The ecology and conservation of hotspots for Hector's dolphin

Tom E. Brough

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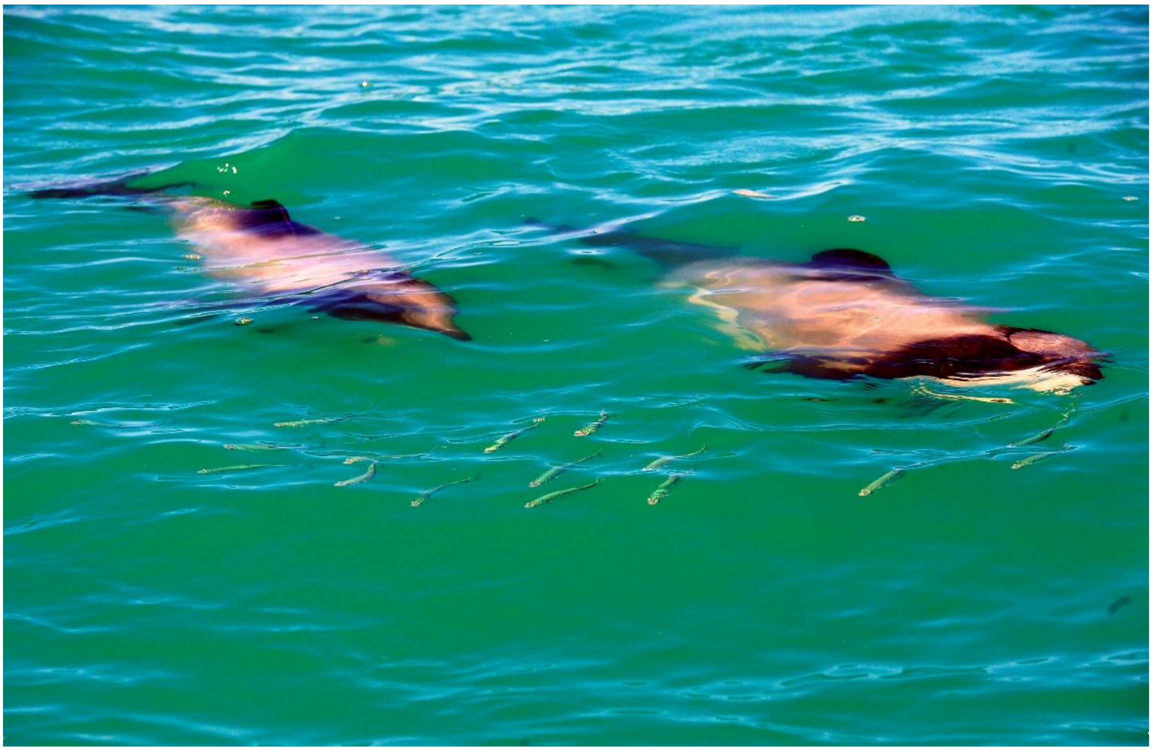
Abstract

Many species of marine top-predator have ‘hotspots’ in their distribution. Hotspots can be defined as areas within the distribution of a population that are used disproportionately more than other locations. Usually identified as consistent, high density aggregations, hotspots are generally locations that are important for certain life history processes or key behaviours such as foraging. Knowledge on what drives the existence of hotspots is crucial for the conservation of species and for understanding ecosystems. New Zealand’s only endemic cetacean, Hector’s dolphin, is endangered and sparsely distributed. This thesis investigates hotspots in the distribution of Hector’s dolphins at Banks Peninsula in order to determine what makes these locations unique and thus to appraise how human disturbance may threaten the ecology of these areas. Three simple questions were considered: Where and when do hotspots exist? Why do the dolphins use these areas? What habitat features make these locations unique?

Hotspot locations were defined using Kernel density analysis (KDe) of a visual sightings database from standardized, boat-based surveys. The analyses showed that fifty percent of sightings, made over 29 years and weighted by search effort, were clustered into only 21% of the study area. The seasonal pattern of hotspots strongly reflected summer distribution patterns, but several hotspots were also important in spring and autumn. Locations of hotspots were consistent over almost three decades. Passive acoustic monitoring showed the highest rates of foraging buzzes at hotspots; suggesting that foraging opportunities shape distribution in this species. The temporal distribution of foraging was complex, with substantial differences among locations over seasonal, diel and tidal cycles.

Data from hydro-acoustic surveys of epipelagic fish showed strong overlap between dolphins and their prey. The depth of prey schools was also important. Prey were generally more abundant, and shallower, at hotspots compared to reference areas. A broad range of habitat variables were pooled from several sources to determine the best predictors of habitat use and the characteristics of hotspots. Covariates were considered that define the physical and biological features of habitat that may be correlated with distribution. Variables significantly related to the relative abundance of dolphins included prey abundance, mud coverage, reef coverage, depth, current velocity, salinity, fluorescence and thermocline depth. However, only the preferred values of prey, depth, dominant habitat type, and to a lesser extent, reef coverage were more common at hotspots.

Confirmation of the locations of hotspots, their stability over time and their importance for foraging provides candidates for areas deserving more protection. Hector’s dolphins in this area face threats associated with fisheries bycatch, vessel strike and noise pollution. Further, information on the characteristics of hotspots provides management with opportunities to prevent degradation of the features that make good quality habitat. With spatially explicit management that focusses on the full range of threats, populations of this ecologically important, taonga species may recover to previous, un-impacted levels.



He rangai maomao ka taka ki tua o Nukutaurua, e kore a muri e hokia[1]

Once the shoal has passed beyond the harbour entrance, it shall never return.

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[1] Whakatauki recited by Hone Toia, Ngapuhi.

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Dedication

This thesis is dedicated to the memory of my Grandad, Bob Denham, who gave me the sea..

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Chapter 1: General Introduction

1.1 - Coastal conservation

Coastal areas are the most accessible marine environments to humans, and so face disproportionately greater anthropogenic impacts associated with commercial and recreational fishing, coastal development, pollution and high shipping traffic among others (Suchanek 1994; Micheli and Halpern 2005; Airoldi and Beck 2007; Crain et al. 2009). For example, anthropogenic impacts on coastal Caribbean coral reefs have resulted in an 80% decline in reef cover (Gardner et al. 2003). In many parts of Europe, critically important coastal ecosystems, such as oyster reefs and seagrass meadows, have been reduced to the point where they are functionally extinct (see Airoldi and Beck, 2007; for a review).

Conservation of the coastal marine environment is important for many reasons. Firstly, the coastal zone provides substantial ecosystem services – benefits to human communities that are freely gained by healthy ecosystems. Thus, the restoration and preservation of coastal ecosystems can have profound benefits for water quality, nutrient cycling and food production (Worm et al. 2006; Lange and Jiddawi 2009; Luisetti et al. 2011). Secondly, restoration of habitat and species assemblages in the coastal zone can have economic advantages for local communities through the provision of better fishing opportunities or through the development of non-consumptive industries, such as tourism (Russ and Alcala 1996; Brunnschweiler 2010; McCook et al. 2010). Also, marine conservation measures can restore vital ecological processes (e.g. food web structuring, regulation of primary productivity, nutrient availability) that increase resilience to future impacts (Hughes et al. 2005; Micheli and Halpern 2005). Often due to restoration of top-predators, marine protected areas can increase trophic complexity (Shears and Babcock 2003; Micheli and Halpern 2005; Byrnes et al. 2006) rendering ecosystems better equipped to withstand future impacts of climate change for example (Graham et al. 2008; McCook et al. 2010).

Marine top-predators have been particularly impacted by anthropogenic impacts in the coastal zone (DeMaster et al. 2001; Myers and Worm 2003; Myers et al. 2007). These species are usually the first targets for fisheries and so have been fished to very low levels globally (Pauly et al. 1998a; Myers and Worm 2003). Further, many predators have life-history characteristics such as low reproductive rates and slow growth that mean recovery from exploitation is a slow process (Schindler et al. 2002; Lotze et al. 2011).

With a few notable exceptions, most coastal marine mammal populations are not harvested. Instead, the main threats to these important taxa are incidental bycatch in fisheries (Read et al. 2006; Chilvers 2008; Slooten and Dawson 2010), ecological impacts from habitat modification (Ribeiro et al. 2007; Jefferson et al. 2009; Karczmarski et al. 2016), anthropogenic noise pollution (Brandt et al. 2011; Castellote et al. 2012) and climate change (Tynan and DeMaster 1997; Burek et al. 2008). In particular, bycatch has resulted in substantial declines in coastal dolphin populations (Read et al. 2006; Slooten and Dawson 2008). The two most endangered cetacean (sub)species, Māui dolphin (*Cephalorhynchus hectori māui)* and Vaquita (*Phocoena sinus)*, owe their current dire status mostly to the effects of fisheries bycatch (Slooten 2013; Taylor et al. 2017).

1.2 - Area based protection for marine top-predators

Management of marine top-predators that are threatened often takes the form of area-based protection (Reeves 2000; Hooker et al. 2011; di Sciara et al. 2016). Such protection usually aims to exclude known threats to species such as direct harvesting (Zacharias et al. 2006; Brunnschweiler 2010; Bond et al. 2012), bycatch (Dawson and Slooten 1993a; D'agrosa et al. 2000) or negative effects from tourism (Lusseau and Higham 2004; Notarbartolo di Sciara et al. 2009). Some marine protected areas (MPAs) aim to protect core habitat in order to prevent negative effects of habitat degradation (Hooker et al. 1999; Hastie et al. 2003), or to protect particular, vulnerable, life history stages (Hooker and Gerber 2004; Schofield et al. 2010; de Castro et al. 2014). Ideally, MPAs for marine top-predators should incorporate all the aforementioned factors (Reeves 2000; Thompson et al. 2000; di Sciara et al. 2016) yet historically this is rarely the case (Hooker et al. 2011). For example, the Southern Ocean Whale Sanctuary (SOS) was implemented by the International Whaling Commission in order to protect baleen whale species from direct harvest in their important summer feeding grounds in the Southern Ocean (Gillespie

2000). In a critical review, Zacharias et al. (2006) discusses how the SOS provides little protection to whales or their ecosystems. This is in part due to the inability of the SOS to address the full range of threats faced by whales in the Southern Ocean and the lack of ecological considerations involved in the gazetting of the sanctuary (Zacharias et al. 2006).

Typically, top-predators are highly mobile species that exhibit wide-ranging and variable distributions and so MPAs for their conservation must place considerable emphasis on the spatial and temporal scale of protection (Game et al. 2009; Hooker et al. 2011). For example, Hartel et al. (2015) found that management areas for bottlenose dolphin (*Tursiops truncatus)* were ineffective due to inappropriate scale and placement. Further, an MPA designed to protect NZ sea lions (*Phocarctos hookeri)* from fisheries bycatch has been shown to be largely ineffective because sea lions regularly forage beyond the boundaries of protection (Chilvers 2008). Robust information on the spatial ecology of marine mammals can be difficult to gather at a scale appropriate for MPA planning. For management be effective, however, it is crucial that managers prioritise the gathering of such data.

1.3 - Fine-scale distribution and hotspots for marine mammals

Studies of marine mammal distribution generally show that particular areas within a populations' range are used more than others (Ingram and Rogan 2002; Scott et al. 2010; Harwood et al. 2014). The term 'hotspot' is often used for locations with disproportionately high habitat-use (Hastie et al. 2004; Bouchet et al. 2015). Hotspots exist for various reasons: they may contain more abundant or more 'catchable' prey (Hastie et al. 2006; Torres et al. 2008; Eierman and Connor 2014), provide shelter from extreme weather (Elwen and Best 2004; Rayment et al. 2015) or represent important breeding habitat (Garaffo et al. 2007; Forney et al. 2012; Keller et al. 2012; de Castro et al. 2014). Whatever the reasons, it is important to understand how marine mammals use their habitat in order to protect against anthropogenic disturbance and subsequent habitat-related effects upon populations. These effects can include displacement from important areas (Bejder et al. 2006; Tezanos-Pinto et al. 2013; Karczmarski et al. 2016), changes to diet (Trites and Donnelly 2003;

Burek et al. 2008), or decreases in reproductive success (Wells et al. 2005; Baker et al. 2007). Clearly, this information is directly relevant to management of endangered species.

Understanding how marine mammals use their habitat also provides important information on ecological processes, such as the spatiotemporal distribution of productivity, marine food-web dynamics and community structuring (Estes 1998; Myers et al. 2007; Scott et al. 2010). For example, as delphinid distribution is usually correlated with that of their lower trophic level prey, the distribution of these top-predators is often related to locations of high primary productivity (Croll et al. 2005; Torres et al. 2008; Scott et al. 2010). Further, areas of high productivity favoured by marine mammals may also represent locations of high biodiversity and ecological complexity (Bowen 1997; Hooker et al. 1999; Palacios et al. 2006; Eierman and Connor 2014). For these reasons, it has been suggested that many top-predators may be 'indicator species' in that their distributions reflect ecological patterns of biodiversity, productivity and food-web complexity (Zacharias and Roff 2001; Hooker and Gerber 2004).

Despite claims that marine mammals may be 'indicator species', few studies link marine mammal distribution to the ecological values that their distribution is thought to reflect. In particular, whether hotspots for marine mammals are also hotspots for other predators and lower trophic levels remains poorly understood, certainly at fine scales. If marine mammal hotspots can be used as proxies for hotspots of a range of species, this may provide evidence that marine mammal distribution can provide information on biodiversity and potentially productivity (Hoyt 2002; Hooker and Gerber 2004). For this reason, studies on marine mammal habitat use often collect data on other predators and most importantly, their prey (Scott et al. 2010; Benoit-Bird et al. 2013).

1.3.2 - Temporal variability in spatial distribution

The way marine mammals use their habitat varies seasonally according to the availability of resources, shelter or the demands or reproduction (Pendleton et al. 2012; O'Toole et al. 2015; Rayment et al. 2015). Thus, it is common to investigate marine mammal habitat use patterns across seasons (Reilly 1990; Wilson et al. 1997; Martin and Silva 2004; Fury and Harrison 2011).

Habitat use may also change over long temporal scales (Scott et al. 1990; Rowntree et al. 2001; Cheney et al. 2014), due to variability in habitat quality (Simmonds and Eliott 2009; Karczmarski et al. 2016), changes in population dynamics (Moore et al. 2003; Cheney et al. 2014) or anthropogenic disturbance (Bejder et al. 2006).

If spatial management of threats fails to account for variability due to seasonal shifts in distribution it is likely that animals will occupy unprotected areas for significant parts of the year (Hooker et al. 1999; Rayment et al. 2010a). Likewise, if the distribution patterns of populations change over time, the boundaries of area-based management may become inappropriate (Hartel et al. 2015). Because marine mammals are likely to be extirpated where anthropogenic impacts are high (Bejder et al. 2006; Tezanos-Pinto et al. 2013), investigating how distribution patterns change on long-term scales may provide valuable insights into threats facing species and their habitat.

1.4 - Distribution of foraging behaviour

High quality foraging habitat and unimpeded access to foraging opportunities are intrinsically connected to the viability of top-predator populations. Foraging success is related to condition, and therefore reproductive success, in a range of species (Atkinsen and Ramsay 1995; Mann et al. 1998; Baker et al. 2007). For example, annual pup mortality in South American sea lion (*Otaria flavescens*) populations can reach 100% during periods when foraging success is low (Soto et al. 2004). Foraging is also a behaviour regularly disturbed by tourism/vessel traffic (Lusseau 2003; New et al. 2013; Pirotta et al. 2015) and habitat modification (Markowitz et al. 2004; Karczmarski et al. 2016). Consequently, the identification and protection of important foraging habitat should take high priority in the management of threatened species.

Distribution patterns of many marine predators are often related to hotspots in foraging behaviour (Hastie et al. 2004; Ashe et al. 2010). For example, Hastie et al. (2004) demonstrated that hotspot areas for bottlenose dolphins in Moray Firth are locations where dolphins have high rates of foraging. Chilean dolphins also exhibit more foraging behaviour at hotspots compared with low density locations in Yaldad Bay, Chile (Ribeiro et al. 2007). Thus, an understanding of hotspots in distribution provides an opportunity to further assess how these areas may represent important foraging habitat.

The onset of foraging behaviour in delphinids is often governed by the same temporal processes that influence overall habitat selection; foremost among these is the temporal availability of prey (Benoit-Bird and Au 2003; Kuhn et al. 2015). Foraging activity has been associated with temporal trends over tidal cycles (Johnston et al. 2005; Bailey and Thompson 2010; Doniol-Valcroze et al. 2012) and diel cycles (Benoit-Bird et al. 2004; Schaffeld et al. 2016). The frequency of foraging is also known to vary on weekly, monthly or seasonal scales (Hastie et al. 2004; Scott et al. 2010; Pendleton et al. 2012; Pirotta et al. 2013). Understanding the temporal patterns of foraging behaviour provides insights into ecological factors influencing prey distribution, and thus coastal productivity generally (Gende and Sigler 2006; Scott et al. 2010; Cotté et al. 2015). Further, knowledge of temporal variation in foraging may allow management of threats to this important behaviour (Ashe et al. 2010; Bailey and Thompson 2010).

Several studies have assessed both the spatial and temporal distribution of foraging behaviour in odontocetes (Benoit-Bird and Au 2003; Pirotta et al. 2013; Schaffeld et al. 2016). Few, however, have conducted this analysis in the context of MPA design. In planning for a marine protected area, Ashe et al. (2010) demonstrated that killer whales (*Orcinus orca*) are 2.7 times more likely to engage in foraging behaviour at a distribution hotspot. Subsequently, an MPA was proposed to encompass the area defined as a ‘foraging hotspot’ to protect against the impacts of vessel traffic and tourism (Ashe et al. 2010). Clearly in order for such MPAs to be effective, the design must consider a broad range of factors that influence when, where and why top-predators aggregate and forage and consider the possibility that these areas may change over time.

1.5 - Overlap between predators and prey

Top-predators in the ocean typically show high spatiotemporal overlap with their prey (Benoit-Bird and Au 2003; Embling et al. 2012; Saijo et al. 2017) and this is particularly true for small marine mammals (Benoit-Bird et al. 2004; Johnston et al. 2005; Miller 2014; Lawrence et al. 2016). These species must maintain very high rates of foraging to sustain the energetic demands of a small, warm body in a cool, heat-sapping medium (Benoit-bird 2004; Yeates et al. 2007; Wisniewska et al. 2016). Smaller predators may also lack the capacity to store sufficient energy reserves for times when prey are scarce (Lockyer et al. 2003; Wisniewska et al. 2016). Thus, quality foraging habitat may be particularly important for species such as Hector's dolphin (*Cephalorhynchus hectori)* and harbour porpoise (*Phocoena phocoena*).

The spatial distribution of top-predators is generally thought to mimic that of their prey (Redfern et al. 2006; Torres et al. 2008). However, there are several aspects of the 'prey-field' (i.e. prey community), other than its abundance, that have a significant effect on the abundance of top-predators. Predators will also forage where and when prey are easier to catch (Benoit-Bird and Au 2003; Embling et al. 2012; Womble et al. 2014), more detectable (Benoit-Bird et al. 2013), or of greater quality (Grémillet et al. 2008b; McCluskey et al. 2016). Thus, parameters associated with prey depth (Benoit-Bird and Au 2003; Embling et al. 2012) and patch size (Benoit-Bird et al. 2013) or the calorific value of prey (McCluskey et al. 2016) have been shown to influence the habitat selection of predators, sometimes more so than prey abundance (Benoit-Bird et al. 2013). Different characteristics of habitat may promote different responses in the prey field. Thus in order to accurately quantify what makes good foraging habitat, it is important to investigate how a range of variables associated with the prey field influence the distribution of top-predators.

As a combination of prey abundance, catchability and foraging energetics influences where a predator chooses to forage, it is important to consider how each of these metrics may affect distribution in different predators. If hotspots of marine mammal distribution are also hotspots for other predators, we would expect these parameters to have similar effects among species. Differences in the effects of prey metrics may underlie niche partitioning among predators

(Friedlander et al. 2009, 2011; Gross et al. 2009), that in turn may result in varied habitat use patterns. Such information is important in assessing whether marine mammal distribution can be indicative of high productivity, food-web complexity and biodiversity.

Knowledge about locations that sustain high overlap between top-predators and their prey can greatly enhance our understanding of ecological processes. Top-down forcing is likely to be particularly dominant where predator-prey overlap is high (McCann et al. 2005; Baum and Worm 2009). Thus, information on such overlap can be used to assess the relative effect of this process on community composition. Also, strong coupling between trophic levels promotes efficient transfer of energy (McCann et al. 2005; Libralato et al. 2010; Griffiths et al. 2017) - an ecological process that is strongly related to ecosystem function and resilience (DeAngelis 1980; Dickman et al. 2008). The vital rates of many populations of predators have been directly connected to the abundance of their prey (Frederiksen et al. 2004; Oro et al. 2004; Baker et al. 2007). Thus knowledge of the locations and times when predator-prey overlap is high can help identify and protect the features that promote such critical interactions and is therefore valuable for endangered species management.

1.6 - Habitat selection studies for marine mammals

The concept of 'habitat use' describes the way in which animals utilise their environment in order to complete their particular life history (Redfern et al. 2008). Habitat can be considered as the range of biological and physical attributes of the environment, and also includes ecological features associated with inter species interactions (predation, competition etc.). Typically, habitat selection studies include observations or measurements of biophysical properties of the habitat that are assumed to relate to an important aspect of a species life history (Balance 1992; Redfern et al. 2008' Heithaus & Dill 2006). Such environmental correlates of distribution are used to define 'critical habitat'. Particularly, in studies of large marine vertebrates, it is not always simple to relate critical habitats to life history processes due to the animals' extensive range and in some cases, limited knowledge on life history. Thus, definition of critical habitat usually relies on understanding the biophysical habitat types that correlate well with distribution and assuming that they are important for the completion of a species life cycle.

The factors that describe how marine mammals aggregate within their range typically involve features of the habitat itself. Environmental parameters such as habitat 'type' (Torres et al. 2008; Goetz et al. 2012; Eierman and Connor 2014) and prey availability (Johnston et al. 2005; Benoit-Bird et al. 2013; Santora 2013), as well as information about spatial distribution of predators (Heithaus and Dill 2006; Wirsing et al. 2008), are often used to investigate the key drivers of habitat selection. Knowledge on how particular 'types' of habitat are favoured allows for understanding of potential habitat related impacts on species. For example, dugongs (*Dugong dugon*) are dependent on seagrass meadows for foraging (Marsh et al. 1999, 2005). Large scale reductions in the quantity and quality of seagrass meadows due to anthropogenic impacts are primarily responsible for the perilous state of many dugong populations (Marsh et al. 2005; Hughes et al. 2009).

Investigations into habitat preferences for marine mammals have advanced rapidly within the last decade (Redfern et al. 2006; Gregr et al. 2013; Palacios et al. 2013). Historically, studies assessed environmental proxies (e.g. sea surface temperature, salinity, turbidity, depth) that were assumed to relate to prey and therefore, marine mammal distribution (Ballance 1992; Smultea 1994; Baumgartner et al. 2003b; Bräger et al. 2003). With advances in technology and statistical modelling techniques, recent habitat studies assess parameters associated with broad habitat 'types' including; seafloor characterisation (Torres et al. 2008; Goetz et al. 2012; Brookes et al. 2013), habitat heterogeneity (Sargeant et al. 2007; Torres et al. 2008; Eierman and Connor 2014), topographic features (Doniol-Valcroze et al. 2012; Bouchet et al. 2015), oceanographic fronts (Bost et al. 2009; Bailey and Thompson 2010; Pirotta et al. 2013), tidal forcing (Skov and Thomsen 2008; Fury and Harrison 2011; Lin et al. 2013), and primary productivity (Scott et al. 2010; Cotté et al. 2015). Importantly, studies are now incorporating parameters directly associated with prey availability (Torres et al. 2008; Goetz et al. 2012; Benoit-Bird et al. 2013; Santora 2013), a crucial step in defining the importance of particular habitat for top-predators (Redfern et al. 2006).

Torres et al (2008) found that environmental parameters such as seafloor type and primary productivity best described fine-scale habitat use of bottlenose dolphins in the Florida everglades. In their study of bottlenose dolphins at Turneffe Atoll, Eierman & Connor (2014) demonstrated that fine-scale use was predicted by density of prey and the abundance of habitat such as seagrass and sand flats. Johnston et al. (2005) found that prey distribution was related to fine-scale habitat use patterns of harbour porpoise in the Bay of Fundy. Prey aggregated in areas that were dominated by oceanographic features such as tidal fronts and eddies. More refined models that assess parameters associated with habitat type allow better definition of the spatial boundaries of important habitat (Doniol-Valcroze et al. 2012; Gregr et al. 2013). This has clear benefits for both management of species and for understanding the ecological implications of top-predator distribution.

1.7 - New Zealand dolphin

1.7.1 - Biology & distribution

New Zealand (NZ) dolphin, also known as Hector’s dolphin, is NZ’s only endemic cetacean, and part of a widely dispersed genus of southern hemisphere delphinids; *Cephalorhynchus* (Pichler et al. 2001). The four species in this genus inhabit temperate coastal waters in New Zealand, along the western and eastern coasts of southern South America, and the west coast of southern Africa (Dawson 2009). Based on morphometric and genetic (Baker et al. 2002; Hamner et al. 2012) differences, NZ dolphins are separated into two subspecies. Hector’s dolphin (*Cephalorhynchus hectori hectori)* exhibits a patchy distribution along the east, south and west coasts of New Zealand’s South Island, whilst Māui dolphin (*Cephalorhynchus hectori māui)* inhabits a small stretch of coastline on the west coast of the North Island between the Kaipara Harbour and the southern Taranaki Bight (Dawson and Slooten 1988; Oremus et al. 2013; Derville et al. 2016; Fig. 1.1). Both sub-species are distributed in shallow, coastal waters including bays, harbours and estuaries. They are very rarely found in waters more than 100m deep (Rayment et al. 2010a, 2011a). Published estimates of abundance for NZ dolphins are approximately 7873 (CV = 0.16) individuals for Hector’s dolphins (Slooten et al. 2002; Slooten and Davies 2012; more recent unpublished surveys are covered later) and 55 (CV=0.15) for Māui dolphin (Hamner et al. 2014). Both these estimates represent a substantial decline to 27% of the 1970 population size (Slooten 2007), which contributes to the endangered and critically endangered status of Hector's and Māui dolphins respectively (Reeves et al. 2013a,b).

NZ dolphins are among the smallest dolphins in the world, reaching a maximum adult length of 1.52m (Dawson 2009). The species has low fecundity, with females reaching sexual maturity after seven years and thereafter giving birth approximately once every three years over a maximum lifespan of approximately 25 years (Slooten 1991; Slooten and Lad 1991). Calves are generally born during the warmer months of the austral summer after an approximately year-long gestation period (Slooten 1991; Dawson 2009). Such low fecundity leads to low population growth rates (1.8-4.9% per year; Slooten 1991), which makes the species particularly vulnerable to anthropogenic impacts (Slooten et al. 2000a; Slooten 2013).

Home ranges of individual Hector's dolphins are among the smallest for any cetacean species (Bräger et al. 2002; Rayment et al. 2009a). This extreme site fidelity, coupled with local impacts, has likely caused the genetic isolation of the major populations (Pichler 2002). Dolphins from within local populations show high relatedness (Hamner et al. 2012). Yet between the four major populations of NZ dolphins (east, south and west coast South Island and Māui dolphin) there is little or no population connectivity in terms of mitochondrial DNA exchange (Pichler 2002). The fragmentation of Hector's dolphin units at population and sub-population scales is likely a product of historical exploitation, and increases the risks posed by further population declines (Hamner et al. 2012).

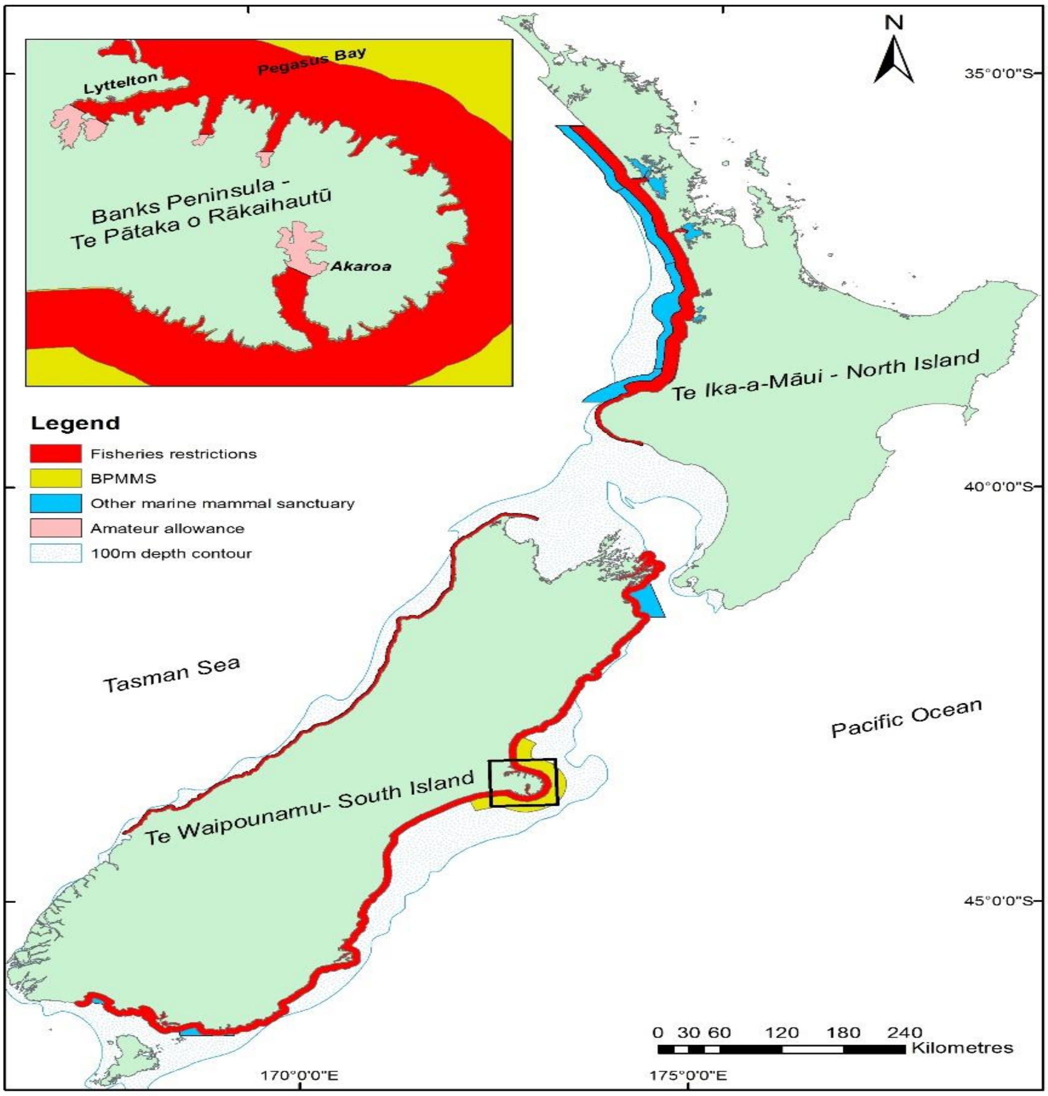

Figure 1.1: The distribution of various types of area based management for NZ dolphins including restrictions to commercial set-net and trawl fisheries and sanctuaries that restrict other threats such as seismic surveying. The 100m depth is considered the offshore extent of the dolphins' range.

1.7.2 - Threats

Bycatch in commercial and amateur set-net fisheries, and to a lesser extent in trawl fisheries, has been the key component in the rapid population decline of NZ dolphins (Dawson 1991a; Slooten et al. 2000a). Between 1984 and 1988 at least 230 Hector's dolphins were bycaught in set-nets in Pegasus Bay and the Canterbury Bight (Fig. 1.1; Dawson 1991a). Population modelling by Davies et al. (2008) estimated annual bycatch in this area peaked at over 100 dolphins per year in the 1980s and declined sharply in the 1990s to between 20 and 40. Observers monitoring the set-net fishery of this region during the summer of 1997/98 recorded 8 dolphins caught in 214 set-net events (Starr and Langley 2000), resulting in an estimated total catch of 17 (Starr 2000; Dawson and Slooten 2005). Using a potential biological removal (PBR) approach, Slooten and Dawson (2010) found the human induced mortality limit for NZ dolphins to be less than one individual per year for most populations. Not surprisingly, a variety of population modelling approaches all indicate that Hector's dolphin populations will decline substantially under historical levels of bycatch (Slooten and Lad 1991; Slooten et al. 2000a; Slooten and Davies 2012).

Vessel strike by recreational craft can cause mortality of Hector's dolphins (Stone and Yoshinaga 2000). Whilst the full extent of this threat is unknown, the fact that Hector's dolphins are often found in high numbers in busy harbours suggests vessel strike events may be reasonably common. Commercial tourism has been shown to impact on the short-term behavioural budget of dolphins at Banks Peninsula (Nichols et al. 2001; Martinez et al. 2010, 2012). The potential for tourism to cause long-term displacement of individuals and other population level effects has not been investigated. Habitat related impacts associated with port development (Brough et al. 2014; Leunissen and Dawson 2018) and aquaculture (DuFresne et al. 2000; Slooten et al. 2000b) have been discussed in terms of displacement of individuals and degradation of habitat quality. Whether such impacts occur and on what scale are currently unknown.

1.7.3 - Management

Banks Peninsula, on the east coast of the South Island (Fig. 1.1), is a stronghold for Hector's dolphins, which have been studied in a long-term research programme since 1984 (Dawson and Slooten 1993a). The vulnerability of the population at Banks Peninsula was recognised with the implementation of the Banks Peninsula Marine Mammal Sanctuary (BPMMS) in 1988 (Dawson and Slooten 1993a). Fisheries-related impacts are now managed by a suite of fisheries restrictions implemented in 2008 (administered by Fisheries NZ) that prevent commercial and amateur set-net fisheries from operating within 4 nautical miles of the Banks Peninsula coastline (Slooten and Dawson 2010). This extended and superseded the protection offered by the BPMMS, which now offers only minor additional protection from impacts such as seismic surveying (DOC 2008). The fisheries restrictions include some allowance for amateur set-netting for flatfish during a reduced ‘season’(Apr-Oct). Trawling within 2 n.mi of shore is restricted to gear used to target flatfish (as defined by low headline height). Hector’s dolphins are regularly seen in associated with vessels engaged in trawling (Rayment and Webster 2009).

The effectiveness of threat management for NZ dolphins may be constrained by a number of factors. Firstly, the fisheries restrictions only partially cover the distribution of the dolphins. Aerial surveys have identified that Hector’s dolphin range at least as far as 19 nautical miles from the coast (Rayment et al. 2010a). Thus management does not prevent bycatch from occurring in a large part of the dolphins’ offshore range. Secondly, the amateur set-net allowance has resulted in several documented cases of dolphin being caught in nets (DOC 2008). Dawson et al. (2013) showed surprisingly high dolphin presence in inner Akaroa Harbour (Fig. 1.1) where and when amateur netting was permissible. Lastly, management provides little or no protection from other potential human impacts upon the dolphins. Impacts associated with trawl fisheries (Rayment and Webster 2009), tourism (Martinez et al. 2012), boat traffic (Stone and Yoshinaga 2000), pollution (Stockin et al. 2010), disease (Roe et al. 2013), coastal development (Brough et al. 2014; Leunissen and Dawson 2018), and general habitat degradation may require further management to safeguard the recovery of populations.

The BPMMS and 2008 fisheries restrictions have proven effective at increasing survival rates of Hector’s dolphins (Gormley et al. 2012). Mean annual survival increased from a pre-sanctuary value of 0.863 (95%CI 0.647-0.971) to 0.917 (95%CI 0.802-0.984). Slooten (2013) found that the improvement in survival rates may not be sufficient to reverse population declines and suggested that protection be extended to the full range (i.e. out to the 100m depth contour) of the dolphins.

As the management framework at Banks Peninsula has proven successful at limiting bycatch, similar management has been extended to cover the known alongshore distribution of Hector’s dolphins and a proportion of Māui dolphin distribution (Slooten 2013). Given that this area-based management model is now the preferred tool for the protection of NZ dolphins, and species elsewhere (Hoyt 2011), understanding the effectiveness of the BPMMS is critically important for the management of NZ dolphins and marine mammals generally.

1.7.4 - Current status

Population monitoring for NZ dolphins is currently undertaken on the West Coast of the North Island and at Banks Peninsula. Abundance estimates for Māui dolphins are produced every second year. Research has suggested a continuation in the decline of Māui dolphins from 110 (95%CI = 48 – 225) individuals at 2004 (Slooten et al. 2006) to 55 (95%CI = 48 – 69) at 2011 (Hamner et al. 2014).

The Hector's dolphin population at Banks Peninsula has received considerable research effort where photo-identification of individuals and line-transect methods have produced estimates for survival rates (Slooten et al. 1992; Cameron et al. 1999; Gormley et al. 2012) and population abundance (Dawson and Slooten 1988; Dawson et al. 2004; Gormley et al. 2005). The abundance calculation by Gormley et al. (2005) produced a value of 1110 (CV= 0.21) at 1996. This is similar to an estimate produced by Dawson et al. (2004) of 900 (for the zone 0-4 n.mi offshore; CV= 0.28) using line-transect surveys of the Banks Peninsula coast during 1997/1998.

In 2012/13 the NZ government commissioned aerial surveys to assess the abundance of Hector's dolphins along the entire east coast of the South Island (MacKenzie and Clement 2014). The study produced abundance estimates of 9130 (CV=0.19) for summer and 7456 (CV=0.18) for winter (MacKenzie and Clement 2014). Summer abundance estimates for inshore (0-4 n.m) strata at Banks Peninsula were 883 (SE=219) for the north side of the peninsula and 1684 (SE=476) for the south. Similar values were produced for offshore (4-12 n.m) strata (MacKenzie and Clement 2014). These values would represent a significant increase in abundance from previous estimates (Dawson et al. 2004), and have introduced considerable uncertainty as to the true abundance of the species in this area (Slooten 2015). Issues associated with the survey design and data analysis of Mackenzie & Clement (2014) have called these estimates into question (Slooten 2015).

1.8 - Fine-scale distribution & knowledge gaps

There have been comparatively few studies assessing fine-scale distribution of *Cephalorhynchus* species. Elwen et al. (2010) investigated the nearshore distribution of Heaviside’s dolphin along 390km of the South African coastline and found a typically clumped distribution. Chilean dolphins in Yaldad Bay spent the majority of time in 21% of the available habitat and were most frequently found in shallow water, close to the coast and river outlets (Ribeiro et al. 2007). Commerson’s dolphins also show preferences for fine-scale ‘hotspots’ (Iñíguez and Tossenberger 2007), and as with other delphinid genera, it seems this pattern of patchy distribution is a consistent feature of *Cephalorhynchus* populations.

Studies of distribution patterns for Hector’s dolphins also demonstrate the existence of hotspots. In an analysis on the home range size and distribution patterns of individually marked dolphins at Banks Peninsula, Rayment et al. (2009) found that some dolphins exhibited consistent overlap in their nearshore core area distribution. These areas were very similar to the locations identified by Clement (2005) who found that dolphin distribution was concentrated into four major hotspots in the nearshore (1km> from coast) zone. Fine-scale (ca. 5km) hotspots also existed in the dolphins’ alongshore distribution on the West Coast of the South Island (Rayment et al. 2011a) and within a portion of Māui dolphin range between the Manukau Harbour and Port Waikato (Derville et al. 2016).

Previous research into nearshore distribution patterns at Banks Peninsula used data from the early (1989-1996) period in the Banks Peninsula monitoring programme (Clement 2005). Now, a far greater volume of data is available to model the distribution patterns of this population. Since the initial investigation, significant change has occurred in coastal habitat due to the expansion of tourism, aquaculture and port industries.

The density of Hector’s dolphins using nearshore habitat decreases during winter (Rayment et al. 2010a; Dawson et al. 2013), yet there is no information concerning seasonal patterns of habitat selection within the nearshore environment at the BPMMS. This information would increase our understanding of the importance of ‘hotspot’ locations, the behaviours they are used for, and the seasonal nature of ecological factors that may persist in these areas.

Very few studies have demonstrated how dolphin habitat use changes on multi-decadal scales (see Cheney et al. 2014, for an exception). Because of the potential for these taxa to be ‘indicator species’, knowledge on whether and how fine-scale distribution may have changed could underlie important ecological changes as well as be necessary for the management of the species.

1.9 - Foraging distribution & knowledge gaps

There have been few studies of the fine-scale distribution of foraging for coastal top-predators in NZ. This information could allow insights into the spatial and temporal distribution of nearshore productivity and hence ecological processes in the coastal environment. Further, as there has been no investigation of foraging distribution for Hector’s dolphins, potentially valuable information is lacking that could be used to better manage threats to this species.

1.10 - Drivers of habitat selection & knowledge gaps

There has been limited published research on the forces driving habitat selection in Hector’s dolphins. Bräger et al. (2003) showed that Hector’s dolphins show a strong preference for shallow water (<39m depth), warm surface temperatures and low water clarity. There is also an indication that tidal cycles correlate with dolphin distribution (Dawson et al. 2013).

Some unpublished research shows that the dolphins show a preference for locations where sea surface temperature (SST) fronts are seasonally common (Clement 2005). Additionally, Miller (2014) found that dolphin distribution is influenced by environmental factors including SST, salinity, and chlorophyll *a* concentrations in both surface and bottom water. She also found that Hector’s dolphins are more frequently encountered in areas where an important prey item, red cod (*Pseudobachus bachus*), is more abundant (Miller 2014).

No studies have directly investigated the role of epipelagic fish in influencing the distribution of Hector’s dolphins. These important prey taxa are common at Banks Peninsula where they make a significant contribution to the diet of several top predators (Allum and Maddigan 2012; Flemming et al. 2013; Miller et al. 2013). Further, predators such as little penguins (*Eudyptes minor*), are regularly sighted foraging at sea, providing an opportunity to assess predator-prey overlap in several predators. This may provide useful information on whether Hector's dolphin distribution is related to that of other, coastal predators.

While there is some information on environmental correlates of Hector's dolphin distribution and those of their prey, no studies have addressed whether particular habitat types sustain these relationships. The nearshore environment of Banks Peninsula offers a wide variety of habitat type featuring highly patchy bottom substrate (Beentjes and Carbines 2005; Brough et al. 2018a), oceanography (Clement 2005; Reynolds-Fleming and Fleming 2005), and dynamic patterns of productivity (Miller 2014). Coupled with high but variable dolphin densities, this offers a unique opportunity to investigate if, and if so, what, habitat types are important in describing the patchy distribution of this species.

By including a wide range of biophysical habitat variables, this thesis aims to better understand links between habitat use and life history processes. Some delphinid species show consistent selection of areas that are used for calving/nursing young (Weir et al.2008; Stockin et al. 2009) and this is certainly well known in baleen whales (de Castro et al. 2014; Rayment et al. 2015). Clearly, access to food resources is important for life history processes and so including information on prey abundance is an important step at relating habitat-use to a the dolphins' life-cycle. Little is known concerning whether particular habitats sustain certain life history processes in Hector's dolphins but Webster et al. (2009) found some evidence that shallow bays were used more frequently by mothers with young calves. The ecologically similar harbour porpoise (*Phocoena phocoena*) spends the majority of its time feeding to maintain a very high metabolism (Wisniewska et al. 2016). In such cases it may be that food resources are the major component of habitat use, with other life history processes (e.g. calving/nursing) being not particularly bound to certain habitat features.

In a wide-ranging literature search, I found no published studies assessing how a broad range of variables including physical habitat type, tidal processes, prey and oceanographic characteristics are related to the distributions of a coastal top-predator. Determining the most important parameters from a broad range of habitat variables will provide valuable information for distribution studies of marine top-predators.

Knowledge on the dynamics of Hector's dolphin distribution provides an opportunity to assess 'what makes hotspots unique', and so shed light on the factors that seem most important in determining habitat selection.

1.11 - Hotspot approach to habitat selection

This thesis aims to fill the gaps identified above by directly investigating the spatial ecology of hotspots in the distribution of Hector's dolphins. By employing a range of sampling methodologies in a multi-disciplinary approach, this thesis attempts to reveal the where, when, why and what of hotspots. A multi-decadal database on visual sightings of Hector's dolphins is used to understand where and when hotspots exist, and to investigate their longevity. Passive acoustic monitoring across hotspots and 'reference areas' is undertaken to investigate why the dolphins aggregate in these areas; are they hotspots for foraging? A simple, repeatable hydro-acoustic method is developed to sample aspects of the epipelagic prey field and relate these to the hotspots. Lastly, a broad range of biophysical habitat characteristics are sampled to assess the habitat types represented at hotspots; what makes these places unique? By building on the substantial body of research on Hector's dolphins at Banks Peninsula, and similar species elsewhere, a novel synthesis of information is undertaken to provide new information on the species' ecology. Such information can be used for the management of Hector's dolphins throughout their range and will provide new insights into the ecology of coastal New Zealand.

1.12 - Thesis goals

This thesis adds to a growing body of knowledge that can be used to support the management of NZ dolphins. It is hoped that the thesis will pave the way beyond a single-species approach, and provide information on the spatial ecology of the species that is relevant for true ecosystem-based management. Research questions specific to each chapter are:

Chapter 2 What are the locations, seasonality and long-term persistence of hotspots for Hector's dolphins at Banks peninsula? .

Chapter 3 What are the functional mechanisms that drive the existence of hotspots for Hectors' dolphins; are these areas important for foraging? Additionally, how does foraging vary on temporal scales within nearshore habitat?

Chapter 4 Can a recreational grade echo-sounder be use used to quantify the relative abundance of epipelagic prey for top predators in coastal habitat?

Chapter 5 How does prey distribution correlate with the distribution of top-predators at Banks Peninsula? What is the relative importance of prey abundance and patch characteristics in terms of their relationships with predators? Are Hector's dolphin hotspots locations where prey is particularly abundant or catchable?

Chapter 6 What are the biological and physical aspects of habitat that correlate with the distribution of Hectors dolphin? What is the relative importance of prey vs. environmental variables? What habitat features make hotspots unique?

Chapter 7 provides a general discussion of the results of this thesis, placing particular emphasis on management outcomes for the species.

1.13 - Conservation outcomes

The Government's management and research directives for NZ endangered species are incorporated into 'Threat Management Plans' (TMP) produced as a joint initiative between the NZ Ministry of Primary Industries, Department of Conservation and stakeholders. The previous TMP for NZ dolphins was developed in 2007 (DOC and MFish 2007), with a review for the Māui dolphin aspect being undertaken in 2012 (MPI 2013). A review of the Hector's dolphin TMP is currently underway. It is hoped that the results of this thesis will be considered in the development of a new TMP for Hector's dolphins and so aid in the future management of the species.

Processes to establish MPAs in other parts of the South Island are currently underway (e.g. south-eastmarine.org.nz). These processes will benefit from new information on what drives habitat selection in coastal top-predators; both for the protection of the species themselves, the ecological factors that shape their distribution, and the ecological functions they support. Such information is currently lacking, but may be relevant for the planning of MPAs throughout NZ coastal waters.

Chapter 2: The spatial and temporal distribution of nearshore hotspots for Hector's dolphins at Banks Peninsula

Chapter status: Published as an article in Marine Mammal Science: Brough TE, Rayment WR, Slooten E, Dawson S. 2018. Fine-scale distribution for a population of New Zealand's only endemic dolphin (*Cephalorhynchus hectori*) shows long-term stability of coastal hotspots. Marine Mammal Science 35: 140-163.

Authorship statement: TB, WR, ES and SD conceived of initial research idea, TB and WR developed research methods, TB, WR, ES and SD contributed to data acquisition, TB performed analyses and wrote the manuscript, WR, ES and SD provided feedback on manuscript preparation.

2.1 - Introduction

Knowledge of the spatial distribution of populations is crucial for understanding the relationships between species and their environment. Quantifying these relationships allows a greater appreciation of the ecological role of species (Gende and Sigler 2006; Scott et al. 2010; Certain et al. 2011), and underpins the successful management of threats (Hastie et al. 2003; Slooten 2013; de Castro et al. 2014).

Patchiness in distribution at a range of scales is a feature of many marine mammal populations (Johnston et al. 2005; Cheney et al. 2012; Williams et al. 2014). Migratory whale species frequently show strong habitat preferences in feeding and breeding areas (Doniol-Valcroze et al. 2007; Gill et al. 2011). Even delphinid populations with relatively small distributions have areas of disproportionate use (Ingram and Rogan 2002; Pirotta et al. 2013). Areas of high density of animals are often termed 'hotspots' (Hastie et al. 2004; Harwood et al. 2014) and may be important for particular behaviors, such as breeding or resting (Garaffo et al. 2007; Notarbartolo di Sciara et al. 2009; Rayment et al. 2015; Tyne et al. 2015). Hotspots may also be locations with high prey abundance or availability (Torres et al. 2008; Benoit-Bird et al. 2013), and so may represent important foraging areas (Scott et al. 2010; Pirotta et al. 2013).

Many marine mammals show a strong preference for coastal waters (Ballance 1992; Barco et al. 1999; Rayment et al. 2010). Coastal habitat is usually productive, sheltered and may provide refuge from predators (Croll et al. 2005; Heithaus and Dill 2006; Rayment et al. 2015). Of all ocean areas, the coastal zone is often the most impacted by human activities (Suchanek 1994; Crain et al. 2009). Because of the importance of coastal waters for many species, and the potential for substantial anthropogenic influence, it is crucial to understand the spatial distribution of marine mammals in these areas.

Analysis of distribution patterns at fine-scales provides the best resolution for examining local relationships among species, habitat and anthropogenic impacts (Hooker et al. 1999; Harwood et al. 2014). Fine-scale analysis of spatial distribution has been undertaken for a variety of dolphin species (e.g. Ingram and Rogan 2002; Hauser et al. 2007; Moulins et al. 2008). Typically, these studies reveal ‘hotspots’, however, few have assessed how these change over time (see Cheney et al. 2014 for an exception). Clearly, knowledge on how hotspots vary temporally is necessary for understanding the importance of these areas, and to assess ecological changes that may be a product of natural and anthropogenic disturbance to species and their habitat (Simmonds and Eliott 2009).

Hector’s dolphin has suffered dramatic declines throughout its range to an estimated 27% of the 1970 population (Slooten and Dawson 2010). This is largely due to fisheries bycatch (Dawson 1991; Slooten and Dawson 2010), but other threats associated with vessel traffic, pollutants and tourism have been documented (Stone and Yoshinaga 2000; Stockin et al. 2010; Martinez et al. 2012). Dolphin protection areas, restricting the use of set-nets and trawling, have reduced bycatch within the most nearshore component of the dolphins’ range (Slooten 2013), but whether populations are recovering is currently unclear. Hector’s dolphins show a strong preference for nearshore waters during the austral summer (Rayment et al. 2010). This preference may be related to foraging opportunities, as some prey species show a similar inshore distribution during summer (Miller 2014). Additionally, the dolphins may seek sheltered, shallow habitat during the summer calving season.

The aim of this chapter is to investigate the existence and locations of hotspots in the nearshore distribution of a population of Hector’s dolphins at Banks Peninsula. Seasonal and long-term consistency of hotspot locations were examined using a 29-year data set. Because of the importance of the nearshore zone to these dolphins, and the potential threats in this area (e.g. increasing pressure from commercial and recreational dolphin watching; Martinez et al. 2012), knowledge of the existence and stability of hotspots is critical information for the management of this endangered species.

2.1.2 Chapter objectives

- To determine the locations of hotspots in the nearshore distribution of Hector's dolphins at Banks Peninsula.
- Investigate the seasonal and long term trends in the density of dolphins at hotspots.

2.2 - Methods

2.2.1 - Sightings data

I conducted a density analysis of visual sightings from systematic boat-based surveys at Banks Peninsula (Fig. 2.1) over 27 yr from 1988-2016. No surveys were carried out in 1998 and 1999. Surveys of the nearshore habitat (<800 m from the coast) were conducted from small (*ca*. 6 m) outboard-powered vessels following a standardised 'strip-transect' methodology, detailed in Dawson and Slooten (1988) and Slooten et al. (1992). Briefly, the vessel was navigated alongshore at speeds between 10 and 15 knots, going into each of the major bays and harbours. The route was established at the beginning of the study (1988) and has been the same for each transect since. Dolphin groups are reliably sighted out to 400 m distance from the vessel (Dawson and Slooten 1988); the vessel was maintained a 400 m distance from shore, resulting in a transect strip width of 800 m. Within Akaroa and Lyttelton Harbours, a predetermined 'zig-zag' survey route was followed that allows for a more thorough search in these larger areas. Two observers were onboard during each transect and scanned an area bound by the bow of the vessel and 90^{o} to either port or starboard. When dolphin groups were sighted, the vessel left the transect route and maneuvered towards the group. Pressing a hotkey on a palmtop computer (Hewlett Packard 200LX) started an 'encounter' in purpose-built software. An encounter was initiated when a group was within 20 m of the vessel. The palmtop was linked via serial port to a GPS unit providing a position and time for each encounter. The location of a dolphin group was approximated by the location of the survey vessel when a group was first encountered. Other information including, group size, number of calves, sea state, and sighting conditions were recorded. When an encounter was terminated, the transect was resumed at the point where the vessel left the transect route. Transects were carried out when Beaufort sea state < 4 and swell < 1.5 m.

As in Rayment et al. (2009) survey effort was summarised in units of ‘sector surveys’ of 15 separate sectors along the coast. Each sector represents a discrete, approximately 6 km length of coastline around the peninsula, or an enclosed harbour (Fig. 2.1). The sectors were placed to allow a full survey of a given sector during a daily transect (i.e. an entire sector is likely to have the same sighting conditions). A sector was surveyed only once per day in an outward or inward direction (relative to port) depending on the most favorable sighting conditions. Due to the size of the study area and variable weather conditions, not all sectors were surveyed in a daily transect; sectors that were missed were typically the focus of subsequent daily transects. A sector survey is a complete, on effort transect through a given sector searching all available habitat; larger sectors (e.g. harbours) required greater survey effort (e.g. 39 km for AK vs. 6 km for SQ; Fig. 2.1) to cover all available habitat. ‘Off-effort’ sightings and transects (e.g. made in transit) were not included in our analysis.

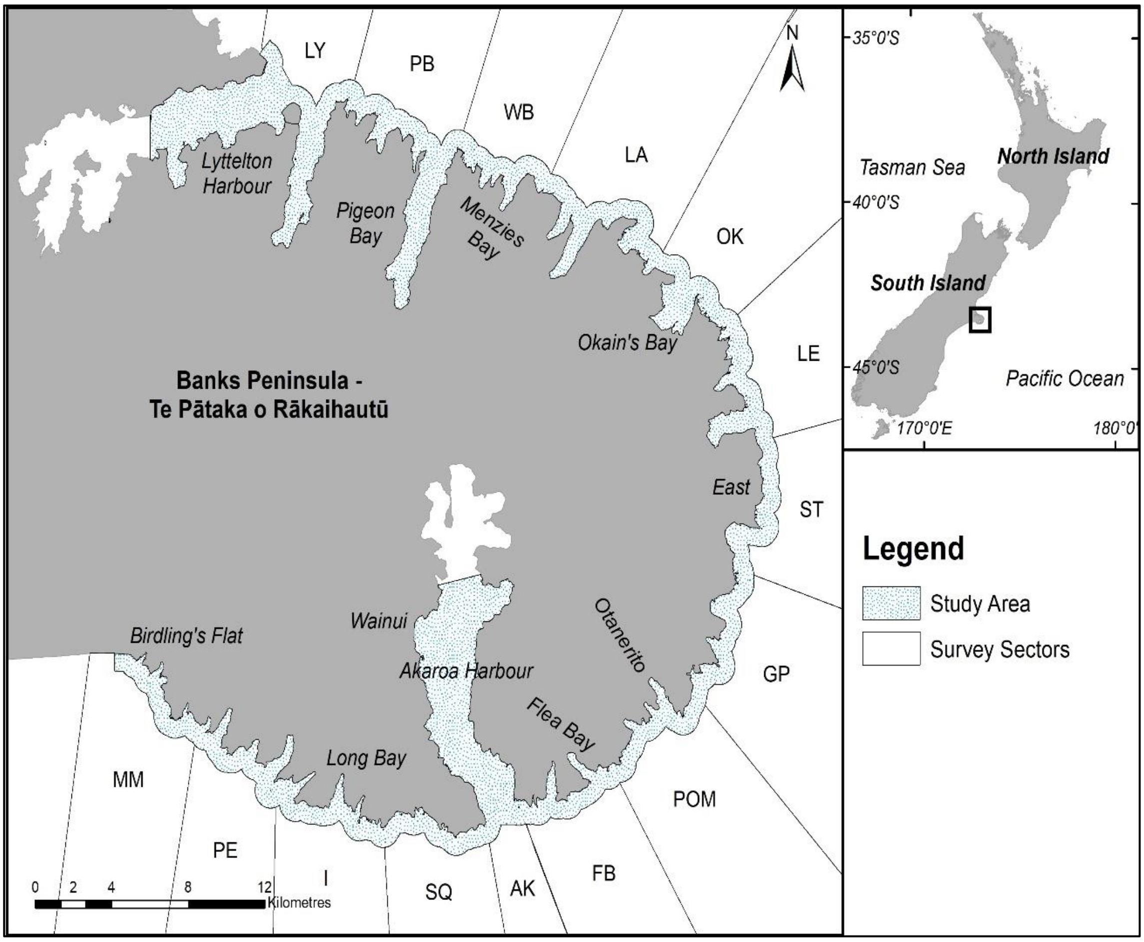

Figure 2.1: The study area for this investigation, Banks Peninsula. Also shown are the survey sectors used to collate sightings and effort data. The location of Banks Peninsula on the east coast of the South Island of New Zealand is shown (inset).

To account for differences in survey effort within the study area and to render density values on a scale of 'per survey', dolphin group sightings were weighted by sightings per unit effort (SPUE; similar to Gill et al. (2011) and Galletti Vernazzani et al. (2012)). The SPUE weight for an individual sighting was calculated using data on surveys of the 15 sectors (Fig. 2.1; Rayment et al. 2009). For each sector, 'relative sector abundance' was calculated as follows,

$$rSA = \frac{n}{V}$$

Where n is the total number of dolphins in all groups observed in a particular sector, and V is the total number of surveys of that sector.

To provide a weight for each sighting, the percentage contribution of a sighting (e.g. group size) to the overall number of dolphins in a sector (n) was calculated. This percentage was then used to apportion rSA among all sightings in a sector. Using the weighted values causes the subsequent density maps to reflect relative rather than absolute density, and has the advantage of making cell density values more comparable throughout the study area and over time.

To investigate how hotspots change among seasons, sightings were combined into four seasonal categories: summer (Dec-Feb), autumn (Mar-May), winter (Jun-Aug), and spring (Sept-Nov). Likewise, to investigate possible changes in hotspots over time, the sightings database was divided into three consecutive time periods; early (1988-1997), mid (2000-2008) and late (2009-2016). A separate calculation of sighting weights was performed for each seasonal and period category using sightings and effort data specific to the respective categories.

2.2.2 - Density and statistical analyses

Fixed kernel density estimation (KDe; Worton 1989) was used to produce maps of dolphin density. The analysis fits a density function to weighted dolphin sightings onto a user defined grid. The toolset Home Range Tools (MacLeod 2013) in ArcMap v 10.3 (ESRI 2014) was used to perform a KDe 'with barriers'. This function allows users to incorporate a barrier to the interpolation of sightings (to ensure that land is excluded).

KDe estimates of home range have been shown to be sensitive to the value chosen for the bandwidth parameter (Fieberg 2007). There are several approaches to choosing an appropriate bandwidth value (Jones et al. 1996; Gitzen et al. 2006). One common method, termed the 'Ad-Hoc approach' (Kie 2013), applies the smallest bandwidth value that produces a single non-broken polygon for the 95% density contour. This approach is well regarded as it allows the spatial variability in the data set to produce a bandwidth value that is 'optimum' for those particular data (Schuler et al. 2014; Signer et al. 2015). Following this approach, an optimum value of 900 m was chosen. This is very similar to the *ca*. 800 m strip-width of the alongshore transects, so has biological relevance for this study.

I defined a grid size of 100 m x 100 m (0.01 km^2) for the KDe analysis. Kernels were constructed in the projected coordinate system New Zealand Geodesic 2000. Separate KDe analyses were undertaken using every on-effort sighting in the database (overall KDe analysis) and using sightings respective to each season and time period. To investigate the existence of 'hotspots', the 50% percentage density contours (PDC) were extracted from the overall kernel analysis. This metric is extensively used to define core areas in wildlife distribution studies and reflects the minimum area in which 50% of the weighted sightings occur (Gill et al. 2011; Leung et al. 2012; Bauer et al. 2015). Contrasting the total area within the 50% PDC with that expected from a uniform distribution (i.e. 50% of the study area) provides an indication as to the existence of 'hotspots'. Data from each KDe analysis were summarized in two ways: 1) The area contained within the 50% PDC was computed for each season to assess how much of the nearshore zone can be considered 'core habitat' among seasons; 2) The density values of each cell within set hotspot and reference areas were extracted to model how these values change over seasons and time.

The density values of KDe cells were obtained for set locations that were consistent for each season and time period. Using the program "Geospatial Modelling Environment" (Beyer 2015), KDe rasters were clipped to match the dimensions of five 'hotspot' and five 'reference area' polygons. Hotspot locations were selected as five separate polygons within the 50% PDC boundary defined by the overall KDe analysis. The hotspots chosen were: Birdling's Flat, Akaroa Harbour, Flea Bay, East and Okain's Bay. These selected hotspots had the five highest dolphin densities among the 50% PDC polygons, were evenly distributed throughout the study area and had a combined area of >80% of the total PDC area (see results). Reference areas were included in this analysis to identify if temporal variation in density is predominant throughout the study area or whether it is confined to hotspots. Further, reference areas help to understand whether changes in density reflect changes in alongshore habitat selection. Polygons denoting reference areas were established outside of the 50% PDC for the overall KDe analysis. Selected reference areas were distributed around the peninsula and had a combined area similar to that of hotspots (24 and 30 km^2 respectively). Reference areas had no fixed size but spanned several of the outer coast bays or large portions of inner harbour areas. Grid cell density values for each hotspot and reference area were exported and summarized as mean, minimum and maximum density for each temporal category at each location. The exact locations of hotspots and reference areas were fixed according to the results of the overall KDe analysis, and the values of these grid cells within each polygon were exported for each temporal category.

Changes in dolphin density at hotspots and reference areas among seasons and over time were investigated with linear mixed effects models using the *lmer* function of package *lme4* (Bates et al. 2015) in *R* (v. 3.2.0, R Core Team 2016). As there were not sufficient data to conduct KDe analysis of seasonal categories within particular time periods, it was not possible to construct a model framework that incorporated both time period and season as factors.

Consequently, two simple families of models were constructed.

$$Dvalue \sim Season\ or\ Period + (RE)Location$$

Where Dvalue is the density value of a particular cell, Season is a categorical factor with four levels and Period is a categorical factor with three levels. Location was specified as a random effect (RE) with 10 levels corresponding to each hotspot or reference area. This random intercept accounts for the autocorrelation among grid cells at the same locations as clearly, cells within each location are not independent datapoints. Using a RE structure to account for a correlated response is common in analyses of ecological data sets (e.g. Bolker et al. 2009; Grueber et al. 2011). Model parameters were estimated via maximum likelihood.

Parameter estimates for each model were extracted and the significance of each effect was inferred by generating 95% confidence intervals (Grueber et al. 2011). The parameter estimates for categorical factors were generated relative to a reference level where $\beta = 0$ (Firth 2003; Grueber et al. 2011). Estimates for the remaining levels therefore indicate the difference in effects compared to the reference level. ‘Summer’ and ‘Early’ were given as reference levels for the seasonal and long-term analysis, respectively.

The effects of season are nested within the effects of period (and vice versa). This could have compromised modelling results had the seasonal distribution of sampling effort been markedly different among the three time periods. To assess whether there was unequal seasonal distribution of sampling effort among periods, the proportion of sector surveys per season was calculated for each period. If these proportions are markedly different among periods, there may be some bias in the results of the temporal analysis.

Inevitably, choice of grid cell size for KDe analysis affects the sample size available for modelling. A small grid cell size means that there are many more samples available per location to model changes in dolphin density across survey sectors. We investigated the sensitivity of model outputs (effect sizes and statistical significance) to changing sample size by randomly subsampling the cell density data at eight different sample regimes (see Appendix 1b).

2.3 - Results

2.3.1 - Sightings and effort

Between 1988 and 2016 there were a total of 3,511 boat surveys across 15 sectors at Banks Peninsula (Fig. 2.2). A total of 9,026 sightings of individual dolphin groups were made across all sectors. Effort was not equally distributed throughout the study area with the Akaroa Harbour (AK) sector receiving noticeably high effort (Fig. 2.2). Not surprisingly, areas that had the highest effort had the greatest number of dolphin group sightings ranging from 3,541 sightings in Akaroa Harbour (AK) to 194 at Lyttelton (LY; Fig. 2.2). Effort was also strongly skewed towards summer months, with the highest proportion of survey effort occurring in summer for each period (Table 2.1). Other than a low proportion of surveys being carried out in winter seasons during the early (1988-1997) period, the seasonal distribution of visual surveys has remained largely consistent over the duration of the study period (Table 2.1*).*

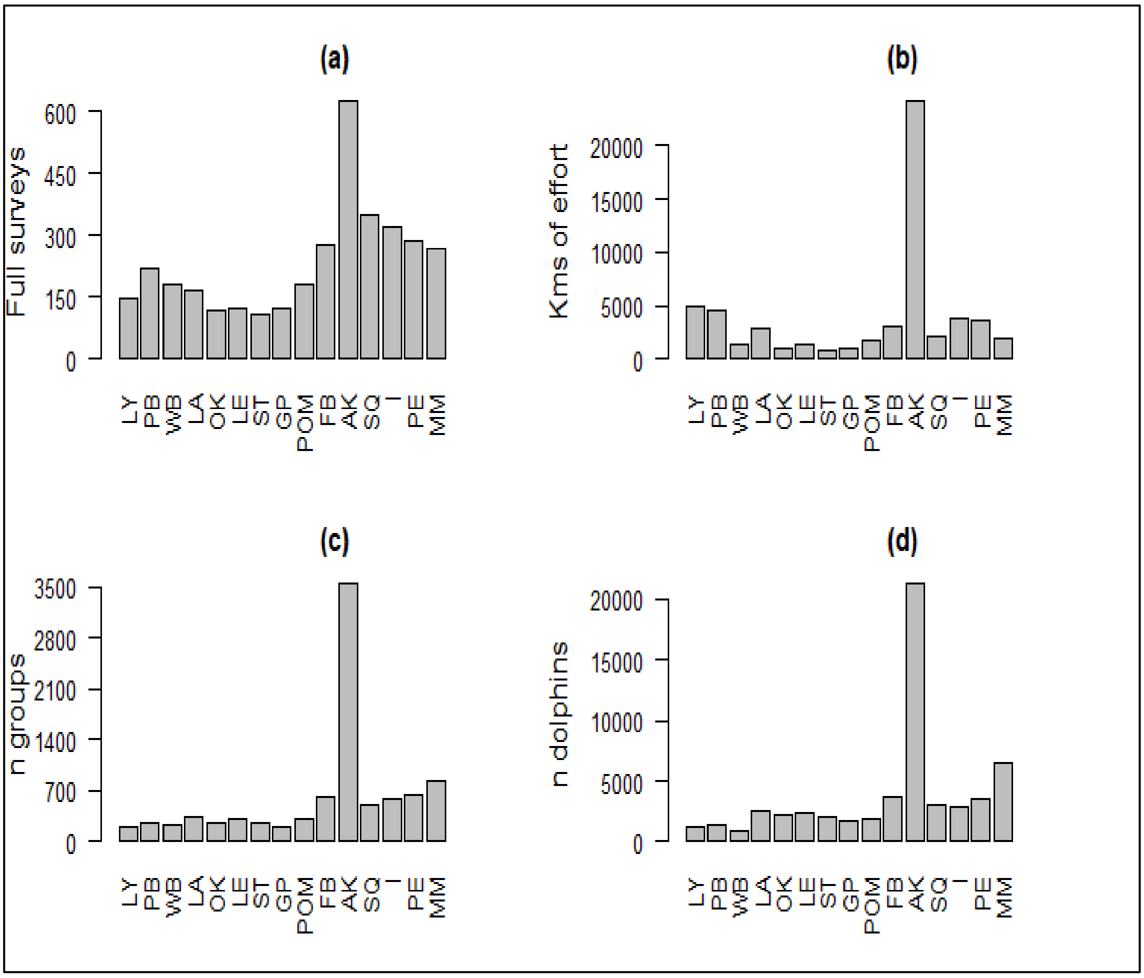

Figure 2.2: Summary of survey effort and sighting information. (a) Number of complete surveys per sector. (b) Survey effort (in km) per sector. (c) Number of dolphin groups encountered per sector. (d) Total number of dolphins encountered per sector. The locations of survey sectors can be seen in figure 2.1.

Table 2.1: Seasonal distribution of survey effort among the three time periods in this study in terms of number of surveys and the percentage of surveys carried out during a certain season at each period.

Season-Period	Sector surveys	Proportion of all surveys in period
Summer 88-97	625	68.2
Autumn 88-97	140	15.3
Winter 88-97	24	2.6
Spring 88-97	128	14.0
Summer 00-08	1014	64.5
Autumn 00-08	163	10.4
Winter 00-08	166	10.6
Spring 00-08	228	14.5
Summer 08-16	653	63.8
Autumn 08-16	148	14.5
Winter 08-16	127	12.4
Spring 08-16	95	9.3

2.3.2 - Density analysis

Hotspots were clearly evident in the overall kernel density analysis (Fig. 2.3, Appendix 1a). Dolphin densities ranged from 0 to 6.8 dolphins per km^2 over the study area. Fifty percent of the weighted sightings occurred within only 21% of the 165 km^2 study area indicating sightings were clustered into particular areas. Major hotspot locations included east of Birdling’s Flat, outer Akaroa Harbour, Flea Bay and around Okain’s Bay (Fig. 2.3). Low density areas were also apparent between Lyttelton Harbour and Menzies Bay, inner Akaroa Harbour and around Long Bay (Fig. 2.3).

The hotspot locations identified by the overall KDe analysis (Fig. 2.3) were consistent with summer distribution patterns (Fig. 2.4). As indicated by inclusion within the 50% PDC area, several hotspots retained high relative density through autumn and spring. These were Birdling’s Flat, Flea Bay, and the far east of the peninsula (Fig. 2.4). Notable declines in the use of the Akaroa Harbour and the Okain’s Bay hotspots were evident outside summer (Fig. 2.4). The distribution of sightings during winter months was not consistent with the hotspot patterns seen during other seasons (Fig. 2.4). The area contained within the 50% PDC was largest during summer at 21% of the entire study area. The 50% PDC area declined to 18%, 19%, and 12% for spring, autumn, and winter, respectively.

While there has been some variation in the shape and size of the 50% PDC polygons, hotspot areas remained consistent over time, changing very little over the early, mid, and late periods of the study (Fig. 2.5). The low density areas also remained consistent over the three time periods.

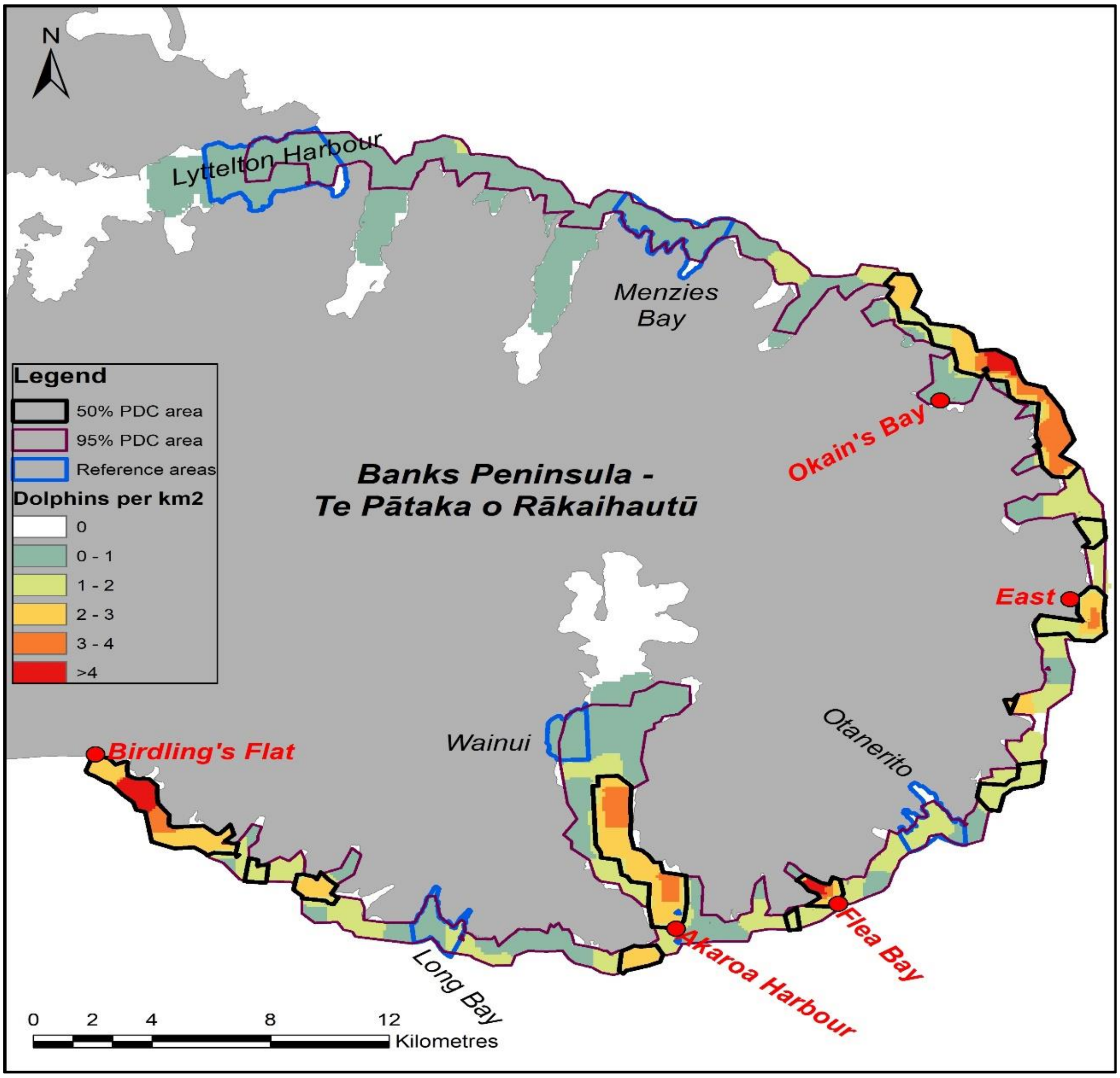

Figure 2.3: KDe analysis of effort weighted dolphin sightings (n=9026) at Banks Peninsula between 1988 and 2016, showing 50% and 95% percentage density contours (PDC). The five hotspot locations are indicated in red adjacent to the respective polygons and the five reference areas are outlined in blue.

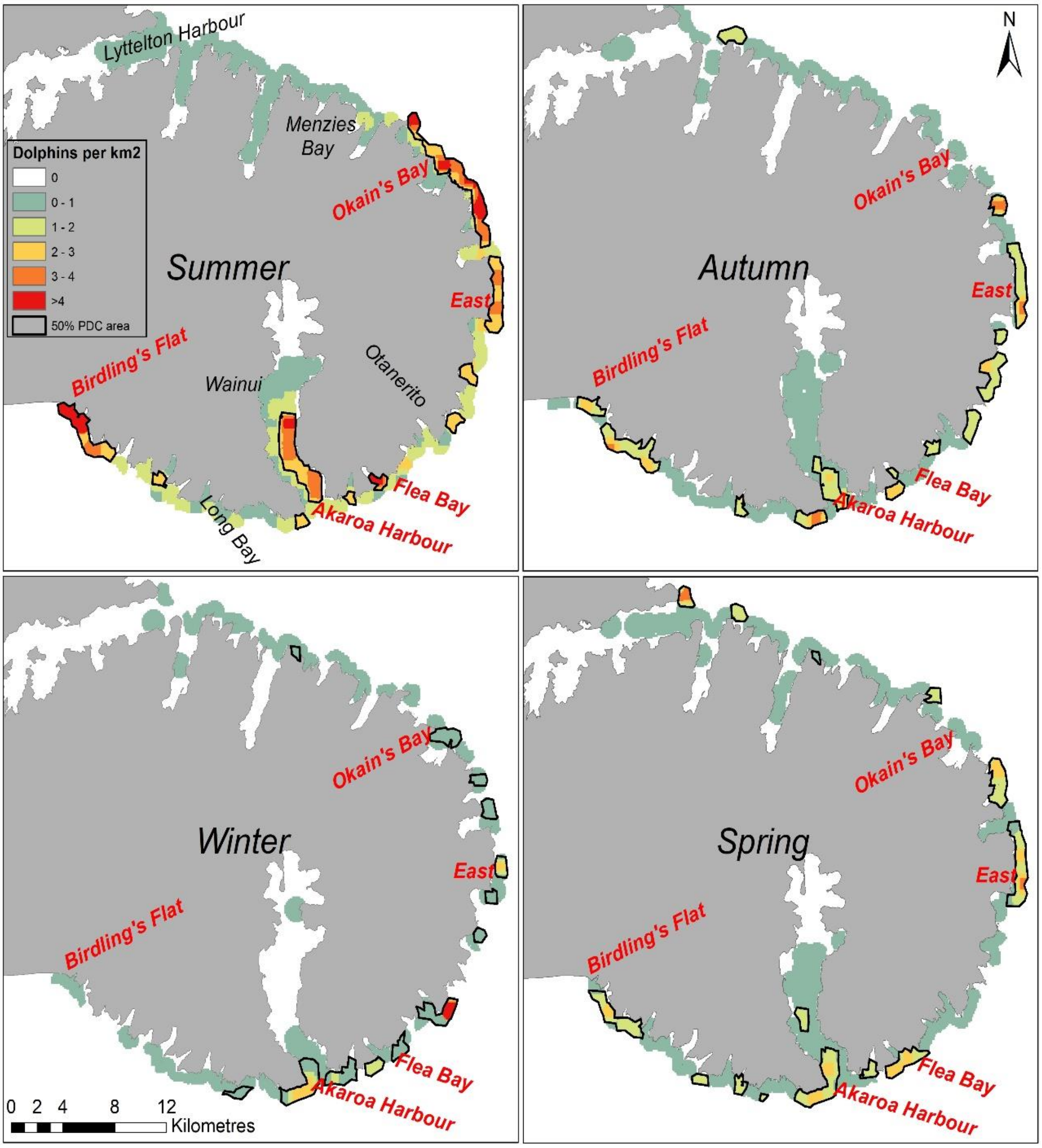

Figure 2.4: Seasonal KDe analysis of Hector's dolphin sightings at Banks Peninsula between 1988 and 2016, showing density for each season and the 50% PDC area. The hotspot locations from the overall analysis (Fig. 2.1) are shown in red.

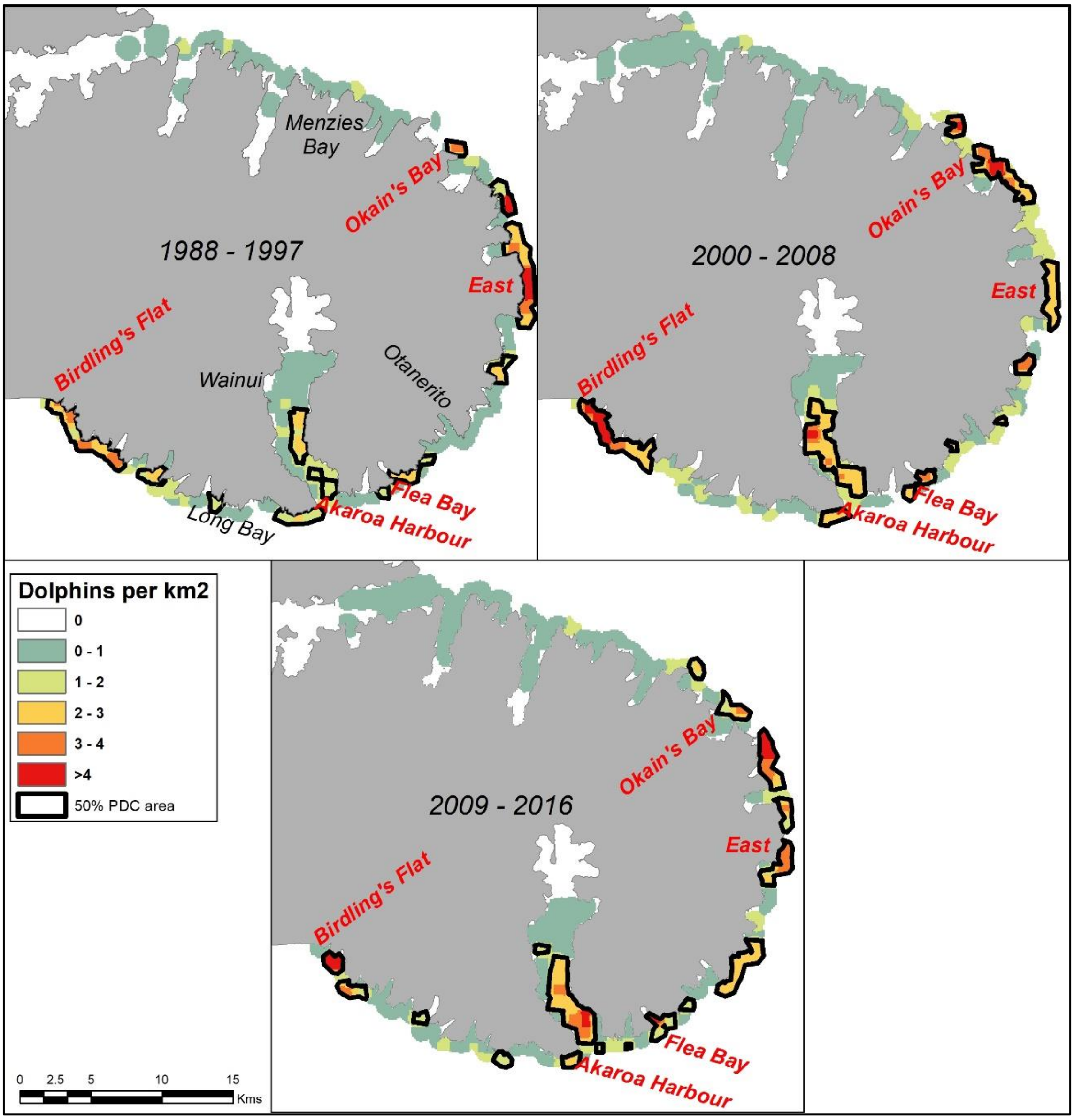

Figure 2.5: Long term KDe analysis of Hector's dolphin sightings at Banks Peninsula between 1988 and 2016, showing density for each period and the 50% PDC area. The hotspot locations from the overall analysis (Fig. 2.1) are given in red.

2.3.3 - Modelling density values

The seasonal KDe investigation shows a clear trend of seasonal variation in dolphin density (Fig. 2.6). Relative dolphin density was highest at all hotspots during summer (Fig. 2.6). In general, the seasonal variation in dolphin density at the reference areas was not as pronounced as hotspots. Differences in relative density between hotspots and reference areas were less apparent in seasons other than summer, with winter densities being similarly low among all locations (Fig. 2.6).

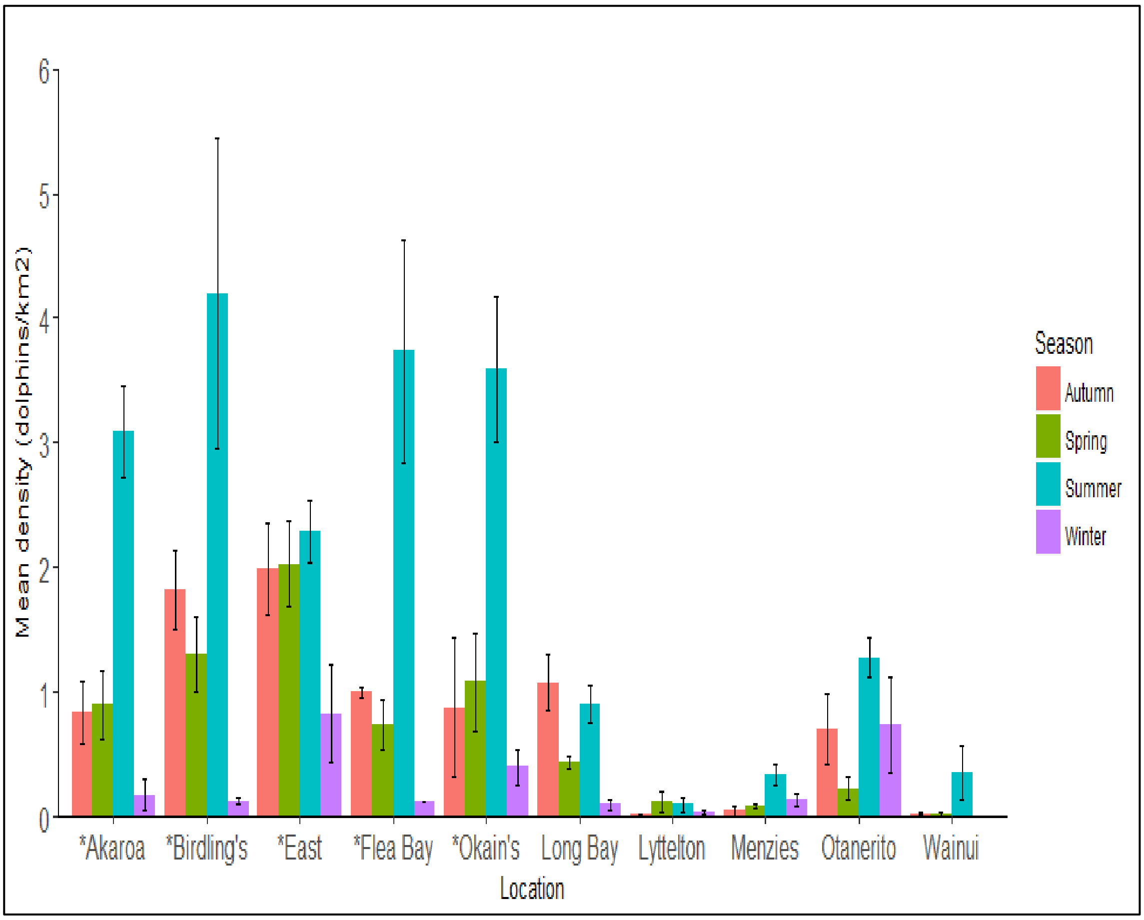

Figure 2.6: Mean relative dolphin density for hotspots and reference locations for the four seasonal categories. Density data were extracted from the KDe analysis for each seasonal dataset. Error bars are +/- standard deviation. The five hotspot locations are on the left of the figure and are shown by *.

Differences in relative dolphin density among seasons were confirmed by modelling changes in the density values of grid cells (Table 2.2). At hotspots, relatively large negative parameter estimates reveal decreases in dolphin density for all seasons compared to summer. These differences are significant given that their 95% confidence intervals do not overlap zero (Table 2.2). Reference areas exhibited similar significant differences in relative density among seasonal categories (Table 2.2). However, the parameter estimates are much smaller, again suggesting there is less seasonal variation in density at reference areas compared to hotspots.

Table 2.2: Summary of the outputs of linear mixed models for the effects of season on relative dolphin density at hotspots and reference areas. The 'summer' season is selected as a reference level, therefore the estimates for the other categorical levels reflect the difference from the summer period.

Hotspot	Estimate	SE	Lower 95% CI	Upper 95% CI
Intercept	3.46	0.18	3.03	3.90
Autumn	-1.70	0.03	-1.77	-1.64
Spring	-1.95	0.03	-2.01	-1.89
Winter	-2.97	0.04	-3.04	-2.89
Reference				
Intercept	0.51	0.13	0.21	0.82
Autumn	-0.13	0.02	-0.16	-0.1
Spring	-0.25	0.01	-0.27	-0.23
Winter	-0.3	0.01	-0.32	-0.27

The comparison of density values over the three time period categories confirmed that hotspots have remained high use areas throughout the 29 yr of this study. Relative to the reference areas, hotspots have exhibited high density values for each time period (Fig. 2.7). Three hotspots (Akaroa, Flea Bay, and Okain's) showed increases in relative density at the latter periods compared to the early (Fig. 2.7). The hotspot area 'East' and the Long Bay reference area show decreases in relative density over time (Fig. 2.7). The remaining locations showed little variation in density with time.

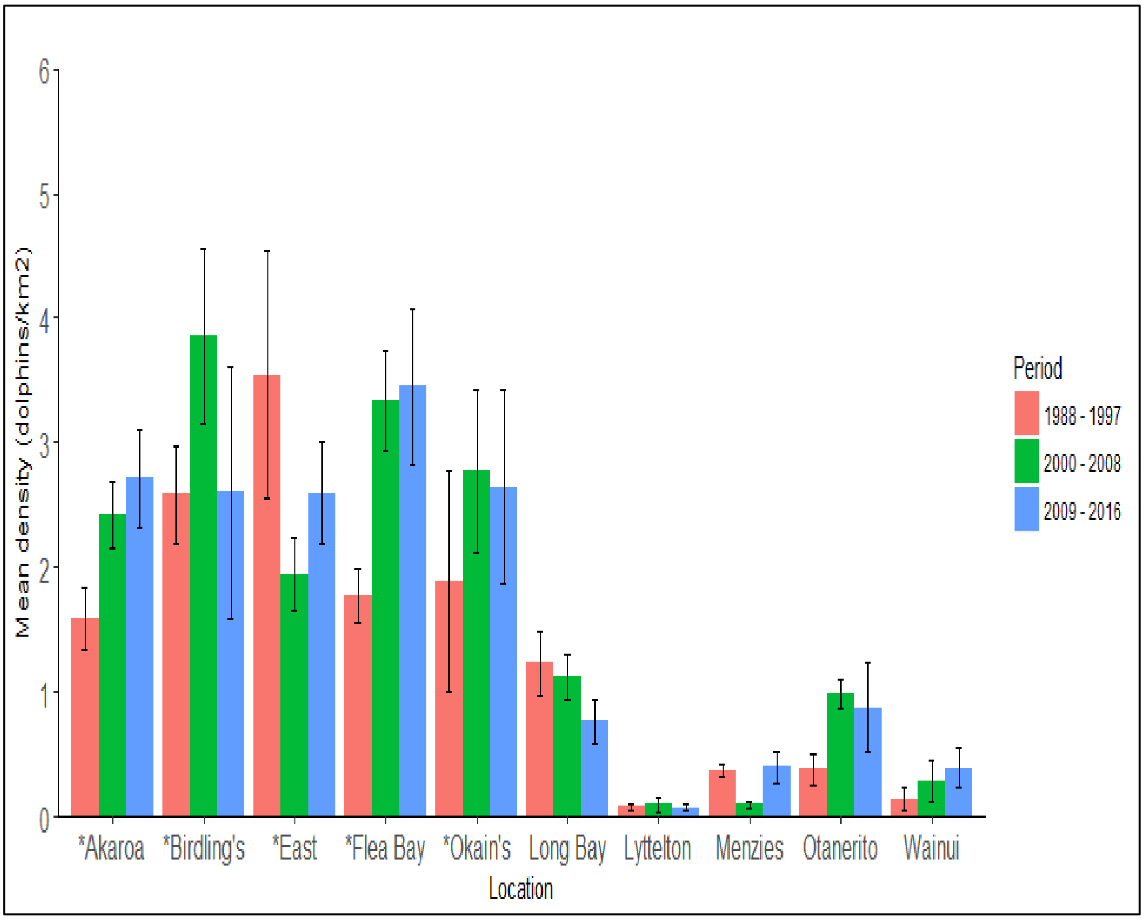

Figure 2.7: Mean relative density of dolphins at hotspots and reference locations for the three time period categories. Density data were extracted from the KDe analysis for each period dataset. Error bars are +/- standard deviation. The five hotspot locations are on the left of the figure and are shown by *.

Model parameter estimates for the mid and late categories represent the difference in the size of the effect of ‘period’ on density relative to the early category. Positive parameter estimates, with confidence intervals that do not overlap zero indicate that density has increased at the mid and late periods relative to early. Larger parameter estimates show that this effect was stronger at hotspots than reference areas. The very small parameter estimates for reference areas suggests that the effect of increasing density over time is small (Table 2.3).

Table 2.3: Summary of the outputs of linear mixed models for the effect of time period on relative dolphin density at hotspots and reference areas. The ‘early’ period is selected as a reference level, therefore the estimates for the other categorical levels reflect the difference from the early period.

Hotspot	Estimate	SE	95% Lower CI	95% Upper CI
Intercept	2.35	0.13	2.05	2.66
Mid	+0.47	0.04	0.40	0.54
Late	+0.42	0.04	0.35	0.49
Reference				
Intercept	0.43	0.15	0.06	0.8
Mid	+0.10	0.01	0.08	0.12
Late	+0.07	0.01	0.05	0.1

2.4 - Discussion

2.4.1 - Hotspot locations

This chapter presents a fine-scale spatial analysis of over 9,000 visual sightings collected in one of the longest running dolphin research programs. The results confirm the existence of hotspots in the distribution of Hector's dolphins at Banks Peninsula. The locations of the hotspots are very similar to the 'hubs' identified by Rayment et al. (2009) in their analysis of the home ranges of individual Hector's dolphins. Hubs were locations where a number of the core areas of individual dolphins overlapped (Rayment et al. 2009a). Our study in combination with Rayment et al. *(*2009) shows that core areas evident at the individual level are very similar to core areas at the level of the population.

Similar fine-scale hotspots have been observed for several coastal dolphin populations (Ingram and Rogan 2002; Hauser et al. 2007; Bailey and Thompson 2009). For example, bottlenose dolphins show significant clustering into two core areas in the Shannon Estuary, Ireland (Ingram and Rogan 2002), while southern resident killer whales also show preferences for particular core areas in the inshore waters of British Colombia and Washington (Hauser et al. 2007). Research on fine-scale distribution patterns of Māui dolphin, also revealed hotspots in distribution, albeit at small sample sizes (Oremus et al. 2013; Derville et al. 2016). The confirmation of hotspots in distribution at Banks Peninsula provides evidence that these patchy distribution patterns are evident in both subspecies of *Cephalorynchus hectori* and provides opportunities to investigate the drivers of distribution for the species.

This study focused on addressing the dynamics of hotspots in the important, nearshore component of the dolphins' habitat. It is well known the dolphins range further offshore than our nearshore study area in all seasons (Rayment et al. 2010a; MacKenzie and Clement 2014). Thus the results of this study cannot establish whether the hotspots identified are important areas in the overall distribution of the population at Banks Peninsula. To investigate this, surveys at greater distances from the coast are required and would provide valuable information on the existence of hotspots in habitat where the predominant threats (i.e. commercial set-net fishing) occur.

It is important to note that the sightings used for analyses in this chapter were made during the daytime. Therefore, it is not possible to resolve whether the hotspots identified in this study are also important during the night. Hector's dolphins are known to prey on *myctophids*, particularly Hector's lanternfish (*Lampanyctodes hectoris*; Miller et al. 2014) that are a vertically migrating species found beyond the nearshore environment on the continental shelf. It may be that dolphins move out into deeper water at night to prey on these species (similar to Dusky dolphins at Kaikoura; Benoit-Bird et al. 2004). If this is the case, the hotspots identified in this study would be less relevant. However, previous passive acoustic monitoring studies have not detected any differences in the diel use of nearshore habitat at Banks Peninsula (Rayment et al. 2010b). There may also be other, more fine scale temporal trends in the use of these areas (i.e. use during certain times of the day) that could not be determined by including the entire sightings database into relatively coarse temporal analyses. Further research on Hector's dolphin hotspots should explore these trends, with different sampling methods (e.g. passive acoustics), that better account for very fine scale spatiotemporal habitat use.

2.4.2 - Variability in habitat selection

Modelling changes in cell density has identified seasonal variability in habitat selection at Banks Peninsula. Seasonal patterns of habitat use are evident in many dolphin populations (Wilson et al. 1997; Barco et al. 1999; Fury and Harrison 2011). These patterns are often influenced by the seasonal availability of prey (Fury and Harrison 2011; Kimura et al. 2012) or particular 'types' of habitat required for seasonal life-history processes, such as reproduction (Barco et al. 1999; Rayment et al. 2015).

Seasonal changes in offshore distribution are well known in Hector's dolphin; the dolphins being more concentrated close inshore in summer than in winter (Rayment et al. 2010a). Low density of dolphins in nearshore habitat during winter is almost certainly a product of the species being distributed further offshore at this time of the year. This means that a greater proportion of the population was missed during winter surveys. Movement offshore in winter is known for several other dolphin species (Goodall et al. 1996; Goodall et al. 1997; Neumann 2001). MacKenzie and Clement (2014) have shown that Hector's dolphins may be distributed further offshore than previously thought. This may contribute to the very low density found throughout the study area during winter.

In this study, the hotspots identified in nearshore distribution of Hector's dolphins were clearly driven by strong summer use, yet several of these areas remained important during spring and autumn seasons. The modelling results confirm this pattern, with summer density values being very high at hotspots compared to other seasons. Unsurprisingly, seasonal differences in density were not as apparent at reference areas. These results suggest that seasonal hotspot dynamics are influenced by biological or social processes that occur at hotspots mainly during summer.

Hotspots are related to foraging behavior in a wide range of marine top-predators (Gende and Sigler 2006; Sydeman et al. 2006; Scott et al. 2010). Hastie et al. (2004) demonstrated that hotspots in bottlenose dolphin distribution were important foraging areas. Similarly, Scott et al. (2010) found that distribution patterns of several marine mammal species were clustered into a small number of core foraging areas in the North Sea. The seasonal use of hotspots may be related to the fine-scale distribution of prey (Gende and Sigler 2006; Pendleton et al. 2012; O'Toole et al. 2015). Certainly, foraging behavior is regularly observed at hotspots, but we have no way of knowing whether this is the primary driver as social behavior is also evident at these locations.

Hector's dolphins feed on a wide variety of prey species with differences between populations probably reflecting local prey availability (Miller et al. 2013). At Banks Peninsula, red cod and epipelagic fish species, e.g. sprat (*Sprattus sp.)* and pilchard (*Sardinops sagax),* are considered the most important prey (Miller et al. 2013). Several demersal prey species, including red cod, seem to be more abundant inshore during summer (Beentjes et al. 2002), which may be related to greater dolphin densities in our study area at that time of the year. Miller (2014) found high red cod biomass at two hotspots (Long Lookout Point and Akaroa Harbour) compared with other nearshore locations. Epipelagic species are thought to be present year-round in inshore waters (Paul et al. 2001; Fraser and Lalas 2004), yet the true temporal and spatial distribution patterns of these species are unknown. Assessing the correlation between aggregations of prey and dolphin hotspots would allow a better understanding of what makes hotspots special.

An additional feature of the seasonal near-shore distribution is that the dolphins exhibit a more uniform distribution during summer. Only 12% of the study area was selected in the 50% PDC in winter compared with 21% in summer. Further, winter space use seems to be concentrated into a reduced number of small areas. A more uniform distribution suggests that more of the study area is important habitat during summer. To confirm this, however, data on offshore sightings would be required to view changes in habitat use within the context of the dolphins' overall (i.e. inshore-offshore and alongshore) distribution. Sveegaard et al. (2011) found that core areas for harbour porpoise show a similar expansion during spring/summer compared to autumn/winter. This seasonal variation in space use could again be related to prey; with prey abundance being less patchy in summer. As calving and mating also occurs in summer, distribution at this time may also reflect these complex social behaviors.

Due to low sampling effort during winter of the early period, some bias may be associated with the modelling results. Low winter sampling effort could cause density of the early period to be biased high and the winter seasonal density to be biased low. As it stands, the early period was shown to have lower dolphin density, and so the low winter effort may mean this is a conservative estimate of the early period's true effect. While the models may have overestimated the effect of low density in winter, evidence from seasonal acoustic (Dawson et al. 2013) and line transect (Rayment et al. 2010a) surveys in this area confirm that dolphin presence is lower in winter. The overall effect of winter on dolphin density in this study is therefore unlikely to be solely an artifact of bias in sampling distribution.

Unlike hotspots, reference areas were not systematically selected based on density values. Instead, reference areas were chosen to represent a range of locations, with variable densities, where it may be possible to detect shifts in distribution with variation in density at hotspots. There is clearly some subjectivity involved in the selection of these locations. If reference areas were located differently, perhaps shifts in distribution may have been detected or temporal trends in density may have been different. Despite this subjectivity, in terms of assessing the longevity and seasonal importance of hotspots the inclusion of the reference areas in this study has been useful. For example, comparison between the hotspots and reference areas has identified something unique to hotspots in summer that causes density values to be very high. Knowledge of the times of year when differences between hotspots and references areas are greatest provides opportunities to assess the drivers of such disproportionate use of habitat.

2.4.3 - Long-term trends

The location and high density of hotspots has remained consistent over time, providing further evidence of the importance of these areas. Fine-scale patterns in habitat use may change on long term scales due to variability in habitat quality (Simmonds and Eliott 2009; Karczmarski et al. 2016), changes in population dynamics (Moore et al. 2003; Cheney et al. 2014), or due to anthropogenic disturbance (Bejder et al. 2006). Hence, studying how hotspots change may present opportunities to assess these factors. This is particularly important for endangered species such as Hector’s dolphin; especially as individuals have very small home ranges relative to other dolphin species (Rayment et al. 2009) and so may be more reliant on localised areas. The consistency of hotspots over time in this study suggests that at least in these locations, habitat quality has remained sufficiently high and/or disturbance has not affected distribution. Alternatively, if habitat quality has declined throughout the dolphins’ range, there may be few incentives to change distribution to similarly ‘poor’ habitat.

Our results indicate that relative density of dolphins increased at some hotspots over the study period. This could be related to an increase in preference for these locations over other nearshore or offshore habitat, or it may be related to growth in the population size at Banks Peninsula. The basin model, proposed by McCall (1990), outlines how spatial distribution is density dependent, with preference for certain habitat features being influenced the opportunities and restraints of variable population abundance. In one of the few long-term studies of dolphin habitat selection, Cheney et al. (2014) found that the use of a core area was related to changes in population status of bottlenose dolphins. Survival rates of Hector's dolphins at Banks Peninsula have increased since the implementation of a protected area in 1988 to reduce fisheries bycatch (Gormley et al. 2012). Before the MPA was created, this population was declining at around 6% per year and now appears to be stable or declining slowly, at no more than 1% per year (Gormley et al. 2012). The current abundance of this population and its relationship with nearshore density is unknown.

2.4.4 - Conclusions

This study has shown the existence and stability of nearshore hotspots in Hector's dolphin distribution at Banks Peninsula. The information will be valuable for management of this population; as it provides detail about candidate areas for further protection from potential threats. Further, this study provides valuable insights on locations that can be used in ecological studies to investigate the biophysical characteristics (e.g. prey density) of important habitat. Determining the factors that describe such small-scale anomalies in distribution will present managers with opportunities to identify and better protect the habitat of this endangered species.

Chapter 3: The distribution of foraging behaviour in Hector's dolphins: Are hotspots driven by foraging?

Chapter status: Accepted as an article in Marine Ecology Progress Series: Brough TE, Rayment WR, Slooten E, Dawson S. (Accepted 2019). The spatiotemporal distribution of foraging in a marine predator: behavioural drivers of hotspot formation, Marine Ecology Progress Series.

Authorship statement: TB, WR, ES and SD conceived of initial research idea, TB, WR and SD developed research methods, TB acquired data, performed analyses and wrote the manuscript, WR, ES and SD provided feedback on manuscript preparation.

3.1 - Introduction

Quantifying the locations and times that predators engage in foraging is important for understanding any ecological system. Obviously, the distribution of predators must overlap, both spatially and temporally, with that of their prey (Sih 1984; Fauchald et al. 2000; Benoit-Bird and Au 2003). In turn, prey species must co-occur with the lower trophic levels they target (Maravelias 1999; Benoit-Bird 2009; Koslow et al. 2014). Therefore, the foraging distribution of high trophic level species can provide insights into how primary productivity is distributed (Smith et al. 1986; Bost et al. 2009; Scott et al. 2010). This information improves the understanding of ecological processes in the ocean (Michaels and Silver 1988; Diaz and Rosenberg 2008), and can aid in the management of areas for conservation (Hooker et al. 1999; Game et al. 2009), fisheries (Pauly and Christensen 1995; Chassot et al. 2010) and ecosystem services (Michaels and Silver 1988; Steinacher et al. 2010).

Adding spatial and temporal information into ecological modelling of marine systems can provide better capacity to predict and assess change (Murphy et al. 2007; Crowder and Norse 2008; Steenbeek et al. 2013). The distribution of interactions within food-webs directly relates to the structuring of ecosystems (Hunt and McKinnell 2006; Ainley et al. 2007; Frank et al. 2007). Thus, the spatiotemporal distribution of foraging in top-predators can provide insights into how top-down forcing is distributed (Frank et al. 2006, 2007; Baum and Worm 2009).

Information on the distribution of foraging has clear benefits for the management of single species. Marine mammals, in particular, have very high energetic demands (Slip et al. 1992; Harding et al. 2005; Wisniewska et al. 2016) and so spend a significant amount of time acquiring food. For this reason, hotspots in the distribution of marine mammals are often hotspots for foraging (Hastie et al. 2004; Gende and Sigler 2006). This is not always the case, however (Miller and Baltz 2007; Eierman and Connor 2014). For example, Eierman and Connor (2014) found foraging behaviour in bottlenose dolphins occurred more often in particular habitat types, despite fewer dolphins being observed in these areas.

The availability and consistency of foraging opportunities have been related to variability in reproductive success in several species (Crawford and Shelton 1978; Atkinsen and Ramsay 1995; Mann et al. 1998; Baker et al. 2007). Drastically reduced juvenile survival in Hawaiian monk seal (*Monachus schauinslandi*) populations has been related to lowered quality of foraging habitat (Craig and Ragen 1999; Baker et al. 2007). Also, the influence of variable sea surface temperature on krill, the main prey for southern right whales (*Eubalaena australis),* was directly related to the calving rate of whales at South Georgia (Leaper et al. 2006).

Marine mammals often show seasonal trends in foraging behaviour (Sergeant 1973; Breed et al. 2006; Schaffeld et al. 2016). This is likely driven by seasonal changes in abundance, predictability and consistency of prey (Macleod et al. 2004; O'Toole et al. 2015). Temporal patterns in foraging are also evident on diel cycles with many species having higher foraging rates at dawn or dusk, or at night (Feldkamp et al. 1989; Allen et al. 2001; Benoit-Bird et al. 2004; Schaffeld et al. 2016). Nocturnal foraging is particularly evident for species that target prey in the mesopelagic deep scattering layer that undergoes diel vertical migration to shallower depths during the night (Benoit-Bird et al. 2004; Soldevilla et al. 2010; Au et al. 2013).

In coastal settings, tidal cycles can influence when top-predators forage (Irons 1998; Johnston et al. 2005; Bailey and Thompson 2010). At particular states of the tide, prey may be more abundant (Johnston et al. 2005; Embling et al. 2012), or easier to catch (Bailey and Thompson 2010). Tidal state has been shown to influence foraging in bottlenose dolphins (Bailey and Thompson 2010; Pirotta et al. 2013), harbour porpoise (Johnston et al. 2005; Nuuttila et al. 2017) and Indo-Pacific humpback dolphins (*Sousa chinensis)* (Lin et al. 2013; Wang et al. 2015b).

Disturbance of animals engaged in foraging, or degradation of foraging habitat, can have severe repercussions for populations (Marsh et al. 1999; Pirotta et al. 2015). Documented threats to this important activity include disturbance from tourism and vessel traffic (Allen et al. 2001; Constantine et al. 2004; Pirotta et al. 2015), noise pollution (Aguilar-Soto et al. 2006; Castellote et al. 2012) and impacts on habitat quality from coastal development (Marsh et al. 1999; Karczmarski et al. 2016) and/or fishing (Watling et al. 1998; Chilvers 2008). In some cases marine mammals compete directly with fisheries for prey (DeMaster et al. 2001), and so the depleted state of many marine fisheries likely reduces the availability of food.

Studying foraging in top-predators is challenging. Several methods have been used to investigate this naturally variable activity, including attaching electronic tags to animals (Thompson and Miller 1990; Abecassis et al. 2015; O'Toole et al. 2015), visual surveys (Irons 1998; Bailey and Thompson 2010; Scott et al. 2010) and passive acoustics (Carlström 2005; Pirotta et al. 2013; Schaffeld et al. 2016). The choice of method depends in part on the ranging patterns of the species and the scale of the investigation. As prey capture events are difficult to observe in-situ, appropriate indicators of foraging are required. These can include deep-diving events (Jaquet et al. 2000; Abecassis et al. 2015; Saijo et al. 2017) or acoustic signatures of foraging (Miller et al. 2004; Hastie et al. 2006; Schaffeld et al. 2016; Guerra et al. 2017).

Because odontocetes make particular types of echolocation sounds whilst foraging (Norris et al. 1961; Au 1993), passive acoustic tools are often used to study this behaviour (Miller et al. 2004; Pirotta et al. 2013; Schaffeld et al. 2016). Echolocating species, including odontocetes and microchiropteran bats, emit clicks with 'regular' repetition rates that are involved in searching for prey (Kellogg 1958; Norris et al. 1961; Au 1993; Johnson et al. 2006; Schaffeld et al. 2016). Following the search phase, 'buzz' sounds, consisting of pulses at high repetition rates (>100Hz), are used as the predator closes in on the prey. It is assumed that buzzes provide greater resolution and thus identification of prey targets at very close proximity to the predator (Norris et al. 1961; Au 1993; Aguilar-Soto et al. 2008; de Ruiter et al. 2009).

Buzzes have been observed in a wide range of odontocetes including sperm whales (Miller et al. 2004; Guerra et al. 2017), beaked whales (Madsen et al. 2005; Johnson et al. 2006), pilot whales (Aguilar-Soto et al. 2008), bottlenose dolphins (Nuuttila et al. 2013; Pirotta et al. 2013), Hector's dolphin (Dawson and Thorpe 1990; Dawson 1991b), Chilean dolphins (Götz et al. 2010), Heavisides dolphins (Leeney et al. 2011) and harbour porpoise (Carlström 2005; de Ruiter et al. 2009; Schaffeld et al. 2016). They also occur at the end of echolocation sequences in bats (Fenton

1980; Barclay 1982). The fact that buzzes are used across such a broad array of species and habitats suggest that they are a generic feature of animal echolocation.

While research on general distribution patterns of Hector’s dolphins has been carried out (Bräger et al. 1999; Clement 2005; Rayment et al. 2009a, 2010a; Miller 2014), no studies directly assess the distribution of foraging activity. This chapter aims to fill this gap by determining whether known hotspots are important for foraging, and when foraging occurs. I also investigate how distribution patterns vary spatially and temporally to assess the relationship between foraging and acoustic measures of relative abundance. This information may provide opportunities to minimise disturbance of this critical behaviour in the locations and at the times where it is most frequently carried out.

3.1.2 – Chapter objectives

- Is the distribution of foraging similar to that of general distribution patterns?
- What is the spatial distribution of foraging activity within the nearshore zone at Banks Peninsula: Are distribution hotspots also foraging hotspots?
- What temporal processes govern when foraging activity occurs?

3.2 - Methods

3.2.1 - Passive acoustic monitoring

Autonomous passive acoustic monitoring (PAM) devices called T-PODs (Chelonia Ltd: versions 4 and 5) were deployed to investigate the distribution of foraging behaviour. T-PODs have been used extensively to study odontocete habitat use (Carlström 2005; Gallus et al. 2012; Brookes et al. 2013; Nuuttila et al. 2017) and behaviour (Cox et al. 2001; Pirotta et al. 2013; Schaffeld et al. 2016), including with Hector's dolphins (Rayment et al. 2010b; Dawson et al. 2013). T-PODs make six sequential scans per minute and log the occurrence and characteristics of echolocation clicks using user-defined settings. Hector's dolphin echolocation consists of narrow-band high frequency clicks centred between 120 to 130 kHz (Dawson and Thorpe 1990; Kyhn et al. 2009). Following previous PAM of Hector's dolphins (Rayment et al. 2011b; Dawson et al. 2013), five of the six scans were configured to target the echolocation clicks of Hector's dolphins (Table 3.1), with the remaining scan set to detect other odontocetes that may occasionally occur at Banks Peninsula; bottlenose dolphin, dusky dolphin *(Lagenorhynchus obscurus)* and common dolphins (*Delphinus delphis).* These species have broad-band echolocation clicks centred at frequencies much lower than Hector's dolphins which allows easy discrimination of the target species from the others. TPODs have a maximum detection range of 431m for Hector's dolphin (Rayment et al. 2009b).

Table 3.1: Parameters used in the setup of TPODs for passive acoustic monitoring of Hector's dolphins

Parameter	**Scans 1 – 5**	**Scan 6**
Target frequency	130 kHz	50 kHz
Reference frequency	92 kHz	70 kHz
Bandwidth	5	5
Noise adaptation	++	++
Sensitivity	10	10
Scan limit	240	240

.

Fifteen individual T-PODs were deployed at ten different locations around Banks Peninsula (Fig. 3.1). The locations consisted of four 'hotspot' and six reference areas as defined by the kernel density analysis in chapter 2 (Fig. 2.3). These 10 study areas differ slightly from those reported in Chapter 2. This is because for this (and subsequent) chapters, it was not possible to sample the full range of hotspots and reference areas denoted by the KDe analyses. The sheer size of some hotspots and their remoteness limited my ability to either obtain meaningful habitat data, or to visit frequently enough to deploy TPODs. Thus, the four hotspots that are the focus of all subsequent investigations in this thesis include three from chapter 2 (Akaroa, Birdling's Flat and Flea Bay) and Long Lookout Point, that is included as a smaller portion of the large 'Okain's Bay' hotspot. The reference areas remain the same as chapter 2 with the inclusion of an addition 'Damon's Bay' reference area to bring the total number of study areas to 10 (Figure 3.1).

TPOD deployments used in this study began in January 2015 and continued until March 2017, although coverage was not continuous over this time (Fig. 3.2). Version 4 and 5 T-PODs have been calibrated with unit specific gain functions to minimise differences in detection rates among units. However to further minimise the chances of T-POD ID influencing results, individual T-PODs were periodically swapped among locations, with no unit being used more than twice in any one location. Deployments had variable duration due to differences in battery consumption among units, issues with extreme weather damaging moorings and infrequent T-POD malfunction. Typically, deployments lasted between 1 and 3 months (Fig. 3.2). T-PODs were attached in midwater to temporary moorings. The positions of T-POD moorings within each area were randomly generated. Because habitat type may vary over small scales within locations, moorings were periodically moved to new randomly generated positions. These were at least 200m from the previous mooring position and at least 200m from shore (Fig. 3.1). At least five sites were sampled from within each location.

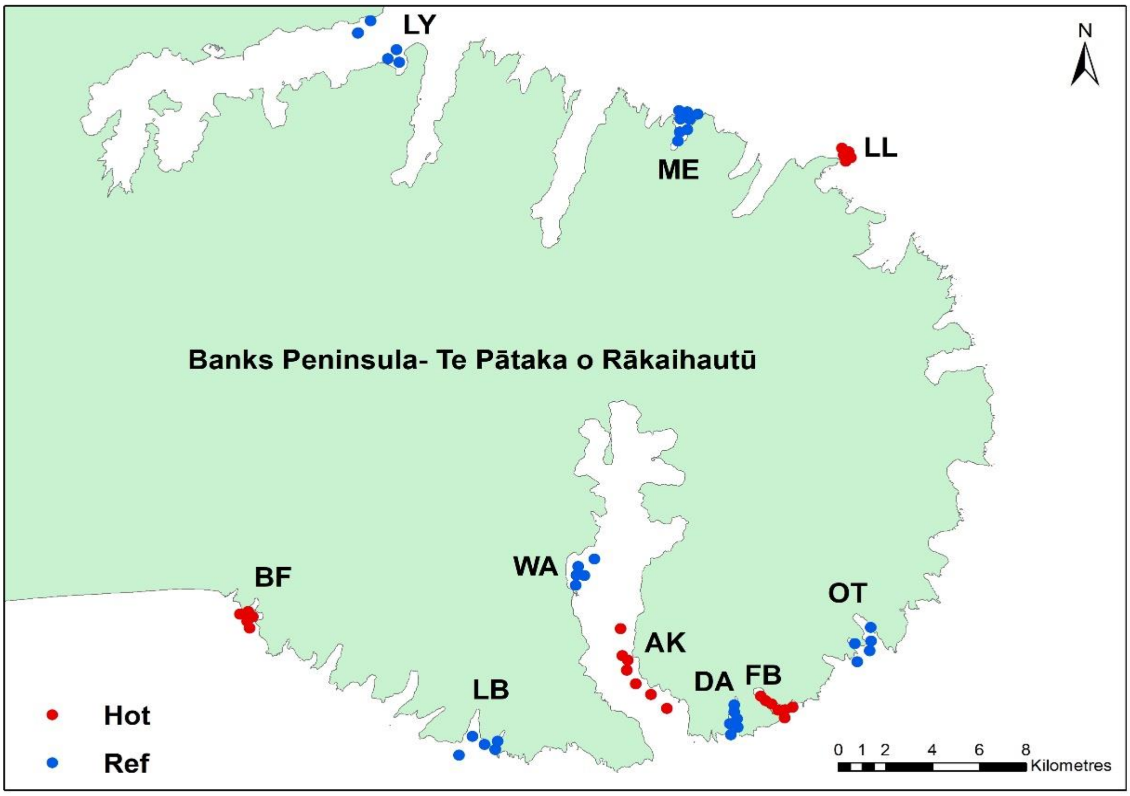

Figure 3.1: Monitoring locations and TPOD deployment positions in this study. The four hotspot (Hot) monitoring locations are Birdlings Flat (BF), Akaroa Harbour (AK), Flea Bay (FB) and Long Lookout Point (LL). Reference locations (Ref) are Long Bay (LB), Wainui (WA), Damon's Bay (DA), Otanerito Bay (OT), Menzies Bay (ME) and Lyttelton Harbour (LY).

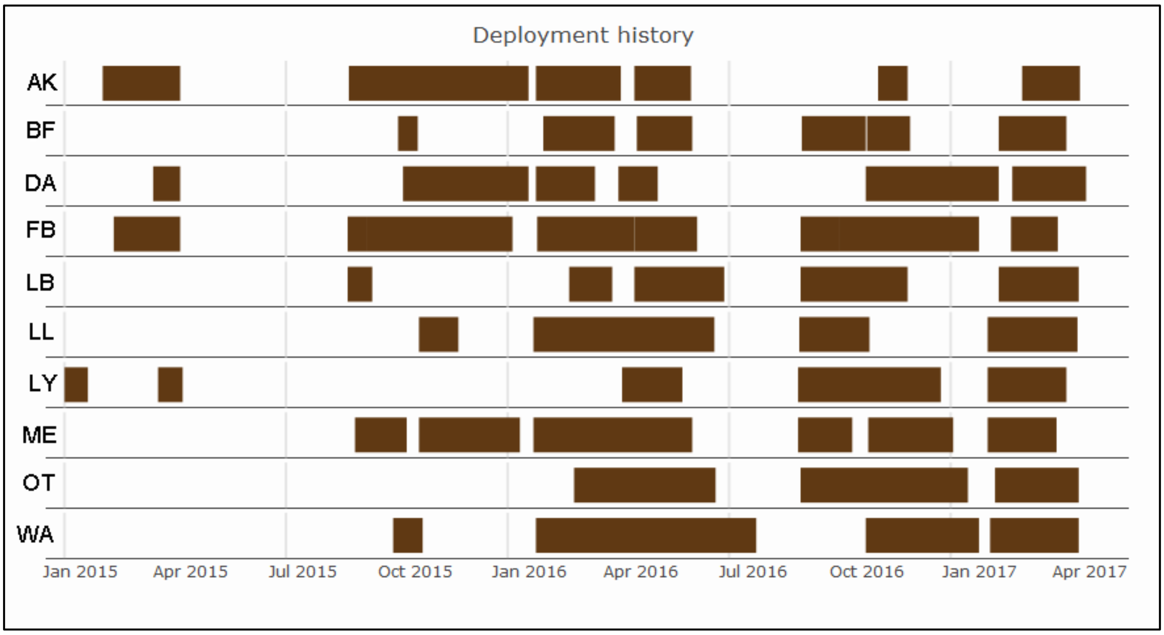

Figure 3.2: Deployment history for passive acoustic monitoring of the ten study locations. Acoustic monitoring began with trials in January 2015 and continued through until March 2017. Location codes are illustrated in figure 3.1.

3.2.2 - Acoustic data processing

Echolocation clicks from T-POD deployments were analysed in the software TPOD.exe (version 8.24; Chelonia Ltd). This purpose-built software classifies clicks into sequences (trains) and assigns a likelihood that a particular click train originates from a cetacean based on pulse duration, pulse repetition frequency, and interclick-interval. Previous study has shown that Hector's dolphins are reliably detected using the CET-ALL category (Rayment et al. 2009b). Thus, this category was used for further analysis. To ensure spurious acoustic signals were not being included in trains, a random sample of raw data from each acoustic deployment was plotted and screened in TPOD.exe. Decision rules developed by Rayment et al. (2011b) were applied to the random subset of data. These were 1) >8 clicks in a train, 2) mean click duration < 300 µs, 3) smooth trend in pulse repetition frequency, 4) no accompanying noise around focal click, and 5) no clicks on the lower frequency scan (scan 6) within 10 minutes.

Information on click trains and individual clicks were exported for each deployment. Using a custom written script in Matlab (version R2014a), clicks were matched to their respective trains by the unique time stamp of each click and train. Inter-click intervals (ICIs) were calculated for every click in each train, defined as the difference in start time between a click and the previous click (Au 1993).

3.2.3 - Buzz classification

ICIs have been used extensively to identify ‘buzz’ sounds in odontocetes (Johnson et al. 2006; Elliott et al. 2011; Pirotta et al. 2013; Schaffeld et al. 2016). Often, an ICI threshold of 10ms is used to classify clicks as buzz activity; click trains with ICIs <10ms (representing a click rate of approximately 100 click/s) are assumed to represent buzzes (Carlström 2005; Leeney et al. 2011; Nuuttila et al. 2013). Because appropriate classification of buzzes may be species specific, I employed a method proposed by Pirotta et al. (2013) in which the multi-modal gaussian distribution of ICIs is used to classify clicks as belonging to particular processes, and therefore different biological functions (Pirotta et al. 2013; Williamson et al. 2017). Using Gaussian mixture models (GMM), the time series of ICIs was analysed to assess the number of modes represented in the dataset, assigning each ICI to one of the observed processes. The GMMs were run with the package *Mixtools* (Benaglia et al. 2009) in R (R Development Core Team 2017) using an expectation maximum algorithm. To determine the number of component distributions (*k)* in the dataset, I specified three models with *k* as either 2, 3, or 4. The most appropriate model was selected by viewing the plotted mixtures and choosing the model that had the lowest AIC score (Akaike 1973) without evidence of overfitting (one component nested entirely within another (Fig. 3.4). ICIs were considered to represent buzz activity if they had a probability >0.99 of belonging to the first component (with the shortest ICIs) (Fig. 3.4), and are hereafter referred to as buzz ICIs.

3.2.4 – Exploratory analyses

Exploratory analyses were used in order to investigate broad trends in dolphin distribution and foraging over different spatiotemporal scales. These analyses were important for identifying broad patterns in the large acoustic dataset and for determining the distribution of the data. As a first step, the raw data were screened. This involved plotting the number of total dolphin trains (for distribution) and the number of buzz trains (for foraging) against the month of the year, time of day and hours since high tide (see Appendix 2b). Secondly, the mean and associated standard error values of the same response data were calculated for each month and for day and night (among monitoring locations) to better visual trends across seasonal and diel scales with the large dataset (Appendix 2c). The effect of tide was investigated by using a smoothed spline to generate mean values of total dolphin detections or foraging trains across hours from high tide. Error around the mean was generated using standardised jacknife residuals to produce a 95% confidence interval (Eubank 1985).

3.2.5 - Statistical modelling

Statistical analyses in this (and subsequent) chapters uses common ecological modelling approaches combined with information theoretic (IT) inference. Such methods are necessary due to the highly complex ecological datasets used in this thesis, that do not satisfy the assumptions of traditional, more simple statistical frameworks (e.g. ANOVA, linear regression) that require normally distributed, independent data points. IT approaches are increasingly favoured over more traditional hypothesis testing due to the lack of reliance on arbitrary p-values and their capacity to weigh evidence for a range of ecological scenarios simultaneously (Burnham and Anderson 2000; Anderson et al. 2000).

Two separate modelling frameworks were developed to investigate general distribution patterns and the distribution of buzzing activity. Both used generalised additive mixed models (GAMMs). GAMMs are an extension of generalised additive models (GAMs; Hastie and Tibshirani 1987) that allow for random effects (RE) structures (Zuur et al. 2009). GAMs are additive models that use non-parametric smoothing functions to model non-linear relationships between predictors and response variables with a range of response distributions (Hastie and Tibshirani 1987; Guisan et al. 2002). Due to this flexibility, GAMs are widely used in ecology (Guisan et al. 2002; Zuur et al. 2009). The incorporation of RE and temporal correlation structures with the GAMM framework provide a powerful tool to model correlated and nested data that are common in ecological datasets (Zuur et al. 2009). Data on the presence/absence of acoustic detections were generated to model the spatial and temporal distribution patterns of dolphins. Hourly monitoring periods at each location that contained dolphin detections were designated a 1 and those without detections a 0. A binomial response was used in this instance due to the strongly zero inflated nature of the dataset (Zuur et al. 2009). For buzz activity, the response variable was foraging trains per hour (FTH); a measure of foraging rate. FTH is the number of click trains that contained buzz activity for each hourly record of each deployment. Similar to Pirotta et al. (2013), only hourly records in which detections of dolphins were made were considered in the modelling framework for buzz distribution. The importance of a location or temporal period for foraging is a product of foraging rate and how regularly animals are present (Pirotta et al. 2013). Thus, the FTH response variable was weighted by detection positive minutes/day (DPM); a common measure of acoustic relative abundance for echolocating species (Leeney et al. 2007; Rayment et al. 2010b; Brookes et al. 2013). This weight prevents rare bouts of high buzzing activity from affecting the analyses of foraging distribution. Each hourly interval was weighted by a DPM value according to the date and location of deployment. DPM was normalised (DPM/meanDPM) to ensure a standardised contribution to the model’s log likelihood (Wood 2017).

Fixed effects included Julian day of the year (DOY), fitted using a circular spline (Wood 2006). DOY determines any seasonal effects. Time of day (Time) was also fitted (using a circular spline) to investigate diel effects on distribution or foraging activity. A parameter for tidal effects (Tide) was defined as the time since the last high tide. Data on tidal state specific for each deployment location was available from the NZ tide forecast model (Goring 2001) produced by the National Institute for Water and Atmospheric research (NIWA). Each fixed effects variable was calculated for the start time of each hourly bin that generated the response variables. The degrees of freedom

(k) for each smoothed effect was set at 'optimum levels', with the final value being determined *via* generalised cross validation (Wood 2006). To prevent unnecessary, highly complex smoothed effects, a maximum k was specified that was the lowest value possible without over-restriction (Wood 2006). Over-restriction was established *via* simulation using the *gam.check* function in *mgcv* (see model diagnostics below).

Multiple deployments from each location are correlated in space. This correlation was investigated by constructing a semi-variogram (Zuur et al. 2009) of the standardized coefficients from a linear model that modelled either the detection or foraging positive hours against each deployment position (59 levels). Significant correlation was observed out to 2km. For this reason, both general distribution and foraging were modelled with a random effects parameter for deployment location. Location corresponded to one of the ten sampling locations (Fig. 3.1). A random intercept allows for correlation within each location (i.e. repeated measures), whilst enabling an assessment of the difference in foraging among locations (Williamson et al. 2017), the key spatial parameter of interest.

Clearly, PAM data are also temporally correlated with successive hourly records from the same location being similar. This can lead to a violation of one of the main GAM assumptions; that model residuals are independent (Wood 2006). For this reason, I used a temporal covariance structure (AR1) following Pirotta et al. (2013) and Nuutila et al. (2017) to account for temporal correlation in the response variables. The AR1 structure builds a covariance matrix that allows temporal correlation within particular time bins (Zuur et al. 2009). The level of covariance is established using autocorrelation function (ACF) plots of the response, and is taken as the ACF value at time lag 1. This was undertaken in R package *itsadug* (van Rij et al. 2017). Days were used as the blocking variable (i.e. a temporal period during which autocorrelation can occur) for the correlation matrix (Pirotta et al. 2013). The covariance matrix was applied to every model used for model selection and inference.

The global GAMM model to investigate the spatial and temporal distribution of dolphins and foraging activity was:

$$FTH \ or \ P/A = s(DOY) + s(Time) + s(Tide) + RE(Location)$$

where s() indicates a smooth term and RE() a random effect. Presence absence (P/A) models for general distribution were fit with a binomial distribution and logit link function. Foraging models were fitted with a poisson distribution and a log link function. The *bam* function of package *mgcv* (Wood 2006) was used to fit the GAMMs in R. *Bam* is formulated similarly to the *gam* function, but is better optimised for larger datasets (Wood 2006). In order to find the best combination of parameters to explain the variation in the response, I generated a model set with every possible combination of parameters. Models were ranked according to the lowest AIC score (Akaike 1973).

It is possible that the temporal fixed effects may have varying levels of influence at different spatial locations. To test this, I fitted three additional models that replaced the singular smoothed term with an interaction term of that temporal parameter with location:

DOY_I -> $FTH = s(DOY, by = Location) + s(Time) + s(Tide) + RE(Location)$

Time_I-> $FTH = s(DOY\ ) + s(Time, by = Location) + s(Tide) + RE(Location)$

Tide_I -> $FTH = s(DOY) + s(Time) + s(Tide, by = Location) + RE(Location)$

Interaction terms were deemed better predictors of the temporal dynamics of foraging if a model ranked higher in terms of AIC compared to the global model (with no interaction terms). When this occurred, interaction terms replaced the single smoothed fixed effect in the formulation of a 'top-model' that contained either an interaction or singular term for each effect. Interaction terms were not included in the global model used for the simulation of all possible model combinations due to the computer power needed to fit models of high complexity to datasets with over 82k hourly data points. The top-model was used for inference and the visualisation of results.

Model selection, and determining the importance of the fixed effects, used a three step process. Firstly, 'automatic' model selection was undertaken using techniques developed by Wood (2006) in package *mgcv*. Using penalised regression splines, shrinkage smoothers were applied to each candidate term in a model framework. Shrinkage smoothers apply a multiple of the identity matrix to each coefficient of a term, so that penalisation can be strong enough for a coefficient to be shrunk to 0, completely penalising a term out of a model. Such 'automated model selection' is regularly used in the studies that employ GAM(M)s as a sole means of model selection (Tepsich et al. 2014; Grüss et al. 2016; Williamson et al. 2017), and prevents overfitting by reducing term's degrees of freedom to 0. The second model selection technique used information theoretic approaches to determine a 'top model' using Akaike's information criterion (AIC; Akaike 1973). As above, every possible combination of input terms was formulated and tested for its parsimony. Only terms retained in the top model were deemed to have some influence on the response variable. Finally, the importance of the various smoothed fixed effects was established by the p-values associated with each smoothed term from the top-model. These p-values are based on Wald's test statistics (Wald 1943) and incorporate Bayesian confidence intervals on the smoothed function (Nychka 1988; Wood 2012). These p-values are approximate, and thus a p-value<0.01 is used as being indicative of a significant effect (Wood 2017; Zuur et al. 2009). The importance of the random effects parameter for spatial distribution is also determined by the p-value associated with the Gaussian random effects term. This p-value is calculated via the likelihood ratio statistic using the relationship between random effects and penalised regression terms (Wood 2013). In summary, in order for a term to be deemed ‘important’ at explaining variation in the response, it must have a) coefficients that have not be shrunk to zero b) be included in the ‘top model’ and c) have a p-value<0.01. This three step process minimises the likelihood of spurious results and prevents overfitting and is the basis for model selection and inference for the all statistical modelling in this thesis. To establish how the distribution of dolphins and buzzing behaviour varied spatially over the ten monitoring locations, the effect of each level of the random intercept term ‘location’ was obtained by prediction using the top foraging model. The temporal effects were set at null values (i.e. excluded from prediction), in order to obtain the true effect of each location independent of the fixed effects. The predicted values are on the scale of the linear predictor.

Accounting for correlation, model fitting, model selection and inference followed the same methods for both model frameworks. The final top-model for the presence/absence of dolphins was used to compare how the temporal and spatial distribution of foraging differs from that of general distribution patterns.

3.2.6 Model checking and diagnostics

A key assumption for GAM and GAMM models is that model residuals have constant variance (Wood 2006). For the foraging models, this was checked by plotting model residuals against fitted values and against the individual smoothed terms. Any trend in residuals across any of these variables would indicate a departure from residual homogeneity (Wood 2006).

The usual residual plots have limited use with models using binomial response variables (Zuur et al. 2009). If sample size permits, binned residual plots can be used to check the assumption that residuals have constant variance (Zuur et al 2009). Therefore, for the binomial models, binned residuals were plotted against fitted values and temporal smoothed effects to examine homogeneity of variance and whether residuals were independent.

Checks for residual independence used ACF plots. These were generated for each global and top-model for the foraging and presence/absence analyses to confirm that the correlation matrices sufficiently accounted for temporal correlation.

The distribution of the model residuals was checked with *qq.gam* in *mgcv* to ensure the distributional assumptions of the binomial (presence/absence) model framework were correctly specified. In the case of the poisson foraging model the package

A particular assumption of additive models is that the degrees of freedom for the smoothed terms (k) is not over-restrictive (Wood 2006). This assumption was checked by plotting partial residuals specific for each smooth function against the smooth itself. Any systematic departure of the mean residual value from the smooth function will indicate k is restrictively low. Further, the effective degrees of freedom were checked using the *gam.check* function in *mgcv* that simulates the residual variance between near-neighbour covariates in each smooth (Wood 2006). A k-index below 1 indicates there is some pattern left in the residuals that may be accounted for by increased *k* (Wood 2017).

Collinearity of model parameters is unlikely to be an issue with this modelling framework as, intuitively, the full range of values for any temporal effect is equally likely to occur at the full range of another temporal parameter. This is especially true given that this dataset was collected over multiple years.

All model checking procedures were applied to the global and top-models for both the foraging and presence/absence dataset.

3.4 - Results

3.4.1 - Acoustic monitoring

TPODs were deployed across the ten monitoring locations from January 2015 to March 2017 (Fig. 3.2). Coverage was not continuous due to recovery and redeployment being limited to two, three month fieldwork seasons (Chapter 5) and the fact that batteries would not typically last between seasons. Over the deployment period, however, every location had a good representation of seasonal, diurnal and tidal sampling (Fig. 3.2. & Table 3.2). The exception to this was the reduced sampling during late June and July at all locations due to battery failure before the winter fieldwork season began (Fig. 3.2).

A total of 82,188 hourly intervals were recorded across the ten monitoring locations (Table 3.2). All locations had a high number of monitoring hours, with Long Bay (LB) having the lowest amount of monitoring at 5903 hours (Table 3.2). Acoustic monitoring was not apportioned equally among seasons; summer and spring had higher monitoring effort than winter and autumn. Despite this unequal sampling effort, a substantial number of hours were recorded throughout the seasons at each location (Table 3.2).

Table 3.2: Summary of acoustic monitoring effort for each location. The number of unique sampling positions per location, total hours and a seasonal breakdown of monitoring hours are given. Location codes are explained in Figure 3.1.

Location	Unique deployments	Total hours	Summer	Autumn	Winter	Spring
AK	7	9341	4327	980	1248	2786
BF	5	6203	2795	1001	1535	872
DA	6	9028	3940	319	455	4314
FB	8	11605	4192	1093	2234	4086
LB	5	5903	2543	809	1745	806
LL	5	7419	3855	1431	1308	825
LY	5	6332	2550	816	1237	1729
ME	7	9931	3465	992	2047	3427
OT	5	7621	2928	1461	1274	1958
WA	6	8805	3761	2185	522	2337
Total	59	82188	34356	11087	13605	23140

3.4.2 Buzz classification

A total of 1.4×10^7 clicks were available to model the gaussian mixture distribution of ICIs. The best model in terms of AIC specified four component distributions (Table 3.3). When plotted, both the three and four component models showed clear signs of being overfitted with the peak of one component being completely nested within another (Fig. 3.3). Therefore I selected the next best model which had no indications of being overfitted; this was the two component model (Table 3.3 & Fig. 3.4).

Table 3.3: Model selection table for the three gaussian mixture models used to investigate the mixture distribution of click ICIs. The degrees of freedom (df), log likelihood (logLik), Akaikes information criterion (AIC), and delta AIC (delta) are given for each model.

Model	df	logLik	AIC	delta
Four component	11	-135131	270285	0
Three component	8	-136193	272404	2119.2
Two component	3	-136768	273548	3262.8

The estimated means of each distribution within the two component gaussian mixture model were 4 ms (SE = 2.9) and 33 ms (SE = 1.5) for the first and second component respectively. A total of 1.1×10^6 ICIs were assigned a probability above 0.99 as belonging to the first component. These clicks were classified as buzz clicks. Buzz clicks had ICIs that ranged between 0.1 and 7.57 ms.

Detections of Hector’s dolphin acoustic presence and foraging behaviour were made at all monitoring locations (Fig. 3.4). The proportion of monitored hours with detections ranged from 76% at Long Lookout Point to 20% at Otanerito Bay (Fig. 3.4). Monitoring hours containing buzzes followed a similar pattern with 52% of hours being foraging positive at Long Lookout and 8% at Otanerito (Fig. 3.4). There was substantial variability in the number of foraging trains per hour across locations (max=314, min=0). On average, Birdling’s Flat had the highest number of foraging trains with a mean of 6.5 per hour (SE=0.17). Wainui Bay had the lowest with a mean of 0.4 foraging trains per hour (SE=0.02).

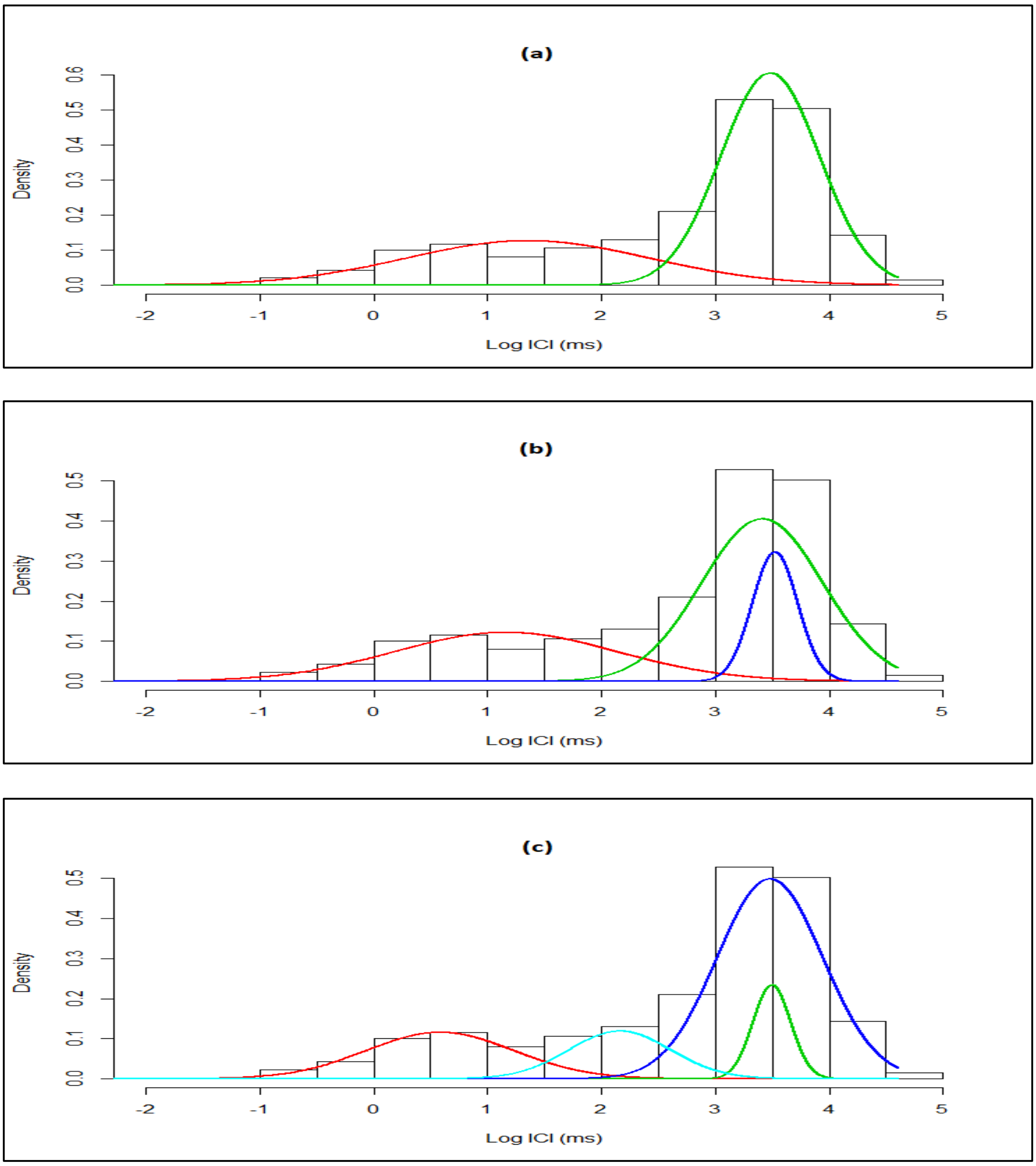

Figure 3.3: Plots of the results of gaussian mixture models of click ICIs with 2 (a), 3 (b) or 4 (c) component distributions. The best model is given by the lowest AIC value from a model that shows no signs of overfitting. Both the 3 and 4 components models show c clear nesting of one distribution within another and so are overfitted.

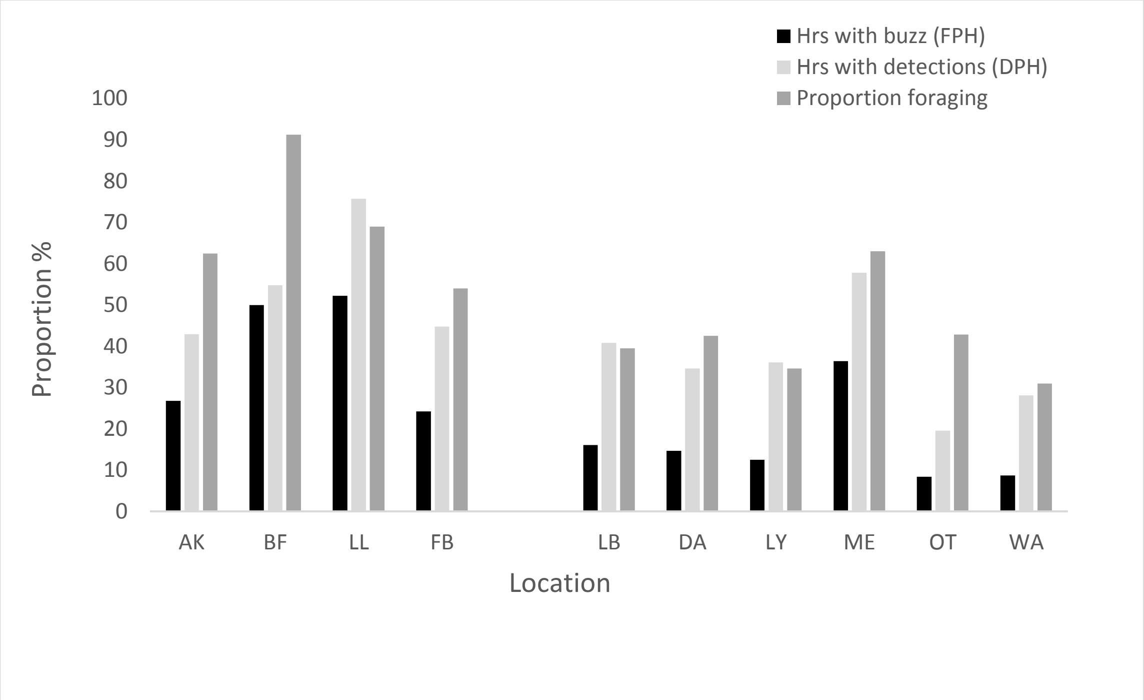

Figure 3.4: Summary of raw data from acoustic deployments. The proportions of monitored hours with buzz content (FPH) and dolphin detections (DPH) are shown for each monitoring location. The proportion of time spent foraging (FPH/DPH) is also given. The hotspot locations from chapter 2 are shown on the left of the figure, with reference areas on the right. Location codes given in Figure 3.1.

There was substantial variability among monitoring locations in terms of the proportion of monitored hours with dolphin detections and foraging trains. The proportion of time spent foraging (FPH/DPH) was also highly variable among locations, with the four hotspots having high values of foraging trains per detection hour. The exception to this was Menzies Bay that had a similarly high proportion of time with foraging signals (Fig. 3.4).

3.4.3 – Exploratory analyses

Other than a general decrease in both dolphin detections and foraging rates across seasons, it was not possible to discern trends in the raw data over temporal scales (Appendix 2b). This is likely a product of the very large dataset and substantial variation therein. Exploratory analyses using mean values did, however, show that both dolphin distribution and foraging varies over temporal scales. Trends were similar with both response variables, with there being a decrease in both dolphin detections (Fig. 3.5) and foraging (Fig. 3.6) in the winter months of June and July. Akaroa, Damon's Bay and Menzies Bay had more detections and more foraging at night compared to the day, while Birdling's flat, Long Lookout and Otanerito had higher values of these response variables during the day. Tide had small effect on both dolphin distribution and foraging, where both of these values were lowest at low tide (Figs. 3.5 & 3.6; Appendix 2c).

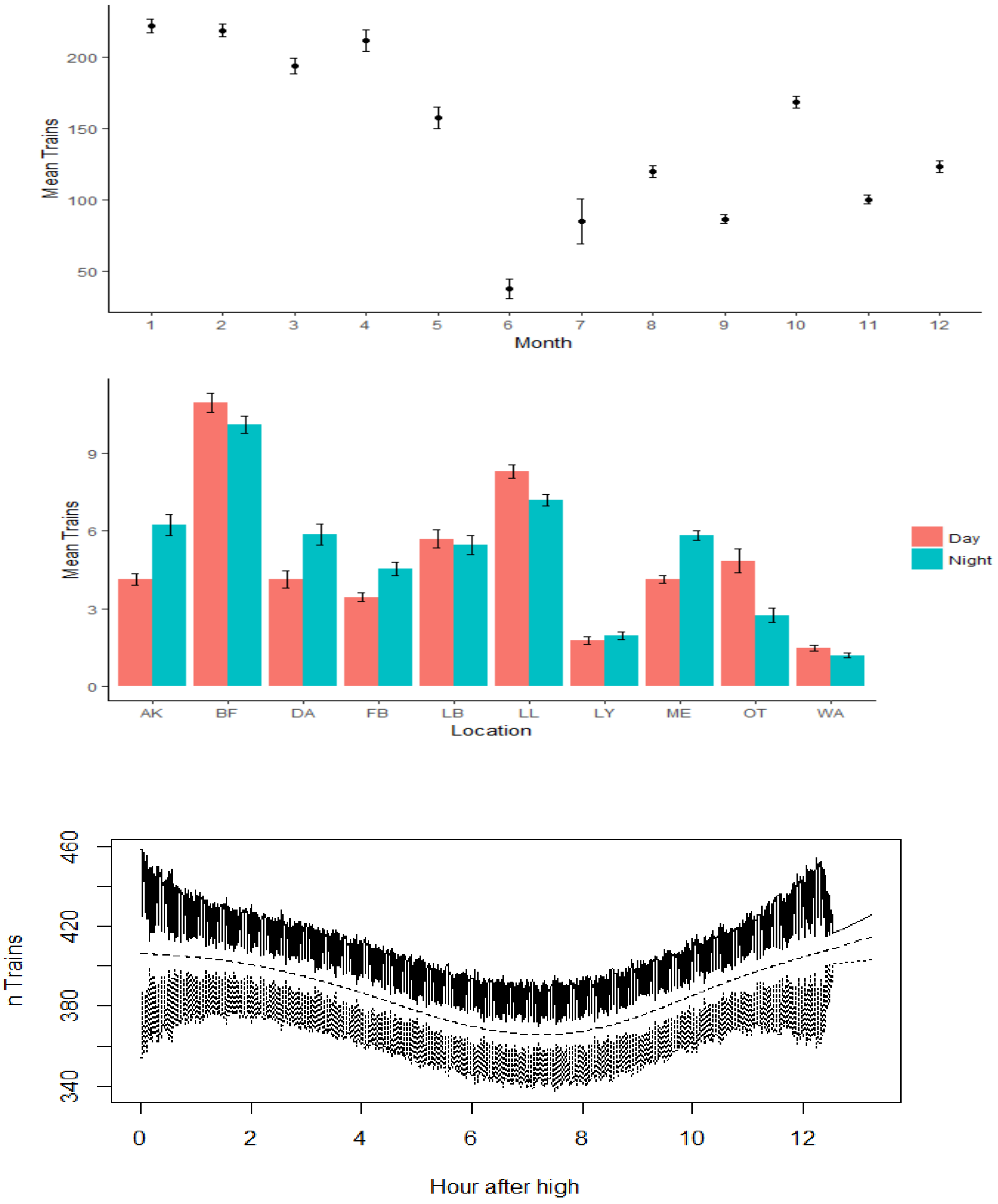

Figure 3.5: Exploratory analyses using data for all deployments at all all locations. Shown is the distribution of dolphin detections (number of trains) over three temporal scales; seasonal (top panel), diel (middle panel) and tidal (bottom panel).

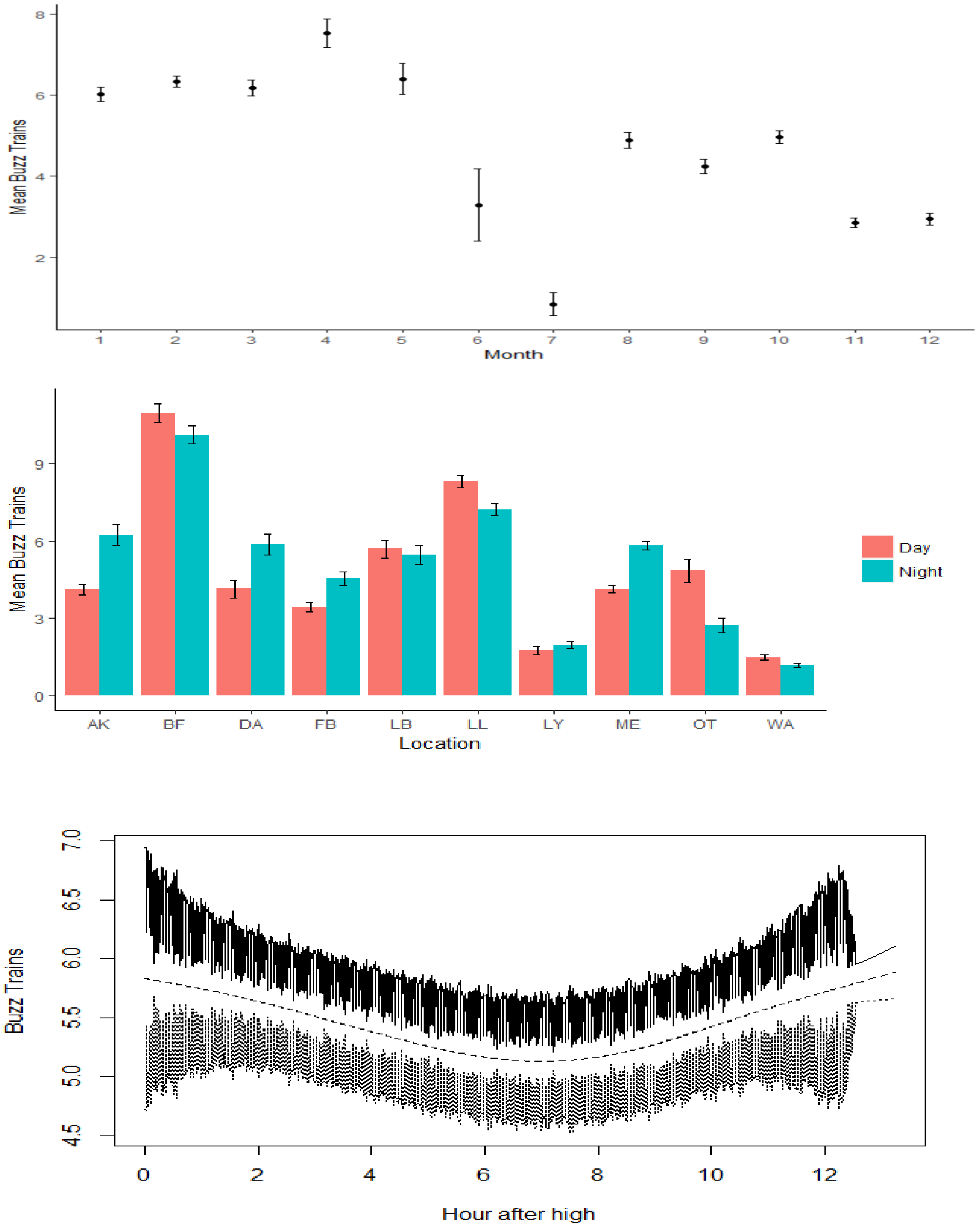

Figure 3.6: Exploratory analyses using data for all deployments at all all locations. Shown is the distribution of foraging buzzes over three temporal scales; seasonal (top panel), diel (middle panel) and tidal (bottom panel).

3.4.4 - General distribution patterns:

The best model to describe the general spatial and temporal distribution patterns of Hector's dolphins was the global model. This model had highest log likelihood, lowest AIC and a model weight of 1 (Table 3.4). All three temporal (fixed effects) parameters; DOY, time, and tide were included in the top-ranked model, as was the random effect of deployment location. When interaction effects were considered in place of the singular smoothed effects, there was good evidence for their inclusion in the top-model (Table 3.5). Therefore the top-model for assessing dolphin distribution included interaction terms between each of the smoothed temporal effects and location. The top-model explained only 14% of the deviance in dolphin presence/absence (see *discussion).*

Table 3.4: Model selection table for the models used to define the best model (without interactions) for dolphin distribution. Models are ranked by AIC and model weight.

Formula	df	logLik	AIC	delta	weight	deviance
DOY+Time+Tide+Location	22	-36369	72784	0	1	8.54%
DOY+Time+Location	18	-36389	72816	32	0	8.51%
DOY+Tide+Location	16	-36403	72839	55	0	8.43%
DOY+Location	12	-36422	72869	86	0	6.88%
Time+Tide+Location	19	-36731	73501	717	0	6.91%
Time+Location	15	-36750	73533	749	0	6.88%
Tide+Location	13	-36764	73555	772	0	6.80%
Location	9	-36783	73585	802	0	6.77%
DOY+Time+Tide	12	-40911	81847	9064	0	1.76%
DOY+Time	9	-40928	81875	9091	0	1.66%
DOY+Tide	7	-40940	81895	9111	0	1.66%
DOY	3	-40957	81921	9137	0	1.63%
Time+Tide	10	-41180	82379	9596	0	0.12%
Time	6	-41197	82407	9623	0	0.01%
Tide	4	-41209	82426	9643	0	0.01%

Table 3.5: Model selection table used to assess evidence for the inclusion of an interaction effect between temporal smoothed terms and location for the prediction of dolphin distribution. Interactions were deemed better predictors of foraging if models with the interaction had lower AIC values.

Model	Formula	df	logLik	AIC	Deviance
DOY_I	DOY*Location+Time+Tide+Location	48	-35583	71264	11.98%
Time_I	DOY+Time*Location+Tide+Location	52	-36152	72409	11.32%
Tide_I	DOY+Time+Tide*Location+Location	35	-36327	72726	9.50%
Global_model	DOY+Time+Tide+Location	22	-36369	72784	8.54%

The smoothed term DOY was a significant predictor of the probability of dolphins being present at all monitoring locations (Table 3.6). Tide was not a significant predictor of dolphin distribution at most locations; being important at Akaroa, Long Lookout Point and Wainui only (Table 3.6). Time of day was a significant predictor of distribution at Akaroa, Birdling's Flat, Damon's & Menzies Bays and Wainui (Table 3.6).

The effects of season (DOY) on the probability of dolphins being present shows a strong trend, at most locations, of higher probabilities during the summer months between December and March (Fig. 3.7). Exceptions to this trend are Akaroa, where the peak in the probability of dolphin acoustic presence occurs later in the season around May. Also, Flea Bay shows very little seasonal variation in the probability of dolphin acoustic presence (Fig. 3.7).

Table 3.6: Statistical significance of the smoothed temporal terms and spatial locations on the probability of dolphin acoustic presence taken from the top-model for general distribution. Significant terms are shown by a low p value and ***.

Term	Chi.sq	p-value	Significant
Location	2166	< 2e-16	***
s(Tide): AK	13	0.001	***
s(Tide): BF	1	0.207	
s(Tide): DA	1	0.266	
s(Tide): FB	1	0.216	
s(Tide): LB	0	0.471	
s(Tide): LL	27	0.000	***
s(Tide): LY	0	0.493	
s(Tide): ME	0	0.302	
s(Tide): OT	0	0.336	
s(Tide): WA	8	0.006	**
s(Htime): AK	37	0.000	***
s(Htime): BF	76	< 2e-16	***
s(Htime): DA	17	0.000	***
s(Htime): FB	0	0.570	
s(Htime): LB	0	0.339	
s(Htime): LL	2	0.132	
s(Htime): LY	2	0.127	
s(Htime): ME	40	0.000	***
s(Htime): OT	2	0.105	
s(Htime): WA	36	0.000	***
s(DOY): AK	800	< 2e-16	***
s(DOY): BF	3256	< 2e-16	***
s(DOY): DA	8995	0.000	***
s(DOY): FB	348	0.000	***
s(DOY): LB	141	0.000	***
s(DOY): LL	168	0.000	***
s(DOY): LY	319	0.000	***
s(DOY): ME	556	< 2e-16	***
s(DOY): OT	1941	< 2e-16	***
s(DOY): WA	1031	< 2e-16	***

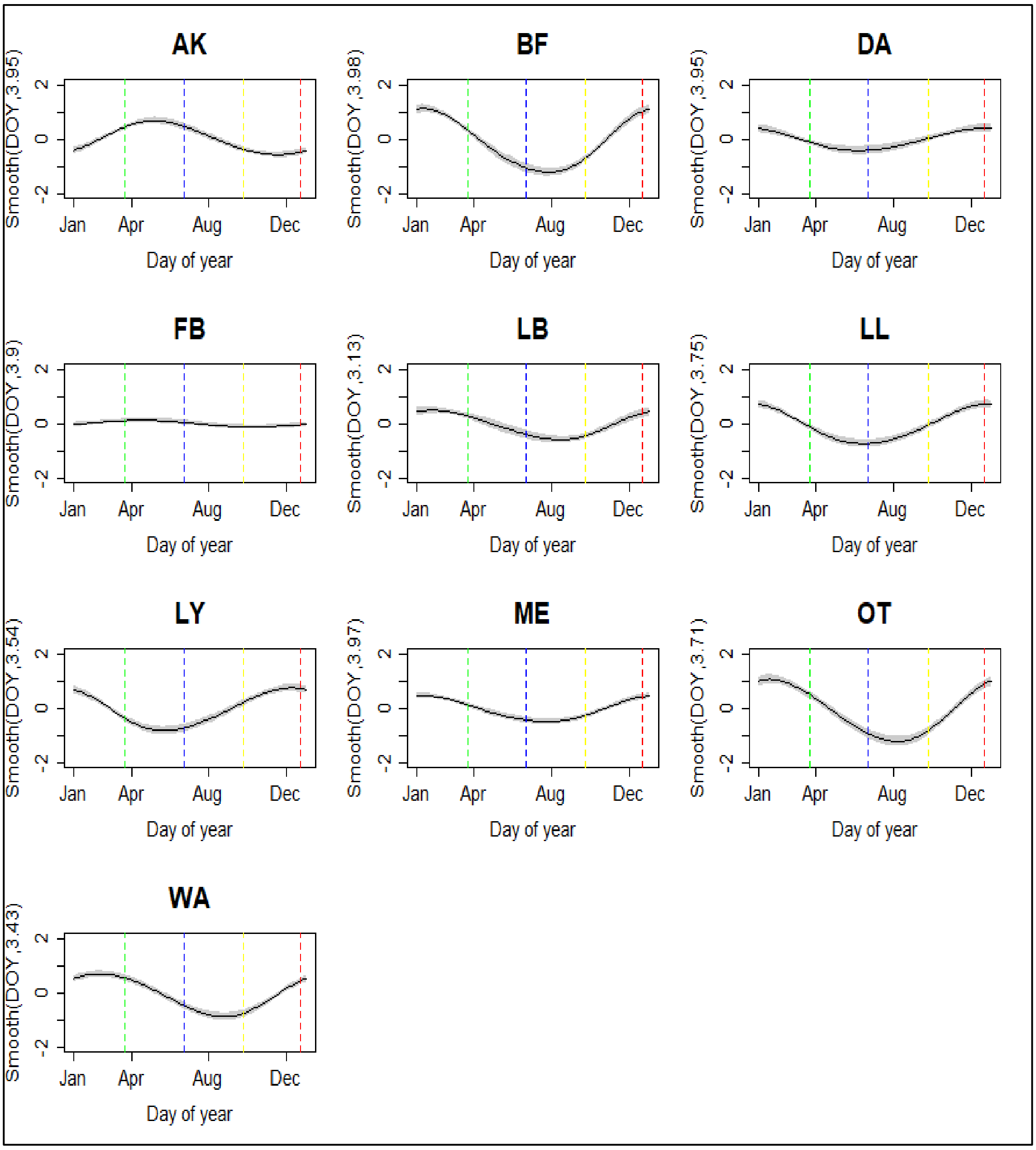

Figure 3.7: The smoothed effect of day of the year (DOY) on the probability of dolphin acoustic presence across the ten monitoring locations. Effective degrees of freedom for each smooth function given on the y-axis. DOY has been fit as a smoothed term with a cyclic spline meaning Dec and Jan are connected. The shaded area represents the 95% confidence band for a given smoothed effect. Dashed lines are given to denote the seasonal changing in the length of the day; green line is the vernal equinox, blue line is the winter solstice, yellow is the spring equinox and red is the summer solstice. Location codes are given in Figure 3.1

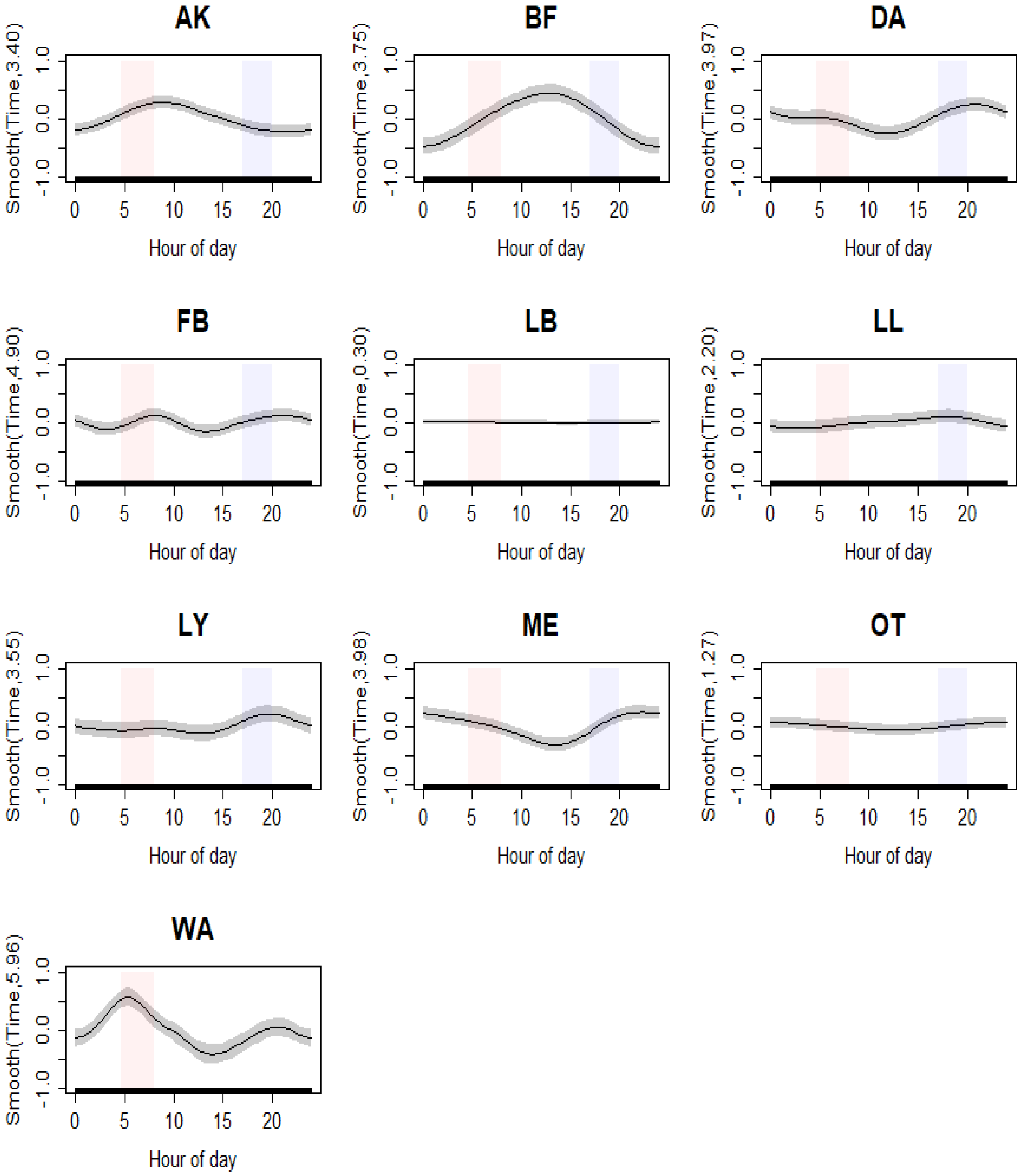

Figure 3.8: The smoothed effect of time (Hour of day) upon the probability of dolphin acoustic presence across the ten monitoring locations. Effective degrees of freedom for each smooth function given on the y-axis. Time has been fit as a smoothed term with a cyclic spline mean 2359 and 0 are connected. The shaded area represents the 95% confidence band for a given smooth. The red vertical shaded area represents the hours of sunrise, blue is sunsent. Location codes are given in Figure 3.1

The influence of time of day on dolphin distribution differs among locations (Fig. 3.8). Akaroa and Wainui had higher probabilities of dolphin detection during the morning. Birdling's Flat showed a peak in the probability of dolphin acoustic presence in the middle of the day and a sharp decline during the night. Menzies Bay and to a lesser extent Damon's Bay exhibited higher dolphin acoustic presence during the night (Fig. 3.8). There was no influence of time of day at the remaining five locations (Table 3.6).

The effect of tide on distribution was weak at most locations (Fig. 3.9). Very small effects were apparent at Akaroa and Wainui where dolphin acoustic presence was highest immediately before high tide (12 & 0 hours; Fig. 3.9). Long Lookout Point was the only location to show a relatively strong association between tidal state and dolphin acoustic presence; here presence was also higher immediately before and at the high tide (Fig. 3.9). The remaining seven locations showed little to no influence of tide upon distribution.

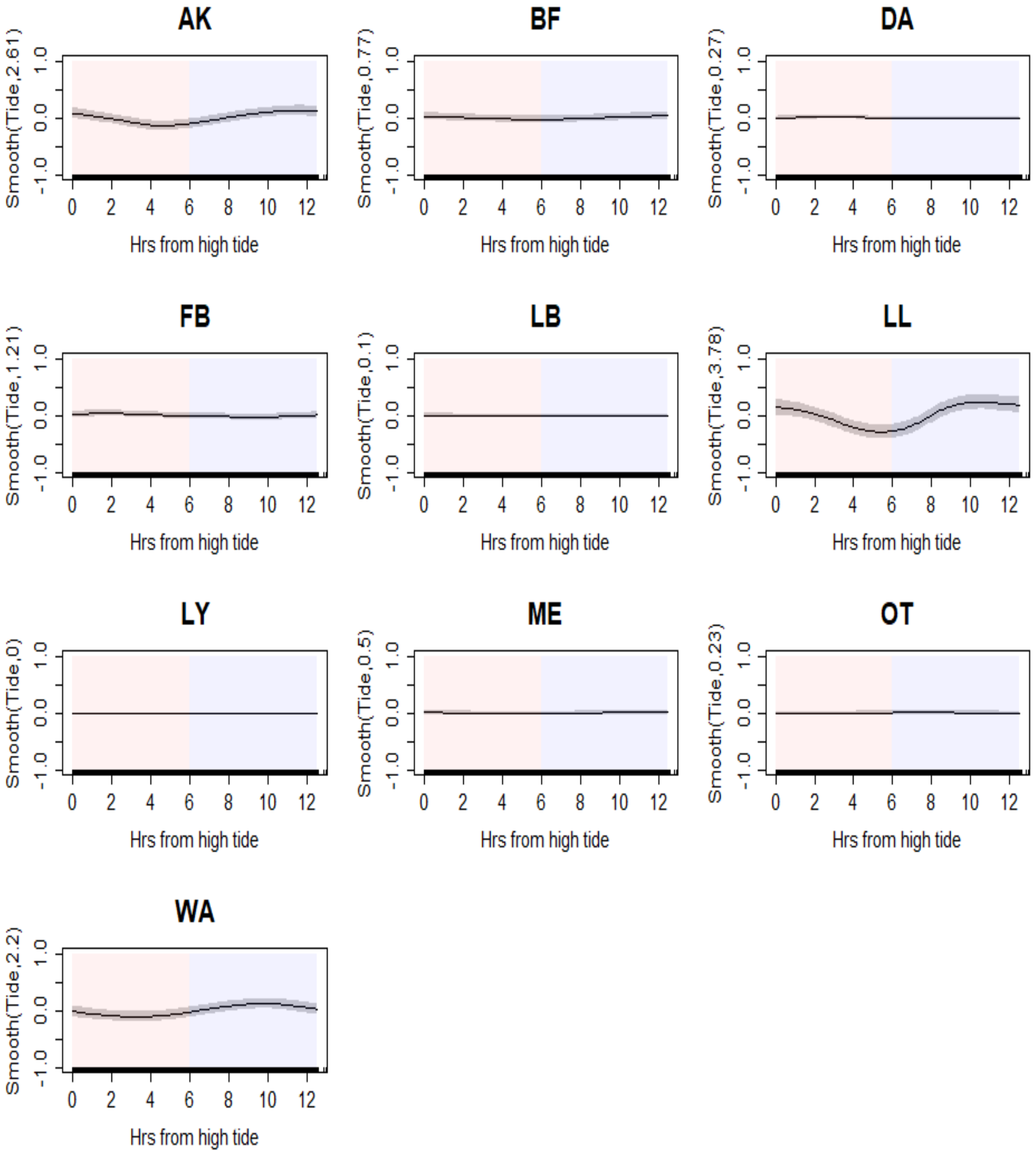

Figure 3.9: The smoothed effect of tide (Hrs from high tide) upon the probability of dolphin acoustic presence across the ten monitoring locations. Effective degrees of freedom for each smooth function given on the y-axis. Semi-diurnal tides persist at Banks Peninsula, with tides approximately 6 hrs apart; 12 and 0hrs represent high tide, 6hrs represents low water. The shaded area represents the 95% confidence band for a given smooth. The red shaded area represents ebb tide, blue is the flow tide. Location codes are given in Figure 3.1.

The effect of location on the distribution of dolphins was highly variable (Fig. 3.10). Predicted values for the effect of location were highest at Long Lookout Pt (1.5), Menzies Bay (0.6) and Birdling's Flat (0.5). Predicted values were lowest and negative at Otanerito Bay, Wainui, Damon's Bay and Lyttelton (Fig. 3.10). With the exception of Menzies Bay, the four hotspots had the highest predicted values for the effect of location. (Fig. 3.10).

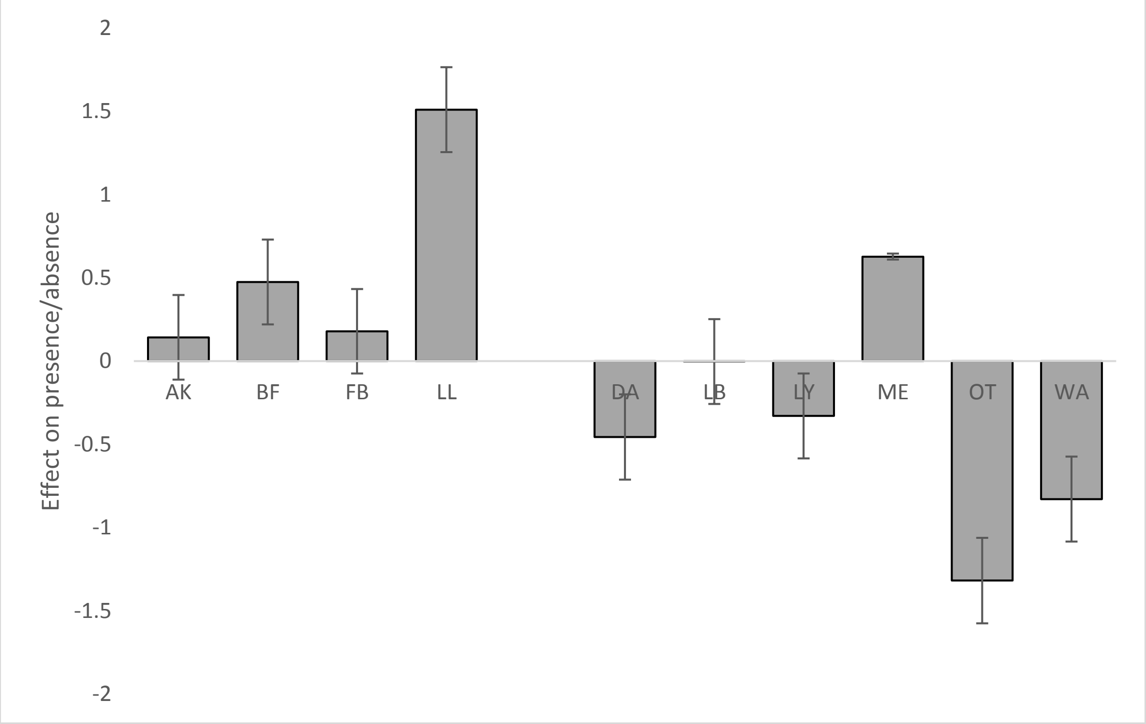

Figure 3.10: The spatial distribution of dolphins. Predicted values for the effect of each level of the random intercept term location from the top-model used to investigate dolphin distribution. Predictions are on the scale of the linear predictor. Hotspot locations are on the left, reference locations to the right. Error bars are +/- standard error on the predicted values. Location codes are given in Figure 3.1.

3.4.5 - Foraging distribution

The best GAMM model (without interactions) for describing the spatial and temporal distribution of foraging was the global model. All three temporal fixed effects parameters; DOY, time, and tide were included in the top-ranked model, as was the random effect of deployment location (Table 3.7). There was strong evidence for this model being favoured above competing models as indicated by higher log likelihood, lower AIC and a model weight of 1 (Table 3.7). However, models without interactions explained only a small amount (max 10.2%) of the deviance in foraging trains per hour.

Table 3.7: Model selection table for the models used to define the best model (without interactions) of foraging behaviour. Models are ranked by AIC and model weight.

Formula	df	logLik	AIC	delta	weight	deviance
DOY+Time+Tide+Location	32	-393202	786470	0	1	10.2%
DOY+Time+Location	24	-393662	787374	904	0	10.0%
DOY+Tide+Location	24	-393840	787729	1259	0	10.1%
DOY+Location	16	-394286	788606	2136	0	9.9%
Time+Tide+Location	25	-402813	805677	19207	0	9.9%
Time+Location	17	-403219	806475	20005	0	7.5%
Tide+Location	17	-403429	806895	20425	0	7.6%
Location	9	-403822	807663	21193	0	7.4%
DOY+Time+Tide	23	-420367	840783	54313	0	3.1%
DOY+Tide	15	-420653	841338	54868	0	3.0%
DOY+Time	15	-421017	842066	55596	0	2.9%
DOY	7	-421289	842595	56125	0	2.8%
Time+Tide	16	-431219	862471	76001	0	0.2%
Tide	8	-431486	862989	76519	0	0.1%
Time	8	-431856	863730	77260	0	0.1%

There was evidence for the inclusion of interaction terms within the top-model for foraging (Table 3.8). Each model that included an interaction between a particular temporal smooth and location had lower AIC values than the global model without interactions. Therefore the top-model for foraging distribution included interaction terms for DOY, time and tide instead of singular smoothed terms. However this model explained only 18% of the deviance in foraging trains per hour (see *discussion*).

Table 3.8: Model selection table used to assess the evidence for the inclusion of an interaction effect between temporal smoothed terms and location. Interactions were deemed better predictors of foraging if models with the interaction had lower AIC values than the global model.

Model	Formula	df	logLik	AIC	Deviance
DOY_I	DOY*Location+Time+Tide+Location	94	-377573	755334	14%
Time_I	DOY+Time*Location+Tide+Location	104	-382541	765292	13%
Tide_I	DOY+Time+Tide*Location+Location	104	-389054	778317	11%
Global_model	DOY+Time+Tide+Location	32	-393202	786470	10%

In the top-model for foraging, the smoothed terms DOY, time and tide were all significant predictors of the number of foraging trains per hour (Table 3.9). All levels of these interactions were statistically significant for each temporal variable (Table 3.9). This suggests that the three temporal variables have some influence on foraging at all monitoring locations and that the nature of each effect is location specific.

Table 3.9: Statistical significance of the smoothed temporal terms and spatial locations on the number of foraging trains per hour taken from the top-model in the foraging set. The top-model contained interaction terms between each temporal variable and deployment location. Significant terms are shown by low p values and ***.

Term	Chi.sq	p-value	Significant
Location	2662	< 2e-16	***
s(Tide): AK	2107	< 2e-16	***
s(Tide): BF	299	< 2e-16	***
s(Tide): DA	1822	< 2e-16	***
s(Tide): FB	431	< 2e-16	***
s(Tide): LB	630	< 2e-16	***
s(Tide): LL	921	< 2e-16	***
s(Tide): LY	79	1.12E-14	***
s(Tide): ME	338	< 2e-16	***
s(Tide): OT	820	< 2e-16	***
s(Tide): WA	212	< 2e-16	***
s(Time): AK	1224	< 2e-16	***
s(Time): BF	953	< 2e-16	***
s(Time): DA	1286	< 2e-16	***
s(Time): FB	978	< 2e-16	***
s(Time): LB	1116	< 2e-16	***
s(Time): LL	1487	< 2e-16	***
s(Time): LY	69	2.22E-13	***
s(Time): ME	2303	< 2e-16	***
s(Time): OT	1760	< 2e-16	***
s(Time): WA	272	< 2e-16	***
s(DOY): AK	8648	< 2e-16	***
s(DOY): BF	4522	< 2e-16	***
s(DOY): DA	65284	1.90E-15	***
s(DOY): FB	2982	< 2e-16	***
s(DOY): LB	6201	< 2e-16	***
s(DOY): LL	3758	< 2e-16	***
s(DOY): LY	2037	4.09E-13	***
s(DOY): ME	2905	< 2e-16	***
s(DOY): OT	1431	< 2e-16	***
s(DOY): WA	1967	< 2e-16	***

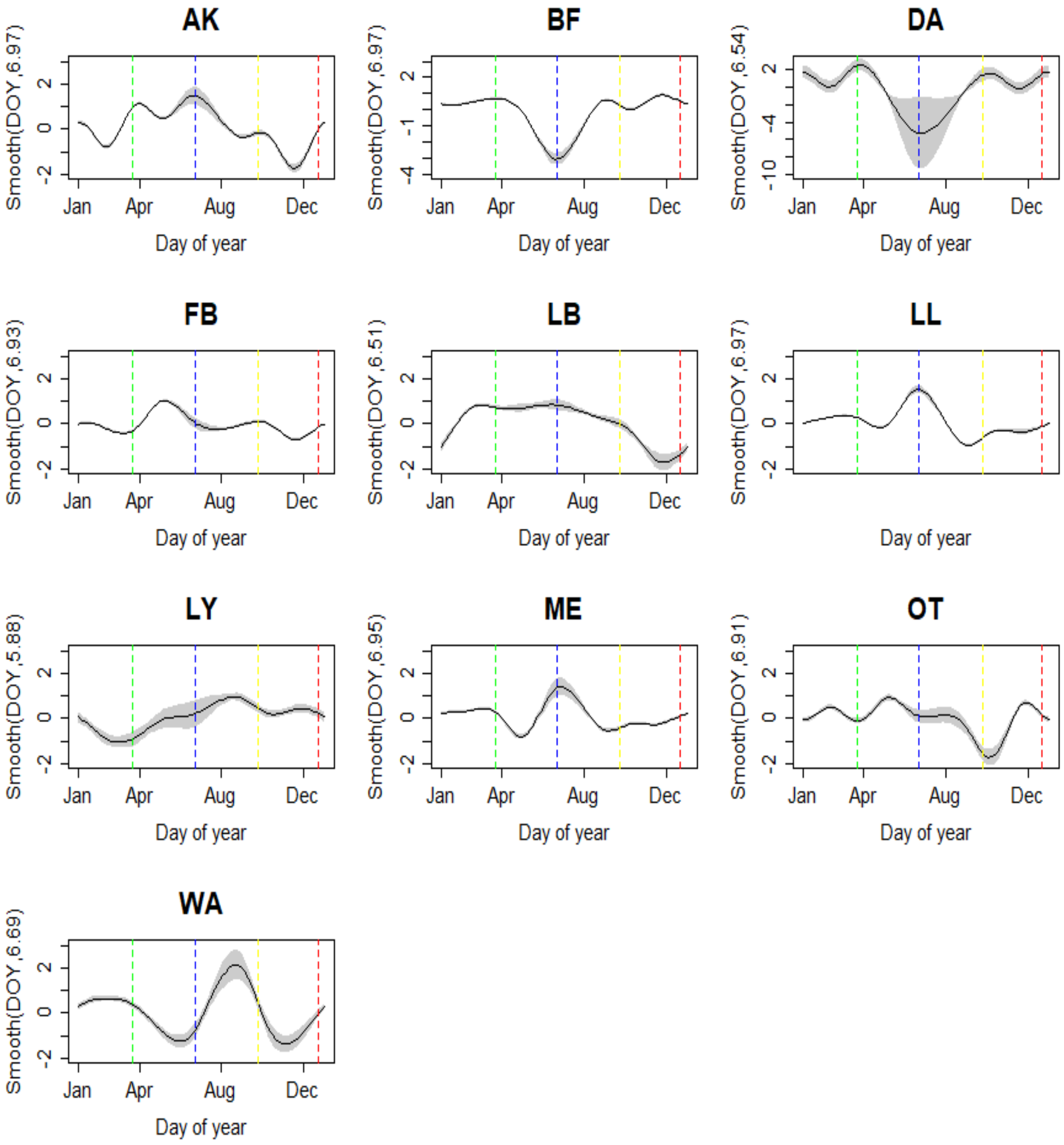

Figure 3.11: The smoothed effect of day of the year (DOY) on the number of foraging trains per hour across the ten monitoring locations. The estimated degrees of freedom for each smooth is given on the y-axis. DOY has been fit as a smoothed term with a cyclic spline meaning Dec and Jan are connected. The shaded area represents the 95% confidence band for a given smooth. Dashed lines are given to denote the seasonal changing in the length of the day; green line is the vernal equinox, blue line is the winter solstice, yellow is the spring equinox and red is the summer solstice. Note the different y-axis scale for DA. Location codes are given in Figure 3.1.

The influence of season (DOY) on the number of foraging trains per hour differs among locations (Fig. 3.11). Some locations show a decline in the amount of foraging during late autumn and through winter (April-August). This is particularly true for Birdling's Flat, Damon's Bay and Otanerito. At Akaroa, foraging peaks between April and June. Flea Bay has limited seasonal variability in foraging, with a small peak around April. Long Bay shows reasonably consistent foraging throughout the year other than a substantial decrease between September and January. Long Lookout also has reasonably consistent levels of seasonal foraging other than a decrease between August and December. Lyttelton Harbour exhibits a strong decline in foraging between January and August. Lastly, Wainui shows a decrease in foraging between April-August but also exhibits a peak in September (spring). There are no obvious trends in terms of seasonal foraging between hotspots and reference locations.

There were substantial differences in diel foraging behaviour among the ten monitoring locations. The number of foraging trains per hour is higher (approx 50%) during the night at Akaroa, Damon's Bay, Menzies Bay and to a lesser extent Flea Bay (Fig. 3.12). Such a trend is also evident in plots of the raw data (Fig. 3.6; Appendix 2c). In contrast, there is more evidence for foraging during daylight hours at Otanerito Bay and foraging peaks in the morning at Wainui. There are small peaks of foraging at dawn and dusk at Long Bay and Long Lookout Pt. Data from Lyttelton show very little effect of time of day upon foraging (Fig. 3.12). Again, there is no clear distinction between hotspots and reference areas in terms of diel foraging behaviour.

Generally, the effects of tide were highly variable and small. Clear effects of tidal state on the number of foraging trains per hour is evident at Akaroa where foraging peaks at high tide (Fig. 3.13). The influence of tide is negligible at Birdling's Flat, Flea Bay, Long Lookout Point and Menzies Bay. Otanerito Bay shows a peak in foraging at mid tide of both ebb and flow (9hrs and 3hrs respectively). Long Bay shows a decline in foraging at high tide. Foraging at Wainui peaks at high tide, yet is highly variable. Other than Akaroa Harbour, all hotspot locations show very little variation in foraging over tidal state (Fig. 3.13).

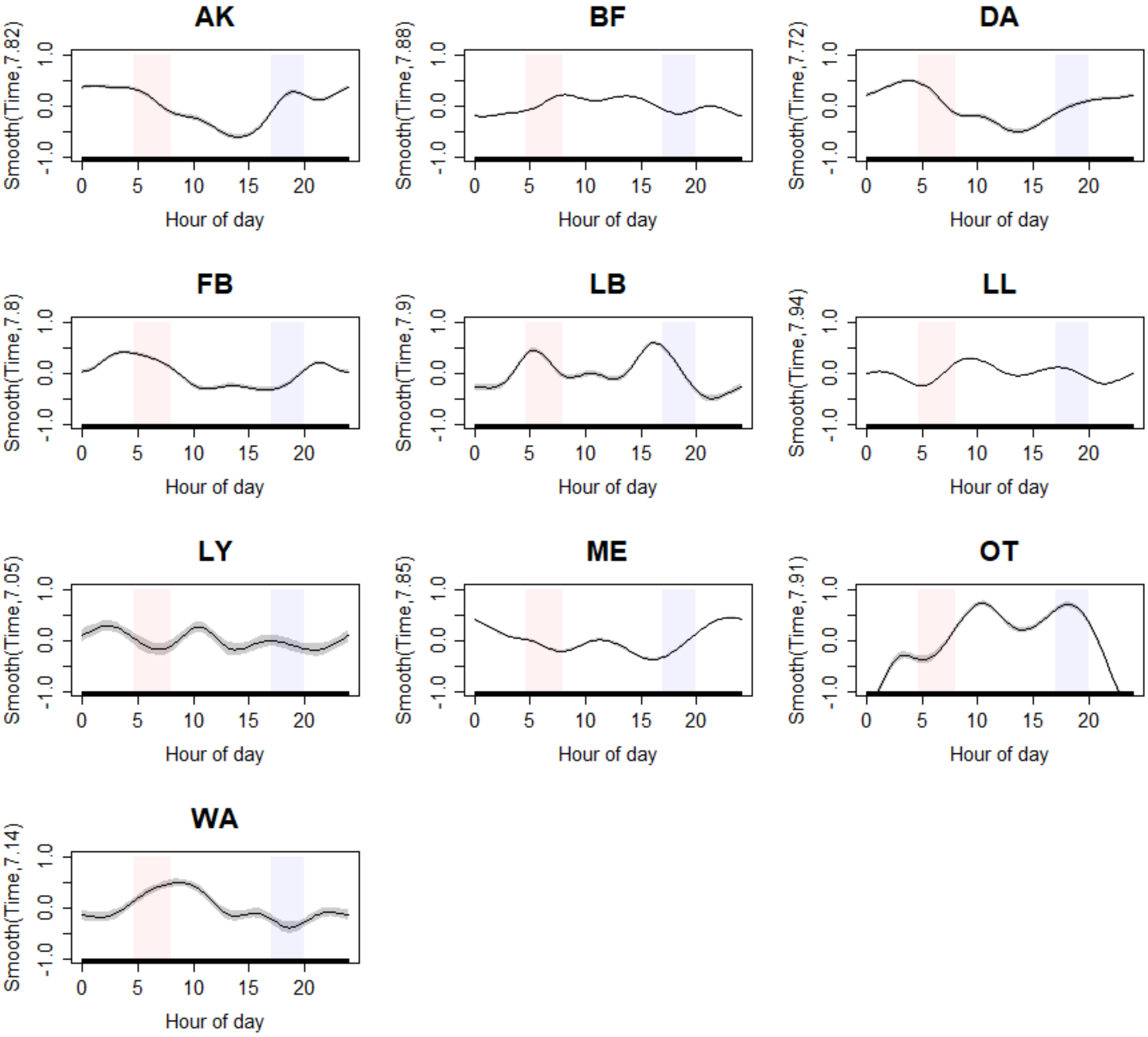

Figure 3.12: The smoothed effect of time (Hour of the day) upon the number of foraging trains per hour across the ten monitoring locations. Time has been fit as a smoothed term with a cyclic spline meaning 24 and 0 are connected. The shaded area represents the 95% co confidence bands for a given smooth. . The red vertical shaded area represents the hours of sunrise, blue is sunset. Location codes are given in Figure 3.1.

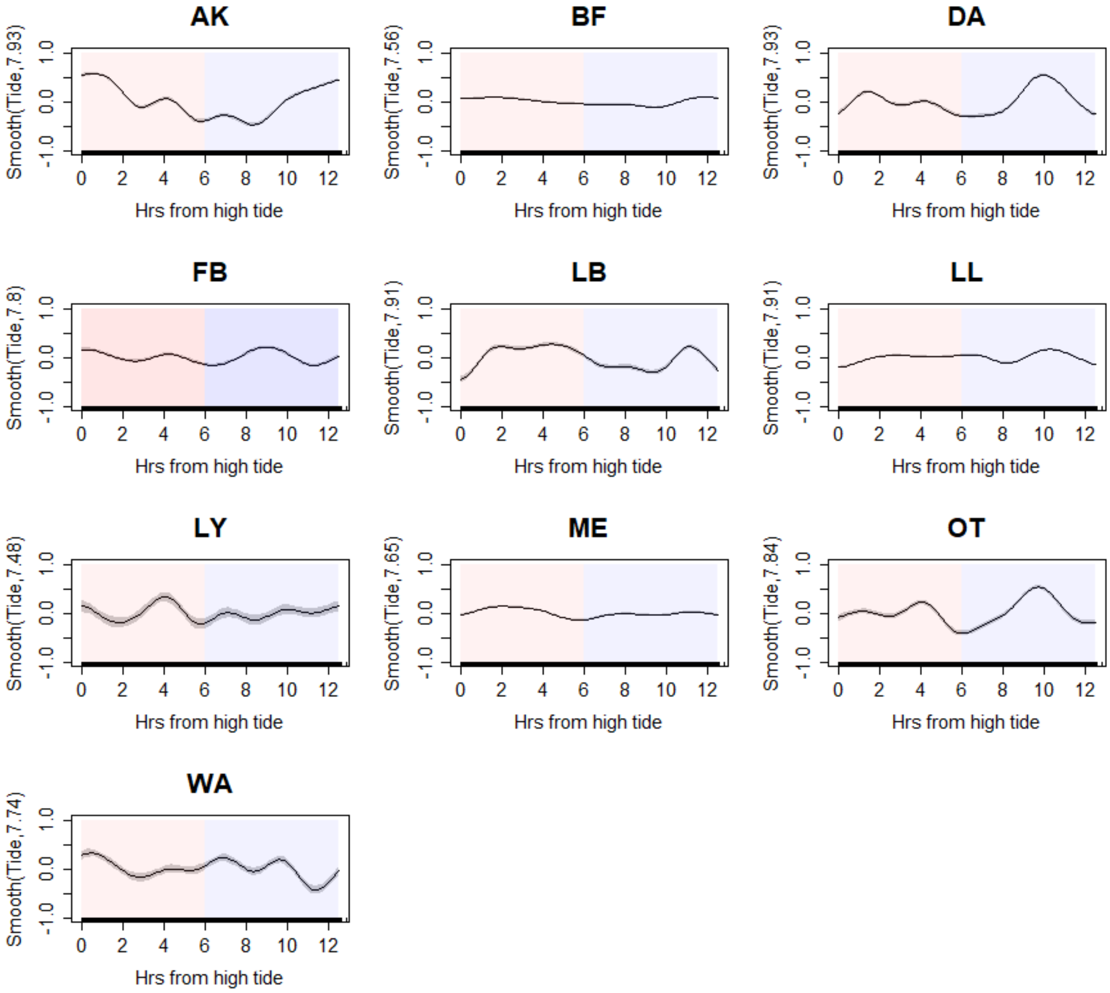

Figure 3.13: The smoothed effect of tidal state (Hrs from high tide) upon the number of foraging trains per hour across the ten monitoring locations. Tides at Banks Peninsula are semi-diurnal with tides approximately 6hrs apart. Therefore 0 and 12 represent high tide and 6 represents low water. Tide has been fit as a smoothed term with a cyclic spline meaning 12 and 0 are connected. The shaded area represents the 95% confidence band for a given smooth. The red shaded area represents ebb tide, blue is the flow tide Location codes are given in Figure 3.1.

The effects of location on FTH showed significant variation in the places where foraging is most often carried out (Fig 3.12). The locations with the largest, positive effect on foraging were Birdling's Flat, Long Lookout Point, Akaroa and Flea Bay respectively (i.e. the four hotspots). However, the difference between Akaroa Harbour (0.41) and Menzies Bay (0.36) is not large. Wainui, Damon's Bay and Lyttelton had strong, negative effects on foraging (Fig. 3.14).

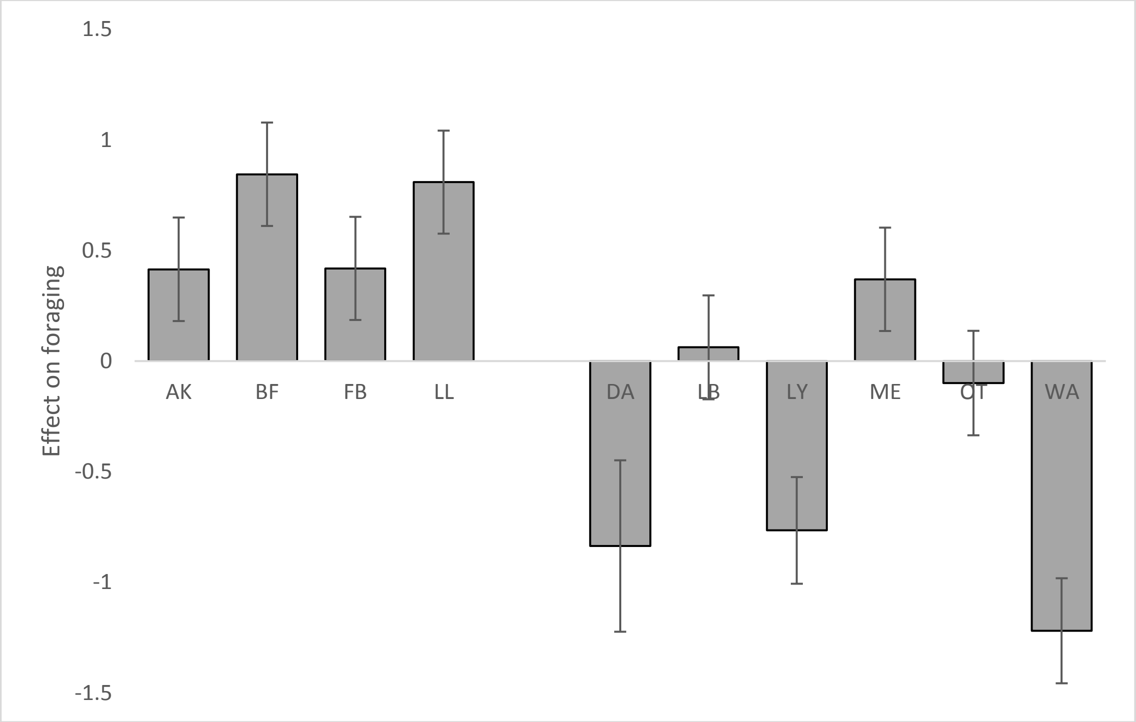

Figure 3.14: The spatial distribution of foraging behaviour among the ten monitoring locations. The predicted effects of foraging were obtained for each level of the random intercept of location from the top foraging model. All fixed effects were set to null. Hotspot locations are on the left, reference locations to the right. Error bars are +/- standard error on the predicted values.

3.4.6 - Model diagnostics

The models used to assess distribution and foraging showed good evidence for homogeneity of variances across fitted values and individual smoothed terms (Appendix 2a). QQ-plots suggested a binomial distribution was correct for the distribution models, yet, the simulation of the foraging residuals suggested a departure from the poisson distribution. Tests on the distribution of the response variable gave good evidence for a poisson distribution. Thus it was likely the marked departure from the QQ-plot distribution is a product of the simulation using discrete data (Wood 2017). The effect of this departure on model performance is unknown.

ACF plots for each model set before and after the application of the AR1 temporal correlation matrix show a substantial decrease in the correlation of model residuals. This confirms the assumption of independent model residuals (Appendix 2a).

The degrees of freedom for the smoothed terms in each model set were set at the lowest value that was not over-restrictive. In some cases however, max *k* had to be increased to relatively high values to ensure no restriction of the terms (Fig. 3.11). This was the case with the temporal effects for the foraging framework, and describes why these terms are more complex compared to the temporal effects on distribution.

3.5 - Discussion

3.5.1 - Buzz classification

Gaussian mixture models (GMM) proved a useful tool for determining likely acoustic signals of foraging. Using all ICIs that had a probability >0.99 of belonging to the first gaussian component, ICIs shorter than 7.6 ms were considered to be ‘buzzes’. This is equivalent to a repetition rate of 129 Hz. The multi-modal distribution of ICIs has been used to determine buzzes in a range of odontocete species (Madsen et al. 2005; Pirotta et al. 2013), including harbour porpoise (Carlström 2005; Williamson et al. 2017) that are acoustically very similar to Hector’s dolphins (Thorpe et al. 1991; Goodson and Sturtivant 1996). Carlström (2005) showed that ICIs within the first gaussian peak were strongly associated with feeding in harbour porpoise. Other studies report similar modal distribution of ICIs as those documented here, with a peak representing foraging behaviour with short ICIs and another representing ‘other’ processes with longer ICIs around 30ms (Pirotta et al. 2013; Williamson et al. 2017).

In this study, processes other than foraging are assumed to be fully represented by acoustic signals that belong to the second gaussian component, referred to as ‘regular ICIs’ in Pirotta et al. 2013. Currently, there is no way to test this assumption. Research on the behavioural context of harbour porpoise acoustics benefits from studies that match in-situ behaviour with the characteristics of acoustic signatures, often in captivity (de Ruiter et al. 2009; Verfuß et al. 2009). Such detailed analysis of Hector’s dolphin acoustics is lacking, however we do know they produce sounds that show the typical buzz characteristics, particularly when approaching objects at close range (Dawson 1991b). Dawson (1991b) also documented acoustic signatures of social behaviours termed a ‘cry’ with repetition rates much higher (>200Hz) than the buzz ICIs used in this study. An additional biological process, with ICIs shorter than buzzes, was not apparent from the distribution of GMM components. Thus, some acoustic signatures of social behaviour may be included as foraging in this study. If behaviours other than foraging are also represented by ICIs shorter than 7.6 ms, it is likely that they are much less common; small delphinids in temperate areas are known to spend the majority of time foraging (Ribeiro et al. 2007; Stockin et al. 2009; Wisniewska et al. 2016).

There may be some coarseness in this buzz classification as every ICI shorter than 7.6 ms may not represent a foraging event. However, it is likely that using GMM to define buzz clicks is a considerable advance on the standard technique that uses an arbitrary 10ms threshold for buzz classification (Carlström 2005; Verfuß et al. 2009; Leeney et al. 2011; Nuuttila et al. 2013; Wang et al. 2015a). Additional confidence in the 7.6 ms buzz threshold may be obtained by conducting a sensitivity analysis to determine the sensitivity of the modelling approach to variable buzz thresholds.

3.5.2 - General distribution patterns

The effect of season on the probability of dolphins being present shows a significant pattern of higher probabilities during the summer months between Jan-Mar. This is a well-established trend in the seasonal distribution of Hector's dolphins; with the dolphins becoming more spread out in their offshore extent during winter (Dawson and Slooten 1988; Rayment et al. 2010a, 2011a; MacKenzie and Clement 2014). Akaroa Harbour was the singular exception to this trend, where dolphin relative abundance peaked in May. This has important connotations for management; amateur set-netting is allowed at some locations in Akaroa Harbour from April through to October, when the dolphins are assumed to be at low densities.

Time of day was a significant predictor of dolphin distribution at four of ten locations. Where it was significant, the probability of acoustic presence agreed closely with the peaks in the number of foraging trains per hour. At these four locations, we can conclude that diel foraging influences dolphin distribution. The fact that in six locations time of day was significant at describing foraging but not distribution suggests that dolphins may occupy these sites throughout the day but forage more at particular times.

Tide was significantly correlated with dolphin distribution at three locations, but of these, effects were strong at Long Lookout Point only, where distribution peaked during the flow tide. Elsewhere, it appears that state of the tide influences foraging rates but not distribution. This is probably explained by foraging rates increasing at locations and times when features such as eddies, wakes and fronts occur, that in turn influence the prey field (Johnston et al. 2005; Bailey and Thompson 2010; Pirotta et al. 2013). Dolphins may choose to be present throughout the tidal cycle in anticipation of particularly good foraging conditions at the onset of such tidal features.

Each hotspot location had a positive effect on the probability of dolphin acoustic presence, but the reference area Menzies Bay had also had a strong positive effect. Visual (Chapter 2) and acoustic methods provide different, and complementary information on the importance of locations to marine mammals (Kimura et al. 2009; Rayment et al. 2018). For example, in Menzies Bay, dolphins seem to be present and forage more at night, when our visual surveys are not carried out. Interestingly, Menzies Bay is the only study location that has aquaculture (cultivation of mussels; *Perna canaliculus*). In NW Spain, bottlenose dolphins have been shown to regularly aggregate and forage at mussel farms (Díaz López and Methion 2017). Research into whether mussel farms influence distribution and foraging in Hector's dolphin at Banks Peninsula is ongoing.

3.5.3 - Temporal distribution of foraging

The results from the GAMM analysis show that foraging varies on several temporal scales. Interestingly, trends in temporal foraging activity were much more complex than general distribution patterns. This suggests that the temporal distribution of foraging is more difficult to predict and may reflect the highly patchy nature of prey. A seasonal effect on foraging was seen at all locations, but this effect was different from one area to another. Peaks in foraging were observed during summer or autumn at five locations- agreeing with the peaks in general distribution. This could be explained by prey being either more abundant, aggregated or catchable at this time of the year at these sites (Macleod et al. 2004; Gende and Sigler 2006; Sveegaard et al. 2011). Some Hector's dolphin prey (e.g. red cod) are more abundant in shallow, coastal waters during summer (Beentjes and Renwick 2001; Miller 2014). Therefore, differences among locations in terms of seasonal foraging may reflect habitat preferences of these prey.

The lowest values of foraging were observed in winter at five locations, but several had small peaks of foraging during winter. This, along with peaks in foraging in spring and autumn, suggest that foraging rates are high throughout the year. The discrepancy between seasonal effects on distribution and foraging is likely influenced by the small bodied dolphins needing to sustain very high foraging rates year-round to meet energetic requirements. In fact, those requirements may actually increase over months when the water is cooler (Wisniewska et al. 2016). There is some evidence that prey such as sprat (Colman 1979) and mullet (MPI 2017) spawn during winter and spring. If spawning occurs at certain locations this could explain some of the variability in seasonal foraging rates.

Foraging varied on diel scales, but with significant variability between locations. Diel trends in foraging behaviour have been observed in a wide range of cetaceans (Baumgartner et al. 2003a; Carlström 2005; Soldevilla et al. 2010; Pirotta et al. 2013; Wang et al. 2015a; Schaffeld et al. 2016). In this study, three locations showed clear evidence of nocturnal foraging (Menzies and Damons Bay, Akaroa). That both general distribution (Fig. 3.8) and foraging (Fig. 3.12) is higher during the night at Menzies and Damon's Bay suggests animals are moving out of these locations during the day. In contrast, distribution in Akaroa peaks during the morning suggesting that animals are preferentially foraging at night while being present in the harbour throughout the day. Some Hector's dolphin prey, including red cod and arrow squid, are reportedly more active at night (Uozumi 1998; Francis 2013). Red cod for example are thought to dwell in caves/cracks in reefs during the day and move onto sediment dominated habitat to feed at night (Francis 2013). Other diel foraging observed in this study included peaks of buzzing at early morning and late afternoon and peaks during daylight hours. Observations of both these diel foraging strategies have been recorded in other marine predators (Oleson et al. 2007; Calambokidis et al. 2008; Regular et al. 2010; Schaffeld et al. 2016). Dusky dolphins in Admiralty Bay spend a substantial amount of time foraging on schooling epipelagic fish during the day (Benoit-Bird et al. 2004). Interestingly, the same species several hundred kilometres further south forages almost exclusively at night on the DSL in the Kaikoura submarine canyon (Benoit-Bird et al. 2004). Such diversity in diel foraging within and among species demonstrates versatility in foraging tactics and suggests that animals adapt to the available prey field in time and space.

Whilst small, the effects of tide on foraging were statistically significant meaning tide does play some role in regulating when Hector's dolphins forage. However, the very large dataset analysed in this study is likely to contribute to the statistical significance of effects that are relatively small and not necessarily biologically significant (similar to Dawson et al. 2013). The effects of tide differed among locations, the most obvious effects occurring when foraging peaked around high tide. Many studies on marine mammals show that tidal state influences when animals are present (Baumgartner et al. 2003a; Johnston et al. 2005; Lin et al. 2013; Wang et al. 2015b) or when they forage (Zamon 2001; Bailey and Thompson 2010; Pirotta et al. 2013). As with the other temporal processes, the effects of tide on foraging are generally thought to relate to the dynamics of the prey field (e.g. Hastie et al. 2004; Bailey and Thomspson 2010).

Tidal influences on marine communities can be significant (Viehman et al. 2015). The state of the tide dictates the flow and set of tidal currents (Goring 2001; Pisoni et al. 2015) and the generation of tidal features such as eddies and wakes (Johnston et al. 2005; Ansorge et al. 2015; Russell and Vennell 2017). These features are known to aggregate fish and increase foraging rates in top-predators (Johnston et al. 2005; Bailey and Thompson 2010). A strong south-north tide flows around Banks Peninsula and creates a large eddy in Pegasus Bay (Reynolds-Fleming and Fleming 2005). How this tidal flow results in fine-scale oceanographic features (i.e. on the same spatial scale as this analysis) is unknown. At Otago Peninsula, localised upwelling derived from enhanced secondary flow is created by the interaction of tidal currents and a prominent headland (Russell and Vennell 2017). The upwelling is more pronounced at tidal states with greater flow (Russell and Vennell 2017). Given the similarity between Banks and Otago Peninsula in terms of tidal range and geomorphology, it is possible that such features also occur at Banks Peninsula.

Understanding the importance of the temporal processes on foraging and distribution provides valuable information for conservation. This chapter has identified three locations where foraging and relative abundance is higher during the night, information not previously available using analyses of visual sightings made during the day (Chapter 2). In order for management to have positive outcomes it is important that to quantify when/where diel trends in habitat selection exist as, seemingly, some important habitat could be overlooked if the classification of hotspots is based solely on daytime data. Similarly, the seasonal analyses shows that some locations are frequently used and/or have high foraging rates at times other than summer. Amateur set-netting is permissible from April to October in some areas on the peninsula, including in parts of Akaroa Harbour where dolphin detections and foraging peaked in April-May. Clearly, this information needs to be considered when appraising the risk of the set-net allowance.

3.5.5 Spatial distribution of foraging behaviour

There were significant differences in foraging behaviour across the ten monitoring locations. Predicted values of foraging were higher at the four 'hotspot' locations than at the reference areas. This provides evidence that hotspot locations are in fact hotspots for foraging. Foraging was also high at Menzies Bay. Although not considered a hotspot by the analysis of visual sightings (Chapter 2), Menzies had high acoustic relative abundance; adding further weight to the relationship between distribution and foraging patterns.

As mentioned earlier, these small dolphins likely have high energetic requirements that require very high foraging rates (Johnston et al. 2005; Kimura et al. 2012; Wisniewska et al. 2016). It is therefore not surprising that hotspots in distribution will also be hotspots for foraging behaviour. Hotspots in distribution are also foraging hotspots for bottlenose dolphins in Moray Firth, Scotland (Hastie et al. 2004). Further, the distribution of Steller's sea lions (*Eumetopias jubatus*) is also explained by the concentration of foraging into discrete patches where forage fish are particularly abundant (Gende and Sigler 2006). It seems inevitable therefore, that the distribution of foraging opportunities shapes the overall distribution patterns of many marine predators.

While foraging is clearly a significant driver of habitat selection, other behaviours and processes also influence where animals aggregate. Behaviours such as resting (Garaffo et al. 2007; Notarbartolo di Sciara et al. 2009; Blasi and Boitani 2012) and breeding/nursing (Weir et al. 2008; Rayment et al. 2015) influence habitat selection. For example, spinner dolphins in the Red Sea use sheltered coral atolls as resting habitat during the day (Notarbartolo di Sciara et al. 2009; Fumagalli et al. 2018). Similarly, common dolphins use the large, sheltered Hauraki Gulf as a calving and nursery area (Stockin et al. 2009). In this study, the effect of Akaroa and Flea Bay on foraging was lower than the other hotspots. Perhaps these shallow, sheltered locations are also important for other behaviours (such as nursing).

Two locations, Wainui and Lyttelton, had low levels of foraging and fewer dolphins. These are also the two locations that have the greatest exposure to human impacts; particularly Lyttelton which has high levels of noise pollution from vessels and industrial activity (Leunissen and Dawson 2018). Noise pollution can cause animals to leave areas of high impact (Morton and Symonds 2002; Madsen et al. 2006) and to alter their 'normal' behaviour (Buckstaff 2004; Guerra et al. 2014; Pirotta et al. 2015). How anthropogenic factors influence foraging in Hector's dolphins is unknown.

3.5.6 Model performance

The models used to assess the dynamics of foraging and distribution provided statistically significant results, but it should be noted that their performance at explaining overall deviance in these variables was relatively low (distribution and foraging top-models; 14 and 18% respectively). This suggests other (unmeasured) variables could better describe variation in these processes. This is not surprising. Dolphins are large brained mammals with complex, sophisticated behaviour (Marino et al. 2007). A myriad of ecological and social factors could influence distribution and foraging. These analyses aimed to assess broad temporal patterns that may be useful for management, and are thus unavoidably coarse.

3.6.6 - Conclusions

The hotspots identified in chapter 2 are indeed areas in which foraging occurs disproportionately often. Thus, foraging opportunities strongly influence the overall distribution patterns of Hector's dolphins. I have also shown that foraging varies broadly over seasonal, diel and tidal temporal scales, but does not always match when dolphins have a higher probability of being present. This is due to temporal trends in foraging being more complex than general distribution patterns.

Effective conservation management can benefit from knowing when and where foraging happens most often. Impacts from tourism, coastal development and high vessel traffic are present throughout the study area (Stone and Yoshinaga 2000; Martinez et al. 2012).

This chapter also provides a platform upon which to investigate the ecological drivers of hotspots and foraging distribution. Further chapters will assess the ecological factors associated with hotspots to determine the biophysical relationships governing where this endangered and ecologically important species aggregates and forages

Chapter 4: A simple hydro-acoustic method to quantify the epipelagic prey of coastal top-predators

Chapter status: In Review as an article in PLoS One: Brough TE, Rayment WR, Dawson S. (In Review 2019). Using a recreational grade echosounder to quantify the potential prey field of coastal predators. PLoS One.

Authorship statement: TB conceived of initial research idea, TB, WR and SD developed research methods, SD provided advice on acoustics, TB acquired data, performed analyses and wrote the manuscript, WR, and SD provided feedback on manuscript preparation.

4.1 - Introduction

The distribution of marine top-predators generally reflects that of their prey (Crawford and Shelton 1978; Baumgartner et al. 2003a; Fauchald 2009; Benoit-Bird et al. 2016). For this reason, studies that investigate the habitat use and distribution of predators greatly benefit from data that quantify prey (Gende and Sigler 2006; Redfern et al. 2006; Benoit-Bird et al. 2013). Such data have been shown to improve the predictive power of habitat models (Torres et al. 2008; Palacios et al. 2013), elucidate threats associated with prey depletion (Bearzi et al. 2006, Bedford et al. 2015) and can contribute to marine spatial planning (Hooker et al. 2002, 2011). Generally, the prey of marine mammals is highly varied within species, and certainly among them (Tollit and Thompson 1996; Gannon and Waples 2004; Morrissette et al. 2006). Diet diversity, coupled with the extreme spatial and temporal patchiness typical of most prey species, greatly increase the difficulty of quantifying prey availability for marine mammals.

Patchiness over multiple temporal and spatial scales (Fauchald 2009; Benoit-Bird et al. 2013; Hazen et al. 2013) is the main challenge with sampling the pelagic prey that make up the diet of a wide range of top-predators (Fauchald and Erikstad 2002; Certain et al. 2011; Bedford et al. 2015). Several methods are used, including mid-water baited underwater video, trawling, set-netting, and hydro-acoustics (Auster et al. 1992; Mhlongo et al. 2015; McCluskey et al. 2016). Baited underwater video (BUV) can be used to measure abundance, species composition and size distribution of pelagic fish (Heagney et al. 2007; Santana-Garcon et al. 2014), and has the advantage of being non-destructive. Relative abundance information is often based on counts of the maximum number of fish of a particular species recorded over a set deployment time (Heagney et al. 2007; Santana-Garcon et al. 2014). Other sampling methods for pelagic fish communities involve fisheries techniques such as trawling (Postuma 1972; Harley et al. 2001; Witteveen et al. 2008) or set-netting (Hansson and Rudstam 1995; McCluskey et al. 2016) to provide similar information on fish abundance, diversity and size. Fishing techniques typically estimate fish relative abundance via catch per unit effort (CPUE) metrics (Harley et al. 2001; Torres et al. 2008).

Increasingly, hydro-acoustics are used to obtain data on pelagic prey (Lawson et al. 2001; Benoit-Bird et al. 2004; Certain et al. 2011; Bedford et al. 2015; Lawrence et al. 2016). In a hydro-acoustic survey, pulses from echo-sounder or sonar transducers are used to ensonify the water column. A set of well-known physical relationships between the properties of the acoustic signal and the environment allow the interpretation of backscattered acoustic energy to provide biologically meaningful information (Simmonds and MacLennan 2005). The quality of this information is dependent on knowledge of the scattering sources at the seafloor and in the water column and the stability of the transmitter. For example, based on the unique acoustic impedance values of biological and physical scattering sources, the amplitude of a reflected signal can identify particular physical features, biological taxa and even species (Lu and Lee 1995; Lawson et al. 2001; Simmonds and MacLennan 2005). Further, when properties of the acoustic beam pattern and geographic location of a pulse are known accurately, acoustic backscatter can provide data on the size of scattering targets (O’Driscoll and McClatchie 1998; MacLennan et al. 2002; Benoit-Bird and Au 2003). Calibration of acoustic equipment (Foote et al. 1987) allows for direct estimation of abundance, density and subsequently biomass of biological aggregations, given that species’ target strength relationships are known (Simmonds and MacLennan 2005).

Hydro-acoustic methods offer many advantages for quantifying prey fields. These include the ability to integrate prey data over multiple spatiotemporal scales (Davoren et al. 2003; Trenkel et al. 2011; Godø et al. 2014), the capacity to measure the patch characteristics of prey (Fauchald and Erikstad 2002; Benoit-Bird and Au 2003; Benoit-Bird et al. 2013) and the compatibility of the method with concurrent observations of predators (Davoren et al. 2003; Benoit-Bird et al. 2004; Certain et al. 2011; Lawrence et al. 2016). In addition, there are clear advantages in the method being non-destructive. For many research programmes, however, the significant cost involved with the purchase or hire of a scientific echo-sounder (SES), and the expertise or logistic requirements to operate such equipment, are major drawbacks. This may reduce the repeatability of prey surveys and therefore constrain the sample size required to resolve a patchy prey field. Several modern, recreational grade echo-sounders (RGE) allow on-board recording of the digital echo-return data, and can, within certain limitations, provide an alternative to SES. RGE systems function in exactly the same way as SES, although they typically have less power and lower signal to noise ratio (Spitael 2007; McInnes et al. 2015). RGE have been used to quantify aspects of predator prey overlap in deep water habitats (Benoit-Bird et al. 2004) and in coastal settings (McInnes et al. 2015), as well as for mapping fish schools in shallow coral reefs (Lotz et al. 2007). Without calibration it is not possible to identify prey aggregations to species level, and therefore RGE systems can only quantify 'potential prey'. Given the generalist diet of many predators and their preference for prey taxa that are most abundant, this may not be a significant drawback. If raw data on echo-returns can be saved by RGE and information is available concerning the properties of the acoustic pulse and beam pattern, RGE systems offer an inexpensive option for obtaining reliable data on prey distribution.

Epipelagic fish and invertebrates are important components of the diet of many coastal marine mammals (Pauly et al. 1998b; Certain et al. 2011; Miller et al. 2013) and seabirds (Crawford and Shelton 1978; Fauchald 2009; Regular et al. 2010). Epipelagic clupeid fishes including pilchards and sardines (*Sardinops spp.*) and anchovy (*e.g. Engraulis spp.)* are often considered high quality prey for top-predators due to their high calorific value (Dahdul and Horn 2003; Grémillet et al. 2008b; Spitz et al. 2010). Very little is known about the distribution of epipelagic schooling fish in NZ waters, particularly at the fine-scales required to determine overlap with marine predators. Knowledge of the distribution and habitat preferences of epipelagic fish is important in its own right as these taxa are vital links in marine food webs between zooplankton and higher predators (Cury et al. 2000; Griffiths et al. 2013). Impacts on temperate epipelagic fish communities from climate change (Jacobson et al. 2001; Chavez et al. 2003) and overfishing (Bearzi et al. 2006; Grémillet et al. 2008b) add further weight to the need to understand the spatial ecology of these important taxa.

Visual surveys of predators, with concurrent observation of prey, offer opportunities to investigate how aspects of the prey field influence the distribution of multiple predators (Scott et al. 2010;

Benoit-Bird et al. 2013). This information can help resolve niche differentiation among predator species and determines habitat-links among oftentimes diverse taxa. Banks Peninsula has an abundance of predators that target epipelagic prey including little penguins, Hector's dolphin, NZ fur seal and spotted shags (Allum and Maddigan 2012; Flemming et al. 2013; Miller et al. 2013). Further, epipelagic species such as NZ sprat (Colman 1979; Whitehead et al. 1985) are known to be particularly abundant in waters around the peninsula. Small, surface-schooling fish form large aggregations in the nearshore habitat of this area (pers obs), which should be readily detected by RGEs. These features provide an opportunity to trial the use of an RGE to quantify aspects of the epipelagic fish community and relate these to the distribution of top-predators.

4.1.2 - Chapter objectives

- Assess the capability of a recreational grade echo-sounder to detect schools of epipelagic fish in shallow coastal habitat.
- Carry out a ground truthing of the echo-sounder with known epipelagic schools to provide information on the school dimensions and relative scattering intensity of the potential prey of top-predators.

4.2 - Materials and methods

4.2.1 - Hydro-acoustic systems

The hydro-acoustic systems used in this study were two similar 'off the shelf' recreational grade echo-sounders produced by Lowrance Marine Electronics (Tulsa, USA) and Simrad (Simrad Ltd. Oslo, Norway). Two systems were used because the original unit (Lowrance) installed on the survey vessel was upgraded in January 2016 to the Simrad system with side scan sonar capabilities (Chapter 6). The Lowrance was a 2014 Elite-7 chirp that powered a hybrid dual imaging (HDI), multi-frequency, dual beam transducer with two elements capable of transmitting and receiving at 50/200kHz and 455/800kHz. The transducer was mounted on the transom 0.5m below the waterline. The Simrad system (2016 NSS7 evo2) used the same transducer.

Both systems offered some user control of the operational settings. Ping rate and gain were set manually after field trials to find optimum values for the survey area (Table 4.1). Source level is automatically configured to the various range settings and could not be quantified reliably or set manually. The Simrad system supplies a maximum of 1000W power, however it is unlikely such power is achieved at 200 kHz transmit frequency (Korneliussen et al. 2008). The Lowrance system has a maximum power output of 250 W. For these surveys the systems were set to 'shallow water mode', which sets pulse length of 0.2ms and applies no time-varied gain function to water column samples (Navico pers. comm.). Other settings at the echo-sounder console included 'noise rejection' and 'surface clarity' functions that reduce unwanted stochastic artefacts from the echogram display. Both functions were set to 'medium', however from inspection of logged data with different values of these settings it seems these functions did not influence the raw data.

Both Simrad and Lowrance are owned and operated by the same parent company (Navico Ltd, Lysake, Norway). Consequently the two echo-sounders were very similar in their operation and, importantly, in the way they stored acoustic data. Navico echo-sounders store data on raw echo returns written to a compressed format in a '.sl2' file. The files consist of binary strings that code for particular parameters associated with the echo return and navigation. The software Sonar TRX (Leerand Engineering Inc.), used for analysis and mosaic construction of side scan sonar data, reads and exports raw data from .sl2 files in 1000 ping clips. Both units also have in-built GPS receivers so latitude, longitude and precise UTC time data are stored from the GPS string respective for every ping.

Table 4.1: Relevant settings for both hydro-acoustic systems used in this study. Both systems used the same transducer.

Parameter	**Simrad NSS7 evo2**	**Lowrance Elite-7**
Transducer	HDI 50/200 455/800 kHz	HDI 50/200 455/800 kHz
Max depth	755 m (@ 50 kHz)	755 m (@ 50 kHz)
3dB beam angle	12°	12°
Frequency	200 kHz	200 kHz
Ping rate	9-13 Hz	9-13 Hz
Sampling rate	3072 bytes per ping	1920 bytes per ping
Pulse length	0.2ms	0.2ms
Gain	System value: 5	System value: 55
Time Varying Gain (TVG)	None	None
Output power	1000 W RMS (Maximum)	250W RMS (Maximum)
Source level	Range specific/unknown	Range specific/unknown

4.2.2 - Hydro-acoustic data acquisition and ground truthing

While RGE systems have documented capabilities for detecting and recording fish schools (Lotz et al. 2007; McInnes et al. 2015, 2017), some background information is required to classify echogram marks as schools. This is not unique to RGE systems; scientific systems also require information on fish behaviour, school dimensions, and/or accurate information on target strength relationships, to enable classification of taxa or species (Lawson et al. 2001; Simmonds and MacLennan 2005; Korneliussen et al. 2009). Very limited information is available concerning epipelagic fish behaviour and schooling characteristics in NZ waters (see O'Driscoll and McClatchie (1998) and O'Driscoll (1998) for exceptions, and there is no information on the acoustic characteristics of these species. Therefore to aid in the discrimination of fish schools in the acoustic data I conducted ground truthing of the hydro-acoustic system with known epipelagic schools.

Fish schools were located opportunistically by visually identifying aggregations at the surface or, more commonly, observing predators corralling and actively foraging on epipelagic species. Such ‘work-ups’ are easily identifiable by the presence of diving seabirds such as white-fronted terns (*Sterna striata*), which have a documented foraging association with Hector’s dolphins (Bräger 1998). A calibration ‘event’ was an instance in which epipelagic aggregations were confirmed, were stable for at least 5 minutes prior to hydro-acoustic data logging, and when weather conditions were calm (beaufort <3, swell <1.5m). Hydro-acoustic and navigation data were logged continuously during each calibration event, with the vessel manoeuvring to ensonify a volume of water as close as possible to where schools had been observed. Georeferenced notes were entered into a HP-palmtop computer connected via serial port to the GPS chartplotter and included information on the top-predators present, fish species present (if possible), weather conditions and survey speeds and directions. When possible we used a Nikon D3 DSLR camera with a Nikkor AF80-200ED f2.8 zoom lens to photograph foraging predators and confirm the prey species (Fig. 4.2). A downwards facing drop-camera (Go-Pro Hero 3+) was used to identify prey in situ when schools were stationary, stable and when water clarity permitted.

Hydro-acoustic and navigation data were written to a micro-SD card in .sl2 file format. Using *R* (version 1.0.153; R Core Team 2017), clips exported from Sonar TRX were merged for a given event and data formatted for analysis. Formatting steps included: 1) Converting UTC timestamps into NZ standard time, 2) Selecting the required variables from the dataset (i.e. date, time [to milliseconds], latitude, longitude, ping number, sampling rate, max/min range, total number of samples per ping and the full sample count), and 3) Transforming the sample count from a linear 8-bit integer to dB scale. Commonly, RGE and some SES systems store echo-return data as 8-bit integers that code for pixel brightness on a scale of 0-255 (Allen et al. 2005; Spitael 2007; McInnes et al. 2015; Zhao et al. 2017). Analysis of hydro-acoustic data for fisheries research is typically performed on the (log) decibel scale (Simmonds and MacLennan 2005). This can then be used to represent the echo-return data in scattering volume (Sv) or target strength (Ts) form, the former being the standard format for abundance and biomass calculation using echo integration

(Simmonds and MacLennan 2005). Using information supplied by the manufacturer, I was able to remap the sample count data to the appropriate dB scale. However, due to the highly proprietary nature of the material I was not able to obtain information concerning the reference for the echo returns, source level or transducer and receiver gain functions. Without this, it was not possible to format the data in a way that allows the calculation of density (MacLennan et al. 2002), preventing estimates of abundance and biomass. Such uncertainty around the scattering volume values and likely instability of non-calibrated equipment limits the direct use of data on volume scattering coefficients. However, the dimensions of schools can still be defined from raw –dB echo returns (Simmonds and MacLennan 2005; Lotz et al. 2007), enabling a calculation of school area and consequently, relative abundance (Misund 1993; Petitgas et al. 2001).

Hydro-acoustic and navigation data for each calibration event were imported into the software Echoview version 7.1 (Echoview Software Pty Ltd) for analysis. The data were screened for bad samples and excess noise (identified as ‘no-data’ regions or uninterpretable, high intensity backscatter). Events that comprised >50% of such samples were discarded. Without correction, acoustic backscatter intensity is highly correlated with depth. In order that the application of a threshold value does not influence the integrity of school morphometric measurements (e.g. degrading the perceived boundaries of schools in the 2D plane), it was important to remove this depth correlation. Information provided by the manufacturer suggested that no time variable gain function had been applied to water column samples (Navico, pers. comm.). To determine the extent of this correlation, and to check the information provided by the manufacturer, I used a 38.1 mm tungsten carbine acoustic calibration sphere to measure the rate of transmission loss. The sphere was lowered directly below the transducer face and acoustic data recorded between the depths of 5 and 35m. In echoview, the relative intensity (in volumetric, Sv format) of the sphere was extracted at 200 points with varying depths. The relationship between depth and intensity was plotted. Application of the 20*log* TVG function (the nominal form for spherical spreading and volumetric backscatter, Foote et al. 1987) clearly overcompensated for the rate of transmission loss. This suggests that some TVG correction had been applied by the acoustic hardware (most likely 10log in the volumetric, or 30log in the single target format). Thus, I generated a TVG curve based on the form for shallow water, representing cylindrical rather than spherical spreading (Marsh and Schulkin 1962; Fine and Lenhardt 1983). The cylindrical spreading function ($10log$) performed better, with no correlation between depth and relative intensity being observed for both the calibration sphere and the school targets (Figure 4.6). It is known that the spherical spreading form may be inaccurate at shallow water depths (Simmonds & MacLennan 2005), thus the cylindrical form was deemed appropriate. The TVG function is therefore:

$$Y = \xi log(\mathrm{R}) + 2\alpha\mathrm{R}$$

Where Y is the TVG function at range (R), ξ is the TVG range coefficient that is set to 10 for cylindrical spreading and α is the acoustic absorption coefficient. Y is applied to the raw data to remove the depth dependency of the intensity values. Acoustic absorption is defined as:

$$\alpha = 10\ log_{10}[I(z)/I(z+\Delta z)]/\Delta z$$

Where I is the intensity of a backscattered wave, z is the depth below the transducer given by a Cartesian coordinate system (MacLennan et al. 2002). The absorption coefficient is calculated and applied for a particular speed of sound in water that in turn is influenced by oceanographic properties including water temperature, salinity, pH and the frequency of the acoustic signal (Simmonds and MacLennan 2005). Temperature and salinity data were available from an RBR Concerto conductivity, temperature and depth (CTD) device, pH was set at an appropriate value (8) for sea water in this region and transmit frequency set at 200kHz. These oceanographic properties were used to formulate α by inbuilt functions in Echoview.

Next, the analysis domain for school detection was set. This isolates the water column from backscatter originating from the seafloor and the surface. Echoview's 'best candidate' bottom picking algorithm was fit to the acoustic data to remove the seafloor from the analysis domain. An editable line fixed at 3m was used to exclude noise from the surface. A background noise removal operator was then used to remove any unwanted noise from the echogram; often this was noise introduced by the application of the TVG curve (De Robertis and Higginbottom 2007).

To detect schools of potential prey, the shoal analysis and patch estimation system (SHAPES) algorithm (Coetzee 2000) was applied in Echoview. SHAPES creates a data matrix of columns (defined by each echo return) and rows (defined by the vertical resolution of a sample). Horizontal resolution varied according to ping rate and vessel speed, but was generally between 20 and 34 centimetres. Similarly, vertical resolution was a product of range settings (as the RGEs store the same number of pixel values regardless of range), but was typically between 1 and 4 cm. The matrix is then reduced by the minimum analysis threshold and a school is considered to be a collection of adjoining samples that meet minimum dimension requirements (Coetzee 2000; Lawson et al. 2001; Burgos and Horne 2007). A minimum analysis threshold was set at -35 dB relative intensity. This value effectively removed lower intensity scattering sources that most likely originated from zooplankton and water column stratification while keeping the integrity of perceived schools of potential prey. Thresholding is commonly using in fisheries acoustics to remove unwanted, low intensity scattering sources (Swartzman et al. 1999; Simmonds and MacLennan 2005; Parsons et al. 2013; Viehman et al. 2015).

SHAPES was applied to the data from ground truthing events, with conservative constraints on school dimensions. A minimum school thickness of 1.5m and school length of 3m were set as initial baseline dimensions. Echograms with detected schools were visually screened to ensure acoustic signals from surface noise, bubbles or wake were not included. The dimensions, depth range, relative scattering intensity and geographic position of schools were exported. Dimension and depth data were plotted to provide an indication of the range of school dimensions and depth distribution of acoustic targets of potential prey that were clearly relevant for the top-predators in this location. Further, the information on the relative scattering intensity and general appearance of potential prey schools from ground truthing assisted with scrutinising of echograms from the standard surveys (Chapter 5), a process that has known observer bias (Lu and Lee 1995; Coetzee 2000).

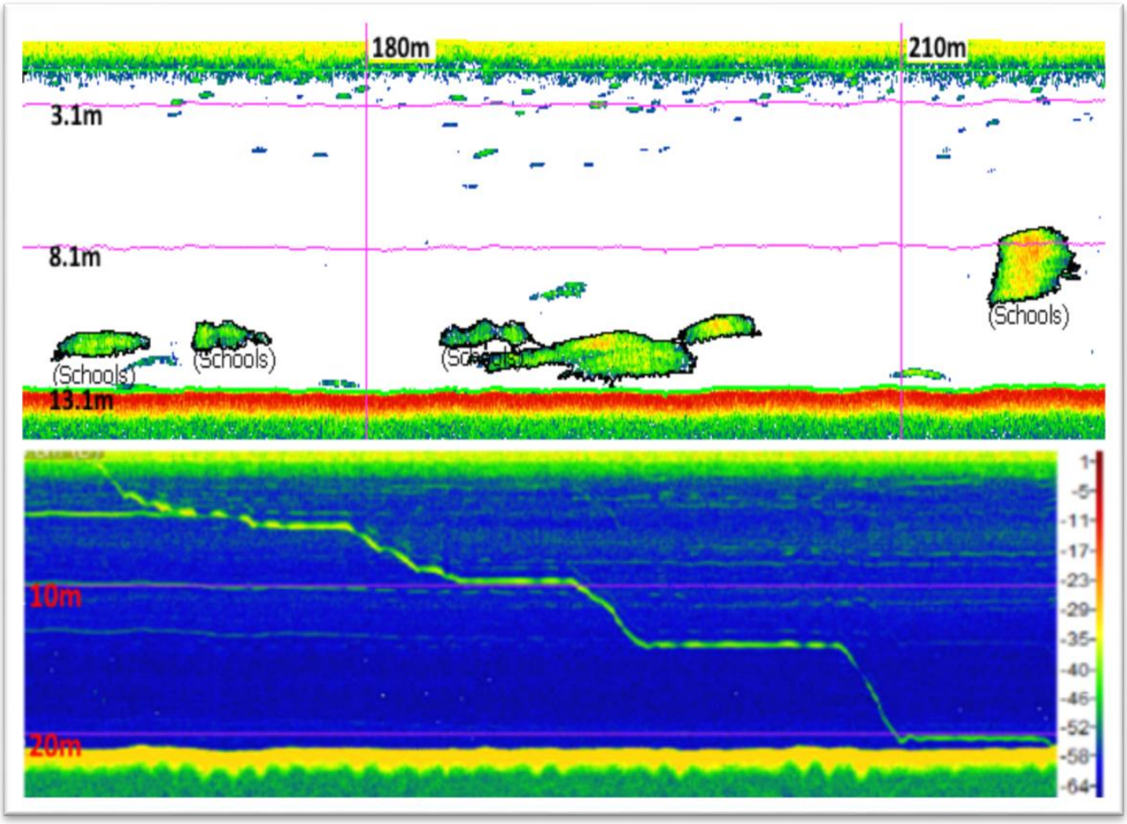

Figure 4.1: Echograms from the recreational grade echo-sounder that show typical schools of epipelagic fish encountered during ground truthing (top) and the decreasing relative intensity of a 30mm tungsten carbine standard target (bottom). Vertical scale is depth (m), horizontal scale is distance along track (m).Aggregations are considered part of the same school if they are <15m apart.

SHAPES provides estimates of a range of school parameters that can be used to quantify relative abundance and patch characteristics of potential prey schools (Coetzee 2000; Burgos and Horne 2007). For this study, the parameters of interest produced by SHAPES included uncorrected length (L), uncorrected thickness *(T*) and uncorrected area (*A*). These are the horizontal (L) and vertical *(T*) dimensions of a hypothetical rectangle around a school region, whilst *A* is a summation of these dimensions for every sample within a school. These parameters are then corrected for beam geometry following Diner (2001) such that corrected length (Lc) is:

$$Lc = L - (2 \times D \times \tan(\phi/2)$$

Corrected thickness (Tc) is:

$$Tc = T - C/2 \times \tau/1000$$

Corrected school area (Ac) is:

$$Ac = A \times \frac{(Lc \times Tc)}{(L \times T)} if\ L \times T \neq 0$$

Where D is mean school depth, ϕ is the 3dB beam angle, C is the speed of sound and τ is the transmitted pulse length.

4.3 - Results

Between September 2015 and March 2017 a total of 36 ground truthing events were carried out on known epipelagic schools. The majority of these (94%) occurred during summer field seasons when foraging aggregations are more common in the study area. Potential prey schools were detected acoustically in 86% of ground truthing events. Identification of prey species was possible either visually or photographically in 55% of calibration events; in the remainder, prey were either not seen sufficiently clearly or were unknown species (possibly juveniles). The most common prey species observed was slender sprat (*Sprattus antipodum),* followed by NZ pilchard (*Sardinops* *sagax)* and yellow-eyed mullet (*Aldrichetta forsteri*) (Table 4.2). The most common predators associated with foraging events were white-fronted terns, Hector's dolphins and spotted shags (*Phalacrocorax punctatus;* Table 4.2). Other taxa often encountered during calibration events included predatory fish such as barracouta (*Thyrsites atun*) and kahawai (*Arripis trutta)* and juvenile squat lobster (*Munida gregaria*). Predatory fish were readily distinguishable in echograms as clusters of 'fish arcs', that are well known echo traces of large fish (Ehrenberg and Torkelson 1996; Ransom et al. 1998). Acoustic signals of *Munida* were similar to proposed potential prey schools but were typically higher intensity, shallower and had much larger dimensions (see *discussion).*

Table 4.2: Summary of information from ground truthing events including the seasonality of events, the number of events with acoustic detections and the number of events with identification of prey species and presence of predators. + includes other large predatory fish species such as barracouta and kahawai, as well as pelagic phase squat lobster.

Season	
Summer	30
Winter	6
Acoustic detections	31
Prey species ID	20
Sprat	11
NZ pilchard	6
Yellow-eyed mullet	3
Predators present	33
White-fronted terns	28
Hector's dolphin	28
Spotted shag	9
Little blue penguin	6
NZ fur seal	4
Other taxa[+]	9

Figure 4.2: Photographic examples of prey identification from ground truthing events. The three most commonly encountered prey species are shown; (a) a slender sprat captured by a white fronted tern, (b) Hector's dolphins corralling a school of NZ pilchard and (c) a yellow-eyed mullet being caught by a Hector's dolphin.

Ground truthing events occurred all around Banks Peninsula from Birdling's Flat in the south to Lyttelton Harbour in the north (Fig. 4.3). Akaroa Harbour had the greatest number of events (13). There was no clear distinction between pilchard and sprat in terms of the locations around the peninsula where these species were encountered. The three times that yellow-eyed mullet were recorded were all inside Akaroa Harbour. The large number of calibration events that contained 'unknown' epipelagic fish as well as the opportunistic nature of ground truthing limits any meaningful comparison of the locations that various epipelagic species were observed.

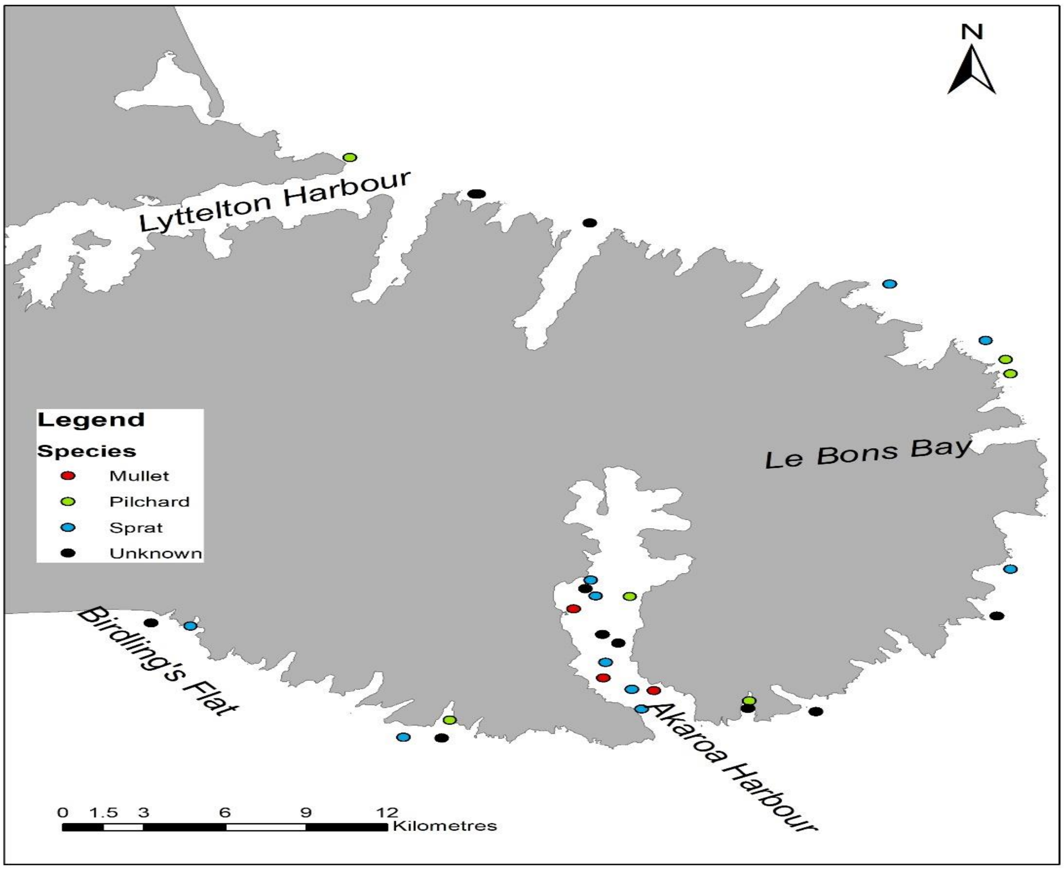

Figure 4.3: The location of ground truthing events and the epipelagic prey species observed at Banks Peninsula.

Two hundred and fifty nine schools were classified as potential prey during ground truthing. There was a wide variety in the mean depth of potential prey schools, ranging from 3 to 34m (Fig. 4.4). School area was similarly variable with the majority of schools being between 5 and 100m^2 in area. The thickness of potential prey schools was strongly clustered at values less than 10m with a peak occurring between 2 and 5m. Similarly the highest proportion of school lengths was less than 20m, although some very long schools (up to 100m) were observed. Although many small clusters of samples were detected, 84% of classified schools had dimensions greater than 2m vertical thickness and 5m length (Fig. 4.4).

The mean relative intensity of schools of potential prey that were detected in ground truthing ranged between -34 and -13 dB (Fig. 4.5). Mean school intensity is summarised as echoview’s ‘Sv_mean’ parameter, with all calculations being undertaken in linear space. The peak in the distribution of mean school intensity was -26 dB. The majority of detected schools had mean intensity values between -30 and -20 dB of relative intensity. Very few schools had high mean intensity above -20 dB (Fig 4.5).

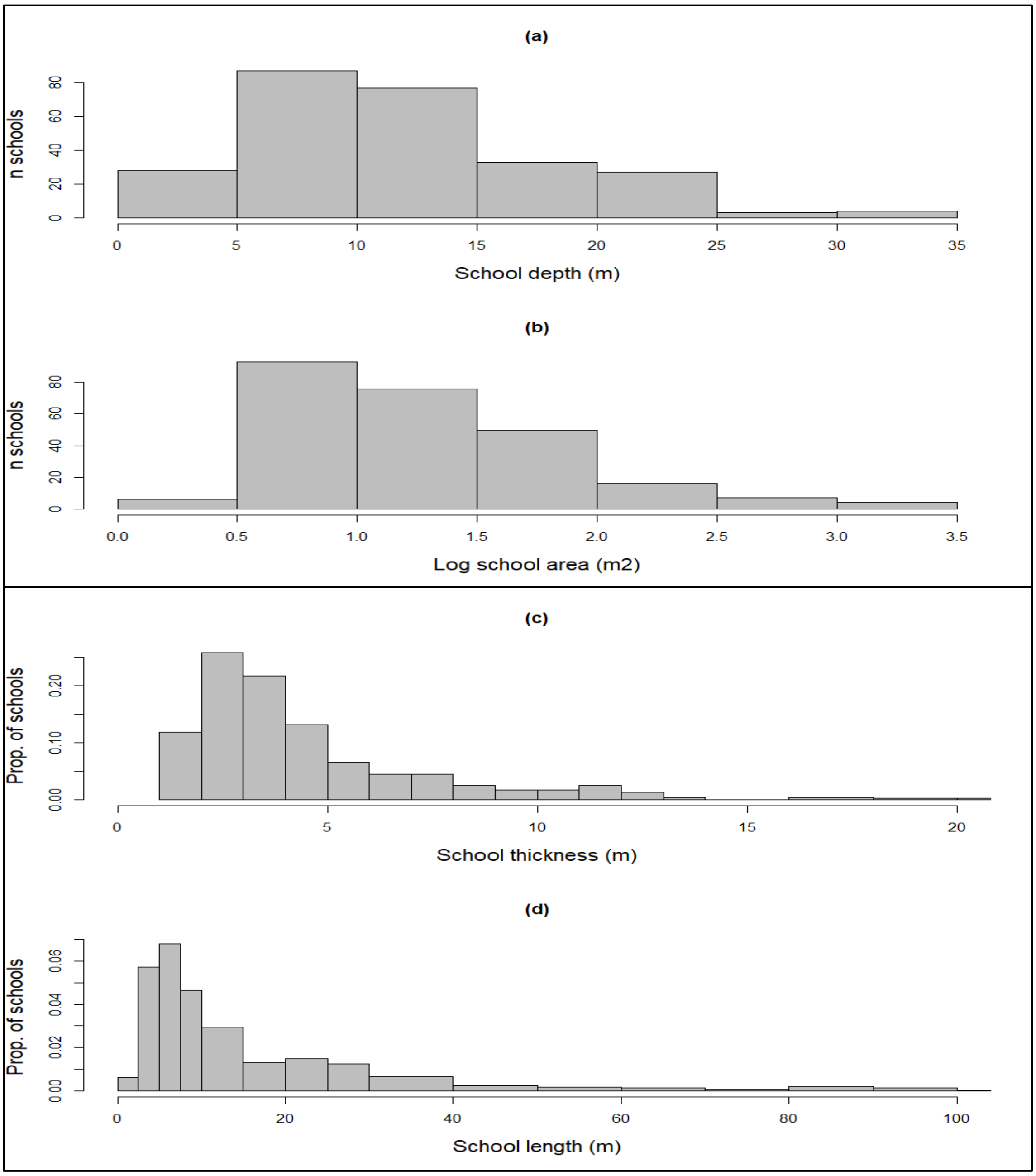

Figure 4.4: Histograms of the distribution of school dimensions from all schools detected in ground truthing events. The mean depth of schools is given in (a), (b) is the distribution of school area. The proportional distribution of (c) school vertical thickness and (d) is school length are also given.

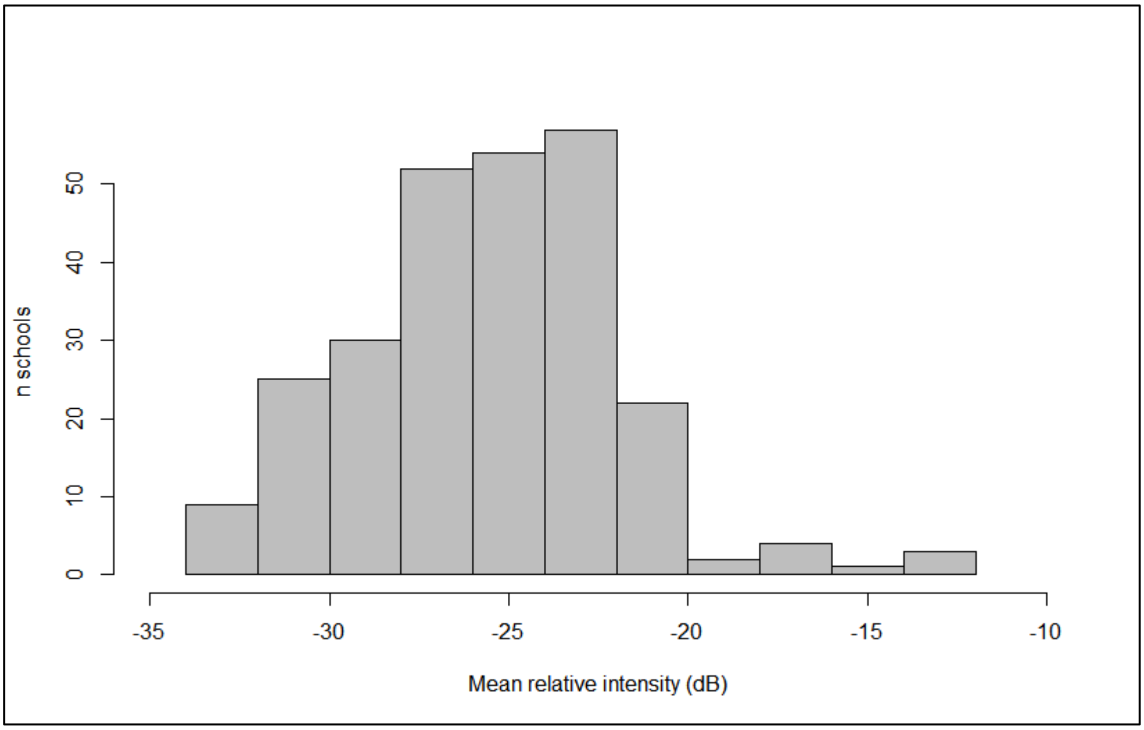

Figure 4.5: Distribution of mean intensity for schools of potential prey detected during ground truthing events. As the hydro-acoustic systems used in this study are not calibrated and there is limited information on crucial parameters concerning the echo-sounders transmit and receive functions, the data represent relative intensity only. Data have been corrected for spreading loss and absorption by the application of a TVG function.

Before the application of the TVG function, the mean relative volume backscatter strength of schools was highly correlated with depth ($R^2 = 0.29$). Using the 10log TVG function successfully minimised the relationship between increasing depth and relative scattering strength of acoustic targets ($R^2 = 0.02$; Fig. 4.6). Thus, thresholding the acoustic data with a constant value (-35 dB relative intensity), is unlikely to influence the perceived morphology of fish schools at various depths in the water column.

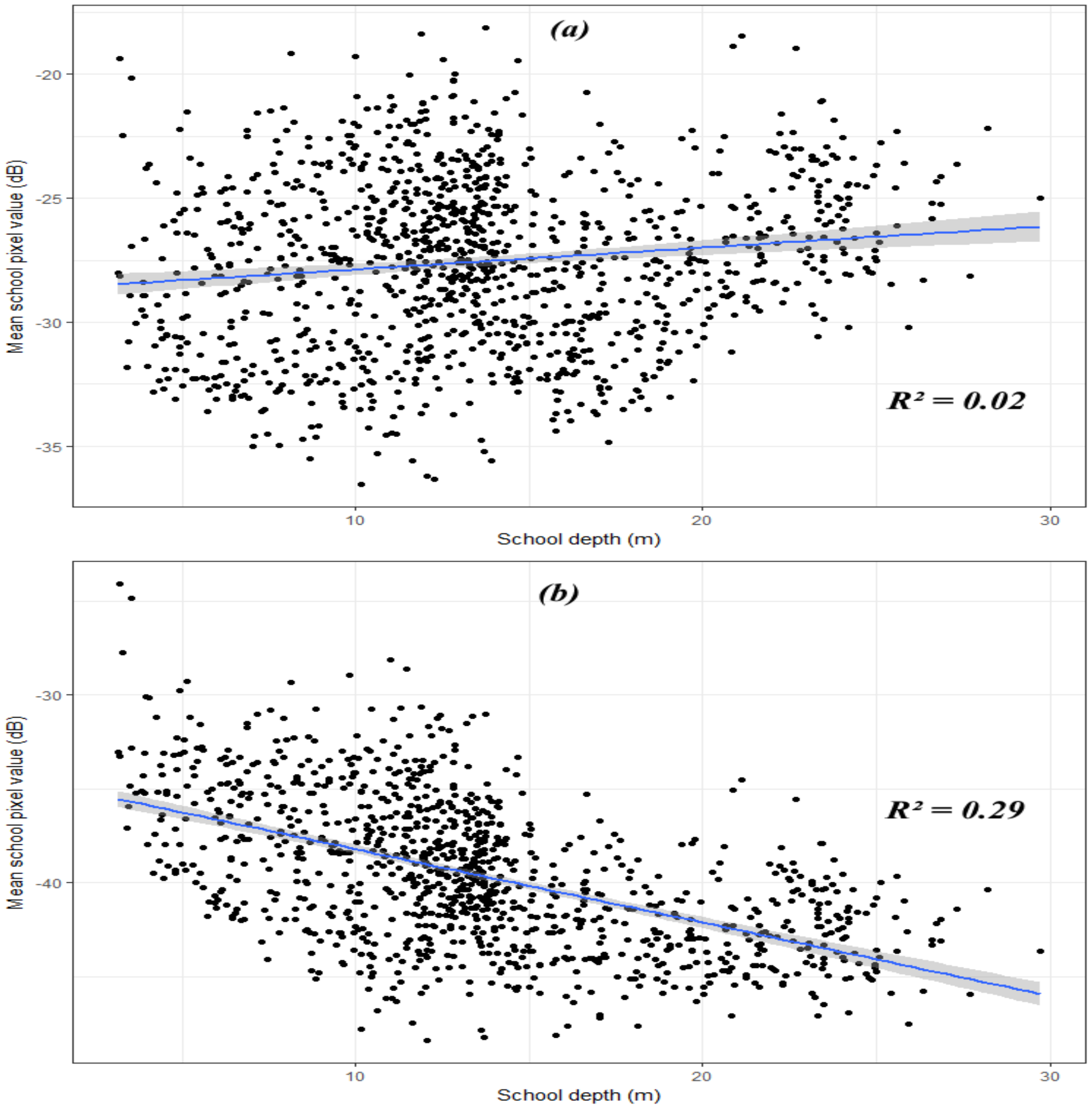

Figure 4.6: Plots showing the effect of the application of the 10log TVG function to remove the depth dependence of relative scattering strength (mean school pixel values). The plot shows the same schools before (b) and after (a) the application of the 10log TVG function.

4.5 - Discussion

Schools of potential prey were readily detected by the RGEs used in this study. This shows that these tools are suitable for obtaining data on the relative abundance and patch characteristics of the prey field of top-predators, at least in shallow water. RGEs have also performed well in other studies used to assess the abundance and/or distribution of small schooling fish (Lotz et al. 2007; McInnes et al. 2015, 2017; Parnum et al. 2017). McInnes et al. (2015) compared a RGE with a Simrad EK60 SES and found the systems closely agreed in the estimation of school depth, area, relative abundance and distribution when the systems ensonified the same schools. They concluded that RGE systems offer an inexpensive option to provide meaningful data on the distribution and relative abundance of the prey of top-predators (McInnes et al. 2015). Panum et al. (2017) also found that a Humminbird RGE performed well at school detection and classification when run alongside a Biosonics SES. Both McInnes et al. (2015) and Parnum et al. (2017) suggest that RGEs may not be appropriate for estimates of density and biomass, largely due to concerns around the stability of non-calibrated equipment and lack of information on the transmit and receive parameters of the acoustic pulses. I also faced these challenges and will therefore limit the quantification of prey field in this thesis to relative abundance and patch characteristics.

The ground truthing procedure was useful for determining the school dimensions of potential prey as recorded by our RGE equipment. It is probable that the distribution of school dimensions would have been skewed to smaller sizes had the SHAPES algorithm been set at smaller minimum dimensions. However, setting smaller school dimensions in SHAPES may have caused problems due to error around the GPS fixes from the navigation systems (average error on fix was approximately 3m; Navico pers comm.), particularly in the alongtrack (length) dimension. Further, other backscattering sources (e.g. stochastic artefact, top-predators) may have been included in detected schools (i.e. false positives) if smaller dimensions had been set in SHAPES. The frequency distribution of school dimensions shows a peak after the minimum values set by SHAPES, thus it is likely that any true schools missed (i.e. false negatives) are comparatively few.

The distribution of the mean relative intensity of schools also showed a peak after the minimum threshold value (-35db) used for the detection of schools. Comparatively few schools had mean relative intensity less than -30 dB. Whilst these values cannot be used in any quantitative sense, the distribution of relative intensity provides useful descriptive information on potential prey schools as recorded by these RGEs in shallow coastal habitats. This information can be used to guide the discrimination of potential prey schools in acoustic surveys and to set an appropriate minimum threshold value.

The three fish species observed at calibration events provide a good representation of the epipelagic prey field of top-predators at Banks Peninsula. All feature in the diet of either Hector's dolphins and/or little blue penguins (Flemming et al. 2013; Miller et al. 2013) that were commonly observed at calibration events. Sprat in particular is a key prey item for both predators; this agrees with sprat being the most commonly observed prey species in this study. No obvious differences in the distribution of schools with verified species identity were apparent, other than mullet being seen inside Akaroa Harbour only. Mullet are known to have a preference for sheltered coastal waters, particularly estuaries (Morrison et al. 2014). However, there was not a sufficient sample size of schools with verified identity to test differences in distribution among species.

Certain limitations of the RGE method warrant discussion. Firstly, there is some inherent uncertainty in the identity of the echo traces classified as 'potential prey' schools using this method. Ground truthing provided valuable information concerning the likely school dimensions and characteristics of known epipelagic prey, but other biological aggregations might share these characteristics. This was a particular issue when aggregations of the pelagic phase of squat lobster (*Munida gregaria*) were abundant throughout the study area in the 2016 summer season. *Munida* aggregations were large, dense and had high relative intensity values similar to those of known epipelagic fish schools. In most cases, *Munida* form aggregations at the surface that are easily visually identified due to their density and bright red colour (Zeldis 1985). These instances were recorded and the aggregations removed from the school detection analysis. However, other studies have made acoustic detections of *Munida* at depths beyond the surface waters (Bertrand et al. 2008; Diez et al. 2016). These studies used multi-frequency acoustics, morphometric or trawl samples to distinguish between *Munida* aggregations and epipelagic fish schools (Bertrand et al. 2008; Gutiérrez et al. 2008; Diez et al. 2016). It is likely therefore, that some of the schools retained as potential prey in this study were actually *Munida*. Although there is no evidence for the top-predators in this area directly targeting *Munida*, it may be part of the diet of little blue penguins and Hector's dolphins. Other *Cephalorhynchus* species regularly eat *Munida* in the south of South America (Heinrich 2006; Riccialdelli and Newsome 2013) and *Munida* is an important component in the diet of many seabirds (Imber 1976; Weiss et al. 2009) including penguins (Thompson 1993; Clausen and Pütz 2002). Therefore it is assumed that some inclusion of *Munida* aggregations will not strongly influence the relevance of the data for top-predators.

The lack of information on volume scattering coefficients of detected schools means an important dimension of prey aggregations is missing and likely results in some coarseness to the data for unravelling predator-prey overlap. Further, due to the lack of in-situ acoustic calibration, the presentation of echo returns in a 'relative intensity' rather than Sv format, and absence of target strength information, it was not possible to draw conclusions about the species that make up potential prey schools. Also, the combination of shallow water, a narrow beam and limited sample size of some species meant classification based on morphometrics (O'Driscoll and McClatchie 1998; Lawson et al. 2001; Korneliussen et al. 2009) was not possible. If certain predators prefer particular epipelagic prey (e.g. Certain et al. 2011; Nøttestad et al. 2014), the inability of the RGE method to identify schools to species level means there will be additional coarseness in unravelling the spatial overlap between trophic levels. Little blue penguins and Hector's dolphins show inherent flexibility in their diet to target the most abundant prey (Cullen et al. 1991; Miller et al. 2013). This suggests that metrics that summarise the characteristics of a general epipelagic prey field may be appropriate for establishing spatiotemporal concurrence.

A final limitation of the RGE method consists of the small volume of water sampled for prey due to the narrowness of the beam in shallow water habitat. This is not a limitation of RGE per se, with

SES facing similar challenges in shallow water (Scalabrin et al. 1996; Lawson and Rose 1999; Boswell et al. 2007). Hydro-acoustic surveys in shallow water increase the risk of fish avoidance behaviour due to the proximity of the survey vessel to targets and the lower volume of water sampled (MacLennan et al 2002). Fish avoidance behaviour can result in horizontal displacement, where schools are not sampled or only partially sampled by the acoustic beam. Vertical displacement is also common in shallow water and results in bias in the estimation of target depth. To reduce the impact of displacement, some studies use side scan or multibeam sonar methods to sample schooling fish in shallow water (O'Driscoll and McClatchie 1998; Trenkel et al. 2008) as, with a much wider beam (particularly in the across-track axis), the chances of ensonifying schools are much greater. In this thesis, if depth is variable among survey areas, the relative abundance of schooling fish may be negatively biased in shallower areas. Additionally, fish schools may be observed deeper in shallower areas due to vertical displacement. As it stands, depth is relatively consistent across survey areas (between 10 and 35m), yet further work is required to determine whether avoidance behaviour is affecting the hydro-acoustic results in this thesis.

When prey biomass is low, the chances of a school being ensonified by a small sample volume are greatly reduced (Lawson and Rose 1999). This may result in a negative bias on the assessment of relative abundance at times when biomass is low. Problems associated with negative bias due to a small sample volume are likely to be greater when the goal is to extrapolate abundance information to density and biomass estimates (Lawson and Rose 1999). It is assumed that the effect on metrics of relative abundance are reduced, however there is limited opportunity to test this assumption without more extensive sampling to groundtruth measures of relative abundance (e.g. concurrent trawl sampling).

Due to the limitations of the RGE at sampling the epipelagic prey field, there is obviously some coarseness in the use of the method to quantify relative abundance. However, it is likely that for predators that have a general preference for epipelagic species in locations where prey density is high, the method will provide meaningful data to quantify predator-prey relationships. The following chapter will test this explicitly, by carrying out hydro-acoustic surveys concurrently with observations of predators. This will determine the true utility of RGE at determining spatial and temporal overlap between predators and prey in coastal settings

Chapter 5: The fine-scale overlap between predators and prey at Banks Peninsula.

5.1 – Introduction

Revealing the spatial and temporal overlap between top-predators and prey is fundamental to understanding of marine systems due to the influence predators have upon food webs (Trites et al. 1997; McCann et al. 2005; Hunsicker et al. 2011; Steenbeek et al. 2013). Ecological processes sustained by predator-prey relationships are currently threatened by complex and interconnected anthropogenic stressors including the impacts of climate change (Tynan and DeMaster 1997; Hunsicker et al. 2013), fisheries (Trites et al. 1997; Pauly et al. 1998a; Cury et al. 2011) and pollution (Fisk et al. 2001; Tanabe 2002). While the spatiotemporal relationships between marine predators and their prey have been studied in both pelagic (Fiedler et al. 1998; Bedford et al. 2015; Benoit-Bird et al. 2016; Saijo et al. 2017) and coastal (Baumgartner et al. 2003b; Torres et al. 2008; Womble et al. 2014; Lawrence et al. 2016) environments, this information is lacking for most predators. Such missing knowledge prevents assessment of disruption to food-webs and undermines protection against the ecological consequences that often follow (Pauly et al. 1998a; Heithaus et al. 2008).

It is axiomatic that availability of foraging opportunities is connected with population viability of marine top-predators (Crawford and Shelton 1978; Oro et al. 2004; Baker et al. 2007; Cury et al. 2011). Particularly for capital breeders, or species restricted in range during their reproductive cycle, variations in prey availability can mean the difference between good and bad breeding seasons (Atkinsen and Ramsay 1995; Lynnes et al. 2004; Hennicke and Culik 2005; Baker et al. 2007; Simmons et al. 2010). Therefore, quantifying the spatiotemporal relationships between predators and their prey could be useful for conservation management. For example, if predator-prey interactions occur more regularly at some locations, these may be more appropriate candidates for protection from the impacts of fishing or habitat degradation (Game et al. 2009; Hooker et al. 2011).

The spatial overlap between marine predators and their prey has been investigated at a range of scales from 100s of kms (Fauchald et al. 2000; Fauchald and Erikstad 2002; Reid et al. 2004), 10s of km; (Rose and Legget 1990; Fauchald et al. 2000; Fauchald and Erikstad 2002) and <5 kms - commonly referred to as 'fine-scale' (Goss et al. 1997; Benoit-Bird and Au 2003; Hazen et al. 2009; Regular et al. 2010; Certain et al. 2011). Fine-scale overlap is observed in many species of seabirds (Lynnes et al. 2004; Hennicke and Culik 2005; Fauchald 2009), marine mammals (Baumgartner et al. 2003a; Benoit-Bird and Au 2003; Gende and Sigler 2006; Hazen et al. 2009) and fish (Rose and Legget 1990; Ciannelli and Bailey 2005). Often, the 'hotspots' in the distribution of predators are thought to reflect locations where prey are either particularly abundant (Gende and Sigler 2006; Wingfield et al. 2011; Hazen et al. 2013), or catchable (Weimerskirch et al. 2005; Bailey and Thompson 2010; Au et al. 2013; Thorne and Read 2013). Gende & Sigler (2006) have shown that hotspots of Steller sea lion distribution are locations where forage fish are abundant and persistent. Also, a high density area for pilot whales (*Globicephala macrorhynchus*) in Hawaii is associated with high abundance of their mesopelagic prey (Abecassis et al. 2015). Many other studies suggest the importance of prey in the formation of hotspots (Ingram and Rogan 2002; Bailey and Thompson 2010; Scott et al. 2010; Hazen et al. 2013), but for most species and habitats this information is lacking.

Despite the obvious need for predators to regularly coincide with their prey, many studies show limited evidence for spatial co-ocurrence (e.g. Russell et al. 1992; Goss et al. 1997; Torres et al. 2008; Fauchald 2009). Some studies show a negative relationship (e.g. Logerwell et al. 1998), often due to mismatches in the scales of sampling needed to resolve distribution across multiple trophic levels (Logerwell et al. 1998; Fauchald 2009; Kuhn et al. 2015). Further, factors other than prey density may be important for describing predator aggregations. Prey patchiness and patch characteristics (Fauchald and Erikstad 2002; Weimerskirch et al. 2005; Benoit-Bird et al. 2013), the presence of refuge habitat (Rose and Legget 1990; Ciannelli and Bailey 2005), prey quality (Grémillet et al. 2008b; McCluskey et al. 2016) and the energetic demands of foraging (Benoit-Bird et al. 2004; Au et al. 2013; Bedford et al. 2015) have each been found to be important. Benoit-

Bird et al. (2013) found that the characteristics of prey patches (including aggregation height, length and depth) predicted the relative abundance of predators in the Bering Sea better than metrics associated with prey biomass and density. McClusky et al. (2016) found mother-calf pairs of bottlenose dolphins focussed on areas with high prey quality (calorific value) even though overall prey biomass was low. Deep-diving predators often show greater overlap with their prey when the prey field is shallower (Benoit-Bird et al. 2004; Au et al. 2013; Abecassis et al. 2015). This is particularly common for predators that forage on prey in the mesopelagic deep scattering layer that is found at shallower depths during the hours of darkness (Au et al. 2013; Naito et al. 2013; Abecassis et al. 2015; Saijo et al. 2017). Most predators are themselves subject to predation that further shapes their distribution and thus overlap with prey. For example, bottlenose dolphins in Shark Bay were encountered infrequently at locations with high prey biomass but greater risk of shark attack, compared to less productive (but less risky) areas (Heithaus and Dill 2006). These examples indicate that the association between predators and prey is complex.

There have been few studies linking predator and prey distribution in New Zealand waters (see O'Driscoll et al. 1998; Benoit-Bird 2004, Miller 2014 for excceptions). Having a diverse assemblage of predators, good knowledge of their diets, and in some cases data on fine-scale distribution patterns, locations like Banks Peninsula offer opportunities to investigate these links. The relative abundance of Hector's dolphins at Banks Peninsula has been shown to be strongly correlated with that of a main prey item, red cod (Miller 2014). With good information about the existence, longevity and seasonality of hotspots (Chapter 2), there are now opportunities to investigate the spatial overlap of the dolphins and their prey, relative to the existence of hotspots. This information will help confirm the mechanisms driving the existence of hotspots and the high foraging rates seen in these locations (Chapter 3).

A further ecological factor of Hector's dolphin hotspots may be high biodiversity and the subsequent food web complexity this often entails (Hooker & Gerber 2004). The 'indicator species' theory, where marine mammal distribution serves as a proxy of habitat of high ecological value, is rarely tested. An important first step towards assessing this theory is to assess whether hotspots for Hector’s dolphins are also hotspots for other predators and/or their prey. Further, differences in the importance of certain prey field characteristics among predators may help to explain the reasons why the ‘indicator species’ theory does not hold true in every case. Thus, predator-prey surveys that make observations of several predators (e.g. Scott et al. 2010; Benoit-Bird et al. 2013) are important undertakings.

Little penguins (*Eudyptes minor)* are a common seabird found in coastal locations around New Zealand and southern Australia (Chiarada et al. 2007). In NZ, the penguins are classified as ‘at risk-declining’ by the Department of Conservation; the main threats involving predation from introduced mammalian predators (Dann 1994). Banks Peninsula is one of the few breeding areas of an endemic subspecies of little penguin, the white-flippered penguin (*Eudytptula minor albosignata)*, that is classified as endangered (Challies and Burleigh 2004). The two subspecies co-exist at Banks Peninsula, and hereafter the common name ‘little penguin’ refers to both. The penguins are central-place foragers, making foraging trips (usually daily) within 20km from fixed nesting colonies (Collins et al. 1999; Hoskins et al. 2008; Chiaradia et al. 2012). A dominant component of their diet is small epipelagic, clupeiform fish such as pilchard, anchovy and sprat (Fraser and Lalas 2004; Flemming et al. 2013). Substantial declines in populations of little penguin have been linked to fluctuations in the abundance of these important epipelagic taxa (Dann 1992; Cannell et al. 2012; Chiaradia et al. 2012). No studies have quantified the overlap between little penguins and their epipelagic prey. Understanding such relationships and how they change over time will be valuable information for the management of this threatened species.

Hydro-acoustic methods offer many advantages for the quantification of epipelagic prey fields. Such surveys can be easily undertaken concurrently with surveys of predators (Davoren et al. 2003; Benoit-Bird et al. 2004; Certain et al. 2011; Lawrence et al. 2016), can provide data on the characteristics of prey patches (Fauchald and Erikstad 2002; Benoit-Bird and Au 2003; Benoit-Bird et al. 2013) and can be integrated over multiple spatio-temporal scales (Davoren et al. 2003; Trenkel et al. 2011; Godø et al. 2014). Further, with significant advances in the technology of recreational grade echo-sounders (RGE), quantitative information on prey are cheaply available. While RGE systems have been shown to produce robust data (McInnes et al. 2015, 2017; Parnum et al. 2017), they have not yet been used to assess overlap between predators and prey.

In this study, I use two RGE systems to investigate the fine-scale overlap between two predators and the epipelagic prey field at Banks Peninsula. Ultimately, this information can be used to assess whether patterns in prey distribution drive the existence of hotspots in Hector's dolphin and other coastal top-predators.

5.1.2 - Chapter objectives

- Determine whether data describing the characteristics of the prey-field sourced from a RGE (Ch. 4) is useful in describing the relative abundance of coastal top-predators.
- Investigate the best metrics of prey abundance and patch characteristics for describing variation in the relative abundance of two common top-predators.
- Assess the fine-scale spatial overlap between top-predators and the relative abundance of potential prey and their patch characteristics.
- Are there differences in the prey field at hotspots when compared to reference areas?

5.2 - Materials and methods

5.2.1 - Hydro-acoustic surveys

The RGE systems used in this study are detailed in Chapter 4 and the settings used for the surveys are given in Table 4.1. Hydro-acoustic surveys were carried out in 'summer' (Jan-Mar) and 'winter' (Aug-Oct) field seasons in ten study areas around Banks Peninsula from August 2015 to March 2017 (Fig. 5.1). Locations were selected to include a diversity of habitat types and represent a gradient in predator density. Four of the locations were known 'hotspots' for Hector's dolphins with the remaining six being 'reference' areas with lower dolphin density (Chapter 2). Limited information is available concerning the at-sea distribution of other predators in this area, but little penguins are encountered in all locations (Challies and Burleigh 2004).

Surveys followed a ‘zig-zag’ pattern in an alongshore direction. A random start point was selected either as close to shore as possible, or at the 800m offshore extent of the near-shore habitat zone (Chapter 2). The survey vessel was a 6m aluminium hulled power-boat with a 115hp 4-stroke outboard engine. Survey speed was kept at 5-6 knots. At the end of each leg of the zig-zag a 150^0 turn was made to bring the vessel on a divergent leg. The ‘zig-zag’ pattern continued until the vessel reached the boundary of the area to be covered (Fig. 5.1). Hydro-acoustic and navigation data were logged continuously during each survey. Metadata associated with a survey including start and end locations and times, sea state, sightings conditions and any relevant notes, entered into a GPS-linked HP palmtop computer.

Counts of Hector’s dolphins and little penguins were made concurrently with hydro-acoustic data acquisition. These species were selected because they use the epipelagic prey field (Flemming et al. 2013; Miller et al. 2013), are common within the study area and represent two very different taxa. In the case of Hector’s dolphin, information on the fine-scale overlap with prey will be used to determine the biological characteristics of hotspots in the species’ distribution (Chapter 6). During hydro-acoustic surveys, two observers scanned sectors bounded by the bow of the vessel and 90^0 to port or starboard. Predator sightings were reported to a recorder who entered data into the HP palmtop along with an estimate of group size. Dolphin surveys at slow speeds and within confined areas carry the risk of positive bias (Dawson et al. 2008). Observers were instructed to maintain constant communication about sightings in order to reduce the risk of double counting.

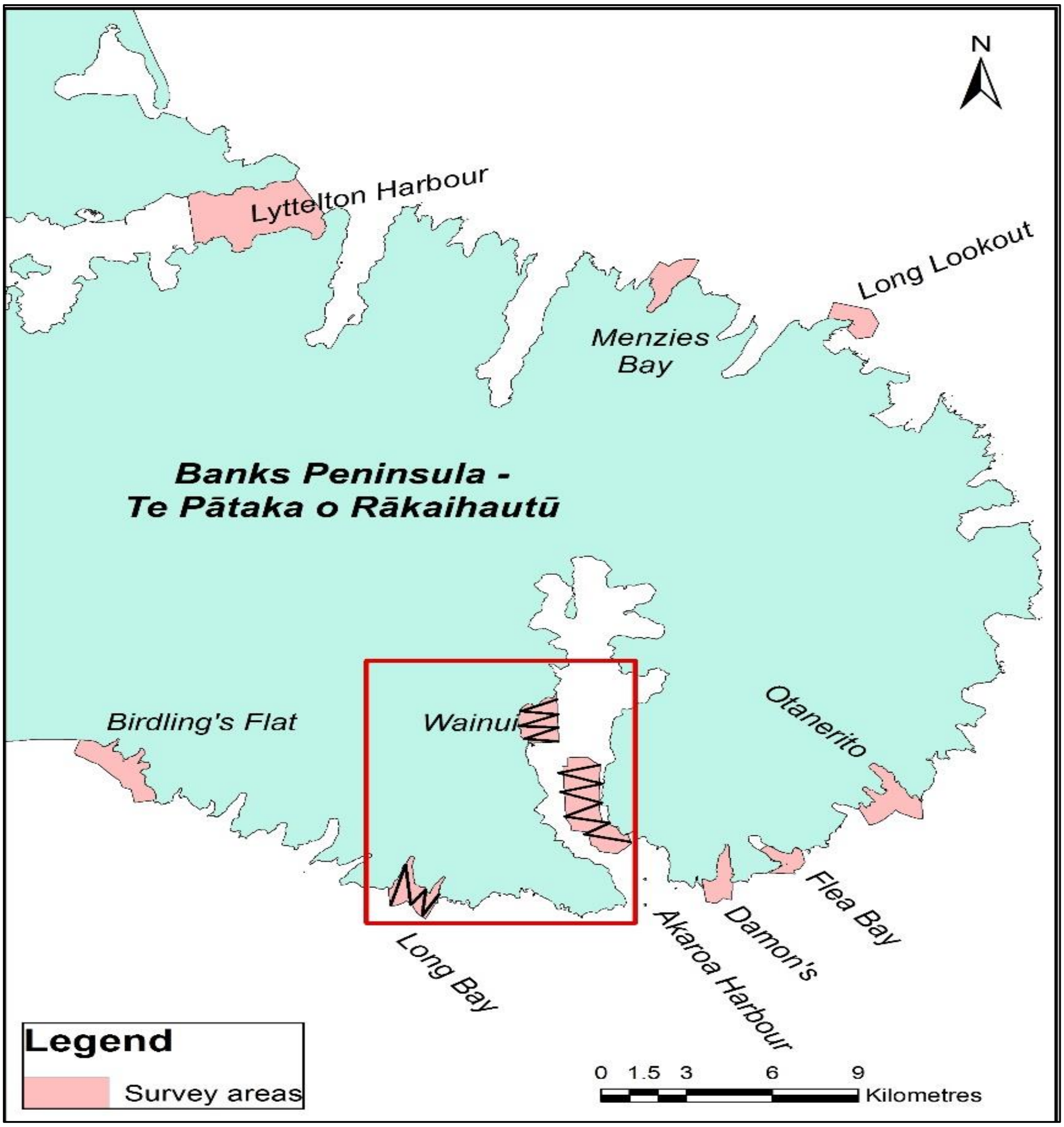

Figure 5.1: Locations of the ten survey areas around Banks Peninsula. Examples of typical hydro-acoustic survey tracks are shown at three survey areas within the red rectangle.

5.2.2 - School detection and analysis

Hydro-acoustic data were processed and formatted following the steps given in section 4.2.2 in Sonar TRX and R. Once data were in the appropriate format, hydro-acoustic and navigational data were imported into Echoview for analysis. Similar to Chapter 4, steps involved setting the analysis domain using editable line functions, applying TVG correction and using the SHAPES algorithm to detect fish schools. A minimum threshold of -35 dB relative intensity was applied based on the results of ground truthing described in Chapter 4. Similarly, the minimum dimensions of schools were taken from information produced by ground truthing and represent school dimensions appropriate for the potential epipelagic prey encountered in this study area as detected by the RGE. These were a minimum vertical height of 2m and a horizontal length of 5m. Multiple aggregations were considered part of the same school if they were within 15m of each other.

Once candidate schools of potential prey were defined, screening was undertaken to remove aggregations of pixels that may have belonged to a scattering source not removed by minimum thresholding (Simmonds and MacLennan 2005). Such aggregations often included wake from boats and turbulent bubble-laden water seen close to the shore at wave-exposed sites; both these were discernible as very high relative scattering intensity that was connected to the surface. Other false positive detections included macro-algae such as *Macrocystis pyrifera* and *Carpophyllum flexuosum*; apparent as a linear extension off an uneven seafloor (i.e. resembling a reef).

School parameters derived from SHAPES include corrected school area, length, thickness and mean depth (section 4.2.2), calculated for every school retained in the SHAPES analysis (after screening). Corrected area was defined as the area of a potential prey school in the 2 dimensional plane of the echogram (MacLennan et al. 2002; D'Elia et al. 2009). This was used to summarise the relative abundance of potential prey (RAPP) in a given survey by calculating the cumulative school area backscatter (C. area) and standardising it for survey distance (SD). This value provides a 'snapshot' of RAPP for schooling epipelagic prey within a particular survey area at the time of survey.

$$RAPP = \frac{c.area_{BS}}{SD}$$

Where C.area$_{BS}$ is a summation of the school area for every school in a survey.

Metrics typically used to assess relative abundance of schooling fish such as area backscattering coefficient (ABC; McClatchie and Dunford 2003; Mcquinn et al. 2005) or nautical area backscattering coefficient (NASC; Axenrot and Hansson 2004; Embling et al. 2012) were not used in this study due to their reliance on scattering volume (Sv) data that were not available from the RGE (due to uncertainty around the data on intensity returns; Chapter 4) . However, as discussed by Lotz et al. (2007) cumulative school area offers an alternative measure of relative abundance based on the strong relationship between the area occupied by schools and true fish abundance (Misund 1993; Pettis et al. 2004).

The standardised c.area$_{BS}$ metric was summarised in several ways to generate a range of possible best candidates for assessing the relationship between RAPP and relative abundance of predators (Table 5.1). Thus, c.area$_{BS}$ was calculated over four fixed 5m depth bins (Bin) and four layers that described the distance from the seafloor (Layer). A school was attributed to a particular depth bin if its mean depth occurred within the given bin. Layers were set at 5m depth intervals off the seafloor and school information was integrated and exported for these cells directly from Echoview (Table 5.1). Layers off the seafloor and depth bins were both considered because they describe different features of the prey field (D'Elia et al. 2009). For example, layers account for the association of schools with the seafloor, which, due to the variable depths of the study areas, may not be adequately captured by absolute depth bins. Depth was variable among the ten survey areas, with some shallow areas not having sufficient depth to generate data in deeper bins or layers further from the seafloor. This means it is not possible to test the influence of all bin and layer metrics at each survey area. The characteristics of prey patches for each survey were summarised as mean school depth, area, length and thickness of all schools detected in a given survey (Table 5.1).

Table 5.1: Summary of metrics used to represent the relative abundance of prey and prey patch characteristics in models that investigate the relationship between predators and the prey field. Relative abundance metrics are summations of school area either over an entire survey or within particular depth bins or layers off the seafloor. Patch characteristics are the mean values of measurable geometries of detected schools within a survey.

Relative abundance	**Term**	**Description**
Cumulative school area backscatter	$c.area_{BS}$	Summation of school area for every school in a survey divided by the survey distance (m^2/km).
Cumulative school area backscatter within depth bin 1.	Bin_1	Summation of school area for every school with a mean depth between 3 and 8m divided by the survey distance (m^2/km).
Cumulative school area backscatter within depth bin 2.	Bin_2	Summation of school area for every school with a mean depth between 8 and 13m divided by the survey distance (m^2/km).
Cumulative school area backscatter within depth bin 3.	Bin_3	Summation of school area for every school with a mean depth between 13 and 18m divided by the survey distance (m^2/km).
Cumulative school area backscatter within depth bin 4.	Bin_4	Summation of school area for every school with a mean depth between 18 and 23m divided by the survey distance (m^2/km).
Cumulative school area backscatter within layer 0	Layer_0	Summation of school area for every school within 5m of the seafloor divided by the survey distance (m^2/km).
Cumulative school area backscatter within layer 1	Layer_1	Summation of school area for every school between 5 and 10m from the seafloor divided by the survey distance (m^2/km).
Cumulative school area backscatter within layer 2	Layer_2	Summation of school area for every school between 10 and 15m from the seafloor divided by the survey distance (m^2/km).
Cumulative school area backscatter within layer 3	Layer_3	Summation of school area for every school between 15 and 20m from the seafloor divided by the survey distance (m^2/km).
Patch characteristics	**Term**	**Description**
Mean depth of schools	Depth_mean	The mean depth of all schools detected in a survey (m)
Mean area of schools	Area_mean	The mean area of all schools detected in a survey (m^2)
Mean length of schools	Length_mean	The mean horizontal length of all schools detected in a survey (m)
Mean thickness of schools	Thickness_mean	The mean thickness of all schools detected in a survey (m)

5.2.3 - Statistical analysis

All analyses were undertaken at the scale of individual surveys, providing a snapshot of the prey field and predator numbers at a particular survey area at the time of survey. Exploratory analyses using scatterplots first determined the distribution of each prey field metric and identified any outliers. Then, in order to assess the best metric for RAPP for each predator species, generalised additive mixed models (GAMMs) were used to assess the relationship between each RAPP candidate parameter and the predator counts for each survey. The nine RAPP candidates (Table 5.1) were fit against count data as a smoothed function using a thin plate regression spline in the form of 9 separate, single parameter models. A random effects variable 'Location' (i.e. one of the ten survey areas) was included in order to account for non-independence of datapoints from within the same survey area. The models were fit in *R* package *mgcv* (Wood 2017), using the *gam* function. A poisson family with a log-link function was used for both the dolphin and penguin models. The effective degrees of freedom *(k)* were estimated at 'optimum' levels using generalised cross validation (Wood 2006). A maximum value for k was set at 5 (i.e. 4 knots; Tepsich et al. 2014; Rayment et al. 2015) to ensure no overfitting (see *model diagnostics* below). R^2, deviance explained and AIC values were exported for each model, and the best index for RAPP chosen based on the model that had the lowest AIC score.

A similar approach was undertaken to assess the relationship between school dimension metrics and predator counts. The four school dimension metrics were fit using smoothed functions (again with a thin plate regression spline). The models were fit with the same families and link functions as above in *mgcv*. School dimension models were compared using R^2, deviance explained and AIC values.

It is possible that a combination of both RAPP and school dimension metrics may best describe variability in predator numbers. To investigate this, I generated a 'top-model' for each predator species using an information-theoretic model selection approach (Burnham and Anderson 1998). Firstly, relevant input parameters were included in a 'global model'. Ideally this would include every RAPP and school metric parameter, however many of these are not independent; this is especially true for the RAPP metrics. Thus, the best RAPP variable (chosen by lowest AIC) was selected for each predator and included in the global model. School dimension metrics were included in the global model if they were not correlated with each-other or the selected RAPP variable. When smoothed terms are present, collinearity is best assessed as concurvity (Wood 2006). The function *concurvity* in *mgcv* was used to generate indices of concurvity between variables. From simulation performed by He et al. (2006), concurvity was deemed to have a negative effect on the slope and variance estimation if the 'estimate' index was higher than 0.3 – (1 indicating a complete lack of identifiability). Where concurvity was apparent, the variable with the lowest AIC score from the single parameter models was retained in the global model.

The response variables of predator counts were not standardised by survey distance (to produce numbers per unit effort) because of problems associated with the poisson family's requirement for whole (i.e. count) numbers. Exploratory analysis using scatterplots and general linear models suggested very little effect of survey distance upon predator counts, yet to account for this a variable 'survey distance' (km) was included in the global models and top-models for each predator. Forcing inclusion of this variable into the models accounts for any variation in predator counts associated with unequal survey effort. To account for spatial autocorrelation among surveys from the same area, a random effects variable 'Location' was included within the global and top-models.

A full model set with every possible combination of input parameters listed in the global model for each predator was produced. Each GAMM model was fit in *mgcv* and compared and ranked in terms of AIC and model weight, with the top-model being the formulation that had the lowest AIC and highest weight (Anderson et al. 2000). The statistical significance of each variable in the top-model was inferred by a p-value <0.01 for smoothed terms (Zuur et al. 2009). The nature and magnitude of the effect of the smooth terms on the relative abundance of predators were assessed by viewing plots of each smoothed effect.

5.2.4 – Model diagnostics

In order to assess model fit and whether GAMM assumptions are upheld, the top-models for each predator were checked using standard procedures (Wood 2006; Zuur et al. 2009). Firstly, the k value set by the selection of an 'optimum' degrees of freedom for the smooth functions was checked to ensure k was not overly restrictive. This was done using the *gam.check* function of *mgcv* and also by plotting the smoothed terms with partial residuals overlaid to determine any systematic departures from the smooth. As mentioned above, the function *concurvity* was used to identify and exclude terms where strong non-independence was observed. Spatial correlation among residuals was investigated using spatial correlograms and bootstrapped 95% confidence intervals that modelled the correlation between pairs of observations as a function of geographic distance (Zuur et al. 2009). Residual checking was undertaken to assess homogeneity of variance and the independence of the response variable. Residuals were plotted against fitted values and each predictor variable retained within each top-model (see Appendix 3a). The distributional assumptions of the models were investigated by producing qq-plots via simulation using the function *qq.gam* in *mgcv* (Appendix 3a).

5.3 - Results

5.3.1 - Hydro-acoustic surveys

A total of 305 hydro-acoustic surveys were conducted between August 2015 and March 2017. Of these, 297 were appropriate for analysis. The remaining eight surveys were excluded based on poor data quality due to adverse weather conditions or interference from the side scan sonar system used in Chapter 6. The ten survey areas did not receive an equal number of surveys (Table 5.2). This is because weather conditions limited access to some locations more than others. For similar reasons there was more survey effort during summer as the weather is more favourable for small boat work during this time (Table 5.2). Despite there being differences among areas, each survey area received a substantial amount of sampling effort (Table 5.2).

Table 5.2: Number of hydro-acoustic surveys for potential prey among survey areas and seasons. Total surveyed distance for each area is also given. The percentage of surveys with detections of potential prey schools (Detections) are given for summer (Su) and winter (Wi) seasons for each survey area. Area codes are given in section 3.3.

Area	*Summer*	*Winter*	*Total*	*Distance(km)*	*Detections %(Su)*	*Detections %(Wi)*
AK	31	20	51	263	100	85
BF	15	8	23	108	100	50
DA	17	10	27	84	100	70
FB	20	11	31	116	100	73
LB	17	6	23	106	100	83
LL	20	14	34	126	100	86
LY	14	8	22	100	86	38
ME	22	13	35	141	86	77
OT	12	7	19	72	100	29
WA	22	10	32	127	86	40
Total	**190**	**107**	**297**	**1246**	**96**	**67**

Detections of potential prey schools were made at all locations and during each season (Table 5.2). All survey areas except Lyttelton, Menzies and Wainui had potential prey detected at every survey during summer. In winter, Long Lookout had the highest number of surveys with prey detection followed by Akaroa, Long Bay and Menzies Bay. Otanerito and Lyttelton had the lowest proportion of surveys with school detections in winter.

There was substantial variation in RAPP among surveys. Cumulative school backscatter area per km of survey ranged from 2605 m^2/km to 0 m^2/km (mean = 159). Prey patch metrics had similarly high levels of variation (Fig. 5.2). The average depth of schools per survey ranged from 4 m to 26 m (mean = 12.4 m). Mean thicknesses of schools per survey were between 1.8 and 10 m (mean = 3 m). The distribution of mean length and mean area of schools was influenced by the detection of a small number of very large prey patches (Fig. 5.2). Mean length of schools ranged between 5 m and 164 m (mean = 17 m). Values for mean area of schools were between 10 m^2 and 326 m^2 (mean = 23 m^2).

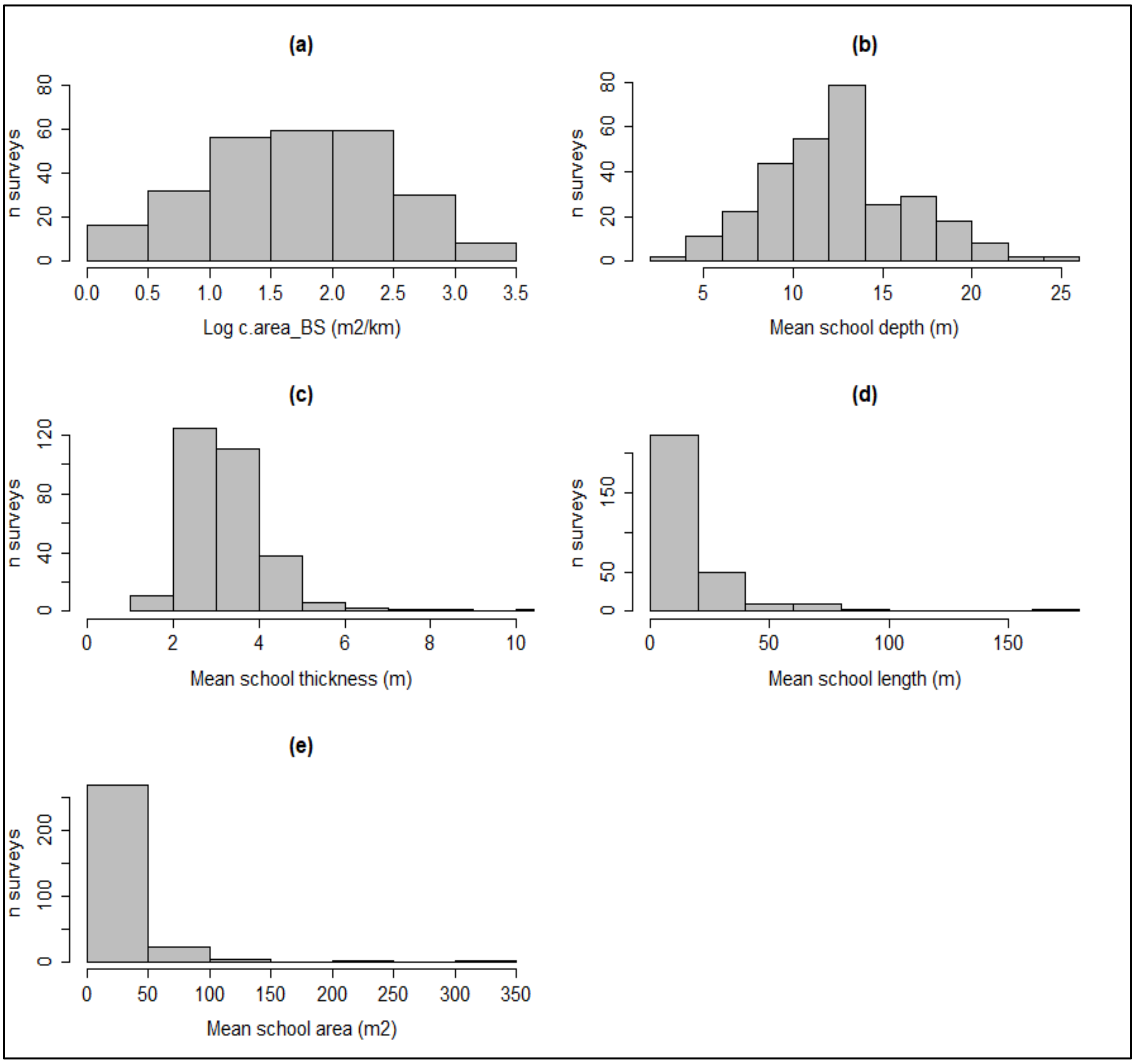

Figure 5.2: Summary of the distribution of the relative abundance of prey and prey patch data obtained during hydro-acoustic surveys and analysed in Echoview. Histograms show the frequencies of mean values of the relative abundance of potential prey as measured by the c.areaBS per km metric (a). Patch characteristics include the mean depth (b), thickness (c), length (d) and area (e) of schools detected during hydro-acoustic surveys.

Numbers of predators recorded during surveys were also highly variable. Hector's dolphin was the most commonly observed predator throughout the study area. Dolphins were frequently recorded at four of the ten survey areas (Akaroa, Birdling's Flat, Flea Bay and Long lookout). Penguins were distributed throughout the study area, but showed high relative abundance at Akaroa, Flea Bay, and Otanerito Bay (Fig. 5.3).

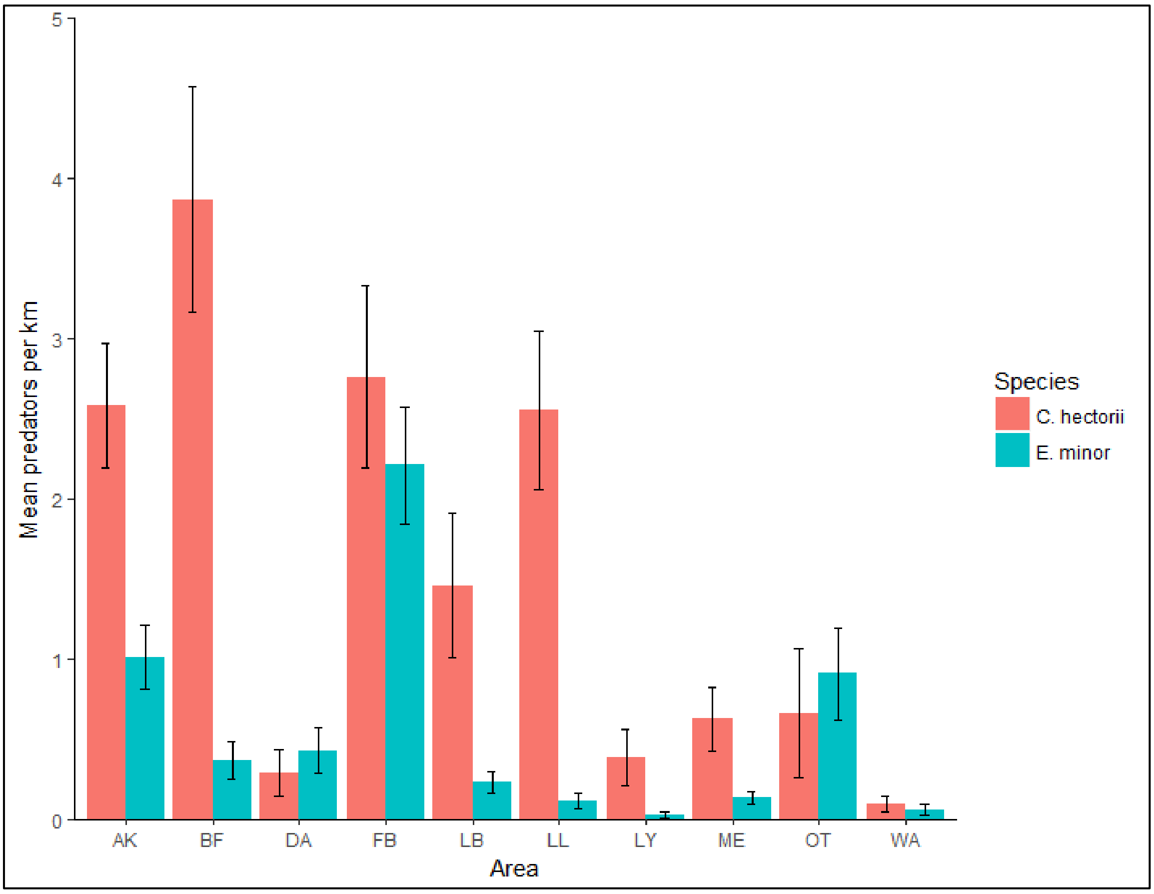

Figure 5.3: Mean counts of Hector's dolphins and little penguins recorded during surveys at ten study areas. Error bars are +/- standard error.

Exploratory data analyses provided hints at meaningful relationships between several prey metrics and the relative abundance of both predators. Relationships between prey relative abundance (cumulative school area) and predator counts were obvious, as were non-linear trends with school depth (Fig. 5.4). Such trends confirm the importance of using models that account for non-linear effects.

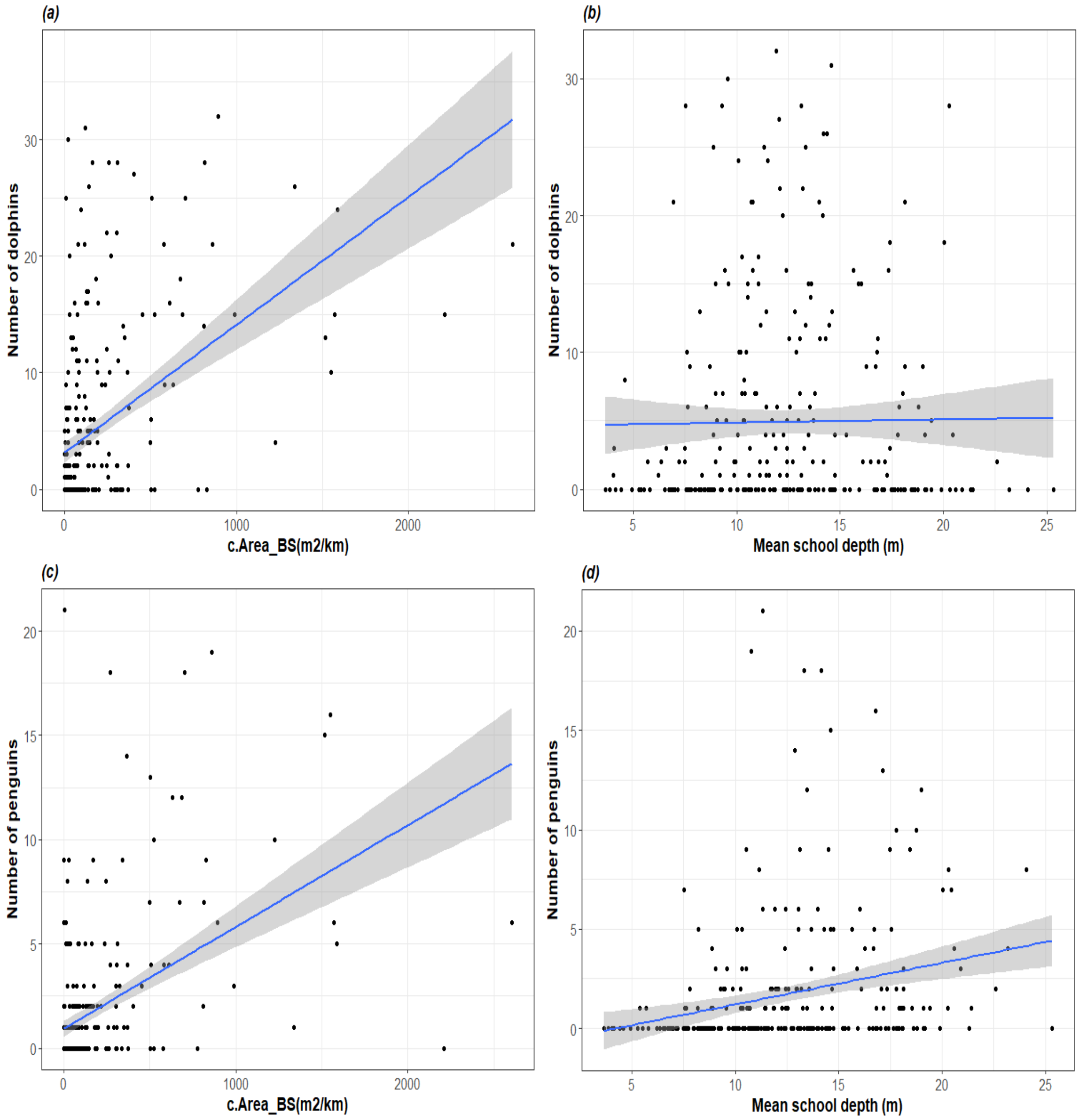

Figure 5.4: Scatterplots and linear trendlines from exploratory analyses of the relationship between predator relative abundance and prey field metrics. Cumulative school area (c.Area_BS) is a measure of prey relative abundance and is compared to counts of both predators (a and c) , as is the mean depth of schools encountered during surveys (b and d).

5.3.2 – Relative abundance of prey

The variable that best described the relationship between RAPP and predators was different for the two predator species (Tables 5.3, 5.4). For dolphins, several indices of prey abundance described variation in dolphin numbers reasonably well, with the best metric being a smoothed function of the cumulative school backscatter area per survey (Table 5.3). This metric had lowest AIC score, and explained 49.6% of the deviance.

The relative abundance of penguins was best described by a variable that quantified the total school backscatter area in a depth bin between 13 and 18m (Table 5.3). This model described 55.9% of the deviance in penguin counts and had the lowest AIC score. The next best index of potential prey abundance for penguins was a smooth of cumulative school backscatter (53.6% deviance).

Table 5.3: Summary of single parameter models used to determine the best metric of potential prey abundance for dolphins. Each model contains a single parameter smoothed function using a thin plate regression spline (s) and includes a random effect for survey location. Definition of each variable is given in Table 5.1 above but can be briefly described as total school backscatter area/km in a given survey (C.area_BS), or the same value summarised into four different depth bins (Bin), or layers off the seafloor (Layer). The null model, describing the 'site effects' of survey area is also given for comparison.

Model	R2	Deviance	df	AIC
Dolphin ~ s(C. area_BS)	0.32	46.10%	12	876
Dolphin ~ s(Layer.0)	0.32	41.50%	12	896
Dolphin ~ s(Bin.2)	0.34	37.30%	11	914
Dolphin ~ s(Bin.1)	0.29	36.40%	12	919
Dolphin ~ s(Bin.3)	0.32	35.60%	11	922
Dolphin ~ s(Layer.1)	0.28	36.10%	12	922
Dolphin ~ s(Layer.2)	0.24	33.10%	12	935
Dolphin ~ s(Layer.3)	0.22	32.80%	12	935
Dolphin ~ Survey area	0.20	28.90%	8	947

Table 5.4: Summary of single parameter models used to determine the best metric of potential prey abundance for penguins. Each model contains a single parameter smoothed function using a thin plate regression spline (s) and includes a random effect for survey location. Definition of each variable is given in Table 5.1 above but can be briefly described as total school backscatter area/km in a given survey (C.area_BS), or the same value summarized into four different depth bins (Bin), or layers off the seafloor (Layer). The null model, describing the 'site effects' of survey area is also given for comparison.

Model	R2	Deviance	df	AIC
Penguin ~ s(Bin.3)	0.537	50.10%	11	473
Penguin ~ s(C. area_BS)	0.47	48.20%	11	481
Penguin ~ s(Layer.0)	0.44	47.40%	11	484
Penguin ~ s(Layer.2)	0.40	44%	12	501
Penguin ~ s(Bin.4)	0.35	43.50%	10	501
Penguin ~ s(Layer.1)	0.37	42.30%	11	508
Penguin ~ s(Layer.3)	0.38	41.70%	11	511
Penguin ~ s(Bin.1)	0.36	41.10%	11	512
Penguin ~ s(Bin.2)	0.36	40.70%	11	516
Penguin ~ Survey area	0.29	38%	8	522

5.3.3 - Prey patch metrics

For both dolphins and penguins, the mean area and length of schools explained a substantial amount of the deviance in the relative abundance of these predators. The mean depth of schools and school thickness also explained a reasonable amount of deviance (Tables 5.5 & 5.6).

Compared to the performance of variables that quantify the relative abundance of potential prey (Tables 5.3, 5.4), prey patch metrics did not describe variation in predator numbers well. In some cases, patch metrics and relative abundance variables can be used together to improve the overall fit of models relating predators to their prey (see below).

Table 5.5: Summary of single parameter GAMMs used to assess the relationship between prey patch metrics and dolphin relative abundance. Each of the four metrics is represented as a smoothed function using a thin plate regression spline (s) and also includes a random effect for location.

Model	R^2	Deviance	df	AIC
Dolphin ~ s(Area_mean)	0.29	37.70%	12	913
Dolphin ~ s(Length_mean)	0.29	37.80%	12	914
Dolphin ~ s(Thickness_mean)	0.27	33.60%	11	931
Dolphin ~ s(Depth_mean)	0.19	29.00%	9	948

Table 5.6: Summary of single parameter GAMMs used to assess the relationship between prey patch metrics and penguin relative abundance. Each of the four metrics is represented as either a smoothed function using a thin plate regression spline (s) and also includes a random effect for location

Model	R^2	Deviance	df	AIC
Penguin ~ s(Area_mean)	0.42	45%	11	496
Penguin ~ s(Length_mean)	0.38	43.30%	11	504
Penguin ~ s(Thickness_mean)	0.34	41.20%	10	512
Penguin ~ s(Depth_mean)	0.30	40.30%	10	515

5.3.4 - Top-models relating predators and prey

Due to the influence of concurvity, not all prey patch metrics could be included within the global model for each predator species. Nevertheless, mean depth of schools and mean school thickness was retained in the top-model for each predator (Table 5.7). The top model for dolphins retained parameters for prey relative abundance and patch characteristics (school depth and thickness). For penguins, only the relative abundance of prey was retained (Table 5.7). However, a second-ranked model, with similar weight (0.31) included mean school depth. Thus, the influence of mean school depth, from the second ranked model is considered in the gam plots below. The top-models for dolphins and penguins both explained a substantial amount of deviance (52 and 50% respectively).

Table 5.7: Top-models chosen by information theoretic model selection for predicting the relative abundance of three predators according to potential prey abundance and patch characteristics.

Predator	Formula	Deviance	df	AIC	weight
Dolphin	s(C. area_BS) + s(School_depth) + s(School_thickness) + Location(RE)	52%	18	883	0.89
Penguin	s(Bin.3) + Location(RE)	50%	12	474	0.38

With one exception (school depth in the penguin model; p. = 0.1) all parameters retained in the top-model for each predator species were statistically significant with p-values <0.01 for smoothed terms (Table 5.8). This shows that both the relative abundance and attributes associated with prey patches have important influences on the predators studied.

Table 5.8: Statistical significance of parameters retained in the top-model of each predator species. The parameter for school depth for the penguin model (*) comes from the second ranked, similarly weighted top model.

Parameter	Species	P-value
s(C. area_BS)	Dolphin	<0.000
s(School_thickness)	Dolphin	0.01
s(School_depth)	Dolphin	0.004
Location(RE)	Dolphin	<0.000
s(Bin.3)	Penguin	<0.000
s(School_depth)*	Pengiun	0.104
Location(RE)	Penguin	<0.000

RAPP had a strong effect on relative abundance of dolphins (Fig. 5.5). As cumulative school area backscatter increases from 0 there is a dramatic increase in the effect on dolphin abundance (Fig. 5.5). The positive relationship between RAPP and dolphin abundance continues until the trend plateaus at approximately 600 m^2/km. Additional increases in RAPP do not influence the effect of this parameter. Further evidence of the importance of this trend is provided by narrow confidence bands that do not overlap zero.

The effect of mean school depth on dolphin relative abundance illustrates a peak between 8 and 15m where the effect of school depth is positive (Fig. 5.5). At depths greater than 15m the influence of mean school depth becomes significantly negative. Depths shallower than approximately 8m also have a negative influence upon dolphin relative abundance. For dolphins there appears to be an ‘optimal prey school depth between 8 and 15m.

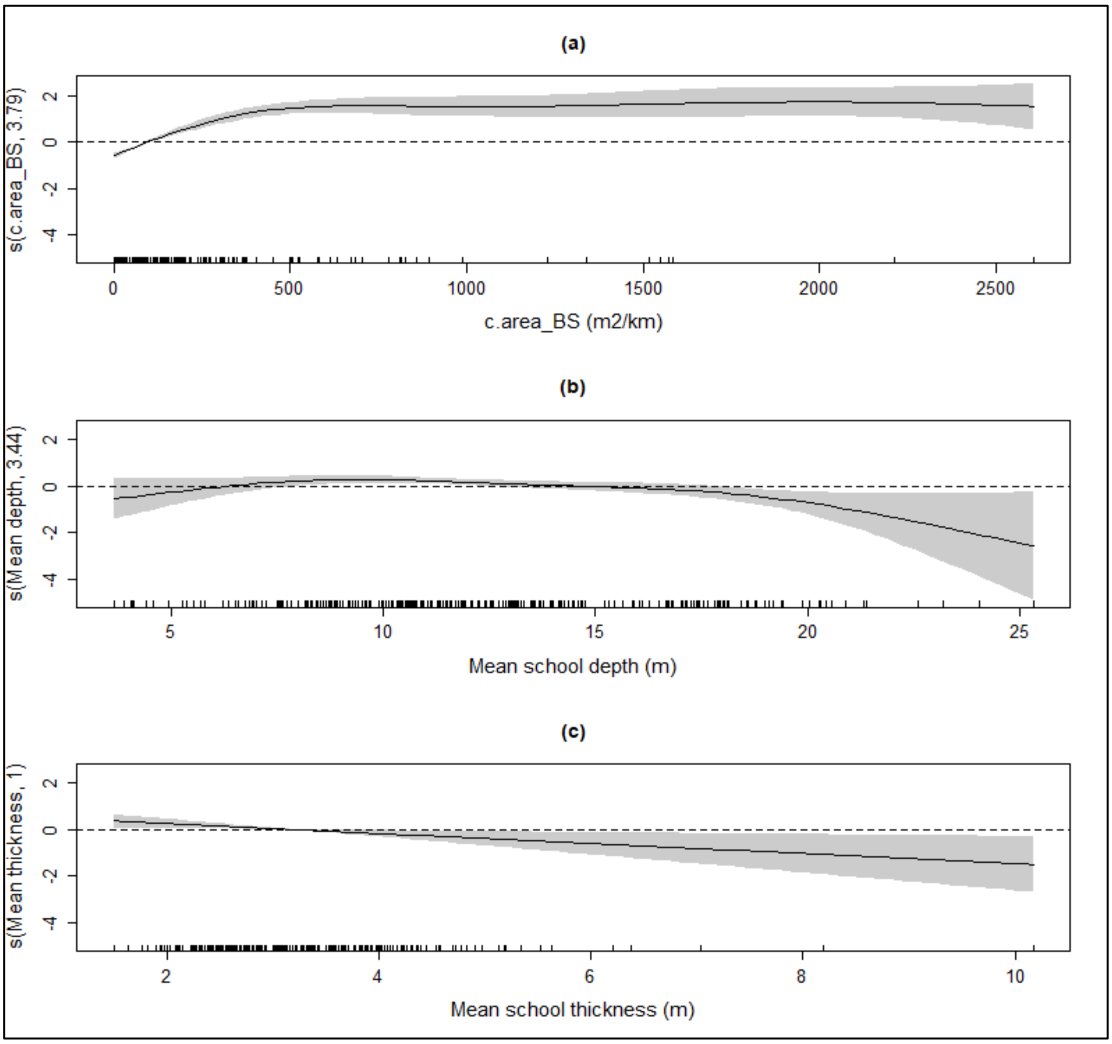

Figure 5.5: Plots of the smoothed effect of relative prey abundance (a), mean school depth (b) and mean school thickness (c) upon dolphin relative abundance. Shaded area represents the 95% confidence band on the given smooth. The effective degrees of freedom for each smoothed effect is given on the y-axis. Tick marks on the x-axis represent values of a variable from a specific survey.

RAPP also had a strong effect on the relative abundance of penguins (Fig. 5.6). An increasing positive effect of prey abundance was observed up to approximately 300 m^2/km, whereafter the effect plateaued. At higher levels of RAPP there was little change in the influence on penguin counts; the apparent decrease at 800 m^2 is associated with wide confidence bands that overlap 0. There are few data points beyond 800 m^2 meaning at these values the trend must be regarded with caution (Fig. 5.6).

The effect of mean depth of schools on the relative abundance of penguins showed increasing penguin numbers with school depth. The effect is strongest at 25m. At depths shallower than 8m the effect of mean school depth becomes significantly negative (Fig. 5.6). It should be noted, however, that the effect of school depth on penguin relative abundance is weak and not statistically significant. This is shown by the confidence intervals that overlap 0 for the majority of the effect, and a p-value > 0.01 (Table 5.7).

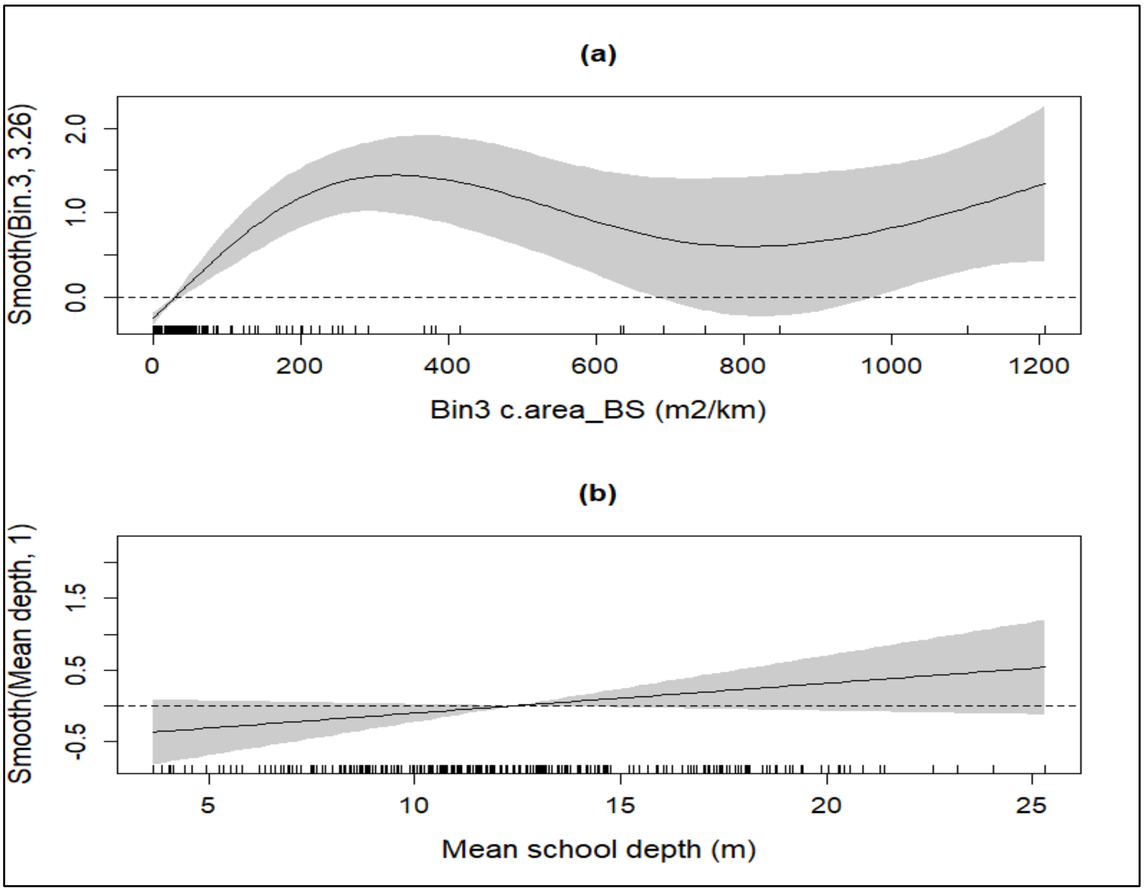

Figure 5.6: Plots of the smoothed effect of the best parameter for prey abundance (a) and mean school depth (b) upon the relative abundance of penguins. Shaded area represents the 95% confidence band on the given smooth. Each of these variables were retained in the top-model two for penguins. The effective degrees of freedom for each smoothed effect are given on the y-axis. Tick marks on the x-axis represent values of a variable from a specific survey.

Diagnostic plots of residuals against predictors or fitted values identified no issues with homogeneity of variance for either of the top-models (Appendix 3a). The independence of the response variable was also confirmed for the top-models for each predator (Appendix 3a). Using the *gam.check* function showed that the degrees of the smoothed terms were not overly restrictive for the dolphin or penguin top-models. Plots of the Pearson residuals overlaid on each smoothed effect from the three top-models showed no systematic departure from the smooth. The residuals of the models for both predators generally approximated the negative binomial distribution as shown by the simulated q-q plots (Appendix 3a*)*. There were some departures from the idealised distribution for the dolphin models at the extreme positive theoretical quantity and in the centre of the distribution for the penguin models. These small departures are assumed to have limited effect on the model outcomes as some departure from the ideal simulated distribution is expected with discrete count data (Wood 2017). In any case, preliminary trials with other response distributions (i.e. poisson) yielded more extreme departures from the idealised distribution, thus negative binomial was the most appropriate for these models.

5.3.5 - Spatial and seasonal distribution of prey

There was significant variation in RAPP among survey areas and seasons. Mean prey abundance was highest during summer (Fig. 5.7). With exceptions of Lyttelton and Otanerito, the difference in RAPP between summer and winter was substantial. In summer, RAPP was highest at Flea Bay, followed by Akaroa, Damon's Bay, Long Lookout, and Otanerito Bay. There was much less variation in RAPP among survey areas in winter. Over both seasons, four "reference" areas had the lowest values of RAPP (Wainui, Lyttelton, Menzies Bay and Long Bay; Fig 5.6).

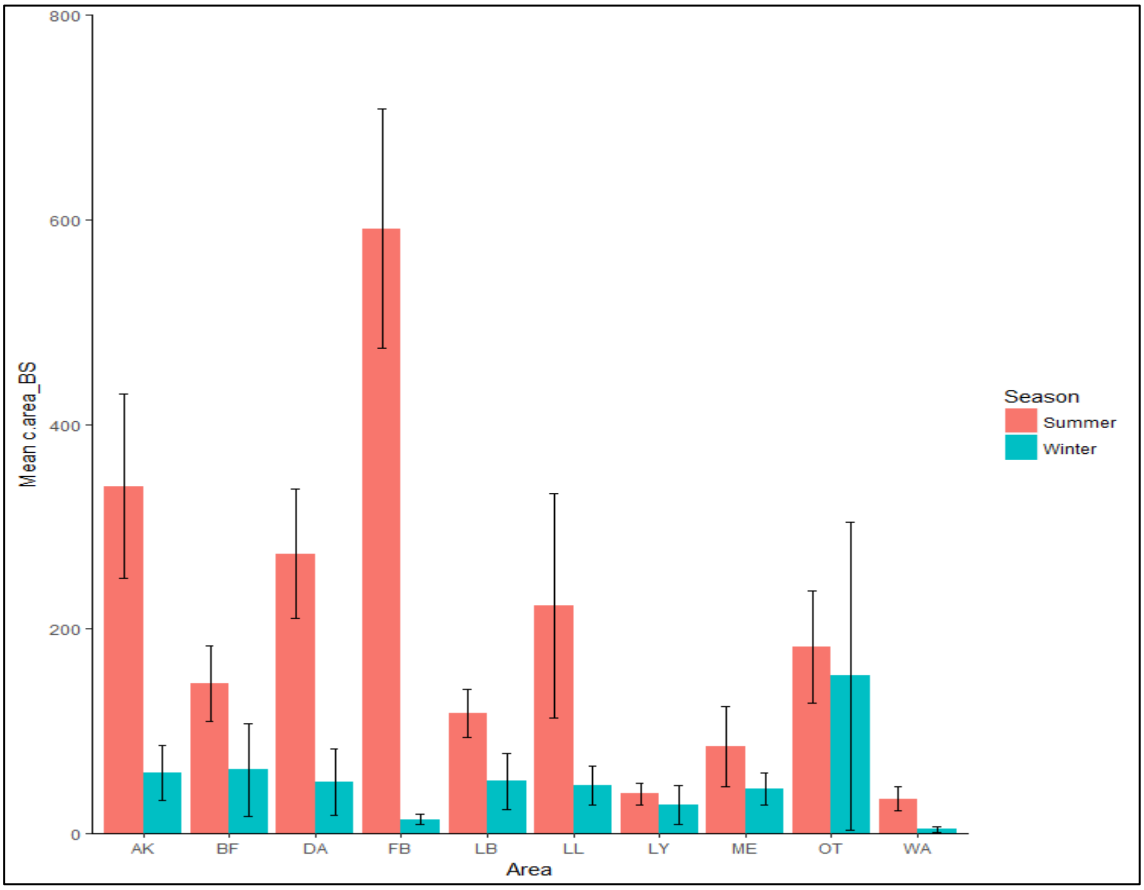

Figure 5.7: The mean relative abundance of potential prey (c.area_BS; m2/km) for all hydro-acoustic surveys conducted at ten survey areas and over two seasons. Error bars are +/- standard error.

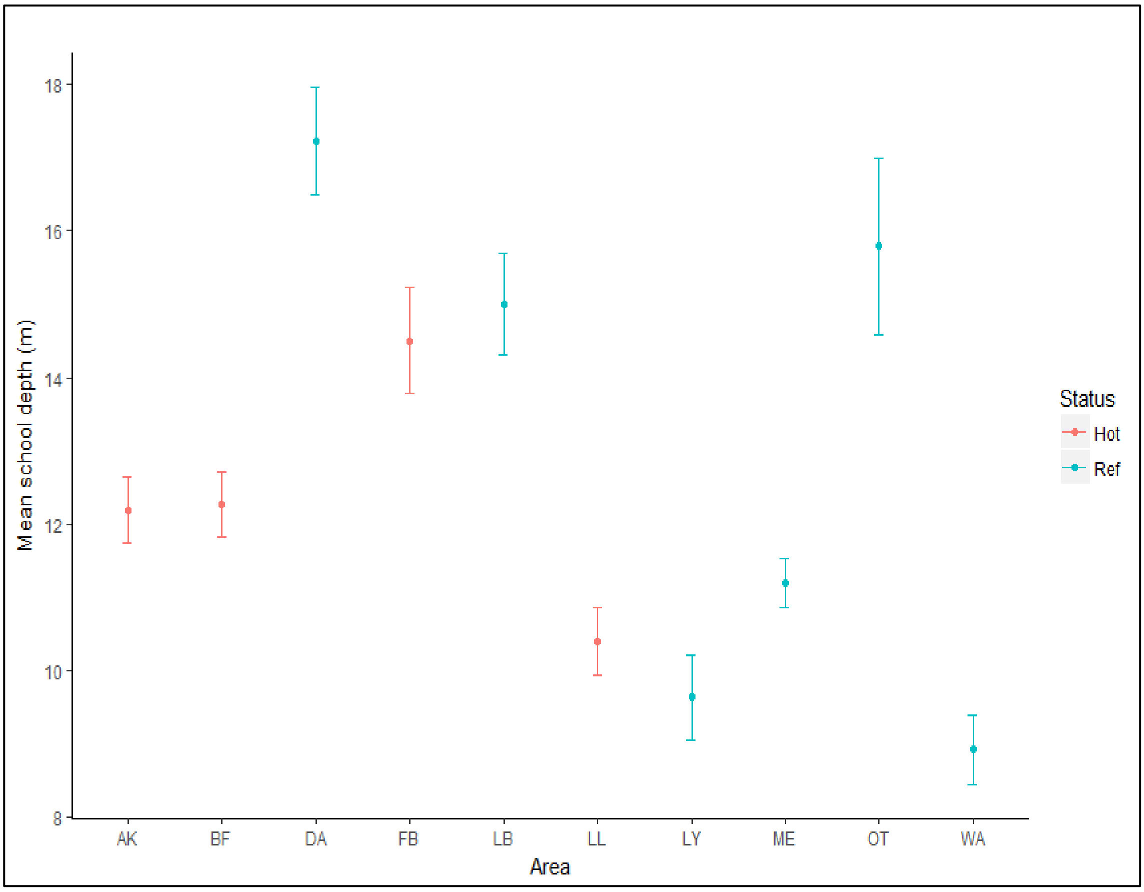

Figure 5.8: The mean depth of schools of potential prey detected in all hydro-acoustic surveys at the ten survey areas. Hotspots (Hot) and lower density areas (Ref) for Hector's dolphins are shown. Error bars are +/- standard error.

There was also substantial variability in the mean depth of schools among survey areas (Fig. 5.8). The depth of schools was deepest at Damon's Bay, Otanerito Bay and Long Bay and shallowest at Wainui, Lyttelton and Long Lookout (Fig. 5.8). The four survey areas that are hotspots for Hector's dolphins had mean school depths between 10 and 15m; a depth range shown to have a positive effect on dolphin abundance (Fig. 5.5).

5.4 - Discussion

5.4.1 Best metrics for relative abundance and prey patches

This Chapter provides clear evidence that meaningful relationships between predator and prey abundance can be discerned using data sourced from RGEs (Figs. 5.4, 5.5). Interestingly, different metrics were seen as the best indicator of RAPP for the two predators. The metric that best described relative abundance of dolphins was total cumulative school area. This suggests that the prey field of dolphins is distributed throughout the water column; a fact confirmed by stomach content analysis of stranded or bycaught dolphins (Miller et al. 2013). While epipelagic prey are a major component of the diet of Hector’s dolphin, benthic and demersal fish such as red cod and ahuru (*Auchenoceros punctatus)* were more important in Miller et al’s sample. Further, Miller (2014) found evidence for fine-scale overlap between Hector’s dolphins and red cod. Little is known concerning the schooling characteristics of red cod, although the species is abundant in the nearshore waters of the Canterbury Bight and Banks Peninsula during summer (Habib 1975; Kemp et al. 2012). The binned prey abundance metric that best explained variation in dolphin abundance was layer zero, the demersal bin adjacent to the seafloor. Canterbury trawl fishermen report that red cod sometimes form dense aggregations just above the bottom (pers comm to S. Dawson); it is conceivable that some near-seafloor schools classified as epipelagic were in fact red cod.

The RAPP metric that best described variation in little penguin counts was cumulative school backscatter in depth bin three; between 13 and 18m of depth. A stronger relationship between the abundance of deeper prey and penguins is surprising, given that with shallower dive depths and shorter dive times (Hoskins et al. 2008; Chilvers 2017), penguins would be assumed to prefer shallower prey than dolphins. The depth range of bin three is slightly deeper than the mean dive depths of penguins reported by studies in Australia (Hoskins et al. 2008; Pelletier et al. 2012) and elsewhere in NZ (Chilvers 2017). This could reflect variability in diving behaviour between penguins at Banks Peninsula and other locations; the species is known to be remarkably adaptable in its foraging strategy (Chiaradia et al. 2007; Hoskins et al. 2008; Chilvers 2017).

The importance of RAPP at greater depths in the penguin models could be related to a specific, preferential prey type that prefers a mid to deep position in the water column (Hoskins et al. 2008; Embling et al. 2012). Perhaps more likely is the influence of habitat characteristics on the formulation of the RAPP metrics. High penguin numbers were found at Flea Bay, Akaroa Harbour and Otanerito; all of which have depths beyond 25m in places. In deeper water, mid-water schools would have a greater mean depth. It should be noted that the process to establish the best RAPP metrics using depth bins may be influenced by vessel avoidance (see below), especially if prey are vertically avoiding the presence of the research vessel.

As the penguins do not usually travel further than 20km from their nesting colonies to forage, proximity to colonies is likely to influence the counts made during surveys. Each surveyed area had at least one penguin colony nearby, yet the size of colonies is highly variable (Challies and Burleigh 2004). Colony size is likely related to the degree of management (i.e. trapping of predators) that occurs at each site. Further research into the distribution of little penguins in this area could incorporate variables that account for distance to the nearest colony and the varying degrees of colony management. Thiswould provide an interesting opportunity to assess both marine and terrestrial drivers of relative abundance.

Metrics of prey patch characteristics were also related to the relative abundance of both predators. Mean school area and length explained a good proportion of the deviance in the counts of dolphin and penguins, yet it is likely that these metrics reflect patterns related to overall prey abundance. For both predators, the RAPP variables were better predictors of relative abundance than patch characteristics. This is in contrast with the results of Benoit-Bird et al. (2013), who found that patch characteristics were better at predicting the distribution of predators. Such a contrast likely reflects differences among predator-prey communities, predator foraging strategies and habitat (Ciannelli and Bailey 2005; Fauchald 2009; Benoit-Bird et al. 2013; Hunsicker et al. 2013; Womble et al. 2014; Bedford et al. 2015). It should be noted that the RGE sampling system may be limited in its capacity to generate accurate prey patch characteristics in shallow water due to the small volume sampled and potential for behavioural avoidance of the survey vessel by prey

(Lawson and Rose 1999; Simmonds and MacLennan 2005). Few other studies compare the relative importance of patch characteristics and prey abundance at describing predator distributions, but both factors have been shown to be independently important for a range of top-predators (Fauchald et al. 2000; Friedlaender et al. 2009; Hazen et al. 2009, 2011).

While some surveys areas had high relative abundance of both predators there was no consistent trend where hotspots for Hector's dolphins also had high abundance of penguins (Fig 5.6). Without incorporating data on a greater range of coastal predators, different prey and true measures of diversity and food-web complexity it would be premature to rule out whether dolphin hotspots have high ecological value. Yet, this perceived mismatch in distribution and the importance of different prey field characteristics provides insights into why the 'indicator species' theory may not always hold true. Likely due to the fundamental differences in foraging ecology between the two predators (e.g. visual vs. acoustic predators, independent vs group foraging), different characteristics of the prey field seem to be important. Additionally, terrestrial impacts on penguin populations (see below) may reduce relative abundance in certain areas so that local prey fields are not fully exploited. Such complexity in the factors that influence predator-prey relationships and spatiotemporal concurrence surely limit the applicability of the 'indicator species' theory at fine scales.

5.4.2 - Fine-scale overlap between predators and prey

Hector's dolphins and little penguins both showed statistically significant overlap with potential prey at fine-scales, suggesting that epipelagic prey have a strong influence on their distribution. The only other study linking Hector's dolphins to prey distribution (Miller 2014) showed fine-scale overlap between the dolphins and red cod. Few studies have linked dolphin and epipelagic prey distributions in coastal systems. Benoit-Bird et al. (2004) demonstrated that the relative abundance of dusky dolphins was strongly associated with potential prey at Admiralty Bay, New Zealand. In an ecosystem study that included a portion of the coastal zone, Certain et al. (2011) found strong spatial association between common dolphins and epipelagic prey such as pilchards

(Sardinops pilchardus) and sprats (*Sprattus sprattus).* There is growing evidence that the distribution of epipelagic prey strongly shapes habitat selection of coastal dolphins, across diverse locations.

While the distributions of several seabird (Crawford and Shelton 1978; Weimerskirch et al. 2005; Fauchald 2009; Regular et al. 2010), and other penguin species (Reid et al. 2004; Bedford et al. 2015) have been quantitatively linked to distribution of their prey, this is the first study to provide this link for little penguins. There is evidence that declines in the availability of epipelagic prey to little penguins are associated with population decline and/or variability (Dann 1992; Chiaradia et al. 2012). Therefore knowledge on the extent of overlap with prey and the locations and times that foraging is carried out may help to understand and so protect these important interactions.

Both predators showed similar trends with increasing RAPP; a strong increase followed by a plateau in the effect. This could be due to some large Munida schools inflating the RAPP metrics (Chapter 4), with predators not responding strongly to such aggregations. However, patches of prey are ephemeral, and the numbers of available predators are limited. Even a large, dense patch of food is unlikely to attract dolphins and penguins from many kilometres away. Thus, there will always be a finite number of predators foraging at a certain prey patch, regardless of its abundance.

Mean depth of schools was retained in the top-models for both predators. Dolphins show a clear optimal depths for prey between 8 and 15m. The mean depth of prey schools for each hotspot was located in this optimal depth. The three reference areas with relatively high prey abundance had the three deepest depths of schools. These results suggests that hotspots for Hector’s dolphins are locations where prey are not just abundant, but within easily accessible depths.

The inclusion of prey depth for assessing the distribution of top-predators in coastal habitat is rare, yet seemingly important (Embling et al. 2012; Womble et al. 2014). Womble et al. (2014) demonstrated that the prey depth influenced the foraging distribution of harbour seals (*Phoca vitulina*) in Alaska. Embling et al. (2012) found that large aggregations of black-legged kittiwakes (*Rissa tridactyla)* frequently occurred when their prey, sand eels (*Ammodytes* spp.), were found near the surface. These examples and the results from this study confirm the importance of considering both abundance and patch characteristics of prey when determining habitat selection by predators.

There was a strong seasonal effect in RAPP, with prey being more abundant in summer than winter in most survey areas. Very little is known about the seasonal distribution of epipelagic fish in NZ waters; to my knowledge this is the first study to show seasonal change in relative abundance. Colman (1979) found sprat eggs to be higher density further offshore in the Canterbury Bight in winter/spring seasons; suggesting that the species spawns beyond the nearshore environment at this time of the year. In Australia, pilchard were also found to spawn off the coast (2-8km) between July and December (Fletcher and Tregonning 1992). In Port Phillip Bay, pilchards are more abundant in summer and autumn than winter months when adult fish migrate further offshore (Neira et al. 1999). It seems possible therefore, that the most common epipelagic species seen in this study (sprat and pilchard) are moving offshore during the winter and spring. Hector’s dolphins show a similar decrease in the use of nearshore habitat during winter (Chapter 2, 3, Rayment et al. 2010), and are found further offshore at this time (Dawson & Slooten 1988; Bräger et al. 2003; Rayment et al. 2010). Miller (2014) regularly caught red cod in her inshore pots in summer, but none in winter. Conversely, in offshore (4 n.m) habitat, red cod catch was higher in autumn-winter-spring, and no cod was caught in summer (Miller 2014). It seems both red cod and epipelagic species share a similar inshore-offshore seasonal distribution that matches that of Hector’s dolphins. This provides evidence that the seasonal use of the nearshore study area of this thesis is closely linked with the presence of prey.

The distribution of epipelagic prey throughout the study area will be influenced by their habitat preferences. Species-habitat relationships are largely unknown for the epipelagic species that feature in this study, but O’Driscoll and McClatchie (1998) found a strong association between epipelagic schools and an eddy system on the Otago Coast. O’Driscoll (1998) found that the distribution of epipelagic barracouta were influenced by the density of their prey (Krill;

Nyctiphanes australis). In Australia, some pilchard stocks seek shallow, nearshore locations as nursery habitat (Neira et al. 1999), and there is some circumstantial evidence for this at locations in NZ (Paul et al. 2001). Depth and seabed type are known to influence the distribution of epipelagic schools in the Mediterranean (D'Elia et al. 2009) and oceanographic variables influence habitat selection for anchovy and sardines in the Bay of Biscay (Planque et al. 2007). A wide variety of physical and oceanographic habitat types are represented in the nearshore environment at Banks Peninsula (Chapter 6). Coupled with good information on predator distribution, this study area offers opportunities to investigate the habitat types that sustain the predator-prey interactions identified in this study as well as determining the species-habitat relationships of important epipelagic taxa.

Understanding when/where prey aggregate provides valuable information for the conservation of marine predators. This chapter has identified locations at Banks Peninsula where an important prey field is abundant and catchable. As good access to prey is intrinsically linked to population vital rates (Atkinsen and Ramsay 1995; Mann et al. 1998; Baker et al. 2007)) this information may be valuable for management. Disturbance to foraging behaviour from anthropogenic sources such as vessel traffic and tourism (Martinez et al. 2010; Brough et al. 2014) or direct impacts on the prey availability (e.g. via overfishing or climate change) are documented or perceived threats to both predators. Thus, careful management would consider mechanisms to protect the vital interactions between predators and prey in the places and the times that they most often occur.

The results of this chapter show how models of distribution and habitat use of marine predators are greatly improved by information on prey. The models performed much better than those of chapter 3 which were based on coarse spatiotemporal parameters. However, this chapter and the analyses of chapter 6 are based on visual sightings, while chapter 3 used acoustic data on dolphin relative abundance and foraging. Visual and acoustic methods sample marine mammal abundance in different ways and at different scales, however the methods often provide compatible information (e.g. Rayment et al. 2018). In this thesis, I do not compare the differences between the two methods in terms of their ability to resolve habitat use patterns. In appendix 3b I provide some information on the relationship between the visual and acoustic response variables, for visual surveys during which TPODs were deployed. A strong correlation between the response variables suggests the two methods are providing similar information on dolphin relative abundance. Further investigations will use both visual and acoustic datasets to assess the relative merits of each method in determining marine mammal habitat use, at multiple scales.

5.4.3 - Conclusions

While recreational grade echo-sounders have important limitations, this chapter has proven their utility for quantifying the spatial overlap between two coastal predators and epipelagic fish. This is the first study to demonstrate overlap between Hector's dolphins, little penguins and their epipelagic prey. Such information can be used to investigate biophysical coupling between trophic levels and better protect foraging habitat for these vulnerable predators. The results from this chapter suggest that prey are an important driver of hotspots of Hector's dolphin distribution, and strongly influence seasonal changes in distribution.

Chapter 6: What makes hotspots unique? Investigating the drivers of habitat selection and the existence of hotspots

6.1 - Introduction

Many studies show that marine top-predators have 'hotspots' of distribution (Hastie et al. 2004; Gende and Sigler 2006; Scott et al. 2010). What drives the formation of hotspots is less well known. In particular, the ecological factors that make hotspots unique are poorly understood; there are few studies that directly assess the unique characteristics of these areas. Species distribution modelling suggests that habitat use by predators is shaped by physical habitat type (Torres et al. 2008; Eierman and Connor 2014), hydrological regime (Johnston et al. 2005; Yen et al. 2006) or a combination of both (Bailey and Thompson 2010; Embling et al. 2012). Further, hotspot formation is also likely to be strongly correlated with the distribution of prey (Gende and Sigler 2006; Hazen et al. 2013).

Understanding the characteristics of important habitat has obvious benefits for the protection and management of species. For example, if the features of hotspots are well understood, it will be easier for management to target the preservation of these features and provide more effective protection of the biodiversity they support. This has been shown in the establishment of "The Gully" MPA in Canada to protect the habitat of resident northern bottlenose whales (*Hyperoodon ampullatus;* Hooker et al. 1999). The whales' habitat preferences were used to define the boundaries of the MPA (Hooker et al. 1999, 2002, 2011). Whilst there are many other examples of MPAs that have considered the spatial distribution of the top-predators they are designed to protect (e.g. Dawson and Slooten 1993; Cheney et al. 2014; di Sciara et al. 2016), few consider the habitat preferences of the species. This is probably due to a lack of the necessary information, and emphasises the need to quantify predator-habitat relationships.

Being able to define important areas based on habitat characteristics may allow the prediction of hotspots in locations that are lacking detailed information on distribution. For threatened or recovering species, ability to predict the locations of important habitat will be invaluable (Guisan et al. 2013; Torres et al. 2013; Roe et al. 2014). For example, Torres et al. (2013) used predictive modelling to identify important habitat for Australasian southern right whales (*Eubalaena australis)*. In the case of Hector's dolphin, little is known about fine-scale habitat use patterns beyond the nearshore environment (e.g. Rayment et al. 2009). If dolphin-habitat modelling in the nearshore can help clarify the relationships between dolphins and their habitat, predictive models may help to identify areas beyond current MPAs that are appropriate for further fisheries restriction. However, such a use of habitat models can only be achieved if the dolphin-habitat relationships from the nearshore environment are similar in offshore settings.

Spatiotemporal patchiness in primary productivity is apparent at scales of 100s of kilometres to 10s of metres (Perry 1986; Alvarez-Borrego and Lara-Lara 1991; Martin et al. 2002) and from days to years (Perry 1986; Barber et al. 1996; Iriarte et al. 2007). This patchiness means it is often difficult to resolve and predict patterns in productivity. Fine-scale patterns are particularly hard to predict. For example, the factors that drive differences in phytoplankton density in apparently similar locations, only kilometres apart, are poorly understood (Owen 1989; Abraham 1998; Lunven et al. 2005). Correlations between productivity and predator distribution have been reported in many studies (e.g. Yen et al. 2006; Scott et al. 2010; Moura et al. 2012; Saijo et al. 2016). Conversely, some studies show a weak or negative relationship between predators and indices of primary productivity (Smith et al. 1986; Redfern et al. 2008; Forney et al. 2012). Often, the relationship between predators and primary productivity is scale dependant, where trends are obvious at certain (often larger) scales but not others (Redfern et al. 2008; Forney et al. 2012). In order to understand if, and when, top-predators may be used as indicators of productive locations, it is necessary to investigate the links among these trophic levels in diverse habitats.

Characteristics of the seafloor have been related to the distribution of several species (Macleod et al. 2004; Torres et al. 2008; Goetz et al. 2012; Brookes et al. 2013). For example, the distribution of harbour porpoise has been linked to sandy habitat (Brookes et al. 2013; Williamson et al. 2017). The spring-time distribution of minke whales (*Balaenoptera acutorostrata*) is also highly correlated with a sand/gravel seafloor type at the Isle of Mull, Scotland (Macleod et al. 2004). Bathymetric factors such as areas of preferred depth (Doniol-Valcroze et al. 2012; Bouchet et al. 2015; Williamson et al. 2017) and slope (Pirotta et al. 2011, 2013; Bouchet et al. 2015) are related to distribution for some marine mammals. Oceanographic features including the dynamics of tidal currents (Bailey and Thompson 2010; Pirotta et al. 2013), eddies (Johnston et al. 2005; Yen et al. 2006; Cotté et al. 2015) and fronts (Sydeman et al. 2006; Bost et al. 2009) strongly influence where some predators aggregate. Oceanic predators in particular have strong associations with frontal systems where primary productivity is high (Louzao et al. 2006; Sydeman et al. 2006; Bost et al. 2009). In coastal locations, tidal flow over uneven topography often results in aggregations of predators (Johnston et al. 2005; Bailey and Thompson 2010).

The most common descriptors of habitat used in distribution models are simple measures of oceanographic conditions such as temperature and salinity (Reilly 1990; Grémillet et al. 2008a; Torres et al. 2008). These variables have been correlated with the distribution of a wide variety of top-predators, and help to explain seasonal shifts in distribution (Reilly 1990; Bräger et al. 2003; Miller and Baltz 2007; Grémillet et al. 2008a; Saijo et al. 2017). Whilst informative, such relationships provide little information for the protection of species and habitat unless there are stable features, such as upwelling, that promote consistent trends in oceanographic properties. Features derived from oceanographic data e.g. thermoclines (Redfern et al. 2008; Hazen et al. 2011) and the degree of mixing (Scott et al. 2010; Embling et al. 2012) are also commonly used in habitat models for top-predators.

In general, each of the above characteristics of habitat are thought to relate to the distribution of predators via their effect on prey. For example, the association of both harbour porpoise and minke whales with sandy habitat reflects a requirement of sand eels (a prey item for both species; Macleod et al. 2004; Williamson et al. 2017). Additionally, tidal eddies and wakes associated with high harbour porpoise densities in the Bay of Fundy were also areas of high prey abundance (Johnston et al. 2005). For some predators, features other than prey abundance, such as detectability, catchability and quality, are important (Au et al. 2013; Benoit-Bird et al. 2013; McCluskey et al. 2016). These factors may be shaped by processes other than those that regulate prey abundance. Consequently, characteristics of habitat may not always serve as appropriate proxies for the aspects of the prey field that best describe predator distribution. For this reason, it makes sense to consider prey abundance as a further characteristic in models of habitat-use in top-predators.

Several studies have assessed the distribution of marine mammals with respect to a broad suite of physical, oceanographic and prey characteristics (e.g Torres et al. 2008; Hazen et al. 2011; Embling et al. 2012), but few have focussed on how such characteristics are represented at known hotspots. In one of the few examples, Bailey & Thompson (2010) showed that a hotspot for bottlenose dolphins in Moray Firth was related to topographic and tidal features that promote foraging opportunities. For Hector's dolphins, previous study has demonstrated that water temperature (Bräger et al. 2003), depth (Bräger et al. 2003), salinity (Miller 2014), chlorophyl concentration (Miller 2014) and oceanic fronts (Clement 2005) are related to distribution. The abundance of dolphins is also highly correlated with the abundance of red cod (Miller 2014). There is little understanding of how these factors are represented at hotspots. Further, the importance of variables associated with physical habitat type, tidal currents and water column stratification remain unknown.

The stability of hotspots over several decades (Chapter 2) and their use for foraging (Chapter 3) illustrate the importance of these areas for Hector's dolphins and substantiate the need to understand what habitat features are represented by these locations.

6.1.2 - Chapter objectives

- What biophysical factors are correlated with the distribution of Hector's dolphins in coastal habitat at Banks Peninsula.
- How are these factors represented in known dolphin hotspots? What makes hotspots hot?

6.2 - Methods

Systematic visual surveys of Hector's dolphins (see Chapter 5 for detail) were used to collect data on the relationship between the distribution of dolphins and the characteristics of their habitat. 'Zig-zag' surveys were carried out in four 'hotspot' and six 'reference area' locations over summer and winter seasons (Chapters 2, 3, 5) and provide an estimate of the relative abundance of dolphins at these locations at the time of survey. Survey effort, number of dolphins seen and sighting conditions were entered into the HP palmtop computer.

6.2.1 - Physical habitat types

Side-scan sonar (SSS) surveys were carried out to map the entire sub-tidal habitat of each area. Modern high frequency SSS provides near photo-realistic images that, when combined with ground-truthing, provide accurate characterisation of the seafloor (McRea et al. 1999; Brown et al. 2002; Kenny et al. 2003; Blondel 2009). All habitat mapping was undertaken in the winter of 2016, mid-way through the study period, using a Simrad NSS7 evo2 equipped with a structure-scan 3D^{TM} transceiver. A structure-scan 455/800Khz transducer was mounted on the transom of a 6m aluminium powerboat on an extendable pole and was fixed 1.2m below the waterline. The transducer produces two side-scanning lobes that ensonify the seafloor out to a maximum of 120m either side of the vessel in a fan shaped beam. However, given the shallow water depths of this nearshore habitat, lateral range was typically restricted to between 30 and 50m, giving a total swath width between 60 and 100m. Acoustic data were sampled at 1400 samples per pulse giving a horizontal resolution of approximately 30cm per pixel. Survey lines were established running parallel to the shore, and extending out to the 800m limit of the nearshore study area. Lines were positioned to ensure a 20% overlap of coverage between adjacent runs. SSS surveys were undertaken in conditions with beaufort<2 and swell<1m to minimise artefacts produced by turbulence around the transducer. Navigation data was sourced from the vessel's GPS system and typically had between 3 and 5m accuracy. Sonar and navigation data was logged directly to a micro-SD card.

The software Sonar TRX was used to process, analyse and create georeferenced mosaics from SSS data. Processing steps included 1) calculating beam angle correction statistics and slant range correcting the hydro-acoustic data, 2) removing the water column from each survey, 3) screening data for serious artefacts (e.g. dropped pings, beam-spreading error, acoustic interference; Blondel 2009), 4) removing data beyond the range extent for the survey and 5) constructing mosaics. Mosaics were constructed at the highest possible resolution in order to aid visual categorization of habitats. Raster mosaic tiles were viewed in ArcMap (version 10.4; ESRI) and the highest quality (i.e. closest to nadir) overlapping tiles selected; these were then merged into a 'master-image' (Fig. 6.1) for each survey area using Sonar TRX.

Classification of physical habitat types followed the NZ marine habitat classification scheme (Dohner 2013). Habitat was classified to level 2, i.e. main abiotic habitats. Hard-substrate (reef) was easily discernible and was classified into bedrock reef, boulder reef and cobble (Table 6.1). Soft-substrate was visually identified by the absence of any high-intensity, rugged seafloor and was classified into mud, sand and coarse sediment (Table 6.1). Demarcations between different habitat types were identified visually by marked changes in the physical appearance and intensity of adjacent areas of the seafloor; known as 'acoustic regions' (McRea et al. 1999; Brown et al. 2002). The boundaries of each region were classified manually by constructing polygon features in ArcMap, which were then merged to form a continuous benthic habitat map for each location. The identity of each region was later categorised by ground-truthing (see below). Due to the variability in swath coverage and the location of boundaries between adjacent swaths (e.g. Fig 6.1), some interpretation is required in establishing the location of habitat boundaries (Blondel 2009). This potentially introduces some observer bias. This was reduced by having one observer responsible for the classification of the entire SSS dataset.

Ground-truthing of habitat types was carried out using a combination of ponar sediment grabs and drop camera deployments. Ground-truthing stations targeted the regions that appeared dissimilar in the master mosaic images for each area. Also, randomly generated points were used to sample additional habitat features and to confirm initial classification. A drop-camera was used when it was expected that a region would be hard substrate, and the ponar grab on soft-substrate. The drop-camera could not be used to identify soft-sediment due to low water visibility conditions making it difficult to distinguish between sand and mud bottom types. Sediment grab samples were photographed and classified in the field based on estimated grain size (Table 6.1). The drop-camera frame had a measurement scale allowing categorisation of boulders and cobbles (Table 6.1). Each location had at least ten samples of different acoustic regions and ten randomly allocated ground-truthing points. Some areas, however, had many more ground truthing points due to the availability of 174 randomly distributed drop camera sites from a baited under-water video survey carried out by the NZ Department of Conservation (Brough et al. 2018b)

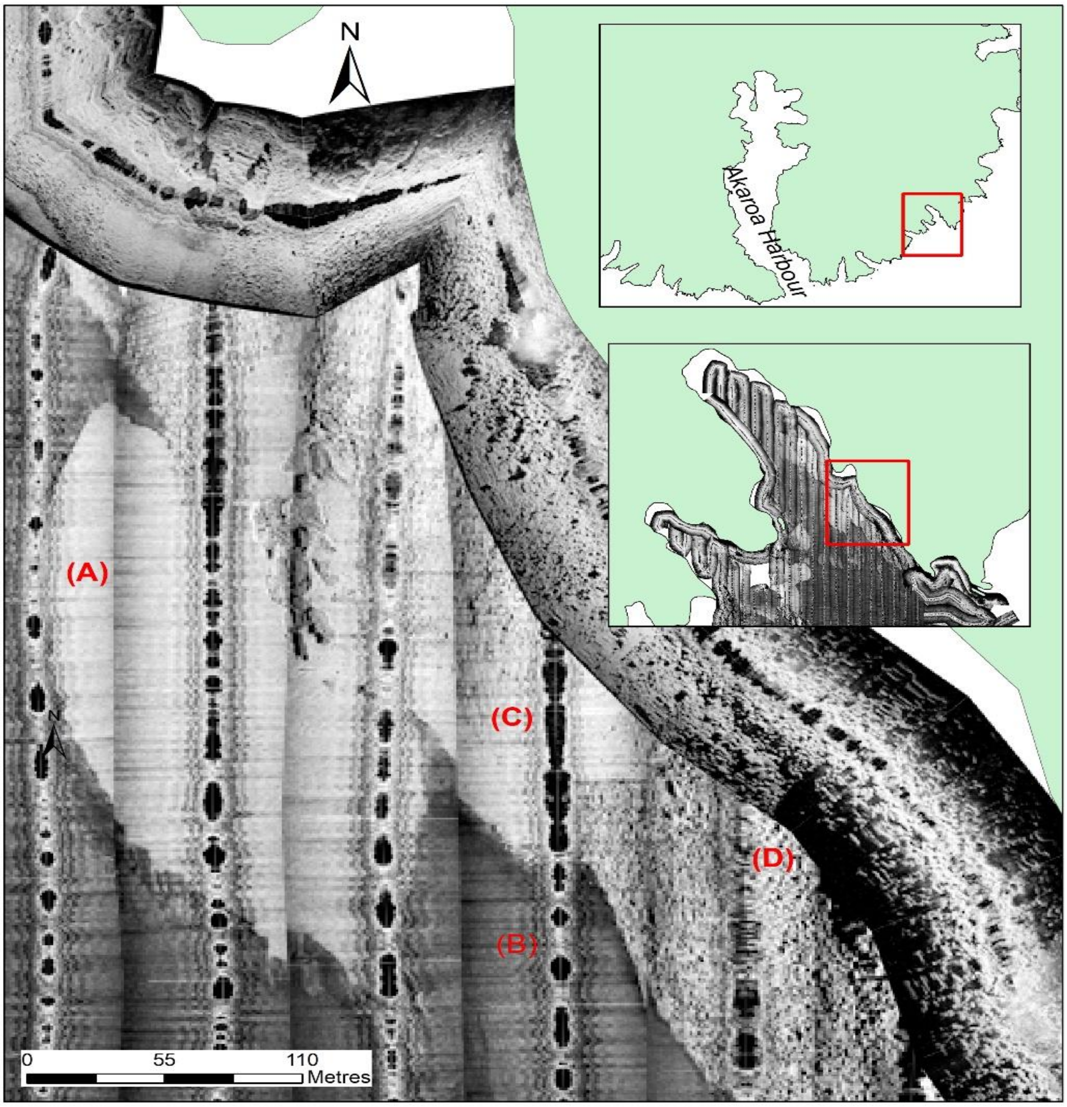

Figure 6.1: Example of side scan sonar imagery from Otanerito Bay that shows the representation of various habitat types. Ground-truthed coarse sediment (A) and mud (B) is shown. The high resolution scanning sonar clearly shows loose cobble (C) and boulder reef (D). The location of this section of the mosaic within Otanerito Bay is shown with the full SSS master image (bottom inset) as is the position of Otanerito Bay on Banks Peninsula (top inset).

Table 6.1: Habitat classification used in this study following the NZ marine habitat classification scheme for physical habitat. Acoustic regions of the seafloor were classified into one of three hard-substrate types or three soft-substrate types. A description of each habitat type is given based on how it was distinguished from side-scan mosaics and ground-truthing samples. Classifications based on size measurements are from Dohner (2013).

Habitat type	NZMHCS number	Description
Hard-substrate		
Bedrock reef	3.2.3	Slabs of continuous, rocky substrate.
Boulder reef	3.2.2	Rounded boulders greater than 256mm in diameter.
Cobble	3.2.1	Small hard structure with diameter less than 256mm
Soft-substrate		
Coarse sediment	3.1.3	Flat areas of the seafloor with high backscatter intensity. Grab samples yield pebbles, gravel, shell-hash or whole shells. Sediment grain size estimated to be above 4mm.
Sand	3.1.1	Flat areas of the seafloor with medium backscatter intensity, sand-waves often visible. Grab-samples yield sediment with obvious grainy structure.
Mud	3.1.2	Flat areas of the seafloor with low backscatter intensity. Grab-samples yield sediment with little or no obvious grainy structure. Anoxia often present.

6.2.2 - Bathymetry

Bathymetric maps of the depth and slope of each survey area were produced using hydro-acoustic data from a single beam echo-sounder that was operated during SSS surveys. Echo-sounder data was also available from the prey surveys (Chapter 5). Raw hydro-acoustic data were uploaded into the software ReefMaster (v. 1.8 Reefmaster Sotware Ltd) and bathymetric surfaces created using the x,y,z data from each data source. Data were corrected for tide level by the generation of tidal models for each area using the software WXtide (v. 4.6; WXtide 32) and data from NZ tide forecast model (Goring 2001). The grid for the bathymetric surface was set at 5 x 5 m. Interpolation of depth information was set at the minimum value needed to construct a complete surface for each area. Given the wide coverage of SSS transects and large number of single beam surveys at each location, interpolation distance was typically less than 50m. Bathymetric surfaces were exported as asci grids into ArcMap. When necessary, a smoothing filter was applied to bathymetric surfaces to remove residual artefacts (observable as unrealistic fluctuations in z-values over short spatial scales; Hell and Jakobsson 2011).

Slope surfaces were created for each area in ArcMap using the slope tool in the 3D analysis toolset. Slope raster files were produced at the same resolution as the original bathymetric data in units of degrees of slope angle.

6.2.3 - Tidal currents

Data on the velocity of tidal derived currents throughout the study area were available from a regional oceanographic modeling system (ROMS) constructed by MetOcean Solutions Ltd and described in detail by Soutelino and Beamsley (2015). The Pegasus Bay ROMs model has an average horizontal resolution of 300m and spans a period between 2003 and 2013. The model estimates horizontal and vertical current dynamics throughout the water column every 3 hours. For this study, I exported data on the depth averaged horizontal current (the dominant aspect) for 10 selected cells, each in the geographic centre of a particular survey area. Due to computational limitations, only the first five years of ROMs data were used (2003-2008). Data on tidal state specific for each location was sourced from the NZ tide forecast model (Goring 2001) for the same period and was matched against the ROMs output. Thus, each ROMS output for each location had an associated tidal state (described as hours from the last high tide). A smoothed spline analysis was used to create a dataset that summarised average tidal current velocity as a product of tidal state for each location (Appendix 4 Fig. 3). The fit of each non-parametric spline to the tidal data was appraised by generating 95% confidence intervals based on the standardized jack-knife residuals (Eubank 1985). This analysis was undertaken in *R*.

6.2.4 - Oceanographic data

Data on local oceanographic conditions at each location at the time of a survey were gained using an RBR Concerto conductivity, temperature and depth device (CTD) that was equipped with a Turner Cyclops fluorometer. CTD casts were made at the completion of each zig-zag survey at a point approximately in the centre of the survey track. After a 2 minute acclimatisation phase at 1m depth, the CTD was lowered through the water-column to within 1m of the seafloor. The CTD was calibrated at the beginning of the study and again midway through (winter 2016). The fluorometer was not ground-truthed; these data represent relative rather than absolute chlorophyll concentrations.

Oceanographic data were processed in Matlab using a custom written script. Excel files of raw data for each cast were processed in the following steps: 1) The acclimatisation phase and upcast sections of the cast were removed, 2) Downcast data were averaged within 1m bins from the 'surface' value (1.5m depth) to remove spikes, 3) variables summarising the temperature, salinity and fluorescence at the surface and maximum cast depth bin were extracted, and 4) Derived variables including metrics associated with the thermocline and water column stratification were calculated. A summary of raw and derived oceanographic variables and how they were calculated is given in Table 6.3.

6.2.5 - Prey

Data on the relative abundance and patch characteristics of prey were collected concurrently with observations of dolphins using hydro-acoustics (Chapter 5). Dolphins showed a strong relationship with the relative abundance and the depth of prey (Chapter 5). Thus, these factors were included as variables the modelling framework.

6.2.6 - Dolphin-habitat-prey database

A database that summarised the physical habitat types, bathymetry, current velocity, oceanography, prey field characteristics, survey effort and relative abundance of dolphins for each survey was generated. Data on the physical habitat types and bathymetry were extracted from feature and raster layers in ArcMap. A digitised track-line of each survey was imported and a buffer with a 400m (i.e. max sighting distance; Chapter 2) radius placed around the track. The resultant 'survey polygon' reflected the total area surveyed for each dolphin-habitat survey. The total area and percentage overlap of each physical habitat type contained within a survey polygon was calculated. The mean and standard deviation of the depth and slope bathymetric surfaces that overlapped a survey polygon were calculated and exported for each survey

A velocity value for the location specific tidal state was extracted from the averaged tidal velocity models (Appendix 4) in *R.* Variables derived from CTD casts were imported into the database and matched against the surveys for which casts were available. Every survey had measures of prey relative abundance and mean school depth. Sighting rate - the number of individual dolphins seen during a survey, divided by the survey length - was the measure of dolphin relative abundance. Survey effort was summarised in units of kilometres 'on effort'.

There is limited information on the relationship between Hector's dolphins and many of the habitat features assessed in this study. From studies of similar species in coastal environments, there is good reason to believe that a wide range of physical, oceanographic and prey variables influence distribution. Such variables can be represented in different forms (e.g. temperature can be surface temperature, bottom temperature, or somewhere in between). For this reason a broad range of habitat characteristics were included as candidate variables (Table 6.2). The best form for a particular characteristic was chosen based on comparing the fit (via AICc) of competing forms in the concurvity exercise (*see below).* Further information on the relationship between habitat variables and dolphin abundance was provided by exploratory analyses using scatterplots

Table 6.2: A summary of the full list of habitat variables considered in modelling dolphin-habitat relationships. Variables are grouped into habitat type, bathymetric, current, prey and oceanographic clusters. Descriptions of each variable are provided.

Variable	Abbreviation	Units	Description
Habitat-type			
Percentage of mud coverage	Perc_mud	Percentage	Percentage of mud habitat type encountered within a survey polygon
Percentage of sand coverage	Perc_sand	Percentage	Percentage of sand habitat type encountered within a survey polygon
Percent reef coverage	Perc_reef	Percentage	Addition of the percentage cover of bedrock, boulder and cobble reef habitat within a survey polygon
Percent coarse sediment coverage	Perc_Coar.sed	Percentage	Percentage of coarse sediment habitat type encountered within a survey polygon
Bathymetric			
Mean depth	Depth	Metres	The average depth of 5x5m grid cell encountered within a survey
Standard deviation of depth	Depth_std	Metres	The standard deviation of all cells contained within the survey polygon for a given survey. A measure of topographic complexity.
Mean slope	Slope_mean	Degrees	The average slope of 5x5m grid cell encountered within a survey
Standard deviation of slope	Slope_std	Degrees	The standard deviation of all cells contained within the survey polygon for a given survey. A measure of topographic complexity.

Tidal current			
Current velocity	Velocity	Metres per second	Averaged horizontal current velocity for the tidal state at the time of a survey.
Prey			
Relative abundance of prey	Prey_RA	Metres squared per kilometre	The total cumulative school area for all potential prey schools encountered within a survey divided by the survey distance.
Mean school depth	School_depth	Metres	Mean school depth for all schools detected within a survey
Oceanography			
Surface temperature	Surf_temp	Degrees Celsius	The temperature of seawater at 1.5m depth
Surface salinity	Surf_sal	Practical salinity units	The salinity of seawater at 1.5m depth
Surface fluorescence	Surf_flr	Micrograms per litre	Measure of relative chlorophyll a concentration at 1.5m depth
Temperature at max depth	Temp_MaxD	Degrees Celsius	The temperature of seawater from the deepest depth window.
Salinity at max depth	Sal_MaxD	Practical salinity units	The salinity of seawater from the deepest depth window.
Fluorescence max	Flr_max	Micrograms per litre	Maximum relative chlorophyll a concertation across all depth windows in a cast.
Depth of max fluorescence	Depth_maxFlr	Metres	Depth of maximum relative chlorophyll concentration.

Depth of thermocline	TC_depth	Metres	The depth window with the greatest variance in temperature values (Hazen & Johnston 2010, Redfern et al. 2008)
Thermocline strength	TC_strength	Degrees Celsius	The variance in temperature values within the thermocline window (Hazen & Johnston 2010, Redfern et al. 2008)
Temperature stratification	Temp_strata	Degrees Celsius	Gradient in temperature with depth. The surface temperature minus the temperature at max depth (Scott et al. 2010)
Salinity stratification	Sal_strata	Practical salinity units	Gradient in salinity with depth. The surface salinity minus the salinity at max depth (Pearl et al. 1998)

6.2.7 - Dolphin-habitat models

As a first step in the modelling process, it was necessary to determine the variation in dolphin relative abundance among survey areas (i.e. hotspots and reference areas). Thus, a 'null model' was used as a baseline with which to compare the performance of the final dolphin-habitat models. The null model was constructed using a GAMM with 'survey area' as a sole, random effect parameter. There was an observation of relative abundance for each of the 256 dolphin-habitat surveys. As in chapter 5, the response variable was sighting rate (dolphins per km of survey effort). The AICc and deviance explained of the null model was calculated and compared to the final dolphin-habitat 'top-models'. This presents an opportunity to determine whether the dolphin-habitat models adequately explain the 'site effects' in dolphin relative abundance. Secondly, using scatterplots of habitat covariates and relative abundance, I investigated possible relationships between environmental data and dolphin distribution. This exploratory data analysis provided some information on the form of dolphin-habitat relationships and was important in ensuring the final habitat models were formulated correctly.

The relationship between the relative abundance of dolphins (sighting rate) and the physical and biological characteristics of habitat were modelled using GAMs. GAMs were fit in *mgcv* (Wood 2017) in *R* with a negative binomial distribution. GAMs were used instead of GAMMs due to an apparent lack of spatial correlation between multiple surveys from the same area (see section 6.3.3). Firstly, it was important to investigate autocorrelation and to determine the best form for competing candidate predictor variables. Autocorrelation was investigated using the *concurvity* function in *mgcv* (Wood 2006; 2017). *Concurvity* generates a correlation matrix with an estimate of the correlation between every model term. A cutoff of 0.3 was used as a maximum cutoff value for correlated variables (Chapter 5; He et al. (2006)). To avoid the need to fit a model containing all 21 input variables (Table 6.2), concurvity was investigated in two steps. Three separate GAMs were constructed that included independent variables associated with 1) habitat type, prey and currents, 2) bathymetry, and 3) oceanography. Concurvity was assessed among variables in these three models and the correlated terms dropped from subsequent analyses. Then, all uncorrelated terms from the three models were included in a global model and the process repeated. When concurvity between variables was apparent, the decision of which to retain was based on the AICc values returned by single parameter GAM models that fit the variable in question against the response (sighting rate). The variable that produced the model with the lowest AIC value was retained.

The resulting global model was constructed and fit in *mgcv*. Each continuous variable was fit as a smoothed function using a thin plate regression spline. The number of degrees of freedom was estimated at ‘optimum’ levels for each term using generalized cross validation (Wood 2006, 2012). Due to the complexity of the model framework, the degrees of freedom for each term were limited to maximum of 5 (i.e. 4 knots; Tepsich et al. 2014, Rayment et al. 2015) in order to minimize the chances of overfitting impacting model selection and interpretation. The decision to limit the complexity of the smooth for each variable was investigated using model diagnostic approaches discussed below.

A model set that contained a formulation for every possible combination of input parameters was constructed and each model fit separately. Model selection was undertaken using AICc (Hurvich and Tsai 1989) and model weight scores (Burnham and Anderson 1998), with the 'top-model' being the formulation with the lowest AICc and highest model weight. Habitat variables retained in the top-model were considered to have some effect on the relative abundance of dolphins. Further inference was based on the *p*-value associated with each smoothed term; a significant effect is considered to be $p<0.001$ (Zuur et al. 2006; Wood 2006). The magnitude of each smoothed effect was determined from plots of each variable in the top-model.

CTD casts were not made during the first season of fieldwork (winter 2015) and the CTD was often unavailable in the early part of summer field seasons (first week or two of January). Therefore, not all dolphin-habitat surveys had associated oceanographic samples. To reduce the effects of missing data values in statistical modelling, a second dataset containing only those surveys with CTD casts was constructed and modelled separately. Thus, two families of GAM models were fit; a family that used every survey undertaken throughout the study period (full-dataset; n = 296 surveys) that used every habitat variable except those derived from the CTD, and a family that contained all variables including CTD data (CTD-dataset; n = 187 surveys). Inference on the importance of the various physical, tidal and prey variables was made with the full-dataset because of the larger sample size. Models using the CTD-dataset were only used to investigate the relative importance of oceanographic variables and to illustrate the relative contribution of these variables to model performance. This was judged by comparing the deviance explained by the top-models between each family.

6.2.8 - Model diagnostics and validation

As in previous chapters, the global and top-models from both model families were checked for the validity of assumptions using a combination of diagnostic plots and functions within *mgcv*. To check that the decision to limit the complexity of smoothed terms was not overly restrictive, the *gam.check* function was used (Appendix 5).

As surveys were undertaken in 10 spatial blocks, there is potential for spatial autocorrelation in the response variable with samples from the same block being similar. Such correlation would typically be dealt with by using random effects structures (i.e. GAMMS) or similar correlation matrices (Dormann et al. 2007). The extent of this correlation was investigated by generating spatial correlograms and bootstrapped 95% confidence intervals that modelled the correlation between pairs of observations as a function of geographic distance (Zuur et al. 2009). Spatial correlation was investigated with both families using the model residuals from the global and top-models (Dormann et al. 2007; Zuur et al. 2009). The centre of each survey polygon was used as the geographic point for which to construct lag distances.

To assess goodness of fit and the predictive capacity of the top-models, the deviance explained was summarised and a validation procedure established. For model validation, each dataset was randomly split into a ‘training’ set that contained two thirds of the total dataset and an ‘evaluation’ set containing the remaining third. The top-model was fit using the training data and used to predict values on the response scale given the values of the variables in the evaluation data. The validation procedure was carried out fifty times with different, randomly selected training and evaluation data for each dataset. Model performance was established by comparing the predicted values with the observed values in the evaluation dataset. The non-parametric Spearman’s correlation coefficient was used as a measure of correlation between the predicted and observed values (Guisan and Zimmermann 2000; Grüss et al. 2016), with a value higher than 0.50 indicating good predictive capacity (Grüss et al 2016 and references therein). The final predictive performance of each top-model was taken as the median Spearman’s coefficient with associated 95% confidence intervals.

6.2.9 - Habitat and hotspot analysis

To link the habitat variables that were important in describing the relative abundance of dolphins to the existence of hotspots, a modified ‘GAMvelope’ method (Torres et al. 2008) was used. A GAMvelope describes the area on a GAM curve where values of a habitat variable (x-axis) have a positive effect on the response (y-axis; Torres et al. 2008; Tepsich et al. 2014; Correia et al. 2015). Extracting these data and examining how they are represented spatially among survey grids allows an appraisal of the location of important habitat (Torres et al. 2008). Due to the use of penalised regression splines in *mgcv,* smoothed functions can be very close to 0 (Wood 2006). I avoided using such uncertain effects by establishing a cutoff where the 95% confidence interval for a smoothed function did not overlap 0. Areas on the curve where the smoothed function and its confidence interval were above 0 were positive GAMvelopes and areas below 0 were negative GAMvelopes. The range of values contained with positive GAMvelopes were considered ‘preferred’ values for that habitat variable, those contained within negative GAMvelopes were ‘avoided’ habitat.

Typically, a GAMvelope is used to establish the locations of survey grid cells where preferred values of habitat variables are represented, and so define important habitat (Torres et al. 2008). In this study, the objective was to assess how habitat variables were represented in locations that we already know are important. Therefore, I summarised the occurrence of preferred values of habitat variables among hotspots and reference areas (defined in Chapter 2). This was undertaken by matching GAMvelope data back to the respective surveys. For each statistically significant habitat variable, the proportion of surveys with ‘preferred’ values were calculated among hotspots and references areas. To provide visual discrimination of important biophysical habitat, the distribution of habitat types and depth were plotted in ArcMap. Overlaying hotspot locations with the distribution of important biophysical features allows appraisal of the spatial relationships between dolphin density and key habitat.

6.3 - Results

Two hundred and ninety six dolphin-habitat surveys were carried out across the ten survey areas. Sixty-five percent of surveys were carried out in summer. The ratio of summer/winter surveys was similar across survey areas (range 1.7 – 2.5) apart from Otanerito Bay, which had 6 times more surveys in summer (see *discussion)*. The number of surveys varied across areas, but each received at least 12 (see table 5.2 in Chapter 5). One hundred and eighty seven surveys had associated CTD casts.

6.3.1 - Habitat characteristics

The full dataset of habitat characteristics is summarised in Appendix 4. A summary of the prey field data across survey areas is given in Chapter 5 (section 5.3.5). In terms of habitat types, hard substrate was rare and generally confined to a coastal fringe (e.g. Fig. 6.1). The most common habitat types were sand and mud. Yet, there was substantial variation in relative coverage of the dominant habitats among survey areas (Appendix 4, Fig. 1.). Menzies Bay, Lyttelton, Wainui and Damon's Bay areas were dominated by mud. Akaroa and Otanerito had high proportions of both mud and sandy habitat, and the remaining four areas were mostly sandy.

Depth varied across the survey areas, ranging from 0.5 to 40 m. The deepest areas were Damon's Bay, Otanerito and Flea Bay with mean depths of 23, 22 & 21m respectively. The shallowest areas were Wainui, Lyttelton and Long Lookout. Steep slope gradients were rare at all locations, with the steepest values being associated with the coastal reef margin. Mean slope values ranged from 0.2 degrees at Lyttelton to 2.2 degrees at Damon's Bay (Appendix 4, Fig. 2). Sloping soft-substrate features were notable at Long-Lookout, Birdling's Flat, Akaroa and Lyttelton.

There were substantial differences in the velocity of tidal currents among areas (Appendix 4, Fig. 3). The highest averaged current velocities were at Long Lookout (0.4 ms^{-1} just before low tide). Damon's Bay and Akaroa also had relatively high current velocities. Interestingly, both Birdling's Flat and Long Bay had very little variation in the velocity of current over the tidal cycle. When variation over the tidal cycle was evident, peak velocities typically coincided with mid ebb and flow of the semi-diurnal cycle. The exception to this was Damon's and Otanerito that did not show a peak in current velocity during the ebb tide (between 0-6 hours after high).

Oceanographic data from CTD casts are summarised in full in Appendix 4. Briefly, mean bottom temperatures were between 13.51 ^{o}C (SE=0.47) at Otanerito and 14.9 ^{o}C (SE=0.96) at Lyttelton. Surface fluorescence varied among locations, with relative chlorophyll concentration between an average of 0.82 mg/L (SE=0.07) at Otanerito and 2.85 mg/L (SE=0.29) at Lyttelton. Otanerito also had the lowest mean sub-surface chlorophyll value (1.87 mg/L, SE=0.19), but Akaroa had the highest with 5.23 mg/L (SE=1.13). The depth of the chlorophyll maximum also varied among locations but no location had its maximum value at the surface. TC depth was shallowest at Wainui (mean=4.93 m, SE=0.85), and was deepest at Damon's Bay (mean=13.56 m, SE=1.78). The strength of the thermocline also varied substantially, with mean values being lowest at Long Lookout and highest at Akaroa.

6.3.2 – Exploratory analyses

Exploratory analyses using scatterplots identified several relationships between dolphin relative abundance and habitat covariates (Fig. 6.2). Important trends were identified with prey relative abundance (Chapter 5, Fig. 5.5), mud and sand habitat and with oceanographic variables including temperature and fluorescence. The exploratory process also successfully ruled out habitat variables that clearly had little correlation with dolphin habitat use (Fig 6.2).

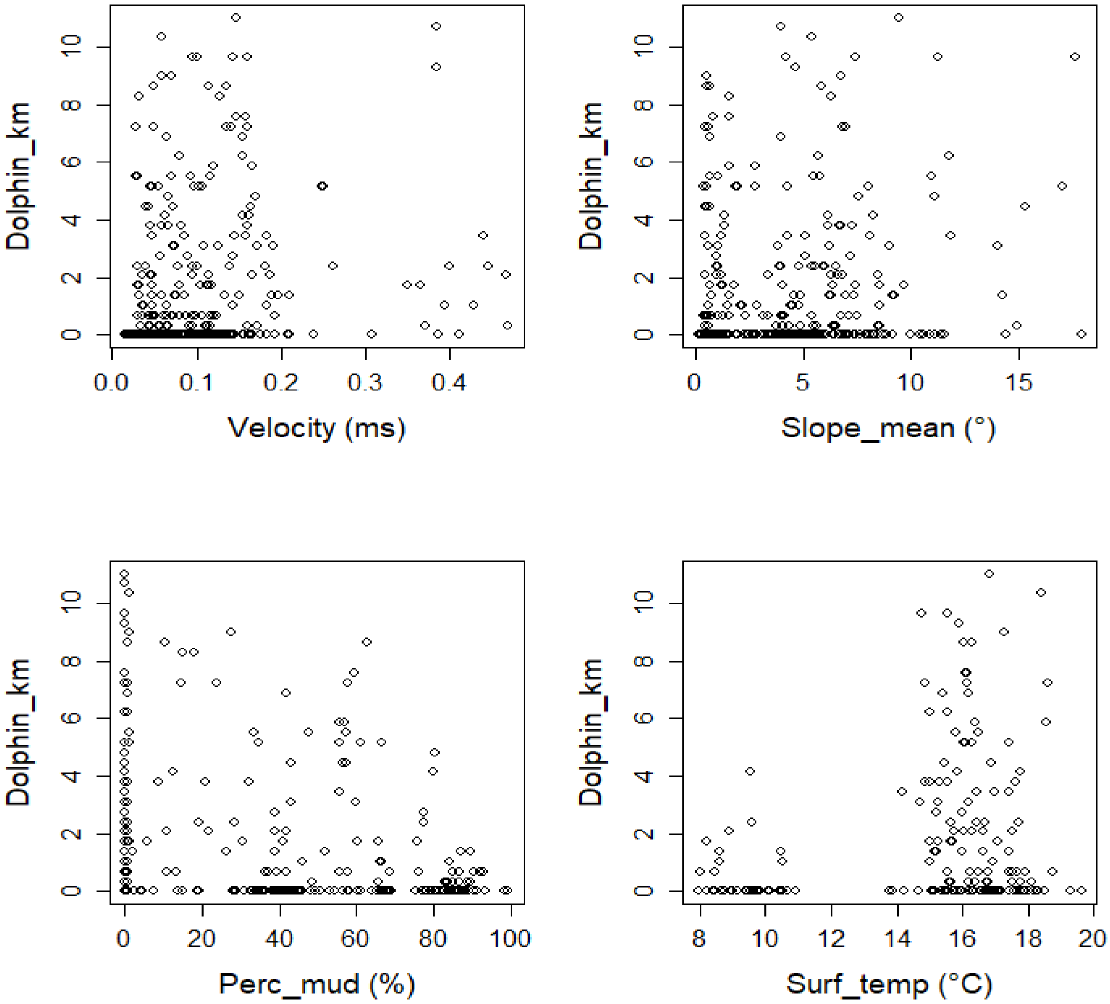

Figure 6.2: Examples of exploratory analyses of the relationship between selected habitat variables and the relative abundance of dolphins (Dolphin_km). Habitat variables are explained in Table 6.2.

6.3.3 - Dolphin-habitat models

Unsurprisingly, many of the habitat variables were highly correlated. For the global model using the full dataset, the number of input parameters was reduced from 14 to seven. Parameters that described each physical, bathymetric, oceanographic and prey characteristic were able to be included in the global model with the exception of a variable describing slope. The best performing variable for slope (mean_slope) explained only 1.70% of the deviance in dolphin abundance.

Similarly, in order to remove correlated variables, the global model for the CTD dataset had a substantially reduced number of terms (from 26 to 13). Again, this is not surprising as many variables were measures of the same characteristic (e.g. temperature) and were included only to find the best metric for each variable.

For the full-dataset. two models ranked almost equally in terms of AICc. The top ranked model explained 46% of the deviance in dolphin relative abundance and had variables for prey relative abundance, mean depth, percentage of reef and percentage of mud habitat (Table 6.3). The second ranked model, with only 0.1 difference in AICc from the top model, incorporated these same variables with an addition of tidal velocity (47% deviance). Due to the models being similarly ranked, inference is based on both models. The top models for the full dataset performed substantially better than the null (site effects) model (deviance explained 29%; Table 6.3).

The top-model using the CTD dataset contained the same variables as the model for the full dataset with the exception that a parameter that described the percentage of coarse sediment was included in place of depth. Additional oceanographic variables included were thermocline depth, surface fluorescence, and surface salinity (Table 6.4). This model explained 54% of the deviance in the relative abundance of dolphins. Similar to the model selection of the full dataset, two models had similar AICc scores, the second ranked model containing an addition of tidal current velocity (Table 6.4). For this reason, the effects of tidal velocity are considered by viewing the plot of the effects (Fig 6.3) from the second ranked model.

Table 6.3: Model selection table used to determine the top-model to define the relationship between Hector's dolphins and habitat characteristics using the full-dataset. The top-model was selected based on lowest AIC score and highest weight. The top 5 models are given. Abbreviations for model terms are given in table 6.2. The null model – illustrating the 'site effects' of a parameter for survey area – is also given for comparison.

Model	df	AICc	weight	Deviance
Prey_RA + Depth + Perc_mud + Perc_reef	14	875.9	0.3	46%
Prey_RA + Depth + Perc_mud + Perc_reef + Velocity	15	876.0	0.3	47%
Prey_RA + Perc_coar.sed + Depth + Perc_mud + Perc_reef + Velocity	16	878.1	0.1	47%
Prey_RA + Depth + Perc_mud + Perc_reef + School depth	15	878.2	0.1	46%
Prey_RA + Depth + Perc_mud + Perc_reef + School depth + Velocity	16	878.3	0.1	47%
Null model (Survey area)	9	1416		29%

Table 6.4: Model selection table used to determine the top-model to define the relationship between Hector's dolphins and habitat characteristics using the CTD-dataset. The top-model is selected based on lowest AIC score and highest weight. The top 5 models are given. Abbreviations for model terms are given in table 6.2. The null model – illustrating the 'site effects' of a categorical parameter for survey area – is also given for comparison.

Model	df	AICc	weight	Deviance
Prey_RA + Perc_coar.sed + Perc_reef + Sur_flr + Surf_sal + D_TC1 + Perc_mud	24	550.7	0.08	54%
Prey_RA + Perc_coar.sed + Perc_reef + Surf_flr + Surf_sal + D_TC1 + Perc_mud + Velocity	25	551.9	0.05	54%
Prey_RA + Perc_coar.sed + Perc_reef + Surf_flr + Surf_sal + Perc_mud	17	552.3	0.04	52%
Prey_RA + Perc_coar.sed + Perc_reef + Surf_flr + Surf_sal + D_TC1 + Depth + Perc_mud	24	553.0	0.03	51%
Prey_RA + Perc_coar.sed + Perc_reef + Surf_flr + Surf_sal + Perc_mud + Velocity	18	553.3	0.02	53%
Null model (Survey area)	9	1416		29%

Each of the habitat characteristics retained in the top two models for the full dataset were statistically significant with p-values<0.01, with the exception of current velocity (Table 6.5), The effects of the shared variables between the top two models were identical. Yet, the magnitude of the effects of the individual terms within models differed markedly. The relative abundance of potential prey was strongly correlated with the relative abundance of dolphins, with the strength of the effect increasing with higher prey abundance (Fig. 6.3). The percentage of reef habitat showed a strong negative relationship on dolphin abundance at values higher than 15% and a positive effect between 0 and 10% (Fig. 6.3). The percentage of mud habitat had a strong negative correlation with relative abundance at values greater than 60%. The mean depth encountered during a survey was strongly related to on dolphin abundance and suggested an optimum depth between 12 and 22m (Fig. 6.3). Current velocity had a weak and inconclusive relationships with relative abundance, with the 95% confidence interval for the trend overlapping 0 for the majority of velocity observations (Fig 6.4).

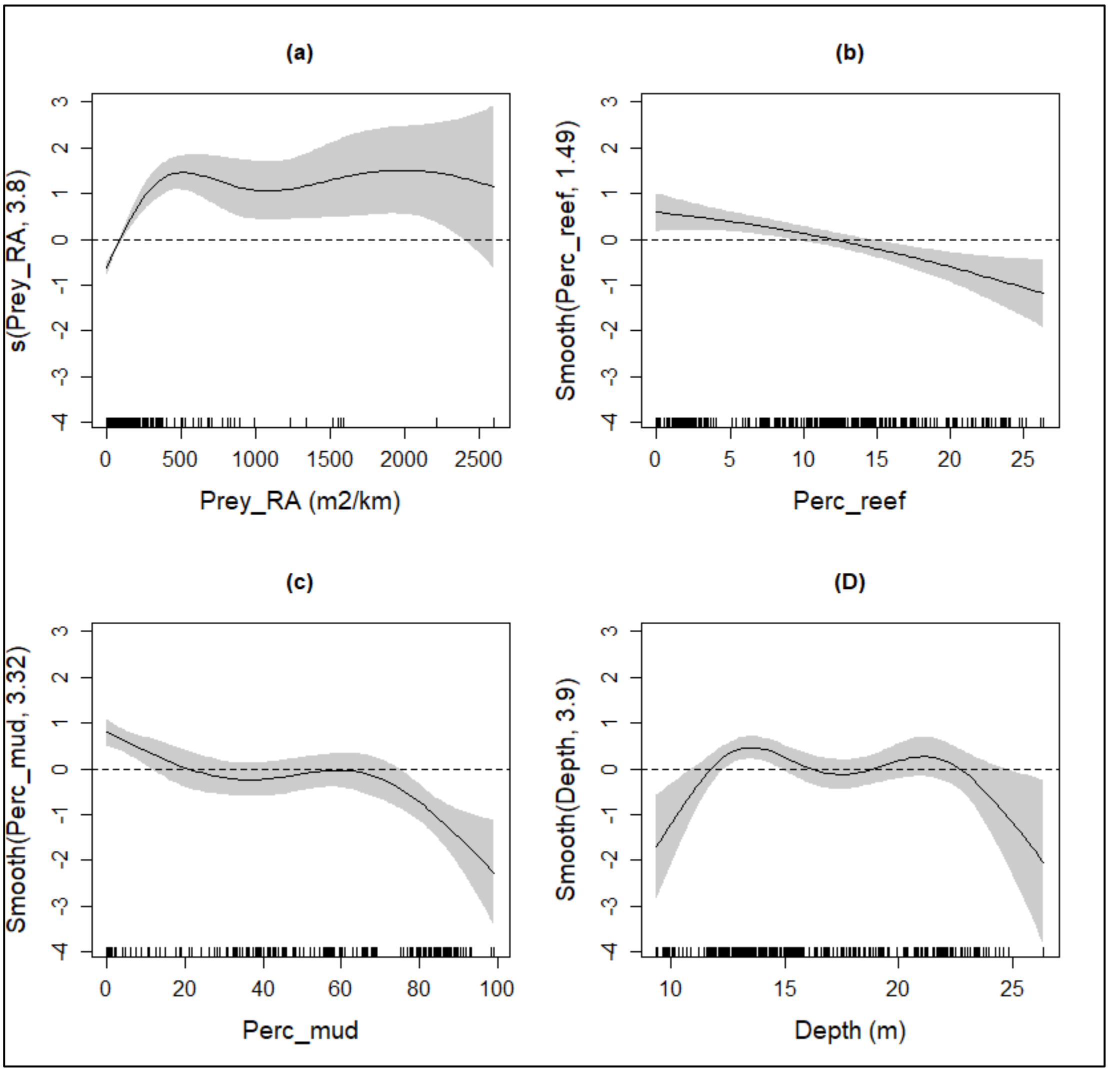

Figure 6.3: Plots of the effects of habitat variables on the relative abundance of dolphins from the top GAM using the full dataset. The full dataset is used to assess the influence of physical habitat types, bathymetry, prey and current. Plots are the effect of the relative abundance of potential prey (a), mean depth of potential prey (b), percentage of reef habitat (b), percentage of mud habitat (c) and mean depth (d). Grey regions are 95% confidence intervals for a given smoothed effect and the degrees of freedom for each smooth is give on the y-axis.

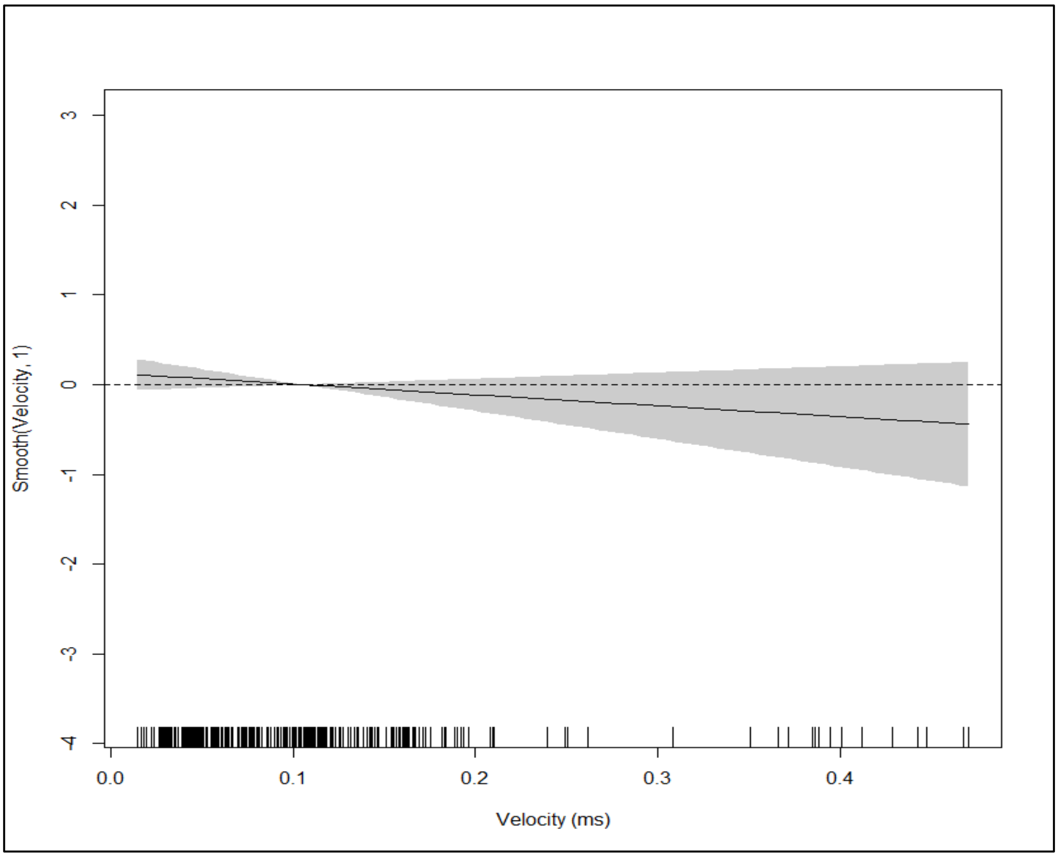

Figure 6.4: Plot for the effect of tidal current velocity on the relative abundance of dolphins generated from the second ranked GAM model using the full dataset.

Every variable retained in the top-model using the CTD dataset was also statistically significant with the exception of thermocline strength (Table 6.5), but again, there were substantial differences in the magnitude of effects. Increasing relative chlorophyll concentration (Surf_Flr) was negatively correlated with dolphin relative abundance (Fig. 6.5). Surface salinity less than approximately 33.5 psu were strongly negatively correlated with dolphin abundance (Fig. 6.5). The depth of the thermocline had a negative association beyond 18 m, but had large error around the estimated trend (Fig. 6.5).

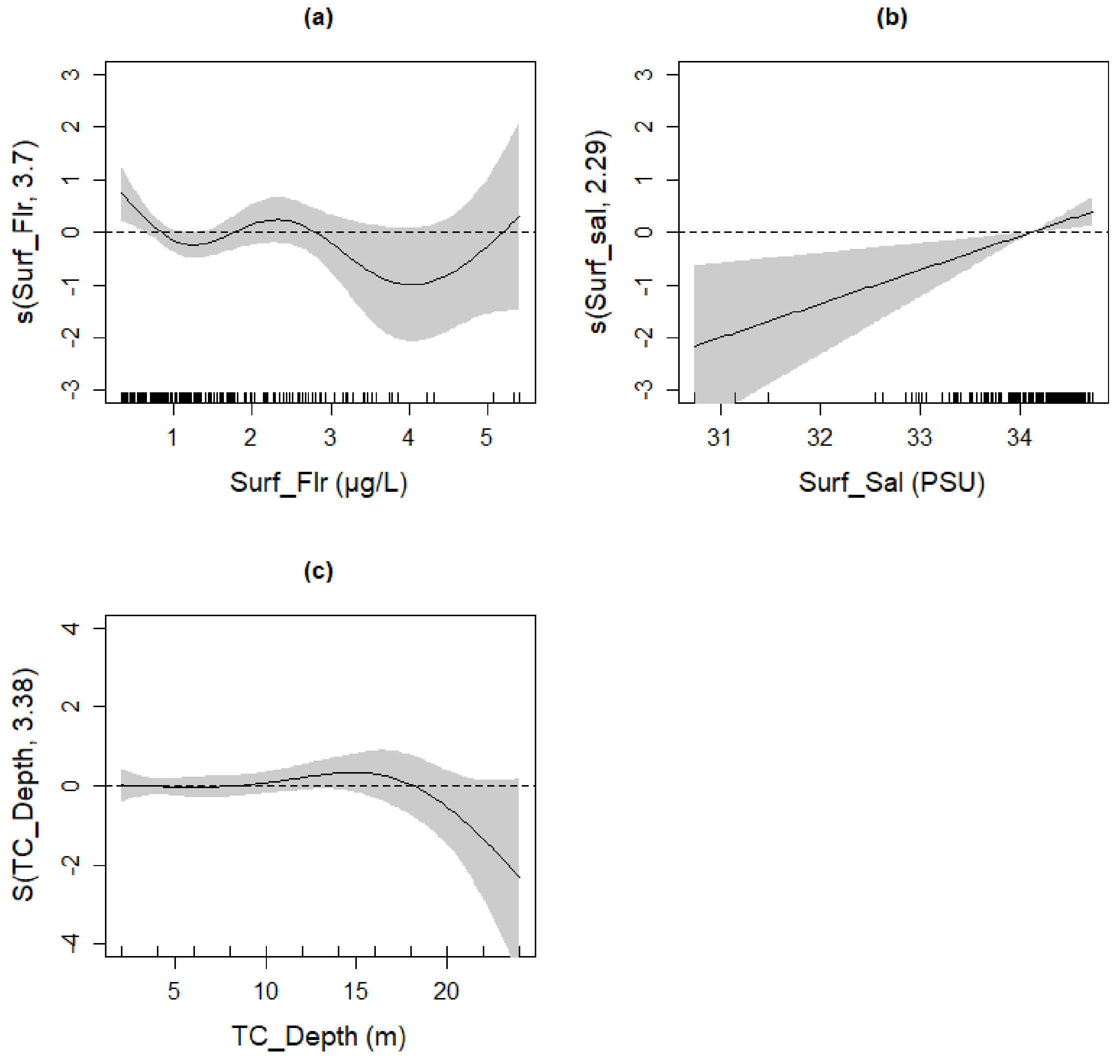

Figure 6.5: Plots of the effects of habitat variables on the relative abundance of dolphins from the top GAM using the CTD dataset. The CTD dataset is used to assess the influence of oceanographic habitat variables. Plots are the effect of the relative chlorophyll concentration (a), surface salinity (b) and thermocline depth). No other CTD variables were retained in the top model. Grey regions are 95% confidence intervals for a given smoothed effect and the degrees of freedom for each smooth is give on the y-axis.

Table 6.5: Summary of the statistical significant of terms retained in the top-models for the full and CTD datasets. P-values for the smoothed terms (s) are taken to be statistically significant effect <0.01. The values provided for each term are the effective degrees of freedom (edf), reference distribution degrees of freedom (ref.df), chi-squared value (Chi sq), p-value and for the parametric terms the parameter estimate (Estimate), standard error (SE) and z-values.

Term	**edf**	**ref.df**	**Chi_sq**	**p-value**
Full_dataset				
s(Prey_RA)	3.71	3.97	19.71	<0.0001*
s(Mud)	3.32	3.70	10.94	<0.0001*
s(Perc_Reef)	1.49	1.83	9.75	0.001*
s(Mean_Dpth)	3.90	3.99	4.18	0.003*
s(Velocity)	1	1	1.63	0.20
CTD_dataset	**edf**	**ref.df**	**Chi_sq**	**p-value**
s(Flr_Surf)	3.79	3.81	13.00	0.004*
s(Surf_sal)	1.00	1.00	8.00	0.005*
s(TC_Depth)	3.34	3.70	1.45	0.31

6.3.4 - Model validation

Model diagnostic techniques did not identify any issues associated with residual homogeneity with fitted values or levels of the variables, lack of independence in the response or residual distribution. These results were evident for both families of models (Appendix 5). *Gam.check* suggested that limiting the complexity of the smoothed effects was not over-restrictive and so there was no need to increase the amount of smoothing for any variable in either model family.

When the correlogram of the model residuals was examined no correlation was evident, suggesting no spatial autocorrelation of datapoints from within the same survey area. Spatial autocorrelation is likely accounted for by the fixed effects (Dorman et al. 2007; Zuur et al. 2009). This confirms the decision to use GAM over the more complex GAMM.

Model validation using training and evaluation data for each data-set provided median Spearman’s correlation coefficients of 0.65 and 0.82 for the full and CTD dataset respectively (Table 6.6). This level of correlation between independent observed and predicted values suggests that the top-model of each family has good predictive performance (Spearman’s >0.50; Grüss et al. 2016), and validates the results of these models.

Table 6.6: Results of model validation for the top-models using the full and CTD dataset. Median Spearman's correlation coefficients are provided for each family after 50 randomly selected training and evaluation subsets of each dataset.

Model family	Median spearman's	CI-Upper	CI-Lower
Full-datset	0.65	0.47	0.73
CTD-dataset	0.82	0.71	0.88

6.3.5 - Habitat and hotspots

‘GAMvelopes’ were defined for each statistically significant habitat variable retained in the top-models for the full and CTD-dataset. The model using the CTD-dataset was used only for the oceanographic variables derived from CTD sampling (Fig. 6.5). Using the 95% confidence interval as a cutoff between positive and negative GAMvelopes ensured areas of the curve within uncertain effects were not included in further analysis (Fig. 6.6).

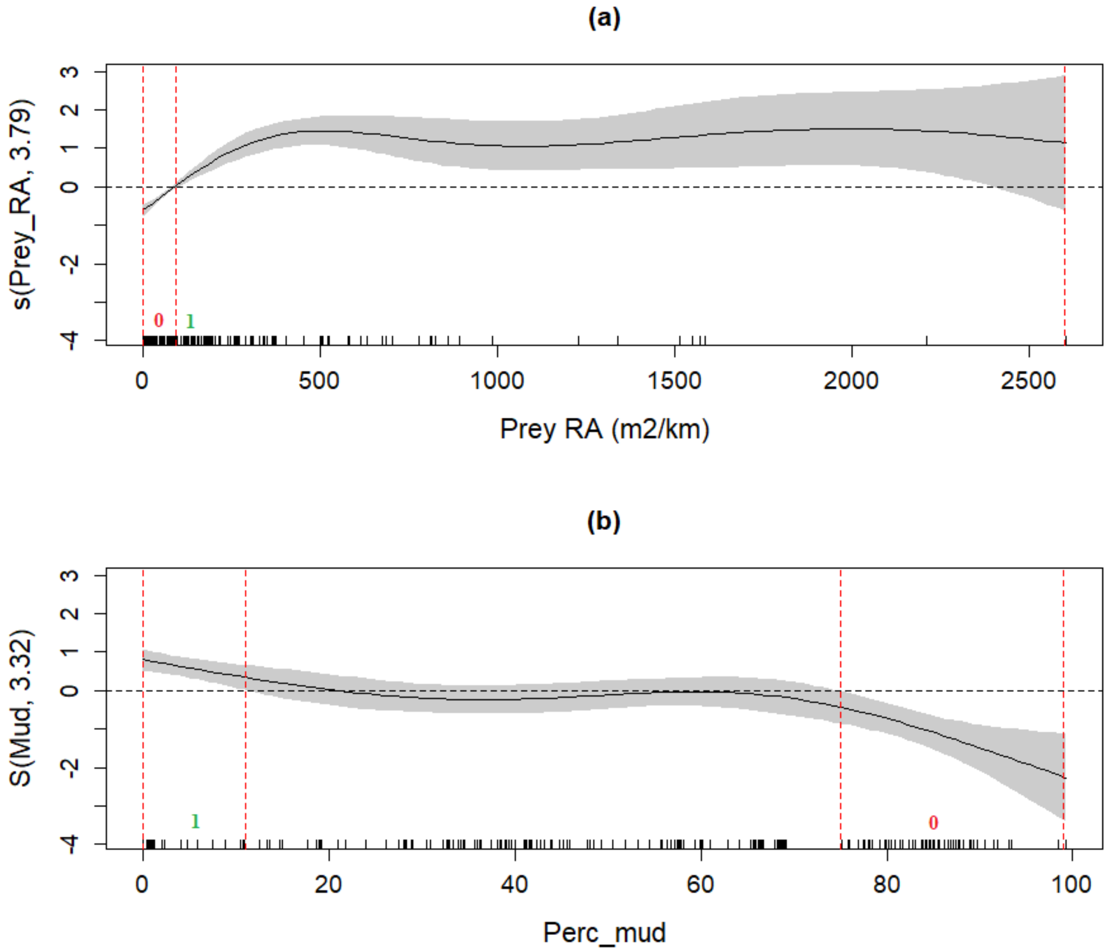

Figure 6.6: Examples of 'GAMvelopes' where the area on a plot of a smoothed effect is used to define values of habitat covariates that have either positive or negative effects on dolphin relative abundance. Examples are given for prey relative abundance (a) and percentage of mud (b). Red 0s indicate negative 'avoided' values of a habitat covariate and green 1s indicate positive, ‘preferred’ habitat.

A greater proportion of surveys at hotspots had preferred values of prey abundance (i.e. high prey relative abundance). A higher proportion of surveys at hotspots had preferred depth values (91%) compared to 48% at reference areas. (Fig. 6.7). Preferred values of mud coverage (i.e. low coverage) were more common at hotspots than reference areas (99% compared to 28%; Fig. 6.7). Forty percent of surveys at hotspots had preferred values of percentage reef coverage (i.e. low reef cover) compared to thirty five percent at references areas. Preferred values of surface fluorescence seemed to be more commonly encountered at reference areas than at hotspots. There was no difference in the distribution of preferred values of surface salinity between hotspots and reference areas. (Fig. 6.7).

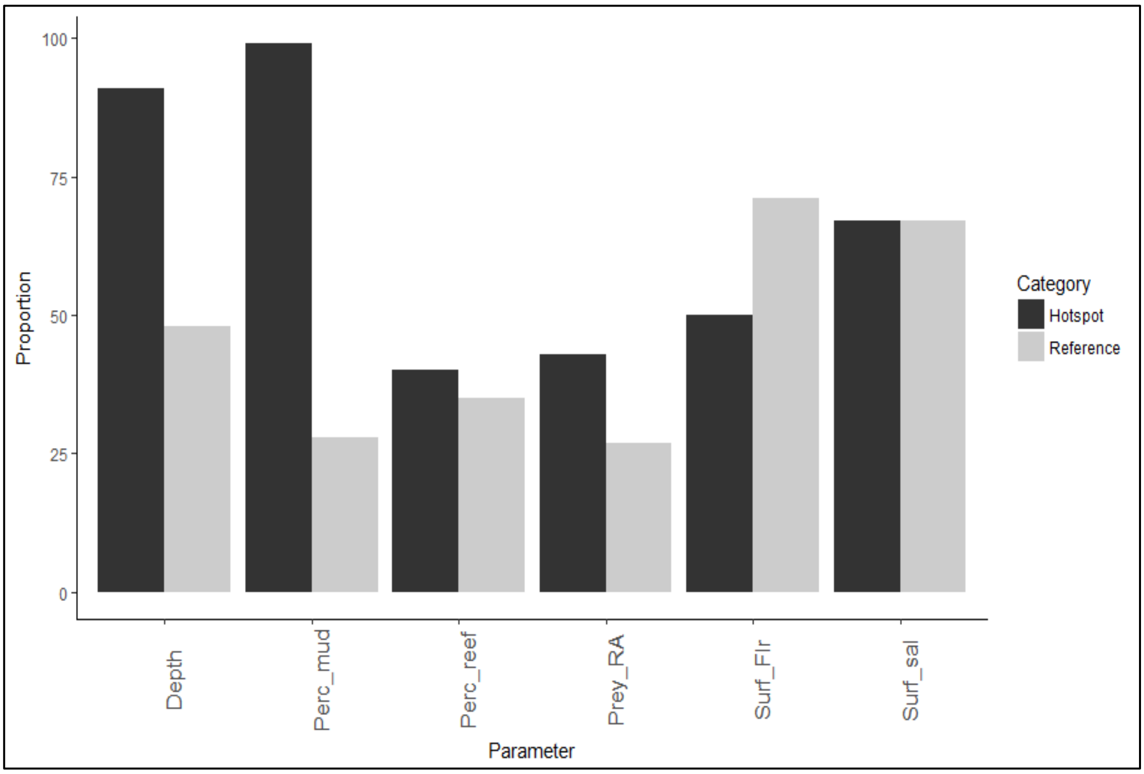

Figure 6.7: The proportion of surveys at hotspots and reference areas that had preferred values of each statistically significant habitat variable retained in the top-models. Preferred values are defined as those values of a variable that have a positive effect on the relative abundance of dolphins as shown by GAMs. Habitat variables are described in Table 6.2.

Mapping the distribution of the biophysical habitat types further revealed the importance of shallow, sandy habitat. All four hotspots have significant area of sandy habitat that is between 11 and 23m (Fig. 6.8). In contrast the only reference area to have a substantial amount of this biophysical habitat type is Long Bay. Incidentally, Long Bay also has high reef coverage, a habitat type that is negatively correlated with dolphin relative abundance (Fig. 6.8).

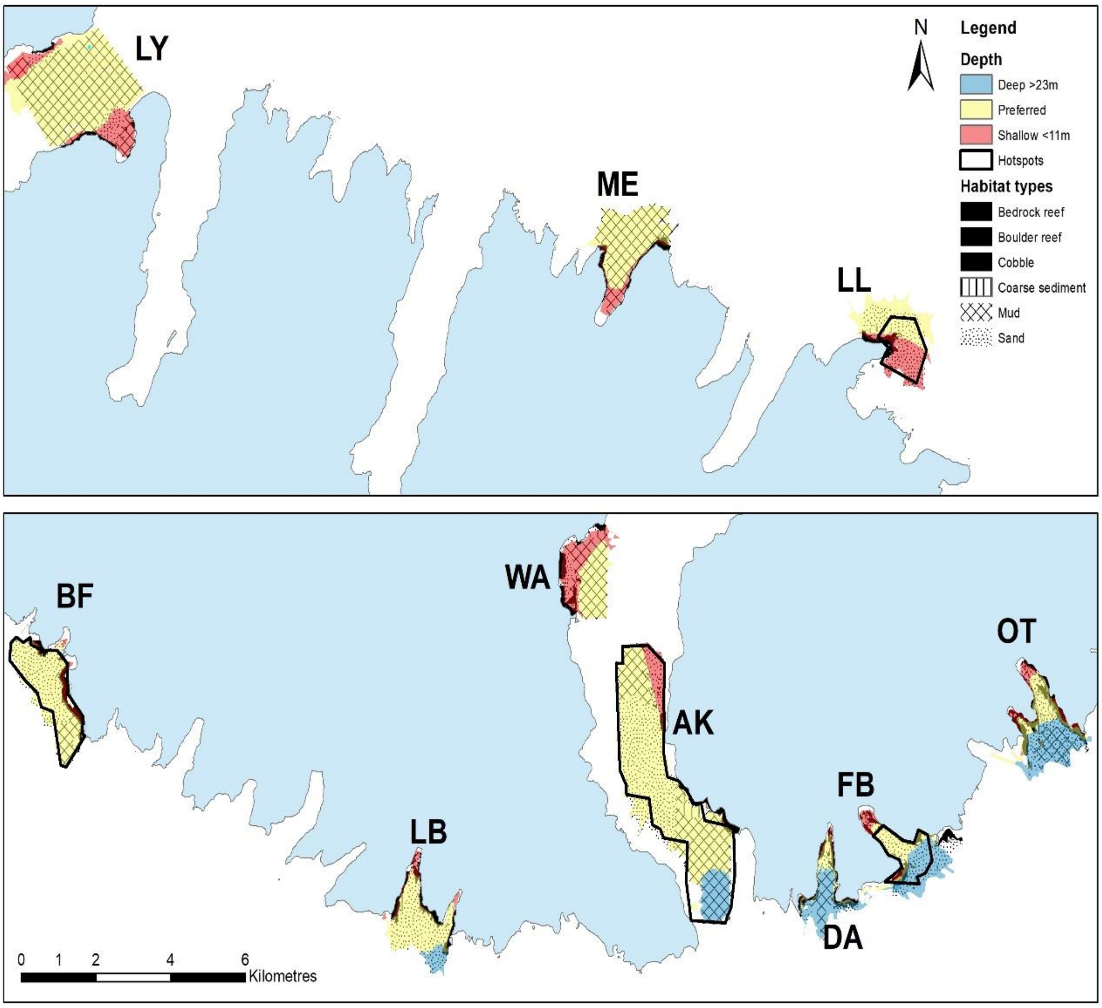

Figure 6.8: The distribution of broad biophysical habitat types that have been shown to correlate with the relative abundance of dolphins. The key physical habitat types identified via side scan sonar are shown with depth information overlaid in order to visualise the distribution of the two most important physical variables. The locations of the hotspots are given in bold outline.

6.4 - Discussion

6.4.1 - Important factors shaping dolphin distribution

Among all the variables, the relative abundance of potential prey had one of the strongest correlations with dolphin abundance. When prey were more abundant, so were the dolphins. This was shown in Chapter 5, but including prey abundance as a biological driver of habitat selection allows an appraisal of the relative importance of the prey field amongst the physical characteristics of habitat. As discussed extensively in Chapter 5, many studies have shown the spatial and temporal overlap between top-predators and their prey (Baumgartner et al. 2003a; Fauchald 2009; Benoit-Bird et al. 2013). Especially for small-bodied marine mammals inhabiting temperate areas, the need to be constantly foraging to satisfy high energetic requirements (Harding et al. 2005; Wisniewska et al. 2016) means that these taxa are likely to exhibit particularly high overlap with prey. That prey abundance is one of the most important parameters in the species-habitat models suggests this is true in the case of Hector’s dolphin.

Few studies include both prey and physical habitat features in models of habitat selection by top-predators. Embling et al. (2012) found that prey abundance was closely related to the abundance of black legged kittiwakes, but that kittwake abundance was also tightly coupled with sub-surface chlorophyll and thermal stratification. Similar results were reported by Hazen et al. (2011), who investigated characteristics of foraging habitat in two beaked whale species. Interestingly, habitat models for bottlenose dolphins performed best using environmental variables only (Torres et al. 2008). It was suggested that, due to the heterogeneity of the study area and subsequent extreme patchiness in prey, environmental variables were better predictors than prey (Torres et al. 2008). Banks Peninsula is more homogenous than the study area of Torres et al. (2008). Further, the hydro-acoustic sampling method of this study may have been better at resolving the patchy prey-field than the trawling methods used in that study.

Prey depth was not retained in either of the top-models, and thus has a significantly reduced importance from that seen in Chapter 5. This is despite being shown to be important in several studies of top-predator distribution in shallow (Embling et al. 2012; Womble et al. 2014) and open-ocean (Benoit-Bird et al. 2004, 2013; Bedford et al. 2015) habitat. The reduction of the importance of prey depth is likely due to some of the effects of this variable being described by the mean depth of a survey that, seemingly, is a better correlated with dolphin relative abundance.

Tidal velocity had very little effect on the relative abundance of dolphins. Several studies have related tidal state to distribution or foraging in marine predators (e.g. Johnston et al. 2005; Bailey and Thompson 2010; Lin et al. 2013; Nuuttila et al. 2017). The use of quantitative information on tidal currents is not as common, despite evidence it is important at describing habitat use (Skov and Thomsen 2008; Marubini et al. 2009; Pirotta et al. 2013; Hunt et al. 1998). Harbour porpoise were found to be more abundant at high tidal stream velocities (Marubini et al. 2009). The velocity of currents is thought to relate to top-predator distribution in several ways that are discussed in detail in Chapter 3 (section 3.5.4). The velocity of the tidal flow may itself be a proxy for features such as eddies, wakes and fronts that occur at particular tidal flow rates and serve to aggregate prey (Johnston et al. 2005; Bailey and Thompson 2010; Russell and Vennell 2017). With high flow rates and complex geomorphology it is likely these features are present at Banks Peninsula. However, the scale of this analysis may have been too coarse to detect the influence of such features. Further habitat modelling, using more fine scale (e.g. passive acoustic data) would better resolve these ephemeral hydrological processes.

The habitat models suggest that reef habitat was not favoured by Hector's dolphins. In temperate areas, reef habitat and the macro-algal communities that it sustains, are important local sources of productivity and provides heterogeneity that promotes high biodiversity (Gladstone 2007; Smale et al. 2013; Rees et al. 2014). The strong negative relationship between Hector's dolphins and reef shows that these top-predators do not respond to these ecological values, at least on the scale of this study. Hector's dolphins seldom target reef associated fish species (Miller et al. 2013), and it may be that reef habitat provides some shelter for prey. Bottlenose dolphins in Florida (Torres et al. 2008) and Belize (Eierman and Connor 2014) also had lower abundance in areas with high reef coverage. In contrast, Indo-Pacific humpback dolphins are more common at shallow reefs that are important foraging areas (Karczmarski et al. 2000). It seems the relationships between top-predators and reef habitat are diverse and adds weight to the need to investigate such links at the species level.

The influence of the depth variable shows that dolphins prefer areas that are between 11 and 22m deep. This window is similar to the preferred depth of dolphin prey seen in Chapter 5 and illustrates the synergy between the prey field and physical habitat variables. Preferences for certain water depths by marine predators is a product of the depth of preferred prey species (Hoskins et al. 2008; Embling et al. 2012), balancing the energetic demands of foraging (Benoit-Bird et al. 2004; Au et al. 2013; Bedford et al. 2015) and the distribution of their own predators (Heithaus and Dill 2006). Longer/deeper dives increase the energetic demands of foraging (Williams et al. 1999; Doniol-Valcroze et al. 2011) and obviously, dive depths are likely to be deeper at locations with greater water depths. This may weigh heavily on the foraging efficiency of small dolphin species such as Hector's.

Mud habitat had a significant negative correlation with dolphin numbers.. Mud and sand were the dominant habitat types in all survey areas. Thus the percentage of sand habitat could not be included in the habitat models because it was highly correlated (inversely proportional) to the percentage of mud. It is likely, therefore that the negative effects of mud habitat suggest a favouring of more sandy areas by the dolphins. At fine-scales, harbour (*Phoca vitulina*) and grey (*Halichoerus grypus*) seals were also less common where bottom types had a high proportion of muddy sediment (Bailey and Thompson 2009). Preference for particular bottom types is probably related to the preference of certain prey for these habitats (Torres et al. 2008; Embling et al. 2012). As mentioned above, the preference for sandy habitat by harbour porpoise and minke whales is almost certainly due to their sand eel prey being found in this habitat type (Macleod et al. 2004; Williamson et al. 2017). To date there have been no studies that investigate the species-habitat relationships for prey of Hector's dolphins.

The effects of the surface chlorophyll variable suggests that dolphins are more common in places or at times of low productivity. These results differ from those reported by Yen et al. (2006), Scott et al. (2010), Moura et al. (2012), and Saijo et al. (2016) who show an increasing abundance of predators with increasing primary productivity. This trend is likely explained by the spatiotemporal lag between the lowest and highest trophic levels (Cushing 1990; Edwards and Richardson 2004; Grémillet et al. 2008a). These 'downstream' effects result in a mismatch between the locations and/or times of high phytoplankton biomass and high abundance of predators (Croll et al. 2005; Soldevilla et al. 2011; Thorne and Read 2013). When the abundance of zooplankton and their predators follows successional rather than aggregational processes (e.g. zooplankton being advected by downwelling or fronts), the lag time between the peaks in abundance of trophic levels can be considerable (Jaquet 1996; Gregr and Trites 2001; Croll et al. 2005; Soldevilla et al. 2011). Generally, it is thought that the higher the trophic level the more removed a species may be from spatiotemporal distribution of primary production. The abundance of two odontocete species in the Gulf of Mexico was closely related to chlorophyll concentration at 4 weeks lag time (Soldevilla et al. 2011). How such a lag is represented at Banks Peninsula is unknown, but would be an interesting avenue for further research.

There was a clear influence of salinity on dolphin abundance, with dolphins less abundant at surface salinities less than 34 psu. The relationship between Hector's dolphin distribution and salinity may reflect some influence of temperature, as evaporation by warm temperatures has a strong influence on salinity in shallow coastal environments (Royer et al. 2001; Anthony et al. 2009). Temperature could not be included in the final habitat models due to strong correlation with other, better predictors. Temperature is, however, a well-known correlate of Hector's dolphin distribution and is related to the inshore-offshore seasonal distribution of the species (Rayment et al. 2010a; Dawson et al. 2013), as it tracks the distribution of prey (Chapter 5; Miller 2014). Alternatively, salinity may influence dolphin distribution itself. Low salinities periods, brought on by excessive rainfall, may inhibit phytoplankton productivity (Royer et al. 2001; Anthony et al. 2009), minimising the biomass available for dolphin prey and ultimately affecting dolphin prey abundance.

6.4.2 - Seasonality

Many of the variables included in the species distribution models have a strong seasonal signature. This is certainly true for many of the oceanographic and prey parameters. Seasonal distribution of sampling effort was very similar among locations, with the exception of the Otanerito area. Prey abundance is higher is summer (Chapter 5) and Otanerito had far higher sampling effort in summer compared to winter. Thus, the estimated level of prey abundance at Otanerito is likely to be biased high. Dolphin abundance was generally low in Otanerito (Chapter 5), thus the relationship between prey abundance and dolphin distribution may be underestimated. Further, the similarity between Otanerito and some hotspots in terms of prey abundance is likely explained by this unequal seasonal sampling distribution.

6.4.3 - Hotspots and habitat types

The GAMvelopes provided some clear indications of how the characteristics of habitat discussed above were represented at hotspots. Differences in the relative abundance of prey, depth, percentage reef cover, and muddy substrate between hotspots and reference areas confirm these components are important characteristics of hotspots. Hotspots typically have depths between 12 and 22 m and most reference areas have mean depth values outside this range. There were also large differences between hotspots and reference areas in their dominant substrate type; sand being more common at hotspots. Typically, on average, prey were more abundant at hotspots. Therefore, I conclude that hotspots are locations dominated by sandy substrate with low reef cover, have high prey abundance and are neither very deep nor too shallow. These conclusions are not absolute, however. Sandy substrate was certainly more common at hotspots, but Akaroa Harbour also had a large proportion of muddy sediment (albeit with high sand-grain content, Fig. 6.8. Prey abundance was high at hotspots but also high at Damon’s Bay (Chapter 5, Fig. 5.7). Such exceptions indicate that in order to be a hotspot, a location needs to exhibit only some of the main characteristics.

A growing body of evidence suggests that top-predator distribution patterns are shaped by both the distribution of their prey and the abiotic features of their habitat (Baumgartner et al. 2003a; Hazen et al. 2011; Embling et al. 2012; Benoit-Bird et al. 2013; Thorne and Read 2013), rather than by environmental parameters acting solely as a proxy for prey distribution. This study suggests this is the case for Hector's dolphins. Each of the abiotic characteristics in this study may be related to dolphin abundance via the habitat preferences of prey. Alternatively, it is possible that the optimum depth, tidal current and reef characteristics are related to increased catchability of prey. Whilst further research is required to confirm this hypothesis, these results confirm the merit of weighing both biotic and abiotic factors in an appraisal of habitat selection.

Interestingly, none of the preferred values of the important oceanographic variables occurred more regularly at hotspots. This suggests that preferred values of these variables are more broadly distributed. For example, thermocline depth and salinity are likely to be correlated with summer when dolphins are more abundant in this nearshore study area.

The biophysical variables identified as characteristics of hotspots in this study are not an exhaustive list. Additional factors including turbidity, wave exposure and the prevalence of oceanic features (e.g. fronts) have been shown to influence Hector's dolphin distribution (Clement 2005; Miller 2014; Dittmann et al. 2016) and may further shape the existence of hotspots. Further, data on additional prey species (e.g. red cod) would likely significantly improve the performance of the species distribution models and the classification of hotspots based on prey abundance.

6.4.4 - Conclusions

This chapter has provided new information on the habitat characteristics that are related to the distribution patterns of Hector’s dolphins. Further, the results of this chapter suggest prey abundance, depth, sandy substrate and to a lesser extent percentage reef cover are important features of distributional hotspots. This information is important for the management of habitat related impacts on this species. Anthropogenic degradation of these features already exists in this study area in the form of aquaculture, dredging, and coastal development. Further, the broad-scale siltation of near-shore habitat at Banks Peninsula due to terrestrial runoff is a dominant impact on the study area (see Chapter 7). This chapter also provides interesting ecological insights into the types of habitat that support high abundance and foraging of a top-predator, provides evidence of a spatiotemporal mis-match between primary productivity and dolphin abundance, and has identified several avenues for further research.

Chapter 7: General Discussion

7.1 - Summary of main findings

In this thesis, I analysed the ecology of hotspots in the fine-scale distribution of Hector's dolphins. The thesis presents a variety of methods and is split into chapters that determine the where and when of hotspots (Chapter 2), why dolphins aggregate at these locations (Chapter 3) and what habitat features are represented at these areas (Chapters 4-6). These investigations provide strong evidence for the importance of these locations for this endangered species, and, have wider implications for understanding the ecology of coastal ecosystems.

7.1.1 - The where and when of hotspots

The kernel density analysis of Chapter 2 provides clear support for the existence of hotspots in the nearshore distribution of Hector's dolphins at Banks Peninsula. Fifty percent of the weighted sightings occurred within only 21% of the study area. Major hotspots were identified around Birdling's Flat, in Akaroa Harbour, Flea Bay, around Okain's Bay and in the far east of the peninsula. Hotspots were driven by strong use in the austral summer, but all hotspots except Okain's Bay were also important in spring and autumn. Hotspots were not, however, heavily used in winter. Each of the major hotspots has remained consistent over nearly 30 years. This consistency implies the importance of these areas to the dolphins' ecology.

The results of Chapter 2 add to a growing body of evidence that hotspots exist in the distribution of a variety of top-predators (Ingram and Rogan 2002; Gende and Sigler 2006; Scott et al. 2010). Importantly, these results are some of the first to show the longevity of hotspots over several decades. For the conservation of Hector's dolphin and its habitat, establishing the locations, seasonality and longevity of hotspots in a zone with extensive human impacts is an important outcome.

7.1.2 - Why: foraging at hotspots

In Chapter 3, I investigated the spatial and temporal distribution of foraging behaviour to determine if hotspots were important foraging areas. The results suggest that foraging is indeed more common at hotspots, although one of the six ‘reference areas’ (Menzies Bay) had similar levels of foraging to hotspots. Comparing PAM data on general distribution patterns with the spatial distribution of foraging provided further evidence that foraging shapes distribution in this species. Trends in temporal foraging patterns were, however, far more complex than temporal trends in distribution. Some areas showed clear diel foraging patterns, while others were influenced by tidal state. Most locations had strong seasonal variability in foraging rates, but the highest rates did not always occur when the dolphins were most abundant (i.e. summer). This shows that foraging rates are high year-round and is likely a product of the high energy requirements of these small dolphins in this cool, temperate area.

The results of Chapter 3 reveal the locations and times when vital foraging behaviour is most frequently carried out, providing managers with opportunities to limit impacts on this behaviour. The identification of areas where foraging rates are high implies there is something unique about the ecology of these areas. Thus, hotspots may be appropriate candidates for protection not only because of their importance to dolphins, but for the protection of wider biodiversity, habitat heterogeneity and ecosystem services. Two hotspots had high diversity of benthic and pelagic fish compared to other areas in the nearshore environment (Miller 2014). Whether such values are represented at all hotspots should be investigated more fully.

7.1.3 - What: Prey distribution and habitat characteristics

In Chapter 4, I developed a method to sample the epipelagic prey field of coastal top-predators. Outputs from a recreational-grade echo-sounder (RGE) reliably detected schools of potential prey and ground truthing provided good information on school dimensions and relative intensity for common prey taxa. In Chapter 5, I show that both Hector’s dolphins and little penguins had strong overlap with their prey at fine-scales. In addition to relative abundance of prey, patch characteristics including school depth were important. Investigation of prey dynamics among survey areas indicated prey were generally more abundant at hotspots; although two reference areas also had high prey abundance. Prey were deepest at these two reference areas. Hotspots, then, are areas where prey are generally abundant, but also shallower and therefore less energetically costly to catch. These results add to emerging evidence that both prey abundance and prey patch characteristics are important at shaping the distribution of predators (Embling et al. 2012; Benoit-Bird et al. 2013). Importantly, these results are the first to demonstrate such trends for a coastal dolphin species.

The distribution of small epipelagic fish is difficult to quantify. Understanding habitat use by these species is important in its own right, as well as for studies on the ecology of their predators (including fisheries). Confirmation of the utility of the RGE to provide quantitative data on the distribution of epipelagic fish is an important output of Chapter 5. RGE systems are cheaply available and easily used in the field, and facilitate high frequency of sampling (e.g. up to 30 transects per area in one season). Such properties make these systems very useful for investigating the distribution of highly patchy species.

Chapter 6 combined information from Chapters 2 (hotspot locations and seasonality), Chapter 3 (importance for foraging) and Chapters 4/5 (prey) in order to determine the biophysical correlates of habitat selection and the characteristics of hotspots. Comprehensive species distribution models were developed using a broad range of variables describing physical habitat type, bathymetry, hydrology, oceanography and prey distribution in a thorough examination of habitat selection. A range of factors were important for describing the relative abundance of dolphins, including the dominant habitat type, the amount of reef habitat, depth, current velocity and oceanographic properties such as temperature and primary productivity. Prey abundance had a strong influence on dolphin abundance. These results reveal the synergy between the dynamics of prey and environmental features that are important at describing habitat selection by top-predators.

Not all of the important factors identified from the species distribution models were represented at hotspots. Hotspots were locations that, generally, had sandier habitat, had depths within a certain range (12-22m) and higher prey abundance. These were not consistent across all hotspots, but hotspots exhibited at least two of these three main features. Notably, no differences in the oceanographic variables were observed between hotspots and reference areas. The importance of these variables is likely to reflect their seasonality and thus correlation with the high density of dolphins in this habitat during summer.

7.2 - Impacts on habitat

Each of the features of hotspots identified in Chapter 6 face varying degrees of human impact. Smothering of sandy habitat and infilling (i.e. changing depth distribution) is likely to occur at some locations on Banks Peninsula. Recent habitat mapping surveys found evidence for smothering of sandy habitat by silt (Brough et al. 2018a), and some inner harbour locations have lost more than 1m of depth since the 1950s (Hart et al. 2009). In Akaroa Harbour, the composition of infaunal communities is strongly related to the mud content of the sediment, with biomass being higher in sandy, outer harbour locations (Fenwick 2004). The mechanisms that link Hector’s dolphins to sandy substrate are, however, unknown.

How natural and/or anthropogenic processes have impacted on the prey of Hector’s dolphins is not known. Considering there is little information about the habitat preferences or general biology of the epipelagic prey species featured in this thesis, establishing causal relationships with changing conditions is not straightforward. In several other locations, the population dynamics of epipelagic fish have been linked to climate changes (Jacobson et al. 2001; Chavez et al. 2003; Mhlongo et al. 2015), overfishing (Murphy 1967; Dalzell and Ganaden 1987) and disease (Gaughan et al. 2000; Paul et al. 2001). There have been dramatic fluctuations in populations of predators that consume epipelagic fish in NZ waters (Jones 2000; Miskelly et al. 2008; Mattern et al. 2017), and reported declines in some epipelagic stocks (Paul et al. 2001). Therefore, anthropogenic impacts on epipelagic species in this area cannot be ruled out.

Information from recreational fishers (Källqvist et al. 2015) and decreased commercial catch rates (MPI 2017), provides evidence for a recent decline in red cod at Banks Peninsula. Whilst not explicitly investigated by this thesis, red cod had high abundance at two hotspots (Akaroa and Long Lookout Pt; Miller 2014). If fishing has impacted red cod availability, this would have a clear impact on an important ecological feature of hotspots.

The flow of tidal currents can be impacted by coastal development such as land reclamation and wharf construction (Jefferson et al. 2009), aquaculture (Grant and Bacher 2001) and dredging (van Maren et al. 2015). These do not currently occur at hotspots, but further resource management of the marine environment at Banks Peninsula should consider the importance of current velocities for Hector's dolphins should industries expand.

7.3 - Further protection: How

A review of the threats to Hector's dolphins is currently underway and will result in an updated Threat Management Plan (TMP) for the species. The TMP will guide management for the species over the next ten years and therefore it is important the most up to date information is available. The results presented in this thesis are clearly relevant to the TMP process; providing new information that can be used to identify and protect important habitat for this endangered species.

The main threat to Hector's dolphin throughout its range is bycatch (Dawson 1991a; Slooten 2013). Commercial and amateur set-net fishing is excluded from hotspots as part of the nearshore fishing restrictions. Compliance and enforcement of these restrictions should, however, take a high priority in future management. Whilst set-net fishing is unlikely to occur at hotspots, a concession granted to amateur fishers allows set-netting in the upper Akaroa Harbour between April and October (Fig. 7.1). Both the relative abundance and foraging rates of dolphins peaked during April in Akaroa Harbour (Chapter 3) and dolphins have been killed in nets during this time (S. Dawson pers. comm.) In order to prevent further captures it is advised that the concession allowing amateur gillnetting in Akaroa Harbour is removed (see also Dawson et al., 2013).

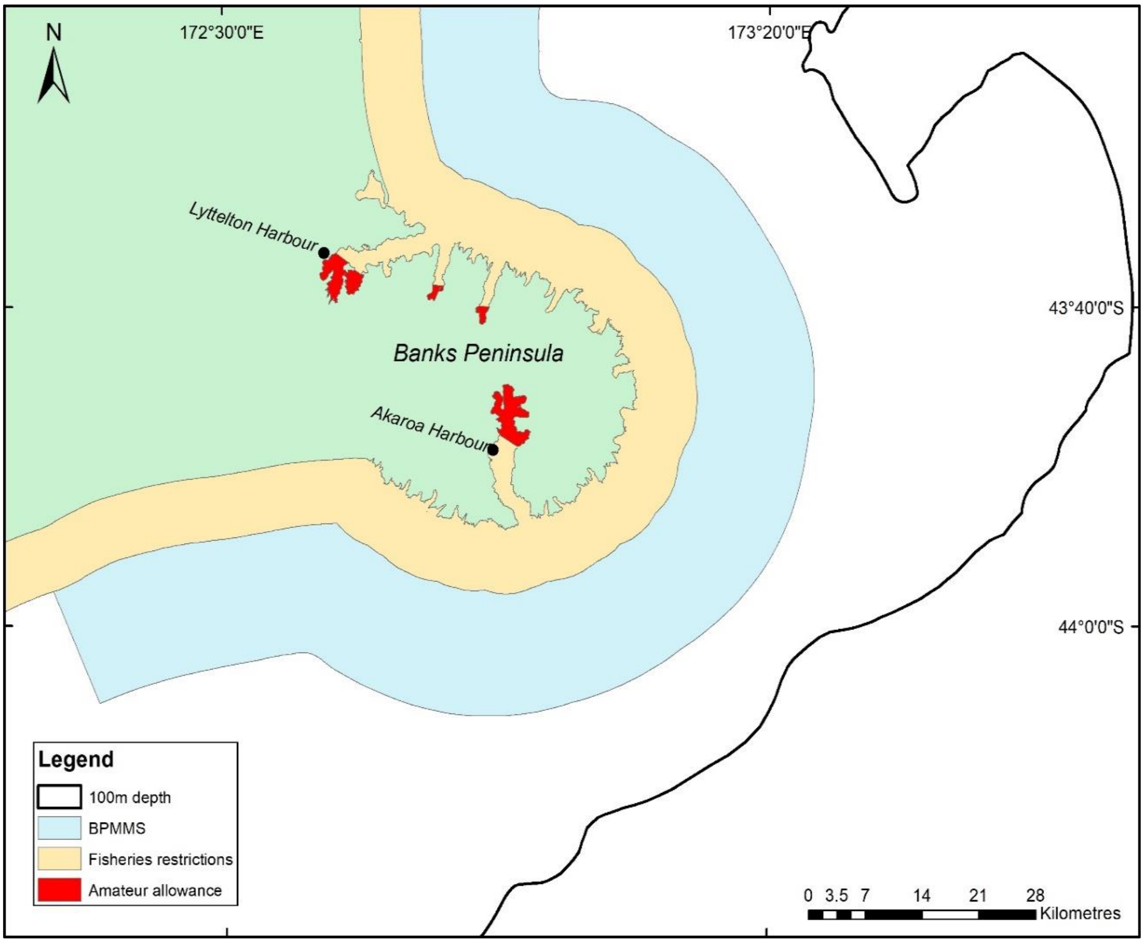

Figure 7.1: Current management of Hector's dolphins at Banks Peninsula. Bycatch is reduced by fisheries restrictions and seismic surveying is prevented in the Banks Peninsula Marine Mammal Sanctuary (BPMMS). Bycatch still occurs in areas where amateur set-netting is allowed, and in the part of the dolphins range not covered by fisheries restrictions (offshore to 100 metres depth).

Additional threats to Hector’s dolphin include: noise pollution (Leunissen and Dawson 2018), impacts of tourism (Martinez et al. 2010, 2012), vessel strike (Stone and Yoshinaga 2000), habitat degradation (Brough et al. 2014), pollution (Stockin et al. 2010) and disease (Roe et al. 2013). The Banks Peninsula Marine Mammal Sanctuary (Fig. 7.1) restricts seismic surveying within 12 n.m of the coastline, but does not address other threats. Compared to bycatch, each of the aforementioned threats are likely to be small. Yet, the cumulative impact of the broad range of threats facing Hector’s dolphins may be significant. It is important therefore, that individual threats receive appropriate attention in the TMP process.

With new information on the ecology of hotspots for Hector's dolphin, additional protection of these areas would be supported by strong evidence. It is likely that similar, fine-scale hotspots exist throughout the range of the species (e.g. Rodda 2014). Protection should be extended to these important areas. The crucial question is; what threats should be managed? At Banks Peninsula, impacts of tourism (Martinez et al. 2010, 2012) and vessel strike (Stone and Yoshinaga 2000) are likely to be greater in the two major harbours on the peninsula. Akaroa Harbour is also a major hotspot. It is probable that the majority of vessel strikes go either unreported or undetected. Yet, during summer when high densities of dolphins and vessels coincide, there is likely to be significant risk of vessel strike. The presence of tour boats interrupts important behaviour at this time of the year in Akaroa Harbour (Martinez et al. 2010). Whether dolphins avoid the harbour, or use it differently when vessel traffic or tourism pressure is high, is not known. Such effects have been observed in other coastal populations of dolphins (Lusseau 2005; Bejder et al. 2006). For these reasons, it makes sense to consider an additional protected area within Akaroa Harbour, the boundaries of which could be defined by the Akaroa Harbour hotspot (Fig. 7.2). This MPA could require vessels to travel slower or limit interactions with dolphins. Similar restrictions on the locations and/or times that tour boats can conduct trips are used in the Bay of Islands (Hartel et al. 2015) and in Doubtful Sound (Lusseau and Higham 2004) in order to protect bottlenose dolphins. Managers should consider these initiatives in the case of Hector's dolphins in Akaroa Harbour.

The other hotspots are far more isolated than Akaroa Harbour and so have little vessel traffic and essentially no commercial tourism. In these areas (as well as Akaroa), management should focus on protecting the features that make good quality habitat. I hope that regulatory bodies consider the results of this thesis when appraising resource consent applications for coastal development. Developments that generate significant siltation (i.e. require major earth works), change the depth of the seafloor (e.g. dredging), or influence current flow (e.g. aquaculture) should be restricted, at least at hotspots. Resource managers should also consider the impacts of coastal development on the important features of dolphin habitat throughout Banks Peninsula. In the absence of region specific species distribution models, precautionary management would consider such impacts throughout Hector's/Maui dolphin range.

Managers should also consider the protection of the predator-prey interactions identified in this thesis. Two small no-take marine reserves (MR) are already present on Banks Peninsula; Pōhatu Marine Reserve (215ha) and Akaroa Marine Reserve (475ha). Akaroa Harbour is also under Taiāpure protection – customary management that aims to recover declining mahinga kai (food resources). At least in the case of Pōhatu, there is some evidence that depleted fish populations are recovering (Brough et al. 2018b), although note that Akaroa MR is only 4 years old. Both reserves are, however, very small and it is unlikely either will sufficiently protect the wide ranging prey of Hector's dolphin. There should be a thorough consideration of the distribution of dolphin prey and the existence of hotspots when planning future marine protection at Banks Peninsula.

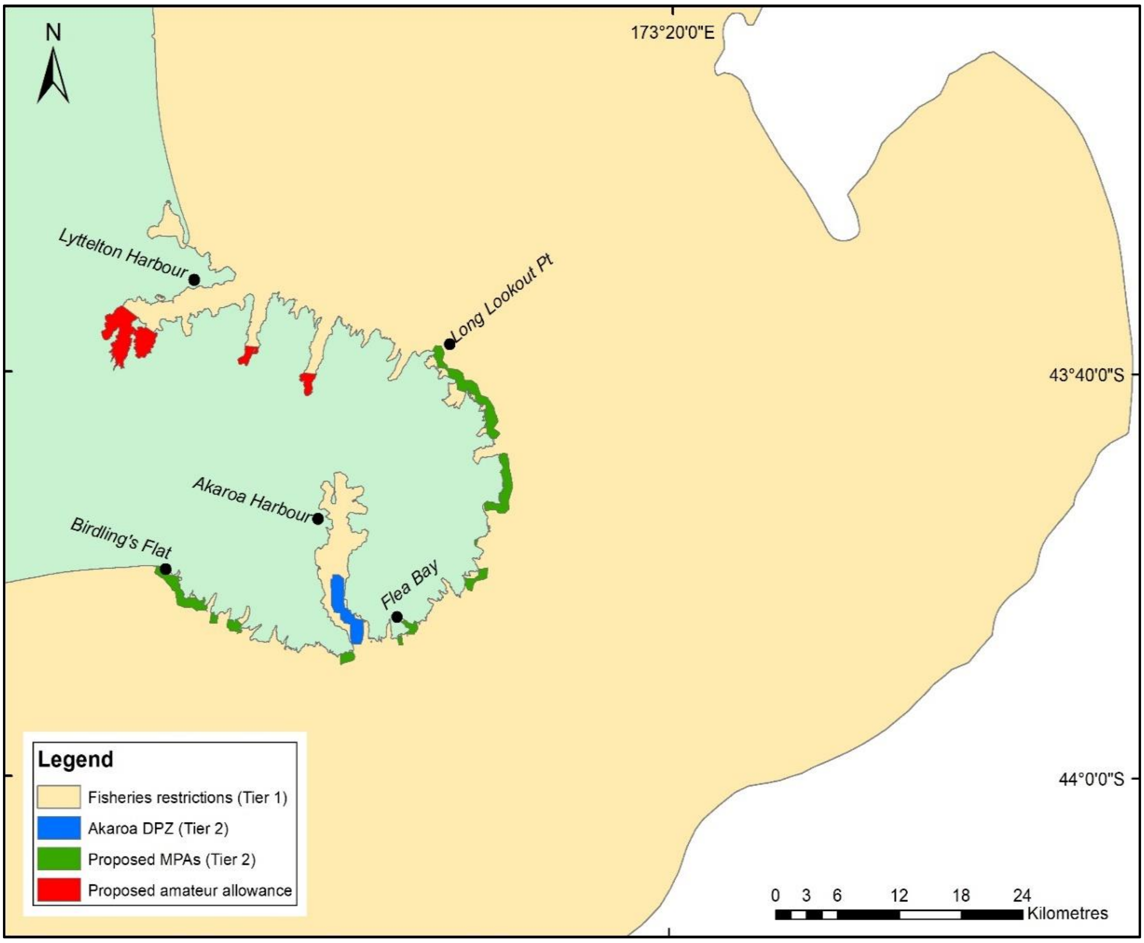

Figure 7.2: Proposed design for hierarchical threat management of Hector's dolphin at Banks Peninsula. Fisheries restrictions (tier 1) are extended to the full offshore range of the species (100m depth) and MPAs are established at hotspots (tier 2) to protect against localised impacts. A dolphin protection zone (DPZ) in Akaroa Harbour is proposed to mitigate the impacts of tourism and vessel strike. The amateur set-netting allowance is removed from Akaroa Harbour.

I suggest that management of this important population, and its habitat, should follow a hierarchical model (e.g. Zacharias and Roff 2000), in which the key threats are managed as a network of management areas with multiple ‘tiers’. Such an approach has been undertaken with the management of endangered North Atlantic right whales; the threats to the species (including ship strike, entanglement in fishing gear, and disturbance of feeding) are managed in multiple MPAs (Hoyt 2011). A lack of protection for the whales throughout their range and the absence of binding legislation have limited the effectiveness of such an approach, however (Hoyt 2011). In the case of Hector's dolphin, the very small home range of the species (Rayment et al. 2009a) means it is ideally suited to area-based management, as the full range of a population can be easily covered. An increase in survival rates after the implementation of fisheries restrictions (Gormley et al. 2012) provides evidence that area-based protection can work for Hector's dolphins. While not explicitly investigated by this thesis, the impacts of fisheries bycatch on this population are still substantial (Slooten 2010). Thus, bycatch, in all forms of fishing, should be further reduced by extending the boundaries of current fisheries restrictions to the offshore limit of the species; the first tier of protection (Fig. 7.2). Within this larger protected area, smaller MPAs can be established, focussing on localised impacts including minimising the risk of vessel strike, the disturbance of critical behaviours, protecting key habitat features, and conserving and/or enhancing prey populations. The hotspots identified in this thesis are clear candidates for such 'second-tier' protection (Fig. 7.2). Such an approach, considering a range of threats and the ecological drivers of distribution, would represent true ecosystem based management (Hoyt 2011).

7.4 - Further research

This thesis has identified multiple avenues for further research.

Firstly, there is still limited information on the fine-scale distribution of Hector's dolphins beyond the boundaries of current protection. Relevant questions include: Do the dolphins show consistent hotspots offshore? Do these hotspots exhibit similar characteristics to nearshore hotspots? And importantly, does set-net fishing show a similar spatiotemporal distribution? Hector's dolphins are found at depths of up to 100m (Rayment et al. 2010a, 2011a). To reduce bycatch, fisheries restrictions prevent commercial set-netting and some trawling out to 4 n.m from the coast (Fig. 7.2). Particularly in winter, there is significant overlap between the distribution of dolphins and areas where fishing occurs (Rayment et al. 2010). There have been no published studies on the fine-scale distribution of set-net fishing beyond 4 n.m; although data on the location of sets are held by Fisheries NZ, and so such analyses are possible. Currently, most bycatch models for the species assume a random distribution of both dolphins and fishing (e.g. Baird and Bradford 1997).

This is however, unlikely to be the case (Chilvers 2008; Herr et al. 2009). Thus, information on the relative distribution of dolphin and fishing hotspots beyond 4 n.m would help quantify the threat that these animals face beyond the current boundaries of protection.

From the results of this thesis and Miller (2014), there is now a good understanding of what drives the distribution of Hector's dolphins at Banks Peninsula. Broad scale correlations with water depth and distance from shore are known from the west coast of the South Island and Kaikoura (Bräger et al. 2003; Rayment et al. 2011a; Weir and Sagnol 2015). Also, fine-scale distribution has been linked to the proximity of river mouths in Te Wae Wae Bay (Rodda 2014). The factors that shape distribution in most other locations are unknown. Several populations are small, fragmented and isolated (Hamner et al. 2012) e.g. Kaikoura (Weir and Sagnol 2015), Otago (Turek et al. 2013) and Porpoise Bay (Bejder and Dawson 2001). Understanding the drivers of habitat selection and the features of important habitat in these populations may help to quantify local impacts on these populations.

Importantly, this thesis has identified substantial gaps in the understanding of the ecology of epipelagic fish in NZ. Given the significant importance of these taxa as prey for top-predators (Flemming et al. 2013; Miller et al. 2013), for supporting fisheries (Paul et al. 2001; MPI 2017), and their critical ecological role (Cury et al. 2000; Griffiths et al. 2013) the lack of research in this area is surprising. Future research should focus on identifying the drivers of population dynamics in pilchard and sprat in particular. These taxa have undergone significant fluctuations in abundance in some areas (including NZ; Paul et al. 2001) and are vulnerable to climate change (Jacobson et al. 2001; Chavez et al. 2003). An assessment of the habitat preferences for these species would assist in understanding how they respond to changing conditions and would allow an appraisal of the pressures faced by top-predators as their prey respond to climate change.

Additional investigations can focus on understanding the ecological values of hotspots, determining the links between predators and certain habitat features and niche differentiation among top-predators at Banks Peninsula.

7.5 - Concluding remarks

Hotspot locations are clearly important. In order to protect this endangered taonga species and its habitat, it is strongly advised that these locations are protected. Such protection can take several forms and can be implemented under a hierarchical model. In this way, Hector's dolphin can be protected from the full range of threats.

After all, he tu te Pahu, he tu te Tai[2]; if the dolphin is well, so are our coasts.

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[2] Maori whakataukī (proverb)

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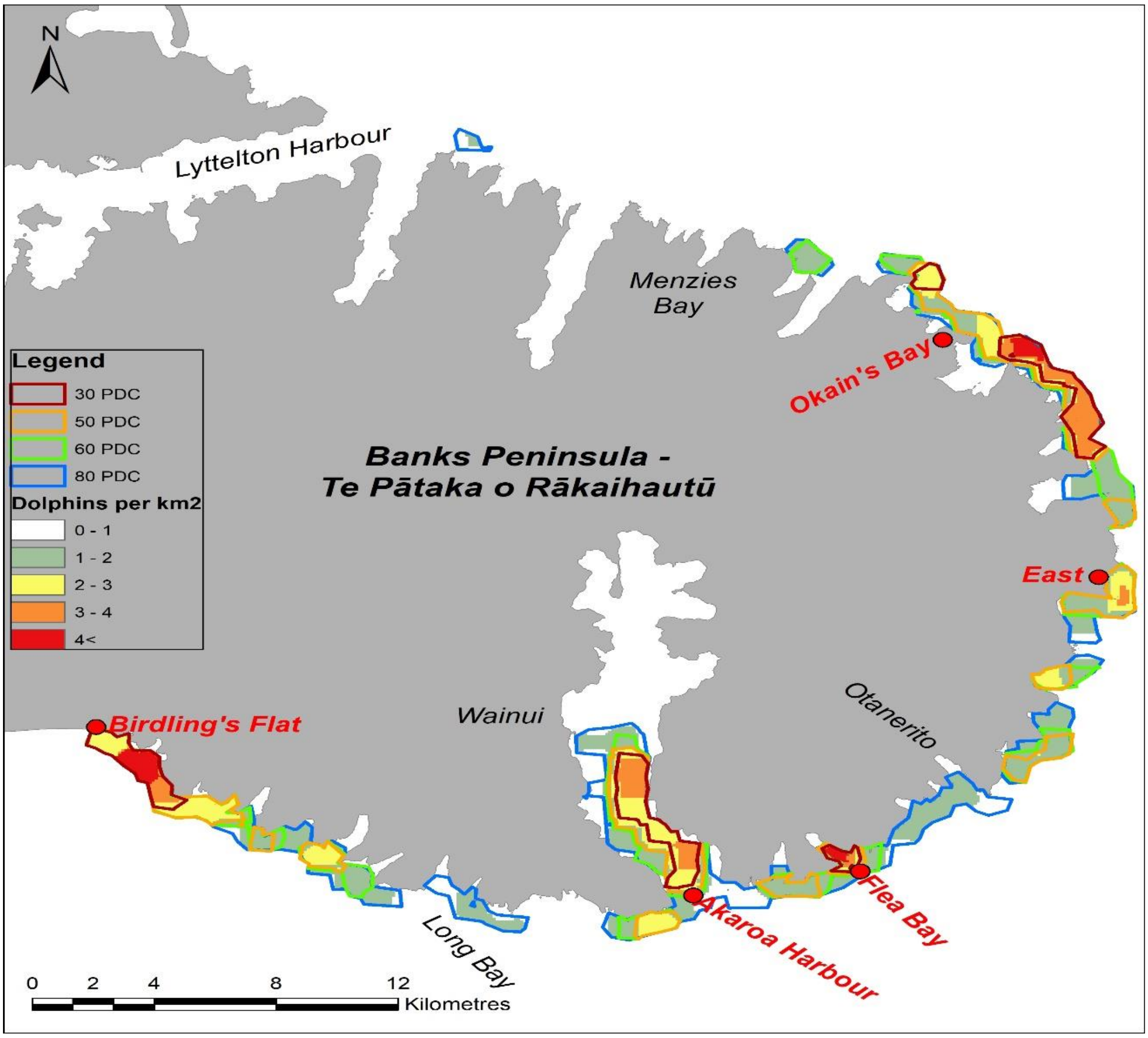
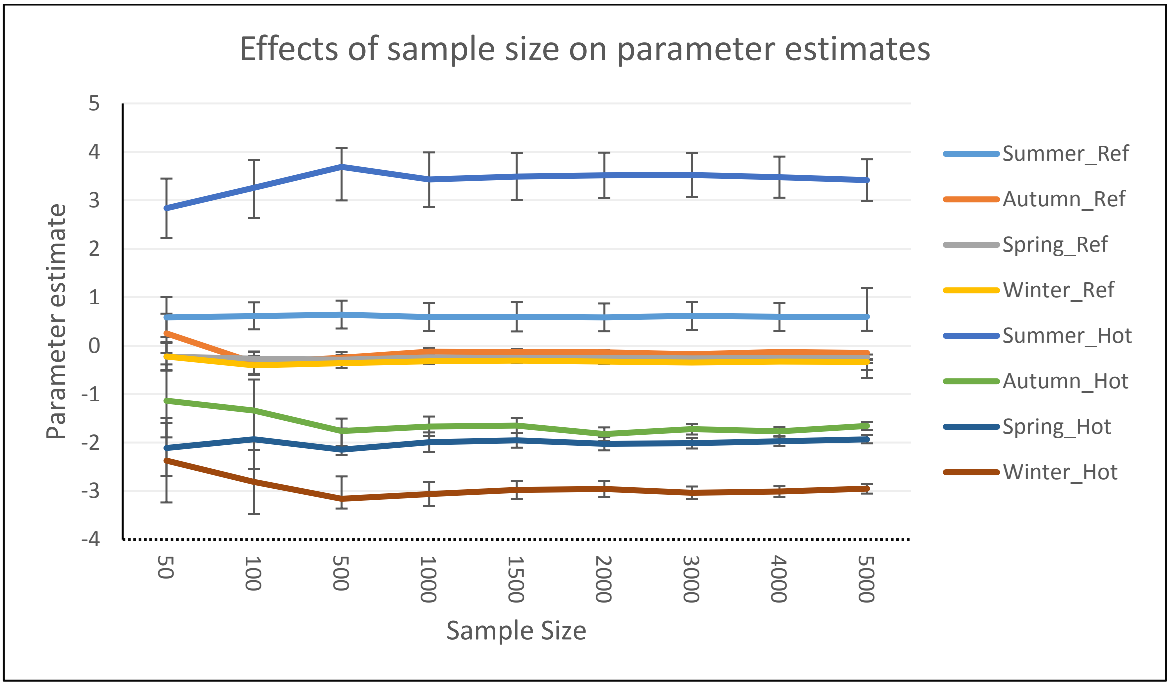
Appendix 1a: Hotspot distribution



Appendix 1a. Overall kernel density estimation of Hector's dolphin sightings at Banks Peninsula between 1988 and 2017. Four percentage density contours (PDCs) are provided (30, 50, 60 and 80). Dolphin density is given as dolphins per km^2.

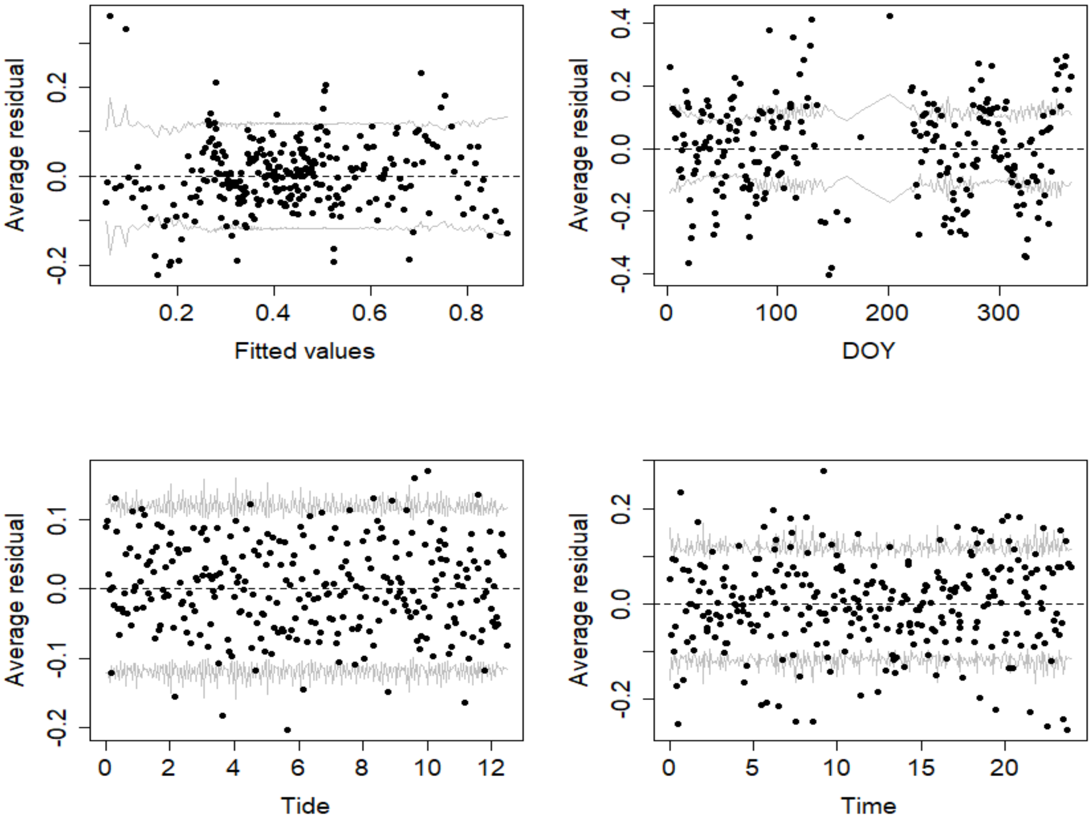
Appendix 1b: Cell size for GLMM modelling

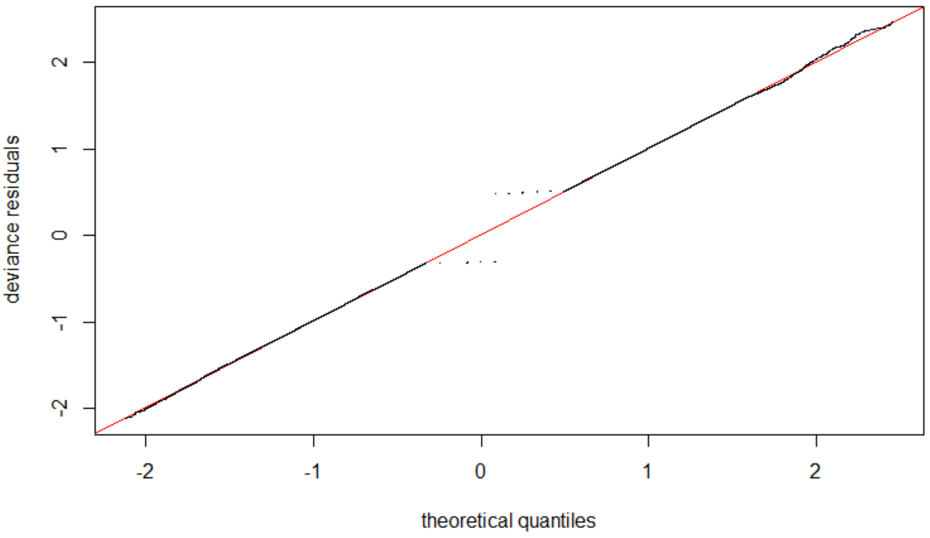


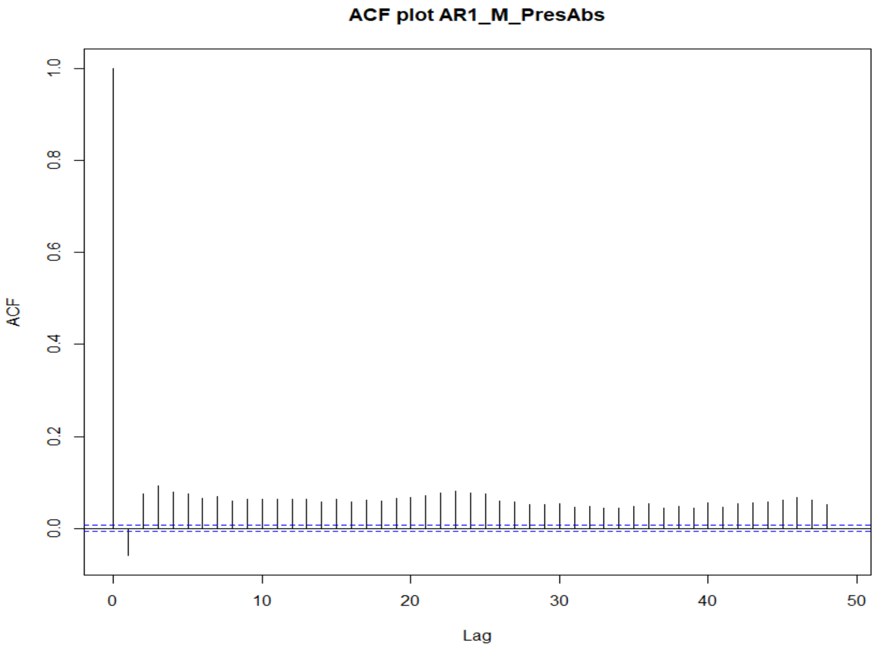
Appendix 1b: The effect of subsampling the original grid cell dataset in order to assess the influence of sample size on the outputs for density models. Results are shown for models that assess variation in density values according to season for both hotspots (Hot) and reference areas (Ref). The original sample size for the hotspot seasonal analysis was 8,234 and for coldspots was 6,344. Error bars are 95% CI around the parameter estimate.

Appendix 2a: Model diagnostics for GAMM of distribution and foraging

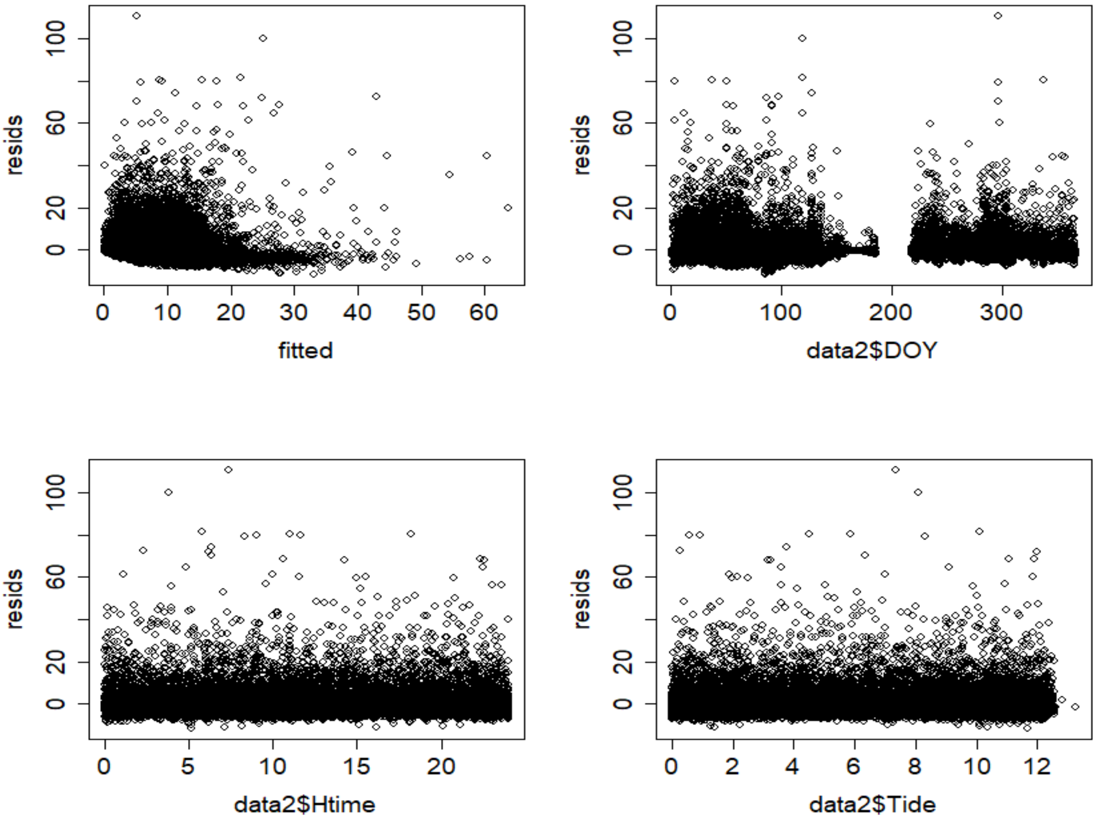
Presence/absence models

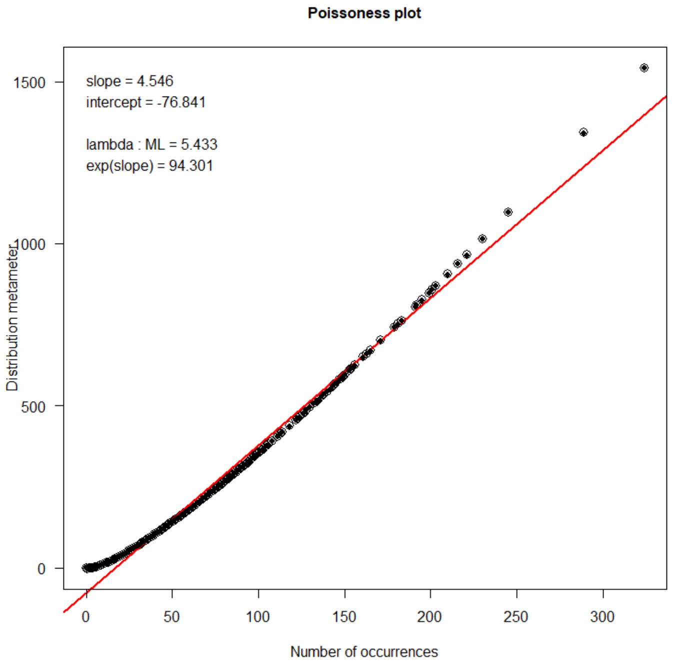


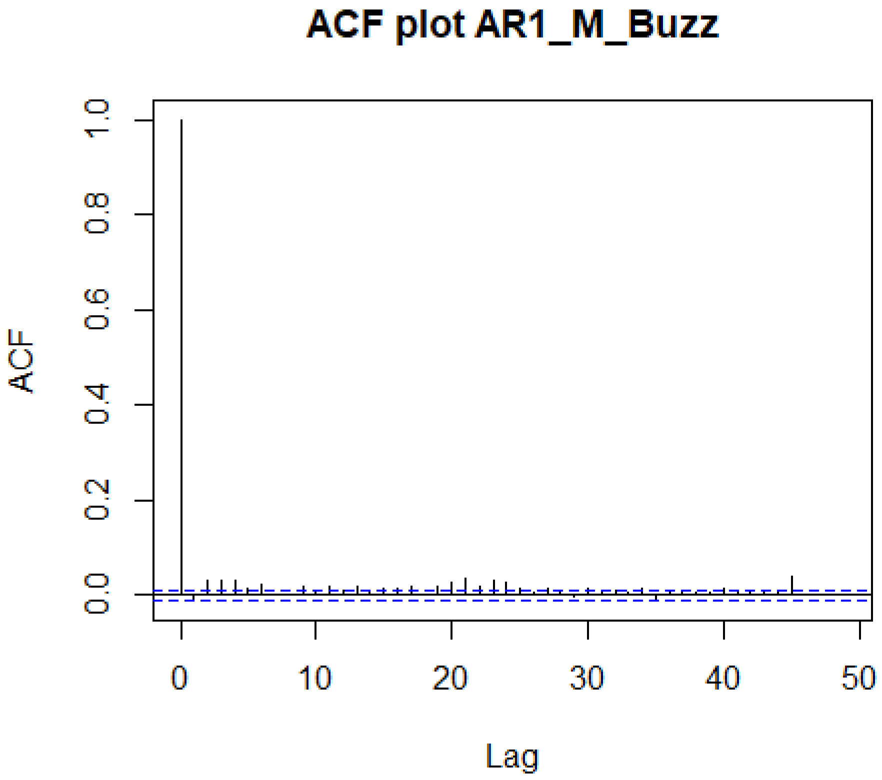




Foraging models

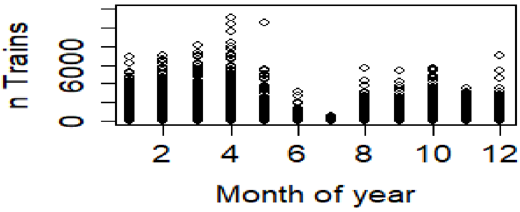


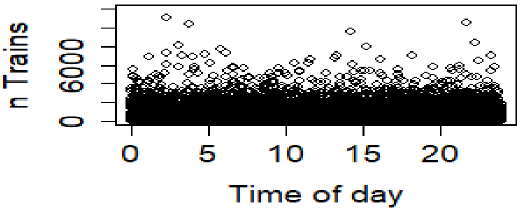

Poissoness plot
slope = 4.546
intercept = -76.841
lambda : ML = 5.433
exp(slope) = 94.301
Distribution metameter
0
500
1000
1500
0
50
100
150
200
250
300
Number of occurrences

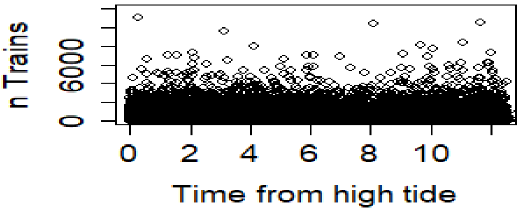

ACF plot AR1_M_Buzz
ACF
0.0
0.2
0.4
0.6
0.8
1.0
0
10
20
30
40
50
Lag

Appendix 2b: Plots of raw data across three temporal scales for both dolphin distribution and foraging.

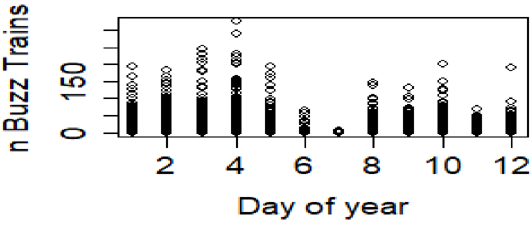
Dolphin distribution

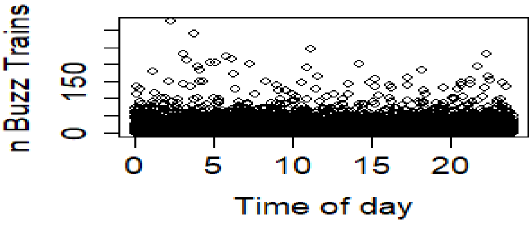


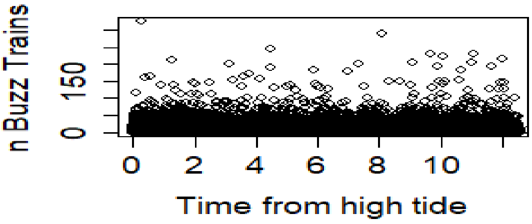




Foraging

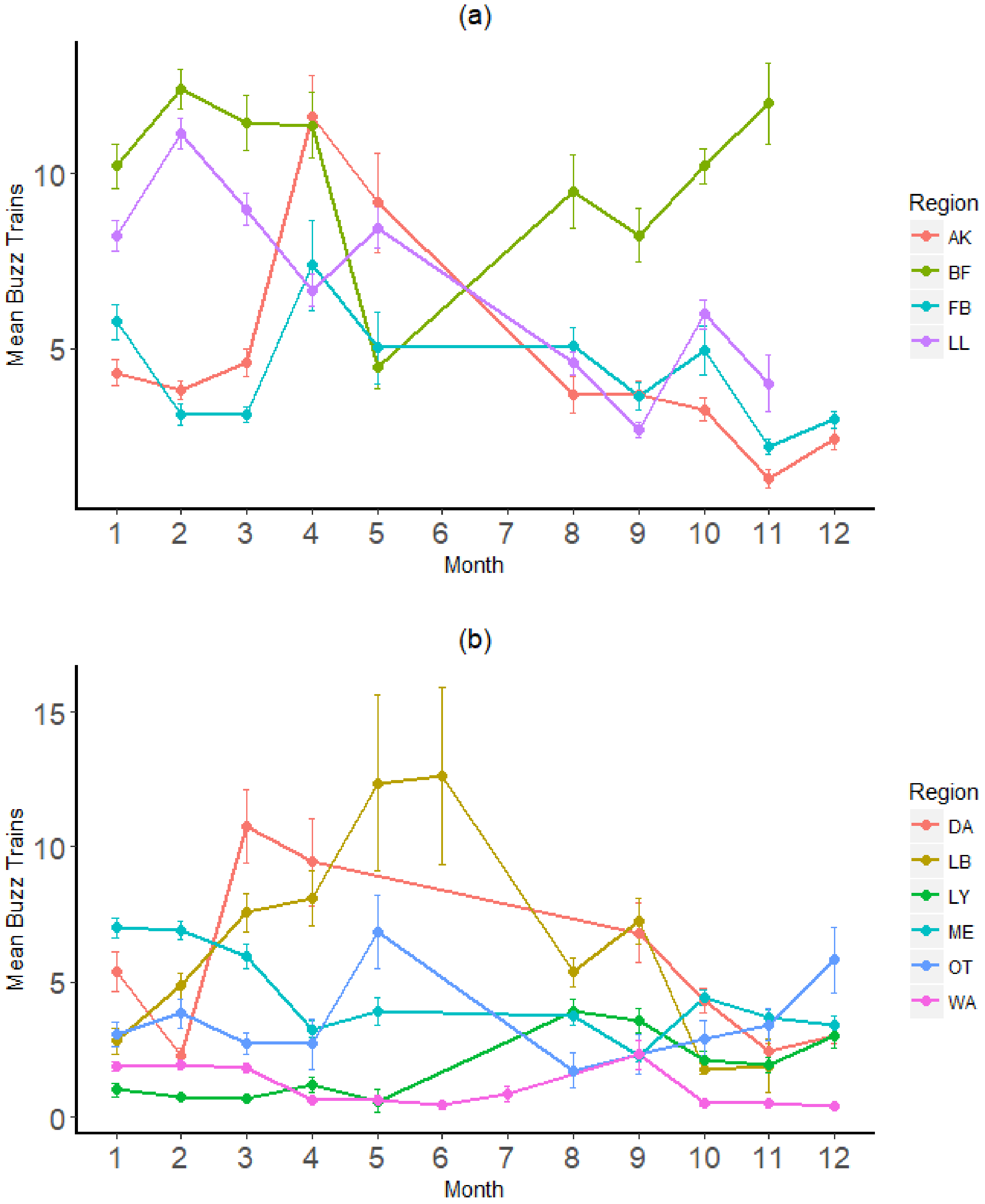




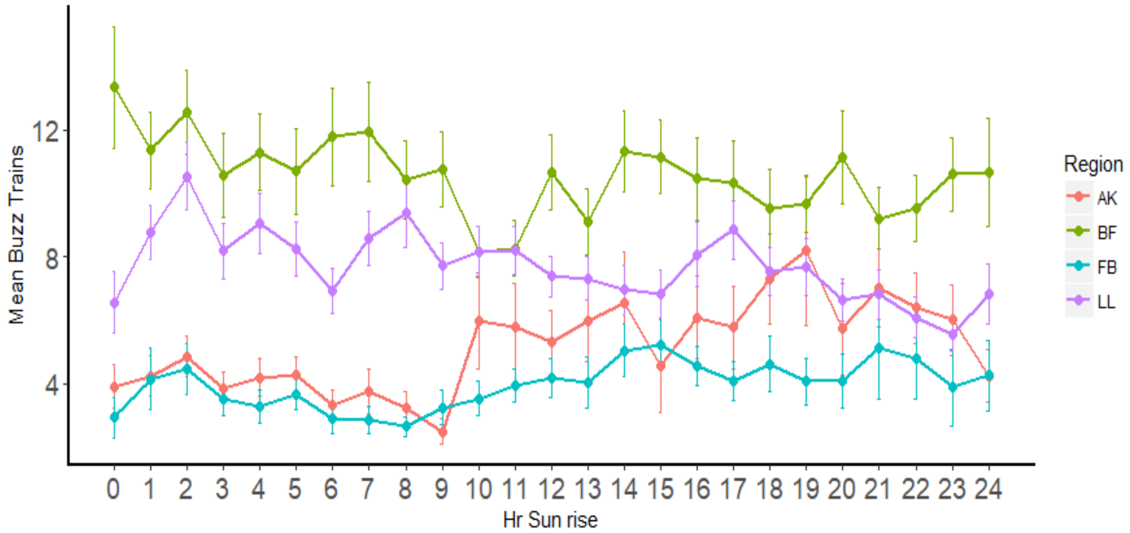


Appendix 2c: Plots of raw data to illustrate trends determined via foraging GAMM models.

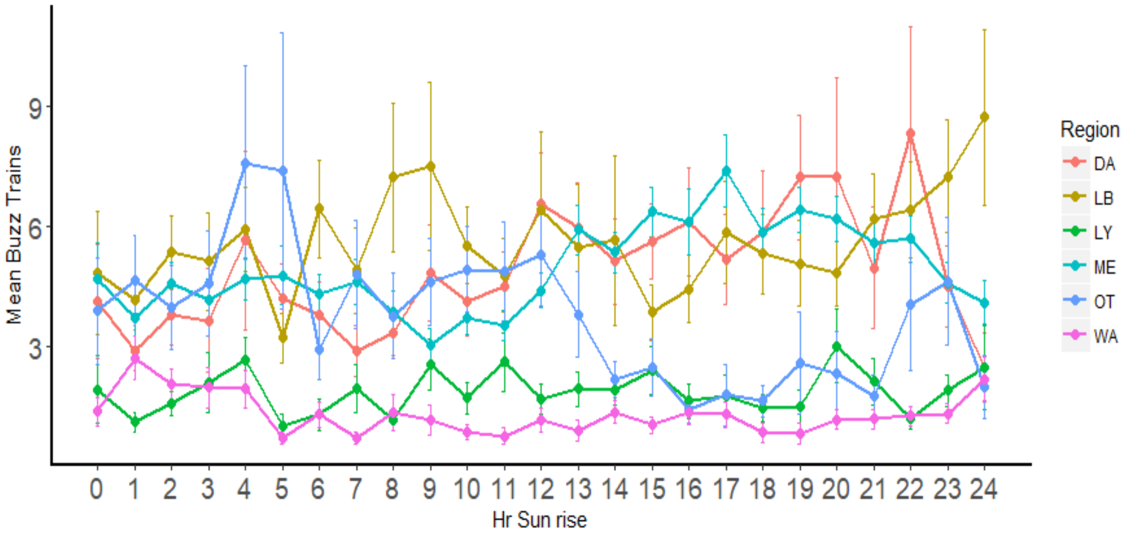
Three figures showing patterns in the raw data between foraging rates and season, hour of day and tide for hotspots (a) and reference areas (b).

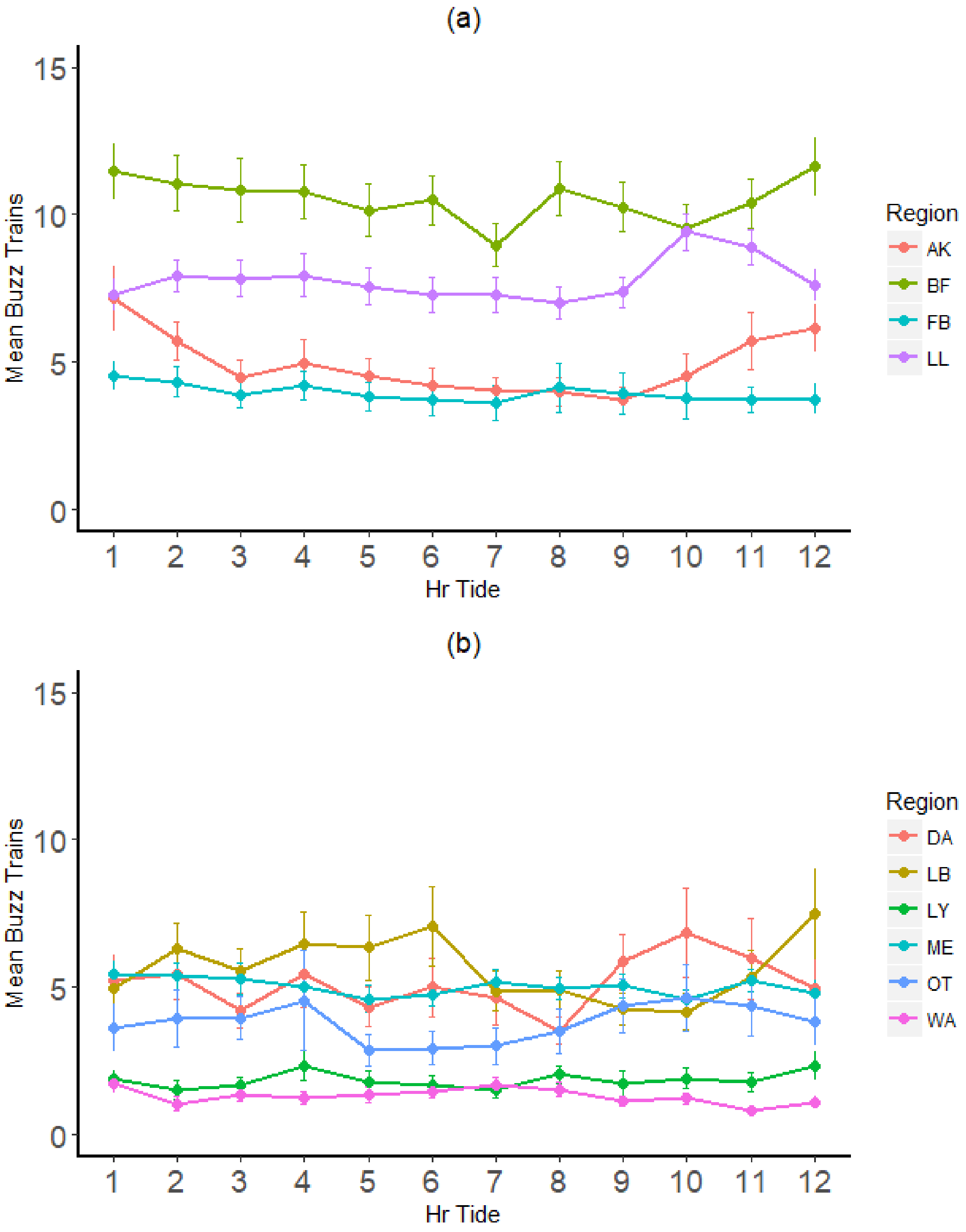


(a)


Mean Buzz Trains
12
8
4
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Hr Sun rise
Region
AK
BF
FB
LL

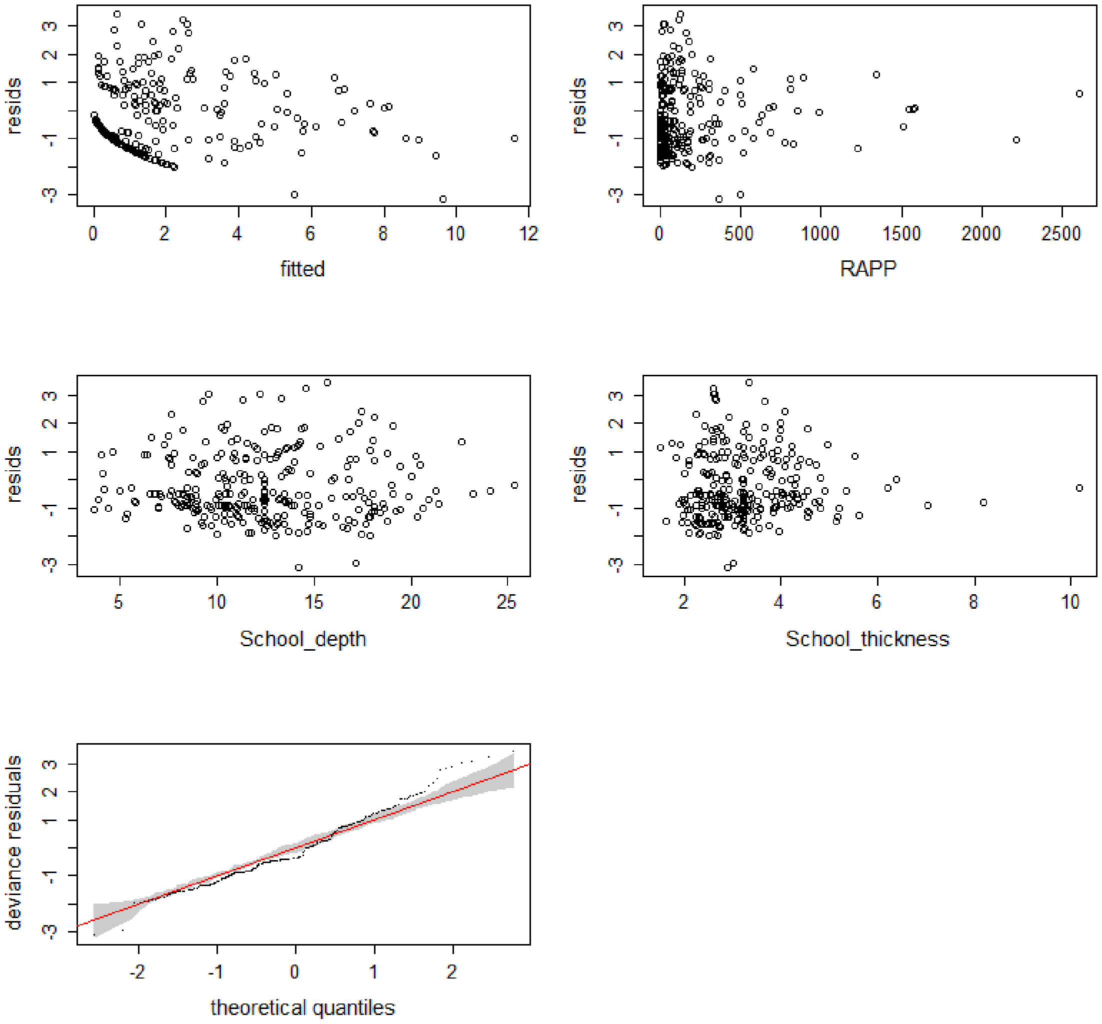
(b)


Mean Buzz Trains
9
6
3
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Hr Sun rise
Region
DA
LB
LY
ME
OT
WA

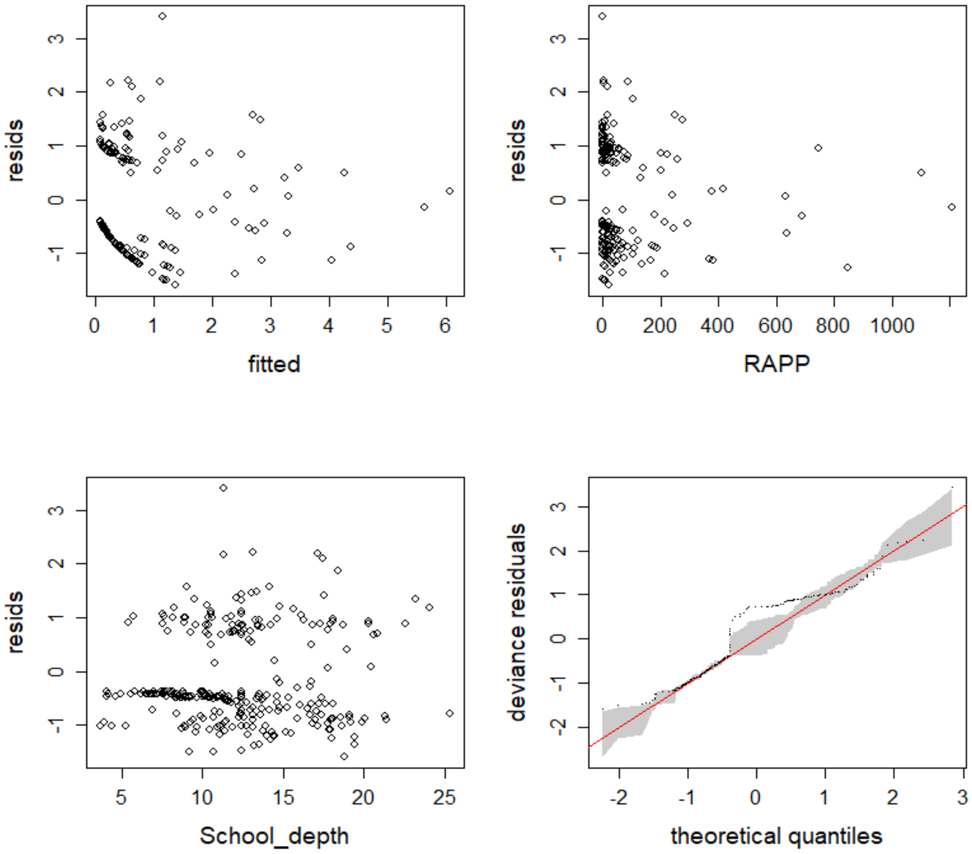

(a)
Mean Buzz Trains
0
5
10
15
1
2
3
4
5
6
7
8
9
10
11
12
Hr Tide
Region
AK
BF
FB
LL
(b)
Mean Buzz Trains
0
5
10
15
1
2
3
4
5
6
7
8
9
10
11
12
Hr Tide
Region
DA
LB
LY
ME
OT
WA

Appendix 3a: Diagnostic plots for predator prey overlap

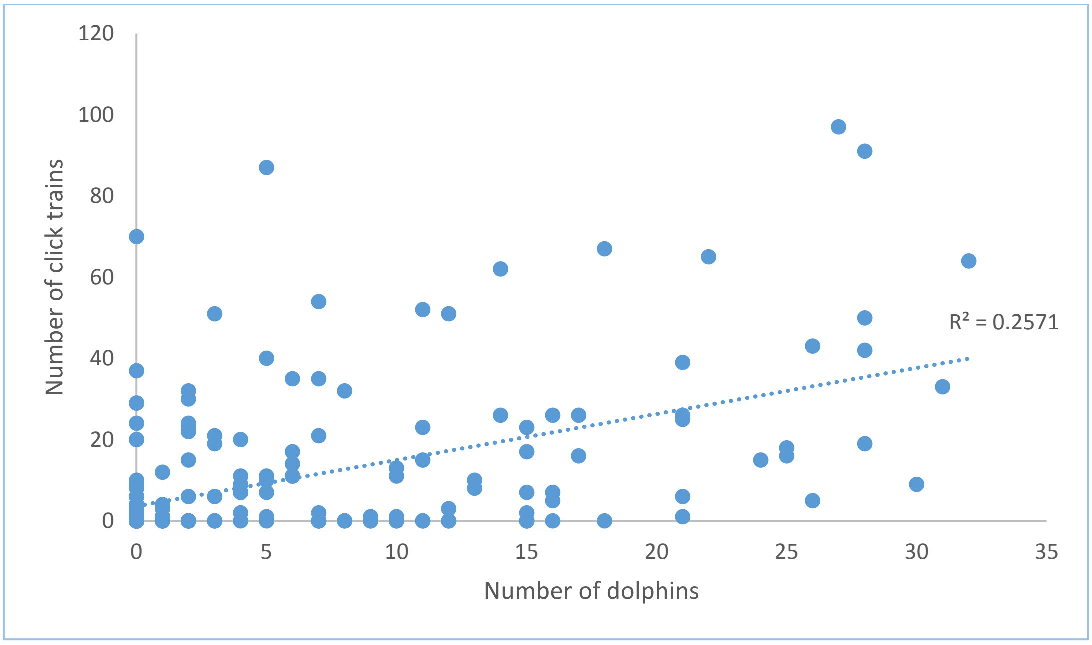
Dolphin top-model



Penguin top-model

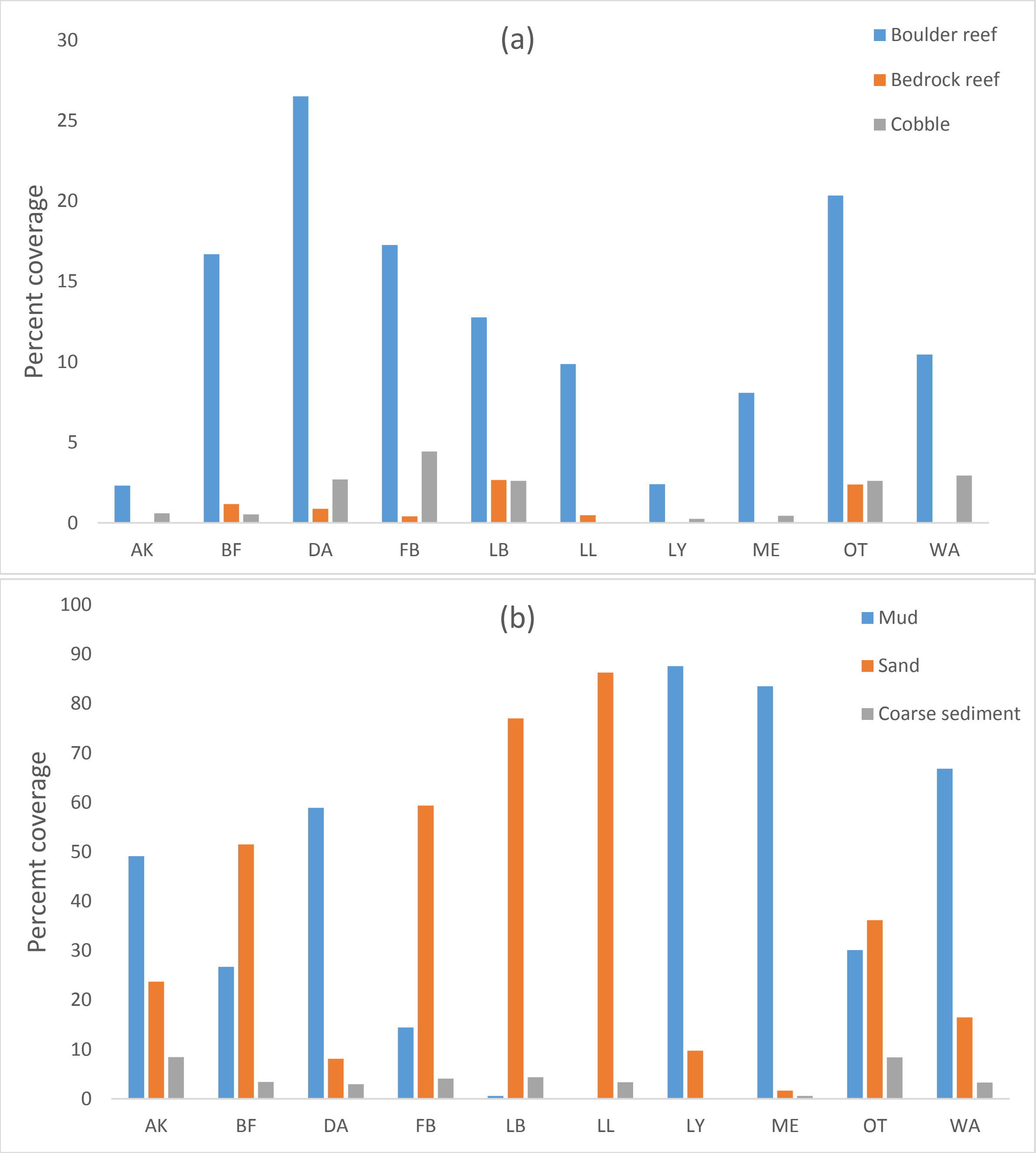


Appendix 3b: Correlation between visual and acoustic data

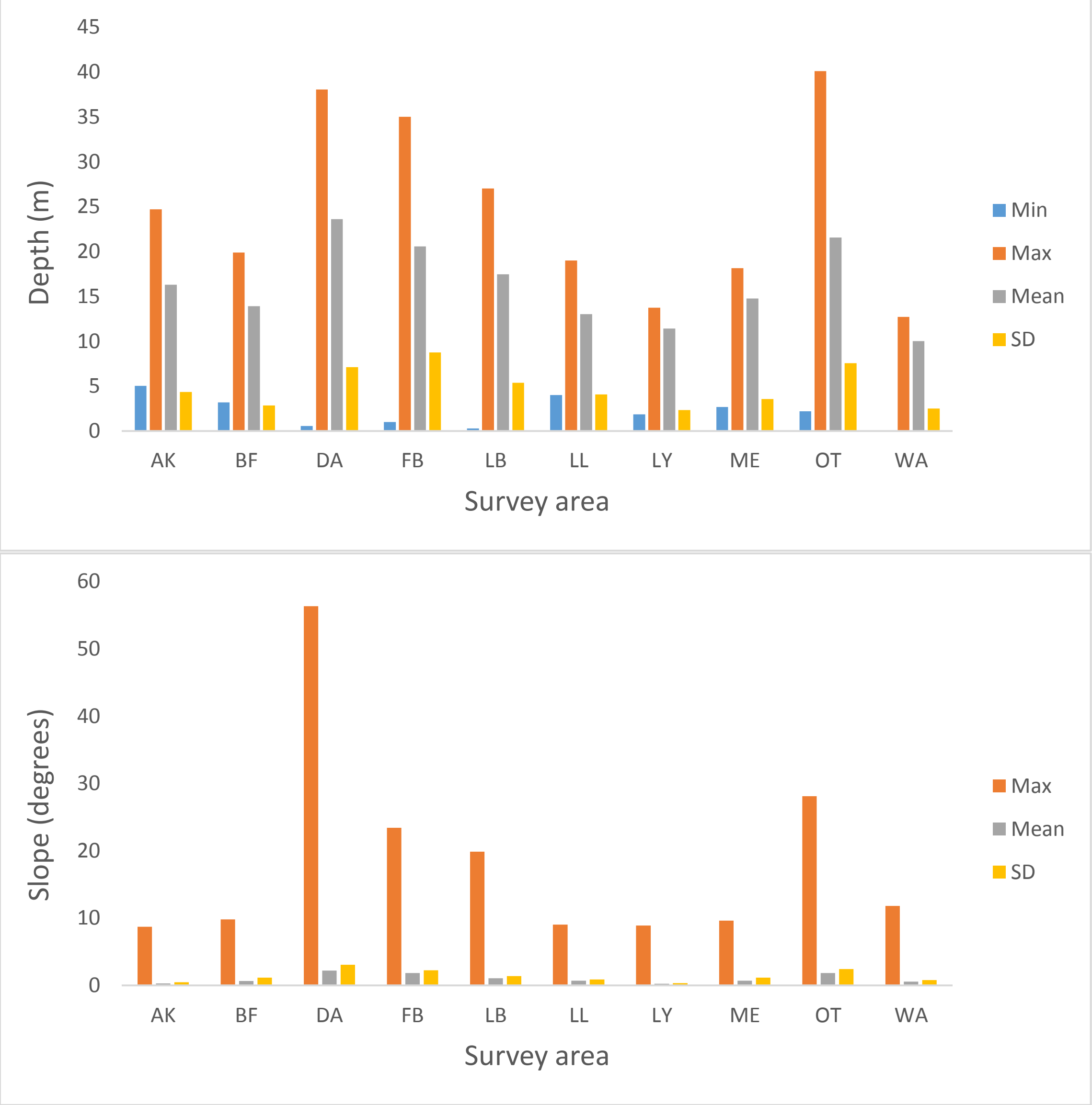


Appendix 3b: The relationship between visual (number of dolphins) and acoustic (number of click trains) data for determining habitat use with visual and acoustic methods respectively. Data points are for visual transects during which a TPOD was deployed. The number of click trains recorded by the TPOD during the nearest hourly interval is used to compare with the number of dolphins sighted during a visual transect. A positive relationship between the two response variables suggests the methods are providing similar information on dolphin relative abundance. Yet, substantial variability around the correlation suggests further investigation into the relative merits of each method is warranted.

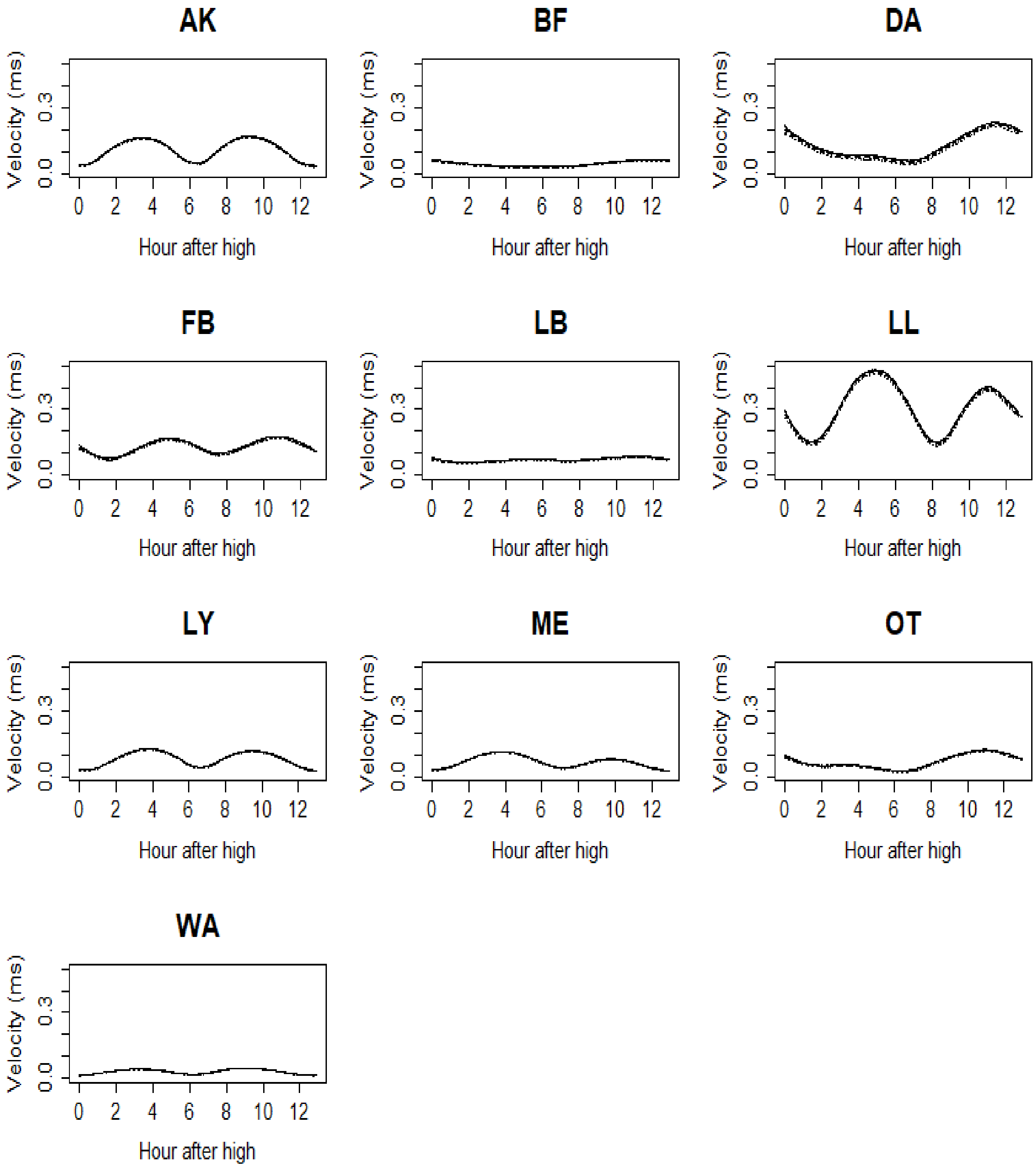
Appendix 4: Summary of data used to define the habitat characteristics for the 10 survey areas.



Appendix 4 Fig. 1: The percentage cover of six habitat types at the ten survey areas. The percentage cover of hard substrate types are given in (a), and soft substrate types given in (b). The value for each habitat type is expressed as a percentage of the total area mapped at each area.



Appendix 4 Fig.2: Summary of covariates sourced from bathymetric data used to define depth and slope for each survey area.



Appendix 4 Fig 3: Averaged velocity of tidal currents at ten locations as a function of the state of the tide. Averages were created using a smoothing spline with 95% confidence intervals on current data derived from the Pegasus Bay ROMS model.

Appendix 4 Table 2: Summary of oceanographic data from CTD casts used to describe the characteristics of the ten survey areas.

Surface temperature

Area	N	Mean	SE
AK	30	15.02	0.54
BF	14	15.03	0.96
DA	18	14.98	0.69
FB	20	14.47	0.61
LB	18	15.03	0.68
LL	21	14.04	0.70
LY	15	15.59	1.05
ME	22	15.06	0.69
OT	13	14.56	0.65
WA	15	14.56	0.87

Surface salinity

Area	N	Mean	SE
AK	30	34.18	0.09
BF	14	33.73	0.26
DA	18	34.06	0.19
FB	20	34.30	0.07
LB	18	33.96	0.22
LL	21	34.24	0.06
LY	15	33.96	0.12
ME	22	34.15	0.06
OT	13	34.43	0.07
WA	15	34.05	0.14

Surface Chlorophyll

Area	N	Mean	SE
AK	30.00	1.77	0.18
BF	14.00	1.17	0.20
DA	18.00	1.14	0.24
FB	20.00	0.92	0.11
LB	18.00	0.82	0.17
LL	21.00	1.82	0.15
LY	15.00	2.85	0.29
ME	22.00	2.11	0.24
OT	13.00	0.82	0.07
WA	15.00	1.62	0.27

Bottom temperature

Area	N	Mean	SE
AK	30	13.78	0.45
BF	14	14.01	0.72
DA	18	13.66	0.51
FB	20	13.66	0.48
LB	18	14.00	0.53
LL	21	13.73	0.67
LY	15	14.91	0.96
ME	22	14.46	0.64
OT	13	13.51	0.47
WA	15	13.58	0.75

Bottom salinity

Area	N	Mean	SE
AK	30	34.44	0.06
BF	14	34.31	0.11
DA	18	34.48	0.08
FB	20	34.50	0.04
LB	18	34.42	0.08
LL	21	34.31	0.06
LY	15	34.11	0.10
ME	22	34.28	0.05
OT	13	34.59	0.06
WA	15	34.25	0.13

Chlorophyll Max

Area	N	Mean	SE
AK	30	4.76	0.52
BF	14	5.23	1.13
DA	18	2.94	0.79
FB	20	1.94	0.20
LB	18	3.43	0.85
LL	21	2.96	0.26
LY	15	4.79	1.01
ME	22	3.46	0.35
OT	13	1.87	0.19
WA	15	4.94	0.86

Appendix 4 Table 2: Summary of derived oceanographic variables from CTD casts used to describe the characteristics of the ten survey areas.

Depth_CMAX

Area	N	Mean	SE
AK	30.00	8.33	0.44
BF	14.00	8.00	0.83
DA	18.00	14.44	1.32
FB	20.00	14.00	1.04
LB	18.00	12.00	0.83
LL	21.00	7.95	0.79
LY	15.00	4.87	0.45
ME	22.00	5.50	0.39
OT	13.00	15.15	1.15
WA	15.00	7.20	0.60

Thermocline depth

Area	N	Mean	SE
AK	30	7.73	0.54
BF	14	7.71	0.96
DA	18	13.56	1.78
FB	20	8.90	1.38
LB	18	9.89	1.03
LL	21	4.95	0.71
LY	15	6.40	0.92
ME	22	5.91	0.64
OT	13	12.31	1.45
WA	15	4.93	0.85

Thermocline strength

Area	N	Mean	SE
AK	30.00	0.67	0.13
BF	14.00	0.45	0.10
DA	18.00	0.41	0.07
FB	20.00	0.30	0.07
LB	18.00	0.34	0.08
LL	21.00	0.17	0.05
LY	15.00	0.30	0.08
ME	22.00	0.25	0.05
OT	13.00	0.33	0.12
WA	15.00	0.54	0.15

Temp_stratification

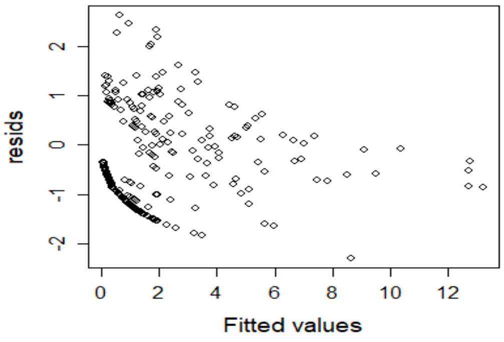
Area	N	Mean	SE
AK	30	1.24	0.23
BF	14	1.03	0.34
DA	18	1.32	0.29
FB	20	0.81	0.24
LB	18	1.03	0.30
LL	21	0.31	0.10
LY	15	0.68	0.24
ME	22	0.60	0.15
OT	13	1.05	0.37
WA	15	0.98	0.27

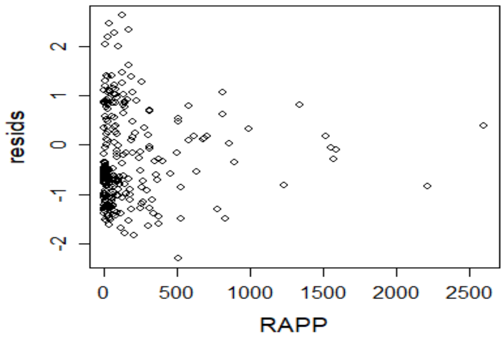
Sal_stratification

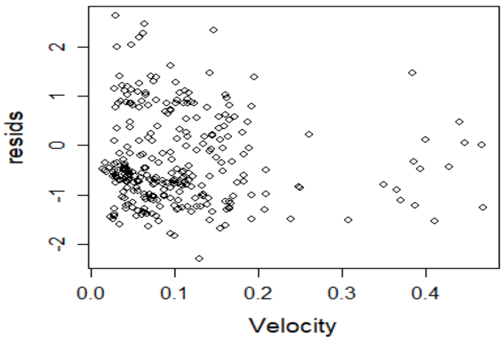
Area	N	Mean	SD	SE
LL	21.00	0.07	0.09	0.02
ME	22.00	0.13	0.17	0.04
LY	15.00	0.15	0.14	0.04
OT	13.00	0.16	0.21	0.06
WA	15.00	0.20	0.17	0.04
FB	20.00	0.20	0.25	0.06
AK	30.00	0.26	0.24	0.04
DA	18.00	0.42	0.55	0.13
LB	18.00	0.46	0.70	0.16
BF	14.00	0.58	0.63	0.17

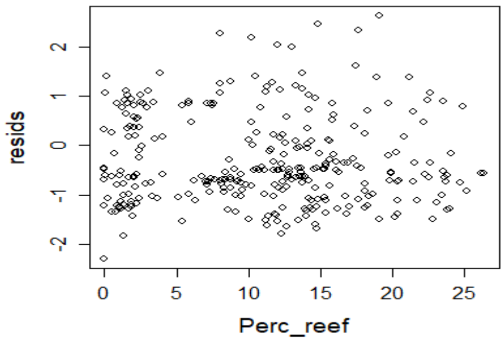
Appendix 5: Model diagnostics for GAMs.

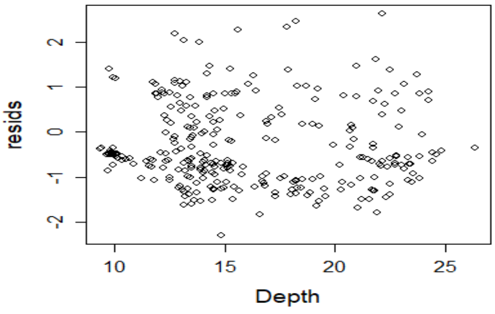
Full-dataset

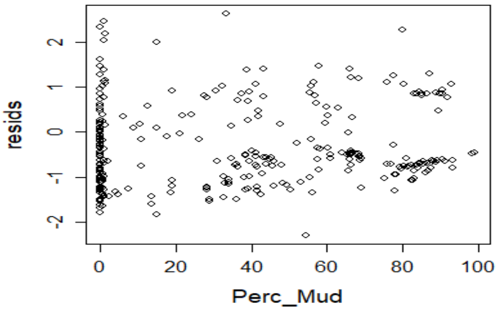


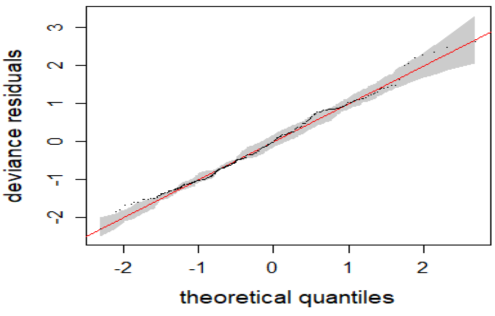












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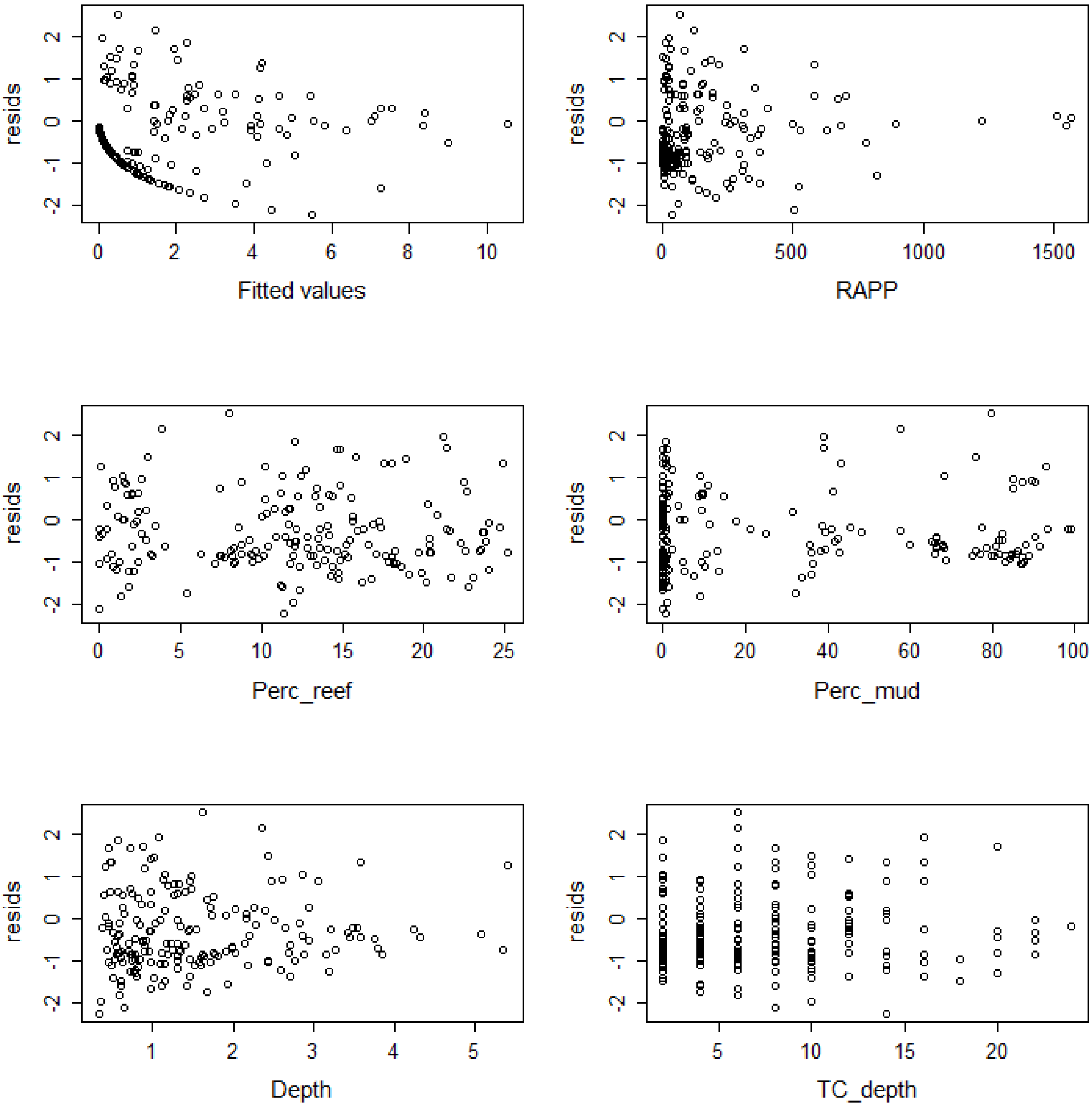
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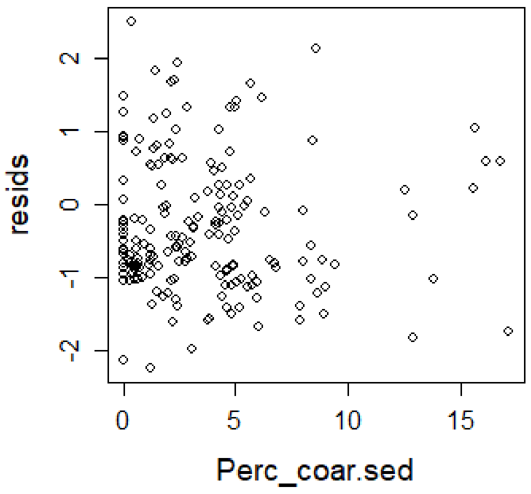
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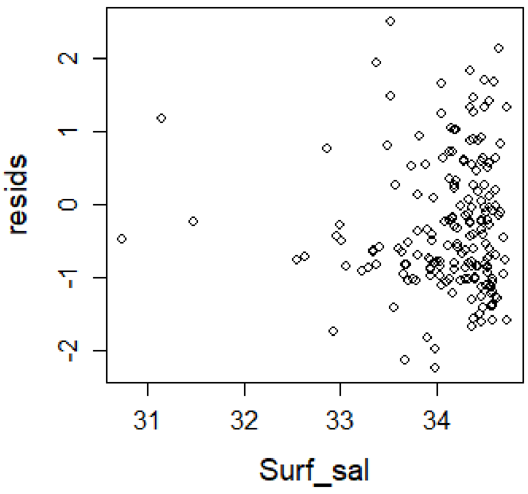
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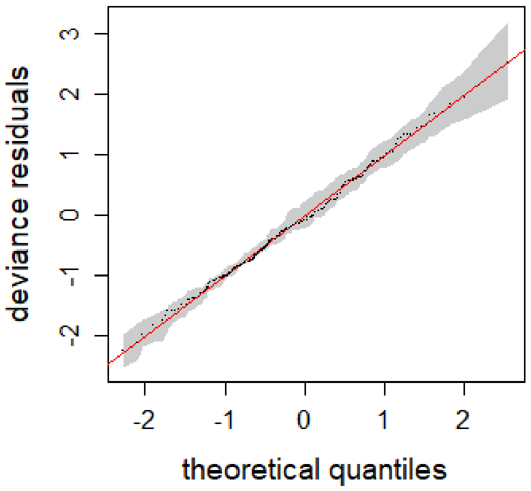
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