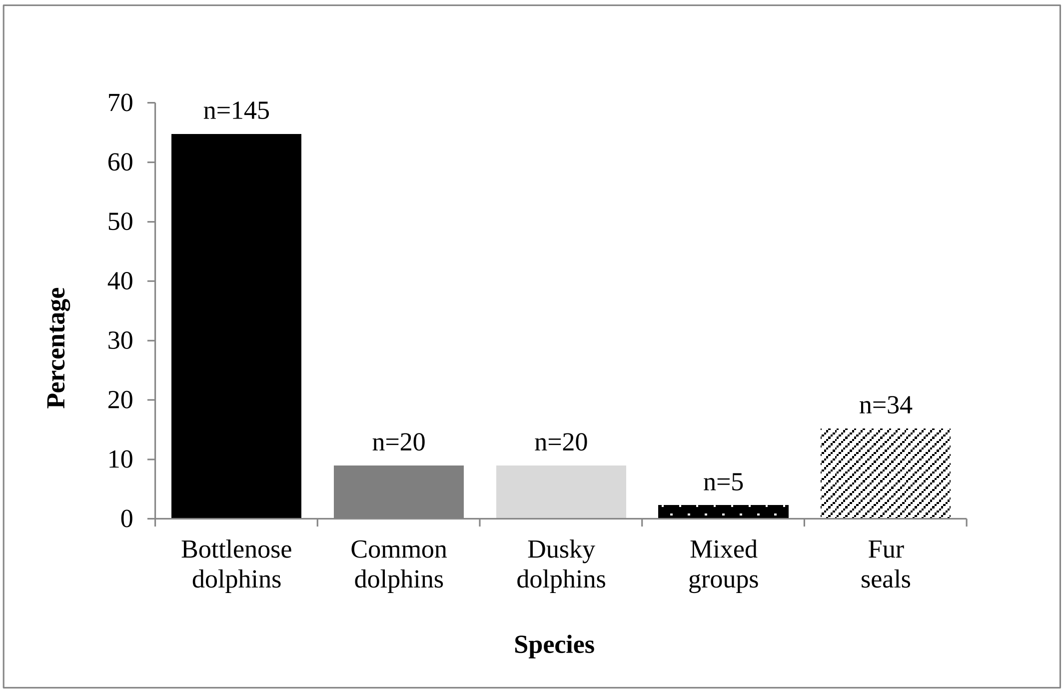


Figure 5.1. The species with which swim encounters took place in QCS from 2011–2014. Note that mixed groups refer to dusky/Hector's dolphin groups.

The mean group size of bottlenose dolphins during swims was 36.9 (SE = 1.66, range = 2–90 animals). During the period of the swim, at least one young (either calf or juvenile) dolphin was observed during 77.9% (n = 113 of 145) of encounters. Of the 139 encounters during which initial behaviour was observed, 43.2% (n = 60) occurred when dolphins were travelling. Variation existed between the proportion of behavioural states prior to initial vessel approach compared to those prior to the first swim attempt. Travelling (swim = 64.3%; n = 89) was comparatively higher prior to the first swim attempt, while the other behavioural states were lower prior to the first swim attempt. The values were: foraging (initial = 28.0%, n = 39; first swim = 15.0%, n = 21) resting (initial = 7.9%, n = 11; first swim = 5.0%, n = 7) socialising (initial = 7.9%, n = 11, first swim = 6.4%, n = 9) and milling (initial = 12.9%, n = 18, first swim = 9.3%, n = 13; $X^2 = 13.3$, $df = 4$, $n = 278$, $p < 0.05$; Figure 5.2).

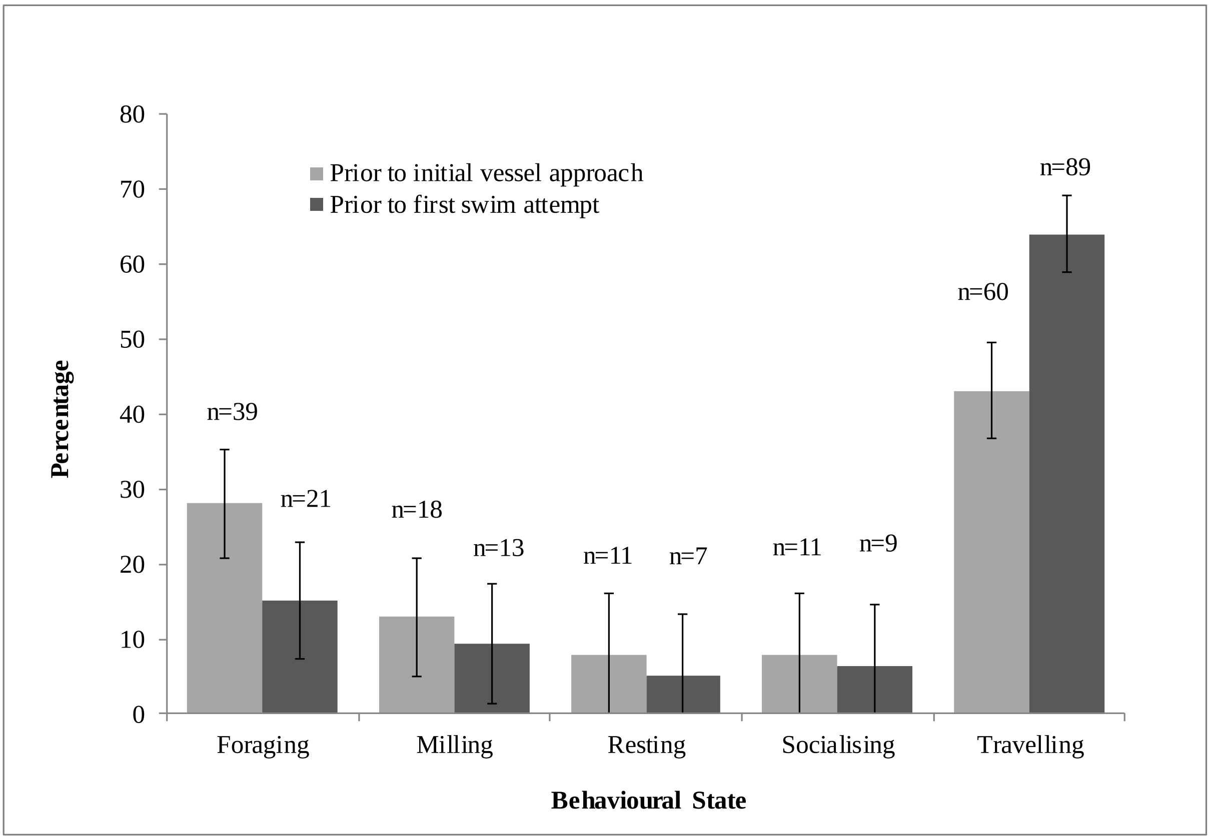


Figure 5.2. Comparison of bottlenose dolphin behavioural categories prior to initial vessel approach and prior to the first swim attempt during swim encounters in QCS from 2011–2014. Error bars represent standard error of the mean.

5.3.1.2 Geographic origin of swim attempts and operator techniques

The majority of swim encounters originated in the middle (48.3%; n = 70) and inner (36.0%; n = 53) Sounds. Only 8.3% (n = 12) originated in the outer Sound while 6.9% (n = 10) in Tory Channel (Figure 5.3). On the majority of trips, the initial number of other vessels present during bottlenose swims was ≤ 3 (90.5%; n = 124) and > 3 during only 9.5% (n = 13) of trips.

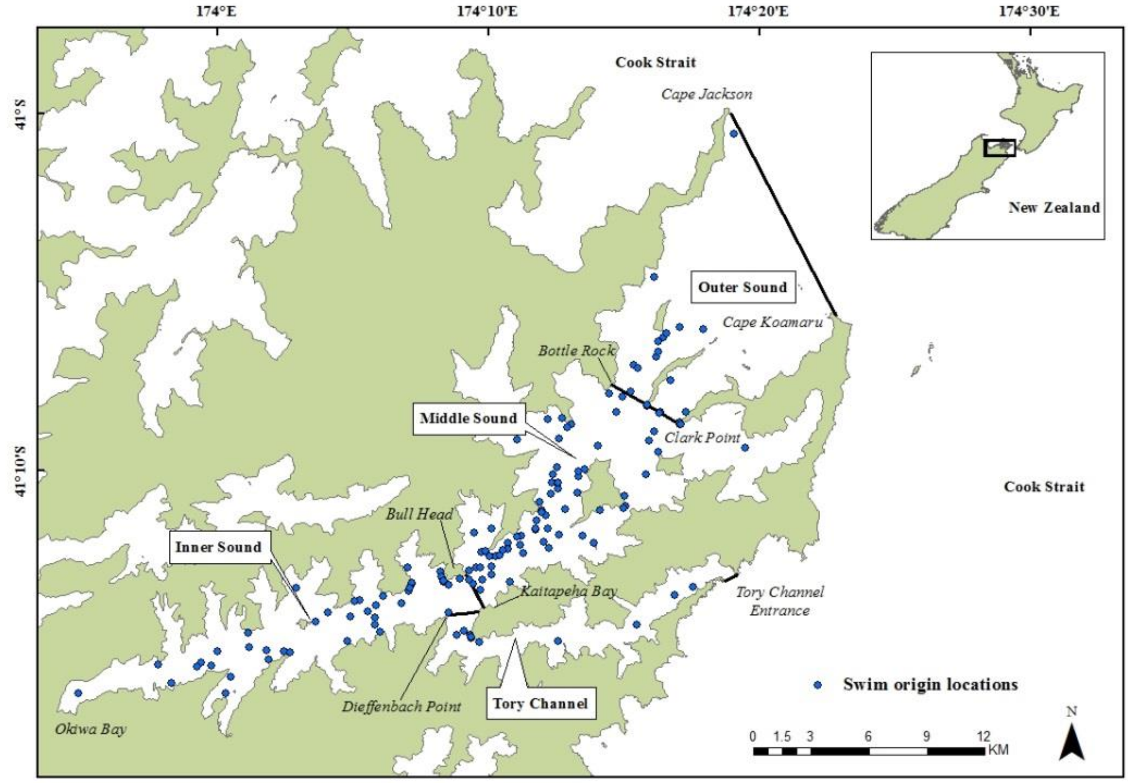


Figure 5.3. Study area indicating the origin of bottlenose dolphin swim encounters.

The majority of vessel approaches observed (74.5%, n = 347) were deemed invasive (*i.e.*, J, in-path, Table 5.7). Swimmer orientation was primarily classified as the in-path method (66.3%, n = 242, Figure 5.4). The mean estimated distance between the vessel and the dolphins, when the swimmers entered the water was 118 m (range = 0–500 m, SE = 5.64, n = 340), while the average number of swim attempts was 3.5 (SE = 0.79, range = 1–5). The mean maximum number of swimmers during encounters was 10.5 (SE = 0.41, range = 2–18, n = 140), with some evidence of annual variation evident (ANOVA: F(2) = 3.5, $p < 0.05$). Post hoc tests indicated that the mean during year three (mean = 11.6, SE = 0.65, range = 2–18, n = 61) was significantly greater than year two (mean = 9.2, SE = 0.66, range = 2–18, n = 41). There was also evidence that mean maximum swimmer number varied on a seasonal basis (ANOVA: F(2) = 17.9, $p < 0.001$). Post hoc tests indicated that values during summer (mean = 12.7, SE = 0.59, range = 2–18, n = 62) were significantly greater than spring (mean = 6.9, SE = 0.80, range = 2–18, n = 21) and autumn (mean = 9.4, SE = 0.55, range = 2–18, n = 57).

Table 5.7. Vessel approach methods by the tour operator during swim encounters with bottlenose dolphins in QCS from 2011–2014. Method definitions were modified from (Scarpaci *et al.*, 2002). For analytical purposes, categories were based on interpretation of the Marine Mammals Protection Regulations (1992).

Category	Method	# Approaches	% Approach Methods
Invasive	J	310	66.5
Invasive	In path	37	7.9
Non-invasive	Parallel	45	9.7
Non-invasive	No approach	2	0.4
Unspecified	Reverse	10	2.1
Unspecified	Direct	62	13.3

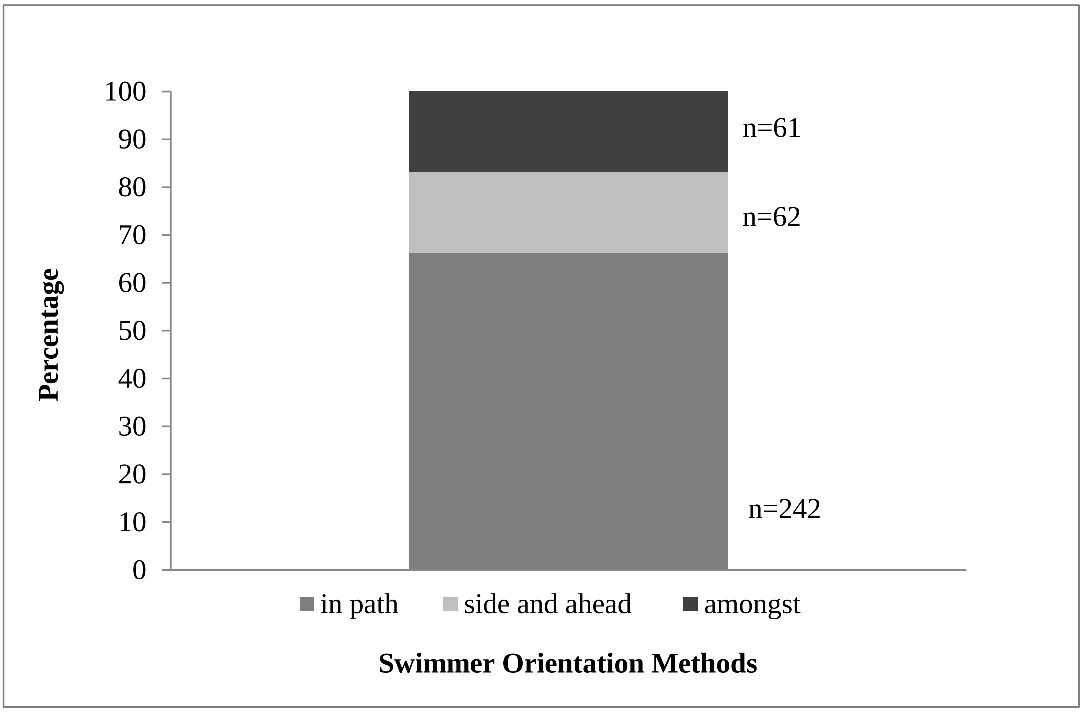


Figure 5.4. Methods of swimmer orientation in reference to bottlenose dolphins during swim encounters in QCS from 2011–2014.

5.3.2 Measures of bottlenose dolphin engagement in swim tourism

5.3.2.1 Likelihood bottlenose dolphin sightings resulted in swim encounters

A total of 184 bottlenose dolphin sightings occurred during dedicated swim trips, of these 78.8% (n = 145) resulted in swim attempts. The optimal GAM for the occurrence of swims during bottlenose sightings was occurrence ~ (year, *df* = 2) + (dolphin group size) which offered strong evidence that swim encounter occurrence varied on a yearly basis ($p < 0.05$) and was influenced by dolphin group size ($p < 0.001$). Post hoc tests indicated that swim encounters were 4.7 times more likely to occur during year three than year one (p = 0.06; 95% CI = 0.9 times less–23.4 times more). Swim encounters were 1.06 times more likely as group size increased by one animal ($p < 0.001$; 95% CI = 1.03–1.1 times). The model explained 22.2% of the deviance (Table 5.8).

Table 5.8. Parameter estimates of significant variables selected in the final GLM (binomial distribution) for the likelihood that a bottlenose dolphin sighting resulted in a swim encounter.

Term	Levels	DF	Estimate	SE	z value	p value	Change in deviance
year		*2*				*0.03*	*32.87*
	2		*0.53*	*0.47*	*1.13*		
	3		*1.59*	*0.59*	*2.68*		
group size			*0.06*	*0.02*	*4.04*	*<0.001 ****	
null deviance 147.77 on 166 df residual deviance 114.90 on 163 df AIC 122.9 deviance explained 22.2%							

5.3.2.2 Duration of bottlenose dolphin swim attempts

Mean individual swim attempt duration was 4.2 min (SE = 0.15, range = 0.7–39.5 min, n = 493), while the mean duration of total combined swim attempts during an encounter was 14.7 min (SE = 0.65, range = 2.7–55.9 min, n = 142) and encounter duration (extent of dolphin sighting from start to finish, inclusive of swim time) was 71.3 min (SE = 2.5, range = 1.6–27.2, n = 145). Thus, the actual presence of swimmers with dolphins (mean duration of cumulative swim attempts), illustrated only a small fraction (20.6%) of the duration that the vessel was in the presence of the dolphins, represented by the mean swim encounter duration (refer to depiction of this in Figure 5.5).

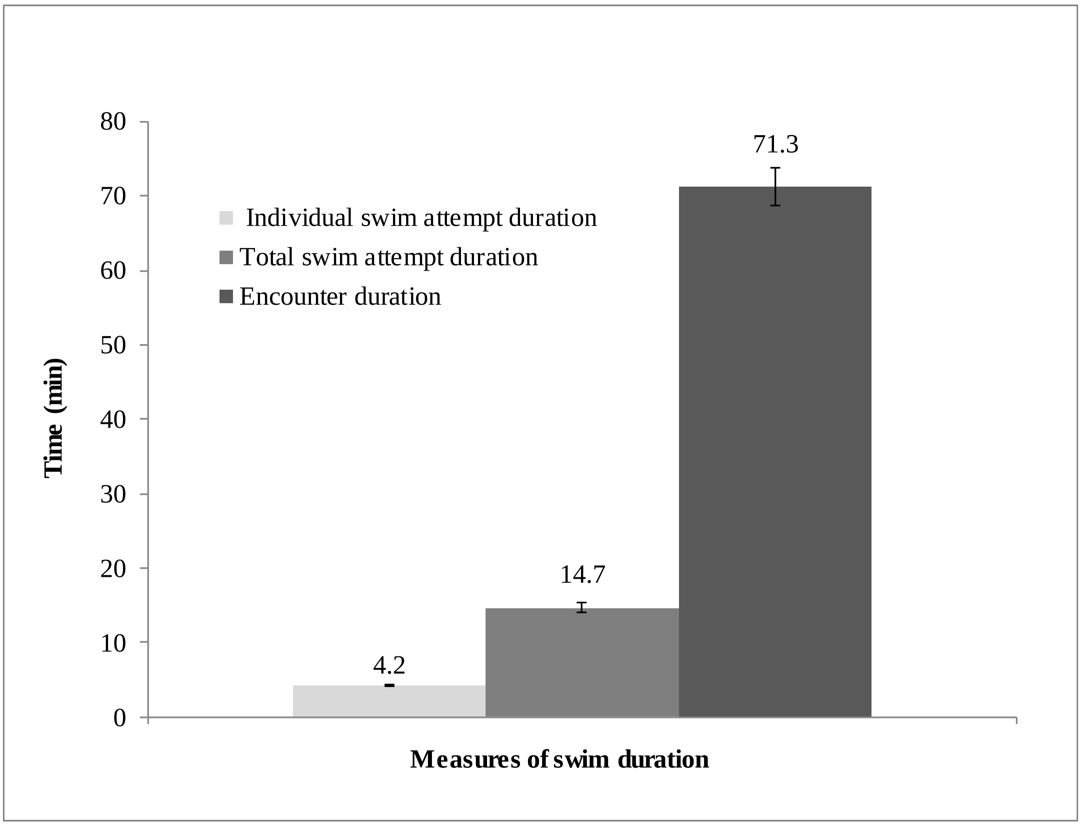


Figure 5.5. Measure of actual swimmer presence amongst dolphins (represented by comparison of mean duration of individual swim attempts and mean duration of total successive swim attempts), versus mean duration of swim encounters (representing vessel presence with dolphins) in QCS from 2011–2014. Error bars represent standard deviation.

Model results

The optimal LM for bottlenose dolphin swim duration was: duration ~ (year, *df* = 2) + (season, *df* = 2) + (section of the Sound, *df* = 3) + (distance of vessel at entrance) + (dolphin group size) + (initial behaviour, *df* = 4) + (presence of juveniles, *df* = 1) + (swimmer number). There was strong evidence that swim attempt duration varied between years ($p < 0.0001$), seasons ($p < 0.05$), sectors of the Sound ($p < 0.001$), with vessel distance ($p < 0.01$), with dolphin group size ($p < 0.001$), with initial behaviour ($p < 0.01$) and in the presence of young ($p = 0.01$; Table 5.9).

Table 5.9. Parameter estimates of significant variables selected in the final LM (with a log link function) for swim attempt duration. Significance codes are indicated by ***0.001, **0.01 and *0.05.

Term	DF	Levels	Estimate	SE	t value	p value
year	*1*					*< 0.001****
		3	*-0.28*	*0.07*	*-4.11*	
season	*2*					*0.03**
		spring	*-0.23*	*0.10*	*-2.02*	
		summer	*-0.16*	*0.07*	*-2.33*	
location	*3*					*< 0.001****
		middle	*0.21*	*0.10*	*2.08*	
		inner	*0.42*	*0.11*	*3.72*	
		Tory	*0.39*	*0.13*	*2.95*	
group size			*0.01*	*0.00*	*4.19*	*< 0.001****
young	*1*					*< 0.01***
		yes	*-0.39*	*0.14*	*-2.90*	
behaviour	*4*					*< 0.01***
		milling	*0.07*	*0.11*	*0.61*	*0.54*
		resting	*0.06*	*0.24*	*2.49*	*0.01*
		socializing	*0.01*	*0.14*	*0.05*	*0.96*
		travelling	*-0.15*	*0.08*	*-1.79*	*0.07*
vessel distance			*0.00*	*0.00*	*2.66*	*< 0.01***
swimmer number			*0.01*	*0.01*	*2.09*	*0.04 **

Res. standard error 0.4985 on 303 df multiple R-squared 0.2237 Adjusted R-squared 0.1879 f-statistic 6.238 on 14 and 303 df p value: 6.04e-11

Since the variable distance of the vessel at swimmer entrance was included, this precluded the use of data from year one in the model. Post hoc tests indicated that swim attempt duration was 24.1% shorter during year three than year two ($p < 0.0001$; CI = 13.0 %–34%) and 15.3% longer during autumn than summer ($p < 0.05$; CI = 0.33%–28.0%). Swim attempt duration was 52.4% longer in the inner than outer Sound ($p < 0.001$; CI = 14.3%–103.0%), 48.5% longer in Tory Channel than the outer Sound ($p < 0.05$; CI = 5.1 %–109%) and 24.1% longer in the inner than middle Sound ($p < 0.05$; CI = 3.1%– 49.3% min). There was a direct relationship between vessel distance and swim attempt duration. For every increase of 100 m, swim attempt duration increased by 8.2% ($p < 0.01$; CI = 2.2%–15.5%). Likewise, there was a direct relationship between dolphin group size and swim attempt duration. As group size increased by each animal, swim attempt duration increased by 0.7% ($p < 0.0001$; CI = 0.3 %–1.0%). As the number of swimmers increased by one person, swim attempt duration increased by 0.1% ($p < 0.05$; CI = 0.01%–0.2%). Swim attempt duration was 52% longer when the initial behavioural state of dolphins was resting versus travelling ($p < 0.01$; CI = 9.0%–74.0%) and 32.4% longer when young were absent ($p < 0.01$; CI = 12.0% –48.2%).

5.3.2.3 Distance operators travelled to track dolphins during swim encounters

The mean distance operators travelled to track dolphins during bottlenose swims was 11.7 km (SE = 0.46, range = 1.6–27.2, n = 140).

Model results

The optimal LM for distance travelled during bottlenose dolphin swim encounters was: distance ~ (section of the Sound, $df = 3$) + (initial behaviour, $df = 4$) + dolphin group size. There was strong evidence that distance travelled was influenced by sector of the Sound ($p < 0.05$), initial behaviour ($p < 0.01$) and dolphin group size ($p = 0.001$; Table 5.10).

Post hoc tests indicate that the distance travelled during swim encounters was 3.0 km longer when swims originated in the inner as opposed to middle Sound ($p < 0.05$; CI = 0.2–5.7 km). An initial behavioural state of socialising resulted in distances travelled of 6.4 km longer compared to foraging ($p < 0.01$; CI = 1.6–11.3 km), 6.3 km longer compared to milling ($p = 0.01$; CI = 1.0–11.7 km), 7.3 km longer compared to resting ($p < 0.05$; CI = 1.0–13.6 km) and 4.9 km longer compared to travelling ($p < 0.05$, CI = 0.1–9.6 km). A direct relationship existed between dolphin group size and the distance travelled whereby distance increase by 0.08 km with the increase of group size by one animal ($p = 0.01$; CI = 0.036–0.15 km).

A test for the interaction effect between dolphin group size and initial behaviour was run (*i.e.,* to see if larger groups may have been observed travelling more or smaller groups were resting more). Similarly, a test for the interaction between the section of the Sound and the number of vessels was run to see if a higher number of vessels in certain areas may have been influential. In both cases interaction effects were not present ($p > 0.5$).

Table 5.10. Parameter estimates of significant variables selected in the final LM for the distance operators travelled to track dolphins during swim encounters. Significance codes are indicated by ***0.001, **0.01 and *0.05.

Term	DF	Levels	Estimate	SE	t value	p value
location	*3*					*0.036**
		middle	*-1.35*	*1.52*	*-0.75*	
		inner	*1.93*	*1.71*	*1.12*	
		Tory	*-2.00*	*2.17*	*-0.92*	
group size			*0.07*	*0.05*	*1.41*	*0.001***
behaviour	*4*					*0.005***
		milling	*0.50*	*2.93*	*0.17*	*0.86*
		resting	*-3.27*	*3.95*	*-0.83*	*0.41*
		socializing	*5.50*	*3.62*	*1.52*	*0.13*
		travelling	*1.20*	*2.49*	*0.48*	*0.63*

Residual standard error: 4.965 on 123 degrees of freedom (7 observations deleted due to missingness) Multiple R-squared: 0.2104, Adjusted R-squared: 0.1591 F-statistic: 4.097 on 8 and 123 DF, p-value: 0.0002342

5.3.2.4 Bottlenose dolphin reactions

The majority of bottlenose dolphin responses were classified as neutral (82.9%; n = 387). Only 9.0% were classified as attraction (n = 42) and 8.1%, avoidance (n = 38).

Model results

The optimal model for a response (either attraction or avoidance) to a swim was reaction ~ (swimmer orientation, *df* = 2) + (initial behaviour, *df* = 4) + dolphin group size. There was strong evidence that group size ($p < 0.01$), initial behaviour ($p < 0.001$) and swimmer orientation ($p < 0.01$) influenced whether or not dolphins reacted to swim attempts. Since the variable swimmer placement was included, this precluded the use of data from year one in the model.

To determine if these factors were associated with a particular response, the data were filtered by attraction and subsequently avoidance and the model was re-run. However, this did not change the results. The model explained 13.6% of the deviance. Post hoc tests indicated that swim encounters were 6.5 times more likely to elicit a response (attraction or avoidance) from dolphins when the behavioural state was socialising as compared to foraging ($p < 0.01$; 95% CI = 1.4–30.0 times more), 6.6 times more likely when the behavioural state was socialising compared to milling ($p < 0.05$; 95% CI = 1.2 time more–35.8 times more) and 0.1 times less likely when travelling compared to socialising ($p < 0.001$; 95% CI = 0.03 times more–0.4 times more).

Swim encounters were 0.3 times less likely to elicit a response if swimmer orientation was amongst dolphins as opposed to in their path of travel ($p = 0.001$; 95 % CI = 0.1 times less–0.6 times less) and 0.3 times less likely if swimmer orientation was to the side and ahead ($p = 0.062$; 95 % CI = 0.1 times less–1.0 times more) as opposed to amongst the dolphins. A response was 0.98 times less likely as group size increased by one animal ($p < 0.01$; 95% CI = 0.96 times less–0.99 times less; Table 5.11; collective model*).

Table 5.11. Parameter estimates of significant variables selected in the final GLM (with binomial distribution and logit link function) for bottlenose dolphin reactions to swim attempts. Significance codes are indicated by ***0.001, **0.01 and *0.05.

Term	DF	Levels	Estimate	SE	z value	p value	Deviance explained
group size			*0.02*	*0.01*	*2.63*	*< 0.01**	*7.72*
behaviour	*4*					*< 0.001****	*19.21*
		milling	*0.02*	*0.56*	*0.03*		
		resting	*0.70*	*1.13*	*0.62*		
		socializing	*-1.87*	*0.57*	*-3.27*		
		travelling	*0.29*	*0.42*	*0.68*		
swimmer placement	*3*					*< 0.01***	*12.22*
		path	*1.36*	*0.39*	*3.51*		
		side/ahead	*1.11*	*0.49*	*2.25*		

Null deviance: 315.76 on 353 degrees of freedom Residual deviance: 272.80 on 346 degrees of freedom
Deviance explained 13.6% (371 observations deleted due to missingness) AIC: 288.8

5.4 Discussion

5.4.1 Measures of bottlenose dolphin engagement in swim tourism

A number of proxies (*i.e.,* likelihood of swim, duration, distance operators were required to travel to track bottlenose dolphins during swim encounters and dolphin reactions) were measured to assess bottlenose dolphin engagement in swim tourism in QCS, including one novel proxy (distance operators travelled to track dolphins during swim encounters), not previously reported within the literature. Operator techniques and dolphin group composition were compared to similar studies and then included as variables to assess the proxies for dolphin engagement in swim-with-dolphin tourism.

5.4.1.1 Likelihood bottlenose dolphin sightings resulted in swim encounters

An increased likelihood for a sighting to result in a swim encounter may be interpreted as a greater tourism industry success rate. However, it may also suggest a growing commitment by the operator to engage in swim events on behalf of patrons, irrespective of guidelines (Whitt & Read, 2006), or potential unfavourable biological consequences. The results here suggest the latter and may infer negative consequences for the bottlenose dolphins targeted for swim tourism. Swims were 4.7 times more likely to occur during the third year, than the first, while model results specified that the presence of young (calves or neonates) and group behaviour were not significant variables. The majority of swim encounters in the present study (77.9%) had at least one young animal present, which was higher than other similar delphinid swim studies. Comparatively, calves were present with conspecifics in the Bay of Islands, NZ during 49.8% of encounters (Constantine, 2002), while neonates were present during 30.6% of swims in Port Phillip Bay, Australia (Scarpaci *et al.*, 2003). Amongst dusky groups in Kaikoura, calves occurred 9% and 52% of the time with small and large groups, respectively (Markowitz *et al.*, 2009). With common dolphins, calves were present during 53.8% of occasions in the Bay of Plenty, NZ (Meissner *et al.*, 2015), while in Akaroa, swims were only attempted with groups of Hector's dolphins in the absence of calves (Martinez *et al.*, 2011).

Regional differences may be attributed to the size and structure of the tourist operations coupled with dolphin group structure. Dolphin tourism in QCS is a small operation that relies on a single daily trip for dolphin swims, compared to larger operations with multiple vessels, trips and the capacity for large numbers of viewers only. As demonstrated previously, calves are found in bottlenose dolphin groups year-round in QCS, particularly with larger groups (Merriman, 2007). In the present study, the location of alternate dolphin groups without calves could have presented a challenge and may have influenced the decision to swim, despite group composition. It is also possible that calves or neonates may have been missed by the operators in an initial assessment, or may have joined groups throughout an encounter as part of fission-fusion activity (Connor *et al.*, 2000).

An alternate hypothesis is that variation in dolphin group composition, as well as group size observed during swims may have been attributed to differences amongst study areas. Bottlenose dolphins in coastal or isolated waters tend to form small groups (Campbell *et al.*, 2002; Kerr *et al.*, 2005; Lusseau *et al.*, 2003), while offshore they can form groups of several hundred individuals (Folkens *et al.*, 2002). From this perspective, in QCS, bottlenose dolphin group size (mean 36.9, range = 2–90) was comparable to conspecifics in the Bay of Islands, NZ (2–50; Constantine, 2002). It was smaller than dusky dolphin group size that ranged from 4–1000 in Kaikoura, NZ (mainly between 100–250 individuals; Markowitz *et al.*, 2009) and common dolphin group size, that ranged from 3–400 in Mercury Bay, NZ (Neumann & Orams, 2006). Most of these studies occurred in areas exposed to open ocean influence, while QCS is a semi-enclosed, relatively shallow, buffered Sound (refer to section 2.2.1).

Furthermore, in QCS, most swims occurred in the lesser exposed mid and inner Sounds, as opposed to the outer Sound and Tory Channel that are subject to variable tidal flux and influence from the Cook Strait (Davidson *et al.*, 2011; Hadfield *et al.*, 2014). Thus, these isolated areas in QCS could provide shelter, where young animals are less vulnerable to predation and where large group size may not have been needed to offer safety (Shane *et al.*, 1986; Srinivasan & Markowitz, 2009). However, with comparatively small group sizes in QCS, it is logical that interactions (with swimmers or the vessel) by different animals are less likely to occur, leading to overall higher exposure and cumulative effects to target individuals (Steckenreuter *et al.*, 2012).

Differences in group dynamics observed amongst study areas may have also been due to the misinterpretation of regulations which currently state: "*persons may swim with dolphins and seals but not with juvenile dolphins or a pod of dolphins that includes juvenile dolphins* (Marine Mammals Protection Regulations, 1992)." The term "juvenile" is not defined in the regulations and is thus, vague and open to interpretation. As such, operators may understand the definition to refer to foetal-fold calves (*i.e.*, neonates). In actuality, the written term likely represents the scientific definition for calves (*i.e.*, animals < 1/2 the size of adults), or more conservatively the scientific definition of juveniles, as written (individuals that are approximately two-thirds the size of adults and often observed swimming in association with their mothers (Constantine, 2002; Fertl, 1994; Mann & Smuts, 1999). The undefined terminology may explain the findings in the present study. However, it is still worth noting that frequent interaction of swimmers or vessels with dolphin groups containing calves or neonates may influence the frequency in which calves separate from their mothers, altering the mother-calf bond that is vital to calves for protection and nursing (Mann *et al.*, 2000) and essential for survival (Mann & Watson-Capps, 2005). This is particularly important since juveniles may be more likely to approach swimmers (Constantine, 2001).

Like group structure, dolphin behaviour was not a significant model variable in the likelihood that a swim encounter occurred during a bottlenose dolphin sighting in QCS. Behavioural assessments may offer insight into the way dolphins utilize an area and how tourist activities can affect this. Most swim attempts in QCS took place when dolphins were travelling, followed by foraging, milling, resting and socializing. Similar behavioural proportions were observed amongst common dolphins in the Bay of Plenty, NZ (excluding the placement of swimmers in the water with resting animals; Meissner, 2015). Dolphin travel is often followed by feeding behaviour and is thought to be linked to the dolphins' need to move around in search of food (Bearzi, 2005a; Stockin *et al.*, 2009). Furthermore, travel in groups and widespread formation has been thought to increase the efficiency with which dolphins encounter prey (Hanson & Defran, 1993). Therefore, the large proportion of travelling behaviour observed in QCS could indicate movement between productive patches, either within QCS or nearby regions outside the Sound (Merriman *et al.*, 2009). Consequently, interaction with travelling dolphins may have an influence on dolphin foraging efficiency.

While the assessment of behavioural proportions can be informative from an ecological perspective, the detection of behavioural changes in reference to tourist activities (*i.e.*, vessel/swimmers) may infer a number of negative consequences. In QCS, the comparison of behavioural state prior to initial vessel approach and prior to the first swim attempt indicated that travelling increased, while the proportion of foraging, milling, resting and socializing decreased. Similar results were observed during tourist activities with bottlenose dolphins off

Zanzibar, Tanzania (Stensland & Berggren, 2007) and during swim encounters with dusky dolphins off Kaikoura (Markowitz *et al.*, 2009). Since travel is an energy consumptive behaviour, transition to increased travel may lead to an energetic drain on dolphins (Bejder & Dawson, 1999; Yazdi *et al.*, 1999), while disruptions in foraging can decrease energy intake (Williams *et al.*, 2006b). Moreover, when foraging, resting or socializing are interrupted (Christiansen *et al.*, 2010; Meissner, 2015; Peters *et al.*, 2013; Stensland & Berggren, 2007; Stockin *et al.*, 2008) it suggests impacts to further biological processes including growth, reproduction, calving and nursing (Hastie *et al.*, 2003b; Lusseau & Bejder, 2007; Stensland & Berggren, 2007). This could result in long-term consequences such as decreased survival (Lusseau & Bejder, 2007; Lusseau *et al.*, 2006) or animal displacement from the area (Lusseau, 2005). Moreover, from a tourism industry perspective, swim encounters largely with travelling dolphins may equate to less interactive swim tours (Markowitz *et al.*, 2009).

In summary, this model offers evidence of an increased likelihood of swim occurrence with bottlenose dolphins in QCS, over time and despite dolphin group dynamics. The results also suggest that dolphin behaviour may be altered by the presence of swim tourism, specifically compromising foraging. These findings and their associated implications suggest that swim activity may not be suitable for bottlenose dolphins in QCS.

5.4.1.2 Duration of bottlenose dolphin swim attempts

The measure for swim attempt duration has been deemed representative of animal interest or affinity for swimmers (Filby *et al.*, 2014a; Markowitz *et al.*, 2009; Martinez *et al.*, 2011). In other words, shorter swim duration equates to low animal interest. The mean value in QCS (4.2 min) was a measure of swim attempts from start to stop (when swimmers entered and exited the water). While values with conspecifics in the Bay of Islands were the same, swim attempt duration there was measured just when the dolphins were in the presence of swimmers (Constantine & Baker, 1997). This means that if it were possible to measure swim attempts in QCS in the same manner as in the Bay of Islands (see explanation in 5.2.2); they may have been comparatively shorter in QCS. Likewise, swim attempts with other species elsewhere (*i.e.*, bottlenose, common, dusky, Hector’s, rough-toothed dolphins (*Steno bredanensis*) and short-finned pilot whales (*Globicephala macrorhynchus*) were all longer than swim attempts in the present study, suggesting animal disinterest in QCS (refer to Table 5.12).

Table 5.12. The mean duration of swim attempts observed during swim-with-dolphin studies with several species in New Zealand and other locations.

Duration (min)	Species	Location	Reference
4.2	bottlenose dolphins (*T. truncatus)*	Bay of Islands, NZ	Constantine *et al.* 1997
4.3	bottlenose dolphins (*T. australis)*	Port Phillip Bay, Australia	Filby *et al.* 2014
8.0	bottlenose dolphins (*T. australis)*	Gulf of St. Vincent, Australia	Peters *et al*. 2013
5.2	common dolphins	Bay of Plenty, NZ	Meissner e*t al.* 2015
5.3	common dolphins	Bay of Islands, NZ	Constantine *et al*. 1997
9.1	dusky dolphins	Kaikoura, NZ	Markowitz 2009
25.0	Hector's dolphins	Akaroa, NZ	Nichols *et al.* 2002
25.3	Hector's dolphins	Akaroa, NZ	Martinez *et al.* 2011
12.0	rough-toothed dolphins	La Gomera, Canary Islands	Ritter *et al.* 2002
14.0	short-finned pilot whales	Tenerife, Canary Islands	Scheer *et al.* 2004

The model suggests decreased dolphin receptivity over time in QCS, as indicated by the significantly shorter attempt duration (24.1%) between year two to three. Furthermore, this may be indicative of lower tolerance; defined as the intensity of disturbance that an individual endures without responding in a defined way (Nisbet, 2000). Evidence of increased tolerance has been suggested from studies with delphinids elsewhere, as a result of elevated exposure and longer measured duration (Constantine, 2001; Filby *et al.*, 2014a; Martinez *et al.*, 2011; Neumann & Orams, 2006). In QCS, swims were 15.3% shorter during summer then autumn. Since summer is the peak tour season, this could suggest a problem for operators. Short swims may not meet the expectations of patrons (Filby *et al.*, 2014b) and could jeopardize economically sustainable tour operations (Lusseau & Higham, 2004). Moreover, despite the high percentage of swim encounters with young present, attempts were actually longer (32.4%) in their absence. From a tourism perspective, it may not be logical to engage with young animals, not only because of the potential implication to calving and survival (refer to 5.4.1.1), but also because this may lead to short, unfavourable swim encounters.

This model also indicated that longer swims were influenced by a higher swimmer number. However, higher swimmer numbers have the potential to increase disturbance due to additional time needed for swimmers to enter and exit the water (Martinez *et al.*, 2012) and the potential for increased noise exposure (Nowacek & Tyack, 2008). The mean maximum swimmer number (10.5; SE = 0.41, range = 2–18, n = 140) in QCS was higher than reported for swims with other species in NZ (dusky, mean = 9.0; Hector's mean = 7.6; Markowitz *et al*., 2009; Martinez *et al*., 2011), while swimmer number was not a significant variable elsewhere (Markowitz *et al.*, 2009). While short swim duration suggests animal disinterest, multiple swim attempts with the same group of dolphins during an encounter further implies that the initial attempts were unsatisfactory; otherwise additional attempts would not have been undertaken. More than one attempt is not essential for swim tours, despite the broad range in QCS and nationwide studies (refer to Table 5.13 for details). Therefore, the number of attempts can be viewed as a reflection of the amount of effort invested in accomplishing a satisfactory interaction. While the range in QCS (1–5) was comparable to that of other studies, the mean number of attempts (3.2) was higher than with bottlenose dolphins or with other species. However, mean swim attempt duration was shorter than most other species elsewhere (as detailed earlier in this section).

Table 5.13. The mean number and range of swim attempts observed during swim-with-dolphin studies in New Zealand.

Measure	Value	Species	Location in NZ	Reference
Range of swim attempts	1 – 6+	dusky	Kaikoura	Markowitz *et al*., 2009
	1 – 5	bottlenose	Bay of Islands	Constantine & Baker, 1997
	1 – 5	Hector's	Akaroa	Martinez *et al.*, 2011
Mean # of swim attempts	2.9	bottlenose	Bay of Islands	Constantine, 2001; Constantine & Baker, 1997
	1.9	common	Bay of Islands	Constantine & Baker, 1997
	2.6	common	Mercury Bay	Neumann & Orams, 2006
	1.6	Hector's	Akaroa	Martinez *et al*., 2011

In summary, short and repeated swim attempts that decreased in duration over time indicate bottlenose dolphin disinterest for swim activity in QCS. According to this proxy, bottlenose dolphins in QCS like *T. australis* in Australia and common dolphins in Mercury Bay, NZ, were not receptive to swim-with-dolphin tourism (Filby *et al.*, 2014a; Neumann & Orams, 2006).

5.4.1.3 Distance operators travelled to track dolphins during swim encounters

The previous proxies that were discussed in this chapter allowed for comparison with other studies. However, distance travelled by the operator during a swim encounter was a novel measure of tour vessel presence amongst dolphins during swim encounters and dolphin engagement/interest. It is a common misconception that if animals are not interested in an interaction that they would leave (Martinez & Orams, 2011). However, findings in this study indicate that this opportunity may be thwarted by extensive lengths to maintain interactions (mean = 11.7 km; SE = 0.46, 1.6–27.2 km) and therefore, suggest operator pursuit. Dolphins may retreat to the inner part of QCS (where 36% of swims originated), because of the calm, still environment (refer to 5.4.1.1); however, the distance travelled amongst them was 3.0 km longer when they originated there. Excessive vessel presence and multiple attempts with the same group may be unnecessary, potentially disruptive and could eventually lead to dolphin displacement from the region (Rako *et al.*, 2013).

The distance travelled, in conjunction with certain operator methods (vessel approach and overall encounter duration) may equate to "leapfrogging," associated with resultant animal evasion that may cause energetic depletion (Williams *et al.*, 2002). The majority of vessel approaches utilized in QCS were invasive (J style or in-path; 74.4%), particularly J style (66.5%). In comparison, this technique was only used 9.4% of the time during swims in Port Phillip Bay (Scarpaci *et al.*, 2003). In Akaroa, NZ, Hector's dolphins initiated approaches in 38.5% of encounters, while vessel-initiated approaches were mostly from the side (61.5%) and in-path approaches were negligible (Martinez *et al.*, 2011). Moreover, the overall duration of swim encounters in QCS were up to twice as long (71.3 min) as conspecific studies that measured this (54 min; Constantine & Baker, 1997) or the presence within 100 m of dolphins (34.8 min; Scarpaci *et al*., 2003). Likewise, they were about 1.6 times longer than dusky dolphin swim encounters (44 min; Markowitz *et al*., 2009). The relatively long encounter duration (vessel presence amongst dolphins) in QCS was despite shorter mean swim attempt duration, collectively representing only 20.6% of the total mean encounter duration (*i.e.*, suggesting animal disinterest; refer to section 5.4.1.2).

The distance travelled amongst dolphin groups in QCS and the associated approach methods may have restricted the dolphins' choices either to carry on toward the vessel and/or swimmers, or to avoid them. These methods raise questions about the level of tour vessel presence amongst dolphins, the lack of recognition for animal disinterest during swim encounters and accordingly if swim-with-dolphin activities are suitable for this dolphin population.

5.4.1.4 Bottlenose dolphin reactions

A final measure of bottlenose dolphin engagement in swim-with-dolphin tourism in QCS was the reaction of dolphins to swim attempts. In response to a potential disturbance, animals may exhibit habituation *i.e.,* "a persistent waning of a response as a result of a repeated stimulation which is not followed by any kind of reinforcement" (Thorpe, 1963). They may also display sensitisation, *i.e*., "an increased behavioural responsiveness" (Richardson *et al.*, 1995). Both of these are longitudinal changes in animal response (Bejder *et al.*, 2009) and are generally viewed as negative consequences with associated long-term implications (Higham & Shelton, 2011). Habituated animals may be "made viewable" through human actions (Knight, 2009). Undesirable associated repercussions of animal habituation to tourist activities may include changes to natural behaviour patterns (Orams, 2002), displays of aggression (Scheer, 2010) and alterations in population levels (Orams, 2002).

The extended duration of tourism operation in QCS coupled with the large proportion of neutral reactions suggest that bottlenose dolphins are habituated to swim tourism in QCS. Wild animals are naturally human-averse and over time inclinations to evade human activity can be replaced with tolerance for it (Knight, 2009). Periods of habituation can often follow sensitization (Domjan, 2010). Therefore, it is also possible that dolphins in QCS displayed periods of sensitization at the onset of swim tourism stimuli and were habituated shortly thereafter. Since this is the first regional study of its kind with no baseline before dolphin swim tourism or tourism were initiated, this cannot be known for sure. However, in the Bay of Islands, the avoidance response increased from 22.0% to 31.0% in the span of a two year study, suggesting the occurrence of sensitization (Constantine, 2001). The inter-regional difference may be explained by the fact that sensitization and habituation occur over time (Bejder *et al.*, 2009). Tourism in QCS had been in operation for 16 years and swim tourism specifically for seven years at the start of the study (refer to section 2.3.4). In contrast, dolphins in the Bay of Islands had only been exposed to tourism for three years prior to the study.

The high proportion (82.9%) of a consistently neutral response could also indicate that avoidance did not offer a suitable option for the dolphins (Gill *et al.*, 2001). Given that the majority of swim attempts (62.9%) commenced with travelling dolphins within the narrow, elaborately shaped Sound (refer to section 2.2.1 for more detail), avoidance, or a change of path may not have always been feasible (*e.g.*, due to the presence of numerous small bays). Thus, a neutral response passing through a group of swimmers may have been a more suitable choice.

This could be because dolphins in QCS are mainly travelling amongst foraging spots and disruption of foraging may lead to declines in energy intake (Bearzi, 2005a; Merriman *et al.*, 2009; Williams *et al.*, 2006b), as explained earlier (refer to section 5.4.1.1). Therefore, the largely neutral response may have been more energetically efficient or cost-effective than avoiding the potential risk of disturbance (*i.e.,* swim activity; Frid & Dill, 2002). Travel in search of, or to follow prey may partially justify the rather low deviance explained (13.6%) by the model. While the response variable here was comprehensively tested against explanatory variables from various categories (*i.e.,* temporal, spatial, group dynamics and operator techniques), prey is a factor that could not be considered here, but may have contributed.

Short-term behavioural assessments alone can be informative, but also limiting. The occurrence of habituation can also be inferred by physiological changes that indicate a decreased stress response, including declines in corticosterone levels, as specified by studies on iguanas and penguins (similar to cortisol levels in mammals; Romero & Wikelski, 2002; Walker *et al.*, 2006). However, chronically stressed animals may also display a reduced stress response (Cyr & Romero, 2009). The interpretation of human-wildlife encounters is very complex (Bejder *et al.*, 2009), especially since negative consequences of stress in long-lived animals may take time to manifest (Walker *et al.*, 2006) and can be difficult to quantify or detect (Orams, 2004). A neutral reaction could mistakenly be viewed as non-problematic, when in fact it could indicate habituation and its associated negative consequences, the absence of a better option for animals, or even chronic stress. These interpretations suggest dolphin disinterest and thus, question the suitability for swim activities with these animals. Misunderstanding animal responses could lead to misguided and potentially detrimental management decisions (Cyr & Romero, 2009; Walker *et al.*, 2006), like issuing further swim permits. It is suggested that such steps do not proceed in QCS without caution. Continued research including the repetition of aspects of this study, investigation of the behavioural budget in the presence and absence of the vessel (Meissner *et al.*, 2015; Stockin *et al.*, 2008) and ongoing monitoring are essential (Ehler, 2008).

5.5 Limitations and conclusions

Although swim-with-dolphin tourism has the potential to contribute to wildlife conservation efforts by increasing awareness, the potential effects on target animals must be thoroughly investigated, particularly in areas with threatened or endangered species. This research was a crucial first investigation of dolphin tourism in QCS. While this work resulted in a number of important outcomes, the data collection and comparative assessments were not free of caveats. The results presented here are representative of the time frame when data were collected and the scope of the study was limited by the research platform. For instance, dolphin behavioural assessments in the presence and absence of the tour vessel were not feasible from this platform. Moreover, like other studies, isolating the stimuli of vessel and swimmer is nearly impossible since swims took place from a boat (Constantine, 1999). In addition, while differences were detected amongst measurements taken in QCS and elsewhere, variation may be attributed to the way that proxies were measured and the actual methods involved in conducting a swim encounter. For instance, slight variation existed amongst regions regarding what defined the start and end of swim attempts. This could have influenced the comparisons of swim attempt duration measurements. Additionally, variation in operator techniques amongst studies may have been attributed to differences in regional permitting. For example, during the first year of sampling, the permit in QCS allowed a maximum of 12 swimmers at any one time with a dolphin group. However, after the first year of sampling, regional permits were adjusted to allow a maximum of 18 swimmers. This alteration was therefore reflected in the observed mean maximum swimmer number in QCS.

Despite accepted limitations, this study comprehensively examined 1) characteristics of swim-with-dolphin tourism with bottlenose dolphins in QCS and 2) bottlenose dolphin engagement in swim-with-dolphin tourism in QCS from several angles. Findings indicated that the adherence to biological recommendations for swim tourism (*i.e.*, regarding group composition and behaviour) because of operator choice, geo-morphology of the region, or clarity of the regulations, might have been difficult. Furthermore, operator methods (*i.e.*, number of swim attempts, swim attempt duration, encounter duration and distance travelled) may lead to biological implications for the dolphins, as well as compromise the success of swims from a tourism perspective. While assessing human/animal tourism relationships is very complicated, through the measurement of several proxies, it can be concluded that swim-with-dolphin tourism in QCS with bottlenose dolphins is not appropriate, unless methods and/or regulations change. Based on the findings presented in this chapter, several specific management recommendations are outlined in the concluding thesis chapter (refer to section 6.2.2.2).

Chapter 6

General Discussion

The sun setting over the hills in Queen Charlotte Sound, New Zealand.

6.1 Summary of research findings

Research findings presented in the data chapters of this thesis led to a number of notable conclusions. Two separate datasets were analysed: dolphin sighting data collated from historical vessel log books (Chapter 2) and opportunistically collected dolphin sighting data (Chapters 3–5), over different time periods (1995–2011 and 2012–2014, respectively). Collectively, the presented analyses indicated the consistent presence of three delphinid species in Queen Charlotte Sound (QCS), New Zealand (NZ) during 1995–2014.

6.1.1 Overall encounter/sighting rates

Data standardization varied slightly between datasets in that dolphin sightings were standardized by the number of trips (TER) in Chapter 2, while in Chapter 3 sightings (and groups) were standardized by the amount of search effort in hours (SR/ER). Despite this difference, the comparison of overall species' TER with SR indicates that during both time periods, Hector's dolphins *(Cephalorhynchus hectori hectori*) occurred more frequently than dusky dolphins (*Lagenorhynchus obscurus*) and at a similar or higher frequency than bottlenose dolphins (*Tursiops truncatus*). These findings, therefore, suggest that during the extended time frame of this study, QCS has been a particularly important area for Hector's dolphins.

6.1.2 Seasonal trends

Findings from both the collated historical records explored in Chapter 2 and opportunistically collected data in Chapter 3 also demonstrated consistent seasonal patterns. Hector's dolphin sightings were more prevalent during summer and autumn, while dusky dolphin sightings increased during winter and spring. These patterns presented in Chapter 2 suggest the early presence of niche partitioning in QCS. This phenomenon was explored further in Chapter 3, through the calculation of both temporal and spatial overlap and with habitat modelling in Chapter 4. The temporal patterns observed in QCS were comparable to those observed elsewhere in NZ and were likely associated with foraging habits and prey availability. Hector's dolphins move offshore during winter in the Banks Peninsula following the movement of prey. This movement likely occurs elsewhere around NZ and would explain decreases in Hector's dolphin sightings inside of QCS during winter/spring. Comparatively, dusky dolphins move north from Kaikoura during the colder months toward Admiralty Bay and likely the other Marlborough Sounds, including QCS. Likewise, bottlenose dolphins pass throughout QCS and the Marlborough Sounds, as part of a broad home range within NZ. Movement by all three species around NZ may explain the temporal patterns within QCS and may contribute to the shared use of the region. Additionally, these patterns may be attributed to the flexibility in diet and/or foraging tactics exhibited by all three species. Competitive exclusion may result amongst similar species if resources are not shared.

6.1.3 Spatial trends

Like the temporal trends revealed in both datasets, comparisons of historical (Chapter 2) and more current (Chapter 3) spatial trends result in noteworthy points. Across historical time frames, Hector's dolphins displayed a spatial shift toward the middle Sound, where the more current range and central range occurred. Both datasets established that a higher density of Hector's dolphins existed in this central area, particularly during the summer and autumn seasons.

Comparatively, both the historical and current bottlenose dolphin data illustrated a broad distribution throughout the study area, but the more recent data suggests that the central range was focused in the middle to outer Sound. Historically, higher density estimates were observed during winter and lower values were observed during spring. However, more obvious seasonal spatial peaks were detected from the recent data. This may partly be due to the higher resolution calculations presented in Chapter 3. Those calculations incorporated animal group size, which, was not consistently available in the historical dataset, so therefore not included in estimates.

Dusky dolphins (like Hector' dolphins), were more apparent in the inner Sound historically and exhibited some shifting toward the middle/outer Sound over time (Chapter 2). Higher density estimates occurred during winter and spring, but animals were more concentrated in the inner Sound during winter and more evenly spread during spring. Likewise, the current data indicated higher density estimates during the same seasons. Hotspots and the central range occurred in the inner Sound during spring, likely due to the occurrence of an exceptionally large dolphin group (Chapter 3).

In summary, over time, both Hector's and dusky dolphins displayed some displacement away from the inner Sound. The central Sound appeared to be important for all three species, particularly Hector's dolphins.

6.1.4 Environmental correlations

The environmental parameters that were tested affected each species differently. However, the influence on individual species' occurrence and density was largely consistent (as discussed in Chapters 2 and 4, respectively). These commonalities were likely indicative of the movement patterns out of the Sound and around NZ (refer to section 6.1.2) and provide further evidence for trophic partitioning within QCS. Occurrence and density data indicated that Hector's dolphins were consistently influenced by higher sea surface temperatures (SST) and dusky dolphins by lower SST. Bottlenose dolphin occurrence exhibited limited association with dynamic variables and density was only influenced by static parameters. Models generated from both datasets suggested that all three species were influenced by temporal variation. Occurrence of all species was influenced by annual variation, while density was influenced by either annual (bottlenose and dusky dolphins) or seasonal (Hector's and dusky dolphins) variation; suggesting the need for continued research to detect any future shifts in these patterns. The model predictions generated in Chapter 4 enhance the information gained from the Kernel Density Estimates (KDE) in Chapter 3, allowing for animal movement (Wilson *et al.*, 2004) within the Sound.

6.1.5 Swim-with-dolphin tourism

The historical trends suggest a steady increase from the early to late 2000s in the percentage of trips that included a swim encounter. Comparatively, more recent trends indicate that during 2012–2014, the likelihood of a swim to occur (specifically with bottlenose dolphins) increased from year one to year three. Thus, the outcomes of this thesis suggest continued expansion of dolphin tourism in QCS, specifically amongst swim-with-dolphin activities. These findings are consistent with trends that have been observed on a global scale (refer to section 1.6). Moreover, it can be concluded that pressure existed to undertake dolphin swim encounters. The historical records indicated that swim encounters began to occur with Hector's dolphins, a non-permitted species. Likewise, the modelled data (Chapter 5) indicated that swim encounters with bottlenose dolphins took place despite dolphin group composition or behaviour; and demonstrated extensive distance travelled by the operator to track dolphins and attain a swim encounter. Overall, the proxies explored in Chapter 5 denoted a lack of bottlenose dolphin engagement in swim activity in QCS.

6.2 Conservation management

6.2.1 Current local management

At present, the Marlborough Sounds Resource Management Plan (MSRMP) aims to encourage the sustainable integrated management of the Marlborough Sounds region. This evolving plan strives to take into consideration all of the natural and physical resources of the Sounds, while mitigating the effects of existing anthropogenic activities (MDC, 2003). This means that any temporal and/or spatial restrictions of activities within QCS would consider all natural resources, including the delphinid patterns presented in this thesis.

Plans are currently in progress to incorporate the MSRMP into a single district-wide Marlborough Environment Plan (MDC, 2017). Both of these represent ecosystem-based management plans, which are area-based and focus on the ecosystem and affiliated activities of a specific place (Crowder & Norse, 2008; McLeod *et al.*, 2005). The ecosystem approach has been referred to by the Convention on Biological Diversity as "a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way (Douvere, 2008)." In addition to the MSRMP, the Marlborough Sounds Integrated Management Trust (MSIMT) was recently established to approach issues in the Sounds in a complementary fashion to MSRMP by considering and finding common ties amongst all stakeholders in the Sounds. Likewise, it aims to sustain the natural resources of the ecosystem within the greater Marlborough Sounds region (Jorgensen *et al.*, 2012).

The MSRMP and MSIMT consider the broader Marlborough Sounds as a whole (Pelorous, Kenepuru and Queen Charlotte Sounds; Admiralty Bay, portions of Tasman Bay and Cook Strait beyond Clifford Bay on the East Coast; refer to Appendix 3.5). While these Bays/Sounds are interconnected via strong tidal currents, the individual Sounds are unique in terms of their physical/biological aspects and anthropogenic influences (Davidson *et al.*, 2011; Hadfield *et al.*, 2014; Markowitz *et al.*, 2004). The MSRMP currently has delineated zones that limit the occurrence of permitted activities including port and harbour functions, marine farming and marine activity in the Sounds. Fine-scale zones are present within the inner QCS along the coast, but within the mid to outer QCS more course zones exist, some of which, extend to neighbouring Sounds (MDC, 2015).

6.2.2 Management applications and recommendations

6.2.2.1 Spatial and temporal trends/habitat use

The delphinid trends established in this thesis have important implications for conservation management that may contribute to the development and goals of the Marlborough Sounds Resource Management Plan (MSRMP).

A valuable application of the findings in Chapter 2–4 is their use in Marine Spatial Planning (MSP) efforts for the region. MSP is a practical, public process of organizing temporal and spatial distribution of human activities in marine areas to achieve social and economic objectives, while protecting the ecosystem. An integral component of MSP involves understanding and mapping temporal and spatial trends (*e.g.*, Bombosch *et al.*, 2014; Pennino *et al.*, 2017), like the ones presented in this thesis. Notably, delphinid species' overlapping range, inclusive of Hector's dolphins' central range, is situated in the mid-upper region of QCS (refer to Figure 3.13), conclusively an important region for all three species. MSP in QCS would ideally consider this area in particular to outline when and where human activities should/should not occur within the Sound (Ehler & Douvere, 2009).

Anthropogenic influences vary regionally and so do the associated potential threats to dolphins. In QCS, vessel traffic, tourism and aquaculture are present. These activities in NZ and elsewhere are accompanied by known threats to dolphins, including vessel strikes (Dwyer *et al.*, 2014; Stone & Yoshinaga, 2000), behavioural effects of tourism (refer to section 1.6) and fisheries bycatch (Dawson & Slooten, 2005; Dawson, 1991a). Potential impacts of aquaculture on dolphin distribution, social structure and behaviour have also been observed in the Marlborough Sounds and abroad (refer to section 1.6 for further detail).

With shared space, potential conflicts may arise between environmental and anthropogenic factors. Conservation management must be approached from a precautionary angle, especially when data are limited as they are in QCS (Tyne *et al.*, 2016). The establishment of a holistic plan prior to further development (*i.e.*, industry expansion, granting of tourism permits) is crucial for shaping the evolution of Sound usage, avoiding user conflict and supporting delphinid/ecosystem conservation. Conservation management recommendations based on the delphinid spatio-temporal patterns presented in this thesis include:

1. Zoning

Zoning is an essential element of effective MSP (Kenchington & Day, 2011). A management plan may operate on a system that identifies multiple zones, with different uses (Klein *et al.*, 2010) and with varying levels of restriction, ranging from general access to zero-use (Douvere, 2008). For example, restriction of vessel speed and/or vessel access amongst delphinid central ranges in QCS may contribute to further subdivision or more specified zones (than those that are currently established; refer to section 6.2.1). In fact, MSP dictates that marine areas managed by zoning should include some areas that are inaccessible to human activity for purposes other than pure education or scientific research (Ehler & Douvere, 2009). Since marine ecosystems are heterogeneous and occur at various spatial scales (Crowder & Norse, 2008), management efforts would ideally recognize the uniqueness of the individual Sounds within the broader region. Restrictions may be relevant only to particular areas within QCS and may not apply holistically to the Marlborough Sounds (for more detail on current management refer to section 6.2.1).

2. Establishment of a Marine Protected Area

QCS may be viewed as an important ecological area because of its endemism (*e.g.*, Hector's dolphins), high biodiversity and its role as a migration stop over point (*i.e.*, as dolphins move between regions; Ehler & Douvere, 2009). Moreover, the model predictions (generated in Chapter 4), allow for biological rational to the placement of boundaries for protective measures (Wilson *et al.*, 2004). The predictions suggest that bottlenose dolphins could use the entire Sound and Hector's and dusky dolphins could be using most of the Sound. From this perspective, all of QCS can be viewed as a potentially important habitat, collectively, for these dolphin species (two of which are endangered). As such, the Sound as a whole, may be considered as a Marine Protected Area (MPA). These are defined as spatially delineated regions of the marine environment that are managed to protect natural resources. While the primary goals include environmental protection and restoration, MPAs may provide a number of other benefits, like education and the collection of baseline data (Upton & Buck, 2010). Management steps in QCS may include efforts to protect the overall health of the entire Sound. Further regulations to coastal development may be needed since associated environmental implications like runoff and sedimentation can influence the benthic habitat and all organisms up the food chain (Morrison *et al.*, 2009; Thrush *et al.*, 2004; Urlich, 2015). Moreover, marine farming can influence the general health of a region (Christensen *et al.*, 2003; Handley, 2015; Keeley, 2013). This must be a consideration, particularly since interest to expand this industry in the

Marlborough Sounds was initiated in the last few years (Baines, 2012; Haworth, 2010). Furthermore, the introduction of vessel speed restrictions (*i.e.,* in delphinid high density areas), increased training to vessel operators and ongoing monitoring would be encouraged as precautionary measures.

Direct management actions in other areas of NZ include *e.g.,* Hector's dolphin sanctuaries that restrict gillnet fishing off of Banks' Peninsula and the North Island West Coast (Dawson & Slooten, 2005), the establishment of vessel exclusion zones to limit interactions with bottlenose dolphins in the Bay of Islands (Hartel *et al.*, 2015) and similarly, "dolphin protection zones" within Doubtful Sound (Department of Conservation, 2008; refer to section 6.2.2.3 for further details). Moreover, similar measures beyond NZ have been actioned. Areas of high harbour porpoise (*Phocoena phocoena*) density off the west coast of Scotland, as well as regions with a high probability of bottlenose dolphin occurrence in the Southern Mediterranean Sea have been used to advise in Special Areas of Conservation (Embling *et al.*, 2010; La Manna *et al.*, 2016). Likewise, habitat preference for several species informed managers of potential conservation priority zones within already established MPAs in the Moray Firth, Scotland (Bailey & Thompson, 2009). In general, MPAs can be classified according to one of five levels of protection, ranging from conditional or seasonal limitations to zero access on a permanent, year-round basis (Al-Abdulrazzak & Trombulak, 2012). While all of QCS may be considered as a MPA, boundaries may be limited on a seasonal basis or solely to the area of overlapping range or delphinid species' central ranges, as suggested by (Silva *et al.*, 2012).

Zoning and the creation of MPAs are practical applications of spatial data and useful management measures. However, successful management is a multi-step process that includes planning and analysis, plan implementation and ongoing monitoring/evaluation (Douvere, 2008; Ehler, 2008). Often underplayed, monitoring is a crucial element to detect changes within dynamic ecosystems, so that management can adapt (Ehler, 2008). Therefore, in QCS it is recommended that future replicate studies be undertaken that may detect changes in delphinid patterns from the present study, alongside any future change within the QCS ecosystem; natural or human-influenced. As implied from Hector's and dusky dolphins' previously broader distribution, shifts in species' use of QCS can occur (refer to Chapter 2). Continued evaluation may indicate if any further shifts take place, in which case management measures (*e.g.,* zoning/MPA boundaries) may need to adjust accordingly.

6.2.2.2 Swim-with-dolphin tourism

The pressure to achieve a swim encounter in QCS is currently high. Applications for additional full tourism permits in QCS were submitted and were a catalyst for the present study. The findings in this thesis (Chapters 2 and 5) may have potentially important implications for the current swim-with-dolphin operations in QCS, since it is only the human-related influences that can be regulated during conservation management efforts (Douvere, 2008). A number of explicit management recommendations are offered:

1. Given the ambiguity regarding the definition for juveniles within the Marine Mammals Protection Regulations, there is a necessity to re-examine terminology to ensure transparency and reduce the need for subjective operator interpretation.

2. Prior to the decision to proceed with a swim encounter, it is recommended that dolphin group dynamics be assessed for a designated period of time, to avoid potentially missing the presence of calves/neonates. In accordance with regulations, swims should not continue with dolphin groups including calves/neonates. Trips could be designed to include swim encounters as opportunistic events contingent upon ideal conditions.

3. A re-consideration of the number of consecutive swim attempts allowed with the same group is suggested in order to limit the extended presence of the vessel amongst the dolphins (*i.e.,* in terms of swim encounter duration and distance operators travelled).

4. Typical dolphin behaviour in QCS (travel), together with the proxies explored during this study, illustrate an overall lack of bottlenose dolphin engagement in swim activity. These findings suggest that swim-with-dolphin tourism in QCS is not functional and therefore may not be appropriate. It is recommended that no further tourism permits be issued in this region.

6.2.2.3 Broader applications of research

The species considered here move between regions within New Zealand waters (*e.g.,* Hector's dolphins move offshore/alongshore, dusky dolphins move between Kaikoura and the Marlborough Sounds and bottlenose dolphins move amongst the Marlborough Sounds; previously explained in section 3.4). Therefore, the applications of the present research is relevant to conservation management of QCS/Marlborough Sounds, but also part of a collective effort to support overall NZ-wide delphinid conservation. Dedicated conservation efforts of these species have been initiated elsewhere in NZ in accordance with similar and/or complementary research to the findings presented here.

Hector’s dolphins face a number of threats including fisheries bycatch, limited gene flow and chemical pollutants (refer to section 1.6.1 for details). Bycatch, in particular, has contributed to the decrease in their estimated population size (Slooten, 2007). Techniques comparable to those in the present study have been used for practical conservation management measures elsewhere to limit their risk of further decline. For example, surveys designed to quantify the West coast distribution and abundance indicate that the existing restrictions on gillnetting aren’t expansive enough to protect the population in this region (Rayment *et al.*, 2011). Recommendations include extending the scope and temporal limitations of the offshore boundary. Moreover, Kernel Density Estimates (KDE) of dolphin home range indicate that the sanctuary off the Banks Peninsula does not encompass the whole range and should be expanded (Rayment *et al.*, 2009). Likewise, more recent aerial surveys suggest that dolphins occur beyond current delineated spatial management areas (Mackenzie & Clement, 2014). Collectively, these studies demonstrate that species conservation management is an adaptive process that is contingent upon the re-evaluation of baseline spatial data, like those presented here for QCS. The present assessment of spatial patterns and habitat use is the impetus for further regional studies and thus, part of the widespread effort to protect the species.

Emergent research also benefits concerted efforts to protect bottlenose dolphins in NZ. Previous studies have focused on the behavioural ecology and abundance of this species in QCS (Merriman, 2007; Merriman *et al.*, 2009). However, the work presented here, similar to that of Dwyer *et al.*, (2014, 2016) in the Hauraki Gulf, results in previously unknown information regarding the spatial patterns within the home range of this species. These studies, like the aforementioned Hector’s dolphins studies, are essential in the scope of NZ-wide spatial planning efforts, such as the placement of useful management area boundaries. Long-term distribution studies for bottlenose dolphins in the Bay of Islands indicate spatial shifts in this species, dictating the need for re-assessment of exclusion zone boundaries to include dynamic limits (Hartel *et al.*, 2015). As per the present research, baseline data for similar long-term monitoring has now been established within QCS for bottlenose dolphins.

Like the other species, data presented here for dusky dolphins is an integral aspect of broader research goals within NZ. Given that this species moves between QCS and nearby Kaikoura (refer to section 3.4), there is a connectivity between the two regions. Studies conducted in Kaikoura provide a wider context to the present research. Like numerous similar studies in NZ and elsewhere (refer to section 1.6.1), Lundquist *et al.*, (2012) observed behavioural changes of dusky dolphins in the presence of tour vessels off Kaikoura. Thus, these findings may highlight the potential need to limit vessel activity in areas of high dolphin density within QCS (refer to the previous section, 6.2.2.1). Similar studies should be replicated in QCS for all delphinid species. Moreover, research in nearby Admiralty Bay indicates that mussel farms may inhibit dusky dolphin coordinated feeding behaviour and lead to area avoidance (Pearson *et al.*, 2012). Comparably, in this study, some avoidance of the immediate areas around marine farms was detected for dusky (as well as Hector's dolphins; refer to Chapter 4). Thus, further development of the marine industry in QCS needs to take this into consideration, particularly in regions of high density and predicted density (refer to Chapters 3 and 4). Behavioural studies of these species around the marine farms and elsewhere in QCS, similar to those conducted by Pearson *et al.*, (2012) may be beneficial.

Since Hector's, bottlenose and dusky dolphins are highly mobile, actions in one area can influence overall, NZ-wide delphinid species conservation efforts. Nationwide regional collaboration is essential, as well as multi-national agreement when issues for these species span international waters (Childerhouse & Baxter, 2010). Ideally, MSP efforts will be adaptive to systematically allow for change, like animal movement and thus, ultimately improve management (Gormley *et al.*, 2015). This future-oriented approach is contingent upon the evaluation of meaningful data, appropriate modifications and a plan for continual research (Ehler & Douvere, 2009).

6.3 Future research

It is recommended that ongoing research in QCS build on the present findings in order to contribute to the further understanding of delphinids in this region. Interpretation of species' range, overlap and habitat associations indicate the occurrence of niche partitioning in QCS and suggest that dolphin species may be accessing different prey. Direct prey sampling alongside future data collection can be incorporated in habitat models, potentially offering more conclusive evidence of this. Prey sampling has been beneficial elsewhere (Lusseau & Wing, 2006; Miller, 2014), at suitable scales (Torres *et al.*, 2008) and can allow for regional baseline assessments and comparisons within NZ waters (Lusseau, 2003c; Miller, 2014; Miller *et al.*, 2013).

In addition, spatial scaling (*i.e.,* resolution) is an important consideration during the design of future studies, especially since the resultant meaning of habitat models can affect management decisions (McGowan *et al.*, 2013). Therefore, further research may include data collected at a higher resolution across the whole study area so that it may be analysed and compared within a smaller grid size, as per Bailey & Thompson (2009). Moreover, it may be beneficial to focus high resolution data in regions of known high delphinid density (*i.e.,* within central ranges) in order to explore more fine scale details of delphinid habitat that may not have been detected in this study. For example, delphinid distribution/density in association with water clarity/turbidity on a finer scale may be informative and directly applicable to coastal development within the region. Moreover, fine scale studies may allow for the identification of animal response to small scale environmental changes (Viddi *et al.*, 2010) and higher resolution predictions.

The habitat models presented in Chapter 4 indicate the significance of distance from marine farms, suggesting that anthropogenic presence may influence delphinid use of the region. Likewise, the spatial shifts noted over time may be associated with an increase in human-related activities (refer to Chapter 2). Therefore, data collection could also include additional anthropogenic variables, like vessel traffic. Such data has proven to affect the distribution of delphinids elsewhere. With anthropogenic expansion on the rise, a dedicated effort to consider potential impacts in QCS may prove beneficial.

From a tourism perspective, continued research and monitoring are crucial in QCS. In particular, as assessment of dolphin behavioural budget in the presence and absence of a vessel, as well as other anthropogenic factors is advised. This could be accomplished from a separate vessel or using drone technology and would benefit the area allowing for comparison with similar studies elsewhere (Meissner *et al.*, 2015; Stockin *et al.*, 2008). Likewise, dedicated research focused on operator compliance as in (Filby *et al.*, 2014b; Kessler & Harcourt, 2013; Scarpaci *et al.*, 2003; Scarpaci *et al.*, 2004) may be useful monitoring necessary for adaptive management (Ehler, 2008), particularly if/when regulations and permits are updated.

6.4 Major contributions and concluding remarks

This study resulted in a number of important scientific contributions. Long-term spatial and temporal trends of delphinids and the presence of tourism were explored using collated historical records, fundamentally establishing an extensive baseline of data for QCS. Shifts in delphinid spatial use were identified, along with some potentially problematic anthropogenic influences as possible contributing factors. Furthermore, insight into long-term habitat associations with dolphin occurrence was gained. From more recent data, calculations of range and core range indicated regions within QCS most frequented by the three key dolphin species. Spatially explicit habitat models identified unique habitat associations for each species, while model predictions suggested areas that dolphins may be using. Lastly, regional bottlenose dolphin swim-with-dolphin tourism was examined for the first time in nearly two decades of existence. Despite extensive effort by operators, overall, dolphins were not engaged in swim-with-dolphin activity. Collectively, the findings in this thesis have advanced the understanding of delphinid species' ecology in QCS.

This research illustrated that alternate data sources (*i.e.*, historical sighting records and government databases) can indeed prove to be very useful. Furthermore, opportunistic vessels, like tour boats and ferries can serve as suitable platforms at little or no financial cost and with no additional environmental impact. Here, the use of historical data led to scientific contributions that would have otherwise been undiscovered. The opportunistic research in this study yielded findings from data that may have been impossible to collect otherwise (*i.e.*, due to logistics; limited funds).

The long-term importance of QCS for three delphinid species, particularly, Hector's dolphins, was demonstrated by the present research. This thesis represents the first investigation of spatio-temporal cetacean patterns in QCS. Likewise, this was the first time habitat modelling was explored for delphinids in this area and for Hector's, bottlenose and dusky dolphins together in the same location. Finally, this research highlighted aspects of regional cetacean swim-with-dolphin tourism, amongst a backdrop of anthropogenic expansion. This study has made noteworthy scientific contributions that will ideally inspire further investigation, ultimately benefitting comprehensive conservation management within Queen Charlotte Sound, New Zealand.

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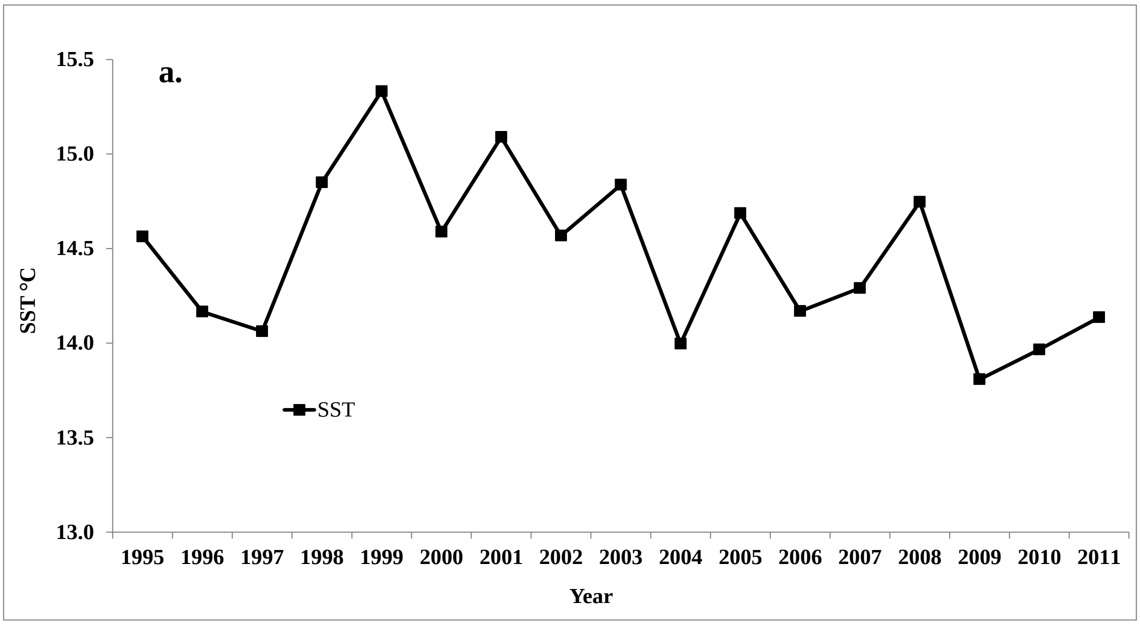
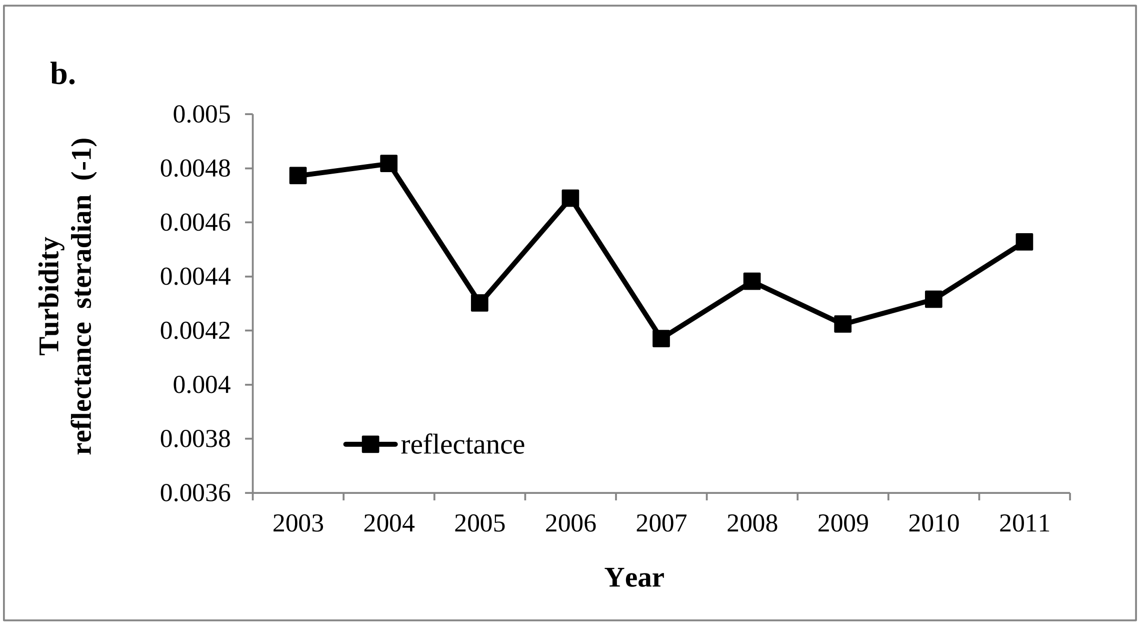
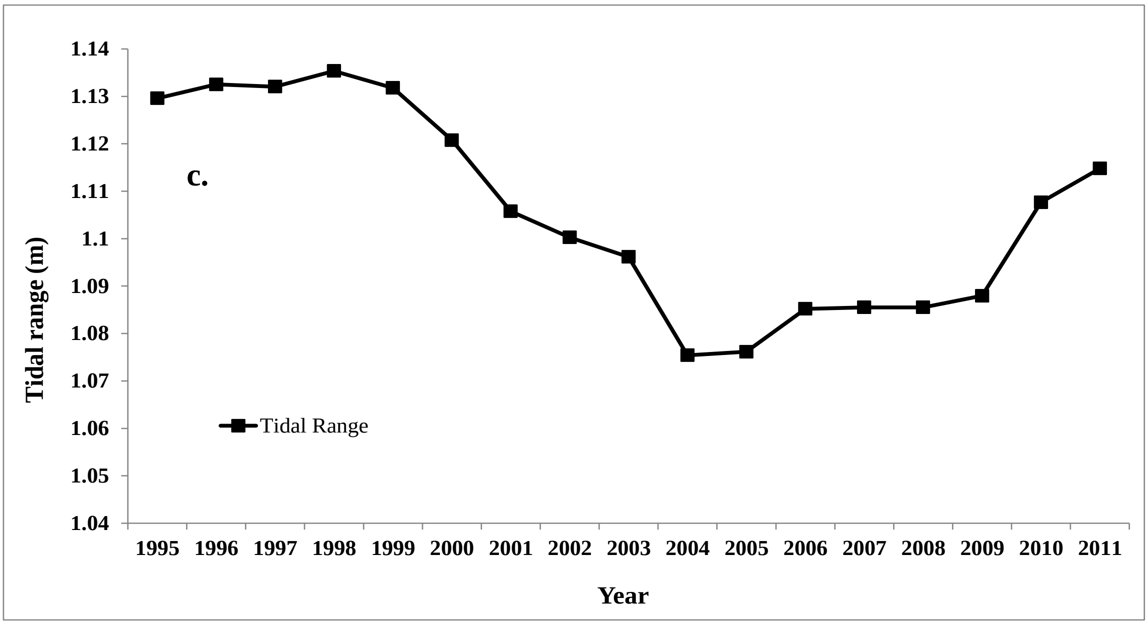
Appendices

Appendix 2.1

Plots of environmental parameters tested as model covariates of delphinid occurrence
a. SST, b. tidal range (1995–2011) and c. reflectance, the proxy for turbidity (2003–2011).




b.
Turbidity
reflectance steradian (-1)
0.005
0.0048
0.0046
0.0044
0.0042
0.004
0.0038
0.0036
reflectance
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year


1.14
1.13
1.12
1.11
1.1
1.09
1.08
1.07
1.06
1.05
1.04
c.
Tidal range (m)
Tidal Range
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
Year

Appendix 2.2

Table 2.2a. Parameter estimates of the variables selected in the best fit GAM for Hector's dolphins during 1995–2002. Significance codes are "***" 0.001, "**" 0.01, '*' 0.05, "." 0.1, " " 1.

Variable			
Smooth terms	edf	χ^2	p value
SST	2.69	145.52	< 0.001***
Year	5.43	25.61	0.0002***

Deviance explained =16.8 %; n = 1289

Table 2.2b. AIC and deviance explained for all candidate GAMs for Hector's dolphins during 1995–2002. Model 2 represents the best fit GAM.

Model	Variables Included	AIC	Deviance Explained (%)
1	s(Year) + s(SST) + s(Tide)	1380.79	16.8
2	**s(Year) + s(SST)**	**1379.16**	**16.8**
3	s(Year)	1627.26	1.3
4	s(SST)	1398.51	15.0

Appendix 2.3

Table 2.3a. Parameter estimates of the variables selected in the best fit GLM for Hector’s dolphins during 2003–2011. Significance codes are “***” 0.001, “**” 0.01, ‘*” 0.05, “.” 0.1, “ ” 1.

Variable		
Terms	estimate	p value
SST	–17890	< 0.001***
Year	1	< 0.001***

Deviance explained = 15.7%; n = 1124

Table 2.3b. AIC and deviance explained for all candidate GLMs for Hector’s dolphins during 2003–2011. Model 2 represents the best fit.

Model	Variables Included	AIC	Deviance Explained (%)
1	Year + SST + s(Tide) + s(Turbidity)	1312.5	16.5
2	Year + SST + s(Turbidity)	1312.6	16.4
3	**Year + SST**	**1317.2**	**15.7**
5	SST	1361.1	12.8
6	Year	1515.8	2.9

Appendix 2.4

Table 2.4a. Parameter estimates of the variables selected in the best fit GAM for bottlenose dolphins during 1995–2002. Significance codes are “***” 0.001, “**” 0.01, ‘*” 0.05, “.” 0.1, “ ” 1.

Variable			
Smooth terms	edf	χ^2	p value
SST	2.6	21.06	0.002 ***
	df	χ^2	p value
Year	1	5.45	0.01 *

Deviance explained = 2.5%; n = 1289

Table 2.4b. AIC and deviance explained for all candidate GAMs for bottlenose dolphins during 1995–2002. Model 2 represents the best fit GAM.

Model	Variables Included	AIC	Deviance Explained (%)
1	(Year) + s(SST) + s(Tide)	1380.9	2.4
2	**(Year) + s(SST)**	**1379.1**	**2.5**
3	s(SST)	1382.1	2.0
4	(Year)	1395.3	1.0

Appendix 2.5

Table 2.5a. Parameter estimates of the variables selected in the best fit GAM for bottlenose dolphins during 2003–2011. Significance codes are “***” 0.001, “**” 0.01, ‘*’ 0.05, “.” 0.1, “ ” 1.

Variable			
Smooth terms	edf	χ^2	p value
Year	6.83	220.7	< 0.001***
	df	χ^2	p value
Turbidity	1	6.22	0.013

Deviance explained = 20.0 %; n = 1123

Table 2.5b. AIC and deviance explained for all candidate GAMs for bottlenose dolphins during 2003–2011. Model 3 represents the best fit GAM.

Model	Variables Included	AIC	Deviance Explained (%)
1	Year + s(SST) + s(Tide) + s(Turbidity)	1160.97	21.2
2	Year + s(SST) + s(Turbidity)	1159.29	21.2
3	**Year + s(Turbidity)**	**1156.93**	**20.0**
4	Year	1164.42	20.4

Appendix 2.6

Table 2.6a. Parameter estimates of the variables selected in the best fit GAM for dusky dolphins during 1995–2002. Significance codes are "***" 0.001, "**" 0.01, '*" 0.05, "." 0.1, " " 1.

Variable			
Smooth terms	edf	χ^2	p value
SST	2.88	146.1	< 0.001 ***
	df	χ^2	p value
Year	1	65.4	< 0.001 ***
Deviance explained = 23.5%; n = 1288			

Table 2.6b. AIC and deviance explained for all candidate GAMs for dusky dolphins during 1995–2002. Model 2 represents the best fit GAM.

Model	Variables Included	AIC	Deviance Explained (%)
1	(Year) + s(SST) + s(Tide)	986.68	23.6
2	**(Year) + s(SST)**	**986.48**	**23.5**
3	s(SST)	1058.16	17.7
4	(Year)	1211.92	5.4

Appendix 2.7

Table 2.7a. Parameter estimates of the variables selected in the best fit GAM for dusky dolphins during 2003–2011. Significance codes are "***" 0.001, "**" 0.01, '*' 0.05, "." 0.1, " " 1.

Variable			
Smooth terms	edf	χ^2	p value
Year	7.78	137.29	< 0.001 ***
SST	2.99	225.73	< 0.001***
Tide	2.24	13.50	0.004 **
Turbidity	2.46	32.63	< 0.001***

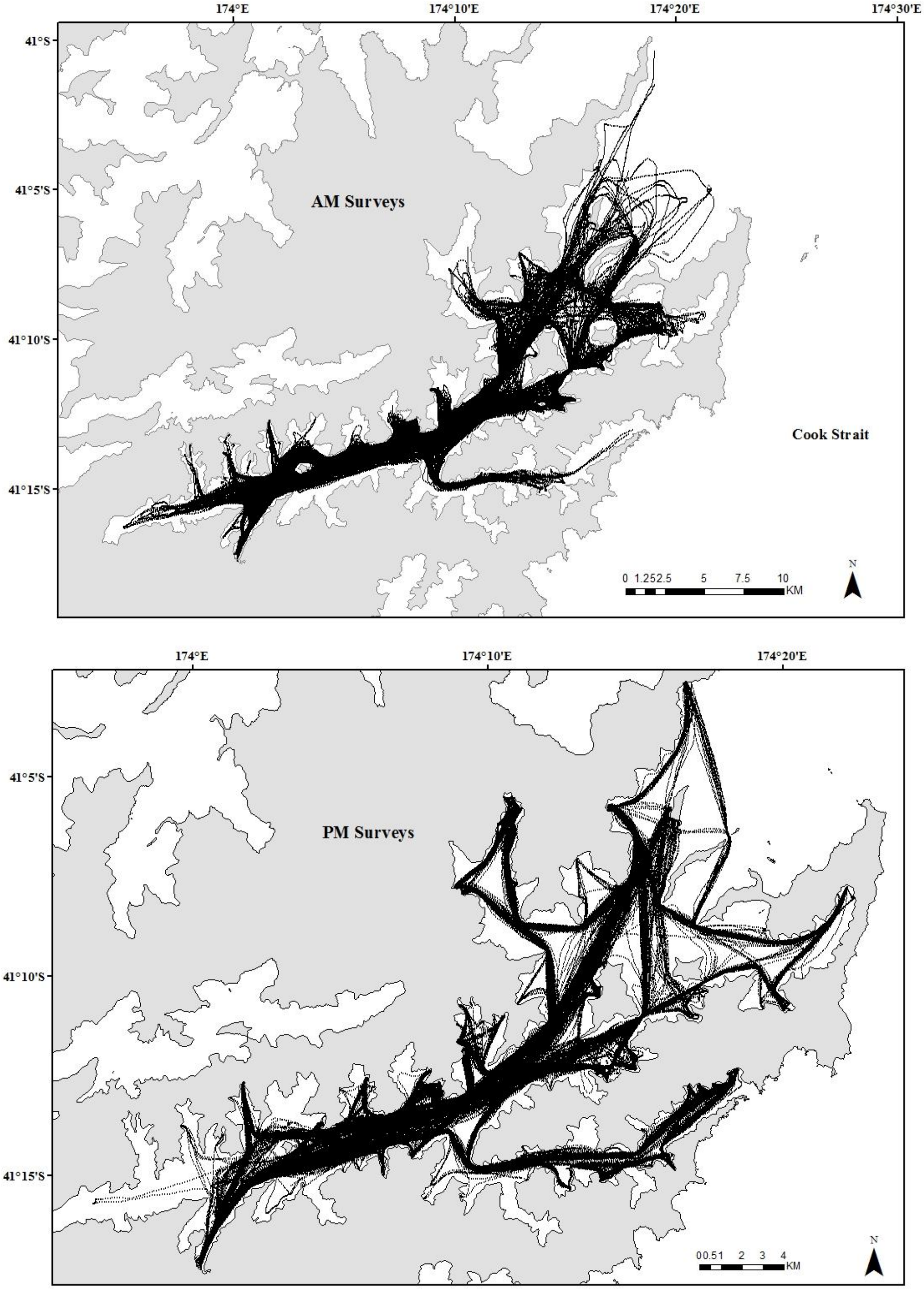
Deviance explained = 43.3%; n = 1123

Table 2.7b. AIC and deviance explained for all candidate GAMs for dusky dolphins during 2003–2011. Model 1represents the best fit GAM.

Model	Variables Included	AIC	Deviance Explained (%)
1	**s(Year) + s(SST) + s(Tide) + s(Turbidity)**	**793.96**	**43.3**
2	Year + s(SST) + s(Turbidity)	805.09	42.1
3	Year + s(SST) + s(Tide)	864.13	39.2
4	s(SST) + s(Tide) + s(Turbidity)	977.43	28.5
5	Year + s(SST)	871.08	38.4
5	s(SST) + s(Turbidity)	990.16	27.2
6	s(SST) + s(Tide)	1042.90	25.1

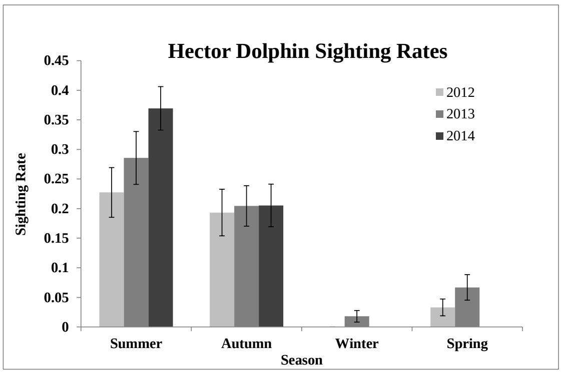
Appendix 3.1

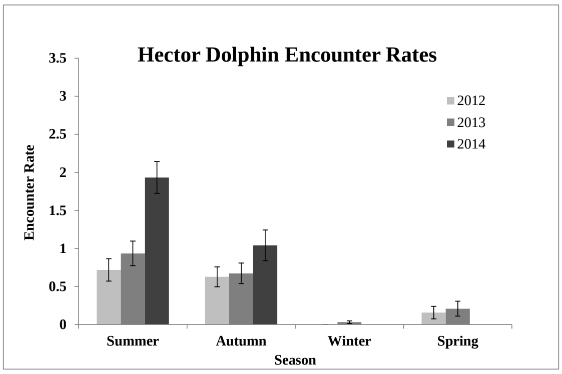
Total survey tracks on effort during morning and afternoon surveys prior to being confined to 3x3 km grid for spatial analysis.

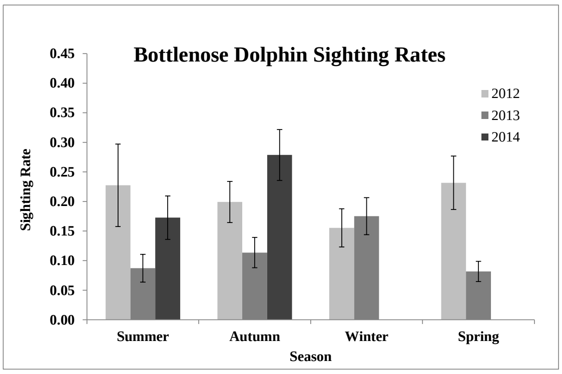


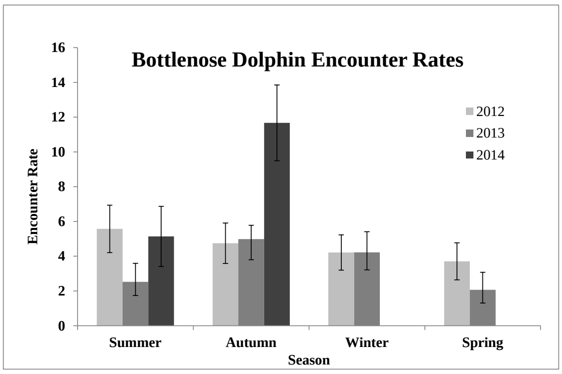
Appendix 3.2

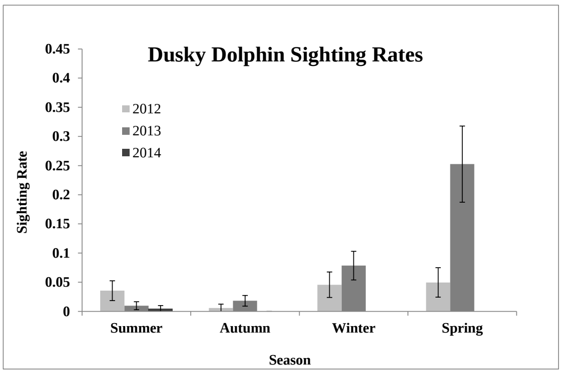
Seasonal and annual sighting and encounter rates (± SD) of Hector's (*Cephalorhynchus hectori*), bottlenose (*Tursiops truncatus*) and dusky dolphins (*Lagenorhynchus obscurus*) during surveys in QCS, NZ during from December 2011–April 2014.

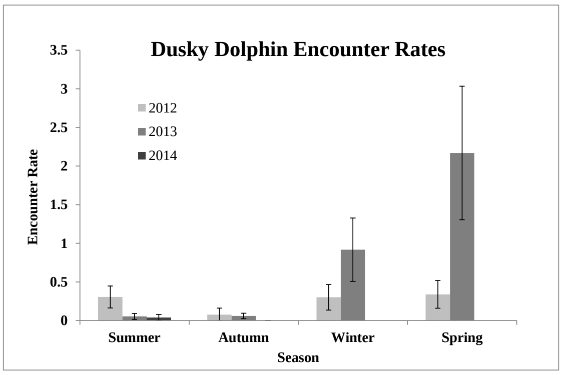






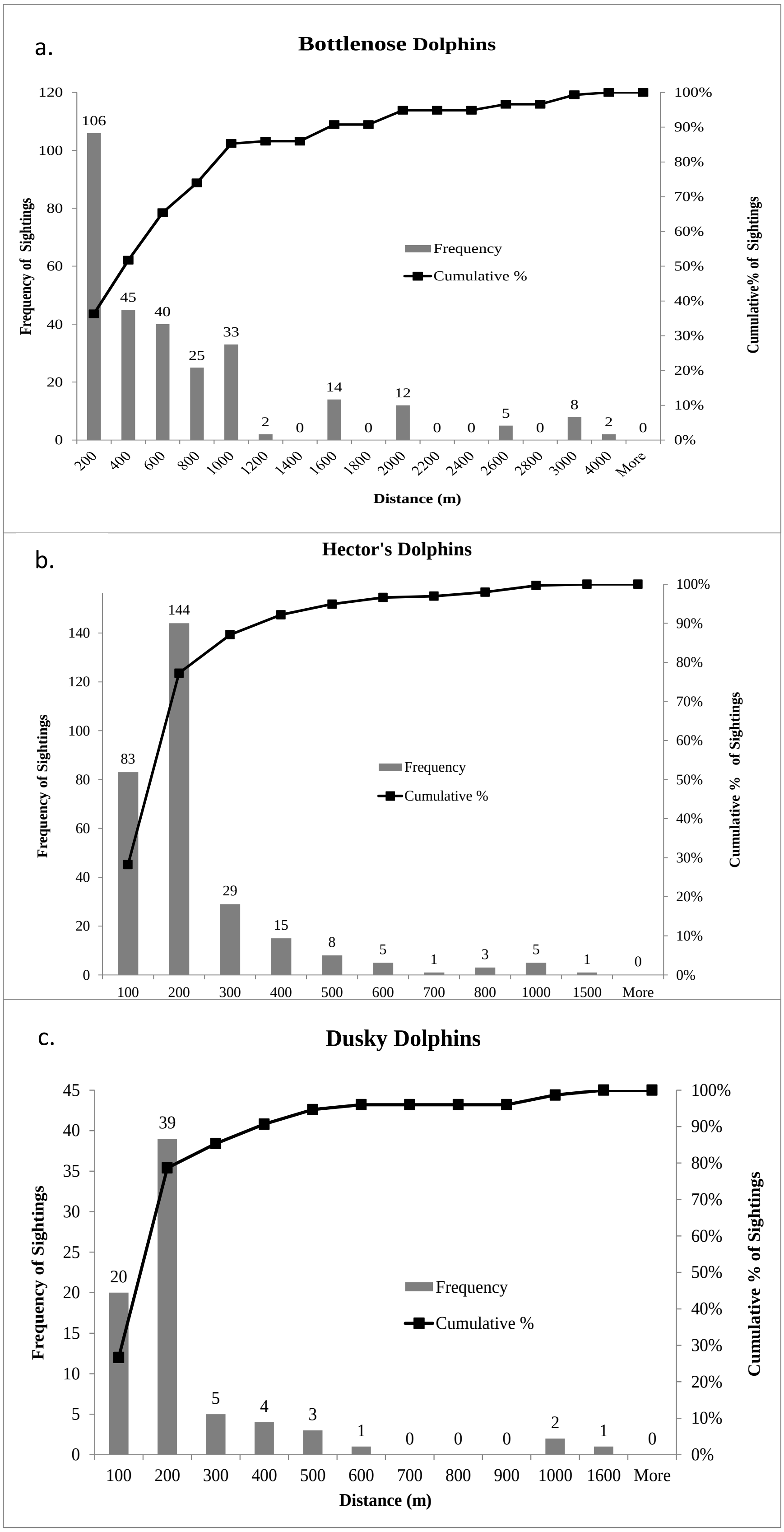






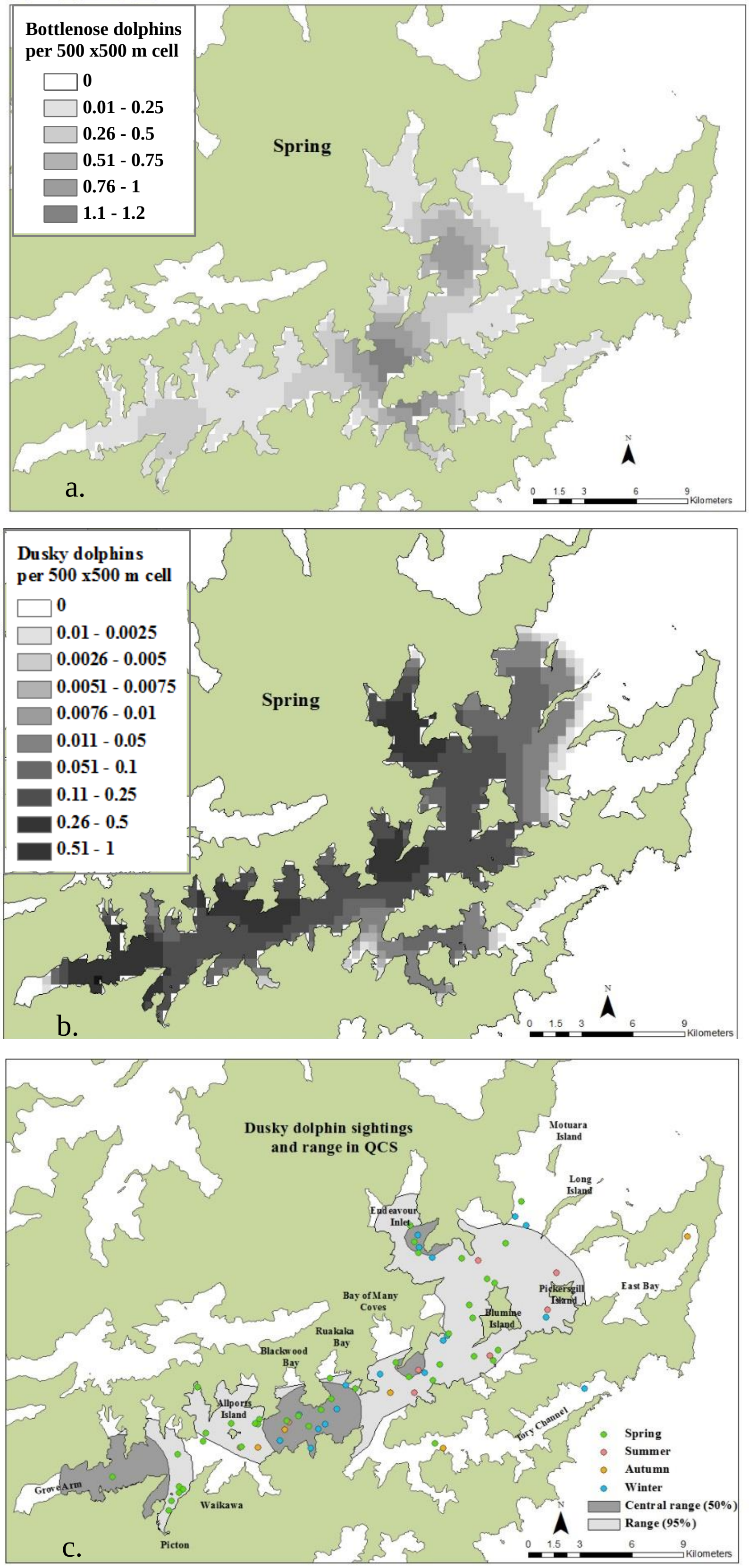
Appendix 3.3

Cumulative frequency histograms depicting sighting distances of a. bottlenose, b. Hector's and c. dusky dolphins during surveys in QCS, NZ from December 2011–April 2014.



Appendix 3.4

Kernel Density Estimates trialled with large sightings removed to investigate the effects of outliers combined with low survey effort for a. bottlenose dolphins during spring b. dusky dolphins during spring and c. the resultant core range of dusky dolphins.



Appendix 3.5

Queen Charlotte Sound study area and the Greater Marlborough Sounds region.