Fine-scale foraging habitat and behavioural responses of pygmy blue whales

by

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BSc (Hons)

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The research carried out for this thesis was only achieved through the efforts and contributions of many individuals and organisations. Specific collaborations are first mentioned, followed by some examples of where and how the research was communicated. Personal acknowledgements are then expressed.

STUDY COLLABORATIONS

This study, and the thesis outcomes, form part of a wider research partnership. It seemed necessary to state the specific contributions of myself and my collaborators, who are expected to be co-authors in the published outputs.

The study of pygmy blue whales off the southern Australian coast has been undertaken through a partnership between Deakin University and the Blue Whale Study Inc. (BWS), a not-for-profit research organisation directed by Dr Peter Gill and myself. Dr Peter Gill's thesis ('*Ecological linkages in the Bonney Upwelling blue whale feeding area*', Gill 2004) was the first study of these whales in Australian waters with a focus on broad-scale linkages between whale distribution and physical habitat. The present study detailed in this thesis was designed to segue from Dr Gill's broad-scale study, with a goal to bring a critical threshold of knowledge together to develop predictive whale-distribution models in the future, and that can make significant contributions to the conservation and management of endangered pygmy blue whales. Partnerships with the BWS extend to a number of other research and industry organisations, with considerable published and unpublished outputs relating to blue whale scientific, conservation and management information since 2000 (some of which are listed below).

My own contributions (MM) to this thesis have involved all aspects of the research. I have led, under most circumstances, the initiation, planning, research design, funding, field logistics, and the collection, processing, analyses and interpretation of research data. I have also instigated research partnerships between Deakin University and the BWS, South Australian Research and Development Institute (SARDI) and Myriax Pty Ltd (Myriax). I have completed all of the writing contained within this thesis, with critical advice from a range of people (outlined below and in the Personal Acknowledgements). The significant contributions of collaborators are listed below.

Dr Alecia Bellgrove (Principal Supervisor, Deakin University): AB worked closely with MM throughout her candidature on all aspects of study, including the study design, and

data analyses and interpretation. AB was also the Principal Investigator for some of the successful research grants that supported the study. AB has been the main writing advisor and thesis reviewer.

Prof. Gerry Quinn (Associate Supervisor, Deakin University): GQ's contribution has been a significant advisor in the analysis phases of the study, and a reviewer.

Dr Toby Jarvis (Research Supervisor, Myriax): TJ has been the main advisor helping MM to process the large amounts of complex hydroacoustic data collected for the study. TJ specifically developed processing templates within Echoview software, and helped MM extract the acoustic data at appropriate temporal and spatial scales. TJ worked closely with MM in discussing conceptual and interpretative ideas to bring the thesis together as a whole. TJ reviewed the whole thesis.

Dr Pete Gill (BWS): PG assisted with the initial project conception and funding, and has generally assisted with field logistics and data collection. PG also provided the broad general knowledge of the upwelling system and blue whales needed to plan and sample appropriately. PG also reviewed some sections of the thesis.

Dr Maria Garcia (Centre for Whale Research, WA): MG assisted MM in general data collection and processing of plankton samples. MG also helped skill MM in software and analyses, particularly to organise and process the integrated data presented in the thesis in an appropriate way. MG also provided conceptual and interpretative advice when dealing with these complex data and analyses. MG reviewed most of the thesis.

Dr Rebecca Pirzl: RP has been a general advisor regarding thesis purpose, structure and continuity. RP particularly advised on model structure in Chapter 3, and reviewed and copy-edited the whole thesis (an unenviable task).

Dr Paul van Ruth (SARDI): PvR has been the key advisor on biological oceanography for Chapter 3. PvR provided critical comment on the Pelagic Habitat Conceptual Model and reviewed Chapter 3.

STUDY EXPOSURE

Due to the iconic nature and endangered status of blue whales, there has been significant interest in the study and the study findings by various government departments, NGOs, industry and the general public. As such, MM gave advice, contributed information and wrote a range of technical and popular material. Communication exposure included: international, national and local radio and television interviews; popular and specialist magazine articles; a major ABC Natural

History Unit production called "The Big Blue"; guest lecturing for Universities, local and regional community talks; and oral and poster presentations at international and national conferences. Specific reporting requirements were also necessary for studying an endangered species. More formal reporting and advising included to: international and national bodies (e.g. International Whaling Commission and its Scientific Committee), Deakin University Ethics Committee, non-government conservation organisations, industry (to assist sensitive management of their activities with regard to whales), and Commonwealth and State Government legislative processes (e.g. recovery plans, marine protected area plans, industry referrals, and collection of scientific data from dead stranded animals). MM, in partnership with blue whale research colleagues, also organised a Southern Hemisphere Blue Whale Workshop. Some examples of where the study outcomes have been reported are listed below:

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I have the very great fortune in being surrounded by the most wonderful and supportive family and friends. I give my enduring appreciation and gratitude to you all. I would particularly like to mention my extended family (there are too many of you to mention you all by name and you are all special), my whale colleagues (above), Pep Rea and family, Mary Anne Lea, Lou Billet, Cindy Hull and family, Helena Psotova, Jan Barton and Adam Pope, Molly Reynolds and Rolf de Heer, Susie Raymond and family, Susie Lyons, Kieran Lawton, Snake, other special friends in Tassie who have particularly provided support to Kiwi, and the Cudgee Community. Also to the wonderful staff at Sherwood Park Daycare Centre who have done a most superb job in helping Kiwi and I raise our kids. All of you have kept the faith, even though you think I'm completely bonkers, and found your own special way to give direct support, or channel energy and good wishes to support the soul. You are all big stars!

To my mum, Helena, and Dad, Jo, I will be forever indebted. Your journey with me and support has been from the very beginning. You have given me much unconditional support in so many ways that I would run out of page to list them. I am truly lucky to have such wonderful parents and inspirers in my life. Thank you.

I also recognise that I need to acknowledge myself, as it must have been those wild visions as a child that allowed me to pursue this endeavour with all the grit and determination that only comes from people slightly mad and obsessed. It was this doggedness that made me continue in times when all seemed lost and completely well above my means. The words of T. S. Eliot ring very true for me … "If you aren't in over your head, how do you know how tall you are?".

It is with the deepest gratitude and affection that I owe my family, Kiwi, Molly and Luke. They have been a rock to keep me grounded when my head was in the clouds, and a nurturing cradle to heal me of the cuts and bruises sustained from a long haul. They have all sacrificed much to enable me to complete this mission. Thankfully, they share my passion for whales and all things wild, and I hope my children will continue that passion in their own way and spread the word.

I dedicate this thesis to blue whales

To their recovery, and

To their special place in the ocean

ABSTRACT

Pelagic habitats support the largest and most threatened animals on the planet, where these top predators perform one of the most essential functions of life, to find enough food to survive and thrive. These predators are vulnerable to changes in their foraging habitat, particularly prey availability. The availability of prey (krill) is arguably the most important factor determining individual and population distribution and growth of any predator. Assessing finescale responses by large predators to their foraging habitat will help explain their broader patterns of population abundance and range changes.

Pygmy blue whales (*Balaenoptera musculus brevicauda*) that migrate to upwelling-influenced coastal waters off southern Australia, recognised as one of the largest foraging grounds in the Southern Hemisphere, are endangered and show no measurable signs of recovery. The central aim of this study was to quantify prey availability, and habitat factors influencing prey, at the fine temporal and spatial scales relevant to the foraging and feeding of the world's largest planktivore. The study occurred in a representative area of the Bonney Upwelling, centrally placed in the world's only northern-boundary current system. This upwelling region was expected to provide consistently profitable foraging for the Australian-Indian Ocean population of pygmy blue whales. Pygmy blue whale prey was predicted to be more abundant in the mid-shelf, since this is where the highest primary production was expected to occur. Pygmy blue whale distribution and foraging behaviour were predicted to closely match prey availability.

PERMANOVA analyses of prey aggregation descriptors (derived from high-resolution hydroacoustic data) were used to characterise the prey field. The observed patterns of prey were explained through conceptual and empirical models of their relationships to habitat features. Pygmy blue whales were followed, and their behavioural responses to prey and other habitat factors were measured and compared to available habitat elsewhere on the shelf.

The study area was found to have abundance of neritic aggregations comparable at times to the most productive ocean regions in the world (e.g. eastern-boundary current systems). Patchiness was observed in prey distribution and abundance over time (years) and space (location on the shelf and depth in the water column). As predicted, the areas occupied by pygmy blue whales were found to be areas of highest prey abundance (including maximum weight densities of krill of 1.64 kg m^{-3}), with the location of upwelled water, access to nutrients and surface phytoplankton more important factors influencing prey availability. At the broad scale, pygmy blue whale

occurrence and movement did not closely reflect the distribution and abundance of their prey; it was at the fine scale that this match was observed. The high-resolution at which whale surface movements were recorded was pivotal in capturing a range of movements and spatial patterns not previously described for blue whales, but predicted from theoretical studies to be important for maximising search efficiency.

The findings of fine-scale interactions between pygmy blue whales and their habitat reported in this thesis, along with the supporting conceptual models and empirical data, will allow rapid assessments of whether a given area is profitable for these whales. This information is critical to effective management of interactions between blue whales and human activities, and to forecasting the effects of changes in foraging habitat in response to longer-term climate change.

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LIST OF COMMON TERMS

1-step upwelling – describes a situation where upwelled water comes directly onto a narrow shelf, < 25-km wide

Access to nutrients – a vertical descriptor of thermal structure, used in this study, calculated from the positional relationship between the upwelled-water front and the mixed-layer depth (Chapter 3, Section 3.2.3)

Acoustic biomass (of aggregations) – the sum of the nautical area backscattering coefficient (ΣNASC, Chapter 2, Appendix, 2, Equation 2) of each proportion of an aggregation within an interval

Aggregation – a contiguous group of corrected acoustic samples (and hence assumed to be of biological origin, Chapter 2, Section 2.2.4)

Area-restricted search – defined by Benhamou (1992) as increasing the search effort after detecting a prey item because of the high probability of encountering other items nearby.

Circular excursions - highly tortuous and roughly circular sections of track in milling movements (Chapter 4, Section 4.3.2)

Counts (of aggregations) – the total number of whole and part aggregations within an interval (Chapter 2, Section 2.2.4)

Demersal - depth strata with mean depth of aggregations within 10 m of the ocean floor (Chapter 2, Section 2.2.5)

Echogram – a visual representation of an acoustic variable

Ekman transport - 90 ° net transport of the surface layer (depth to which wind penetrates) due to wind forcing (http://en.wikipedia.org/wiki/Ekman_transport)

Extensive movement - oriented or ranging/relocation behaviour that matched the movement mode criteria developed in Chapter 4, Section 4.2.2

High-S_v (aggregation) – an aggregation detected on an echogram with sample S_v values ≥ -70 dB (Chapter 2, Section 2.2.4)

Intensive movement - area-restricted search movements that matched the movement mode criteria developed in Chapter 4, Section 4.2.2

Interval - a section of cruise track 1 km in length, calculated as the cumulative ping-to-ping straight-line distance using the WGS84 projection for the shape of the Earth (Chapter 2, Section 2.2.4)

Layer – a partially-transected aggregation, i.e. where the first and/or last pings of the aggregation coincide with the extent of the transect (Chapter 2, Section 2.2.4, and see 'school' below)

Low-S_v (aggregation) – an aggregation detected on an echogram with sample S_v values from -89 to < -70 dB (Chapter 2, Section 2.2.4)

Midwater - depth strata with mean depth of aggregations from 10 m depth to 10 m from the ocean floor (Chapter 2, Section 2.2.5)

Milling – area-restricted search movements that matched the movement mode criteria developed in Chapter 4, Section 4.2.2

Neritic – coastal waters extending from the low tide mark to the edge of the continental shelf

Non-surface-feeding interval - all intervals in both the survey and track data in which there were no whales feeding at the surface (Chapter 4, Section 4.2.5)

Non-whale interval - intervals not associated to whale sightings, from survey data (Chapter 4, Section 4.2.5)

Optimal environmental window – a situation where the effects of limiting factors are minimised (Figure 3 in Cury & Roy 1989)

Patch – an aggregation of prey (i.e. areas where the local resource (prey) density is higher than the mean overall resource (prey) density, (Benhamou 1992). Where specified, refers to aggregations of krill 'swarms' that occur at spatial scales of 1 to 100s kilometres, from days to months (Figure 2-1; Murphy et al. 1988, Wiens 1989)

Percentage occupation (of aggregations) – for each interval, the proportion of the total number of acoustic samples that were in aggregations (Echoview: ΣSamples_In_Domain) relative to the total number of acoustic samples in the interval (Echoview: C_good_samples + C_no_data_samples), expressed as a percentage (Chapter 2, Section 2.2.4)

Percentage upwelled-water - a vertical descriptor of thermal structure, calculated from the difference in the depths of each water column position and the depth of the upwelled-water front (i.e. 14.7 °C), as a percentage (Chapter 3, Section 3.2.3)

Profitable (prey, area) - provides high energy returns in terms of food resources, greater abundance of prey and more prey patches (Barraquand & Benhamou 2008)

School – a completely-transected aggregation, i.e. where the first and last pings of the aggregation lie completely within the extent of the transect. An aggregation was defined as a polygon in Echoview's 'schools detection algorithm' (Chapter 2, Section 2.2.4, and see 'layer' above)

Surface – depth strata with mean depth of aggregations within 10 m of the sea surface (Chapter 2, Section 2.2.5)

Surface event - period of time a whale surfaced, from track data (Chapter 4, Section 4.2.2)

Surface-feeding interval - intervals where whales were observed to be surface feeding, from survey and track data (Chapter 4, Section 4.2.5)

Surface-habitat descriptor – surface descriptor used in empirical model analyses, including sea surface temperature, surface chlorophyll-a and alongshore wind-stress Chapter 2, Section 3.2.2)

Surface sequence - between consecutive surface events (particularly between the terminal position prior to a dive), from track data (Chapter 4, Section 4.2.2)

Swarm - an aggregation of krill that occurs at a spatial scale of 1 to 100s metres, and a temporal scale of hours to days (Chapter 2, Figure 2-1; Murphy et al. 1988)

Vertical-habitat descriptor – vertical descriptors of ocean structure derived from vertical profiling data, including 'percentage upwelled-water' and 'access to nutrients'

Whale interval - intervals associated with whale sightings, from survey data (Chapter 4, Section 4.2.5)

LIST OF ABBREVIATIONS

AIC – Akaike's Information Criterion (Chapter 3, Section 3.2.3)

BIC - Bayesian Information Criterion (Chapter 3, Section 3.2.3)

Chl-*a* – surface chlorophyll-*a* (Chapter 3, Section 3.2.2)

CTD – conductivity-temperature-depth (Chapter 2, Section 2.2.4 and Chapter 3, Section 3.2.2)

ENSO – El Niño-Southern Oscillation (Chapter 2, Section 2.4.2)

ER – encounter rate (Chapter 4, Section 4.2.1)

GAB – Great Australian Bight (Chapter 2, Section 2.1, Chapter 3, Section 3.1)

GLM – Generalised linear model (Chapter 3, Section 3.2.3)

MLD – Mixed-layer depth (Chapter 3, Section 3.2.2)

ΣNASC – sum of the nautical area scattering coefficient (Chapter 2, Section 2.2.4, Table 2-2 and Appendix 2, Equation 2)

$N_{ext}ND$ – Next neighbour distance (Chapter 2, Section 2.2.4)

SST – sea surface temperature (Chapter 3, Section 3.2.2)

S_v – (Mean) volume backscattering coefficient (Chapter 2, Section 2.2.4, Table 2-2 and Appendix 2, Equation 1)

PHCM – Pelagic Habitat Conceptual Model (Chapter 3, Section 3.2.2)

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Southern Ocean

Chorus 3

Margaret Scott[1]

The fishing fleet sways in gold on the morning ocean.

The wind comes fresh from the continent of ice.

Beneath the waves silver curtains of fish,

Shells, stars, the shadows of predators,

Weave through the feathered bones of long-drowned ships.

Travel the whale-road out to the far horizon

Where dolphins plunge and the albatross swings high.

Enter the thread cross-hatching the gray-green wave,

The dazzle of anchovy swarms, the seal's swerve.

Rise from the depths of the past into slanting light.

Move to your neighbour's step, turn in the stranger's spirit

As the gull veers in the blue.

Pray for the ousting of greed and the self's dead eye.

Ride on the life-bearing currents of ocean sky into coming day …

08/2013
Molly
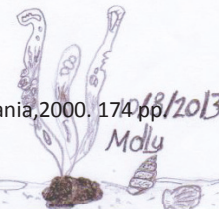
1. GENERAL INTRODUCTION AND THESIS OVERVIEW

1.1. GENERAL INTRODUCTION

Animals use foraging habitats to perform one of the most essential functions of life, to find enough food to survive and thrive. The trend of increasing degradation of marine habitats is recognised as a global problem, and is occurring at rates beyond those predicted (Jackson 2008). These changes are profoundly altering community structure, biodiversity, biophysical interactions and ecosystem resilience, and in turn the considerable ecosystem services that habitats provide (Lotze et al. 2006, Halpern et al. 2008, Jackson 2010, Doney et al. 2012). Marine foraging habitats of large predators are typically characterised by ecological processes that enhance primary productivity, with cascading effects through the food web (Cury et al. 2000, Ware & Thomson 2005, Benoit-Bird & McManus 2012). Ocean habitats provide system-wide abundant food resources, albeit periodically, and are shaped by global, regional and local weather and ocean forcing.

"*Vast movements of ocean and air currents bring dramatic change throughout the year. And in a few special places, these seasonal changes create some of the greatest wildlife spectacles on Earth*"(Attenborough 2009).

Pelagic habitats, where environmental conditions are suitable for biota to aggregate are useful areas for ecologists to investigate the ecosystem-level effects of changing resource availability. Quantifying whole-of-ecosystem dynamics is difficult, and many studies use selected species as representative of trophic groups. This approach allows these species to be used as indicators of how well an ecosystem is managing under change, and under the processes that may shift stability (Cury et al. 2000, Atkinson et al. 2004, Baum & Worm 2009, Newson et al. 2009, Letessier et al. 2011, Doney et al. 2012). Pelagic habitats support the largest and most threatened animals on the planet, and conservation of those vulnerable populations is pivotal in conserving their habitats (Hooker 1999, Redfern et al. 2006, Azzellino et al. 2012). Human use of the oceans is increasing and moving from coastal to open-ocean domains, areas where knowledge is fragmented and hard to acquire. The traditional approach to conserving biodiversity is through systems of protected areas (e.g. marine protected areas, MPAs). Management paradigms under MPA systems are limited in the extent to which they can protect pelagic and far-ranging predators where critical resources, such as prey, move (Humphries et al. 2010, Bull et al. 2013). Knowledge of the important mechanisms driving pelagic predator distribution and abundance has been acquired by using robust

empirical datasets, and has been pivotal in leading to positive conservation outcomes for pelagic communities (Berman-Kowalewski et al. 2010, Redfern et al. 2013).

Current approaches for understanding aquatic domains now include regional ecosystem models. Such models are generally purpose-built for individual systems or management needs (e.g. Botsford et al. 2003, Fulton et al. 2007, Bulman et al. 2011, Goldsworthy et al. 2013). However, their sophistication is allowing them to be used in other aquatic domains, and to incorporate a wide spectrum of system interactions. Model components include interactions between trophic levels and physical habitat, with increasing complexity and resolution of scale (Fairweather & Lester 2010, Lambert et al. 2011). Some models have also been designed to elucidate foraging responses of predators; these are parameterised for particular scenarios according to interactions between the 'preyscape', physical habitat and predators (Wiedenmann et al. 2011, Bestley et al. 2013). Relationships are complex, and often some of the key predator-prey interactions used in models have to speculated where no empirical data exists. Predictive models and the specific scenarios they test can be extremely useful management tools for the long-term conservation of species (Louzao et al. 2011, Azzellino et al. 2012). Making these model predictions realistic and relevant, and useful as forecasting tools for 'novel' observations such as those that may eventuate from climate change, will require high quality empirical data. Currently the highest resolution data to quantify water column fauna is collected using acoustic techniques. Measurements of underwater acoustic echoes have long been used to assess composition, biomass and behaviour of zooplankton and fish populations (Petitgas et al. 2001, Simmonds & MacLennan 2005). Hydroacoustic data can be collected over very fine- and broad- temporal and spatial scales (Brierley et al. 1998, Petitgas et al. 2001, Lawson et al. 2008b). Appropriate acoustic hardware, collection and processing settings, and ground-truthing, can provide rapid assessments of fauna throughout the water column (Simmonds & MacLennan 2005).

Many large marine predators find food using a diverse range of horizontal and vertical search patterns, designed to provide optimal foraging paths within their patchy habitats (Hays et al. 2006, Weimerskirch 2007, Sims et al. 2008, Fauchald 2009, Hays et al. 2012). Search patterns follow general rules, as described by foraging theory (Stephens & Krebs 1986, Stephens et al. 2007), with more search effort where prey is most available and profitable. This strategy provides energy benefits and, ultimately, reproductive and survival benefits (Weimerskirch 2007, Barraquand & Benhamou 2008, Beyer et al. 2010, Santora et al. 2011a).

CHAPTER 1

Horizontal movements of predators occur at distinct spatial scales. Fine-scale movements influence broad-scale movements and reflect the hierarchical regional- and local-dynamics that shape prey resources (Murphy et al. 1988, Kotliar & Wiens 1990, Weimerskirch 2007). Predator movement and distribution has been linked to the horizontal and vertical patchiness and density of their food (McClatchie et al. 1989, Piatt & Methven 1992, Sims & Quayle 1998, Baumgartner & Mate 2003, Friedlaender et al. 2006, Fauchald 2009, Hazen et al. 2009, Almenar et al. 2013, Benoit-Bird et al. 2013b). Predator-prey interactions can be dependent on a host of factors such as the distribution, density and behaviour of both predators and prey. For example, prey thresholds of predators (the point at which a particular predator behaviour is elicited) can change contingent upon prey availability (Piatt & Methven 1992, Bowers & Matter 1997, Sims 1999, Fauchald et al. 2000, Baumgartner & Mate 2003, Simon et al. 2009). Incorporating fine-scale interactions into models provides important context for explaining predator-prey relationships (Beyer et al. 2010, Azzellino et al. 2012, Pendleton et al. 2012).

Plankton is a dynamic and abundant food resource that typically aggregates, and can dominate marine ecosystems. Zooplankton flourish in the most productive regions of ocean such as upwelling-influenced ecosystems (e.g. boundary current systems). Zooplankton are also characterised by temporal variability in distribution and abundance over decades, years and within-seasons as a consequence of ocean-basin, regional and local weather and ocean forcing (Edwards et al. 2000, Napp et al. 2002, Hays et al. 2005, Coyle et al. 2008, Baird et al. 2011). The diversity, motility and aggregating properties of zooplankton are exploited by large ectothermic and endothermic planktivores that show convergent evolution in their movement and feeding strategies (Gleiss et al. 2011, Potvin et al. 2012). Ram feeders (represented by basking sharks (*Cetorhinus maximus*), right whales (*Eubaleana spp.*) and bowhead whales (*Balaena mysticetus*)) typically feed on diffuse layers of less agile microzooplankton (Sims & Quayle 1998, Sims 1999, Baumgartner & Mate 2003, Simon et al. 2009). Lunge feeders (represented by fin whales (*Balaenoptera physalus*) and blue whales (*Balaenoptera musculus*)), have adopted a technique (although energy-exacting) that enables a large transfer of prey and energy in single mouthfuls (Goldbogen et al. 2006, Goldbogen et al. 2012, Goldbogen et al. 2013b). Lunge feeders therefore select for very dense aggregations of agile meso- and macrozooplankton, and move rapidly between prey patches. There are very few studies that have quantified the fine-scale interactions between planktivores and their prey (e.g. Sims & Quayle 1998, Sims 1999, Baumgartner et al. 2003, Baumgartner & Mate 2003, Croll et al. 2005). An understanding of these interactions is fundamental to managing the recovery of iconic and vulnerable marine predators, some being the largest predators on Earth,

particularly as their habitats undergo influences from large-scale climate and ocean change (Hays et al. 2005). Finding measures that represent foraging habitat structure and availability of these top predators, and characterising their behavioural responses to changes to this habitat, will help explain broader patterns of their population abundance and range changes.

Blue whales, with their voluminous size and huge energy needs, range constantly across vast areas of ocean, moving annually between polar/temperate and tropical waters to find profitable prey patches (Stafford et al. 1999, Acevedo-Gutiérrez et al. 2002, Croll et al. 2005, Bailey et al. 2010, Wiedenmann et al. 2011, Goldbogen et al. 2012, Goldbogen et al. 2013b). There is some evidence that blue whale movement patterns and the organisation of their prey are linked hierarchically (Bailey et al. 2010, Doniol-Valcroze et al. 2012). This is demonstrated in Figure 1-1, which shows that the scale of blue whale movement matches the spatial scale at which krill aggregate. Blue whale-krill interactions make a good case study for understanding planktivore habitat selection and scales of predator-prey interactions.

Knowledge of blue whale habitat suitability and selection varies from advanced in some populations, such as the California Current and the St. Lawrence Estuary, to low in others, such as Southern Hemisphere populations. Nevertheless, studies consistently show that the movement and prey choices of blue whales are dictated by attempts to maximise their foraging efficiencies (Croll et al. 1998, Croll et al. 2001a, Croll et al. 2001b, Acevedo-Gutiérrez et al. 2002, Croll et al. 2005, Calambokidis et al. 2007, Doniol-Valcroze et al. 2011, Goldbogen et al. 2011, Goldbogen et al. 2012, Potvin et al. 2012, Goldbogen et al. 2013b, Shadwick et al. 2013). The success of blue whales in finding profitable prey has only been effectively measured in a few studies, and these demonstrated the highly variable nature of blue whale prey (Schoenherr 1991, Fiedler et al. 1998, Croll et al. 2001b, Croll et al. 2005). Krill may change their range extents, abundance and community structure over days, months, seasons and decades (e.g. Hewitt et al. 2003, Atkinson et al. 2004, Cox et al. 2011, Santora et al. 2012); this variability can have far-reaching population effects on their predators. Post-whaling populations of blue whales exhibit substantial range change, attributable to ocean basin-scale regime shifts in productivity (i.e. pronounced and prolonged climate-linked changes in biological systems; Benson & Trites 2002, Hays et al. 2005, Calambokidis et al. 2009). These broad-scale patterns are integrally linked to krill availability and fine-scale behavioural responses of blue whales, and again highlight the critical value of baseline data at a range of scales from which future change can be measured.

CHAPTER 1

Blue whale movements   **Krill organisation**

Fine scale
Inter-swarm movements
within a patch

PATCH

Meso scale
Inter-patch movements
within a concentration
(foraging area)

CONCENTRATION

Broad scale
Inter-concentration
movements within a
population

POPULATION
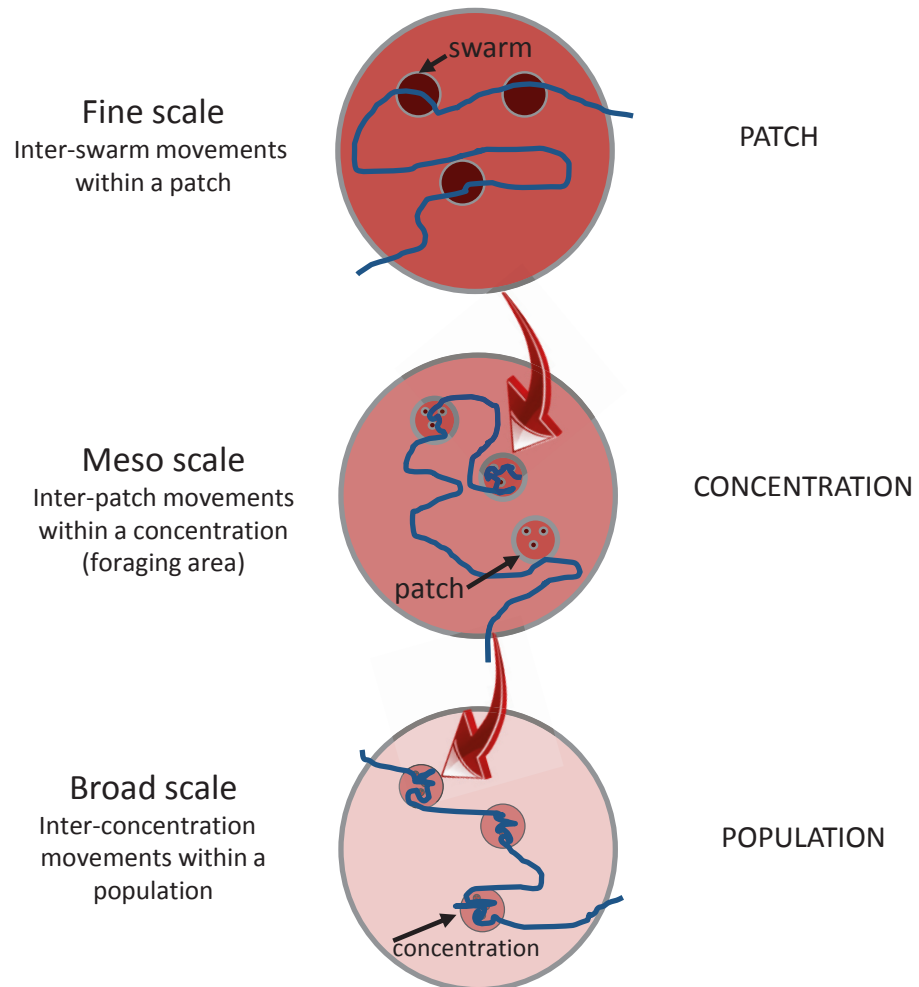
Figure 1-1. The hierarchy of blue whale movements as they relate to krill distribution from fine-scale inter-swarm movements within a patch (dark red), to meso-scale inter-patch movements within krill concentrations (medium red), and to broad-scale inter-foraging area movements across the blue whale's home range (adapted from Murphy et al. 1988, Kotliar & Wiens 1990, Weimerskirch 2007, and Fauchald 2009 Figure 4).

The goal of this study was to better understand the fine-scale nature of the foraging habitat and behavioural responses of a lunge-feeding planktivorous predator, the pygmy blue whale (one of two recognised subspecies in the Southern Hemisphere, putatively *B. m. brevicauda*; Ichihara 1966, Attard et al. 2010). It was predicted that foraging habitat would provide a variable resource, and that prey would be profitable in areas where optimal sets of ocean processes led to high nutrient and hence high

5

phytoplankton productivity. It was also predicted that the scale of whale behaviour would match the scale of prey availability, and that whales that were feeding would be in the most profitable patches. Once profitable habitat features are quantified for these endangered whales, the ensuing knowledge can be used to manage human activities and their effect on foraging areas.

The foraging habitat of pygmy blue whales off southern Australia was chosen as a model system to conduct fine-scale predator-prey research. The region is characterised by a narrow shelf and seasonal coastal upwelling. It was predicted to be a highly-productive foraging habitat for pygmy blue whales due to the known regular occurrence of these whales foraging and feeding in the area (Gill et al. 2011). Previous studies of the influence of environmental factors on pygmy blue whale distribution, surveyed by air from the Great Australian Bight to Bass Strait over six upwelling seasons, found 48% of sightings were associated with surface krill swarms and 62% of sightings in one area of this region were best explained by cooler sea surface temperature (Gill et al. 2011). Moreover, the study area provided convenient accessibility to the continental shelf to test predictions that pygmy blue whales and profitable feeding areas would be in the middle of the shelf. The study was conducted over three feeding seasons (austral spring to autumn) to investigate the interannual variability in the system, and how this might affect pygmy blue whale occurrence. The system studied also offered an opportunity to look at the relative profitability of krill as prey (Jarman et al. 2002, Gill 2004) through the water column, due to the regular (and generally unusual) habit of the indigenous krill, *Nyctiphanes australis*, of forming both diurnal and nocturnal surface aggregations (Blackburn 1980, Young et al. 1993, Gill 2004). Multidisciplinary field data and remote-sensed data were used to better understand the mechanistic links between pygmy blue whales and their habitat.

1.2.   RESEARCH APPROACH AND THESIS ARRANGEMENT

This study characterised the fine-scale foraging habitat and behavioural responses of a large marine planktivorous predator, the pygmy blue whale. A bottom-up approach was taken: a habitat framework from prey to predator was built, with a focus on the fine-scale interactions that occur between the two trophic groups, and the ocean processes that shape those interactions. The first step was to characterise the prey field of pygmy blue whales in the context of how that resource was structured (size, shape and density), and how available it was within the foraging ground. The fine-scale patterns observed in prey distribution and abundance were explained by investigating the influences of habitat structures that operated on the shelf off southern Australia during the upwelling period. Predator habitat selection was described according to the

prey and habitat structures, and how they associated with predator occurrence, horizontal movement and feeding events.

The fine-scale nature of a marine foraging habitat and the complexity of predator-prey interactions were demonstrated with the largest planktivore, the pygmy blue whale, and its prey (krill) in a coastal upwelling system. The investigations were structured around the suite of conceptual frameworks highlighted in the General Introduction (Section 1.1). These frameworks form the basis of predictions about how the characteristics of the foraging habitat of pygmy blue whales determine whale foraging and feeding responses.

Chapter 2 ('*Acoustic characterisation of neritic aggregations in a pygmy blue whale foraging ground, southern Australia*') investigates the temporal and spatial patterns of neritic faunal aggregations that constitute the prey of pygmy blue whales. No study has previously documented the neritic fauna of this shelf region, and high-resolution hydroacoustic data were collected during small-vessel surveys in order to quantify where aggregations were distributed and how they were structured (size, shape, density). Predictions were tested about when and where prey resources would be profitable for whales. More specifically, the study examined how prey abundance and spatial organisation varied temporally (interannually) and spatially (across the shelf and through the water column). The observed patterns of prey were explained in the context of their suitability as a food resource for pygmy blue whales (high-energy users).

Chapter 3 ('*Influences of fine-scale upwelling habitat structure on aggregating neritic macrozooplankton and fish*') employs a conceptual model to establish the ocean processes expected to operate in this northern-boundary current system (particularly the narrow-shelf region). Empirical models were used to determine which fine-scale habitat structures were most influential on the distribution and abundance of aggregating neritic prey. The same temporal and spatial patterns investigated in Chapter 2 were considered in the model structures.

Although knowledge of the broad-scale horizontal movement patterns and vertical dive behaviour of blue whales is well advanced for some ocean regions, there has been varying success in explaining behaviour with respect to habitat. Few studies have investigated blue whale-prey interactions at the scale of prey 'swarms'; even rarer are studies in regions where surface swarms make up a potentially important component of this resource. No study has investigated the integrated relationships between the combination of prey availability and whale occurrence, fine-scale horizontal movement, and surface feeding events. Chapter 4 ('*Fine-scale habitat selection and behaviour of a*

constant forager') uses simple analytical techniques, drawing on the prey and habitat patterns detailed in Chapters 2 and 3, to test the prediction that pygmy blue whales occupy profitable areas in terms of food resources. This was approached in two ways: 1) by comparing the habitat associated with whale occurrences to overall habitat availability, and 2) by comparing the habitat selected by whales in different movement modes and feeding states.

The study used integrated real-time data and remotely-sensed data to build a framework to describe the foraging habitat and behaviour of pygmy blue whales. The three data chapters of the thesis (Chapters 2 to 4) are interlinked through their concepts and methodology, but have been written as independent draft journal papers. Where possible, repetition has been avoided to allow the story to flow. The General Discussion and Conclusions (Chapter 5) summarise the key findings of the thesis and their significance in the context of the broader conceptual framework and aims stated in the General Introduction (Chapter 1). Conclusions are drawn in relation to the contribution of the study's findings to foraging habitat and movement models of blue whales, and to conservation management outcomes.

2. ACOUSTIC CHARACTERISATION OF NERITIC FAUNAL AGGREGATIONS IN A PYGMY BLUE WHALE FORAGING GROUND, SOUTHERN AUSTRALIA

2.1. INTRODUCTION

The coastal waters of southern Australia hosts one of the largest documented feeding grounds of endangered pygmy blue whales (one of two recognised subspecies of blue whales in the Southern Hemisphere, putatively *Balaenoptera musculus brevicauda*; Ichihara 1966, Attard et al. 2010) . This feeding ground extends over ~38,000 km^2 from the Great Australian Bight (GAB) to Bass Strait and western Tasmania (Gill et al. 2011), and is one of 18 consistently used blue whale feeding grounds worldwide (Branch et al. 2007). It is characterised by the most extensive region of seasonal coastal upwelling off Australia, with the most prominent known as the Bonney Upwelling (Lewis 1981, Herzfeld 1997, Herzfeld & Tomczak 1997, 1999, Middleton & Cirano 2002, Middleton & Platov 2003, Gill 2004, Kämpf et al. 2004, Middleton & Bye 2007). The upwelling enriches surface waters with nutrients that boost primary production and, in turn, support an exceptionally diverse and productive pelagic ecosystem (McClatchie et al. 2006, Ward et al. 2006, van Ruth et al. 2010b, van Ruth et al. 2010a).

There is evidence that the southern-Australian pygmy blue whale population is struggling with observations of emaciated, skin-diseased and parasitised animals (Gill and Morrice unpublished data). These whales are constant foragers with a continuous demand for food intake and relatively low fat reserves. However, little is known about how they make feeding decisions, what governs their feeding success or where they go throughout the rest of year. With the added pressure of increasing human activities in the region (e.g. energy development, whale watching) and uncertainty around climate change impacts, it is increasingly important to understand the nature of this foraging habitat for long-term pygmy blue whale conservation.

A common approach to explaining whale occurrence is to measure the degree of spatial correlation between whale distribution and aspects of their environment (Gregr & Trites 2001, Barlow et al. 2008). However, it is often challenging to provide robust explanations for the distribution and foraging success of individual whales, not least because the relationship between predator and prey distribution is scale dependent in both time and space (O'Driscoll & McClatchie 1998, Fauchald 2009).

CHAPTER 2

Large marine predators, such as seabirds, turtles, seals and whales, use hierarchical search patterns that match encounters of particular levels of prey patchiness (i.e. greater search effort with more profitable patches; Piatt & Methven 1992, Hays et al. 2006, Weimerskirch 2007, Fauchald 2009, Santora et al. 2009). Despite these complexities, prey distribution has been successfully used to explain aspects of the ecology of a range of these predators (Young et al. 1993, Fiedler et al. 1998, O'Driscoll & McClatchie 1998, Fauchald et al. 2000, Hewitt et al. 2003, Reid et al. 2004, Mills et al. 2008, Schumann et al. 2008, Santora et al. 2009, Thompson et al. 2012, Benoit-Bird et al. 2013a). For example, Benoit-Bird et al (2013b) found that the scale of foraging behaviour of northern fur seals (*Callorhinus ursinus*) were linked to the patchiness of their prey.

Just as large pelagic predators have hierarchical foraging patterns, krill and other smaller pelagic biota also aggregate in ways that are organised hierarchically from the individual to the population (Murphy et al. 1988). In this study, the hierarchical level of interest was the 'swarm' (or in the case of fish, the 'school'). In the hierarchical search behaviour of blue whales the swarm is likely to be the scale at which they search once they have detected that they are in a prey 'patch' or 'concentration' (Figure 2-1).

In addition to distribution, the species composition, packing density and size of prey aggregations influences blue whale behaviour (Piatt & Methven 1992, Croll et al. 1998, Croll et al. 2005). Blue whales typically feed on dense aggregations of krill and it has been proposed they will only feed above certain density thresholds (Croll et al. 1998, Croll et al. 2005, Goldbogen et al. 2011). The pygmy blue whales off southern Australia feed on the neritic krill *Nyctiphanes australis* (Jarman et al. 2002, Gill 2004), which has been observed during daylight across the shelf (Gill 2004). *N. australis* is endemic to shelf waters off New Zealand and south-east Australia where it contributes significantly to shelf productivity, and shows diversity in its shelf and water column distribution, and associated demographics (Sheard 1953, Blackburn 1980, Hosie 1982, Ritz & Hosie 1982, Bradford & Chapman 1988, McClatchie et al. 1989, Young et al. 1993, Haywood 2002). *N. australis* also has an unusual habit (for krill) of swarming at the surface (Blackburn 1980, Young et al. 1993, Gill 2004, Gill et al. 2011). Although the occurrence of surface swarms is variable (with observations off Australian waters in all seasons, during day and night; Hosie 1982, Ritz & Hosie 1982, O'Brien 1988, Young et al. 1993, Gill 2004), surface swarms are likely to be a relatively cost-effective food resource for pygmy blue whales. This is because blue whales typically lunge when feeding, expending significant effort that increases with the depth of prey (Goldbogen et al. 2011, Goldbogen et al. 2012).
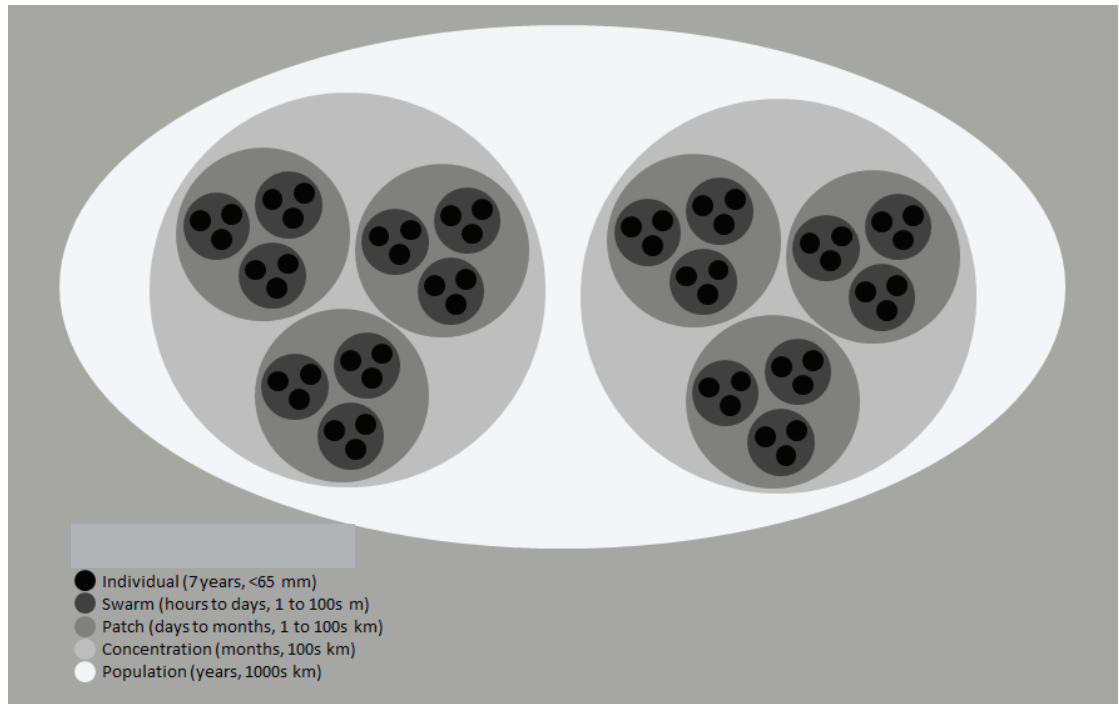
Figure 2-1. Schematic of hierarchical organisation of krill based on *Euphausia superba* and adapted from Murphy (1988). NB. Krill off southern Australia, *Nyctiphanes australis*, are expected to have life expectancies of 1 year and to be < 30 mm.

Quantifying the food resource used by pygmy blue whales off southern Australia posed a challenge. Knowledge of the dynamics of the southern Australian neritic community was restricted to areas in Bass Strait and the eastern GAB, where there are commercial pelagic fisheries and previous studies of the breeding and feeding success of seals and seabirds (e.g. Bunce 2004, Page et al. 2005, Ward et al. 2006, Dann et al. 2008, Kirkwood et al. 2008, Hobday et al. 2011).

The goal of this study was to understand the structure and availability of neritic faunal aggregations in the Bonney Upwelling in the context of pygmy blue whale foraging. This understanding is critical to ongoing sustainable management of the pygmy blue whale foraging ground, as successful foraging is central to population viability. Prey aggregations were detected and characterised from high-resolution acoustic measurements. These measurements included aggregation abundance, spatial organisation and structure of potential pygmy blue whale prey. PERMANOVA analyses were used to test whether the characteristics of aggregations varied significantly in time and space. In particular, the analyses were structured to test predictions that aggregations would vary year-to-year, and they would show profitable characteristics

in areas where pygmy blue whales were expected to preferentially forage (i.e. in mid-shelf and in surface- and midwater strata).

2.2. METHODS

2.2.1. Study area

The study area comprised ~1424 km^2 on the continental shelf off southern Australia (Figure 2-2). Situated near Portland, Victoria, it was considered representative of the narrow shelf region of the southern-Australian pygmy blue whale feeding ground, on the basis of regular sightings of pygmy blue whales and surface-swarming krill (Gill 2004, Gill et al. 2011), and a complex of abiotic features likely to be influencing productivity. Abiotic features considered likely to influence productivity included a narrow continental shelf (~30-km wide), slope submarine canyons, complex coastal circulation (including upwelling jets at Capes Nelson, Bridgwater and Duquesne and associated fronts and filaments) and headland-influenced eddies (Kämpf et al. 2004, Middleton & Bye 2007, Nieblas et al. 2009, Harris & Whiteway 2011).

2.2.2. Survey design

Hydroacoustic surveys were conducted in the study area from small boats during the mid-late period of the pygmy blue whale feeding season (Mar- May, Gill 2004) in 2003, 2004 and 2007. Surveys were designed as a series of cross-shelf transects running perpendicular to bathymetry. Transects were spaced 5.6 km (3 nmi) apart and were randomly selected for survey on any given day. In 2004 and 2007 transects were aligned with existing aerial survey transects (Gill 2004, Gill et al. 2011) to facilitate future data comparisons. A total of 37 vessel transects covering 1074 km (580 nmi) were completed in daylight hours over 24 separate survey days (Table 2-1).

The transect extents were deliberately chosen to incorporate three locational strata based on water depth (Table 2-1). Depth strata were chosen using previous aerial survey results, which indicated that whales mostly occurred in the mid-shelf region i.e. 81 % of sightings occurred between 60 – 100 m depth (Gill 2004).
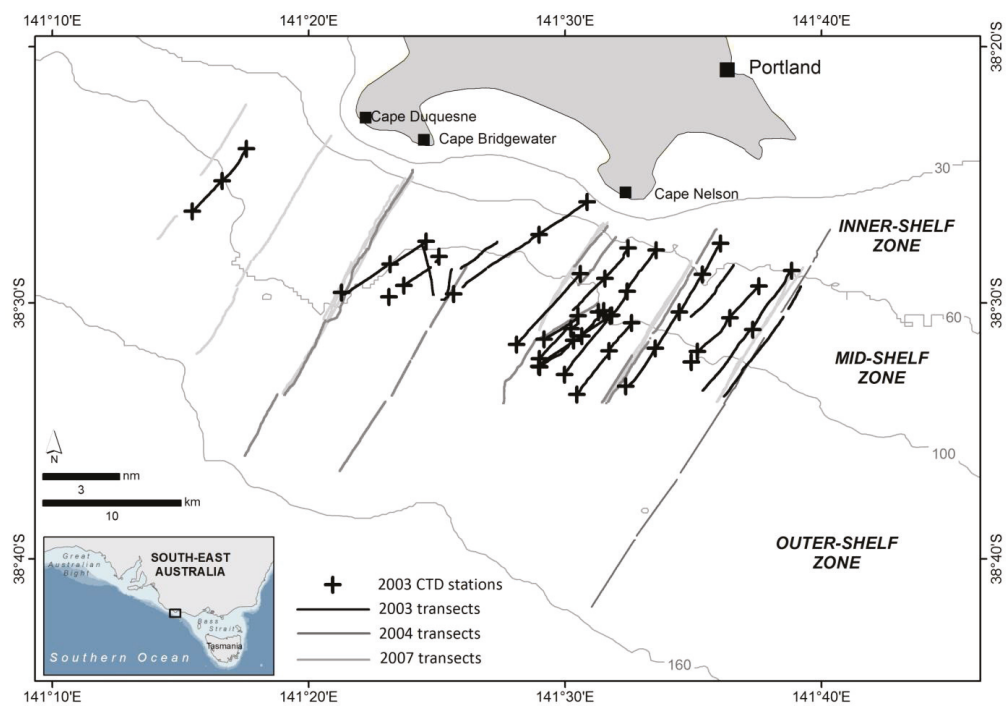
Figure 2-2. Map of study area showing positions of hydroacoustic survey transects for each sampling year off southern Australia. Also shown are CTD stations (✕), continental shelf strata used in analysis, and associated bathymetry (m, bathymetry courtesy GEOSCIENCE 2011).

Table 2-1. Hydroacoustic survey effort for each year and shelf strata: distance surveyed (km) and number of survey days.

Shelf strata	Depth range (m)	Effort each year (km)		
		2003	**2004**	**2007**
Inner-shelf	30-60	20.0	24.5	13.9
Mid-shelf	61-100	158.6	84.0	246.6
Outer-shelf	101-160	172.1	193.9	159.9
Total annual effort		**350.7**	**302.4**	**420.4**
Number survey days		**10**	**7**	**7**

2.2.3. Acoustic data collection

The characteristics of neritic aggregations were quantified acoustically using a portable Simrad ES60 echosounder system (Simrad AS, 2000). The echosounder system consisted of a 1 kW 38/200 kHz General Purpose Transceiver (GPT) housed in a pelican case, and a single-beam 120-kHz (120-25-E) transducer housed in a streamlined steel blister and pole. The transducer pole was attached to each vessel via a purpose built, articulated assembly, and positioned on either the port or starboard beam, depending on the vessel. The transducer was set to transmit vertically with a 1-m draft to minimise surface-associated noise, while still capturing near-surface aggregations.

Simrad ES60 software (v1.4.3.64) run from a laptop computer was used to control the transmission of pings and logging of digital data (to Simrad RAW format) via ethernet connection to the GPT. Samples of received echo power (acoustic data) were collected at an operating speed of 11.1 km h^{-1}. For acoustic system specifications and data collection settings see Section 2.5.1, Appendix 1. Acoustic data were integrated with date, time (Coordinated Universal Time, UTC) and position using a Garmin III global positioning system (GPS, accuracy 15 m, Garmin, 1999).

2.2.4. Acoustic data processing

The logged acoustic data collected along transects in 2003, 2004 and 2007 were processed using Echoview software (v5.0.69.19064, www.echoview.com). A semi-automated algorithm was developed within Echoview to perform acoustic data

correction (e.g. apply corrections to acoustic samples from echosounder system calibration and removal of noise, see Section 2.2.4.1 below), aggregation detection and aggregation characterisation.

2.2.4.1. Data correction

Calibration

Parameters describing the acoustic characteristics of the environment and the properties of the echosounder system and vessel were applied to the acoustic data in order to calculate absolute (mean) volume backscattering strength (S_v in dB re 1 m^{-1}; Section 2.5.2, Appendix 2, Equation 1) and locate the acoustic samples correctly in space and time. The parameters required for the calculation of S_v and related acoustic products were applied by means of an Echoview Calibration Supplement file (Section 2.5.2, Appendix 1, Section 2.5.3, Appendix 3).

Transducer gain (on-axis transducer sensitivity) and the s_A (or NASC, $m^2\,nmi^{-2}$; Section 2.5.2, Appendix 2, Equation 2) correction (a Simrad-specific offset for estimating the effective pulse duration) were estimated by means of a calibration experiment on 22 April 2003 in Portland Harbour (38° 21' S, 141° 37' E). Mean water temperature (measured by thermocouple from 0 to 5 m depth) was 13.88 °C, salinity was nominally defined as 35 psu (not measured directly) and water depth was 12 m. Following manufacturer guidelines (Simrad, 2003) a 38.1-mm diameter, tungsten-carbide sphere was suspended beneath the transducer at a depth of 8 m (range from transducer 7 m). Being a single-beam transducer, the location of the beam axis was approximated by observing the backscatter values of the sphere samples as the sphere was moved across the beam, and identifying the point at which these values peaked. With this point located, the sphere was held on axis and acoustic samples logged for 15 minutes at a transmit power of 1000 W and a pulse duration of 0.256 ms. Echoview was used to estimate transducer gain and s_A correction from the data according to the Help-file guidelines (http://www.echoview.com/files/WebHelp/Echoview.htm).

Sound speed (c in m s^{-1}) and absorption coefficient ($\alpha_{120\,kHz}$ in dB m^{-1}) for each survey were estimated from down-cast CTD (conductivity-temperature-depth) data collected in 2003 (Falmouth Scientific Inc., model FSI MCTD 3"). A survey-mean profile across all casts was generated for both temperature and salinity, and final values for temperature (14.77 °C), salinity (35.27 psu) and depth (64.43 m) calculated as the mean of the profile samples weighted for sampling effort (to account for variable spacing of the CTD measurements over depth). Assuming a nominal pH of 8 (Simmonds &

MacLennan 2005), c and $\alpha_{120\,kHz}$ were calculated using the equations of Mackenzie (1981) and Francois and Garrison (1982).

Transducer equivalent two-way beam angle (Ψ in dB) was calculated as the factory measurement (-18.08 dB; Section 2.5.2, Appendix 2, Equation 3) and compensated for the sound speed during the survey (Section 2.5.2, Appendix 2, Equation 4).

Noise removal

Simmonds and MacLennan (2005) define echosounder signal as the component of the measurement corresponding to transmitted sound backscattered onto the transducer, and noise as the remainder. Common sources of noise on vessel-based acoustic surveys include propeller cavitation, water flow over the hull, sounds and bubbles produced by animals and the environment, and electrical noise from the echosounder and other equipment. 'Background' noise is defined as noise extending continuously over multiple echosounder pings with an S_v at 1 m < -125 dB, and 'intermittent' noise as all other noise signatures.

Background noise was estimated and subtracted from the data using the technique developed by De Robertis and Higginbottom (2007). For this technique to be effective, a proportion of the acoustic data in any given time interval must represent background noise only. This requirement was not always met, and even with the small resample interval chosen for estimating background noise (two pings along-track by 0.5-m depth), there were instances where it was not possible to estimate the true background-noise level. For this reason, a noise-maximum threshold value (Noisemax, *sensu*, De Robertis & Higginbottom 2007) was applied (equivalent to S_v at 1 m = -125 dB), with noise estimates greater than this being set to the threshold level. The estimated background-noise level was subtracted from the original data and a signal-to-noise ratio threshold (threshold$_{SNR}$; *sensu*, De Robertis & Higginbottom 2007) applied to suppress the S_v noise values greater than the noise estimate. The S_v noise values greater than the noise estimate and those with S_v values less than the noise estimate were converted to -999 dB, which is an Echoview default value to denote zero backscatter in the linear domain. Threshold$_{SNR}$ was defined from visual inspection of the noise-subtracted echogram as the value at which the 'speckling' from acoustic samples in empty-water regions of the echogram was removed. Threshold$_{SNR}$ values estimated in this way ranged from 12.5 to 17 dB across the complete dataset.

Intermittent noise manifested in the data as high density acoustic samples (S_v at 1 m generally > -125 dB, and generally > -100 dB) occurring together over a small proportion of a given ping. The source of intermittent noise was unclear, but was

probably due in some cases to inverter interference. In many cases, intermittent-noise samples were found at the same range in one or more adjacent pings. An algorithm was developed to search for the characteristic signature of these samples in order to detect and filter them. The algorithm scanned the data chronologically from ping to ping at each sample range and detected samples with S_v values that showed an increase from the previous sample and a decrease to the next by more than a given threshold value. Samples detected as such were labelled 'true'; all other samples were labelled 'false'. After visual inspection of a subset of the survey data from each year, a threshold of 9 dB was found to satisfactorily identify intermittent-noise samples. A Boolean 'OR' operator was used in the algorithm to manage the situation where intermittent-noise samples were found in up to seven adjacent pings at the same range. 'True' samples were replaced with an S_v value equal to the minimum of the set of samples extending three pings before and three pings after at the same range.

The echograms were visually inspected for any remaining intermittent-noise samples. These were manually delineated into polygon regions using Echoview's selection tools and labelled 'bad'; all other samples were implicitly considered as 'good'. 'Bad' samples were replaced with an S_v value equal to the mean of the 'good' samples within a surrounding cell of dimension 50 pings along-track by 10-m depth.

Surface and seafloor exclusion

The acoustic samples close to the transducer (i.e. near the sea surface) were typically dominated by noise due to transducer ringdown and bubbles entrained into the water column by wave action. For each survey, the upper extent of the data was fixed between 3.5 and 5.5 m based on the visual assessment of the depth of the surface noise on the echogram. The lower extent of the data was defined as a line 2-m above the seafloor; seafloor depth was manually defined on the echogram using Echoview's line-drawing tool.

2.2.4.2. Aggregation detection

Contiguous groups of corrected acoustic samples were considered to represent biological aggregations. These were delineated into polygon regions using Echoview's 'schools detection' algorithm (after Barange 1994, Coetzee 2000, Diner 2001). This algorithm is typically used to detect completely-transected aggregations ('schools') because they can be easily defined and interpreted (Reid et al. 2000). Partially-transected aggregations ('layers'), especially 'diffuse' layers, are often complex in shape and can extend contiguously across whole transects and all depths; layers are therefore less-easily defined and interpreted, and for this reason are often ignored when

considering aggregations in acoustic datasets. However, there was no *a priori* reason to consider layers to be of lesser ecological relevance to the study, so an objective detection procedure was sought for both schools and layers.

A visual inspection of a subset of the acoustic survey data from each year showed that the samples within layers typically had S_v values < -70 dB. The corrected acoustic samples were therefore thresholded into 'high-S_v' ($S_v \geq$ -70 dB) and 'low-S_v' (S_v -89 to < -70 dB) echograms (with thresholded samples converted to -999 dB), and the schools-detection algorithm applied to each echogram according to the settings in Table 2-2. These settings are user defined, and in the study were tuned to delineate aggregations equivalent in scale to the krill 'swarm' described in Figure 2-1 (i.e. 1 – 100s m, Murphy et al. 1988). Detecting aggregations at small scales equivalent to krill 'swarms' has the benefit of yielding a dataset from which the complete range of aggregation scales can be determined, including prey aggregations considered likely to influence whale foraging and feeding behaviour.

Table 2-2. Schools detection settings applied to delineate both high-S_v and low-S_v aggregations in the study area. See text for details.

Detection parameter	Value (m)
Minimum total length	8
Minimum total height	2
Minimum candidate length	4
Minimum candidate height	1
Maximum vertical linking distance	3
Maximum horizontal linking distance	12

2.2.4.3. Aggregation descriptors

The detected aggregations were characterised using a combination of primary and derived acoustic descriptors (Table 2-3). Echoview was used to calculate and export a comprehensive suite of metrics (Echoview 'analysis variables') from the corrected acoustic data at two scales: 1) by aggregation by transect; and 2) by aggregation by 1-km along-track interval. The by-interval scale provided effort-normalised metrics for both complete aggregations and portions of aggregations encountered within each interval.

Additional acoustic descriptors were derived from the exports to further describe the abundance and spatial organisation of aggregations. Abundances of aggregations were described in terms of:

1) counts (the total number of whole and part aggregations within an interval),
2) acoustic biomass (the sum of the nautical area backscattering coefficient (ΣNASC, Section 2.5.2, Appendix, 2, Equation 2) of each proportion of an aggregation within an interval), and
3) percentage occupation (the proportion of the total number of acoustic samples that were in aggregations, relative to the total number of acoustic samples in the interval, expressed as a percentage).

Spatial organisation of aggregations was described in terms of next neighbour distance (N_{ext}ND, in m). N_{ext}ND was calculated for each aggregation in the transect data, as the distance from the centre of one aggregation to the centre of its closest neighbour in one direction (i.e. in the order that they were detected along transect). N_{ext}ND was calculated using the Pythagorean equation (adapted from Nero & Magnuson 1989, Barange 1994, Petitgas et al. 2001):

$$N_{ext}ND = \sqrt{a^2 + b^2}$$

where a is the horizontal distance and b is the vertical distance to the next aggregation measured along track. N_{ext}NDs between all low-S_v aggregations with corrected lengths < 1000 m were calculated to look at the organisation between shorter aggregations that were expected to be associated with long layers. Only one high-S_v layer was detected. This was excluded from further analyses, therefore all high-S_v aggregations were classed as 'schools'.

A set of variables was selected from the transect exports for multivariate tests of aggregation structure (energy, size and shape) and their likely contribution to structuring aggregations. Linear relationships between variables were assessed using scatterplot matrices (R software, v2.15.0, R: A Language and Environment for Statistical Computing, R Core Team; package: Car; Fox & Weisberg 2011).

For a complete list of Echoview output and derived acoustic descriptors used in analysis and associated information, see Table 2-3. All variables were transformed prior to analysis to normalise distributions and homogenise variances across the dataset. Aggregation descriptors were grouped into five types (Reid et al. 2000): 1. position - spatio-temporal position (Section 2.2.5); 2. morphometric - shape and size; 3. energy - acoustic backscatter (MacLennan et al. 2002); 4. environment - such as water depth (Section 2.2.5); and 5. derived.

2.2.4.4. Species identification

The acoustic data were also assessed to ascertain whether zooplankton could be distinguished from fish. For example, De Robertis et al. (2001) reported target strength (TS) values of -95 to -66 dB for 7 - 22 mm krill at 120 kHz. If a maximum possible packing density for a dense aggregation of 22 mm individuals (assuming they are cubes as krill will have minimum inter-individual spacing) of 94,000 n m^{-3} (which falls within the range summarised in Table 4.1, Watkins 2007) is considered, then the maximum possible S_v for an aggregation of 22 mm krill (TS = -66 dB) would be -16.2 dB re 1 m^{-1}. The numerical density and aggregation density values could be much higher or lower using different lengths and modelling them, for example, as rectangles. The S_v values cover the full range of aggregation densities that were observed (e.g. maximum aggregation density -25 dB re 1 m^{-1}), providing no unambiguous S_v threshold for separating krill from fish in the acoustic data. The net samples collected during this study (methodology see Section 2.5.4, Appendix 4, Morrice unpublished data) provided a only a limited degree of ground-truthing for acoustic data due to the study's limited access to appropriate vessels and trawl gear for targeted sampling. The samples were able to conclude that:

a) krill including *Nyctiphanes australis* occur in the study area;
b) krill of different sizes (0.6 - 23.2 mm) occur in close proximity to each other;
c) krill of all life-history stages occur in the surface layer; and
d) a range of zooplankton species occur in the study area, in close proximity to krill.

Therefore, it was determined that it was not possible to differentiate between krill and fish given the single acoustic frequency, limited ground-truthing and no prior information about the water column ecology of the region. The acoustic descriptors (Table 2-3) therefore represent 'neritic aggregations' for which differences in distribution, abundance, organisation and structure were tested.

2.2.5. Aggregation analysis

Based on the knowledge that the abundance, spatial organisation and structure of different aggregations (e.g. macrozooplankton and fish) may not be consistent over space and time, acoustic descriptors of aggregations were analysed with a multi-factor crossed design comparing differences between group levels of the *a priori* temporal and spatial strata expected in the data including:

a) years (3 levels: 2003, 2004, 2007),

b) shelf strata (3 levels: inner-shelf, mid-shelf, outer-shelf (Table 2-1, Figure 2-2)), and

c) depth strata (3 levels: surface, midwater and demersal).

Depth strata categories were based on the assumptions that krill and fish show depth preferences driven by their prey and other biological needs, and that there are depth-dependent weather and physical forcing factors at play. The 'surface' depth stratum was defined as mean depth of aggregations within 10 m of the surface; 'demersal' as mean depth of aggregations within 10 m of the ocean floor; and 'midwater' as everything between surface and demersal.

Aggregations in both transect and interval data were assigned to each stratum. To account for sampling bias across the shelf, any given aggregation or interval that was positioned across shelf strata was excluded from further analysis. It was also recognised in the analysis of the depth strata, that the greater volume of the midwater compared to surface and demersal waters meant greater effort in the midwater part of the water column. A random subset of transects was selected across years to balance sampling effort (Table 2-1). Intervals that contained greater than 30 % in off-effort periods (i.e. not on transect) were excluded from analyses. It is thus estimated, that a small proportion of intervals used in the analyses had the potential to contain some off-effort periods. Consequently, abundances in these intervals will have been slightly under-estimated. This impact is likely to be spread across shelf- and water-column-positions, contributing to unexplained variation in the analyses, but it is possible there may be a temporal bias as there were higher rates of off-effort krill sampling in 2003, than 2004 and 2007.

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Table 2-3. Acoustic descriptors calculated for aggregations and used in univariate and multivariate tests.

Descriptor	Unit	Data source	Descriptor type	Analysis	Transform	Reference
Count	-	Interval	Derived	Distribution & abundance	$\sqrt[4]{}$	
Percentage occupation	%	Interval	Derived	Distribution & abundance	$\log(x+2)$	
Sum acoustic density (ΣNASC)	$m^2\,nmi^{-2}$	Interval	Derived	Distribution & abundance	$\log(x+1)$	App.2, Equ.2
Next neighbour distance ($N_{ext}ND$)	m	Transect	Derived	Organisation	$\sqrt[4]{}$	
Corrected mean volume backscattering strength (S_v)	$dB\ re\ 1\ m^{-1}$	Transect	Energy	Structure	-	Diner (1998), App.2, Equ.1
Standard deviation of uncorrected S_v (SD)	$dB\ re\ 1\ m^{-1}$	Transect	Energy	Structure	$\log(x)$	
Coefficient of variation of corrected S_v (CV)	%	Transect	Energy	Structure	$\log(x)$	
Skewness	$dB\ re\ 1\ m^{-1}$	Transect	Energy	Structure	$\log(x)$	
Kurtosis	$dB\ re\ 1\ m^{-1}$	Transect	Energy	Structure	$\log(x)$	
Vertical roughness coefficient (V roughness)	$dB\ re\ 1m^2\ m^{-3}$	Transect	Energy	Structure	$\log(x+1)$	
Horizontal roughness coefficient (H roughness)	$dB\ re\ 1m^2\ m^{-3}$	Transect	Energy	Structure	$\log(x)$	
Mean height (height)	m	Transect	Morphometric	Structure	$\log(x)$	
Corrected length (length)	m	Transect	Morphometric	Structure	$\log(x)$	Diner (2001)
Corrected perimeter (perimeter)	m	Transect	Morphometric	Structure	$\log(x)$	Diner (2001)
Corrected area (area)	m^2	Transect	Morphometric	Structure	$\log(x)$	Diner (2001)
Image compactness (compactness)	–	Transect	Morphometric	Structure	$\log(x)$	Perimeter^2/ area

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Analysis of variance based on permutations was applied to all univariate and multivariate tests using PERMANOVA (Anderson et al. 2008) in the PRIMER-E statistical package (PRIMER-E v6.1.15 statistical package, Anderson 2001, Clarke & Gorley 2006) with the PERMANOVA+ add-on package (v1.0.5, Anderson 2001). Where significant interactions were found for 3-factor analyses (year, shelf and depth), the models were reduced to 2-factor (shelf and depth) for each year, or further to 1-factor analyses comparing depth strata for each year- and shelf-strata combination. These were all performed using type III sums of squares due to the unbalanced designs, and 9999 permutations of residuals under a reduced model, except in 1-factor tests where unrestricted permutations of raw data were more appropriate. Post-hoc pair-wise comparisons using the permutational procedure were also performed to investigate patterns among levels of groups that had significant results. Tests for homogeneity of dispersions within groups were carried out using PERMDISP (Anderson et al. 2008) with distance to centroids, and where sample numbers were < 10, distance to spatial medians. Monte Carlo (MC) p-values were also reported for tests with low sample numbers. For most analyses, observation numbers were sufficient due to the large number of aggregations detected from the acoustic data and the long distances sampled.

Ordination plots using non-metric multi-dimensional scaling (NMDS, Kruskal 1964) in PRIMER software (25 restarts, min. stress 0.01, Kruskal fit scheme 1, Clarke 1993, Clarke & Gorley 2006) were useful in some cases for visualising group differences and patterns of dispersion. Further visualisation was provided from plots of variable means (± SE).

2.2.5.1. Abundance

Univariate 3-factor PERMANOVAs (Anderson et al. 2008) were used to test whether mean aggregation counts, percentage occupation and ΣNASC for 1-km interval data differed across years, shelf and depth strata. All tests were carried out on the combined aggregation-interval dataset, and for high-S_v schools. Only tests for occupation were performed on low-S_v aggregations, as tests of counts and density were not of interest for this group. Dissimilarity distance resemblance matrices were constructed with transformed data using Bray-Curtis distance for counts due to low numbers in cells, and Euclidean distance for percentage occupation and ΣNASC.

2.2.5.2. Spatial organisation

Univariate 2-factor PERMANOVAs were performed on mean $N_{ext}NDs$ for high-S_v schools measured from transect data both throughout the water column and separately

between surface, midwater and demersal schools, using Euclidean distance to test for differences across years and shelf strata. These tests allowed a comparison of the differences in mean $N_{ext}NDs$ depending on where schools were in the water column. The differences in $N_{ext}NDs$ was not formally tested for low-S_v layers or schools as layers did not have defined end points, and low-S_v schools were assumed to be components of layers.

2.2.5.3. Structure

Multivariate 3-factor PERMANOVAs were used to test whether there were differences in the energy, size and shape (structure) of low-S_v aggregations and high-S_v schools across years, shelf and depth strata. A dissimilarity distance resemblance matrix was constructed with a selection of transformed and normalised aggregation structure variables (Table 2-3) by Euclidean distance. Key aggregation descriptors driving differences in aggregation structure across group levels were identified using similarity percentages (SIMPER, in PRIMER, Clarke 1993).

2.3.   RESULTS

2.3.1. Abundance

A total of 6958 individual aggregations were detected on the continental shelf in the austral autumn over the three years of this study. These comprised 5040 low-S_v aggregations and 1918 high-S_v schools. Low-S_v layers were detected across all years and shelf positions and mostly occupied surface and midwater depth strata. One low-S_v layer was up to 25-km long. Where high numbers of low-S_v schools were encountered, they typically occurred adjacent to layers and looked to be fragmented sections of horizontal layer structures on the shelf (Figure 2-3).

On average, 7.68 (SE ± 0.52) aggregations were detected per interval. Of the aggregation types, low-S_v aggregations were significantly more abundant than high-S_v schools (8.44 ± 0.41 vs 3.29 ± 0.10 schools km^{-1}; univariate PERMANOVA's Pseudo-$F_{(1,1305)}$ = 82.40, p = 0.0001). Similarly, low-S_v aggregations occupied significantly more of each interval than high-S_v schools (9.59 ± 0.44 vs 0.54 ± 0.06 % km^{-1}; Pseudo-$F_{(1,1305)}$ = 655.36, p = 0.0001). In contrast, high-S_v schools contributed significantly more ΣNASC per interval than low-S_v aggregations (391.96 ± 122.76 vs 7.38 ± 0.40 m^2nmi^{-2} km^{-1}; Pseudo-$F_{(1,1305)}$ = 358.75, p = 0.0001).
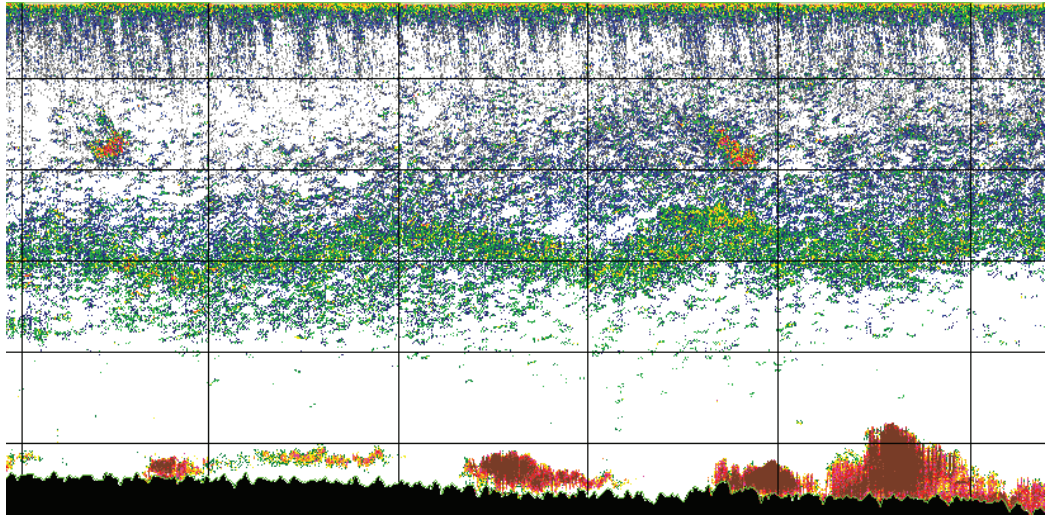
Figure 2-3. Echogram showing the occurrence of scattering layers at the surface and in midwater strata. Discrete high-Sv aggregations can be seen between these layers and just above the ocean floor in demersal water.

2.3.1.1. *Temporal patterns in aggregations*

Interannual differences in abundance were found in tests on combined, as well as within, low-S_v aggregations and high-S_v schools, although some of this variability was due to interactions between temporal and spatial strata (all univariate 3-f PERMANOVAs year*shelf*depth interaction $p < 0.05$). For combined aggregations, 2004 had significantly lower counts (3-f PERMANOVA Pseudo-$F_{(2,1258)}$ = 16.30, p = 0.0001, pairwise 2004*2003 and 2004*2007 $p < 0.0001$) and occupation km^{-1} than 2003 and 2007 (3-f PERMANOVA Pseudo-$F_{(2,1280)}$ = 8.41, p = 0.0002, pairwise 2004*2003 and 2004*2007 $p < 0.05$). Low-S_v aggregations also occupied less space in 2004 than in 2003 and 2007 (1-f PERMANOVA Pseudo-$F_{(2,657)}$ = 64.76, p = 0.0001, all pairwise comparisons $p < 0.05$; Figure 2-4).

Number and occupation of high-S_v schools was lowest in 2004 (counts Pseudo-$F_{(2,620)}$ = 4.77, p = 0.006; occupation Pseudo-$F_{(2,644)}$ = 5.62, p = 0.004; pairwise 2004*2003 and 2004*2007 $p < 0.05$; Figure 2-4 and Figure 2-5), with dispersion effects contributing to this difference (PERMDISP $p < 0.05$; 2004<2003 and 2007). ΣNASC was significantly less in 2003 than in 2004 and 2007 for high-S_v schools, explained by a difference in location only (PERMANOVA year main effect Pseudo-$F_{(2,620)}$ = 4.25, p = 0.01; pairwise 2003*2004, 2003*2007 $p < 0.05$; PERMDISP $p > 0.05$; Figure 2-4 and Figure 2-5). The contribution of generally more occupation and ΣNASC of high-S_v schools in 2007 can be attributed to a few large and very dense schools occurring on 26 March 2007 off Cape Nelson (Figure 2-5).
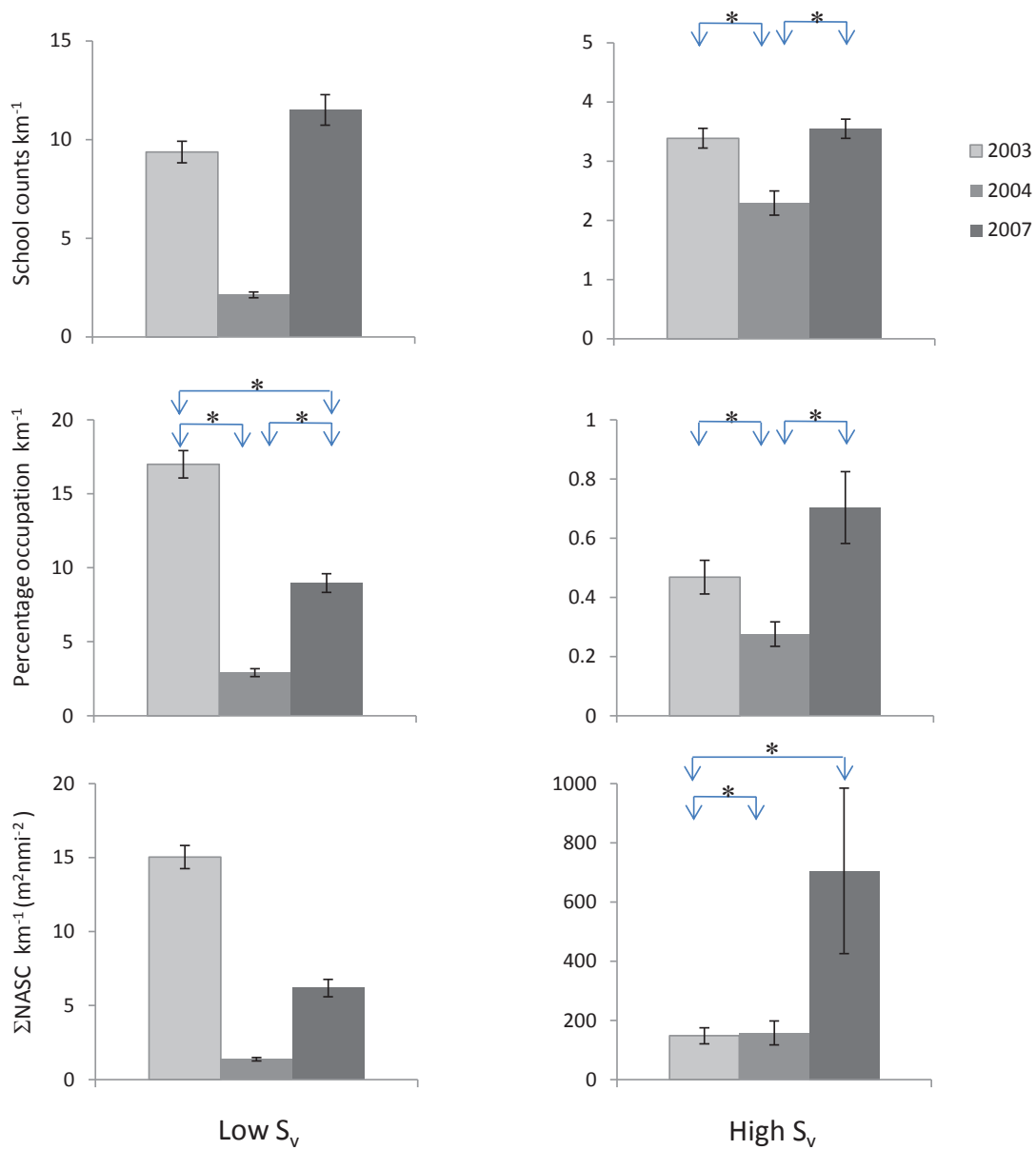
Figure 2-4. Distribution and abundance (mean ± SE) km^{-1} interval of low-S$_v$ aggregations and high-S$_v$ schools for each year shown for numbers, percentage occupation and acoustic biomass (ΣNASC). Asterisks and associated arrows represent significant post-hoc pair-wise comparisons where tested, $p < 0.05$, PERMANOVA. Tests on low-S$_v$ aggregations only performed for occupation.

a)
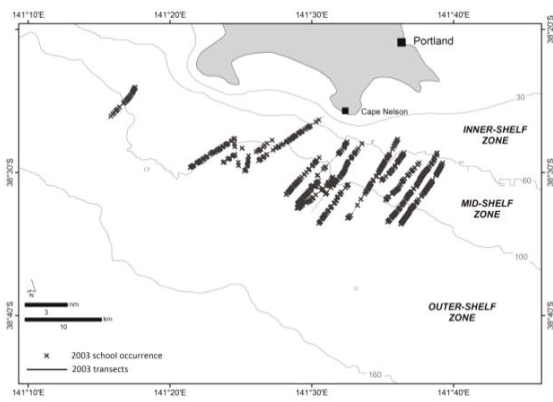
2003

School counts

b)

School ΣNASC
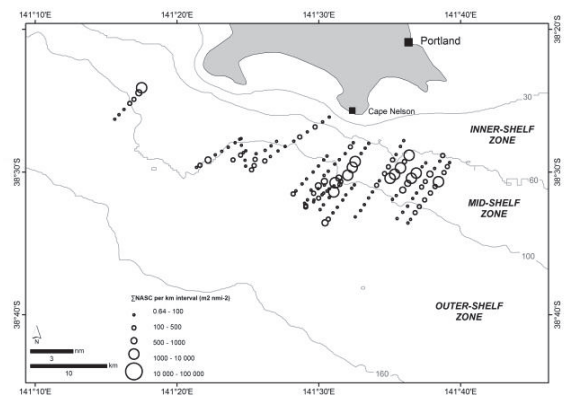
c)
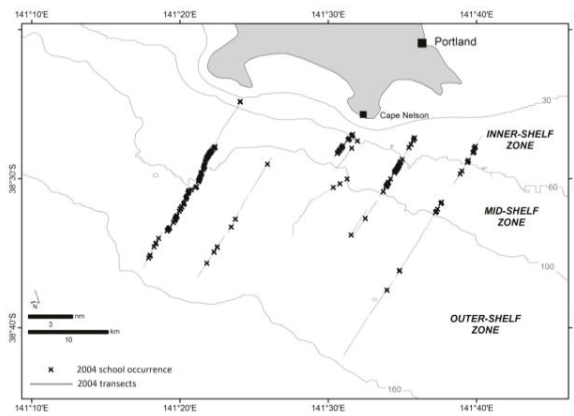
2004

School counts

d)

School ΣNASC
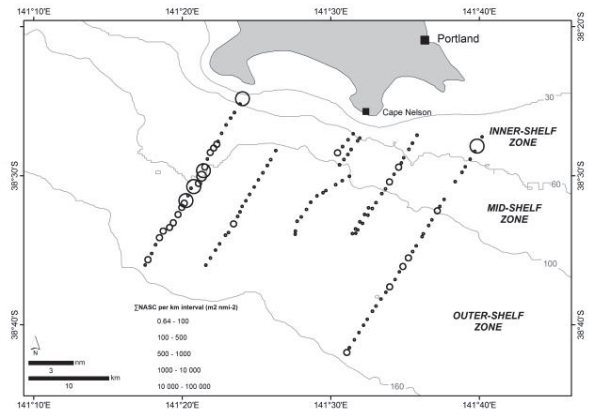
e)
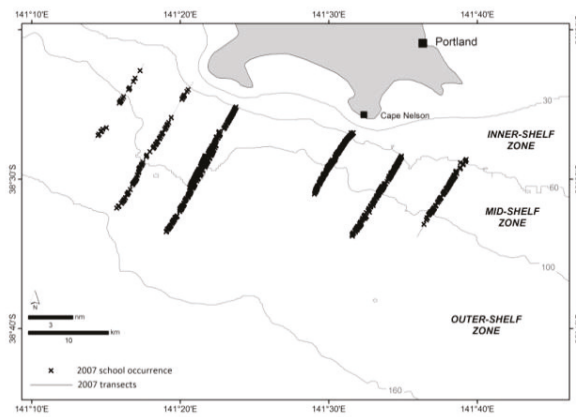
2007

School counts

f)
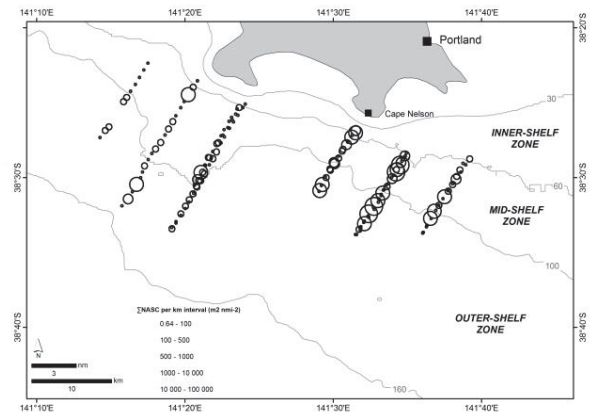
School ΣNASC

Figure 2-5. High-S_v school counts and acoustic biomass (mean ΣNASC km^{-1}, m^{2}nmi^{-2}) for: a-b) 2003, c-d) 2004 and e-f) 2007, for each interval sampled across the shelf.

2.3.1.2. *Spatial patterns in high-S_v schools*

Differences in counts of high-S_v schools were consistent for the shelf and depth strata across years (univariate PERMANOVAs shelf and depth main effects: Pseudo-$F_{(2,620)}$ = 4.52 and 4.88 shelf and depth respectively, $p < 0.05$). The mid-shelf had significantly more mean (± SE) high-S_v school counts (3.71 ± 0.11) than the outer-shelf (2.93 ± 0.10), and significantly more counts than the inner-shelf (2.55 ± 0.19) across all years, all driven by location effects (univariate PERMANOVA's Pseudo F pairwise comparisons $p < 0.05$; PERMDISP $p > 0.05$). In contrast, there were no differences in the occupation and ΣNASC of high-S_v schools km^{-1} across the shelf (PERMANOVA occupation Pseudo-$F_{(2,620)}$ = 2.73; ΣNASC Pseudo-$F_{(2,620)}$ = 1.42, $p > 0.05$).

The results of tests on distribution and abundance across depth strata showed the midwater to have significantly lower mean (± SE) high-S_v school counts km^{-1} (2.47 ± 0.08) than surface (3.90 ± 0.33) and demersal waters (3.55 ± 0.10). Mean (± SE) school occupation (0.23 ± 0.04 %) was significantly lower in surface waters than in mid- (0.91 ± 0.10 %) or demersal waters (0.45 ± 0.03 %; univariate PERMANOVA's pairwise comparisons $p < 0.05$). As a significant interaction was detected for year and depth differences in ΣNASC km^{-1} (PERMANOVA year*depth interaction Pseudo-$F_{(4,620)}$ = 3.96, $p < 0.05$), separate tests for each year were run. These showed that all depth strata were different to each other in 2003 and 2004. The midwater contained the highest ΣNASC, driven only by differences in location (PERMANOVA all pairwise comparisons $p < 0.05$, PERMDISP $p > 0.05$; Figure 2-6). This result was likely due to the greater area of water sampled in the midwater stratum. In 2007 there were no differences in ΣNASC km^{-1} across all depth strata, even though the mean ΣNASC for the midwater stratum was the highest across all years. (1-f PERMANOVA Pseudo-$F_{(2,279)}$ = 1.28, $p > 0.05$; PERMDISP $p < 0.05$, M>D>S; Figure 2-6). This was probably due to the high variability in the mean ΣNASC measure.

ΣNASC km^{-1} (m²nmi^{-2})
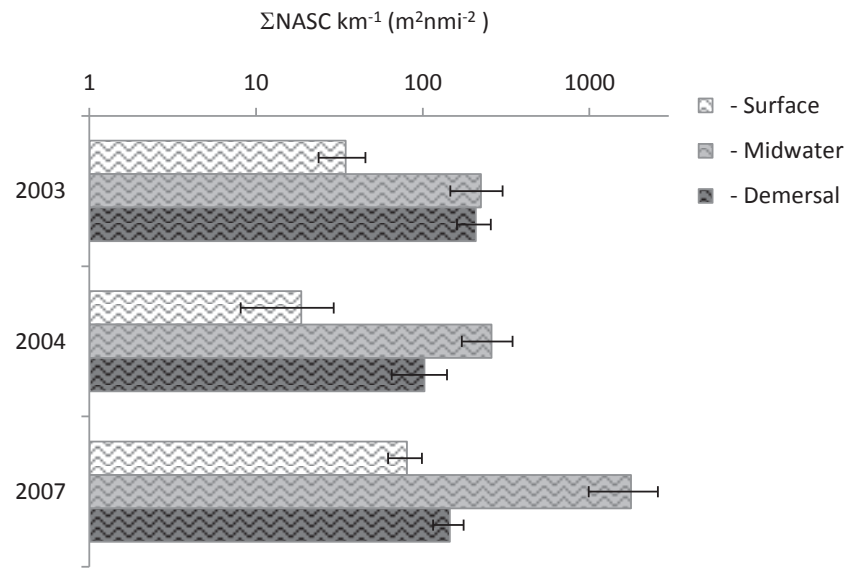
Figure 2-6. Acoustic biomass (mean ΣNASC ± SE, logarithmic scale) of high-S_v schools km^{-1} for each year and depth strata. For 2003 and 2004 all post-hoc pair-wise comparisons were significant ($p < 0.05$, PERMANOVA); in 2007 all post-hoc pair-wise comparisons were not significant ($p > 0.05$, PERMANOVA).

2.3.2. Spatial organisation

2.3.2.1. Temporal patterns in schools

The empirical cumulative distribution function (eCDF) plot of next neighbour distances ($N_{ext}NDs$) for low-S_v schools (i.e. less than 1-km length) for each year showed schools in 2004 were distributed further apart than in 2003 and 2007 (mean ± SE; 193.27 ± 13.66, 83.23 ± 2.54, 56.77 ± 1.19 years respectively; Figure 2-7a). A similar pattern was found in $N_{ext}NDs$ for high-S_v schools, with greater distances between schools (and higher variation about the mean) in 2004 than in 2003 and 2007 (mean ± SE; 183.66 ± 18.70, 134.72 ± 4.64, 153.14 ± 5.35 years respectively; Figure 2-7b). The point of inflexion on the curve for 2003 and 2007 eCDFs was approximately 300 m (Figure 2-7b); 90 % of all schools occurred within this distance. The equivalent proportions of schools in 2004 were over 400 m from each other. When mean $N_{ext}NDs$ were tested between all high-S_v schools throughout the water column, $N_{ext}NDs$ in 2004 were significantly further apart than other years (1-f univariate PERMANOVA year main effect: Pseudo-$F_{(2,1717)}$ = 4.09; p = 0.02; pairwise comparisons 2004*2003 and 2004*2007 $p < 0.05$, Figure 2-8a). Differences were driven at least in part by dispersion (PERMDISP $p < 0.05$). Mean $N_{ext}NDs$ for separate water column strata could not be tested across years due to a year*shelf*water column interaction (3-f univariate PERMANOVA: Pseudo-$F_{(4,1439)}$ = 2.68; p = 0.03).
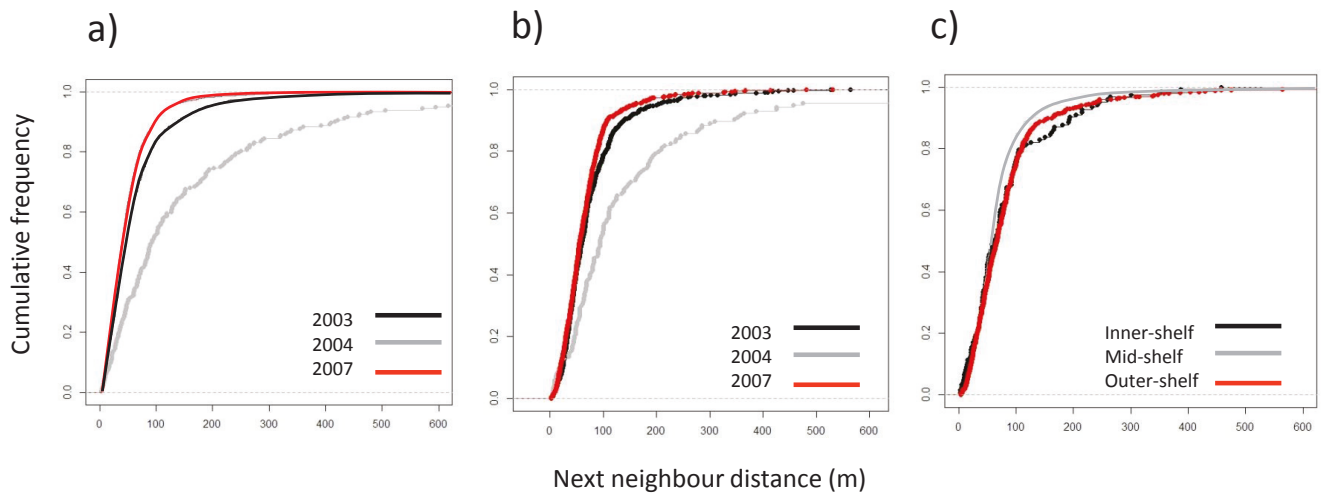
Figure 2-7. Empirical cumulative distribution function (eCDF) plots for next neighbour distances between a) all low-S_v aggregations for each year; b) all high-S_v schools for each year; and c) all high-S_v schools for each shelf strata. All schools > 1-km length excluded.
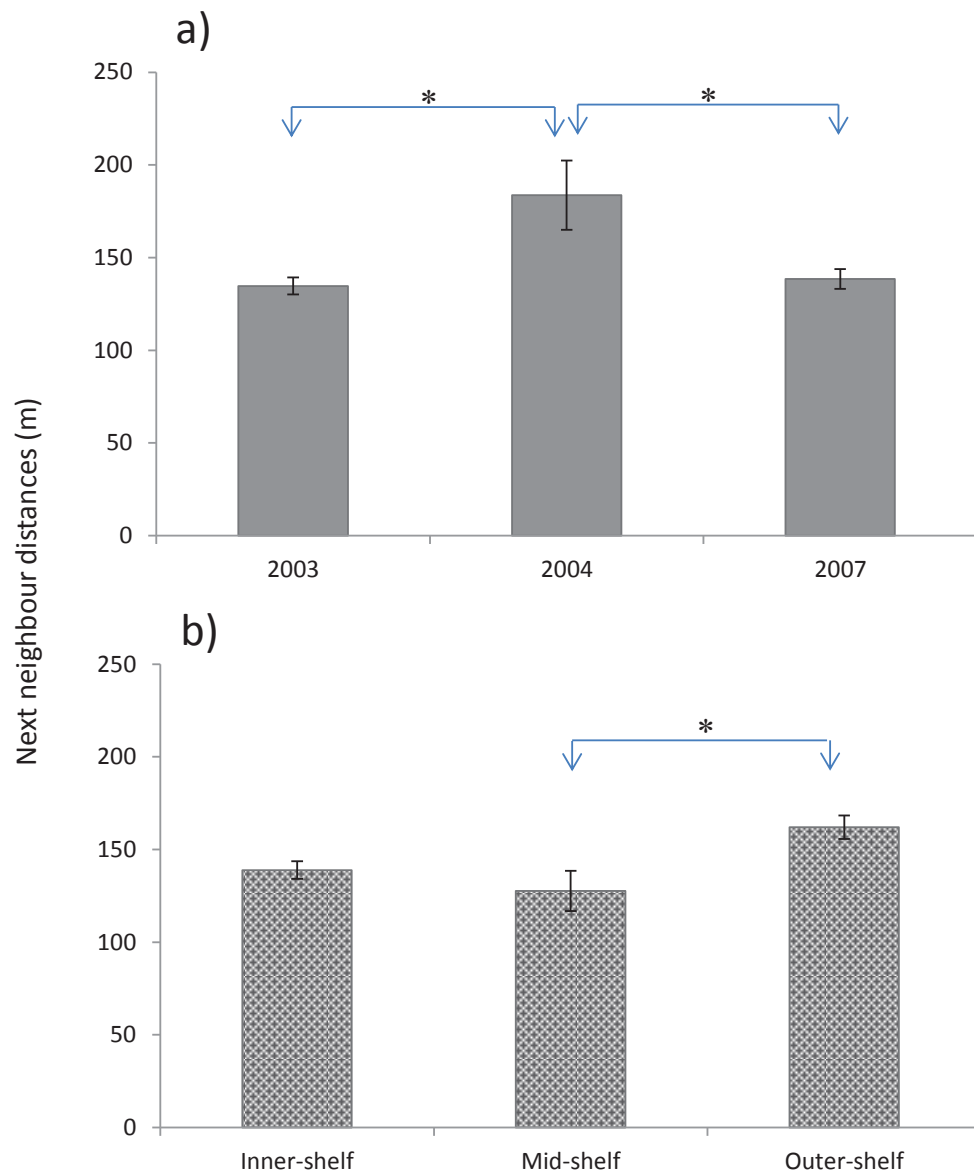
Figure 2-8. Next neighbour distances (mean ± SE) for all high-S_v schools for each a) year, and b) shelf strata. Asterisks and associated arrows represent significant post-hoc pair-wise comparisons, $p < 0.05$ from PERMANOVA tests.

2.3.2.2. Spatial patterns in high-S_v schools

Differences in $N_{ext}NDs$ for high-S_v schools across shelf strata were only apparent near the curve inflexion (Figure 2-7c). Tests of school organisation showed that mid-shelf schools were closer together than outer-shelf schools (1-f univariate PERMANOVA shelf main effect: Pseudo-$F_{(2,1717)}$ = 7.36; p = 0.0006; pairwise mid-shelf*outer-shelf p < 0.0001, Figure 2-8b). Dispersion effects also contributed to this difference (PERMDISP p < 0.05).

When mean $N_{ext}NDs$ were tested across shelf and water column positions for each year, there were no differences across the shelf or depth in 2004 (1-f univariate PERMANOVAs shelf and depth main effects: Pseudo-$F_{(2,99)}$ = 0.96, p = 0.38; Pseudo-$F_{(2,99)}$ = 0.27, p = 0.77 respectively). Analysis of high-S_v school mean $N_{ext}NDs$ for each depth strata were analysed separately for mid-shelf and outer-shelf schools in 2003 and 2007 due to significant interactions (2-f univariate PERMANOVAs shelf*water column interaction: Pseudo-$F_{(3,631)}$ = 7.53, p = 0.0001; Pseudo-$F_{(4,709)}$ = 3.12, p = 0.02 respectively). The inner-shelf was not included in these analyses because it was not significantly different to other shelf positions when compared across the whole water column. There were no detected differences in mean $N_{ext}NDs$ between water column strata for the mid-shelf in 2003 (1-f PERMANOVA Pseudo-$F_{(2,358)}$ = 1.88, p = 0.15). There were, however, significant differences between schools in the outer-shelf in 2003 and for both shelf positions in 2007 (1-f univariate PERMANOVAs 2003 outer-shelf: Pseudo-$F_{(2,235)}$ = 7.58, p = 0.0009; 2007 mid-shelf: Pseudo-$F_{(2,444)}$ = 17.24, p = 0.0001; 2007 outer-shelf: Pseudo-$F_{(2,235)}$ = 3.13, p = 0.04). In summary, high-S_v schools at the surface were significantly closer together than demersal schools in the outer-shelf in 2003 and in both shelf strata in 2007, and midwater schools were closer than demersal schools in the outer-shelf in 2003 and 2007 (these pairwise comparisons p < 0.05; Figure 2-9). Midwater high-S_v schools in the mid-shelf in 2007 were further apart than both surface and demersal schools (pair-wise comparisons p < 0.05; Figure 2-9). Of interest is that surface and midwater schools had similar $N_{ext}NDs$ for the outer-shelf across all years (pair-wise comparisons p > 0.05).

Next neighbour distance (m)
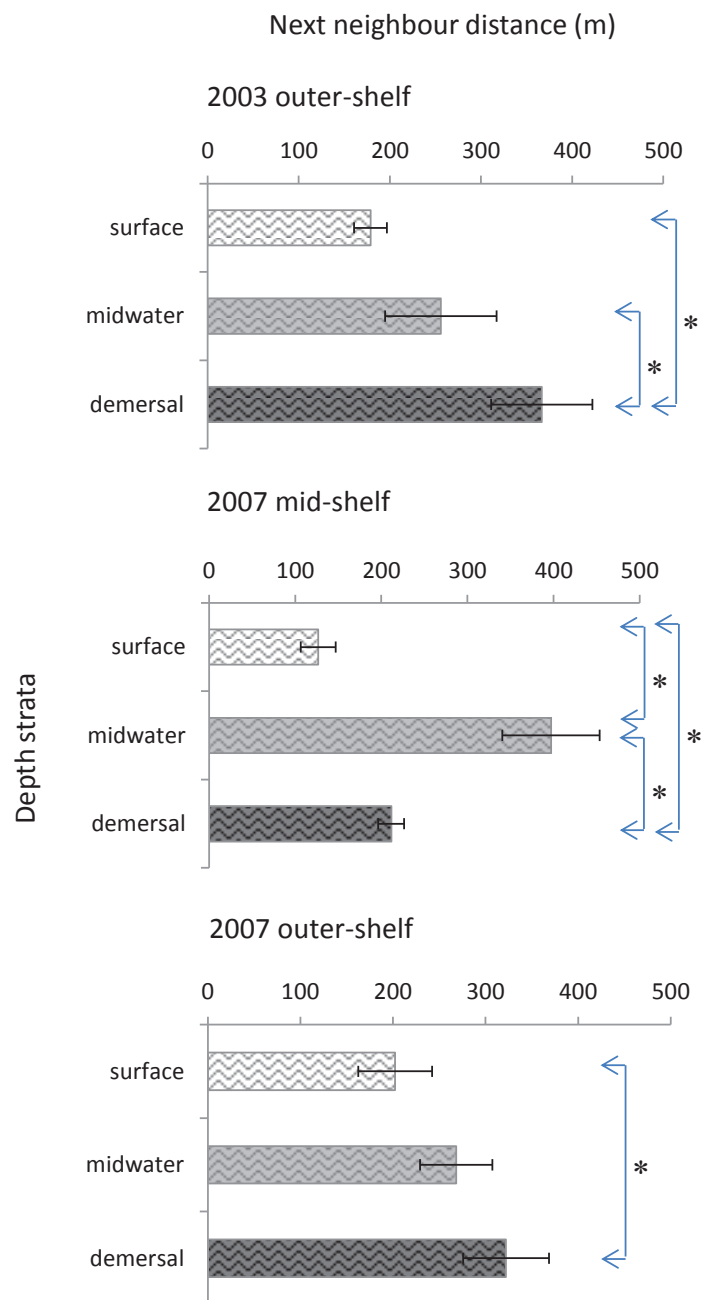
Figure 2-9. Next neighbour distances (mean ± SE) for all high-S_v schools within each depth strata for year and shelf strata where significant differences tested. Asterisks and associated arrows represent significant post-hoc pair-wise comparisons, $p < 0.05$ from PERMANOVA tests.

2.3.3. Structure

Multivariate tests for aggregation structure (energy, shape and size) differences showed variability across years, shelf and depth strata for both low-S_v aggregations and high-S_v schools (PERMANOVA low-S_v: year*shelf*depth interaction Pseudo-$F_{(4,5018)}$ = 4.04, p = 0.013; high-S_v: year*depth interaction Pseudo-$F_{(4,1892)}$ = 10.29, p = 0.0002; and shelf*depth interaction Pseudo-$F_{(4,1892)}$ = 2.75, p = 0.015). Subsequently, tests focussed on the differences in aggregation structure between the mid- and outer-shelf, where most of the productivity occurred (Section 2.3.1).

2.3.3.1. Patterns in low-S_v aggregation structure

The structure of surface and midwater low-S_v aggregations were significantly different in the outer-shelf in 2003, and across the mid- and outer-shelf in 2004 and 2007, driven by location effects (Table 2-4). These differences in 2003 and 2004 were explained by a combination of morphometric and energy variables (SIMPER: 2003 mid-shelf = 42.54 %, 48.52 %; 2004 mid- and outer-shelf = 47.13 %, 46.89 % respectively), and in 2007 mostly by morphometric variables alone (SIMPER: mid-shelf = 65.69 %, outer-shelf = 88.72 %). Morphometric variables also explained differences between surface and demersal low-S_v aggregations in 2007 (SIMPER: mid-shelf = 60.89 %, outer-shelf = 85.77 %).

Differences in structure between midwater and demersal low-S_v aggregations in the mid-shelf in 2003, and both mid- and outer-shelf in 2007, were explained mainly by energy distribution and dispersion variables (SIMPER: 2003 = 82.59 %; 2007 mid-shelf = 58.85 %, outer-shelf = 62.33 %). Although the contributions of each variable to the differences were very similar (SIMPER range 5 – 22 %), the mean height of low-S_v aggregations was plotted to illustrate the importance of morphometric variables for explaining differences between year, shelf and depth strata described above (Figure 2-10). In particular, the mean heights of low-S_v aggregations, which included layers and schools, were narrower in 2004 than in either 2003 or 2007, across both mid- and outer-shelf. In addition, aggregations in the surface stratum were higher than in either midwater or demersal strata. These patterns were consistent with the height characteristics of low-S_v layers observed in echograms.

2.3.3.2. Patterns in high-S_v school structure

Differences in the structure of surface and midwater high-S_v schools were found across all years and between mid-shelf and outer-shelf strata. The differences were driven by a combination of location and dispersion effects (Table 2-4, Figure 2-11), except the

outer-shelf in 2004 where no surface schools were present. A combination of morphometric and energy variables helped explain the differences between surface and midwater schools for the outer-shelf in 2003 and the mid-shelf in 2004 (SIMPER: 2003 = 50.81 %, 41.70 %; 2004: 40.68 %, 54.16 % surface and midwater schools respectively). In contrast, variables representing energy distribution and dispersion explained most of the differences in the mid-shelf in 2003 and across both offshore strata in 2007 (SIMPER: 62.52 %, 64.45 % respectively).

Differences between surface and demersal high-S_v schools across years and shelf strata were explained to a large degree by energy variables (SIMPER: 2003 mid-shelf = 59.91 %, outer-shelf = 63.54 %; 2004 mid-shelf = 63.48 %; 2007 = 61.66 %). Differences between midwater and demersal schools were explained by both morphometric and energy variables in 2003 and 2004 (SIMPER: 2003 mid-shelf = 42.23 %, 48.26 %; outer-shelf = 49.35 %, 41.60 %; 2004 outer-shelf = 41.87 %, 50.56 % respectively), and mostly by energy variables in 2007 (64.45 %). The high-S_v school mean densities (S_v) were plotted against depth strata to illustrate some of the differences in structure described above. During 2007, density of high-S_v schools was higher across the mid- and outer-shelf than during 2003 and 2004. This contributed to the higher, although variable, acoustic energy recorded for 2007 (Figure 2-4f). Midwater schools in 2007 were generally higher density than those in other depth strata, except for outer-shelf demersal schools in 2004 and mid-shelf schools in 2007 (Figure 2-12).

Table 2-4. 1-factor PERMANOVA and dispersion results for depth strata showing significant differences for aggregation structure for year and shelf strata (* indicates all pair-wise comparisons significant at p < 0.05; ** indicates all pair-wise comparisons significant at p <0.0001, ~ indicates tests where one depth strata had no schools present; ^ indicates Monte Carlo p-values the same as those derived from permutations for levels with sample sizes < 10; DS = depth strata; S = surface, M = midwater, D = demersal positions; PERMDISP results for centroid and spatial median distances).

School energy group	Year	Shelf strata	Source	Df	MS	Pseudo-F	p	PERMDISP
Low	2003	Inner-shelf	DS Residual	1 107	67.38 11.48	5.86	0.0075~ ($M_{vs}D$)	p>0.05, no difference in dispersion, location effect only, M = D
		Mid-shelf	DS Residual	2 728	255.59 8248.80	22.55	0.0001^ (pair-wise $M_{vs}D$ P<0.0001)	p<0.05, significant difference in dispersion, and perhaps location effect, D>M
		Outer-shelf	DS Residual	1 699	130.03 11.83	10.99	0.0018~ ($S_{vs}M$)	p>0.05, no difference in dispersion, location effect only, S = M
	2004	All	DS Residual	1 259	419.76 9.15	45.86	0.0001**~($S_{vs}M$)	p<0.05, significant difference in dispersion, and perhaps location effect, S>M
	2007	Inner-shelf	DS Residual	2 95	138.98 9.32	14.90	0.0001*^	p<0.05, significant difference in dispersion, and perhaps location effect, D>(M = S)
		Mid-shelf	DS Residual	2 1629	1123.10 10.63	105.6	0.0001**	p>0.05, no difference in dispersion, location effect only, S = M = D
		Outer-shelf	DS Residual	2 1501	268.28 11.65	23.01	0.0001*^	p>0.05, no difference in dispersion, location effect only, S = M = D
High	2003	Inner-shelf	DS Residual	2 59	77.47 9.78	7.92	0.0001^ (pair-wise $S_{vs}M$, $S_{vs}D$ P<0.05)	p>0.05, no difference in dispersion, location effect only, S = M = D
		Mid-shelf	DS Residual	2 453	296.75 10.74	27.62	0.0001*	p<0.05, significant difference in dispersion, and perhaps location effect, S>D
		Outer-shelf	DS Residual	2 319	139.22 11.20	12.42	0.0001*	p<0.05, significant difference in dispersion, and

							perhaps location effect, S<(M = D)
2004	Mid-shelf	DS Residual	2 89	30.77 11.57	2.65	0.01 (S_{vs}M & S_{vs}D P<0.05)	p>0.05, no difference in dispersion, location effect only, S = M = D
	Outer-shelf	DS Residual	1 55	53.33 11.24	4.74	0.001~(M_{vs}D)	p>0.05, no difference in dispersion, location effect only, M = D
2007	All	DS Residual	2 888	114.56 11.11	10.31	0.0001**	p<0.05, significant difference in dispersion, and perhaps location effect, M>(D = S)
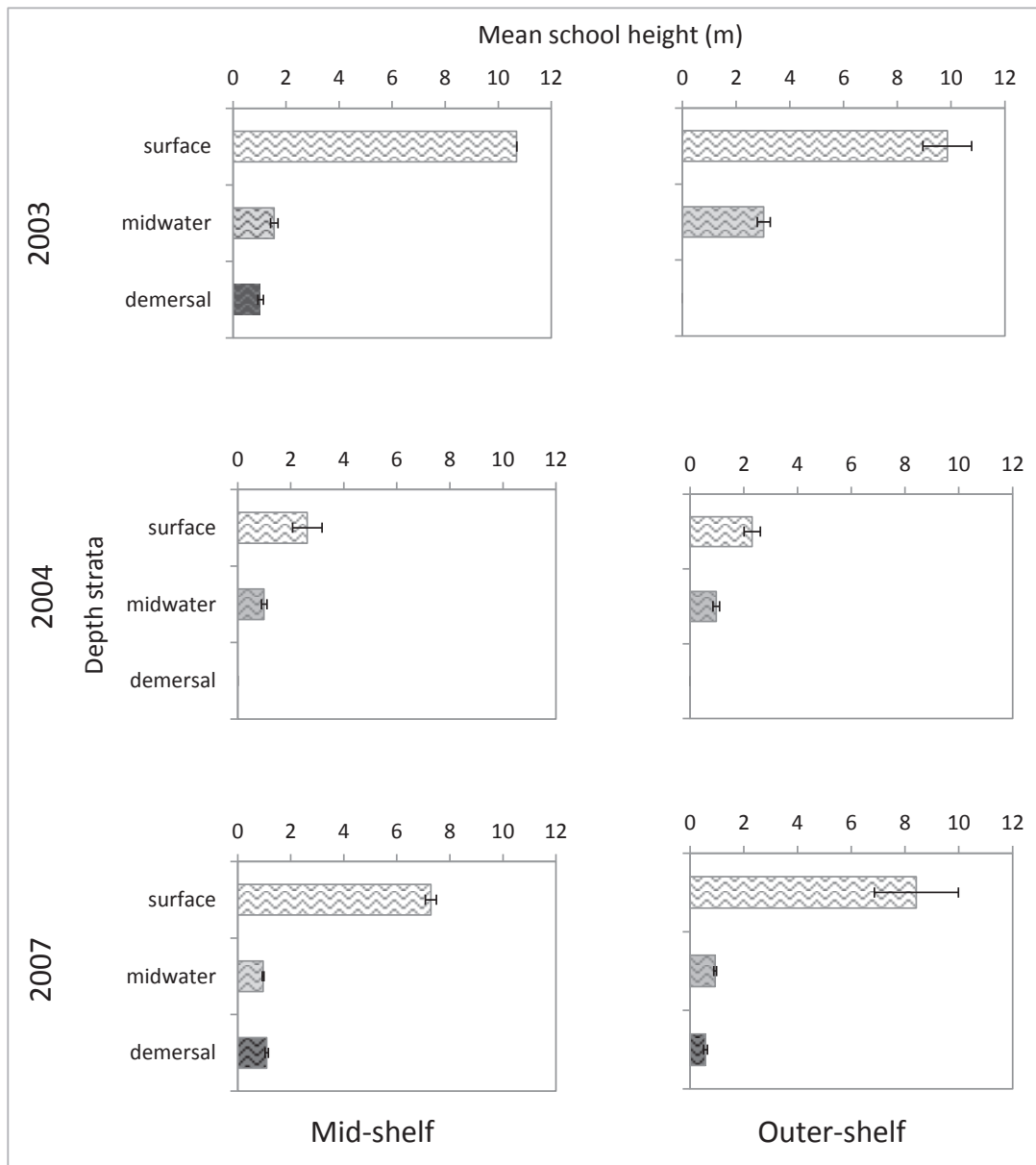
Figure 2-10. Height of low-S_v aggregations (mean ± SE) for each year, shelf and depth stratum.
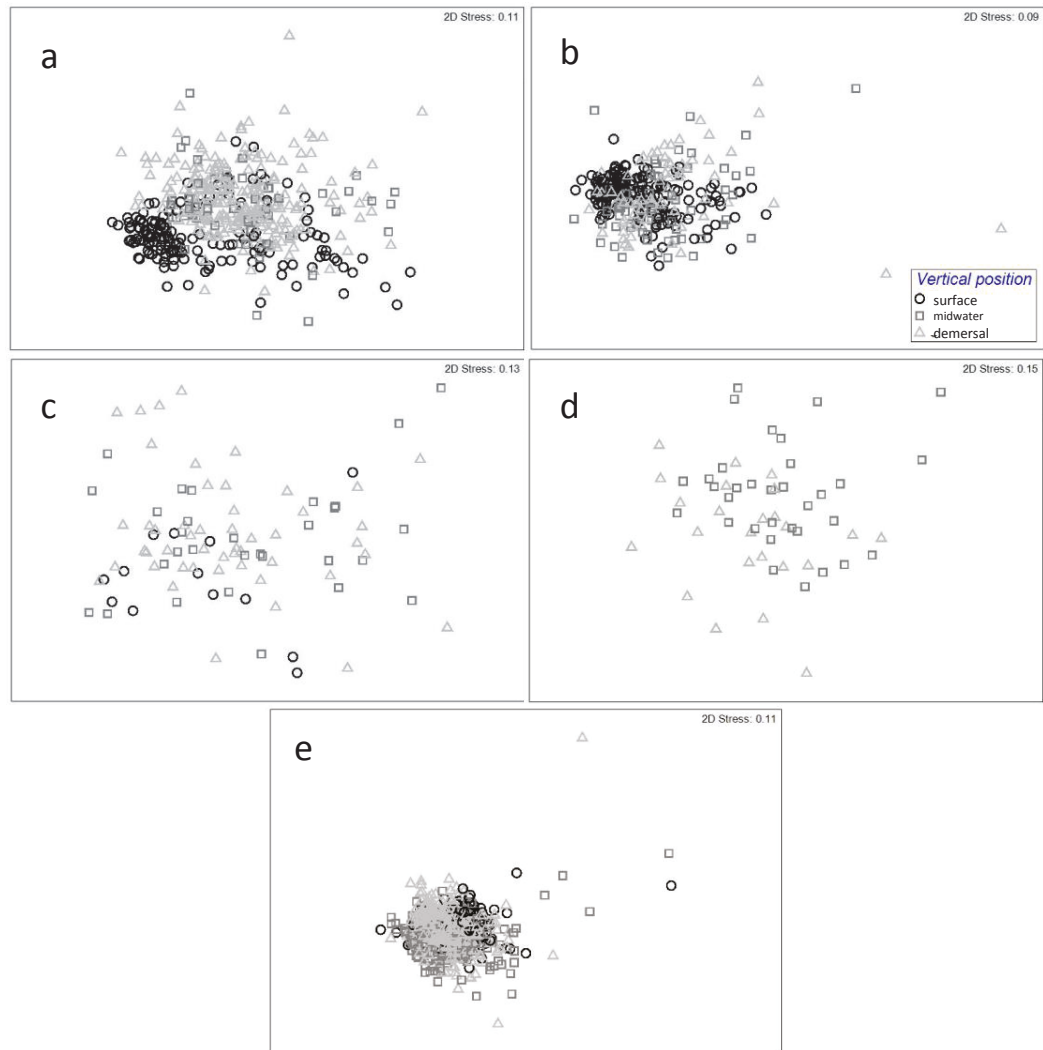
Figure 2-11. nMDS ordination plots of high-S_v schools showing location differences for schools recorded in surface (o), midwater ( ) and demersal (Δ) depth strata for: a) 2003 mid-shelf excluding a small subset of data, b) 2003 outer-shelf, c) 2004 mid-shelf, d) 2004 outer-shelf (no surface schools recorded), and e) 2007 for mid- and outer-shelf strata.
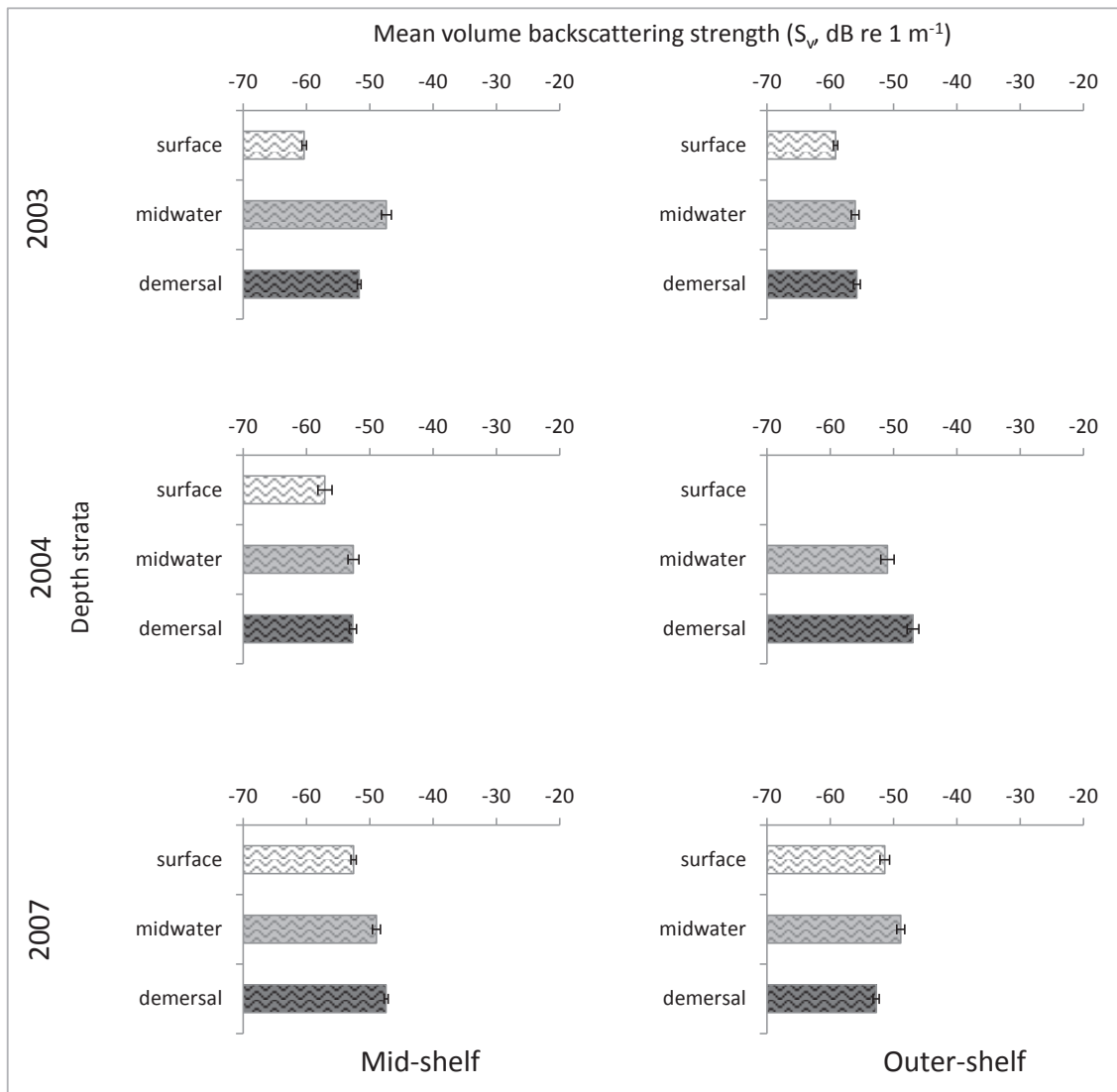
Figure 2-12. Acoustic density (mean $S_v \pm SE$) of high-S_v schools for each year, shelf and depth stratum.

2.4. DISCUSSION

The availability (abundance and spatial organisation) and variability of shelf neritic faunal aggregations were acoustically quantified for the first time in the Bonney Upwelling region, known to be an important pygmy blue whale foraging ground and expected to have productivity similar to the eastern Great Australian Bight and other upwelling regions in the world (Ward et al. 2006, van Ruth et al. 2010a). The combination of descriptors of prey aggregations used in this study was important for showing heterogeneity at broad temporal and finer spatial resolutions. Although the relative contribution of all macrozooplankton, including the krill *N. australis* known to be pygmy blue whale prey (Jarman et al. 2002, Gill 2004), could not be distinguished from that of other neritic fauna, strata where krill aggregations were predicted to be and the likely implications of these biotic patterns in driving pygmy blue whale distribution, are discussed.

2.4.1. Predominance of diffuse layers

A major and unexpected feature of aggregations in the study area was the predominance of diffuse scattering layers (as opposed to completely-transected schools) over the entire survey region in all years. Diffuse scattering layers extended right across the shelf, and occupied significant portions of the water column in the near-surface and midwater depths.

Scattering layers, although not previously acknowledged as a pelagic feature off southern Australia, are major features of many marine systems. Elsewhere they vary in persistence, horizontal and vertical extent, diel patterns of distribution, density gradients, plankton composition and significance to surrounding biota (Brierley et al. 1998, Watkins & Murray 1998, Lawson et al. 2004, McManus et al. 2005, Lawson et al. 2008a, Benoit-Bird et al. 2009a, McManus et al. 2012). The occurrence and distribution of thin layers (< 5 m height), similar to some layers recorded in this study, have been linked to the nature and persistence of physical structures of the water column, such as thermal stratification and internal waves (Brierley et al. 1998, Lawson et al. 2004, McManus et al. 2005, McManus et al. 2012). Layers may also be structured by the needs of the fauna that make up their communities, such as requirements for foraging, predation avoidance and reproduction.

Studies of Antarctic krill (*Euphausia superba*) sampled at night off the Antarctic Peninsula found that krill layers played an important role in the formation and dispersal of krill swarms, and individual krill lengths, sex and stages of maturity (Watkins & Murray 1998). *E. superba* layers extended for kilometres and contributed significantly

to the variation in local biomass, with dense regions separated by more diffuse regions (Watkins & Murray 1998). The large number of low-S_v schools adjacent to layers in this study can be attributed to the variable structure of layers (Lawson et al. 2008a). This was particularly prevalent in 2007 where layers were split at varying depths, as shown by varying mean school heights. Numerous small and closely spaced schools occurred in the same depth ranges. These low-S_v discrete schools would have been incorporated into layers had different schools detection parameters been used, such as slightly greater vertical- or horizontal-linking distances.

Analysis of net samples collected during this study (Appendix 4, Morrice and Garcia-Rojas unpublished data) showed layers to be comprised of mixed assemblages of zooplankton (21 Orders) dominated by calanoid copepods and salps. This diversity is similar to the diversity previously recorded for shelf waters off southern and southeastern Australia (Harris et al. 1991, van Ruth & Ward 2009, Baird et al. 2011). Similar layers studied elsewhere are shaped by herbivorous zooplankton, such as copepods, and zooplanktivores, such as siphonophores, large krill and larval fish (Brierley et al. 1998, Lawson et al. 2004, Lawson et al. 2008a, Benoit-Bird et al. 2009a). They are often in separate but parallel layers (Brierley et al. 1998). Such a pattern of variability in the vertical component of layers may explain the variable heights of layers recorded in the study, particularly in 2007 when separate layers of single species aggregations may have occurred, rather than mixed assemblages. The combination of vertical layers may have played a role in the spatial distribution and composition of the surface krill aggregations detected in close proximity to surface layers, and provided an important source of food from detritus and smaller plankton such as diatoms, dinoflagellates and copepods (Sheard 1953, Hosie 1982, Pilditch & McClatchie 1994, Haywood 2002, McManus et al. 2005). In some cases, sampled layers in this study incorporated aggregations of macrozooplankton or fish, although this was uncommon due to the thresholds set in the schools detection.

Benoit-Bird et al. (2009b) showed the occurrence and composition of zooplankton scattering layers to be persistent, with variation in diel migration and acoustic energy important in driving the distribution of dolphins that fed within these layers off Hawaii and New Zealand. In comparison, layers detected in the study were consistently low energy ($S_v$mean < 70 dB re 1 m^{-1}) and unlikely to support large marine predators. Studies of the persistence of layers over time and space will better determine their significance to planktivores and the wider pelagic community.

2.4.2. Temporal patterns in aggregations

2004 was a significantly different year from 2003 and 2007 with respect to the abundance and spatial organisation of aggregations. Between-year differences were masked to some extent by high within-year variability in shelf and depth strata results, possibly from within-season affects; and may have been skewed in some cases by inclusion of off-effort data. Despite this variability, differences between 2004 and other years remained apparent. In particular, 2004 was marked by lower average-occurrence and occupation of aggregations and greater inter-aggregation mean distances. The pattern of lower school abundance in 2004 than in other years was reasonably consistent across low-S_v aggregations and high-S_v schools. The main exceptions were that high-S_v schools in 2004 had higher ΣNASC than 2003, primarily due to the presence of a few midwater schools in 2004 with very high biomasses. Similarly, no difference was detected between 2007 and 2004 in the ΣNASC of high-S_v schools, due to the high variability in this measure. Patterns of structure in high-S_v schools were not clear at an annual temporal resolution and could not be used to differentiate interannual differences. Some of the interannual variability in the abundance of low-S_v layers was explained by the differences in mean heights of aggregations. For example, occupation was higher in 2003 than in either 2004 or 2007. In addition, layers in 2007 were patchier (higher school counts and shorter inter-aggregation distances), and more variable in height (less occupation) than 2003.

Studies of *N. australis* off New Zealand and Tasmania found phytoplankton and zooplankton abundance to be lower when ocean temperatures were warmer during either El Niño or La Niña events (depending on the local influences of these climatic patterns; Harris et al. 1987, Young & Davis 1992, Haywood 2002). Relationships between El Niño-Southern Oscillation (ENSO) events and upwelling and production indices off southern Australia have been found to be weak due to the high interannual and inter-seasonal variability in these indices (Nieblas et al. 2009). However, 2003 had a higher upwelling-favourable wind stress, lower anomolies for sea surface temperature, sea level and ENSO index (Niño-3.4), and a larger upwelling-plume area than 2004 (Middleton et al. 2007, Nieblas et al. 2009). These patterns suggest that very large-scale climate signals almost certainly influence oceanographic conditions in the study area, despite the fact that no definitive links have yet been described. While increased upwelling does not necessarily equate to increased productivity (as conditions may be less optimal for plankton growth; Cury & Roy 1989, Coyle et al. 2008), wind and circulation activities in the preceding year or season may pre-condition the system for summer-autumn productivity and therefore influence interannual differences (Middleton et al. 2007, Mills et al. 2008, Thompson et al. 2012). Seasonal

and annual patterns of upwelling and downwelling are almost certainly linked to interactions between ENSO cycles and Southern Ocean climate patterns, such as the Southern Annular Mode (SAM, Hall & Visbeck 2002, Middleton et al. 2007, Cai et al. 2011). This in turn influences the distribution and abundance of aggregations of pygmy blue whale prey.

2.4.3. Spatial patterns in aggregations

The spatial pattern of neritic aggregations across the shelf followed the prediction that the mid-shelf would be more profitable (in terms of prey availability) than other shelf areas. The mid-shelf stratum had higher numbers of aggregations with closer spatial organisation, occupying more of the water column than other shelf strata. The exception was the ΣNASC, which showed no difference across the shelf, possibly because the high variability in this measure made differences difficult to detect.

Some of the cross-shelf variability detected in this study is likely to result from within-season effects of upwelling strength and periodicity, as mentioned earlier, and variable offshore extent of upwelling (Lawson et al. 2008a). Greater frequency of upwelling-favourable winds, and associated larger volumes of upwelled water and Ekman transport, will extend the influence of upwelling and physically move planktonic pelagic biota further offshore (Botsford et al. 2003). There is also a temporal-lag between nutrient input and its effect on primary and secondary production. Hewitt et al. (2004) found that productivity of Antarctic krill shifted offshore later in the austral summer; this is similar in the finding in this study of higher abundances of aggregations in the mid-shelf region. A shift of productivity offshore later in summer has also been found locally, with the highest densities of zooplankton and sardine (*Sardinops sagax*) larvae occurring offshore of cooler upwelled waters in the eastern GAB (Ward et al. 2006, McClatchie et al. 2007). Additionally, some of these aggregating pelagic species may be restricted by 'local-thermal critical limits' (Ward et al. 2006). This is unlikely for *N. australis* as it has been found to have an optimal temperature range of 12 - 18 °C, tolerating as low as 9 °C (Sheard 1953, Hosie 1982, Haywood 2002), which accords with the range in temperature of the upwelled water in the study region (McClatchie et al. 2006, Middleton et al. 2007, Middleton & Bye 2007, van Ruth et al. 2010a).

Comparison of inter-aggregation distances with other studies was confounded by different parameters used in school detection, and different methods of estimating distance. Krill aggregations off the Western Antarctic Peninsula showed 81-88 % of aggregations were within 100 m of each other, and up to 99 % within 1 km (Lawson et al. 2008a). Such distances are within the ranges detected in this study, where all high-S_v schools were < 1 km apart. Further investigation of 'patch' detection and metrics across

the spatial range of hierarchical organisation and temporal resolutions expected for zooplankton and schooling fish may reveal greater complexity in distribution patterns (Petitgas 2003).

Further resolution in spatial patterns of aggregations was achieved when differences were tested across depth strata. The patterns reported in this study are similar to those reported for other shelf systems, including systems dominated by Antarctic krill (Pauly et al. 2000, Lawson et al. 2008a). Near-surface waters typically had small, low-density aggregations that were close together (within 200 m). In contrast, a few large aggregations contributed to the greater biomass of aggregations in the midwater stratum. It is expected that the relative importance of surface aggregations of *N. australis*, sampled by plankton net, would have been higher if surface waters could have been acoustically sampled more effectively (the top 3 - 5 m of data were excluded due to noise-effects). Surface and sub-surface aggregations may be a profitable food resource for blue whales and other lunge feeders, as whales have greater energetic demands when they feed at depth (Goldbogen et al. 2011). While benefits may accrue from whales accessing the denser aggregations likely to be encountered in midwater depths (as recorded in this study), foraging efficiencies may arise from feeding on less dense but more abundant surface aggregations. Whales may also force surface aggregations to increase their packing densities by driving them from underneath towards the ocean surface, prior to engulfment. Humpback whales have been recorded repeatedly reverse looping through the same area near the surface whilst lunge-feeding (Ware et al. 2011). *N. australis* have also been observed to be repelled when driven towards a 'barrier' (O'Brien 1987, 1988), thus potentially locally and instantaneously increasing the density of a swarm.

The variability in the vertical spatial pattern of aggregations may be explained by some pattern of vertical movement not detected in the study. Diel changes in spatial distribution are a regular feature of zooplankton aggregations worldwide (Hays 2003), and greatly influence predator-prey interactions. Reverse diel patterns have also been observed, such as in the blue whale feeding ground off California (Watkins & Murray 1998). It is unknown whether the zooplankton in aggregations detected in this study were shaped by patterns of vertical dispersal. There is no evidence of *N. australis* undertaking diel migrations off the east coast of Tasmania (Young et al. 1993), however, the species may at times use its capacity to vertically migrate either during the day or night to maintain its position relative to particular shelf and/or depth strata to maximise food availability (Pilditch & McClatchie 1994).

2.4.4. Structure of aggregations

The structure of *N. australis* swarms and fish schools can be 'plastic' (O'Brien 1988, O'Driscoll & McClatchie 1998). As a result, the size and shape of aggregations detected in the study could not be used as a reliable method to distinguish between *N. australis* and other zooplankton and fish aggregations. It follows that image compactness, a measure of the shape of an aggregation, did not rank highly in explaining the differences between high-S_v schools. As low-S_v aggregations had a more consistent shape, their mean height provided the best comparative measure. Some studies of marine systems where small pelagic fish predominate have shown stability in particular structural variables, such as measures of shape, with strong correlations to water depth. However variability in these patterns appears to increase with increasingly mixed assemblages, and across different temporal and spatial regimes (Scalabrin & Massé 1993, Barange 1994, Maravelias 1997, Muino et al. 2003, D'Elia et al. 2009). Better ground-truthing of acoustic data using combinations of dB differencing and video/net sampling techniques will allow assemblages within the study area to be differentiated. This would provide higher resolution measures of krill availability to pygmy blue whales.

2.4.5. Summary

Neritic aggregations of the Bonney Upwelling, considered trophically to drive this regionally rich and abundant shelf system, have now been characterised for the first time. Areas expected to be occupied by pygmy blue whales (i.e. midwater depths of the mid- and outer-shelf) coincided with areas of highest abundance of neritic aggregations. As predicted, patterns of abundance were variable across broad temporal and finer spatial scales, with strong indications that interannual variation is driven by both very large-scale and local-scale weather and ocean processes. Midwater patterns of abundance and spatial organisation reflected the patchiness of the resource, and the marked influence that aggregations have on the overall patterns of resource abundance. Despite the variability in midwater aggregations, these, and surface aggregations, are expected to be an important food resource for planktivores and other predators. The trophodynamic significance of diffuse layers in supporting dense aggregations remains to be investigated in this region, as does the influence of biophysical processes on these pelagic layers. The spatial organisation of aggregations was reasonably consistent with that expected for the organisation of 'swarms'. 'Patch' detection will be an important next step in spatial pattern analyses.

CHAPTER 2

This study captured some of the interannual and spatial variability inherent in the shelf system studied off southern Australia. The neritic community was influenced by abiotic and biotic interactions occurring at hierarchical scales, which posed particular challenges for predicting the system's dynamic interactions. The pattern of aggregations found in the study area provides information not previously available on the foraging resources of pygmy blue whales. The findings of the study also establishes a basis for future work to further elucidate the region's suitability and predictability for foraging pygmy blue whales.

2.5.   APPENDICES

2.5.1. Appendix 1. Echosounder system specifications, and collection and processing settings.

	Collection settings	Processing settings
Transducer depth (m)	*Sea Hawk* 2003: 1.0	*Sea Hawk* 2003: 1.22
	Sea Hawk 2004: 0.0	*Sea Hawk* 2004: 0.77
	Pelican: 0.0	*Pelican*: 0.8
	Bonney Blue: 0.0	*Bonney Blue*: 1.0
Transmitted power (W)	1000	1000
Pulse duration (τ in ms)	0.256	0.256
Absorption coefficient (α in dB m^{-1})	0.0373	0.04402
Sound speed (c in m s^{-1})	1500	1507.33
Transducer gain (dB)	23.2	20.285
sA correction (dB)	0	-0.61
3 dB beamwidth[a] ($^\circ$)	9.5	9.5
Equivalent two-way beam angle (Ψ in dB)	-17.5	-18.02[b]
TVG range correction (no. of samples offset)	Not applicable	2[c]

[a] Major-axis value not provided by manufacturer; circular beam assumed based on supplied minor-axis value

[b] Compensated for water temperature (see Appendix 2, Equation 4)

[c] Applied in Echoview as the "Simrad Ex60" setting (see Appendix 3)

2.5.2. Appendix 2. Symbols and formulae.

Equation 1: (Mean) volume backscattering strength (S_v in dB re. 1 m^2 m^{-3}) (after MacLennan et al. 2002)

$$S_\mathrm{v} = \mathrm{Pr} + 20\log_{10}R + 2\alpha_f R - 10\log_{10}\left(\frac{\mathrm{P_t}\mathrm{G}_0^2\lambda^2 c\tau\Psi_{\mathrm{comp}}}{32\pi^2}\right) - 2(s_A \text{ correction})$$

Where:

P_r = Received echo power (dB re 1 W)

R = Sample range (m), corrected for transceiver delays (+2$c\tau$ for Simrad ES60 data)

α_f = Absorption coefficient (dB m^{-1}) at frequency f (Hz)

P_t = Transmitted power (W)

G_0 = $10^{(\text{Transducer gain}/10)}$ (with Transducer gain in dB)

λ = Acoustic wavelength (m) = c/f

c = Sound speed (m s^{-1})

τ = Pulse duration (s)

Ψ_{comp} = Temperature-compensated equivalent two-way beam angle (dB) (see Appendix 2, Equation 4)

s_A correction = Simrad-specific offset (dB) for estimating the effective pulse duration

See Appendix 1 for further details.

CHAPTER 2

Equation 2: Nautical area scattering coefficient (s_A or NASC in m^2 nmi^{-2})

$$s_A = 4\pi(1852^2) \times 10^{\frac{\overline{S_v}}{10}} \times T$$

Where:
1852 = m nmi^{-1}
$\overline{S_v}$ = Aggregation or interval mean S_v (in dB re 1 m^2 m^{-3})
T = Aggregation or interval mean height (m)

A note about s_A

s_A is an acoustic areal-density metric, expressed as a columnar density for a column surface area of 1 nmi^2 (for historical reasons) and a defined column height (in m). It is commonly used in fisheries acoustics to provide a simple metric for the total amount of backscatter (acoustic biomass) in a given volume of water; typically this volume is either an alongtrack distance interval or an individual aggregation, both of which must be reported along with their mean height in order for the measurement to be compared.

s_A is an acoustic unit that can be divided by the mean target strength (TS in dB re 1 m) of the contributing targets in order to give true biomass in terms of numbers of individuals (from which weight biomass can then be derived). However, it is a non-trivial (and often impossible) task to know both the identity of the acoustic targets (Horne 2000) and their TS (see e.g. Conti & Demer 2006). Hence, the relationship between s_A (acoustic biomass) and true biomass is not straightforward, especially in mixed assemblages. s_A is therefore best viewed as a rough proxy for true biomass, which can be reasonably expected to reflect the dominant patterns of true biomass over space and time.

Equation 3: Equivalent two-way beam angle (Ψ in dB)

$$\Psi = 10 \log_{10} \left(\frac{ab}{5800} \right)$$

Where:
a = Minor (alongship or longitudinal) 3dB beamwidth (˚)
b = Major (athwartship or latitudinal) 3dB beamwidth (˚)

See Appendix 1 for further details.

Equation 4: Temperature-compensated equivalent two-way beam angle (Ψ_{comp} in dB) (Demer 2004)

$$\Psi_{comp} = 10\log_{10}\left(2\,\frac{c}{c_0}\right) + \Psi$$
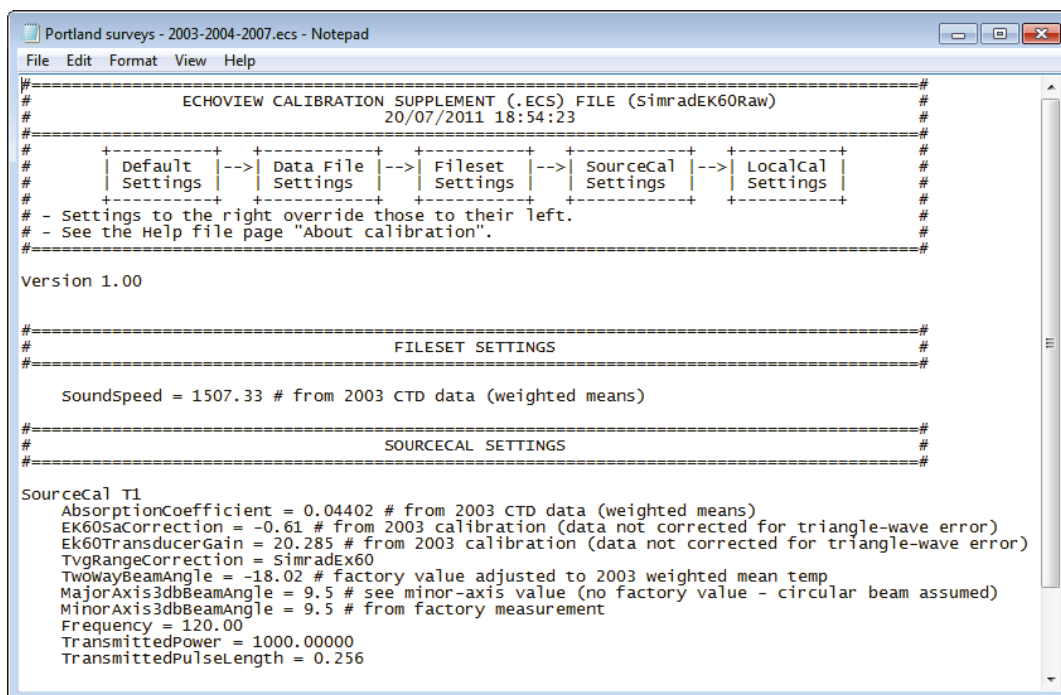
Where:

c = Sound speed on survey (m s^{-1})

c_0 = Sound speed during factory measurements (m s^{-1}): This was not provided by the manufacturer, so was nominally defined as the 2003 Portland Harbour calibration-experiment value (1503.14 m s^{-1}) see Section 2.2.4

Ψ = Equivalent two-way beam angle (dB; see Appendix 2, Equation 3)

2.5.3. Appendix 3. Echoview Calibration Supplement (ECS) file used during data processing

2.5.4. Appendix 4. Methods for net sampling of krill in the study area.

Validation of some acoustic sample data was achieved by targeted net sampling with concurrently recorded hydroacoustic data. As validation samples were opportunistic and focussed mainly on surface samples, they were not fully representative of the survey area. Tow samples of the water column were collected using a 40-cm wide hand-held plankton dip net (mesh size 380 μm) and a 1-m wide ring net (mesh size 500 μm). As a result, stages larger than furcilia I (1.8 mm, Hosie 1982) were sampled. Most sampling occurred with the dip net at the surface at ~4 kts forward of the vessel for varying sample times and when krill could be seen entering the net, to improve the representativeness of the catch. Tows from the ring net were integrated to the target depth. Samples were fixed and stored in 75-95% ethanol. Large net samples were sub-sampled using a Folsom splitter, allowing a minimum of 300 individuals per sample (Young et al. 1993, De Silva-Dávila et al. 2002). These were then identified to at least Family (Dakin & Colefax 1940, Hosie 1982, Watson & Chaloupka 1982). Individuals identified as *Nyctiphanes australis*, were counted and measured according to size classes in Hosie (1982)(i.e. eggs, metanauplii 0.45-0.80mm; calyptopis I 0.80-1.28mm, calyptosis II 1.50-1.98mm, calyptosis III 1.5-2.55mm; furcilia I 1.82-3.43mm, furcilia II 2.25-4.55mm, furcilia III 3.18-6.60mm; postlarvae 4.75-8.95mm, adolescents 6.55-11.63mm and adults – 11.00-20.75mm). The total length of individuals was measured from the anterior tip of the short rostral plate to the tip of the postero-lateral spines of the telson (Hosie 1982, Watkins et al. 2007) under magnification using a SV-6 Carl Zeiss stereomicroscope fitted with a cross micrometer ($\pm$ 0.1 mm). Length frequency histograms were then plotted separately for samples collected at the surface and those integrated by depth. Combined with each sample's acoustic energy, they provided examples of euphausiid size-class and acoustic densities found in the study area.

3. INFLUENCES OF FINE-SCALE UPWELLING HABITAT STRUCTURE ON AGGREGATING NERITIC MACROZOOPLANKTON AND FISH

3.1. INTRODUCTION

Neritic macrozooplankton and small fish that aggregate in the water column are a key trophic component of shelf ecosystems (Schwartzlose et al. 1999, Ward et al. 2006, Fielding et al. 2012). They contribute significantly to biomass and therefore sustain a large diversity of marine predators (Worm et al. 2003, Munger et al. 2009, Santora et al. 2011a). They are also significant targets for fisheries worldwide (Everson et al. 2007). Understanding the patterns of distribution and abundance of neritic fauna, and the underlying processes shaping those patterns, are key areas of marine research in the management of fisheries, biodiversity, climate change, and predators of high conservation significance (Edwards et al. 2000, Frank et al. 2007, Embling et al. 2012, Goldsworthy et al. 2013).

Regional ecosystem models are being used more frequently as a tool to understand ecosystem linkages, and as a basis to make management decisions for neritic communities and populations (Goldsworthy et al. 2013). Ecosystem models are built to explain complex trophic interactions from primary producers to apex predators. They are often developed in the context of physical drivers underpinning trophic interactions, and they are used to assist management (Botsford et al. 2003, Fulton et al. 2007, Bulman et al. 2011, Lester & Fairweather 2011, Goldsworthy et al. 2013). The power of such models for estimating current, and predicting future, ecosystem relationships depends on the input of field-measured, regional and local biophysical parameters (Bulman et al. 2011). Rarely, however, do relevant quantitative analyses that could validate these models exist (Ward et al. 2006, van Ruth et al. 2010a, Benoit-Bird & McManus 2012).

Systems where aggregating macrozooplankton and small fish dominate are often associated with ocean-basin-scale eastern-boundary currents (i.e. California, Canary, Peru and Benguela; De Silva-Dávila et al. 2002, Barth et al. 2007, Santora et al. 2011b) and meso-scale flows such as the world's only northern-boundary current, the Flinders Current, off southern Australia (Middleton & Cirano 2002, Middleton & Platov 2003, McClatchie et al. 2006, Ward et al. 2006, Middleton et al. 2007, Middleton & Bye 2007, Currie et al. 2012). Complex dynamics between weather and ocean-circulation patterns in such systems create habitat features that favour productivity. For example, the southern Australian shelf system is a complex temperate region, with ocean-basin and

regional patterns of air- and sea-forcing working in concert with local topography to configure local water circulation (Lewis 1981, Schahinger 1987, Gill 2004, Kämpf et al. 2004, McClatchie et al. 2006, Middleton & Bye 2007, Nieblas et al. 2009, van Ruth et al. 2010b, van Ruth et al. 2010a, Gill et al. 2011). From spring to autumn each year patterns of circulation distribute nutrients and make them available for phytoplankton production – and it is from there that the fate of grazers and higher trophic groups are determined. This general pattern is mirrored in many upwelling-influenced coastal regions (Mann & Lazier 2006); however each region has a unique suite of physical conditions that shapes its biota. A worldwide review of the fluctuations observed in sardine (*Sardinops sagax*) and anchovy (*Engraulis spp*.) populations by Schwartzlose et. al. (1999) concludes there are three main physical processes, mostly driven by wind, that determine favourable habitat for these small aggregating fish. The processes are enrichment (e.g. upwelling, mixing and eddies), concentration (e.g. fronts, turbulent mixing and Ekman convergence) and retention (e.g. lack of offshore transport, enclosed gyres and stable currents). These processes are also influential for high productivity of phytoplankton and krill (Brierley et al. 1998, Lawson et al. 2004, McManus et al. 2005, Taylor et al. 2010, McManus et al. 2012).

Even when relationships between macrozooplankton and small fish and their habitat are found, the mechanisms driving them are usually complex. Complexity arises due to dynamic interactions between physical forcing, nutrient cycling and predator-prey relationships. Such complex dynamics often lead to mismatches in the strength and direction expected of predator-habitat relationships (Bertram et al. 2001, Gremillet et al. 2008, Certain et al. 2011). For example, Certain et al. (2011) describes 'spatial anchors' that may affect the patterns of predator-prey relationships in the Bay of Biscay, such as the availability of prey resources elsewhere in the region of study, predator avoidance, and ocean currents that can either concentrate or move prey away from optimal feeding environments. Temporal and spatial mismatches may also be a consequence of trophic interactions in any particular system. As Cury and Roy (1989) state a "wide spectrum of trophodynamic scenarios may be observed during upwelling as well as relaxation periods", including a range of food web pathways (Harris et al. 1987, Cury & Roy 1989). Prey-switching will affect top-down and bottom-up controls. For example, dominant omnivorous predators, such as the krill *Nyctiphanes australis* (endemic to southeastern Australia and New Zealand; Sheard 1953, Blackburn 1980, Hosie 1982, Ritz & Hosie 1982), can influence food web interactions and community structure (McClatchie et al. 1989, Young et al. 1993, Hughes et al. 2013).

The greatest degree of temporal and spatial matching would occur for species in their 'optimal environment window' (where the effects of the limiting factors are minimised;

Figure 3 in Cury & Roy 1989, Coyle et al. 2008). In the eastern Bering Sea, conditions were optimal for zooplankton when high water-column stability coincided with a nutrient reservoir available below the thermocline, along with optimal temperatures for growth (Coyle et al. 2008). A maximum threshold of water-column stability forced by wind was thought to apply, over which abundance of zooplankton declines due to the effects of passive advection and active vertical movement away from optimal habitat (Cury & Roy 1989, Botsford et al. 2003, Coyle et al. 2008). Local conditions will also influence the trophic interactions in the system, where perturbations from regional- and ocean-basin-scale climate change and anthropogenic pressures can lead to population shifts and switching of dominant trophic levels (Cury et al. 2000, Baum & Worm 2009, Bulman et al. 2011, Certain et al. 2011). As biological processes and habitat interactions typically cascade up to higher-trophic levels (Cury & Roy 1989), a better understanding of lower-level interactions will allow changes in the distribution and abundance of top marine predators to be better explained and predicted (Certain et al. 2011).

Of particular interest to this study are the habitat features influencing the distribution and abundance of prey for a population of pygmy blue whales (*Balaenoptera musculus brevicauda*) known to forage and feed off the southern Australian shelf (Gill 2004). The influence of habitat on pygmy blue whale and prey occurrences is of critical conservation interest for this endangered, and previously highly exploited population (Branch et al. 2007). Understanding the mechanisms driving the distribution and abundance of pygmy blue whales is particularly important. The pygmy blue whale is recognised as a subspecies of blue whale (*Balaenoptera musculus*) and is currently showing no measurable signs of recovery, encounter rates of calves are low and there is evidence of individuals in nutritional stress (Gill 2002, Gill et al. 2011). Also, the shelf habitat on which these whales depend for food is shared with current and emerging anthropogenic activities known to impact them (e.g. energy development and shipping; Croll et al. 2001b, Douglas et al. 2008, Berman-Kowalewski et al. 2010, Di Iorio & Clark 2010, Melcon et al. 2012, Redfern et al. 2013).

Pygmy blue whales regularly aggregate along the narrow shelf between Portland (38° 21' S, 141° 37' E), western Victoria, and Robe (37° 2' S, 139° 12' E), South Australia (Gill 2004, Gill et al. 2011). The shelf is characterised by a series of seasonal upwellings that regularly surface adjacent to headlands and capes, collectively known as the Bonney Upwelling (Butler et al. 2002, Kämpf et al. 2004). Some knowledge exists of the physical processes operating in the Bonney Upwelling region (Lewis 1981, Schahinger 1987, Gill 2004, Middleton et al. 2007, Middleton & Bye 2007, Levings & Gill 2010). However, biophysical processes for the upwelling are not clear, and upwelling is predicted to

follow a 1-step process (where upwelled water comes directly onto the narrow shelf, < 25 km). Primary productivity and biomass are expected to be higher where the shelf is narrower than where it is broader, and to occur throughout the euphotic zone (P. van Ruth, pers. comm.). No study has linked the weather and ocean processes that occur in the Bonney Upwelling region to primary productivity and to grazers such as krill and small fish.

The eastern Great Australian Bight (GAB), west of the Bonney Upwelling, where biological oceanography studies have occurred, has a wide shelf (> 50 km) and a 2-step process where upwelled water is pooled off Kangaroo Island (McClatchie et al. 2006, van Ruth et al. 2010a). The eastern GAB is also directly influenced by warm-water masses of the central GAB (McClatchie et al. 2006, Ward et al. 2006, Middleton & Bye 2007, van Ruth et al. 2010a, van Ruth et al. 2010b). Primary production in eastern GAB hotspots (1600-3900 mg C m^{-2} day^{-1}) is comparable to that in eastern-boundary current systems (van Ruth et al. 2010a). Enrichment of the water column from upwelled water (10 – 16 °C), and then its retention in the euphotic zone (through stratification and upwelling-favourable winds and mixing), distributes nutrients and allows phytoplankton production to occur in both upwelling and downwelling periods (van Ruth et al. 2010b, van Ruth et al. 2010a, van Dongen-Vogels et al. 2012). Of particular significance in the eastern GAB is large phytoplankton concentrations (represented by chlorophyll maxima) associated with upwelled water just below the surface mixed-layer ($\sim$ 35 m; van Ruth et al. 2010a). Relationships between phytoplankton and nutrients as well as water mass features are characterised by temporal and spatial variability (van Ruth et al. 2010a). Productivity has been shown to decline when mixing processes entrain phytoplankton into waters below the critical depth, where productivity losses due to respiration exceed productivity gains due to photosynthesis (van Ruth et al. 2010b). In addition, changes in phytoplankton community structure, which affect predator food resources, have been associated with changes in enrichment, mixing and stratification (van Dongen-Vogels et al. 2011, 2012). East of the Bonney Upwelling, from Portland to western Bass Strait, the shelf widens again. There, water flows from the west of Bass Strait and Tasmania are expected to influence water circulation, particularly adjacent to canyons.

Pygmy blue whales forage and feed on the krill *N. australis* in the Bonney Upwelling region (Gill 2002, Jarman et al. 2002, Gill 2004). Despite *N. australis'* assumed trophic importance the Bonney Upwelling system, there have been no studies of its distribution and abundance or relational links with habitat. Studies off the east coast of Australia, including Tasmania, and off New Zealand where different shelf processes occur, show that *N. australis'* abundance and distribution displays much temporal and

spatial variation (Sheard 1953, Mauchline & Fisher 1969, Blackburn 1980, Hosie 1982, Ritz & Hosie 1982, Bradford & Chapman 1988, O'Brien 1988, McClatchie et al. 1989, Young et al. 1993, Young et al. 1996, Haywood 2002, Schultz 2003, Nicol & Brierley 2010). For example, years of strong upwelling-favourable winds created optimal conditions for 'new' primary production from large diatoms (as opposed to 'recycled' production from regenerated nutrients) and associated high abundance of *N. australis* swarms (Harris et al. 1991). The abundance of adult and larval *N. simplex,* a similar Northern Hemisphere krill in regions of the southern California Current system, was coupled to local coastal physiography of embayments, and water-flow regimes such as eddy structures. Those conditions led to water stability, optimal-food quality and quantity, and larval retention and recruitment (De Silva-Dávila et al. 2002).

Much of the pelagic niche probably used by *N. australis* is shared with other zooplankton, such as copepods and small pelagic fish and their larvae (Hosie 1982, Ritz & Hosie 1982, O'Brien 1988, Young & Davis 1992, Young et al. 1993, Young et al. 1996, Young et al. 1997, Ward et al. 2006, van Ruth 2009, van Ruth & Ward 2009). The composition of these assemblages is expected to vary in terms of species dominance from west to east, along with longitudinal environmental conditions (Young & Davis 1992, Young et al. 1993, Ward et al. 2006, McClatchie et al. 2007, Bulman et al. 2011, Condie et al. 2011, McLeod et al. 2012). Studies from the eastern GAB and southeastern Australia show that the habitat structures expected to be important for shaping the distribution and abundance of aggregating zooplankton and small fish are the position of water turbulence, stratification and upwelled water, and the distribution and abundance of prey (Harris et al. 1991, Young et al. 1993, Reid et al. 2000, Ward et al. 2006, Currie et al. 2012, McLeod et al. 2012).

Chapter 2 of this thesis provides the first quantitative data of the fine-scale distribution and abundance of neritic aggregations for the Bonney Upwelling, which is a productive narrow-shelf region. Acoustic characterisation of the water column over three years showed heterogeneity in the abundance of aggregating macrozooplankton and small fish over time (years) and space (shelf and water column). Abundance was generally greater in the mid-shelf, where pygmy blue whales aggregate to forage and feed (Gill et al. 2011; refer to Chapter 4). Temporal and spatial variability in weather and physical processes that dominate shelf-circulation patterns and primary productivity in the region were expected to shape neritic aggregation patterns.

In this Chapter, both conceptual and empirical models were developed and tested to understand the relationships between neritic aggregations and their habitat in the Bonney Upwelling. Aggregations were derived from high-resolution hydroacoustic data

at a scale representative of krill aggregations likely to be encountered by foraging pygmy blue whales. The conceptual model was built to provide an *a priori* picture of the biophysical structures and processes likely to be shaping neritic aggregation distribution and abundance. Empirical models were developed to explore the influence of local biophysical structures on the distribution and abundance of neritic aggregations. Model structures included temporal (interannual) and spatial (horizontal and vertical) patterns found to influence neritic aggregation abundance in Chapter 2, and the main forcing features occurring in the region. Empirical model results were given context through the conceptual model and characterisation of the structural conditions of the habitat occurring at the time of sampling.

3.2.   METHODS

3.2.1. General data collection

Simultaneous visual and hydroacoustic surveys were conducted from small boats in a study area selected for its narrow continental shelf, and suitability as foraging habitat for pygmy blue whales (Chapter 2, Figure 2-2) during the autumns of 2003, 2004 and 2007. Surveys were designed as a series of cross-shelf transects (i.e. perpendicular to bathymetry) distributed 3.0 nmi (5.6 km) apart, and randomly selected for survey on any given day. Acoustic data were collected with a calibrated, portable Simrad ES60 echosounder system (Simrad AS, 2000; for system specifications see Chapter 2, Section 2.2.4). Standard-visual, line-transect survey protocols were followed to detect blue whales. Port and starboard observers scanned ahead and to 90 ° abeam of the vessel using the naked eye for sightings of pygmy blue whales and oceanographic features. Weather and effort datasets were collected using dedicated logging software linked to a GPS. Further details of data collection and processing methods can be found in Chapter 2 or below for individual habitat variables.

3.2.2. Characterisation of habitat structure

3.2.2.1. Pelagic Habitat Conceptual Model (PHCM)

A 2D pelagic habitat conceptual model (PHCM) was developed to outline the expected biotic responses to key abiotic habitat structures operating for a region with wind-forced upwelling and a narrow continental shelf (i.e. influenced by 1-step Ekman-type upwelling). The model was constructed to couple the distribution and abundance of aggregating macrozooplankton and small fish to patterns in weather, ocean circulation and primary production. The PCHM was considered in terms of the temporal processes (interannual) and spatial strata (shelf and water column) likely to influence these

abiotic-biotic relationships. The PHCM was informed by a number of conceptual models: primary productivity and mixing (van Ruth et al. 2010b), primary productivity, water mass formation and nutrient enrichment (van Ruth et al. 2010a), water circulation (Currie et al. 2012), Nutrient-Phytoplankton-Zooplankton (NPZ) (Botsford et al. 2003), and regional ecosystem models formulated for southern Australia (Harris et al. 1991, Fulton et al. 2007, Bulman et al. 2011, Goldsworthy et al. 2013). The relationships expressed in the PHCM developed here were used to identify the most appropriate variables and scale for empirical models of pelagic 'schools' (i.e. aggregations of macrozooplankton and fish as defined by hydroacoustics), and to help interpret empirical model results.

3.2.2.2. Remote and in situ characterisation of habitat conditions

The choice of habitat descriptors selected to represent the structures likely to be influencing the abundance of neritic aggregations through the water column was based on: previous relationships described for krill and fish species (Harris et al. 1991, Young & Davis 1992, Schwartzlose et al. 1999, De Silva-Dávila et al. 2002, Lawson et al. 2004, Siegel 2005, Ward et al. 2006, Lawson et al. 2008a), local climatic, ocean circulation and primary production patterns described in the PHCM (reported in Section 3.3.1), accessibility, and temporal and spatial resolution. Descriptors were also selected if they were expected to cause, either directly or as proxies, patterns of neritic aggregation distribution and abundance. Two sets of abiotic and biotic habitat descriptors were considered: 1) horizontal habitat, referred to as 'surface habitat'; and 2) vertical habitat.

Surface-habitat descriptors

The remotely-sensed measurements of sea surface temperature (SST, °C) and surface chlorophyll-*a* (chl-*a*, mg m^{-3}) represent proxies for the distribution of surface-upwelled water and phytoplankton concentration respectively. Chl-*a* was also expected to closely correlate with the distribution and abundance of krill swarms near the surface, that in turn would influence patterns of neritic fish distribution and abundance, with unknown relationships at depth. Even though regions of low SST were considered to represent areas where nutrient-rich water was available to primary producers, SST was also considered with respect to the likely temporal and spatial lag in its influence on patterns in neritic aggregations through the water column. SST and chl-*a* were accessed from the Thematic Real-Time Environmental Distributed Data System (THREDDS, Pacific Fisheries Environmental Laboratory) using extraction software developed for R (Xtractomatic, Environmental Research Division, Southwest Fisheries Science Centre and US National Marine Fisheries Service), both available through NOAA's CoastWatch

West Coast Node (http://coastwatch.pfel.noaa.gov). SST and chl-*a* were acquired for data available to within 0.01 ° radius of the mid position of each 1-km transect interval used to calculate neritic school abundance (see Section 3.2.3.1). SST was available for a blended-weighted mean product from multiple microwave and infrared sensors (AMSR-E, MODIS, Imager, AVHRR) and satellite platforms (Aqua, GOES, POES) for 5-day composite and 0.1 ° resolution. Chl-*a* was derived from MODIS Aqua data (ERDDAP v.1.42) for 8-day averages from a combination of 0.05 ° and 0.025 ° resolution.

Wind forcing is the primary driver of local circulation patterns, and was expected to be a better measure of structures at depth than the above remotely-sensed SST and chl-*a*. Alongshore wind-stress (τ_0, at 315 ° T representing local coastline orientation) was used to represent habitat structures that would have both direct (physical turbulence and stratification, strength of surface currents) and indirect (index of upwelling intensity, relative position of upwelled water on the shelf) effects on the distribution and abundance of schools. For example, positive values of τ_0 correspond with active upwelling (van Ruth et al. 2010b). Wind stress was averaged for the period from the mid-sampling time of neritic school 1-km transect intervals to 24 hours prior (best fit when compared to range of time lags trialled), to account for the lag effects of upwelling or downwelling activity. Wind stress (τ) was calculated according to the equation (van Ruth et al. 2010b):

$$\tau = \rho_a C_D \mathbf{U} |\mathbf{U}|$$

where ρ_a is the density of air (1.2 kg m^{-3}), C_D is the drag coefficient given by Gill (1982), and **U** is wind speed and direction for each half-hourly interval (Cape Nelson automatic weather station, Australian Bureau of Meteorology).

Vertical-habitat descriptors

The vertical water mass was characterised using *in situ* measures of temperature and salinity recorded with a calibrated CTD (conductivity-temperature-depth) instrument (Falmouth Scientific Inc., model FSI MCTD 3"; accuracy: C = ± 0.05 mS cm^{-1}, T = ± 0.4 °C, D = ± 0.45 m; and resolution: C = ± 0.01 mS cm^{-1}, T = ± 0.1 °C, D = 0.03 m). Only data for the May 2003 survey period were used (Chapter 2, Figure 2-2, for sampling locations) due to instrument failure in 2004 and 2007. YSI EcoWatch® software was applied for hardware configuration and deployment, and data retrieval and display.

Three hydrographic strata were considered: upwelled water, stratified water and mixed water (ICES 2000; refer to PHCM in Section 3.3.1). Positions of upwelled water and stratification across each transect were estimated by extrapolating between

temperature and salinity profiles from CTD casts using an optimal interpolating tool in Ocean Data View software (v4.5.2; Schlitzer, R., Ocean Data View, http://odv.awi.de, 2012; DIVA gridding – Data-Interpolating Variational Analysis). Temperature and salinity profiles were then exported as data and images using the 2D Estimation export tool for a subset of depth positions, for each water column position in each school 1-km transect interval (Section 3.2.3.1). Regions influenced by upwelled water and stratification were identified by a combination of relationships between temperature and salinity, visual interpretation of profiles, and comparison to known characteristics of upwelled water in the region. An x-y plot of temperature and salinity for all 2003 casts combined showed a trend for waters with temperatures below 14.7 °C to have salinities below 35.23 psu (Figure 3-1). Waters at or below this temperature and salinity were therefore characterised as being influenced by upwelled water sourced from the Flinders Current. The spikes of lower salinity water seen in Figure 3-1 were expected to be from the input of freshly upwelled water. Similar physical properties were seen in depth profiles of the Bonney Canyon, west of the study area, where a constant salinity of between approximately 35.1 – 35.3 psu was recorded for shelf waters between 12 – 14.5 °C, indicating interaction between well mixed upwelled-water masses and warmer shelf-water masses (see Figure 5 in Currie et al. 2012). These water mass signatures were also seen further west in the eastern GAB (van Ruth et al. 2010b).

The mixed-layer depth (MLD) was derived, where suitable data were available, using a density-based criterion according to the equation in Kara et al. (2000):

$\Delta\sigma_t = \sigma_t\,(T + \Delta T,\, S,\, P) - \sigma_t\,(T,\, S,\, P),$

where σ_t is density, T is temperature, ΔT = 0.8°C (determined as the optimal estimate of turbulent mixing penetration), S is salinity and P is pressure (set to zero). In brief, the MLD is the depth at which the density has increased by $\Delta\sigma_t$ (refer to Figure 3 (Kara et al. 2000), which is determined using a chosen temperature difference, ΔT. Firstly, the $\Delta\sigma_t$ is calculated for a reference density ($\sigma_{t\,ref}$) and temperature (T_{ref}) at 10 m. The depth profile is then explored to find the base of the uniform density layer (i.e. $\sigma_{t\,n}$, where the difference in σ_t is less than or equal to 0.1 $\Delta\sigma_t$ from the $\sigma_{t\,ref}$). $\Delta\sigma_t$ is then added to $\sigma_{t\,n}$ to get the base density, $\sigma_{t\,b}$. The depth at which $\sigma_{t\,b}$ occurs is the MLD.

As an additional descriptor of the water column habitat the approximate depth of the euphotic zone was inferred from the MLDs using the relationship between MLD and euphotic depth as previously calculated from selected casts in the eastern GAB in 2005, just west of the study area (see Figure 8 in van Ruth et al. 2010a; slope = 0.462, regression coefficient = 0.811).

Temporal and spatial patterns in the habitat-structural variables were described in terms of the horizontal and vertical patterns encountered in the data, and relative effects of patterns between sampling periods.

3.2.3. Pelagic School Empirical Models (PSEMs)

3.2.3.1. Response variable selection and treatment

Neritic aggregations were detected and processed from logged acoustic data using Echoview software (v5.0.69.19064, www.echoview.com; Chapter 2, Section 2.2.4). The schools detection algorithm was applied to each echogram according to data-specific settings (Chapter 2, Table 2-2). School descriptors were exported from Echoview separately for schools by intervals (proportions of schools within a given 1-km, transect interval, herein referred to as 'interval'). The detected aggregations were sorted into 'high-S_v' ($S_v$mean ≥ -70 dB) and 'low-S_v' ($S_v$mean -89 to < -70 dB). Only high-S_v schools (referred to as schools) were included into model analyses as they were most likely to contain pygmy blue whale prey (i.e. neritic aggregating macrozooplankton, Chapter 2, Section 2.2.4.2). From these high-S_v schools three acoustic descriptors of aggregation abundance were derived and described in terms of:

1) counts (the total number of whole and part aggregations within an interval),
2) acoustic biomass (the sum of the nautical area backscattering coefficient (ΣNASC, Chapter 2, Appendix 2, Equation 2) of each proportion of an aggregation within an interval), and
3) percentage occupation (the proportion of the total number of acoustic samples that were in aggregations relative to the total number of acoustic samples in the interval, expressed as a percentage).
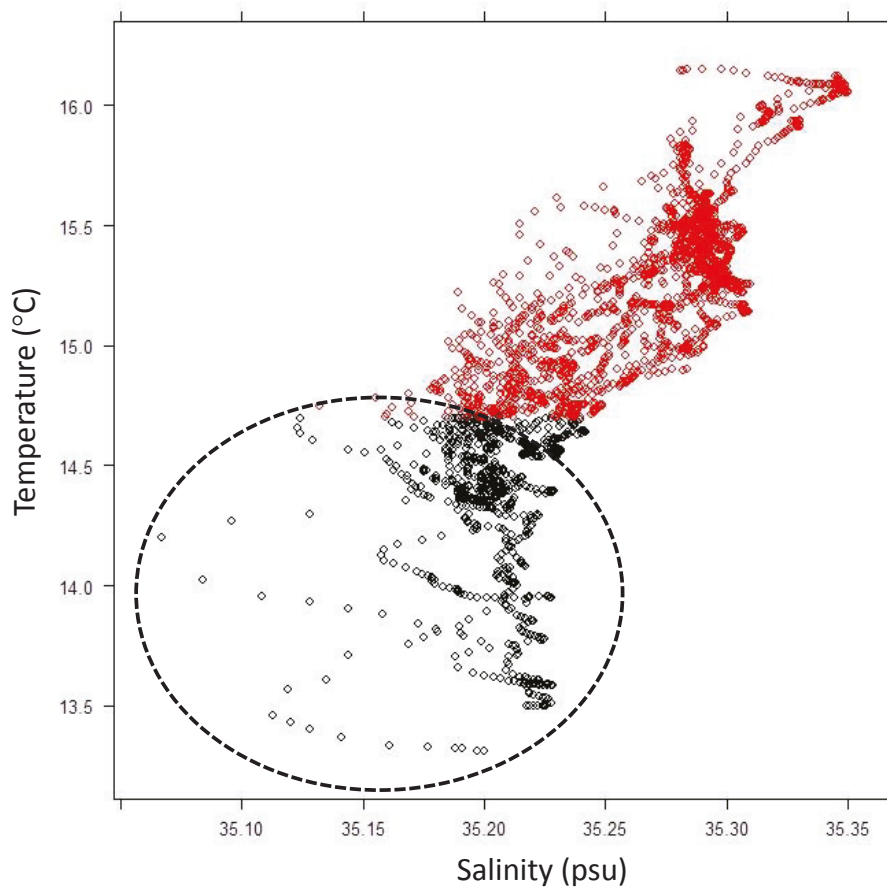
Figure 3-1. Relationship between temperature and salinity from CTD casts deployed in 2003 across the shelf off Portland, Victoria. Red denotes samples with temperature values > 14.7 °C, black < 14.7 °C. Dashed circle highlights estimated boundary of upwelled water mass characterised for this region.

Schools were further classified into water column positions because different habitat variables and their combinations were expected to have different influences on schools depending on where they occurred in the water column (i.e. surface, midwater and demersal; as defined in Chapter 2, Section 2.2.5).

Assumptions of normality, homogeneity and independence for school abundance were checked via exploratory tests. Transects were taken as spatially independent because the sampling design and selection of transects was randomised (Chapter 2, Section 2.2.5). Intervals within transects were chosen to represent independent samples of schools (Carroll & Pearson 2000, Keitt et al. 2002) as the inter-interval distance was based on the longest recorded inter-school distance (i.e. 1 km, from assessment of next

neighbour distances, N_{ext}NDs, Chapter 2, Sections 2.2.4.3). Interval independence was also confirmed via Pearson's correlation coefficients and x-y plots (R software, v2.15.0, R: A Language and Environment for Statistical Computing, R Core Team; packages: Base and Lattice) of pair-wise Euclidean-distance matrix data for inter-interval distances and their respective abundances (counts: R^2 = -0.088, p = 0.003; ΣNASC: R^2 = 0.009, p = 0.75; percentage occupation: R^2 = -0.101, p = 0.0006). School abundances in some intervals may have been biased by off-effort samples, however the effect of these samples is considered low for analyses outcomes. Boxplots and histograms were plotted to examine the data for normality and the presence of outliers (R software, packages: Car and Graphics). All abundance measures were highly skewed with outliers. Counts were less skewed than ΣNASC and percentage occupation. This non-normality was accounted for in model structures.

3.2.3.2. Habitat descriptor selection and treatment

The number of habitat descriptors chosen as explanatory variables for pelagic habitat models were minimised to enhance model performance and avoid collinearity. The surface-habitat descriptors used were SST, chl-*a* and alongshore wind-stress. Two vertical-habitat descriptors were derived from the 2003 CTD data: 'percentage upwelled-water' and 'access to nutrients', which were regarded as vertical descriptors of thermal structure. The percentage upwelled-water was calculated from the difference in the depths of each water column position and the depth of the upwelled-water front (i.e. 14.7 °C), as a percentage. This was calculated only for the midwater and demersal depths as no upwelled water was detected in surface waters. Access to nutrients (a variable representing the vertical limit that phytoplankton had 'access to nutrients' sourced from upwelled water) was calculated from the positional relationship between the upwelled-water front and the MLD. For example, the greater the depth of the mixed-layer below the upwelled-water front, the greater expected access to nutrients in the upper water column. MLD was only derived for midwater depths in 2003 as the MLD was always positioned in that part of the water column. All variable observations were checked for normality and collinearity using histograms, x-y plots and correlation coefficient (using 'Pearsons' method) matrices (R software, packages: Graphics, Lattice, Car, Stats).

3.2.3.3. Modelling approach

Models were developed to determine the habitat structural variables that best explained the distribution and abundance of acoustically detected schools. Generalised Linear Models (GLMs) were chosen to examine these relationships as they were

assumed to be 'linear', but there were non-linear sampling effects, interannual interactions, and non-normality in the response variables to be considered (GLMs; R Core Team, package: Stats; Quinn & Keough 2002, Zuur et al. 2009). Measures of goodness of fit (Burnham & Anderson 1998, Zuur et al. 2009, Burnham et al. 2011) were used to select the best explanatory model/s from the combination of all fitted models i.e. 'best' method procedure. These were Akaike's Information Criterion (AIC), Bayesian Information Criteria (BIC, or Schwarz's Bayesian criterion, a more conservative estimate; BIC function, R Core Team), and Akaike's Information Criterion for small sample sizes (AICc). The best (ranked by information criteria) and full (with the full set of variables) models were then evaluated by checking their dispersion parameter output and plots of their residuals (Pearsons and deviance methods; R software, package: Graphics, plot function; Zuur et al. 2009). Habitat variables that were most influential in the best model/s in explaining the abundance of schools were identified using a combination of t or z values and their respective levels of significance ($p < 0.05$). The intercept was always included in the models but its value had no biological interpretation. Hierarchical partitioning (R software, package: hier.part, C. Walsh, Monash University; based on Mac Nally 2000), which provides the independent and conjoint contribution of each explanatory variable in the best model as a percentage of the total likelihood (Quinn & Keough 2002), was also applied where appropriate using a log-likelihood for Poisson distributions, and R-squared for Gaussian distributions.

3.2.3.4. Model structure

Separate GLMs were run to investigate the relationships of each abundance measure (count, ΣNASC, percentage occupation) with various combinations of water column positions, and surface- and vertical-habitat descriptors (Table 3-1). The aim of these six combinations of model structures was to see if habitat descriptors at depth would perform better than surface descriptors at describing the abundance of schools at depth. As the MLD could not be estimated for all the 2003 subset data (as not all parameters were available for its calculation), separate models and hierarchical partitioning were run for midwater schools with the full (subset A) and reduced dataset (subset B) for 2003 using vertical-habitat descriptors. This allowed an assessment of the influence of missing MLDs on the model outcomes. Models using 2003 data had relatively low sample sizes (full dataset n = 34, reduced dataset n = 22), thus such model outcomes were not considered as reliable as the models using all years data (n > 300).

Table 3-1. Explanatory variables used per model group to investigate how the relationships of surface- and vertical-habitat descriptors relate to each school abundance measure (count, ΣNASC, percentage occupation).

Model group	Year	Water column position	Explanatory variables				
			SST	Chl-*a*	Wind stress	Percentage upwelled water	Access to nutrients
1	2003 2004 2007	Surface Midwater Demersal	X	X	X	-	-
2	2003 subset A	Midwater Demersal	X	X	X	-	-
3	2003 subset A	Midwater Demersal		X	X	X	-
4	2003 subset B	Midwater	X	X	X	-	-
5	2003 subset B	Midwater	-	X	X	X	-
6	2003 subset B	Midwater	-	X	X	-	X

As all school abundance measures showed different levels of over-dispersion (i.e. left skewed distributions), different families and link functions were applied. Raw counts were applied with a Poisson distribution (dispersion parameter ψ taken to be 1) in combination with either a 'log', 'square root' or '4th root' link function to see which model performed the best in terms of their residual patterns. Quasi-poisson was not considered as it didn't provide an AIC value. A negative binomial with a 'log' link (R software, package: MASS) was also considered to account for overdispersion, but was found to not perform well in residual plots and was likely over compensating for dispersion in the response data. Although the GLMs showed similar explanatory model/s when run with the different link functions, not all of them could run for all water column data, therefore the Poisson (log-link) model was reported as it showed a good pattern of the residuals. The ΣNASC and percentage-occupation measures were found to still have high dispersion parameters (> 5) as measured by the model when run as raw data using a Gaussian distribution ($\psi = \sigma^2$) and a 'log' link. They were consequently run as log-transformed ($\log(x+1)$) response variables to normalise their mean and variance across the full range of data, using a Gaussian distribution with an 'identity' link. Model outcomes were not affected by the presence of outliers, thus all data were included in the ΣNASC and percentage occupation models.

The structure of these GLMs was designed to account for a number of *a priori* patterns in the data. GLMs for midwater schools accounted for the different areas of water

sampled by each interval with the inclusion of an 'offset' term for the mean depth of each interval (Zuur et al. 2009). In addition, the effect of different sampling years on each abundance measure, which was assumed from the interannual differences found in the Chapter 2 PERMANOVA analyses, was also included in the model structure (i.e. year was added as a nominal variable (factor) to each model-set combination). Not all possible interaction terms could be included in the model structure as they would be collinear with the main effects. Nonetheless, it was recognised that the effects of wind stress and upwelling activity could vary from year to year (Middleton et al. 2007, Middleton & Bye 2007, Nieblas et al. 2009, van Ruth et al. 2010b), and this was considered in the interpretation of the model results.

3.3.   RESULTS

3.3.1. Characterisation of habitat structure

3.3.1.1.   *Pelagic habitat conceptual model (PHCM)*

The PHCM built here has four main abiotic-biotic patterns that are likely to be encountered in the mid-late upwelling season, for regions with a narrow continental shelf, 1-step upwelling process and coastline parallel to upwelling-influential winds (Figure 3-2).

Pattern 1: *Shelf waters are well mixed and therefore there is little or no stratification of the water column*. This pattern is driven by extended periods of high wind stress from the west and south-west, causing downwelling. Under these circumstances no enrichment of shelf waters from nutrient-rich bottom water off the shelf (originating from the Flinders Current and Tasmanian Subantarctic Mode Water,Middleton & Bye 2007) would be expected, leading to low primary productivity (Scenario 1, Figure 1 in van Ruth et al. 2010a, and van Ruth et al. 2010b). Aggregating macrozooplankton and fish would not be expected to be structured into any particular part of the water column, but to be relatively evenly distributed across the shelf in low numbers. In addition, as horizontal and vertical physical stratification would be low or non-existent, abiotic parameters chosen to represent stratification patterns would similarly have weak relationships with the distribution and abundance of aggregating macrozooplankton and fish. The exception to this pattern would occur when alternative food sources not dependent on access to nutrients and light were available, such as those delivered by microbial food pathways.

Pattern 2: *The occurrence of upwelling-influential winds from the south-east changes the across-shelf and water column physical stratification leading to transport of deep nutrient-rich water onto the shelf*. This would shoal the thermocline and MLD, but not as far as the euphotic depth (Z_{eu}), also resulting in low primary productivity (Scenario 2, Figure 1 in van Ruth et al. 2010a; and Scenario 3, Figure 1, van Ruth et al. 2010b). This pattern could still occur during weak- and mid-downwelling winds following a period of upwelling. Under these circumstances, macrozooplankton and fish and their relationships to abiotic parameters would be similar to Pattern 1.

Pattern 3: *Sustained upwelling, from an extended period of upwelling-favourable winds, and further shoaling of the thermocline to above the euphotic depth (Scenario 3, Figure 1 in van Ruth et al. 2010a; and Scenario 2, Figure 1, van Ruth et al. 2010b) enhances nutrient availability to phytoplankton in the euphotic zone*. This would result in increased productivity available to macrozooplankton and fish. The depth of maximum abundance of phytoplankton, and therefore grazers, would depend on a set of optimal physical conditions affecting water column stability (Coyle et al. 2008). These include the volume of upwelled water onto the shelf, which would in turn depend on the strength and periodicity of upwelling favourable winds and other influential physical forces that affect local water circulation. Under strong Pattern 3 conditions, upwelled water would reach the ocean surface and increased primary production would occur throughout the water column (Scenario 4, Figure 1 in van Ruth et al. 2010a). Surface upwelled water is expected to be transient, becoming regularly mixed with local, warmer, surface waters, or driven down through the water column during downwelling-influential winds. Grazers and their predators would be found in high abundance associated with the distribution and abundance of primary producers. This scenario would occur particularly downstream (i.e. down current) of upwelled water due to the time lags associated with phytoplankton responding to increased nutrients and then further time for macrozooplankton and fish aggregations to exploit the increased abundance of phytoplankton or grazers. Factors that may affect zooplankton and fish reaching, or optimally using, these primary food resources could be: physiological and behavioural drivers (such as temperature effects of nearby water masses on metabolism), and movement of neritic aggregations out of their optimal feeding areas (due to strong current systems such as surface Ekman-driven currents). Such movement could be passive (e.g. non-motile juveniles carried in currents) or active (e.g. adult zooplankton and small fish regulating their position in the water column). Such factors will cause a temporal mismatch in expected grazing interaction.

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Pattern 4: *During sustained low-wind (and therefore quiescent) periods after an upwelling event/s surface turbulence decreases but the depth of the MLD (that depends on previous wind and circulation patterns) still circulates nutrients to the surface.* Nutrients would be used by phytoplankton (as they passively sink through them). Surface krill swarms would probably be most prevalent during this pattern as they consume the available phytoplankton and are likely to associate with zooplankton layers in this zone (Chapter 2). Pelagic fish are also likely to use increased concentrations of prey in surface and upper-midwaters during this pattern. Primary and secondary productivity would not be as temporally mismatched as in Pattern 3, although grazing pressure may be more prevalent.

3.3.1.2. Remote and in situ characterisation of habitat conditions

Figure 3-3 provides the daily means (± SE) for each of the surface habitat variables used in the empirical models across the three years of sampling. It shows that all variables were represented by both within-day and between-day variability, where sampled consecutively, particularly for alongshore wind-stress and chl-*a*. The intensity of

upwelling varied across the sampling periods and across years, with periods of upwelling (positive wind stress) being more intense than periods of downwelling (negative wind stress, Figure 3-3). This showed that the late-autumn-winter pattern of downwelling and mixing (PHCM, Pattern 1 and 2, Figure 3-2) had not occurred and that Patterns 3 and 4 in the PHCM best reflected habitat conditions. The pattern of wind stress from day to day generally matched chl-*a*, with periods of increased upwelling-favourable winds corresponding to elevated primary production (Figure 3-3). Although wind stress and chl-*a* showed low linear correlation (r = 0.276), strong time lag (i.e. greater than 24 hours) from increased wind stress to increased primary production could be expected.

The effect of wind stress on upwelling was further demonstrated by looking at the pattern of upwelling intensity across the whole sampling period for each year (Figure 3-4). Wind stress data show that the days prior to each period of sampling were characterised by either highly-positive or highly-negative wind stress, and in some cases both, corresponding to cycles of upwelling and downwelling, because sampling occurred during low wind activity. Prior oceanographic activity (greater than 1 – 3 days prior to sampling) would have therefore influenced the availability of light and nutrients, and thus, primary production. Of note was that SST was never below 14.7 °C, indicating limited direct surface expression of upwelled water during sampling, regardless of where intervals were sampled on the shelf. However, upwelled-influenced water offshore of upwelling plumes can be seen in Figure 3-5 where

movement of a high-pressure ridge through the study area caused strong north to northwesterly winds. These winds carried upwelled-influenced surface waters from the main upwelling jets at Capes Nelson, Bridgwater and Duquesne offshore, directly through the study area. Typically, upwelling jets move to the west and northwest, forced by prevailing southeasterly winds (Figure 12 in Middleton & Bye 2007).
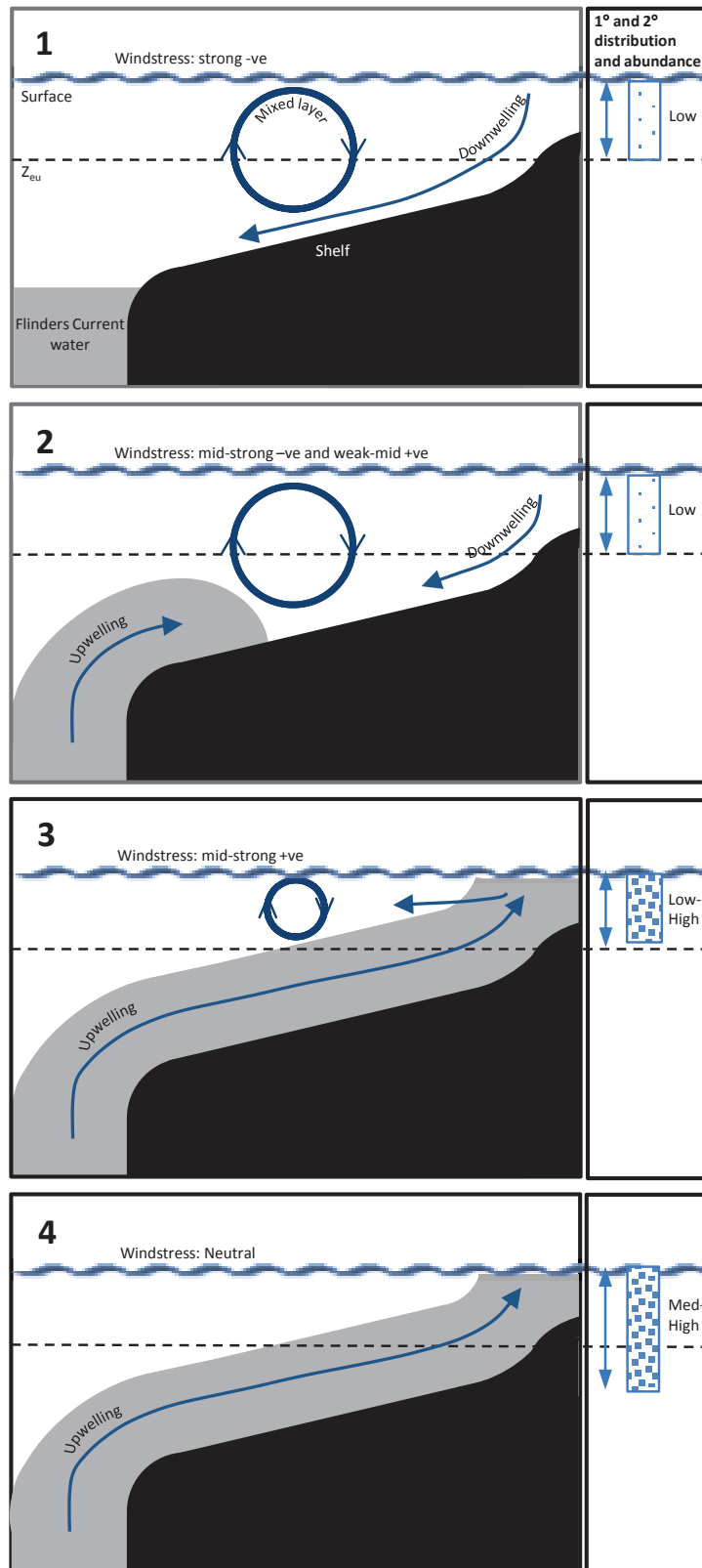
Figure 3-2. Conceptual model of the four main weather and ocean circulation spatial patterns expected to occur across the narrow continental shelf off southern Australia during the mid to late upwelling season, and associated distribution and abundance of phytoplankton (1°) and pelagic aggregations (2°). Alongshore wind-stress (τ_0) is an index of upwelling intensity; positive values correspond to upwelling (van Ruth et al. 2010b). The approximate depth of the mixed-layer (MLD) is shown by the rotating circle, no MLD is indicated for Pattern 4 as it will depend on previous wind activity. The euphotic depth (Z_{eu}) is shown by the dashed line, and the Flinders Current upwelled water is dark grey. The main direction of water flow is indicated by arrows. The right-hand panel shows the expected depth range (⟷) of phytoplankton and macrozooplankton and small fish, the pattern of distribution (Dispersed = ⬚ , Clumped = ▨), and the range of abundance (low-high) relative to this region at this time of year. Refer to text for more detail. Ocean circulation and phytoplankton model adapted from van Ruth et al. (2010b, 2010a).
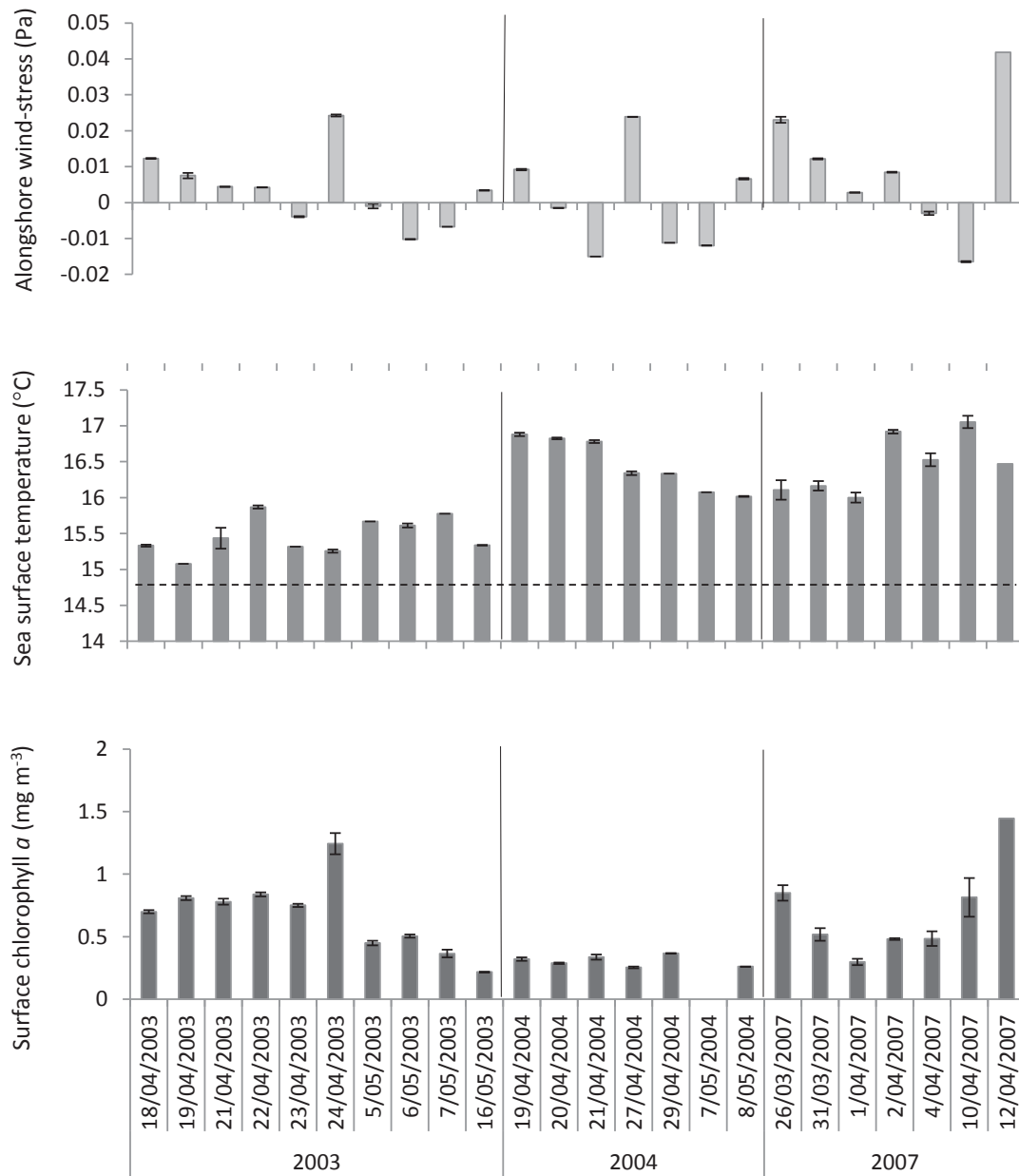
Figure 3-3. Daily means (± SE) for the habitat variable values from each school interval used in the GLMs from 2003 to 2007. Years demarcated by the solid vertical lines. Positive values of alongshore wind-stress indicate upwelling, negative values downwelling. A dashed line shows the upwelled-water front at 14.7 °C.

Figure 3-4. Daily-mean, alongshore wind-stress for the entire sampling period for each year. Sampling days are marked by the dashed vertical lines, and years by solid lines.
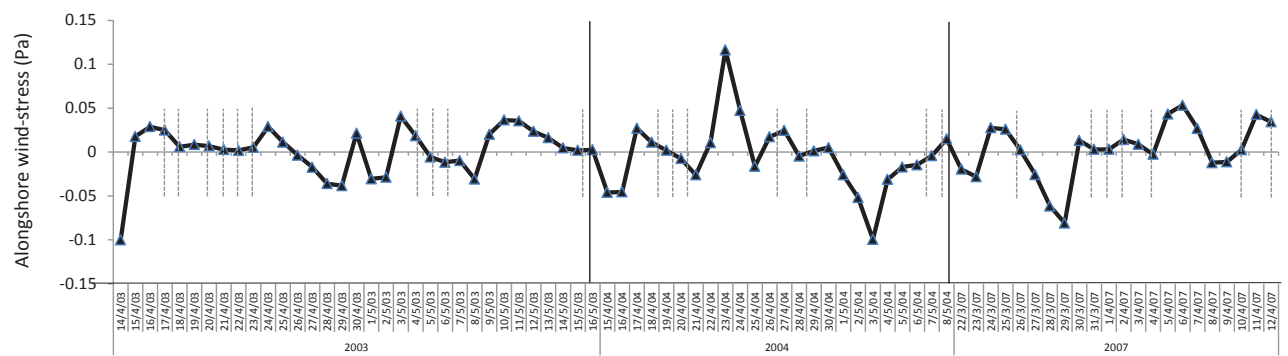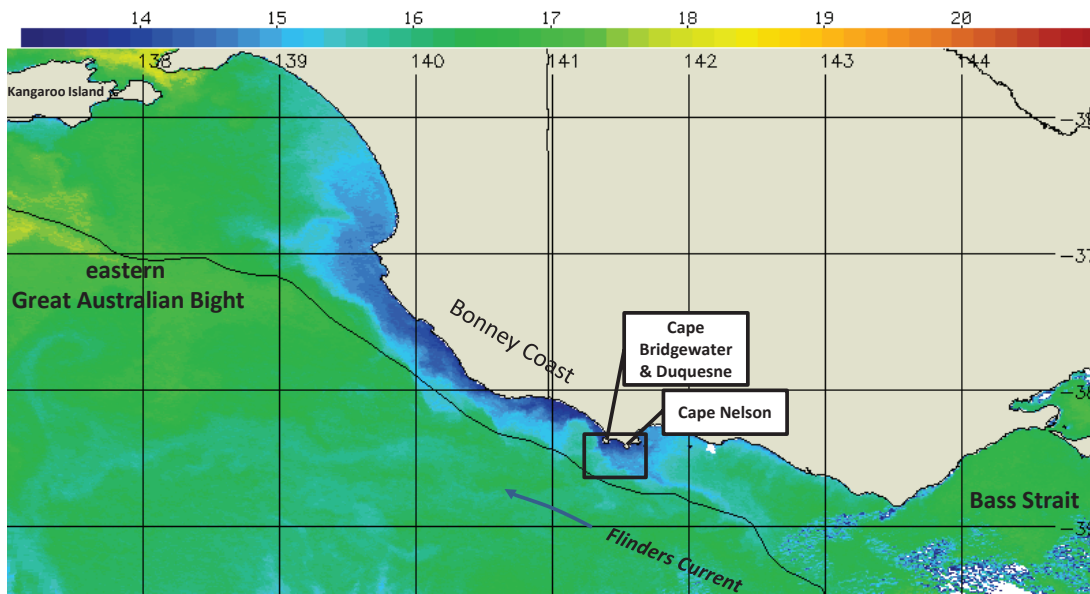
Figure 3-5. Remotely-sensed image of sea surface temperature, showing the dispersion of the upwelling plume to the south and south-east from their surface origins north-west of Capes Duquesne, Bridgewater and Nelson. Box indicates approximate boundary of study area. Temperature scale shown above image. 100 m isobath shown.

The patterns in the surface habitat variables used in modelling were further complemented by examining the vertical habitat structure from data available for 2003. The period of sampling late in the season (i.e. 5 – 7 and 16 May 2003) covered a period of strengthening upwelling. The coldest and lowest salinity water was found near the ocean floor and towards the edge of the shelf on Transect 16 (minimum 13.30 °C, 35.06 psu; Figure 3-6, 16a, b). This indicated a water mass that was closer to the source of the Flinders Current, likely from an adjacent canyon, one of the deepest in the study area (see Figure 3 in Harris & Whiteway 2011). This is in contrast with areas where water temperatures above 14.7 °C had gradually increasing salinities (Figure 3-1, Figure 3-6), and generally corresponded to waters close to the edge of the surface mixed-layer (i.e. above the MLD; Figure 3-6, 13 - 18b). The pattern of a more structured water column (i.e. more extensive presence of upwelled water on to the shelf to within 40 m of the surface; as described in the PHCM, Pattern 3) later in the sampling period (i.e. prior to and during Transects 17 and 18) was supported by an upwelling-favourable wind pattern (Figure 3-4). This was also supported by calculations of the euphotic depth (Z_u) that extended to the ocean floor in all except one case in Transect 17 (not shown in figures). This indicates that the full water column was not limited by light for primary producers during the sampling period.
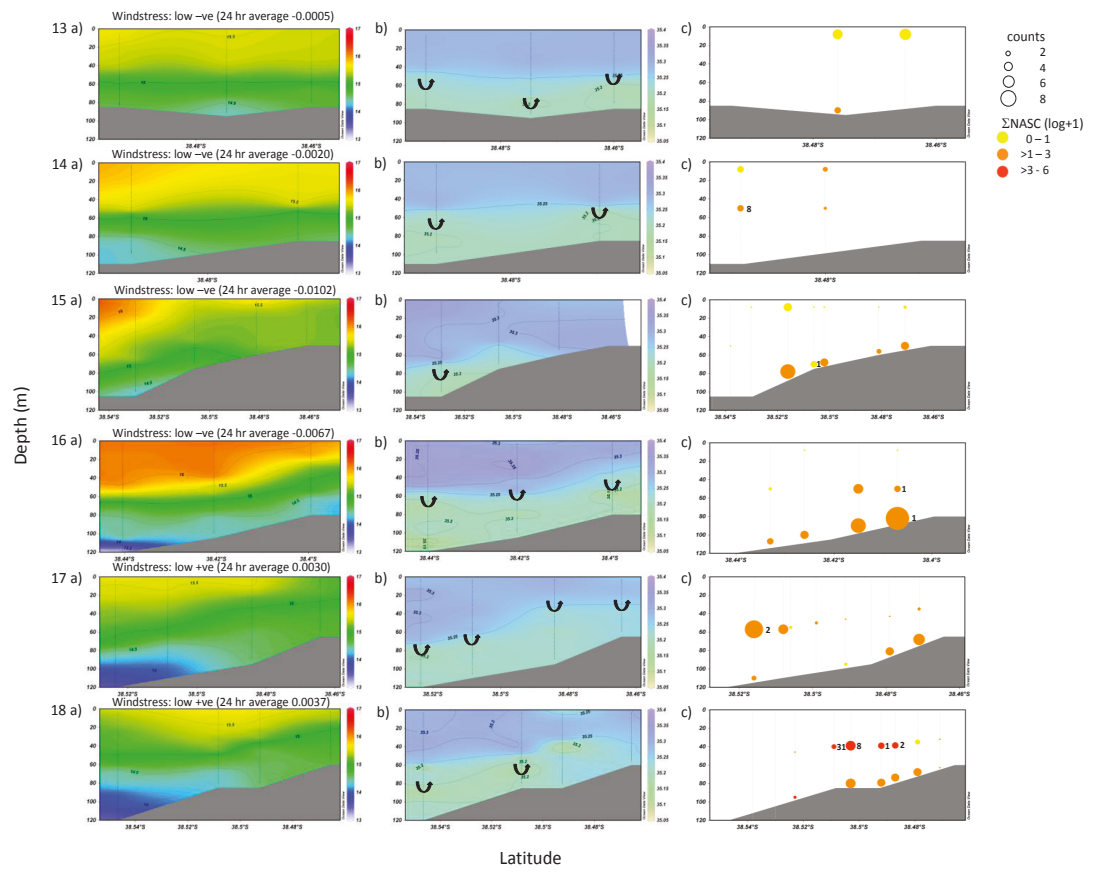
Figure 3-6. Cross-shelf hydrological characteristics of the water column in relation to the abundance of schools for a subset of the 2003 data. Plots are for transects 13 – 18 showing a) interpolated temperature profile, b) interpolated salinity profile, and c) the abundance of schools for each interval used in modelling. The maximum depth of the mixed-layer is marked by the symbol $\cup$. The 24-hourly wind stress for each transect is shown above each temperature profile. Counts are indicated by circle sizes, ΣNASC by colour gradients, and percentage occupation by numbers (shown in the figure to the right of interval positions where values were greater than 1 percent).

3.3.2. Pelagic School Empirical Models (PSEMs)

3.3.2.1. Models using surface habitat structures across years (Model Group 1)

Surface schools

The models with chl-*a*, wind stress and year ranked the best in explaining the relationship between the counts of schools near the ocean surface and the selected habitat variables (Table 3-2a). Although all variables were influential, chl-*a* and wind stress had high relative *z*-values (Table 3-2d) and larger independent percentage contributions to the total likelihood (wind stress: I = 33 %, chl-*a*: 35 %; Figure 3-7), based on the full model with all variables.

The models best explaining the ΣNASC of schools near the surface were the full model with all variables (Model 4), and a reduced model excluding SST (Model 5; Table 3-2a). This confirmed that chl-*a* and wind stress were the most influential variables (Table 3-2d; Figure 3-7), having positive relationships with ΣNASC. Chl-*a* had the highest independent contribution (I = 66 %). Once again, the inclusion of year was important between all year combinations, although less so between 2004 and 2007 (Table 3-2d).

Chl-*a*, wind stress and year were found to best explain the percentage occupation of surface schools (Table 3-2a). Chl-*a* was the most influential variable having higher *t*- and I-values than wind stress, and both having a positive relationship with percentage occupation of schools (Table 3-2d; Figure 3-7). The inclusion of year as a factor had some influence on the model outcome, particularly 2003 versus 2004 and 2007 (Table 3-2d).

Midwater schools

The counts of midwater schools were best explained by the model with all habitat variables (Model 7) and the model without SST (Model 8; Table 3-2b). Although a fully comparable hierarchical partitioning statistic could not be achieved for midwater schools (as the offset for different sampling depths could not be considered), chl-*a* was the most influential explanatory variable (*z*-value = -2.6, p = 0.009; I = 29 %; Table 3-2e; Figure 3-7). Chl-*a* was influenced heavily by the variation between all year combinations (I = 52 %; Figure 3-7e).

The ΣNASC for schools in the midwater was best explained by the model with all habitat variables (Model 9; Table 3-2b). All variables were influential, but wind stress made the highest contribution (I = 44 %; Table 3-2e; Figure 3-7). SST and chl-*a* had a negative relationship with midwater school ΣNASC (similar to counts), and wind stress

had a positive relationship. The differences in midwater school ΣNASC between 2007 and both 2003 and 2004 influenced these relationships (Table 3-2e).

Wind stress and year best explained the percentage occupation of schools in the midwater (Table 3-2b). The least influential variable was chl-*a*, which also made the lowest independent percentage contribution to the likelihood (I = 5%, Figure 3-7). SST had a negative relationship with percentage occupation (Table 3-2e) and had the highest I-value (I = 44%; Figure 3-7); wind stress had a positive relationship. The inclusion of the differences in percentage occupation between 2004 and 2007 was important in improving the model fit (Table 3-2e).

Demersal schools

The model best explaining counts of demersal schools was the model with all variables (Model 15; Table 3-2c). There was no clear distinction between the explanatory variables driving the pattern of demersal counts (Table 3-2f; Figure 3-7), however chl-*a* was slightly more influential and had a significant positive relationship with counts, compared to wind stress and SST that had negative relationships. There were also differences in counts between years (Table 3-2f).

The pattern of habitat relationships for the ΣNASC for demersal schools was best represented by models with chl-*a*, year and/or SST (Model 16 and 17; Table 3-2c). Wind stress was the least influential variable (lowest I = 4%; Figure 3-7); SST the most influential, having a negative relationship with ΣNASC along with chl-*a* (Table 3-2f; Figure 3-7). Year differences between 2004 and 2003, and 2004 and 2007 had an effect on these relationships (Table 3-2f).

The model with only wind stress and year ranked as the most parsimonious across all model combinations for explaining the percentage occupation of demersal schools (Model 18; Table 3-2c). Although wind stress contributed to the independent percentage of the total likelihood, other variables such as SST also contributed when compared across the full model (wind stress I = 18 %, SST I = 48%; Table 3-2f; Figure 3-7). This was also reflected in the fact that models with SST were ranked 2nd and 3rd by the AIC and BIC (Table 3-2c). The differences between 2004 and 2003, and 2004 and 2007 were important in explaining the relationship between demersal school percentage occupation and habitat variables (Table 3-2f).

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Table 3-2. GLM results for school intervals for Model Group 1 at a) surface, b) midwater and c) demersal depths, performed for each abundance measure using all possible combinations of habitat variables. Only the 'best' model/s (out of the total 16 models) are presented using a combination of AIC and BIC. Where there was disagreement between AIC and BIC, then the group of best models are tabled, ordered by AIC, with the 'best' BIC in bold. Chl-a = surface chlorophyll-a; SST = sea surface temperature; df = degrees of freedom; ψ = overdispersion parameter; P = number of parameters in each model; N = number of samples in the model. Figures d) to f) show model results for each habitat variable for surface, midwater and demersal depths respectively; z or t statistic provided with their respective p-values (p < 0.05 in bold).

a)

Name	Model	AIC	BIC	null deviance	df	residual deviance	df	ψ	P	N/P ratio
Count										
Model 1	chl a + wind stress + year	992.15	1011.02	1329.42	321	674.84	317	2.13	3	110
Model 2	sst + chl a + wind stress + year	994.02	1016.67	1329.42	321	674.72	316	2.13	4	83
Model 3	wind stress + year	995.27	**1010.47**	1351.41	329	679.96	326	2.09	2	165
NASC										
Model 4	sst + chl a + wind stress + year	553.91	580.33	134.98	321	100.83	316	0.32	4	83
Model 5	chl a + wind stress + year	557.51	**580.16**	134.98	321	102.60	317	0.32	3	110
Occupation										
Model 6	chl a + wind stress + year	-852.05	**-829.40**	1.76	321	1.29	317	0.00	3	110

b)

Name	Model	AIC	BIC	null deviance	df	residual deviance	df	ψ	P	N/P ratio
Count										
Model 7	sst + chl a + wind stress + year + depth	1127.80	1150.38	794.15	320	719.11	315	2.28	5	66
Model 8	chl a + wind stress + year + depth	1128.70	**1147.60**	794.15	320	722.10	316	2.29	4	83
NASC										
Model 9	sst + chl a + wind stress + year + depth	978.52	1004.92	404.67	320	379.28	315	1.20	5	66
Model 10	sst + chl a + year + depth	979.42	**1002.05**	404.67	320	382.73	316	1.21	4	83
Occupation										
Model 11	wind stress + year	-120.32	-101.32	13.56	329	13.02	326	0.04	2	165
Model 12	sst + year	-119.35	-100.39	13.55	327	12.95	324	0.04	2	165
Model 13	sst + wind stress + year	-118.86	-96.10	13.55	327	12.89	323	0.04	3	110
Model 14	wind stress	-114.80	**-103.40**	13.56	329	13.40	328	0.04	1	330

c)

Name	Model	AIC	BIC	null deviance	df	residual deviance	df	ψ	P	N/P ratio
Count										
Model 15	sst + chl a + wind stress + year	1525.10	**1547.76**	1076.94	321	939.11	316	2.97	4	83
NASC										
Model 16	sst + chl a + year	875.11	897.76	299.05	321	275.10	317	0.87	3	110
Model 17	chl a + year	875.78	**894.66**	299.05	321	277.39	318	0.87	2	165
Occupation										
Model 18	wind stress + year	-441.72	**-422.73**	5.47	329	4.92	326	0.02	2	165

d)

Name	Model	sst			chl a			windstress			year (2003:2004)		year (2003:2007)		year (2004:2007)	
		slope	z	p	slope	z	p	slope	z	p	z	p	z	p	z	p
Count																
Model 19	chl a + wind stress + year				0.273 (0.139)	1.960	0.050	61.794 (5.137)	12.031	<2e-16	-9.944	<2e-16	-10.328	<2e-16	6.183	6.28e-10
Model 20	sst + chl a + wind stress + year	0.053 (0.148)	0.356	0.722	0.280 (0.140)	1.997	0.046	61.890 (5.120)	12.112	< 2e-16	-9.042	< 2e-16	-6.629	3.38e-11	6.194	5.87e-10
Model 21	wind stress + year							68.709 (3.775)	18.200	< 2e-16	-11.291	< 2e-15	-11.248	< 2e-16	6.925	4.37e-12
NASC																
Model 22	sst + chl a + wind stress + year	0.208 (0.088)	2.356	0.019	0.452 (0.107)	4.219	3.21e-05	13.165 (2.836)	4.643	5.05e-06	-4.265	2.64e-05	-3.657	0.0003	2.073	0.039
Model 23	chl a + wind stress + year				0.483 (0.107)	4.510	9.16e-06	10.371 (2.594)	3.998	7.95e-05	-3.796	0.0002	-2.852	0.005	1.551	0.122
Occupation																
Model 24	chl a + wind stress + year				0.070 (0.012)	5.872	1.09e-08	1.228 (0.291)	4.224	3.14e-05	-2.526	0.012	-3.384	0.0008	-0.273	0.785

e)

Name	Model	sst			chl a			windstress			year (2003:2004)		year (2003:2007)		year (2004:2007)	
		slope	t	p	slope	t	p	slope	t	p	t	p	t	p	t	p
Count																
Model 25	sst + chl a + wind stress + year + depth	-0.224 (0.131)	-1.718	0.086	-0.494 (0.190)	-2.606	0.009	11.031 (4.733)	2.331	0.020	-2.399	0.016	3.302	0.001	7.403	1.3E-13
Model 26	chl a + wind stress + year + depth				-0.530 (0.190)	-2.839	0.005	13.750 (4.340)	3.168	0.002	-4.863	1.16e-06	2.976	0.003	7.875	3.41e-15
NASC																
Model 27	sst + chl a + wind stress + year + depth	-0.397 (0.172)	-2.310	0.022	-0.240 (0.210)	-1.146	0.253	9.326 (5.510)	1.693	0.091	0.420	0.674	2.409	0.017	2.483	0.014
Model 28	sst + chl a + year + depth	-0.519 (0.157)	-3.312	0.001	-0.111 (0.200)	-0.569	0.570				1.298	0.195	3.153	0.002	2.097	0.037
Occupation																
Model 29	wind stress + year							1.773 (0.842)	2.107	0.036	-1.939	0.053	1.047	0.296	3.062	0.002
Model 30	sst + year	-0.069 (0.030)	-2.480	0.014							0.631	0.530	2.510	0.013	2.585	0.010
Model 31	sst + wind stress + year	-0.055 (0.030)	-1.813	0.071				1.121 (0.919)	1.220	0.223	0.201	0.841	2.051	0.041	2.698	0.007
Model 32	wind stress							1.690 (0.851)	1.987	0.048						

f)

Name	Model	sst			chl a			windstress			year (2003:2004)		year (2003:2007)		year (2004:2007)	
		slope	t	p	slope	t	p	slope	t	p	t	p	t	p	t	p
Count																
Model 33	sst + chl a + wind stress + year	-0.363 (0.104)	-3.507	0.0005	0.261 (0.111)	2.346	0.019	-13.460 (3.442)	-3.909	9.25e-05	-2.516	0.012	3.625	0.0003	7.286	3.20e-13
NASC																
Model 34	sst + chl a + year	-0.215 (0.132)	-1.626	0.105	-0.0073 (0.165)	-0.445	0.657				-1.251	0.212	1.871	0.062	4.278	2.5e-05
Model 35	chl a + year				-0.0064 (0.165)	-0.388	0.699				-3.418	0.0007	1.004	0.316	4.538	8.05e-06
Occupation																
Model 36	wind stress + year							-0.660 (0.520)	-1.268	0.206	-5.378	1.44e-07	-0.739	0.460	4.848	1.93e-06
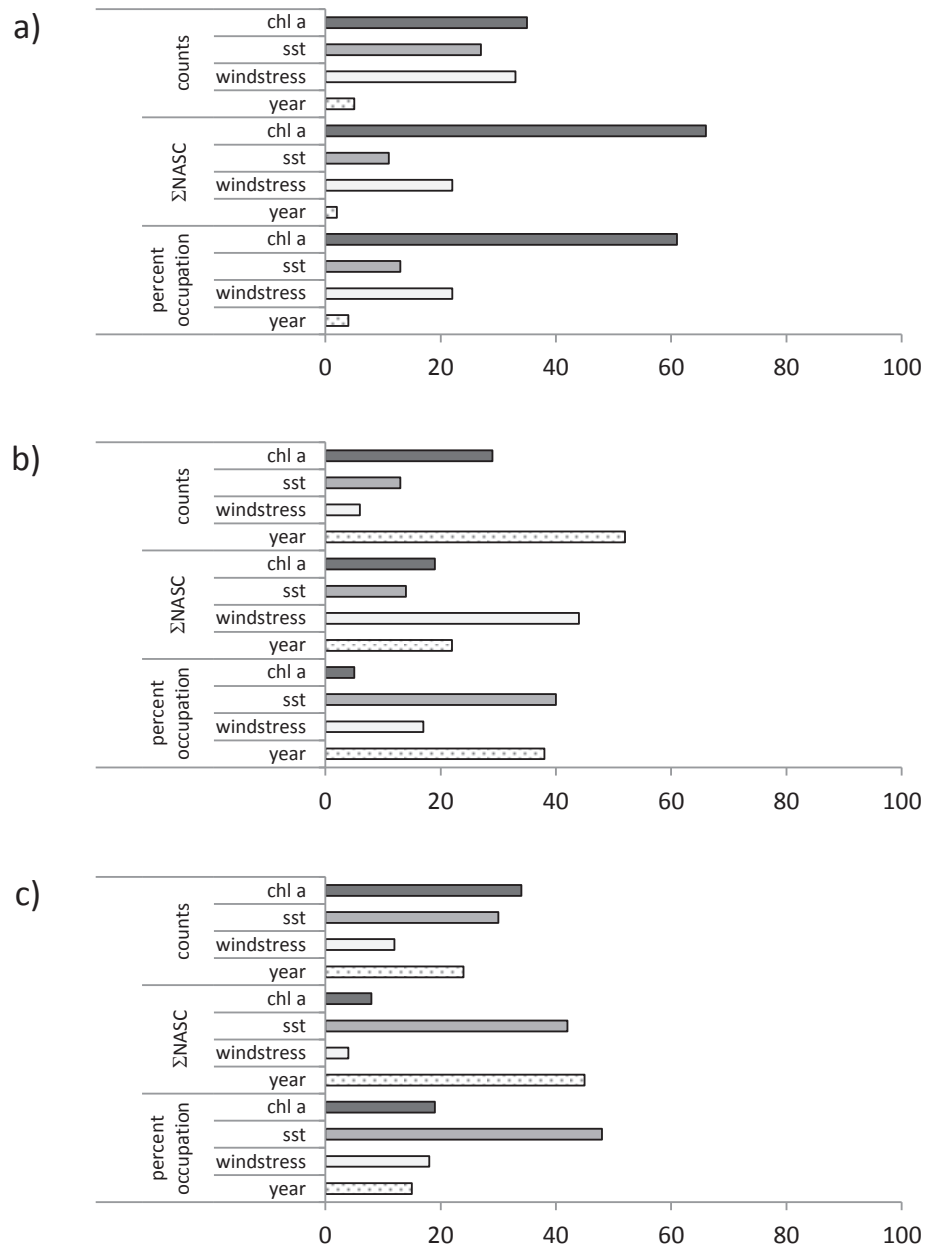
Figure 3-7. Percentage contributions of independent effects for each habitat variable calculated from hierarchical partitioning (HP) for the GLMs for Model Group 1 explaining a) surface, b) midwater and c) demersal schools separately for each abundance measure across all years. Percent occupation = percentage occupation, chl-*a* = surface chlorophyll-*a*, SST = sea surface temperature. The midwater HP values are not fully comparable with the surface and demersal GLMs for count and ΣNASC as they could not account for different water depths across the intervals, but they give an indication of the patterns encountered.

3.3.2.2. Models using vertical habitat structures in 2003 (Model Groups 2-6)

Midwater schools

The patterns in the counts of midwater schools in 2003 were explained by different models when the three different measures of thermal structure were used (i.e. SST, percentage upwelled-water and access to nutrients). The model run with SST (Model Group 2, Table 3-1) was best explained by models with all variables and with only wind stress (Model 1 and 2; Table 3-3a). When SST was replaced by the percentage upwelled-water (Model Group 3), the best model included only wind stress for all information criteria (Model 2; Table 3-3a), closely followed by the model with chl-a (ΔAIC = 0.22, not shown). This model selection was similar when the percentage upwelled-water was replaced by access to nutrients (Model Group 6), with the chl-a model ranked the best for all information criteria (Model 3; Table 3-3a) followed by the model with wind stress (ΔAIC = 0.32, not shown). These relationships were reflected in the hierarchical partitioning analysis that showed there were no dominant variables across the model runs, although chl-a (that had a negative relationship with counts, Table 3-3c) was always slightly higher in contributing to the independent effects, or the same in the case of the model using access to nutrients (Figure 3-8a).

The model containing wind stress clearly best described the pattern of midwater acoustic biomass (ΣNASC) of schools in 2003 (Model 4; Table 3-3a). This model was the most parsimonious for all information criteria, regardless of the thermal structure variable used (Table 3-3a). The model containing chl-a alone was consistently ranked second (with a range in the ΔAIC of 0.80 – 1.32) to the model containing wind stress (not shown). Wind stress was also the variable that consistently made a higher independent contribution of the total likelihood (Figure 3-8b), with the use of the percentage upwelled-water (Model Group 3) being slightly better than SST (Model Group 2) and access to nutrients (Model Group 6) in midwater (Figure 3-8b).

The model containing wind stress (Model 5) was also the most parsimonious across the full set of models for the percentage occupation of midwater schools in 2003 when SST (Model Group 2) and percentage upwelled-water (Model Group 3) were used as the variables representing vertical thermal structure (Table 3-3a). These thermal variables, however, still contributed to explaining the pattern of occupation of schools in the GLM and hierarchical partitioning analyses, being included in the top three models (not shown); the percentage upwelled-water also had the second highest I-value (I = 27 %) following wind stress (I = 48 %; Figure 3-8c). When access to nutrients was included in the models (Model Group 6), it was the most influential variable, being ranked as the

top model across all information criteria (Model 6; Table 3-3a and c) and the highest I-value (I = 59%; Figure 3-8c).

When models were run with the reduced dataset where MLDs were available (Model Groups 4-5), there was little change to the rankings in the models and percentage contributions to the total likelihood, as calculated by hierarchical partitioning (results not shown), and therefore some confidence was given to comparison of the results with the full dataset. The main difference was for midwater counts when percentage upwelled-water was used. This gave greater influence to percentage upwelled-water, with the top two ranking models being chl-*a* and percentage upwelled-water, and wind stress and percentage upwelled-water.

Demersal schools

Different explanatory models were selected for counts of demersal schools when using the different variables for thermal structure. Although the model run using SST (Model Group 2) ranked the model with just SST as the best for all information criteria (Model 7; Table 3-3b), the AIC difference was only 0.06 between it and the next ranked model containing chl-*a* and wind stress (not shown). This model (Model 8) and the model with only wind stress (Model 9) were identified as the best models when the percentage upwelled-water was included (ΔAIC = 0.16). Wind stress, which was in the best models and had a negative relationship with demersal schools (Table 3-3d; compared to having a positive relationship with midwater schools), had the highest independent percentage contribution of the total likelihood for the models run with the different thermal structures (Model Groups 2, 3 and 6; Figure 3-8d). Of the two thermal structures, SST had a higher I-value (I = 37 %) than the percentage of upwelled water (I = 18 %).

The model using wind stress (Model 10) was ranked the best for explaining the ΣNASC of demersal schools when using SST (Model Group 2). When SST was replaced with the percentage upwelled-water (Model Group 3), this measure of thermal structure was much better at explaining variation in the biomass of demersal schools (Model 11; Table 3-3b; Figure 3-8e), and showed a negative relationship with biomass (t = -1.29, I = 80 %; Table 3-3d). The models using only wind stress or a measure of thermal structure both ranked well in explaining the occupation of demersal schools (Table 3-3b). Those variables had a negative relationship with the occupation of demersal schools (Table 3-3e). Wind stress had the highest I-value for the model set including SST (Model Group 2; I = 53%; Figure 3-8f), compared to the model set with the percentage upwelled-water where that variable had the highest I-value (Model Group 3; I = 46%; Figure 3-8f).

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Table 3-3. GLM results for 2003 school intervals for Model Groups 2, 3 and 6 at a) midwater and b) demersal depths, for each abundance measure using surface- and vertical-habitat variables. The 'best' model/s are presented using a combination of AIC, BIC and AIC_c. Where there was disagreement between AIC, BIC and AIC_c the group of best models are tabled, ordered by AIC, with the 'best' BIC and AIC_c in bold). z or t statistic provided with their respective p-values ($p < 0.05$ in bold). % upwelled water = percentage upwelled-water; df = degrees of freedom; ψ = overdispersion parameter; P = number of parameters in each model; N = number of samples in the model. The model runs with access to nutrients (demarcated by a dotted line) cannot be compared to other model sets with sea surface temperature and % upwelled water as they used a smaller subset of the data.

a)

Model Group	Name	Type	Model	AIC	BIC	AICc	null deviance	df	residual deviance	df	ψ	P	N/P ratio
	Count												
2	Model 1	sst	sst + chla + wind stress	147.33	153.43	148.13	98.79	33	81.99	30	2.730	3	11
	Model 2		wind stress	147.77	**150.82**	**147.90**	98.79	33	86.43	32	2.701	1	34
3	Model 2	% upwelled water	wind stress	147.77	**150.82**	**147.90**	98.79	33	86.43	32	2.701	1	34
6	Model 3	access to nutrients	chl a	123.33	**125.69**	**123.51**	77.31	23	73.52	22	3.341	1	24
	NASC												
2	Model 4	sst	wind stress	115.88	120.46	116.01	62.82	33	50.41	32	1.575	1	34
3	Model 4	% upwelled water	wind stress	115.88	120.46	116.01	62.82	33	50.41	32	1.575	1	34
6	Model 4	access to nutrients	wind stress	87.52	91.06	87.70	48.56	23	41.97	22	1.908	1	24
	Occupation												
2	Model 5	sst	wind stress	25.74	30.32	25.87	3.94	33	3.56	32	0.111	1	34
3	Model 5	% upwelled water	wind stress	25.74	30.32	25.87	3.94	33	3.56	32	0.111	1	34
6	Model 6	access to nutrients	nutr	25.44	28.97	25.62	3.50	23	3.16	22	0.144	1	24

b)

Model Group	Name	Type	Model	AIC	BIC	AICc	null deviance	df	residual deviance	df	ψ	P	N/P ratio
	Count												
2	Model 7	sst	sst	198.36	**201.41**	**198.49**	133.85	33	124.92	32	3.904	1	34
3	Model 8	% upwelled water	chla + wind stress	198.42	203.00	198.81	133.85	33	122.99	31	3.967	2	17
	Model 9		wind stress	198.58	**201.63**	**198.71**	133.85	33	125.14	32	3.911	1	34
	NASC												
2	Model 10	sst	wind stress	97.81	102.39	97.94	29.69	33	29.63	32	0.926	1	34
3	Model 11	% upwelled water	perc upwelled	96.15	100.73	96.28	29.69	33	28.22	32	0.882	1	24
	Occupation												
2	Model 12	sst	wind stress	-44.12	-39.54	-43.99	0.46	33	0.46	32	0.014	1	34
3	Model 13	% upwelled water	perc upwelled	-44.42	-39.84	-44.29	0.46	33	0.45	32	0.014	1	34

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c)

Model Group	Name	Type	Model	sst			chl a			windstress			% upwelled water			access to nutrients		
				slope	z	p	slope	z	p	slope	z	p	slope	z	p	slope	z	p
	Count																	
2	Model 1	sst	sst + chl a + wind stress	3.234 (1.794)	1.80	0.071	-3.867 (2.262)	-1.710	0.087	122.289 (64.086)	1.908	0.056						
	Model 2		wind stress							87.664 (27.380)	3.202	**0.001**						
3	Model 2	*% upwelled water*	wind stress							87.664 (27.380)	3.202	**0.001**						
6	Model 3	*access to nutrients*	chl a				-2.388 (1.270)	-1.881	0.060									
	NASC																	
2	Model 4	sst	wind stress							103.784 (36.982)	2.806	**0.008**						
3	Model 4	*% upwelled water*	wind stress							103.784 (36.982)	2.806	**0.008**						
6	Model 4	*access to nutrients*	wind stress							103.328 (55.405)	1.858	0.077						
	Occupation																	
2	Model 5	sst	wind stress							18.281 (9.825)	1.861	0.072						
3	Model 5	*% upwelled water*	wind stress							18.281 (9.825)	1.861	0.072						
6	Model 6	*access to nutrients*	nutr													0.008 (0.005)	1.532	0.1398

d)

| Model Group	Name	Type	Model	sst			chl a			windstress			% upwelled water			access to nutrients		
				slope	t	p	slope	t	p	slope	t	p	slope	t	p	slope	z	p
	Count																	
2	Model 7	sst	sst	1.626 (0.542)	3.00	**0.003**												
3	Model 8	*% upwelled water*	chl a + wind stress				-2.430 (1.684)	-1.443	0.149	-94.951 (36.226)	-2.621	**0.009**						
	Model 9		wind stress							-48.098 (16.189)	-2.371	**0.003**						
	NASC																	
2	Model 10	sst	wind stress							-6.834 (28.354)	-0.241	0.811						
3	Model 11	*% upwelled water*	percupwelled										-0.006 (0.005)	-1.289	0.207			
	Occupation																	
2	Model 12	sst	wind stress							-0.614 (3.517)	-0.174	0.863						
3	Model 13	*% upwelled water*	percupwelled										-0.0003 (0.0006)	-0.561	0.579			
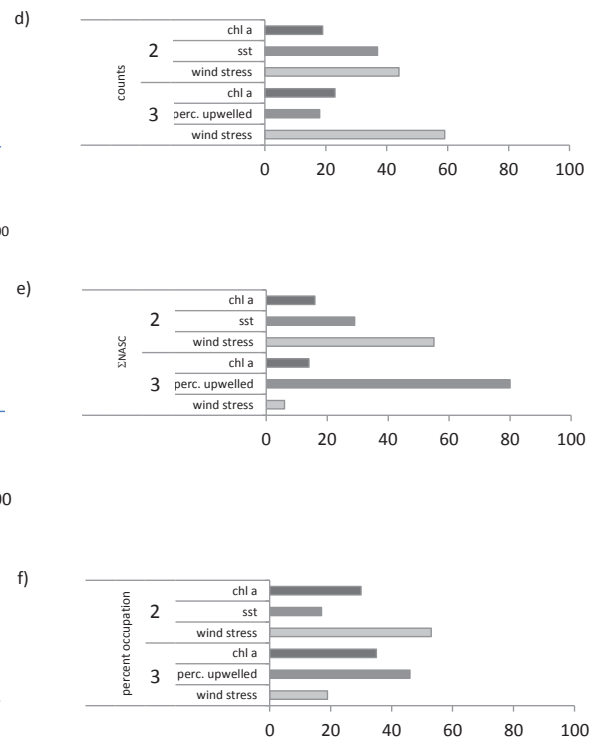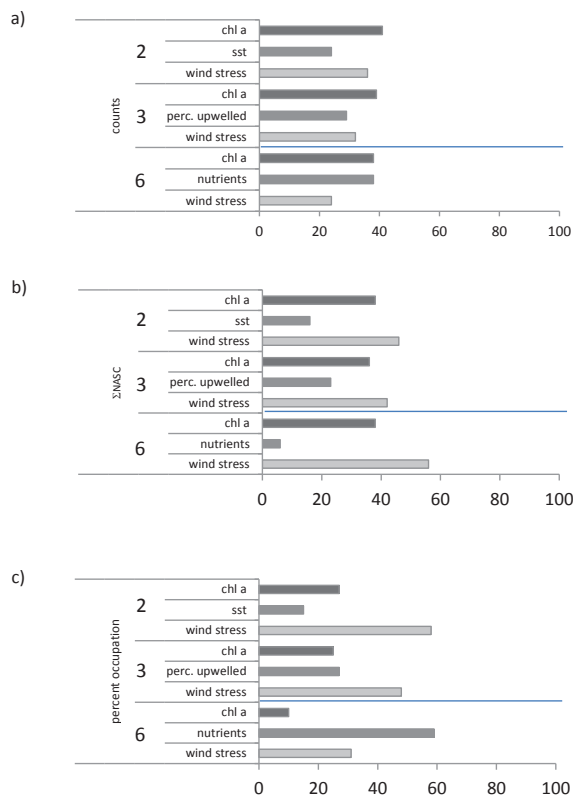
Figure 3-8. Percentage contributions of independent effects for surface and vertical habitat variables calculated from hierarchical partitioning (HP) for the GLMs explaining the a) – c) midwater and d) – f) demersal schools in 2003 separately for each abundance measure. The Model Group numbers are indicated. Percent occupation = percentage occupation, chl-*a* = surface chlorophyll-*a*, SST = sea surface temperature, perc. upwelled = percentage upwelled-water. The midwater HP values are not fully comparable with the demersal GLMs for count and ΣNASC as they could not account for different water depths across the intervals, but they give an indication of the patterns encountered. Also, the HP values for the set with access to nutrients (demarcated with a line) are not comparable as they used a smaller subset of data in comparison to the datasets used with sea surface temperature and percentage upwelled-water.

3.4.   DISCUSSION

The main weather and ocean forcing expected to operate in the northern-boundary current system, where upwelled water was drawn onto and circulated across the shelf, occurred during the period of the study. The key habitat descriptor representing weather forcing of the shelf system (alongshore wind-stress) was also consistently influential in explaining key habitat structures at depth, particularly the intensity of upwelling, position of upwelled water and stratification. To a large extent wind stress explained the distribution and abundance of neritic aggregations. Wind stress also worked well in combination with measures of surface phytoplankton concentration (chl-a) and thermal structure (SST, percentage upwelled-water and access to nutrients). The variability in the importance of wind stress and its changing relationship with school abundance with depth appeared to be a condition of variability in the wind's periodicity and strength. This in turn would have affected the level of nutrients accessible to primary producers, and other conditions optimal for productivity. Wind stress probably also influenced the position of aggregations in the water column by driving surface turbulence. Periods of high wind activity prior to sampling are likely responsible for some of the mismatches between primary production and neritic aggregations (Cury & Roy 1989), such as the reduced influence and negative relationship at times between deeper schools and chl-a. The inclusion of vertical habitat variables was important in improving model relationships. This was particularly so for the variable representing access to nutrients, which was better at explaining the occupation of midwater schools. The relationships between neritic schools and habitat variables in the study were well represented by the PHCM both across the shelf and for the main vertical strata thought to operate in this shelf habitat.

Weather and ocean circulation acted together over many temporal and spatial scales to provide the conditions, either suitable or not, for secondary production. The relationship between school abundance and habitat structures was found to not only vary between abundance measures (i.e. counts, acoustic biomass and percentage occupation) and through the water column, but also interannually. The temporal variation in these relationships showed just how ephemeral habitat-conditions could be, also shown by the influence of the offshore movement of the upwelling plume on near-surface schools in 2003. Below, the patterns and mechanisms likely to be driving temporal variation in relationships are described in more detail.

3.4.1. Consistent habitat structural influences on surface schools

The variables that were most representative of surface prey (chl-*a*), turbulence and the position of upwelled water (wind stress), were consistently the most influential in their relationship with the abundance of near-surface schools, expected to predominantly comprise krill swarms (Morrice, unpublished data). Chl-*a* and wind stress both had a positive relationship with all measures of abundance and generally agreed with each other in their patterns across time, suggesting the *a priori* mechanistic pathways between surface habitat structures and surface schools, as described in the PHCM, were occurring. The influence of wind stress on bringing upwelled water to the surface may not have been as pronounced during the periods of sampling as its effect on turbulence, preventing stratification and maintaining the mixed-layer at depth, therefore limiting surface phytoplankton's access to 'new' nutrients. Phytoplankton could have been sustained from nutrients already circulating in the upper-water column (e.g. enriched from upwelling-favourable winds prior to sampling). This was shown by the presence of near-surface schools early in sampling in 2003 (where the depth of the mixed-layer was above upwelling-influenced bottom water; Figure 3-6) and any primary production would have been relying on nutrients already in the system. Similar pre-conditioning of systems has been suggested as an explanation for observed coastal productivity in the absence of strong sources of nutrient supply off the west coast of North America (Ware & Thomson 2005). The lack of upwelled water at the surface reported in the study (evident from remotely-sensed and *in situ* measures of temperature)(McClatchie et al. 2006) could explain the lesser influence and positive relationship of SST with abundance in surface waters (i.e. higher temperatures related to higher school abundance). Even though the system studied is characterised as having a 1-step upwelling process (refer to Introduction and PHCM), there must be a level of wind forcing and local circulation required to bring cold water to (or near) the surface, offshore of coastal upwelling jets. Similar shelf thermal-structuring has been observed further west in the eastern GAB, where surface waters were generally 15.2 – 23.9 °C during the summer-autumn period, but were cooler inshore along sections of coastline that ran parallel to prevailing winds associated with upwelled water (McClatchie et al. 2006, Ward et al. 2006, Middleton & Bye 2007, van Ruth et al. 2010a, van Ruth et al. 2010b).

The effect of turbulence on the abundance of near-surface schools was expected to not only be on nutrient circulation in upper-shelf waters, but also on moving neritic schools away from optimal habitat (when wind-forcing and/or local circulation was strong enough). Larger zooplankton and fish are more able to regulate their position in the water column relative to strong currents, however juvenile and less-motile zooplankton

and fish stages would be passively moved (Watkins 2007). Zooplankton off British Columbia were displaced by surface and deeper circulation patterns generated by the slope and shape of canyon walls (Allen 2001). This movement effect was incorporated into nutrient-trophic models by Botsford et al. (2003) on a shelf of similar width to the one in this study (i.e. 25 km). In such situations, advection should occur with wind speeds greater than 5-6 m s^{-1} (12 knots), and will likely be very location specific. This wind-speed threshold was also important in explaining pelagic fish recruitment (Cury & Roy 1989). High abundances of zooplankton and sardine eggs were recorded in warm surface waters and it was thought mismatches were due to movement of zooplankton away from inshore 'coldspots' and elevated primary productivity (Ward et al. 2006, van Ruth & Ward 2009). Such a pattern is also seen in other upwelling systems (Mann & Lazier 2006). It is considered less likely that advection played an important role in the relationships found in the study, as a strong positive relationship was found with chl-*a*. However, it cannot be discounted that there were mixed-food pathways and diet switching occurring in zooplankton and small fish found near the surface, depending on the dominant sources of nutrients and prey in the system. Mixed-food pathways and diet switching may explain, to some degree, the presence of surface aggregations in periods where little circulation of nutrients and low productivity of large phytoplankton were expected. Another possible explanation is that omnivorous *N. australis* were utilising prey in sub-surface diffuse scattering layers recorded across the shelf (Chapter 2, and Morrice and Garcia-Rojas unpublished data). Further clarification of advection and food pathways operating in the system will improve knowledge of mechanisms driving mismatches in surface predator-prey-habitat relationships.

Some of the variation in surface school relationships with habitat could be attributable to temporal influences, both intra-seasonal and interannual. The factor year appeared in all the best explanatory models, although less so between 2004 and 2007. This may be explained by the difference in the spatial organisation of near-surface schools between years (Chapter 2, Section 2.3.2.2), and interactions between wind stress and year. For example, cooler temperatures were seen across the study area in mid-April 2003 due to the forcing by north to northwest winds. It was also likely the combination of relatively weak and variable wind forcing and El Niño conditions encountered over the sampling period varied the transport of upwelled water to the surface (Chapter 2, Discussion). High surface temperatures could have led to reduced surface productivity in 2004, a trend of warming oceans (Ware & Thomson 2005), whereby those areas of ocean had reduced nutrient availability coincident with increased biota-metabolism requirements. Zooplankton patterns in the eastern GAB and krill, such as *Nyctiphanes australis,* in waters off the east coast of Tasmania were also influenced by interannual and along-shelf variation in physical forcing, and by the availability of preferred

phytoplankton (Harris et al. 1991, Ward et al. 2006). *N. australis* also have an optimal temperature range of 12 - 18 °C, which is likely to affect their abundances in surface waters of higher temperatures (Sheard 1953, Hosie 1982, Haywood 2002). Coastal water masses from the east and west, the latter containing warm waters and low-nutrient flows from the Southern Australian Sea, may have also influenced relationships (Middleton & Bye 2007).

Other mechanisms that may have caused variability in surface relationships include: 1) schools exhibiting other habitat or behavioural drivers for being at the surface; 2) predator-prey interactions occurring between sampled schools and higher-trophic levels that feed at the surface (such as larger fish, seabirds and marine mammals; Cury et al. 2000, Feyrer & Duffus 2011); and/or 3) changes in fish composition, whereby different species exhibiting different habitat responses. For example, a change in dominance of surface zooplankton from large krill to small warm-water tolerant copepods was associated with the movement of warmer, nutrient-poor waters of the East Australian Current off eastern Tasmania (McLeod et al. 2012). This had significant upper-trophic consequences for the distribution and diet of jack mackerel (*Trachurus declivis*), redbait (*Emmelichthys nitidus*) and Australian salmon (*Arripis trutta*) (Harris et al. 1987, Harris et al. 1991, Young & Davis 1992, Young et al. 1993, McLeod et al. 2012, Hughes et al. 2013), and likely surface predators such as seabirds dependent on those species as prey resources (McClatchie et al. 1989, Chiaradia et al. 2003).

3.4.2. Dynamic forces affect midwater school abundance

The pattern of surface-habitat variables influencing school abundance was less clear at midwater and demersal depths when modelled with all the data. This was expected due to the reduced influence of surface-habitat variables away from the surface. Midwater depths have a higher likelihood of mixed assemblages of neritic schools (Barange 1994, Barange & Hampton 1997, McLeod et al. 2012). This would increase the variation in their response to their habitat, including with respect to the number, density and size of schools. In general, the combination of wind stress and year was consistently included in the best explanatory models across all abundance measures for all years, with varying inputs of chl-*a* and SST. The patterns were more consistent for the 2003 data, with wind stress and chl-*a* being the most influential variables for all abundance measures when modelled with the different thermal-structure variables. The only exception was for percentage occupation where access to nutrients (having a positive relationship with abundance) ranked better than wind stress. The greater influence of access to nutrients in this case was due to the few occasions during sampling where the MLD was positioned below the upwelled-water front, allowing

enrichment of upper waters and presumably increasing primary productivity and abundance. For occupation, and less so for counts, it was beneficial to include a variable that was more representative of thermal structures at depth.

Of interest was the negative relationship between chl-*a* and the abundance of midwater schools compared to the relationship between chl-*a* and abundance of near-surface schools. This may be interpreted a number of ways. Firstly, chl-*a* measures may not represent phytoplankton abundance and their grazers at depth, particularly when productivity is limited at the surface. Deep-chlorophyll maxima are not represented well in studies of relationships between primary production and higher trophic levels (De Silva-Dávila et al. 2002), and are likely to be responsible for weaker relationships with these trophic groups (Gremillet et al. 2008). van Ruth et al. (2010a), in a study of the physical forcing influencing primary production in the eastern GAB, found variation in the depth of chlorophyll maxima; it regularly sat just below the surface mixed-layer within the euphotic zone, and associated with an upwelled water mass. The negative relationship between chl-*a* and the abundance of midwater schools may also be an artefact of grazing pressure on phytoplankton in the midwater part of the water column, as grazing accounts for some of the daily integral phytoplankton losses (van Ruth et al. 2010b). The higher biomass of grazers expected amongst aggregations that occurred in the study area could exert a top-down control on phytoplankton abundance. This functional relationship is well known to be driven by lower-trophic groups in upwelling-influenced systems (Cury & Roy 1989, Baum & Worm 2009, Taylor et al. 2010, Bulman et al. 2011; Chapter 3, Introduction). As described for surface schools, there may also be a temporal and spatial mismatch associated with the different movement of surface and deeper waters, some resulting from Ekman spiralling (Mann & Lazier 2006).

In conditions of greater wind forcing, which occurred between sampling times, it is expected there would have been more occasions where nutrients would have been more available through the water column with a shoaling of the upwelled-water front and deepening of the MLD. Vertical profiling data in 2003 show that midwater depths probably fell within an 'optimal-light window' (i.e. the euphotic depth extended to the ocean floor), as described by Coyle et al. (2008). Limitations on productivity would therefore have been driven by nutrient availability, as was highlighted in Pattern 3 of the PHCM, and any effect of temperature on metabolism. These patterns reflect how dynamic midwater depths were. Midwater depths were influenced by processes above and below them, such as the positions of upwelled water and the mixed-layer, and also by the variation in circulation and primary productivity patterns year to year.

3.4.3. Patterns in demersal school abundance under-represented by surface habitat structures

The abundance of demersal schools showed a variety of relationships with surface habitat variables, similarly to midwater schools, with no clear model or variable explaining the relationship across all abundance measures for all years. SST and chl-*a* were consistently more influential than wind stress, having characteristic negative relationships with abundance. This is intuitive if reduced temperatures at the surface do reflect upwelling at depth, even though SST had a positive relationship with surface school abundance. Measures of vertical-thermal structure also highlighted the importance of upwelled water, as the percentage upwelled-water exceeded wind stress as the most influential variable when it replaced SST for the acoustic biomass and occupation of schools in 2003. Currie et al. (2012) found that demersal fish were associated with thermal-water boundaries. As described for midwater patterns in this study, chl-*a* measures at depth would be a better descriptor for explaining the abundance of higher-trophic levels at depth. For example, demersal chl-*a* concentrations has been found to have a significant positive relationship with demersal fish biomass (Currie et al. 2012). Grazing pressure and increasing primary productivity losses to respiration at depth may also influence the negative relationship with chl-*a* (van Ruth et al. 2010b).

The relationship between wind stress and demersal schools was not consistent with surface and midwater schools. Wind stress was negatively related to abundance in all the models, in contrast to its positive relationships in surface and midwater depths. It was the dominant variable for some models across all year data and for most models in 2003. The change in influence of wind stress on the abundance of schools from year to year is likely a response to the periodicity and strength of upwelling and whether these conditions were conducive to high, low or moderate primary and secondary productivity. In the case of the 2003 data, the general path of upwelled water into shelf waters was along the seafloor, with varying degrees of mixing occurring above that. Features such as the steep submarine canyons in the study area (Heap & Harris 2008, Harris & Whiteway 2011) are known to influence local upwelling and circulation and in turn pelagic communities (Allen 2001, Currie et al. 2012). It follows that there would be a time lag of some days from the entrance of this water into demersal shelf waters (from increased alongshore wind-stress) to its effect on increasing phytoplankton productivity at fronts (and at the surface). This is shown by a lack of schools in the very coolest waters in 2003. It may also explain the highest demersal fish biomasses at water mass boundaries in Currie et al. (2012). Optimal conditions for zooplankton and fish growth have also been found downstream of upwelled-water fronts (Barange

1994), with reduced abundance in the very coldest water as prey and predator metabolism reduces. An additional temporal and spatial lag from surface productivity to its effect on demersal schools was evident in the negative relationship between the abundance of demersal schools and surface chl-*a*. Inclusion of wind data averaged over longer times may provide increased correlation to surface productivity and neritic aggregation abundance at depth. It should also be considered that the pattern of distribution and abundance in demersal schools may have been better represented by a suite of static descriptors that link them to the complexity of the sea floor such as rugosity, slope and substratum type (Ierodiaconou et al. 2011, Monk et al. 2011, Hasan et al. 2012).

3.4.4. Implications of model approaches and results on future research

The outcomes of modelling in this study highlight the need to consider not only key structures driving biotic patterns in upwelling shelf systems, but how their influence varies according to the biota's position in the water column, likely temporal and spatial lags in relationships, and the effects of system pre-conditioning prior to sampling.

Stratifying schools by select temporal and spatial *a priori* patterns expected in the data, as guided by the PHCM, was very informative for highlighting the different influence habitat structures had on shaping school distribution and abundance. In particular, it highlighted the different relationships, in both strength and direction that schools had with habitat structures, depending on where they were in the water column. These structures were influential in shaping not only how many schools prevailed, but also their biomass and occupation at different depths.

Empirical models of school abundance were also strengthened by the use of pre-conceived patterns in shelf dynamics and the use of habitat structures expected to influence school abundance at depth (i.e. thermal stratification and access to nutrients). Surface-habitat descriptors appeared to work well only in describing schools in the midwater and demersal depths in the presence of upwelling-front waters. Midwater and demersal school relationships with habitat at these depths varied due to the timing of upwelling activity and position of sampling along the shelf relative to pathways of this water. As the strongest relationships occurred between surface schools and surface habitat variables, particularly with chl-*a* (the proxy for food), future modelling exercises would also be well served to include vertical measures of phytoplankton production and composition. This could improve the physical-trophic linkages described here for schools at depth. In addition, measures of nutrient characteristics of the water column would identify which food pathway was dominant

(i.e. production generated by 'new' versus 'recycled' nutrient pathways; e.g. Harris et al. 1987).

Other shelf-system processes not accounted for in this study may have influenced the relationships between neritic aggregations and their habitat. Sampling in this study occurred towards the end of the upwelling season, when prior intra-seasonal trends in wind forcing and ocean circulation would have influenced the observed patterns. Some consideration of the duration and magnitude of stability in the system prior to sampling would help to understand what and where resources were limited. It could also help explain any mismatch between abiotic and biotic measures of productivity occurring at the time of sampling. For example, descriptors such as the magnitude of turbulence (Cury & Roy 1989, Coyle et al. 2008), or a measure of the timing and magnitude of the seasonal peak in upwelling and/or primary productivity (Bertram et al. 2001) have helped incorporate prior-system conditions in relationship building.

The patterns described here can only provide a window into the stability of the predator-prey controls likely operating earlier in the upwelling season, and in another year. As modelling is an iterative process, model robustness, validation and efficacy for use in a predictive capacity would only occur by testing these models on independent datasets. Test datasets that incorporate more of the temporal and spatial variability in the system would be particularly useful. For example, sampling under greater wind speeds would identify whether relationships shift, becoming non-linear under thresholds of wind, and describe the parameters of 'optimal environmental windows' (where the effects of the limiting factors are minimised, see Figure 3 in Cury & Roy 1989). Also, further investigation of the influence of different shelf widths and canyon features would help determine the relative lag effects of nutrient availability in the system, which in the California Current system is about 10 days between upwelling and peak primary productivity (Croll et al. 2001b).

It has to be remembered that the school-habitat interactions described here did not occur in isolation. Predator-prey interactions are expected to have exerted some level of effect on school abundances, particularly in a local context as whales are expected to locally deplete their prey resource to below threshold levels before moving on to the next resource. Therefore, better knowledge of the next level of trophic interaction (i.e. between neritic zooplankton and small fish and their predators) will enable managers and researchers to better understand the underlying forces driving predator distribution in upwelling systems, including resource use and the implications of shifts in top-down and bottom-up controls.

4. FINE-SCALE HABITAT SELECTION AND BEHAVIOUR OF A CONSTANT FORAGER

4.1. INTRODUCTION

Understanding the processes that influence the distribution and movement patterns of animals is a key area of ecological research. Knowledge of these processes and the ability to predict suitable habitats for animals is central to the conservation and management of vulnerable and far-ranging species (Tynan et al. 2005, McMahon & Hays 2006, Redfern et al. 2006, Mills et al. 2008).

Habitat selection and suitability has been quantified for many terrestrial and aquatic species and systems (e.g. Freitas et al. 2008, Schofield et al. 2009, Monk et al. 2011, Martín et al. 2012). Studies have measured the overlap between species distribution and various habitat metrics at a variety of temporal and spatial scales (Legendre & Fortin 1989, Wiens 1989, Bowers & Matter 1997, Houghton et al. 2006, Redfern et al. 2006, Benoit-Bird et al. 2013b). Species-habitat relationships are characterised by variability. Improved predictive power is achieved when species occurrence is measured against those factors most directly influencing how individuals or aggregations occupy time and space. Quantifying how habitat selection changes as a function of habitat availability, and how behavioural context can be applied to make functional links between animal habitat use and foraging success, are recognised as important focuses for future research (Beyer et al. 2010).

Animals in their foraging habitat are expected to spend more time in areas where prey is most available and profitable (i.e. prey provides high energy returns), as this strategy will ultimately provide reproductive and survival benefits (Weimerskirch 2007, Barraquand & Benhamou 2008, Beyer et al. 2010, Santora et al. 2011a). Terrestrial and aquatic predators have evolved a large range of strategies to optimise their search efficiencies in finding prey (e.g. Bradshaw et al. 2004, McMahon & Hays 2006, Weimerskirch 2007, Humphries et al. 2010, Almenar et al. 2013, Avgar et al. 2013). Migration or transiting movements are strongly oriented behaviours and are generally used for moving between breeding and foraging areas, or between foraging areas (Benhamou 1994, Barraquand & Benhamou 2008). Animals will intensify their search effort in areas where they encounter more productive foraging areas (e.g. area-restricted searches), then often switch to more extensive searching upon prey becoming sparser and unpredictable (Benhamou 1992, Humphries et al. 2010, Barton & Hovestadt 2013). Foraging areas are sometimes vast, covering 1000s km^2, requiring

individuals to search over broad-, medium- and fine-scales in response to hierarchical system dynamics that shape their prey resources (e.g. Avgar et al. 2013).

Marine predator movements and distributions have been linked to the horizontal and vertical patchiness and density of their food. For example, the habitat use of three co-occurring marine predators (black-legged kittiwakes, *Rissa tridactyla*, thick-billed murres, *Uria lomvia*, and northern fur seals, *Callorhinus ursinus*) in the southeastern Bering Sea was consistently predicted (irrespective of time of day, year and source colony) by vertical prey distribution and patchiness as opposed to more traditional measures of prey abundance (i.e. biomass or density; Benoit-Bird et al. 2013a). Based on these relationships, the authors concluded that prey needs to be sampled as discrete aggregations rather than averaged over pre-determined and often arbitrary grids that do not always match the scale at which predator-prey processes are occurring (Benoit-Bird et al. 2011, Benoit-Bird et al. 2013b). Predator-prey interactions can be density- and behaviour-dependent, for example, thresholds in prey selected by predators can change contingent upon prey availability (Piatt & Methven 1992, Bowers & Matter 1997, Sims 1999, Fauchald et al. 2000, Baumgartner & Mate 2003, Simon et al. 2009). Predator-prey studies highlight the importance of understanding the behavioural context as well as incorporating the most synoptic data to better explain relationships (Azzellino et al. 2008, Beyer et al. 2010, Azzellino et al. 2012, Pendleton et al. 2012).

The largest marine vertebrates filter feed on plankton, with a large transfer of mass from prey to predator. They show convergent specialisation in their patterns of movement and prey engulfment, based on how plankton aggregate, that has allowed them to fill particular habitat niches (Sims et al. 2008, Gleiss et al. 2011, Goldbogen et al. 2012, Goldbogen et al. 2013b). Plankton is generally structured into diffuse, long layers of plankton with limited motility, or very dense, patchily distributed aggregations of agile zooplankton that are engulfed using ram- and lunge-feeding respectively. Ram feeders, represented amongst cetaceans by bowhead (*Balaena mysticetus*) and right whales (*Eubaleana spp.*), filter feed by swimming with their mouth agape through plankton at slow, steady speeds (Baumgartner & Mate 2003, Simon et al. 2009). Lunge feeders, represented by fin (*Balaenoptera physalus*) and blue whales (*Balaenoptera musculus*), approach prey aggregations at high speeds, engulfing large volumes of zooplankton in single mouthfuls (Goldbogen et al. 2006, Goldbogen et al. 2012, Goldbogen et al. 2013b). Lunge feeding is an energy-intensive technique, essential to capture highly-mobile plankton such as krill (O'Brien 1987). Lunge feeders must not only consume dense aggregations (Goldbogen et al. 2011), but also be manoeuvrable and streamlined, and able to move rapidly between prey patches. There are very few

studies worldwide on how such planktivores respond to their prey at fine scales, or on the characteristics of profitable prey (Sims & Quayle 1998, Sims 1999, Baumgartner et al. 2003, Baumgartner & Mate 2003).

The world's largest planktivore, the blue whale, has very high energy requirements that drive its need to constantly search for and consume large quantities of prey (Acevedo-Gutiérrez et al. 2002, Croll et al. 2005, Wiedenmann et al. 2011, Goldbogen et al. 2012, Goldbogen et al. 2013b). Blue whales annually range over vast areas of ocean between polar, temperate and tropical waters (Stafford et al. 1999, Bailey et al. 2010). Across this range they show characteristic hierarchical movement, from broad-scale transiting between foraging grounds (Bailey et al. 2010) to meso-scale concentrated search effort within 'traditional' foraging grounds and areas of ocean where they could expect enhanced biological productivity (Figure 1-1; Doniol-Valcroze et al. 2007, Bailey et al. 2010).

Within their foraging grounds, blue whale distribution and abundances have highly variable relationships with measures of habitat, and success in predicting associations has been variable (Benson et al. 2002, Davis et al. 2002, Baumgartner & Mate 2003, Croll et al. 2005, Doniol-Valcroze et al. 2007, Gill et al. 2011, Doniol-Valcroze et al. 2012). High variability likely results from a range of factors. These include use of indirect habitat measures whose relationship to whales may lag significantly from more causal mechanisms such as prey distribution and abundance. Habitat dynamics, individual whale responses to habitat and the prior body-condition of whales will also affect the relationships that whales have with their habitat. Better predictive power in building habitat-suitability models and in estimating foraging efficiency has transpired when local- and meso-scale oceanographic features (Doniol-Valcroze et al. 2007), feeding events (Doniol-Valcroze et al. 2012) and prey distribution and abundance have been incorporated (Schoenherr 1991, Fiedler et al. 1998, Croll et al. 2001b, Croll et al. 2005). These studies highlight the importance of considering the function and value of such habitat and behavioural metrics (Baumgartner & Mate 2003, Beyer et al. 2010, Doniol-Valcroze et al. 2012).

Studies of whale-prey relationships using integrated methods have shown that blue whales adopt a range of strategies to maximise their search efficiencies at the surface and at depth, with the majority of their food resources occurring at depth (Croll et al. 2001b, Croll et al. 2005, Doniol-Valcroze et al. 2011). Their ability to feed can be dependent on the density of prey, and can require prey density to be above a certain threshold to initiate feeding (> 0.1 kg m^{-3}; Croll et al. 1998, Croll et al. 2005, Goldbogen et al. 2011, Wiedenmann et al. 2011). Few studies, however, have characterised the

fine-scale interactions between whales and individual 'swarms' of prey, and the weather and oceanographic processes influencing prey. No study has characterised the fine-scale horizontal-movement responses of blue whales, including the more subtle transitional responses that may be important for whales managing the spatial and temporal variability of their food resources.

Pygmy blue whales (*B. m. brevicauda*, a recognised subspecies of blue whale; Ichihara 1966) utilise the upper-slope and shelf region off southern Australia to forage and feed on krill aggregations. These blue whales are distributed across a region of over 38,000 km^2 from the Great Australian Bight (GAB) to Bass Strait and western Tasmania, with much temporal and spatial variability (Gill et al. 2011). Whales off southern Australia share population features with animals recorded off Western Australia, such as genetic relatedness, and there have been resightings of individual whales between regions (Blue Whale Study Inc. and Centre for Whale Research unpublished data; Attard et al. 2010, Attard et al. 2012). Tentative estimates for the Australian-Indian Ocean population lie between 570 and 1700 individuals (Jenner et al. 2008). There are currently no measureable signs of population recovery from severe exploitation during whaling operations (Blue Whale Study unpublished data; Branch et al. 2007). Individuals from the Australian-Indian Ocean population have been tracked as far south as the Subtropical Convergence in summer (Blue Whale Study and Centre for Whale Research unpublished data) and north to the Indonesian Archipelago in winter (Branch et al. 2007). Both regions have been documented for their ocean productivity (Clementson et al. 1998, Susanto et al. 2001, Hamilton 2006). The southern-Australian foraging ground is the only area where whales have been consistently recorded over the entire spring-autumn period. The region off southern Australia is therefore expected to provide a consistently profitable foraging ground for pygmy blue whales from the Australian-Indian Ocean region.

One of the reasons the southern-Australian region is likely to be profitable for pygmy blue whales is that the species of krill known to dominate the water column, *Nyctiphanes australis*, has a surface-swarming habit both day and night (Young et al. 1993). *N. australis* swarms can be a ubiquitous feature of these waters, forming large concentrations that can extend over kilometres of ocean (Chapter 2; Gill et al. 2011). These swarms coincide with regular observations of surface-feeding pygmy blue whales (Gill 2004, Gill et al. 2011), and also support other rorqual whales including humpback (*Megaptera novaeangliae*), fin, sei (*B. borealis*), Antarctic-minke (*B. bonaerensis*) and dwarf-minke (*B. acutorostrata*; Gill et al. In review). There is also acoustic evidence to suggest that the region is visited by Antarctic blue whales (*B. m. intermedia*; R. McCauley unpublished report). Surface swarms are expected to provide a very

profitable food resource for these whales. Surface swarms would constitute more suitable food than prey at depth, which would require greater expenditure of energy to capture. The region is thus a good model system to study fine-scale habitat selection by pygmy blue whales, particularly in response to surface aggregations of krill and measures of ocean productivity.

In this chapter a combination of predator occurrences and high-resolution surface observations of behaviour are used with descriptors of habitat (including prey) to gain insights into the mechanisms that influence predator-prey interactions at fine scales. Simple analytical techniques are applied to test the prediction that pygmy blue whales occupy relatively profitable areas. Similarly, behavioural contexts (including surface movement modes and feeding behaviour) are used to determine the effect on relationships between whales and prey. Findings are considered in relation to the expected sources of variability contributing to these patterns, the foraging efficiency of preying on surface swarms, habitat selection and foraging behaviour reported for other marine predators including planktivores, and contributions to foraging-habitat and foraging-movement models.

4.2. METHODS

4.2.1. Collection of survey data

Sightings of pygmy blue whales were collected during the autumns of 2003, 2004 and 2007 in systematic small vessel surveys of a study area (Chapter 2, Figure 2-2) selected for its narrow continental shelf and known suitability as foraging habitat for pygmy blue whales. Detailed survey methods are given in Chapters 2 and 3. Whale sightings within 1.5 km of a transect line were assigned to the closest transect interval (Section 4.2.3) using the line-measuring tool in ArcGIS (v10.1, ESRI 2013). Daily whale-encounter rates (ERs) were calculated for comparison with ERs of prey, by dividing the number of sightings by the transect distance (km) covered on any given survey day. Whales within 100 m of each other for longer than a transient pass ($\sim$ 30 min) were assigned to the same group and were presumed to be interacting.

4.2.2. Collection of track data and characterisation of surface movement

Surface movements of individual pygmy blue whales were characterised from observations of surface behaviour in order to test the differences in prey abundance and other habitat features between movement modes. Fine-scale transitional states (i.e. more subtle movement changes within area-restricted search modes; see Introduction) were as important to distinguish as broader movement changes (Barton

& Hovestadt 2013). Movement was characterised to differentiate between area-restricted search behaviour (classified here as 'intensive' and 'milling') and oriented or ranging/relocation behaviour (classified here as 'extensive' movements; Benhamou 1994, Barraquand & Benhamou 2008, Barton & Hovestadt 2013). Intensive and milling movements were predicted to represent movements between prey swarms (i.e. as described by Murphy et al. 1988), and extensive movements were predicted to occur within and between prey patches within a foraging ground (Figure 1-1).

Orientation and angle variables (see below), derived from whale surface behaviour, were used in a rules-based approach to characterise three modes of foraging movement (i.e. intensive, milling and extensive). A rules-based method was chosen over more analytical methods (e.g. random-walk and state-space modelling, used for inferring movements from bio-logging data; Jonsen et al. 2005, Jonsen et al. 2013) because the data came from direct surface observations over very short temporal and spatial scales, and all movements were assumed to have a foraging function. Orientation and angle variables were chosen due to their common application in characterising animal search behaviour at broad and fine scales (Jonsen et al. 2005). Speed (derived from measures of distance and time between surface events) was not included as a movement variable because it was highly variable across the length of tracks.

Whales were followed by vessel in 2007. Time, GPS position and behaviour (breaths and behaviour state, including surface feeding) data were recorded for each surface event (i.e. period of time the whale surfaced). All followed whales were individually identified (using photo images of unique dorsal markings; Calambokidis 1990) to account for individual variability in movements and to associate paired whales. Whale disturbance was minimised when possible by keeping behind and 200 m offset of the whale track.

Variables representing orientation (i.e. bathymetry gradient (m), track orientation (cardinal points), and bearing (°)) and turning angle (°) were derived using GPS position data between consecutive surface events (particularly between the terminal position prior to a dive; herein referred to as a 'surface sequence') in ArcMap™ (v10.1, ESRI, 2012). Criteria for bathymetry gradient (1: perpendicular, 2: parallel) were selected from the orientation of bathymetry between surface sequences, with parallel gradients representing extensive moves. Criteria for track orientation (1: NW, 2: SE) were selected from the orientation of the shelf and calculated from the net longitudinal displacement of the whole track. Bearing criteria were calculated for each surface sequence and relative to the track orientation (i.e. 1: $= \geq \pm 135°$, 2: $= \pm 45° > x < \pm$

135°, 3: = ≤ ± 45°). It was presumed that bearings more similar to the track orientation demonstrated extensive moves (i.e. criteria 3). Turning angle criteria are shown in Figure 4-1b. Angle criteria were based on the assumption that a greater change in angle indicated more intensive searching in an area. For example, intensive movement was differentiated from milling by the degree of angle change for a given surface sequence, and the requirement for more than one consecutive change. Movement modes were then assigned to each surface sequence where all criteria matched up across movement measures, otherwise they were assigned as milling. As a check of the performance of these modes, the track 'tortuosity' or 'search efficiency' was calculated separately for sections of track with different movement modes (Figure 4-1c). The Straightness Index (ST) was selected over other measures of tortuosity as tracks were found to mostly orient to the northwest (Figure 4-1a), likely in response to the alignment and narrowness of the shelf. The ST was calculated by the equation:

$$ST = dE/L$$

where dE is the Euclidean distance between the beginning and end of the path, and L is the total path length (where values closer to 1 show higher search efficiency; Batschelet 1981, Codling et al. 2008, Almeida et al. 2010). The pattern of movement modes used by whales was then described, including the proportion of time spent in each mode.
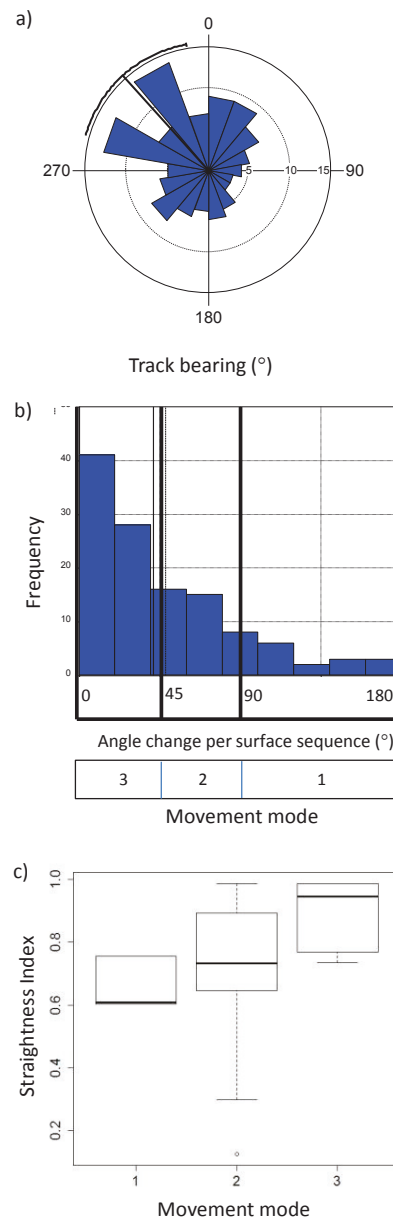
Figure 4-1. Distribution of orientation and angle variables (a: bearing, b: turning angle and c: Straightness Index) used to classify movement modes (i.e. 1: intensive, 2: milling and 3: extensive) for each surface sequence of a whale track. Criteria for track bearing were based on net displacement along the shelf. Turning angle was the difference between two consecutive bearings. Straightness Index was the difference between the straight-line distance between two positions and the actual distance travelled by the whale (values closer to 1 showed higher search efficiency).

4.2.3. Prey distribution and abundance

Measures of prey availability were derived from hydroacoustic samples collected simultaneously with visual observations using a calibrated, portable Simrad ES60 echosounder system (Simrad AS, 2000). High-density schools (i.e. $S_v$mean ≥ -70 dB), expected to represent pygmy blue whale prey 'swarms', were detected and processed from logged acoustic samples using a schools detection algorithm in Echoview software (v5.0.69.19064, www.echoview.com; Chapter 2, Section 2.2.4). The vessel track avoided crossing whale tracks to reduce excessive noise in the hydroacoustic data caused by turbulence.

To investigate relationships between whale sightings and behaviour and prey abundance, three descriptors of school abundance were derived from hydroacoustic data for each 1-km interval along transect (herein referred to as 'interval', Chapter 2, Section 2.2.4.3):

1) counts (the total number of whole and part aggregations within an interval),
2) acoustic biomass (the sum of the nautical area backscattering coefficient (ΣNASC, Chapter 2, Appendix, 2, Equation 2) of each proportion of an aggregation within an interval), and
3) percentage occupation (the proportion of the total number of acoustic samples that were in aggregations relative to the total number of acoustic samples in the interval, expressed as a percentage).

School abundance data were integrated by intervals over 1-km distances in order to make school data independent for analyses (for further detail on tests for data independence see Chapter 3, Section 3.2.3.1). Data were checked for normality and the presence of outliers using boxplots and histograms (R software, packages: Car and Graphics). All abundance measures were highly skewed with outliers and thus were transformed (counts: $\sqrt[4]{}$, ΣNASC and percentage occupation: log(x+1)). Schools were further stratified into water column positions (surface (refers to near-surface), midwater and demersal; Chapter 2, Section 2.2.5) to assess whether the vertical location of schools influenced whale activity.

4.2.4. Habitat structure descriptors

Descriptors of ocean structure were used to further assess the relationship between pygmy blue whale distribution and movement and habitat structure. Only surface-habitat descriptors were available for all years. For a full description of these parameters, see Chapter 3, Section 3.2.2. In brief, remotely-sensed measurements of

sea surface temperature (SST) (°C, 5 day composite, 0.1 ° resolution) and chlorophyll-*a* (chl-*a*) (mg m^{-3}, 8-day averages, 0.05 -0.025 ° resolution) were acquired for the most synoptic data available to within 0.01 ° radius of the midpoint for each school interval.

Alongshore wind-stress (τ_0, at 315 ° T from local coastline orientation, Pa) was averaged for the period from the sampling-time midpoint to 24 hours prior for school intervals, to account for the lag effects of upwelling or downwelling activity. Wind stress (τ) was calculated according to van Ruth et al. (2010b) using half-hourly wind (speed and direction) data from the Cape Nelson automatic weather station (Australian Bureau of Meteorology). All habitat-structure descriptors had normal distributions and did not require transformation.

4.2.5. Data analysis

Simple descriptive and univariate analytical techniques were used to characterise habitat selection by pygmy blue whales in their foraging area. Two approaches were investigated: 1) to assess general habitat selection by pygmy blue whales, by comparing the environmental characteristics in areas of whale and non-whale occurrence, and 2) to assess the influence of behaviour on whale habitat selection, by comparing the environmental characteristics across whale movement modes and in surface-feeding and non-feeding states. In some instances, these were described in the context of overall habitat availability.

4.2.5.1. General habitat selection by pygmy blue whales

Empirical modelling of the relationships between profitability (in terms of prey abundance and surface environmental features) of areas where whales were encountered compared to available areas, and an investigation of the variables driving these relationships was not feasible. This was due to: 1) low numbers of whale sightings (n = 15), and 2) lack of true absences since the whole study area is foraging habitat and pygmy blue whales are from a depleted population. Similarly, presence-only habitat-suitability modelling such as Ecological-Niche Factor Analyses (ENFA; Hirzel et al. 2002) require at least 30 occurrences to perform well (Wisz et al. 2008, Monk et al. 2011, Doniol-Valcroze et al. 2012).

Descriptive and analysis-of-variance statistics were therefore applied to identify the range of habitat likely to be most influential in determining whale distribution, and likely useful in prospective multivariate-modelling analyses. Correlation coefficients (using 'Pearsons' method; R software, packages: Car, Graphics, Stats) and univariate PERMANOVA's (PRIMER-E statistical package v6.1.15; PERMANOVA+ add-on package

v1.0.5; Anderson 2001, Clarke & Gorley 2006, Anderson et al. 2008) were used to test the hypothesis that there were differences between mean habitat-variable values (as described in Sections 4.2.3 and 4) measured for intervals associated with whale sightings (herein referred to as 'whale intervals') and the 'environmental window' available to them (i.e. intervals not associated to whale sightings, herein referred to as 'non-whale intervals'). Only intervals that were surveyed on days when whales were sighted were used in analyses, as intervals surveyed outside those days were considered 'unavailable' (Beyer et al. 2010). PERMANOVAs were carried out using type III sums of squares due to the unbalanced designs, with 9999 permutations of residuals under unrestricted permutations of raw data, and Monte Carlo (MC) p-values. Tests for homogeneity of dispersions within groups were performed using PERMDISP (Anderson et al. 2008). Ranges in habitat-variable values for whale intervals and non-whale intervals were compared to values encountered along whale tracks. Boxplots were used to visualise the spread in values (in contrast to mean ± SE displayed in Chapter 2).

4.2.5.2. Habitat selection during movement modes and feeding states

Univariate PERMANOVAs were used to test the hypothesis that there were differences in mean habitat-variable values (as for Section 4.2.5.1): 1) between movement modes; and 2) between 'surface-feeding' and 'non-surface-feeding' intervals. Surface-feeding intervals were defined as those intervals where whales were observed to be surface feeding; and non-surface-feeding intervals were defined as all other intervals in both the survey and track data. Post-hoc pair-wise comparisons using the permutational procedure were also performed to investigate patterns among levels of movement groups that had significant results. Further evidence of the scale of movement and feeding response to prey abundance was provided by comparing the overall change in school counts and maximum-acoustic density (volume backscattering strength, Chapter 2, Appendix 2, Equation 1; $S_v$max, dB re 1 m^{-1}) for sections of track (using two 1-km intervals for each movement mode) where: 1) whales switched movement modes, and 2) that preceded or proceeded surface feeding. The $S_v$max was selected over averaged measures of school density (i.e. $S_v$mean) as it was presumed that whales cue in on the highest abundance values of prey when searching.

The school-weight density (kg m^{-3}) metric is commonly used as a measure of prey availability, and was calculated in this study as a comparison to studies elsewhere. School-weight densities were calculated (for equation refer to Chapter 4, Appendix 1) for the $S_v$max of surface and demersal schools from 1-km interval data associated with surface feeding whales. As acoustic samples could not be sufficiently ground-truthed (Chapter 2, Section 2.2.4.4), the parameters used to calculate the school-weight density

metric included the observed school $S_v$max (i.e. surface $S_v$max range -23.63 to -39.09, demersal $S_v$max range -36.85 to -42.14), the best available estimate for krill Target Strength (TS, -80; based on average values for 22 mm krill; De Robertis 2001; Chapter 2, Section 2.2.4.4), and the mean weight of an individual target. Weight values were based on dry weight-length relationship for *N. australis* (3.77 x 10-6; Hosie 1982, Ritz & Hosie 1982).

4.3. RESULTS

4.3.1. General habitat selection by pygmy blue whales

A total of 18 sightings of pygmy blue whales were recorded over 291 km of vessel effort during 2003, 2004 and 2007. Fifteen of these sightings were within 1.5 km of transects, covering 12 days of survey and 139 km of effort (Table 4-1). Of these sightings, whales were observed in pairs four times (generally *B. musculus* pairs comprise a lead female with a trail male generally following within four body lengths, J. Calambokidis pers. comm.). Whales remained in this formation for the period of observation. Encounter rates (ERs) of whales per day varied from 0.04 km^{-1} to 0.45 km^{-1} (Figure 4-2). Neritic school ERs had a similar order of magnitude range (from 0.61 to 11.68 km^{-1}). There was a significant but moderate relationship between whale and school ERs (r = 0.49, p < 0.05; Figure 4-2), with sample sizes being too low to confidently fit a non-linear curve.

Table 4-1. Summary of effort, and number of pygmy blue whales and prey schools recorded for vessel survey days where blue whales were sighted in 2003, 2004 and 2007.

Date	No. transects	No. 1-km intervals	Effort (km)	No. whale sightings (individuals)	Whale Behaviour	No. pelagic schools
18-Apr-03	2	10	8.58	1 (2)	Milling	22
21-Apr-03	1	7	6.90	1 (1)	Milling	38
22-Apr-03	3	16	13.96	2 (2)	Feeding	85
23-Apr-03	2	10	6.60	3 (3)	Feeding	76
24-Apr-03	2	17	15.72	1 (1)	Unconfirmed	177
07-May-03	1	4	3.94	1 (1)	Milling	46
21-Apr-04	1	12	11.55	1 (1)	Unconfirmed	29
08-May-04	1	14	13.06	1 (1)	Milling	8
02-Apr-07	1	7	5.77	1 (2)	Feeding	14
04-Apr-07	2	31	27.97	1 (2)	Milling	135
10-Apr-07	2	20	18.13	1 (2)	Milling	102
12-Apr-07	1	7	6.69	1 (1)	Unconfirmed	84
Total	19	155	138.86	15 (19)		816
Average				1.25		68
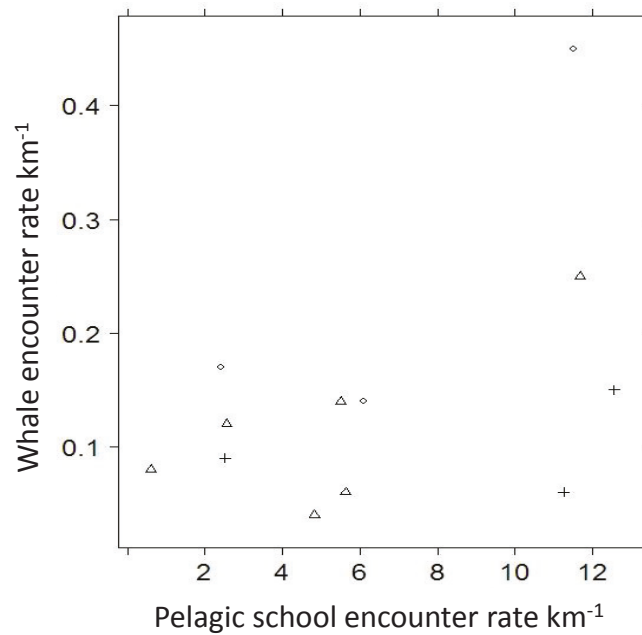
Figure 4-2. Daily encounter rates per kilometre of effort (ER km^{-1}) for whale sightings and prey schools from survey data. Observed surface behaviours of whales are also indicated (i.e. ○ = feeding, △ = milling, + = unconfirmed).

The habitat (prey and habitat structure) occupied by whales was similar to the habitat available elsewhere (Chapter 4, Appendix 2; univariate PERMANOVAs for prey abundance and other habitat variables $p > 0.05$). There was only a significant difference in the mean percentage occupation of midwater schools, which is likely explained by the significant dispersion between whale and non-whale intervals (Pseudo-$F_{(1,153)}$ = 4.52, MC p = 0.03, permdisp $p < 0.05$).

Nine individual whales were followed during the autumn period in 2007 for a cumulative total of 10.5 h and 56.6 km (Table 4-2). The habitat values recorded along all whale tracks combined were within the range of values occurring over the survey more generally, with slightly higher maximum prey abundance values and elevated surface productivity (as measured by the presence of surface-upwelled water (< 14.7 °C) and higher chl-*a* concentrations and upwelling-favourable winds; Appendix 2).

Table 4-2. Summary of effort for individual whale tracking data. Hydroacoustic data were collected within 200 m of whale tracks. Surface sequences were the track sections between consecutive whale terminal dive positions. Movement modes: 1 = intensive, 2 = milling, 3 = extensive. * denotes track where surface feeding recorded.

Date	Whale sighting ID	No. whales	No. surface sequences	Total time of whale track (hrs)	Total distance of whale track (km)	Total distance (time) in movement mode		
						1	2	3
9-Mar-07	1143	1	46	2:17:02	10.11	1.24 (0:14:00)	6.67 (1:31:22)*	2.06 (0:21:41)
14-Mar-07	1149	1	8	0:44:00	3.46	0.86 (0:12:09)	2.30 (0:20:51)	0
14-Mar-07	1153	2	43	2:56:42	14.53	0	9.45 (1:59:00)*	3.76 (0:54:00)*
15-Mar-07	1157	1	19	0:58:01	6.45	0.53 (0:11:00)	1.12 (0:12:00)	4.01 (0:43:00)
31-Mar-07	1158	1	7	0:33:00	3.24	0	2.40 (0:24:45)	0
1-Apr-07	1159	2	6	0:17:56	1.53	0	0	1.53 (0:18:20)
2-Apr-07	1160	2	11	1:25:00	9.67	0	4.65 (0:43:20)	4.00 (0:31:50)
4-Apr-07	1161	1	7	0:43:40	2.52	0	1.77 (0:09:50)	0
10-Apr-07	1162	1	7	0:36:20	5.05	0	4.21 (0:28:40)	0
Total	9	12	154	10:31:41	56.56	2.64 (0:37:09)	32.52 (5:49:48)	15.36 (2:48:51)

4.3.2. Habitat selection during movement modes

Within the three movement modes classified for whale tracks, whales spent 63 % of their time milling, 30 % extensively moving and 7 % intensively moving (Table 4-2). Only two whales, whose tracks spanned over 6 km, exhibited all three movement modes (Figure 4-3a, b). All tracks less than 3.4 km showed one movement mode, either milling or extensive movements. All whales except one (i.e. whale 1159 with the shortest track, Table 4-2) showed milling behaviour, and spent between 20 – 100 % of their time in this mode.

There was an overlap in the range of tortuosity exhibited between movement modes (Figure 4-1c). Milling covered the full range of tortuosity, with highly tortuous sections of track corresponding to circular excursions of up to 1 km from a whale's main path (Figure 4-3b, c). These were classified as milling as only one surface sequence fell into the turning angle criteria of 1.

Whale 1143
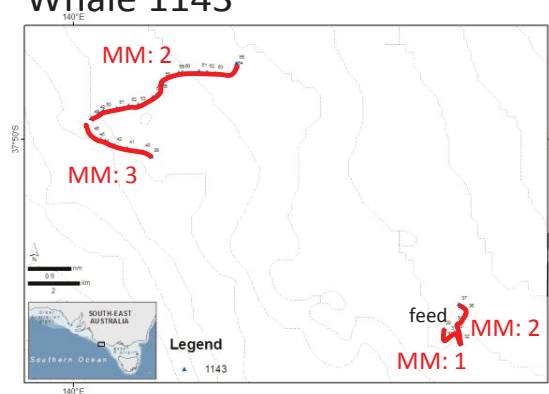
Whale 1153
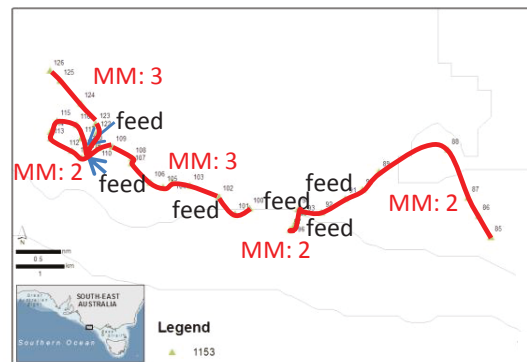
Whale 1157
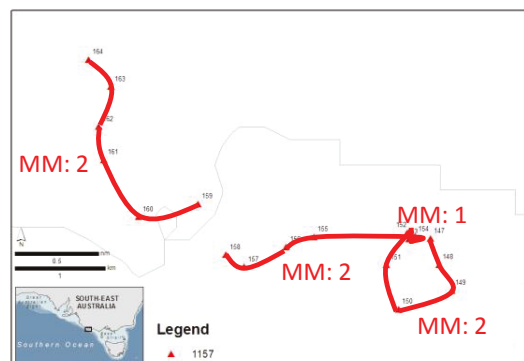
Figure 4-3. Three examples of whale tracks recorded in 2007, showing individual whale surface movements. Shown are: position of terminal positions of diving whales (▲); movement modes (MM, 1 = intensive, 2 = milling and 3 = extensive), and feeding events. Bathymetric contours at 10 m.

Whales also used a range of effort (distance, time, speed) within each mode, as measured for each surface sequence. Milling movement showed the highest variation in speed (Figure 4-4). Interestingly, the distribution of all three effort measures for all follows combined were bimodal at (e.g. speed ~ 5 and 9 km hr^{-1}; NB. distance and time

used to derive speed were highly correlated; r = 0.70, p < 0.05), although this modality was not explained by any relationship with any other measure of effort or movement.
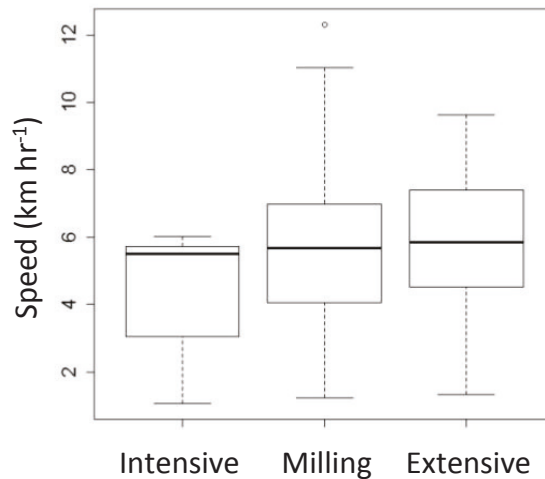
Figure 4-4. Boxplot (median, 1st and 3rd quartiles, and outliers) showing the range of speeds observed between movement modes.

Whales showed some selection for habitat according to movement modes. Near-surface and midwater school abundance was elevated during intensive movements compared to milling and extensive movements (Appendix 2, Figure 4-5; univariate PERMANOVAs surface ΣNASC: Pseudo-$F_{(2,82)}$ = 3.14, MC p = 0.05, pairwise 1,3 p < 0.05, permdisp p > 0.05; midwater percentage occupation: Pseudo-$F_{(2,82)}$ = 3.16, MC p = 0.05, pairwise 1,2 p < 0.05, permdisp p > 0.05). The mean values for other measures of near-surface and midwater prey abundance were also generally higher for intensive compared to other movement modes (Appendix 2). Whales also followed through areas of elevated surface productivity during intensive movements (Appendix 2). Only chl-*a* had significantly different means for intensive and extensive movements, with chl-*a* for intensive movements having higher values (explained by either dispersion or location effects; Pseudo-$F_{(2,82)}$ = 1.88, MC p = 0.16, pairwise 1,3 p < 0.05, permdisp p < 0.05).

In support of the patterns described above, the sections of track where whales were 'switching' markedly between intensive and either milling or extensive movements showed changes in prey abundance of between 1.5 and 2.5 numbers of near-surface schools km^{-1} and 0 to 2.5 demersal schools km^{-1}. Areas associated with intensive movements had higher school counts. The change in the density of schools was not as clear and appeared influenced by the school counts and the surface-feeding activity of

whales in adjacent areas. Neither switching between milling and extensive movements, or to circular excursions within milling behaviour, could be explained by a change in school counts or density (i.e. both positive and negative changes in prey abundance were observed).
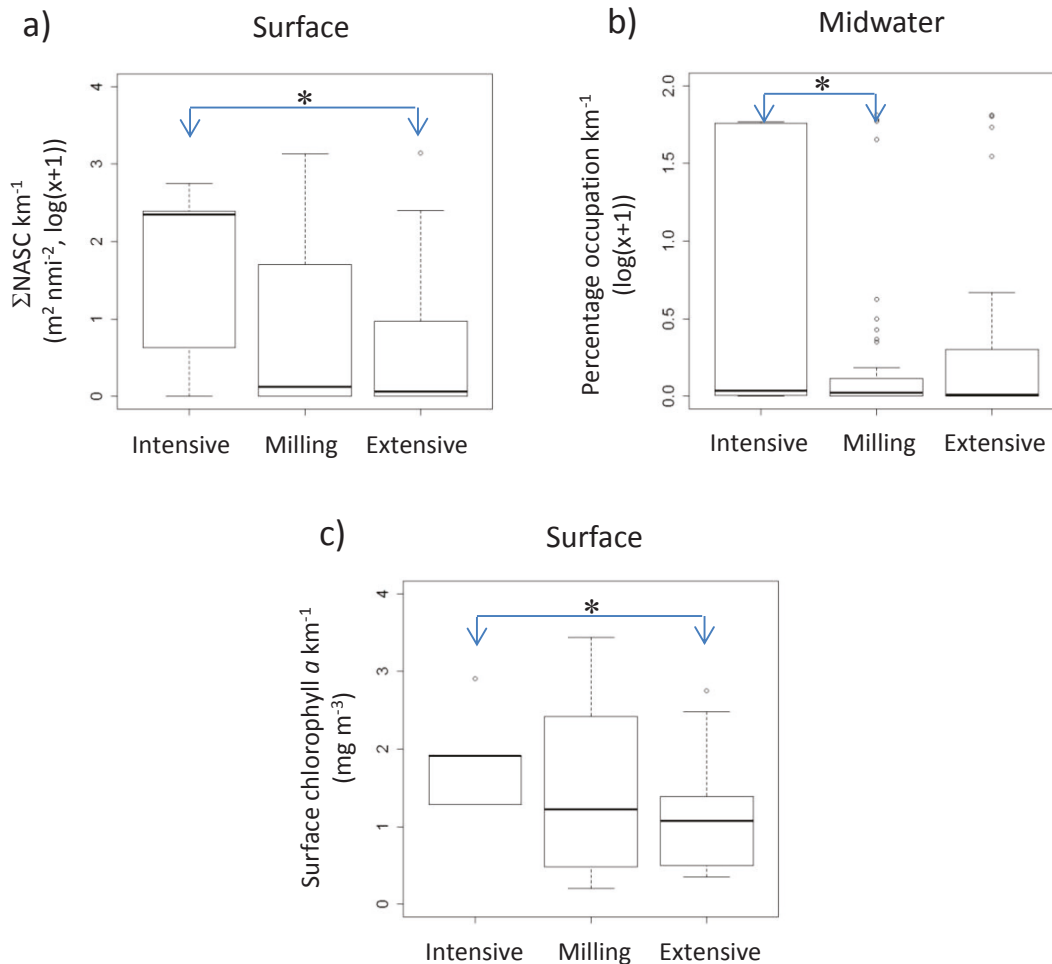
Figure 4-5. Boxplots (median, 1st and 3rd quartiles, and outliers) of transformed prey abundance per km-interval: a) surface acoustic biomass (ΣNASC), and b) midwater percentage occupation; and c) surface chlorophyll-*a* for each movement mode (intensive n = 5, milling n = 84, and extensive n = 66). Asterisks and associated arrows represent significant post-hoc pair-wise comparisons, $p < 0.05$, PERMANOVA.

4.3.3. Habitat selection by feeding whales

Eleven surface feeding events were recorded in survey (n = 5) and tracking (n = 7; Table 4-2) data. Six of the seven feeding events occurred in milling mode and one in extensive movement mode. Surface feeding events during milling included two

adjacent to, and associated with, intensive and circular movements (Figure 4-3). There was no difference in whale speeds for surface sequences where whales were feeding and non-feeding (mean ± SE; feeding: 4.34 ± 0.86 km h^{-1}; non-feeding: 5.81 ± 0.22 km h^{-1}; univariate PERMANOVA Pseudo-F$_{(1,115)}$ = 2.66, p > 0.05).

The occurrence of surface feeding whales was influenced by prey abundance, although the very low number of observations requires that these results to be interpreted with caution. From the survey data, demersal school abundance, particularly school acoustic biomass and percentage occupation, were significantly higher in feeding intervals than non-feeding intervals (Figure 4-6a, b; univariate PERMANOVAs ΣNASC: Pseudo-F$_{(1,153)}$ = 8.86, MC p = 0.004, permdisp p > 0.05; percentage occupation: Pseudo-F$_{(1,153)}$ = 3.63, MC p = 0.06, permdisp p > 0.05). From the track data, near-surface and demersal school counts (Figure 4-6c,e) and acoustic biomass (Figure 4-6d, f) were significantly higher for feeding intervals than non-feeding intervals, with some of the differences explained by dispersion and location effects (univariate PERMANOVAs surface counts: Pseudo-F$_{(1,83)}$ = 7.09, MC p = 0.009, permdisp p < 0.05; surface ΣNASC: Pseudo-F$_{(1,83)}$ = 6.88, MC p = 0.01, permdisp p > 0.05; demersal counts: Pseudo-F$_{(1,83)}$ = 8.72, MC p = 0.004, permdisp p < 0.05; demersal ΣNASC: Pseudo-F$_{(1,83)}$ = 3.87, MC p = 0.05, permdisp p < 0.05).

Consistent with findings, from the survey data, the highest ER of whales and prey schools corresponded to feeding whales (Figure 4-2). Unsurprisingly, however, there was variance in this observation, with some intervals associated with feeding whales exhibiting low school counts (i.e. 0.14 and 0.17 km^{-1}; Figure 4-2). Further, when the section of track where whale 1153 was surface feeding (Figure 4-3) was compared for its difference in school prey abundance to the preceding track section where no feeding was observed, there was a large shift from high to low counts for both near-surface and demersal schools (i.e. difference of 3.3 and 5.4 schools km^{-1} respectively). Also, the maximum density (S$_v$max, dB re 1 m^{-1}) of near-surface schools decreased by 10.84 dB re 1 m^{-1} from feeding to non-feeding track sections, with no real change in midwater and demersal maximum densities (i.e. -1.86 and -1.71 dB re 1 m^{-1} respectively).

The estimated maximum weight densities schools (Methods, Section 4.2.5.2) occurring around surface feeding whales were consistently higher for near-surface schools. Maximum weight densities for near-surface schools ranged from 0.05 to 1.64 kg m^{-3}, compared with a range of 0.02 to 0.08 kg m^{-3} for demersal schools. These equate to numerical densities of between 12,331 and 433,510 n m^{-3} for near-surface schools and between 6,109 and 20,653 n m^{-3} for demersal schools.

The track data showed that waters where whales surface-fed also had elevated surface productivity (Figure 4-6g-i; Appendix 2; univariate PERMANOVAs SST: Pseudo-$F_{(1,83)}$ = 9.78, MC p = 0.002, permdisp p > 0.05; univariate PERMANOVAs sea chl-*a*: Pseudo-$F_{(1,83)}$ = 11.45, MC p = 0.001, permdisp p > 0.05; univariate PERMANOVAs alongshore wind-stress: Pseudo-$F_{(1,83)}$ = 3.45, MC p = 0.06, permdisp P < 0.05).
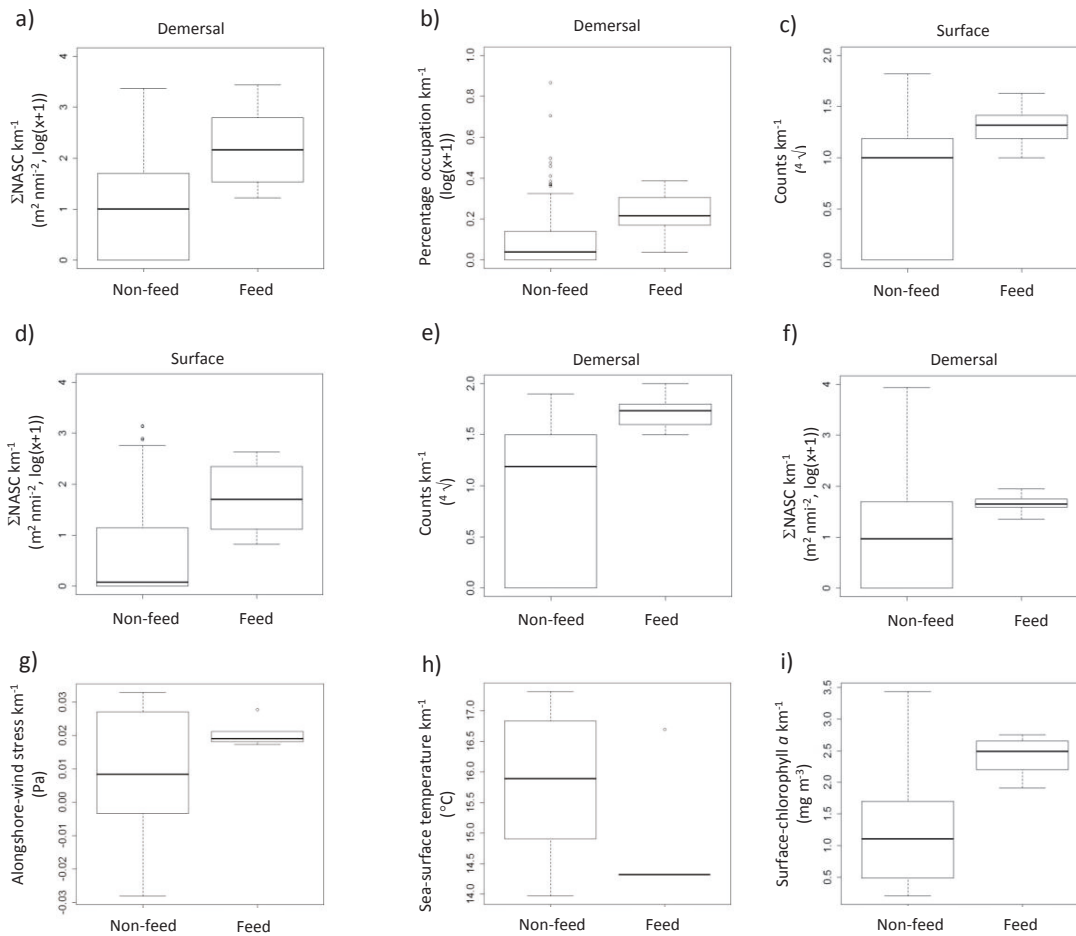
Figure 4-6. Boxplots (median, 1st and 3rd quartiles, and outliers) of transformed prey abundance and untransformed habitat-structure descriptors per km-interval from survey data (a – b); and tracking data (c – i), for non-feeding and feeding whales. All PERMANOVA tests p < 0.05.

4.4. DISCUSSION

Pygmy blue whales showed diverse movement patterns and responses to their habitat at very fine scales. Although distributed throughout the range of shelf habitat available to them, they selected profitable habitat (i.e. greater prey abundance and more prey patches) when in more intensive search modes. Further coherence was observed for areas where whales were surface feeding. Surface feeding areas were characterised by high near-surface and demersal prey abundance (school counts, and acoustic biomass and density), and habitat values representing enhanced water column productivity. These results highlight the importance of accounting for fine-scale patterns in predator-prey interactions, including the behavioural context of predators and the vertical distribution and abundance of prey.

4.4.1. General whale habitat selection

Pygmy blue whales recorded on survey were not distributed in any particular 'environmental window' on the shelf, and occupied highly variable habitat. The habitat available to pygmy blue whales recorded on survey was also found to have prey and other habitat characteristics similar to characteristics recorded throughout the study area (Chapter 2 and 3). This pattern, of whales generally occupying available habitat, held true when comparing the horizontal distribution of whales (not accounting for behaviour) with multiple horizontal and vertical measures of prey abundance.

Moderate relationships were found between whale and prey school ERs for survey data. Only the very highest ERs of whales and schools showed a correlation (although with low sample sizes), and equated to a threshold of 10 schools km^{-1} day^{-1} in the study area before whale ERs increased. Areas occupied by whales were also characterised by higher midwater school occupation than areas not occupied by whales. However, the low number of intervals with whales and the highly variable relationships between whales and habitat limited the capacity to fully interpret these results. The broad range of habitat values associated with surveyed whales, therefore likely reflected environmental conditions at the time of sampling. Although direct comparisons with other baleen whale studies are challenging due to different measures of prey abundance and habitat structure, rorqual whales generally forage and feed in ocean areas with elevated productivity associated with upwelled water (Croll et al. 1998, Fiedler et al. 1998, Croll et al. 2001b, Davis et al. 2002, Baumgartner 2003, Baumgartner et al. 2003, Doniol-Valcroze et al. 2007, Gill et al. 2011). For example, similar low and variable ERs of rorquals were recorded during vessel surveys in the California Current, and whale ERs were generally influenced by krill density and

upwelling over short time scales (Croll et al. 2001b). As one might expect, there is variability in these relationships, and in the environmental factors that influence them (Certain et al. 2011). Studies of baleen whale abundance off eastern Canada found that variability in whale abundance was associated with capelin (*Mallotus villosus*) abundance, and that some of this variability was explained by differences in capelin abundance from year to year (Piatt & Methven 1992).

Whales also moved through a broad range in habitat, which was generally more profitable than that recorded for whales observed on survey. This was evident in higher midwater prey abundance and chl-*a* concentrations (as high as 3.4 mg m^{-3}; equivalent to high values in the region; Chapter 3 and van Ruth et al. 2010a), and lower minimum SSTs (i.e. 13.9 °C). Surface-upwelled water (i.e. < 14.7 °C; Chapter 4, Section 3.2.2.2) is a feature uncommon outside coastal-upwelling plumes across the study area and in other shelf areas off southern Australian (McClatchie et al. 2006, Ward et al. 2006, Middleton & Bye 2007, van Ruth et al. 2010b, van Ruth et al. 2010a, Gill et al. 2011).

There are clearly a number of mechanisms affecting whale-habitat relationships. The pygmy blue whale-habitat relationships found in the study highlight that these patterns are expected to change depending on factors affecting the availability of prey, such as school size and density, upwelling features and whale activity.

4.4.2. Behavioural plasticity

The simple methods used here to characterise fine-scale surface movements of whales provided the flexibility required to distinguish between a diversity of movement modes. These broadly represented the range of hierarchical search patterns expected for a predator moving between prey swarms (inter-swarm distances: 0.004 – 1 km; as reported in Chapter 2, Figure 2-7a, b) and within and between patches (expected average patch size: > 1 – 100's kms; Figure 1-1; Murphy et al. 1988). Although three distinct modes were characterised, switching between modes was sometimes abrupt (e.g. between circular excursions and extensive moves) and at other times more subtle (e.g. between milling and extensive moves), revealing a plasticity in fine-scale behavioural response, as has been documented in basking sharks (*Cetorhinus maximus*; Sims & Quayle 1998). This complexity in response and tendency to switch gradually has previously been captured in models assessing the optimality of search efficiency in predators (Barton & Hovestadt 2013).

There was also variability in the tortuosity recorded between movement modes, expressly highlighted by the circular excursions during milling. Tortuosity may reflect random search paths similar to larger 'looping' for central-place foraging seabirds,

where scale-dependent adjustments are made to foraging modes, likely in response to the predictability of prey (Weimerskirch 2007). Movement patterns characterised in this study had similar horizontal patterns to broader-scale transiting and area-restricted searches described and quantified for marine predators (Fauchald & Tveraa 2006, Hays et al. 2006, Weimerskirch 2007, Bestley et al. 2013), including blue whales (Bailey et al. 2010). Although track lengths were too short to quantify the spatial extent of movements, the data suggest that switching between all modes can occur at very short distances (e.g. < 6 km). Movement data showed that the least time was spent in intensive movement and the most time in milling across the shelf (Table 4-2). This was also shown by the range of depths in which whales foraged (milling movements ranged more widely across the shelf). Such ranging behaviour may also explain the range of habitat encountered for surveyed and followed whales, described above. Blue whales tracked by satellite had a spatial range for area-restricted search movements of between 10 and 360 km radius (mean 50 km; using First-Passage Time analysis; Bailey et al. 2010). These spatial search distances would be equivalent to larger inter-patch distances (Figure 1-1), possibly occurring across the southern-Australian foraging ground.

Measures of movement effort (i.e. breaths, distance, time and speed) were variable within each movement mode. This was unexpected, as speed has been used consistently to characterise movement at broad scales (Bailey et al. 2010, Jonsen et al. 2013). However, the measures of effort used in this study are more commonly applied to differentiate feeding events in ram feeders (Sims 1999, Baumgartner & Mate 2003, Simon et al. 2009), and for large movements in ram and lunge feeders (Bailey et al. 2010). Lunge feeders, such as blue whales, can show large variability in speeds across dive intervals due to their dynamic dive behaviour and the effect of variable prey depths. For example, blue whales use acceleration, deceleration and gliding during the lunge, filtering and engulfment phases, as well as mostly gliding during dive descents, and active swimming during dive ascents (Acevedo-Gutiérrez et al. 2002, Goldbogen et al. 2006, Calambokidis et al. 2007, Goldbogen et al. 2010, Goldbogen et al. 2011, Doniol-Valcroze et al. 2012, Goldbogen et al. 2012). Calambokidis et al. (2007) reported that diving behaviour varied by region and period, being more uniform for individuals in the same area. Coupled with dive effort are corresponding surface recovery times that will affect overall horizontal speed (Doniol-Valcroze et al. 2011). The two modes found in swim speeds in this study across all tracks ($\sim$ 5 and 9 km hr^{-1}) probably represent bimodal patterns in the vertical habitats used by pygmy blue whales. Similar modality in feeding behaviour (where increase in feeding events at depth correlate to increase in speed recorded over a dive interval) occurs in blue whales off California (Goldbogen et al. 2011) and in the Gulf of St. Lawrence (Doniol-Valcroze et al. 2011).

Blue whales used depth strata at different times of the day, linked to the vertical movement of krill (Doniol-Valcroze et al. 2011). The speed modalities reported here may therefore reflect the depth ranges covered by foraging whales, and the associated time and distances to cover those depths, along with feeding effort at those depths.

The suite of foraging movements described in the study must contribute to optimising each whale's horizontal and vertical search efforts for heterogeneous prey, and allow them to respond and adapt to changing conditions encountered at fine- and broad-scales. Of interest is how fine-scale surface movements interact with meso-scale (within foraging ground) and broad-scale (between foraging ground) patterns of movement, and what internal and external mechanisms drive switches.

4.4.3. Improved resolution of habitat selection by using movement modes

Higher prey abundances were observed when whales were more intensively searching, and when switching to an intensive mode. Intensive movements were associated more frequently with higher near-surface- and midwater-prey abundance than other movement modes. Patterns of association between areas where whales switched movements and prey abundance showed that prey patchiness (as measured by school counts) was more influential than density, with changes of up to 2.5 near-surface and demersal schools km^{-1} occurring at sites between intensive and other movements.

The only evidence to explain whale movements switching to circular excursions was the width of such excursions (~ 1 km), which matched the overall school patchiness measured in the study (Chapter 2). The length of intensive movements (< 1 km) also matched this spatial scale, providing further evidence that this distance may be an optimal intensive-search distance for pygmy blue whales in this region. The extent of forage areas where fin and blue whales in the California Current spent extended time was a similar horizontal scale to this study where prey may have similar scales of patchiness (1 km^2; Acevedo-Gutiérrez et al. 2002). Search patterns at distinct spatial scales, including as small as 8 m were found in northern fur seals in the eastern Bering Sea and were coupled to the patchiness of their prey, juvenile walleye Pollock (*Theragra chalcogramma*; Benoit-Bird et al. 2013b). The scale of predator-prey interaction found in studies elsewhere suggest pygmy blue whale search patterns may, to some extent, operate in a 'hierarchically-nested system' (Fauchald 2009). Broader prey-patch analyses, and recording of whale tracks over longer distances, will resolve whether coherence occurs at larger scales than could be detected here, and whether the relationships between pygmy blue whale movement and habitat found in the study align to studies that have measured predator-habitat interactions across similar scales (Weimerskirch 2007, Benoit-Bird et al. 2013b). The few circular and intensive

movements recorded in the present study also suggest that the area in which whales were followed had relatively low food resources.

4.4.4. Fine-scale habitat coherence for feeding whales

Pygmy blue whales fed at the surface in areas characterised by higher prey abundance and surface primary productivity, highlighting the improved coherence in predator-prey interactions achieved when incorporating behavioural context. Whales selected for near-surface and demersal prey abundance, and for habitat structure that represented elevated surface primary productivity (Figure 4-6). More specifically, near-surface and demersal prey counts and acoustic biomass were consistently higher in areas where whales fed, irrespective of movement mode. Some of the counts of demersal schools were the highest recorded for all survey and track data, and for the study area (Chapter 2, Figure 2-4); however, demersal school densities were lower than those of near-surface schools recorded concurrently. Abundance of near-surface schools was consistently higher in areas where whales were feeding compared to adjacent sections of track. Prey abundance was also less variable in areas where whales were feeding than elsewhere, which possibly indicates more specific selection by surface feeding whales. It may also be an artefact of the low sample sizes for feeding whales.

Results of the study were consistent with the prediction that surface feeding whales would select dense and locally aggregated surface schools. Feeding rates were consistently higher in blue whales in the St. Lawrence River estuary for surface feeding than feeding at greater depths. This indicated that whales may select surface prey for foraging efficiency reasons, and therefore concentrate their foraging effort at night when krill are at the surface (Doniol-Valcroze et al. 2011). In the present study surface schools were found to be discrete and dense, and therefore very suitable resources for pygmy blue whales in terms of both food availability and foraging efficiency. Estimated maximum-weight densities of all near-surface swarms associated with feeding whales recorded in the study were above the 0.1 kg m^{-3} threshold set for blue whales (Croll et al. 2005, Goldbogen et al. 2011, Wiedenmann et al. 2011). Numerical densities of these near-surface swarms were also high (12,331 and 433,510 n m^{-3}, based on maximum density estimates) compared to those observed for feeding blue whales elsewhere (4403 n m^{-3}, based on mean density estimates, Croll et al. 2005), and krill generally (O'Brien 1988, Watkins 2007). Estimates of the numerical densities of schools in the study are speculated to be higher than the estimated maximum packing density of krill in Chapter 2 (i.e. 94 000 n m^{-3}, Section 2.2.4.4) due to the varying lengths, orientations and species of macrozooplankton and fish that may be encountered in the study area. Depending on the predictability of the resource provided by surface schools, feeding on

surface schools would considerably reduce the need to search for prey at depth, with a consequent reduction in energy expenditure. However, near-surface schools did not occur consistently across the shelf, and except in areas where near-surface schools were highly aggregated, it is unlikely that they provide a predictable food resource.

It appeared that whales were searching and using the whole water column, with potentially profitable resources occurring at various depths, depending on prevailing conditions. Whales associated with schools at a range of depths including midwater schools, which at times were a locally significant resource, albeit more ephemeral than other parts of the water column (Chapter 2). Whale effort elsewhere in the water column was also demonstrated by surface feeding occurring in both oriented and milling searches, with no significant change in behaviour observed after whales surface fed. Associations between surface feeding whales and demersal schools may be due to a combination of biological and environmental controls that couple these schools. Such controls may include the different vertical migration, feeding and breeding needs of sub-groups of the same prey aggregations, and shared environmental preferences for productive water or benthic substrate (Wakefield et al. 2012). It is likely that shelf areas containing surface and demersal schools had productive water throughout the water column (as represented in Pattern 3, PHCM, Chapter 3).

Demersal schools were not considered available to surface or diving lunge-feeding whales because they were 10 m above the ocean floor and blue whales typically approach prey from below (Goldbogen et al. 2013b). Although humpback whales (*Megaptera novaeangliae*) are specialist bottom feeders (Friedlaender et al. 2009, Hazen et al. 2009), fin and blue whales feed at both the surface and midwater depths (Croll et al. 2001b, Croll et al. 2005, Calambokidis et al. 2007, Goldbogen et al. 2013b). Diving at depth is more marginal in terms of energetic efficiency when prey densities are too low for net energy gain (Doniol-Valcroze et al. 2011, Goldbogen et al. 2011). However, demersal schools recorded in the study were consistently numerous and may represent a food resource when schools may move up in the water column.

Relationships between marine predators that are confined to the surface and their deep prey have been observed in seabirds. Most seabirds have a limited diving capacity to reach deeper prey from the surface, and it is believed they rely on environmental cues that indicate when prey will be accessible (Fauchald 2009). For example, the distribution of black-legged kittiwakes (*Rissa tridactyla*) in the eastern Bering Sea was strongly predicted by prey abundances that were deep and in-accessible (Benoit-Bird et al. 2013a). Fin and blue whales, and other planktivores, change their dive depths in response to changes in prey distribution, with gradual shallowing of dive depths at dusk

in concert with the vertical migration of krill to the surface (Croll et al. 1998, Calambokidis et al. 2007, Benoit-Bird et al. 2011, Doniol-Valcroze et al. 2011). The diel behaviour of krill off southern Australia has not been quantified, and it remains to be seen how prominent vertical migration is, how it influences surface aggregations, and the consequences for plankton predators.

It appeared that prey abundances associated with surface feeding whales in the study were also coupled with ocean-surface productivity. In the study area in 2003 (Chapter 3), the vertical position and abundance of schools were influenced by the availability of surface phytoplankton, which in turn was influenced by the availability of upwelled water and upwelling-influential winds. It is unknown whether whales use environmental cues to search for prey. However, the fact that signatures for surface-upwelled water were only apparent in the follow data where whales fed (Figure 4-6) indicates that it is more likely that these associations were due to elevated-prey abundance, as suggested by Benoit-Bird (2013a). Collection of whale feeding and ocean physical data at higher resolutions and at depth will help resolve this.

Some variability in the relationship between feeding whales and prey reported here may also have been driven by con-specific interactions occurring between paired whales. Paired associations between whales are thought to be early-breeding behaviour prior to their migration to winter breeding and foraging grounds, as most of these encounters are between a lead female and trail male (Blue Whale Study unpublished data; Calambokidis et al. 2007, Bortolotti 2008). Paired whales in the study were still engaged in foraging and feeding behaviour, and moved over potentially suitable foraging ground, indicating they may 'multi-task' while in foraging grounds.

4.4.5. Conclusions

This research highlights the improved understanding of predator-prey and environmental relationships that is achieved when fine-scale predator behaviour is integrated with multiple measures of prey distribution and abundance. Pygmy blue whales were found to constantly forage over highly variable habitat; this variability was comparable to the variability in the entire habitat available to them. This may explain their variable relationships with meso-scale environment factors found in other studies. Whales followed over kilometres displayed great plasticity in horizontal movement patterns, with a variety of movements occurring over small areas of shelf. Switching to more intensive movements occurred when prey patchiness increased. There was some evidence to suggest consistency in intensive-search areas (possibly optimal at < 1 km) that matched overall school patchiness. Surface feeding whales had the most predictable relationship with habitat, selecting for profitably-structured near-surface

schools. Demersal schools were selected either due to their food potential or due to their association with surface schools in areas where productivity occurred throughout the water column (leading to bentho-pelagic coupling of these schools). Both horizontal speeds and foraging movements revealed that pygmy blue whales, even amongst profitable surface prey, were still expending considerable effort searching for prey at depth.

CHAPTER 4

4.5. APPENDICES

4.5.1. Appendix 1. School-weight density equation

$$w_{\text{school}} = w_{\text{ind}} \times \frac{s_v}{\sigma_{bs}}$$

Where:

w_{school} = aggregation weight-density in kg m^{-3}

w_{ind} = the mean weight of an individual in kg

s_v = the volume backscattering coefficient of the aggregation in m^2 m^{-3}

σ_{bs} = the backscattering cross-section of an individual in m^2

And:

$$s_v = 10^{S_v/10}$$

Where:

S_v = (Mean) volume backscattering strength in dB re 1 m^2 m^{-3} (see Chapter 2, Appendix 2, Equation 1)

And:

$$\sigma_{bs} = 10^{TS/10}$$

Where:

TS = the target strength of an individual in dB re 1 m^2

4.5.2. Appendix 2. Summary of untransformed prey and habitat structure descriptor values (mean ± SE, ranges) for interval groups used for comparison within survey and track data.

Groups included whale and non-whale, and feeding and non-feeding (inclusive of whether whales were present or not) intervals within survey data; and movement modes, and feeding and non-feeding intervals within track data. Significant PERMANOVA results (p < 0.05) indicated by separate notations for paired interval groups.

Interval group	Data type	Variables						
Prey abundance		School counts		School ∑NASC (m^2 nmi^{-2})		School percentage occupation		
Surface								
non-whale	survey data	1.76 ± 0.26	(0-15)	20.44 ± 6.15	(0-668)	0.14 ± 0.03	(0-2.15)	
non-feeding	survey data	1.79 ± 0.25	(0-15)	26.30 ± 8.36	(0-926)	0.13 ± 0.03	(0-2.15)	
	track data	1.53 ± 0.24°	(0-11)	93.81 ± 29.45^	(0-1381)	0.17 ± 0.03	(0-1.44)	
whale	survey data	1.67 ± 0.71	(0-9)	72.78 ± 61.41	(0-925)	0.05 ± 0.02	(0-0.23)	
	track data	1.67 ± 0.22	(0-11)	97.32 ± 26.00	(0-1381)	0.19 ± 0.03	(0-1.44)	
movement mode	intensive	2.6 ± 0.93	(0-5)	205.66 ± 101.77#	(0-554)	0.28 ± 0.09	(0-0.52)	
	milling	1.55 ± 0.3	(0-11)	104.10 ± 34.92	(0-1369)	0.20 ± 0.05	(0-1.44)	
	extensive	1.59 ± 0.4	(0-8)	66.32 ± 51.44#	(0-1381)	0.13 ± 0.05	(0-1.06)	
feeding	survey data	0.6 ± 0.6	(0-3)	1.60 ± 1.60	(0-8)	0.03 ± 0.03	(0-0.13)	
	track data	3.29 ± 0.75°	(1-7)	137.03 ± 61.80^	(5-164)	0.35 ± 0.12	(0.04-0.93)	
Midwater								
non-whale	survey data	0.98 ± 0.13	(0-10)	113.65 ± 66.76	(0-8905)	0.15 ± 0.04*	(0-3.21)	
non-feeding	survey data	0.99 ± 0.13	(0-10)	109.70 ± 62.35	(0-8905)	0.18 ± 0.04	(0-3.59)	
	track data	1.82 ± 0.26	(0-10)	570.47 ± 232.26	(0-15519)	6.10 ± 1.97	(0-64)	
whale	survey data	1.33 ± 0.47	(0-7)	39 ± 23.82	(0-351)	0.46 ± 0.25*	(0-3.58)	
	track data	1.80 ± 0.23	(0-10)	539.01 ± 202.22	(0-15519)	6.69 ± 1.84	(0-63.6)	
movement mode	intensive	2.4 ± 1.12	(0-6)	948.14 ± 598.44	(0-2943)	22.80 ± 13.94~	(0-57.7)	
	milling	1.83 ± 0.31	(0-10)	532.71 ± 310.84	(0-15519)	4.52 ± 2.08~	(0-63.5)	
	extensive	1.63 ± 0.41	(0-8)	495.53 ± 290.06	(0-7505)	8.21 ± 3.80	(0-63.6)	
feeding	survey data	1.6 ± 1.36	(0-7)	8.26 ± 8.22	(0-41)	0.22 ± 0.22	(0-1.10)	
	track data	1.57 ± 0.57	(0-4)	183.99 ± 87.66	(0-500)	13.37 ± 8.87	(0-58)	
Demersal								
non-whale	survey data	2.46 ± 0.24	(0-14)	96.63 ± 25.40	(0-2314)	0.32 ± 0.05	(0-4.1)	
non-feeding	survey data	2.46 ± 0.23	(0-14)	91.07 ± 23.76+	(0-2314)	0.31 ± 0.04*	(0-4.1)	
	track data	3.10 ± 0.37◊	(0-13)	156.75 ± 110.44<	(0-8687)	0.54 ± 0.11	(0-6.34)	
whale	survey data	3.07 ± 0.75	(0-9)	250.93 ± 183.84	(0-2758)	0.78 ± 0.41	(0-6.34)	
	track data	3.59 ± 0.38	(0-16)	147.92 ± 96.02	(0-8687)	0.57 ± 0.10	(0-6.34)	
movement mode	intensive	3.6 ± 2.06	(0-11)	73.07 ± 44.44	(0-213)	0.59 ± 0.34	(0-1.55)	
	milling	3.87 ± 0.54	(0-16)	196.28 ± 163.42	(0-8687)	0.53 ± 0.10	(0-3.58)	
	extensive	2.89 ± 0.59	(0-9)	69.47 ± 42.48	(0-1149)	0.63 ± 0.25	(0-6.34)	
feeding	survey data	4.4 ± 1.44	(0-9)	726.49 ± 519.51+	(15-2758)	1.98 ± 1.10*	(0.47-6.34)	
	track data	9.14 ± 1.44◊	(5-16)	48.33 ± 7.86<	(22-87)	0.82 ± 0.16	(0.38-1.59)	
Habitat structure		alongshore-wind stress (Pa)		sea-surface temperature (°C)		surface-chlorophyll a (mg m^{-3})		shelf depth (m)
non-whale	survey data	0.003 ± 0.001	(-0.02-0.04)	16.17 ± 0.06	(14.7-17.6)	0.70 ± 0.03	(0.2-2.0)	96.34 ± 2.03 (50.1-137.6)
non-feeding	survey data	0.003 ± 0.001	(-0.02-0.04)	16.16 ± 0.06	(14.7-17.6)	0.70 ± 0.03	(0.20-2.02)	97.08 ± 1.97 (50.1-137.6)
	track data	0.007 ± 0.002#	(-0.03-0.03)	15.88 ± 0.11~	(13.9-17.3)	1.26 ± 0.10"	(0.2-3.4)	93.51 ± 3.71 (35-157)
whale	survey data	0.003 ± 0.004	(-0.02-0.04)	16.02 ± 0.17	(15.2-17.1)	0.67 ± 0.08	(0.2-1.4)	103.99 ± 6.59 (67.2-134.6)
	track data	0.008 ± 0.002	(-0.03-0.03)	15.78 ± 0.11	(13.9-17.3)	1.35 ± 0.10	(0.2-3.44)	90.08 ± 3.45 (35-157)
movement mode	intensive	0.006 ± 0.014	(-0.03-0.03)	15.57 ± 0.46	(14.6-16.7)	1.86 ± 0.30^	(1.3-2.9)	81.15 ± 3.24 (70-87)
	milling	0.010 ± 0.002	(-0.03-0.03)	15.86 ± 0.15	(14.3-17.3)	1.41 ± 0.14	(0.2-3.4)	95.74 ± 5.13 (35-157)
	extensive	0.004 ± 0.004	(-0.03-0.03)	15.71 ± 0.20	(14.0-17.3)	1.09 ± 0.13^	(0.4-2.8)	81.36 ± 5.31 (44-130)
feeding	survey data	0.00 ± 0.003	(-0.004-0.008)	15.82 ± 0.35	(15.3-17.1)	0.73 ± 0.05	(0.53-0.81)	97.08 ± 13.68 (71.0-131.1)
	track data	0.020 ± 0.001#	(0.01-0.02)	14.66 ± 0.34~	(14.3-16.7)	2.41 ± 0.13"	(1.9-2.7)	51.34 ± 5.10 (45-82)

5. GENERAL DISCUSSION AND CONCLUSIONS

Herein I discuss the contribution of this study for understanding the interactions between pygmy blue whales (*Balaenoptera musculus brevicauda*) and their habitat, and predator-prey interactions more generally. Particular emphasis is given to defining habitat that is profitable (in terms of food resources), describing how pygmy blue whales search this habitat efficiently to find food, and presenting suggestions for further studies to improve the resolution of the study's findings. Concluding comments are made with regard to the significance and utility of the findings for pygmy blue whale conservation.

5.1. PYGMY BLUE WHALE FORAGING HABITAT

The study confirmed that the foraging habitat of pygmy blue whales off southern Australia is temporally and spatially variable, and productive, with densities of neritic fauna aggregations and chlorophyll-*a* concentrations similar at times to the most productive marine regions in the world (Mann & Lazier 2006, Ward et al. 2006, Gremillet et al. 2008, van Ruth et al. 2010a, Santora et al. 2011b). High spatial and temporal variability was found in both biophysical features and the distribution and abundance of the neritic fauna (macrozooplankton and small fish). The analytical approach (of combining and spatio-temporally stratifying the acoustically-derived characteristics of neritic aggregations) provided a comprehensive picture of the prey available to, and selected by, pygmy blue whales.

A combination of habitat factors was found to influence the abundance and variability of neritic aggregations, with surface wind patterns and their interannual differences being of particular importance. The 1-step upwelling process thought to operate in this northern-boundary current system was indeed active during the study period, with increased southeasterly winds found to be concurrent with the presence of upwelled water and its circulation through the water column. The variability in the importance of wind stress, and its changing relationship with abundance of neritic aggregations over depth, appeared to be dependent on the wind's periodicity and strength. This in turn would have affected the level of nutrients accessible to primary producers, and potentially other conditions optimal for productivity. Wind stress probably also influenced the position of aggregations in the water column through the generation of surface turbulence. Periods of high wind activity prior to sampling (which occurred in relatively calm weather) were probably responsible for some of the mismatches between surface phytoplankton concentrations and neritic aggregations, since high

winds make conditions less optimal for primary production (Cury & Roy 1989). The inclusion of vertical-habitat variables was important in improving model relationships. Vertical-habitat variables gave a more complete picture of the habitat features affecting overall aggregation abundance at depth, particularly access to nutrients by phytoplankton. This showed that the Pelagic Habitat Conceptual Model (PHCM) worked well in articulating patterns not just across the shelf, but also in the main vertical strata thought to operate in neritic waters.

Pygmy blue whales were observed across the whole shelf, thereby ranging over the diverse habitat features available to them. Such variable habitat use was likely a response to the variable weather and ocean processes interacting during the upwelling season. The mid-shelf region, as predicted, was the most productive part of the shelf, and whales predominantly occurred there. Aggregation counts and percentage occupation were found to be consistently high in the mid-shelf region, whereas, acoustic biomass was highly variable across the shelf. The mid-shelf region was generally more profitable for pygmy blue whales (i.e. more and denser prey patches) than inner-shelf or outer-shelf regions. This was due to the influence of upwelled water and its associated primary and secondary productivity. For example, higher frequency of upwelling-favourable winds and the effect of Ekman transport will extend the influence of upwelling offshore, and physically move the neritic fauna (Botsford et al. 2003, Lawson et al. 2008a). This spatial movement of fauna, combined with the temporal lag between nutrient input from upwelled water and its effect on primary and secondary production, results in most productivity occurring in the mid-shelf region. A higher neritic biomass offshore (offshore of cooler water) has been seen in the eastern Great Australian Bight (Ward et al. 2006, McClatchie et al. 2007).

The shelf-wide patterns described here also affected the productivity within the water column. Variability in the vertical abundance of neritic aggregations was dependent on where they occurred across the shelf. Diffuse sub-surface layers were persistent across the study area. Although not previously recorded off southern Australia, they likely contributed to overall shelf productivity as an important food resource for surface and sub-surface planktivores. For example, there was evidence that dense aggregations were associated with the diffuse layers, and that layers consisted of mixed assemblages of mostly herbivorous micro- and macrozooplankton, including species recorded as prey for both *Nyctiphanes australis* and small fish (Chapter 2). Studies that quantify the temporal persistence and interactions of diffuse layers with other pelagic biota and physical processes will better define the ecosystem function of plankton layers. Such studies will be particularly important as diffuse layers play significant roles in structuring planktonic and other pelagic communities (Brierley et al. 1998, Watkins &

Murray 1998, Lawson et al. 2004, McManus et al. 2005, Lawson et al. 2008a, Benoit-Bird et al. 2009a, McManus et al. 2012).

Interannual habitat variability consistently influenced the distribution and abundance of neritic aggregations. The abundance of aggregations was positively correlated with wind strength over the sampling years (Chapter 3), as well as other indicators of upwelling strength and periodicity over the same period (including El Niño-Southern Oscillation cycles; Middleton et al. 2007, Nieblas et al. 2009). Broader-scale weather and ocean patterns (including those in the Southern Ocean) are likely to have influenced the entire foraging region (i.e. from the eastern GAB to Bass Strait), which extends both east and west of the study area.

Neritic aggregations exhibited a range of characteristics that made them a profitable food resource for pygmy blue whales. Across the study area, schools varied in size and showed consistency in their organisation. Most were < 1 km apart, suggesting that they were organised hierarchically. Inter-school distances were equivalent to those of krill off the Western Antarctic Peninsula (Lawson et al. 2008a), and may represent a common euphausiid patch organisation.

Near-surface schools, that may have been predominantly krill, were characterised as particularly profitable prey. Whales appeared to show a preference for tightly packed and very dense schools when intensively searching and surface feeding. This was in contrast to elsewhere in the study area where near-surface swarms were further apart and of lower density. The mechanistic pathways predicted to influence surface schools (according to the PHCM) concurred with the influence of habitat variables that represented the availability of upwelled water, primary productivity and turbulence at the surface. Clearly, conditions suitable for supporting high abundance of surface phytoplankton and krill occurred where whales were feeding, since those areas were found to have the highest productivity for the study area. This was in contrast to the general patterns in ocean processes affecting near-surface schools, with wind keeping the mixed-layer, and likely associated phytoplankton productivity, at depth.

This study was unable to test whether whales preferred near-surface schools over resources at depth. Areas associated with the presence of whales had both high midwater and demersal school abundance, and whale horizontal search patterns did not change after they fed at the surface. Often aggregations at depth were denser and took up more of the water column than near the surface (particularly the midwater), and those aggregations might be expected to sustain whales for longer than surface schools. However, midwater schools were more ephemeral and affected by the ocean processes above and below them. Although demersal schools were not considered

available to surface or diving lunge-feeding whales (as this resource was 10 m above the ocean floor; Goldbogen et al. 2013b), they were a consistent pelagic feature and appeared coupled to near-surface schools. Whales were either actively searching for deeper aggregations, or their association with deeper aggregations may have been due to productivity occurring throughout the water column. Demersal schools may represent more diffuse krill aggregations that shelter from predators at depth during the day, and migrate to surface waters to maximise their own prey availability at night (Pilditch & McClatchie 1994, Hays 2003). The diel behaviour of krill off southern Australia has not been quantified; it remains to be seen how prominent this behaviour is, how it influences surface aggregations, and what the consequences of vertical migration are to planktivores. Ocean processes influencing schools at depth were less clear than those influencing schools at the surface. This again highlights the importance of collecting habitat data at appropriate temporal and spatial scales, including vertical profiling and consideration of the effects of system pre-conditioning prior to sampling (refer to Chapter 2 and 3 Discussions).

5.2.   FINE-SCALE SEARCH STRATEGIES

Pygmy blue whales followed over fine scales in the study were found to use more dynamic search strategies than has previously been reported more generally for blue whales in the literature. Most horizontal movements reported in this study showed similar characteristics to the range of random and non-random search patterns described for large foraging animals (Fauchald & Tveraa 2006, Hays et al. 2006, Weimerskirch 2007, Bestley et al. 2013), including blue whales (Bailey et al. 2010). This suggests that the fine-scale search strategies that blue whales apply in foraging grounds may operate hierarchically, and are nested within meso- and broad-scale movements (Fauchald 2009, Benoit-Bird et al. 2013b). For example, intensive movements were constrained within 1-km areas where whales were moving between swarms within a patch, and may represent an optimal intensive-search area learnt from the expected patchiness in their prey. The same search areas have been documented for fin whales (*Balaenoptera physalus*), blue whales and seabirds (Acevedo-Gutiérrez et al. 2002, Weimerskirch 2007). Milling movements were characterised by animals moving over larger areas of shelf in a zigzag fashion, not dissimilar to movements detected at broad scales (Figure 1-1; Bailey et al. 2010). These are likely to represent inter-patch movements at meso-scales (> 1 km; Fauchald 1999). The more oriented behaviour characterised as extensive movements in this study is expected to represent a directional strategy of movement between larger patches of prey along the foraging ground. This is consistent with the transiting movement between foraging areas across ocean basins described elsewhere for blue whales (Bailey et al. 2010). The diverse

types of movement in the study could only be detected by tracking animal movements for each surfacing, as the resolution of movement response would otherwise be lost. The detail in movement metrics also showed features not typically detected in foraging studies, yet considered to provide optimal efficiencies when searching for patchy prey (Weimerskirch 2007, Barton & Hovestadt 2013, Lundy et al. 2013). These included relatively gradual switching between movement modes, and circular excursions within milling movements, both of which are probably scale-dependent responses to underlying prey patterns.

Interpretation of the range of horizontal movement patterns detected in the study was assisted by development of a simple conceptual fine-scale horizontal-movement model for blue whales in their foraging habitat (discussed below). The model contributes to the observational data recorded for a small dataset of individual pygmy blue whale movements (Chapter 4). It relies heavily on general observations made in the field during the study (not reported), and observations recorded for other blue whale populations (refer to Chapter 4). The model also draws upon conceptual and empirical movement models developed for other marine predators (e.g. Fauchald 1999, Weimerskirch 2007, Fauchald 2009). It will be important to test this model with larger datasets in the future. The conceptual model provided below is demonstrated for pygmy blue whale movements off southern Australia (Figure 5-1).

Pygmy blue whales select the region off southern Australia due to their knowledge of its predictability in providing food over the summer-autumn period. Selection of this habitat by whales may be instinctive or learnt, passed on by their mothers in their first year of life while they are still closely bonded (supported by the occurrence of 10 mother-calf pairs in the Bonney Upwelling between 2002 and 2007, Gill et al. 2011). Whales may enter the foraging ground from the west, south or east depending on their prior residence at other regional foraging grounds (i.e. within the Indian, Southern or Pacific Oceans respectively). Early in the season most whales are probably transiting across the Indian Ocean from their presumed foraging/breeding ground in the north-eastern Indian Ocean (e.g. Savu and Banda Seas, as shown by generally higher occurrence to the west of the Bonney Upwelling early in the season; Gill et al. 2011). However, whales may readily move between foraging grounds; satellite-tagged whales show movements between the Bonney Upwelling and Subtropical Convergence, and between the Perth Canyon and the Savu Sea (Gill and Jenner unpublished data).

Blue whale movement

Inter-patch and inter-concentration	• Extensive
Inter-patch	• Milling (zigzag) • Milling (circular)
Inter-swarm	• Intensive (zigzag, < 1 km)

Increasing prey availability
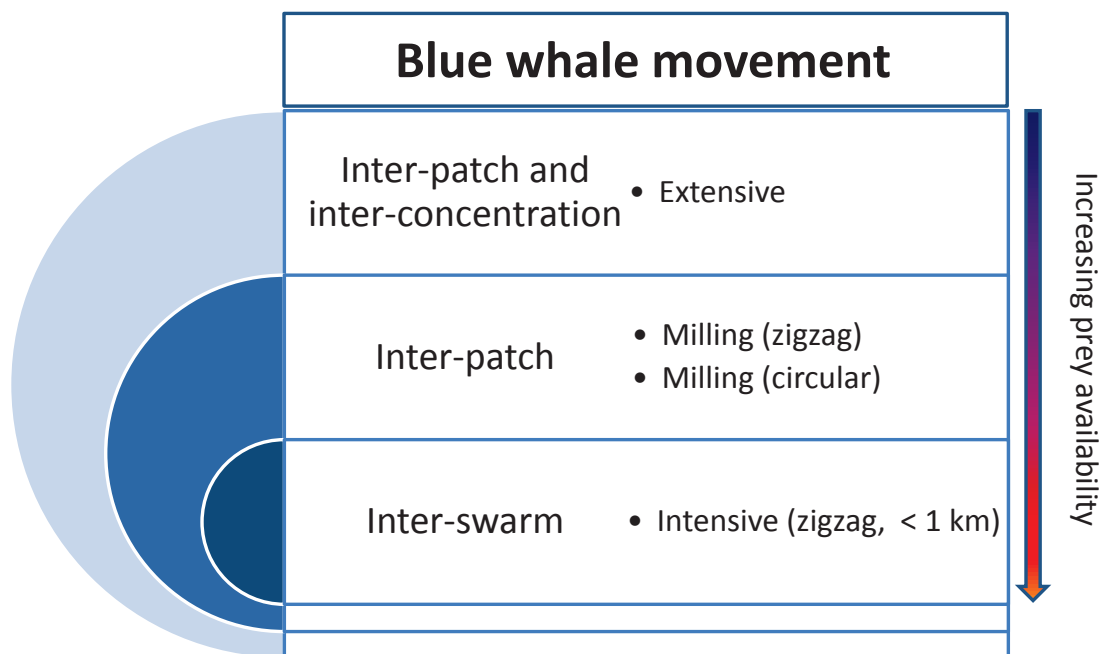
Figure 5-1. Fine- and meso-scale horizontal movement model for blue whales within their foraging ground, as characterised by movements detected in this study and with respect to krill organisation.

Whilst in their foraging habitat pygmy blue whales are likely to most often exhibit milling movements, searching widely for prey. They may change between milling and oriented movements when prey is less profitable or absent (as indicated in Chapter 4). Higher search efficiency is likely applied once pygmy blue whales encounter higher prey availability, and the level of search efficiency would depend on the rate of change in prey availability. Movements are characterised by restricting shelf coverage by circling an area (i.e. circular excursions) or more intensively searching using short zigzags. The search width would be dependent on the scale of prey patchiness (in this case < 1 km, Chapter 4). Whales would remain in this pattern as long as the patch is profitable, otherwise they would resume milling or extensive movements. Most feeding on swarms at depth is expected to occur during more intensive search movements. Surface feeding may occur in any movement mode (Chapter 4) due to the more unpredictable and easily detectable nature of this resource. For example, surface krill are silhouetted against surface light for whales diving beneath them (Calambokidis et al. 2007, Goldbogen et al. 2013a). When prey is anticipated to be more profitable elsewhere, whales would move to another area of the foraging ground or another foraging ground by switching to a more extensive movement (e.g. Macarthur & Pianka 1966, Viswanathan et al. 1999, Humphries et al. 2010).

5.3. CONCLUSIONS AND IMPLICATIONS OF THE STUDY FOR CONSERVATION MANAGEMENT

The study characterises, for the first time, the fine-scale foraging habitat of pygmy blue whales off southern Australia. The study revealed highly dynamic and periodically abundant fauna across the shelf, characteristics that attract numbers of pygmy blue whales and other planktivorous predators every year. The region, from the eastern GAB to western Bass Strait, is recognised as one of the largest foraging regions in the Southern Hemisphere for endangered pygmy blue whales. The study area, centrally placed in the world's only northern-boundary current system, exhibited pelagic biota abundance that make it comparable to the most productive ocean regions in the world (De Silva-Dávila et al. 2002, Santora et al. 2011b). Neritic aggregations, recorded at high-resolution throughout the water column were closely tied to the measured weather and ocean features. The availability of upwelled water containing nutrients and surface phytoplankton was the dominant process shaping the distribution, abundance and structure of aggregations. The habitat conditions perceived to provide the most optimal conditions for water-column productivity mostly occurred at depth, downstream of the upwelled-water front. At depth, higher productivity occurred inshore of the front, whereas higher surface productivity was found offshore of the front.

Individual pygmy blue whales that were followed for short periods exhibited strategies that would allow them to contend with the variability in their foraging habitat. The study was able to characterise the fine-scale horizontal movements of pygmy blue whales for the first time, albeit with a small number of animals. The high-resolution at which movements were recorded was pivotal in capturing a range of movements and spatial patterns not previously described for blue whales, but predicted from theoretical studies to be important for maximising search efficiency (Benhamou 1992). For example, fine-scale movements (1 – 15 kms) showed similar characteristics to movements at broad scales (10 – 1000 kms) for other large marine predators, including blue whales in the eastern-Pacific Ocean (Bailey et al. 2010). Further, the spatial scales of intensive movements matched the organisational structure of neritic schools (< 1 km), which likely included krill swarms. This 1-km spatial scale has been recorded for krill aggregations in the Antarctic (Lawson et al. 2008a). This spatial area matches foraging movements recorded for seabirds and other rorqual whales (Acevedo-Gutiérrez et al. 2002, Weimerskirch 2007, Fauchald 2009).

The present study provided solid evidence that whales were successful in finding profitable prey patches. A marked change in school availability was detected when

whales were intensively moving and surface feeding. The near-surface schools detected in those areas had the highest abundances recorded for all surveys, rivalling the highest densities detected for krill worldwide (Watkins 2007), and within (and at times above) the proposed thresholds set for blue whales (i.e. > 0.1 kg m^{-3}, Croll et al. 2005). However, it was also apparent that whales spent longer searching for aggregations than they spent searching within confined patches. Whales also selected aggregations that were in potentially less optimal parts of the water column. Integrated studies that can quantify the search efforts and feeding events of whales throughout the water column in relation to the availability of their prey (night and day) will be better able to quantify the relative use of deeper resources. The ephemeral nature of the food resource was supported by the high degree of temporal and spatial variability of neritic schools across the survey area, and the wide range of habitat used by whales.

The findings of the study can be applied to conservation measures to assist the recovery of pygmy blue whales. Primarily, the study provides a research benchmark and the first fine-scale information about habitat interactions within a pygmy blue whale foraging ground from which to measure future change in the study area and broader foraging region. Climate change, and the considerable uncertainty it is bringing to the world's weather and ocean processes, is undeniably a great risk to the recovery of endangered populations, such as pygmy blue whales of the Australian-Indian Ocean sector. The effects of sustained changes in wind patterns on pygmy blue whales and their prey are unknown for this region or for other alternate foraging grounds. There are predictions that wind forcing will increase in eastern- and northern-boundary current systems, and there is some evidence to support this off southern Australia (Middleton et al. 2007). However, this does not necessarily mean an increase in shelf production, as wind thresholds may exceed the optimal conditions required by phytoplankton and upper trophic levels such as krill. Blue whales under future scenarios are likely to encounter more 'novel' conditions than those they are currently adapted to, and may have to search further afield for sufficient prey. The significant but moderate correlation between whale and prey encounter rates in the study indicate that the whale-prey relationship may be density dependent, and that the foraging region may support even more variable numbers of pygmy blue whales in future years. The resilience of pygmy blue whales to change and their reliance on the foraging ground off southern Australia will also be influenced by the availability of prey in alternate foraging grounds. Areas such as the Subtropical Convergence (arguably the largest pygmy blue whale foraging ground in the world), the waters off New Zealand and the Indian Ocean are little studied and expected to be just as variable, albeit with different weather and ocean forcing factors. Major shifts in blue whale populations are known from the Northern Hemisphere (Bortolotti 2008, Calambokidis et al. 2009).

Whether blue whales are equipped with enough strategies to continue to adapt to ongoing change will need to be monitored using long-term, multidisciplinary datasets.

Protecting areas of ocean is not a secure strategy for wide-ranging foragers, such as blue whales. The approaches taken will have to be as novel as the conditions of change that whales will encounter. These changes include a raft of current and emerging human uses of blue whale habitats; ironically they include industry (wind, wave and tidal) being developed to combat climate change. By their nature, blue whale foraging habitats are attractive environments for exploitative human activities, being known for their important fisheries, oil and gas deposits, high wind and wave energy, and tourism potential with their wealth of ocean life. Through these activities, and medium to high density coastal human occupation, these ocean habitats are also at risk of higher-than-average levels of pollution. For an endangered species that has an energy-exacting feeding technique and requires large amounts of dense prey to sustain itself (Goldbogen et al. 2011, Goldbogen et al. 2012, Potvin et al. 2012), ocean uses that adversely affect habitat and food availability may have severe consequences to the recovery of pygmy blue whales. There is some capacity in Australia via State, and (primarily) Commonwealth legislation to manage human activities and to mitigate their effects. However, there are no mechanisms to deal with cumulative and overlapping activities.

Based on the wide range of habitats occupied by pygmy blue whales in the study area, and the plasticity in their movement responses, pygmy blue whales are considered reasonably resilient to habitat change under current conditions. However, pygmy blue whales clearly have specific criteria for food they consider profitable enough to spend effort searching for and feeding on. Profitable prey characterised in the study were very dense, and areas where suitable prey occurred were limited. In the event that whales were disturbed enough to leave a patch of food, they may have to travel long distances to encounter another. Smart strategies need to be developed, in partnership with managers, scientists and industry, for rapid detection of profitable areas of ocean for blue whales that are also being proposed for potentially disturbing activities, and whales' access to alternate food resources. Relatively permanent offshore structures may be problematic if they interfere with pygmy blue whale habitat, and their appropriate placement and design will require thoughtful consideration to minimise disturbance to whales and their prey. Whale-watching guidelines will need to be redrawn to incorporate special consideration of activities considered 'critical' to survival, such as feeding.

The study provides the first conceptual models and fine-scale empirical data for interactions between pygmy blue whales and their habitat for the region. The robustness of these findings needs to be tested with datasets that incorporate a wider set of habitat scenarios to make firm hierarchical links between whales and their habitat. Regional ecosystem models provide a grounded framework to incorporate the dynamic predator-habitat interactions detailed in the study. The inclusion of the study findings in ecosystem models and foraging-movement models will improve model robustness in predicting whale-habitat interactions. These findings will also allow the rapid assessment of areas considered profitable for whales, important to manage whale interactions with human activities, and to forecast the likely effects of ongoing change in foraging-habitat conditions caused by changing weather and climate. Investment in conserving our ocean's productive areas is also an investment in the enormous ecosystem services these areas provide, including to the giant of our planet, the blue whale.

"We shall not cease from exploration

And the end of all our exploring

Will be to arrive where we started

And know the place for the first time."

T.S. Eliot, *Four Quartets*

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