Spatial Ecology and Conservation of Cetaceans using the Hauraki Gulf, New Zealand

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ABSTRACT

Understanding species' distributions and habitat use, and how they change spatially and temporally, is crucial for conservation management. The Hauraki Gulf, North Island, New Zealand is a highly productive marine ecosystem that is important for a range of marine megafauna, including cetaceans. This study investigated the spatial and temporal distribution and habitat use of three focal species: common dolphin (*Delphinus* sp.), Bryde's whale (*Balaenoptera edeni*) and bottlenose dolphin (*Tursiops truncatus*) in the Hauraki Gulf, with the overarching goal of providing scientific information for conservation and management. A dedicated research vessel was used for data collection and surveys were focused in the inner Hauraki Gulf (IHG) and off the west coast of Great Barrier Island (GBI; outer Hauraki Gulf). The likely spatial use of the Hauraki Gulf by cetaceans, and how that likelihood changes seasonally, was investigated using species distribution modelling (SDM). A novel approach to SDM for cetaceans that incorporates detection probability was investigated with occupancy models and compared with generalised linear model (GLM) outputs. Additionally, photo-identification was used to assess the population ecology of bottlenose dolphins using GBI waters for the first time in light of the reported decline in abundance in what has formerly been recognised as the core region (i.e. Bay of Islands) for the North Island population.

Survey effort totalled 20,803 km in IHG and GBI waters during 279 survey days between January 2010 and November 2012. Central northern IHG regions were important for common dolphins year-round, with increased probabilities of encounter during winter and spring compared with summer and autumn at GBI. The inshore movement of common dolphins in Hauraki Gulf waters during winter may represent an overall offshore to inshore shift in distribution, combined with an influx of dolphins into the Gulf from the wider surrounding areas of the northeast coast. This is likely to be related to prey distribution. Estimates of the functional habitat models suggested that the use of more southerly waters in the IHG during summer and autumn reflects habitat use by nursery rather than by feeding dolphin groups. However, the overall predictive maps were more temporally and spatially similar to the feeding than the nursery group predictions, indicating that prey availability likely has important implications for the general distribution and habitat use patterns of common dolphins in the Hauraki Gulf. Furthermore, occupancy model outputs showed similar spatial and temporal trends in distribution and habitat use of common dolphins in the IHG as the GLMs. While incorporating detection probability reduced the bias in parameter estimates, the depth covariate was still identified as the most important predictor of seasonal occurrence using both model types.

Overall, the spatial and temporal distribution patterns of Bryde's whales were the most unpredictable of the focal species, particularly inter-annually off GBI. Notably, habitat use by Bryde's whales and common dolphins in GBI waters was considerably different, unlike in IHG waters. This may be indicative of whales foraging more frequently on krill in outer Hauraki Gulf waters than in the IHG, albeit dependent on inter-annual variation in prey availability. It is important to note that the results of this study occurred under predominantly La Niña conditions. Given the strong effects of winds on ocean circulation in the Hauraki Gulf, variations in patterns described here may vary under more neutral and El Niño conditions.

The high encounter rates of bottlenose dolphins at GBI compared with the IHG support the hypothesis that GBI is a hotspot for the North Island population. Groups using GBI waters were larger than previously reported for the North Island population and predominantly contained neonates and calves. In particular, the southwest coast of GBI appeared important for bottlenose dolphins, possibly due to a combination of factors including food availability, its suitability for breeding or calving, and the likely decreased levels of anthropogenic pressures associated with other regions of the population's home range. Photo-identification analyses confirmed overall site fidelity (MSR = 0.33) to the GBI region was high, albeit with variable re-sighting patterns among individuals. A total of 171 dolphins (CI = 162–180) used the area during the study period, representative of a significant proportion of the North Island population. Seasonal abundance estimates peaked in summer and autumn and were lower during winter months, with individuals leaving the study area for multiple seasons but subsequently returning. Thus, individuals of the North Island population clearly spend extended periods of time outside of what has formerly been recognised as their core home range. It is apparent that the GBI region is not simply being used as a corridor to reach other destinations but instead is a key location for at least a part of the North Island population.

A number of important baselines have been identified via this study and the future challenge will lie in securing enough resources to ensure continuity in research and monitoring for further conservation purposes. The fact that the use of GBI waters by bottlenose dolphins has been overlooked until now highlights the need for researchers, managers and funding agencies to maintain an open outlook on their population of interest as a whole when conducting or funding research. For management of North Island bottlenose dolphins to be effective, a comprehensive approach including the entire home range of this population along the northeast coast is required.

This research also demonstrated for the first time that occupancy models can be successfully applied to cetacean sighting data to assess habitat use while simultaneously accounting for imperfect detection. There was strong agreement between predicted areas of high use for common dolphins identified by the GLMs and occupancy models. This congruency between different model types suggests that the predictive maps presented here provide reliable seasonal distributional information that will be useful to support current and future conservation initiatives. An improved understanding of the processes driving the differences in habitat use will enable refined predictions of spatial and temporal distribution, which is required for effective management and conservation of cetaceans using the Hauraki Gulf.

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LIST OF ABBREVIATIONS

AIC	Akaike's Information Criterion
ANOVA	Analysis of Variance
BIC	Bayesian Information Criterion
BOI	Bay of Islands
BOP	Bay of Plenty
BPMMS	Banks Peninsula Marine Mammal Sanctuary
CI	Confidence interval
CJS	Cormack-Jolly-Seber
Contd.	Continued
CSV	Comma separated values
CV	Coefficient of variation
df	Degrees of freedom
DOC	Department of Conservation
EAUC	East Auckland Current
ECBOP	East Coast Bay of Plenty
e.g.	For example
ENSO	El Niño Southern Oscillation
ER	Encounter rate
ESRI	Environmental Systems Research Institute
Fig.	Figure
GAM	Generalised additive model
GBI	Great Barrier Island
GIS	Geographic Information System
GLM	Generalised linear model
GME	Geospatial Modelling Environment
GPS	Global Positioning System
HGBDC	Hauraki Gulf Bottlenose Dolphin Catalogue
HGMPA	Hauraki Gulf Marine Park Act
h	Hours
hp	Horse power
i.e.	That is
IHG	Inner Hauraki Gulf
IQR	Interquartile range
IUCN	International Union for Conservation of Nature
km	Kilometre
LME	Large marine ecosystem
m	Metre
ML	Maximum likelihood
MMAP	Marine Mammal Action Plan
MMPR	Marine Mammals Protection Regulations
MPA	Marine protected area
MPI	Ministry for Primary Industries
MSP	Marine spatial planning
MSR	Monthly sighting rate

NIWA	National Institute of Water and Atmospheric Research
NA	Not applicable
NE	Not estimated
NP	Number of parameters
NPP	Net primary production
OHG	Outer Hauraki Gulf
PAU	Proportion of area used
PDU	Probability of common dolphin use
Pr	Probability
SAC	Special Area of Conservation
SD	Standard deviation
SDM	Species distribution modelling
SE	Standard error
SPUE	Sightings per unit effort
SR	Sighting rate
SSM	Safe Ship Management
SSR	Seasonal sighting rate
SST	Sea surface temperature
USA	United States of America
VGPM	Vertically Generalised Production Model
VIF	Variance inflation factor

Chapter 1

General Introduction

Surveying for marine mammals in the Hauraki Gulf. Photo: Sarah Dwyer.

1.1 INTRODUCTION

Understanding species' distributions and habitat use, and how they change in space and time, is crucial for conservation management. Species distribution modelling (SDM) relates observational data to environmental variables in order to predict spatial and temporal environmental suitability (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). This approach, developed in the 1980s, has variously been named as niche-based habitat modelling, ecological niche modelling, habitat suitability modelling or climate envelope modelling (Lobo et al. 2010). SDM has now become a widely accepted tool for predicting species distributions (Rocchini et al. 2011) and is particularly relevant given global climate change and the demand for future projections of species distributions or at worst, extinctions (Dormann 2007). The majority of SDMs have been applied in conservation planning (Robinson et al. 2011), where they can be used as key tools for decision making, reducing the impact of biological invasions or enabling identification of critical habitats (Guisan et al. 2013).

The research presented in this thesis is primarily spatially focused, with the overarching goal of informing conservation management. The spatial and temporal distribution and habitat use of three focal cetacean species: common dolphin (*Delphinus* sp.), Bryde's whale (*Balaenoptera edeni*) and bottlenose dolphin (*Tursiops truncatus*), in the Hauraki Gulf, North Island, New Zealand, were investigated. The population ecology of bottlenose dolphins using the west coast of Great Barrier Island (outer Hauraki Gulf) waters was also assessed in light of the reported decline in abundance in the Bay of Islands, part of the home range of the North Island population (Tezanos-Pinto et al. 2013).

In this introductory chapter, distribution and habitat use are described in relation to their application in this thesis, the distribution and habitat use of the focal cetacean species are detailed based on a review of the literature, and their conservation and management in the Hauraki Gulf is outlined. The rationale and structure of the thesis are presented at the end of the chapter.

1.1.1 Distribution, density, and habitat use

The field of ecology encompasses the study of the distribution and abundance of organisms (Krebs 1988). It is well known that distribution and abundance are very closely related. Put simply, distribution is concerned with *where* and abundance with *how many*. Distribution is defined in this thesis as the geographical range of a population (Lawrence 2000). The term density is another way to describe abundance and is used to describe the number of individuals per unit of area (Bush et al. 1997). Identifying the factors that determine species range limits and quantifying distributions is a key focus of ecological studies (Guisan & Thuiller 2005; Broennimann et al. 2012).

Quantifying patterns of spatial and temporal variation in distribution and density can provide important information for conservation planning and management, such as using mapping to understand the extent to which conservation priorities may overlap with key areas for human activities that may be destructive for the species involved (Margules & Pressey 2000). There are many reasons why the field of distribution ecology is important and has shown considerable growth in recent years, particularly with the increased interest in SDM. Guisan & Thuiller (2005) and Franklin (2010) discuss many of these reasons, including tackling applied problems like management of rare species, ecological restoration, mapping suitable sites for species reintroductions, and assessing the impact of climate change and other environmental changes on species distributions. This emphasis on spatial knowledge in conservation decision making translates to a higher demand for more accurate maps of species distributions (Guisan et al. 2013).

Understanding how animals use the space in which they are distributed is also necessary for guiding management decisions. Hall et al. (1997) applied the term 'habitat use' to the way an animal uses a collection of physical and biological components in a habitat, and scientists often use this term to describe correlations with specific habitat features (Bergin 1992). Habitat use is also defined in relation to the proportion of time that animals spend in a particular habitat (Beyer et al. 2010). The term 'habitat selection' is the process (often behavioural) by which an animal actively chooses a particular habitat from others (Johnson 1980; Beyer et al. 2010) and 'habitat preference' refers to the ratio of habitat use relative to its availability (Aarts et al. 2008).

Habitat use studies investigate a wide range of factors, both biotic and abiotic, that ecologists may consider important for their focal species and study areas. In terrestrial environments, habitat use is often assessed in relation to landscape characteristics. Examples include the investigation of land use conflict among feral horses (*Equus ferus*), livestock, wildlife and native grassland conservation in the Rocky Mountain Forest Reserve, Canada (Girard et al. 2013), or determining factors that influence habitat use at migration stopover areas for wetland birds (Webb et al. 2010). In marine environments, the association of habitat use with environmental factors is typically classified as a secondary relationship for cetaceans, indirectly linked to the distribution of their prey (Heithaus & Dill 2002; Bräger et al. 2003; Azzellino et al. 2008; Dawson et al. 2013; Eierman & Connor 2014), which for the marine environment is known to be patchy and heterogeneous (Weimerskirch 2007). Identifying changes in habitat use over time is vital for conservation, especially where static protected areas may become futile for management if changes in habitat use result in changes in spatial distribution (Hartel et al. 2014).

Biological factors that may affect habitat use are varied, ranging from the distribution of predators (Lima & Dill 1990; Heithaus & Dill 2002; Nicholson et al. 2014) to the effects of group composition (Cañadas & Hammond 2008; Hartel et al. 2014). Linking cetacean behaviour with distribution can also enable a better understanding of the function behind habitat use patterns (Hastie et al. 2004). A well-known example for marine mammals is the spinner dolphins (*Stenella longirostris*) of the Hawaiian Islands, USA, that use shallow, sandy areas to rest during the day and deep waters to forage at night (Norris & Dohl 1980).

Various approaches have been used to model species distributions and/or habitat use including maximum entropy (Maxent), generalised linear models (GLMs), generalised additive models (GAMs), and regression trees (Guisan & Zimmermann 2000; Franklin 2010). Different models are suitable for different types of data; Maxent was specifically developed for presence-only data (Dudík et al. 2007) while GLMs and GAMs are forms of regression analysis that are commonly used with presence-absence data in cetacean studies (e.g. Cañadas et al. 2005; Becker et al. 2010; Silva et al. 2014). GLMs comprise a response, a predictor and a link function that describes the relationship between the expected value of the response and the predictors (Brigham & Schwarz 2003). GAMs are a non-parametric extension of GLMs, in which one of the parametric functions of the predictor variables is replaced by a smoothing function (Brigham & Schwarz 2003; Becker et al. 2010). One of the greatest advantages of using GAMs is their flexibility in capturing non-linear relationships; however, GAMs are less efficient than GLMs when interactions among predictor variables are present (Redfern et al. 2006). This thesis uses GLMs and GAMs, and also explores the first use of occupancy models that incorporate detection probability (MacKenzie et al. 2002) to assess cetacean habitat use.

The detection of groups/individuals in wildlife studies is rarely perfect (Bailey & Adams 2005). True absence and non-detection (i.e. false absence) are often confounded when detection probability is less than one. Animals may mistakenly be counted as absent from a habitat when in reality they were present at the time of the survey, but for some reason were not observed (i.e. false absence; MacKenzie et al. 2002; Bailey & Adams 2005). Imperfect detection (detection probability < 1) will always result in underestimation of true distribution or abundance (MacKenzie et al. 2003; 2004; Bailey & Adams 2005). As such, parameter estimates will be biased if detection probability is not accounted for (MacKenzie et al. 2002; 2003; 2004).

Detection probabilities are usually accounted for in line transect surveys for cetaceans that aim to estimate absolute density or abundance (e.g. Hammond et al. 2013). In distance sampling, the trackline detection probability, or g(0), has been shown to be highly variable for different marine mammal species (Barlow 2015), and varies according to factors such as the average dive duration of the species (Stockin et al. 2001). For example, estimates of g(0) used in a cetacean abundance study for Hawaiian waters were significantly lower (i.e. 0.23–0.45) for more cryptic beaked whale species than for small groups of conspicuous delphinids such as striped dolphins (*S. coeruleoalba*, 0.76; Barlow 2006). Furthermore, environmental conditions, particularly sea state, are also known to negatively affect the detection of cetaceans at sea (Barlow et al. 1988; Forney 2000; Gannier 2005).

In most distribution or habitat use studies, attempts are made to reduce heterogeneity in detection probability as much as possible during field surveys by placing limits on suitable conditions for surveys. However, detection probability is often not explicitly accounted for in the spatial analyses (Viddi et al. 2010; Hartman et al. 2014). This exclusion can be problematic because covariates that mainly bias detection probability may in fact mistakenly appear to be important factors of habitat use. This type of situation was described by MacKenzie (2006) using an example of pronghorn antelope (*Antilocapra americana*) in Wyoming, USA.

In response to a lack of appropriate techniques that could account for imperfect detection, occupancy models were developed in the early 2000s (MacKenzie et al. 2002; 2006). The premise of occupancy modelling is that the probability of species occurrence and detection probability are modelled simultaneously. Model parameters (occupancy and detection probability) are estimated using maximum likelihood methods and can be functions of covariates such as habitat type (MacKenzie et al. 2004). Since visual surveys for cetaceans are known to be affected by imperfect detection, and occupancy models offer a method of modelling habitat use in conjunction with detection probability, this thesis has used occupancy techniques to model habitat use by a cetacean species for what is thought to be the first time.

1.2 Study site and species

The Hauraki Gulf, the study site for this thesis, is a relatively shallow, semi-enclosed body of water on the northeast coast of the North Island, New Zealand (Fig. 1.1; Paul 1968; Manighetti & Carter 1999; Black et al. 2000). Circulation in the Hauraki Gulf is strongly influenced by surface winds and their interaction with tidal currents, in addition to physical barriers such as headlands and islands that enhance local upwellings (Black et al. 2000). Warm waters from the East Auckland Current flow into the northerly entrance of the Hauraki Gulf during summer and autumn, when easterly winds and downwellings are more prevalent (Zeldis et al. 2004). Westerly winds that are favourable for upwelling prevail in late winter and spring (Chang et al. 2003; Zeldis et al. 2004). Since seasonal upwellings are responsive to the wind, hydrodynamics are largely affected by broad-scale variability in climate conditions, namely the influence of the El Niño Southern Oscillation (ENSO).

Figure 1.1 Hauraki Gulf, North Island, New Zealand. Map Source: NIWA.

Renwick et al. (2010a) provide an overview of ENSO and its effect on the New Zealand climate, which is summarised as follows: An El Niño event occurs when there is a breakdown in the regular east to west pattern of the Trade Winds across the tropical Pacific Ocean. This causes a decreased difference in SSTs between the warmest waters in the west and coolest water in the east. For La Niña, the opposite occurs and the normal pattern is intensified, resulting in an increased difference in SSTs. The Southern Oscillation Index (SOI) is a commonly used measure of ENSO; a positive SOI and La Niña are associated with stronger than usual Trade Winds while a negative SOI and El Niño are associated with weaker than usual Trade Winds. For New Zealand, an El Niño translates to increased westerly and southwesterly winds and therefore cooler seasons than normal. Conversely, for La Niña, westerlies decrease and northerly winds are more frequent, with warmer than usual seasons. The probability of El Niño or La Niña conditions occurring during any year is equally likely, each at approximately 25% of the time. When neither El Niño nor La Niña phases are underway, the conditions are described as neutral.

During the years of this study, from 2010 to 2012, conditions were primarily La Niña or neutral, with El Niño conditions only fully developed at the beginning of the study in summer 2010 (Fig. 1.2; National Climate Centre 2013). From spring 2010 to the end of autumn 2011, a strong La Niña was underway (National Climate Centre 2013). While more westerly winds could be expected in the Hauraki Gulf during El Niño, the region typically experiences more northeasterly winds associated with higher rainfall during La Niña conditions (Wratt et al. 2014).

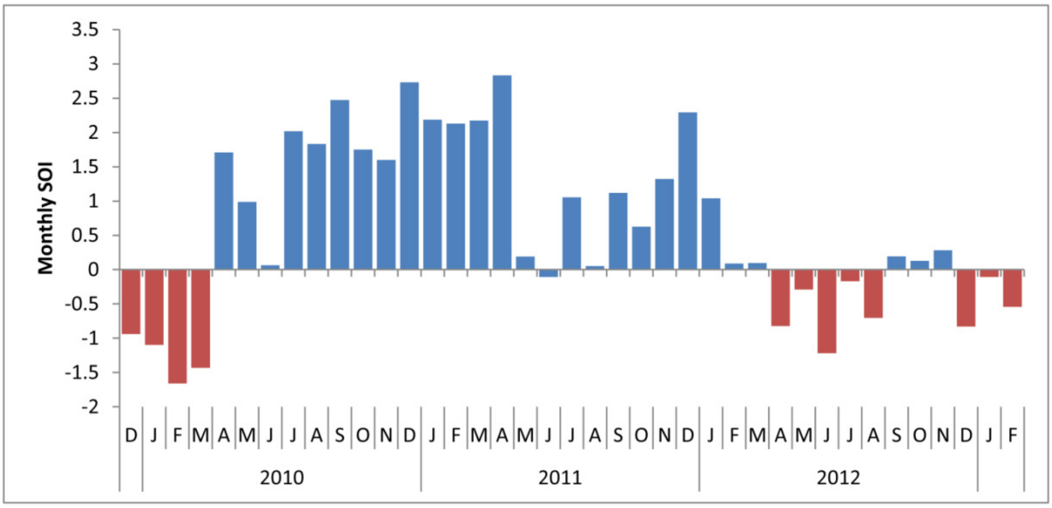

Figure 1.2 The Southern Oscillation Index (SOI) from summer 2009/10 to summer 2012/13. Values of +1 or more indicate the presence of La Niña conditions, while values of -1 or less indicate the presence of El Niño conditions. Data source: NIWA

The Hauraki Gulf is a highly productive marine ecosystem (Zeldis et al. 2005; Hauraki Gulf Forum 2011; MacDiarmid et al. 2013) and is important for a diverse range of megafauna including seabirds (Stephenson et al. 2008; Machovsky Capuska et al. 2011; Gaskin & Rayner 2013) and marine mammals (Visser 1999; O'Callaghan & Baker 2002; Berghan et al. 2008; Stockin et al. 2008a; Wiseman et al. 2011; Dwyer et al. 2014a). A diversity of marine mammal species have been sighted in Hauraki Gulf waters including killer whales (*Orcinus orca*; Visser 2000; O'Callaghan & Baker 2002), pilot whales (*Globicephala melas*; O'Callaghan & Baker 2002; this thesis), Arnoux's beaked whales (*Berardius arnouxii*; O'Callaghan & Baker 2002) and southern right whales (*Eubalaena australis*; Carroll et al. 2014; this thesis). This thesis focused on the three most frequently sighted species in the Hauraki Gulf, i.e. common dolphins, Bryde's whales and bottlenose dolphins.

1.2.1 Common dolphin

Common dolphins (*Delphinus* spp.), members of the Delphinidae family, have a widespread distribution (Fig. 1.3) with considerable geographic and morphological variation (Amaha 1994; Murphy et al. 2006). While confusion regarding the taxonomic status of *Delphinus* in particular regions of the world has been clarified to some degree (Heyning & Perrin 1994; Natoli et al. 2006; Amaral et al. 2007), the global taxonomy of the genus remains unresolved. In the South Pacific, the short-beaked form (*D. delphis*) has been confirmed in southern Australian waters (White 1999; Bell et al. 2002; Bilgmann 2007); however, the taxonomic status of common dolphins in New Zealand waters remains unclear (Stockin et al. 2014). Although most New Zealand haplotypes clustered with short-beaked common dolphins from the Pacific and Atlantic Oceans, some also clustered with the long-beaked form (*D. capensis*) from the North Pacific (Stockin et al. 2014). Similar morphological variation has been identified in a recent cranial morphometric study (Jordan et al. 2015). As a result, New Zealand common dolphins are referred to herein as *Delphinus* sp.

1.2.1.1 Common dolphin distribution

Common dolphins have a widespread global distribution (Fig. 1.3) across tropical, subtropical and temperate shelf and oceanic waters, but the species is absent from polar waters (Dohl et al. 1986; Gaskin 1992). Described as cosmopolitan, common dolphins are found in the eastern (Gaskin 1992; Notarbartolo di Sciara et al. 1993; Weir et al. 2001; Bearzi et al. 2003; Gannier 2005; Cañadas & Hammond 2008; Jefferson et al. 2008; Robinson et al. 2010) and western Atlantic (Selzer & Payne 1988;

Gaskin 1992; Lawson et al. 2009; Jefferson et al. 2009; Oviedo et al. 2010), Indian (Cockcroft & Peddemors 1990; Smeenk et al. 1996) and Pacific Oceans (Banks & Brownell 1969; Evans 1982; Gaskin 1992; Carretta et al. 2000). A critical review of common dolphin records in the western Atlantic Ocean found that the species does not appear to be widespread in tropical waters as previously suggested, but rather is restricted to mainly temperate regions (Jefferson et al. 2009).

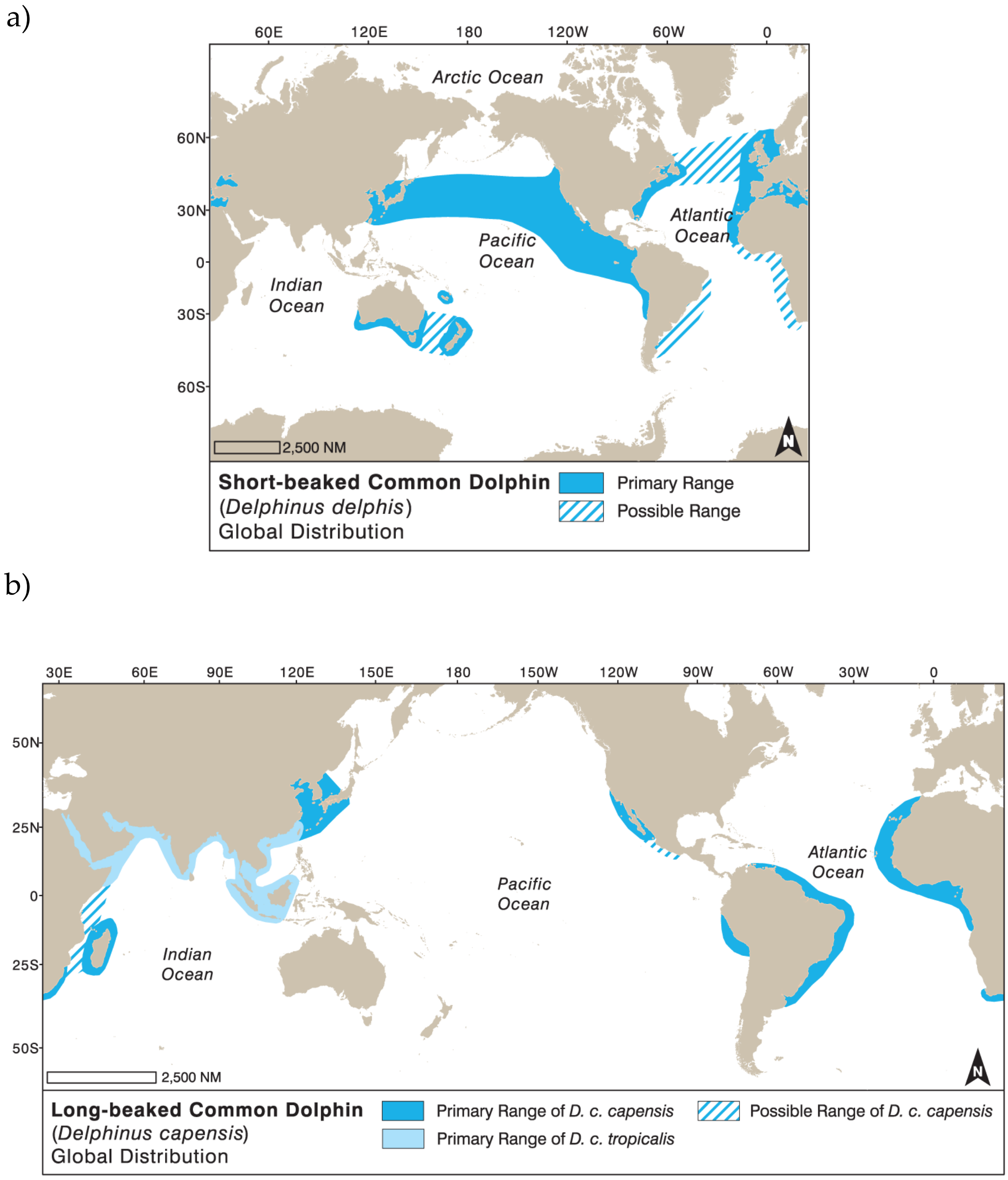

Figure 1.3 Global distributions of **a**) short-beaked common dolphin (*Delphinus delphis*) and **b**) long-beaked common dolphin (*D. capensis*). Map sourced from Jefferson et al. 2008.

In the western South Pacific, distribution studies remain limited. In Australia, short-beaked common dolphins are reported in subtropical and temperate waters spanning the southern and southeastern coasts and reaching into southern Queensland waters (Jefferson & Van Waerebeek 2002; Möller et al. 2011). Dedicated studies assessing range and movement are scarce, with the first assessment of common dolphin distribution in Australian waters published only recently (Gulf St. Vincent, South Australia, Filby et al. 2010). In New Zealand waters, common dolphins have been recorded around much of the coastline, particularly during the austral summer when water temperatures exceed 14° C (Gaskin 1968). New Zealand common dolphins display similar patterns in seasonal distribution to *Delphinus* in South African waters (Cockcroft & Peddemors 1990), with year-round presence in some regions and only seasonal occurrence in others (Stockin & Orams 2009). Early studies conducted during the New Zealand summer reported common dolphins in waters around the majority of the South Island coastline, from the Marlborough Sounds in the north and as far south as Doubtful Sound (Webb 1973; Bräger & Schneider 1998). Large aggregations have been documented during the austral winter months in Cook Strait and in the Hauraki Gulf (Stockin & Orams 2009). However, both sighting and stranding data suggest this species is the most concentrated off the northeastern coast of the North Island (Stockin & Orams 2009).

Seasonality

Seasonality in common dolphin occurrence and distribution has been well-documented. Summer movements into more northerly waters have been recorded on both sides of the Atlantic Ocean, off the coast of Scotland and in the waters off Newfoundland (Gaskin 1992; Lawson et al. 2009). In the southwestern Mediterranean, a shift in distribution towards deeper offshore waters was observed in winter compared with summer (Cañadas & Hammond 2008). Conversely, in the English Channel and the Bay of Biscay, short-beaked common dolphins move closer inshore in winter (Brereton et al. 2004). In the Southern California Bight, seasonal changes in distribution are evident in the summer when the common dolphin population (*Delphinus* spp.) expands its use of the region, in contrast to a more confined distribution closer to shore in winter-spring (Dohl et al. 1986; Becker et al. 2014). An inshore shift in distribution has also been documented further north off the

Californian coast in winter (Forney & Barlow 1998). Off the southeast coast of South Africa, *D. delphis* show a varied seasonal distribution, apparent in some areas year-round yet present in the north only during the winter, coinciding with the annual sardine run (Cockcroft & Peddemors 1990).

In New Zealand waters, common dolphins were recorded moving further offshore in autumn compared with spring and summer in the western Bay of Plenty (Neumann 2001a) and the East Coast Bay of Plenty (Meissner et al. 2014). An absence of sightings in winter in the western Bay of Plenty was presumed to represent a shift in distribution beyond the limits of the study area (Neumann 2001a). Winter sightings in the East Coast Bay of Plenty were also sparse; however, winter effort was very low (7%) compared with summer (57%; Meissner et al. 2014). In the Bay of Islands, common dolphins were reported further offshore in summer and were more frequently found inside the bay, i.e. closer to shore, in the winter (Constantine & Baker 1997). In the Hauraki Gulf, common dolphins have been recorded in shallower waters during summer compared with autumn (Stockin et al. 2008a).

1.2.1.2 Common dolphin habitat use

Common dolphin distribution is known to be affected by a number of environmental parameters, such as depth, slope, and chlorophyll concentrations, that may indirectly affect prey distribution (Hui 1979; Au & Perryman 1985). Depth has been identified as an important predictor of common dolphin occurrence in many habitat use studies (e.g. Cañadas et al. 2005; Azzellino et al. 2008; Moura et al. 2012). Common dolphins are found in a range of water depths, using shallow (< 100 m) shelf waters in some locations including the eastern Ionian Sea in the Mediterranean (Bearzi et al. 2005), the Gulf St. Vincent, Australia (Filby et al. 2010), the Hauraki Gulf (Stockin et al. 2008a) and Bay of Plenty, New Zealand (Meissner et al. 2014). In other regions such as the western Ligurian Sea (Azzellino et al. 2008) and around the Azores in the mid-Atlantic Ocean (Silva et al. 2014) they use deeper pelagic waters (> 1000 m). In large-scale sampling that includes shelf and oceanic waters, bimodality in common dolphin abundance with respect to depth has also been reported (Cañadas & Hammond 2008; Becker et al. 2014). In the Mediterranean Sea, Cañadas & Hammond (2008) suggested the two peaks in abundance observed in shelf edge and deep waters could be related to the locations of upwellings. However, in the western Atlantic Ocean, the use of shallow waters north of 26° S but deeper offshore waters south of 26° S has been tentatively suggested to be a consequence of two species of common dolphins occurring in those waters (Jefferson et al. 2009). Conversely, Hui (1979) found that occurrence was higher in areas of high sea floor relief and that depth did not appear to influence distribution in the Southern California Bight.

A number of studies have found that common dolphins show a preference for slope areas or regions with steep topographic features including canyons and escarpments (Bearzi 2005; Petroselli 2006; Kiszka et al. 2007; Oviedo et al. 2010). However, as with other parameters, it should be noted that slope is not always a significant predictor of common dolphin distribution, as in the case of the northeastern Alboran Sea (Cañadas et al. 2002).

In the absence of prey data, oceanographic variables used as proxies for biological factors can act as good predictors of common dolphin distribution and density. Au & Perryman (1985) suggested that areas in the eastern tropical Pacific prone to seasonal upwelling with highly variable oceanographic features (including large seasonal changes in sea surface temperature (SST) and thermocline depth) hold greater concentrations of common dolphins. However, in the Mediterranean Sea, habitat models predicted a higher use of areas with a lower temporal variability in average SST and cooler waters than the overall average (Cañadas et al. 2005). Despite the nature of the relationships, SST and thermocline properties have been identified as important variables influencing occurrence and encounter rates of common dolphins at various study sites (e.g. Redfern et al. 2008; Cañadas & Hammond 2008). Other factors such as oceanographic fronts have also been hypothesised to relate to seasonal movements of common dolphins (Goold 1998).

Chlorophyll concentration was identified as the most important variable (compared with depth and SST) associated with short-beaked common dolphin distribution off the Portuguese coast (Moura et al. 2012). The authors suggested that this was a reflection of a strong local dependency on sardine (*Sardina pilchardus*), which feed mainly on plankton. That study and another in the Mediterranean (Cañadas &

Hammond 2008) identified a strong relationship between common dolphin abundance and higher chlorophyll concentrations. However, in the eastern tropical Pacific, encounters unexpectedly peaked in waters with intermediate chlorophyll concentrations (Redfern et al. 2008).

Common dolphins typically feed on small pelagic shoaling fish (Pusineri et al. 2007) including sardine (*Sardina* spp.), anchovy (*Engraulis* spp.), pilchard (*Sardinops* spp.), and mackerel (*Trachurus* spp.), as well as cephalopods such as *Nototodarus* spp. (Cockcroft & Peddemors 1990; Young & Cockcroft 1994; Silva 1999; Meynier et al. 2008). Although prey data are typically not available for direct investigations into habitat use, links have been made with fisheries data where possible. Short-beaked common dolphin distribution off South Africa has been linked to the sardine run (Cockcroft & Peddemors 1990) and higher densities of common dolphins (*Delphinus* spp.) in Venezuelan waters coincide with the main location of the sardine fisheries (Oviedo et al. 2010). Additionally, median group sizes were significantly higher in the Southern Californian Bight when anchovies were reportedly more available (Hui 1979). Seasonality of different prey species may also explain differences in dolphin habitat use. In the Black Sea (Reeves & Notarbartolo di Sciara 2006), dolphins are attracted to feeding grounds of anchovy in southeastern areas in winter compared with sprat in central and northern regions in summer. Although not a habitat use study *per se*, a comparison of short-beaked common dolphin diet in oceanic compared with neritic waters of the Northeast Atlantic suggested that while prey type (i.e. small aggregating species available in the epipelagic layer) and feeding behaviour were similar, diet was taxonomically distinct between the two habitats (Pusineri et al. 2007).

When habitat use is also analysed in terms of biological factors such as behaviour or age class, further trends in habitat use may become apparent. Feeding groups were associated with shallow waters up to 200 m off southern Spain (Cañadas et al. 2002), found closer to the shelf edge off northeastern Venezuela (Oviedo et al. 2010) and found in deepest waters in the Hauraki Gulf (Stockin et al. 2009a). Groups with calves used more coastal waters in the southwestern Mediterranean (Cañadas & Hammond 2008); however, there was no significant difference in depth between groups containing immature or only mature individuals in the Hauraki Gulf (Schaffar 2004; Stockin et al. 2008a).

1.2.2 Bryde's whale

The Bryde's whale is a member of the Balaenopteridae family and is distributed in most tropical and temperate waters worldwide (Fig. 1.4). Taxonomic confusion still exists for Bryde's whales, with recognition of two species *B. brydei* and *B. edeni* by some (Wada et al. 2003; Kanda et al. 2007) and of two subspecies *B. edeni brydei* and *B. edeni edeni* by others (Committee on Taxonomy 2011; Kershaw et al. 2013). In addition, a third species *B. omurai* has been described for the Indo-Pacific region (Wada et al. 2003).

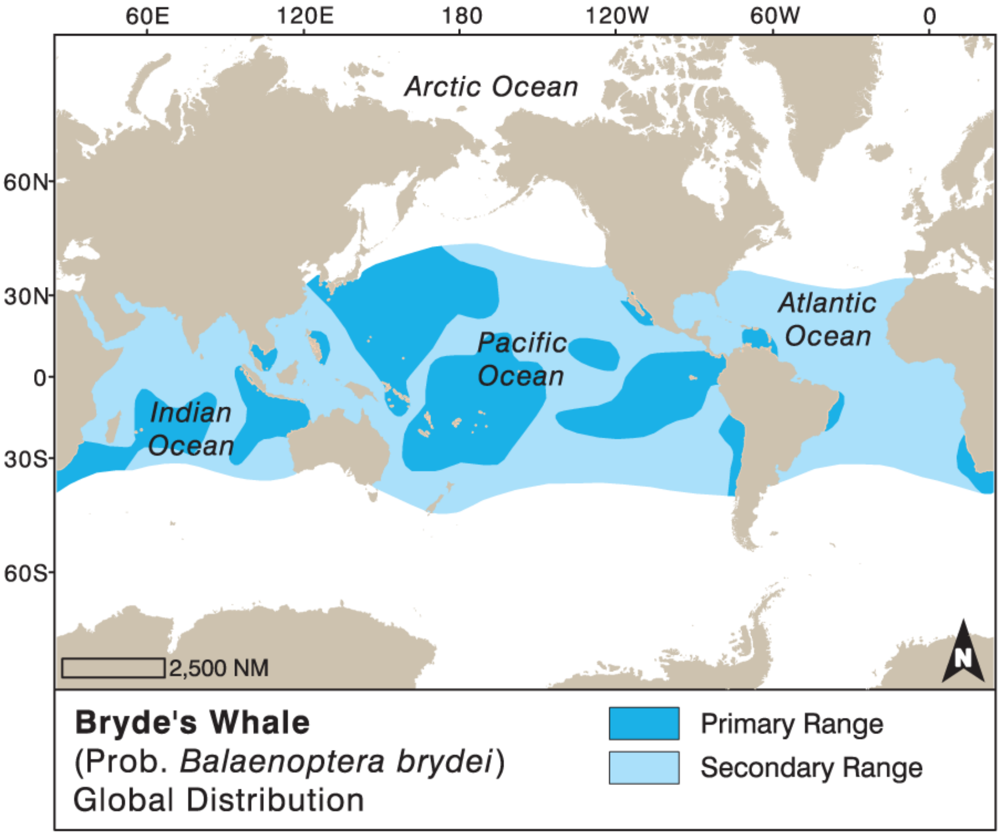

Figure 1.4 Global distribution of Bryde's whales (*Balaenoptera brydei*, *B. edeni*). Map sourced from Jefferson et al. 2008.

1.2.2.1 Bryde's whale distribution

Unlike most baleen whales, Bryde's whales do not make extensive polar migrations between warm water breeding grounds and cold water feeding grounds (Jefferson et al. 2008), and are typically distributed in waters between 40° N and 40° S (Best 1977; Kanda et al. 2007; Kato & Perrin 2009). Occurrence has been documented in the eastern and western Atlantic (Best 1977; Mullin & Fulling 2004; Siciliano et al. 2004; De Boer 2010; Weir 2010), eastern and western Pacific (Tershy 1992; Gerrodette & Forcada 2002; Carretta et al. 2011; Watanabe et al. 2012; Sasaki et al. 2013) and Indian (Kanda et al. 2007; Braulik et al. 2010) Oceans.

In the southwest Pacific, information about the distribution of Bryde's whales is limited. Occurrence is known for all Australian states except Northern Territory (Bannister et al. 1996). Within New Zealand waters, Bryde's whales have been recorded off the northeast of the North Island in both coastal and offshore regions (Gaskin 1972; Baker & Madon 2007). However, most of the information about the species comes from studies carried out in the Hauraki Gulf (O'Callaghan & Baker 2002; Baker & Madon 2007; Stockin et al. 2008b; Wiseman 2008; Behrens 2009; Wiseman et al. 2011; Constantine et al. 2012; Riekkola 2013). These studies concur that Bryde's whales are found year-round in the Hauraki Gulf (Baker & Madon 2007; Behrens 2009; Wiseman et al. 2011). Baker & Madon (2007) conducted aerial surveys from North Cape to the Hauraki Gulf and concluded that more whales occur in the Hauraki Gulf than in northern waters. They reported more whale sightings in summer than winter; however, Wiseman et al. (2011) found the highest number of whale sightings per day during winter.

Seasonality

Many studies have demonstrated seasonality in Bryde's whale occurrence. Tershy (1992) conducted a study over a four year period and reported Bryde's whales most abundant in summer and autumn in the Gulf of California. In Plettenberg Bay on the southeast coast of South Africa, a three year study found encounter rates peaked in autumn and then declined throughout winter and spring (Penry et al. 2011). Following a three year study in the Hauraki Gulf, Wiseman et al. (2011) reported a significantly higher trip encounter rate in winter than spring or summer. However, studies spanning a longer temporal period have failed to detect a significant seasonal pattern. In the southern Gulf of California, Salvadeo et al. (2011) analysed a twenty year dataset and did not find a well-defined seasonal pattern of occurrence. Similarly, no significant differences were detected for the number of whales using Hauraki Gulf waters in the cool or warm water seasons based on a ten year dataset (Behrens 2009), despite an apparent peak in sightings during May–June.

1.2.2.2 Bryde's whale habitat use

To investigate why Bryde's whales exhibit seasonality in occurrence and distribution, studies have examined visual or acoustic detections of whales in relation to a number of environmental and geographic variables including SST (Tershy 1992; Wiseman et al. 2011; Penry et al. 2011; Kerosky et al. 2012; Sasaki et al. 2013), chlorophyll concentrations (Penry et al. 2011; Salvadeo et al. 2011), climatic conditions (Salvadeo et al. 2011), depth (Wiseman et al. 2011; Sasaki et al. 2013), distance to shore (Tershy 1992) and prey species (Watanabe et al. 2012).

Bryde's whales feed on a range of prey items including euphausiids (order Euphausiacea) and small fish such as anchovy, pilchards and mackerel (Best 1977; Tershy 1992; Jarman et al. 2006; Wiseman 2008). Changes in the distribution of these prey species are considered to be the primary driver of changes in whale occurrence (Tershy 1992; Salvadeo et al. 2011; Penry et al. 2011). However, while relating Bryde's whale occurrence to the presence of prey may often be the preferred option for habitat studies, data relating to prey occurrence and distribution are typically unavailable and environmental variables are used instead. This is often the case for many cetacean studies.

With the benefit of an extensive temporal dataset to enable examination of large scale climatic variables, Salvadeo et al. (2011) suggested that inter-annual changes in Bryde's whale occurrence in the Gulf of California may be related to climate variability that affects availability of food resources. They found a significant relationship between the relative abundance of whales and both the Northern Oscillation Index and SST anomalies. While water temperature is known to affect the distribution of Bryde's whales on a broad scale, i.e. whales are not found using colder waters poleward of 40° N and 40° S (Kato & Perrin 2009), SST may or may not be an important predictor of occurrence on smaller scales. Some studies have reported a positive relationship between SST and sighting rates (Tershy 1992; Penry et al. 2011), while in the Hauraki Gulf there was a negative correlation; sighting rates increased as SST decreased (Wiseman et al. 2011). Conversely, an acoustic study found no significant relationship between Bryde's whale call rates and SST in the Southern California Bight (Kerosky et al. 2012). Furthermore, a recent increase in the occurrence of Bryde's whale off southern California is postulated to relate to short-term changes in water temperature along with changes in prey distribution and abundance that may be related to climate change (Kerosky et al. 2012; Smultea et al. 2012).

Although many environmental variables have been linked to Bryde's whale occurrence, chlorophyll concentration was not a significant predictor for studies in South Africa (Penry et al. 2011) or the Gulf of California (Salvadeo et al. 2011). Wind speed has been used as a proxy for local upwellings (Penry et al. 2011); however, the importance of this variable can be hard to interpret given wind speed is also a factor that affects detection of cetaceans in the first place.

1.2.3 Bottlenose dolphin

Two species of bottlenose dolphin are formally recognised, *T. truncatus* and *T. aduncus*. A third species, the Burrunan dolphin (*T. australis*), has recently been described in Australian waters (Charlton-Robb et al. 2011), but is not currently accepted by the Committee on Taxonomy for marine mammal species and subspecies (Committee on Taxonomy 2011). Common bottlenose dolphins (*T. truncatus*), hereafter referred to as bottlenose dolphins, are globally distributed (Fig. 1.5) and found in a variety of offshore and coastal habitats. *T. truncatus* is the only species found in New Zealand waters, and most research to date has been focused on the coastal form (e.g. Constantine 2001; D. Lusseau 2003; Currey et al. 2008; Merriman et al. 2009; Tezanos-Pinto et al. 2013; Dwyer et al. 2014a; Hartel et al. 2014). More recently, Zaeschmar et al. (2013; 2014) documented the offshore ecotype that is known to associate with false killer whales (*Pseudorca crassidens*). The coastal and offshore ecotypes are distinguished by morphological differences in addition to scars presumed to originate from cookie cutter shark (*Isistius* sp.) bites (Dwyer & Visser 2011). The bottlenose dolphins referred to in this thesis are of the coastal form.

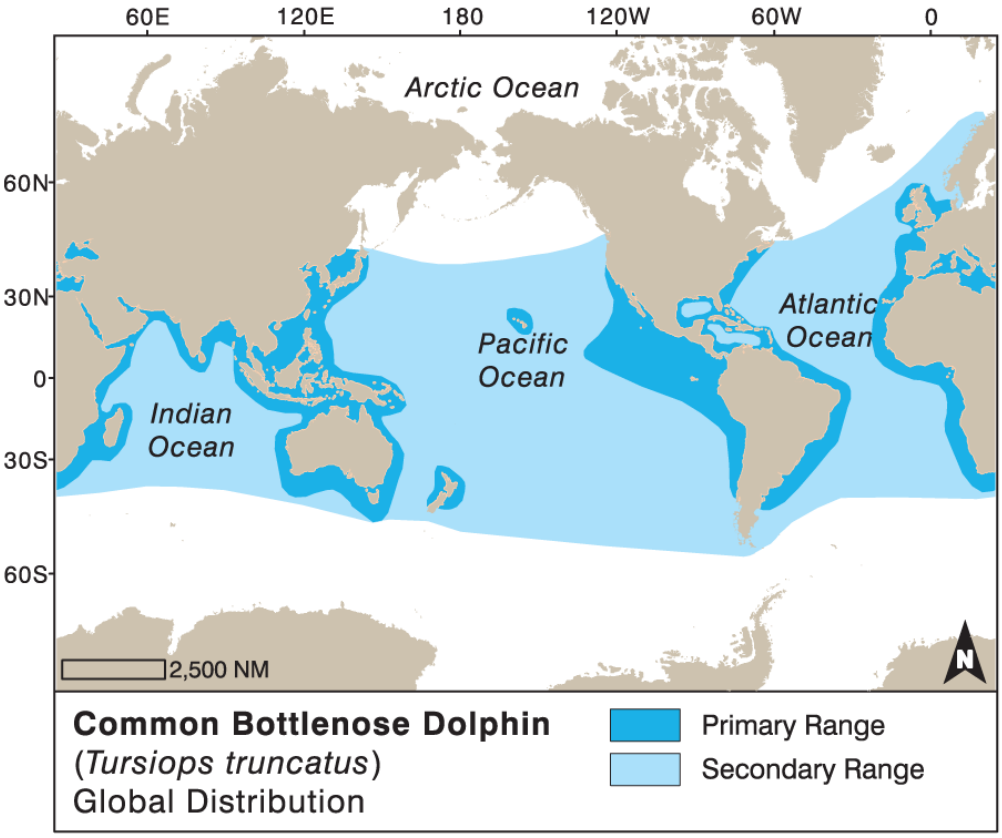

Figure 1.5 Global distribution of common bottlenose dolphins (*Tursiops truncatus*). Map sourced from Jefferson et al. 2008.

1.2.3.1 Bottlenose dolphin distribution

Bottlenose dolphins are widely distributed around the world, inhabiting waters ranging in temperature from approximately 10 to 32° C (Wells & Scott 2009). They are found in all of the world's major oceans and occur in most enclosed or semi-enclosed seas including the Mediterranean Sea (Bearzi et al. 2009), North Sea (Hammond & Thompson 1991) and Gulf of Mexico (Leatherwood 1975). The species is not typically found poleward of 45° (Jefferson et al. 2008); although there are some exceptions. Bottlenose dolphins have been recorded in the southern Okhotsk Sea in the North Pacific (Jefferson et al. 2008), and off Canada (Leatherwood et al. 1976), Norway (McBrearty et al. 1986) and Scotland (Evans 1980; Cheney et al. 2013) in the North Atlantic. In the southern hemisphere, bottlenose dolphins are known from the cool waters of Tierra del Fuego, Argentina (Wells & Scott 1999) in the South Atlantic and Fiordland, New Zealand in the South Pacific (Webb 1973; Currey et al. 2008).

Coastal bottlenose dolphins occur in three geographically discrete populations in New Zealand waters (Baker et al. 2010), with low levels of gene flow among them (Tezanos-Pinto et al. 2009). The three main areas for these populations are 1) off the northeastern coast of the North Island (Constantine 2002), 2) centred around the Marlborough Sounds (Merriman et al. 2009) and 3) Fiordland (Webb 1973) regions of the South Island. The North Island population is known to primarily range from Doubtless Bay to Tauranga on the east coast of the North Island (Constantine 2002), although infrequent sightings of known individuals outside of these areas has more recently extended the known range to the west coast of the North Island (Tezanos-Pinto et al. 2013). Research on the North Island population has focused on the Bay of Islands region, an area in which tourism is highly developed (Constantine 2001; Constantine et al. 2004). Consequently, while the North Island population has been extensively studied within the confines of the Bay of Islands, prior to the work in this thesis (Dwyer et al. 2014a; Chapter 5) only one species-specific study (Berghan et al. 2008) had been published to represent other regions within the greater home range of the population. From the work conducted herein, it appears that Great Barrier Island in the outer Hauraki Gulf is also an important region for North Island bottlenose dolphins that has been overlooked until recently.

1.2.3.2 Bottlenose dolphin habitat use

Bottlenose dolphins occupy a wide range of habitats from pelagic waters to shallow coastal areas, estuaries, river mouths, and deep fiords (e.g. Williams et al. 1993; Zolman 2002; Ingram & Rogan 2002; Bearzi 2005; Chabanne et al. 2012). Their diverse range of foraging techniques and prey species (Connor et al. 2000) allow them to exploit these different habitats. For example, in Shark Bay, Western Australia, bottlenose dolphins use sponges as a tool to protect their rostrum while probing the benthos for prey (Smolker et al. 1997; Mann et al. 2008). Other populations intentionally strand to capture fish chased onto shore (e.g. Silber & Fertl 1995).

Bottlenose dolphins also respond to food patches created by humans (Chilvers & Corkeron 2001; Ansmann et al. 2012), as demonstrated by trawler foraging in Moreton Bay, Australia (Corkeron et al. 1990).

Bottlenose dolphin habitat use has been extensively studied in relation to environmental variables and occurrence is often highly correlated with water depth, with the species often found year-round in shallow waters (e.g. Cañadas et al. 2002; Bearzi 2005; Blasi & Boitani 2012). There is evidence for increased use of steep slope areas which have been suggested to aid dolphins in their foraging activities (Ingram & Rogan 2002; Cañadas et al. 2005), and relationships with SST and chlorophyll concentrations have been documented (Barco et al. 1999; Torres et al. 2008). Additionally, temporal variation in occurrence has been recorded in many regions, such as the Moray Firth, Scotland, where numbers have been shown to peak in summer and autumn (Wilson et al. 1997). Temporal variation in habitat use has also been reported for bottlenose dolphins (Chilvers et al. 2003), with use of deeper waters during warmer months and shallower waters during cooler months off the northeast coast of the North Island, New Zealand (Dwyer et al. 2014a; Hartel et al. 2014).

Biological factors affecting habitat use by bottlenose dolphins have been widely studied. Following examination of the effects of food availability and risk of predation on habitat use in Shark Bay, Australia, Heithaus & Dill (2002) suggested that bottlenose dolphin distributions reflected a trade-off between food availability and tiger shark (*Galeocerdo cuvier*) predation risk. The effects of group composition have been investigated and groups containing calves are typically recorded using shallower waters than groups without calves (Mann et al. 2000; Hartel et al. 2014). Anthropogenic disturbances may also affect habitat use, for example Allen (2000) suggested that dolphins near Clearwater, Florida, USA decreased their use of primary foraging areas during times of high boat density. In the Mediterranean Sea, bottlenose dolphins appeared to be more attracted to a particular region following the installation of a fish farm that may have increased foraging opportunities (Diaz López et al. 2005).

In New Zealand, habitat use patterns vary among the different populations and habitats that they use. The Fiordland population in Doubtful Sound uses inner fiord sites most often in summer and autumn, and outer fiord sites during winter and spring (Elliott et al. 2011). In contrast, the North Island population uses inshore waters more during winter and spring and can be found further offshore during summer and autumn (Dwyer et al. 2014a; Hartel et al. 2014). Reasons for these seasonal variations have been tentatively attributed to changes in prey distribution at both locations, and/or avoidance of lower water temperatures in winter by calves for the Fiordland dolphins. Conversely, seasonal variation in habitat use was not detected for the Marlborough Sounds population (Merriman 2007).

1.3 Conservation and management

The Department of Conservation (DOC) is the regulatory body responsible for the management of marine mammal species in New Zealand waters. DOC administers the New Zealand Threat Classification System (Townsend et al. 2008) that was developed to list species according to their threat of extinction (Molloy et al. 2002). The New Zealand system is intended to complement the IUCN Red List by providing a more sensitive classification that takes into account the small size of New Zealand, the period over which recent declines have occurred, and the small population sizes and restricted ranges of many of the New Zealand taxa (Molloy et al. 2002). The latest available conservation assessment of New Zealand marine mammals was conducted in 2009 (Baker et al. 2010) using the New Zealand Threat Classification System (Townsend et al. 2008).

Common dolphins are listed under a variety of criteria in the IUCN Red List of Threatened Species depending upon the (sub)species or subpopulation. The short-beaked form (*D. delphis*) is classified as 'Least Concern' (Hammond et al. 2008a), with the exception of the Mediterranean subpopulation that is listed as 'Endangered' (Bearzi 2003) and the Black Sea common dolphin (*D. delphis* ssp. *ponticus*) that is 'Vulnerable' (Birkun Jr. 2008). The long-beaked form (*D. capensis*) is classified as 'Data Deficient' (Hammond et al. 2008b). In New Zealand, common dolphins are currently listed as 'Not Threatened' under the New Zealand threat classification system (Baker et al. 2010), although are acknowledged as 'data poor'. While the species has been reported in New Zealand waters since as early as 1884 (Hector 1884), no studies have focused on their nation-wide distribution, density or abundance. From a conservation perspective, this is an issue because these basic data requirements are imperative to appropriately manage the species. Changes in density or abundance of species can highlight causes for concern, as evident for short-beaked common dolphins in the Mediterranean Sea. A marked decrease in encounter rates from 2.18 to 0.40 encounters per 100 km was detected over the period 1997 to 2003 and was attributed to prey depletion (Bearzi et al. 2005). Consequently, and combined with reported declines in the Adriatic, Balearic and Ligurian Seas, the Mediterranean subpopulation was classified as 'Endangered' by the IUCN in 2003 (Bearzi 2003).

Currently, common dolphins remain the only resident delphinid in New Zealand waters to lack management under a species-specific action plan (Suisted & Neale 2004). This is problematic given this species is known for by-catch in the jack mackerel fishery (Stockin & Orams 2009; Berkenbusch et al. 2013; Thompson et al. 2013), is subject to set net entanglement (Stockin et al. 2009b) and is affected adversely by a range of other human activities including tourism (Stockin et al. 2008c) and pollution (Stockin et al. 2007). Given the paucity of demographic data, Stockin (2008) argued that a more appropriate New Zealand Threat Classification System listing for common dolphins would be 'Data Deficient'.

Globally, Bryde's whales are listed as 'Data Deficient' in the IUCN Red List of Threatened Species since the taxonomy of the species remains unresolved (Reilly et al. 2008). Locally, Bryde's whales were listed as 'Nationally Critical' under the New Zealand Threat Classification System in 2002 (Hitchmough 2002) and retained that status following the most recent conservation assessment of marine mammals (Baker et al. 2010). The reasons for this were the small population size and limited distribution of Bryde's whales in New Zealand waters (Baker et al. 2010). Mark-recapture abundance estimates for the Hauraki Gulf for the period 2003–2006 indicated a small population size of $n = 159$ ($CV = 0.35$) using a closed population model and $n = 46$ ($CV = 0.08$) using an open population model (Wiseman 2008). A more recent estimate (Tezanos-Pinto & Stockin 2014) concurs with a small population size of fewer than 120 whales using the Hauraki Gulf.

One of the most significant threats to Bryde's whales using Hauraki Gulf waters is the high level of mortality due to ship strike (Stockin et al. 2008b; Wiseman 2008; Behrens 2009; Constantine et al. 2015). Of the Bryde's whale carcasses collected between 1996 and 2014 for which the cause of death could be determined, vessel strike was attributed to 85% of cases — a mortality rate that is considered to be unsustainable (Constantine et al. 2015). A recent study used tagging information to determine that the whales spent 91% of their time at depths where the risk of collision with large vessels is most likely to occur (Constantine et al. 2012). Additionally, spatial analyses of whale sighting data by Riekkola (2013) indicated that the areas of the Hauraki Gulf with the highest probability of encountering whales were also the areas with the highest levels of vessel traffic. Diverting the shipping routes does not appear to be a viable management option (Riekkola 2013), instead conservation efforts are currently focused on reducing the speed of ships transiting through the Hauraki Gulf (Constantine et al. 2012). Overseas research has shown that the probability of a lethal injury to a whale from a vessel collision decreases with decreased vessel speed (e.g. Vanderlaan & Taggart 2007). A voluntary protocol is currently in place to reduce the risk of collisions with whales by encouraging ships to reduce their speed when transiting the Hauraki Gulf (Ports of Auckland 2013).

The global conservation status of bottlenose dolphins is low risk 'Least Concern' (Hammond et al. 2012). Under the New Zealand Threat Classification System, the species was listed as 'Not Threatened' up until 2002 (Hitchmough 2002) and subsequently up-listed to 'Range Restricted' in 2005 (Hitchmough et al. 2007). A further reclassification to 'Nationally Endangered' in 2009 (Baker et al. 2010) was based on apparent declines in abundance in two of the three coastal populations, coupled with reports of high calf mortality (Currey et al. 2009a; Tezanos-Pinto et al. 2013). The Fiordland population was also recognised as 'Critically Endangered' by the IUCN (Currey et al. 2011) based on the reduction in population size, geographic range and probability of extinction (Currey et al. 2009b). The abundance of the

Marlborough Sounds population has not been reassessed since it was first estimated using photo-identification data collected between 2003 and 2005 (Merriman et al. 2009); therefore, population trends for that region are currently unknown.

As already highlighted in this chapter, the Hauraki Gulf is important for common and bottlenose dolphins and Bryde's whales. The Hauraki Gulf Marine Park Act (HGMPA 2000) is legislation that recognises the significance of the Hauraki Gulf region and management objectives include protecting the life-supporting capacity and natural and physical resources of the Hauraki Gulf environment (HGMPA 2000). In order to follow this mandate, New Zealand's first marine spatial plan was commissioned in 2013 for the 1.2 million hectare Hauraki Gulf Marine Park (Fig. 1.6).

Figure 1.6 The Hauraki Gulf Marine Park, Tikapa Moana Te Moananui a Toi. The white dashed line indicates the boundary of the marine park. Map source: www.seachange.org.nz

The Hauraki Gulf marine spatial plan, named 'Sea Change — Tai Timu Tai Pari' (hereafter referred to as Sea Change), is currently under development until 2015. According to Ehler & Douvere (2009), marine spatial planning (MSP) is defined as "*a public process of analysing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic, and social objectives that are* *usually specified through a political process*." Sea Change aims to better understand the pressures on the Hauraki Gulf and identify long term solutions in order to improve the ecology and economy of the Gulf. Although the plan itself will not be legally binding, it is purported to provide a strong framework to guide the management of the Hauraki Gulf and help shape future statutory plans. A diverse range of stakeholders are part of Sea Change, including DOC.

1.4 Thesis rationale and structure

Within the Hauraki Gulf, cetaceans are exposed to a variety of anthropogenic impacts, including pollution (Stockin et al. 2007; Young & Adams 2010), tourism (Stockin et al. 2008c), fisheries by-catch (Stockin et al. 2009b) and ship strike (Stockin et al. 2008b; Behrens 2009; Martinez & Stockin 2013; Riekkola 2013; Dwyer et al. 2014b). To understand the potential effects of these anthropogenic threats, insight into the distribution, density and habitat use of the cetaceans using the Hauraki Gulf is required. This is particularly pertinent given the importance of the region for feeding (Wiseman 2008; Stockin et al. 2009a) and nursery groups (Stockin et al. 2008a; Wiseman 2008; Dwyer et al. 2014a) of common and bottlenose dolphins and Bryde's whales. However, spatial information for the Hauraki Gulf is lacking for common and bottlenose dolphins and currently restricted to data collected from platforms of opportunity for Bryde's whales.

This research aims to address these management requirements by investigating the distribution, density and habitat use of common and bottlenose dolphins and Bryde's whales using inner and outer Hauraki Gulf waters. A dedicated research vessel was used and surveys were focused in Great Barrier Island waters for the first time. Additionally, a novel approach for modelling distribution and habitat use of cetaceans while simultaneously accounting for imperfect detection was investigated with occupancy models. Finally, in light of the declines in abundance of two of the New Zealand populations (see Section 1.3) and the absence of prior knowledge of bottlenose dolphins using Great Barrier Island waters, abundance and demographic parameters were estimated and site fidelity was assessed.

This thesis comprises four research chapters (Chapters 2–5) with a general introduction (Chapter 1) and a general discussion (Chapter 6) chapter. Each research chapter has been written in publication format and represents a manuscript that is either published (Chapter 5) or in preparation for publication (Chapters 2–4). As such, the format resulted in some unavoidable repetition; however, this has been minimised where possible. The scope of each chapter is as follows:

Chapter 1 contains background information relating to the themes of this thesis, i.e. distribution and habitat use, and their importance for conservation. The concept of imperfect detection and its relevance in distribution ecology is also introduced. A literature review of the global distribution and habitat use of the three focal species (i.e. common dolphin, Bryde's whale and bottlenose dolphin) of this thesis is presented, followed by an overview of the conservation and management of these species in the context of the Hauraki Gulf Marine Park.

Chapter 2 describes the geographic distribution and density patterns of common dolphins, Bryde's whales and bottlenose dolphins in inner and outer Hauraki Gulf waters. Data were collected year-round during a three year study in the inner Hauraki Gulf (2010–2012) and a concurrent two year study off the west coast of Great Barrier Island in the outer Hauraki Gulf (2011–2012). Relative densities were examined seasonally by assessing changes in the number of groups and individuals encountered. A geographic information system (GIS) was used to further examine temporal and spatial trends by conducting kernel density analyses. Data collection and analyses were performed by S.L. Dwyer. The chapter was written by S.L. Dwyer and improved by edits and suggestions provided by D.M. Clement and K.A. Stockin.

Chapter 3 investigates habitat use by common dolphins, Bryde's whales and bottlenose dolphins in the inner and outer Hauraki Gulf. Spatial and environmental variables that may be important predictors of occurrence were examined using GLMs and GAMs. From these models, predictive maps depicting the probability of encountering these species in the Hauraki Gulf are presented. Additionally, the inclusion of behavioural data to help further explore habitat use was conducted for feeding and nursery groups. Data for this chapter were collected by S.L. Dwyer.

Assistance with modelling was kindly provided by M.D.M Pawley. The chapter was written by S.L. Dwyer and improved by edits and suggestions provided by M.D.M. Pawley, D.M. Clement and K.A. Stockin.

Chapter 4 assesses the feasibility of using a novel approach, i.e. occupancy models, for modelling cetacean distribution and habitat use. This method simultaneously models the probability of occurrence and probability of detection, and was applied to common dolphin data collected in the inner Hauraki Gulf by S.L. Dwyer. The spatial predictions of the occupancy models were compared with those of the GLMs presented in Chapter 3. Data analysis was performed by S.L. Dwyer, following advice kindly provided by D. MacKenzie and D.M. Clement. The chapter was written by S.L. Dwyer and improved by edits and suggestions provided by D.M. Clement and K.A. Stockin.

Chapter 5 evaluates the importance of the Great Barrier Island region for bottlenose dolphins. Group dynamics were examined in relation to group composition. Photographic mark-recapture methods were used to investigate individual site fidelity to the region. Abundance and demographic parameters were also estimated. This chapter is a reformatted version of a paper published in *Endangered Species Research*, co-authored with G. Tezanos-Pinto, I.N. Visser, M.D.M Pawley, A.M. Meissner, J. Berghan and K.A. Stockin. Data for this chapter were collected by S.L. Dwyer between January 2010 and January 2013 during Hauraki Gulf surveys. Photographic data from regions outside of the Hauraki Gulf were provided by A.M. Meissner and I.N. Visser. Group dynamics and site fidelity analyses were conducted by S.L. Dwyer, and assistance with abundance estimation was kindly provided by G. Tezanos-Pinto. The manuscript for this chapter was written by S.L. Dwyer, with specific sections of the methodology text relating to abundance estimation contributed by G. Tezanos-Pinto. The manuscript was improved by edits and suggestions provided by all co-authors.

Chapter 6 concludes by synthesising the findings of the research chapters for each species. The significance of the research is placed into context for conservation management.

Chapter 2

Distribution and relative density of cetaceans in the Hauraki Gulf

Common dolphin (*Delphinus* sp.), Bryde's whale (*Balaenoptera edeni*) & bottlenose dolphin (*Tursiops truncatus*) in the Hauraki Gulf. Photos: Sarah Dwyer.

2.1 INTRODUCTION

Understanding the distribution or geographical range of a species is a key factor when attempting to prioritise conservation initiatives (Ando et al. 1998; Brooks et al. 2001; Fortin et al. 2005). Knowledge of a species' distribution is vital for a number of reasons, particularly in applied conservation. Quantitative characterisation of a species' geographic range is necessary to determine the effects of climate change on populations, such as assessing the probability of species extinctions (Moreno-Rueda et al. 2012). In the marine environment, marine spatial planning (MSP) relies on an understanding of the spatial and temporal distribution of organisms in conjunction with the distribution of human activities (Ehler & Douvere 2009) in order to manage environmental protection alongside a range of human activities (Day 2008).

New Zealand's first marine spatial plan is currently being developed for the Hauraki Gulf, North Island. The Hauraki Gulf, part of the wider Hauraki Gulf Marine Park, is a highly productive marine ecosystem (Booth & Søndergaard 1989; Chang et al. 2003; Hauraki Gulf Forum 2011) that provides a number of ecosystem services such as the nursery role played by seagrasses and mangroves (MacDiarmid et al. 2013). The Gulf has been identified as a significant area for a range of apex predators, including seabirds (Machovsky Capuska et al. 2011; Gaskin & Rayner 2013) and marine mammals (Visser 1999; O'Callaghan & Baker 2002; Berghan et al. 2008; Stockin et al. 2008a; Wiseman et al. 2011). However, spatial distribution patterns of cetaceans using the Hauraki Gulf are not well understood.

Our preliminary understanding of the distribution of the three most frequently sighted cetacean species (common dolphin (*Delphinus* sp.), Bryde's whale (*Balaenoptera edeni*) and bottlenose dolphin (*Tursiops truncatus*)) of the Hauraki Gulf comes from previous studies conducted primarily within inner Hauraki Gulf (IHG) waters (see Fig. 2.1 for the inner and outer Hauraki Gulf boundary). Common dolphin studies to date have primarily focused on behaviour (Schaffar 2004; Stockin et al. 2009a; de la Brosse 2010), anthropogenic effects (Stockin et al. 2007; 2008c; 2009b; Martinez & Stockin 2013) and ecology (Burgess 2006; Stockin et al. 2008a; Petrella et al. 2012). The occurrence of common dolphins in the IHG has been described in relation to environmental parameters (Stockin et al. 2008a); however, spatial distribution and density have not been previously assessed. The same parameters remain unexamined for bottlenose dolphins using Hauraki Gulf waters, with only one species-specific study published for the IHG region that focused on individual photo-identification (Berghan et al. 2008). The distribution of Bryde's whales in the Hauraki Gulf has been assessed in a number of studies; however, these were mainly restricted to using data collected from platforms of opportunity that had limited operating ranges that did not include Firth of Thames or Great Barrier Island waters (Behrens 2009; Wiseman et al. 2011; Riekkola 2013).

Great Barrier Island, the largest of New Zealand's northern offshore islands (285 km^2), is located in the outer Hauraki Gulf (see Fig. 2.1). Previously, dedicated marine mammal research conducted in the Great Barrier region has been limited to baleen whale acoustics (Kibblewhite et al. 1967; Helweg 1998; McDonald 2006). Aerial surveys for Bryde's whales were conducted in northeastern New Zealand waters between 1999 and 2003 (Baker & Madon 2007), with a small portion of the Hauraki Gulf transects covering waters off the west coast of Great Barrier Island. No delphinid studies have been conducted in the area, possibly due to the logistical constraints of fieldwork in this comparatively remote location of the Hauraki Gulf. As such, no information was available within the scientific literature describing dolphins off the coast of Great Barrier Island prior to this study and information for Bryde's whales remains limited.

In order to assess spatial distribution and density patterns of cetaceans using the Hauraki Gulf, dedicated boat-based surveys were conducted in inner and outer Gulf waters, the latter off the west coast of Great Barrier Island. The overall aim was to define areas that may be of particular importance for some species and provide new information about previously unstudied regions, such as the Firth of Thames and Great Barrier Island, that may warrant further dedicated surveys. Great Barrier Island was chosen as the study site for the outer Hauraki Gulf for practicality reasons due to the logistics of conducting small boat surveys in offshore environments. By conducting surveys during a concurrent time period in the IHG and at Great Barrier Island, distribution and density patterns could be compared between these regions.

The objectives of this chapter were to describe the geographic distribution and density patterns of common and bottlenose dolphins and Bryde's whales occurring in both inner and outer Hauraki Gulf waters by:

- Investigating temporal relative densities in relation to the number of groups and individuals encountered at a seasonal level; and
- Describing any patterns in spatial distribution and relative density.

2.2 MATERIALS AND METHODS

2.2.1 Study area

The Hauraki Gulf is a relatively shallow, semi-enclosed body of water on the northeast coast of the North Island, New Zealand (Fig. 2.1; Manighetti & Carter 1999; Black et al. 2000). The Gulf is landlocked to the west and south, partially enclosed to the east by the Coromandel Peninsula and Great Barrier Island, and exposed to the north. Water circulation in and out of the Hauraki Gulf is via three channels; Jellicoe Channel between the mainland and Little Barrier Island, Cradock Channel between the Barrier Islands, and Colville Channel between Great Barrier Island and the northern Coromandel Peninsula (Fig. 2.1). The Hauraki Gulf contains a diverse range of marine habitats from open ocean environments to shallow bays, inlets and the intertidal flats of the Firth of Thames (Hauraki Gulf Forum 2011).

The dividing line between inner and outer Hauraki Gulf waters has been variously defined in previous studies as: a line between Cape Rodney and Cape Colville (Paul 1968; Berghan et al. 2008), a latitude line parallel with the northern tip of the Coromandel Peninsula (Greig & Proctor 1988), or a line between Takatu Point and the tip of the Coromandel Peninsula (Wiseman et al. 2011). Based on the operating limits of the research vessel in the first year of data collection, the delineating line in this study was between Takatu Point on the mainland and Kaiiti Point on the Coromandel Peninsula (Fig. 2.1), i.e. the same as Wiseman et al. (2011).

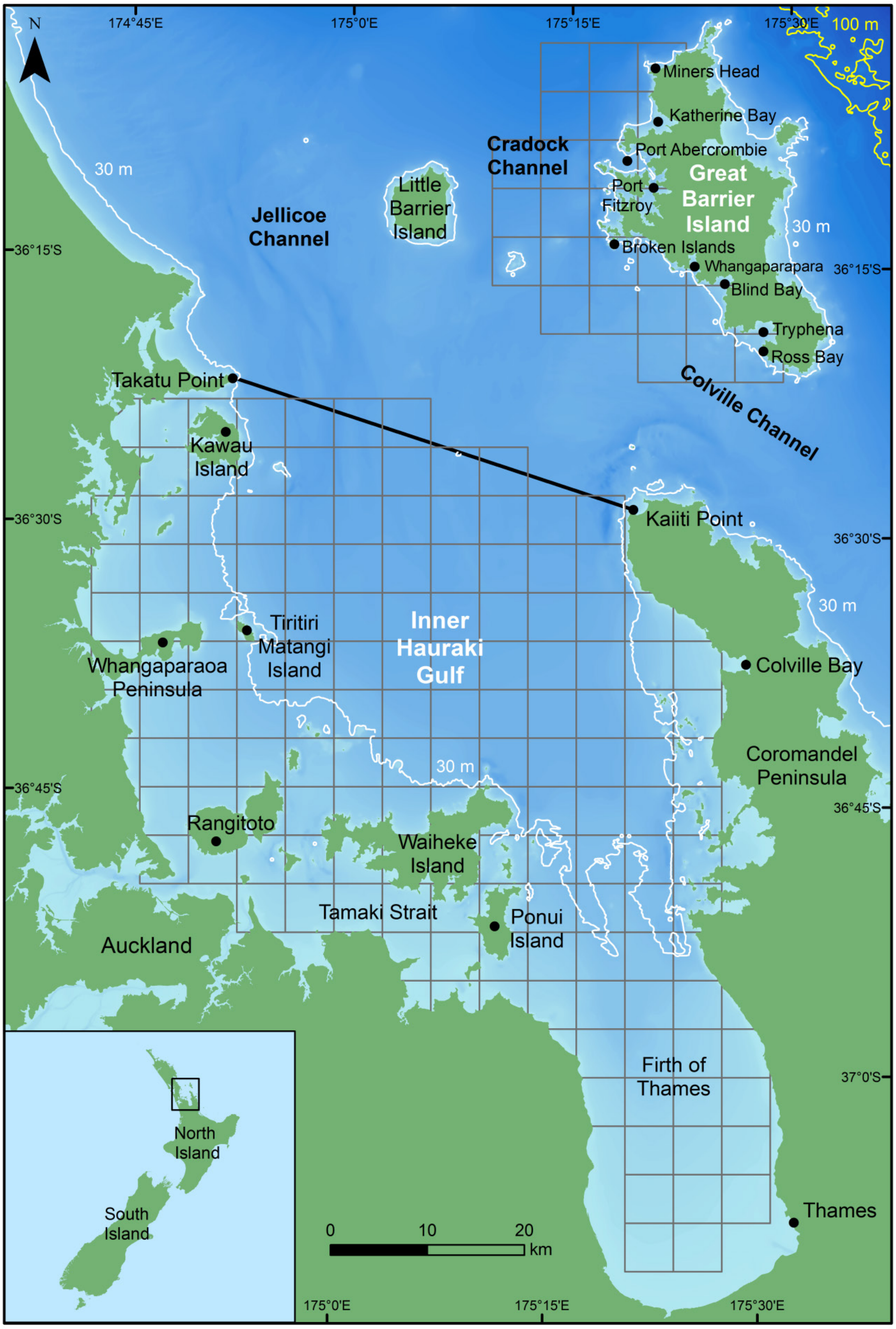

Figure 2.1 Map of the Hauraki Gulf, New Zealand. The solid black line (from Takatu Point to Kaiiti Point) indicates the boundary between the inner and outer Hauraki Gulf, the white lines show the 30 m isobath and the yellow lines the 100 m isobath. Bathymetry is depicted with darker shades of blue representing deeper waters; data courtesy of NIWA (Mackay et al. 2012). 5 x 5 km grid cells are shown in grey. Inset: Location of the Hauraki Gulf, North Island, relative to New Zealand.

The IHG is adjacent to Auckland city, New Zealand's largest urban area, and also borders a number of other urbanised regions (Edbrooke et al. 2003). The IHG sampling area included all waters south of the delineating line (Fig. 2.1; see Section 2.2.3.2), including the southerly reaches of the Firth of Thames, and covered 3480 km^2. Approximately 40% of the IHG consists of waters less than 20 m deep, while 30% falls within the 20 to 40 m depth contours (Paul 1968). Great Barrier Island (GBI) is situated in the outer Hauraki Gulf, approximately 80 km northeast of Auckland city (Fig. 2.1). The 542 km^2 study site[1] in the outer Gulf mainly incorporated the coastal waters off the western side of GBI, i.e. all waters between Miners Head in the north and Ross Bay in the south, up to a distance of 10 km offshore (Fig. 2.1). The west coast of GBI is characterised by numerous shallow embayments and a predominantly rocky shoreline. GBI has a low human population density, with 68% of the land administered by DOC (Norgrove & Jordan 2006). Most of the west coast remains uninhabited. Off the west coast of GBI, water depths reach up to 100m.

Circulation in the Hauraki Gulf is strongly influenced by surface winds and their interaction with tidal currents, in addition to physical barriers such as headlands and islands that enhance local upwellings (Black et al. 2000). SST typically ranges from 12.5 to 22° C across the Hauraki Gulf (Paul 1968). Warm waters from the East Auckland Current (EAUC) flow into the northerly entrance of the Hauraki Gulf during summer and autumn, when easterly winds and downwellings are more prevalent (Zeldis et al. 2004). Westerly winds that are favourable for upwellings prevail in late winter and spring (e.g. Chang et al. 2003; Zeldis et al. 2004). Since seasonal upwellings are responsive to the wind, hydrodynamics are largely affected by broad-scale variability in climate conditions, namely the influence of the El Niño Southern Oscillation (ENSO).

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[1] The study site was limited to the research vessel operating area, which was permitted in accordance with the Maritime New Zealand Safe Ship Management (SSM) system for commercial vessels. For GBI, the operating area for the research vessel was restricted to waters off the western side of the island only.

2.2.2 Data collection

Marine mammal sighting data were collected during dedicated monthly boat surveys conducted between January 2010 and November 2012 from the Massey University research vessel *Te Epiwhania*, a 5.5 m Stabicraft boat powered by a 100 hp four-stroke engine (Fig. 2.2). A non-systematic survey design was employed in order to maximise survey effort, since the geography of the Hauraki Gulf would allow some areas but not others to be surveyed in certain weather conditions. Survey tracks and the direction of travel were selected based on prevailing weather and sea conditions, and on the extent to which any particular area had been previously surveyed within that month. The overall aim was to cover the study area as equally as possible each month. Surveys were conducted in conditions of Beaufort sea state 3 or less (see Section 4.2.2, Chapter 4 for further details). Time spent travelling along survey tracks actively searching for marine mammals, with vessel speed maintained at ~10 knots, was classified as *on effort*.

Figure 2.2 The Massey University research vessel *Te Epiwhania* used during this study. Photo: Karen Elliott

Starting in January 2011, monthly research trips averaging four days in duration were made to GBI when possible (i.e. when weather and sea conditions permitted).

Where feasible, routes were selected to achieve equal survey coverage of the west coast and to include both nearshore and offshore waters up to 10 km from land within any given month. Effort was also made to survey the latitudinal extent of the GBI west coast in order to cover both northern and southern regions in any given day.

While *on effort*, two experienced observers continuously scanned to the horizon in a 270° arc in front of and to the sides of the vessel. Dolphins and whales were detected by the naked eye and/or binoculars (10 x 50 magnification). Visual clues indicating cetacean presence included splashing, water disturbance and sighting of blows or dorsal fins (e.g. Stockin et al. 2008a; Wiseman et al. 2011). When the vessel left the survey track to approach cetaceans, the survey mode was *off effort* until returning to the track to resume searching. *Off effort* mode also included all other occasions when the vessel was away from the survey track (e.g. returning to harbour due to deteriorating sea conditions or collecting data on a sighting group).

When a cetacean group/individual was detected, the vessel stopped on the transect line to record the sighting cue and estimated distance to the sighting from the vessel. The distance was always estimated by the author to prevent inter-observer bias. The vessel subsequently left the track (i.e. *off effort*), approached to within 50 m of the group/individual, and commenced data collection. In accordance with the Marine Mammal Protection Regulations (Part 3, MMPR 1992), the research vessel was operated so as not to disrupt the normal movement or behaviour of any marine mammal. When the vessel was within 300 m of any marine mammal, the vessel was manoeuvred at a constant slow speed at idle or 'no wake' speed in such a way that no marine mammal was separated from a group or caused any members of such a group to be scattered. This involved approaching groups/individuals from behind and parallel to, and moving in the same direction as the group/individual (Stockin et al. 2008b). After observational data were logged, the vessel returned to the survey route and resumed *on effort* in order to continue searching for independent groups or individuals (i.e. spatially and/or temporally separated to prevent the same individuals becoming resampled (Stockin et al. 2009a)).

Water depth (± 0.1 metre) was measured using an on-board depth sounder at the location of the group when first sighted. All observational and environmental data were collected using an XDA Orbit II Windows Mobile device. CyberTracker version 3 software (Steventon et al. 2002) was programmed for logging observational data (e.g. group size) and to record the GPS position of the vessel every 60 seconds throughout the survey. Beaufort sea state was recorded every 15 minutes.

Group size was visually assessed and recorded for each encounter. A group of common or bottlenose dolphins was defined as any number of individuals observed in apparent association, moving in the same general direction and often, but not always, engaged in the same activity (Shane 1990). Groups were considered independent if they were encountered at a spatial or temporal scale that prevented the same individuals becoming resampled (Stockin et al. 2009a). Where feasible, this was additionally confirmed via photo-identification. A group of Bryde's whales was defined as the maximum number of individuals within 100 m of each other (Wiseman 2008). Group size was recorded at sea using minimum, maximum and best estimate counts (following Kiszka et al. 2007) and was later confirmed or amended using photo-identification data where applicable.

Photo-identification of individual animals was conducted following standard methods (Würsig & Jefferson 1990) using a Canon EOS 7D or 400D digital SLR camera fitted with 100–400 or 70–300 mm lenses, respectively. While photo-identification was attempted for all bottlenose dolphin groups, common dolphins and Bryde's whales were photographed only opportunistically to avoid prolonged periods away from the survey track.

2.2.3 Data analysis

2.2.3.1 General methods

Grids of 5 x 5 km cells were created for the IHG and GBI using the grid index features tool. Cell size was determined by the size of the study areas and the overall coverage of survey effort in order to ensure adequate spatial replication, i.e. that there were sufficient sampling occasions per grid cell for all analyses conducted in this thesis. This included following the recommendation for a minimum of three sampling occasions per grid cell for occupancy modelling (Chapter 4; MacKenzie & Royle 2005). The regions of land within cells were erased from all grid cells leaving the total area of water available to search for marine mammals as 3480 km^2 for the IHG and 542 km^2 for GBI.

Austral seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) to facilitate comparisons with previous studies on common dolphins (Stockin et al. 2008a), bottlenose dolphins (Berghan et al. 2008) and Bryde's whales (Wiseman et al. 2011) in the Hauraki Gulf. Only *on effort* sighting data were included in analyses and 'best estimate' group sizes were used unless otherwise stated.

SPSS version 20.0 (SPSS Inc., Chicago, Illinois, USA) was used for statistical analyses. Sighting data (see Sections 2.2.3.3–2.2.3.5) were initially tested for normality using the Shapiro-Wilk test. If the data passed the test of homogeneity of variances but the distribution of non-normal data did not improve following square root transformation, parametric techniques could still be used (Tiku 1971). However, if the data were non-normal and did not exhibit homoscedasticity, non-parametric techniques were applied. Where applicable, a series of Bonferroni or Dunn-Bonferroni *post hoc* tests were used. The significance level was set at 0.05.

2.2.3.2 Effort

Search effort was quantified by calculating the number of kilometres of effort per 5 x 5 km grid cell per survey day using ArcGIS version 10.0 (ESRI, Redlands, California, USA) and Geospatial Modelling Environment (GME) version 0.7.2.0 (Beyer 2012). The New Zealand Transverse Mercator (NZTM2000) projection was used for all GIS analyses.

Vessel tracks were downloaded from CyberTracker and processed as CSV files to remove all *off effort* portions of the tracks before importing into ArcMAP. Survey tracks were intersected by the respective grid polygons and the *sumlinelengthsinpolys* command in GME was used to calculate the amount of effort in kilometres in each grid cell. Any grid cell that contained less than 10 km of effort or was sampled on fewer than five occasions during the study period was removed from the analysis to ensure all grid cells contained enough sampling replicates for analyses (Chapters 3 & 4). Any sightings associated with those tracks were reclassified as *off effort*. Consequently, waters between the northern limit of the IHG and southerly boundary of the GBI study area did not receive sufficient survey effort to be included in analyses (see Appendix 2.1 for a map of the total *on effort* tracks). The Kolmogorov-Smirnov Goodness of Fit test was applied to the seasonal survey effort data to test whether effort was evenly distributed across grid cells.

2.2.3.3 Sightings and group sizes

All sighting data were exported from CyberTracker and added to a MySQL database. Queries on the sighting data were performed using the open source HeidiSQL management software.

In order to identify any potential outliers in the data for the three most frequently sighted cetacean species (i.e., the focal species; common and bottlenose dolphins and Bryde's whales), sighting distances were explored. Distances were binned into 200 m intervals and the cumulative frequency was calculated for each distance class and expressed as a percentage. The distances within which the majority of sightings (i.e. 95%) were reliably recorded were determined and subsequently used as the sighting limit. Any sightings detected at further distances were considered unreliable and were removed where applicable. Beaufort sea state was also expected to affect the distances at which sightings could be reliably detected. Scatterplots and boxplots were produced for each species to determine the frequency of each sighting distance for Beaufort sea states 0–3, in addition to identifying extreme outliers. Once completed, the HeidiSQL database was updated to account for data truncation. All *off effort* sightings and the outliers identified by the above assessments were removed from the final *on effort* dataset and stored in an *off effort* sightings database.

Sighting records of all cetaceans, both *on* and *off effort*, were collated. *On effort* group sizes of the three focal species were described at a seasonal level, primarily to help understand distribution and density patterns. A one-way ANOVA was used to test for seasonal differences in the average group size for each species. For common dolphins that showed the greatest variation in group size, groups were categorised as small (< 10 dolphins), medium (10–49 dolphins) and large (> 50 dolphins), in line with previous studies in the Hauraki Gulf (Stockin et al. 2008a; 2009a), for relating variation in group sizes to temporal relative densities.

2.2.3.4 Temporal relative density

The relative densities of common and bottlenose dolphins and Bryde's whales were assessed using sighting rate (SR) and encounter rate (ER) indices. These types of relative abundance indices have been used in a number of cetacean studies to make comparisons among different areas or monitor changes in populations over time (e.g. Bearzi et al. 2005; De Boer 2010; Filby et al. 2010; Blasi & Boitani 2012). SR (number of groups encountered per kilometre travelled) and ER (number of individuals encountered per kilometre travelled) were calculated using the ratio n / L, where n is the number of groups or individuals and L is the number of kilometres spent *on effort* (Forcada & Hammond 1998; Bearzi et al. 2005; Cañadas et al. 2005) within the study area. Both SR and ER were used in this study to facilitate comparisons with other studies that only used one of these indices. While Bryde's whale SRs and ERs were not expected to vary greatly due to primarily sighting singletons, both indices were included in analyses for consistency.

Seasonal SRs and ERs were calculated by combining the total number of sightings/individuals and the total number of kilometres for each austral season. The sampling variance of the seasonal sighting and encounter rates was calculated using the formula (Buckland et al. 1993, Bearzi et al. 2005)

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

where n is the total number of groups or individuals in a season, L is the total number of km spent on effort in a season, n_i is the number of groups or individuals in a survey day, l_i is the number of kilometres spent on effort in a survey day and k is the number of days surveyed in a season. Daily SR and ER values were weighted by the corresponding proportion of seasonal effort to test for significant temporal trends. Since data were non-normal and transformation did not improve normality or meet the assumption of equal variances, non-parametric Kruskal-Wallis tests were applied. Histograms were plotted to visually assess intra- and inter-annual patterns. Mean SR and ER values for each species and region were also calculated to enable comparisons with other studies.

To determine whether seasonal sighting data could be pooled across years for further analyses, inter-annual variation in SR and ER were tested for each species using ANOVAs or a non-parametric Mann-Whitney U test. The ranks of monthly SRs and ERs were tested for those months with data for all years, i.e. January–November for the IHG and January, March, April, May, August and October for GBI. If no significant differences among survey years were detected, data could be pooled for overall seasonal analyses (Clement 2005).

2.2.3.5 Spatial relative density

To examine seasonal trends in relative densities across the study area, kernel density estimates were calculated in ArcMAP using the Spatial Analyst tool *Kernel Density*. Kernel density estimates are often used to estimate the home ranges of animals (Moland et al. 2011; Monsarrat et al. 2013). Here, they were applied in the same manner as Hauser (2006) as a measure of relative space use. This method calculates a density value based on the value of each dolphin or whale sighting within each grid cell (standardised by number of individuals and effort) and is weighted by any sightings in neighbouring cells within a defined search radius (McCoy et al. 2001). Seasonal weighted values were obtained by standardising sightings by the total number of individuals and kilometres per 5 x 5 km grid cell for each season. Cell size for the kernel density estimation was set at 1 x 1 km and the search radius was set to 7.5 km (Euclidean distance) to limit searching to adjacent 5 x 5 km grid cells only. The smaller cell size selected for the kernel density estimation was to avoid creating an output raster that was a poor approximation to a continuous surface (Beyer 2012) but realistic for the scale of the sampling resolution. Scaling factors were constant within species and across study sites but not among species, therefore comparing relative density values for different species was not possible. The resulting kernel density maps were visually assessed in order to identify any high density regions, i.e. hotspots (Clement 2005).

Additionally, distance to shore was used to further describe the geographic distribution of cetaceans within the study areas. Distance to shore (km) was calculated using the ArcMap *near* tool to measure the distance to the nearest point of land. Seasonal differences in distances from shore were tested using a one-way ANOVA or a Kruskal-Wallis test if the assumption of equal variances was violated.

2.3 RESULTS

2.3.1 Effort

2.3.1.1 Inner Hauraki Gulf

From January 2010 until November 2012, 233 days of survey effort were conducted in the IHG. A total of 887.6 h were spent *on effort* searching for marine mammals, with 16,785.8 km of *on effort* tracks within the IHG grid cells that remained for analyses (Table 2.1, Fig. 2.3). An additional 555.9 h were spent *off effort* in the region — a combination of time spent making group observations, conducting photo-identification, travelling to or from the home port (Whangaparaoa, Fig. 2.1) of the research vessel etc.

Surveys were conducted in the IHG during every month of the study period. Effort was greatest in the first year of data collection and was approximately double that of the final two years (Table 2.1) when surveys were also being conducted at GBI. Not accounting for heterogeneity in spatial distribution, seasonal survey effort was relatively even for the first year, high in summer and lower in autumn of the second year and high in summer but lower in spring of the third year. Overall, the summer season received the most survey effort (Table 2.1).

Table 2.1 Seasonal survey effort in the inner Hauraki Gulf (IHG), New Zealand in 2010–2012. Year 1 = January–November 2010, Year 2 = December 2010–November 2011, Year 3 = December 2011–November 2012.

	Summer	**Autumn**	**Winter**	**Spring**	**TOTAL**
Survey days	67	53	60	53	**233**
km *on effort* Year 1	1953.2	2463.8	2029.7	2062.4	**8509.1**
km *on effort* Year 2	1723.6	483.3	916.0	1209.6	**4332.5**
km *on effort* Year 3	1368.3	1052.3	976.4	547.2	**3944.2**
TOTAL EFFORT (km)	**5045.1**	**3999.4**	**3922.1**	**3819.2**	**16785.8**

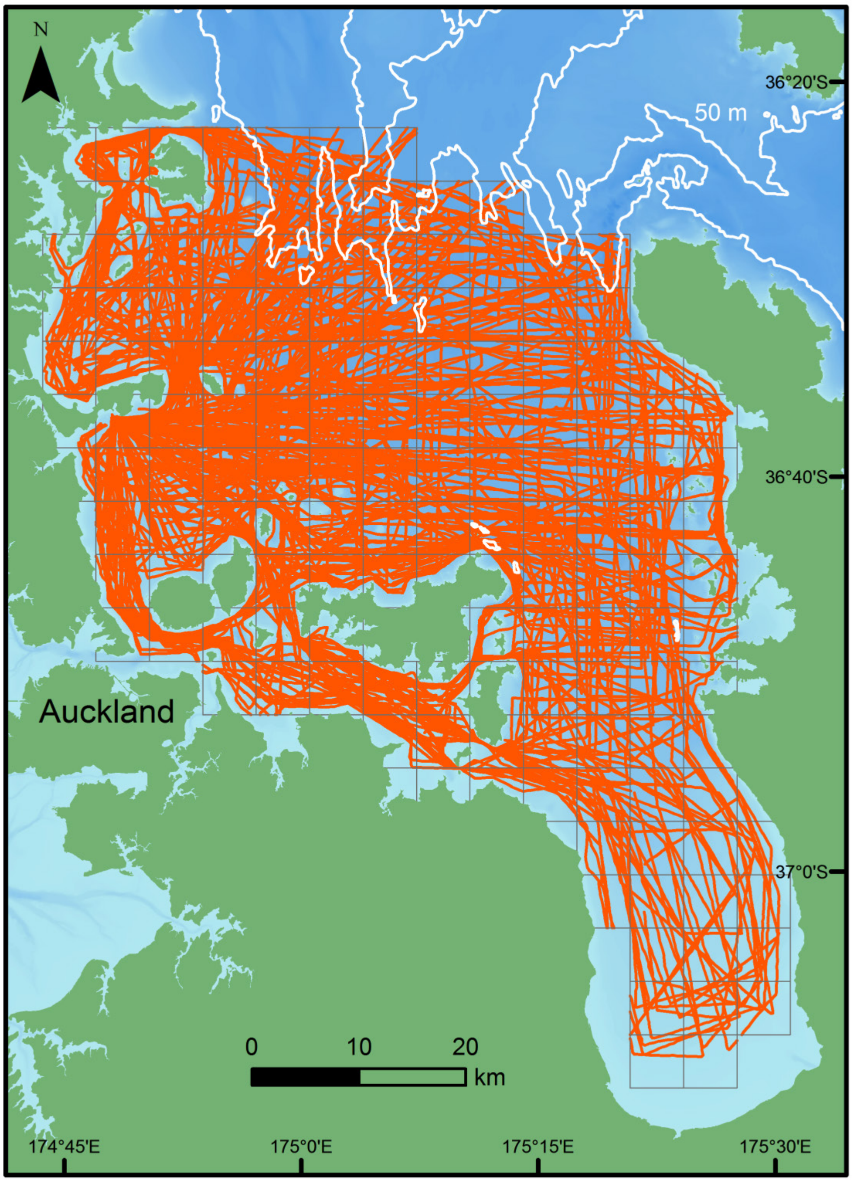

Figure 2.3 Search effort in the inner Hauraki Gulf (IHG), New Zealand in 2010–2012. Red lines represent *on effort* boat survey tracks and 5 x 5 km grid cells are shown in black. Bathymetry is depicted with darker shades of blue representing deeper waters, data courtesy of NIWA (Mackay et al. 2012). The 50 m isobath is shown in white.

When considering the total survey effort per grid cell, the distribution was non-uniform (one-sample Kolmogorov-Smirnov: Z = 3.201, $p < 0.001$; Fig. 2.4). Total effort per grid cell ranged from 10.1 to 282.4 km (median = 109.1, IQR = 69.6–147.8, n = 150). Typically, grid cells located furthest from the home port of the research vessel at Whangaparaoa (e.g. cells at the southern reaches of the Firth of Thames; see Fig. 2.1) received the lowest amount of effort. Survey effort was also non-uniformly distributed across all grid cells each season (one-sample Kolmogorov-Smirnov: Z = 11.658, $p < 0.001$; Fig. 2.4). Total effort per grid cell per season ranged from 0 to 114.9 km (median = 25.4, IQR = 15.8–38.0, n = 600). All 150 grid cells were sampled in winter and spring. However, in summer, four grid cells at the extremities of the survey area were not sampled and one grid cell received no survey effort in autumn.

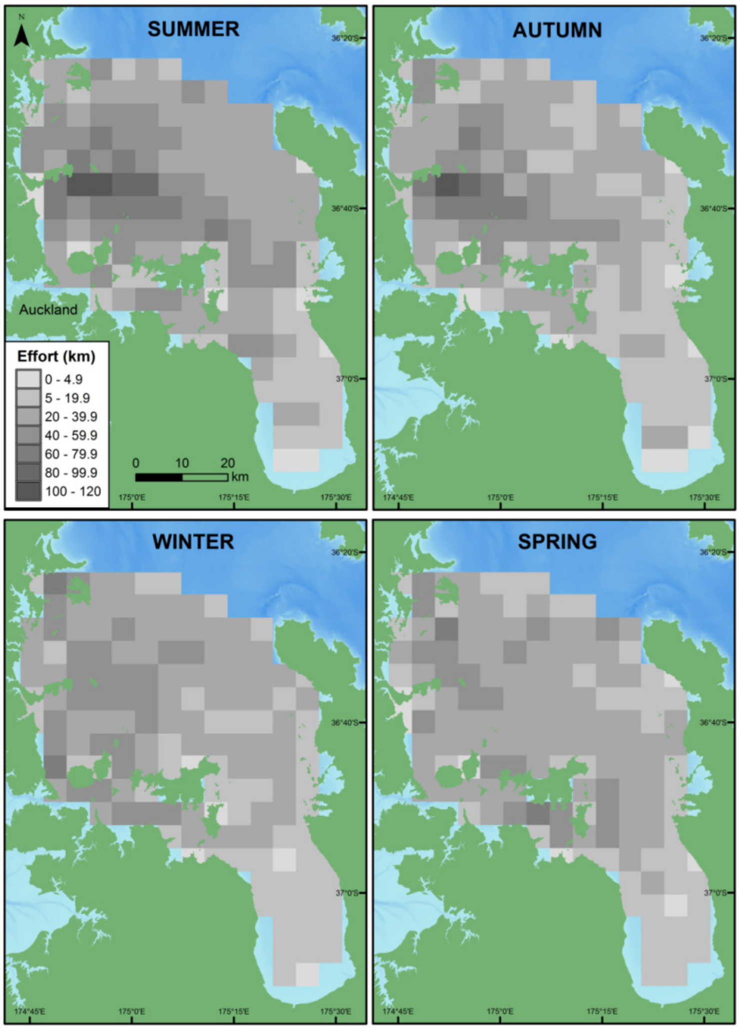

Figure 2.4 Distribution of seasonal survey effort in the inner Hauraki Gulf (IHG), New Zealand in 2010–2012. Bathymetry is depicted with darker shades of blue representing deeper waters, data courtesy of NIWA (Mackay et al. 2012).

2.3.1.2 Great Barrier Island

Between January 2011 and October 2012, a total of 243.9 h were spent *on effort* searching for marine mammals in the GBI study area (Fig. 2.5). The *on effort* survey tracks in the final GBI grid cells amounted to 4017.1 km (Fig. 2.5, Table 2.2). An additional 274.2 h were spent *off effort* in the region, while making group observations, conducting photo-identification, travelling to or from the island etc.

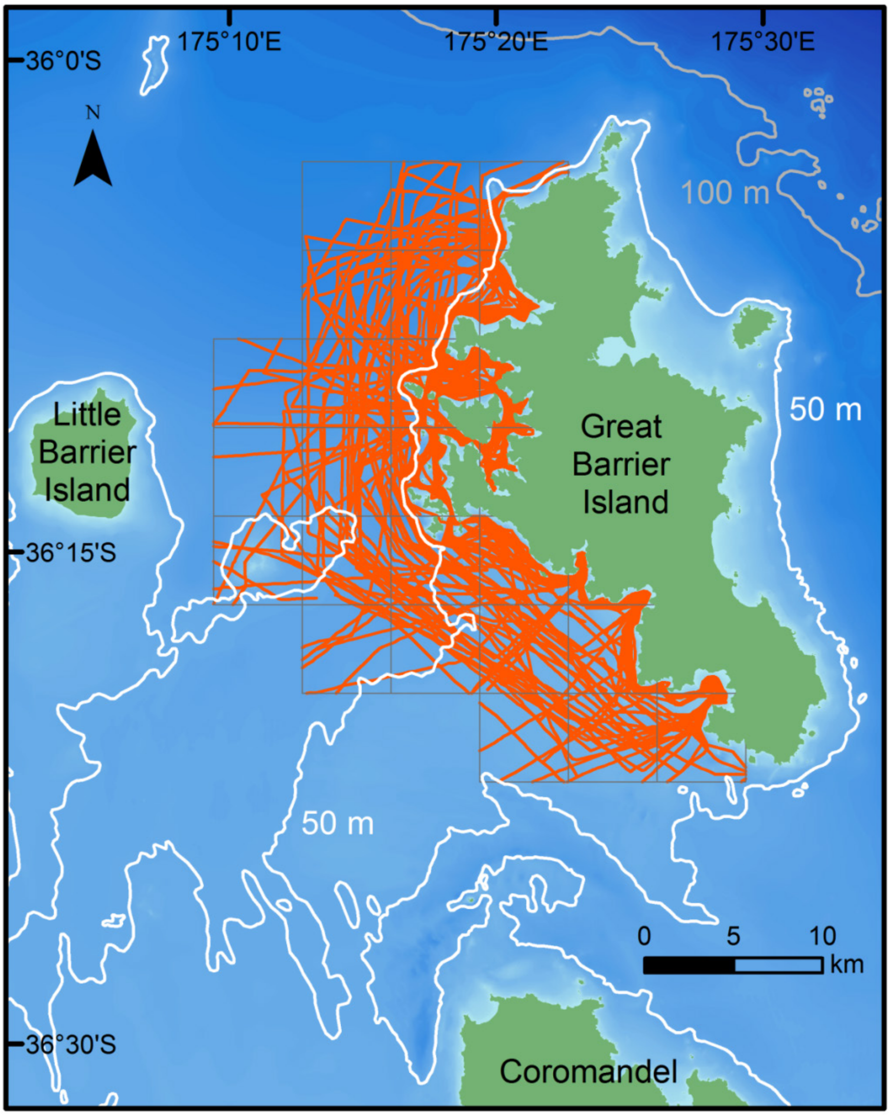

Figure 2.5 Search effort off the west coast of Great Barrier Island (GBI), New Zealand in 2011–2012. Red lines represent *on effort* survey tracks and 5 x 5 km grid cells are shown in black. Bathymetry is depicted with darker shades of blue representing deeper waters, data courtesy of NIWA (Mackay et al. 2012). The 50 m isobath is shown in white and the 100 m isobath in grey.

Surveys were conducted at GBI during nine months of the year for both 2011 and 2012. In 2011, surveys were carried out in January, March, April, May, July, August, October, November and December. In 2012, surveys were conducted in January, February, March, April, May, June, August, September and October. Although effort was approximately equally distributed across the two calendar years (2004.1 km in 2011 and 2012.9 km in 2012), effort was greater in summer 2011–2012 (841.7 km) compared with summer 2010–2011 (216.6 km; Table 2.2) due to surveying during three months during summer 2011–2012 (December–February) but only one month during summer 2010–2011 (January). Not accounting for the spatial distribution of effort, seasonal survey effort was relatively even across years for the other seasons (Table 2.2), with less effort recorded during spring of both years due to this being the windiest season in New Zealand (Renwick et al. 2010b).

Table 2.2 Seasonal survey effort at Great Barrier Island (GBI), New Zealand in 2011–2012. Year 2 = January 2011–November 2011, Year 3 = December 2011–October 2012. Note: surveys were not conducted at GBI during Year 1.

	Summer	**Autumn**	**Winter**	**Spring**	**TOTAL**
Survey days	16	22	18	12	**68**
km *on effort* Year 2	216.6	662.3	501.7	336.9	**1717.5**
km *on effort* Year 3	841.7	497.8	495.7	464.4	**2299.6**
TOTAL EFFORT (km)	**1058.3**	**1160.1**	**997.4**	**801.3**	**4017.1**

When considering the total survey effort per grid cell, the distribution was non-uniform (one-sample Kolmogorov-Smirnov: Z = 1.367, p = 0.048, Fig. 2.6). Total effort per grid cell ranged from 23.5 to 366.9 km (median = 126.5, IQR = 65.6–216.9, n = 27). Grid cells located furthest from the coast typically received the lowest amount of effort (Fig. 2.6). Survey effort was also not uniformly distributed across all grid cells each season (one-sample Kolmogorov-Smirnov: Z = 3.924, $p < 0.001$; Fig. 2.6). Total effort per grid cell per season ranged from 0 to 130.6 km (median = 31.6, IQR = 16.0–51.8, n = 108). Most grid cells were sampled during all seasons, with the exception of three grid cells at the extremity of the study area, one of which was not sampled during winter and two were not sampled during spring.

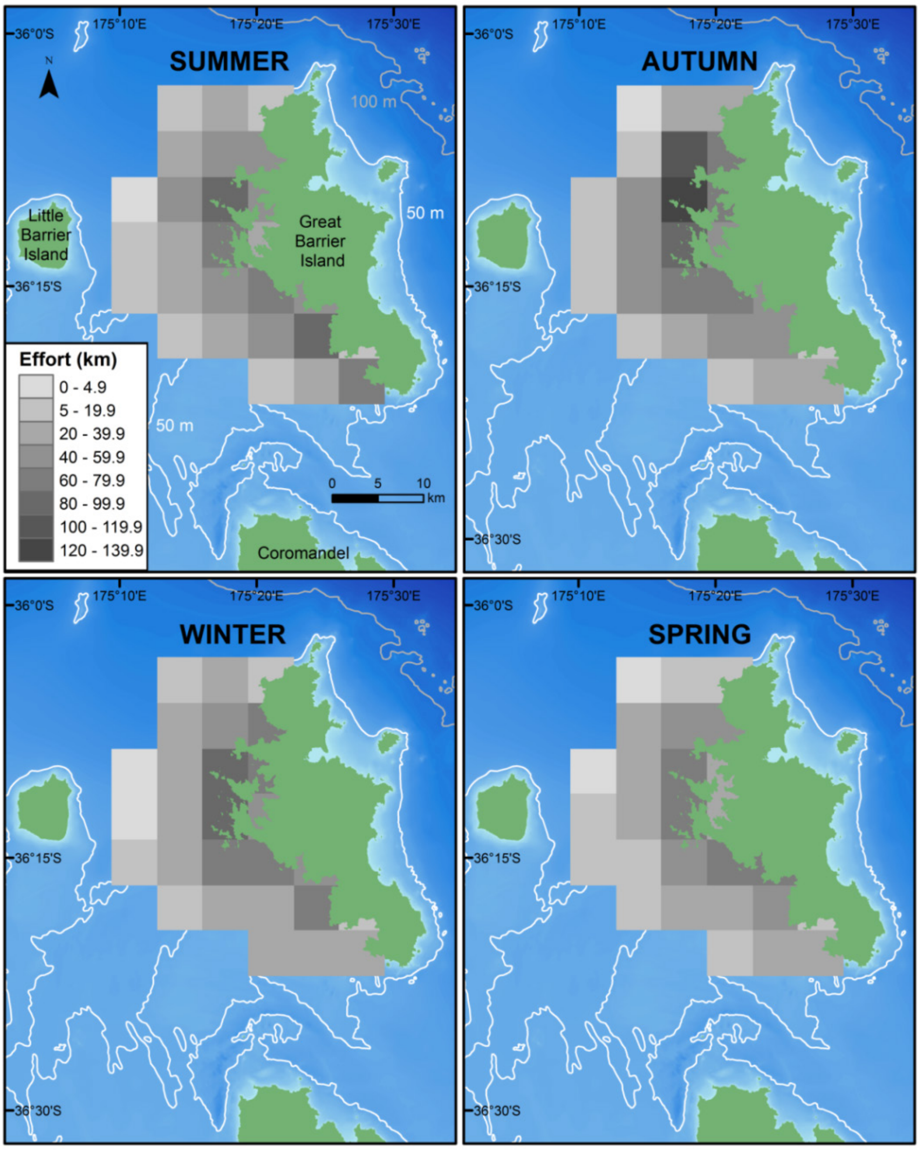

Figure 2.6 Distribution of seasonal survey effort (km) in each 5 x 5 km grid cell off Great Barrier Island (GBI), New Zealand in 2011–2012. Bathymetry is depicted with darker shades of blue representing deeper waters, data courtesy of NIWA (Mackay et al. 2012). The 50 m isobath is shown in white and the 100 m isobath in grey.

2.3.2 Sightings and group sizes

2.3.2.1 Data processing

Common dolphins were sighted up to estimated distances of over 2400 m from the research vessel, with 50% and 95% of sightings detected within ~450 m and ~1500 m, respectively. Outliers were found for sighting distances greater than 1600 m and dolphins were not detected at distances greater than 1600 m in Beaufort seas state 3, i.e. maximum survey conditions (Appendix 2.2). As this species could not be reliably detected at distances greater than 1500 m, those sightings (n = 21) were removed from the final dataset and added to the *off effort* sightings database.

Bryde's whales were sighted up to 2400 m from the research vessel, with 50% and 95% of sightings within ~700 m and ~2200 m, respectively. The whales were sighted at greater maximum distances compared with the dolphins, likely due to the long distance over which whale blows can be detected. Whales were sighted at distances of up to 2000 m in Beaufort sea state 3 (Appendix 2.2). However, given the relatively small sample size and that most whales were sighted within this distance, the small number of sightings (n = 6) at distances of between 2000 and 2400 m were not removed from the final dataset.

Bottlenose dolphins were detected up to 1800 m from the research vessel, with 50% and 95% of sightings within ~300 m and ~1600 m, respectively. Outliers were detected at distances greater than 1100 m (Appendix 2.2) and groups were only detected up to 1200 m in Beaufort sea state 3. However, given the relatively small sample size for this species and small number of outliers, no bottlenose dolphin sightings were removed from the final dataset.

2.3.2.2 Inner Hauraki Gulf cetacean sightings

A total of 603 independent cetacean sightings were recorded in the IHG; 463 *on effort* and 140 *off effort* (Table 2.3; Appendix 2.3). Eight cetacean species were observed. Overall, the common dolphin was the most frequently sighted cetacean (83% of *on effort* encounters), followed by the Bryde's whale (13%). These two species were encountered year-round. Bottlenose dolphin, killer whale (locally known as orca, *Orcinus orca*), southern right whale (*Eubalaena australis*), minke whale (*B. acutorostrata*), pilot whale (*Globicephala melas*) and false killer whale (*Pseudorca crassidens*) were encountered only rarely (all < 2% of *on effort* encounters; Table 2.3; Appendix 2.3).

Table 2.3 Cetacean sightings by season in the inner Hauraki Gulf (IHG), New Zealand, 2010–2012. Numbers in parentheses are *off effort* encounters.

	Summer	**Autumn**	**Winter**	**Spring**	**TOTAL**
Common dolphin	67 (13)	45 (6)	156 (64)	118 (36)	**386 (119)**
Bryde's whale	20 (0)	5 (2)	20 (2)	16 (1)	**61 (5)**
Bottlenose dolphin	–	4 (1)	1 (2)	2 (3)	**7 (6)**
Killer whale (orca)	0 (1)	1 (1)	1 (5)	2 (2)	**4 (9)**
Southern right whale	–	–	1 (1)	–	**1 (1)**
Minke whale	–	–	1 (0)	–	**1 (0)**
Pilot whale	1 (0)	–	–	–	**1 (0)**
False killer whale	1 (0)	–	–	–	**1 (0)**
Unidentified cetacean	1 (0)	–	–	–	**1 (0)**
TOTAL	**90 (14)**	**55 (10)**	**180 (74)**	**138 (42)**	**463 (140)**

2.3.2.3 Great Barrier Island cetacean sightings

A total of 201 independent cetacean sightings were recorded; 185 *on effort* and 16 *off effort* (Table 2.4; Appendix 2.3). Five cetacean species were observed. Overall, the common dolphin was the most frequently sighted species (41% of *on effort* encounters), followed by the Bryde's whale (36%) and bottlenose dolphin (19%). These three species were all encountered year-round. Blue whale (*B. musculus*) and killer whale (orca) were rarely encountered (1.6% and 1.1% of *on effort* encounters, respectively).

Table 2.4 Cetacean sightings by season at Great Barrier Island (GBI), New Zealand, 2011–2012. Numbers in parentheses are *off effort* encounters.

	Summer	**Autumn**	**Winter**	**Spring**	**TOTAL**
Common dolphin	10 (1)	26 (2)	36 (7)	4 (0)	**76 (10)**
Bryde's whale	22 (0)	13 (0)	19 (0)	12 (0)	**66 (0)**
Bottlenose dolphin	10 (0)	9 (2)	7 (2)	10 (1)	**36 (5)**
Blue whale	–	–	–	3 (0)	**3 (0)**
Killer whale (orca)	1 (0)	0 (1)	–	–	**1 (1)**
Unidentified cetacean	1 (0)	–	1 (0)	1 (0)	**3 (0)**
TOTAL	**44 (1)**	**48 (5)**	**63 (9)**	**30 (1)**	**185 (16)**

2.3.2.4 Common dolphin group sizes

In the IHG, common dolphin group sizes were the largest and most variable of the delphinids (maximum > 500 dolphins; Table 2.5). Lower mean and median group sizes were recorded during winter (mean = 17.8, median = 7.0; Table 2.5), and the largest average group sizes were recorded during summer (mean = 26.8, median = 19.0; Table 2.5). However, there was no evidence for a difference in group size according to season (ANOVA: F = 0.939, p = 0.422). Although large groups (> 50 dolphins) were recorded during all seasons, group sizes were right-skewed, with 91% of groups consisting of fewer than 50 individuals and 46% of groups containing fewer than ten individuals.

For GBI, the largest overall group sizes were recorded for common dolphins (maximum = 250; Table 2.5). The mean group size for common dolphins in winter (mean = 8.3, SD = 11.5; Table 2.5) was lower than all other seasonal mean group sizes for common dolphins in the Hauraki Gulf. There was evidence of a seasonal difference in group size at GBI (ANOVA: F = 17.5, p < 0.0001), with *post hoc* tests showing group sizes were significantly lower in winter than in all other seasons (p < 0.0001). Group sizes were right-skewed, with 82% and 47% of groups consisting of fewer than 50 and fewer than ten individuals, respectively.

Table 2.5 Group sizes of common dolphins sighted *on effort* in the inner Hauraki Gulf (IHG) and off Great Barrier Island (GBI), New Zealand, in 2010–2012 and 2011–2012, respectively.

	Mean	**Median**	**SD**	**Range**	**n**
IHG					
Summer	26.8	19.0	33.0	3–225	67
Autumn	22.3	17.0	21.8	1–89	45
Winter	17.8	7.0	38.7	1–333	156
Spring	25.2	12.0	59.4	1–580	118
Overall	**22.2**	**11.0**	**43.9**	**1–580**	**386**
GBI					
Summer	67.4	70.0	50.0	2–145	10
Autumn	34.0	24.0	32.6	3–148	26
Winter	8.3	4.5	11.5	1–52	36
Spring	73.8	19.5	117.7	6–250	4
Overall	**28.3**	**10.5**	**41.7**	**1–250**	**76**

2.3.2.5 Bryde's whale group sizes

Bryde's whale group sizes in the IHG demonstrated little seasonal variation (Kruskal-Wallis: H = 2.510, p = 0.474), ranging from only one to two individuals (Table 2.6). The majority of IHG groups (89%) consisted of singletons. Similarly, group sizes at GBI also showed little seasonal variation (ANOVA: F = 0.445, p = 0.722), ranging from one to three individuals. The majority of GBI groups (82%) consisted of just one whale, with a group of three whales recorded only once.

Table 2.6 Group sizes of Bryde's whales sighted *on effort* in the inner Hauraki Gulf (IHG) and off Great Barrier Island (GBI), New Zealand, in 2010–2012 and 2011–2012, respectively.

	Mean	**Median**	**SD**	**Range**	**n**
IHG					
Summer	1.2	1.0	0.4	1–2	20
Autumn	1.0	1.0	0	1	5
Winter	1.1	1.0	0.3	1–2	20
Spring	1.1	1.0	0.3	1–2	16
Overall	**1.1**	**1.0**	**0.3**	**1–2**	**61**
GBI					
Summer	1.2	1.0	0.4	1–2	22
Autumn	1.2	1.0	0.4	1–2	13
Winter	1.3	1.0	0.6	1–3	19
Spring	1.1	1.0	0.3	1–2	12
Overall	**1.2**	**1.0**	**0.4**	**1–3**	**66**

2.3.2.6 Bottlenose dolphin group sizes

Bottlenose dolphin groups in the IHG typically consisted of fewer than ten individuals (71%). Seasonal trends in group sizes could not be precisely estimated due to an overall small sample size (n = 7; Table 2.7). For GBI, there was evidence of a seasonal difference in group size (ANOVA: F = 3.236, p = 0.035), with *post-hoc* testing identifying lower group sizes in autumn compared with summer (p = 0.026). Group sizes were larger during all seasons for GBI compared with the IHG (Table 2.7).

Table 2.7 Group sizes of bottlenose dolphins sighted *on effort* in the inner Hauraki Gulf (IHG) and off Great Barrier Island (GBI), New Zealand, in 2010–2012 and 2011–2012, respectively.

	Mean	Median	SD	Range	n
IHG					
Summer	–	–	–	–	0
Autumn	10.0	5.5	11.5	2–27	4
Winter	3.0	3.0	–	3	1
Spring	15.5	15.5	10.6	8–23	2
Overall	**10.6**	**7**	**10.1**	**2–27**	**7**
GBI					
Summer	47.2	54.5	23.8	3–76	10
Autumn	18.9	14.0	15.9	1–43	9
Winter	30.4	31.0	14.0	8–50	7
Spring	39.1	47.0	24.4	3–67	10
Overall	**34.6**	**35**	**22.5**	**1–76**	**36**

2.3.3 Temporal relative density

2.3.3.1 Common dolphins

Inner Hauraki Gulf

In the IHG, a greater number of common dolphin groups were detected during winter of all survey years, the majority of which were small (< 10 dolphins; Table 2.5; Fig. 2.7a–b). Dolphins were less dispersed during summer and autumn, resulting in fewer but generally larger groups (Table 2.5; Fig. 2.7a). There was a statistically significant difference in seasonal SRs (Kruskal-Wallis: $H = 20.001$, $p < 0.001$), with lower SR in autumn compared with both winter ($p < 0.001$) and spring ($p = 0.001$). Overall, the temporal relative density, i.e. SR, of common dolphin groups was greatest during winter and spring and gradually declined over summer, decreasing to the lowest values in autumn (Fig. 2.7a). This trend was also evident in the *off effort* sighting data (Appendix 2.3), with increased sightings in winter and spring compared with summer and autumn.

A significant difference in seasonal ER was also detected (Kruskal-Wallis: $H = 15.215$, $p = 0.002$), with lower relative densities of common dolphins in autumn compared with winter ($p = 0.002$) and spring ($p = 0.010$). The exception to this general trend was a relatively high ER for autumn 2011, exceeding both summer and winter values for that year (Fig. 2.7b). The result for autumn 2011 may have been biased by a relatively low amount of effort as it was the season that received the lowest overall survey effort (2.9% of the total effort; Table 2.1). The mean SR for common dolphins in the IHG was 0.024 groups/km (SD = 0.012, n = 12), and mean ER was 0.515 individuals/km (SD = 0.240, n = 12). No significant differences were detected between years for monthly SRs (ANOVA: F = 0.204, p = 0.816) or ERs (ANOVA: F = 0.821, p = 0.450). Seasonal data from all years could therefore be pooled for common dolphins.

Great Barrier Island

Overall, there were a small number of large groups (> 50 dolphins) of common dolphins recorded during summer, with more groups of varying sizes encountered during autumn (Table 2.5; Fig. 2.7c–d). During winter, dolphins were generally more dispersed and groups were mainly small (< 10 dolphins). The pattern for spring was not clear due to inter-annual variation in some results and a small sample size (n = 4).

Although an overall significant difference in seasonal SR was detected (Kruskal-Wallis: H = 8.344, p = 0.039), there were no significant values between pairwise comparisons at the alpha = 0.05 level, with p = 0.55 and p = 0.146 for winter compared with summer and spring, respectively. Common dolphin groups were sighted more frequently in winter and autumn during both 2011 and 2012 (Fig. 2.7c). The absence of sightings during summer 2011 (Fig. 2.7c–d) was likely an artefact of only one monthly trip to GBI and should be treated with caution. SR was low during spring of both years (0.006 in 2011 and 0.004 in 2012; Fig 2.7c). The temporal relative densities of common dolphins did not vary seasonally (Kruskal-Wallis: H = 4.344, p = 0.227), despite noticeably low ERs in winter (0.085) and spring 2012 (0.065). ER was consistently high in autumn of both years; however, these rates were associated with large standard errors (Fig. 2.7d). Values for the other seasons were variable across years (Fig. 2.7d). Mean SR and ER for common dolphins at GBI was 0.017 groups/km (SD = 0.016, n = 8) and 0.465 individuals/km (SD = 0.360, n = 8), respectively. Seasonal data from both years were pooled for common dolphins off GBI since no significant differences were detected between years for monthly SRs (Mann-Whitney: U = 11.000, p = 0.310) or ERs (Mann-Whitney: U = 12.000, p = 0.394).

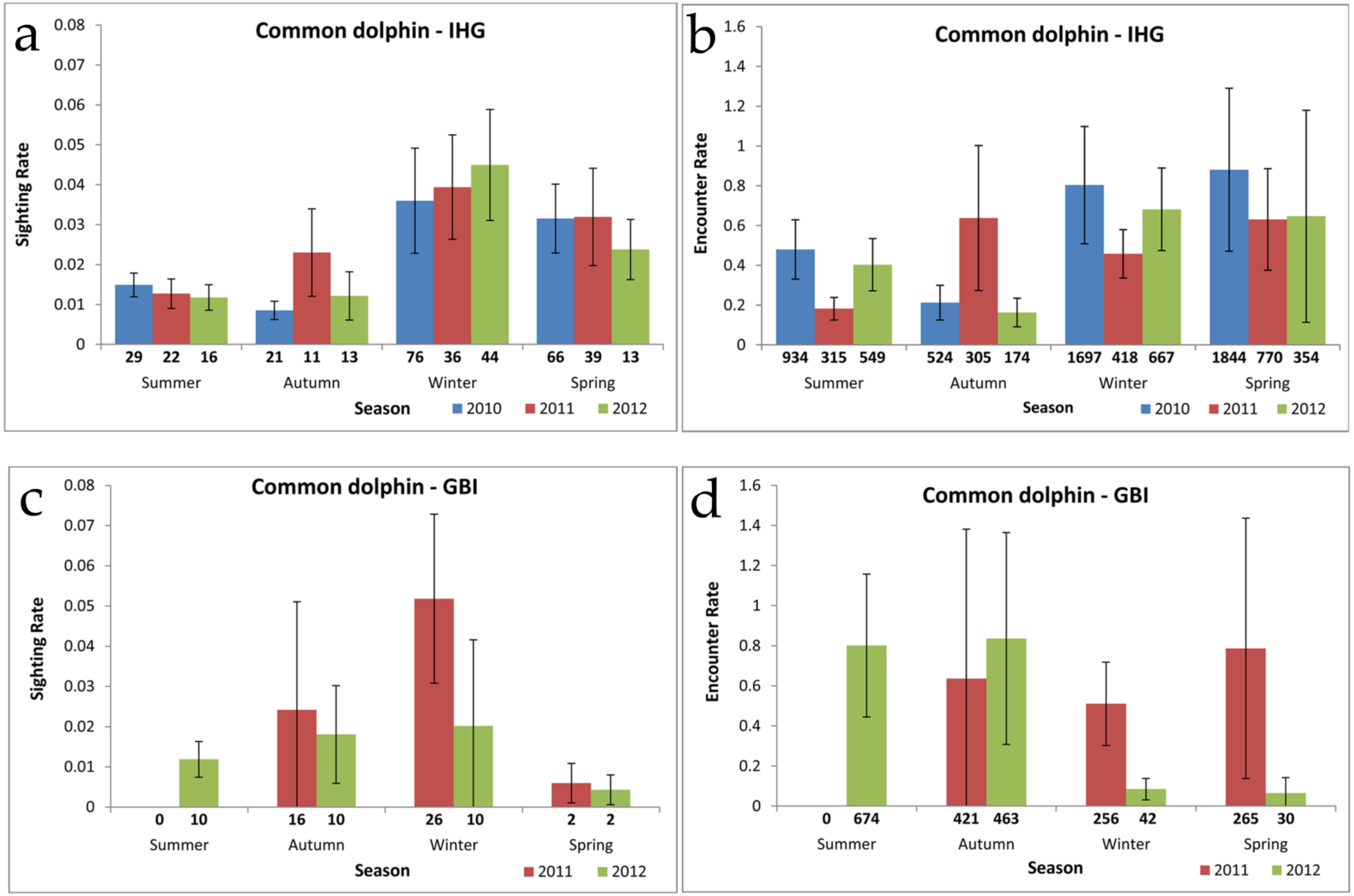

Figure 2.7 SR (sighting rate) and ER (encounter rate) by season (± SE) of common dolphins using a–b) inner Hauraki Gulf (IHG) waters in 2010-2012 and c–d) Great Barrier Island (GBI) waters in 2011–2012. Sample sizes (number of groups and number of individuals, respectively) are shown for each season and year.

2.3.3.2 Bryde's whales

Inner Hauraki Gulf

Bryde's whales were encountered year-round in the IHG (Table 2.6) with more whales detected in 2010 and 2012 than during 2011 (Fig. 2.8a–b). Although seasonal patterns in relative densities were not distinct due to inter-annual variation, sightings were consistently lower during autumn of all years (Fig. 2.8a–b). Overall, there was little variation in seasonal SRs (Kruskal-Wallis: $H = 3.436$, $p = 0.329$). Since Bryde's whale groups consisted of only 1 to 2 individuals, there was little difference between the relative values of SR and ER compared with the dolphin species (Fig. 2.8). As such, a significant difference across seasonal ER values was not found (Kruskal-Wallis: $H = 3.507$, $p = 0.320$) and mean SR and ER values were the same (0.004, $SD = 0.004$, $n = 12$).

No significant differences were detected between years for monthly SRs (ANOVA: $F = 1.582$, $p = 0.222$) or ERs (ANOVA: $F = 1.402$, $p = 0.262$), therefore seasonal data from all years could be pooled for further spatial analyses for Bryde's whales sighted in the IHG.

Great Barrier Island

Bryde's whales were encountered in the GBI study area year-round; however, given the variation between survey years (Fig. 2.8c–d), no overall trends in seasonal SRs or ERs could be detected. Again, there was little difference between the relative values for SR and ER because Bryde's whale groups consisted of only 1 to 3 individuals. Neither SR (Kruskal-Wallis: $H = 1.609$, $p = 0.657$) or ER (Kruskal-Wallis: $H = 1.754$, $p = 0.625$) varied seasonally. Furthermore, the low SR/ER at GBI during winter 2012 coincided with a peak in the IHG at that time. Mean SR and ER were greater at GBI than in the IHG ($SR = 0.019$ groups/km, $SD = 0.015$, $n = 8$ and $ER = 0.022$ individuals/km, $SD = 0.018$, $n = 8$).

In general, more whales were detected per km of search effort in the first year than the second (Fig. 2.8c–d). Differences were detected between years for monthly SRs (Mann-Whitney: $U = 2.000$, $p = 0.009$) and ERs (Mann-Whitney: $U = 2.000$, $p = 0.009$). Therefore, data from different years were not pooled for further seasonal analyses.

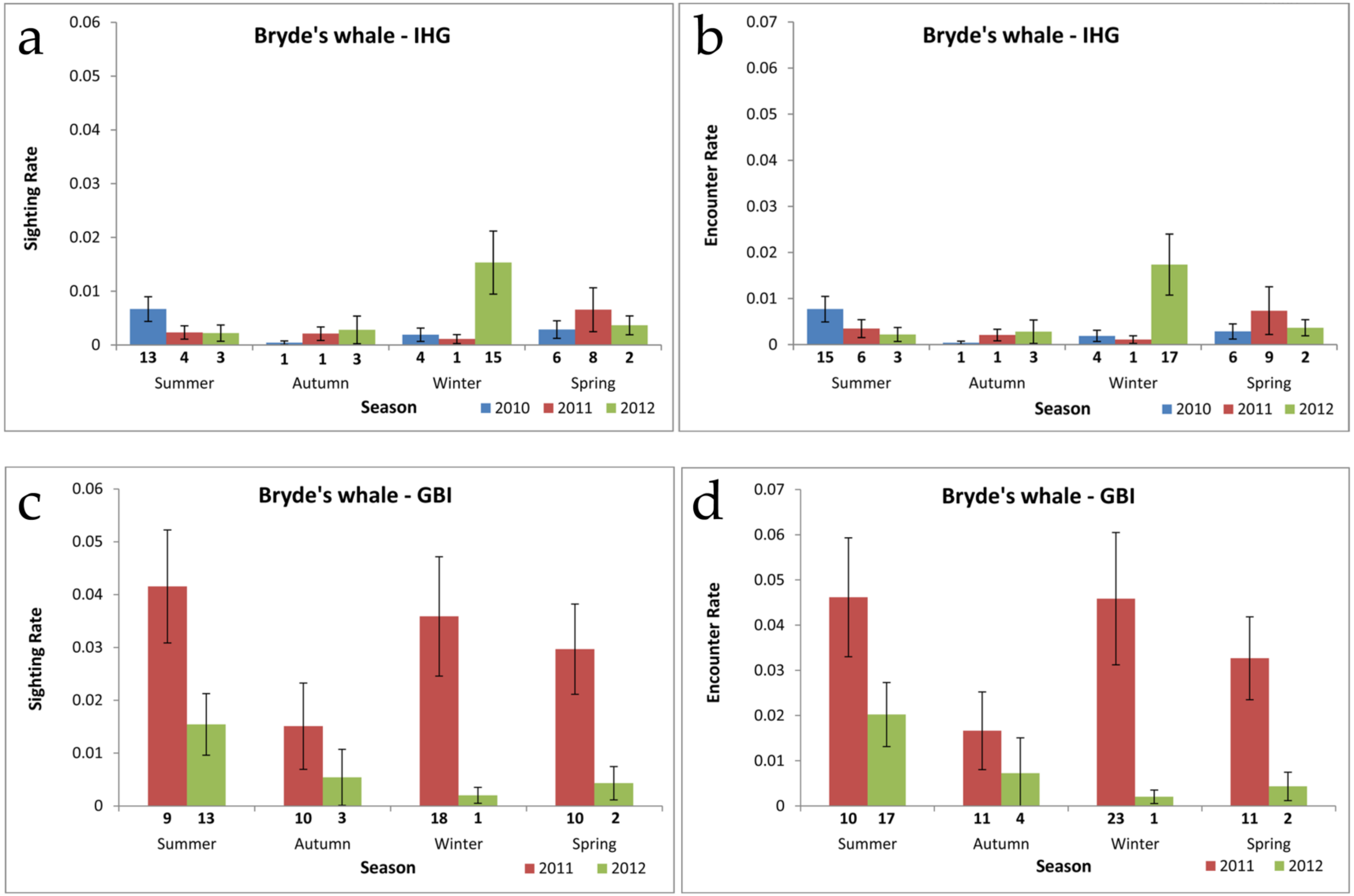

Figure 2.8 SR (sighting rate) and ER (encounter rate) by season (± SE) of Bryde's whales using a–b) inner Hauraki Gulf (IHG) waters in 2010–2012 and c–d) Great Barrier Island (GBI) waters in 2011–2012. Sample sizes (number of groups and number of individuals, respectively) are shown for each season and year.

2.3.3.3 Bottlenose dolphins

Inner Hauraki Gulf

Bottlenose dolphins were not frequently sighted during IHG surveys. Detections were made during *on effort* surveys only in autumn and winter 2010, spring 2011 and autumn and spring 2012 (Fig. 2.9). No sightings (*on effort* or *off effort*; Appendix 2.3) were made in summer of any survey year. The greatest number of sightings and individuals were recorded during autumn, followed by spring (Fig. 2.9a–b). Mean SR and ER were 0.0004 groups/km (SD = 0.0006, n = 12) and 0.0054 individuals/km (SD = 0.0089, n = 12). Due to the small sample size, no statistical tests were carried out on the bottlenose dolphin data for the IHG.

Great Barrier Island

Bottlenose dolphins were recorded at GBI during all seasons and years (Fig. 2.9c–d). Although there was little variation in the number of groups sighted each season (Kruskal-Wallis: H = 7.657, p = 0.054), there was a significant difference in seasonal ERs (Kruskal-Wallis: H = 9.781, p = 0.021), with more dolphins detected in spring compared with autumn (p = 0.024). The low ERs for autumn reflect the typically smaller group sizes recorded during that season (Table 2.7). All seasonal ER patterns were consistent between survey years (Fig. 2.9). Mean SR and ER were 0.010 groups/km (SD = 0.004, n = 8) and 0.318 individuals/km (SD = 0.156, n = 8), respectively.

Seasonal data for bottlenose dolphins in 2011 and 2012 could be pooled for spatial analyses since no significant differences were found between years for monthly SRs (Mann-Whitney: U = 15.500, p = 0.699) and ERs (Mann-Whitney: U = 16.500, p = 0.818).

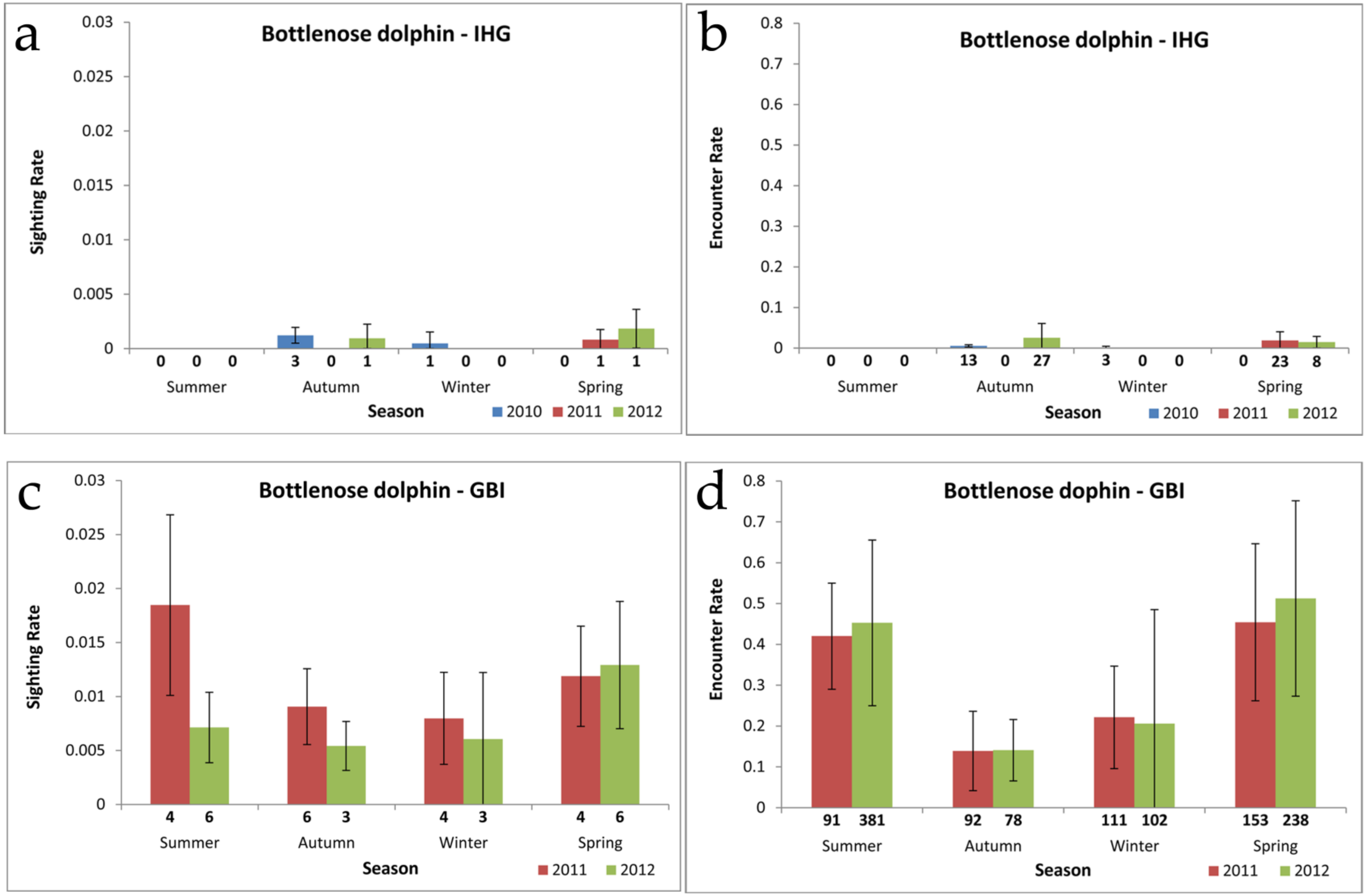

Figure 2.9 SR (sighting rate) and ER (encounter rate) by season (± SE) of bottlenose dolphins using a–b) inner Hauraki Gulf (IHG) waters in 2010–2012 and c–d) Great Barrier Island (GBI) waters in 2011–2012. Sample sizes (number of groups and number of individuals, respectively) are shown for each season and year.

2.3.4 Spatial relative density

2.3.4.1 Common dolphin

Inner Hauraki Gulf

The distribution and density of common dolphins in the IHG varied with season, with the highest density grid cells recorded during winter and spring (Fig. 2.10). Dolphins were most widely distributed throughout the IHG during winter and were the least widespread during autumn, when densities were also the lowest.

Common dolphins were found in central regions of the IHG during all seasons. In the northwestern IHG, common dolphins were sighted close to and inshore of Kawau Island during winter and spring. Sightings close to Auckland city in the southwestern IHG were rare, with only one group recorded in the Tamaki Strait (in winter) during the three year study period. Common dolphins were infrequently encountered in the Firth of Thames and only during summer and winter. Their distribution spanned eastern regions of the IHG (i.e. off the west coast of the Coromandel Peninsula) the most during winter. There was a statistical difference in seasonal distance from shore (ANOVA: $F = 4.914$, $p = 0.002$), with winter distances (mean = 3.64 km, SD = 4.08) significantly lower than summer (mean = 8.60, SD = 4.08, $p = 0.008$) and autumn (mean = 8.63, SD = 4.53, $p = 0.030$).

High density regions were concentrated further south during winter compared with spring. In winter, high density cells were located in the eastern central IHG, approximately 20 km west of Colville Bay and also off the northwestern coast of Waiheke Island, where a small number of large groups were detected. In spring, the highest density cells were found approximately 15 km northeast of Tiritiri Matangi Island (Fig. 2.10).

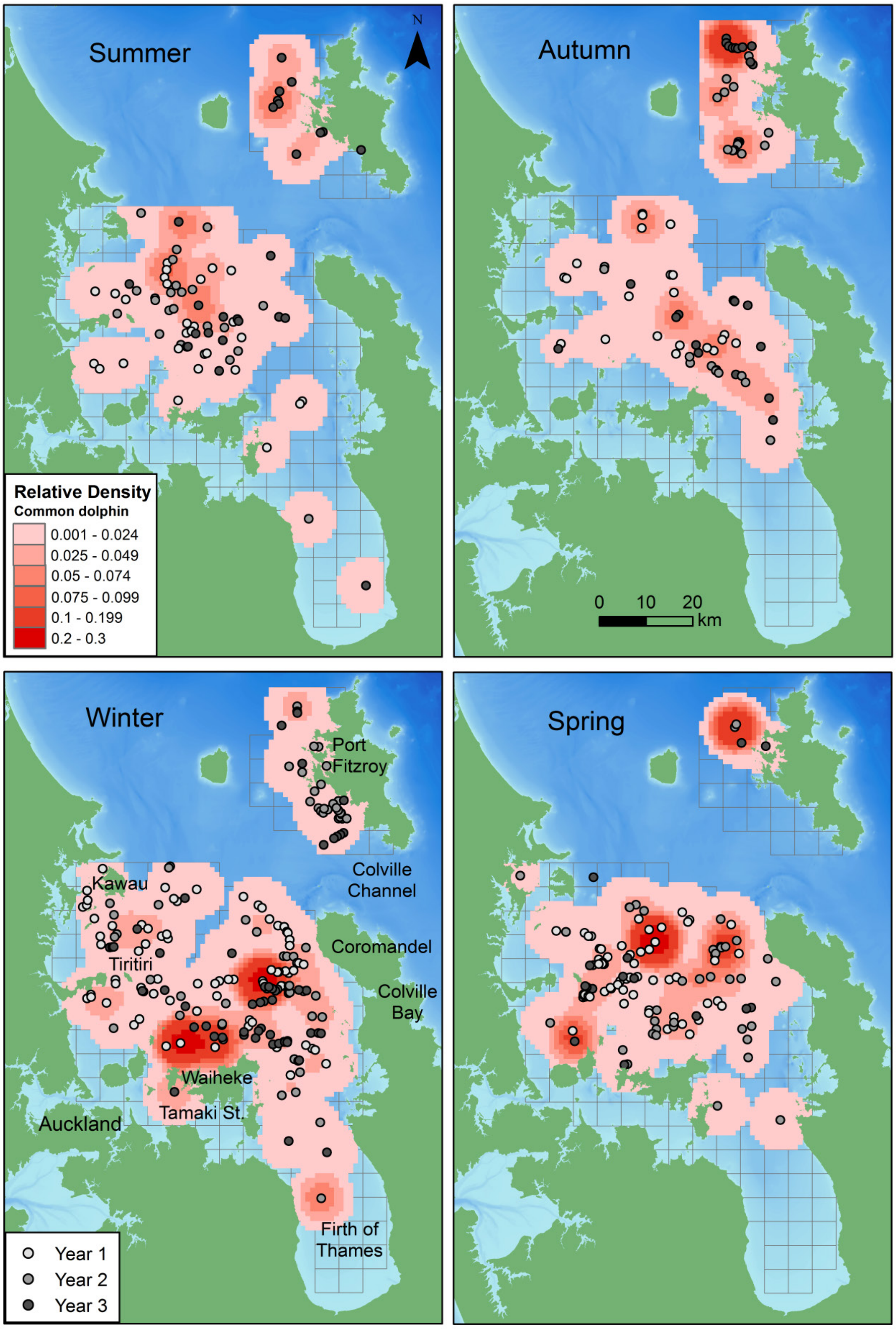

Figure 2.10 Seasonal relative densities of common dolphins in the inner Hauraki Gulf (IHG) in 2010–2012 and off Great Barrier Island (GBI) in 2011–2012. Darker shading represents higher density cells. The sighting position of each common dolphin group is indicated by a shaded grey dot according to year. Year 1: January–November 2010, Year 2: December 2010–November 2011, Year 3: December 2011–November 2012. Bathymetry is depicted with darker shades of blue representing deeper waters, data courtesy of NIWA (Mackay et al. 2012). The 5 x 5 km grid is also shown.

Great Barrier Island

The distribution and density of common dolphins off GBI varied with season. The consistent factor across all seasons was the presence of common dolphins off the northwestern coast of GBI (associated over or near the Cradock Channel region) rather than more southeastern regions, and in more offshore waters rather than within the bays and ports of GBI. Common dolphins were widely distributed across the study area during most seasons with the exception of spring (Fig. 2.10). Distribution spread furthest into southeastern regions during winter. Groups were sighted at significantly different distances from shore according to season (ANOVA: $F = 10.937$, $p < 0.001$), with dolphins found closer to shore in winter (mean = 2.71 km, SD = 2.12) compared with autumn (mean = 5.99, SD = 2.26, $p < 0.001$). This was also apparent from the *off effort* sightings (Appendix 2.3). Winter was the only season when common dolphins were found in the sheltered inshore bays of Port Fitzroy (Fig. 2.10).

Overall, the relative density maps (Fig. 2.10) show GBI waters were used by a much greater density of common dolphins in autumn relative to the other seasons. Despite a large number of winter sightings, the relatively low winter density was due to the large proportion of small groups (mean = 8.3, SD = 11.5; Table 2.2) of dolphins spread more evenly across most of the survey area. Summer densities, while similar to winter; were due to a few large groups of dolphins equally spread across similar regions, albeit in more enclosed waters during winter and with higher densities over the Cradock Channel region in summer.

2.3.4.2 Bryde's whale

Inner Hauraki Gulf

Bryde's whale distribution was generally similar across most seasons, with the exception of autumn when whales were spatially concentrated in eastern areas of the IHG (Fig. 2.11). Overall, distribution was concentrated around central and more northern regions with no whales detected anywhere south of the northern coast of Waiheke Island (Fig. 2.11) during any season. Distance from shore differed significantly according to season (ANOVA: $F = 5.252$, $p = 0.003$), with whales found closer to land in winter (mean = 6.73 km, SD = 3.72) compared with spring (mean = 13.06 km, SD = 5.53, p = 0.002). Bryde's whales were distributed closest to the Coromandel coast during winter. Sightings were not recorded in the western IHG during autumn or spring, but whales were encountered in northwestern regions (i.e. between Tiritiri Matangi and Kawau Islands, Fig. 2.11) during summer and winter.

Densities were similar in all seasons except for autumn when only a small number (n = 5) of whales were detected. In winter, the high density cells were located furthest to the east while in spring and summer, hotspots were found in northern mid-IHG waters.

Great Barrier Island

Since data could not be pooled across years, kernel density maps for Bryde's whales were produced using only the 2011 sightings. While kernel density estimation was not carried out for the 2012 data due to low seasonal sample sizes, the 2012 sighting positions are represented for distribution. Bryde's whales were unevenly distributed across the study area, particularly 2011 encounters (Fig. 2.11). Sightings were concentrated off the southwest coast of the island closer to the Colville Channel and over the 40 m shelf region, with an absence of whales in the Cradock Channel in winter and spring of both years and in summer 2011. Whales were distributed closest inshore during summer (mean = 1.76 km, SD = 1.83) and winter (mean = 2.73, SD = 1.39) and furthest from the coast in spring (mean = 4.61, SD = 2.34). This seasonal difference was significant (ANOVA: F = 5.636, p = 0.002) for spring distances compared with summer (p = 0.001) and winter (p = 0.048). Overall, densities were similar for winter and spring, with high density cells off the southwest coast, but with a slight offshore movement in spring. Whales used more northerly waters during summer and autumn.

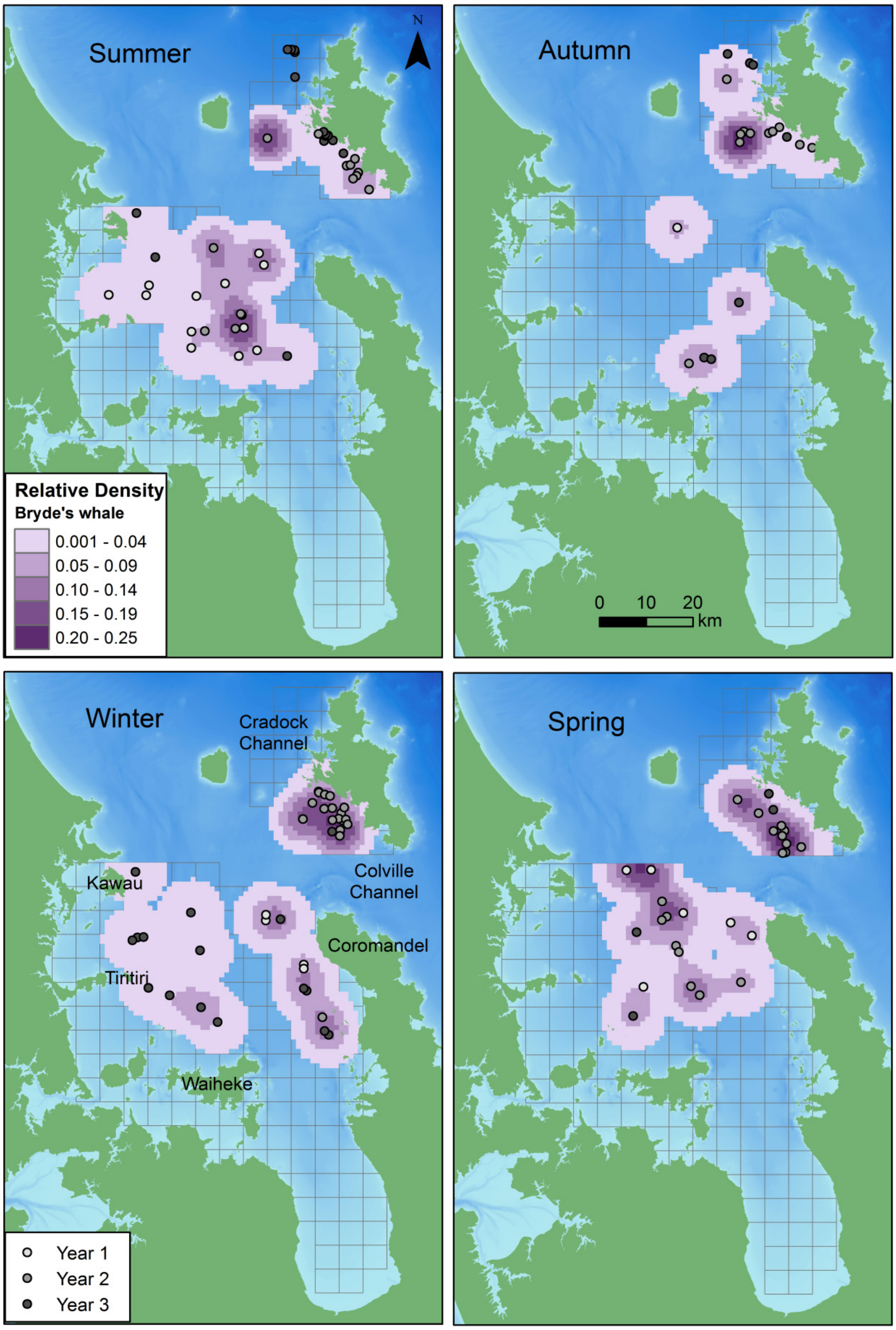

Figure 2.11 Seasonal relative densities of Bryde's whales in the inner Hauraki Gulf (IHG) in 2010–2012 and off Great Barrier Island (GBI) in 2011. Darker shading represents higher density cells. The sighting position of each Bryde's whale group is indicated by a shaded grey dot according to year. Year 1: January–November 2010, Year 2: December 2010–November 2011, Year 3: December 2011–November 2012. Bathymetry is depicted with darker shades of blue representing deeper waters, data courtesy of NIWA (Mackay et al. 2012). The 5 x 5 km grid is also shown.

2.3.4.3 Bottlenose dolphin

Inner Hauraki Gulf

Bottlenose dolphins were sighted infrequently in the IHG, yet they were detected in all seasons except for summer (Fig. 2.12). Although based on a very low number of sightings (n = 7), it appears that bottlenose distribution varied seasonally, with groups sighted furthest from the coast in autumn (mean = 7.82 km, n = 4) and found close to shore during winter (1.46 km, n = 1) and spring (mean = 3.88 km, n = 2). Slightly more groups were detected during autumn. Due to the small seasonal sample sizes, kernel density analyses were not conducted for the IHG.

Great Barrier Island

Bottlenose dolphins were generally found close inshore and within bays and harbours during all seasons (Fig. 2.12). While a similar number of groups were detected year-round, group sizes were much larger during spring and summer (see Table 2.7). The southwestern region of the coastline was generally used by more dolphins than the northwestern area. Dolphins were found within 1 and 2 km of the coast for 84% and 96% of encounters, respectively. Bottlenose dolphins were found very close inshore during winter (median = 0.13 km, SD = 0.18) and were distributed furthest from the coast during summer (median = 0.94 km, SD = 1.26). This seasonal difference was significant (Kruskal Wallis: H = 10.937, p = 0.002).

The highest seasonal densities of bottlenose dolphins were recorded during summer and spring (Fig. 2.12). In summer, winter and spring, the highest density cells were all located around the Whangaparapara to Blind Bay region of coastline (Fig. 2.12) in the southern half of the study area. Use of the west coast of GBI appeared to be slightly more uniform during autumn.

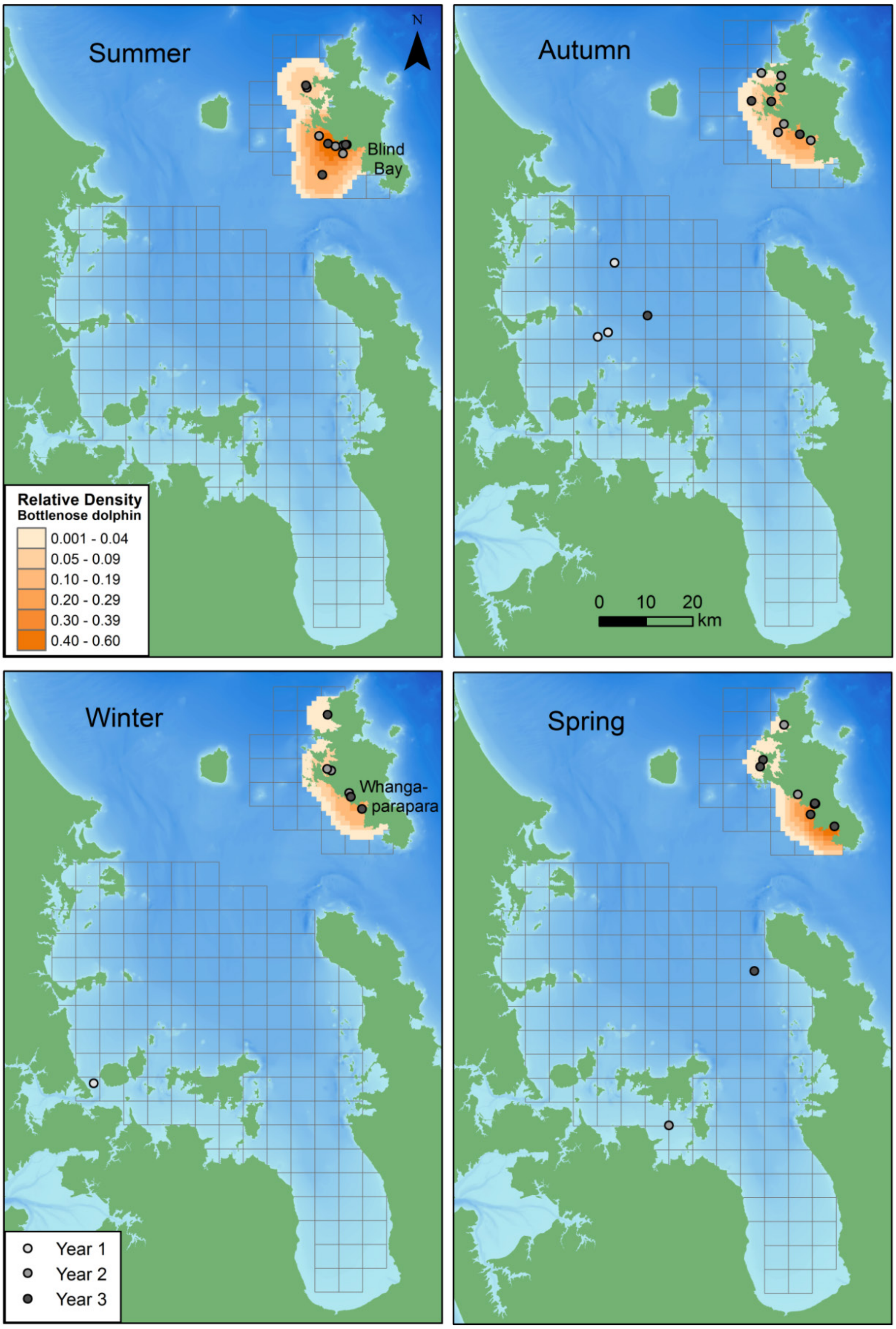

Figure 2.12 Seasonal relative densities of bottlenose dolphins off the west coast of Great Barrier Island (GBI), New Zealand in 2011–2012. Darker shading represents higher density cells. Sighting positions of each bottlenose dolphin group detected in the inner Hauraki Gulf (2010–2012) and off GBI are indicated by a shaded grey dot according to year. Year 1: January–November 2010, Year 2: December 2010–November 2011, Year 3: December 2011–November 2012. Bathymetry is depicted with darker shades of blue representing deeper waters, data courtesy of NIWA (Mackay et al. 2012). The 5 x 5 km grid is also shown.

2.4 DISCUSSION

The distribution and density of cetaceans using IHG and GBI waters have been described in this study to provide baseline data for conservation management. Furthermore, these results help give spatial and temporal context to the following chapters (Chapters 3 and 4), which investigate habitat use in relation to environmental parameters.

2.4.1 Common dolphin

Common dolphins were generally widely distributed across IHG and GBI waters during all seasons. Similar to the Gulf St. Vincent, Australia (Filby et al. 2010) and the eastern Ionian Sea, Greece (Bearzi et al. 2005), small group sizes of fewer than ten individuals were most prevalent in this study. However, only groups of a maximum of 30 individuals were recorded for those overseas populations. Common dolphin group size in the Hauraki Gulf was highly variable, ranging from small groups of fewer than ten dolphins to large aggregations of more than 500 animals. This is more consistent with common dolphin populations in other parts of the world, such as the Bay of Biscay (Kiszka et al. 2007) and Alboràn Sea (Bearzi et al. 2003), where group sizes range from singletons to 600 dolphins.

Hypothesising about the similarities or differences among SR and ER indices of different populations is difficult because the sizes of the study areas and survey designs alone may account for a considerable amount of the variation among indices. For example, if this study had not included Tamaki Strait and Firth of Thames waters where common dolphins are only sighted infrequently, the relative abundance indices reported herein would have been considerably higher. However, some comparisons with other regions are made since similarities may suggest that general life history traits affecting population dynamics may be functioning at a global level. Sighting rates (SR, groups per kilometre) of common dolphins in the IHG (mean = 0.024) and off GBI (mean = 0.017) were most similar to those reported for the Alboràn Sea, Mediterranean (0.023 groups/km), where common dolphins remain relatively abundant compared with other regions of the Mediterranean (Bearzi et al.

2003). Similar values were also reported for the Bay of Biscay (0.010 groups/km, Kiszka et al. 2007) and the Gulf St. Vincent, Australia (0.03 groups/km, Filby et al. 2010). The IHG and GBI values were lower than those reported for southern Spanish waters (0.038 groups/km, Cañadas et al. 2005), one of the most important remaining Mediterranean habitats for the species (Cañadas & Hammond 2008). However, relative densities were considerably larger than for the Gulf of Vera, Mediterranean (0.007 groups/km, Bearzi et al. 2003). The mean ERs (individuals per kilometre) for the IHG (0.52) and GBI (0.47) were greater than those reported for the Gulf St. Vincent (0.16 individuals/km, Filby et al. 2010), likely due to the presence of larger groups in the Hauraki Gulf. ER values for the Hauraki Gulf were lower than those reported for the Alboràn Sea (1.74 individuals/km) where the average group size is large (mean = 68.4), but greater than the Gulf of Vera (0.36 individuals/km) where groups are smaller (mean = 47.5, Bearzi et al. 2003). Overall, SRs and ERs for common dolphins in the Hauraki Gulf fell within the range of values previously reported for common dolphin populations in other warm temperate waters. Most importantly, the results of this study will be beneficial when used for monitoring the Hauraki Gulf population over time. This was demonstrated by Bearzi et al. (2005) who recorded a local decline of short-beaked common dolphins in the eastern Ionian Sea, Mediterranean, as a likely consequence of prey depletion.

Group size was variable across seasons, with the greatest proportion of small groups recorded during winter. Comparing with other southern hemisphere temperate regions, this corresponded with Stockin et al. (2008a), who found that both small groups and large aggregations were most frequent during winter. In the Gulf St. Vincent, relative abundance data were collected only between the months of September and May (Filby et al. 2010); therefore it is unknown whether similar peaks also occur in Australian waters during austral winter months. However, off the southeast coast of South Africa, common dolphin densities were greatest in winter and coincided with the annual 'sardine run' (Cockcroft & Peddemors 1990). In the Hauraki Gulf, the increased SRs and ERs during winter were consistent across IHG and GBI waters. Similar to this study, Stockin et al. (2008a) also reported highest sighting rates (based on SPUE, defined as the number of common dolphin sightings per 60 min of search effort) in the IHG in winter. Kernel densities were highest in

IHG waters during winter and spring, which may be related to increased foraging opportunities, since the winter and spring seasons are when foraging groups are most prevalent (Stockin et al. 2009a; Chapter 3).

The inshore movement in Hauraki Gulf waters during winter may represent an overall offshore to inshore shift in distribution since the same pattern was reported for the Bay of Islands (Constantine & Baker 1997). This may also be combined with an influx of dolphins from the wider surrounding areas, which could be feasible given the high winter densities in the IHG and decreased winter sightings in the Bay of Plenty (Neumann 2001a; Meissner et al. 2014). While these changes in distribution are correlated with changes in water temperature, it is unlikely that cooler temperatures alone would push dolphins northwards given that common dolphins are also sighted further south when temperatures are at their coolest, for example, in Admiralty Bay, South Island (Halliday 2013). Additionally, common dolphins were more abundant in Admiralty Bay towards the winter months (Halliday 2013), suggesting that the inshore movements of common dolphins during winter may be more specifically localised to particular bays or sheltered waters around the country. This is likely to be related to prey distribution, given that common dolphin prey such as pilchard (*Sardinops neopilchardus*) are known to be more abundant in bays and harbours in New Zealand when water temperatures are cooler (Ministry for Primary Industries 2013).

While there is a paucity of published data relating to the ecology of the main prey species of common dolphins such as jack mackerel (*Trachurus novaezelandiae*) and pilchard (Meynier et al. 2008), local fishermen observe that it is more difficult to catch species such as pilchards close to the surface when water temperatures are warmer (Dave Kellian, pers. comm.). If more dolphins are required to work a school of fish closer to the surface during foraging when water temperatures are warmer, this could also be an important factor that affects the size of common dolphin groups in the Hauraki Gulf. This concurs with Burgess (2006) who investigated the foraging ecology of common dolphins in the IHG during summer/autumn and found that larger groups spent more time devoted to foraging activity compared with smaller groups, with coordinated group foraging strategies observed more frequently than individual strategies.

In the Hauraki Gulf, neonates are most frequently recorded during summer months (Stockin et al. 2008a). A study in the IHG by Schaffar (2004) found that groups with neonates were larger than groups containing all other age classes (from neonate through to adult only). Coinciding with peak seasons for neonates and calves may explain the larger groups encountered during summer (mean 26.8 for IHG and 67.4 for GBI) and spring (mean 25.2 for IHG and 73.8 for GBI) in the present study. However, high densities were not recorded in summer for the IHG or GBI, suggesting individuals may also be moving to other regions or at least beyond the IHG and GBI study areas. This corresponds with increased sightings of common dolphins to the south of the Hauraki Gulf in the East Coast Bay of Plenty (ECBOP) during summer (Meissner et al. 2014). Furthermore, individual dolphins have been photo-identified in both the Hauraki Gulf and western Bay of Plenty (Neumann et al. 2002), with individuals photographed in the Hauraki Gulf in winter/spring recorded in BOP in summer/autumn (Massey University, unpubl. data).

Decreased SRs and ERs in the IHG in autumn corresponded with increased SRs and ERs at GBI, suggesting a possible seasonal offshore movement of dolphins. Further evidence of such an offshore movement during autumn was in the decreased distances from shore that dolphins were sighted during winter compared to summer and autumn. This is in line with Neumann (2001a), who reported that for the east coast of the Coromandel Peninsula, distance from shore increased from spring through to autumn as a likely consequence of changes in the distribution of common dolphin prey. Similarly, Meissner et al. (2014) reported common dolphins further offshore in autumn compared with summer.

A discrepancy in the lowest seasonal sighting rates between autumn in the present study and spring for the 2002–2004 survey period in Stockin et al. (2008a) could be related to methodological differences, such as surveying from different platforms and measuring sighting rates based on kilometres travelled compared with the number of hours spent searching. Comparing data between platform types has previously been suggested to be problematic (Evans & Hammond 2004). Alternatively, discrepancies could be related to environmental conditions, since the 2002–2004 period was dominated by El Niño conditions, in which southwesterly winds are more common during autumn (Wratt et al. 2014). The 2010–2012 period was mostly in the La Niña phase (National Climate Centre 2013) when north-easterly winds were more characteristic. Given that upwellings in the IHG are known to be associated with westerly winds (Chang et al. 2003), El Niño conditions are likely to provide more favourable foraging conditions and therefore possibly more dolphin groups.

2.4.2 Bryde's whale

Bryde's whales were consistently observed as singletons, or in groups of two or three on occasion, across all seasons and both regions. This aligns with previous research overseas (Tershy 1992; De Boer 2010) and within the Hauraki Gulf (O'Callaghan & Baker 2002; Wiseman 2008), although the maximum group size (n = 3) was lower in this study compared with other studies in the IHG that used a platform of opportunity (n = 8, Wiseman 2008; n = 10, Behrens 2009; n = 10, Martinez et al. 2010; n = 7, Riekkola 2013). Bias in group size estimates from the platform of opportunity may have arisen if observers and group size definitions were not consistent during the respective studies (Hupman et al. 2014).

Bryde's whale encounter rates were generally quite variable across the Hauraki Gulf, with peaks in different seasons in the IHG each survey year. At GBI, sightings were high throughout 2011 and continually decreased throughout 2012. A study in the Gulf of California, USA that examined inter-annual changes in Bryde's whale occurrence over a 20 year period found that whales did not have a well-defined pattern of seasonal occurrence, and suggested changes could be driven by variability in food availability that was related to climate fluctuations (Salvadeo et al. 2011). Conversely, in Plettenberg Bay, South Africa, Bryde's whale encounter rates (sightings per day) peaked in autumn and were generally highest between the months of November to May, when water temperatures were greater than 18° C (Penry et al. 2011). The data compiled here found the opposite to Penry et al. (2011); encounter rates remained low in autumn in both IHG and GBI waters, despite the lack of any clear seasonal trends, and there was also an absence of *off effort* sightings during autumn (Appendix 2.3). In an earlier study in the Hauraki Gulf, Wiseman et al. (2011) reported a significant difference in the seasonal (but not annual) occurrence of Bryde's whales during 2003 to 2006, with increased trip encounter rates during winter compared with spring and summer. Although Behrens (2009) also reported a peak in sightings during May–June and fewer sightings in December–February, this result was not statistically significant and the study concluded that no significant seasonal differences for either the number or distribution of whales were detected using data collected between 2000 and 2009. When examining temporal variation in encounter rates in the IHG, it is important to consider the use of the wider Hauraki Gulf region. The results of the winter 2012 season clearly show that decreased sightings at GBI corresponded with a peak in occurrence in the IHG. Therefore, apparent decreased encounter rates in either the IHG or outer Hauraki Gulf alone may not be representative of the overall use of the Hauraki Gulf. The importance of scale is discussed in Chapter 3.

Finding a presence (Wiseman et al. 2011) or absence (Behrens 2009; this study) of a seasonal pattern in the occurrence of Bryde's whales could be related to factors like differences in methodologies and/or annual climate fluctuations. Wiseman et al. (2011) used only presence/absence data to calculate their trip encounter rate. In the present study, relative density indices were calculated based on the number of whale sightings per survey, rather than the presence/absence of a sighting. Behrens (2009) noted that the highest number of annual sightings between 2000 and 2009 occurred in the years 2003–2005, coinciding with the Wiseman et al. (2011) study period when conditions were predominantly El Niño. This was the opposite of the data presented herein that were collected during mainly La Niña conditions. The differing results of the Hauraki Gulf studies and the inter-annual variability in sighting rates in this study could well be explained by such a climate driven system, as was reported by Salvadeo et al. (2011). For instance, the change from La Niña to neutral conditions in 2012 may have had some effect on the distribution of whales off GBI between 2011 and 2012, possibly linked to changes in prey distribution. Indeed, evidence for the significant top-down effects of inter-decadal climate variability on oceanic ecosystems were described for the Gulf of Alaska, where climate was linked to an increase in predatory fishes, with subsequent declines in forage fish that in turn affected bird and mammal populations (Francis et al. 1998).

Bryde's whale distribution was relatively consistent across seasons in the IHG, with central northerly regions commonly used, as reported in previous studies (O'Callaghan & Baker 2002; Baker & Madon 2007; Behrens 2009; Wiseman et al. 2011). The high density areas (south of Kawau Island and west of Coromandel town) predicted by Riekkola (2013) from platform of opportunity data were not identified as hotspots in this study, most likely due to differences in survey methodologies and analyses. The data presented by Riekkola (2013) were primarily collected from platforms of opportunity that were restricted by factors such as permit limitations and sailing times. If search effort on board platforms of opportunity is not evenly distributed in space or time due to logistical constraints (Redfern et al. 2006), the distribution of sightings will likely be more representative of the vessels and observers than true animal distribution (Sveegaard 2011). The benefits of using an independent research vessel in the present study were that search effort was not restricted by set departure schedules, and broader, more uniform spatial coverage of the Hauraki Gulf could be achieved.

In the IHG, relative hotspots were located further south in winter and further north in spring, in similar regions to common dolphin hotspots during those same seasons. Common dolphins and Bryde's whales consume some of the same prey species such as pilchards and jack mackerel (Meynier et al. 2008; Wiseman 2008), and are known to feed in multi-species feeding associations with other marine predators such as Australasian gannets (*Morus serrator*, Burgess 2006; Machovsky Capuska et al. 2011). Since prey species such as pilchards are pelagic (Kendrick & Francis 2002), foraging locations for common dolphins and Bryde's whales may be significantly affected by circulation patterns, particularly in the case of the Hauraki Gulf, where surface winds play an important role in ocean dynamics (Black et al. 2000). Therefore, the similar distributions of these species in the IHG during the colder seasons may be linked to the distribution of their prey more so than at other times of the year when reproductive requirements may influence habitat use to a greater degree. Penry et al. (2011) also suggested the decrease in whale encounter rates in Plettenberg Bay in winter may have been associated with prey movements, since increased sightings of whales further north along the coast coincided with the annual north-eastward migration of sardine. Movements of pilchards and other small schooling fish such as anchovy are poorly known for the northeast coast of the North Island, and large-scale movements akin to the 'sardine run' in South Africa are not known in New Zealand waters. Instead, pilchards are present year-round and show variability in seasonal and annual abundances (Young & Thomson 1926; Paul et al. 2001).

While whales used similar regions of the IHG across all survey years, the data were more variable for GBI. Densities were high off the southwest coast of GBI in 2011 but fewer encounters were made in 2012, and these were located further north in summer and autumn of that year. There were also significant differences between whale and common dolphin distributions off GBI, with whales found almost exclusively off the southwest coast of GBI in 2011 and common dolphin densities highest in northern waters associated with the Cradock Channel. This raises the question as to whether Bryde's whales feed more frequently on fish in IHG waters but more often on krill in outer Hauraki Gulf waters, akin to Bryde's whales in South Africa feeding primarily on krill in pelagic waters and fish in coastal waters (Best 1977).

When southeasterly winds reach moderate velocities, the strongest upwellings in the Hauraki Gulf occur on the leeward side of GBI (Black et al. 2000). This corresponds with the Bryde's whale hotspot that was particularly evident in 2011 when La Niña conditions were strong and therefore more easterly winds were prevalent (Renwick et al. 2010a). If these upwellings from the Colville Channel are more highly associated with krill than other regions, it could explain some of the variation in Bryde's whale and common dolphin distributions in GBI waters. There is currently no available evidence as to whether Bryde's whales are more likely to feed on krill or fish in outer Hauraki Gulf waters. However, krill are known to be present in outer Gulf waters yet scarce in the IHG (Jillet 1971), and DNA from ray-finned fish was present in all ten Bryde's whale faecal samples collected in IHG waters (Jarman et al. 2006), but krill and amphipod DNA were only present in seven and three samples, respectively. The results of the DNA study may be suggestive of a higher incidence of whales feeding on fish compared with krill in the IHG, as reported by Wiseman (2008). Feeding preferences of whales using GBI waters remain unknown.

2.4.3 Bottlenose dolphin

Bottlenose dolphins were infrequently encountered in the IHG, but were regularly encountered at GBI across all seasons. Unfortunately, sample sizes for the IHG were too small to conduct any meaningful statistical analyses, rendering the discussion of bottlenose dolphin distribution in the IHG considerably limited. SR for GBI (0.010 groups per kilometre) was similar to the values reported for bottlenose dolphins in other warm temperate waters like the eastern Ionian Sea, Greece (0.011 groups per km, Bearzi et al., 2005), Northern Evoikos Sea, Greece (0.010 groups per km, Bonizzoni et al. 2014) and off southern Spain (0.004–0.012 groups per km, Cañadas & Hammond 2006). ERs (individuals per kilometre) for GBI were high during spring and summer when group sizes were largest and calves were most prevalent (Dwyer et al. 2014a; Chapter 5). The lowest densities at GBI were consistently recorded during autumn when group sizes were smallest, which also coincided with the highest number of encounters in IHG waters in this study, and the most observations in an opportunistic photo-identification study conducted in the IHG between 2000 and 2003 (Berghan et al. 2008). Based on individual photo-identification (Dwyer et al. 2014a; Chapter 5), there appears to be some movement of frequently sighted individuals away from the GBI region in autumn when the lowest number of frequent users was recorded, which also coincides with an influx of occasional visitors to the GBI area.

Distribution at GBI varied according to season, with groups found closest to shore in winter and spring and furthest from the coast in summer. This pattern was consistent across years and concurs with research conducted in the Bay of Islands, Northland, where bottlenose dolphins were distributed in shallower waters during winter and deepest waters during summer (Constantine & Baker 1997; Constantine 2002). A definitive cause for this seasonal shift could not be determined in the Bay of Islands due to a paucity of data on prey movements, and the same is true for GBI. This warrants further investigation as it may have implications for the general movement patterns of this population and subsequent management plans. Additionally, while both northern and southern regions of the coast were used in all seasons, the Whangaparapara to Blind Bay area was a hotspot for bottlenose dolphins in all seasons except for autumn, when distribution and density were more uniform along the coast. That southwestern region of the coast appears to be important for groups with calves, as discussed in Dwyer et al. (2014a) and Chapter 5.

Populations of bottlenose dolphins around the world are known to reside within limited home ranges, with changes in seasonal distribution within those home ranges typically proposed to relate to prey movement (Scott et al. 1990; Elliott et al. 2011). This appears to be the case for the North Island bottlenose dolphin population, with some areas like the Bay of Islands and GBI used more frequently than others, such as the IHG or ECBOP (Constantine 2002; Berghan et al. 2008; Dwyer et al. 2014a; Meissner et al. 2014). Prey distribution, rather than reproductive requirements or predation pressure, has previously been considered the main driver of bottlenose dolphin movements in the Bay of Islands (Hartel 2010). An influx of different prey species from the EAUC in the warm season has been suggested to explain the seasonal movements of bottlenose dolphins to deeper waters (Constantine & Baker 1997; Hartel 2010). If this is the case and dolphins maximise foraging opportunities in regions that are more directly affected by the EAUC, it could also help to explain the absence of sightings in the IHG during summer, given that the EAUC only passes by the northerly entrance of the IHG (Zeldis et al. 2004). This concurs with increased sightings of coastal bottlenose dolphins in ECBOP waters during summer; however, the ECBOP data were based on small sample sizes and a large proportion (57%) of survey effort in summer (Meissner et al. 2014), making it difficult to draw any strong inferences. Nevertheless, bottlenose dolphins observed in the ECBOP were predominantly engaged in foraging activity (Meissner et al. 2014), providing support for the hypothesis that seasonal movements of bottlenose dolphins in this region may be predominantly related to prey movements. The consistent seasonal use of GBI waters, albeit by varying densities of dolphins, suggests a sufficient year-round food supply to support a population. GBI also offers a similar type of habitat to the Bay of Islands, with sheltered bays located adjacent to deeper shelf waters influenced by the EAUC. As discussed for common dolphins and Bryde’s whales, it is apparent that more information about prey distribution, movements and abundance are required to understand bottlenose dolphin distribution patterns.

There were considerable differences in the encounter rates of bottlenose dolphins in the IHG compared with GBI. However, the sizes of the two study areas may have had some effect on results since the IHG study area was much larger than the GBI study site (3480 km^2 *cf*. 542 km^2 of search area within grid cells) and could not be fully surveyed in a single day. This likely lowered the probability of encountering a group of bottlenose dolphins in the IHG on any given day if, for example, there was only one group available to be detected, relative to the greater proportion of the GBI study area that could be surveyed in one day. However, even taking this into account, it appears that GBI is a potential hotspot for bottlenose dolphins in the Hauraki Gulf, especially considering the relatively high levels of individual site fidelity to the area (Dwyer et al. 2014a; Chapter 5).

2.4.4 Summary

Hauraki Gulf waters are clearly important year-round for a number of cetacean species. Distribution and density patterns were strongly seasonal for bottlenose dolphins, less so for common dolphins that exhibited some levels of inter-annual variability, and highly variable for Bryde’s whales that may be influenced to a greater degree by changes in climate systems that influence ocean circulation patterns. Central northern IHG regions were important for common dolphins and Bryde’s whales year-round. The inshore movement of common dolphins in Hauraki Gulf waters during winter may represent an overall offshore to inshore shift in distribution, combined with an influx of dolphins into the Gulf from the wider surrounding areas of the northeast coast. This is likely to be related to prey distribution, given that common dolphin prey such as pilchards are known to be more abundant in bays and harbours in New Zealand when water temperatures are cooler. Common dolphins also appear to move offshore during summer and autumn, when densities are low in the IHG but high off GBI.

The west coast of GBI was important for bottlenose dolphins during all seasons, and was variable for Bryde’s whales in one survey year compared to the other. Again, this variability for Bryde’s whales is likely related to changes in prey availability as a consequence of changes in climate conditions. The disparity between common dolphin and Bryde’s whale distributions in GBI waters compared with IHG waters raises the question of whether whales feed more frequently on fish in IHG waters but more often on krill in outer Hauraki Gulf waters, at least during some years.

Bottlenose dolphins were sighted infrequently in the IHG, but were regularly encountered at GBI across all seasons. The consistent seasonal use of GBI waters, albeit by varying densities of dolphins, suggests a sufficient year-round food supply to support the population. The year-round high encounter rates at GBI compared with the IHG support the hypothesis that GBI is a hotspot for bottlenose dolphins of the North Island population.

It is important to remember that the results of this study occurred under predominantly La Niña conditions. Given the strong effects of winds on ocean circulation in the Hauraki Gulf, variations in patterns described here may vary under more neutral and El Niño conditions. The results presented here provide useful seasonal distribution and density information to support management initiatives, in particular marine spatial planning — a scheme currently under development for the Hauraki Gulf. Additionally, relative abundance indices not only enable global comparisons with other populations of these species, but also provide baseline values for the Hauraki Gulf that can be used for future monitoring purposes.

Chapter 3

Habitat use by cetaceans in the Hauraki Gulf

Common dolphin (*Delphinus* sp.) of neonate age class, Bryde's whale (*Balaenoptera edeni*) feeding, and bottlenose dolphins (*Tursiops truncatus*) close to shore in the Hauraki Gulf. Photos: Sarah Dwyer.

3.1 INTRODUCTION

Understanding how animals use the space in which they are distributed is important for guiding management decisions in conservation. The term 'habitat use' has been applied to the way an animal uses a collection of physical and biological components in a habitat (Hall et al. 1997). Scientists often use the term to describe correlations with specific habitat features (Bergin 1992). Habitat use may also be defined in relation to the proportion of time that animals spend in a particular habitat (Beyer et al. 2010). This chapter focuses on the habitat use of the three focal cetacean species within the Hauraki Gulf, specifically describing the potential relationships with physical and biological components of the Gulf environment.

In terrestrial and aquatic systems, key extrinsic factors known to influence habitat use include food availability, distribution of predators, and the effects of inter- and intraspecific competition (e.g. Sinclair 1985; Lima & Dill 1990; Turner 1996; Lurz et al. 2000; Acevedo-Gutiérrez 2009). However, such data are often difficult to obtain at the appropriate spatial and temporal scales. As a result, most cetacean habitat use studies investigate the relationship between occurrence and environmental predictors of these factors that are more readily obtainable (e.g. Panigada et al. 2008; Marubini et al. 2009; Garaffo et al. 2010; Santora 2011). For instance, cetacean associations with environmental factors such as sea surface temperature (SST) are often classified as a secondary relationship, indirectly used as a proxy for prey distribution (Heithaus & Dill 2002; Bräger et al. 2003; Azzellino et al. 2008; Dawson et al. 2013; Eierman & Connor 2014).

Biological factors of the cetaceans themselves, such as group composition, are also known to affect habitat use. Hartel et al. (2014) identified that bottlenose dolphin (*Tursiops truncatus*) group composition affected habitat use in the Bay of Islands, New Zealand, with groups containing calves found in shallower water with a lesser degree of benthic slope than groups without calves. A similar trend was detected for short-beaked common dolphins (*Delphinus delphis*) in the southwestern Mediterranean (Cañadas & Hammond 2008), where groups containing calves were found in shallower waters closer to shore. This suggests nursery groups may be preferentially using shallower more protected waters than other group members.

Since habitat heterogeneity and the biological requirements of a species interact to produce patterns in geographical distribution and habitat use (Ballance 1992), linking behaviour to information on distribution enables a better understanding of the function behind any habitat use patterns (Hastie et al. 2004). For example, Chilean dolphins (*Cephalorhynchus eutropis*) off Chiloé Island, Chile, use areas close to rivers and streams intensively, which mostly correlates with feeding (Ribeiro et al. 2007). Spinner dolphins (*Stenella longirostris*) in the Hawaiian Islands, USA, rest in shallow, sandy areas during the day and forage in deep waters at night (Norris & Dohl 1980). Habitat use by snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback (*Sousa chinensis*) dolphins in Queensland, Australia, also appeared to be driven by foraging preferences (Parra et al. 2006a).

A suite of modelling techniques has been used in habitat use studies over the years, with multiple regression approaches such as generalised linear models (GLMs), generalised additive models (GAMs) or regression trees commonly applied (Guisan & Zimmermann 2000). In addition to understanding which variables may be more important, habitat models also serve a predictive purpose and are useful tools in guiding conservation and management. Models may be used to define boundaries of proposed Special Areas of Conservation (SAC; Cañadas et al. 2005) or guide initiatives such as marine spatial planning (MSP; Redfern et al. 2013) and marine protected area (MPA) design (Silva et al. 2012).

This chapter uses habitat modelling to examine cetacean habitat use in the Hauraki Gulf, New Zealand; a body of water for which the first national marine spatial plan is being developed. The Hauraki Gulf supports a range of megafauna including a diversity of marine mammal species (O'Callaghan & Baker 2002; Berghan et al. 2008; Stockin et al. 2008a; Wiseman et al. 2011; Dwyer et al. 2014a). Common dolphins (*Delphinus* sp.) and Bryde's whales (*Balaenoptera edeni*), the most commonly sighted species, have been the focus of the majority of the cetacean research conducted in the Gulf over the past fourteen years (e.g. O'Callaghan & Baker 2002; Schaffar 2004;

Burgess 2006; Baker & Madon 2007; Stockin et al. 2008c; 2009a; Behrens 2009; de la Brosse 2010; Wiseman et al. 2011; Riekkola 2013). As a result, the importance of the region for feeding (Stockin et al. 2009a; Wiseman 2008) and nursing (Stockin et al. 2008a; Wiseman 2008) for these species has been highlighted. Bottlenose dolphins, the third most frequently sighted species in the Hauraki Gulf, have received less attention, in part due to the lack of dedicated study (Berghan et al. 2008).

The aims of this chapter were to investigate habitat use by cetaceans in the Hauraki Gulf by using species distribution modelling (SDM) in the form of GLMs/GAMs to address the following objectives:

- Identify important variables that may affect the occurrence of common and bottlenose dolphins and Bryde's whales in inner Hauraki Gulf (IHG) and west coast of Great Barrier Island (GBI) waters;
- Use models to make predictions for the probability of encountering each dolphin or whale species in the IHG or off GBI; and
- Include behavioural information that may help further explain habitat use, i.e. predictors of feeding and nursery groups.

3.2 MATERIALS AND METHODS

3.2.1 Study area

The Hauraki Gulf (Fig. 3.1) is a relatively shallow, semi-enclosed body of water on the northeast coast of the North Island, New Zealand (Manighetti & Carter 1999; Black et al. 2000). Information about the Hauraki Gulf, including its geography and factors affecting hydrodynamics, is provided in Chapter 2 (Section 2.2.1). Two regions of the Hauraki Gulf were sampled in this study, the IHG and GBI (Fig. 3.1). Further details about the two study sites, including average water depths and SSTs, are also provided in Chapter 2 (Section 2.2.1).

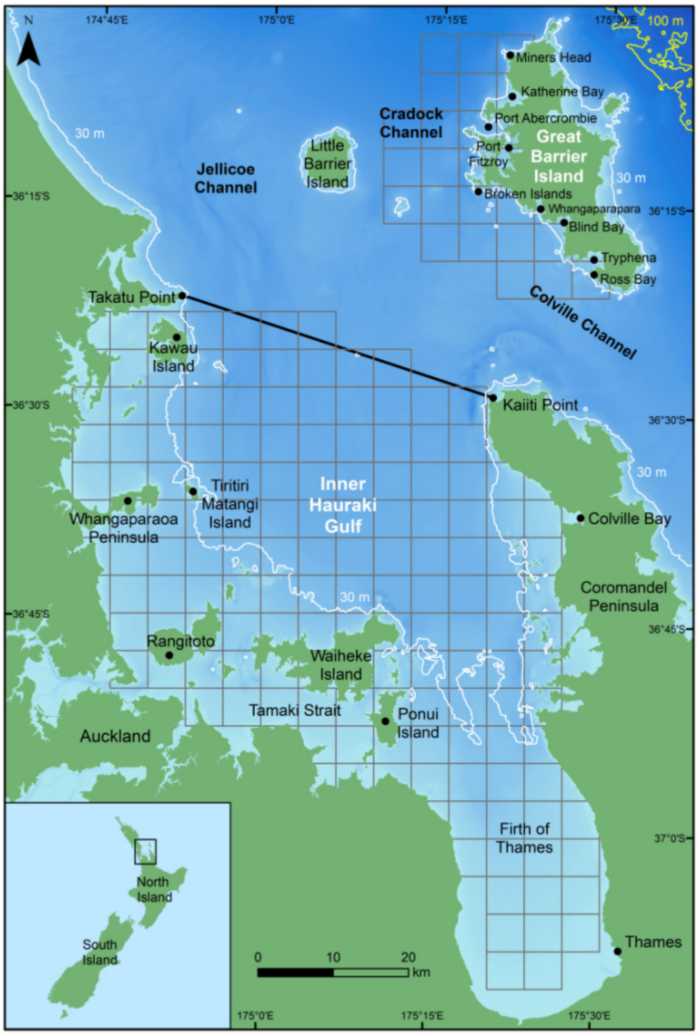

Figure 3.1 Map of the Hauraki Gulf, New Zealand. The solid black line (from Takatu Point to Kaiiti Point) indicates the boundary between the inner and outer Hauraki Gulf, the white lines show the 30 m isobath and the yellow lines the 100 m isobath. Bathymetry is depicted with darker shades of blue representing deeper waters; data courtesy of NIWA (Mackay et al. 2012). Inset: Location of the Hauraki Gulf, North Island, relative to New Zealand.

3.2.2 Data collection

Sighting data were collected during dedicated monthly boat surveys conducted between January 2010 and November 2012 from the Massey University research vessel *Te Epiwhania*, a 5.5 m Stabicraft boat powered by a 100 hp four-stroke engine. Starting in January 2011, monthly research trips averaging four days in duration were made to GBI when possible (i.e. when weather and sea conditions permitted). Survey design is described in detail in Chapter 2 (Section 2.2.2). In brief, time spent travelling along survey tracks actively searching for marine mammals, with vessel speed maintained at ~10 knots, was classified as *on effort*. When the vessel left the survey track to approach marine mammals, the survey mode was *off effort* until returning to the track to resume searching. *Off effort* mode also included all other occasions when the vessel was away from the survey track (e.g. returning to harbour due to deteriorating sea conditions and collecting data on a sighting group).

When a cetacean group/individual was detected, the vessel stopped on the transect line to record the sighting cue and estimated distance to the sighting from the vessel. The distance was always estimated by the author to prevent observer bias. The vessel subsequently left the track (i.e. *off effort*), approached to within 50 m of the group/individual, and commenced data collection. Water depth (± 0.1 m) was measured using an on-board depth sounder at the location of the group when first sighted. All observational and environmental data were collected using an XDA Orbit II Windows Mobile device. CyberTracker version 3 software (Steventon et al. 2002) was programmed for logging observational data (e.g. group size) and to record the GPS position of the vessel every 60 seconds throughout the survey day. Beaufort sea state was logged at 15 minute intervals. After observational data were logged, the vessel returned to the survey route and resumed *on effort* in order to continue searching for independent groups.

Group size and composition (i.e. age class of individuals) and the initial behavioural state were visually assessed and recorded for each encounter. Details relating to group size are presented in Chapter 2. Group composition was recorded in the same manner as group size, using minimum, maximum and best estimate counts (following Kiszka et al. 2007) of all age classes. The initial behavioural state of the group/individual was assessed before the vessel reached within 50 m. When determining the behavioural state of dolphin groups, all dolphins were scanned from left-to-right. This ensured inclusion of all individuals in the group and avoided potential biases caused by specific individuals or behaviours (Mann 1999). The behavioural state was determined as the category in which > 50% of individuals were involved in, with all represented behaviours logged when an equal proportion of the group were engaged in different behaviours (Stockin et al. 2009a).

3.2.2.1 Age class and behaviour definitions

Age class and behaviour definitions follow those previously described for these three species using Hauraki Gulf waters. Due to relatively limited sample sizes for Bryde's whales and bottlenose dolphins, group composition and behavioural data were not included in habitat use analyses. Therefore, only common dolphin age classes and definitions are listed here. Bryde's whale and bottlenose dolphin definitions can be found in Appendix 3.1.

Common dolphin age class definitions follow those used by Stockin et al. (2008a):

- **Neonate**: Small calves which exhibited diagnostic features indicative of newborns such as the presence of dorso-ventral foetal folds.
- **Calf**: Animals that were approximately less than or equal to one-half the length of an adult and were consistently observed in close association with an adult animal.
- **Juvenile**: Animals approximately two-thirds the size of an adult animal and frequently observed swimming in association with an adult animal but not in the infant position, suggesting that they were weaned.
- **Adult**: Fully grown dolphins not included in the prior classifications.

Common dolphin behaviour definitions follow those used by Stockin et al. (2009a):

- **Forage/feed**: Dolphins involved in any effort to pursue, capture, and/or consume prey, as defined by observation of fish chasing (*herding*), coordinated deep diving and rapid circle swimming. Prey frequently observed at the surface during foraging activity of the dolphins.
- **Mill**: Dolphins exhibited non-directional movement, frequent changes in heading that prevent animals from making headway in any specific direction.
- **Rest**: Dolphins observed in a tight group (< 1 body length between individuals), engaged in slow manoeuvres with little evidence of forward propulsion. Surfacing appears slow and is generally more predictable than those observed in other behavioural states.
- **Social**: Dolphins observed chasing, copulating, or engaged in any other physical contact with other dolphins (excluding mother-calf pairs). Aerial behaviours such as breaching are frequently observed.

- **Travel**: Dolphins engaged in persistent, directional movement, making noticeable headway along a specific compass heading.

3.2.3 Data analysis

3.2.3.1 Spatial extent

As detailed in Chapter 2, grids of 5 x 5 km cells were created for the IHG and GBI study areas using the grid index features tool in ArcGIS version 10.0 (ESRI, Redlands, California, USA). Cell size was determined by the size of the study areas and the overall coverage of survey effort in order to ensure adequate spatial replication. All spatial data were processed using ArcGIS and Geospatial Modelling Environment (GME) version 0.7.2.0 (Beyer 2012), as per Chapter 2.

3.2.3.2 Sampling data

Search effort was expressed as the number of kilometres of effort through a grid cell per survey day. Vessel tracks were downloaded from CyberTracker and processed as CSV files to remove all *off effort* portions of the tracks before importing into ArcMap. Survey tracks were intersected by the respective grid polygons and the *sumlinelengthsinpolys* command in GME was used to calculate the amount of effort in kilometres in each grid cell.

Beaufort sea state values were assigned to each 5 x 5 km grid cell for each sampling occasion (i.e. each time the vessel track passed through a cell on a survey day). The value corresponded with the sea state recorded at the mid-point of the vessel track within each grid cell.

A detailed account of how sighting data were processed is provided in Chapter 2. Following on from data truncation to remove outliers from the dataset, the final *on effort* sighting data were collated for each species with respect to each sampling occasion for each grid cell. Any sighting(s) of a species in a grid cell were denoted by a ‘1’ and an absence of sightings was denoted by a ‘0’. Additionally, feeding groups were classified as all groups for which the initial behavioural state ‘forage/feed’ was recorded. Nursery groups of dolphins were defined as groups including at least one neonate. This conservative definition was selected rather than 'groups that contained at least one neonate and/or calf' because calves are present in the Gulf year-round and are found in a high proportion of groups (Stockin et al. 2008a). Nursery groups of Bryde's whales were groups that contained at least one mother-calf pair. Feeding and nursery groups were then assigned a '1' and groups initially observed in other behavioural states or that did not include neonates were assigned a '0'.

3.2.3.3 Environmental data

The following static and dynamic environmental variables were considered to influence the distribution of common and bottlenose dolphins and Bryde's whales: Depth, slope, tidal current, SST, net primary production (NPP), and predominant monthly wind direction. The mean depth (m) and slope (°) of grid cells were calculated in ArcMap using the NIWA Hauraki Gulf bathymetric dataset (Mackay et al. 2012) and the Spatial Analyst tools *slope* and *zonal statistics*. Depth data for cells where cetaceans were recorded (i.e. presence) were collected using the on-board depth sounder and within 100 m of the position of the group when it was first sighted. For cells where cetaceans were not encountered (i.e. absence), depth was retrieved at the midpoint of the track segment in each cell surveyed using the NIWA Hauraki Gulf bathymetric dataset (Mackay et al. 2012). The mean maximum tidal current for each grid cell was extracted from the existing New Zealand Marine Environment Classification raster 'tidal_curr', which was calculated as the depth averaged maximum tidal current speed in metres per second (Snelder et al. 2005).

For temporally dynamic variables, daily SST data (° C) were obtained from the Physical Oceanography Distributed Active Archive Centre (PO.DAAC, NASA Jet Propulsion Laboratory, Pasadena, California, USA) at a 1 km spatial scale and subsequently averaged for each 5 x 5 km grid cell. These data were used to calculate the monthly mean SST values for each region. The SST within-month standard deviation was calculated for each grid cell as a measure of variability that is expected to be large where strong oceanographic activity occurs in regions of strong spatial gradients (Hadfield et al. 2002). NPP data (mg C/m**2) were remotely collected (www.science.oregonstate.edu/ocean.productivity) and based on the Vertically Generalised Production Model (VGPM; Behrenfeld & Falkowski 1997). The VGPM is a model that estimates net primary production from chlorophyll using a temperature-dependent description of chlorophyll-specific photosynthetic efficiency. NPP values were extracted as 8-day averages for each grid cell and NPP within-month standard deviation was also calculated. NPP values could not be obtained for all IHG grid cells, mainly due to cloud cover. Given the influence of wind direction on the occurrence of upwellings in the Hauraki Gulf, hourly wind data were extracted from the NIWA CliFlo database (CliFlo: NIWA's National Climate Database on the Web) to determine the most frequent wind direction each month. The Whangaparaoa weather station (36° 36′ S, 174° 50′ E) was selected based on its latitudinal position near the overall centre of the study areas and because data were available for the entire study period *cf*. the Cape Colville weather station (36° 29′ S, 175° 20′ E). Seasonal wind roses were plotted using www.enviroware.com to visualise the wind data.

3.2.3.4 Spatial data

The spatial variables considered for the models were easting, northing, distance to shore, and distance to Colville Channel (dist_channel). Distance to Colville Channel was chosen as a proxy for the local environment since the Colville Channel experiences the strongest currents in the Hauraki Gulf (Manighetti & Carter 1999). Distance to shore (km) and distance to Colville Channel (km) were calculated using the *near* tool to measure the distance between the centroid of each grid cell and the nearest point of land or the midpoint of the Colville Channel, respectively. If a cell centroid was located on land, the distance to shore was classified as zero.

3.2.3.5 Models and predictions

The data were examined for evidence of non-linearities and since none were found (with the exception of common dolphin feeding groups for which a GAM was fit), GLMs were chosen over GAMs to model the probability of encountering a species, where the response variable was the presence (positive observation) of a sighting in a grid cell. A binomial distribution was used with a logit link function. Given the different characteristics and sampling periods for the IHG and GBI study sites, separate models were fit for each species in each region. After modelling overall occurrence, the probability of encountering feeding or nursery groups was modelled separately where possible (i.e. where sample size allowed). Analyses were carried out in R version 3.1.0 (R Core Team 2014).

The following were fit as covariates in the initial model: year, season, northing, easting, depth, slope, distance to shore, distance to Colville Channel, tidal current, SST, SST within-month standard deviation, NPP, NPP within-month standard deviation, predominant monthly wind direction, effort, Beaufort sea state, and all meaningful interactions among the variables. These variables were selected based on their hypothesised biological importance and the feasibility of obtaining reliable measurements, with northing and easting included as proxies for unknown variables. Austral seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) to facilitate comparisons with previous studies conducted on common dolphins (Stockin et al. 2008a), bottlenose dolphins (Berghan et al. 2008) and Bryde's whales (Wiseman et al. 2011) in the Hauraki Gulf. Since NPP data could not be obtained for all IHG grid cells, models were initially run using only the grid cells for which NPP data were available. If the NPP variable was not considered a significant factor, the models were re-run using the full set of grid cells and omitting the NPP variable.

The variance inflation factor (VIF) was used to assess multicollinearity. Predictors with a VIF greater than 2 were considered highly correlated (i.e. conservative approach selecting threshold of 2, see Kutner et al. 2004). In such cases, the most biologically meaningful variable was typically selected. The initial model fit all remaining variables that could plausibly be useful in predicting the distribution of the species. Typically, this led to an extremely large candidate set of possible models (when including pair-wise interactions). The candidate set was investigated using the *glmulti* package in R (Calcagno 2013). The top five models were examined using BIC (Bayesian Information Criterion) and were used as a basis for further investigation into variable selection. A more parsimonious model was then fit using step-wise selection with manual intervention ensuring important covariates (i.e. effort and Beaufort sea state) were still included. Beaufort sea state was retained in all models because of its known effect on detecting cetaceans during field studies (e.g. Barlow et al. 1988; Gannier 2005) and by including it as an explanatory variable models could consider at least some detection effects (Forney 2000). Similarly, effort was retained in all models to account for the fact that more search effort is expected to yield more sightings. Confidence intervals for each parameter were calculated assuming asymptotic normality. A likelihood-ratio test was used to check pairs of models for the deviance explained by each covariate, or the interaction between two covariates (where applicable). These pairs consisted of the final model that was compared with the same model but with a single variable dropped.

Predicted values for each grid cell were calculated at the annual or seasonal level, dependent upon which factor was significant in the final model for a given species and region. The inverse link transformation was used to obtain probability values on the scale of the original response variable since the results of the calculations were based on the scale of the linear predictor (Guisan & Zimmermann 2000). For binomial GLMs, the inverse logistic transformation is

$$p(y) = \frac{\exp(LP)}{1 + \exp(LP)}$$

where *LP* is the linear predictor fitted by logistic regression. This transformation provided probability values for each grid cell that were used to create predictive maps using ArcGIS. Predictive values were not calculated for a small number of grid cells that were not sampled in all seasons (IHG: n = 5; GBI: n = 3). These cells were not colour-coded but remained white on the predictive maps.

3.3 RESULTS

3.3.1 Sampling data

From January 2010 to November 2012, 233 days of survey effort were conducted in the IHG. A total of 887.6 h were spent *on effort* searching for marine mammals, totalling 16,785.8 km of *on effort* tracks within the IHG grid cells (Fig. 2.4; Chapter 2). Between January 2011 and October 2012, 243.9 h were spent *on effort* in the GBI study area, with track effort totalling 4017.1 km (Fig. 2.6; Chapter 2). Although attempts were made to cover all areas homogeneously, effort was not uniform across either study site (see Chapter 2).

The resulting sightings for each species are presented in Table 3.1. Some grid cells contained more than one encounter per day, but a grid cell received a '1' regardless of the number of sightings (i.e. presence, maximum one per day); hence, both total sightings and total grids with sightings are presented. Common dolphin groups could not always be assessed behaviourally or for the presence of neonates. Initial behavioural state was recorded for 350 and 65 IHG and GBI groups, respectively, with 353 IHG groups and 63 GBI groups assessed for the presence of neonates. Only occurrence models could be developed for Bryde's whales and bottlenose dolphins due to relatively small sample sizes for feeding and nursery groups (Table 3.1), therefore maps were created to show the sighting locations of feeding and nursery groups (Appendix 3.2).

Table 3.1 Sighting data for common and bottlenose dolphins and Bryde's whale in the Hauraki Gulf, New Zealand. IHG = inner Hauraki Gulf, GBI = Great Barrier Island.

Model type	IHG sightings (total)	IHG sightings (grid cell)	IHG model?	GBI sightings (total)	GBI sightings (grid cell)	GBI model?
Common dolphin occurrence	386	274	Yes	76	44	Yes
Common dolphin feeding	59	52	Yes	12	6	No
Common dolphin nursery	39	37	Yes	3	3	No
Bryde's whale occurrence	61	51	Yes	66	45	Yes
Bryde's whale feeding	21	20	No	25	18	No
Bryde's whale nursery	2	2	No	6	5	No
Bottlenose dolphin occurrence	7	7	No	36	36	Yes
Bottlenose dolphin feeding	0	0	No	7	7	No
Bottlenose dolphin nursery	3	3	No	26	26	No

3.3.2 Environmental data

For the IHG, grid cells with deeper waters were located centrally and further north, while areas with increased slope were observed close to shore (although not in southerly regions, e.g. Firth of Thames; Fig. 3.2). Regions with strong tidal currents were apparent in the Firth of Thames, close to the Colville Channel and in the channels between islands (Fig. 3.2). At GBI, water depths were greater for northern grid cells, regions of increased slope mostly occurred in grid cells closer to shore, and the greatest tidal currents were adjacent to the Colville Channel and between Little and Great Barrier Islands (Fig. 3.2).

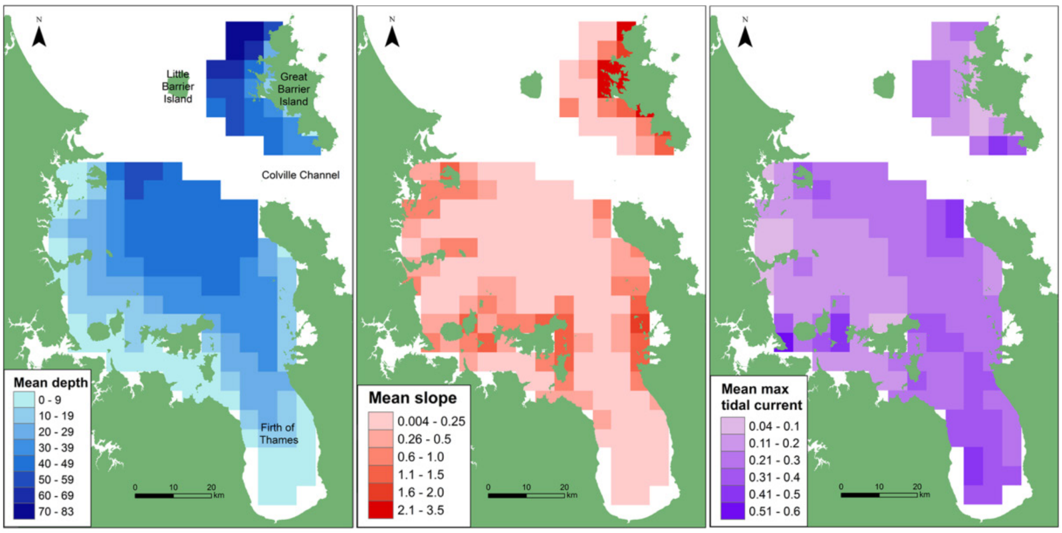

Figure 3.2 Summary of the static environmental variables depth, slope, and tidal current used in IHG (inner Hauraki Gulf) and GBI (Great Barrier Island) habitat models. Values represent weighted means for each 5 x 5 km grid cell, with darker shades for higher values.

Mean monthly SSTs revealed the coolest and warmest water temperatures were experienced in August (IHG: 13.2 ± 0.2 ° C; GBI: 14.3 ± 0.3 ° C) and February 2011 (IHG: 22.0 ± 0.1 ° C; GBI: 21.6 ± 0.1 ° C), respectively (Fig. 3.3). Temperatures were slightly less variable at GBI than in the IHG, where both the highest and lowest temperatures were recorded. Waters also remained comparatively warmer at GBI for longer in autumn and winter (Fig. 3.3). During summer, GBI inshore waters were cooler than IHG waters, especially compared with western and southern regions of the IHG where average temperatures were the highest (Fig. 3.4). In winter, GBI waters were warmer than IHG waters, with average temperatures decreasing with increasing latitude (Fig. 3.4).

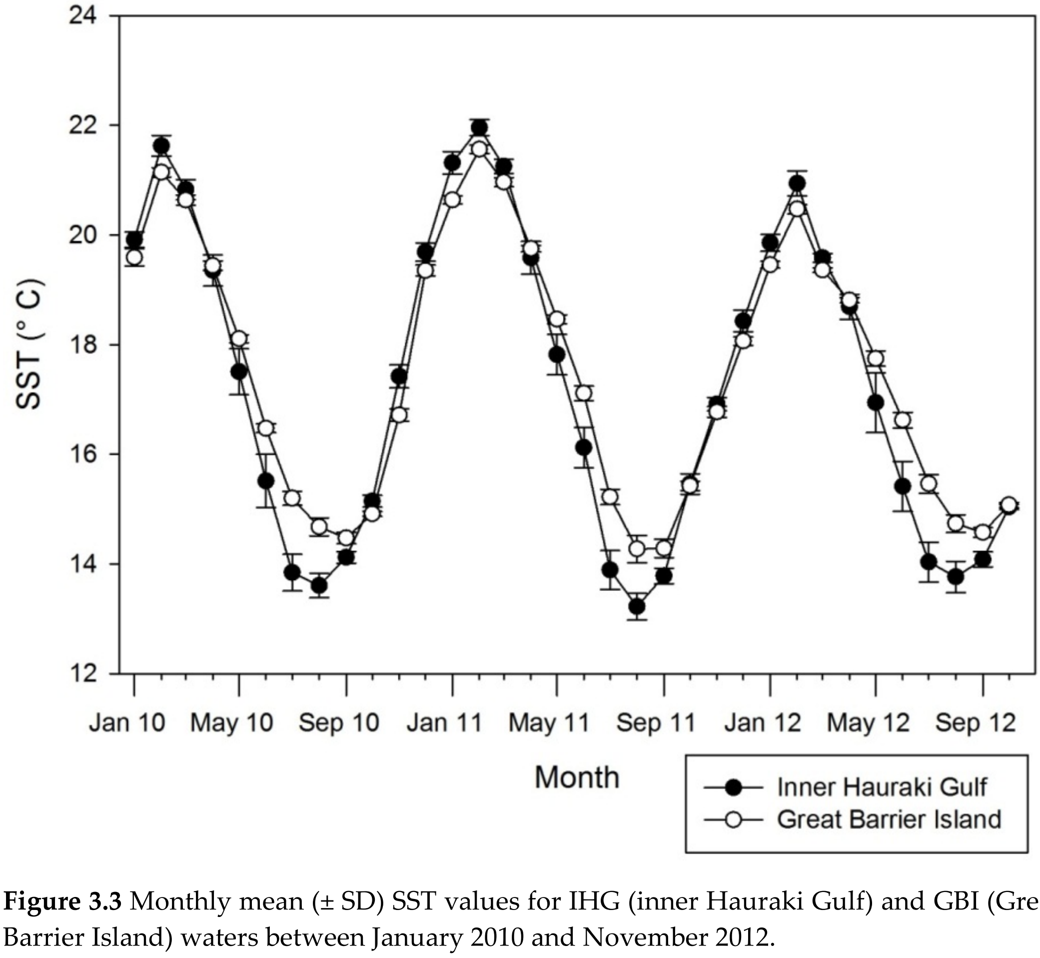

Figure 3.3 Monthly mean (± SD) SST values for IHG (inner Hauraki Gulf) and GBI (Great Barrier Island) waters between January 2010 and November 2012.

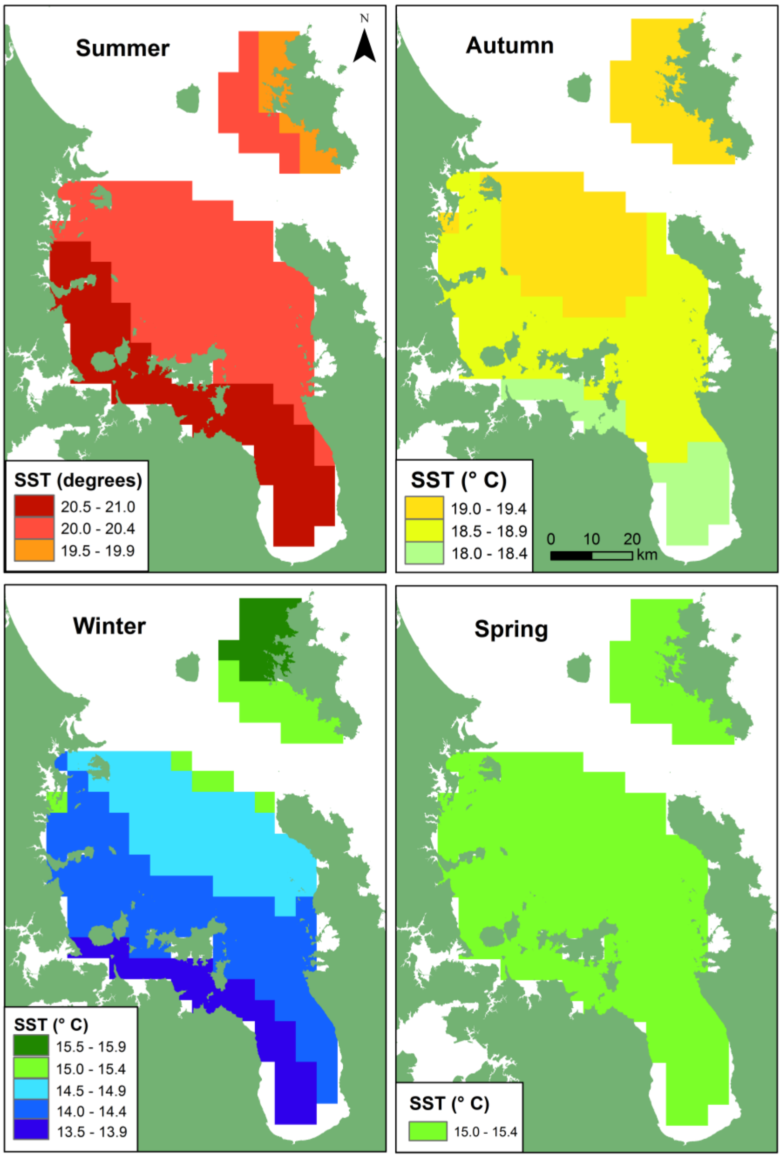

Figure 3.4 Seasonal mean SST values for IHG (inner Hauraki Gulf) and GBI (Great Barrier Island) waters between January 2010 and November 2012.

NPP values could not be obtained for all grid cells (Fig. 3.5a). Using the values that were available, the data showed some consistency across regions in 2010 and 2012, with a noticeable spike in October 2010. However, in 2011, peaks in IHG values did not correspond with peaks in GBI values and vice versa (Fig. 3.5b).

There was little temporal variability in the results of the wind data analyses, with westerly winds predominant for most months (71%, n = 24). The greatest variation occurred in 2012, when north-northeasterly winds were most frequent in summer and east-southeasterly winds dominated in autumn (Fig. 3.6).

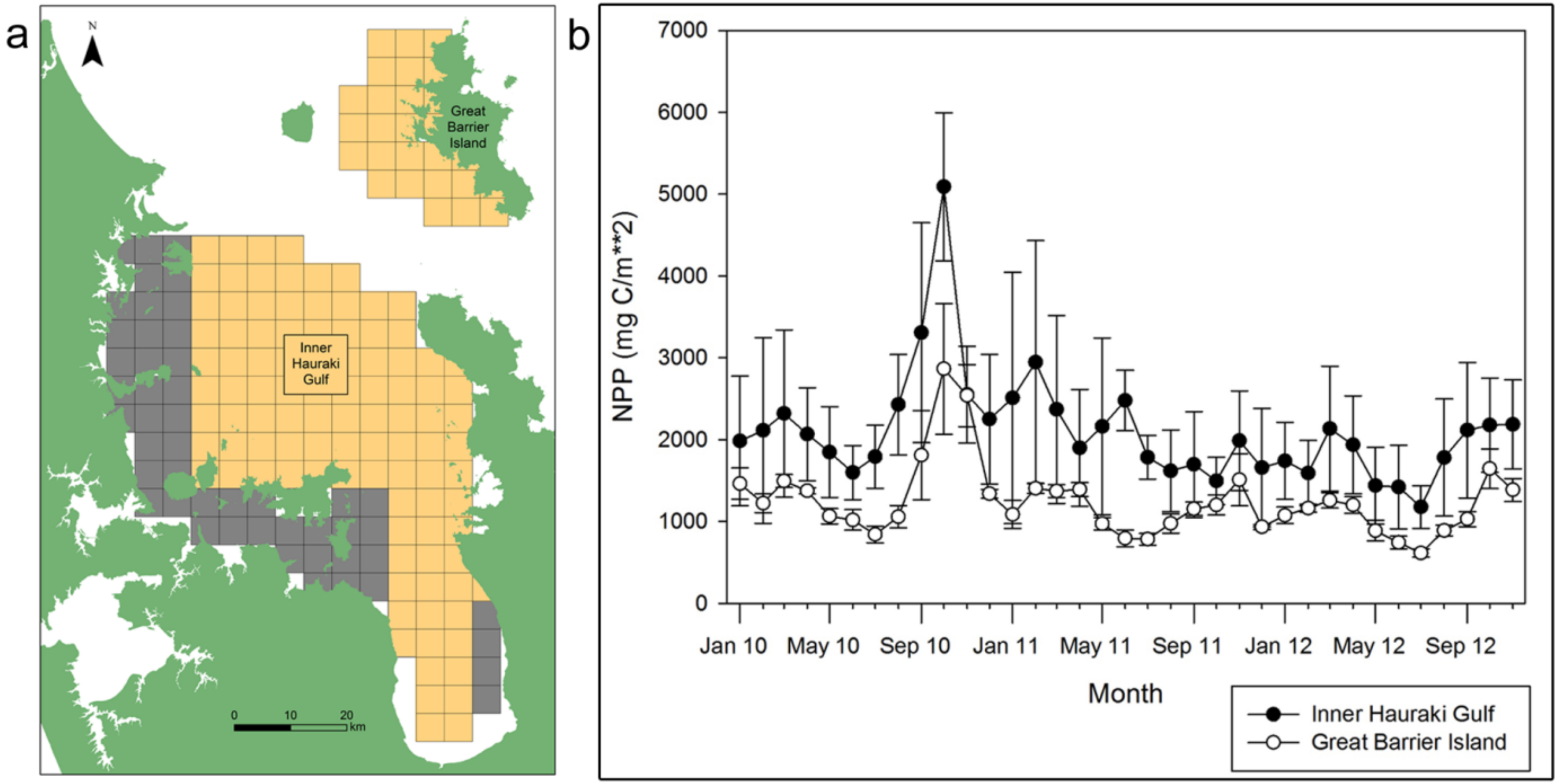

Figure 3.5 a) Values of NPP (net primary production) could not be obtained for grid cells shaded grey. Cells for which data could be obtained are yellow; b) Monthly mean (± SD) NPP values for IHG (inner Hauraki Gulf) and GBI (Great Barrier Island) waters between January 2010 and November 2012.

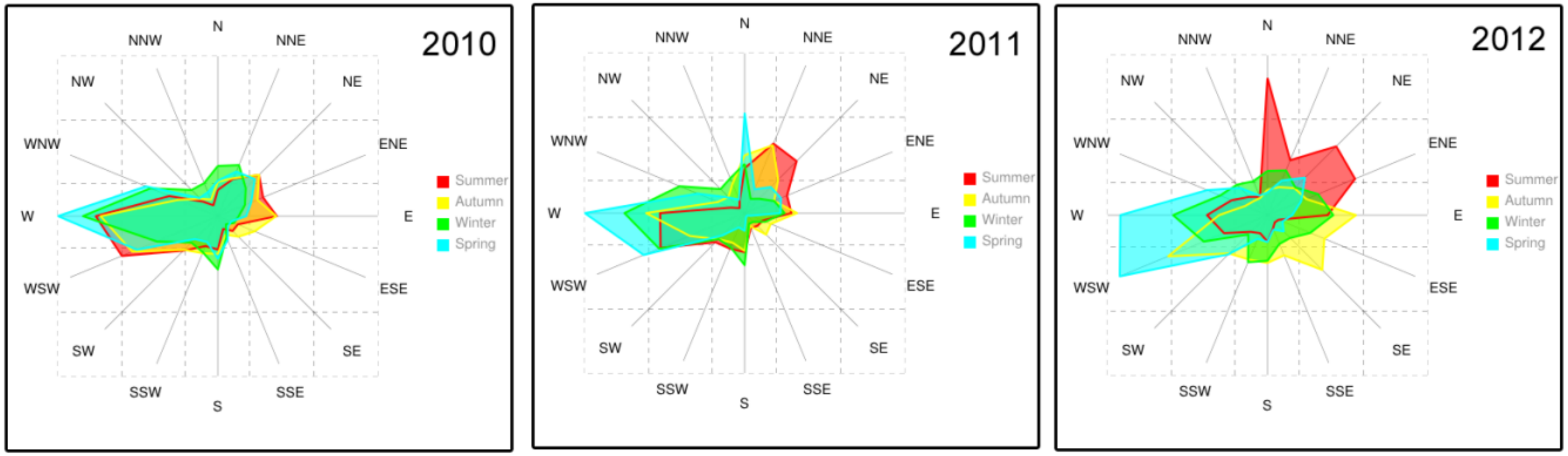

Figure 3.6 Wind roses showing predominant monthly wind direction in the Hauraki Gulf, New Zealand, between December 2009 and November 2012.

3.3.3 Habitat models

Environmental variables that were frequently important in the habitat models were depth, slope, current and SST. Wind direction and NPP were not included in any of the final models. Since the NPP variable was not considered important for models using the reduced set of grid cells (Fig. 3.5a), this variable was dropped and all subsequent models for the IHG included the full set of grid cells. For highly correlated variables, SST was selected over season, depth was chosen over distance to shore, and distance to Colville Channel was used for GBI Bryde's whale models because it had a cleaner interpretation than northing. A scatterplot and correlation matrix of key variables is shown in Appendix 3.3.

3.3.3.1 Common dolphin habitat use

The final IHG and GBI common dolphin occurrence models explained 15.3% and 11.4% of the deviance, respectively (Table 3.2). The models suggested that probability of encounter was greater in cooler water temperatures, in areas of decreased tidal current and slope, and generally in deeper waters. The exception was for GBI, where probability of encounter was greatest in shallower waters with very low SSTs (13° C; Fig. 3.7). The spatial aspect (i.e. easting) indicated probability of occurrence increased from west to east for the IHG but from east to west for GBI, although these patterns were not highly significant. Overall, the most significant variables in the common dolphin models were depth and SST (Table 3.2). Additionally, effort and Beaufort sea state were highly significant factors for the IHG, suggesting that the chances of encountering common dolphins increased with increased survey effort and decreased with higher sea states. However, neither of these variables were significant in the final GBI model.

Predictive maps indicated central northern regions of the IHG had the greatest probabilities of encountering common dolphins during all seasons (Fig. 3.8). The overall probability of encountering common dolphins increased within the IHG over winter and spring when water temperatures were cooler. Cells closer to shore also had increased probability values when SSTs were lower. At GBI, probability of encounter was greater in northern and deeper regions in summer and autumn, and greater in southern, shallower regions over winter.

Table 3.2 Parameter estimates of significant variables selected in the final common dolphin models (GLM with binomial distribution and logit link function) for the inner Hauraki Gulf (IHG) and Great Barrier Island (GBI). Interaction terms are denoted by (-); significance codes are *** 0.001, ** 0.01, * 0.05.

Area	Term	Estimate	SE	z value	p value	Explained Deviance
IHG	Intercept	2.87E-01	6.08E-01	0.472	0.6369	–
	Depth	6.09E-02	6.87E-03	8.857	< 2e-16 ***	100.130
	SST	-1.89E-01	2.44E-02	-7.747	9.41e-15 ***	63.809
	Slope	-1.88E+00	4.24E-01	-4.439	9.03e-06 ***	26.077
	Current	-5.86E+00	1.46E+00	-4.028	5.63e-05 ***	17.082
	Easting	1.69E-05	6.72E-06	2.516	0.0119 *	6.322
	Beaufort	-3.44E-01	7.14E-02	-4.821	1.43e-06 ***	23.130
	Effort	2.01E-01	3.56E-02	5.635	1.75e-08 ***	33.318

Null deviance 1997.6 on 3997 degrees of freedom
Residual deviance 1692.3 on 3990 degrees of freedom
% of deviance explained: 15.3

Area	Term	Estimate	SE	z value	p value	Explained Deviance
GBI	Intercept	1.02E+01	3.48E+00	2.929	0.00341 **	–
	SST-Depth	1.12E-02	3.86E-03	2.892	0.00383 **	12.128
	Depth	-1.77E-01	6.62E-02	-2.681	0.00734 **	–
	SST	-6.64E-01	2.06E-01	-3.221	0.00128 **	–
	Slope	-7.03E-01	2.58E-01	-2.728	0.00638 **	9.038
	Current	-7.10E+00	3.26E+00	-2.174	0.02971 *	6.247
	Easting	-9.18E-05	4.63E-05	-1.982	0.04753 *	4.480
	Beaufort	-5.16E-02	1.73E-01	-0.298	0.76575	0.088
	Effort	3.27E-02	6.46E-02	0.506	0.61251	0.255

Null deviance 341.67 on 807 degrees of freedom
Residual deviance 302.83 on 799 degrees of freedom
% of deviance explained: 11.4

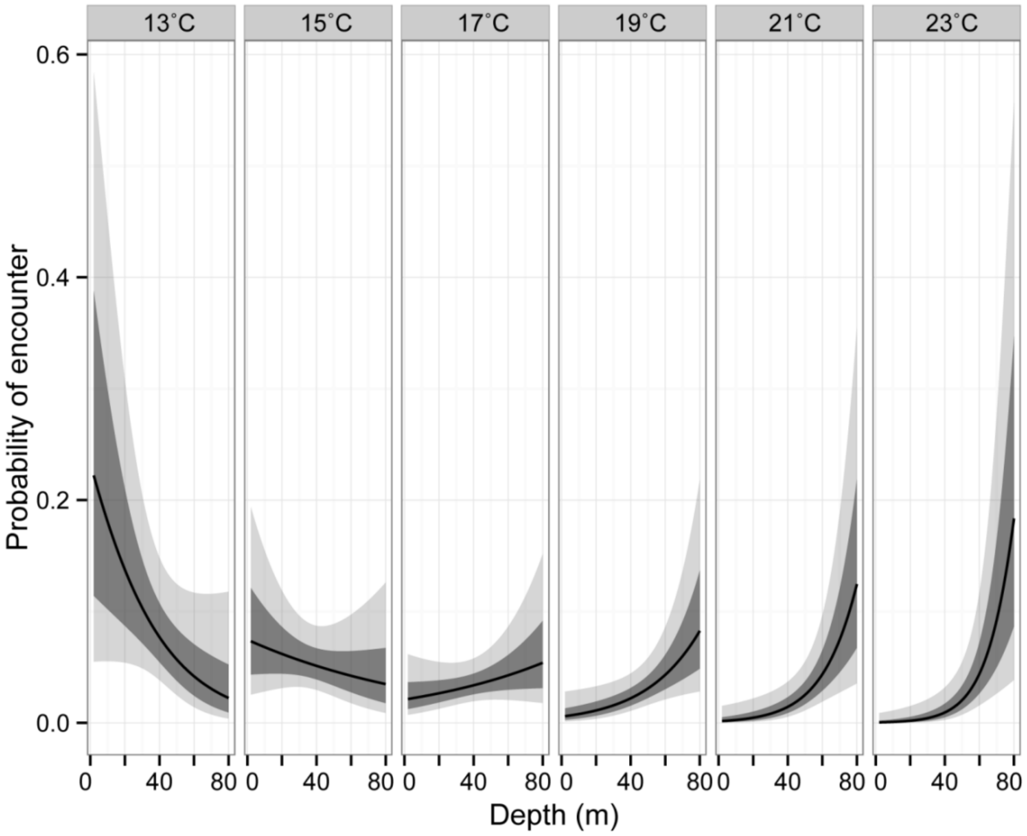

Figure 3.7 Interaction between depth and sea surface temperature (SST) on the probability of encountering common dolphins at Great Barrier Island (GBI), New Zealand. The black line is the average probability; shaded areas show one- and two-standard error intervals.

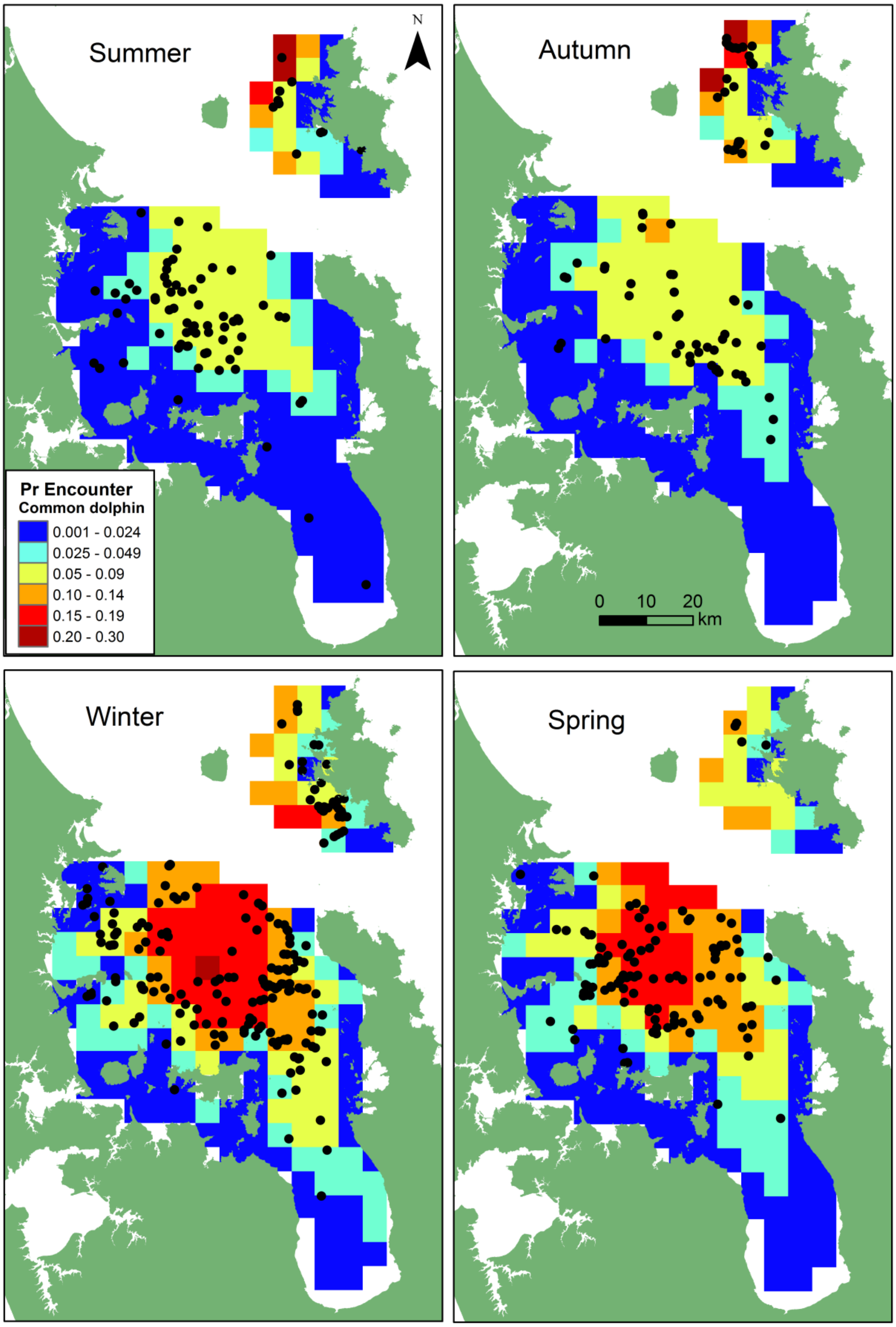

Figure 3.8 Predicted seasonal probabilities of encounter for common dolphins in the Hauraki Gulf, New Zealand. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show actual sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012 and Great Barrier Island (GBI) surveys in 2011–2012.

3.3.3.2 Common dolphin habitat use by feeding groups

Sighting data were too sparse to fit specific feeding or nursery group models for the GBI region; therefore results refer only to IHG waters. The final common dolphin model for feeding groups explained only 11.5% of the deviance (Table 3.3). The predictive maps (Fig. 3.9) showed similar patterns to the overall common dolphin occurrence maps (Fig. 3.8), with greater chance of encountering feeding groups in northern and central regions during all seasons and increased probabilities in winter and spring compared with summer and autumn. The probability of encountering feeding groups was greatest in cooler waters, in areas of decreased slope (Table 3.3) and depths of approximately 40 m (Fig. 3.10). The depth variable accounted for the most deviation in the final feeding model (Table 3.3). Effort was also a significant factor suggesting the chances of encountering a feeding group increased with survey effort.

Table 3.3 Parameter estimates of significant variables selected in the final common dolphin model (GAM with binomial distribution and logit link function) for feeding groups in the inner Hauraki Gulf (IHG). Significance codes are *** 0.001, ** 0.01, * 0.05; edf: estimated degrees of freedom.

Area	Term	Estimate	SE	z value	p value	Explained Deviance
IHG	Intercept	-2.71735	1.01389	-2.680	0.00736**	–
	SST	-0.15943	0.05291	-3.013	0.00258**	9.542
	Slope	-1.60923	0.93702	-1.717	0.08591	2.555
	Beaufort	0.05092	0.16047	0.317	0.75102	0.069
	Effort	0.19113	0.06844	2.793	0.00523**	6.776

	edf	χ^2 statistic	p value	Explained Deviance
Depth	3.04	18.15	0.00105**	29.640

% of deviance explained: 11.5

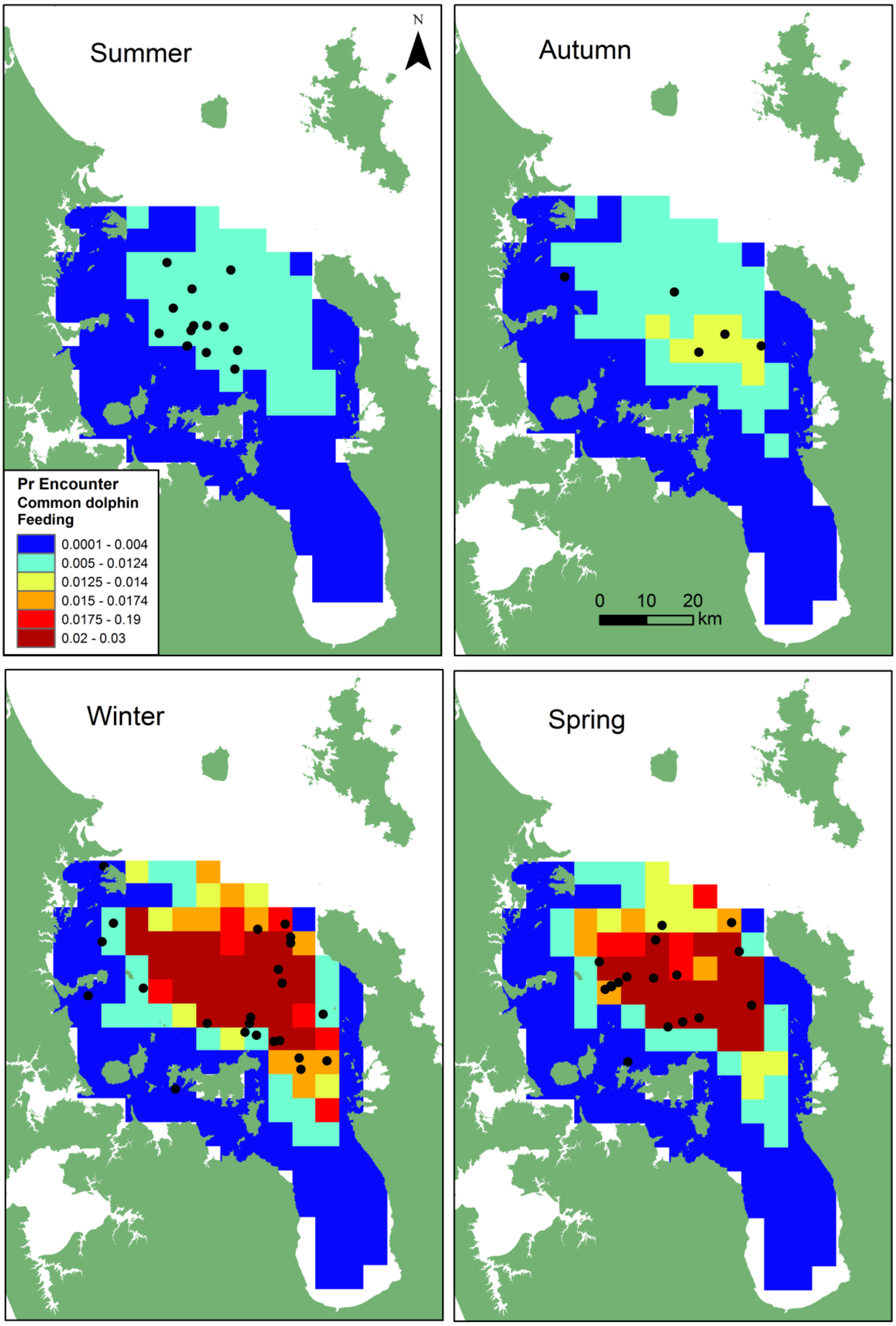

Figure 3.9 Predicted seasonal probabilities of encounter for feeding groups of common dolphins in the Hauraki Gulf, New Zealand. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show actual sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012.

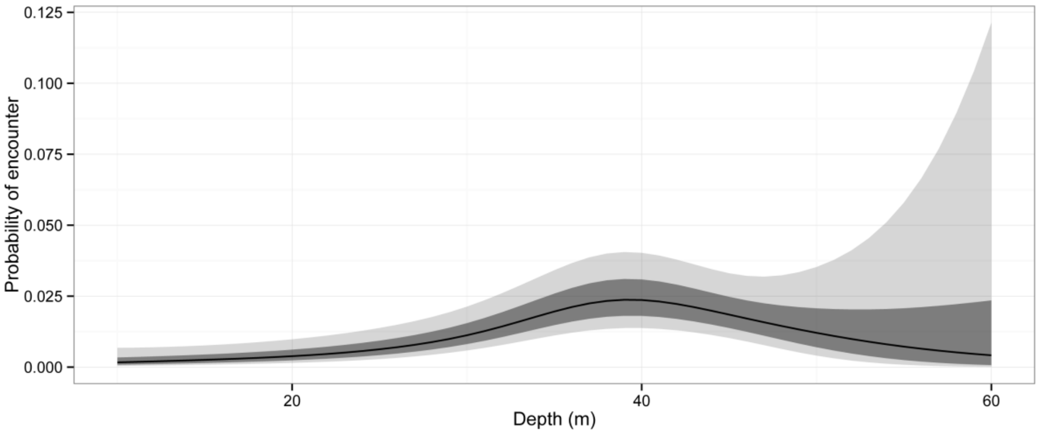

Figure 3.10 Relationship between depth and probability of encountering feeding groups of common dolphins in the inner Hauraki Gulf (IHG), New Zealand. The black line is the average probability; shaded areas show one- and two-standard error intervals.

3.3.3.3 Common dolphin habitat use by nursery groups

The final common dolphin nursery group model explained 15.1% of the deviance (Table 3.4). Probability of encounter for nursery groups was greater in warmer, slightly offshore waters in areas of decreased slope and slow tidal currents. The predictive maps suggested that the probability of encountering nursery groups was greater in summer and autumn and within more central regions of the Gulf, further south (i.e. closer to Waiheke Island) than for feeding groups (Fig. 3.11). Beaufort sea state was also a significant factor suggesting the chances of sighting a nursery group increased in calmer sea states.

Table 3.4 Parameter estimates of significant variables selected in the final common dolphin model (GLM with binomial distribution and logit link function) for nursery groups in the inner Hauraki Gulf (IHG). Significance codes are *** 0.001, ** 0.01, * 0.05.

Area	Term	Estimate	SE	z value	p value	Explained Deviance
IHG	Intercept	275.22350	120.87308	2.277	0.02279 *	–
	Depth	0.08705	0.02886	3.016	0.00256 **	10.511
	SST	0.19463	0.06778	2.871	0.00409 **	9.327
	Current	-8.51421	3.21963	-2.644	0.00818 **	7.614
	Slope	-4.55678	1.88018	-2.424	0.01537 *	10.020
	Northing	-0.04771	0.02041	-2.337	0.01943 *	5.781
	Beaufort	-0.51376	0.18032	-2.849	0.00438 **	8.117
	Effort	0.10445	0.07420	1.408	0.15924	1.832

Null deviance 420.17 on 3997 degrees of freedom
Residual deviance 356.72 on 3990 degrees of freedom
% of deviance explained: 15.1

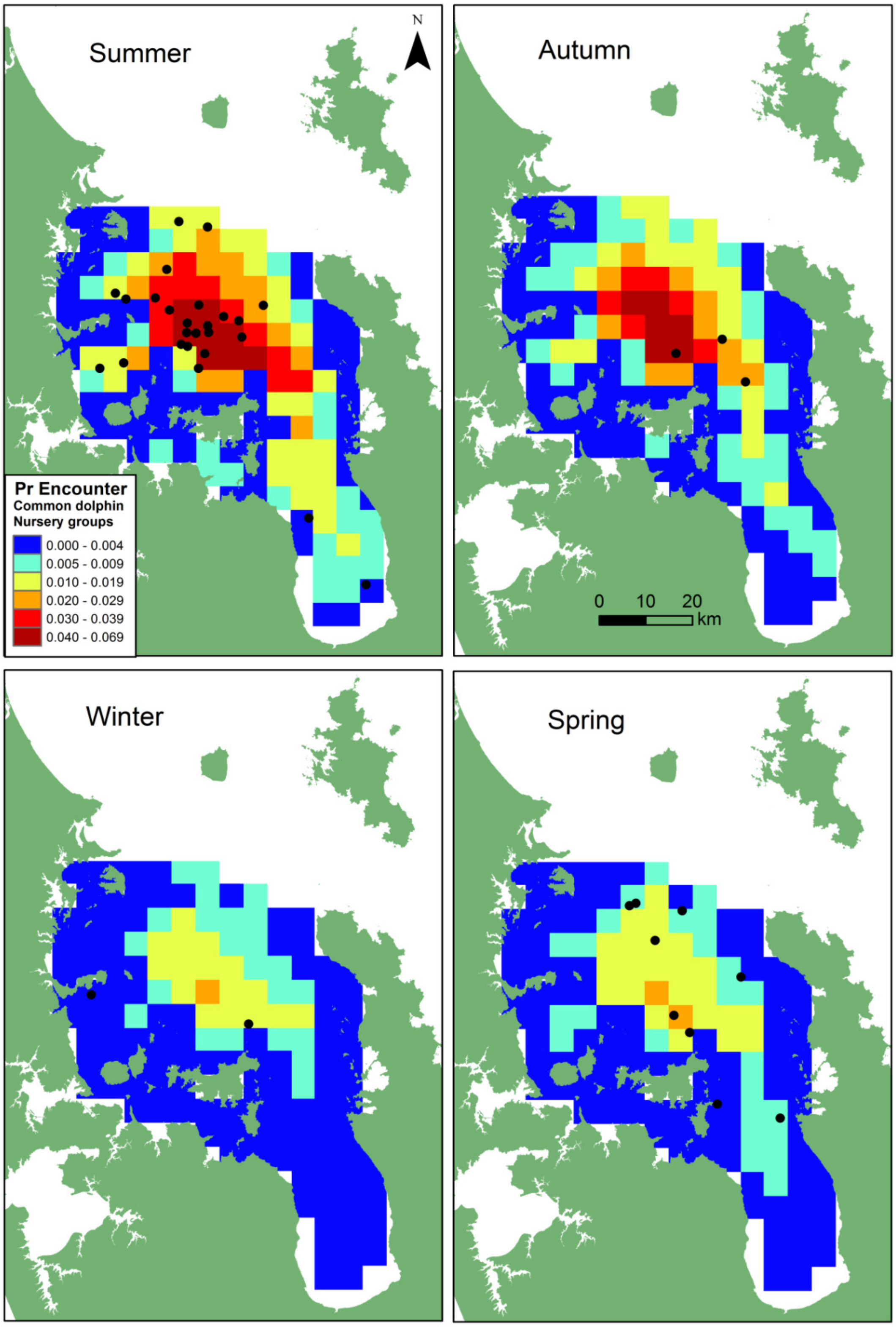

Figure 3.11 Predicted seasonal probabilities of encounter for nursery groups of common dolphins in the Hauraki Gulf, New Zealand. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show actual sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012.

3.3.3.4 Bryde's whale habitat use

The final IHG and GBI Bryde's whale models explained 16.8% and 24.4% of the deviance, respectively (Table 3.5). Depth was highly significant for both IHG and GBI models. For the IHG, whales used deeper waters with decreased slope and there was a survey year effect (Table 3.5). For GBI, whales also used deeper waters and there was a strong survey year effect with the importance of the spatial aspect 'distance to Colville Channel' dependent on survey year. The probability of encountering Bryde's whales in the GBI region was significantly higher in 2011 compared with 2012 (Fig. 3.12), particularly for grid cells closest to the Colville Channel (Fig. 3.13). Effort was also a significant factor suggesting the chances of encountering whales increased with survey effort.

The predictive maps showed consistent use of northern and central regions of IHG waters with the highest probability of encounters during 2012 (Fig. 3.13). The annual pattern was the opposite for GBI, with an overall higher probability of encountering whales in 2011 than in 2012 and a shift in location from the southwestern coast in 2011 to the northwestern coast in 2012.

Table 3.5 Parameter estimates of significant variables selected in the final Bryde's whale models (GLM with binomial distribution and logit link function) for inner Hauraki Gulf (IHG) and Great Barrier Island (GBI). Interaction terms are denoted by (-); significance codes are *** 0.001, ** 0.01, * 0.05.

Area	Term	Estimate	SE	z value	p value	Explained Deviance
IHG	Intercept	-676.09915	334.75369	-2.02	0.04342 *	–
	Depth	0.11133	0.02079	5.356	8.53e-08 ***	46.286
	Year	0.33206	0.16644	1.995	0.04604 *	3.875
	Slope	-2.34087	1.11167	-2.106	0.03523 *	6.502
	Beaufort	-0.27197	0.15194	-1.79	0.07346	3.176
	Effort	0.19619	0.0705	2.783	0.00539 **	7.211

Null deviance 546.24 on 3997 degrees of freedom
Residual deviance 454.59 on 3992 degrees of freedom
% of deviance explained: 16.8

GBI	Intercept	1.04E+04	2.63E+03	3.952	7.74e-05 ***	–
	Year	-5.17E+00	1.31E+00	-3.953	7.72e-05 ***	–
	Depth	5.74E-02	1.66E-02	3.448	0.000565 ***	15.398
	Dist_channel	-3.46E+02	1.10E+02	-3.153	0.001613 **	–
	Year-Dist_channel	1.72E-01	5.45E-02	3.152	0.001622 **	10.302
	Beaufort	-3.04E-01	1.77E-01	-1.713	0.086772	2.915
	Effort	1.43E-01	6.40E-02	2.230	0.025765 *	4.955

Null deviance 347.36 on 807 degrees of freedom
Residual deviance 262.77 on 801 degrees of freedom
% of deviance explained: 24.4

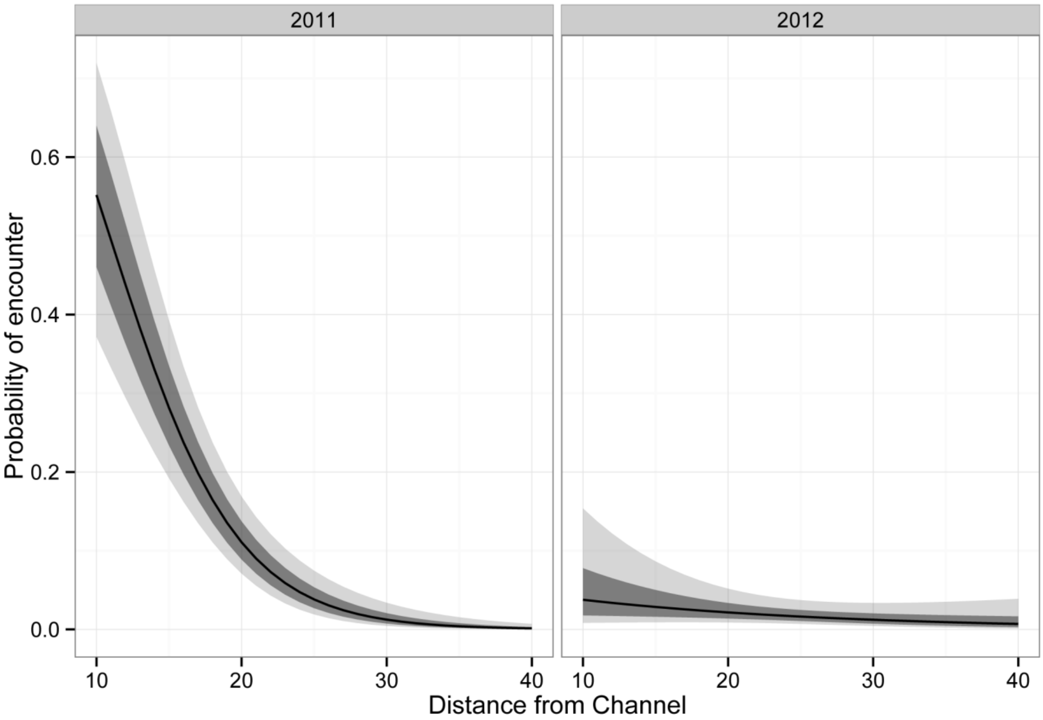

Figure 3.12 Interaction between year and distance to Colville Channel (km) on the probability of encountering Bryde's whales at Great Barrier Island (GBI), New Zealand. The black line is the average probability; shaded areas show one -and two-standard error intervals.

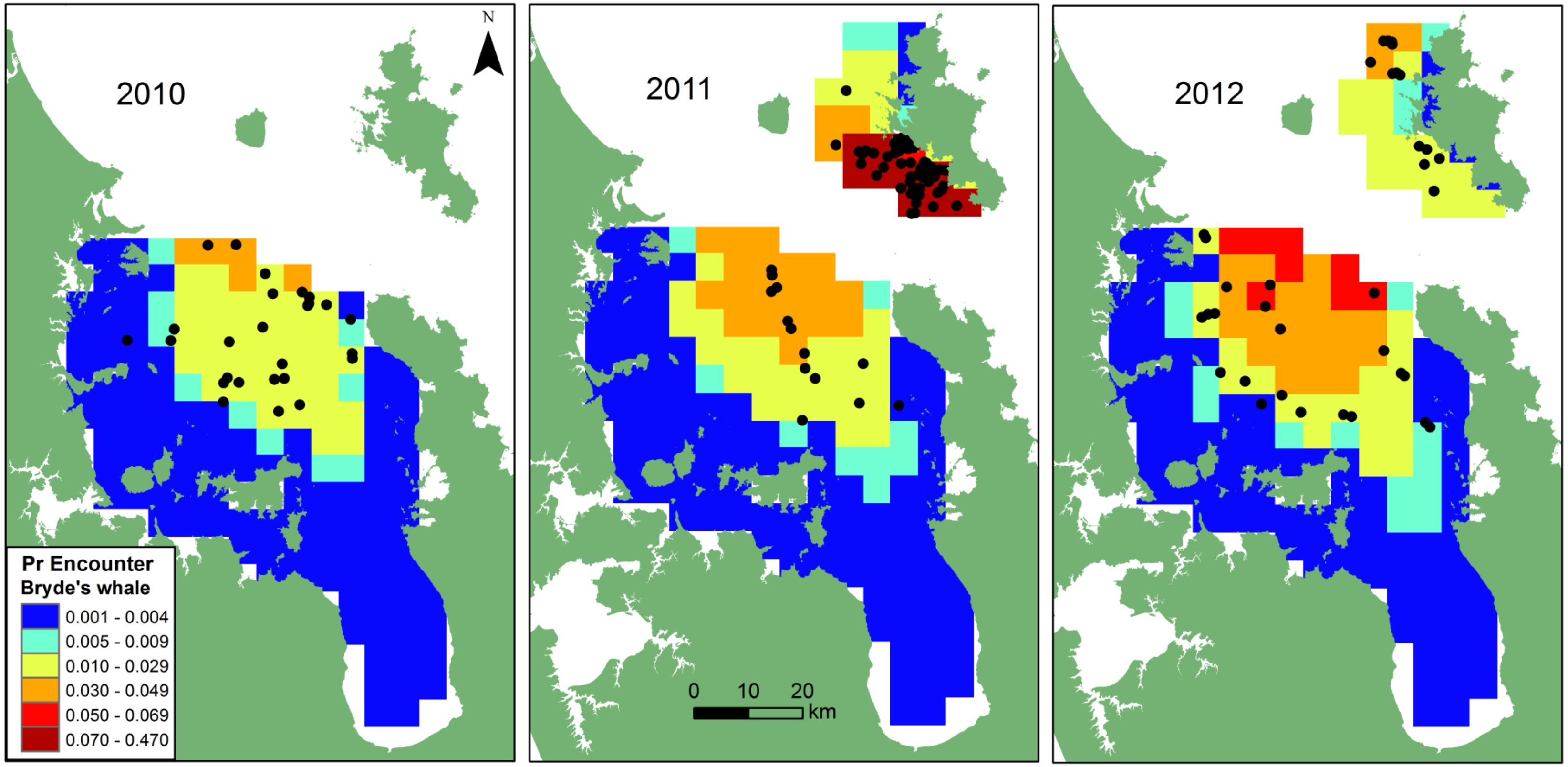

Figure 3.13 Predicted annual probabilities of encounter for Bryde's whales in the Hauraki Gulf, New Zealand by sampling year. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show actual sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012 and Great Barrier Island (GBI) surveys in 2011–2012.

3.3.3.5 Bottlenose dolphin habitat use

Bottlenose dolphin sightings were too sparse to fit models for the IHG region; therefore results refer only to GBI waters. The final model explained 20.5% of the deviance and suggested that probability of encounter was greater in shallower waters with increased slope (Table 3.6). There was strong evidence of an interaction between depth and SST, with the effect of depth dependent upon SST. The model suggested an increased probability of encountering bottlenose dolphins in shallow water in winter and spring when waters are at their coldest and in deeper, generally warmer waters in summer (Fig. 3.14). The extreme inshore use of bays and harbours by the bottlenose dolphins that were sighted within GBI waters is clear from the predictive maps, particularly over winter and spring (Fig. 3.15).

Table 3.6 Parameter estimates of significant variables selected in the final bottlenose dolphin model (GLM with binomial distribution and logit link function) for Great Barrier Island (GBI). Interaction terms are denoted by (-); significance codes are *** 0.001, ** 0.01, * 0.05.

Area	Term	Estimate	SE	z value	p value	Explained Deviance
GBI	Intercept	4.406740	2.546264	1.731	0.0835	–
	SST-Depth	0.021361	0.005486	3.894	9.87e-05 ***	42.221
	Depth	-0.461249	0.106398	-4.335	1.46e-05 ***	–
	SST	-0.391216	0.145569	-2.687	0.0072 **	–
	Slope	0.454359	0.205258	2.214	0.0269 *	4.829
	Beaufort	0.338320	0.21885	1.546	0.1221	2.426
	Effort	0.036353	0.069057	0.526	0.5986	0.275

Null deviance 294.37 on 807 degrees of freedom
Residual deviance 234.11 on 801 degrees of freedom
% of deviance explained: 20.5

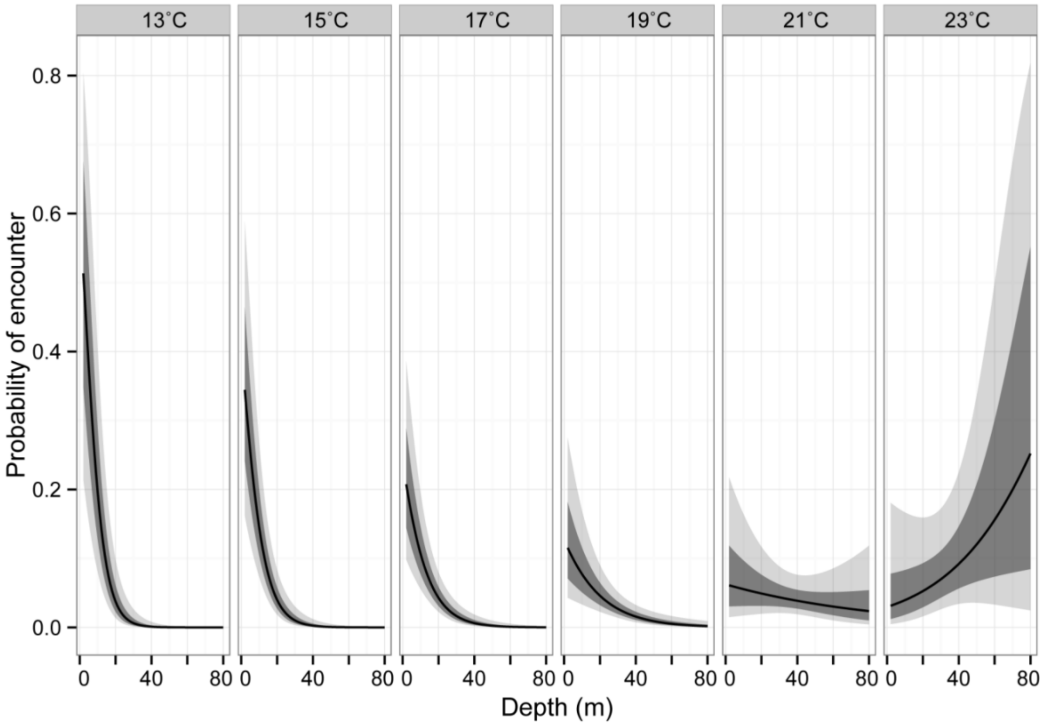

Figure 3.14 Interaction between depth and sea surface temperature (SST) on the probability of encountering bottlenose dolphins at Great Barrier Island (GBI), New Zealand. The black line is the average probability; shaded areas show one- and two-standard error intervals.

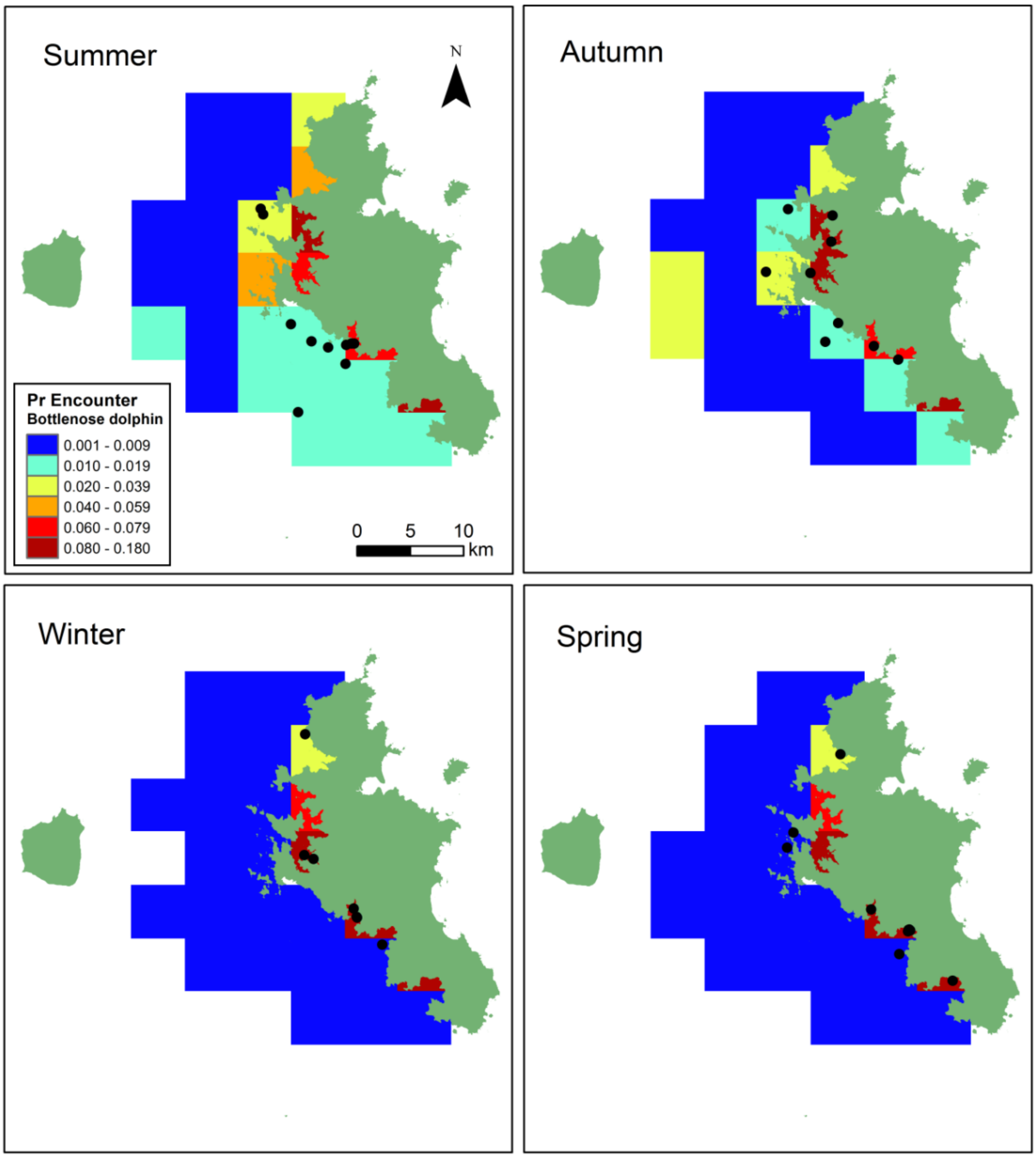

Figure 3.15 Predicted seasonal probabilities of encounter for bottlenose dolphins off Great Barrier Island (GBI), Hauraki Gulf, New Zealand. Red and blue represent the highest and lowest probabilities, respectively, as shown in the probability of encounter key. Black dots show actual sighting locations from surveys in 2011–2012.

3.4 DISCUSSION

This chapter represents the first spatial modelling of cetacean data for the Hauraki Gulf. The results of the predictive mapping improve our current understanding of the spatial and temporal habitat use of the Hauraki Gulf by common dolphins, Bryde's whales and bottlenose dolphins to support conservation management. Modelling the occurrence of mobile species inhabiting a highly dynamic environment is challenging given the degree of random variability and the large number of possible explanatory variables used to try to capture the heterogeneity in environmental conditions. The most frequent environmental variables that were important in the habitat models presented here were depth, slope, current and SST. However, while some variables were highly significant for certain species and regions, the deviance explained by the models was relatively low. Such results are often typical for this type of data (e.g. Ferguson et al. 2006; Cañadas & Hammond 2008; Embling et al. 2010) and have been attributed to factors such as the spatial scale of the study area (Cañadas & Hammond 2008) or a mismatch in predictor variables used as proxies for prey distribution or abundance (Ferguson et al. 2006)

3.4.1 Common dolphin habitat use

Model results indicated that the greatest probability of encountering common dolphins within the IHG was during the colder months of winter and spring and within deeper waters (40–60 m). The effect of depth was consistent with a previous study (Stockin et al. 2008a) of common dolphin presence using GAMs which is reassuring given the differences in analyses between the studies, with the absences for the GAM analysis based on sightings records of other cetacean species compared with this study that used grid cells where dolphins were not sighted during surveys for the absence data. It should be noted that the predicted high probability of encounter cells in winter in the central northern IHG had fewer actual sightings than expected, likely due to sampling error. The highest chances of encountering common dolphins off GBI was also in deeper waters (50–80 m), but during summer and autumn; or in shallow waters (< 20 m) during very low SSTs of 13° C. There did not appear to be any well-defined spatial trends in SST that could explain these patterns.

In addition to depth and SST, other important variables included tidal current and slope. Previous studies (e.g. Bearzi 2005; Kiszka et al. 2007; Oviedo et al. 2010) have typically associated common dolphin habitat use with areas of complex topography or slope regions that may be rich feeding areas and advantageous for prey capture. However, results from this study suggested greater use of areas with lesser slope. The differences could in part be related to the scale of the study areas and the relatively homogeneous topography of the sea floor in the Hauraki Gulf (compared with oceanic shelf regions). Common dolphins used areas with decreased tidal current, a variable that was identified as more important for the IHG than GBI. Spatially, this corresponded with infrequent sightings in areas of higher currents directly adjacent to the Colville Channel, in the Firth of Thames, and in the channels between IHG islands.

Although local effects of surface winds upon currents is known for the Hauraki Gulf (Black et al. 2000), a significant relationship between predominant monthly wind direction, localised tidal current and probability of dolphin encounter was not detected. This could potentially be due to a failure to select the appropriate spatial resolution (here 5 x 5 km) for the analyses in order to capture the variability in hydrodynamics. In a study of dolphin habitat use in the eastern tropical Pacific (Redfern et al. 2008), investigations into scale-dependence did not identify significant differences in selected variables, their functional forms, or high and low density regions of predictive maps for different spatial resolutions that were assessed. However, other studies have highlighted the importance of well-defined temporal and spatial scales when interpreting cetacean distribution or habitat use results (Jaquet 1996). The overall scale of the study area in the study by Redfern and colleagues (2008) was extremely large (19.6 million km^2) compared with the Hauraki Gulf study sites (4022 km^2 combined). It remains unknown whether the spatial resolution chosen in the present study was appropriate to capture the relationships between the habitat features and dolphin occurrence. Future comparisons with the results of a study currently underway using aerial survey data may provide further insight, since the aerial survey study is using two spatial scales of 420 metres and 2775 metres for analyses (Lily Kozmian-Ledward, pers. comm.).

Perhaps the temporal scale that some of the data were analysed at was problematic, and monthly rather than seasonal scales would have been more appropriate, but it was difficult to collect enough sighting data for more fine-scale temporal analyses. A spatial disconnect between regions of upwelling and blue whale (*B. musculus*) sightings in the South Taranaki Bight, New Zealand, was hypothesised to relate to a spatial lag in wind, currents and temporal lags in zooplankton growth (Torres 2013). Such a temporal or spatial lag between localised upwelling events and dolphin occurrence offers an alternative explanation for why a significant relationship with some of the environmental covariates was not detected in the present study.

Northern and central regions of the IHG were used year-round by common dolphins, while for shallow inshore waters, the probability of encounter increased during winter and spring. Short-beaked common dolphins (*D. delphis ponticus*) in the Black Sea are known to move from offshore waters to shallow coastal waters to feed on Black Sea anchovy (*Engraulis encrasicolus ponticus*) and Black Sea sprat (*Sprattus sprattus*) in the winter and summer, respectively (Reeves & Notarbartolo 2006). A change in prey availability and/or seasonal distribution within Gulf waters may have also affected the change in common dolphin habitat use.

Although the occurrence of clupeid fish, such as pilchards (*Sardinops neopilchardus*) and sprats (*Harengula antipoda*), has been documented as erratic and their migrations difficult to predict (Young & Thomson 1926), they have been described as locally abundant in some regions of New Zealand, such as Wellington harbour, in winter and spring (Young & Thomson 1926; Ministry for Primary Industries 2013). Changes in seasonal abundance or movements of pilchards in the Hauraki Gulf have not been assessed, as with other important species in the diet of common dolphins, such as jack mackerel (*Trachurus* spp.). However, limited fisheries catch data obtained from the Ministry for Primary Industries for the period of this study (Appendix 3.4), whilst regarded cautiously, shows some alignment with the findings of this chapter, with a significant proportion of the annual pilchard catch taken during one winter month (August). Baker (1972) suggested that minimum water temperatures of around 14° C may be warm enough to support year-round spawning of pilchards off northeastern New Zealand. Such a consistent source of prey could explain the year-round use of the Hauraki Gulf by common dolphins, as suggested by Stockin et al. (2008a).

The inclusion of functional data into the models provided further information about habitat use, as previously demonstrated by Cañadas & Hammond (2008) for short-beaked common dolphins in the southwestern Mediterranean. Feeding groups were predicted to occur more commonly in northern-central regions of the IHG during winter and spring. These data correspond well with the results of an earlier (2002–2005) behavioural study that found most foraging common dolphins were found in the deepest waters of the IHG and mainly during winter and spring (Stockin et al. 2009a). While feeding groups were generally observed in deeper waters, the chance of encountering a feeding group in shallow regions was still possible but only when SSTs were at their lowest. Overall, the predictive occurrence maps were temporally and spatially similar to the feeding predictions, suggesting prey availability likely has important implications for the general distribution and habitat use patterns of common dolphins in the IHG.

Nursery groups in the IHG were most prevalent during summer and autumn when temperatures were warmest, in line with other North Island studies (Constantine & Baker 1997; Neumann 2001a; Stockin et al. 2008a; Meissner et al. 2014) and common dolphin research conducted overseas (Cañadas & Hammond 2008). Although latitude was found to be a significant spatial predictor, with a greater probability of sighting nursery groups in more southerly waters, there were no distinctive hotspots for nursery or feeding groups. Instead, the same general areas of the IHG were used for both functions, although there is some suggestion that groups move into more sheltered waters for nursing since moving further south into the IHG provides more protection from open waters to the east (due to the position of the Coromandel Peninsula, see Fig. 3.1).

The prediction for increased use of areas with similar water depths (~40 m) by nursery groups and the general population did not correspond with Stockin et al. (2008a) who found that groups with neonates were typically observed in shallow waters of less than 20 m depth. It is not clear whether the different observations represent a change in habitat use over the period of the two studies, or are due to differences in survey methodologies. The latter seems less likely given that the majority of the data analysed in Stockin et al. (2008a) was collected from a tour vessel that spent more time in deeper waters searching for whales and would thus presumably have had more opportunities to encounter neonates in deeper waters. Similar to this study, Meissner et al. (2014) reported that common dolphin groups were encountered in similar water depths regardless of group composition in the ECBOP. Unfortunately, small sample sizes precluded the fitting of functional models for GBI to provide additional results for habitat use by nursery groups of common dolphins. As a result, it is not clear why probability of encounter was greater in northerly regions in summer and autumn, but greater in southern regions in winter. The question was raised by Stockin et al. (2008) as to whether inshore movements of common dolphins during the reproductive season relate to reproductive requirements or are secondary responses to prey availability. For the Hauraki Gulf, it appears the use of more southerly waters in summer and autumn in this study reflects habitat use by nursery rather than by feeding groups.

3.4.2 Bryde's whale habitat use

Water depth was the single most influential variable for the Bryde's whale models. The year of the survey and its interaction with the distance to Colville Channel was also important for GBI, with slope and year showing some importance for IHG. Whales generally used the deeper waters of the Hauraki Gulf, yet showed considerable inter-annual variability in their actual occurrence, particularly within GBI waters.

Significant inter-annual variability in whale occurrence has been documented in other regions. A decrease in blue whale sightings in inshore regions off southern Sri Lanka occurred in 2011 (de Vos et al. 2014). The authors hypothesised this was due to a shift in blue whale prey following anomalous rainfall and higher turbidity from river discharge, which affected inshore productivity. For Bryde's whales (*B. edeni*) in the southwestern Gulf of California, large-scale inter-annual changes in occurrence have been documented over a twenty-year period from 1988 to 2006 (Salvadeo et al. 2011). The California study did not find any consistent seasonal patterns of occurrence, but attributed annual variability in whale occurrence to climate conditions and effects on prey availability, with more whales recorded during La Niña conditions and fewer whale sightings during El Niño. In the present study, the probability of encountering Bryde's whales varied annually both within and between IHG and GBI regions. Although a large temporal dataset is required to ascertain any correlations with ENSO conditions, for most of 2011 when the probabilities of encounter were the greatest for GBI waters, a strong La Niña was underway (National Climate Centre 2013). It would be useful to understand whether the increased northeasterly winds and higher rainfall experienced under La Niña conditions affect the occurrence of whales off the southwest coast of GBI.

Contrary to this study, Wiseman et al. (2011) found no inter-annual variation in Bryde's whale occurrence in the IHG from 2003 to 2006, but did report a significantly greater encounter rate during winter compared with other seasons. Conversely, Behrens (2009) found no seasonal difference for either the number or distribution of whales in the IHG based on data collected between 2000 and 2009. Given that long-term temporal datasets are required to assess the effects of large-scale climate conditions (Holmgren et al. 2001; Burrows et al. 2012), the relatively short-term nature of this study and that of Wiseman et al. (2011) may explain the discrepancies and variations in annual versus seasonal occurrence.

The peak in occurrence at GBI in 2011 was significantly greater than for all other years in both regions, suggesting conditions may have been particularly favourable for prey that year off the southwestern coast of GBI. In general, little is known about the existence of any specific breeding grounds for Bryde's whales (Kato & Perrin 2009), so whether an increase in sightings could be related to a socially driven factor such as mating is open to question. Calves have been reported throughout the year in the Hauraki Gulf, with a peak in the late summer/early autumn (Wiseman et al. 2011). While mother-calf pairs were observed in most seasons in this study (Appendix 3.2), the prevalence of feeding whales compared with mother-calf pairs (Appendix 3.2) suggests prey availability may be the most likely factor affecting Bryde's whale habitat use in the Gulf. When southwesterly winds predominate, fishermen report a clustering of krill and other plankton that becomes entrapped against the southwest coast of GBI due to the geography of the Hauraki Gulf (see Fig. 3.1) and the nature of the currents (Dave Kellian, pers. comm). In this study, sightings were also clustered north of the Colville Channel, an area known for its strong currents (Black et al. 2000).

Notably, habitat use by Bryde's whales and common dolphins off GBI was considerably different, unlike IHG waters. Whales used similar areas of the IHG as common dolphins, consistent with previous studies in the region that have documented multi-species feeding associations (Burgess 2006; Stockin et al. 2009a; Machovsky Capuska et al. 2011). Although robust prey data were absent for this study (Appendix 3.4), Bryde's whales are known to feed on both fish and krill in the Hauraki Gulf (Wiseman 2008), and krill are known to be present in outer Hauraki Gulf waters but scarce in the IHG (Jillet 1971). The differential use of GBI waters by Bryde's whales and common dolphins supports the concept that whales may forage more frequently on krill in outer Hauraki Gulf waters than in the IHG, albeit dependent on inter-annual variation in prey availability, as suggested in Chapter 2.

While whales used similar waters as common dolphins in the IHG, the whales were not recorded in the same range of water depths as the dolphins, possibly as a consequence of body size affecting their ability to exploit very shallow waters (Acevedo-Gutiérrez 2009). The inshore form of Bryde's whales off the coast of South Africa are associated with scarring on the underside of their bodies, mainly towards the tail flukes, that has been attributed to scratches acquired when swimming close to the sea floor (Best 1977; Penry 2010). This has not been documented for Bryde's whales using Hauraki Gulf waters, but such observations would be interesting to assist in further understanding habitat use. While Bryde's whales are not typically known to frequent waters less than 15 m deep in the Hauraki Gulf, tagging results have shown that they spend more than 90% of their time between the surface and depths of 12 m, and are consequently at a high risk of collision with shipping traffic traversing the Gulf (Constantine et al. 2012).

The results of the GLMs provide some insights into the habitat use of Bryde's whales in the Hauraki Gulf; however, many questions remained unanswered. Is inter-annual variability in Bryde's whale occurrence and distribution related to prey availability? To what extent is this driven by climate conditions? Do feeding whales and whales with calves use Hauraki Gulf waters differently? Future studies should aim to use data collected over large temporal scales (i.e. minimum of 10 years) to try and answer some of these questions.

3.4.3 Bottlenose dolphin habitat use

Habitat models could not be fit for bottlenose dolphins in IHG waters due to a very low number of *on effort* sightings during three years of surveys. However, bottlenose dolphins used GBI waters year-round, with the general spatio-temporal pattern for use of shallow inshore waters, the extent of which varied seasonally. Overall, depth and SST were the most important variables in determining bottlenose dolphin distribution at GBI. The final bottlenose dolphin model explained a greater percentage of the deviance than most other models for common dolphins and Bryde's whales in this chapter, likely due to the dolphins' clear use of inshore waters relative to the study area.

Depth has been consistently reported as an important factor affecting the distribution of bottlenose dolphins (e.g. Cañadas et al. 2002; Azzellino et al. 2008; Blasi & Boitani 2012). In this study, a general seasonal onshore-offshore movement between shallow and deeper waters was found to correspond with the same trend identified in the Bay of Islands, North Island. In both cases, dolphins were distributed in shallower waters during winter and in deeper waters during summer (Constantine 2002; Hartel et al. 2014). As discussed in Chapter 2, investigations into fine-scale dolphin habitat use in conjunction with prey distribution may help to understand the reasons behind this seasonal shift. The models also predicted use of areas with increased benthic slope, which has been shown in other studies of bottlenose dolphins in temperate waters (e.g. Wilson et al. 1997; Ingram & Rogan 2002; Hastie et al. 2003). It has been suggested these areas may support higher concentrations of fish (Ingram & Rogan 2002), but this is another unknown factor for GBI waters.

Modelling habitat use of bottlenose dolphin feeding and nursery groups was not possible in this study due to limited sample sizes; however, the southwest coast did appear important for nursery groups based on distribution alone (Appendix 3.2; Chapter 5). The Colville Channel, that passes between GBI and the northern tip of the Coromandel Peninsula (see Fig. 3.1), is characterised by the strongest currents in the Hauraki Gulf (Manighetti & Carter 1999). Strong upwellings occur off GBI and around the Colville Channel (Black et al. 2000) and thus, this region may be subject to increased biological activity. The shallow bays and harbours (e.g. Whangaparapara, Blind Bay, Tryphena; Fig 3.1) adjacent to the Colville Channel may provide bottlenose dolphins with an environment that offers consistent food availability, is suitable for breeding or calving, and lacks the level of anthropogenic pressures associated with other regions of their home range (Chapter 5; Dwyer et al. 2014a).

Habitat use by bottlenose dolphins and common dolphins was quite distinct in this study, similar to the differentiation described for the two species in the Bay of Islands (Constantine & Baker 1997) and western Bay of Plenty (Neumann 2001b). While common and bottlenose dolphins have been recorded in association in the Hauraki Gulf on occasion (Stockin & Visser 2005), they were not observed together in the present study, despite being separated spatially by only a few kilometres at times. Habitat partitioning has been described for common and bottlenose dolphins in other regions, for example in Santa Monica Bay, California (Bearzi 2005) and Admiralty Bay, New Zealand (Halliday 2013). While spatial partitioning between common and bottlenose dolphins has been hypothesised to relate to avoidance of the larger bottlenose dolphins (Halliday 2013) that are known for their aggressive interactions with other delphinids (Barnett et al. 2009), the disparity in habitat use by the two delphinid species in the Hauraki Gulf is more likely a consequence of different prey preferences. While common dolphins target small pelagic shoaling fish (Neumann & Orams 2003; Meynier et al. 2008; Stockin et al. 2009a), coastal bottlenose dolphins typically select fish with a strong association to the rocky reef and other benthic habitats (Constantine 2002; S. M. Lusseau 2003; Hartel et al. 2014). Indeed, bottlenose dolphins in GBI waters were primarily observed chasing and capturing fish, such as John Dory (*Zeus faber*), close to shore (pers. obs.).

3.4.4 Study limitations and future recommendations

While some of the variables fit in the habitat models were highly significant for certain species and regions, the deviance explained by the models was relatively low. While this is common for marine mammal habitat use studies (Ferguson et al. 2006; Cañadas & Hammond 2008; Embling et al. 2010), future cetacean studies in the Hauraki Gulf should consider other variables that were not incorporated here in order to better capture the variability in oceanographic processes. The use of different spatial and temporal scales may be beneficial since species distribution patterns may be governed by processes at multiple scales (Dormann 2007). Future studies could test the effects of different spatial resolutions on the prediction of dolphin or whale occurrence with the aim of improving our understanding of the roles of the environmental variables, as suggested by Silva (2007). Additionally, the seasons in this study were defined in the same manner as previous cetacean studies in northern New Zealand waters in order to facilitate the comparison of results. However, the monthly water temperatures presented in this chapter suggest the conventional terrestrial seasonal definitions may not be the most appropriate for marine mammals and their prey. For example, the warmer months in terms of SSTs were January to March, rather than December to February as defined herein. This warrants further consideration in future marine mammal studies.

The NPP data used in this study were not considered reliable due to the inaccuracy of satellite data in coastal, nearshore waters that can render even relative comparisons inconsistent when *in situ* data is not available for validation. Therefore, the insignificance of the NPP variable in the habitat models may have been a consequence of inaccurate data rather than a real lack of association. This could be addressed in the future by collecting *in situ* chlorophyll α data that can help validate remotely collected NPP data. Additionally, the inclusion of prey data could improve models, although the scale of the data collection would likely be important. While the addition of prey data is often anticipated to provide further understanding of habitat use patterns, a fine-scale study that incorporated prey distribution data to model bottlenose dolphin habitat use found that models were actually more successful using appropriate environmental variables than the prey data, in part due to the spatial variability of prey patches (Torres et al. 2008).

The Bryde's whale and bottlenose dolphin occurrence models were fit for all sightings, regardless of factors such as behaviour, density or group composition. By analysing all sightings together, interpretation can become complicated and areas used only occasionally but for critical behaviours are likely to be under-predicted by occurrence models (Silva 2007). The development of models that include behavioural observations can help to delineate the functional mechanisms behind habitat use (Hastie et al. 2004), as found for common dolphin feeding and nursery groups in this study and noted in other previous studies (Cañadas & Hammond 2008; Hartel et al. 2014).

Further improvements to the analyses conducted in this chapter would include evaluating the predictive power of the models, ideally using two independent datasets (Guisan & Zimmermann 2000). Collecting cetacean sighting data at sea is known to be challenging (Kiszka et al. 2007; Viddi et al. 2010; Kaschner et al. 2012) and this study was no exception. During three years of year-round data collection, sighting data were insufficient to subdivide into training and evaluation datasets. Future studies should aim to collect enough sighting data for two independent datasets, possibly by allocating more effort to high predictive regions (i.e. central northerly areas) and less effort to regions where dolphins were not frequently recorded (e.g. Firth of Thames).

The detection of species in ecological studies has important consequences when examining trends over space or time, since changes in detection may be interpreted as changes in occupancy or abundance if detection probabilities do not remain constant (MacKenzie & Kendall 2002). Survey protocols in the present study were kept consistent during the entire fieldwork period to try to minimise factors affecting detection, and variables that were deemed to have significant effects on the detection of cetaceans during boat surveys were incorporated into the habitat models. This included Beaufort sea state, which is known to affect the detectability of cetaceans at sea (Forney 2000), and the amount of effort in a grid cell. Both of these variables had a significant effect in many of the models. However, even though they were incorporated into the models, they did not account for detection probability explicitly or spatially. Therefore, the results presented in this chapter will underrepresent true levels of habitat use since imperfect detection will result in negatively biased results (MacKenzie et al. 2002). Chapter 4 uses occupancy modelling to further investigate the effects of detection probability on the distribution and habitat use of common dolphins in the Hauraki Gulf.

3.4.5 Summary

This chapter documents the first spatial modelling of cetacean habitat use for the Hauraki Gulf. Northern and central regions of the IHG were used consistently by common dolphins, with the greatest probability of encountering dolphins during the colder months of winter and spring and within deeper waters (40–60 m). The probability of encounter in shallow inshore waters also increased during winter and spring. While the greatest chances of encountering common dolphins off GBI was also in deeper waters (50–80 m), it was at different times of the year, i.e. during summer and autumn. Spatially, this corresponded with decreased sightings of common dolphins in areas of higher currents directly adjacent to the Colville Channel, in the Firth of Thames, and in the channels between IHG islands. During summer and autumn, it appears the use of more southerly waters in the IHG reflects habitat use by nursery rather than by feeding groups. However, overall predictive occurrence maps for common dolphins were more temporally and spatially similar to the feeding rather than the nursery group predictions, suggesting prey availability likely has important implications for the general distribution and habitat use patterns of common dolphins in the Hauraki Gulf.

Bryde’s whales showed considerable inter-annual variability in habitat use, particularly within GBI waters. Whales generally used the deeper waters of the Hauraki Gulf, although this varied spatially off GBI according to year. Depth was the most important predictor in the habitat models. The prevalence of feeding whales compared with mother-calf pairs suggested prey availability may be the most likely factor affecting Bryde’s whale habitat use in the Hauraki Gulf. Notably, habitat use by Bryde’s whales and common dolphins in GBI waters was considerably different, unlike IHG waters. This differential use of GBI waters by Bryde’s whales and common dolphins may be suggestive of whales foraging more frequently on krill in outer Hauraki Gulf waters than in the IHG, albeit depending on inter-annual variation in prey availability.

The habitat use patterns for bottlenose dolphins showed a general seasonal onshore-offshore movement between shallow and deeper waters depending on SST. In particular, the southwest coast of GBI appeared important for bottlenose dolphins, possibly due to a combination of factors that includes a consistent availability of food, its suitability for breeding or calving and the potentially decreased levels of anthropogenic pressures associated with other regions of the population's home range. The disparity in habitat use by common and bottlenose dolphins in the Hauraki Gulf is likely a consequence of different prey preferences. While common dolphins target small pelagic shoaling fish, coastal bottlenose dolphins typically select fish with a strong association to the rocky reef and other benthic habitats.

The results of this study show that the collection and analysis of long-term datasets is needed for all three species, but specifically required for Bryde's whales due to significant inter-annual variability in habitat use. Fine-scale studies that incorporate functional data with habitat use analyses are also required to better understand common and bottlenose dolphin use of GBI waters.

Chapter 4

Occupancy models to assess spatial use of the Hauraki Gulf by common dolphins

Common dolphins (*Delphinus* sp.) in the inner Hauraki Gulf. Photo: Sarah Dwyer.

4.1 INTRODUCTION

Many wildlife ecology studies seek to explain patterns and dynamics in species occurrence. Information about the abundance or distribution of species is vital for conservation management; however, a common problem with these studies is that detection of groups/individuals is rarely perfect (Bailey & Adams 2005). As a consequence, parameter estimates will be biased if detection probability is unaccounted for (MacKenzie et al. 2002; 2003; 2004). Occupancy is concerned with the locations where a species is present and is defined as the proportion of area, patches, or sample units that are occupied (MacKenzie et al. 2006). The concept of occupancy has been used in a variety of contexts (MacKenzie & Bailey 2004), for example, as a coarse surrogate for actual abundance (MacKenzie & Nichols 2004) or in habitat modelling where the aim is to relate species presence/absence to environmental or physical characteristics of the sampling sites (Martin et al. 2010; Cove et al. 2013).

Occupancy modelling techniques were only recently developed in the early 2000s (MacKenzie et al. 2002; 2003; 2004) to address the problem of discerning true absence from non-detection. The two are often confounded because a non-detection can be either a) a true absence, or b) a false absence (i.e. the species was present but not detected) if the probability of detecting the species was less than one (MacKenzie et al. 2002; Bailey & Adams 2005). Imperfect detection (i.e. detection probability < 1) will always result in underestimated levels of occupancy (MacKenzie et al. 2003; 2004; Bailey & Adams 2005).

Occupancy modelling (MacKenzie et al. 2002) consists of two components that simultaneously model; 1) occurrence of the species and 2) the probability of detecting the species across multiple surveys (MacKenzie 2006). Model parameters (occupancy and detection probabilities) are estimated using maximum likelihood methods and can be functions of covariates such as habitat type (MacKenzie et al. 2004). Missing observations (i.e. occasions when a site was not sampled) are also permitted.

In cetacean studies, detection probabilities are usually accounted for in line transect surveys that aim to estimate absolute density or abundance (e.g. Hammond et al. 2013). Trackline detection probabilities (or g(0) in distance sampling terminology) have been shown to be highly variable for different marine mammal species (Barlow 2015), depending on factors such as the average dive duration of the species (Stockin et al. 2001), an example of availability bias. Other factors known to affect detection probabilities include sighting methods, sighting cues, search conditions and group size (Barlow et al. 2001). Some studies have used multiple survey methods to try and reduce detection bias, with a recent combined visual and acoustic survey of Ganges river dolphins (*Platanista gangetica gangetica*) demonstrating improved precision of abundance estimates compared with single methods only (Richman et al. 2014). Detection probability is not always explicitly accounted for in spatial analyses of distribution or habitat use (e.g. Viddi et al. 2010; Hartman et al. 2014), although most studies attempt to reduce heterogeneity in detection probability as much as possible during field surveys (e.g. by placing limits on suitable conditions for surveys).

One of the critical assumptions when modelling occupancy is that sites are closed to changes in occupancy state within sampling seasons (MacKenzie et al. 2002; MacKenzie 2003). This closure assumption may be relaxed if a species moves in and out of sites in a random manner, as is often the case for highly mobile species such as cetaceans or wide-ranging carnivores (Midlane et al. 2014). While the parameter estimates for occupancy and detection remain valid, their interpretation changes to one of use rather than occupancy (MacKenzie et al. 2004; 2006). Occupancy modelling has been applied to a range of semi or fully-terrestrial species including amphibians (Corn et al. 2005), reptiles (Griffiths & McKay 2007), birds (Olson et al. 2005), mammals (Long et al. 2011) and invertebrates (MacKenzie 2003). To date, the method has been scarcely used for marine species (Issaris et al. 2012; D'Souza et al. 2013) and not previously applied to cetaceans.

Given the known detectability issues associated with visual surveys for cetaceans and the importance of accounting for detection bias, this study was focused on the application of occupancy models to common dolphin (*Delphinus* sp.) sighting data in the inner Hauraki Gulf (IHG), New Zealand. Common dolphins were considered the ideal species for this study because they are the most frequently sighted cetacean species in the IHG (O'Callaghan & Baker 2002; Chapter 2), hence analyses would not be limited by sample size. Since common dolphin movements in the Hauraki Gulf violate the assumption of geographic closure, the interpretation of occupancy and detection changed for this study. Occupancy was interpreted as 'use', i.e. the probability that common dolphins used a site. Detection probability was a combination of two components: the probability that dolphins used a site and the probability that they were detected given that the site was being used (MacKenzie et al. 2004; 2006; Midlane et al. 2014).

This chapter aims to extend the results of the generalised linear models (GLMs) presented in Chapter 3 by addressing the following objectives:

- Investigate the feasibility of applying occupancy models to a cetacean species for the first time;
- Assess changes in the seasonal distribution and habitat use of common dolphins in the IHG while simultaneously accounting for imperfect detection; and
- Compare spatial predictions of the occupancy models with those of the GLMs presented in Chapter 3.

4.2 MATERIALS AND METHODS

4.2.1 Study area

The Hauraki Gulf is a relatively shallow, semi-enclosed body of water on the northeast coast of the North Island, New Zealand (Fig. 4.1; Manighetti & Carter 1999; Black et al. 2000). Circulation in the Hauraki Gulf is strongly influenced by surface winds and their interaction with tidal currents, in addition to headlands and islands that enhance local upwellings (Black et al. 2000). Warm waters of the East Auckland Current (EAUC) flow into the entrance of the Hauraki Gulf during summer and autumn, when easterly winds and downwellings are more prevalent (Zeldis et al. 2004). Westerly winds that are favourable for upwellings prevail in late winter and spring (Chang et al. 2003; Zeldis et al. 2004). Further detailed information about the study area is provided in Chapter 2.

The sampling area in the IHG consisted of a grid of 5 x 5 km cells that covered 3480 km^2 (excluding land that fell within cells; Fig. 4.1). In the IHG, approximately 40% of the area consists of waters less than 20 m deep, while 30% falls within the 20 to 40 m depth contours, with sea surface temperature (SST) typically ranging from 12.5° to 22° C (Paul 1968).

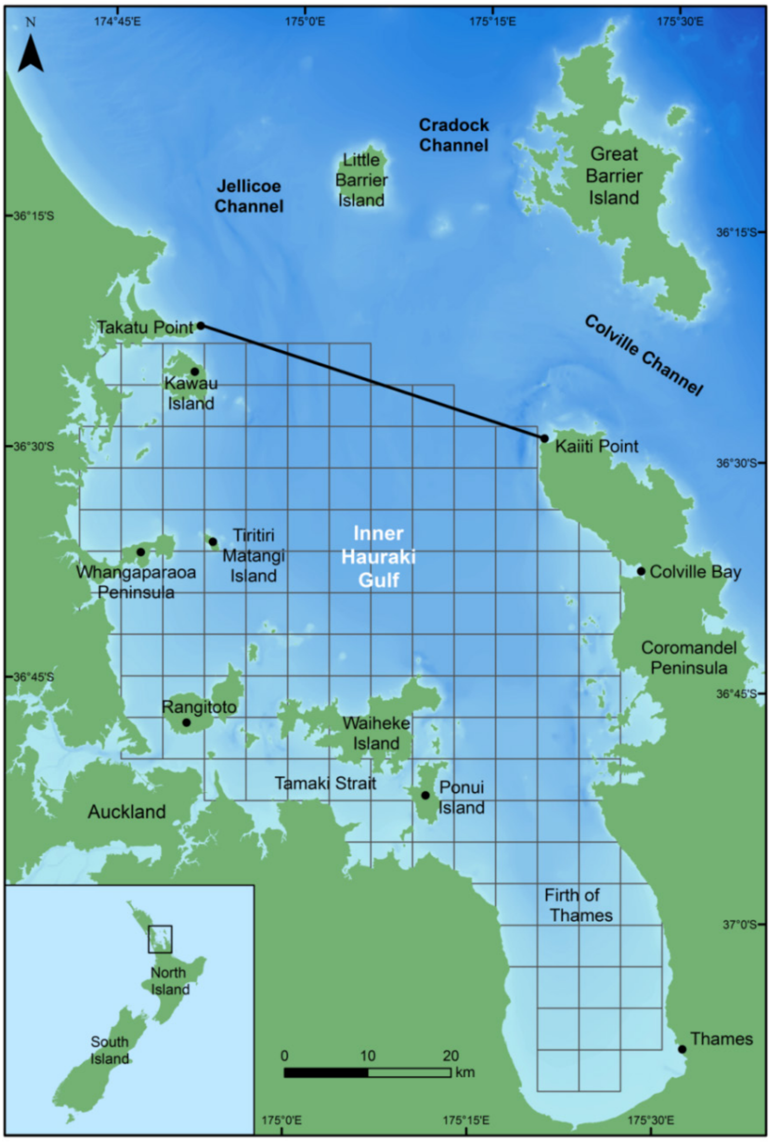

Figure 4.1 Map of the Hauraki Gulf, New Zealand. The solid black line (from Takatu Point to Kaiiti Point) indicates the boundary between the inner and outer Hauraki Gulf. A grid of 5 x 5 km cells is shown in grey. Bathymetry is depicted with darker shades of blue representing deeper waters; data courtesy of NIWA (Mackay et al. 2012). Inset: Location of the Hauraki Gulf, North Island, relative to New Zealand.

4.2.2 Data collection

Common dolphin sighting data were collected during dedicated monthly boat surveys conducted between January 2010 and November 2012 from the Massey University research vessel *Te Epiwhania*, a 5.5 m Stabicraft boat powered by a 100 hp four-stroke engine. A non-systematic survey design was employed, with survey tracks and the direction of travel selected based on prevailing weather and sea conditions, and on the extent to which any particular area had been previously surveyed within that month. The overall aim was to cover the study area as equally as possible each month.

Large vessels that conduct visual surveys in offshore waters typically survey in conditions of up to Beaufort sea state 5 or 6 (e.g. Barlow 2006; 2013); and Beaufort sea states 0 to 5 have been used in estimating line-transect detection probabilities for common dolphins (*D. delphis* and *D. capensis*, Barlow & Forney 2005). Beaufort sea state 3 was considered appropriate as the limit for this study based on the small size of the vessel with decreased observer height (~2 m) and because large swells were not frequent in the IHG since the semi-enclosed bay is only exposed to the open ocean at the northern entrance. Time spent travelling along survey tracks searching for dolphins, with vessel speed maintained at ~10 knots, was classified as *on effort*.

While *on effort*, two experienced observers continuously scanned to the horizon in a 270° arc in front of and to the sides of the vessel, as detailed in Chapter 2. Dolphins were detected by the naked eye, and visual clues indicating cetacean presence included splashing, water disturbance and sighting of dorsal fins (Stockin et al. 2008a). A group of dolphins was defined as any number of individuals observed in apparent association, moving in the same general direction and often, but not always, engaged in the same activity (Shane 1990). When the vessel left the survey track to approach a group, the survey mode was *off effort* until returning to the track to resume searching for independent groups (i.e. groups separated spatially and temporally). *Off effort* mode also included all other occasions when the vessel was away from the survey track (e.g. returning to harbour due to deteriorating sea conditions).

Data were collected using an XDA Orbit II Windows Mobile device. CyberTracker version 3 software (Steventon et al. 2002) was programmed for logging sighting data and to record the GPS position of the vessel every 60 seconds throughout the survey day. Beaufort sea state was logged at 15 minute intervals.

4.2.3 Data analysis

4.2.3.1 Modelling framework

Likelihood-based occupancy modelling (MacKenzie et al. 2002; 2006) estimates both site occupancy (ψ, probability that a species occupies a site) and detectability (p, probability that a species is detected at a site) from detection/non-detection data. The term detection/non-detection is equivalent to presence/absence, but considered more correct since it describes the outcome of the sampling process rather than the biological occurrence of a species at a site (MacKenzie 2005a). MacKenzie et al. (2002) outlined the modelling procedure, whereby a detection history describes the sequence of detections (1) and non-detections (0) that results from multiple surveys of each sampling unit (site). A model is built from the detection histories for each site using probabilistic arguments and allows maximum likelihood estimation of the model parameters. Sampling effort is not required to be equal across all sites since the model allows for missing observations. If sampling does not take place, then no information is contributed to the model likelihood for that site on the occasion(s) it was not sampled.

The single season occupancy model is described as follows (MacKenzie et al. 2002; 2006; Bailey & Adams 2005; MacKenzie 2012):

- ψ_i is the probability the target species is present at the *i*th sampling unit (site)
- (1 - ψ_i) is the probability the *i*th site is empty
- p_{ij} is the probability of detecting the species in the *j*th survey in the *i*th site given the species is present
- (1 - p_{ij}) is the probability of not detecting the species in the *i*th site during the *j*th survey, given presence
- *s* is the number of sites

Detection histories denote the sequence of detections and non-detections for each survey at each site. For example, the detection history

$$h_i = 1010$$

shows that the site was occupied and the species was detected during the first and third surveys. The probability statement for this detection history is:

$$\Pr\,(h_i = 1010) = \psi_i \, p_{i,1}(1 - p_{i,2})p_{i,3}(1 - p_{i,4}).$$

Sites where the target species was never detected (e.g. h_i = 0000) could either be unoccupied (i.e. true absence) or occupied but the target species was not detected (i.e. false absence) during the surveys. Both of these probabilities must be determined and then added together in the probability statement:

$$\Pr\,(h_i = 0000) = \psi_i(1 - p_{i,1})(1 - p_{i,2})(1 - p_{i,3})(1 - p_{i,4}) + (1 - \psi_i).$$

The model likelihood, given the set of detection histories from the s sites surveyed, is defined as

$$L = \prod_{i=1}^{s} \Pr(h_i)$$

The model likelihood for the observed set of data can be maximised to obtain maximum likelihood estimates of the parameters.

Missing observations (e.g. due to bad weather) can be readily incorporated into the models, e.g.

$$h_i = 1–10$$

where the site was occupied and the species was detected during the first and third surveys, and not detected during the fourth survey (nothing can be said about the second survey since it did not take place at this site). The probability statement for this encounter history is:

$$\Pr\,(h_i = 1–10) = \psi_i \, p_{i,1} \, p_{i,3}(1 - p_{i,4}).$$

Covariate information can also be incorporated into the modelling framework. Occupancy and detection probabilities can be modelled as a function of site and survey-specific covariates by using the logit-link function, e.g.:

$$logit(\psi_i) = ln\left(\frac{\psi_i}{1-\psi_i}\right) = \alpha_0 + \alpha_1 x_{1,i} + \alpha_2 x_{2,i}$$

$$logit(p_{ij}) = ln\left(\frac{p_{i,j}}{1-p_{i,j}}\right) = \beta_0 + \beta_1 x_{1,i} + \beta_2 x_{2,i} + \beta_3 y_{1,ij} + \beta_4 y_{2,ij}$$

where ln is the natural logarithm, the x's and y's are site-specific and survey-specific covariates respectively, and the α and β parameters are the regression coefficients to be estimated. These resulting equations are in the form of logistic regression equations. An important consideration to note is that detection probability can be modelled as a function of either site-specific or sampling-specific covariates; however, occupancy can only be modelled as a function of site-specific covariates (Bailey et al. 2007).

4.2.3.2 Key model assumptions

There are four critical assumptions of single season occupancy models that can be met using design-based or model-based approaches. These assumptions (MacKenzie et al. 2002; 2006; Bailey & Adams 2005) and details of how they were met in this study are as follows:

a) Sites are closed to systematic changes in occupancy during a sampling season:

Common dolphins are highly mobile animals that do not adhere to the assumption of geographic closure. However, this assumption can be relaxed if a species moves in and out of sites in a random manner, although the interpretation of the parameter estimates changes. As such, this study examined common dolphin 'use', i.e. the probability that dolphins used a site; and detection probability, i.e. both the probability that dolphins used a site and the probability that they were detected given that the site was used (MacKenzie et al. 2004; 2006; Midlane et al. 2014). The term 'proportion of area used' (PAU) was applied rather than 'proportion of area occupied' and the model predictions were interpreted as 'probability of dolphin use' (PDU) rather than 'probability of dolphin occupancy'. As explained in MacKenzie et al. (2006), the terms referring to the proportion of area occupied/used and the underlying probability that a site within a group of sites is occupied/used are often used interchangeably since the observed proportion can be used as an estimate of the underlying probability.

b) No false detections:
Surveys were designed to ensure there was no misidentification of species, i.e. that species were never falsely detected when absent. In this study, the research vessel left the transect line and approached dolphin groups to ensure the dolphins were correctly identified.

c) Detections are independent:
It is assumed that detection of a species at a site is independent of detection of the species at other sites. Boat surveys were conducted such that animals could not be detected at multiple sites during a survey (i.e. on the same day). The issue of 'trap response' was also not a concern when conducting visual boat-based surveys because dolphins were not subject to being easier to detect at a site where they had already been detected on a previous survey.

d) No unmodelled heterogeneity:
Occupancy and detection probabilities are assumed to be constant across sites or differences can be explained with covariates that are included in the model. In this study, information was collected about the factors that were considered to cause heterogeneity in occupancy or detection probability for incorporation into the models. The covariates that were considered to cause variation in occupancy or detectability are detailed in Sections 4.2.3.4–4.2.3.5.

4.2.3.3 Sampling units, survey periods and detection histories

A grid of 150 cells, each 5 x 5 km in size, was created for the IHG using the *grid index features* tool in ArcGIS version 10.0 (ESRI, Redlands, California, USA). Each grid cell constituted a sampling unit, or site. All spatial data were processed using ArcGIS and Geospatial Modelling Environment (GME) version 0.7.2.0 (Beyer 2012). The New

Zealand Transverse Mercator (NZTM2000) projection was used for all spatial analyses.

Detection histories were collated for each site for each month of each austral season, (defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November)) to facilitate comparisons with previous studies conducted on common dolphins in New Zealand waters (e.g. Neumann 2001a; Stockin et al. 2008). Since annual variability in common dolphin occurrence was not detected in the Hauraki Gulf (Chapter 3), seasonal data were pooled across years. A grid cell received a '1' for a detection, regardless of how many groups were encountered in the cell per sampling month. A non-detection received a '0'.

4.2.3.4 Site covariates

The following environmental and spatial variables were considered to influence the habitat use of common dolphins, similar to Chapter 3: depth, slope, tidal current, SST within season standard deviation, easting, northing, and distance to shore (Chapter 3). The mean depth (m) and slope (°) of grid cells were calculated in ArcMAP using the NIWA Hauraki Gulf bathymetric dataset (Mackay et al. 2012) and the Spatial Analyst tools s*lope* and z*onal statistics*. The mean tidal current for each grid cell was obtained from the New Zealand Marine Environment Classification raster 'tidal_curr', which was calculated as the depth averaged maximum tidal current in m/s (Snelder et al. 2005). Daily SST data (° C) were obtained from the Physical Oceanography Distributed Active Archive Centre (PO.DAAC, NASA Jet Propulsion Laboratory, Pasadena, California, USA) at a 1 km spatial scale and subsequently averaged over each grid cell. The SST within-month standard deviation was calculated for each grid cell as a measure of variability that is expected to be large where eddy activity occurs in regions of strong spatial gradients (Hadfield et al. 2002). Distance to shore (km) was calculated using the *near* tool to measure the distance between the centroid of each grid cell and the nearest point of land. If a cell centroid was located on land, the distance to shore was classified as zero.

4.2.3.5 Sampling covariates

The amount of search effort in a grid cell and Beaufort sea state were considered to be the main variables acting on detection probability and were also fitted in the GLMs (Chapter 3) for comparative purposes. Other factors known to influence cetacean detectability include the number of observers, group size and behaviour (Barlow et al. 2001; Silva et al. 2014). The number of observers was kept constant in this study and the effects of group size and behaviour were not accounted for here since these variables could not readily be incorporated into the common dolphin single season models in PRESENCE.

Search effort was expressed as the number of kilometres of effort through a grid cell per survey day. The processing of track data is detailed in Chapter 2. Briefly, the total number of kilometres of effort in each grid cell per survey month was calculated using the *sumlinelengthsinpolys* command in GME. Beaufort sea state values were assigned to each grid cell for each sampling occasion. The value corresponded with the sea state recorded for the mid-point of the vessel track within each grid cell. The weighted average was then calculated for any grid cells that were sampled more than once in a given month.

4.2.3.6 Model building and selection

Prior to modelling, site covariates were examined for pairwise correlations (Appendix 4.1). The Spearman correlation coefficient (r_s) was used since most site covariates were not normally distributed. For highly correlated variables with $r_s > 0.7$ (González-Suárez et al. 2013), the most biologically meaningful variable was typically retained. A final set of four site covariates (depth, slope, current and easting) remained for model building.

Single season occupancy models were built in program PRESENCE version 6.4 (Hines 2006a). First, naïve occupancy estimates (the proportion of cells where dolphins were detected) were compared with the constant habitat model (holding ψ constant and varying p for effort and Beaufort sea state), to assess the effect of false absences on seasonal PAU. While this is not the best representation of the data, it provides a basic comparison of unadjusted (i.e. naïve) and adjusted proportions

(Connell et al. 2006). PDU was then modelled as a function of site-specific covariates while modelling detection probability as a function of the sampling-occasion covariates.

AIC_C values (Akaike Information Criterion adjusted for small sample sizes) were used to rank candidate models (Burnham & Anderson 2002). Model weights were used to assess the evidence for a given model being the best model in the candidate set. If no model received > 90% of the weight, the top ranked models constituting the 95% confidence set (i.e. the top ranking models with Akaike weights summing to 0.95) were selected and model-averaged estimates of ψ were calculated (Burnham & Anderson 2002; Long et al. 2011). The estimated effects of coefficients for site covariates were also compared across seasons using each single site covariate model in combination with the sampling occasion covariates acting on detection probability (e.g. ψ(depth), p(effort+beaufort)). Model fit was evaluated using the program PRESENCE by comparing the observed Pearson χ^2 statistic from the most general model with χ^2 statistics from 10,000 simulated parametric bootstrapped datasets (MacKenzie & Bailey 2004; MacKenzie et al. 2006; Long et al. 2011).

4.2.3.7 Predicted distribution maps and comparison of occupancy and GLM predictions

The resulting model-averaged predictive values were applied to each 5 x 5 km grid cell to create a map of spatially explicit PDU for each season. Additionally, PDU predictions from occupancy models were compared to the GLM probability of encounter predictions for common dolphins in the IHG (GLMs presented in Chapter 3). Since the predictive values from the different modelling techniques were not directly comparable, the Spearman correlation coefficient (r_s) was used to evaluate the cell rankings from highest to lowest. The predictive maps were also compared visually after rescaling as deciles (Gormley et al. 2011). Outputs were rescaled independently for each season and model type.

4.3 RESULTS

4.3.1 Models

Common dolphins were detected in 89 of the 150 grid cells sampled during 233 survey days between January 2010 and November 2012. The average number of secondary sampling periods per season was 5.3 in summer, 4.4 in autumn, 4.6 in winter, and 4.5 in spring. Of the 253 total detections, winter had the most detections per season (n = 98) across the most sites (n = 64). Therefore, winter had the highest naïve PAU estimate (0.427, Table 4.1). Similar naïve estimates were recorded for spring (0.293) and summer (0.247), while the lowest PAU was recorded during autumn (0.188; Table 4.1).

Table 4.1 Common dolphin occupancy model data collected in the inner Hauraki Gulf (IHG) in 2010–2012, with naïve and modelled estimates of the seasonal proportion of area used (PAU). Naïve estimates represent the proportion of grid cells used during each season without accounting for imperfect detection. The modelled estimates of ψ are based on the $\psi(.)p$(effort+beaufort) model accounting for heterogeneity in detection probability due to sampling effort and Beaufort sea state.

Model	Number of sites with detections	Number of detections	Naïve estimate of use	Modelled estimate of use (ψ)	SE	95% CI
Summer	36	54	0.247	0.476	0.093	0.305–0.653
Autumn	28	34	0.188	0.547	0.158	0.257–0.808
Winter	64	98	0.427	0.660	0.069	0.515–0.781
Spring	44	67	0.293	0.515	0.082	0.358–0.669

For all seasons, the probability of detection increased with increased effort, and decreased with increasing Beaufort sea state (Table 4.2). The model $\psi(.)p$(effort+beaufort) holding occupancy constant estimated PAU, after adjusting detection probability to vary with effort and Beaufort sea state, as 0.66 (95% CI: 0.52–0.78; Table 4.1) for winter. Unlike the naïve estimate, the modelled estimate for autumn had the second highest seasonal value at 0.55 (95% CI: 0.26–0.81). Overall, the model estimates indicated more constant use of the IHG across all seasons when compared with the naïve estimates, with the detectability-corrected estimates 22.2–35.9% higher than the naïve estimates (Table 4.1).

Table 4.2 Untransformed estimates and standard errors of sampling occasion coefficients acting on detection probability for constant habitat models $\psi(.)p(\text{effort+beaufort})$ for common dolphins in the inner Hauraki Gulf (IHG), New Zealand.

Model	$\hat{\beta}$(effort)	SE	$\hat{\beta}$(beaufort)	SE
Summer	0.105	0.030	-0.359	0.195
Autumn	0.094	0.045	-0.783	0.240
Winter	0.169	0.040	-0.437	0.162
Spring	0.133	0.038	-0.401	0.170

The site covariates depth, slope, current and easting remained after removing correlated variables (Table 4.3). All model results indicated some degree of model selection uncertainty (Tables 4.4–4.7); therefore model averaging of the predictions was performed for all seasonal models. For all seasons except autumn, all four site covariates appeared in the top ranking models (Table 4.4, 4.6, 4.7). For autumn, the top models contained all covariates except current (Table 4.5). The candidate set for autumn was smaller than for other seasons because some models (with a combination of the depth covariate and one or more other covariates acting on ψ) gave spurious results (i.e. only estimates of 0 or 1) and were subsequently removed from the set (Table 4.5). No evidence of overdispersion was detected for any of the models ($\hat{c} < 1$).

Table 4.3 Untransformed estimates and standard errors of coefficients for site covariates affecting the probability of common dolphin use (PDU). Estimates are from models with only the named site covariate acting on PDU, e.g. $\psi(\text{depth})\ p(\text{effort+beaufort})$.

Model	$\hat{\beta}$(depth)	SE	$\hat{\beta}$(slope)	SE	$\hat{\beta}$(current)	SE	$\hat{\beta}$(easting)	SE
Summer	1.489	0.413	-1.913	0.642	-0.802	0.389	-0.462	0.337
Autumn	4.357	1.670	-1.807	0.702	0.055	0.755	3.447	2.359
Winter	3.658	1.121	-1.007	0.325	0.066	0.356	1.133	0.695
Spring	2.535	0.683	-1.760	0.512	-0.462	0.314	-0.117	0.314

Depth appeared to be the most important variable since it was always in the top ranking models and did not appear in any of the low ranking models, unlike the other site covariates (Tables 4.4–4.7). The directions of the model parameter estimates for depth and slope were consistent across seasons, with a strong positive effect of depth and a negative effect of slope (Table 4.3). The effect of depth was strongest in autumn (4.36 ± 1.67; Table 4.3), with increased probability of dolphins using deeper waters. The effect of current was variable since it was negative in summer and spring and weakly positive in autumn and winter, although the autumn and winter estimates had large standard errors relative to the estimates (Table 4.3). The estimates suggested higher PDU in more westerly regions of the IHG during spring and summer, but further east in autumn and winter (Table 4.3).

Table 4.4 Model selection results of single season occupancy analysis for common dolphins using inner Hauraki Gulf (IHG) waters during summer. The top ranked models (i.e. the top ranking models with Akaike weights summing to 0.95) used in model-averaging are in bold.

Model	**AIC_C**	**Δ AIC_C**	**AIC_C weight**	**-2 Log likelihood**	**No. parameters**
ψ(depth + current + slope), *p* (effort + beaufort)	343.47	0.00	0.4078	327.04	7
ψ(depth + easting + slope), *p* (effort + beaufort)	345.22	1.75	0.1700	328.79	7
ψ(depth + current), *p* (effort + beaufort)	345.45	1.98	0.1515	331.66	6
ψ(depth + current + slope + easting), *p* (effort + beaufort)	345.99	2.52	0.1157	326.79	8
ψ(depth + slope), *p* (effort + beaufort)	346.91	3.44	0.0730	333.12	6
ψ(depth + current + easting), *p* (effort + beaufort)	348.04	4.57	0.0415	331.61	7
ψ(depth + easting), *p* (effort + beaufort)	349.60	6.13	0.0190	335.81	6
ψ(depth), *p* (effort + beaufort)	350.51	7.04	0.0121	339.26	5
ψ(slope + easting), *p* (effort + beaufort)	352.89	9.42	0.0037	339.10	6
ψ(slope + current), *p* (effort + beaufort)	353.14	9.67	0.0032	339.35	6
ψ(current + easting + slope), *p* (effort + beaufort)	354.50	11.03	0.0016	338.07	7
ψ(slope), *p* (effort + beaufort)	355.91	12.44	0.0008	344.66	5
ψ(current), *p* (effort + beaufort)	366.89	23.42	0.0000	355.64	5
ψ(current + easting), *p* (effort + beaufort)	369.43	25.96	0.0000	355.64	6
ψ(.), *p* (effort + beaufort)	370.17	26.70	0.0000	361.35	4
ψ(easting), *p* (effort + beaufort)	370.63	27.16	0.0000	359.38	5
ψ(.), *p* (.)	381.90	38.43	0.0000	377.66	2

Table 4.5 Model selection results of single season occupancy analysis for common dolphins using inner Hauraki Gulf (IHG) waters during autumn. The top ranked models (i.e. the top ranking models with Akaike weights summing to 0.95) used in model-averaging are in bold.

Model	AIC_C	Δ AIC_C	AIC_C weight	-2 Log likelihood	No. parameters
ψ(depth), p (effort + beaufort)	226.14	0.00	0.6106	214.00	5
ψ(depth + slope), p (effort + beaufort)	228.38	2.24	0.1992	213.27	6
ψ(depth + easting), p (effort + beaufort)	229.02	2.88	0.1447	213.91	6
ψ(depth + current + easting), p (effort + beaufort)	231.33	5.19	0.0456	213.02	7
ψ(easting + slope), p (effort + beaufort)	251.43	25.29	0.0000	236.32	6
ψ(slope), p (effort + beaufort)	252.14	26.00	0.0000	240.00	5
ψ(current + easting), p (effort + beaufort)	252.49	26.35	0.0000	237.38	6
ψ(current + slope), p (effort + beaufort)	254.24	28.10	0.0000	239.13	6
ψ(current + easting + slope), p (effort + beaufort)	254.56	28.42	0.0000	236.25	7
ψ(easting), p (effort + beaufort)	257.11	30.97	0.0000	244.97	5
ψ(.), p (effort + beaufort)	260.71	34.57	0.0000	251.33	4
ψ(current), p (effort + beaufort)	263.47	37.33	0.0000	251.33	5
ψ(.), p (.)	270.03	43.89	0.0000	265.64	2

Table 4.6 Model selection results of single season occupancy analysis for common dolphins using inner Hauraki Gulf (IHG) waters during winter. The top ranked models (i.e. the top ranking models with Akaike weights summing to 0.95) used in model-averaging are in bold.

Model	**AIC$_C$**	**Δ AIC$_C$**	**AIC$_C$ weight**	**-2 Log likelihood**	**No. parameters**
ψ(depth), p (effort + beaufort)	496.63	0.00	0.2866	485.98	5
ψ(depth + easting), p (effort + beaufort)	496.79	0.16	0.2646	483.87	6
ψ(depth + current), p (effort + beaufort)	498.50	1.87	0.1125	485.58	6
ψ(depth + slope), p (effort + beaufort)	498.81	2.18	0.0964	485.89	6
ψ(depth + slope + easting), p (effort + beaufort)	498.89	2.26	0.0926	483.65	7
ψ(depth + current + easting), p (effort + beaufort)	499.11	2.48	0.0829	483.87	7
ψ(depth + current + slope), p (effort + beaufort)	500.78	4.15	0.0360	485.54	7
ψ(depth + current + slope + easting), p (effort + beaufort)	501.26	4.63	0.0283	483.64	8
ψ(slope), p (effort + beaufort)	533.24	36.61	0.0000	522.59	5
ψ(slope + easting), p (effort + beaufort)	534.63	38.00	0.0000	521.71	6
ψ(slope + current), p (effort + beaufort)	535.04	38.41	0.0000	522.12	6
ψ(current + slope + easting), p (effort + beaufort)	536.87	40.24	0.0000	521.63	7
ψ(easting), p (effort + beaufort)	540.27	43.64	0.0000	529.62	5
ψ(current + easting), p (effort + beaufort)	541.14	44.51	0.0000	528.22	6
ψ(.), p (effort + beaufort)	542.52	45.89	0.0000	534.09	4
ψ(current), p (effort + beaufort)	544.70	48.07	0.0000	534.05	5
ψ(.), p (.)	564.96	68.33	0.0000	560.83	2

Table 4.7 Model selection results of single season occupancy analysis for common dolphins using inner Hauraki Gulf (IHG) waters during spring. The top ranked models (i.e. the top ranking models with Akaike weights summing to 0.95) used in model-averaging are in bold.

Model	**AIC_C**	**Δ AIC_C**	**AIC_C weight**	**-2 Log likelihood**	**No. parameters**
ψ(depth + current + slope), *p* (effort + beaufort)	368.89	0.00	0.4288	352.99	7
ψ(depth + current), *p* (effort + beaufort)	369.80	0.91	0.2721	356.40	6
ψ(depth + current + slope + easting), *p* (effort + beaufort)	371.40	2.51	0.1222	352.92	8
ψ(depth + current + easting), *p* (effort + beaufort)	372.30	3.41	0.0779	356.40	7
ψ(depth + slope + easting), *p* (effort + beaufort)	373.41	4.52	0.0447	357.51	7
ψ(depth + easting), *p* (effort + beaufort)	374.55	5.66	0.0253	361.15	6
ψ(depth + slope), *p* (effort + beaufort)	375.44	6.55	0.0162	362.04	6
ψ(depth), *p* (effort + beaufort)	375.93	7.04	0.0127	364.95	5
ψ(slope), *p* (effort + beaufort)	394.81	25.92	0.0000	383.83	5
ψ(slope + current), *p* (effort + beaufort)	395.31	26.42	0.0000	381.91	6
ψ(slope + easting), *p* (effort + beaufort)	395.68	26.79	0.0000	382.28	6
ψ(current + slope + easting), *p* (effort + beaufort)	397.44	28.55	0.0000	381.54	7
ψ(current), *p* (effort + beaufort)	414.08	45.19	0.0000	403.10	5
ψ(.), *p* (effort + beaufort)	414.29	45.40	0.0000	405.64	4
ψ(current + easting), *p* (effort + beaufort)	416.18	47.29	0.0000	402.78	6
ψ(easting), *p* (effort + beaufort)	416.48	47.59	0.0000	405.50	5
ψ(.), *p* (.)	425.84	56.95	0.0000	421.65	2

4.3.2 Predicted distribution

The seasonal maps derived from the model-averaged results predicted widespread use of the IHG by common dolphins, with low predicted occurrence for the Tamaki Strait and Firth of Thames regions (Fig. 4.2). High PDU (> 0.5) cells were contiguous across central and northern regions in all seasons (Fig. 4.2), although fine-scale seasonal patterns were apparent. Overall, common dolphin occurrence was predicted to be most widespread and with a greater proportion of high PDU cells in winter (60.7%), with decreasing numbers of high PDU cells as water temperatures increased through spring (43.3%) and summer (33.3%). The number of high PDU cells increased again in autumn (41.3%), although this was spatially restricted to deeper water areas. Areas with low PDU (< 0.2) were most prevalent during autumn (52.7%) and in inshore waters, particularly in western areas (Fig. 4.2). In winter, only 26.7% of cells had a PDU of < 0.2.

4.3.3 Comparison of occupancy model and GLM predictions

There were strong positive correlations (Summer: r_S = 0.958, autumn: r_S = 0.837, winter r_S = 0.825, spring: r_S = 0.934) between the rankings of cells based on the different model types (occupancy models and GLMs from Chapter 3). Cells with higher probability of encounter values from the GLMs also had higher PDU values from the occupancy models. After rescaling the outputs to deciles, minor spatial differences were observed for the highest ranked cells (decile 10, Fig. 4.3) in autumn and winter, with those cells located slightly further north for occupancy models. Cells in coastal areas were generally ranked higher for the GLMs, although these rankings remained lower overall. Hence, while the GLM predictions were negatively biased overall (maximum probability of encounter 0.2, Chapter 3) by not accounting for imperfect detection, the same high use areas were identified by both model types.

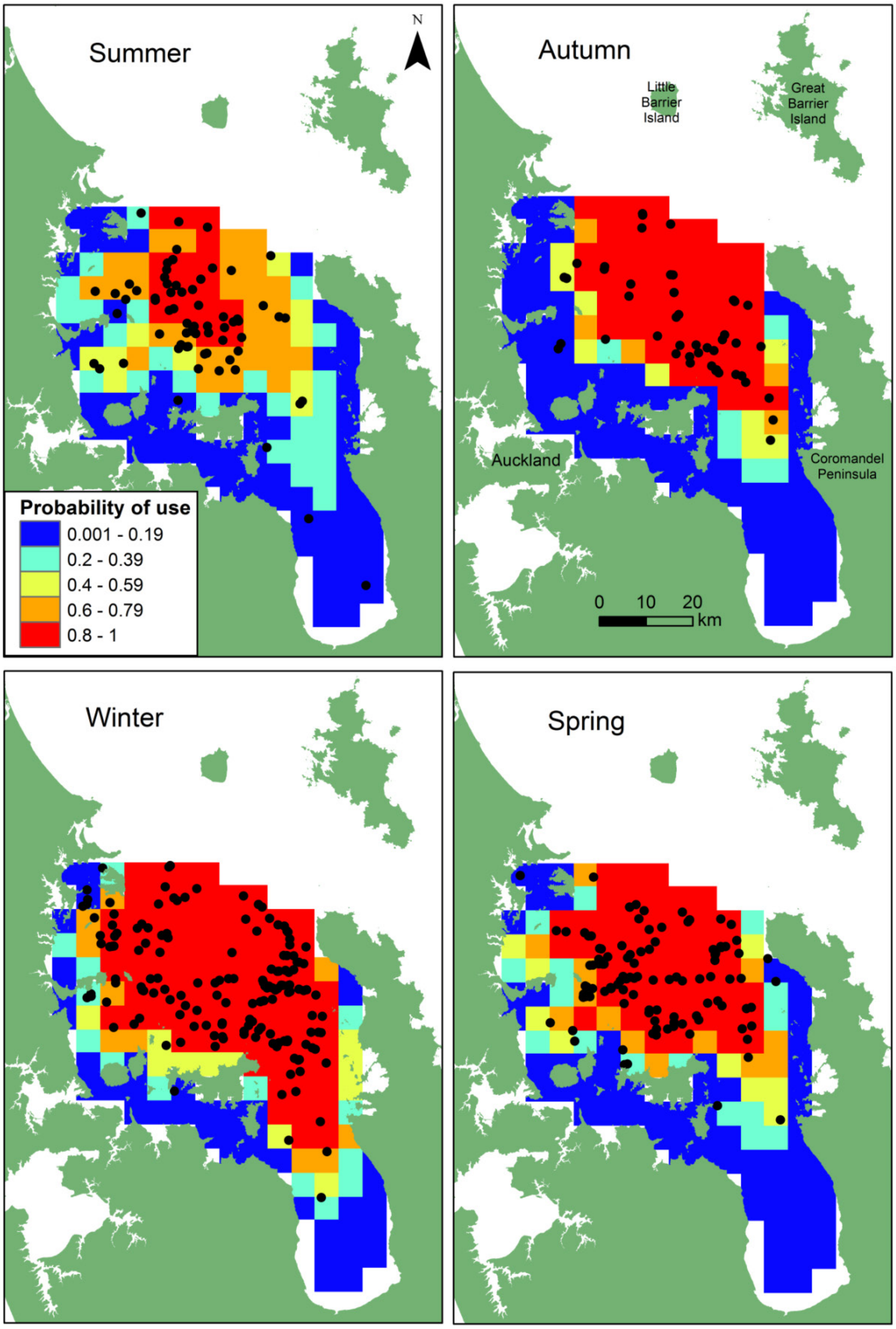

Figure 4.2 Predicted seasonal estimates of ψ (probability of dolphin use, PDU) for common dolphins. Red and blue represent the highest and lowest probabilities, respectively, as shown in the key. Black dots show actual sighting locations from inner Hauraki Gulf (IHG) surveys in 2010–2012.

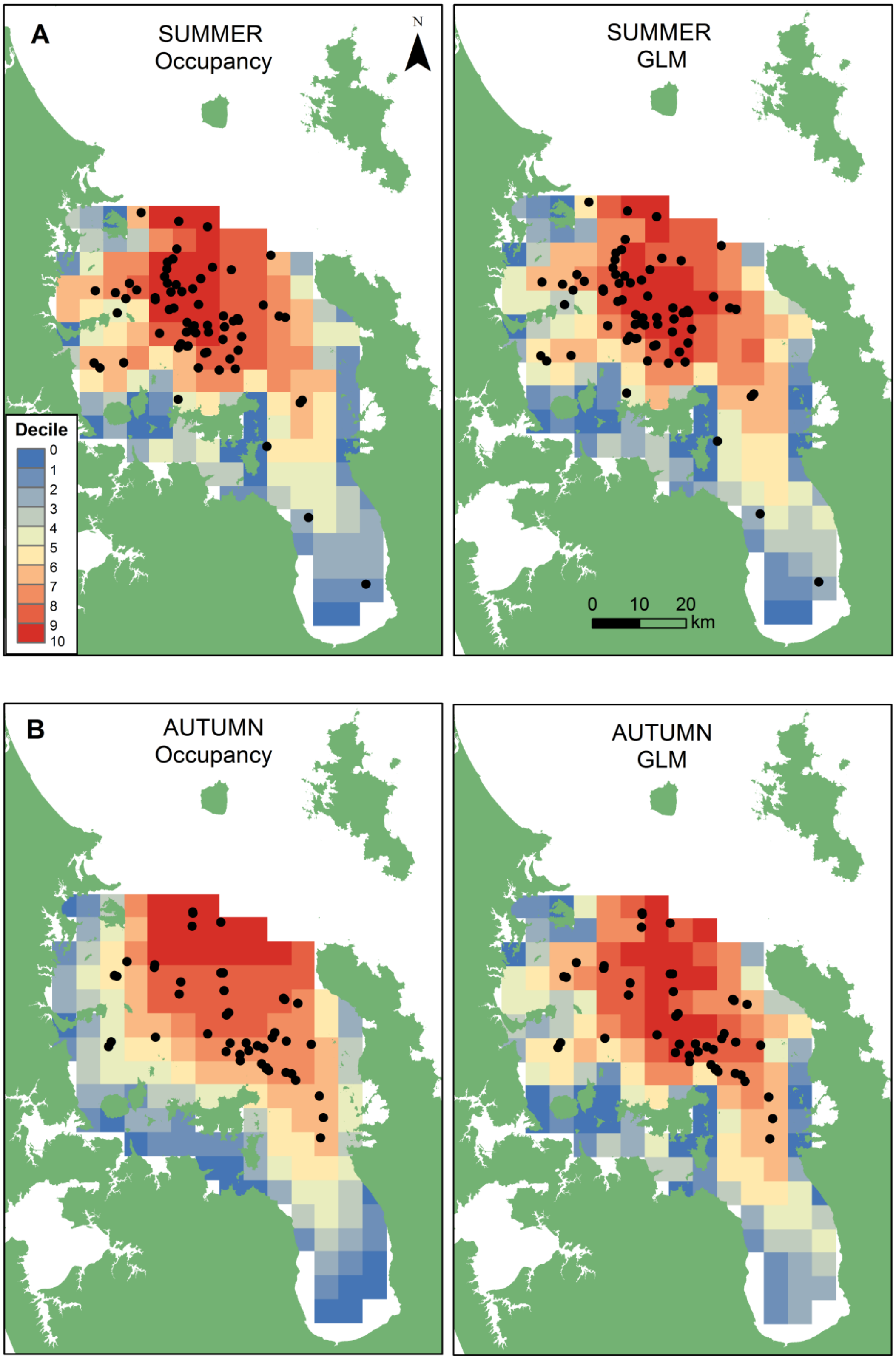

Figure 4.3a–b Seasonal outputs of occupancy models and GLMs rescaled as deciles. Red and blue represent the highest and lowest probabilities, respectively, as shown in the key. Black dots show actual sighting locations of common dolphins from inner Hauraki Gulf (IHG) surveys in 2010–2012. Note: Each season was scaled independently; therefore inter-seasonal comparisons cannot be made.

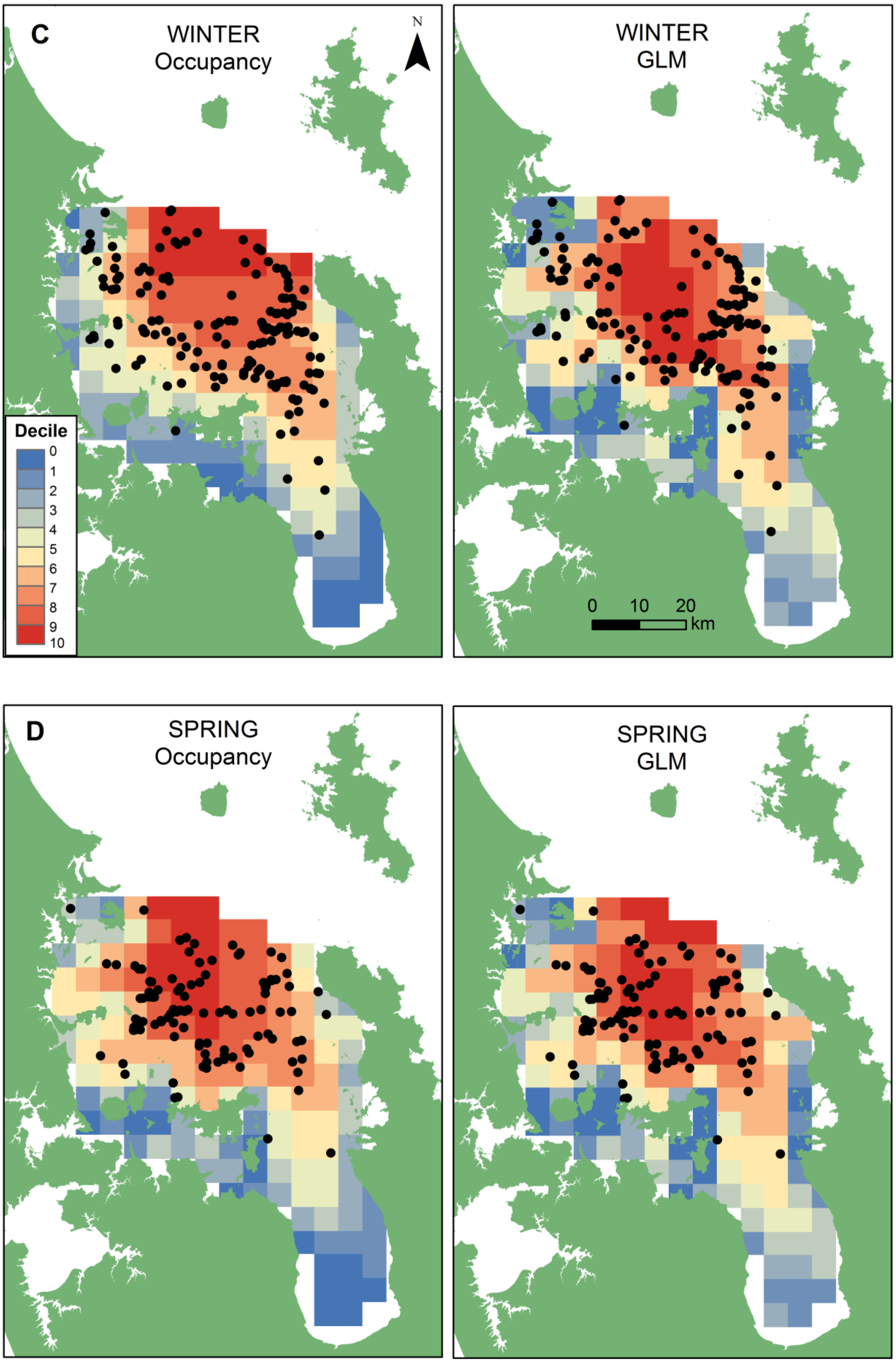

Figure 4.3c–d contd. Seasonal outputs of occupancy models and GLMs rescaled as deciles. Red and blue represent the highest and lowest probabilities, respectively, as shown in the key. Black dots show actual sighting locations of common dolphins from inner Hauraki Gulf (IHG) surveys in 2010–2012. Note: Each season was scaled independently; therefore inter-seasonal comparisons cannot be made.

4.4 DISCUSSION

This study demonstrates for the first time, that occupancy models can be successfully applied to cetacean sighting data to assess habitat use while simultaneously accounting for imperfect detection. A literature search suggests that occupancy modelling has previously only been used to investigate long-term occupancy trends in dugong (*Dugong dugon*, D'Souza et al. 2013).

Results of the field surveys alone suggested that common dolphins used 19–43% of the IHG when the concept of imperfect detection was ignored. These seasonal PAU (proportion of area used) estimates increased substantially to 48–66% when accounting for detection probability. This shows the importance of taking into consideration the negative biases that occur when detection probability is less than one, as previously described by MacKenzie et al. (2002). The direction of the effects of effort and Beaufort sea state on detection probability were as expected, based on the results of the GLMs (Chapter 3) and from previous studies that have reported the negative effect of sea state on detection probability (Forney 2000; Barlow et al. 2001). Interestingly, the models suggested detection probability was lower in autumn than other seasons. However, due to violation of the closure assumption in this study, detection probability was confounded with probability of use. As such, the decreased detection probabilities for autumn may be representative of decreased probability of use rather than decreased detection probabilities because survey methods were consistent across all seasons, the proportions of the different sea states did not vary significantly between seasons, and total effort in autumn was similar to winter and spring (Chapter 2). As discussed in Chapter 2, common dolphins are known to move offshore during autumn in other regions, e.g. Bay of Plenty (Neumann 2001a; Meissner et al. 2014), corresponding with fewer encounters in the IHG (Chapters 2, 3, 4). Alternatively, another covariate that was unaccounted for in the models may have affected the seasonal detection probabilities. This highlights the general problem of detection probability being confounded with presence in non-closed populations.

MacKenzie et al. (2006) highlighted that heterogeneity in detection probability will often lead to negatively biased occupancy estimates. If animals are attracted to the observer, or in this case the research vessel, this could be a potential source of bias in detection probability. Some species such as Hector's dolphins (*Cephalorhyncus hectori hectori*) are known to be attracted to boats (Dawson et al. 2008) and while the responsive movement (whether positive or negative) of common dolphins to boats was not assessed in this study, common dolphins have also demonstrated positive responsive movements to boats in previous studies (Goold 1996; Filby et al. 2010). This warrants further investigation since it may be an additional source of heterogeneity in detection probability that was not accounted for in this study.

It was reassuring, although not surprising given that both techniques are based on logistic regression (Guisan & Zimmermann 2000; MacKenzie & Nichols 2004), that the effects of the habitat covariates were similar between the occupancy models and the GLMs (Chapter 3). Depth appeared to be an important predictor of common dolphin occurrence. This corresponded with the results of Chapter 3, and with a previous study using GAMs that reported depth to be a highly significant predictor of common dolphin presence (Stockin et al. 2008a). The relationship of dolphin occurrence with depth was especially apparent during autumn, when distribution was more restricted to deeper areas of the IHG. The higher PDU across the IHG during winter corresponds with the highest seasonal level of feeding (Stockin et al. 2009a) and aligns with the previously suggested importance of the IHG for feeding groups of common dolphins (Stockin et al. 2008a; 2009a).

There was strong agreement between the rankings of the two types of model predictions, suggesting that the identification of high and low use areas was relatively consistent whether detection probability was explicitly accounted for or not. In a study of sambar deer (*Cervus unicolor*) in Victoria, Australia, some low habitat suitability areas were ranked higher using a Maxent model compared with an occupancy model (Gormley et al. 2011), as was the case when comparing the lower ranking coastal cells from the GLMs with the occupancy models in this study. Gu & Swihart (2004) showed that occupancy estimation can be positively biased if detectability at a site is not random but is related to habitat characteristics (e.g. a clearing in a forest that may enable deer to be more easily detected). In this study, detectability seems unlikely to be affected by habitat characteristics because the variations in the characteristics of the Hauraki Gulf grid cells (depth, slope, current, SST) were related to the subsurface habitat. Factors such as sea state (a characteristic of the sampling conditions) were more likely to affect detection probability because surveys were conducted topside.

Regardless of the discrepancies and the underestimation of the GLM predictions, the top ranking cells were spatially consistent for both model types, which is reassuring for studies concerned with the geographic location of hotspot areas. If conservation managers are concerned mainly with the distribution of species or relatively high use areas, then occupancy may not necessarily be a better choice than other models. For example, Welsh et al. (2013) argue that adjusting occupancy models for non-detection can be just as misleading as ignoring non-detection altogether if detection depends on abundance. However, if more accurate predictive probabilities of temporal or spatial use are required for specific management directives, then occupancy modelling may be a useful approach since predictions will be corrected for detection bias.

The occupancy approach has many benefits for cetacean studies, including the capacity for incorporating missing observations (i.e. missed sampling of a site; MacKenzie et al. 2002; MacKenzie 2005b) that are often the status quo in marine mammal studies due to deteriorating weather conditions (e.g. Hammond et al. 2002; Mannocci et al. 2014). Other benefits include that the detection probabilities are modelled using the same sighting data, therefore additional independent observers are not required. Since detection probabilities may be a function of survey-specific variables (MacKenzie et al. 2002; MacKenzie 2005b), factors such as sea state (which is known to affect the detection of cetaceans at sea) may be incorporated into the models relatively easily. Furthermore, the assumption that all sites are closed to changes in occupancy can be relaxed (and the inference changed to ‘probability of use’) for species that move in and out of sites in a random manner (MacKenzie 2005a), as is the case for many cetacean species.

As with any method, there are inevitably limitations of using occupancy techniques in cetacean studies. One of the challenges innate to all cetacean habitat use studies is relating occurrence to the characteristics of a highly dynamic environment (Redfern et al. 2006; Gómez de Segura et al. 2007). For occupancy modelling, site covariates can be used for estimating occupancy (or use) or detection probabilities, but sampling occasion covariates can only be used for estimating detection probabilities. Therefore, site covariates associated with each grid cell must be static (e.g. depth) or averaged across sampling periods. This limitation could prove problematic in some fine-scale studies where averaging covariates across sampling periods could result in the inability to appropriately capture the variability in oceanographic conditions. However, static variables can be good predictors of cetacean occurrence (Cañadas et al. 2002), especially if models are run at a scale that accounts for some of the unknown variability in hydrodynamics.

Another potential challenge with occupancy modelling for cetaceans is the difficulty in obtaining enough detections (sightings) during field surveys. As with any ecological study, it is important to consider survey design before commencing data collection (MacKenzie 2005a; Dawson et al. 2008). Program GENPRES (Hines 2006b) can be used as a tool during the survey design process to explore design trade-offs of a particular study system and its sampling limitations (Bailey et al. 2007). However, for some cetacean species that are rarely detected, it may still be futile to use occupancy models if sample sizes remain too small to conduct any meaningful analyses.

The single-season modelling framework was chosen for this study since one of the objectives was to compare outputs with those of the GLMs presented in Chapter 3, rather than to estimate local extinction and colonisation of sites. However, a variety of options are available that should be explored in relation to cetacean habitat studies, such as the multi-season models (MacKenzie et al. 2003), multi-state models (MacKenzie et al. 2009) or species co-occurrence models (MacKenzie et al. 2004).

4.4.1 Summary

The application of occupancy modelling to cetacean habitat use studies appears promising. This study combined data from field surveys with statistical techniques that incorporate detection probability to model and predict the seasonal distribution of common dolphins in the Hauraki Gulf. The estimates of the proportion of the Hauraki Gulf used by common dolphins were significantly greater when detection probability was accounted for. However, the effects of the habitat covariates were similar between the occupancy models and the GLMs (Chapter 3), with depth identified as an important predictor of common dolphin occurrence. The increased probability of use across the IHG during winter corresponded with the highest levels of seasonal feeding identified in previous studies, again highlighting the importance of the Hauraki Gulf for feeding groups of common dolphins. Overall, there was strong agreement between the rankings of the occupancy and GLM predictions, suggesting that the identification of high and low use areas was relatively consistent whether detection probability was accounted for or not. In conclusion, the models and predictions provide conservation managers with a tool to understand the likely spatial use of the Hauraki Gulf by common dolphins, and how and possibly why that likelihood changes seasonally.

Chapter 5

Population ecology of bottlenose dolphins at Great Barrier Island

Bottlenose dolphin (*Tursiops truncatus*) off the southwest coast of Great Barrier Island. Photo: Sarah Dwyer.

This chapter is a reformatted version of the manuscript:

Dwyer et al. (2014a) Overlooking a potential hotspot at Great Barrier Island for the nationally endangered bottlenose dolphin of New Zealand. ***Endangered Species Research*** **25: 97–114.**

5.1 INTRODUCTION

Worldwide conservation efforts employed to date have typically relied on a triage system, whereby a species/population only receives protection after it has been demonstrated that there is an urgent requirement to do so (Hooker & Gerber 2004). Often, management efforts instigated to conserve these endangered populations subsequently focus on the protection of key areas and habitats of rare species (Komdeur 1996; Clapham et al. 1999; Wright et al. 2008). However, optimal protection would need to encompass the population's year-round distribution (Reeves 2000), with an understanding of its abundance, assuming that is even known.

A lack of knowledge is not the only obstacle to species protection, with most conservation initiatives constrained by economic circumstances. In New Zealand, the majority of the scientific evaluation of marine mammal species and populations has historically been driven by concerns about either incidental fisheries bycatch (common dolphin (*Delphinus* sp., Stockin et al. 2009b; Thompson et al. 2013), Hector's dolphin (*Cephalorhyncus hectori hectori*, Slooten & Lad 1991; Slooten 2007; Rayment & Webster 2009), Maui's dolphin (*Cephalorhyncus hectori maui*, Slooten et al. 2006), New Zealand sea lion (*Phocarctos hookeri*, Chilvers et al. 2005; Chilvers 2008) or tourism effects (bottlenose dolphin (*Tursiops truncatus*, D. Lusseau 2003; Constantine et al. 2004), common dolphin (Neumann & Orams 2006; Stockin et al. 2008a), dusky dolphin (*Lagenorhynchus obscurus*, Lundquist et al. 2012), Hector's dolphins (Bejder et al. 1999; Martinez et al. 2011), sperm whale (*Physeter macrocephalus*, Richter et al. 2006)). Herein, the term 'user-pays research' is used to refer to the type of system illustrated by these examples, whereby a stakeholder provides research funding to address specific conservation or management needs. As such, research objectives are often specifically based on industry-driven requirements. Although the appropriate feedback can be directly provided to industry stakeholders regarding any potential impacts, the system can be flawed if funding motives become limited over time towards certain research interests, populations or geographic regions.

Although the global conservation status of bottlenose dolphins is low risk 'Least Concern' (Hammond et al. 2012), the Mediterranean Sea and Fiordland (New Zealand) populations have been recognised as 'Vulnerable' (Bearzi et al. 2012) and 'Critically Endangered' (Currey et al. 2011), respectively. Coastal bottlenose dolphins occur in three geographically discrete populations in New Zealand waters (Baker et al. 2010), with low levels of gene flow among them (Tezanos-Pinto et al. 2009). Under the New Zealand Threat Classification System, the species was listed as 'Not Threatened' up until 2002 (Hitchmough 2002) and subsequently uplisted to 'Range Restricted' in 2005 (Hitchmough et al. 2007). A further reclassification to 'Nationally Endangered' in 2009 (Baker et al. 2010) was based on apparent declines in abundance in two of the three coastal populations, coupled with reports of high calf mortality (Currey et al. 2009a; Tezanos-Pinto et al. 2013).

The coastal bottlenose dolphin population of the northern North Island (hereafter referred to as the North Island population), primarily ranges from Doubtless Bay to Tauranga on the east coast of the North Island (see Fig. 5.1; Constantine 2002); although infrequent sightings of known individuals outside of these areas has recently extended the known range to the west coast of the North Island (Tezanos-Pinto et al. 2013). A decline in abundance has been reported for the Bay of Islands (BOI; Tezanos-Pinto et al. 2013), where studies on bottlenose dolphins have formed the basis of our understanding of the North Island population. Research on the species in this region has primarily been driven by funding generated from dolphin tourism levies through the Department of Conservation (DOC), the government agency responsible for managing New Zealand's marine mammal species (Constantine & Baker 1997; Constantine et al. 2003; Hartel et al. 2014). As a result, research on this population has not only been heavily focused on tourism effects (Constantine 2001, Constantine et al. 2004), but perhaps more importantly, was primarily restricted to the specific areas in which tourism is highly developed (BOI in the case of the North Island population). Consequently, while the North Island population has been extensively studied within the confines of BOI, there remains only one species-specific study published to represent other regions (i.e. the inner Hauraki Gulf; Berghan et al. 2008) within the greater home range of this population.

Great Barrier Island (GBI) is situated in the outer Hauraki Gulf and within the home range of the North Island population (Constantine 2002). Previous marine mammal research efforts (prior to this thesis) in the GBI region have been limited to large whale acoustics (Kibblewhite et al. 1967; Helweg 1998; McDonald 2006). No dedicated delphinid studies have been conducted in the GBI area, likely due to a combination of an absence of direct interest from stakeholders and the logistical constraints of fieldwork in this comparatively remote location. Thus, no information is presently available within the scientific literature describing bottlenose dolphins or indeed any other delphinids off GBI.

Given assessments of distribution (Chapter 2), habitat use (Chapter 3), and abundance are vital in understanding the conservation requirements of a population, the aims of this chapter were to assess the importance of GBI waters for bottlenose dolphins by:

- Examining seasonal group dynamics by assessment of group size in relation to the presence or absence of calves;
- Investigating individual site fidelity of bottlenose dolphins to the GBI region and determining whether individuals observed at GBI exhibit any movements away from the area; and
- Estimating demographic parameters, temporary emigration rates, and seasonal and overall abundances of bottlenose dolphins using GBI waters during the study period.

5.2 MATERIALS AND METHODS

5.2.1 Study area

GBI, situated approximately 80 km northeast of Auckland city, is located within the outer Hauraki Gulf (Fig. 5.1). The west coast of GBI, adjacent to Cradock Channel in the north (36°12′S 175°11′E) and Colville Channel in the south (36°23′S 175°25′E), is characterised by numerous shallow embayments and a predominantly rocky shoreline. The study site[2] included all waters up to a distance of 10 km offshore between Miners Head in the north and Ross Bay in the south (Fig. 5.1) and therefore encompassed ~500 km². Water depths in the study area are relatively shallow and reach a maximum of 90 m (Chart NZ 522, Land Information New Zealand). GBI is the largest of New Zealand's northern offshore islands at 285 km², but has a low human population density and 68% of the land is administered by DOC (Norgrove & Jordan 2006). Most of the west coast remains uninhabited and there are currently no commercial marine mammal tourism operations based or operating within GBI waters.

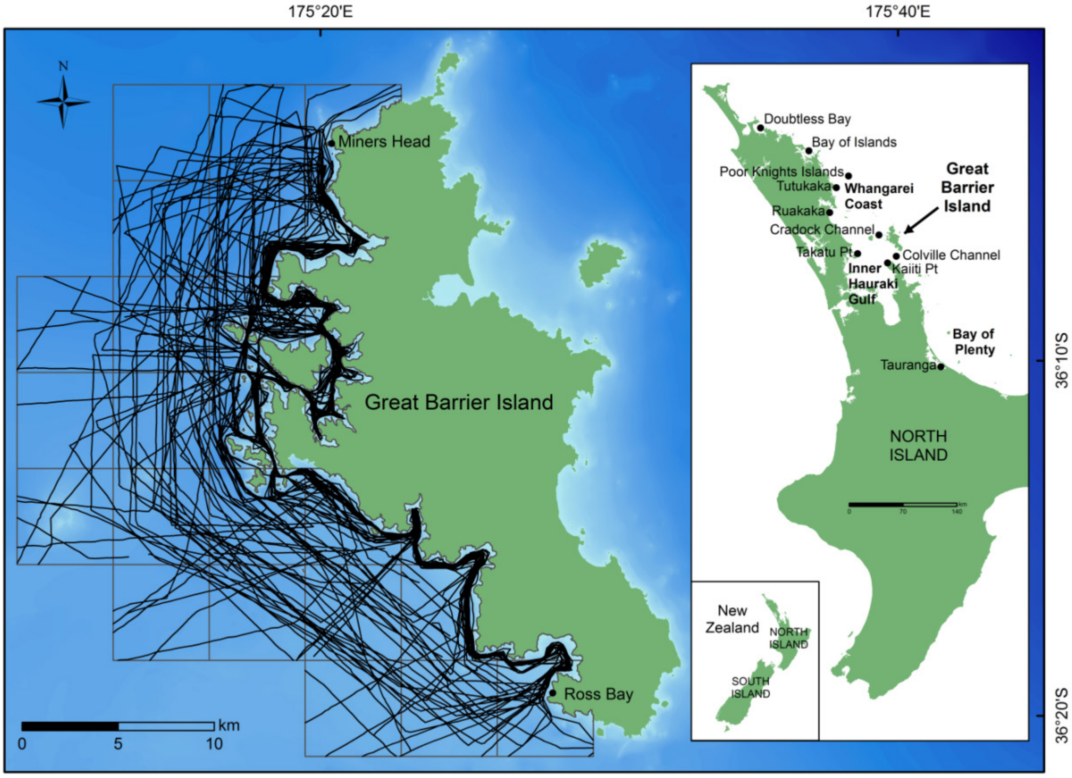

Figure 5.1 Survey tracks off the west coast of Great Barrier Island (GBI), New Zealand, between January 2011 and January 2013. Only *on effort* tracks (black lines) are displayed. Grey lines show the 5 x 5 km grid cells. Bathymetry is depicted with darker shades of blue representing deeper waters; data courtesy of NIWA (Mackay et al. 2012). Inset: Location of GBI and other places referred to in the text in relation to the North Island of New Zealand.

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[2] The study site was limited to the research vessel operating area, which was permitted in accordance with the Maritime New Zealand Safe Ship Management system for commercial vessels. For GBI, the operating area for the research vessel was restricted to waters off the western side of the island.

5.2.2 Data collection

Data were collected across all austral seasons between January 2011 and January 2013. When possible (i.e. when weather and sea conditions permitted), monthly research trips averaging four days in duration were made to GBI. Boat-based surveys were conducted on the research vessel *Te Epiwhania*, a 5.5 m aluminium boat powered by a 100 hp four-stroke outboard engine. A non-systematic survey design was employed, with survey tracks selected based on prevailing weather, sea conditions, and on the extent any particular area had been previously surveyed within that month. Full details about surveying methods are provided in Chapter 2.

Group size was recorded at sea using minimum, maximum and best estimate counts and was later confirmed or amended using photo-identification data. If all individuals in the group were not photographed (e.g. due to time constraints), the best estimate was selected for group size. The number of neonates, calves and juveniles was also estimated visually at sea using minimum, best and maximum counts and was later confirmed or amended using photo-identification data.

Age class definitions follow those previously described for the North Island population (Constantine 2002, Tezanos-Pinto 2009):

- **Neonate**: Presence of obvious white dorso-ventral foetal folds and often uncoordinated upon surfacing to breathe; typically observed up to three months old.
- **Calf**: Approximately half the size or less of an adult, closely associated with an adult and often swimming in the 'infant position'.
- **Juvenile**: Approximately two-thirds the size of an adult and frequently observed in association with the mother but not in the 'infant position'.
- **Adult**: Fully grown dolphin of > 3.0m in length.

Photo-identification of individual bottlenose dolphins was conducted for all groups following standard methods (Würsig & Jefferson 1990) using a Canon 7D or 400D camera fitted with 100–400 and 70–300 mm lenses, respectively. As described in Chapter 2, a group of dolphins was approached from the rear or parallel to the group to avoid disturbance. Attempts were made to photograph all individuals in the group, regardless of the degree of mark distinctiveness of the dorsal fin. Both left and right sides of the fin were photographed where possible.

After observational data were logged and photo-identification completed, the research vessel returned to the survey route and resumed *on effort* in order to continue searching for independent groups (i.e. groups separated spatially and temporally as confirmed by no photographic matches). Multiple independent groups could therefore be observed during any one given survey.

5.2.3 Data analysis

Search effort was calculated as kilometres *on effort* per grid cell per survey day using Geospatial Modelling Environment version 0.7.2.0 (Beyer 2012) and ArcGIS version 10.0 (ESRI, Redlands, California, USA). Both *on* and *off effort* sighting data were included in analyses unless otherwise stated. As with earlier chapters, austral seasons were defined as summer (December to February), autumn (March to May), winter (June to August) and spring (September to November) in accordance with previous studies on this population (Constantine 2002; Berghan et al. 2008; Tezanos-Pinto 2009).

5.2.3.1 Group dynamics

Statistical analyses were carried out using SPSS version 20 (SPSS Inc., Chicago, Illinois, USA) for investigations into group dynamics. Since data were not normally distributed, Mann-Whitney U tests were used to test for significance at $p < 0.05$.

5.2.3.2 Photo-identification analysis

Photographs included in analyses, and in the Great Barrier Island Bottlenose Dolphin Catalogue (S. Dwyer, unpubl. data), were selected based on four photo-quality criteria described in Berghan et al. (2008), to account for angle, focus, relative size and contrast of the fin. Following Tezanos-Pinto et al. (2013), only excellent and good quality photographs were included in the analyses. Individual dolphins were primarily identified and matched based on the nicks and notches on the dorsal fin, with secondary features such as scarring (including rake marks) and overall fin shape also used for identification (Würsig & Jefferson 1990). Dolphins were considered marked if they exhibited at least one primary or at least two secondary features, the latter feasible given that this study was conducted over a short time period. All matching of images was performed by this author and cross-checked by two experienced researchers. Sighting information was recorded in a database for each identified individual. Mother-calf associations were confirmed using photographs from ≥ 2 independent encounters (Tezanos-Pinto 2009).

5.2.3.3 Site fidelity

Site fidelity at GBI was investigated using monthly (MSR) and seasonal sighting rates (SSR), as defined by Parra et al. (2006b). These were calculated by expressing the number of months a dolphin was identified as a proportion of the total number of months in which at least one survey was conducted; and the number of seasons a dolphin was identified as a proportion of the total seasons surveyed (Parra et al. 2006b, Cagnazzi et al. 2011). MSR could therefore range between 0.05 for an individual sighted in only one survey month, to 1 for an individual sighted in all 20 survey months. Similarly, SSR could range between 0.25 for individuals sighted in only one season to 1 for individuals sighted in all four seasons. To minimise the chance of dependence in the data, only one sighting record per individual per day was used (Parra et al. 2006b; Cagnazzi et al. 2011). Based on previously published values for high and low MSR for dolphins (e.g. a high mean MSR = 0.26 (Cagnazzi et al. 2011), a low MSR = 0.10 (Parra et al. 2006b)), individuals were subsequently and conservatively (i.e. using higher minimum values than those previously reported) classified into one of three categories based on MSR and SSR:

- **Occasional visitors**: MSR ≤ 0.15, irrespective of SSR,
- **Moderate users**: MSR > 0.15 and < 0.35, and SSR ≥ 0.5,
- **Frequent users**: MSR ≥ 0.35, and SSR ≥ 0.75.

Therefore, frequent users were defined as animals sighted on average at least once every three months and were observed during at least three seasons of the year. A weighted ratio of the total number of sighting records per unique individual was calculated for each category to assess the relative changes by season.

In order to assess whether dolphins sighted at GBI were also recorded outside the study area, each individual in the Great Barrier Island Bottlenose Dolphin Catalogue was cross-referenced (using standard photo-identification methods described herein) with images and published records of bottlenose dolphins photographed in three other regions of the North Island population home range (Fig. 5.1):

1) Inner Hauraki Gulf — South of GBI. All waters south of a line between Takatu Point on the mainland and Kaiiti Point on the Coromandel Peninsula. Data from 2000 to 2006 (Hauraki Gulf Bottlenose Dolphin Catalogue (HGBDC))[3] were combined with data from 2009 to 2013 (S. Dwyer, unpubl. data).
2) Bay of Plenty — South of GBI. Coastal Tauranga region up to 40 km offshore. Photographs were analysed from data collected during dedicated surveys conducted between 2010 and 2013 (A. Meissner, unpubl. data).
3) Whangarei Coast — North of GBI. Coastal waters between Tutukaka and Ruakaka, including the Poor Knights Islands located 20 km offshore. Bottlenose dolphins were photographed opportunistically on 20 occasions between 2002 and 2011 (I. Visser, unpubl. data).

5.2.3.4 Abundance, temporary emigration and apparent survival

Mark-recapture techniques using the Robust Design (Pollock 1982; Kendall et al. 1997) were used to estimate abundance, apparent survival and temporary emigration rates. The Robust Design incorporates open (primary) periods, which are comprised of a number of closed (secondary) periods (Pollock 1982). Closure is assumed within primary periods but not between them. To ensure this assumption is not violated, the Robust Design relies on secondary periods being close together temporally (Kendall 2004). Bottlenose dolphins along the North Island have variable patterns of residency and home ranges (Constantine 2002; Tezanos-Pinto 2009) that may result in unequal capture probabilities between individuals (Tezanos-Pinto et al. 2013). The Robust Design allows for temporary emigration, resulting in a useful model to estimate the abundance of species that move in and out of the study area. The Schwarz and Arnanson 'super-population' parameterization of the Jolly-Seber model (i.e. POPAN;

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[3] Hauraki Gulf Bottlenose Dolphin Catalogue: J. Berghan, K. Algie, K. Stockin, N. Wiseman & G. Tezanos-Pinto, unpubl. data

Schwarz & Arnanson 1996; Williams et al. 2002) was implemented to estimate the total number of dolphins that visited GBI during 2011–2013 (i.e. the super-population).

5.2.3.4.1 Data organization

A 'sighting' refers to an individual photograph of a uniquely identified dolphin and the associated data (e.g. date, GPS position, group composition) collected during the encounter with that individual. The complete sighting record constitutes the encounter history of an individual. Individual photo-identification data were structured for the Robust Design to estimate the number of dolphins present at GBI in each season as well as rates of apparent survival and temporary emigration between seasons. This hierarchical structure was comprised of primary sampling occasions (seasons) and secondary sampling occasions (survey days) within the primary samples. For this reason, the dataset employed for abundance estimates is different to the site fidelity dataset that includes the full sighting records for GBI. Sighting data were selected in closely adjacent clusters of days with discrete breaks between clusters to implement the selection of secondary samples within primary periods. Secondary periods consisted of near-consecutive survey days with a minimum of 2 and a maximum of 5 survey days (median 3 survey days), and primary samples were separated by a minimum of 56 days (0.15 decimal years) and a maximum of 112 days (0.31 decimal years) between their mid dates (median 91 days or 0.25 decimal years). There were a total of nine primary samples consisting of 28 secondary samples.

Seasonal data for POPAN were selected to estimate the total number of dolphins that used the area during the course of the study (the super-population) by considering one sighting per season for each dolphin (Williams et al. 2002, Nichols 2005), meaning that either the dolphin was captured (1) or not-captured (0) during that season.

5.2.3.4.2 Mark ratio

Not all individuals in a population exhibit sufficient marks for individual recognition. To account for unmarked dolphins photographed at GBI, a mark ratio

(Jolly 1965) was estimated. All quality-controlled photographs were counted, including all age-classes, to estimate the ratio of individually identifiable dolphins (i.e. marked animals) during 2011–2013. Only those encounters in which all dolphins, irrespective of their marks, were photographed several times were included for this estimate. The proportion of marked dolphins (P_m) was estimated (Gormley et al. 2005) as the ratio between the number of marked dolphins and the total number of dolphins observed on each survey, averaged over all surveys (Cantor et al. 2012). P_m and its variance (Gormley et al. 2005) were estimated as follows:

$$\hat{P}_m = \frac{\sum_{i=1}^{k} \frac{I_i}{T_i}}{\mathrm{k}}, var(\hat{P}_m) = \left(\sum_{i=1}^{k} \frac{\hat{P}_{m_i}(1 - \hat{P}_{m_i})}{T_i} \right) / \, k^2$$

where I_i is the number of identifiable (i.e. marked) dolphins per survey, T_i is the total number of dolphins sighted during the ith survey day and k is the total number of survey days for which I/T was calculated (k = 34), for each $\hat{P}_{m_i} = I_i / T_i$. Abundance estimates were scaled by the mark-ratio to obtain the total abundance $\hat{N}_{total}$ (Williams et al. 1993) as follows:

$$\hat{N}_{total} = \frac{\hat{N}_m}{\hat{P}_m}$$

where $\hat{N}_m$ is the abundance of marked dolphins. The variance (var) and standard error (SE) of $\hat{N}_{total}$ were calculated (Wilson et al. 1999) as follows:

$$var(\hat{N}_{total}) = (\hat{N}_{total})^2 \, (var(\hat{N}_m)/(\hat{N}_m)^2 + var(\hat{P}_m)/(\hat{P}_m)^2), SE(\hat{N}_{total}) = \sqrt{var(\hat{N}_{total})}$$

Log-normal confidence intervals were calculated (Burnham et al. 1987) as follows:

$$\hat{N}_{lower} = \hat{N}_{total}/C \text{ and } \hat{N}_{upper} = \hat{N}_{total} * C, \text{ where } C = exp\left(z_{\alpha/2} \sqrt{log_e \left[1 + \left(cv(\hat{N}_{total})\right)^2\right]} \right)$$

where $\hat{N}_{lower}$ is the lower bound of the confidence interval, $\hat{N}_{upper}$ is the upper bound of the confidence interval, $z_{\alpha/2}$ is the normal deviate, α = 0.05 and cv is the coefficient of variation.

5.2.3.4.3 Assumptions of mark-recapture methods

Mark-recapture methods are subject to a number of assumptions; those relevant to this study are detailed as follows (Williams et al. 2002; Cooch & White 2011):

a) Heterogeneity of capture: All individuals should be equally available for capture. Mark-recapture methods assume that the marking process does not affect the probability of capturing individuals. Photo-identification techniques are not expected to affect the behaviour of an individual because photographing them should not elicit a capture response. Therefore, recapturing individuals in this study should be unaffected by the capture event. However, in some cases, individuals may display preferential use of a particular habitat (e.g. avoid particular areas), avoid/prefer vessels or surface less/more than other individuals, all of which may result in variable capture probabilities among individuals (i.e. heterogeneity of capture). To assess potential behavioural effects that would suggest a behavioural response to capture (i.e. 'trap-happy' or 'trap-shy'), TEST 2.CT was implemented in U-CARE version 2.2 (Choquet et al. 2005). Bottlenose dolphins of the North Island population show varied re-sighting patterns and individuals have not been exclusively observed in only one region (Constantine 2002; Berghan et al. 2008; Tezanos-Pinto 2009). This results in variation in individual heterogeneity, with capture probabilities higher for dolphins that spend more time in the study area (i.e. frequent users). TEST 2.CL was used to examine whether there was variation in the time between re-encounters for captured and non-captured individuals. A significant result may indicate that the trapping effect lasts for more than one occasion.

b) Equal probability of survival: All individuals in the population have the same probability of survival between sampling occasions. In Cormack-Jolly-Seber (CJS) models, death is confounded with emigration and birth is confounded with immigration, therefore survival is referred to as 'apparent survival'. As such, variations in apparent survival may be the result of changes in mortality/emigration or births/immigration. In the Bay of Islands, transient dolphins (i.e. animals that visit the area only once) are known to occur (Tezanos-Pinto et al. 2013). When the capture history of transient dolphins is incorporated into Mark-recapture studies, they cause an underestimate of survival. This is because emigration and mortality are confounded in open models. TEST 3.SR was implemented in U-CARE to determine if there was an excess of 'transient' individuals (i.e. individuals only sighted once). In addition, TEST 3.SM was implemented to evaluate if the timing of recapture depended on whether the animal was captured previously or not (Choquet et al. 2005). TEST 3.SM evaluates whether the capture probability of newly marked individuals is different from previously caught individuals.

c) Mark recognition: All marked individuals must be recognised with certainty if recaptured. To reduce the likelihood of false positives or false negatives, only good quality photographs were used in analyses and the photo-identification catalogue was checked by at least two independent researchers, using a combination of marks, notches and scars to confirm matches (see Section 5.2.3.2).

d) Mark loss: Marks are not lost during the course of the study. Nicks and notches on the trailing edge of bottlenose dolphin fins remain relatively stable over several years (Tezanos-Pinto 2009). Without two independent marking methods it was not possible to assess the rate of mark loss in this study. However, both primary and secondary markings were used to minimise any mark loss errors (see Section 5.2.3.2).

e) Instantaneous sampling and immediate release: Birth, immigration, death or emigration do not occur during the resampling process and each release is made immediately after the sample is taken. Nothing changed within the samples during photo-identification surveys and photo-identification techniques do not require any animals to be physically handled; therefore, this assumption is fulfilled.

f) The study area is constant: The size of the GBI study area did not change during the course of the study, therefore this assumption is fulfilled.

5.2.3.4.4 Robust Design model

Pollock's Robust Design models were run in MARK version 5.1 (White & Burnham 1999). The intervals between seasons were specified in decimal years between their mid dates to obtain consistent per annum estimates of apparent survival. Capture probability (*p*) and abundance ($\hat{N}$) of dolphins at GBI were estimated for each season. Three parameters were estimated from the intervals between seasons: the apparent survival probability (φ), the probability that an animal was outside the study area in a sampling occasion given that it was inside the study area in the previous occasion (γ''), and the probability that an animal was outside the study area in a sampling occasion given that it was outside the study area in the previous occasion (γ', Kendall et al. 1995; Kendall et al. 1997). Estimates of apparent survival were calculated for adults and juveniles combined and for adults only to enable comparisons with other studies. Temporal variation in capture probabilities between (s = seasons or primary samples), within (t = surveys within a season or secondary samples), and both between and within primary periods ($s*t$) was considered for all models. Recapture probabilities were constrained to equal capture probabilities on each occasion for all models since there was no evidence of a behavioural effect. Models were fitted with no temporary emigration ($\gamma'' = \gamma' = 0$), random ($\gamma'' = \gamma'$) and Markovian temporary emigration ($\gamma'' \neq \gamma'$) (Huggins 1991; Kendall et al. 1997). To provide parameter identifiability for the Markovian models, either apparent survival (φ) was constrained to be constant or a constraint (session k = session k-1) was added resulting in the last two parameters in the time series set to equal (Kendall et al. 1997). AIC_C (Akaike Information Criterion adjusted for small sample size) was used to evaluate model fit. The best fitting model was identified as having the lowest AIC_C value (Burnham & Anderson 2004).

5.2.3.4.5 POPAN super-population models

A 'super-population' approach, based on a re-parameterization of the Jolly-Seber (JS) model with an additional parameter $\hat{N}_{super}$ that denotes the size of the 'super-population', was applied in POPAN to estimate the abundance of the 'larger' population that used the area during the course of the study. Another additional parameter β (probability of entry) was estimated to measure the proportion of 'new' individuals entering the study area (Williams et al. 2002). Models with constant (.) and temporal variation (t) in capture probabilities between seasons were considered. A constraint was added to the first and last two capture probabilities to provide parameter identifiability for all models (Cooch & White 2011).

5.2.3.4.6 Goodness of fit tests and model selection

Although the Robust Design does not have a goodness of fit test, traditional tests can be applied because the method is a combination of open and closed models. As such, each season was tested for closure using CloseTest (Stanley & Burnham 1999). A CJS framework was used to carry out goodness of fit tests (TEST 2.CT and 2.CL, and TEST 3.SM and 3.SR) in U-CARE (Choquet et al. 2005) and evaluate potential violations of assumptions. Broadly, TEST 2 is concerned with identifying 'recapture problems' and TEST 3 with 'survival problems'. More specifically, TEST 2.CL is used to examine whether there is variation in the time between re-encounters for captured and uncaptured individuals among sampling occasions. TEST 2.CT tests for trap-dependence, TEST 3.SM explores the effect of capture on apparent survival and TEST 3.SR tests for transience (Choquet et al. 2005).

5.3 RESULTS

Between January 2011 and January 2013, over 4000 km were surveyed off the west coast of GBI (Fig. 5.1) during 71 survey days in 20 months. A total of 44 independent groups of bottlenose dolphins were recorded, 36 encountered *on effort* and eight *off effort* (Table 5.1). Photo-identification effort at GBI totalled 78.2 h during 37 survey days across all seasons. A total of 1412 sighting records (i.e. sighting of an identified individual on a discrete day) of 154 individuals photographed at GBI were used in the analyses. Individual sighting frequencies ranged from 1 to 27 (mean = 9.17, SD = 7.93).

Table 5.1 Bottlenose dolphin encounters by season at Great Barrier Island (GBI), New Zealand, between January 2011 and January 2013. Groups encountered: *on effort* totals for all years combined (*off effort* totals in parentheses); Sighting records: total number of individual dolphin sighting records for a discrete day, as confirmed by photographic matches; Unique individuals: number of unique individuals identified in that season.

	Summer	Autumn	Winter	Spring	Overall
Groups encountered	10 (3)	9 (2)	7 (2)	10 (1)	36 (8)
Sighting records	524	217	237	434	1412
Unique individuals	100	116	77	98	154

5.3.1 Group dynamics

Group size ranged from 1 to 82 individuals (median = 35, mean = 36.39, SD = 23.36, n = 44) and varied with depth and season (Fig. 5.2). A relatively large proportion (32%) of groups consisted of ≥ 50 individuals, all of which were recorded in the southern region of the study area (Fig. 5.3) and primarily during spring and summer (86%). Conversely, all small groups of < 10 individuals (18%) were recorded in the northern region (Fig. 5.3). A solitary dolphin was encountered during autumn and the largest group size (n = 82, as confirmed by photo-identification), was recorded during spring. Larger groups were sighted more frequently in spring and summer, and smaller groups were most prevalent in autumn (Fig. 5.2).

Two independent groups, confirmed by a lack of photographic matches, were observed on the same survey day on seven occasions. This included 109 individuals recorded at GBI on 18 February 2012 in two groups of 60 and 49 dolphins, separated by a distance of 19.4 km. The majority of groups (82%) contained immature dolphins, i.e. neonates and/or calves and/or juveniles. Group size (comparing only the number of adults within groups) was significantly higher (Mann-Whitney U = 384.50, $p < 0.001$) in groups containing neonates or calves (median = 40, IQR = 28.5–52.3) than groups containing only adults or adults and juveniles (median = 8, IQR = 3.0–22.0). Groups with neonates and calves were therefore, on average, five times the size of groups with only adults or adults and juveniles. All adult only groups contained fewer than 22 individuals (median = 7, IQR = 3.0–15.0).

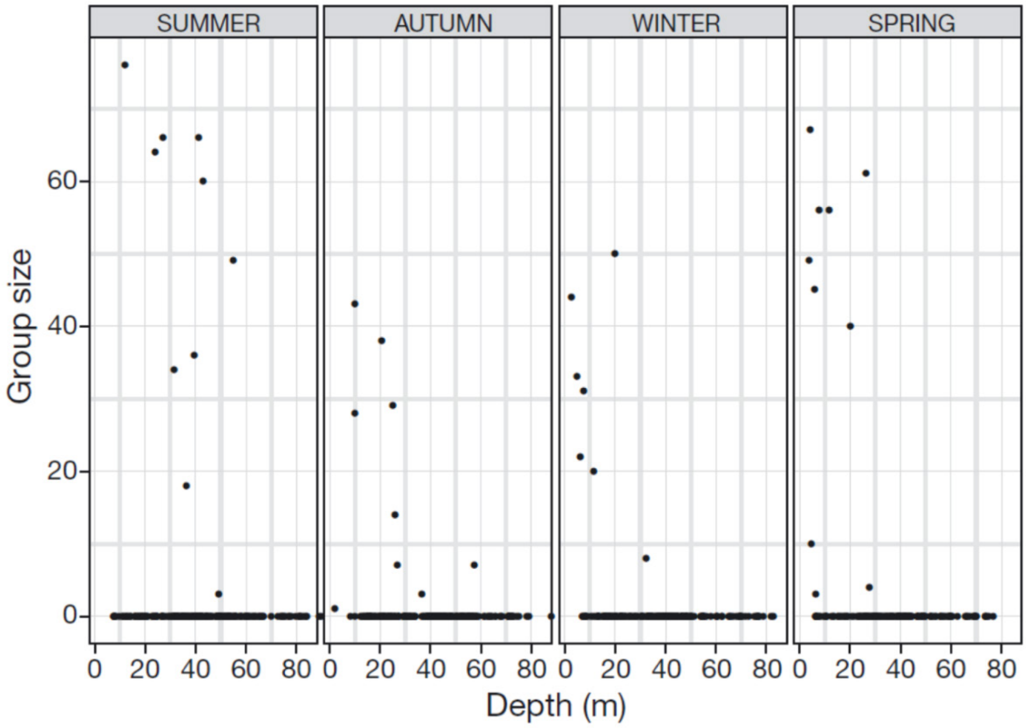

Figure 5.2 Group size of bottlenose dolphins (*on effort* sightings only) at Great Barrier Island (GBI), New Zealand varies with depth and season. Black dots at zero group size indicate non-detections during sampling of a grid cell.

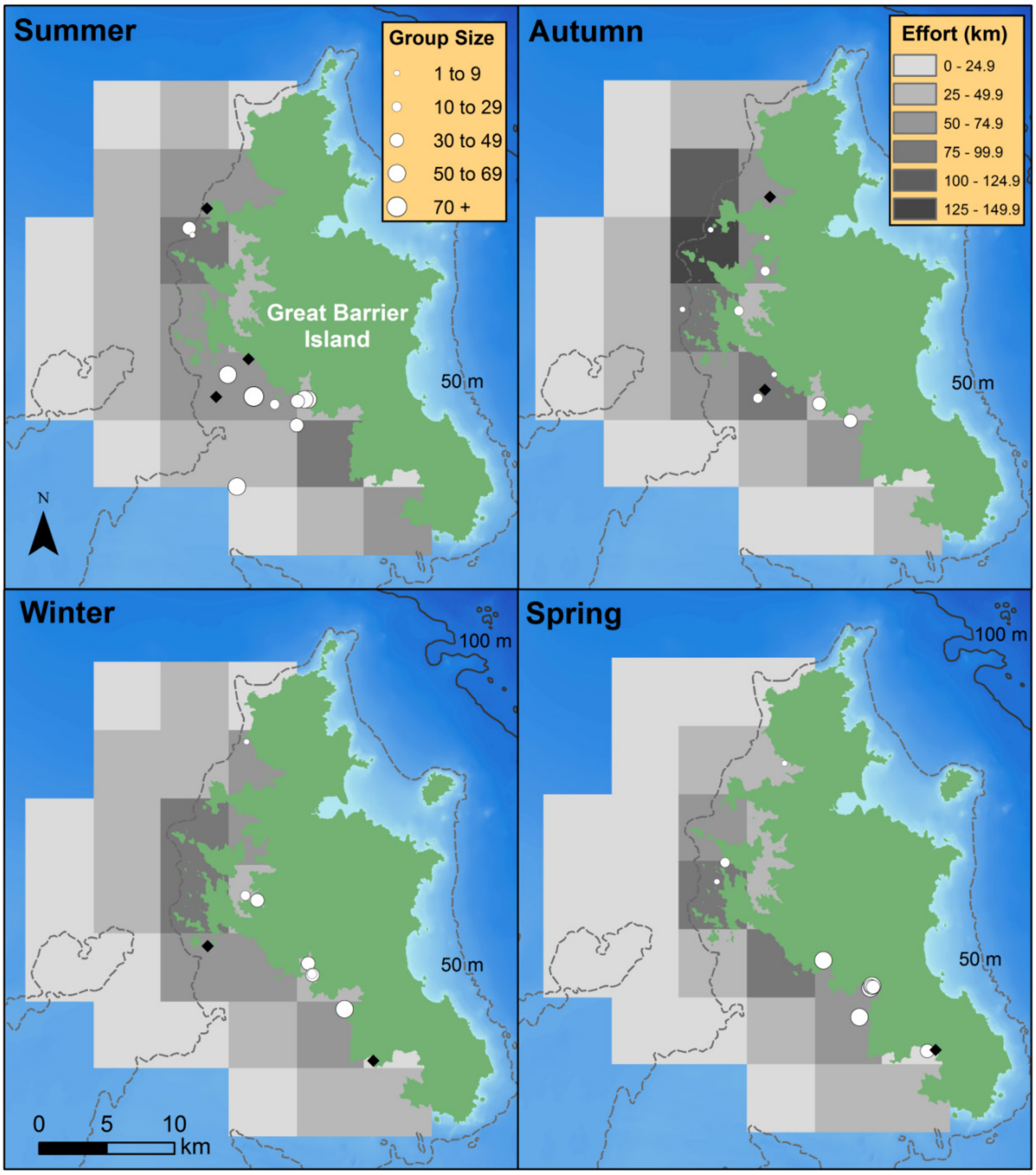

Figure 5.3 Initial sighting locations of bottlenose dolphin groups encountered off Great Barrier Island (GBI), New Zealand between January 2011 and January 2013. White circles represent groups sighted *on effort* and black diamonds are *off effort* sightings. Survey effort per 5 x 5 km grid cell is shaded in grey. The dashed line represents the 50 m isobath and the solid the 100 m isobath.

Neonates and calves were observed across all seasons in 70% of groups. Where present, the number of neonates in groups ranged from one to four (SD = 1.15) and number of calves ranged from one to nine (SD = 2.47). Forty-three percent of groups contained at least one neonate, with the highest proportion of these groups encountered during summer (54%) followed by spring (26%) and autumn (16%). Only one group was recorded with a neonate during winter. Parturition was not directly observed in the field; however, very young neonates were observed at GBI. For example, individual TM027 was recorded 27 times without a calf between 26 January 2011 and 28 December 2012 before being photographed with a neonate (Fig. 5.4) on 2 January 2013. During the study, 12 photo-identified adults were recorded consistently associated with neonates.

Figure 5.4 A neonate showing foetal folds, maximum five days old, observed on 2 January 2013 off Great Barrier Island (GBI), New Zealand. Photo: Sarah Dwyer.

5.3.2 Photo-identification

Bottlenose dolphins were encountered during 19 out of 20 survey months. The discovery curve (Fig. 5.5) showed a steep ascent during early surveys before reaching a plateau in May 2012, with only eight new individuals identified after this plateau during the final quarter of the study. Thirty-five dolphins (23%) were sighted only once in the study area; however, a larger proportion of individuals (37%, n = 57) were sighted ≥ 10 times. Most re-sighted individuals (87%, n = 134) were recorded in the study area in more than one year. The total number of individual sighting records in summer and spring were double those of autumn and winter (Table 5.1), in part due to the higher proportion of large group sizes observed in summer and spring (Fig. 5.2).

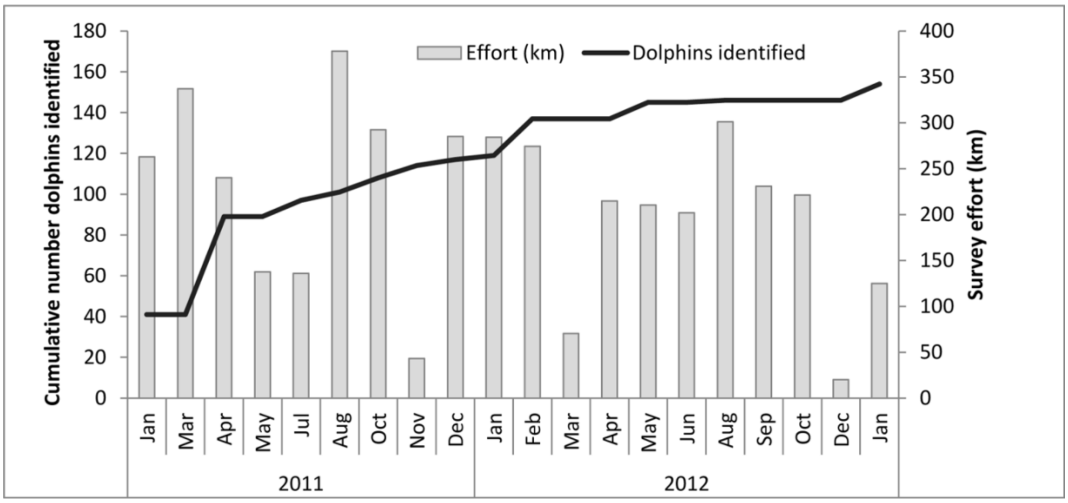

Figure 5.5 Discovery curve of bottlenose dolphins off Great Barrier Island (GBI), New Zealand, with cumulative number of individuals photo-identified per survey month between January 2011 and January 2013. Bars represent the number of km spent *on effort* searching for dolphins (refer to Section 5.2 Materials and Methods).

5.3.3 Site fidelity

Relative to the total number of months surveyed, bottlenose dolphins showed varying degrees of site fidelity to the west coast of GBI (Fig. 5.6). Higher proportions of both occasional visitors (41%) and frequent users (40%) and a lower number of moderate users (19%) were observed. Overall, site fidelity was relatively high (mean MSR = 0.33, SE = 0.022, range 0.05–0.85). Over 32% of all identified individuals were sighted in more than 50% of the total survey months. SSR was also high (mean = 0.70, SE = 0.025; Fig. 5.6), with 117 individuals (76%) sighted in the study area during at least two different seasons. Just under half (44%) of all identified individuals were recorded at GBI in all four seasons. Using a weighted ratio of the total number of sighting records per unique identified individual, the highest proportion of occasional visitors and frequent users per season were observed during autumn (30%; Fig. 5.7) and winter (63%; Fig. 5.7), respectively.

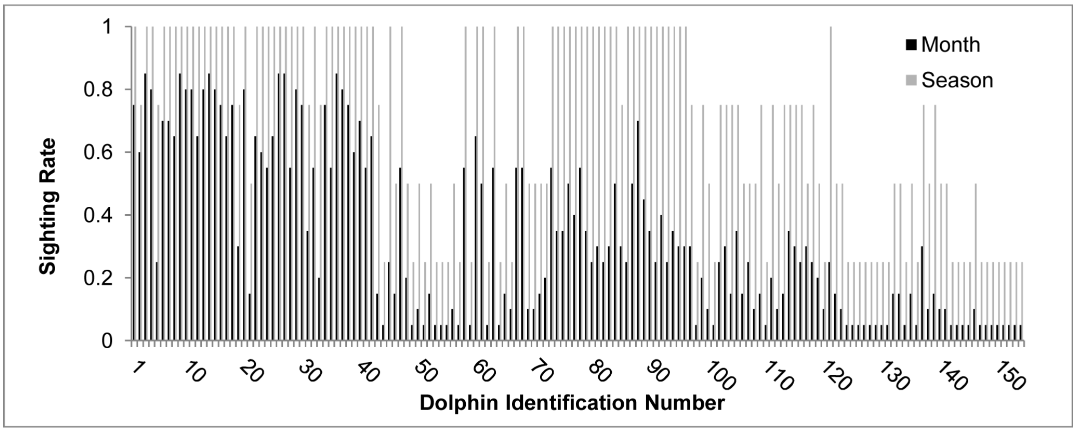

Figure 5.6 Monthly and seasonal sighting rates of bottlenose dolphins at Great Barrier Island (GBI), New Zealand. Rates are the number of months (black) and seasons (grey) a dolphin was photo-identified as a proportion of the total number of months and seasons surveys were conducted.

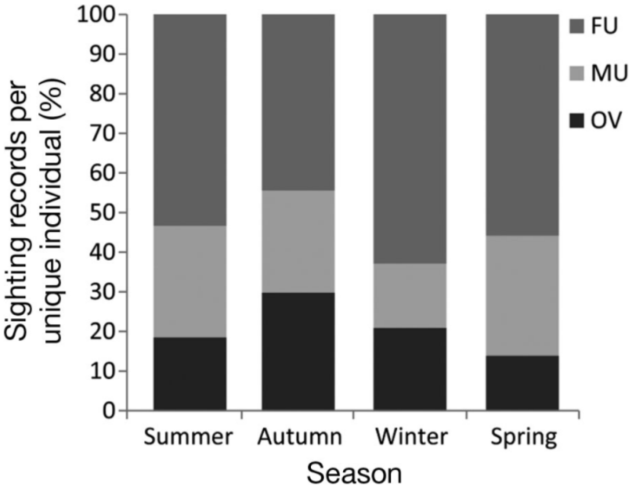

Figure 5.7 Seasonal weighted ratio (expressed as a percentage) of the total number of sighting records per unique identified individual bottlenose dolphin at Great Barrier Island (GBI), New Zealand. FU: Frequent User, MU: Moderate User, OV: Occasional Visitor.

The majority (85%) of individuals identified at GBI were recorded in at least one of the other regions within the North Island home range for which photo-identification data were available (Table 5.2). Sixteen individuals were recorded in all of these regions. Unsurprisingly, there were a high number of matches (n = 115) to the nearby inner Hauraki Gulf. Since all frequent users of GBI (n = 61) were sighted in at least one neighbouring region, even individuals regularly using GBI waters left the area at least seasonally to visit other regions up to 200 km away.

Table 5.2 Number of bottlenose dolphins identified at Great Barrier Island (GBI) and sighted in other regions of the North Island population home range.

Region	GBI individuals (n = 154)	GBI frequent users (n = 61)
Inner Hauraki Gulf	115	47
Bay of Plenty	89	49
Whangarei Coast	51	5

Although more dolphins were counted during summer (n = 524) and spring (n = 434), a higher number of unique individuals were sighted in autumn (n = 116) than in any other season (Table 5.1). This was due to seasonal variations in re-sighting patterns and group dynamics, with a larger proportion of occasional visitors present at GBI during autumn (Fig. 5.7) in overall smaller group sizes (Fig. 5.2).

5.3.4 Abundance, temporary emigration and apparent survival

5.3.4.1 Mark ratio

A total of 1423 quality-controlled photographs collected from 34 surveys during 2011–2013 were used to estimate the mark ratio (P_m). From those, 1260 images were represented identifiable individuals (I) and P_m was estimated at 0.885 (SE = 0.012), or 88.5%.

5.3.4.2 Goodness of fit

The results of the goodness of fit tests were highly significant for TESTS 2.CT, 3.SM and 3.SR (Table 5.3). Failure of TEST 2.CT (a behavioural effect to capture, i.e. 'trap happy') was interpreted as a result of the higher capture probabilities of frequent users because they are more available for capture, rather than a true behavioural response to the photo-identification technique. Similarly, the results of TEST 3.SR were indicative of a number of individuals (n = 26) sighted only once (i.e. transiency, resulting in unequal capture probabilities and overestimated mortality). Failure of TEST 3.SM was interpreted according to the emigration patterns observed at GBI. Briefly, dolphins showed a pattern of Markovian emigration, which means that their presence in the study area was conditional on their presence/absence in the area on the previous occasion (see Robust Design results; this section).

Table 5.3 Results of the goodness of fit tests conducted in U-CARE 2.02 for the seasonal dataset in a Cormack-Jolly-Seber (CJS) framework for bottlenose dolphins at Great Barrier Island (GBI), New Zealand.

	TEST 2.CT	**TEST 2.CL**	**TEST 3.SM**	**TEST 3.SR**
Seasonal dataset	$\chi^2 = 41.2$ $p < 0.0005$ Stat = -5.4 $p < 0.0005$	$\chi^2 = 14.01$ $p = 0.02$	$\chi^2 = 51.3$ $p < 0.005$	$\chi^2 = 35.1$ $p < 0.0005$ Stat = 4.3 $p < 0.0005$
Sum of tests	$\chi^2 = 141.8$ $p < 0.005$			

5.3.4.3 Robust Design

Robust Design models (Table 5.4) with fully time-varying (t) capture probabilities were strongly favoured over models with constant (.) capture probabilities or capture probabilities varying between seasons (s). AIC_C indicated that models with Markovian temporary emigration (models 1, 2, 4 & 8; Table 5.4) received more support from the data than models with random temporary emigration (models 3 & 6; Table 5.4). The best fitting model assumed constant apparent survival, fully time-varying Markovian temporary emigration and fully time-varying capture probabilities (model 1; Table 5.4), and accounted for 93% of the AIC_C weight in the model set. As expected, the likelihood ratio test rejected models with no temporary emigration (models 5 & 7; Table 5.4) when tested against models with random ($\chi^2 = 58.4$, df = 11, $p < 0.0001$) and Markovian ($\chi^2 = 91.2$, df = 10, $p < 0.0001$) temporary emigration.

Table 5.4 Model selection for sighting data of bottlenose dolphins at Great Barrier Island (GBI) during 2011–2013. Model results are for seasonal Robust Design data (top), and POPAN (below). The lowest AIC_C value represents the model that has the most support from the data (in **bold**). Abbreviations: apparent survival (φ), capture (p), recapture (c) and temporary emigration (γ) probabilities, probability of entry (β). ML: maximum likelihood; NP: number of parameters; Dev: deviance. The notation (.) indicates that a given parameter was kept constant and (t) indicates that a given parameter was allowed to vary with time, (s) indicates that a parameter was allowed to vary between seasons, and k is a constraint (session k = session k -1). Notation: $\gamma'' = \gamma' = 0$: no temporary emigration; $\gamma'' = \gamma'$: random temporary emigration model; $\gamma'' \neq \gamma'$: Markovian temporary emigration model (following Kendall et al. 1997).

		Model	AIC_C	Delta AIC_C	AIC_C Weight	ML	NP	Dev
Robust Design	1	$\varphi(.)\ \gamma'(t, k=k\text{-}1)\ \gamma''(t, k=k\text{-}1)\ c=p(t)$	**-765.77**	0.00	0.93362	1	51	1681.36
	2	$\varphi(t)\ \gamma'(t, k=k\text{-}1)\ \gamma''(t, k=k\text{-}1)\ c=p(t)$	-760.48	5.29	0.06638	0.0711	58	1671.08
	3	$\varphi(t)\ \gamma'=\gamma''(t, k=k\text{-}1)\ c=p(t)$	-730.80	34.97	0	0	52	1714.12
	4	$\varphi(t)\ \gamma'(.)\ \gamma''(.)\ c=p(t)$	-711.65	54.12	0	0	42	1755.18
	5	$\varphi(t)\ \gamma=0\ c=p(t)$	-696.46	69.31	0	0	41	1772.54
	6	$\varphi(t)\ \gamma'=\gamma''(.)\ c=p(t)$	-696.46	69.31	0	0	41	1772.54
	7	$\varphi(.)\ \gamma=0\ c=p(t)$	-680.26	85.51	0	0	38	1795.22
	8	$\varphi(.)\ \gamma'(t, k=k\text{-}1)\ \gamma''(t, k=k\text{-}1)\ c=p(s)$	-610.49	155.27	0	0	32	1877.83
POPAN	9	$\varphi(.)\ p(t)\ \beta(.)$	553.15	0.00	0.87145	1	12	4.46
	10	$\varphi(.)\ p(t)\ \beta(t)$	557.91	4.76	0.08067	0.0926	19	-5.55
	11	$\varphi(t)\ p(t)\ \beta(.)$	558.99	5.84	0.04705	0.0540	19	-4.47
	12	$\varphi(t)\ p(t)\ \beta(t)$	567.09	13.94	0.00082	0.0009	27	-13.68

Capture probabilities were variable within (range 0.13–0.90) and between (range 0.33–0.70) seasons. Overall, spring and summer presented the highest capture probabilities (0.70, SE = 0.022 and 0.63, SE = 0.034, respectively) when compared to autumn (0.33, SE = 0.024) and winter (0.35, SE = 0.026; Fig. 5.8). Estimates of abundance also varied; unfortunately abundance estimates for summer had very low and high standard errors and were deemed unreliable (Fig. 5.8). Seasonal estimates varied from a low of 60 dolphins (95% CI = 53–67) in winter 2012, to a high of 131 during autumn 2012 (95% CI = 114–151; Fig. 5.8), including the correction for unmarked dolphins. Overall, seasonal abundances were lower during winter (Fig. 5.8) when compared to autumn.

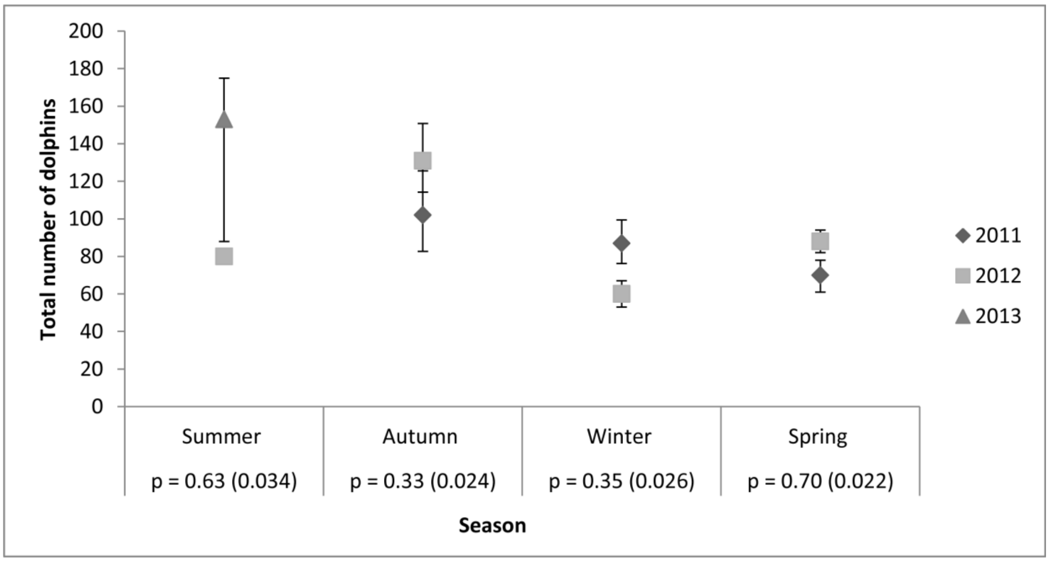

Figure 5.8 Seasonal abundance estimates of bottlenose dolphins at Great Barrier Island (GBI), New Zealand (marked and unmarked dolphins), with the Robust Design including confidence intervals, capture probabilities (*p*) and standard error (in parentheses). Note: For summer 2011–12, SE was inestimable.

The temporary emigration rates of being absent based on the previous period state of being present (γ'') were low and ranged from 0.00–0.04 with a peak in winter 2012 and a mean value of 0.01 (SE = 0.006; Table 5.5). The temporary emigration rates of being absent based on the previous period state of also being absent (γ') were higher and ranged from 0.03–0.75 with a peak in winter 2012, with a mean of 0.267 (SE = 0.140). The 'return rate' of temporary emigrants ($1\text{-}\gamma'$) was lower between winter and spring and higher between summer and autumn (Table 5.5). The model yielded an apparent survival estimate of 0.918 (SE = 0.058, 95% CI = 0.70–0.98) for adults and juveniles combined, or 0.950 (SE = 0.081, 95% CI = 0.40–0.99) for adults only.

Table 5.5 Temporary emigration rates for the best fitting model for bottlenose dolphins, including return rates of temporary emigrants (1-γ'). There are two rates of temporary emigration: γ'' is the probability of being a temporary emigrant if the animal was present in the previous period while γ' is the probability of being a temporary emigrant if the animal was absent in the previous period. Standard error is shown in parentheses. NA: not applicable; NE = this parameter could not be estimated.

	Temporary emigration rates		**Return rate**
	(γ'')	(γ')	(1-γ')
Autumn–Winter 2011	0.003 (0.0001)	NA	NA
Winter–Spring 2011	0.009 (0.001)	NE	NA
Spring–Summer 2011–12	0.019 (0.005)	0.655 (0.025)	0.345
Summer–Autumn 2011–12	0.000 (0.0008)	0.029 (0.004)	0.971
Autumn–Winter 2012	NE	0.112 (0.019)	0.888
Winter–Spring 2012	0.040 (0.014)	0.752 (0.052)	0.248
Spring–Summer 2012–13	0.000 (0.0001)	0.047 (0.008)	0.953

5.3.4.4 POPAN super-population models

Several models were evaluated, including those that held parameters constant or allowed variations with time (Table 5.4). The best-fitting model (87% of the AIC$_C$ weight) incorporated constant apparent survival, time-varying capture probability and constant probability of entry (model 9; Table 5.4). Model averaging was used to estimate the parameters. However, given that this dataset violated goodness of fit tests (Table 5.3), only the ‘super-population’ estimate was considered here. This is because the aim was to estimate the total number of dolphins that used GBI from 2011–2013 regardless of their re-sighting pattern (i.e. occasional visitor, moderate user or frequent user). The super-population (i.e. total number of dolphins that visited GBI during the course of the study) was estimated at 171 dolphins (CI = 162–180) including the correction for unmarked animals.

5.4 DISCUSSION

Considering all regions within the home range of a population is important when determining appropriate conservation management. GBI, a previously undescribed region for delphinids, appears to be a potential hotspot for bottlenose dolphins of the New Zealand North Island population. This study found a high level of individual site fidelity, large average group size and high year-round use of the area by groups that predominantly contain neonates and calves. A total of 171 dolphins (CI = 162–180) used the area during the study period. Even within the narrow scope of this focused study at GBI, it is apparent that many individuals spend extended periods of time outside of what has formerly been recognised as the core home range for this population (i.e. BOI). Additionally, it is clear that the GBI region is not simply being used as a corridor to reach other destinations but instead, is a key site for at least a part of the North Island population.

Until now, our understanding of group dynamics within the North Island population has been based on studies conducted solely in BOI. Median and maximum group sizes for BOI have been reported as 8–12 and 60, respectively (Constantine 2002; Tezanos-Pinto 2009). It was therefore surprising to report considerably larger group sizes at GBI (median = 35, maximum = 82). Group size for bottlenose dolphins worldwide is often reported as relatively small at approximately 2–15 animals (Shane et al. 1986; Mann et al. 2000; Bearzi et al. 2009); however, groups of more than 15 individuals are not uncommon in New Zealand waters (Lusseau et al. 2003; Merriman et al. 2009). Although it is unclear why bottlenose dolphins at GBI repeatedly form large groups, one possible explanation may be related to food availability. The southwestern coast of GBI, where all groups of more than 50 individuals were recorded, is associated with the Colville Channel. This area is characterised by the strongest currents in the Hauraki Gulf (Manighetti & Carter 1999). As discussed previously in this thesis, strong upwellings occur at GBI and around the Colville Channel under southeasterly winds (Black et al. 2000) and thus, the use of the area by large groups of dolphins may be attributed to a localised increase in biological productivity. Alternatively, GBI may act as a social hub where smaller groups fuse for socialising. In this study, all adult only groups contained fewer individuals than groups comprised of calves, the latter accounting for all groups of more than 22 dolphins. Nursery groups have previously been shown to be largest when containing calves up to three months old, likely a protective measure against predators (Mann et al. 2000), which may also in part explain the formation of large groups of bottlenose dolphins at GBI.

Based on the variable patterns of site fidelity and habitat use observed in BOI (Constantine 2002; Tezanos-Pinto 2009; Tezanos-Pinto et al. 2013; Hartel et al. 2014), it was anticipated that new individuals would continue to be photo-identified for the duration of the study. The discovery curve reached a plateau after 17 months of field effort; however, with a further eight new individuals added to the catalogue in the final summer season. It is thus expected that a number of individuals that do not frequently use GBI waters have yet to be identified. Similarly, some dolphins may only visit the area rarely (i.e. transient dolphins), something that has also has been noted for BOI (Tezanos-Pinto et al. 2013).

Overall site fidelity (MSR = 0.33) to the GBI region was high, although re-sighting patterns were variable among individuals. The large proportions of both frequent users and occasional visitors are similar to the variable patterns of residency reported for BOI (Constantine 2002; Tezanos-Pinto 2009). Based on records of GBI individuals outside the study area, it is clear that most bottlenose dolphins recorded at GBI cannot be classified as permanent residents, despite a large proportion of individuals spending considerable periods of time there. It has been hypothesised that dolphins from BOI move to the Hauraki Gulf during winter, based on a seasonal low of individuals in BOI (Tezanos-Pinto 2009). However, given the relatively lower abundance and decreased number of sighting records for GBI during winter, it seems unlikely that dolphins are congregating there when absent from BOI. Furthermore, peaks in bottlenose dolphin sightings have been reported for autumn in the inner Hauraki Gulf (Berghan et al. 2008). This corresponds with records of high numbers of occasional visitors at GBI during autumn and the highest return rate for temporary emigrants between summer and autumn. While individuals using BOI (super-population estimate for 1997–2006 of 483, CI = 358–653; Tezanos-Pinto et al. 2013) are known to frequent GBI waters (Tezanos-Pinto 2011), it is currently unclear what proportion of the North Island population are using GBI waters and to what extent. A previous photo-identification study by Berghan et al. (2008) identified that 59% of individuals opportunistically photographed in the Hauraki Gulf matched to animals in the BOI catalogue. However, the fact that 41% of individuals could not be cross-matched suggested a possible larger population size than was previously thought or perhaps individuals overlap in range between at least two sites along the coastline. Future studies should therefore investigate the seasonal movements of North Island bottlenose dolphins across the entire known range to try and discern these apparent trends.

The estimates of temporary emigration were highly variable and sometimes large. Such large fluctuations in abundance and temporary emigration rates indicate variable use of the area through time. Interestingly, the analyses suggested seasonal differences in abundance estimates. Despite the low precision of the summer estimates, the data suggested that abundance is lower during winter and spring. Specifically, abundance estimates varied from a low of 60 dolphins (95% CI = 53–67) during winter 2012 to a high of 131 (95% CI = 114–151) during autumn 2012 (excluding summer estimates). This is comparable to a recent study conducted on a coastal population of bottlenose dolphins in Bunbury, Western Australia, that implemented the Robust Design (Smith et al. 2013). This population also exhibited a seasonal fluctuation in abundance with peak numbers detected in summer and autumn (139 dolphins in autumn 2009) and lower numbers during winter months (63 dolphins in winter 2007). In BOI, a seasonal fluctuation was also apparent with a lower number of dolphins during winter months (Tezanos-Pinto et al. 2013).

In this study, models incorporating Markovian temporary emigration were deemed better than both random temporary emigration and models with no temporary emigration. Temporary emigration rates varied between seasons for the best fitting Markovian model, with higher rates during time intervals when animals had been absent in the previous period (γ') than the rates for those present in the previous period (γ''). This implies that some individuals leave the study area for multiple seasons but subsequently return. Temporary emigration rates estimated in Bunbury (γ' = 0.34–0.97; Smith et al. 2013) were similar to those estimated in this study (γ' = 0.03–0.75) and also varied seasonally. The apparent survival estimated here for adults and juveniles combined (0.918, SE = 0.058) is marginally lower than the estimate for adults only (0.950, SE = 0.081). This is consistent with studies conducted in other areas that reported lower survival rates for juveniles (Stolen & Barlow 2003). During the two years of this study, one bottlenose dolphin using GBI waters was presumed to have died following a boat strike incident and was identified as a juvenile (Dwyer et al. 2014b; Appendix 5.1). Adult survival estimates for GBI are slightly higher than those reported for BOI (0.928, SE = 0.008) during 1997–2006 (Tezanos-Pinto et al. 2013) but similar to Bunbury (0.95, SE = 0.02) for adults and juveniles (combined) during 2007–2009 (Smith et al. 2013).

In Bunbury, seasonal fluctuations in abundance were explained by an influx of adult males into the study area during the breeding season (summer/autumn) and their subsequent departure during the non-breeding months (Smith et al. 2013). Breeding is also seasonal in BOI (Constantine 2002; Tezanos-Pinto 2009) so it is possible that a similar situation occurs in GBI waters, where the sex of most dolphins is currently largely unknown, especially males and non-reproductive females.

The importance of the GBI region has likely been overlooked at least partly as a consequence of the user-pays research system. Since core long-term research on the North Island population has primarily focused only on areas where bottlenose dolphins are subject to tourism activities, it remains unclear how long and to what extent GBI and potentially other regions of unstudied coastline have been important for this population. It is therefore strongly recommended that other poorly studied areas within the home range be examined so their relative importance in the context of the North Island population can be assessed. While the number of individual sighting records was considered ample for this study, a greater number of group encounters would be beneficial in future studies in order to conduct more robust group dynamics and habitat use analyses. Further studies to estimate abundance, in addition to reproductive and demographic parameters, across the entire range of the North Island population are also recommended. This is particularly relevant following the decline in local abundance of bottlenose dolphins in BOI, where it is unclear whether the reported 5.8% annual rate of decline is due to mortality, low recruitment, emigration or a combination of these (Tezanos-Pinto et al. 2013). Use of the Robust Design is recommended for the North Island population as it appears to be the best framework for the dolphins using GBI and BOI regions, where models with temporary emigration (Markovian or random, respectively) were considered better than models with no temporary emigration (Tezanos-Pinto et al. 2013; this chapter).

5.4.1 Summary

In conclusion, GBI appears to be a potential hotspot for bottlenose dolphins of the North Island population. Photo-identification results showed individuals of this population spend extended periods of time outside of what has formerly been recognised as the core home range (i.e. BOI). Overall site fidelity (MSR = 0.33) to the GBI region was high, albeit with variable re-sighting patterns among individuals. Seasonal abundance estimates peaked in summer and autumn and were lower during winter months, with individuals leaving the study area for multiple seasons but subsequently returning. A total of 171 dolphins (CI = 162–180) used the area during the study period. Groups were typically large and predominantly contained neonates and calves. Based on these results, and the relatively low encounter rates of bottlenose dolphins in IHG waters (Chapter 2), it is apparent that the GBI region is not simply being used as a corridor to reach other destinations but instead, is a key site for at least a part of the North Island population.

It remains unclear how long and to what extent GBI and potentially other regions of unstudied coastline have been important for North Island bottlenose dolphins. It is therefore recommended that other poorly studied areas within the home range be examined so their relative importance in the context of the North Island population can be assessed. This is important for management due to the decline in local abundance of bottlenose dolphins in the BOI.

Chapter 6

General Discussion

The research vessel *Te Epiwhania* at anchor at Great Barrier Island. Photo: Sarah Dwyer.

6.1 Conservation management

Marine conservation lags behind its terrestrial counterpart in relation to protected areas, with approximately 13% of the world's terrestrial surface area protected in reserves, but only a little over 1% in marine environments (Secretariat of the Convention on Biological Diversity 2012). Marine conservation management strategies that have been proposed or implemented over the years include marine protected areas (MPAs; Halpern 2003), MPA networks (Hinch & De Santo 2011), marine spatial planning (MSP; Douvere et al. 2007), the large marine ecosystem (LME) approach (Elvin 2014), and biodiversity indices (Azzellino et al. 2014). These single-species or ecosystem approaches are all underpinned by sound knowledge of species' distributions and abundances.

In conservation science, the general trend has been to shift away from single-species management towards ecosystem strategies (Hyrenbach et al. 2000; Geijer & Jones 2015), exemplified for cetaceans by the advocacy for large-scale MPA networks (Bearzi 2012; Guidetti et al. 2013; Portman et al. 2013). A system-level approach is considered attractive in the marine environment since coastal and pelagic ecosystems can be integrated into a single big picture to understand the effects of multiple stressors (Guidetti et al. 2013; Azzellino et al. 2014). When focusing at the ecosystem level, ecological knowledge of keystone species remains important (Power et al. 1996). Despite their relatively low biomass, cetaceans have been identified as keystone species in marine ecosystems (Coll et al. 2007; Bănaru et al. 2013) and serve as sentinels of the health and status of lower trophic levels (Wells et al. 2004; Alessi & Fiori 2014). From this point of view, ecological knowledge of cetacean species or functional groups (Azzellino et al. 2014) remains important, regardless of the management approach being utilised.

In New Zealand, marine mammal management has previously taken a single-species approach in the form of the DOC Marine Mammal Action Plan (MMAP; Suisted & Neale 2004). The main aims of the MMAP for 2005–2010 were separated into species protection (species-led approach) and management of human interaction and use (issue-led approach). Recent evidence from New Zealand has demonstrated that a species-led approach such as an MPA can work for marine mammals (Gormley et al.

2012), illustrated by the case of the Banks Peninsula Marine Mammal Sanctuary (BPMMS) that was established in 1988 to protect endangered Hector's dolphins (*Cephalorhyncus hectori hectori*, Dawson & Slooten 1993). However, DOC is now focused on an ecosystem-based approach to management. As a result, the MMAP will be replaced with a risk assessment framework that combines the species- and issues-led approaches (Laura Boren, DOC Wellington, pers. comm.).

The importance of incorporating an adaptive management approach into a required monitoring process was highlighted for the BPMMS, where newly acquired scientific information regarding the seasonal distribution of Hector's dolphins suggested that the existing protective measures should be modified (Rayment et al. 2010). A change in habitat use by bottlenose dolphins in the Bay of Islands, New Zealand, also prompted recommendations for an adaptive management approach specifically for that population and generally for other wide-ranging species (Hartel et al. 2014). Similarly, Douvere & Ehler (2010) emphasised the importance of monitoring and evaluating the efficacy of management measures in MSP ecosystem approaches by using ecological and socio-economic indicators. Future protected areas require an explicitly defined process in which all parties agree that regular monitoring is constantly reviewed and regulations will be revised as needed. For instance, if new information suggests that a species has a seasonal shift in distribution, the boundaries of the protected area will be allowed to shift seasonally or be extended to incorporate both regions. In terms of marine conservation, it is clear that an understanding of cetacean distribution and habitat use, and how they continue to change in space and time, is crucial for management.

6.2 Summary of research findings

The main research findings of this thesis are summarised for each species. It is important to note, particularly for Bryde's whales (*Balaenoptera edeni*), that the results of this study are based on data collected during predominantly La Niña conditions. Consequently, spatial and temporal trends described herein may be expected to vary under neutral and El Niño conditions, as discussed in more detail in previous chapters.

6.2.1 Common dolphins

Common dolphins (*Delphinus* sp.) were distributed year-round in central northern regions of the inner Hauraki Gulf (IHG) and used inshore and more southerly waters most frequently during winter when small groups were most prevalent (Fig. 2.10; Chapter 2). Temporal and spatial patterns were generally quite consistent across years, with the greatest dolphin densities recorded during winter. Habitat models estimated that the greatest probability of encountering dolphins was during the colder months of winter and spring and within deeper waters (40–60 m). The probability of encounter in shallow inshore waters also increased during winter and spring. Spatially, this corresponded with decreased sightings of common dolphins in areas of higher currents directly adjacent to the Colville Channel, in the Firth of Thames, and in the channels between IHG islands (Fig. 3.9; Chapter 3).

While the greatest chance of encountering common dolphins off the west coast of Great Barrier Island (GBI) was also in the deepest region of the study area (50–80 m), it occurred at different times of the year, i.e. during summer and autumn (Fig. 3.9; Chapter 3). The inshore movement of common dolphins in Hauraki Gulf waters during winter may represent an overall offshore to inshore shift in distribution, combined with an influx of dolphins into the Gulf from the wider surrounding areas of the northeast coast. This is likely related to prey distribution, given that common dolphin prey species such as pilchards (*Sardinops neopilchardus*) are known to be more abundant in bays and harbours in New Zealand when water temperatures are cooler (Ministry for Primary Industries 2013). Common dolphins also appear to move offshore during summer and autumn, when densities are lower in the IHG but higher off GBI. Estimates of the functional habitat models suggested that the use of more southerly waters in the IHG during summer and autumn reflects habitat use by nursery rather than by feeding groups. However, the overall predictive maps were more temporally and spatially similar to the feeding than the nursery group predictions, indicating that prey availability likely has important implications for the general distribution and habitat use patterns of common dolphins in the Hauraki Gulf.

Occupancy model outputs showed similar spatial and temporal trends in distribution and habitat use of common dolphins in the IHG as the GLMs (Chapter 4). While incorporating detection probability reduced the bias in parameter estimates, the depth covariate was still identified as the most important predictor of seasonal occurrence using both model types. There was strong agreement between the rankings of the occupancy and GLM predictions, suggesting that the identification of high and low use areas were relatively consistent between model types.

6.2.2 Bryde's whales

Overall, the spatial and temporal distribution patterns of Bryde's whales were the most unpredictable of the focal species. Distribution and density patterns within the Hauraki Gulf were highly variable for Bryde's whales (Figs. 2.8 & 2.11; Chapter 2). Although seasonal trends were not detected, central northern IHG regions were important for Bryde's whales year-round, similar to common dolphins. However, the significance of GBI's west coast waters to Bryde's whales appears to be highly variable from one year to the next. The considerable inter-annual variability is likely related to changes in prey availability as a consequence of changes in climate conditions that influence ocean circulation patterns.

Whales generally used the deeper waters of the Hauraki Gulf, although this varied spatially off GBI according to year. The prevalence of feeding whales compared with mother-calf pairs suggested prey availability may be the most likely factor affecting Bryde's whale habitat use in the Hauraki Gulf. Notably, habitat use by Bryde's whales and common dolphins in GBI waters was considerably different, unlike in IHG waters (Chapter 3). This differential use of GBI waters by Bryde's whales and common dolphins may be suggestive of whales foraging more frequently on krill in outer Hauraki Gulf waters than in the IHG, albeit dependent on inter-annual variation in prey availability.

6.2.3 Bottlenose dolphins

Bottlenose dolphins (*Tursiops truncatus*) were sighted infrequently in the IHG, but were regularly encountered off the west coast of GBI during all seasons. The consistently high year-round encounter rates at GBI compared with the IHG support the hypothesis that GBI is a hotspot for the North Island population of bottlenose dolphins. Habitat use patterns showed a general seasonal onshore-offshore movement between shallow and deeper waters depending on SST, i.e. use of shallower waters during cold temperatures and deeper waters during warm temperatures.

Photo-identification analyses of bottlenose dolphins using GBI waters provided additional insights into their use of the Hauraki Gulf. Overall site fidelity to the GBI region was high, albeit with variable re-sighting patterns among individuals. A total of 171 dolphins (CI = 162–180) used the area during the study period, representative of a significant proportion of the North Island population. Seasonal abundance estimates peaked in summer and autumn and were lower during winter months, with individuals leaving the study area for multiple seasons but subsequently returning. Thus, individuals of the North Island population clearly spend extended periods of time outside of what has formerly been recognised as the core home range (i.e. Bay of Islands). Groups using GBI waters were larger than previously reported for the North Island population and predominantly contained neonates and calves. Based on these results, and the relatively low encounter rates of bottlenose dolphins in IHG waters (Chapter 2), it is apparent that the GBI region is not simply being used as a corridor to reach other destinations but instead, is a key location for at least a part of the North Island population. The southwest coast of GBI appeared particularly important for bottlenose dolphins, possibly due to a combination of factors that includes a consistent availability of food, its suitability for breeding or calving and the likely decreased levels of anthropogenic pressures associated with other regions of the population's home range (Chapter 5; Dwyer et al. 2014a).

The disparity in habitat use by common and bottlenose dolphins in the Hauraki Gulf is likely a consequence of different prey preferences. While common dolphins target small pelagic shoaling fish, coastal bottlenose dolphins typically select fish with a strong association to the rocky reef and other benthic habitats.

6.3 Significance and contribution of research findings

In order to successfully manage a species, it is imperative to understand spatial and temporal variations in the distribution and abundance of that species. In this thesis, I present new information about the spatial ecology of cetaceans using the Hauraki Gulf. Mapping of cetacean distributions in previously unstudied regions, such as the Firth of Thames and west coast of GBI, represent new contributions to current knowledge. Species distribution modelling (SDM) of cetaceans using the Hauraki Gulf, utilising data that was not constrained by collection from a platform of opportunity, was conducted for the first time to assess habitat use. This provided an understanding of the likely spatial use of the Hauraki Gulf by cetaceans and how that likelihood changes seasonally. A new method of SDM for cetacean sighting data that incorporates detection probability was also evaluated through occupancy modelling. The occupancy estimates for the probability of dolphin use were significantly greater when detection probability was accounted for, but the predicted high use regions were the same as those identified by the GLMs. Additionally, more fine-scale information about bottlenose dolphin use of GBI waters was investigated through individual photo-identification analyses. This further highlighted the importance of the region, as initially suggested by the spatial data.

Changes in encounter rates over time can be related to natural environmental fluctuations, or they may be indicative of a potential problem affecting a population. In the Mediterranean Sea, a marked decrease in encounter rates of short-beaked common dolphins resulted in the subpopulation being classified as 'Endangered' by the IUCN (Bearzi 2003). Prey depletion was suggested to be the most likely cause for the population decline (Bearzi et al. 2005). The SR and ER values presented for the focal species in the Hauraki Gulf in this study (Chapter 2) will be useful for conservation management, particularly from a monitoring perspective. Now that the first baseline values are available, the challenge will be to ensure continuity in research over the long-term to enable meaningful re-evaluations of these populations in the future.

The identification of significant differences in encounter rates of bottlenose dolphins in the IHG and GBI waters led to the identification of a previously unknown hotspot at GBI for the North Island population. This is an important contribution to knowledge and crucial for management given the local decline in abundance of bottlenose dolphins in the Bay of Islands (Tezanos-Pinto et al. 2013). From a management perspective, commercial tourism should not be allowed to target marine mammals in the GBI region until further research has been conducted into the relative importance of the area for the North Island population. GBI also offers a unique opportunity as a control site to compare against other regions of the home range that are heavily exposed to tourism. For management to be effective, a comprehensive approach including the entire home range of this population along the northeast coast is required. The fact that the use of GBI waters by bottlenose dolphins has been overlooked until now highlights the need for researchers, managers and funding agencies to maintain an open outlook on their population of interest as a whole when conducting or funding research.

While the west coast of GBI was identified as a hotspot for bottlenose dolphins in the Hauraki Gulf, clear areas of high use for common dolphins and Bryde's whales were not apparent. The southwest coast of GBI was obviously important for Bryde's whales in 2011, but this was not a consistent trend identified in the following year. A factor shared by all three focal species was the limited information about the ecology of their prey. The habitat use of common dolphins and Bryde's whales seemed to be most influenced by feeding behaviour, but this was not restricted to any specific spatial boundaries within the wider Hauraki Gulf that could be easily isolated for protection. If protection of the wider area is not feasible, it may be more appropriate to consider other ecosystem-based conservation approaches, such as the management of their prey species.

While searching the literature for information about seasonal abundances and movements of shared prey species of common dolphins and Bryde's whales, it was surprising to discover the extremely low levels of research into fish species such as pilchard, jack mackerel (*Trachurus* spp.) and anchovy (*Engraulis australis*) in New Zealand waters. Close to a century ago, Young & Thomson (1926) investigated the feasibility of establishing a fishing industry founded on pilchards and sprats (*Harengula antipoda*) in New Zealand waters. They concluded their research by stating "*At present it is clear no definite statements could be made. The problem illustrates the importance of systematic and careful scientific investigation of marine conditions.*" It seems we are not much further along in our understanding of the distributions, abundances and movements of these species. In New Zealand, fisheries research tends to focus on the larger and more commercially valuable stocks, and little if any work has been done on pilchards in the last twenty years (Bruce Hartell, NIWA, pers. comm.). It is concerning that these species are commercially fished in New Zealand waters, yet their ecology is poorly known and stock assessments are typically unavailable (Ministry for Primary Industries 2013). Further still, the effect on the ecosystem of extracting thousands of tons of these kinds of fish is unknown (Ministry for Primary Industries 2013). It is disconcerting that the main prey species of the Hauraki Gulf cetaceans are being removed at levels that may or may not be sustainable, especially given the impacts of prey depletion on marine megafauna that have been documented in other parts of the world (Bearzi et al. 2005; 2006; Cury et al. 2011). There are also consequences at the ecosystem level, given the importance of these prey species for other marine megafauna of the Hauraki Gulf e.g. Australasian gannets (*Morus serrator,* Machovsky Capuska et al. 2011). Gathering information on species that belong to lower trophic levels has been highlighted as a major priority for improving our understanding of the ecology of top-level predators (Lehodey & Maury 2010). This provides further impetus to invest in the research of these fish species that are perhaps mistakenly considered of low commercial value, and to ensure that their management is not overlooked. Here, an ecosystem approach to management is vital.

Comparisons of the outputs of several different model types are useful for improved management of marine species (Robinson et al. 2011). There was strong agreement in the predictive outputs of the GLMs (Chapter 3) and occupancy models (Chapter 4) for common dolphins in terms of areas of high use. Despite differences in the actual predicted values when imperfect detection was unaccounted for in the GLMs, very similar areas of high use were identified by both model types. This suggests that the predictive maps presented in this thesis provide reliable seasonal distributional information that will be useful to support current and future conservation initiatives such as *Sea Change*, the MSP scheme currently under development for the Hauraki Gulf.

6.4 Future research

This thesis presents a significant body of new data about the ecology of cetaceans using the Hauraki Gulf. Some aspects improve our current understanding and others extend knowledge; however, there are several avenues for future work.

There are a number of factors that should be investigated to build on the results of the habitat models presented in this thesis. This includes testing different temporal and spatial scales to investigate their effects on the model outputs. For example, the classification of seasons based on months that are most similar in terms of SST could be more appropriate for assessing seasonal trends in the marine environment rather than using the terrestrial definitions. Testing a range of different spatial scales would also be useful in future studies given that species distribution patterns may be governed by processes at multiple scales (Dormann 2007). The incorporation of different variables that were not used in this thesis may help to improve the deviances explained by the habitat models. This could involve the collection of prey data whilst simultaneously conducting cetacean surveys or at least conducting prey surveys during the same period as the cetacean surveys. Covariates that account for some of the anthropogenic impacts affecting the Hauraki Gulf marine environment should also be considered when building habitat models. For example, high nutrient loading from land uses associated with dairy farming is causing oxygen depletion in some regions of the IHG (Hauraki Gulf Forum 2014) that may have implications for species such as cetaceans that occupy high trophic levels.

Additional modelling considerations include using the number of individuals as well as the number of groups encountered, i.e. counts as well as presence-absence data. Furthermore, a larger dataset than is presented in this thesis is required to investigate the functional relationships between bottlenose dolphins and Bryde's whales and their habitat. Modelling the distributions of feeding and nursery groups of these species will improve our understanding of their use of Hauraki Gulf waters. For Bryde's whales in particular, there is a clear need to conduct long-term studies to better understand the effects of climate conditions on their occurrence given the effect of year on their distribution that was identified in this study (Chapters 2 & 3).

Further investigations into the suitability of occupancy models for cetacean data should be conducted. This could include the multi-season model (MacKenzie et al. 2003) to understand the rates of change between seasons or the Royle/Nichols heterogeneity model (Royle & Nichols 2003) to account for heterogeneity in detection probability due to variation in abundance of the target species. The multi-state models could be adopted to investigate the distribution of groups according to a particular behavioural state. For example, a multi-state model (Nichols et al. 2007) could be used to estimate the probability of encountering feeding groups, where the probability that a group is present but not feeding, and the probability that a group is present and feeding are both represented in the models.

For bottlenose dolphins, it would be beneficial to conduct surveys around the entire coastline of GBI (only the western side was surveyed in this study due to the permitted operating area of the research vessel). If dolphins are found on the eastern side of the island when absent from the western side, this would further highlight the importance of the GBI region for the species. As highlighted in Chapter 5, assessments of abundance and movement should be conducted for the entire North Island population. This should include examination of other poorly examined areas (e.g. eastern side of the Coromandel Peninsula) since other previously unstudied regions may also be important for the population.

6.5 Concluding statement

In conclusion, the Hauraki Gulf ecosystem supports the year-round occurrence of three cetacean species that show seasonal and/or annual variation in distribution and habitat use patterns. A number of important baselines have been identified through this research and the future challenge will lie in securing enough resources to ensure continuity in research and monitoring for further conservation purposes. The collection and analysis of long-term datasets is required for all three focal species, and especially for Bryde’s whales due to significant inter-annual variability in habitat use patterns. The answer may be found in adopting a multidisciplinary approach;

with simultaneous collection of physical habitat, prey and fisheries, and multiple megafauna data. An improved understanding of the processes driving the differences in habitat use will enable refined predictions of spatial and temporal distribution, which is required for effective management and conservation of cetaceans using the Hauraki Gulf.

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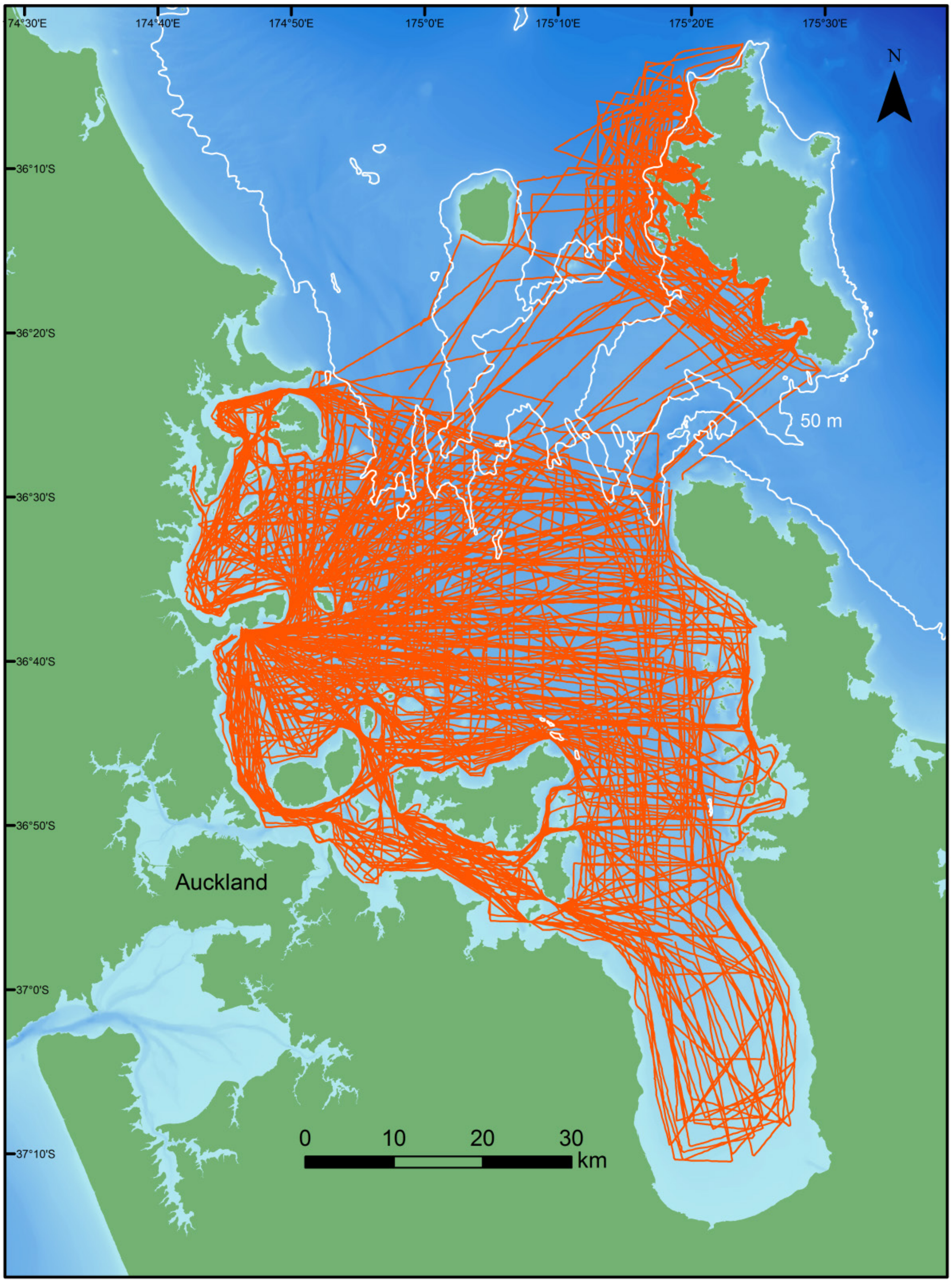
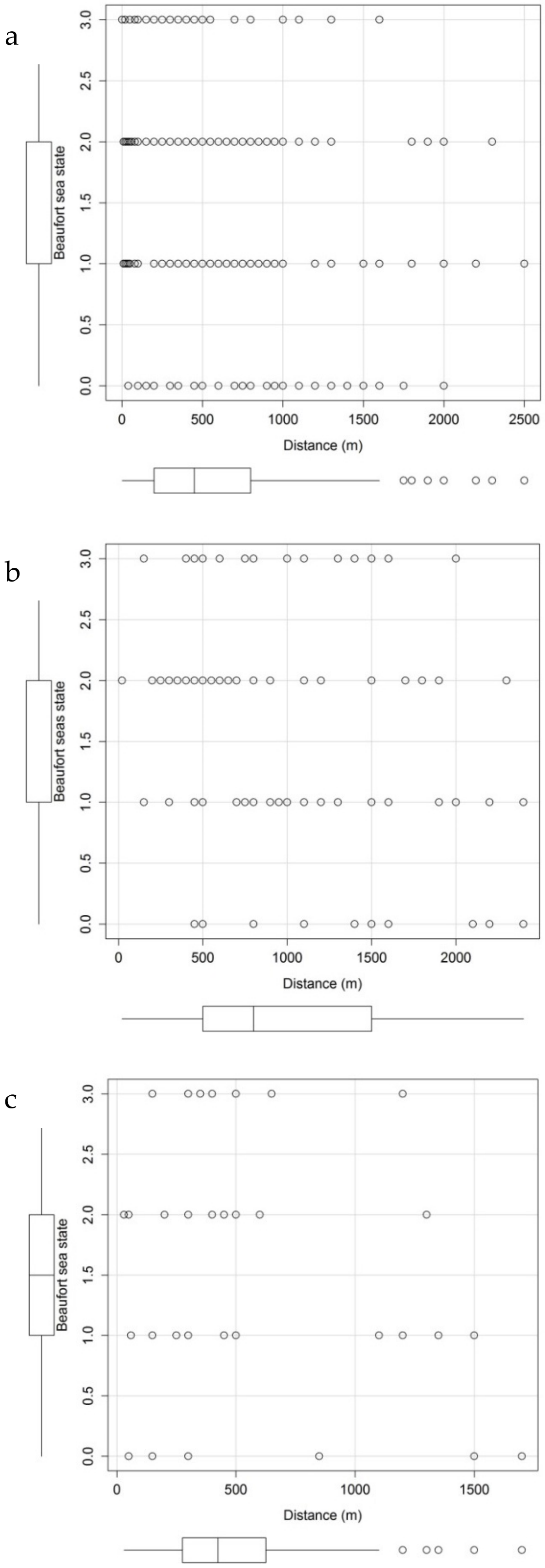
APPENDIX 2.1

Total *on effort* survey tracks in the Hauraki Gulf (prior to tracks being intersected by 5 x 5 km grid polygons for spatial analyses).



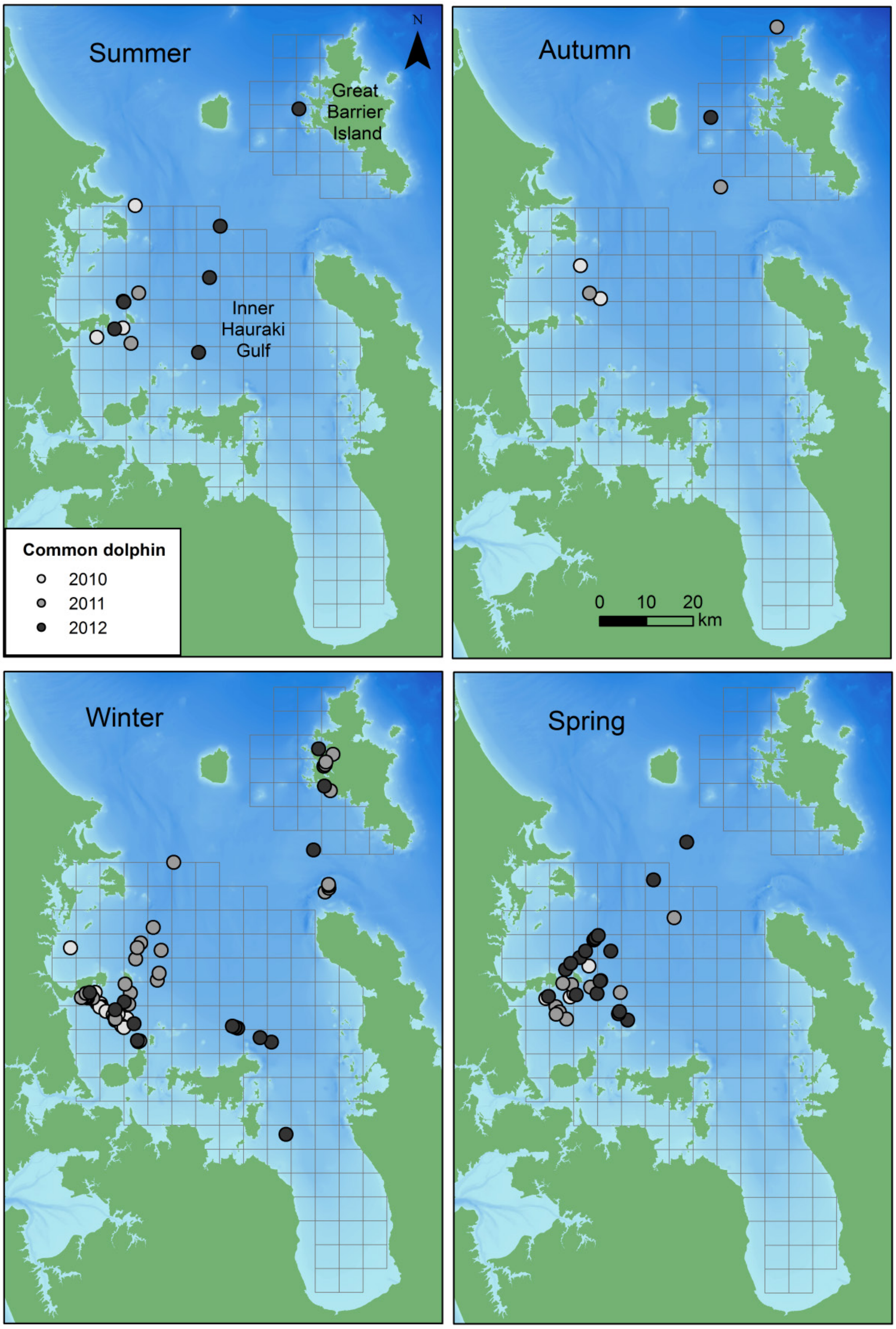
APPENDIX 2.2

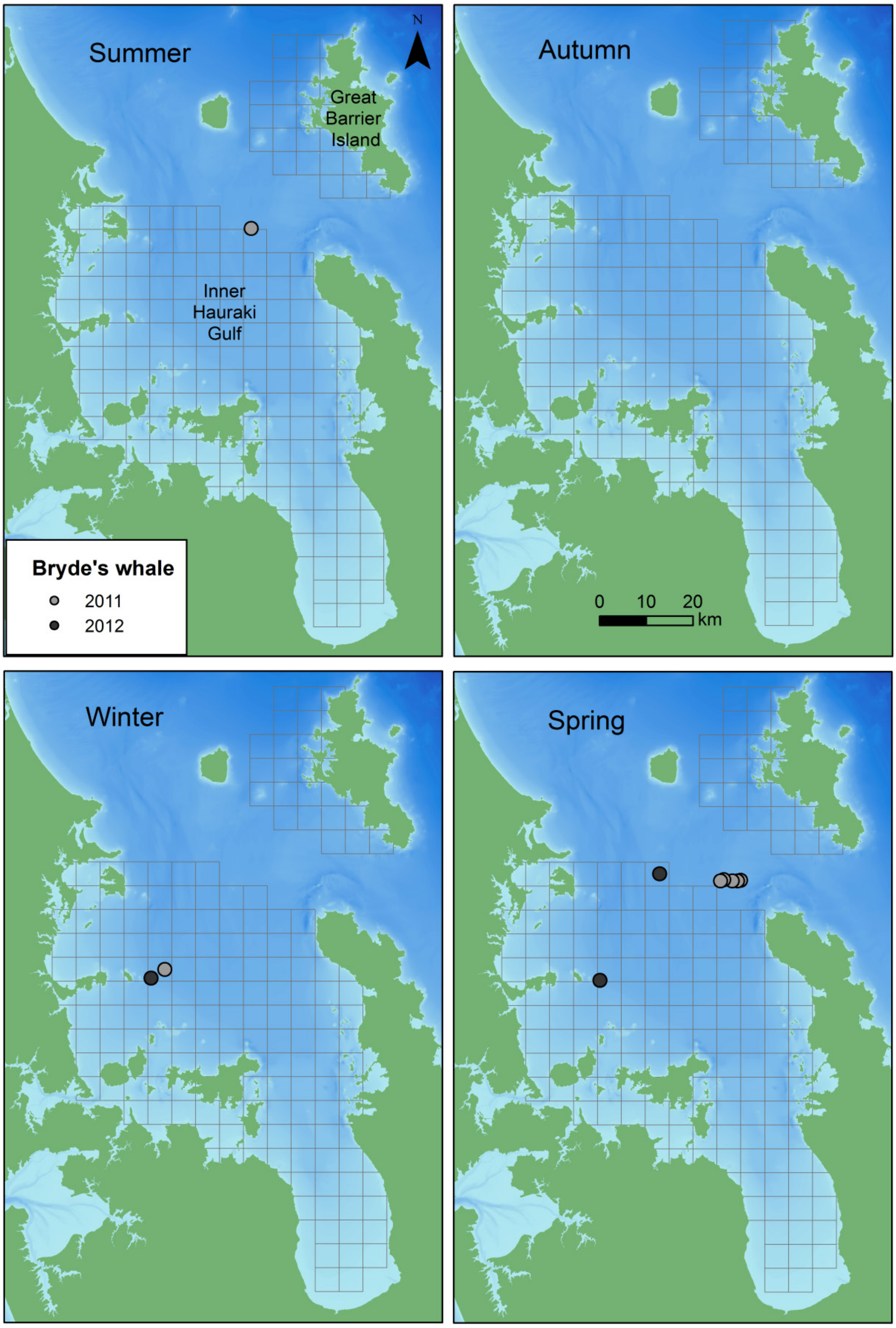
Distribution of sighting distances in Beaufort sea states 0–3 for **a**) common dolphins **b**) Bryde’s whales and **c**) bottlenose dolphins sighted in the Hauraki Gulf, New Zealand, January 2010–November 2012.

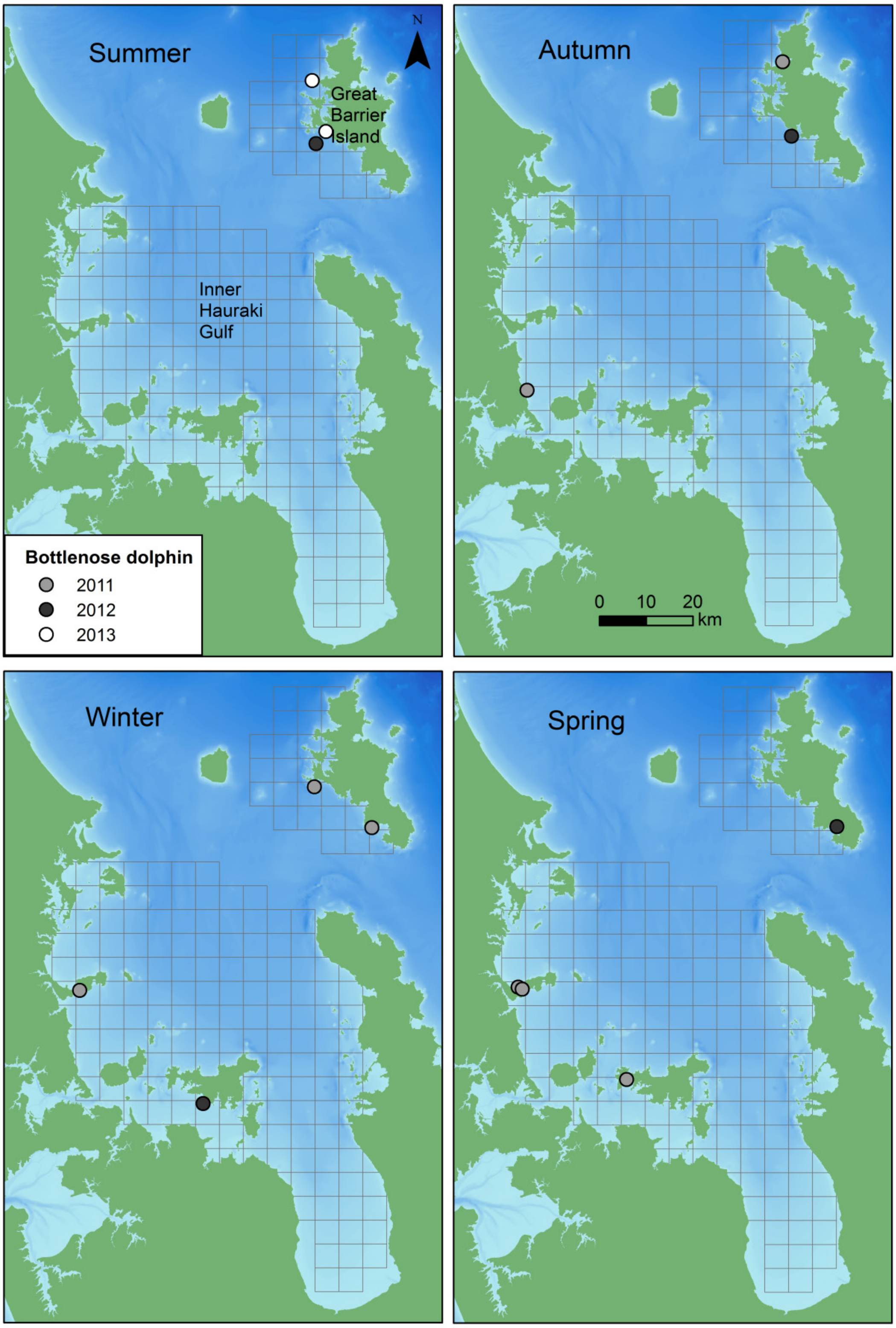


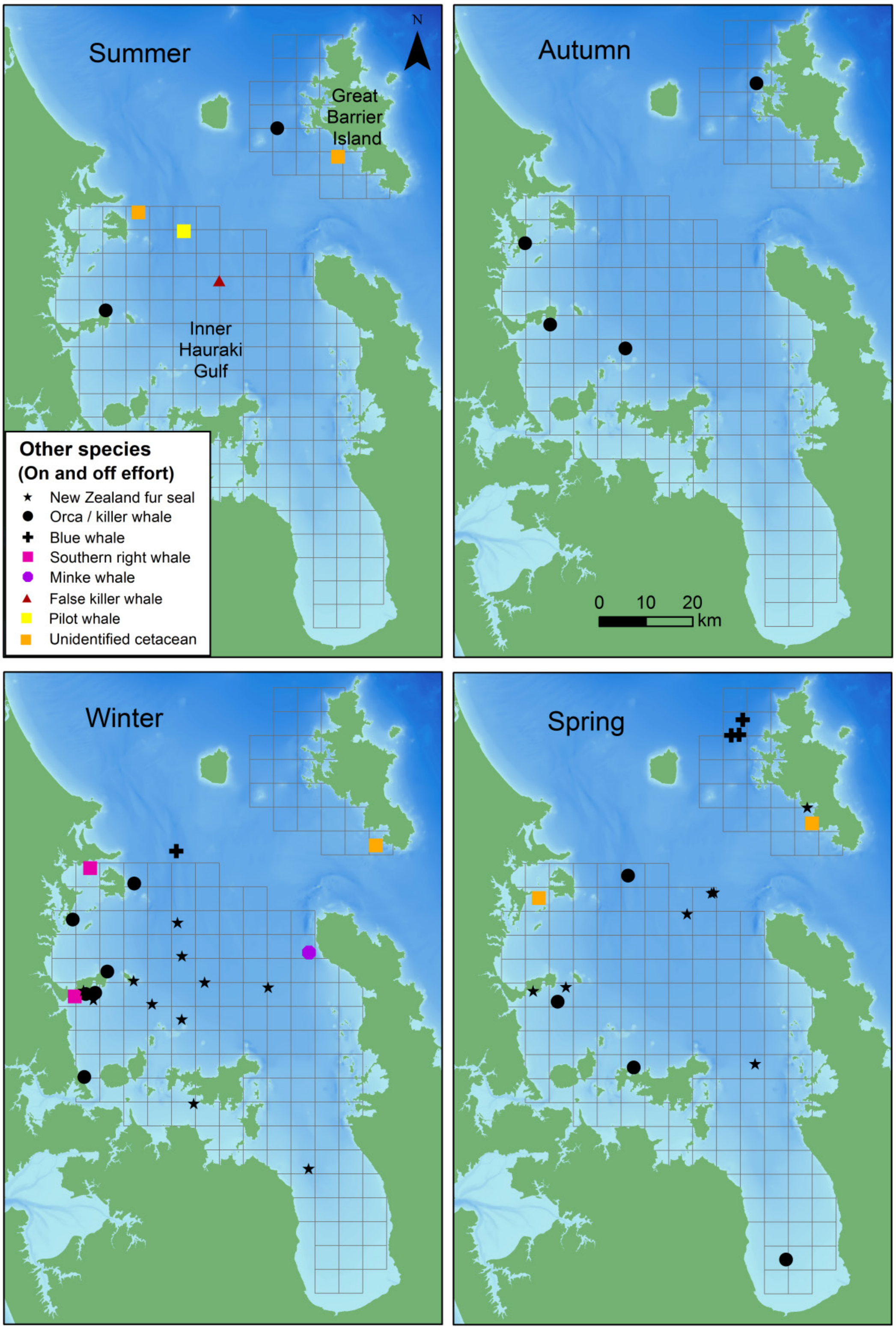
APPENDIX 2.3

Off effort sightings of common dolphins, Bryde's whales and bottlenose dolphins in the Hauraki Gulf, January 2010–January 2013; and *on* and *off effort* sightings of other marine mammal species (i.e. cetaceans and pinnipeds). Sightings from December 2012–January 2013 were opportunistic and mainly used for photo-identification (Dwyer et al. 2014a; Chapter 5). Bathymetry data is courtesy of NIWA (Mackay et al. 2012).




Summer
N
Great
Barrier
Island
Inner
Hauraki
Gulf
Bryde's whale
2011
2012
Autumn
0 10 20
km
Winter
Spring


Summer
N
Great
Barrier
Island
Inner
Hauraki
Gulf
Bottlenose dolphin
● 2011
● 2012
○ 2013
Autumn
0 10 20
km
Winter
Spring


Summer
Autumn
Winter
Spring
N
Great Barrier Island
Inner Hauraki Gulf
Other species (On and off effort)
★ New Zealand fur seal
● Orca / killer whale
✚ Blue whale
■ Southern right whale
● Minke whale
▲ False killer whale
■ Pilot whale
■ Unidentified cetacean
0 10 20 km

APPENDIX 3.1

Age class and behaviour definitions for Bryde's whales (*Balaenoptera edeni*) follow those previously described for the Hauraki Gulf (Wiseman 2008; Wiseman et al. 2011).

Age Class	**Definition**
Calf	Body length equal to, or less than, the length of the accompanying adult. Calves are very closely associated with adults, with the majority of surfacings within 10 m, but up to 100 m, from the adult.
Adult	Fully grown whale that was not classified as a calf.

Behaviour	**Definition**
Feeding	Surface feeding behaviour observed as skim-feeding or lunge-feeding. Skim-feeding is defined as slow swimming through dense surface swarms with the mouth agape, lunge-feeding is defined as an energetic body thrust through the water's surface into a school of prey.
Non-feeding	Engaged in behaviours not described for feeding, including travelling.

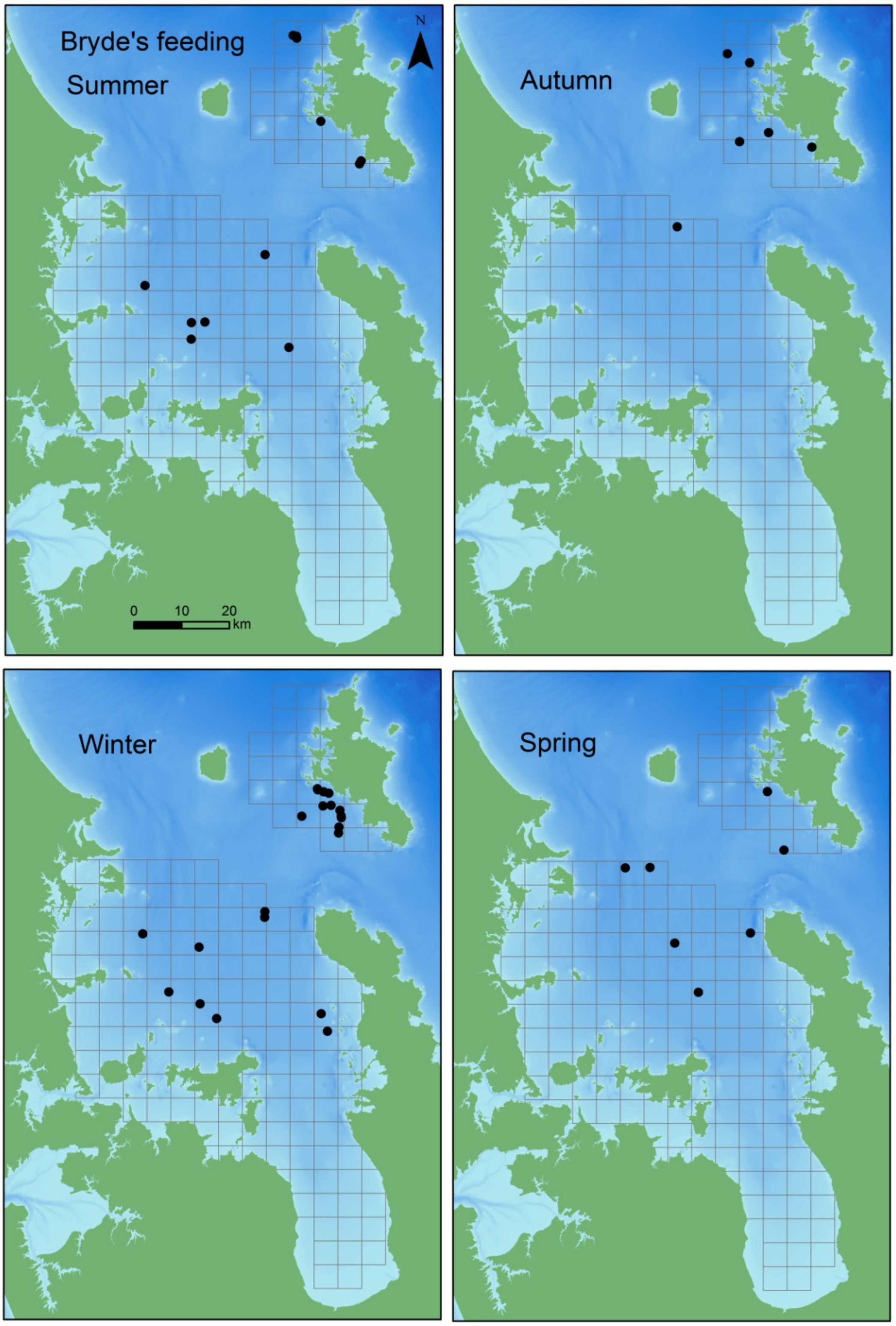
Age class and behaviour definitions for bottlenose dolphins (*Tursiops truncatus*) follow those previously described for the North Island population (Constantine 2002, Tezanos-Pinto 2009).

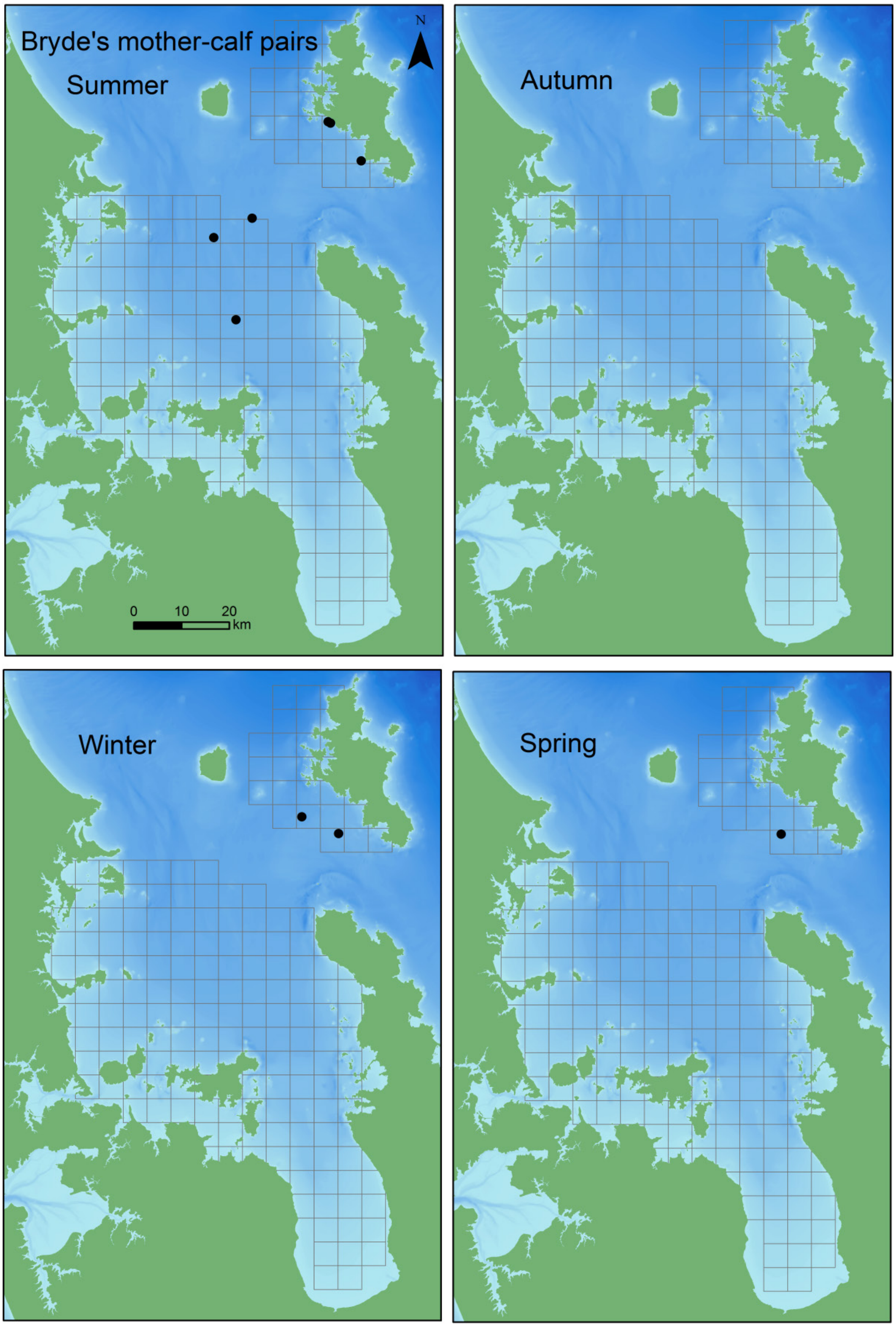
Age Class	**Definition**
Neonate	Presence of obvious white dorso-ventral foetal folds and often uncoordinated upon surfacing to breathe; typically observed up to 3 months old.
Calf	Approximately half or less the size of an adult, closely associated with an adult and often swimming in the 'infant position'.
Juvenile	Approximately two-thirds the size of an adult and frequently observed in association with the presumed mother but not in the 'infant position'.
Adult	Fully grown dolphin of > 3.0 m in length.

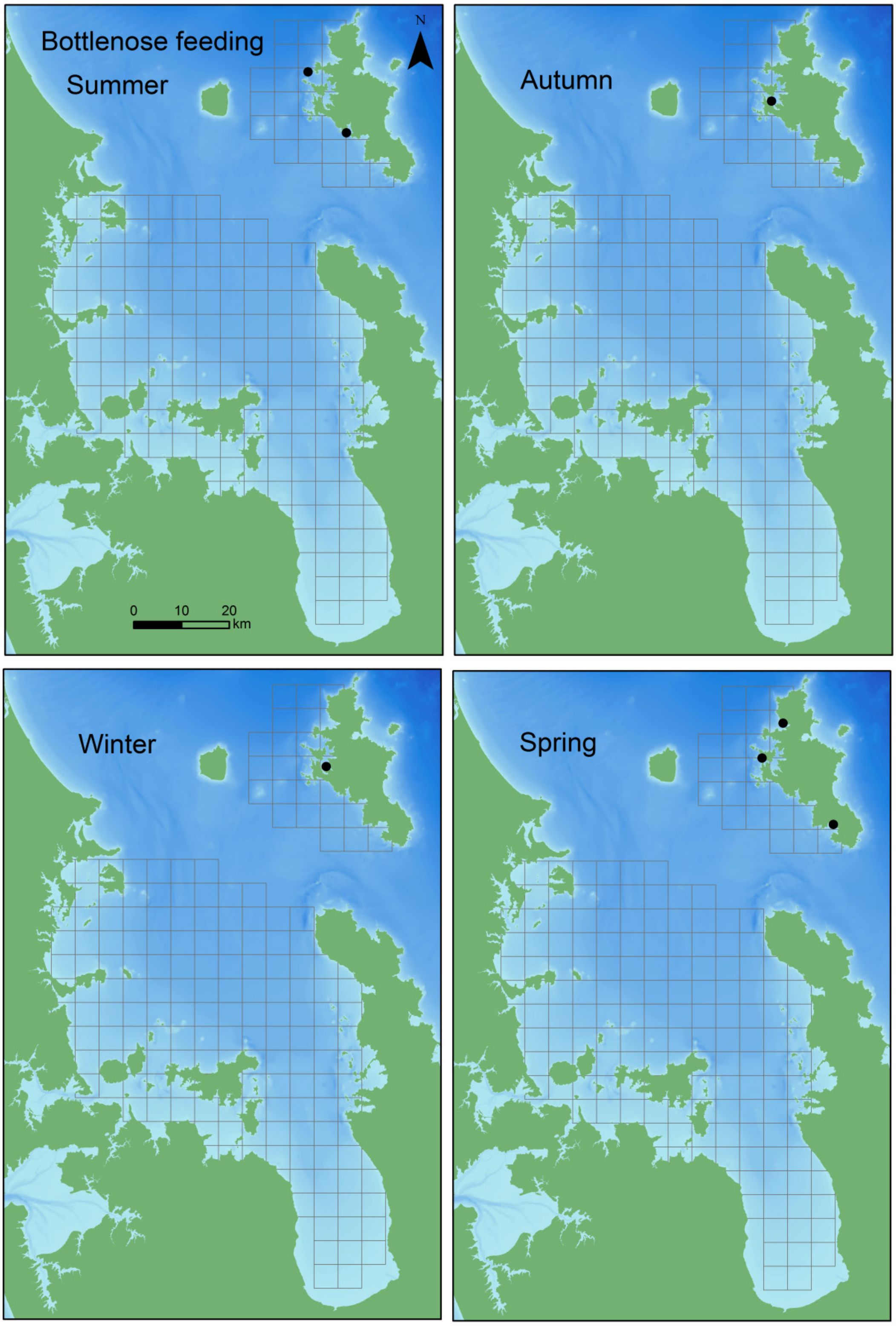
Behaviour	**Definition**
Travel	Dolphins involved in persistent directional movement.
Social	Dolphins observed leaping, chasing and engaged in body contact with other dolphins involved aspects of play (including carrying seaweed) and copulation.
Forage/Feed	Dolphins involved in any effort to capture and consume prey, including fish chasing on the surface, co-ordinated deep diving and no contact between individuals (as often observed when socialising), and rapid circle swimming (but not chasing another dolphin). Prey was sometimes observed in the dolphin's mouth.
Mill	Dolphins showing frequent changes in heading that can appear as a transition behaviour between other behavioural states.
Rest	Dolphins engaged in very slow movements as a tight group and lacking the active components of the other behaviours.

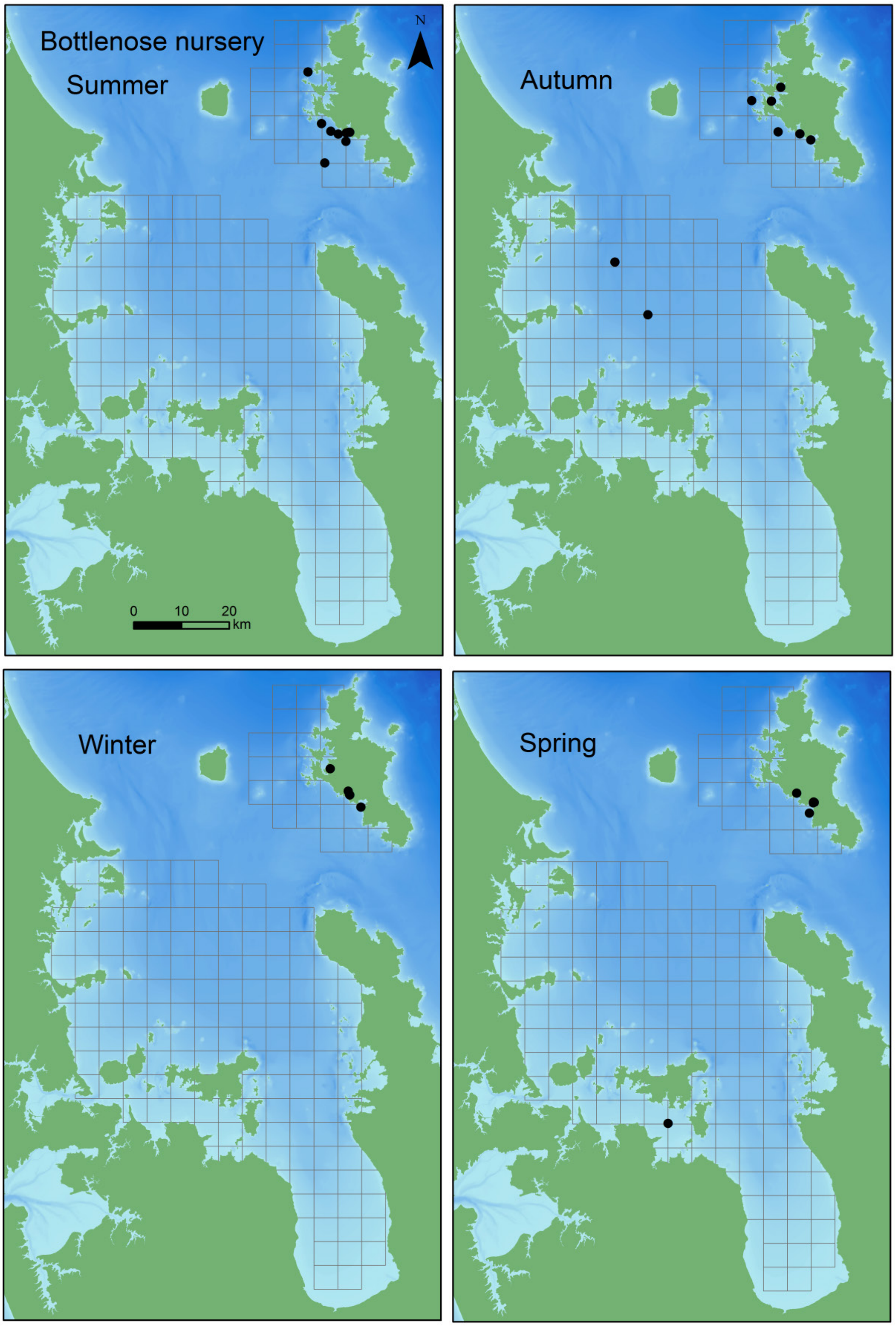
APPENDIX 3.2

Maps depicting *on effort* sightings of feeding and nursery groups of Bryde's whales and bottlenose dolphins. Feeding groups were classified as all groups for which the initial behavioural state 'feeding/foraging' was recorded. Nursery groups of bottlenose dolphins were defined as groups including at least one neonate or calf. For consistency of terminology, nursery groups of Bryde's whales were groups that contained at least one mother-calf pair.



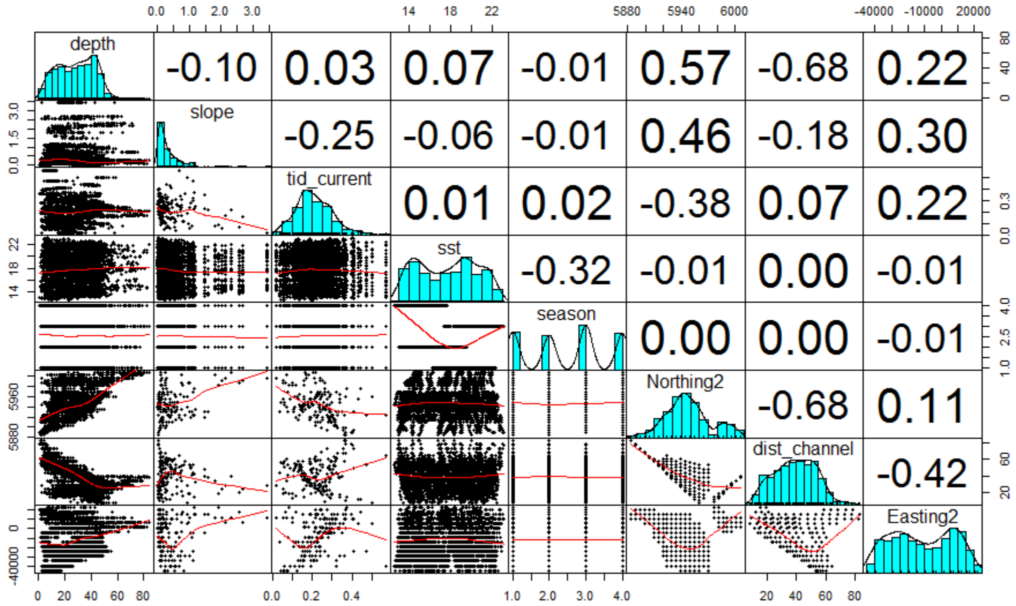

Bryde's mother-calf pairs
Summer
N
0
10
20
km
Autumn
Winter
Spring


Bottlenose feeding
Summer
N
0
10
20
km
Autumn
Winter
Spring


Bottlenose nursery
Summer
N
0
10
20
km
Autumn
Winter
Spring

APPENDIX 3.3

Scatterplot and correlation matrix for the key variables used in common and bottlenose dolphin and Bryde's whale habitat models. Numbers are correlation coefficients and smoother lines (red lines) are shown for scatterplots.



APPENDIX 3.4

Commercial fisheries catch data for some of the main prey species of common dolphins and Bryde's whales were obtained from the Ministry for Primary Industries (MPI), the government agency responsible for fisheries management. Catch weights of anchovy (*Engraulis australis*), pilchard (*Sardinops neopilchardus*), jack mackerel (*Trachurus* spp.) and arrow squid (*Nototodarus* spp.) were obtained for commercial fisheries statistical areas 005 (outer Hauraki Gulf northwards of a line from Cape Colville to Cape Rodney, includes the GBI region from this study), 006 (mid regions of the inner Hauraki Gulf north of Waiheke Island and offshore from all islands) and 007 (inshore inner Hauraki Gulf waters, including the Firth of Thames and Tamaki Strait). An absence of (or very little) catch data represents either no catch or no catch reported for the species since only the top five to eight weight species are reported on fishing returns.

Fisheries catch data for the inner Hauraki Gulf (IHG, statistical areas 006 and 007) and outer Hauraki Gulf (OHG, statistical area 005) between 2010 and 2012. Missing values represent either no catch or no catch reported for this species by fishermen. Catch weights are in kilograms. Data source: Ministry for Primary Industries.

Species	Year	IHG catch weight	IHG fishing days	IHG weight/ day	OHG catch weight	OHG fishing days	OHG weight/ day
Anchovy	2010	130.0	2	65.0	–	–	–
	2011	1062.0	4	265.5	–	–	–
	2012	–	–	–	–	–	–
Pilchard	2010	37902.3	39	971.9	–	–	–
	2011	80056.0	49	1633.8	–	–	–
	2012	91437.7	61	1499.0	2	1	2.0
Jack mackerel	2010	1320.9	143	9.2	25259.0	39	647.7
	2011	7228.6	193	37.5	6238.0	39	159.9
	2012	7407.0	68	108.9	259.0	17	15.2
Arrow squid	2010	348.5	69	5.1	219.0	34	6.4
	2011	88.0	19	4.6	63.0	13	4.8
	2012	42.0	11	3.8	32.0	9	3.6

APPENDIX 4.1

Correlation matrix for site covariates: easting, northing, depth, slope, current distance to shore (dist_shore), and SST within season standard deviation (sst_sd_summer etc.). NA denotes pairs of variables that were never used in the same model set.

	easting	northing	depth	slope	current	dist_shore	sst_sd_summer	sst_sd_autumn	sst_sd_winter	sst_sd_spring
easting	1.00									
northing	-0.53	1.00								
depth	-0.01	0.64	1.00							
slope	-0.20	-0.05	-0.39	1.00						
current	0.59	-0.34	0.07	-0.14	1.00					
dist_shore	0.18	0.27	0.69	-0.85	0.18	1.00				
sst_sd_summer	-0.45	-0.23	-0.46	0.02	-0.30	-0.32	1.00			
sst_sd_autumn	-0.06	-0.76	-0.85	0.20	0.02	-0.47	NA	1.00		
sst_sd_winter	-0.04	0.77	0.83	-0.29	-0.02	0.54	NA	NA	1.00	
sst_sd_spring	-0.20	-0.61	-0.74	0.04	-0.07	-0.31	NA	NA	NA	1.00

APPENDIX 5.1

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SHORT COMMUNICATION

Short-term survival of severe propeller strike injuries and observations on wound progression in a bottlenose dolphin

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Until recently, vessel collisions with small cetaceans were presumed rare, mainly as a consequence of limited reporting. Observations on dolphin wound healing from propeller strike injuries also remain scarce. We present an extreme case of a bottlenose dolphin (*Tursiops truncatus*) with multiple propeller wounds, including a penetration to the bone, where survival was possible for at least 23 days post injury. We used photographic records in conjunction with field observations to describe wound progression in the absence of treatment. Considering the severity of the wounds, it was surprising that the injuries were not immediately fatal. A practical solution remains to be found for the problem of odontocete vessel collisions, in particular for small highly mobile species using neritic waters. In view of the ongoing problem in the Hauraki Gulf and, indeed, worldwide, we recommend continued evaluation of cases and reporting of incidents, in addition to investigations into mechanisms that may reduce the risk of occurrence of vessel collisions with cetaceans.

Keywords: vessel collision; propeller strike; bottlenose dolphin; *Tursiops truncatus*; New Zealand

Introduction

Vessel collisions with marine mammals manifest in the form of blunt trauma and/or propeller strike injuries (Andersen et al. 2007; Calleson & Frohlich 2007; Van Waerebeek et al. 2007; Byard et al. 2012), with the latter typically characterised by curvilinear parallel incised wounds and lacerations (Byard et al. 2012, 2013). Until recently, such vessel collisions with small cetaceans were presumed rare, mainly as a consequence of limited reporting and monitoring worldwide (Van Waerebeek et al. 2007). Observations on dolphin wound healing from propeller strike injuries also remain scarce (Bloom & Jager 1994; Elwen & Leeney 2010).

The documentation of vessel collision injuries and fatalities in cetaceans is challenged by the difficulties in observing injuries in the first instance and subsequently monitoring recovery or recording fatality in these highly mobile animals. The frequency of injuries and fatalities is unknown for most cetacean species for a number of reasons. These include inconclusive or unconfirmed necropsy findings due to decomposed carcasses (Moore et al. 2013), fatally-struck carcasses that are simply not recovered (Dolman et al. 2006; Van Waerebeek et al. 2007), a lack of visible evidence of blunt trauma for cases where necropsy is not performed (Dolman et al. 2006; Moore et al. 2013) and an overall problem of under-reporting when probable or definite collisions are witnessed (Byard et al. 2013). Consequently, the shortage of adequately documented cases is the main obstacle in accurately assessing for vessel collision (Van Waerebeek et al. 2007), and the primary reason for this report.

In New Zealand, vessel collision and propeller strike have been reported for a number of large and small cetacean species (see Martinez & Stockin 2013). In bottlenose dolphins (*Tursiops truncatus*),

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propeller strike scars have been reported for individuals of the Fiordland population (Lusseau 2002; Currey 2008), including one calf that was not resighted following an observed collision (Lusseau 2002). The likelihood of survival from vessel collision injuries can be difficult to ascertain in bottlenose dolphins due to their notable ability to heal from extreme injuries (Zasloff 2011). When assessment of visible external injuries in the field is possible, it is typically difficult to track survivorship of an injured free-ranging individual over time.

Under the New Zealand Threat Classification System (Hitchmough et al. 2007), bottlenose dolphins are classified as Nationally Endangered owing to declines in abundance in two of the three local populations, alongside reports of high calf mortality (Baker et al. 2010). Given that neonates, calves and juveniles appear to be particularly vulnerable to vessel collisions (Stone & Yoshinaga 2000; Laist et al. 2001; Dolman et al. 2006), documentation of any threats to survival is important for these populations.

From previously published records it appears that injuries that penetrate deeply through the muscle, and certainly through the bone, are likely to be fatal (Stone & Yoshinaga 2000; Byard et al. 2012, 2013). We describe herein the most severe propeller strike injuries we are aware of that have been reported for a living free-ranging bottlenose dolphin. We use photographic records in conjunction with field observations to describe wound progression in the absence of treatment.

Methods

The study site included the west coast of Great Barrier Island and all Inner Hauraki Gulf waters south of a line between Takatu Point on the mainland east coast and Kaiiti Point on the Coromandel Peninsula. Boat-based surveys were conducted on the research vessel *Te Epiwhania*, a 5.5 m Stabicraft powered by a 100 hp four-stroke outboard engine. Survey data were collected during all months of the year between January 2010 and January 2013, with Inner Hauraki Gulf Surveys commencing in January 2010 and Great Barrier Island surveys commencing in January 2011.

Photo-identification of individual bottlenose dolphins was conducted for all groups encountered following standard methods (Würsig & Jefferson 1990) using a Canon 7D or 400D camera fitted with 100–400 mm and 70–300 mm lenses, respectively. Attempts were made to photograph all individuals in the group. Photographs included in analysis and in the subsequent Great Barrier Island Bottlenose Dolphin Catalogue (S. Dwyer, Massey University, unpubl. data) were selected based on four criteria described in Berghan et al. (2008), to account for angle, focus, relative size and contrast of the fin. All images were subject to a quality control procedure and were not included in analysis if more than two of the above criteria were compromised. Nicks and notches in the dorsal fin were used, in conjunction with secondary features (i.e. scarring, including tooth rake marks), to identify and match individuals (Würsig & Jefferson 1990). All matching of images was performed by the first author and cross-checked by two observers experienced in photo-identification. Sighting information was recorded in a database for each identified individual.

Results

Background

Individual TM007 was first recorded pre-trauma in the Hauraki Gulf on 17 May 2010 (Table 1). Based on size (approximately half the size of an adult bottlenose dolphin) and associated swimming in the infant position with adult TM009, TM007 was identified as a calf. This presumed mother-offspring association was recorded during four subsequent encounters at Great Barrier Island in 2011 and 2012. No external injuries or deformations were observed on TM007 during these encounters, the fourth of which was on 22 August 2012.

Injury observations

Observation day 1

On 19 September 2012, individual TM007 was photographed with one large open wound on the

Table 1 Sighting records with photographic evidence (✓) of bottlenose dolphins TM007 and TM009 pre- and post-trauma. Great Barrier Island is located approximately 50 km to the northeast of the Inner Hauraki Gulf and 170 km northwest of Tauranga.

TM007	TM009	Date	Location	Latitude	Longitude	Observer(s)
✓	✓	17/05/10	Inner Hauraki Gulf	−36.5094	174.9728	S Dwyer
✓	✓	24/10/11	Great Barrier Island	−36.2623	175.4337	S Dwyer
✓	✓	25/10/11	Great Barrier Island	−36.2628	175.4354	S Dwyer
✓	✓	18/02/12	Great Barrier Island	−36.1445	175.2959	S Dwyer
✓	✓	22/08/12	Great Barrier Island	−36.2526	175.4002	S Dwyer
✓	✓	19/09/12	Great Barrier Island	−36.2636	175.4330	L Kozmian-Ledward; S Dwyer
✓	✓	20/09/12	Great Barrier Island	−36.2621	175.4343	L Kozmian-Ledward; S Dwyer
✓	✓	10/10/12	Great Barrier Island	−36.3284	175.4764	B Kearney
✓	✓	11/10/12	Great Barrier Island	−36.3064	175.4862	S Dwyer
×	✓	01/01/13	Great Barrier Island	−36.1354	175.3103	S Dwyer
×	✓	27/02/13	Tauranga	−37.6085	176.1810	J Bradbury

caudal peduncle immediately caudal to the dorsal fin, and two smaller wounds along the midpoint of the peduncle and on the left tail fluke (Fig. 1). These three evenly spaced parallel wounds were consistent with propeller strike injuries (Byard et al. 2013). Additionally, evidence of blunt trauma in the form of bruising and swelling to the dorsal region of the thorax cranial to the dorsal fin was visible (Fig. 1A).

The largest incised wound (X2; Figs. 1–2) partially transected the caudal peduncle, and penetrated deeply through the skin, blubber, muscle and at least one spinal process of the lumbar vertebrae (Fig. 2A). The incised wound along the midpoint of the caudal peduncle (X3; Fig. 1) also penetrated the skin, blubber and muscle; however, it was not clear if damage was sustained to the caudal vertebrae due to difficulties in observing and photographing this wound. The laceration to the left tail fluke (X4; Fig. 1) was shallower than X2 and X3 and the fluke remained intact. A raised deformation of the dorsal region of the thorax just cranial to the dorsal fin (X1; Fig. 1) was evident and indicative of blunt force trauma. X2 was more deeply incised on the right side of the body (Fig. 2). No haemorrhage was evident from any of the wounds; however, the caudal open face of X2 appeared relatively fresh according to the clear demarcations of the respective layers of skin, blubber and muscle as well as the freshly peeling skin of normal dark grey colouration. The skin surrounding X2 and X3 was intact around the cranial aspects but was peeling away from the smooth blubber layer on the caudal margins and was completely absent in places. The cranial face of X2 was darker and showed an orange to red discolouration of the blubber layer with orange coloured tissue visible on the exposed muscle region (Fig. 2C). Given the apparent freshness of the wounds we suggest the dolphin was likely injured within the previous week.

Observation day 2

External changes in wounds appeared minimal between the first and second day of observations. Differences were only detected for the caudal edge of X2 where further deterioration of the skin was visible on the left side and cream coloured necrotic tissue was observed trailing outside the wound.

Observation day 23

Significant changes in wound appearance were recorded 23 days after first observing the injuries. By 11 October 2012, X2 was filled with granulation tissue across the full extent of the wound. Skin and underlying soft tissue caudal to X2 was necrotic.

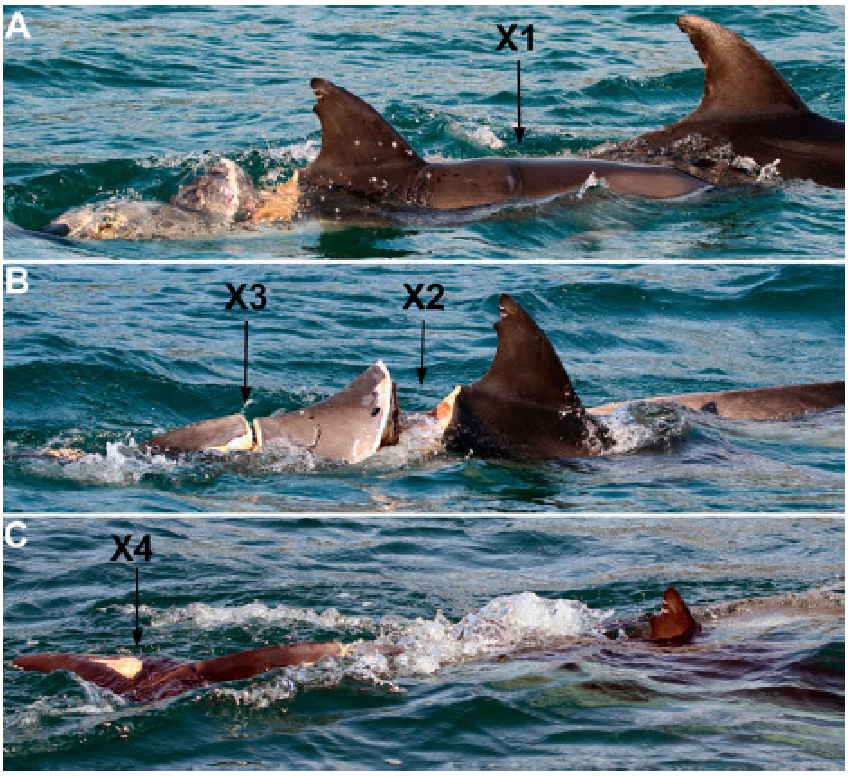

Figure 1 Locations of four externally visible injuries (X1–X4) on a free-ranging bottlenose dolphin *Tursiops truncatus*. Individual TM007 (the injured dolphin) is accompanied by presumed mother TM009. **A**, Evidence of blunt trauma (X1) to the dorsal region of the thorax cranial to the dorsal fin. **B**, Incised wounds X2 and X3 caudal to the dorsal fin. **C**, Wound X4 on the left tail fluke. Photographs by SL Dwyer.

Injuries X3 and X4 were only photographed through the water; therefore, descriptions of wound progressions are limited. X3 was open to a greater degree and both white and pink discolouration could be observed through the water. X4 appeared to be a similar size across all observation days. X1 was still present in the shape of a dorsal deformation and, furthermore, a region of skin was missing, exposing the underlying subdermal surface.

Field observations

During all post-injury encounters the dolphins stayed within a small area of each of the shallow bays at Great Barrier Island at a distance of less than 400 m from shore; therefore overall group movements were small. TM007 and TM009 were consistently observed swimming together in very close proximity (less than one body length apart; Figs. 1, 3) and frequently touching. TM007 was only recorded apart (greater than five body lengths) from TM009 twice; on 19 September 2012 when TM007 was observed alone at a distance of c. 200 m from the group for a period of less than 10 minutes and on 11 October 2012 when TM009 was observed alongside three other adults c. 150 m away from TM007. Following both of these spatial separations, TM009 re-joined TM007 and continued to maintain very close proximity for the remainder of the encounter.

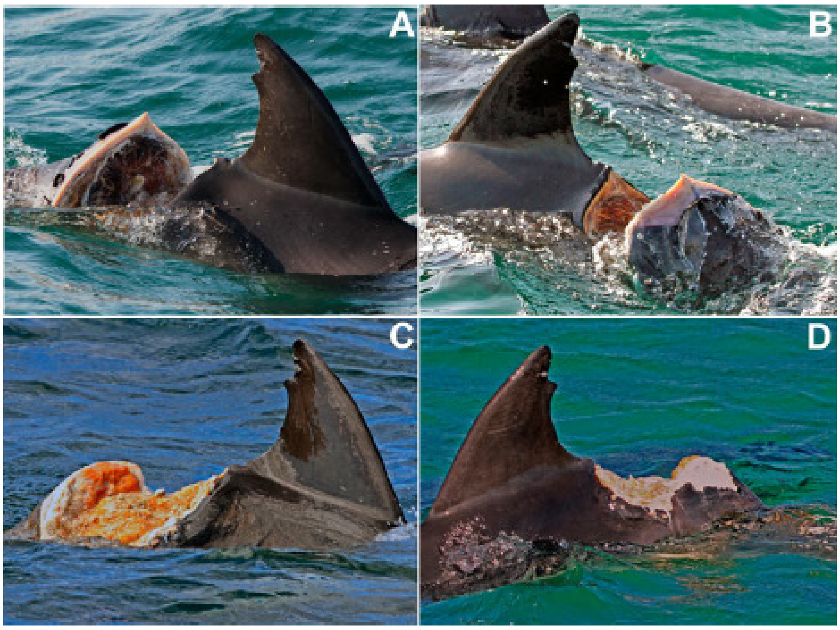

Figure 2 Progression of wound healing associated with the largest incised wound (X2) located immediately caudal to the dorsal fin. **A**, Right side aspect on 19 September 2012. **B**, Left side aspect on 19 September 2012. **C**, Right side aspect on 11 October 2012. **D**, Left side aspect on 11 October 2012. Photographs by SL Dwyer.

Surfacing behaviour of TM007 appeared non-typical, with hyperflexion of the spine beyond what is normally observed for bottlenose dolphins (Fig. 3). Although swimming appeared inhibited and relatively slow, TM007 could maintain spatial proximity to the group and at least shallow diving was possible. Although no photographic evidence could be obtained, TM007 was further reported south of Little Barrier Island on 2 October 2012 (T. Wilson, DOC, pers. comm. 2 October 2012) at a minimum distance of 30 km from the Great Barrier Island sightings. Foraging by TM007 was not observed during any of the post-injury encounters.

TM007 was last photographed on 11 October 2012 (Table 1); however, a sighting without photographic evidence was reported on 21 October

Figure 3 Surfacing behaviour of individual TM007 alongside presumed mother TM009 on 19 September 2012. Photograph by SL Dwyer.

2012 (B. Kearney, Chaos Charters, pers. comm. 24 October 2012). On 1 January 2013, TM009 was resighted at Great Barrier Island in an adult only group, where TM007 was not present. On 27 February 2013, TM009 was further photographed off Tauranga (170 km southeast of Great Barrier Island), where again TM007 was not observed (Table 1). Since a carcass has not been recovered, it cannot be completely ruled out that TM007 is still alive. However, given the historical associations of TM007 and TM009, where neither individual was previously sighted without the other (Table 1), and given that TM009 has since been sighted twice without TM007, we presume that TM007 did not survive the extensive injuries endured.

Discussion

The wound-healing process in dolphins is often considered remarkable in terms of the severity of wounds that can be survived as well as the speed of recovery (Orams & Deakin 1997; Zasloff 2011). We present an extreme case of a dolphin with multiple propeller wounds, including a penetration to the bone, where survival was possible for at least 23 days post injury. Considering the severity of the wounds, it was surprising that the injuries were not immediately fatal. It was also remarkable that the animal was still capable of swimming and maintaining group cohesion with conspecifics for at least three weeks post trauma.

Constant irrigation of a wound with salt water has been cited as a possible aid to wound healing (Corkeron et al. 1987), although in this case the flow of water over X2 may have in fact hindered recovery since the force of the water flow would likely have caused the wound to remain open or even gape further as a consequence of the dolphin's movement through the water. This was evident in the degree of skin loss at the wound peripheries. The skin on the cranial edges of the wounds remained intact compared with the skin at the caudal edges of the wounds, which peeled away in the direction of the water flow over the caudal peduncle. Much of the open wound cavity of X2 had filled in with granulation tissue by observation day 23 and therefore appeared to be healing.

While we acknowledge that survival cannot be completely ruled out due to the absence of carcass retrieval, we presume TM007 did not survive the assumed vessel collision injuries in the long term, based on the strong social bond of the mother-offspring pair that was evident over two and a half years of sighting records. Neither individual was sighted separately prior to the vessel collision event and up to the last known sighting record of TM007. A combination of nurturant and succorant behaviour (Caldwell & Caldwell 1966) was displayed by TM009 towards TM007 in the form of repeated touching and what appeared at times to be a supporting position of TM007 at the surface. A high level of epimeletic care has been documented for bottlenose dolphins, to the extent of mothers carrying the decomposing remains of their dead calves for extended periods (e.g. Harzen & dos Santos 1992; Fertl & Schiro 1994). Considering this, and the social bond between a mother and her calf that typically lasts for several years (Wells et al. 1987), we believe TM009 would have unlikely abandoned her injured offspring if still alive. Since the injuries sustained were a combination of blunt and sharp force trauma and not immediately fatal, factors contributing to the presumed death may have included emaciation and/or dehydration, infection at the site of the propeller wounds, internal injuries caused by blunt trauma or a combination thereof (Byard et al. 2012; Martinez & Stockin 2013).

Fatal vessel collisions in the Hauraki Gulf region have been reported previously for common dolphins (*Delphinus* sp.; Martinez & Stockin 2013) and Bryde's whales (*Balaenoptera brydei*; Stockin et al. 2008; Behrens 2009). The probability of fatality for a vessel strike with a large whale has been shown to decrease by reducing the speed of shipping traffic (Vanderlaan & Taggart 2007), and rerouting shipping traffic outside of critical areas is also being proposed to reduce risk (Vanderlaan et al. 2008; Conn & Silber 2013; Redfern et al. 2013). Resolving the problem of odontocete vessel collisions remains challenging for small highly mobile species using neritic waters. Boat speed restrictions show evidence for reducing deaths in manatees (*Trichechus* sp.; Laist & Shaw 2006) and crocodilians (*Caiman crocodilus*; Grant & Lewis 2010); however, for species that are not territorial or are widely dispersed this may simply not be practical or enforceable. Another problem is that risk of collision according to vessel type is unknown. A study of propeller wounds on manatees (Beck et al. 1982) found that the lengths of the longest incised wounds varied greatly, likely due to variation in the torque of the motor, the position of the manatee in the water and vessel speed. The results of that study suggested larger vessels (over 7.3 m long), mainly powered by inboard engines, were responsible for most of the manatee fatalities attributed to propeller strike. Since the length, spacing and depth of the wounds could not be measured in this study, we cannot draw any conclusions about the type of vessel involved. Furthermore, many small cetaceans may be classified as 'propeller positive', a term used by Visser (1999) for describing cetaceans that actively seek out the wash caused by propellers. The use of propeller guards has therefore been suggested as a mitigation measure (Visser 1999; Van Waerebeek et al. 2007). Experiments with loggerhead sea turtles *Caretta caretta* did not show any significant improvement in animal safety when propeller guards were used (Work et al. 2010); however, their effectiveness is not known for dolphins.

Although legislation (Marine Mammals Protection Regulations [MMPR 1992]) is in place regarding the appropriate manner to operate a vessel around marine mammals, it is clear that these rules alone are not sufficient to protect cetaceans from boat strikes. A number of reported incidents have shown a peak in vessel collisions at times of the year when recreational vessel traffic is at its maximum (Wells & Scott 1997; Martinez & Stockin 2013). In this case, however, the incident occurred at the end of the austral winter when vessel traffic is typically at its lowest. The risks are therefore present year round and increased mitigation efforts at particular times of the year may not be effective.

This case further supports previous evidence that suggests it is unlikely a free-ranging cetacean can survive an injury that has penetrated to the bone. It also demonstrates that such injuries may not be immediately fatal. In view of the ongoing problem of vessel collisions with cetaceans in the Hauraki Gulf and indeed worldwide, we recommend continued evaluation of cases and reporting of incidents. Further discussion and investigations into the mechanisms to reduce the risk of occurrence (e.g. the effectiveness of propeller guards for small cetaceans) are clearly required.

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APPENDIX 6

The following publications have been produced during the PhD candidature as a result of the research presented in this thesis:

Publications

Dwyer, S. L., Tezanos-Pinto, G., Visser, I. N., Pawley, M. D. M., Meissner, A. M., Berghan, J., & Stockin, K. A. (2014). Overlooking a potential hotspot at Great Barrier Island for the nationally endangered bottlenose dolphin of New Zealand. *Endangered Species Research 25*: 97–114.

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Zaeschmar, J. R., Visser, I. N., Fertl, D., **Dwyer, S. L.**, Meissner, A. M., Halliday, J., Berghan, J., Donnelly, D., & Stockin, K. A. (2014). Occurrence of false killer whales (*Pseudorca crassidens*) and their associations with common bottlenose dolphins (*Tursiops truncatus*) off north-eastern New Zealand. *Marine Mammal Science 30*(2): 594–608.

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Dwyer, S. L., Visser, I. N., Tezanos-Pinto, G., Meissner, A. M., Berghan, J., & Stockin, K. A. (2013). Overlooking an important habitat within the known home range of a nationally endangered species: The case of bottlenose dolphins at Great Barrier Island, New Zealand. The 20th Biennial Conference on the Biology of Marine Mammals, Dunedin, New Zealand.

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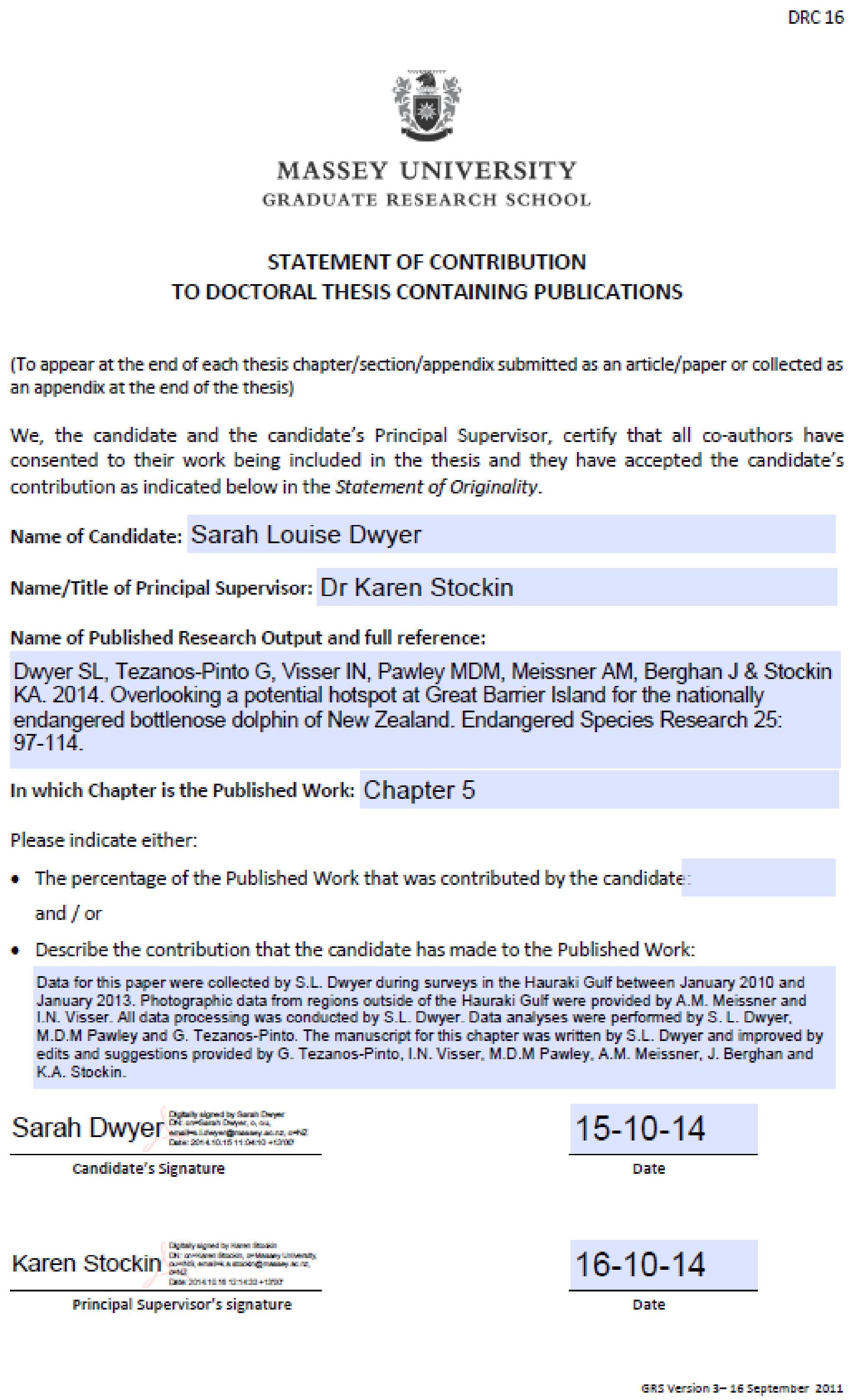
APPENDIX 7



DRC 16

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Sarah Louise Dwyer

Name/Title of Principal Supervisor: Dr Karen Stockin

Name of Published Research Output and full reference:

Dwyer SL, Tezanos-Pinto G, Visser IN, Pawley MDM, Meissner AM, Berghan J & Stockin KA. 2014. Overlooking a potential hotspot at Great Barrier Island for the nationally endangered bottlenose dolphin of New Zealand. Endangered Species Research 25: 97-114.

In which Chapter is the Published Work: Chapter 5

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Data for this paper were collected by S.L. Dwyer during surveys in the Hauraki Gulf between January 2010 and January 2013. Photographic data from regions outside of the Hauraki Gulf were provided by A.M. Meissner and I.N. Visser. All data processing was conducted by S.L. Dwyer. Data analyses were performed by S. L. Dwyer, M.D.M Pawley and G. Tezanos-Pinto. The manuscript for this chapter was written by S.L. Dwyer and improved by edits and suggestions provided by G. Tezanos-Pinto, I.N. Visser, M.D.M Pawley, A.M. Meissner, J. Berghan and K.A. Stockin.

Sarah Dwyer
Candidate's Signature

15-10-14
Date

Karen Stockin
Principal Supervisor's signature

16-10-14
Date

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