Conservation requirements of a threatened migratory species: the importance of habitat and energetics to humpback whales

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This thesis is presented for the degree of Doctor of Philosophy of The University of Western Australia

Faculty of Science
School of Animal Biology

November 2014
“An expert is a person who has made all the mistakes that can be made in a very narrow field.”

Niels Bohr
Abstract

Habitat protection is a principle strategy for threatened species conservation management. The effectiveness of this strategy relies on the correct identification of habitats important for species recovery. The challenge here is to evaluate the importance of habitats in relation to their influence on population persistence, such as their role in promoting survival and reproduction. Conservation physiology is an emerging research field that seeks, in part, to quantify the physiological condition of an animal in relation to the habitat it encounters. In doing so, the contribution of habitats to population demography can be assessed, as survival and reproductive success rely to a large degree on the physical condition of an animal. In this thesis, I took a conservation physiology approach to assessing the conservation requirements of humpback whales (*Megaptera novaeangliae*). These animals engage in annual long-distance migration to breed, supported entirely on stored energy reserves. As they are largely unable to top-up energy stores during the journey, budgeting energy use will be a critical component to the successful completion of migration and reproduction before stores are exhausted. I found that coastal habitats used for resting during the migration journey were associated with conserving energy use and promoting calf growth, driving both the social spacing of resting whale pods, and habitat selection to calmer environmental conditions in resting areas. The quality of foraging habitat was also found to be an important determinant of the initial energy stores of whales commencing their migration. Specifically, annual fluctuations in humpback whale body condition, estimated from whaling records, were linked to sea ice conditions and prey abundances in the Southern Ocean foraging region of these whales with reductions in sea ice leading to worsening condition of humpback whales. Finally, a bioenergetics model of humpback whale energetics revealed that the optimal migration strategy of whales to minimise energy use reflects average migration velocity and time allocated for resting. Cumulative disturbance to both the activity level of humpback whales and the length of resting time can therefore have adverse effects to energy use and reproductive success. Establishing the energetic link between migrating whales and their habitat use enabled me to evaluate the importance of habitat in relation to population persistence, and assess the potential impact of disturbance scenarios to demographic outcomes.
Acknowledgements

There are a number of people to whom I am greatly indebted, and without whom this thesis might not have been written.

I begin by thanking my parents, who have been an inspiration to me throughout my life, and unwavering in their support and encouragement during my PhD. Mum and Dad, words are not enough to express my gratitude for all you have done for me. I would also like to say a big thank you for the support of other members of my family who have been living in Perth, and in particular my brother Ben.

Marko, you have been my rock over the past couple of years. I will especially remember how you cared for me when I broke my elbow.

To all my close friends who have supported me through the tough times, and celebrated with me in the good, thank you! Betty, Val, and Eric, I describe you as my ‘Perth parents’, and am ever grateful for your kind friendship and support.

I would like to thank my supervisors, Jessica Meeuwig, Matt Hipsey, and Curt Jenner, who have patiently guided me through my research. To Jessica, my principle supervisor, rescuer, role-model, and friend. You have been an inspiration to me in your enthusiasm and advocacy for science and conservation. Thank you for allowing a ‘whale person’ to join your research group, and for making my thesis possible.

I am fortunate to have worked with many brilliant colleagues and collaborators throughout my candidature, and in particular I would like to acknowledge the Centre for Whale Research (WA), and their personnel, for collecting and providing data used in my thesis research. I am also grateful to the University of Western Australia for financing my PhD scholarship.
Publications arising from thesis

Braithwaite, JE, Meeuwig, JJ, Jenner, KCS (Submitted) Identifying protected areas for cetaceans: from distributions to culture. *Aquatic Conservation: Marine and Freshwater Ecosystems* (Chapter 2)


Braithwaite, JE, Meeuwig, JJ, Jenner, KCS (Submitted) Evidence of fine-scale humpback whale (*Megaptera novaeangliae*) habitat selection during non-foraging periods. *Animal Conservation* (Chapter 4)

Braithwaite, JE, Meeuwig, JJ, Letessier, TB, Jenner, KCS, Brierley, AS (Submitted) From sea ice to blubber: linking whale condition to krill abundance using historical whaling records. *Polar Biology* (Chapter 5)

Braithwaite, JE, Meeuwig, JJ, Hipsey, MR (In prep.) Optimal migration energetics of humpback whales and the implications of disturbance. *Journal of Theoretical Biology* (Chapter 6)
Statement of candidate contributions

This thesis is presented as a series of five manuscripts in journal format, plus a general introduction and general discussion.

These papers were developed from my own ideas and approaches, under guidance and discussion with my supervisors. I designed the methodology and theoretical models based on these discussions, and carried out all data analyses supporting these papers. Prof. Andrew Brierley (University of St Andrews) provided additional expert guidance in the development of Chapter 5.

Raw aerial survey data for Exmouth Gulf were made available by the Centre for Whale Research, and I completed all subsequent analyses of these data (Chapters 3 and 4). All other raw data were sourced from publicly available datasets, and access to the historical whaling database used in Chapter 5 was facilitated by Dr. Tom B. Letessier.

I wrote all chapters, with feedback from Prof. Jessica Meeuwig (all chapters), Mr. Curt Jenner (Chapters 1-5, 7), A/Prof. Matthew Hipsey (Chapters 1, 6-7), and Andrew Brierley (Chapter 5).
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Chapter 1

General Introduction

Present global trends in conservation place significant emphasis on protecting areas representative of the ecosystem and biodiversity “hotspots” through networks of protected areas (Myers et al., 2000; Gaston et al., 2008). However, there is concern that by prioritising representative habitats and biodiversity hotspots, threatened species are inadequately protected (Dulvy, 2013). Only half of the top 100 threatened species in the world have conservation measures in place (Baillie & Butcher, 2012), and often this is the result of their habitat ranges coinciding with protected areas (Dulvy, 2013). To improve threatened species conservation, species-specific requirements need to be addressed, both by protecting habitat important to these species and by enforcing effective regulations that reduce disturbance to these animals (Baillie & Butcher, 2012; Dulvy, 2013).

Conservation physiology is an emerging field of research associated with understanding the physiological relationships between an animal and its habitat (Cooke et al., 2013). Physiological maintenance is important for animals as individual condition can directly affect survival and reproduction rate (Huey, 1991; Schneider, 2004). Knowledge of physiological relationships can therefore aid in identifying areas important for population maintenance, and assess how an animal’s condition is altered in response to changes in environmental conditions, driven, for instance, by disturbance (Stevenson, 2006; Cooke et al., 2013). This approach is particularly useful for migrating animals where journeys are energetically demanding endeavours, and disturbance that reduces energy stores needed to support migration will leave animals vulnerable to mortality. Locating habitat important for energy regulation, and protecting animals from disruptions to energy gain or expenditure along the migration route are therefore needed to support population recovery and potentially survival.
The focus of this thesis is the application of a conservation physiological approach to the assessment of the energetic requirements of a threatened migratory species by understanding how specific habitats are used to support migration, and determining the consequences of energetic disturbance to the successful completion of these journeys. I focus specifically on the humpback whale (*Megaptera novaeangliae*) as a model species, as these large animals migrate long distances to breed, supported entirely by stored energy. Whilst humpback whales have some species-specific requirements for their migration journey, such as utilising coastal areas for resting, the insights and analysis introduced in this work have general applicability to other long distance migratory species, where energy balance is a key component to migration and reproductive success.

### 1.1 The challenge of threatened species conservation

Threatened species are, by definition, at risk of extinction. There are many reasons why a species may become threatened, often related to human activity that causes direct or indirect mortality, and habitat loss or fragmentation (Tilman *et al.*, 1994; Vitousek, 1997; Brook *et al.*, 2008). Counteractive measures therefore need to be implemented to alleviate negative impacts, and secure the survival and recovery of such species. Protected areas are a fundamental strategy for achieving conservation outcomes, and form a central role in the recovery plans for rare and threatened species (Groom *et al.*, 2006). By protecting specific habitats, the resources needed by the species for survival and growth are secured and protected against negative human impacts. However, the effectiveness of protected areas to promoting recovery of a particular threatened species depends on correctly identifying an area as important (Devillers *et al.*, 2014) and enforcing strict regulations within this area (Allison *et al.*, 1998; Taylor *et al.*, 2011; Dulvy, 2013).

The establishment of protected areas has focused on prioritising protection of ecologically representative habitats and biodiversity hotspots (Myers *et al.*, 2000; Gaston *et al.*, 2008). This is a popular strategy, as conserving biodiversity “hotspots” provides protection to the most species at the least cost, benefiting both ecosystem functioning and management (Myers *et al.*, 2000; Gaston *et al.*, 2008). Protecting areas representative of ecosystems serves to maintain both species diversity and key ecological processes (Kelleher, 1996; Olson & Dinerstein, 1998; Day *et al.*, 2002). However, there is growing evidence that the bias towards protecting biodiversity hotspots and representative habitats may be compromising the conservation of threatened and rare species (Dulvy, 2013). For instance, Prendergast *et al.* (1993) demonstrated many high diversity hotspots (species-rich areas) for UK animal and plant taxa contained no rare species, defined as those species with restricted
distributions. A more recent study in Australia also found a lack of overlap between terrestrial protected areas and threatened species’ ranges (Watson et al., 2011). Many of these protected areas were established with the goal of obtaining a representative terrestrial protected area system across Australia (Sattler & Taylor, 2008; Watson et al., 2011), however 12.6% of threatened species were not present in the protected area network, and 80.4% of species had less than 10% of their range protected (Watson et al., 2011). These studies illustrate that areas deemed valuable for many species (i.e. high biodiversity) or for ecosystem representation do not necessarily coincide with areas valuable to threatened species. Thus, a more focused species-specific approach is needed so that the species in most need of protection will obtain the most effective conservation measures. This approach may also have broader biodiversity and ecosystem benefits, as the protection of habitat for one species (e.g. a focal or ‘umbrella’ species) can serve to improve the status of other co-occurring species (Branton & Richardson, 2011). Furthermore, since the relative abundances of different species within an ecosystem can alter ecosystem properties (Hooper et al., 2005), the recovery and maintenance of threatened species can contribute to ecosystem functioning and stability. The integration of species-specific requirements into conservation management is therefore an essential part to both threatened species and ecosystem conservation.

1.2 The challenge of migratory species protection

Migration is defined as the seasonal movement pattern of animals between specific regions, commonly between breeding and non-breeding locations (Webster et al., 2002). Animal migration is an adaptive response to varying requirements and resource availability. By moving from areas less suitable for their current activity to those of higher suitability, animals can increase their fitness through selecting the best habitat for survival and reproduction in a spatiotemporally varying environment (Dingle & Drake, 2007). For instance, a number swallow species (family Hirundinidae) breed in northern latitudes during spring, but migrate southwards for winter when their main prey of flying insects become scarce in the north (Elphick, 2007). The successful migration of a population can be hindered by human disturbance. Habitat degradation can reduce the availability of food required to fuel energy-intensive migration journeys (Myers, 1983; Moore et al., 1995; Drent et al., 2003; Newton, 2006), while obstructions, such as fences placed across a path, can incur expensive energy costs, or cut off migration completely (Bolger et al., 2008; Castro-Santos & Letcher, 2010). However, it is essential for these species to be able to complete their migration patterns, otherwise survival and population growth will be compromised.
Animal migration presents unique challenges for conservation (Runge et al., 2014). A migrating population is a ‘moving target’, whose current state and needs at one point in time can depend on the conditions encountered previously. Local management will therefore be limited in its effectiveness if other vulnerable points along the migration lack protection (Martin et al., 2007). For example, migrating birds rely on multiple stopover habitats to fuel the next leg of their journey (Moore et al., 1995; Newton, 2006; Elphick, 2007). The protection of food resources at one stopover area in the journey will be inconsequential if the birds are unable to reach this area from inadequate energy replenishment earlier on. Even when migration is completed, the cumulative impact from disturbance en route can impact reproductive success, as less energy is available to invest into offspring (Drent et al., 2003; Newton, 2006; Castro-Santos & Letcher, 2010; McElroy et al., 2012). Effective conservation of migratory species therefore relies on determining which points along the migration route are crucial to the completion of the journey, and minimising disturbance to migrants in these areas (Martin et al., 2007), so that animals can ultimately maximise reproductive success.

Migration is an energetically demanding activity, with migrants relying on limited food supplies to fuel long journeys, whether this be in stages, as for birds (Elphick, 2007), or for the entire journey, such as in baleen whale migration (Stern, 2009). Where migration is linked to breeding, enough energy must also be obtained for investment in reproduction. The success of migration is therefore highly linked to controlling energy balance, and disturbances to this balance can affect mortality and reproduction rates. For example, a reduction in food intake in bird stopover areas due to habitat degradation or disturbance has directly impacted their population mortality and reproductive success (Myers, 1983; Drent et al., 2003; Newton, 2006). In river-spawning fish species, the presence of dams obstructing their path cause delays and increase energy expenditure, negatively impacting survivorship and spawning success (Castro-Santos & Letcher, 2010). The balance between energy gain and expenditure is a therefore critical component to the fitness of migrating animals, directly affecting survival and reproduction. Those habitats that animals utilise to maximise energy gain or minimise energy use en route are therefore areas where migrants will be most vulnerable to disturbance that change energy use. Thus, the identification of areas required for animals to maintain optimal physiological condition for successful migration and breeding is useful to direct conservation priorities, and assist in the recovery of threatened migratory species.
1.3 Conservation physiology

Conservation physiology is an emerging field of research (Cooke et al., 2013). A key focus of conservation physiology is to understand and quantify the physiological relationships between an animal and its habitat, and thus the importance of different resources to the condition and performance of an animal or population (Stevenson, 2006; Wikelski & Cooke, 2006; Cooke et al., 2013). Such cause-and-effect relationships are of great benefit to conservation management (Tomlinson et al., 2014). Survival and reproductive success are strongly linked to an animals’ physiological condition, which in turn is connected to its habitat (Huey, 1991; Schneider, 2004). For example, an animal can only survive with adequate net energy gain, and only reproduce successfully when sufficient energy is available to support offspring investment. Ascertained physiological animal-habitat relationships can predict the physiological consequences to changes in habitat use, either through natural or human causes, and thus quantify their effects on animal fitness and long-term population trends (Wikelski & Cooke, 2006; Homyack, 2010; Cooke et al., 2013).

Energy acquisition and subsequent use is fundamental to determining physiological condition. Animals rely on energy to support basic functioning, daily activities, and to reproduce. A net loss of energy means an animal will perish, while a net gain provides surplus energy which can be allocated towards reproductive investment. Maintaining a positive net intake of energy is therefore vital for an animal’s fitness, and for population growth. The energy balance of an animal is strongly related to the environmental conditions it encounters, both in terms of energy gain and energy loss: higher food availability will promote energy intake, while traversing difficult landscapes will increase expenditure (Kooijman, 2009). For example, the reproductive success of reindeer (Rangifer sp.) was linked to both nutrient availability in summer, and changes in body mass over winter (Parker et al., 2009). More food in the summer results in high energy intake, promoting reproductive investment, however harsher winter conditions had the opposite effect, as moving in thicker snow conditions incurs significantly higher energetic costs due to the greater sinking depth (Parker et al., 2009). In fact, deep snow conditions and longer periods of snow cover negatively influence the body condition, mortality, and reproductive success of several ungulate species (Jacobson et al., 2004; Adams, 2005; Garroway & Broders, 2005; Parker et al., 2009), suggesting that energy conservation is a vital endeavour when food is scarce. Mapping the cost of movement to create ‘energy landscapes’ for animals can reveal how costs, and thus foraging efficiency, can alter in different environments (Wilson et al., 2012; Shepard et al., 2013). For example, small hills were found to considerably increase the movement costs of African savannah elephants (Loxodonta africana), explaining the animals’ avoidance of foraging in hilly areas despite the abundance of food (Wall et al., 2006b).
Insights on species habitat use in relation to energetics, such as movement costs, can explain species distribution patterns and the energetic cost of displacement to other areas. Understanding how changes to habitat conditions and habitat use influence energy balance is therefore an important component to conservation management.

Bioenergetic models mathematically represent the use of energy by an organism and energy flow between an organism and its environment (Grodzinski et al., 1975). These models can therefore assist in assessing resource gain and loss, both important to the energy balance of an animal. For example, an analysis of killer whale (Orcinus orca) bioenergetics identified the amount of prey required to support successful reproduction, suggesting the recovery of this population will require the protection of Chinook salmon (Oncorhynchus tshawytscha) from fishing pressure to ensure sufficient food availability (Williams et al., 2011). Similarly, a study by Hooker et al. (2002) revealed that the energetic requirements of bottlenose whales (Hyperoodon ampullatus) could not be sustained by the level of primary productivity in The Gully where they reside, and food must be subsidised from outside The Gully. They recommend that habitat protection should be extended to areas important for food influx processes to occur (Hooker et al., 2002). These two studies illustrate the requirements of conservation to extend protection to other trophic levels in the ecosystem (Williams et al., 2011) or to habitats critical for food supply (Hooker et al., 2002). Bioenergetic models can also determine sources of energy drain for animals. River spawning fish species select the most energy conserving paths (McElroy et al., 2012), and in the American shad (Alosa sapidissima), increased energy expenditure from introduced obstacles along the migration reduced the energy available for investment in spawning, lowering reproductive success (Castro-Santos & Letcher, 2010). Quantifying the animal-habitat bioenergetic interactions can therefore identify those habitats important to maintaining optimal energy balance, directing conservation efforts to support beneficial energy balance, and determine the consequences of energetic disturbance, in relation to population reproductive success.

A physiological approach to conservation, particularly relating to energetics, is appropriate for both threatened and migratory species management. In both cases, the identification of valuable habitat is the key for promoting population growth, by securing the resources needed for survival, migration, and reproductive success. This can be achieved through understanding and quantifying how an animal’s physiological condition is influenced by its habitat. Those habitats necessary for maintaining an optimal energy balance through high energy intake or by minimising expenditure will be important to protect from detrimental human activities. This is of particular importance to migratory species where energy balance is a vital component to the successful completion of the migration journey. Animal-habitat bioenergetic relationships can also estimate the cumulative cost of human activities to an animal’s physical condition, either from direct disturbance or through habitat degradation, and translate this to long-term
population trends (Humphries et al., 2004; Williams et al., 2006; Heinrichs et al., 2010). Thus, both the value of a habitat, and the consequences of disturbance, can be identified, informing conservation management on where to place protection, and the countermeasures needed to mitigate negative interferences, thereby promoting the long-term recovery of threatened, migratory species.

In this thesis, I apply a conservation physiology approach to assessing the requirements of a threatened migratory species by understanding the dynamics of energy gain and loss in relation to habitat use. This approach will allow the identification of valuable habitat for successful migration and reproduction, and establish priorities for conservation management to promote population recovery. I use humpback whales as a model species, as these slow-reproducing animals migrate over thousands of kilometres to breed, supported entirely on energy reserves accumulated during summer foraging. Energy balance is therefore a crucial component to successfully completing migration without exhausting these stores.

1.4 Humpback whales as a model species

Humpback whales annually migrate between their summer foraging grounds in the polar regions and their winter breeding areas in warmer tropical waters. Upon leaving foraging grounds, adult whales do not actively feed again until returning to the polar waters approximately eight months and 16,000 km later (Chittleborough, 1965; Rasmussen et al., 2007). While humpback whale populations have been found to stop at topographical features associated with high productivity during migration, such as seamounts (White et al., 2007; Garrigue et al., 2010), that may provide feeding opportunities, any food here will be minor in comparison to the energy demand of such a long migration journey. Thus, during migration whales largely rely on their energy reserves, accumulated during summer feeding and stored as blubber, to meet the energetic demands of migration, breeding, and, in the case of females, nursing a calf. This dependence on a finite energy store renders these whales vulnerable to disturbances that affect their energy balance, either through reduced foraging, or increases in expenditure when migrating. Negative changes to energy balance will have consequences on their ability to successfully complete migration before stores are depleted. As humpbacks specifically migrate to breed, reduced energy reserves will also have direct implications for reproductive success and population growth.

Humpback whales are a recovering species. Populations were decimated by unsustainable commercial whaling in the early 1900s (Clapham & Baker, 2009). In 1963, when the International Whaling Commission (IWC) banned exploitation of humpbacks in the southern
hemisphere, around 200,000 individuals had been killed since whaling began in the early 1900s (Mori & Butterworth, 2006), reducing many populations to endangered levels (Reilly et al., 2008). For instance, the two populations of humpbacks occurring in Australian waters were reduced to approximately 3.5-5% of pre-whaling estimates (Dept of the Environment and Heritage, 2005). Since the 1963 ban, humpback whale numbers have increased (e.g. Noad et al., 2006; Barlow et al., 2011; Salgado Kent et al., 2012; Ruegg et al., 2013), and the IUCN status of the species as a whole was changed in 2008 from ‘Vulnerable’ to ‘Least Concern’ (Reilly et al., 2008). Despite this promising species reclassification, the status of local populations varies. For example, the IUCN classifies both the Oceania and Arabian sea subpopulations as ‘Endangered’ (Childerhouse et al., 2008; Minton et al., 2008) due to continuing population declines. The Australian government lists the two populations found in its waters as ‘Threatened’ under the Commonwealth Environment Protection and Biodiversity Conservation (EPBC) Act 1999. As such, these populations require continued protection from actions that are likely to have a “significant impact” on the population (Dept of the Environment, 1999). I therefore focus my thesis on Australian humpback whales, specifically the population that migrates along the western Australian coastline (breeding stock D (IWC, 1998)).

Poleward migration routes of humpback whales are closely associated with the coast (Jenner et al., 2001), that offer calmer, more sheltered conditions for new born calves, in comparison to the open ocean. This coastal affiliation exposes humpback whales to relatively high levels of human activities, which are also concentrated along the coastline. Humpback whales are vulnerable to human disturbance that can have significant adverse effects on cetaceans and their habitats (Clapham et al., 1999; Marsh et al., 2003). Entanglement in fishing gear has been regularly documented for humpback whales, resulting in scarring and mortality (Lien, 1994; Wiley et al., 1995; Robbins & Mattila, 2004; Neilson et al., 2009; Cassoff et al., 2011; Meyer et al., 2011). While mortality rates from entanglement are generally low (Lien, 1994), it can still have a significant impact to the recovery rate for smaller populations (Volgenau et al., 1995), with small whales and juveniles at higher risk (Lien, 1994; Cassoff et al., 2011). Collisions between ships and whales cause injury and can be fatal (Laist et al., 2001). For some small populations of whales, such as the North Atlantic right whale (Eubalaena glacialis), this is a significant source of mortality hindering recovery (Knowlton & Kraus, 2001). The occurrence of ship strikes are associated with coastal areas, where shipping activity is high, and whales are thus at greater risk of a collision (Wiley et al., 1995; Laist et al., 2001; Guzman et al., 2013). Humpback whales, like all cetaceans, rely on sound to navigate and communicate and the presence of human-generated noise has the potential to interfere with whale signals and, in extreme circumstances, cause physical damage to hearing (Ketten et al., 1993). Avoidance behaviour
in humpback whales has been reported in the presence of certain sonar frequencies (Maybaum, 1993; McCauley et al., 2000; Gordon et al., 2003), and in the presence of boats, particularly loud and fast boats (Baker & Herman, 1989; Au & Green, 2000). Changes in the singing behaviour of male humpback whales as they court females have also been documented in areas of high noise levels, with males singing for longer in the presence of low-frequency active sonar (Miller et al., 2000; Fristrup et al., 2003). Like all migratory species, energy is a critical component to the success of humpback whale migration and breeding. Of those disturbances that are not fatal, many are likely to generate significant energy costs. It is currently unclear how disturbances to normal humpback behaviour along the migration route impact the energy use of humpback whales, or the long-term consequences of potential energy disruptions to achieving migration and breeding.

Another aspect to the energetics of migrating humpback whales is their need to obtain adequate energy stores from summer foraging to fuel the long journey. The main food source for southern hemisphere humpback whales is Antarctic krill (Euphausia superba), which are also commercially fished (Nicol et al., 2012). Presently, catch from this fisheries is relatively small (211,984 tonnes in 2009/10 of an estimated 40.2 million tonnes total (Hewitt et al., 2002)), and precautionary limits have been set by the Commission for the Conservation of Antarctic Marine Living Resources (CCLAMR) to secure this resource for predators (Hewitt et al., 2002). However, annual catch is trending upwards (Nicol et al., 2012), and currently little is known about how changes in krill abundance may impact migrating baleen whales (Nicol et al., 2008). Krill abundance is also linked to environmental variables, most notably sea ice which is thought to promote krill recruitment (Siegel & Loeb, 1995; Loeb et al., 1997). Krill is therefore subject to future environmental changes, such as those associated with climate change, with potential knock on effects to the nutritional condition of their predators, including humpback whales (Nicol et al., 2008). If the physical condition of migrating whales is linked to food availability in the Southern Ocean, then the energy budget of these whales will change with both the environmental conditions and significant increases in krill catch.

The successful recovery of humpback whale populations relies on individual whales being able to migrate and breed, which in turn will be a function of their physical condition. The adequate intake of energy and its efficient use during the migration journey are critical factors to completing this journey and reproducing. The potential of human disturbances to alter both energy intake and expenditure may impact population recovery. Conservation of this threatened migratory species would therefore benefit from a physiological approach that identifies areas important to their successful migration. Understanding the link between habitat and energy use will reveal those areas important to regulating energy use, and thus areas where disturbance should be mitigated. For example, during the southbound
migratory species, the humpback whale, by determining the value of habitats to their energy balance, both in terms of energy gain and energy expenditure, and the consequences of disturbance. This will be achieved by addressing the following specific aims:

1) Determine how areas valuable for population persistence for cetaceans are currently identified by assessing existing procedures used for defining the value of habitats to cetacean species through the collection and interpretation of different data types. This review provides a basis for subsequent analyses in this thesis.

2) Establish foundational knowledge on how and why migrating humpback whales use resting areas, by analysing resting behaviour and spatial habitat preferences, and how this relates to energy balance.

3) Investigate annual fluctuations in whale body condition, and whether this is linked to food availability in humpback whale foraging habitat.

4) Develop a bioenergetic model of humpback whale migration, to determine the energetic consequences to disturbance along the migration route.
1.6 Thesis Outline

Cetaceans are wide-ranging animals, so protecting their entire distribution range is impractical. Locating specific areas important for protection requires an understanding of how to identify areas of value to the population. In Chapter 2, I review the literature on methods used to identify protected areas for cetaceans, assessing the advantages and difficulties of collecting and integrating varied data types associated with cetaceans into the designation of effective protected areas. Further, I discuss the effectiveness of defining critical habitat (i.e. those areas essential for species survival) to the conservation of cetacean species.

To assess the value of habitat selection to the energy conservation of migrating humpback whales, a foundational understanding on how and why whales use particular areas along the route is required. Such an assessment provides insights into whether energy conservation is an important aspect to the behaviour and habitat use in particular areas, from which the consequences of disturbance can be evaluated. I focus my research on humpback whale resting areas, as little is currently known on the importance of resting behaviour to migrating whales, and whether disturbances here will have significant impact on population recovery. Chapter 3 investigates the carrying capacity of resting humpback whales in a known resting area in Western Australia (Exmouth Gulf), to determine the number of animals it can support based on resource availability. I hypothesise that space will be the limiting resource for resting humpback whales as food, the traditional method for calculating carrying capacity, is inconsequential to these fasting adults during their migrations. Chapter 4 examines the spatial distribution of whales resting within the gulf, to identify key areas of value and the environmental drivers behind their distribution. This is achieved using statistical habitat modelling techniques.

Disturbances that affect the energy use along a migration route could impact the ability of a whale to successfully complete migration, including supporting a growing calf. However, the severity of energetic disturbance will depend upon both the body condition of the whale and how disturbance impacts the energy usage during migration. In Chapter 5, I quantify the effect of annual fluctuations in food availability in the Southern Ocean on the body condition of migrating whales. Body condition is estimated from historic whaling records, using oil yield as an indicator of condition, and links these changes to fluctuations in Antarctic krill abundance in their foraging habitat. Chapter 6 models the energetics of migrating humpback whales to quantify the impact of disturbances on energy use. I derive an individual based model of energetics for adult lactating females, and nursing calves, and use it to first establish whether there is an energetic advantage to resting during migration and then to test for significant
changes in energy use and growth rates of calves based on different scenarios of disturbance to resting behaviour.

Finally, I synthesise the main findings of my thesis in Chapter 7, and discuss how these insights on humpback whale migration energetics can be applied to the identification of valuable habitats critical for protection. Furthermore, I evaluate the benefit of an energetics approach to assessing the specific conservation requirements of threatened migratory species, and discuss how the knowledge gained here can be translated to other migratory species.

Figure 1.1: Diagrammatic representation of thesis outline
Chapter 2

Identifying protected areas for cetaceans: from distributions to culture

2.1 Abstract

A common approach to conservation is the creation of protected areas around important and critical habitats. Identifying appropriate areas for protection requires accurately translating collected data into areas of ecological importance. This can be difficult for wide-ranging cryptic animals like cetaceans, where information on area use requires data collection across large spatial and temporal scales and thus, is hindered by logistical and financial costs. Here, I examined four different types of data used to assess the ecological value of areas: distribution, habitat, behaviour, and culture, where culture is defined as a form of social learning. Each data type provided a unique perspective on how and why a population is distributed such that the incorporation of several different data types is required to capture the complex relationship between populations and areal use. I also discuss the application of “critical” habitat for conservation, finding that where legal designation is required, the detailed information needed can hinder protection, particularly for cetaceans where data collection is difficult. This review provides a framework for the application of different data types to the identification and interpretation of biologically important areas for cetacean conservation.
2.2 Introduction

Species conservation requires effective management to mitigate disturbance and promote population growth and persistence. The creation of protected areas around important habitats for key species is one approach to achieving conservation outcomes (Kelleher, 1996; Roberts et al., 2003; Hoyt, 2005; Hodges & Elder, 2008), but its effectiveness depends on correctly interpreting an area as important and drawing appropriate boundaries around such areas (Hoyt, 2005; Williams et al., 2009). Assessing the value of a habitat to a population is complex. First there may be several reasons why an area is used by a population (Hoyt, 2005), some of which are difficult to quantify such as cultural importance (Laland & Hoppitt, 2003). Second, the value of an area may be temporally and spatially variable and for mobile animals, like cetaceans, distributions will shift to match environmental fluctuations (e.g. Benson et al., 2002; Schick et al., 2004; Rayment et al., 2010). Appropriate data collection and interpretation are therefore fundamental to correctly assessing which areas are important to a population, and discerning why. There are a variety of approaches and data types to assess the value of a habitat, from general population-level distribution patterns to more specific individual behavioural structures. While there are excellent guidelines for the general establishment of cetacean focused marine protected areas (MPAs) (Hoyt, 2005), no specific framework exists on the application of different data types when identifying areas of importance. In this review, I synthesise information from four data categories: distribution, habitat use, behaviour, and culture, and discuss their application to the identification of areas important for conservation.

I focus this review on cetaceans, as defining important areas for the conservation of these species has the added complication of their large ranges, high mobility (Forney, 2000), limited observational availability (Redfern et al., 2006), and capability for cultural learning (Rendell & Whitehead, 2001). A large number of cetacean species are IUCN red-listed as threatened or data deficient and so meet the requirement for habitat protection (Hoyt, 2005). The slow-reproducing nature of cetaceans makes the rate of population recovery vulnerable to persistent human-induced mortality, as small perturbations in the adult population can significantly impact population reproduction rates (Gilpin & Soulé, 1986), and creating protected areas can serve to mitigate these detrimental interactions (Hoyt, 2005). However, while the majority of cetacean species require relatively urgent protection, there are large knowledge gaps of global abundance and distribution, reflecting the challenges associated with cetacean data collection (Kaschner et al., 2012). As many of these challenges also apply to other terrestrial and marine taxa of megafauna, such as big cats (Sanderson et al., 2002; Wikramanayake et al., 2008), elephants (Douglas-Hamilton et al.,
An additional dimension to protected area management is the concept of ‘critical habitat’, those habitats that are essential to species survival (Hoekstra et al., 2002). While the legal criteria for critical habitat designation vary among countries, the identification of critical habitat areas can aid in species conservation by indicating core zones in need of more strict regulation (Hoyt, 2005). Furthermore, where legal designation of critical habitat exists, more stringent regulations on human activities can be implemented, benefiting endangered species (Taylor et al., 2005). However, there is a lack of consensus on how critical habitat is defined, leading to conflicting views among researchers and governments on whether a habitat can be classified as critical (Patlis, 2001). As the ‘burden of proof’ tends to lie with those petitioning for habitat protection, the standards for providing evidence to justify critical habitat designation are arguably set too high by governance (Hodges & Elder, 2008), perhaps due to a lack of understanding on the challenges inherent in obtaining detailed information on species-habitat associations. This discrepancy in defining critical habitat can therefore hinder endangered populations from receiving the necessary protection. Given the issues associated with cetacean data collection, such as the financial and logistic costs with surveying large areas of the ocean, the appropriateness of designating critical habitat for cetacean populations requires assessment.

I review the application of data on distribution, habitat, behaviour, and culture to the protection of habitat for cetacean conservation, discuss the relevance of defining critical habitat for cetaceans under the existing legal terminology, and present two case studies to examine the application of data to the implementation of legislatively protected areas.

### 2.3 Application of data to identifying protected areas

#### 2.3.1 Distribution and abundance

Establishing the distribution and abundance of a population is fundamental to the identification of important areas, and forms the basis for future research (Hoyt, 2005). Detecting patterns in cetacean distributions over space and time identifies the overall habitat range, aggregation areas, and any routine shifts in these patterns, as well as providing essential information in the design of protected areas for highly mobile animals where distributions can change relatively quickly in response to population needs. For cetaceans, these distribution movements can appear in the form of predictable life history movements, e.g., migrating baleen whales (Lockyer & Brown, 1981), seasonal shifts in
response to changing foraging conditions, e.g. Hector’s dolphins (Rayment et al., 2010), and long-term changes in the environment, e.g. bottlenose dolphins (Wilson et al., 2004). While distribution data are foundational to designating protected areas, a recent study by Kaschner et al. (2012) revealed that globally, the area of ocean surface coverage that has been mapped for cetacean distributions from line-transect surveys is less than 25%, and only 6% is of a quality needed to establish temporal trends. So despite concerted effort to establish cetacean distributions worldwide, reflected in some 430 surveys conducted between 1975-2005 covering 90 million km$^2$ of ocean (Kaschner et al., 2012), there remain large knowledge gaps, and approximately 40% of threatened cetacean species are still categorised by the IUCN as data deficient, based on the 2008 IUCN red list of threatened species (IUCN, 2008).

The limit to distribution data coverage are likely due to the logistic and financial costs associated with gathering distribution data on wide-ranging, cryptic, ocean megafauna (Kaschner et al., 2011). Currently, the standard method for collecting distribution data is line-transect surveys performed from a boat or plane, where systematic transects across a specified area are followed by the survey platform and observers record cetacean sightings. The resulting spatial pattern of detections can then be used to locate possible areas of importance, such as those regions with higher density of sightings. This sampling method has been used for cetaceans since at least the 1950s (Doan & Douglas, 1953), with the bulk of surveys occurring after the mid-80s (Branch et al., 2007; Kaschner et al., 2012), and has contributed a large proportion of the knowledge on abundance and distributions. The development of statistical techniques, such as distance sampling (Buckland et al., 2001) that reduces observation and perception biases, has also assisted in the use of transect surveys for accurately mapping distributions. However, transect surveys from boats or planes spanning the large geographic range of cetacean species are expensive, and financial constraints can create a quality-quantity trade-off, where the need to survey geographically large areas compromises the level of detail obtained within the survey area. Furthermore, accessing remote areas such as the polar regions can be difficult and incur significant costs. For some areas, the application of autonomous aerial vehicles to aid data collection is beginning to be explored for cetacean surveys and may prove to be a more cost effective alternative (Hodgson et al., 2013).

While line-transect surveys are the general method used for collecting distribution data, other alternatives exist, including ships of opportunity, acoustic monitoring, and satellite tracking, that can provide benefits where line-transects are lacking. Taking advantage of ships not specifically employed for cetacean research purposes, such as ferries (Redfern et al., 2006; Kiszka et al., 2007; Cotté et al., 2009) and seabed survey ships (Wall et al., 2006a), as platforms for observation can provide a cost effective method for gathering
Chapter 2. Identifying protected areas for cetaceans: from distributions to culture

distribution data (Kiszka et al., 2007). However, with this method, there is little control in survey design and observer bias, resulting in variable effort across the area and localised effort on shipping lanes and coastal zones. These issues need to be carefully accounted for during analysis to avoid misinterpretations, such as a perceived aggregation resulting from a concentration of effort (Kenney & Winn, 1986). Passive acoustic monitoring uses hydrophones to detect cetacean calls within range of a receiver, and has been found to be a useful technique for detecting smaller cetaceans in certain management areas, especially when visual identification is difficult (Akamatsu et al., 2001; Oswald et al., 2003). For larger cetaceans, such as blue whales, louder calls at lower frequencies can be detected over hundreds of kilometres, enabling abundances to be estimated (McDonald & Fox, 1999) and stock differentiation (Samaran et al., 2013) of these widely dispersed animals. Whilst fixed position hydrophones can be used to estimate abundance (Mellinger et al., 2007), their strength lies in their ability to be deployed over long time periods (Clark et al., 1996; Maclntyre et al., 2013), making them more efficient than repeated transect surveys in some areas. Finally, satellite tracking gathers spatiotemporal data of individual animals by attaching a radio transmission tag that tracks movements. Information of space use through time among individuals can be used to establish the range of distribution (Baird et al., 2010), areas of high use (Sveegaard et al., 2010), seasonal patterns in distributions (Baumgartner & Mate, 2005), and site fidelity (Schorr et al., 2009), while being able to track animals over large distances along migration corridors and to remote areas, such as Antarctica (Dalla Rosa et al., 2008). The development of space-state models (Patterson et al., 2008) allows the behaviour at locations along tracks to be estimated, such as in seals (Breed et al., 2009), turtles (Jonsen et al., 2007), and whales (Bailey et al., 2009). Again, the quantity and quality of data from tags can be limited by the price of both the tags and boat time to deploy the tags, and as only a limited numbers of animals are tagged, results may not necessarily reflect the patterns of the entire population (Hebblewhite & Haydon, 2010).

A common theme emerging among cetacean distribution studies is the need to integrate temporal and spatial flexibility into the management of protected areas (e.g. Hooker et al., 1999; Williams et al., 2009; Embling et al., 2010). Highly mobile cetaceans are adaptable to the variable nature of the ocean, and can quickly alter distributions in response to changing conditions. To remain effective, protected areas need to also respond to these changes, and the ability to detect spatial and temporal patterns in distributions may be paramount to achieving this outcome. The snapshot of distributions in time obtained by transect surveys provides detailed population positions in space, but lacks information to establish temporal trends without repeat surveys, which can be costly and time consuming. Passive acoustics and satellite tracking, on the other hand, can produce seasonal and long-term, trends in distribution patterns, but lack the spatial detail gathered by transect surveys as passive
acoustics can position cetaceans only to the area of the receiver (MacIntyre et al., 2013), while satellite tagging tracks a limited number of individuals in the population (Rosenbaum et al., 2014). Using a combination of methods may offer a forward solution to establishing longer-term spatial and temporal patterns. For example, passive acoustic surveys can identify time periods to conduct annual transect surveys, thereby minimising costs of monitoring long-term distribution patterns. Satellite tracks that provide large-scale spatial patterns of movement can also be used to guide both acoustic and transect survey design.

Distribution data are the foundation for establishing areas of importance, regardless of the method used. However, building on this knowledge of how a population is distributed, to an understanding of the environmental drivers that create distribution patterns, allows for greater predictive capacity in managing area use. For more effective conservation, distribution data will need to be complimented by habitat modelling to improve understanding of spatial and temporal area use.

### 2.3.2 Population-habitat relationships

Understanding habitat use by animal populations can provide insights as to why an area is important to a population beyond what is available from distribution-only data. Habitat use guides the defining of appropriate boundaries for protected areas that include those ecosystem functions important to the focal population. For example, if a population uses an area for foraging, then regulations regarding prey populations can also be considered. A common method to define population-habitat relationships is the application of habitat preference models. These models correlate population distributions with physical and biological environmental variables to identify the main drivers behind the spatial distribution pattern (Guisan & Zimmermann, 2000; Redfern et al., 2006). In doing so, the model reveals which habitat is preferred by the population and so can be used to infer reasons behind habitat use, which can then be integrated into protected area design for more effective management. A number of habitat preference models show that cetacean distributions are largely driven by static environmental variables (Baumgartner, 1997; Hooker et al., 1999; Gregr & Trites, 2001; Cañadas et al., 2002; Ingram & Rogan, 2002; Cañadas et al., 2005; Hastie et al., 2005; Praca et al., 2009). Such patterns may in part be an indirect effect reflecting habitat preferences of prey. For instance, bottlenose dolphins (*Tursiops truncatus*) in the Shannon estuary, Ireland, show a preference for greater depths and slope, the type of habitats that provide a high concentration of prey fish (Ingram & Rogan, 2002). Setting boundaries around static variables, such as a depth contour, can provide fixed protected areas that encompass both the population and the important aspect of the habitat. However, some habitat preference models reveal that distributions can also be linked with
more dynamic variables, such as chlorophyll-a concentrations (Panigada et al., 2008). Here, the boundaries to a protected area would either need to be flexible enough to capture population distribution shifts caused by the dynamic drivers, or large enough to encompass any distribution changes (Granatham et al., 2011; Hooker et al., 2011).

The quality of habitat preference models relies on accurate and unbiased distribution and habitat data (Redfern et al., 2006). For example, it is important to use data spanning several years to minimise false correlations that may occur from snapshot data (Cañadas et al., 2005). Indeed, habitat preference data can be used to gain more temporally stable distribution estimates by using common drivers from yearly data to produce predicted densities integrated over time (Embling et al., 2010), allowing for more fixed protected areas boundaries to be set. However, these data can be difficult and expensive to collect, particularly on a multi-year basis where temporal variability is important. Where insufficient data exist to develop habitat preference models, Kaschner et al. (2006) suggest that habitat suitability models can be used to predict distribution patterns instead. Their Relative Environmental Suitability (RES) model uses qualitative data about habitat use for a range of cetacean species in order to deduce suitable habitat ranges for each species. Although they recognise the limitations of this model in predicting the actual species abundance, particularly at smaller spatial scales, the model is presented as an alternative when data are too deficient for more sophisticated models, and the resulting suitability maps can be used to direct future survey sites in order to gather data (Kaschner et al., 2006). A more detailed ‘logical deduction’ suitability approach by Gregr & Trites (2008) for the Stellar sea lion (Eumetopias jubatus), was able to predict boundaries of suitable habitat that encompassed a larger portion of sightings than the currently designated ‘critical habitat’ boundaries. These two examples present alternate methods of gaining information about population habitat preference when detailed distribution surveys are not available, and could be used as independent measures to strengthen conclusions about particular regions of interest.

Appropriate interpretation of habitat models is crucial for understanding habitat use, but model outputs can be confounded by data artefacts (Dormann, 2007; McPherson et al., 2004; McPherson & Jetz, 2007). Two of the more common problems relate to autocorrelation, which can generate relationships that appear stronger than they are, and collinearity, which can confound predictor variables and underlining drivers (Heikkinen et al., 2004; Redfern et al., 2006; Dormann, 2007). Autocorrelation arises from a population’s response to internal influences, such as social or herding behaviour, meaning the spatial distribution is not entirely due to the influence of external environmental variables (Legendre, 1993; Borcard et al., 2011). In cetaceans, for example, autocorrelation may arise from social interaction, and the location of one animal will depend on the positions of other nearby animals. As each position is not completely independent, this can increase the
chances of making a type I error (detecting a relationship where one does not exist) or increase the apparent strength of existing relationships (Dormann et al., 2007). Errors associated with autocorrelation can be reduced by first testing for autocorrelation (e.g. with a semi-variogram (Legendre, 1993)) and, if necessary, by including autocorrelation structure in the model (De Stephanis et al., 2008; Zuur et al., 2009). Collinearity is a well-recognised phenomenon when exploring statistical relationships (Farrar & Glauber, 1967; Mac Nally, 2000; Hocking, 2005; Harrell, 2001; Graham, 2003; Christiansen et al., 2013), and arises when there are strong correlations between predictor variables. The occurrence of collinearity can result in important variables appearing insignificant in a model due to the significance of correlated, but perhaps less ecologically important, variables (Graham, 2003). While the outcome would be the statistically optimal model, it may not reflect the causal or more ecologically plausible relationship (Mac Nally, 2000). Consequently, the base understanding of habitat associations is lost, and while distributions can be accurately predicted within the study area, these cannot be generalised to other areas. The exploration of collinearity among habitat variables (e.g. using correlation coefficients (Zuur et al., 2009)) is therefore a fundamental step in habitat modelling (Redfern et al., 2006). In general, the purpose of habitat modelling is to understand causal relationships in species distribution patterns, and the ecological implications of such relationships. Accounting for potential sources of error, such as autocorrelation and collinearity, within these models is therefore important for the correct interpretation of results.

Habitat modelling is a useful tool for advancing our understanding of habitat use, providing valuable information for the improvement of protected area design and management. Moreover, this information can be used to direct further survey design by, for example, directing surveys to areas where cetaceans are likely to occur based on habitat suitability (e.g. Kaschner et al., 2006), or using passive acoustic data collection in habitat associated with species (Mellinger et al., 2007). However, while habitat modelling identifies correlations between population distributions and the environment, it does not necessarily elucidate how animals use the habitats in which they are found. These models therefore need to be used in conjunction with biological knowledge to ensure results are modelled and interpreted appropriately. Interpreting habitat preferences can be augmented by the addition of behavioural data, which provides information on what populations are actually doing while occupying a particular area.

2.3.3 Behaviour

Observing the behaviour of animals while they inhabit particular areas can aid in the interpretation of their habitat use (Hastie et al., 2004), direct placement of priority areas for
conservation (Ashe et al., 2010), and the monitoring of the impact of disturbance (Williams et al., 2006). Analyses of behavioural data can allow for a more functional understanding of animal-habitat relationships. However, the detailed nature of these data is also the major drawback, as collecting behavioural data can require considerable time, effort, and expense.

Traditionally, behavioural data have been collected in situ, where an animal (or group) is followed for a period of time and changes in behaviour are recorded (Constantine et al., 2004). The development of tag-based technologies now allows for the remote sensing of behaviour using, for instance, satellite tags that monitor such variables as depth, speed, orientation, and vocalisation (Miller, 2004; Mate et al., 2007; Costa et al., 2010). Changes in behaviour can then be determined from these tags and used, for example, in state-space models, to delineate areas associated with particular behaviour (Bailey et al., 2009). Tagging animals is a highly valuable approach for animals with large distributions, or which travel into difficult-to-reach environments (Cooke et al., 2004).

Disturbance is often measured by short-term behavioural changes (Richardson & Würsig, 1997). A critical question, therefore, is how these short-term responses to disturbance affect populations in the long-term (Bejder et al., 2006a). Recently, studies have explored the method of predicting the probability of a behavioural change given the current behavioural state and the presence or absence of vessel traffic, modelled from collected behavioural data (Williams et al., 2006; Stockin et al., 2008; Christiansen et al., 2013). A key pattern emerging is the interruption of foraging behaviour, and while the direct energetic costs are difficult to quantify (Williams et al., 2006), continual reduction in feeding will have a cumulative long-term impact on energetics and thus the condition and possible breeding success of a population (Williams et al., 2006; Christiansen et al., 2013). When considering protected area placement, the potential for disturbance of foraging behaviour highlights vulnerable areas. For example, killer whales (Orcinus orca) in the north east Pacific are 2.7 times most likely to be foraging in an area close to the south shore of San Juan Island (Ashe et al., 2010). Given the reduced foraging behaviour of killer whales in the presence of vessels (Williams et al., 2006), this area can be identified as vulnerable on behaviour and in need of protection, as suggested by Ashe et al. (2010).

While the value of integrating behaviour into conservation management is disputed (Caro, 2007), ‘conservation behaviour’ is gaining recognition as a research field (Buchholz, 2007; Moore et al., 2008; Berger-Tal et al., 2011), and frameworks are starting to develop to enable the practical application of behaviour to conservation (Berger-Tal et al., 2011). For cetaceans, behavioural data provide information on the drivers of habitat use, confirming spatial modelling predictions and enabling the designation of protected areas. Appropriate regulation and enforcement of protected areas are important to avoid the trap of creating non-effective ‘paper parks’, but can be impractical for wide-ranging marine megafauna
which generally require large protected area boundaries. These priority zones can therefore
provide a valuable strategy for focusing management efforts and increase the conservation
effectiveness of reserves. Furthermore, behavioural data can also be used to determine
whether social learning, sometimes described as ‘animal culture’, is present among
populations and species (e.g. Krützen et al., 2005).

2.3.4 Culture

The existence of culture among non-human animals, including non-human primates, is a topic
As there is no universal definition of culture, the presence of culture in animals is arguably a
subjective assessment, with Laland & Hoppitt (2003) describing culture as being as “rare or
as common among animals as it is defined to be”. Evaluating whether a group behavioural
pattern is a cultural trait requires demonstration that the behaviour is socially learned, and
requires elimination of alternative explanations such as genetic inheritance. An example of
reported cetacean culture is ‘sponging’ in bottlenose dolphins (Tursiops sp.) in Shark Bay,
Western Australia, where marine sponges are used as a foraging tool by individuals in the
population (Krützen et al., 2005). Krützen et al. (2005) discount genetic explanations for this
behaviour and suggested cultural learning as the mechanism of transmission of this unique
behaviour, while Laland & Janik (2006) argue that the behaviour is likely a combination of
genetic, learned, and cultural traits. The capability of cetaceans for social learning, whether
considered as culture or not, is evidential (Rendell & Whitehead, 2001; Whitehead et al., 2004)
and has implications for species conservation (Whitehead, 2010). The importance of social
learning to the identification of protected areas is the potential vulnerability it can place on
populations in response to environmental and human-induced stresses. In particular, two
related social learning traits are relevant: cultural conformity and loss of information.

Social learning can both aid and inhibit the adaptability of animals to a changing
environment. The ability to quickly learn, for example, prey capture techniques from other
conspecifics can assist the rapid adaptation to an alteration in habitat, such as an absence of
preferred prey species due to fishing pressure (Whitehead et al., 2004). However, cultural
conformity can lead to maladaptive behaviours and inflexibility to changes in the
environment, even when it is having a negative impact (Krützen, 2012). This may result in
the continued use of an area through tradition, when staying has a detrimental impact to
individual and population health (Osborne, 1999). Such retained areas are therefore
important for protection, however the identification of culturally important areas, where
they exist, is very difficult. Indeed, the only indication of conformity to use of a particular
area, regardless of environmental conditions, will only be apparent once conditions become
unfavourable and there is no evidence of dislocation. Information on migration routes and good foraging areas are also thought to be socially learned behaviour from previous generations (Rendell & Whitehead, 2001). For example, the loss of information on habitat use has been identified as a partial reason for the absence of North Atlantic right whales (*Eubalaena glacialis*) from the Labrador Sea, and their slow recovery rate (Whitehead *et al.*, 2004). Whitehead *et al.* (2004) argue that by killing a large proportion of the population, information on how to use Labrador waters, which was occupied pre-whaling, was lost to the detriment of recovery rates. Humpback whale (*Megaptera novaeangliae*) populations are also consistent in their migration route, returning to the same breeding ground each year (although some individuals have been found to interchange (Noad *et al.*, 2000)). Knowledge of each route is thought to be transferred to a calf by its mother during its first migration (Baker *et al.*, 1990), and populations may be inflexible to change. Areas important for migration, such as humpback whale resting areas (Jenner *et al.*, 2001), therefore need to be considered for protection.

The difficulty in obtaining clear evidence for cultural associations generally renders this information secondary to better-defined data, such as those for distribution and habitat preference, when considering the establishment of protected areas. This limitation is due in part to the controversial nature of defining culture in animals, and because obtaining evidence from wild populations is challenging, especially when translocation experiments, as suggested by Laland & Janik (2006), are impractical. However, the capacity of cetaceans for social learning and cultural traits can be useful for conservation by, for example, providing a possible answer when reasons for habitat use are unclear, and remains a consideration to identifying important areas for protection.

### 2.4 Critical habitat

Whilst the above types of analyses are useful for identifying important areas for protection, a further progression is to determine which areas can be considered as critical habitat, and thus in need of more stringent protection. Ecologists refer to critical habitat as areas essential to species conservation, the loss of which would directly drive population declines (Rosenfeld & Hatfield, 2006). Demonstrating a habitat is critical can be ecologically tricky (Hagen & Hodges, 2006; Rosenfeld & Hatfield, 2006), as it requires evidence that without a habitat, a population (or species) would decline to extinction, while assuming the animals are unable to utilise other habitats. Despite these difficulties, critical habitat forms the basis for significant conservation legislation in some jurisdictions, most notably the United States.
In the United States, critical habitat is legally defined in the *US Endangered Species Act (1973)* to protect specific habitats of a species range essential for its recovery and long-term persistence (Heinrichs *et al.*, 2010). However, the level of detail needed about habitat use for legal designation as critical habitat is high (Hodges & Elder, 2008), and many cases are dismissed in court as “not determinable” due to insufficient data (Hoekstra *et al.*, 2002; Hagen & Hodges, 2006). Even when critical habitat status is successfully designated, the benefits to long-term population recovery are unclear. For example, (Taylor *et al.*, 2005) found the inclusion of critical habitat improved the likelihood of recovery, while other studies argue a negligible influence of critical habitat on recovery programs (Hoekstra *et al.*, 2002; Male & Bean, 2005; Kerkvliet & Langpap, 2007). The insignificant impact of critical habitat on species recovery is echoed by Clark *et al.* (2002), who found no difference in status trends (e.g. improving, stable, declining) between species with and without critical habitat protection. A recent study by Gibbs & Currie (2012) for mammal species found population status to be negatively related to critical habitat designation, and positively related to funding. Gibbs & Currie (2012) also argued that the benefits of critical habitat found by Taylor *et al.* (2005) are weak given the low percentages (between 1% and 10%) of variance explained. Therefore, while protecting critical habitat is intuitively attractive, the legal framework can be counterproductive to species conservation.

The purpose of defining critical habitat is to conserve areas of most value to a population, and thereby promoting species recovery. For cetacean conservation, the highly detailed information needed for official critical habitat designation (Hodges & Elder, 2008), coupled with the significant cost and effort associated with collecting and analysing cetacean data, make the identification of critical habitat an unreasonable goal. This difficulty is reflected in how critical habitat is defined among focal studies, which is at a significantly lower threshold of relative importance (Ingram & Rogan, 2002; Lusseau & Higham, 2004; Panigada *et al.*, 2008) when compared to legal definitions (Hoekstra *et al.*, 2002), presumably so that classification can reflect the information available. A broader definition of critical habitat might therefore be advantageous in the delivery of conservation outcomes for cetaceans, such that habitats of high value are allocated protection without the constraints of strict definitions, such as in the United States, that hinder conservation outcomes.

### 2.5 A tale of two species: how habitat definitions affect conservation outcomes

The following two case studies demonstrate how understanding of habitat use and subsequent definitions of critical habitat can affect conservation outcomes.
2.5.1 Hector’s dolphins

Hector’s dolphins (*Cephalorhynchus hectori*) are an endangered species of coastal dolphins endemic to New Zealand. This species has declined to approximately 27% of 1970 estimated population numbers (Slooten, 2007), with by-catch from commercial gillnet fisheries a significant source of mortality. The Banks Peninsula Marine Mammal Sanctuary (BPMMS) was established in New Zealand in 1988 to protect the Hector’s dolphin population from human-induced mortality, and extended around the Banks Peninsula coastline (South Island) out to a distance of four nautical miles. These boundaries were set based on the spatial distribution of Hector’s dolphins, established through boat transect surveys (Dawson & Slooten, 1988) and incidental sightings (Cawthorn, 1988). While it was understood that there were seasonal variations in distribution, with dolphins moving further offshore than four nautical miles during winter (Dawson & Slooten, 1988), this knowledge was not incorporated in boundary setting at that time, as the majority of fishing effort was during the summer, and boundaries were set to reflect this risk.

Despite the extra protection of the BPMMS, which nominally improved the probability of species survival (Gormley *et al.*, 2012), Hector’s dolphins continued to decline due to slow reproduction rates of around 2% per annum (Slooten & Lad, 1991) and continuous fishing mortality (Martien *et al*., 1999; Slooten & Davies, 2012). The slow reproductive potential of these small delphinids means even relatively low mortality from fishing can significantly hinder population recovery, and models of future population trends predicted that 100% protection from fishing by-catch would be the only scenario likely to ensure a population increase (Slooten & Dawson, 2010). In 2002, more spatially extensive surveys quantified the seasonal changes in dolphin distribution, and while the sanctuary encompassed 79% of sightings during summer, this was reduced to just 35% during winter (Slooten *et al*., 2006), a pattern consistent across years (Rayment *et al*., 2009), and likely associated with prey patterns in winter followed by calving and nursing in sheltered waters in summer (Rayment *et al*., 2009). In 2008, the government increased the size of the BPMMS in response to this seasonal distribution pattern coupled with evidence of continued by-catch outside the boundary zones (Starr & Langley, 2000; Slooten *et al*., 2006), and the sanctuary now extends further northwards along the coast, and reaches out to 12 nm from the coastline. While to date, there is no study assessing the effectiveness of these new boundaries, the integration of temporal distribution patterns into the BPMMS boundaries is likely to have improved the recovery prospect of this dolphin species.
2.5.2 North Atlantic right whales

North Atlantic right whales (NARW) (*Eubalaena glacialis*) are one of the most endangered cetacean species in the world, following their decimation by commercial whaling, now estimated to be 40% of the estimated population of 1000 individuals pre-whaling (NOAA, 2012). Whalers specifically targeted this species early on, naming them as the ‘right’ whales to kill, until the hunting ban in 1935. Despite having legally defined critical habitat areas in the United States and Canada, this population shows a very slow population recovery of 2.4% per annum (Waring et al., 2012). Critical habitat was designated in the US in 1994 (NOAA, 1994), and despite two petitions in 2002 and 2009 to extend these areas for more effective conservation (NOAA, 2002; Center for Biological Diversity et al., 2009), the original boundaries remain.

Establishing distribution patterns for NARW is difficult. Cetaceans, in general, are challenging creatures to survey given their mobile and cryptic nature, but this is further exacerbated for NARWs where very low population numbers, currently estimated at 396 individuals (Waring et al., 2012) make sightings data sparse. Detecting clear spatial and temporal patterns in distribution will therefore be problematic. NARW sightings, both surveys and opportunistic, have been collated in the ‘Right Whale Consortium’ (RWC) database since 1986 and as this database has grown, patterns such as migration timings, and foraging and calving areas, have become better understood. For example, the database was used by Firestone et al. (2008) to characterise migratory movements and timings, assisting the direction of surveys and mitigation strategies. The advances in computational power and statistical modelling techniques have also facilitated in ‘filling in the data gaps’ and detecting non-linear relationships in habitat associations, and are now being applied to NARW to better quantify habitat use, such as calving habitat (Keller et al., 2012), assisted also by greater data availability.

The US government has failed to revise critical habitat boundaries despite two petitions and strong indication of a lack of adequate protective measures, acknowledged in their own review (NOAA, 2012). The petition made in 2002 was declined based on inadequate data on habitat use: “The revisions proposed by the petitioner are largely based on where whales have been found and general information on what the whales may be doing in those areas rather than on the specific nature and location of the physical or biological features of the habitat that are essential to the conservation of the species” (NOAA, 2003). At that time, there were indications of wide-ranging patterns of movement (Mate et al., 1997) and that calving areas extended further offshore than previously thought (Waring et al., 1999). However these relationships were not quantified to the satisfaction of the National Marine Fisheries Service (NMFS) to warrant critical habitat status (NOAA, 2003). Given that the RWC
database had only been in effect for six years, and that statistical habitat modelling, which is a distinct advantage for NARW given the sparse nature of the data, was not as well established and accessible in the early 2000s (Elith & Leathwick, 2009), quantifying detailed habitat use for NARW was arguably an unreasonable task. Indeed, the limitations to data collection for such a sparsely distributed population did not allow for easy habitat associations until the advancement and availability of new statistical modelling methods. However, the endangered status and very slow recovery of NARWs should have instigated a sense of urgency rather than delay, and the standards for designating critical habitat by the US government are arguably too high for this population of whales, preventing them from receiving the protection they require. The more quantitative assessment of habitat associations used in the 2009 petition will hopefully lead to the establishment of larger, more effective critical habitat boundaries, although five years on, no action has been taken. Government agencies therefore need to understand that the slow reproductive rates in cetaceans require immediate conservation action, including protection of occupied habitat, and the challenges of data collection need to be considered when assessing research for the purpose of designating critical habitat.

2.6 Conclusion

Effective protected area design requires the accurate translation of data into the identification of biologically important areas. The complexity of the relationship between populations and habitat requires the incorporation of several data types on a temporal and spatial scale, including the four considered here: distribution patterns, habitat use, behaviour, and culture. The more information gained about how and why a population is distributed, the better areas of value can be estimated, and improve protected area designation. The case study on Hector’s dolphins presented here is an example of modifying boundaries based on better knowledge on patterns of habitat use while the case study of NARW is an example of a failure to protect important habitat. Establishing a population’s distribution is the foundation to locating areas of relative value, however single surveys provide a ‘snapshot’ of data, which is insufficient to capture temporal and spatial patterns without continual data collection. The next logical step is to assess habitat associations through statistical modelling of distributions with environmental variables. This is an essential step to understanding the drivers behind distribution patterns, enabling temporal and spatial patterns to be predicted. Behavioural studies are helpful in providing detailed information of habitat use, to validate habitat models and to inform conservation management decisions. Finally, cetaceans have arguably demonstrated the capacity for culture, and while cultural associations with habitats are difficult to quantify and thus
integrate into protected area design, it can be a source of vulnerability for populations and needs consideration in conservation management, even if it is a more qualitative contribution.

A common theme across cetacean research is the difficulty of data collection in terms of cost, logistics and time. The one exception to this is habitat modelling, which after distribution data are collected, is a relatively easy step to take given the ease of access to environmental variables through satellite databases, and new statistical modelling techniques. However, the burden of proof to justifying protected area boundaries generally lies with the researchers, who are required to use data to substantiate claims of protection requirements. Given the challenges associated with cetacean data collection, the requirements for justification should be set at the level of ecologically achievable knowledge to underpin conservation outcomes. This is particularly acute for the designation of critical habitat, where the requirements can be inordinately high, and the time taken to reach this quality of data serves to hinder population recovery, as discussed in the NARW case study. The legal definition of critical habitat is therefore not appropriate for cetaceans, and a less rigorous assessment of important habitat is required.

2.7 Acknowledgements

JE Braithwaite would like to acknowledge the University of Western Australia for providing a PhD scholarship.
Chapter 3

Estimating cetacean carrying capacity based on spacing behaviour

3.1 Abstract

Conservation of large ocean wildlife requires an understanding of how they use space. In Western Australia, the humpback whale (*Megaptera novaeangliae*) population is growing at a minimum rate of 10% per year. An important consideration for conservation based management in space-limited environments, such as coastal resting areas, is the potential expansion in area use by humpback whales if the carrying capacity of existing areas is exceeded. Here I determined the theoretical carrying capacity of a known humpback resting area based on the spacing behaviour of pods, where a resting area is defined as a sheltered embayment along the coast. Two separate approaches were taken to estimate spacing distance. The first used the median nearest neighbour distance between pods in relatively dense areas, giving a spacing distance of 2.16 km (±0.94 km). The second estimated the spacing distance as the radius at which 50% of the population included no other pods, and was calculated as 1.93 km (range: 1.62-2.50 km). Using these estimates, the maximum number of pods able to fit into the resting area was 698 and 872 pods, respectively. Given an average observed pod size of 1.7 whales, this equates to a carrying capacity estimate of between 1187 and 1482 whales at any given point in time. This study demonstrates that whale pods maintain a distance from each other, which may determine the number of animals that can occupy aggregation areas where space is limited. This requirement for space has implications when considering boundaries for protected areas or competition for space with the fishing and resources sectors.
3.2 Introduction

An important consideration for conservation is the population size that a given habitat can support. Estimating this carrying capacity provides a baseline against which changes to habitat can be assessed with respect to the maintenance of conservation values (Goss-Custard et al., 2002). Here, carrying capacity is defined in terms of density limitation in a particular area at a given time, rather than the overall population carrying capacity (K) (Leopold, 1987). The limit to animal density in an area is generally related to the total amount of resources available in the habitat and the resource needs of each individual. It is well recognised that density scales inversely with body size across many plant and animal communities (Damuth, 1981; Brown, 1984; Peters, 1986; Carbone & Gittleman, 2002), as does home-range size in top predators (McNab, 1963; Peters, 1986; Jetz, 2004). Individual energy demand is the main explanation for these trends, with larger animals requiring more food and thus a larger area for foraging. Therefore, carrying capacity is often calculated based on food supply (Goss-Custard et al., 2003; Beck et al., 2006): for example, the estimated carrying capacity of sites used by migratory birds is calculated using a ‘daily ration model’, whereby the total consumable food of the site is divided by the individual energetic requirement (Alonso et al., 1994; Goss-Custard et al., 2002, 2003). However, this conventional approach to calculating carrying capacity is limited, and other studies have found that carrying capacity can also be influenced by predation risk (Heithaus & Dill, 2002), freshwater availability (Western, 1975), shelter (Armstrong & Griffiths, 2001), and the availability of nesting sites (Tiwari et al., 2010). As the space requirement of an animal, for example its home range, is generally related to the availability of resources, space itself can be considered as a resource that will limit density.

According to Tilman (1982) “all things consumed by a species are potentially limiting resources for it”, where the term ‘consumed’ describes those things used, such as an occupied wood hole for a squirrel. Following this definition, I argue that space is a resource, as animals consume space due to the physical requirements to perform behaviours, such as individual fish within a school (Krause & Ruxton, 2002), or due to a behavioural preference of the animal, for example social density in primates (Cowlishaw, 1999). The concept of space as a resource is also reflected in research into the welfare needs of animals in captivity, such as livestock or zoo animals with welfare positively correlated to size and complexity of enclosures. A classic example is caged hens (Gallus gallus domesticus), where a behavioural study on the confinements of laying hens in the late 1980s found that the existing cage measurements, based on the physical size of the bird (excluding wing-span), did not permit essential behaviour movements for the hens (Dawkins & Hardie, 1989; Nicol, 2007). Increased space availability in livestock has shown to improve welfare, such as
playfulness in juveniles (Jensen et al., 1998), conflict avoidance (Li et al., 2007; Petherick, 2007), and reduced muscle damage and fatigue during transportation (Tarrant et al., 1988; Petherick, 2007). In aquaculture, the stocking density of fish can affect growth rate (Holm et al., 1990) and mortality (Wedemeyer, 1996), however this is not only associated with the behavioural requirement of space for the individual, but with having space to allow for the circulation of high quality water and flow rates (Wedemeyer, 1996). A study by Clubb & Mason (2007) claims that success for carnivores in captivity is linked to home-range sizes in the wild, whereby infant mortality and stereotypic locomotive behaviour was positively correlated with increasing natural home-range sizes. In captivity food is plentiful, suggesting that the space use and natural ranging behaviour of carnivores in the wild can be a factor when considering animal welfare in captivity, regardless of the correlation between home-range size and foraging needs. Many of these examples are of animals in captivity and there has been little research on space as a resource in wild populations. Yet in naturally confined environments, the space requirements of an individual will determine the density limitation of animals in that area.

Migrating humpback whales in resting areas present a unique opportunity to investigate spacing behaviour in the wild, and the potential limitation this may have on the carrying capacity of the area. During migration, adult humpback whales are not actively feeding, eliminating energy requirements as a factor in density limitation. While calves and juveniles are feeding to varying degrees (Jenner, pers. obs.), their typical presence within a pod containing a fasting adult, where calves are feeding on their mother’s milk, means that feeding is unlikely to be a contributing factor to density limitation. Resting areas are found in relatively enclosed coastal areas, which provide shelter from open oceanographic conditions and protection from potential predators such as killer whales (Orcinus orca), and are therefore space limited. Along the coast of Western Australia, the use of coastal areas by the migrating humpback population is an important conservation issue; the humpback whale population is increasing at near maximum rates (Salgado Kent et al., 2012), while the coastline is becoming increasingly developed. For example, the large offshore oil and gas developments around the Pilbara region of Western Australia have resulted in the creation and expansion of coastal ports, increases in marine vessel traffic and noise, potentially creating competition with migrating whales for space in the ocean. This competition for space is of particular concern in resting areas, which provide the distinct conditions for humpback whales to rest, but are also limited in available space.

Here, I used innovative techniques to explore the concept of a space-defined carrying capacity in a natural environment by examining the spacing behaviour of humpback whales in Exmouth Gulf, a recognised resting and nursing area (Chittleborough, 1953; Jenner et al., 2001), during the 2004 and 2005 migrations. Temporal use was estimated using aerial line-transect surveys,
and overall space use was investigated through the abundance-occupancy relationship. Two different approaches were then used to determine the average distance maintained between pods. This spacing distance was calculated across whale pods in various behavioural states, to obtain a representative distance across the population occupying the Gulf at that point in time. Based on this space use I determine the carrying capacity of the area, which represents the theoretical maximum number of whales able to occupy Exmouth Gulf during the 2004-2005 seasons. I highlight the implications of having a space-defined carrying capacity in the context of an expanding population given current temporal and spatial use of the Gulf.

### 3.3 Materials and Methods

#### 3.3.1 Study area

Exmouth Gulf (Figure 3.1) is located on the Northwest shelf of Australia, between 21°45′S - 22°33′S and 114°08′E - 114°40′E. This embayment is approximately 3000 km² in size, with a mean depth of 9 m and maximum depth of about 20 m. The Gulf is located in the tropical zone and experiences an average sea surface temperature (SST) of 22-23°C during October when whale numbers peak. Exmouth Gulf is a recognised resting area for breeding stock D humpback whales as they migrate southwards from their calving grounds in Camden Sound (northern Western Australia) to the Southern Ocean each year between August and November (Jenner et al., 2001). The Gulf is constrained by coastline on three sides, with a northern opening to the Indian Ocean.

#### 3.3.2 Aerial surveys

A total of 17 aerial surveys were conducted in Exmouth Gulf between 7th July 2004 and 15th October 2005, of which 10 flights included observations of humpback whales (Table 3.1). Surveys were conducted in a twin-engine, overhead winged aircraft (Cessna 337) maintaining a cruising speed of 222 kmh⁻¹ (120 knots) and an altitude of 305 m (1000 feet). Data were collected using distance-sampling methods, with the plane following a systematic parallel line transect course across the Gulf (Figure 3.1) in passing mode (no deviations from the track), following Buckland et al. (2001). The parallel transects were spaced approximately 10 km apart to minimise overlap in the covered strips (Hedley et al., 2009; Salgado Kent et al., 2012). Personnel aboard the aircraft included the pilot, two observers and a data recorder. During the survey, the pilot recorded the angle of drift away from the flight path. For each pod sighting the observer measured the vertical and horizontal angles
from the plane, as well as the GPS location of the plane, and the pod size and composition (number of adults and calves, determined based on size). At the beginning of each flight the devices were calibrated to ±1 sec accuracy. Sea state, glare, wind speed, and visibility were also recorded throughout the survey, to monitor changes in sighting conditions. The position of each whale pod was then calculated following the method in Salgado Kent et al. (2012).

![Figure 3.1: A typical course flown by the aircraft during surveys, with the flight path was split into nine parallel transects spaced approximately ten km apart.](image)

### 3.3.3 Abundance

Population transect surveys are subject to availability and perception biases, whereby animals could be missed if they were not available to be seen, or they were available but not seen by the observer (Redfern et al., 2006). Therefore, distance-sampling was used to reduce any errors caused by perception bias and provide more accurate estimates of abundance (Buckland et al., 2001). This method models the probability of detection of an animal group as a function of the perpendicular distance from the transect. The probability detection function can also take into account the variation in sighting conditions, by introducing covariates such as observer and sea state. Once a detection function has been
fit, it is used to estimate the actual number of animals in the survey area, including those likely to have been missed by the observer (the perception bias).

The sightings data were right-truncated at 5 km from the transect line, removing 5% of the data, following the general ‘rule of thumb’ to remove extreme values prior to fitting detection functions (Buckland et al., 2001). In aerial surveys, it is also difficult to make observations on the transect line as it lies directly beneath the plane. However, the method of fitting a detection function assumes that all animals at the surface (available to be seen) on the transect line were observed. To account for the discrepancy, a standard left-truncation at 0.1 km was set to obtain a better detection function fit, however this did not result in any loss of data as no observations were made within this distance. Distance 6.0 (Thomas et al., 2009) was used to fit different detection function models (half-normal and hazard-rate) for each flight, taking into account covariates that may affect detection probability such as observer, sea state, pod size, and day of flight. Model selection for each flight was based on the Akaike’s Information Criterion (AIC), Q-Q plots, and the Kolmogorov-Smirnov and Cramer-von Mises goodness-of-fit tests. If two or more models were too similar to make a selection based on the above criteria, the parsimonious model was selected. The abundance of whales in Exmouth Gulf for each flight was then estimated in Distance 6.0 using the best probability detection function, and 95% confidence intervals were obtained using a bootstrap.

Availability bias was not accounted for in this analysis, and therefore the model will underestimate abundance. However, we believe this difference to be small as the Gulf is relatively shallow, and resting whales tend to display passive behaviours such as surface lying or surface travelling (Jenner et al., 2010). Therefore pods are more likely to be at the surface and available to be seen from aerial surveys.

Pods with calves have previously been demonstrated to lag in the migration (Chittleborough, 1965; Dawbin, 1966). By looking at the seasonal variation in calves in the Gulf and comparing this to the total abundance of all whales using the Gulf, I can determine if a lag also exists in resting areas. If there were no lag, this would indicate that mainly mothers with calves are likely to be using resting areas. If a lag does exist, then comparing the length of this lag with those found by Dawbin (1966) in the main migration pattern will indicate which groups are using the Gulf. The change in the number of pods with calves over times was plotted to test this prediction for this population of humpbacks. As many of the flights contained a small sample size of pods with calves (< 20), distance sampling was not used in this analysis.
3.3.4 Abundance-occupancy relationship

The abundance-occupancy relationship (AOR) describes the relationship between the abundance of a species and the size of their ranges within a region, and reflects the pattern of abundance covarying with the total area occupied (Brown, 1984; Gaston, 1996). As AOR is usually evaluated across many sites within a region, abundance is calculated as the mean density across all occupied patches, and the occupancy as the sum area of all the occupied patches (Gaston, 1996). In the basic AOR pattern, density remains constant while the occupied area increases, meaning that abundance increases in proportion to the area. However, for most species the AOR is positive; as the density increases so does the occupied area (Gaston, 1996; Gaston et al., 1997; Fisher & Frank, 2004; Frost et al., 2004). In these cases, the population size is increasing at a greater rate than would be expected simply by a range expansion. Alternatively, the AOR pattern may reflect increases in density while the occupied area remains constant. In this case, population abundance increases but the range size stays the same. Understanding the AOR relationship has important implications for conservation; if there is a positive AOR then any reduction in habitat will result in a greater loss in individuals proportional to the AOR (Lawton, 1993). To investigate the AOR for humpback whales in Exmouth Gulf, the occupancy area for each flight was estimated by a convex hull analysis (Barber et al., 1996; Cornwell et al., 2006), which calculates the minimum area occupied by the population by fitting the smallest polygon possible that encompasses all the humpback whale sightings. The abundance was then estimated by calculating the density of humpback whales within the convex hull area (CHA).

3.3.5 Factors affecting pod density

To calculate the carrying capacity of pods in Exmouth Gulf, it is important to first determine what factors may influence their spatial organisation and nearest neighbour distances. The two factors I investigated here were pod size and pod composition, where a pod is defined as a group of one or more animals. During the breeding season, humpback whales are usually found in pods of 2-3 animals, however pod size can range from 1 to 20 animals (Silber, 1986). Pod size could affect spacing behaviour in that, for example, larger pods may prefer more space. The type of animals present in a pod may also influence their nearest neighbour distances regardless of pod size. For example, during the breeding season mother and calf pairs receive the attention of adult males who are looking to compete for and mate with the now receptive female (Tyack, 1981), which may alter the spacing of animals around pods with a calf.
To investigate the effect of pod size, the nearest neighbour distance for each pod in each flight was estimated. The pods from all the flights were then grouped together based upon pod size, ranging from 1 to 8 animals. As there were less than three observations for pods containing 5 or more animals, these groups were excluded from the analysis. The nearest neighbour distances in each of the remaining four group types were distributed non-normally (Kolmogorov-Smirnov test, $p < 0.05$ for all groups). Therefore, the median nearest neighbour of each group size was compared using a Kruskal-Wallis test.

Pod composition was defined as those with calf present (wCP) and those without (nCP), due to the limitation of aerial surveys to specify composition in more detail, such as singing males. The nearest neighbour distances for each pod in the two categories were also distributed non-normally (Kolmogorov-Smirnov test, $p < 0.05$ for both groups), and thus the spacing around the different pod types was tested by comparing the median nearest neighbours using a Kruskal-Wallis test.

3.3.6 Spacing behaviour

I defined spacing behaviour as the distance maintained between pods under relatively dense conditions. To determine the spacing of individual whale pods, I first needed to see if the distribution in the flights followed the same pattern of space use. The harmonic mean position of pods for each flight dataset was estimated, and the CHA was then calculated by including increasing percentages of pods closest to the harmonic mean, starting at 10% and increasing to 100% in increments of 10%. Two distinct trends of space use emerged with increasing number of pods included in the analysis (Figure 3.2): flights 4, 5, 6, and 8 used more space for fewer numbers of pods due to the low number of whales recorded on those days, due to being at the beginning and the end of the season (Table 3.1) while flights 1, 2, 3, 7, 9 and 10 occupied less area per number of pods. As I wanted to calculate the distance maintained in relatively high density conditions, flights with low densities (4, 5, 6, 8) were excluded from further analysis.

Two distinct methods were used to calculate pod spacing to assess consistency of the estimates. The first method used the nearest neighbour distances between pods, whereas the second investigated the number of whales within a given radius of a pod.

Method 1: For each pod in each flight, the distance to the nearest neighbour pod was calculated. A nearest neighbour analysis (Clark & Evans, 1954) was conducted for each flight, which calculates the ratio ($R_n$) between the observed mean nearest neighbour distance ($NND$) and the expected mean $NND$ given a random distribution. Randomly distributed animals will give an $R_n$ value of 1, clustered animals will have a value less than 1, and
Figure 3.2: The minimum polygon area (convex hull area) around whale pods was repeatedly calculated for each survey flight to include increasing number of pods closest to the centre of aggregation, starting at the nearest 10% until all pods were encompassed by the polygon. A scatter plot of these changes in area occupied reveals two patterns in area use; the first group of flights are indicated by open symbols (△ flight 4, ◇ flight 5, ◊ flight 6, ◻ flight 8) and the second group by closed symbols (● flight 1, ■ flight 2, ▲ flight 3, + flight 7, − flight 9, ⭐ flight 10).

uniformly spaced animals will have a value greater than 1. This analysis indicated that pods in Exmouth Gulf were not uniformly spaced, but had a tendency to cluster (Rn = 0.8; mean across 6 flights). As such, the nearest neighbour distance will vary depending on the distance between the pod and the centre of aggregation. I thus grouped pods based on how close they were to the centre of aggregation because I needed to study the pod arrangement when humpbacks were in relatively high density conditions, each group included 10% of the pods; the 0-10% group contained the 10% of pods closest to the harmonic mean, the 10-20% group was the next closest 10% to the mean, and so on. I used a one-way analysis of variance (ANOVA) to compare the mean nearest neighbour distances for each percentage category. The mean nearest neighbour distances in the 90-100% group were significantly higher than the rest of the groups (p < 0.05; Tukey-Kramer. Figure 3.3) and so were excluded from this analysis. The nearest neighbour distances of the remaining 90% of the pods were also non-normal (Kolmogorov-Smirnov test, p < 0.05), so the overall
Chapter 3. Estimating cetacean carrying capacity based on spacing behaviour

Figure 3.3: The nearest neighbour distance (mean of flights ± standard error) of groups of pods based on how close they are to the centre of aggregation, i.e. the 10% mark contains the closest 10% pods to the mean, the 20% mark contains the closest 10 - 20%, and so on up to the 90 - 100% group. The only group with a significantly different nearest neighbour distance was the 90-100%, which was much higher than the rest.

distance maintained between pods was calculated as the median nearest neighbour distance. As there will be individual variability in pods, variation in this distance was estimated by calculating the median absolute deviation (MAD).

Method 2: For each flight, sequential circular boundaries at a radial distance of 0.001 km were drawn around every pod from a minimum radius of 0.001 km to a radius where all the pods had another pod present in the boundary. The proportions of the pods that had at least one pod present within these radii were then calculated. This approach produced a cumulative density of the proportion of pods that had other pods present within a radius of increasing length for each flight. A curve was then fitted to the data using the least squares method (Bates & Watts, 1988) and an exponential model. Here, the distance maintained between pods was estimated to be at the 50% mark, analogous to the use of LD50 curves in toxicology (Weil, 1952) and size at maturity curves in fisheries (Trippel & Harvey, 1991). At this point, half the pods have no other pods within the boundary and half of the pods have at least one other pod within the boundary, providing an estimate of pod spacing for each flight. As a preliminary regression analysis indicated no season trend in the radii ($p > 0.05$), the overall population pod spacing estimate was taken as the mean radius of the six flights, and the error range as the lowest and highest radius over the flights.
3.3.7 Carrying capacity

Assuming that all pods maintain an area of space, the maximum number of pods able to fit in Exmouth Gulf at any one time can be estimated as the highest density of pods allowing for distance between pods to be maintained within the area utilised by the population. The distances from the two above methods were used as a radius to determine a circular boundary of space around a pod. The maximum area used by the population of humpback whales was taken to be the CHA around all recorded pods over all the flights. The pods, plus their circular space, were arranged in a lattice formation, the densest concentration of circles on a single plane (Steinhaus, 1999), within the CHA while allowing the circles to overlap to the length of the radius so that the nearest neighbour to a pod was no closer than the spacing radius. This maximum number of pods for each of the methods was then multiplied by the average pod size to obtain two estimates of the carrying capacity for Exmouth Gulf. The error range for method 1 was calculated using the median absolute deviation (Mosteller & Tukey, 1977) while the error range for method two was estimated by calculating the carrying capacity from the maximum and minimum 50% radii of the six cumulative density curves.

Table 3.1: A summary of the aerial surveys carried out during the 2004 and 2005 humpback whale season (August - November) in Exmouth Gulf. The selected detection function (Det. Func.) for the survey was either a half-normal (HN) or hazard (HZ) function, with two surveys needing an additional covariate of either observer (Obs) or pod size (Pod). The abundance was estimated using this detection function and the 95% lower and upper confidence intervals (CI) were calculated using a bootstrap.

<table>
<thead>
<tr>
<th>Aerial Survey Flight Date</th>
<th>Whales</th>
<th>Calves</th>
<th>Det. Func.</th>
<th>Abundance</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7th Oct 04</td>
<td>135</td>
<td>29</td>
<td>HN (Obs)</td>
<td>409</td>
<td>232</td>
</tr>
<tr>
<td>2</td>
<td>14th Oct 04</td>
<td>97</td>
<td>16</td>
<td>HZ</td>
<td>144</td>
<td>73</td>
</tr>
<tr>
<td>3</td>
<td>26th Oct 04</td>
<td>62</td>
<td>12</td>
<td>HZ</td>
<td>71</td>
<td>30</td>
</tr>
<tr>
<td>4†</td>
<td>2nd Nov 04</td>
<td>26</td>
<td>6</td>
<td>HN</td>
<td>44</td>
<td>22</td>
</tr>
<tr>
<td>5</td>
<td>7th Aug 05</td>
<td>7</td>
<td>0</td>
<td>HN</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>6</td>
<td>21st Aug 05</td>
<td>35</td>
<td>2</td>
<td>HN</td>
<td>138</td>
<td>54</td>
</tr>
<tr>
<td>7</td>
<td>4th Sep 05</td>
<td>79</td>
<td>4</td>
<td>HN</td>
<td>248</td>
<td>127</td>
</tr>
<tr>
<td>8</td>
<td>10th Sep 05</td>
<td>41</td>
<td>3</td>
<td>HN</td>
<td>84</td>
<td>43</td>
</tr>
<tr>
<td>9</td>
<td>25th Sep 05</td>
<td>126</td>
<td>17</td>
<td>HN (Pod)</td>
<td>459</td>
<td>250</td>
</tr>
<tr>
<td>10</td>
<td>15th Oct 05</td>
<td>95</td>
<td>13</td>
<td>HN</td>
<td>279</td>
<td>167</td>
</tr>
</tbody>
</table>

† Seven other surveys, flown on 18th Feb, 7th Mar, 3rd Apr, 26th Apr, 22nd May, 12th Jun, and 12th Jul 2005, no humpback whales were observed.
* The abundance was not calculated for flight 5, as the sample size was too small (<20) to obtain reliable results from distance sampling.
3.4 Results

A total of 703 individual whales were sighted in the Exmouth Gulf region during the 2004-2005 aerial surveys (Table 3.1). The abundance estimates for each flight, using distance sampling, showed a maximum of 459 whales within the Gulf at any one time, and a total of 1270 whales over the entire period (CI 670 - 2080), assuming a maximum two week residency period for each whale (KCS Jenner, estimated from photo ID re-sights; each whale is represented only once in the total estimate). The abundance of whales in the Gulf clearly changed over time (Figure 3.4A), with whales beginning to enter the Gulf from the north around the first week of August, peaking at the end September, before departing until the start of November. The number of calves within the Gulf follows a similar temporal pattern, but peaks about a week or two after the main migration (Figure 3.4B), in early October.

![Graph A](image)

**Figure 3.4:** A. For each flight, the total number of whales resident in Exmouth Gulf was estimated using distance sampling. The error bars mark the 95% confidence interval, calculated using a bootstrap in Distance 6.0. There is clear temporal pulse of whales in the Gulf, with the peak occupancy towards the end of September. B. The total number of calves observed during each survey flight also displays a temporal pulse to occupancy, but the peak here is slightly later in the first week of October.
Chapter 3. *Estimating cetacean carrying capacity based on spacing behaviour*

**Figure 3.5**: The total area occupied was calculated as the convex hull area for each flight, and the density as number of whales per km$^2$ in this area. The pattern emerging is that of a constant area used with increasing density, as highlighted by the grey shaded area. One survey (flight 5), marked as an open circle, is an outlier to this pattern.

**Figure 3.6**: Neither pod size (A) or type (B) showed significant difference in median nearest neighbour distances (Kruskall-Wallis test: pod size $p = 0.80$, pod composition $p = 0.58$). For pod type, wCP are pods with calves present and nCP are pods with no calves observed.
Estimating cetacean carrying capacity based on spacing behaviour

Whales in Exmouth Gulf follow an abundance-occupancy relationship whereby the area occupied remains relatively constant as abundance increases (Figure 3.5; shaded area), and consequently density is increasing with abundance. The area of the first value (marked as an open circle) is less than half that of the other areas. This may be an anomaly in observation, or it may indicate that a constant abundance-occupancy relationship exists only above a threshold of at least 0.04 whales per km$^2$.

Estimating the carrying capacity of whales in Exmouth Gulf requires an understanding of how pods spatially organise themselves within the Gulf, which may be influenced by pod characteristics. However, the two characteristics I investigated here, pod size and composition, had no effect on the median nearest neighbour distance of the pods (Kruskall-Wallis test: pod size $p = 0.80$, pod composition $p = 0.58$; Figure 3.6). Therefore, these variables were not incorporated in analyses to calculate carrying capacity.
TABLE 3.2: Carrying capacity of whales and pods in Exmouth Gulf estimated from two distinct methods. The first method was based on nearest neighbour distances, and the second based on the presence of pods within a certain radius. The total carrying capacity of pods was calculated by fitting the maximum number of pods, including their radius distance, into the convex hull area encompassing the entire population. The carrying capacity of whales is the number of pods multiplied by the mean pod size.

<table>
<thead>
<tr>
<th>Method</th>
<th>1</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radius (km)</td>
<td>2.16</td>
<td>1.93</td>
</tr>
<tr>
<td>Pod carrying capacity</td>
<td>698</td>
<td>872</td>
</tr>
<tr>
<td>Mean pod size</td>
<td>1.7</td>
<td>1.7</td>
</tr>
<tr>
<td>Whale carrying capacity</td>
<td>1187</td>
<td>1482</td>
</tr>
<tr>
<td>Density (whales km(^{-2}))</td>
<td>0.43</td>
<td>0.54</td>
</tr>
</tbody>
</table>

The first method for estimating the spacing between pods, using the median NND of 90% of the population, generated a radius of 2.16 km (MAD \(\pm\) 0.94 km). In the second method, the saturation curve fit to an exponential model (Figure 3.7) estimated the mean distance within which half the population had a pod as 1.93 km (lowest 1.62 km; highest 2.50 km). Fitting the pods into the maximum CHA area of 2742 km\(^2\) in a lattice formation yielded maximum pod estimates of 698 (method 1; range 345 - 2160) and 872 (method 2: range 523 - 1242). Given an average observed pod size of 1.7 whales, this equates to carrying capacity estimates of 1187 and 1482 whales, respectively, and density estimates of 0.43 and 0.54 whales km\(^{-2}\) (Table 3.2). The two distinct approaches to estimating the distance maintained between pods were within 0.1 km of each other, translating into a difference in total carrying capacity of approximately 175 pods or 295 whales.

3.5 Discussion

Our premise is that in limited-space conditions the carrying capacity of an area for resting humpback whales is linked to the space requirement of the animals that occupy it, rather than more typically encountered pressures such as competition for food, and predator avoidance. The results suggest that pods do maintain a distance from each other under relatively high-density conditions, demonstrating that space itself is a resource for these animals and that this space can be determined. I then used this spacing distance to calculate the theoretical carrying capacity of a humpback whale resting area. The implications of having a capacity limit, under the currently increasing population of WA humpback whales, can only be assessed once the
current use of Exmouth Gulf is understood. Therefore, I also investigated how the humpback whale population presently uses Exmouth Gulf, both spatially and temporally.

There is a clear temporal pulse to peak whale occupancy of Exmouth Gulf, starting from late September to early November, which conforms with the timing of movement of the whale population down the WA coast (Chittleborough, 1965; Jenner et al., 2001). This temporal pulse could be caused by an environmental signal that triggers the whales to leave particular areas and continue on their migration, such as a change in temperature or day length, however the influence of environmental cues on the migration of baleen whales is still poorly understood (Baker et al., 1985). As adult humpback whales need to complete migration before energy reserves are exhausted, leaving the Gulf may also be triggered by a certain level of depletion in these reserves.

The number of pods containing calves peaks in the Gulf after the main migration, supporting previous observations that mothers with calves follow the main migration (Chittleborough, 1965; Dawbin, 1966). The timing offset between the two peaks in this study was approximately two weeks, which is shorter than that estimated by Chittleborough (1965). However, the Chittleborough (1965) study used commercial catch data, which reflect hunting near migratory areas and thus were likely to capture the timing of the entire population of migrating whales, whereas these data were concentrated on a resting area. Therefore, the disparity between peak timings could mean only a portion of the migrating whales are using Exmouth Gulf to rest during the southbound migration; if the vanguard of the migrating population are not using Exmouth Gulf then the peak of whale abundance in the Gulf would appear to be later than if sampling the entire population. The match in timing difference between peaks of mature males and lactating females found by Dawbin (1966) indicates that it is these groups of whales which are mostly present in the Gulf, supporting the conclusion that resting areas are particularly important for mothers with calves (McCauley et al., 2000), but also that it is an area where mature males and lactating females are mating. It is important to note that, as distance sampling was not applied to the calf data due to the small sample sizes, the perception bias (the calf is available to be seen, but is not observed) was not corrected for, and thus the total number of calves within the Gulf could not be estimated. To further investigate calf presence in this resting area will require more detailed surveys.

The importance of resting areas to migrating whales is still unknown, however during migration a calf requires sufficient food from its mother to enable it to grow and gain adequate energy reserves to continue migrating towards the Southern Ocean. Mothers are therefore expending their own limited stores to meet both their own energetic requirements and that of the calf. Spending time resting in sheltered embayments, such as
Exmouth Gulf, during migration allows calves to increase energy stores more efficiently, as they will be expending less energy when compared to resting and feeding in open ocean conditions, and thus slowing the rate of energy loss. Furthermore, wind speed is known to influence the energetic surface active behaviours of humpback whales, with rising wind speed increasing behaviours like breaching, pectoral fin slapping, and tail slapping (Dunlop et al., 2010). This correlation is linked to a change in communication strategies during periods of higher wind-dependant background noise (Dunlop et al., 2010). Therefore, the flatter the surface conditions, the more the humpback whales can rest. The wind conditions in Exmouth Gulf are typically characterised by diel changes in speed, creating calmer conditions during the day and for several hours wind speed can drop to nothing. During the October period in northern Western Australia, these extended low wind, flat water conditions are unique to Exmouth Gulf. These conditions create the ideal resting environment along the Western Australian coast for whales, particularly mother with calves, at perhaps a critical stage of their migration towards polar waters. In the Australian context, this unique opportunity to boost calf energy reserves mid-migration may increase long term survivability of calves for this population and partly explain the higher population growth rate measured in west Australia’s Stock D versus east Australia’s Stock E (Noad et al., 2006; Salgado Kent et al., 2012). Considering resting areas are predominately used by mother and calf pods, I theorise that these pods are driving the spacing behaviour in this resting area, perhaps due to mothers regulating the social stimulus of the calf. However, further research will be required to determine if this is the driver behind the spacing behaviour.

### 3.5.1 Abundance-occupancy

The abundance-occupancy relationship of humpback whales within the Gulf demonstrates that the total space used within the Gulf remained constant regardless of whale abundance. The one exception to this rule is at the lowest abundance observed suggesting there could be a positive AOR below a particular threshold of whales. However this holds little significance to the overall understanding of space use as for the majority of the time, the Gulf is occupied at abundance levels above this threshold value.

The AOR analysis uses the average density of whales across the total space used by all the whales (the CHA area) over the duration of each flight, and therefore does not capture any information on the arrangement of whales within this area. However, this spatial arrangement is an important consideration as it has the potential to confound the spacing behaviour analysis. Given that the area used remains constant, if pods are spacing evenly throughout the area then the distance maintained between pods will decrease as density within the area increases. Alternatively, if the pods are aggregating within the area, then
average maintained distance will remain relatively constant and core area of aggregation will continue to expand within the limits of available resting area. The nearest neighbour analysis indicated a tendency towards aggregative behaviour, suggesting the second spatial arrangement. As outlying pods, the 90-100% furthest away from the centre for aggregation, were removed from the spacing behaviour analysis, the results are not confounded by having a constant AOR.

The constant AOR relationship found for humpback whales in the Gulf is different to other cetacean species investigated (Hall et al., 2010), which tend to show a positive AOR. This could reflect the difference in the population’s situation at the time of study; for example, the Minke whales (Balaenoptera acutorostrata) were analysed while they were foraging (Hall et al., 2010), whereas the humpback whales in this study were not feeding and so distributions were not driven by food patchiness. The consequence to having a constant AOR is that as more whales enter the Gulf, the Gulf becomes increasingly dense. Given that there is a minimum requirement for space between individual pods, at some point maximum density, and thus carrying capacity, will be reached.

3.5.2 Implications of spacing behaviour

The two approaches I took to calculate spacing between pods arrived at very similar estimates of approximately 2 km between pods. While both estimates are derived from the same dataset, the answers are distinct due to fundamental differences in the approaches used in the estimation of spacing distance. The first method concentrated on only the measured distance to the nearest neighbour for each pod, ignoring any other pods in the vicinity, while the second approach took account of all the pods within a given radius, regardless of which was nearest.

Pod size and composition did not affect the distance maintained between pods, and so density of pods within the Gulf will be the same regardless of these factors. There were very few observations of pods containing more than four animals, so an effect on nearest neighbour distance may still exist at higher pod sizes. However, given the few instances of large pod sizes in Exmouth Gulf over the season, this will have little consequence on the overall pod carrying capacity within the Gulf, assuming that a recovering population does not lead to larger pods. Pod composition could also be further disaggregated to investigate difference between, for example, singing males or competitive males. However, these aerial survey derived data did not allow us to distinguish such individuals. Other factors that may influence pod density, but were not able to be investigated here, are pod activity, habitat preference, and competitive exclusion. However, the distance maintained between pods calculated here is representative
across the population occupying the Gulf at a point in time, so represents an average over pods in various states of activity and habitat preference. Competitive exclusion is likely to be a factor only once the Gulf approaches maximum density and space to arriving whales becomes unavailable, which appeared not to be the case in the 2004-2005 seasons. Another potentially confounding variable when calculating the spacing distance of pods is movement of and interaction amongst pods. However any extremes in this variation, such as a closer than normal distance between interacting pods, or larger than normal from pods requiring more space, would be accounted for in the analysis by looking at the central tendency in distances, resulting in a representative spacing distance across the population occupying the Gulf at that point in time.

The knowledge that resting humpback whales maintain spacing has implications for their interactions with vessels. Seismic vessels have strict guidelines when operating around and approaching whales, which outline observation, low power, and shutdown zones depending on the distance from the whales (Dept of the Environment, 2008). The 2 km spacing of whale pods matches the 2 km low power zone for vessels operating above 160 dB (Dept of the Environment, 2008), however below this source level the low power zone is reduced to 1 km, which could be viewed as an invasion of space for the pod. Tourism vessels also have guidelines when approaching whales (Dept of the Environment, 2005), with a caution zone of 300 m and a no approach zone of 100 m while fishing vessels have to keep a distance of at least 100 m, all of which are well within the behavioural spacing of humpback pods as calculated here. A specific humpback whale sanctuary established in Camden Sound, the calving grounds for this population (Jenner et al., 2001), has increased this 100 m no approach zone to 500 m for mother and calf pods, however this still falls short of the 2 km distance maintained between pods found in this study. I do not dispute that these regulations are adequate to avoid disturbance to the whales, indeed the population is recovering at near maximum rate (Zerbini et al., 2010; Salgado Kent et al., 2012), however vessels spending too long within the boundary of a pods’ space may end up increasing calf interaction and activity levels, and therefore energy consumption, at a time when net energy levels are intended to be increasing. So while the immediate impact of displacement and/or increased activity may not be apparent, there may be longer term implications to the survivability of the calf mid-migration which is drawing on fixed energy reserves from its mother. I would therefore recommend a precautionary approach to management decisions when considering increasing vessel density in areas likely to contain resting whales.

I calculated the theoretical carrying capacity of Exmouth Gulf to be around 700-850 pods (1200-1500 whales), based on the spacing between pods and the maximum CHA used by the whales. There are moderate errors surrounding the carrying capacity estimates, with ranges calculated as 345-2160 pods and 523-1242 for methods 1 and 2 respectively, but estimates
Chapter 3. Estimating cetacean carrying capacity based on spacing behaviour

of overall carrying capacity are comparable. Considering the constant AOR relationship, whereby the population is occupying the same amount of area regardless of the number of whales within the Gulf, there will likely be no change in the total area used by the whales until carrying capacity is reached. The area the whales are currently occupying (2,742 km$^2$) encompasses most of the Gulf. In the context of a currently increasing numbers, there is little room within the Gulf for the expansion of whale populations. Therefore, if the response of the population is to expand the resting area, then this expansion will extend outside of the Gulf. Alternatively, the whales will seek other appropriate areas in which to rest along the coast, which is of particular concern given the current coastal developments in the northwest of Australia for extractive industries. It is also important to realise that, as space is the limiting factor for carrying capacity, then any reduction of space within the Gulf available for whales to rest will result either in a reduction to the total carrying capacity of the Gulf or a decrease in spacing between pods. As maximum carrying capacity in the Gulf was not observed in this study, it is difficult to predict the consequence of reaching carrying capacity based on space limitations.

To calculate carrying capacity, this study assumed that space limitation exists in the Gulf. The consistent area occupied by the whales over varying densities suggests that there are physical constraints with respect to the area used by humpback whales, making space a limited resource. To determine whether the approximate 2 km spacing distance found in the 2004-2005 seasons is maintained across years will require additional appropriate aerial surveys such that interannual variability in spacing distance as a function of population size can be evaluated. It may be that as the population off the West Australian coast continues to grow, the average space between pods will decrease to accommodate the increase in whales. However, this will depend on the drivers behind spacing behaviour between resting pods. Here, I used the 2004-2005 season to illustrate the concept that space is a resource for resting whales, and distance maintained between pods can be used to calculate carrying capacity at a given point in time, which has important management applications. This study forms the foundation to further work exploring the spacing behaviour of wide-ranging megafauna, and how this may limit carrying capacity in space-limited areas.

3.6 Conclusion

Our study shows that carrying capacity for humpback whales can be calculated based on their behavioural space requirement under relatively dense conditions regardless of pod size or composition, and that this distance can be consistently estimated using two separate approaches. I estimated the carrying capacity of Exmouth Gulf, a migration resting area, to
be approximately 1187-1482 whales. Although there has been considerable research into the spacing of other aggregating animals, such as fish and birds, this study is a new approach to understanding the habitat use of large ocean wildlife when they are not feeding, and how the spacing behaviour can determine a habitat’s carrying capacity. The consequence of a carrying capacity in Exmouth Gulf is that, when exceeded, the resting area may expand in time or space, or the whales will begin to utilise other areas along the coast for resting. Given that the whale population is sharing the coastal waters with human activities, such as mining developments, it will be important to ensure any expansions in resting area habitat use are monitored and that the areas whale populations expand into are disturbance free, in order to promote the continued healthy population growth for this recovering species.

3.7 Acknowledgements

I thank Ben Fitzpatrick for statistical support, Philippe Bouchet for advice on the distance sampling analysis, Straits Resources who funded the aerial surveys, and Micheline Jenner and Emily Wilson who assisted with data collection. JE Braithwaite also thanks the University of Western Australia for providing a PhD scholarship.
Evidence of fine-scale humpback whale habitat selection during non-foraging periods

4.1 Abstract

A key area of research for ecology and conservation is the relationship between a species and its habitat. This knowledge is particularly useful for species-specific conservation, where protection of important habitat is needed. Many studies of species-habitat relationships have indirectly linked distributions with areas likely to support high concentrations of prey, however little research has been conducted when prey is less influential. Here, I use resting humpback whales (Megaptera novaeangliae) in Exmouth Gulf (Western Australia) as a model system to investigate the habitat limitations and preferences of generally non-foraging large ocean wildlife, using presence-absence and abundance data. I find that in the absence of a foraging influence, humpback whales still demonstrate habitat preferences, showing an influence of longitude and sea surface temperature variation on distribution patterns that likely reflect the need to minimise energetic expenditures and promote calf growth. The knowledge of spatial habitat use within Exmouth Gulf is of particular significance where new, infrastructure-intensive, coastal and offshore industrial developments have the potential to significantly modify this, and other, shallow embayments. As many animals use specific habitats for non-foraging activities, the need for energy conservation may also drive their habitat associations, as found here for resting humpback whales. Minimising disruption to energy during these vulnerable times will be essential to habitat management and conservation.
Chapter 4. Humpback whale habitat selection during non-foraging periods

4.2 Introduction

Networks of globally representative protected areas are established to preserve biodiversity and maintain ecological processes (Kelleher & Kenchington, 1992; Kelleher, 1996; Myers et al., 2000). However, there is concern that the trend to protect ecologically valuable habitat has adversely impacted the conservation and recovery of threatened species (Dulvy, 2013). Individual species require specific habitats in relation to their resource requirements, which may not reflect broader biodiversity outcomes. Habitats important to threatened species may therefore be left unprotected where efforts focus on representative networks as a mechanism to protect biodiversity and ecosystem function. A refocus to species-specific conservation, based on scientific evidence, is thus necessary to actively support the recovery of threatened species (Baillie & Butcher, 2012).

The ecological relationship between a species and its habitat is fundamental to conservation and management. Understanding species-habitat associations assists in determining which habitat resources are valuable to the species, and where these high value habitats are located. Statistical modelling is commonly used to determine the environmental drivers behind species distribution patterns (Guisan & Zimmermann, 2000; Mac Nally, 2000; Redfern et al., 2006), and so provides quantitative information for identifying specific areas in need of protection e.g. (Hooker et al., 1999; Franco & Sutherland, 2004; Cañadas et al., 2005; Gunnarsson et al., 2006; Nielsen et al., 2006; Embling et al., 2010), and predicts how these areas may alter in space and time as the environment changes (Guisan & Thuiller, 2005). In general, distributions have been indirectly linked with areas likely to support higher concentrations of prey (Livingston et al., 1990; Stirling et al., 1993; Baumgartner, 1997; Gregr & Trites, 2001; Cañadas et al., 2002; Broomhall et al., 2003; Martínez et al., 2003; MacLeod et al., 2008; Skov et al., 2008), suggesting the importance of conserving food resources in habitat management. Currently, there has been little research conducted on the relationship between animal distribution and habitat when prey is not a driving influence. Many species have discrete foraging and non-foraging habitats to accommodate life history patterns such as moulting (e.g. seals), hibernation (e.g. grizzly bears), breeding (e.g. penguins, seals, turtles, and whales), and resting during migration (e.g. birds and whales). Habitat preferences within non-foraging habitats may also be significantly different to foraging habitats. Understanding species-habitat associations during non-foraging periods is therefore vital to improve protection for animals that partition their habitat use in space and time as a function of their behaviours.

The aim of this research is to apply habitat modelling techniques to determine habitat associations of a threatened marine species during non-foraging periods. This study focuses on humpback whales (Megaptera novaeangliae) as a model species, as these whales
repeatedly use the same specific sheltered coastal areas for breeding, calving, nursing, and resting during migration (Dawbin, 1966). In particular, I focus on the recognised resting area of Exmouth Gulf, Western Australia (Chittleborough, 1953; Jenner et al., 2001), an area that is also subject to increasing in industrialisation as a result of an expanding resources industry (mining and offshore oil and gas). I look at distribution patterns and habitat preferences within the Gulf, using both presence-absence (PA) and abundance data as a function of environmental characteristics such as depth, slope, sea surface temperature (SST), and SST variability (SSTv).

4.3 Materials and Methods

4.3.1 Study area

Exmouth Gulf is a coastal embayment located on the Northwest shelf of Australia (Figure 4.1) and is a recognised nursing and resting area for breeding stock D humpback whales during their southern migration (Chittleborough, 1953; Jenner et al., 2001). This embayment is approximately 3400 km\(^2\) in area, with mean and maximum depths of 9 m and 20 m respectively. The tropically located Gulf experiences annual SST ranging from about 17\(^\circ\)C to 30\(^\circ\)C (Kangas et al., 2006). The peak of humpback whale aggregations in Exmouth Gulf coincides annually with a temperature rise, as the winter offshore wind pattern weakens and radiant heating in calm surface waters creates a unique warm water area along this section of the coastline, with an average SST of 22-23\(^\circ\)C (Chittleborough, 1953; Jenner & Jenner, 2005). During October/November, when humpback whale numbers peak, the SST inside Exmouth Gulf can be 2-3\(^\circ\) warmer than surrounding oceanic temperatures.

4.3.2 Surveys

Aerial surveys were carried out in Exmouth Gulf between 7\(^{th}\) July 2004 and 15\(^{th}\) October 2005, using a twin-engine, overhead winged aircraft (Cessna 337) maintaining a cruising speed of 222 km h\(^{-1}\) (120 knots) and an altitude of 305 m (1000 feet). The plane followed a systematic parallel line transect course across the Gulf in passing mode, following distance sampling methods (Buckland et al., 2001) (Figure 4.1). Parallel transects were spaced about 10 km apart to minimise overlap in the flight bands (Hedley et al., 2009; Salgado Kent et al., 2012). For each humpback whale group (pod) sighting, data were collected using a voice recorder by two observers (port and starboard-side) on pod composition (where possible) and pod size (individuals per pod), declination angle and bearing to humpback whales, and
the plane GPS location, which were used to calculate both the position of the pods, and the perpendicular distance of pods from the transect, following the method in Salgado Kent et al. (2012). Sighting conditions were monitored throughout the survey by recording sea state, glare, wind speed, and visibility.

Figure 4.1: A typical course flown by the aircraft during surveys, with the flight path was split into nine parallel transects spaced approximately ten km apart.

4.3.3 Grid cell design

The study area was divided into 86 grid cells with a resolution of 10 km in the latitude direction and 4.25 km in the longitude direction. This grid cell size was chosen based on the distance between horizontal transects (10 km), and the resolution of the coarsest environmental observations (SST; approximately 4 km between observations). Each grid cell was characterised by humpback whale presence/absence and total abundance, environmental variables, and the central position of the cell (latitude and longitude).
4.3.4 Humpback whales

Distance-sampling was used to estimate the actual number of animals in the survey area and reduce error from perception bias (animals missed by the observer) (Buckland et al., 2001; Redfern et al., 2006). Availability bias was not accounted for in this analysis as whale pods resting in the shallow Gulf are highly likely to be at the surface and thus available to be seen (Jenner et al., 2010). The detection function assumes that all animals available to be seen on the transect line were observed. This is unlikely in aerial surveys as the transect line is directly beneath the plane. A standard left truncation of 0.1 km was therefore set to obtain a better detection function fit. As no observations were made within this area, due to the restricted field of view beneath the plane, no data were excluded. To remove extreme values, the sightings data were right-truncated at 5 km either side of the transect line to coincide with the total grid cell width, removing 5% of the data (Buckland et al., 2001). One flight was also removed from the analysis as the sample size was too small (< 20) to obtain reliable results from distance sampling (Table 4.1). Distance 6.0 (Thomas et al., 2009) was used to fit half-normal and hazard-rate detection function models for each of the remaining flights, following the same method as Braithwaite et al. (2012). Covariates that may affect detection probability such as observer, sea state, pod size, and day of flight, were also taken into account when fitting the models. Models for each flight were selected based on the Akaike’s Information Criterion (AIC), Q-Q plots, and the Kolmogorov-Smirnov and Cramer-von Mises goodness-of-fit tests. The most parsimonious model was chosen when two or more models were too similar to make a selection based on the above criteria.

Detection functions for each flight were extracted to R (R Development Core Team, 2009), and used to obtain an estimated abundance in each cell. This was achieved by multiplying the expected number of groups seen per observation by its expected group size (calculated in Distance 6.0). These ‘whales per observation’ estimates were grouped according to grid cell, producing an abundance estimate for each cell in each flight. Grid cell abundances were summed across all flights, along with total transect length, to obtain the overall abundance of whales in each cell with a corresponding measure of effort. The presence or absence of whales in grid cell was also determined.

4.3.5 Environmental variables

The environmental variables correlated with humpback whale data were SST, SSTv, SSTv relative to the yearly mean (SSTv), depth, and slope. The three variables derived for SST allowed us to account for potential interannual variability. I used the Aqua MODIS data archive (Feldman & McClain, 2013) to obtain 8 day average daytime SST data at a 4 km
resolution for each flight. For each grid cell, the mean SST across all flights was calculated from these data to obtain the average spatial SST in the Gulf across both years. As these SST data were at a 4 km resolution, any temperature points less than 2 km outside the grid cell were also used in mean SST calculations. The overall variability in SST (SSTv) across years in each cell was then calculated by subtracting the minimum SST recorded with the maximum. Finally I determined the SST variability relative to the mean SST for that year (SSTrv). The difference between each cell SST for each flight and the mean SST for the corresponding year was calculated, and overall SSTrv in each grid cell was then estimated as the difference between the lowest and highest relative value across both years.

The mean depth for each grid cell was calculated from bathymetry data with 0.0167° resolution, as mapped by Geoscience Australia (Geoscience Australia, 2009). Mean slope for each cell was estimated using a finite differencing method (Burrough et al., 1998). The overall mean slope in each cell was then calculated from the average gradient along parallel grid boundaries on both the latitude \((dlat)\) and longitude \((dlon)\) axis using:

\[
Slope = \tan^{-1} \sqrt{dlat^2 + dlon^2}
\]  

4.3.6 Statistical modelling

Collinearity between predictor variables violates the assumption of independence, resulting in a loss of power in the model and redundancy among the variables (Zuur et al., 2009). I investigated the strength of collinearity among variables by calculating Pearson’s correlation coefficients between all pair-wise combinations of variables, which were then grouped according to the strength of these coefficients. Only one variable from each group was entered into the model to minimise the risk of collinearity.

Generalised additive models (GAM) were used to test the significance of environmental variables on the presence and abundance of whales in Exmouth Gulf. Variations in survey effort and water area between cells were accounted for by including both total survey area (summed over all flights) and water area in each grid cell as a model offset. As model offsets are calculated as a log effect, cells with zero survey effort results in an infinite value. Six cells were therefore removed from the analysis due to having zero survey effort, retaining 80 grid cells for analysis. Overdispersion in the data was accounted for by using a quasi-binomial (logit-link function) error distribution in the PA models, while a negative binomial (log-link function) was used for abundance (Zuur et al., 2009). I used cubic regression spline smooths applied with a shrinkage term (Zuur et al., 2009). Restricted maximum likelihood (REML) was used for the smoothing parameter estimation model, as this method has been shown to
penalise overfit more severely than the standard generalised cross-validation method (Wood, 2011). I limited the effective degrees of freedom by setting the maximum number of knots for each parameter to four in the negative binomial model (abundance), and three in the binomial models (PA), following the general recommendation of Keele (2008) based on sample size. Models were fit using ‘MGCV’ package (Wood, 2012) in the R statistical package (R Development Core Team, 2009).

The probability outputs of the PA model were transformed to a binary presence/absence value based on a probability threshold. As PA modelling is sensitive to prevalence, the relative proportion of presence and absence in the sample (Jiménez-Valverde & Lobo, 2006), I calculated the threshold value based on the prevalence in the grid area (Liu et al., 2005).

4.3.7 Autocorrelation, model evaluation and bootstrap

Spatial structure can arise from either external forcing (induced spatial dependence) or from the internal processes of the population (spatial autocorrelation) (Borcard et al., 2011). Here, I was interested in the external environmental forcing on spatial structure. Semivariograms of the model residuals, generated using the ‘geoR’ package for R (Ribeiro & Diggle, 2001), were used to evaluate the degree of spatial autocorrelation in the distribution of whales.

Presence-absence model performance was evaluated based on the precision (ratio of true positives to actual positives) and the Kappa value, which calculates the proportion of true presence after accounting for the probability of change agreement (Liu et al., 2005). The performance of the abundance model was evaluated using Pearson’s correlation coefficient and linear regression (Potts & Elith, 2006) in order to quantify the similarity of observed and predicted values.

I used a non-parametric bootstrap to estimate model precision in each grid cell for both the PA and abundance models. Linear regressions of abundance across time (flights) for each cell did not produce any significant temporal relationships of abundance changes in time, and therefore flight was used as the independent sampling unit for the bootstrap. The bootstrap was run for 1000 iterations to produce a coefficient of variation (CV) for each model output in each cell.
Chapter 4. Humpback whale habitat selection during non-foraging periods

4.4 Results

Humpback whale pods were observed on ten flights over 2004-2005 within Exmouth Gulf. One flight that sighted humpback whales was excluded in the distance sampling analysis as it had too few observations to obtain accurate estimates (Table 4.1). Based on the distance sampling analysis, a total of 1822 whales over the nine flights were predicted to be in the Gulf.

Correlations existed among environmental variables. Depth, SST, SSTv, and SSTrv showed strong (>|0.7|) or weak (|0.3| - |0.7|) associations among themselves and were thus placed in a single group. Longitude and slope showed no correlations with these variables or each other and thus were considered independently (Table 4.2). Latitude covaried with all other variables and thus was only used in the model without any of the other variables.

Table 4.1: A summary of the aerial surveys carried out during the 2004 and 2005 humpback whale season (August - November) in Exmouth Gulf. The selected detection function (Det. Func.) for the survey was either a half-normal (HN) or hazard (HZ) function, with two surveys needing an additional covariate of either observer (Obs) or pod size (Pod). The abundance was estimated using this detection function and the 95% lower and upper confidence intervals (CI) were calculated using a bootstrap.

<table>
<thead>
<tr>
<th>Aerial Survey</th>
<th>Flight Date</th>
<th>Whales</th>
<th>Calves</th>
<th>Det. Func.</th>
<th>Abundance</th>
<th>Lower CI</th>
<th>Upper CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7th Oct 04</td>
<td>135</td>
<td>29</td>
<td>HN (Obs)</td>
<td>409</td>
<td>232</td>
<td>598</td>
</tr>
<tr>
<td>2</td>
<td>14th Oct 04</td>
<td>97</td>
<td>16</td>
<td>HZ</td>
<td>144</td>
<td>73</td>
<td>250</td>
</tr>
<tr>
<td>3</td>
<td>26th Oct 04</td>
<td>62</td>
<td>12</td>
<td>HZ</td>
<td>71</td>
<td>30</td>
<td>116</td>
</tr>
<tr>
<td>4*</td>
<td>2nd Nov 04</td>
<td>26</td>
<td>6</td>
<td>HN</td>
<td>44</td>
<td>22</td>
<td>70</td>
</tr>
<tr>
<td>5</td>
<td>7th Aug 05</td>
<td>7</td>
<td>0</td>
<td>HN</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>6</td>
<td>21st Aug 05</td>
<td>35</td>
<td>2</td>
<td>HN</td>
<td>138</td>
<td>54</td>
<td>235</td>
</tr>
<tr>
<td>7</td>
<td>4th Sep 05</td>
<td>79</td>
<td>4</td>
<td>HN</td>
<td>248</td>
<td>127</td>
<td>411</td>
</tr>
<tr>
<td>8</td>
<td>10th Sep 05</td>
<td>41</td>
<td>3</td>
<td>HN</td>
<td>84</td>
<td>43</td>
<td>126</td>
</tr>
<tr>
<td>9</td>
<td>25th Sep 05</td>
<td>126</td>
<td>17</td>
<td>HN (Pod)</td>
<td>459</td>
<td>250</td>
<td>816</td>
</tr>
<tr>
<td>10</td>
<td>15th Oct 05</td>
<td>95</td>
<td>13</td>
<td>HN</td>
<td>279</td>
<td>167</td>
<td>413</td>
</tr>
</tbody>
</table>

* Seven other surveys, flown on 18th Feb, 7th Mar, 3rd Apr, 26th Apr, 22nd May, 12th Jun, and 12th Jul 2005, no humpback whales were observed.
* The abundance was not calculated for flight 5, as the sample size was too small (<20) to obtain reliable results from distance sampling.
TABLE 4.2: Correlations between environmental variables, measured using Pearson’s r coefficients. Values in bold indicate correlations > |0.30|. Numbers after the variable names indicate group membership for modelling.

<table>
<thead>
<tr>
<th></th>
<th>Lat (1)</th>
<th>Lon (2)</th>
<th>Depth (3)</th>
<th>SST (3)</th>
<th>SSTv (3)</th>
<th>SSTrv (3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope (4)</td>
<td>0.36</td>
<td>0.09</td>
<td>0.11</td>
<td>0.23</td>
<td>-0.25</td>
<td>-0.2</td>
</tr>
<tr>
<td>SSTv (3)</td>
<td>-0.79</td>
<td>0.08</td>
<td>-0.77</td>
<td>0.87</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>SSTv (3)</td>
<td>-0.80</td>
<td>0.11</td>
<td>-0.76</td>
<td>0.87</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SST (3)</td>
<td>0.66</td>
<td>-0.24</td>
<td></td>
<td>0.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth (3)</td>
<td>0.72</td>
<td>0.21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lon (2)</td>
<td>0.43</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**FIGURE 4.2:** GAM models for A. longitude and B. SSTrv, fitted to the presence-absence data, and C. longitude and D. SSTrv fitted to the abundance data. Each smooth was constrained to a maximum of three knots in A and B, and four knots in C and D to avoid overfitting.
4.4.1 Presence-absence

The best model to predict the PA of whales in Exmouth Gulf included the variables longitude and SSTv (deviance explained = 61%; Table 4.3). The probability of a presence decreased with increasing longitude (towards the east) and with increasing SSTv after a value of approximately $3^\circ$ is reached (Figure 4.2). Prevalence was calculated as 0.73, and used as the threshold value to convert the probabilities to presence or absence. The model gave a precision and Kappa value of 0.91 and 0.73 respectively, indicating a strong agreement between observed and predicted presence even when random chance is taken into account. The model captured the presence of humpback whales in the west side of the Gulf, but underestimated their presence in the south and east areas (Figure 4.3).

4.4.2 Abundance

Similar to the PA model, abundance was best predicted by longitude and SSTv (deviance explained = 63%; Table 4.3), with abundance decreasing with increasing latitude, and remaining constant with increasing SSTv until a value of about $4^\circ$ was reached, after which abundance decreased sharply (Figure 4.2). There was a relatively strong correlation between observed and predicted abundances ($r = 0.72; p < 0.001$), however, the linear regression between the observed and predicted values indicated that the model overestimated low

### Table 4.3: The performance of habitat models tested. The model in bold was considered to be the best model based on the deviance explained (Dev) and REML score

<table>
<thead>
<tr>
<th>Model</th>
<th>Dev</th>
<th>REML</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SSTv*</td>
<td>0.51</td>
<td>292</td>
</tr>
<tr>
<td>Depth*</td>
<td>0.42</td>
<td>300</td>
</tr>
<tr>
<td>SST</td>
<td>0.22</td>
<td>305</td>
</tr>
<tr>
<td>Lat*</td>
<td>0.20</td>
<td>309</td>
</tr>
<tr>
<td>SSTv*</td>
<td>0.63</td>
<td>17</td>
</tr>
<tr>
<td>Depth*</td>
<td>0.54</td>
<td>25</td>
</tr>
<tr>
<td>SST^</td>
<td>0.29</td>
<td>39</td>
</tr>
<tr>
<td>Lat^</td>
<td>0.11</td>
<td>46</td>
</tr>
</tbody>
</table>

Significance is indicated by: *0.001 + 0.01 ^0.05
abundances and underestimated high abundances (Figure 4.4) Nevertheless, the spatial predictions (Figure 4.3D) effectively captured the area of relatively high abundance of whales towards the west side of the Gulf in the mid-latitude range (Figure 4.3C).

No spatial autocorrelation was present in the PA or abundance models. The bootstrap analysis indicated the spatial variation in model performance by estimating the CV for each grid cell, indicating larger CV values around the edges of the Gulf, particularly along the southern coastline, suggesting relatively poor model performance along the edges (Figure 4.5).

The spatial variability of SSTv indicated that temperature in the north west area varied a small amount across survey flights (< 2°C variation), while the southern and eastern edge varied the most in SSTv (> 2°C variation; Figure 4.6).

**Figure 4.3**: The A. observed and B. predicted presence or absence of humpback whales in Exmouth Gulf. White cells denote the presence of a whale, while black cells indicate their absence. The C. observed and D. predicted abundance of humpback whales in Exmouth Gulf.
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**Figure 4.4:** Predicted vs. observed numbers of whales by grid cell, fitted with a linear regression (solid line; Predicted = 10.61 + 0.57 × observed). The dotted line indicates the 1:1 relationship. The correlation coefficient between predicted and observed abundances was 0.72 (p < 0.001).

**Figure 4.5:** The coefficient of variation (CV) for each grid cell for both the A. presence-absence and B. abundance models, calculated using a non-parametric bootstrap with 1000 iterations.
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**Figure 4.6**: The relative sea surface temperature variability (SSTrv, in °C) in each grid cell across survey flights. SSTrv is calculated from the differences in flight SSTs to the mean SST of the corresponding year.

### 4.5 Discussion

Non-foraging humpback whales have predictable habitat preferences while resting in Exmouth Gulf. The PA and abundance models captured the clustering of whales within the Gulf, and in both cases showed the influences of longitude and SSTrv when predicting spatial habitat use. These models of habitat preference indicate the western area of the Gulf is high value habitat for resting humpback whales. While the best model for predicting spatial habitat use included longitude and SSTrv, the high collinearity between the model variables depth, SST, SSTv, and SSTrv, means any (or all) could be the environmental driver of humpback whale habitat preference within the Gulf, alongside longitude. Before habitat associations can be established, the ecological significance of each covarying variable therefore needs to be considered, in the context of resting whale needs, to understand the probable drivers of habitat relationships.

Longitude was the most important habitat variable, predicting a high presence and abundance of humpback whales towards the western side of the Gulf. There is a contrast of
environmental and hydrodynamic conditions between the west and east side of the Gulf, associated mainly with wind and tide. First, water on the western side is in the lee of North West Cape, with respect to the prevalent south-westerly winds, and therefore tends to stay calm and flat for the longest periods each day (Jenner, KCS pers. obs.), creating less energetically demanding conditions for resting whales. Second, the water movements in Exmouth Gulf are largely driven by tides (Massel & Brinkman, 1996) and tidal currents in and out of the Gulf are strongest near the Cape, on the north west tip of the Gulf (Verspecht, 2002). Humpback whales on the western side can thus ride the strong ebb tide when they choose to leave the Gulf, further conserving energy. The association with longitude is therefore likely driven by a preference for the less energetically demanding conditions in the western side of the Gulf.

The best predictive model for humpback whale distribution included SSTrv, with a high presence and abundance found in the seasonally consistently warmer waters of the north west area of the Gulf. However, individual whales only stay within the Gulf for approximately two weeks (Jenner, KCS unpubl. data based on photo-ID resights and satellite tags), and would not experience the full variation in temperatures across the season. The seasonally stability of temperature, as expressed in the model, is therefore unlikely to be detected by individual whales. However, as calf growth and development is promoted by warmer waters (Rasmussen et al., 2007), and resting areas are primarily important for female humpback whales with newly born calves (McCauley et al., 2000; Braithwaite et al., 2012), the model may reflect a general preference for warmer, calm waters, which are consistently found in the north west area.

The inclusion of depth also produced a significant model for predicting PA and abundance of whales in the Gulf, indicating a preference for deeper waters. Adult humpback whales have a mean length of 13-14 m (Clapham, 2000) and a “draft” of 3-4 m (Jenner, KCS pers. obs.), which places a physical limitation on the minimum depth they can inhabit, excluding them from shallower waters. Water depth is also a factor in humpback mating patterns, where males court females through complex songs (Tyack, 1981), generally singing in depths greater than 10 m (Frankel et al., 1995; Mercado & Frazer, 1999; Mercado et al., 2007). Singing is likely to be occurring in Exmouth Gulf, as whale are known to sing during the first half of the southbound migration (Clapham & Mattila, 1990).

Understanding species habitat associations and their drivers can be difficult, particularly when many of the environmental variables are collinear. Here, several ambient conditions may be influencing humpback whale distribution patterns in Exmouth Gulf including warmer waters, sheltered conditions, tidal influences, and deeper waters. Fundamentally, many of these variables are linked with energy conservation and calf development: warm conditions
promote calf growth, while the less energetically demanding environment allows calves to allocate energy intake towards growth rather than to fuel activity, and tidal influences may serve to reduce energy expenditure upon leaving the Gulf. This link to energy is consistent with findings for breeding humpback whales in the West Indies (Whitehead & Moore, 1982) and Ecuador (Felix & Botero-Acosta, 2011), where females with calves in particular frequented calmer, more sheltered environments. These low energetic conditions are advantageous to calf growth, as a greater amount of energy can be allocated towards growth rather than being expended through swimming (Whitehead & Moore, 1982; Felix & Botero-Acosta, 2011). Other animals have also demonstrated a preference towards energy conserving habitat during periods of low-food availability, such as polar bears (Derocher & Stirling, 1990) and river-spawning fish species (McElroy et al., 2012). I therefore suggest that energy conservation can be an important driver to habitat selection during non-foraging periods.

The importance of protecting foraging habitat for threatened species is intuitive, as all animals require adequate sustenance to survive. However, this study demonstrates that non-foraging habitats can also hold value to a population. I speculate that habitat preferences of resting humpback whales are linked with conserving energy, and thus with promoting calf growth. Extending conservation to these resting areas, and protection against energetically costly disturbances, would therefore benefit population recovery. As many species use specific habitat for non-foraging activities, knowledge of habitat preferences during these times is an important consideration for their effective conservation of these species.

4.6 Acknowledgements

I would like to thank Straits Resources who funded the aerial surveys, and Micheline Jenner and Emily Wilson who assisted with data collection. JE Braithwaite also thanks the University of Western Australia for providing a PhD scholarship.
Chapter 5

From sea ice to blubber: linking whale condition to krill abundance using historical whaling records

5.1 Abstract

Krill (*Euphausia superba*) are fundamentally important in the Southern Ocean ecosystem, forming a critical foodweb link between primary producers and top predators. Krill abundance fluctuates with oceanographic conditions, most notably variation in winter sea ice, and is susceptible to environmental change. Although links between local krill availability and performance of land breeding, central place foragers are recognised, the effects of krill variability on migratory top predators such as baleen whales remain largely unclear because concurrent long-term data on whale condition and krill abundance do not exist. Here, I quantify links between whale body condition and krill abundance using a simple model that links krill abundance to sea ice extent. Body condition of humpback whales (*Megaptera novaeangliae*) caught in west Australian waters between 1947 and 1963 was estimated from oil yields in whaling records. Annual estimates of krill abundance in the Southern Ocean where these whales forage (70°-130°E) was correlated ($R^2 = 0.34$, $p = 0.0066$) to contemporary annual winter sea ice extent. I hindcast sea ice extent for the whaling period from temperature, and from that estimated historic krill abundance. Whale body condition was significantly correlated to hindcasted winter sea ice extent ($R^2 = 0.38$, $p = 0.008$), supporting the hypothesis that variations in body condition are likely mediated by associated krill fluctuations. As humpback whales migrate and breed on finite energy stores
gained during summer foraging in the Antarctic, changes in sea ice have long-term implications for their condition and reproductive success.

5.2 Introduction

Antarctic krill (*Euphausia superba*) is a functionally vital species in the Southern Ocean, feeding directly on primary producers and providing food for large numbers of top predators. Annual fluctuations in regional krill abundance have been linked to natural variation in sea ice dynamics, indicating that the krill-centric ecosystem is vulnerable to potential climate-driven ice loss (Chittleborough, 1965; Atkinson *et al.*, 2004; Nicol, 2006). Good evidence exists that, on local scales, reproductive success of central place foragers such as penguins, seals, and seabirds (Croxall *et al.*, 1999; Reid *et al.*, 2005; Atkinson *et al.*, 2008) is influenced by fluctuations in krill abundance. However, it remains unclear how variability in krill abundance affects baleen whales, which are migratory top predators, because analyses require long-term data on the condition of whales alongside concurrent data on krill abundance (Atkinson *et al.*, 2008; Nicol *et al.*, 2008). The few studies that have been conducted on fin whales (*Balaenoptera physalus*) in the North Atlantic indicate an association between prey availability and body condition, with repercussions to fecundity and reproduction (Lockyer, 1986; Williams *et al.*, 2013).

Historical whaling records provide a valuable long-term dataset, detailing the number and species of whales caught and, in many cases, the individual lengths and total oil yield. Since the amount of oil extracted from a whale depends on its blubber (fat) content, oil yield may provide an indicator of body condition and the variability therein throughout the historic whaling era (1900 - 1963). However, data on krill abundance during that era are scarce, making direct comparisons between food availability and whale condition difficult.

Associations between krill abundance and sea ice extent and duration have been observed in the Southern Ocean on a range of scales (Siegel & Loeb, 1995; Loeb *et al.*, 1997; Nicol *et al.*, 2000; Brierley *et al.*, 2002; Atkinson *et al.*, 2004) from local to sectoral. While the exact mechanisms behind the krill-sea ice relationship are still unclear to some degree (Fraser *et al.*, 1992; Loeb *et al.*, 1997; Nicol, 2006), it is generally understood that sea ice extent and duration influence krill recruitment because ice provides a feeding habitat and nursery ground for krill (Siegel & Loeb, 1995; Loeb *et al.*, 1997). Around the Antarctic Peninsula, elevated krill recruitment is evident following years of heavy ice conditions (Hewitt, 2003; Atkinson *et al.*, 2004).
Associations between krill and sea ice provide an avenue to explore the possible link between whale condition and food availability. Using contemporary krill and sea ice data (1979-2007), I investigate a temporal relationship between krill abundance and sea ice extent (SIE). I estimate humpback whale (*Megaptera novaeangliae*) body condition from historic whaling records, and relate this to hindcast SIE, in order to link whale condition to changing ice conditions via impacts on their food source, krill.

### 5.3 Materials and Methods

#### 5.3.1 Humpback whale body condition

I obtained data from the International Whaling Commission (IWC) on total oil yield (tons) per whaling expedition, and individual whales (identified to species, and length measured (m)) for all southern hemisphere whaling stations. Data were filtered to compile a summary detailing which stations landed humpback whales, the total number of expeditions (returning voyages landing whales) per station per year, and the number of these with corresponding oil yields (75% of expeditions had oil yield data), and a high percentage of humpback whales (> 90%) so that error from estimating humpback whale oil yield from multispecies catches were minimised. I restricted the analyses to post-WWII data only (from 1947 onwards) because of the technological advancements during the war that likely augmented whaling and oil extraction efficiencies (Tønnessen & Johnsen, 1982). Changes in efficiencies after 1947 are difficult to determine, so I assumed they remained constant. This study focused on the 'Australia west' (AusW; 35 expeditions) and 'Australia east' (AusE; 20 expeditions) landing regions, as they comprised 75% of the total southern hemisphere humpback whale catch between 1947 and 1963.

Individual length records for all whales were converted to weight (tons) using species-specific conversion scaling coefficients (Lockyer, 1976). In a very small number of expeditions (4 expeditions of 35 for AusW, and 1 expedition of 18 for AusE) the number of lengths reported was less than the number of humpback whales recorded in the summary, meaning that the total weight calculated from the length data would be underestimated. To adjust for this difference I approximated the weight for the missing whale records as the average for that expedition. Since the number of records missing was very small (9 records of 14,383 for AusW, and 26 of 6,720 for AusE), any error introduced by assuming average values for these records is likely negligible.

Individual whale weights were then summed by expedition to obtain the total weight of whales caught per species per expedition. Total oil yield per expedition included oil from all
baleen whales, with sperm whale oil recorded separately. Catches were comprised exclusively of humpback whales on 86% of expeditions. For multispecies expeditions, the humpback whale oil yield was estimated as the ratio of the weight of humpbacks to all baleen species. For example, if the weight ratio between humpback whales and all other baleen species for a particular expedition was 99:1, then humpback whale oil yield was estimated to be 99% of the total oil yield. Since other baleen species represented less than 2% of the total weight per expedition, significant error was unlikely, despite the likely interspecific variation in oil yields per unit body weight (Lockyer, 1981). The resulting humpback whale oil yields and total weights were summed by year to obtain annual estimates of weight and oil yields attributed to humpback whales.

Several variables have been found to influence the blubber content of baleen whales, including weight, sex, reproductive condition (e.g. pregnant or lactating), age (e.g. mature or immature), and time of year of catch (Chittleborough, 1965), and may contribute to the annual variability of oil yield. Sex composition was assessed as a ratio of males to females in the total catch for each year in each region (west and east Australia). Where sex was not recorded, or recorded as hermaphrodite, a sex composition of 0.5 was assigned (equally male or female). Reproductive condition was calculated as the proportion of pregnant or lactating whales in the total catch for each year in each region. Age was discounted as a variable in the analysis, as only one immature whale was reported killed in the west and east Australian catch regions. The remaining whales were reported as mature or unknown. I assumed unknown aged whales to be mature given the minimum legal length requirement of 35 feet (10.6 m) (Chittleborough, 1965). Time of year of catch was calculated as the mean Julian day of whales caught in each year for each region.

A multiple regression was fit between mean oil yield per humpback whale per year, and catch variables (mean weight, sex ratio, reproductive condition, and mean Julian day) per year in each region. Mean weight was the only significant factor influencing yearly oil yield ($p = 0.0047, n = 28$), so the remaining variables were excluded from the model (sex $p = 0.87$; reproductive condition $p = 0.80$; Julian day $p = 0.24$). The residuals from this oil to weight relationship were used as an indicator of relative humpback whale body condition for a given year: positive residuals indicate years with more ‘fat’ whales (having higher blubber content), while negative residuals indicate years with ‘thinner’ whales. Residuals were converted to a percentage to control for body size: a +1 ton residual for a small whale with a standard yield of, for example, 5 tons equates to a +20% body condition indicator whereas it equates to +12.5% for a larger whale with a standard yield of, for example, 8 tons.
Krill abundance data in the Southern Ocean coinciding with the whaling era (pre-1963) are scarce, making direct associations between body condition and food availability difficult to investigate. Krill abundance is however influenced by sea ice extent (SIE). The relationship between krill abundance and SIE was established for years post-1979 using standardised krill density measurements obtained from KRILLBASE (Atkinson et al., 2008). KRILLBASE is a compilation of data from krill surveys conducted in the Southern Ocean between 1926 and 2003, that has been standardised to account for differences in sampling techniques and catchability (Atkinson et al., 2008). KRILLBASE therefore provides a uniquely large dataset for the exploration of large-scale spatial and temporal trends, and is the only database of krill densities available that spans several years across the east Antarctic region. Data were split into 10° sectors around the Southern Ocean. The annual mean krill densities (no.m⁻²) over the austral spring to autumn seasons (between October of previous year and April of the present year) across each of the 10° sectors comprising the foraging zones (AusW: 70°-130°E, AusE: 130°E-170°W (Donovan, 1991)) were calculated. Sectors with fewer than five observations were removed from the analysis to reduce potential error from under-sampling. The total number of krill density samples, mean latitude and longitude of sampling sites, mean net depth, mean Julian day, and mean day or night measurement, were also determined for each sector across each year to test for sampling biases. Entries in the database were already categorised as occurring at day or night, and designated as a one (day) or zero (night). The mean of these day or night values was therefore used as an indicator of whether sectoral means of krill densities were skewed towards day sampling or night sampling.

In the AusE foraging region, there were a total of 16 sector measurements for mean krill density value post-1979, with 65% (9 of 16 sectors) of these values recorded as zero. I therefore eliminated the AusE region from further analysis, as the zero-inflated, low sample size data were insufficient for robust analysis. In the AusW foraging region, there were 20 sector measurements with no values recorded as zero.

For each sector in the AusW foraging region, I calculated the mean maximum winter SIE, between 1979 and 2007 (Raymond, 2009), and sea ice duration between 1979 and 2008. To calculate sea ice duration, daily sea ice concentration data were obtained from the National Snow and Ice Data Centre (NSIDC) (Cavalieri et al., 1996) that provides data from October 1978 at a spatial resolution of 25 x 25 km grid cell. Cells with more than 15% of ocean area covered by sea ice were, by convention, classified as ‘ice-covered’, a threshold used by the NSIDC (e.g. Stroeve et al., 2007). The total area of ice-covered cells for each 10° sector in the 70°-130°E region was calculated, resulting in a time series of sea ice advance and retreat in
each sector. The trend of ice advance/retreat for each day was calculated as the gradient of ice area change over seven days, i.e. including three days before and after each day. By taking this seven-day gradient, irregular daily fluctuations could be eliminated and a general trend in ice growth and decay obtained. Sea ice duration is the time between when the ice starts advancing to when it stops retreating. I defined the start of ice advance as the point at which the gradient of change was consecutively positive for at least five days, signalling the continual growth of ice (Massom et al., 2013). Likewise, the end of the sea ice retreat was defined as the last point in which the gradient was consecutively negative for five days, signalling the end of continual retreat. Sea ice duration was thus the number of days between the start of sea ice advance and the end of sea ice retreat.

Interannual variability in krill density in the AusW foraging region (n = 20 sectors) was explored in a multiple linear regression framework with respect to winter SIE and duration from the previous year. Sampling variables (total number of krill density samples, mean latitude and longitude of samples, mean net depth, mean Julian day, and mean day or night measurement) were also included in the multiple linear regression to test for sampling bias.

### 5.3.3 Body condition vs. sea ice extent

Empirical SIE data do not exist for the whaling period, between 1947 and 1963. Historical sea ice edge locations have been estimated through direct observations and the use of whaling records (de la Mare, 2008). However, whaling data are limited to October through April, excluding winter months, during which whaling in the Southern Ocean ceased. As krill abundance variation is thought principally to be connected with winter sea ice dynamics (e.g. Loeb et al., 1997; Atkinson et al., 2004), these summer-only whaling-derived ice edge data were not appropriate for this analysis. Instead, I hindcast winter SIE from sea surface temperature (SST) data, as SIE has been found to be significantly correlated with temperature (Fraser et al., 1992; Loeb et al., 1997). I split the Southern Ocean into 10° sectors to correspond with the krill data, and regressed mean maximum winter SIE across longitudes between 1979 and 2007 for each sector on mean winter (June-August) sea surface temperature for the Southern Ocean region (south of 60°S) using historic SST data reconstructed by the National Oceanic and Atmospheric Administration (NOAA, 2007). This relationship enabled us to hindcast winter SIE in each 10° sector of the AusW foraging region to obtain yearly mean winter SIE for each sector. To assess the accuracy of the hindcast SIE data, I compared them to historic sea ice edge positions derived from direct observations and whaling records (de la Mare, 2008). I calculated the mean ice edge latitude across the west Australian whale foraging area (70°-130°E) for each available season (October-April), as

The relationship between whale body condition and krill abundance for the AusW foraging region during the whaling era for which oil data were available (1947-1963) was explored using the hindcasted winter SIE as a surrogate for krill density. This analysis assumes west Australian humpback whales largely forage in the 70-130°E area. Whilst a small level of interchange has been found between east and west Australian humpback whale populations (Chittleborough, 1965; Dawbin, 1966; Noad et al., 2000), current evidence suggests a relatively low presence of west Australian whales in the neighbouring east Australian foraging region (130°E-170°W) (Constantine et al., 2014). As sea ice provides an overwintering habitat for krill, there could be a lag between winter SIE and krill abundance, under the hypothesis that recruitment may largely occur over winter. I therefore regressed body condition against winter SIE of the previous year and 2, 3, and 4 year running means of previous winter SIE to investigate possible cumulative effects of sequential high or low food availability.

5.4 Results

Mean oil extracted per whale was significantly (p = 0.005) correlated to the mean weight of humpback whales caught off Australia, with larger whales providing higher oil yields (Figure 5.1; $R^2 = 0.27, p = 0.005$). Residuals indicate that mean oil yield per whale ranged from -50% to 20% of expected yield.

In the west Australian humpback whale foraging region, the annual mean density of krill (no.m$^{-2}$) was correlated significantly with the maximum recorded winter SIE of the previous year (Figure 5.2A; $R^2 = 0.34, p = 0.0066$). Longitude and day or night sampling also influenced krill density, however the influence of these variables was much weaker than SIE (Longitude: $R^2 = 0.25, p = 0.02$; Day or night: $R^2 = 0.20, p = 0.50$), and there were no improvements over the SIE model with the addition of these variables.

Humpback whale body condition in west Australia was significantly correlated with hindcast winter SIE in their Southern Ocean foraging area (70°-130°E), with higher oil yields in years with greater winter SIE in previous years ($R^2 = 0.25, p = 0.04$). The relationship was strongest when considering winter SIE averaged over the previous three years (Figure 5.2C; $R^2 = 0.38, p = 0.008$).
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Figure 5.1: Mean oil per whale for each catch year increased with mean weight per whale ($R^2 = 0.27$, $F_{1,26} = 9.59$, $p = 0.005$, $n = 28$), across both west (solid circle) and east (open circle) Australian regions. The dashed lines represent the 95% confidence intervals.

There was a significant positive correlation between the mean hindcast winter SIE from this analysis, and the mean ice-edge latitude of the preceding spring-autumn season derived by de la Mare (2008) from historic whaling records across $70^\circ$-130$^\circ$E (Figure 5.3; $R^2=0.29$, $p < 0.0001$), so that a reduced sea ice retreat during summer is followed by a greater maximum sea ice extent in winter across this region. The fluctuation in sea ice, as captured by the hindcast winter SIE data, therefore corresponds well to other estimates of sea ice conditions in the west Australian humpback whale foraging area for seasons spanning between 1931/32 to 1986/87.

Temperature is a reliable predictor of winter sea ice extent (Figure 5.2B), and krill abundance is predicted well by winter sea ice extent. It is therefore robust to make inferences about variability in whale condition as driven by availability of their main food, krill, using sea ice as a proxy for krill abundance.
Figure 5.2: A. Significant relationship between krill abundance in the 70°-130°E Southern Ocean sector and regional winter sea ice extent (SIE) of the previous year ($R^2 = 0.34, F_{1,18} = 9.41, p = 0.0066, n = 20$, spanning 1981-1996, totalling 611 station measurements). B. Highly significant relationship between winter SIE and winter sea surface temperature (June-August) ($R^2 = 0.45, F_{1,27} = 21.8, p < 0.0001, n = 29$, data between 1979 and 2007). C. Highly significant relationship between body condition of whales killed in AusW and the three year running mean of winter SIE in their foraging region over the previous year ($R^2 = 0.38, F_{1,15} = 3.21, p = 0.008, n = 17$). Solid circles denote present-day SIE measurements (A and B), open circles represent hindcast SIE values (C). Dashed lines represent the 95% confidence intervals.
Figure 5.3: Significant relationship between mean hindcast maximum winter sea ice extent (SIE) and mean approximate ice edge latitude of the previous spring to autumn season ($R^2 = 0.29$, $F_{1,35} = 14.14$, $p < 0.0001$, $n = 37$), across the west Australian humpback whale foraging area ($70^\circ$-$130^\circ$ E). Dashed lines represent the 95% confidence intervals.

Figure 5.4: A schematic illustrating the temporal availability of data. Arrows show the relationships investigated with corresponding linear regression p-values.
5.5 Discussion

Humpback body condition for whales caught in the west Australian region was significantly correlated with hindcast winter SIE in their Southern Ocean foraging area, suggesting that changing environmental conditions in their foraging area can impact body condition. Within this same foraging area, krill abundance was significantly correlated with observed winter SIE. I therefore propose that the correlation between whale condition and SIE is mediated by fluctuations in abundance of the whales’ key food, krill. This temporal relationship between krill abundance and sea ice, although based on smaller samples sizes, is consistent with the large-scale link between SIE and krill abundance exposed for the Atlantic region using KRILLBASE (Atkinson et al., 2004). The krill-SIE relationship is also consistent with the concept that sea ice and associated biota provide a source of food and nursery habitat for krill (Nicol et al., 2000; O’Brien et al., 2011), as spatially evident at a broader scale in the west Australian whale foraging region, where krill are more abundant in regions of greater ice cover (Nicol et al., 2000).

Our model linking whale body condition to krill abundance, via sea ice, illustrates the influence of large-scale environmental fluctuations on the annual condition of humpback whales. I recognise that factors additional to those considered here may contribute to variability in the body condition of humpback whales. For example, sizeable reductions to baleen whale numbers during the whaling era would potentially change the level of inter- and intra-specific food competition over time, influencing per capita prey intake: the fewer whales present at the end of the whaling era may have had more krill per capita than whales present prior to exploitation. Whilst changes to intraspecific competition during the study period (1947-1963) may factor into determining average body condition, the relevance of interspecific competition is debatable, as competition between foraging baleen whale species is thought to be unlikely (Clapham & Brownell, 1996; Friedlaender et al., 2006). The incorporation of ecosystem considerations would benefit understanding of those factors contributing to changes in whale body condition, however this simple model of trophic links isolates and quantifies the significant link between body condition, krill, and sea ice for humpback whales, and provides a basis for further development.

This research suggests that in the Southern Ocean foraging grounds of humpback whales that breed off western Australia (70°-130°E), krill abundance fluctuates with ice extent, as has been demonstrated for other Southern Ocean regions (Nicol et al., 2000; Atkinson et al., 2004). While there is a level of uncertainty in these findings, due to limitations in the data available for this large-scale trophic analysis, based on the best evidence available, this study indicates a correlative link between humpback whale condition and krill abundance. Whilst it is not surprising that the condition of a predator is linked to abundance of its prey, quantification
of this link enables predictions to be made and scenarios explored. If ice extent declines in the future, as predicted under some climate change scenarios, whale food will decline and, in turn, energy acquisition will be hindered. After a sequence of reduced ice / low food years, whales will be migrating and breeding on reduced energy input, potentially impacting their ability to successfully complete the breeding cycle. If winter SIE in the west Australian foraging region declines in response to a changing climate, we may see future deterioration in whale body condition, fitness, and ultimately, reproductive success.

5.6 Acknowledgements

I thank the numerous contributors to the KRILLBASE database and to Angus Atkinson, Volker Siegel, and Evgeny Pakhomov for making these data available to us, via the ICED website. I also thank Cherry Allison at the International Whaling Commission for providing the historical whaling database, and Jan Erik Ringstad and Dag Ingemar Bårresen at the Whaling Museum, Norway, for insight into whaling history and culture. JE Braithwaite also thanks the University of Western Australia for providing a PhD scholarship.
Chapter 6

Optimal migration energetics of humpback whales and the implications of disturbance

6.1 Abstract

Whales migrate large distances and reproduce on a finite store of energy. Budgeting the use of this limited energy reserve is an important factor to ensure survival over the migration route and to maximise reproductive investment. Migration routes are closely associated with coastal areas, exposing whales to high levels of human activity. It is currently unclear how disturbance to whales during migration can impact their energy balance, and how this might translate to long-term demographic changes. Here, I develop a theoretical bioenergetic model for migrating humpback whales to investigate the optimal migration strategy in minimising energy use. Average velocity was an important factor in energy use, and the optimal velocity predicted of $1.1 \text{ m s}^{-1}$ was comparable to documented observed migration speeds, suggesting whales migrate at a speed that conserves energy. Furthermore, the amount of resting time during migration was influenced by both transport costs and feeding rates. I simulated disturbance to optimal migration strategy in two ways, by altering average velocity to represent changes in behavioural activity, and by increasing total travelled distance to represent displacement along the migration route. In both cases, disturbance increased overall energy use, with implications for the growth rates of calves.
6.2 Introduction

All animals require energy to sustain life. Energy consumed from the environment is used to maintain basic functioning, support daily activities, and to reproduce. Maximising the efficiency of energy intake and subsequent use drives foraging patterns (Perry & Pianka, 1997), life history traits such as breeding strategy (Gadgil & Bossert, 1970) and hibernation (Nedergaard & Cannon, 1990; French, 1992), and natural selection (Lotka, 1922). Fundamentally, the survival and reproductive success of a population requires sufficient energy intake and efficient energy use. Any natural or human-induced disruptions to these processes, such as a reduction in food availability or increase in energy demands, will have long-term implications for population survival and growth. The energetic repercussions of human disturbance therefore provide an important consideration to conservation management (Cooke et al., 2012, 2013), though it has largely been unexplored as a management tool for humpback whales (Megaptera novaeangliae) whose migration routes can be disturbed by coastal developments.

Organisms allocate energy to processes such as basal metabolism, thermoregulation, activity, reproduction, storage, and growth. The division of energy between these depends on the sex and life-stage of the animal, and environmental conditions (Kooijman, 2009). For example, a pregnant female will require more energy for reproduction, while an animal in cold environments may need to thermoregulate by increasing its metabolic rate. The optimum allocation of resources is an important component to fitness and selective pressure, as reproductive success requires enough energy investment at the right time (Perrin & Sibly, 1993). When energy intake is limited, increased demand to one process may compromise the energy available for others, potentially reducing reproductive effort. In birds, the introduction of disturbance to parental foraging reduced the amount of food delivered to the chicks, even when the amount of food collected remained similar suggesting the extra energy demand for activity reduced the allocation to reproduction (Fernandez & Azkona, 1993; Verhulst et al., 2001). For Magellanic penguins (Spheniscus magellanicus), increased foraging trip distance and duration, signalling higher locomotive costs, negatively affected breeding success (Boersma & Rebstock, 2009). In more general terms, it is apparent that changes in the environment, including the introduction of human disturbance, can alter energy allocation potentially to the detriment of reproduction and population resilience.

There are two general strategies available to an animal to supply the energy needed for reproduction: income and capital breeding (Jonsson, 1997; Stephens et al., 2009). For income breeders, energy replenishment occurs concurrently with breeding, while capital breeders are fasting, supplying the energy for reproduction from stores accumulated previously (Jonsson, 1997; Stephens et al., 2009). For capital breeders, reproductive effort
and success is related to maternal mass, with larger females positively influencing traits such as pregnancy occurrence (Boyd, 2000), lactation length (Wheatley et al., 2006), milk delivered (Crocker et al., 2001), and offspring weaning mass (Derocher & Stirling, 1990; Bowen et al., 2001a, 2006; Wheatley et al., 2006), while reproductive traits of income breeders are more dependent on the fluctuating environment and food availability (Bowen et al., 2001b). Reproductive success is therefore related to the energy available to be invested into offspring. However, the stored energy of capital breeders is finite, meaning that any increases to energy demands for other processes will reallocate energy away from breeding, with repercussions on reproductive success. As these energy stores cannot be replenished until after the breeding season, capital breeders are also vulnerable to exhausting energy reserves before foraging grounds are reached (Jonsson, 1997). Disturbance to energy use during the breeding season therefore has implications for the reproductive success, growth rates, and ultimately survival.

Humpback whales are at the extreme end of capital breeding. They annually migrate thousands of kilometres between foraging grounds in the polar regions and breeding grounds in the tropics. During this migration adults are not feeding, relying on energy stores to fuel the 8-9 month journey in addition to breeding requirements. Increases to energy expenditure therefore have the potential to impact the reproductive success of these animals, and ability to complete the migration cycle before stores are depleted. Disturbance from human activities have been documented to change the behaviour and activity of large whales (Corkeron, 1995; Miller et al., 2000; Richter et al., 2006; Stamation et al., 2009), particularly groups containing females and calves (Lundquist et al., 2008; Stamation et al., 2009). Higher activity levels may impact reproduction by diverting the limited energy available away from lactation in females or growth in calves. The close association of migration routes with the coastline exposes whales to high levels of human activities, increasing the likelihood of disturbance. In Australia, humpback whales are also known to aggregate in sheltered coastal areas to rest during their journey (Chittleborough, 1953; Jenner et al., 2001). The high densities of whales in these areas, where groups contain a high proportion of females with calves (McCauley et al., 2000; Braithwaite et al., 2012), also increase their vulnerability to disturbance from human activities. While local disturbances to behaviour may seem minor, the costs of repeated disruptions may accumulate over the long journey, collectively having a major impact to the energy stores of whales. Further, whales may be more vulnerable to increases in energy use during those periods of resting, where energy conservation appears to be important in habitat selection (Whitehead & Moore, 1982; Felix & Botero-Acosta, 2011; Braithwaite et al., subm.a).

In this study, I develop a bioenergetic model for migrating humpback whales. This model is first used to understand optimal migration strategies for minimising energy use under
varying swimming speeds and resting vs. travelling scenarios, with a focus on lactating females that expend the most energy. I then simulate disturbance to whales through two drivers: increased swimming speed to mimic increased activity, and increased distance travelled to mimic diversion from the migration route through displacement. Changes to the growth rates of calves are assessed under these two disturbance scenarios. Energy is a valuable and finite resource for humpback whales, required to support survival and reproduction. It is therefore crucial to understand how disturbances along the migration route may disrupt optimal energy use, and impact fitness and reproduction, so that adequate protection can be implemented where required.

6.3 Model description

The energy use of a migrating humpback whale was allocated among maintenance, activity, lactation, and growth, depending on the age and sex of the whale. An adult male will use energy for maintenance and activity, an adult female will use additional energy in lactation, and a calf uses energy for growth (Fortune et al., 2013; Winship et al., 2002). The calculations for each of these components are outlined in the following sections. Thermoregulation was considered and discounted as a significant energy drain for migration humpback whales. A change in metabolic rate for thermoregulatory purposes is only relevant outside an animal’s thermoneutral zone; within this zone physiological adaptations are enough to maintain a constant body temperature (Willmer et al., 2005). Evidence suggests that the lower critical temperature for large cetaceans, including their calves, is much lower than the minimum seawater temperature (Lavigne et al., 1990). The upper critical temperature of large whales has not been identified. However, the water temperatures experienced remain lower than core body temperatures, so heat will continually be lost from the animal. Further, physiological and behavioural mechanisms exist to regulate the efficiency of heat lost (Pabst et al., 1999). I therefore assume that humpback whales do not reach their upper critical temperature, and stay within their thermoneutral zone during migration.

6.3.1 Basal metabolic rate

The energy required to support the basic functioning of an organism at rest is generally defined as the basal metabolic rate (BMR). Kleiber (1975) identified an allometric relationship between BMR and body mass among animals, calculated as 

\[ E_{BMR} = 70M^{0.75}, \]

where \( E_{BMR} \) is measured in kcal per day, and mass \( (M) \) in kg. This
relationship describes interspecific variation, and its application to calculating intraspecific variation is unclear (Boyd, 2002), as the scaling of intraspecific metabolism is highly variable (Glazier, 2005). However, as no intraspecific relationship has been established for humpback whales, I used the standard Kleiber (1975) equation in these models. The $E_{BMR}$ of a calf was estimated to be twice that of an adult to account for the elevated metabolic rates of immature animals (Lavigne et al., 1986; Worthy, 2001).

6.3.2 Activity/cost of transport

The main activity of migrating humpback whales is travelling (swimming). Thus, I generalised energy expenditure of all activity as the cost of transport. Resting and travelling behaviours were categorised based on swimming speed, with resting whales swimming at slower speeds than travelling whales (Jenner & Jenner, 2011).

I calculated the cost of a whale swimming through the water based on amount of energy required ($E_{COT}$, J s$^{-1}$) to overcome the drag forces ($D$, kg m s$^{-2}$) of actively swimming at a constant speed ($V$, m s$^{-1}$) (Hind & Gurney, 1997):

$$E_{COT} = D \times V$$  \hspace{1cm} (6.1)

where drag is calculated as:

$$D = \frac{1}{2} \rho S C_d V^2$$  \hspace{1cm} (6.2)

with $\rho$ as the density of water (kg m$^{-3}$), $S$ the surface area (m$^2$), and $C_d$ is the drag coefficient. The drag coefficient is assumed constant across velocities, as the large body of a whale produces a high Reynolds number (turbulent flow) (Batchelor, 1967; Hind & Gurney, 1997). Equation 6.2 is derived for a passive object moving through a medium, whereas whales are active swimmers and will therefore be creating extra drag through body movements. The equation is therefore scaled by the ratio of active to passive drag ($\lambda$), to account for this extra drag (Hind & Gurney, 1997). The energy required to swim will also depend on the efficiency in which metabolised energy is converted into mechanical work (aerobic efficiency, $\varepsilon_A$), and the efficiency in which muscle movements are converted into forward motion (propulsive efficiency, $\varepsilon_P$) (Fish, 1996; Hind & Gurney, 1997). For cetaceans, which are lift-based swimmers, aerobic efficiency typically reaches 20%, while propulsive efficiency is at least 80% (Fish, 1996). Finally, a coefficient for tortuosity ($\theta$) was also included to account for deviations from a straight line travel path (Codling et al., 2008), as
the less straight a path is, the larger the distance travelled. For instance, whales oscillate between the surface to breathe and fully submerged when diving, creating a vertical zig-zag path. Tortuosity has a value of 1 for a straight path, and increases as a path becomes more complex. As no tortuosity values are available for whales, I added a 5% cost (i.e. $\theta = 1.05$) for not swimming in a direct line. The total energetic cost of transport for a migrating whale is therefore calculated as:

$$D = \left( \frac{\lambda \theta}{2 \varepsilon A \varepsilon P} \right) \rho SC_d V^3$$

(6.3)

Water motion also influences the cost of transport, with the aligned flow reducing $E_{COT}$, and opposing flow increasing it. For the purpose of this research, I assumed fluctuations in $E_{COT}$ due to water motion was equalled out over the migration cycle, and thus considered constant, though it could be accounted for by modifying the net migration velocity for studies over shorter time-scales.

### 6.3.3 Lactation

The energy demands of a migrating female with a calf include lactation alongside BMR and COT, to produce enough milk to support the maintenance and growth of the calf. The energy required for lactation depends upon the energy content in the milk produced, which in turn is a function of the protein and lipid content. The metabolic demand of producing a quantity of milk in a given time ($E_{LAC}$, e.g. kJ s$^{-1}$) can be described as:

$$E_{LAC} = M_m \times [(M_{lip} \times ED_{lip}) + (M_{pro} \times ED_{pro})]$$

(6.4)

where $M_m$ is the mass of milk transferred in a given time (kg s$^{-1}$), $M_{lip}$ is the proportion of lipid in the milk, and $M_{pro}$ is the proportion of protein in the milk. $ED_{lip}$ and $ED_{pro}$ are the energy densities of lipid and protein, respectively (kJ kg$^{-1}$, see growth section).

Cetacean milk generally contains water, protein, fat, and ash, and the constituent concentrations change over time (Ofstadal, 1997). For humpback whales, numbers are only provided for 4-7 months postpartum, so I assumed these values for the model. The quantity of milk required needs to meet the energy needs of the calf, and offset the assimilation efficiency of digesting (see growth section). Thus, 110% of the total energy requirements of the calf needs to be provided in the milk.
6.3.4 Growth

A calf requires sufficient energy to support maintenance (BMR, COT) and growth. The length of a new born humpback calf is approximately 4.3 m, and the length of weening approximately 8.8 m (Boyd et al., 1999). Using the Lockyer (1976) species-specific length to weight relationship, this equates to an initial mass of approximately 1,200 kg, and weening mass of approximately 10,050 kg. Thus, approximately 8,850 kg of mass is accumulated through growth over a 10-11 month weening period (Boyd et al., 1999). According to the allometric relationship between sculp (blubber and skin) and body mass, defined by Ryg et al. (1993), approximately 1,644 kg of mass growth will be stored as blubber, using sculp as a proxy for blubber mass. The remaining 7,206 kg of mass growth is categorised here as lean tissue.

The energy requirement for growth was estimated following the methods of Winship et al. (2002). Growth requires the synthesis of protein and lipid. The energy required for growth in a given time \( E_G \), e.g. \( \text{kJ s}^{-1} \) is therefore the total mass gain in lipid and protein, multiplied by their respective energy density values:

\[
E_G = dM \times \left[ (P_{lip} \times ED_{lip}) + (P_{pro} \times ED_{pro}) \right]
\]

where \( dM \) is the change in mass due to growth in a given time period (e.g. kg s\(^{-1}\)), \( P_{lip} \) and \( P_{pro} \) are the proportions of lipid and protein growth, respectively, and \( ED_{lip} \) and \( ED_{pro} \) are the energy densities of lipid and protein (kJ kg\(^{-1}\)) respectively (Winship et al., 2002; Fortune et al., 2013).

Lipid is found in both the blubber and lean tissue of whales, in differing amounts. As I could find no lipid content values separated for blubber and muscle recorded for humpback whales, I took the available values for fin whales to approximate the relationship (Lockyer & McConnell, 1985). The lipid content of fin whale blubber is estimated at 87%, while in muscle it is only 7% (Lockyer & McConnell, 1985). Based on the earlier mass growth values (1,644 kg blubber, 7,206 kg lean tissue), this calculates to 22% of growth stored as blubber (16% in blubber, 0.06% in lean tissue). Since muscle was used to generalise across all lean tissue, this will be an underestimate.

Lean tissue growth is assumed as anything that is not lipid. However, lean tissue also contains water. Thus, the amount of protein in the lean tissue will be \( 1 - P_w \), where \( P_w \) denotes the proportion of water in lean tissue. Thus, equation 6.5 can be rewritten to match the equation of Winship et al. (2002):
Finally, the total energy demand also needs to account for the assimilation efficiency of milk, as a portion of ingested energy will be lost through faeces and urine (Winship et al., 2002; Fortune et al., 2013). Assimilation efficiency for pre-weaned blue and fin whales have been estimated as 86% and 93%, respectively (Lockyer, 1981). I therefore estimated assimilation efficiency to be 90%, meaning that energy required needs to be 110% that of growth to sustain a particular growth rate. The daily energy requirement of a calf ($E_{CALF}$, kJ day$^{-1}$) is summarised as:

$$
E_{CALF} = E_{BMR} + E_{COT} + 1.1E_G 
$$

$$
= 293.1M^{0.75} + \left( \frac{86,400 \lambda \theta}{2\pi A_{eff}^2} \right) \rho SCDV^3 + 1.1dM 
$$

$$
\times \left[ (P_{lip} \times ED_{lip}) + (1 - P_{lip})(1 - P_w) \times ED_{pro} \right] 
$$

(6.7)

6.4 Simulation approach

The energetics model was run for several simulations to investigate optimal energy use in varying migration scenarios defined by swim speed, and the rest to travel time ratio. These simulations focused on lactating females, as they use the most energy, and are thus more vulnerable to exhaustion. Simulations were also limited to the southbound migration (breeding to feeding grounds), as this is when females will be lactating, and when whales are known to rest (Jenner et al., 2001). The second set of simulations centred on the impact of disturbance to calf growth, as energy diverted away from either lactation or growth will have the most impact on young calves. Simulations were programmed in Python programming language (www.python.org).

6.4.1 Ideal migration velocity

The ideal migration velocity was investigated using the adult female model ($E_{FEMALE} = E_{BMR} + E_{COT} + E_{LAC}$). Starting female mass was set at 30,000 kg, while a new-born calf mass was 1,200 kg, derived from the length to weight relationship of Lockyer (1976) for a female of length 13 m, and calf of 4.3 m. For a calf to increase in mass by 8,850 kg over the 10.5 month weening period, it must grow by an average of approximately 28 kg per day. The energy demand of lactation was therefore computed based on this growth rate.
Daily energy expenditure was recorded as the mass of blubber lost, calculated by dividing energy use by the energy density of lipid. Energy expended through $E_{BMR}$, $E_{COT}$, and $E_{LAC}$ were recalculated each day, taking into account mass lost by the female, and mass gain of the calf from the previous day.

Average migration velocity was varied between 0.1 m s$^{-1}$ to 4 m s$^{-1}$ over a migration distance of 8,500 km (Rasmussen et al., 2007), to accommodate the range of swimming speeds of humpback whales (Table 6.1). For each velocity, the total energy expended over the southbound migration for the female was recorded, and the proportion of total blubber utilised calculated assuming a starting blubber amount according to the Ryg et al. (1993)

### Table 6.1: Model parameters with corresponding values used in simulations

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$BMR$ (kJ day$^{-1}$)</td>
<td>292.88M$^{0.75}$</td>
<td>(Kleiber, 1975)</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>0.7</td>
<td>(Hind &amp; Gurney, 1997)</td>
</tr>
<tr>
<td>$\theta$</td>
<td>1.05</td>
<td>see text</td>
</tr>
<tr>
<td>$\varepsilon_A$</td>
<td>0.2</td>
<td>(Fish, 1996)</td>
</tr>
<tr>
<td>$\varepsilon_P$</td>
<td>0.8</td>
<td>(Fish, 1996)</td>
</tr>
<tr>
<td>$\rho$ (kg m$^{-3}$)</td>
<td>1,027</td>
<td>standard for sea water</td>
</tr>
<tr>
<td>$S$ (m$^2$)</td>
<td>0.045M$^{0.696}$</td>
<td>(Ryg et al., 1993)</td>
</tr>
<tr>
<td>$C_d$</td>
<td>0.0034 (minke whale)</td>
<td>(Hind &amp; Gurney, 1997)</td>
</tr>
<tr>
<td></td>
<td>0.00306 (sperm whale)</td>
<td>(Miller, 2004)</td>
</tr>
<tr>
<td></td>
<td>0.0026 (fin whale)</td>
<td>(Miller, 2004)</td>
</tr>
<tr>
<td></td>
<td>0.0029 (killer whale)</td>
<td>(Fish, 1998)</td>
</tr>
<tr>
<td></td>
<td>0.003</td>
<td>used is this study, mean for whale values</td>
</tr>
<tr>
<td>$dM$ (kg)</td>
<td>8,850</td>
<td>over 10.5 months, see text</td>
</tr>
<tr>
<td>$P_{lip}$</td>
<td>0.22</td>
<td>see text</td>
</tr>
<tr>
<td>$P_w$</td>
<td>0.672</td>
<td>(Fortune et al., 2013)</td>
</tr>
<tr>
<td>$ED_{lip}$ (kJ kg$^{-1}$)</td>
<td>39,300</td>
<td>(Schmidt-Nielsen, 1997)</td>
</tr>
<tr>
<td>$ED_{pro}$ (kJ kg$^{-1}$)</td>
<td>18,000</td>
<td>(Schmidt-Nielsen, 1997)</td>
</tr>
<tr>
<td>$M_{lip}$</td>
<td>0.438</td>
<td>(Ofstadal, 1997)</td>
</tr>
<tr>
<td>$M_{pro}$</td>
<td>0.091</td>
<td>(Ofstadal, 1997)</td>
</tr>
<tr>
<td>$V$ (m s$^{-1}$)</td>
<td>0.5-1 (slow)</td>
<td>(Jenner &amp; Jenner, 2011)</td>
</tr>
<tr>
<td></td>
<td>1-2.5 (medium)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;2.5 (fast)</td>
<td></td>
</tr>
</tbody>
</table>

See text for parameter definitions.
mass-sculp relationship. A whale travelled at the defined speed until the 8,500 km journey was completed, so that the faster the velocity, the shorter the travel time. However, food in the Southern Ocean is only available during the summer months, so completing the migration journey early does not translate into the end of fasting for the whales. Those whales that arrived before food was available were therefore designated to ‘wait’ until 90 days was ended. Waiting whales were defined to be actively searching for food but not benefitting from prey acquisition. Wait velocity was assigned a value of 1.5 m s$^{-1}$, corresponding to the slowest average foraging dive speeds recorded for humpback whales (Dolphin, 1987).

6.4.2 Ideal resting time

Humpback whale mother-calf pods select calm habitat in which to rest and breed (Whitehead & Moore, 1982; Craig & Herman, 2000; Ersts & Rosenbaum, 2003; Rasmussen et al., 2007; Oviedo & Solis, 2008; Felix & Botero-Acosta, 2011; Braithwaite et al., 2012; Cartwright et al., 2012; Smith et al., 2012). These habitats conserve energy, maximising the efficiency at which milk can be converted into growth, thus migrating whales need to adopt a rest-travel strategy in order to feed calves. To test for an energetic advantage to resting, the energy use of a female whale was examined across varying rest-travel strategies over a 90 day migration: as the number of resting days increased, the number of travel days decreased accordingly. Resting was defined as slow velocity travel (0.5 m s$^{-1}$), in which no distance of migration was achieved (meandering in one area). Travel velocity was calculated as the speed necessary to complete the 8,500 km journey across the number of travel days remaining, i.e. fewer travel days resulted in faster swimming speeds. Lactation during resting times is required to offset any mass lost by the calf during travelling, and ensure the optimal growth mass of 2,520 kg over the 90 days (28.5% of the 8,850 kg growth mass over 10.5 months), maintaining the average rate of 28 kg per day. The rate of milk delivery required to supply the energy needed by the calf in the allotted resting days was also calculated, and compared to large baleen whale feeding rates.

6.4.3 Disturbance to calf growth

To investigate the impact of disturbance to calf growth rate, two measures of disturbance were used. The first was an increase in mean migration velocity, simulating disturbance within resting areas: females and calves can use the resting area but are unable to rest. The second increased the distance value, simulating an increase in migration distance due to avoiding human activities. The impact to calf growth was measured as the proportion of
ideal growth, where ideal growth is defined as 28 kg per day, reaching 2,520 kg over a 90 days migration. Lactation (thus the energy intake of the calf) was set to a fixed value that supplied the energy to grow at this ideal rate when migrating at the optimal velocity (see section 6.3.2). For the second measure of disturbance (distance), the extra migration time to accommodate the longer distance was also determined.

### 6.5 Results

#### 6.5.1 Ideal migration velocity

The energy expended for a lactating female initially decreased with increasing velocity, reaching a minimum at 1.1 m s\(^{-1}\). After this point, total energy expended increased with velocity (Figure 6.1A). At slow velocities, the majority of energy expended was for BMR and lactation, with transport costs minimal, and wait costs non-existent. At high velocities, BMR and lactation remained reasonably constant, while transport and wait time became increasingly energy expensive. This pattern of convergence to a minimum energy use can also be seen across varying travel times (Figure 6.1B). When the time to travel the 8,500 km migration distance took 90 days (at a velocity of 1.1 m s\(^{-1}\)), total energy used by a lactating female whale was minimised. A greater time spent travelling (i.e. slower velocities), resulted

![Figure 6.1: A. The proportion of blubber stores required for a lactating female to complete a 8,500 km southbound migration across a range of velocities, where food is set to appear after 90 days. If the whale completes the 8,500 km in less time than 90 days, it is assigned to ‘wait’ at 1.5 m s\(^{-1}\) for the remaining time. B. The proportion of blubber stores used across the varying travelling times under the same conditions as A. Travel time is defined as the number of days to complete the 8,500 km distance. The total amount of energy used has been divided in that allocated for basal metabolic rate (BMR), lactation, transport, and waiting.](image-url)
in greater BMR and lactation costs, while less time spent travelling (faster velocities) led to increased transport and wait costs.

6.5.2 Ideal resting time

When the number of rest to travel days was varied, the energy use of whales decreased with increasing numbers of travel days (Figure 6.2). To limit energy expended to 50% of blubber reserves, a female would need to travel for 66 days, resting for 24 days. Milk delivery rate increased exponentially with increasing number of travel days (Figure 6.2), so the energy saved with more travel and fewer resting days is counteracted by the increased milk delivery rate required over the shorter resting time. Assuming a maximum milk delivery rate of 70 kg per day, close to that of a fin whale (Lockyer, 1981), a female would need to rest for at least 35 days.

![Figure 6.2: Changes in female blubber and lactation rate in different travel/resting regimes. Calf feeding was limited to resting days, and ideal calf growth rate of 2520 kg over 90 days was assumed, so that any increase in calf maintenance costs through travelling are met by the mother, and all energy required by the calf for growth is transferred during resting. The green line indicates the proportion of blubber used by the female for migration and lactation, while the blue line is the transfer rate of milk required per day to meet the energy needs of the calf.](image-url)
Figure 6.3: Changes in the growth of calves at increasing migration travel velocity over a 90 day migration. Ideal growth is defined as 28 kg per day, and milk intake is fixed at the amount required to meet the ideal growth rate at 1.1 m s$^{-1}$ (optimal average migration speed, see 6.2A).

Figure 6.4: A. The change in calf growth rates, and B. number of days late to the foraging ground, as a function of increased migration distance. Ideal growth is defined as 28 kg per day, and milk intake is fixed at the amount required to meet the ideal growth rate at 1.1 m s$^{-1}$ (optimal average migration speed, 6.2A). Extra distance is measured in both km (marked on bottom axis) and as a percentage of total migration (marked on top axis).
6.5.3 Calf disturbance

In the first disturbance scenario, where velocity was varied to simulate increased activity, the growth rate of a calf decreased with increasing velocity (Figure 6.3). A doubling of average speed, from $1.1 \text{ m s}^{-1}$ to $2.2 \text{ m s}^{-1}$, resulted in an 85% reduction in calf growth. When distance was used as a measure of disturbance, there were two effects: ideal calf growth decreased, and the number of days whales arrived late to the foraging grounds increased (Figure 6.4). For example, a migration journey with an extra 850 km resulted in a 10% reduction in calf growth, with whales arriving to the foraging grounds about five days behind schedule. For this 10% reduced growth rate to occur, due to coastal disturbance, the southbound migration route would need to be diverted an extra 500 km offshore of the West Australian coast (Figure 6.5).

![Figure 6.5: A representation of a deviated route (open circles) that would add approximately 10% distance to a typical southbound migration journey (solid circles). A deviation of 500 km offshore would be required to achieve this increase in distance.](image)


6.6 Discussion

Energy is an important resource for migrating whales. These capital breeders rely entirely on stored energy (blubber) to fuel long migrations in order to breed, without the option of replenishment. Budgeting energy use will therefore form a crucial component to ensure migration is successfully completed, and reproductive investment maximised. In this study, I developed a theoretical bioenergetic model for migrating whales, and determined the optimal migration strategy to minimise energy use over the southbound leg of the migration cycle. The two main factors contributing to energy conservation were average migration velocity and the amount of time spent resting vs. travelling. Velocity, in particular, had a large influence on total transport costs. Disturbance to migration energetics, either by increasing average velocity or migration distance, changed the allocation of energy in whales, increasing total energy use and impacting the growth rates of calves.

6.6.1 Optimal migration

The optimal velocity to minimise energy use was a trade-off between the accumulation of daily maintenance costs at slow velocities, and the expensive transport cost of high velocities. Slow migrations minimise energy expended through transport, but accrue daily maintenance costs to support the extended journey time. Indeed, travelling too slowly will exhaust energy stores before migration is completed, resulting in mortality. The accumulation of daily maintenance costs can be reduced by travelling faster, however faster velocities incur higher transport costs due to the increase in drag. Furthermore, as the occurrence of food for humpback whales is seasonal, reaching the foraging grounds early yields no energetic advantage as whales are required to wait for food to become available. Thus, daily maintenance costs are only reduced to a point, defined by length of time until food appears. In migrating birds, optimising speed of flight is also a compromise between minimising the total duration of the migration journey and minimising total energy expenditure (Alerstam & Lindström, 1990; Alerstam, 2011). When it is beneficial to arrive early to a destination, a faster speed to reduce migration time is advantageous, whereas if no early arrival benefit accrues, flying slower to reduce the total cost of flight transport is appropriate (Hedenstrom & Alerstam, 1995). It appears, from observed flight speed, that birds maximise the distance flown per unit of work done, thereby minimising total energy costs (Hedenstrom & Alerstam, 1995). However, the proximity of measured speeds to optimal predictions varies with other factors, such as body mass (Pennycuick, 1997; Pennycuick et al., 2013). Regardless, the same trade-off exists with respect to optimising
energy use by balancing the timing of migration and the cost of transport for long-distance migrants.

Travelling at an average migration speed that balances daily maintenance with transport costs not only minimises energy use but also reduces the likelihood of mortality en route. The optimal migration velocity of a female travelling 8,500 km in 90 days predicted by the model was 1.1 m s$^{-1}$. This speed is comparable to, but a slight underestimate of observed migration velocities (Chittleborough, 1953), who noted female humpback whales with calves travelled slowly at velocities around 1.4 - 1.8 m s$^{-1}$ (2.8 - 3.5 knots). However, these observations were taken while whales were travelling between resting areas, and this model estimates the mean speed for the entire migration. Assuming a slower swim velocity in resting areas in comparison to travelling (Jenner & Jenner, 2011), the average velocities for the entire migration would be slower than those observed during periods of travel, accounting for the discrepancy between this model and observed values.

When organisms divide limited resources among competing energy demands, the expected evolutionary outcome is an allocation that maximise reproductive outcomes (Perrin & Sibly, 1993). Alerstam et al. (2003) reviewed several factors that may contribute to the evolution of long-distance migration strategies. For example, refuelling at stopover sites by migrating birds reduces the energy used for transport through minimising heavy fuel load costs (Alerstam et al., 2003), and migrating birds that arrive at breeding grounds with more fat stores experience greater reproductive success (Smith & Moore, 2003). For a migrating humpback whale, minimising energy expended for transport and maintenance enables more energy to be invested into reproductive output. Thus, the observed migration speeds of humpback whales may reflect the evolutionary selection for a migration strategy that maximises the energy available for reproductive investment.

A second energy-saving strategy exists through optimising the amount of time a whale spends resting vs. travelling. Longer resting periods mean less time available for travel, and whales are required to swim at faster speeds to complete the migration journey, resulting in higher transport costs. Consequently, less time spent resting reduces the energy expended through transport. However, in this model I assumed that the majority of nursing occurs in resting areas, where conditions are calm and feeding efficiency can be maximised (Braithwaite et al., subm.a). A minimum resting period is therefore needed to transfer enough energy from mother to calf, given the limitation to milk delivery rates (Lockyer & Brown, 1981). The optimal resting period to minimise total energy use was predicted to be about 30 days (24 - 35 days), leaving approximately 60 days (55 - 66 days) for travelling. Whilst humpback whales are known to aggregate in specific coastal areas for a period of time during the southbound migration (Chittleborough, 1953; Jenner et al., 2001), the total
amount of resting time along the entire journey remains unknown. To a calf, resting is analogous to bird stopover areas, using the area for food acquisition to fuel migration. Validating the optimal resting time predicted by this bioenergetic model through, for example, state-space modelling using tracking data (Bailey et al., 2009), would reveal whether these whales optimise their rest-travel strategy for energy conservation as per the model predictions. The ideal time spent in stopover sites for birds is related to factors such as fuel deposition rates and distances between these sites (Alerstam, 2011). Given the effect of resting time on milk transfer rates, it may be that similar optimisation criteria exist in resting areas, and the ideal time spent resting will depend upon the rate of energy gain. Thus, the conditions of resting areas to efficiently transfer energy from mother to calf may influence the ideal migration strategy.

6.6.2 Disturbance

Both timing and energy balance are important components to successful migration and breeding, and disturbance to either of these can have repercussions to the migrant. Delays to anadromous fish migrations due to river dams, for example, affect both reproductive outcomes, by changing the time and area of spawning, and mortality rates (Castro-Santos & Letcher, 2010). Similarly, human disturbance in bird stopover sites can reduce energy gain, resulting in lower reproductive success from poorer adult body condition at the breeding grounds (Drent et al., 2003). Human activity has the potential to disturb humpback whales during their migration, particularly when occupying shared space in coastal regions (Baker & Herman, 1989; Maybaum, 1993; Au & Green, 2000; McCauley et al., 2000; Miller et al., 2000; Fristrup et al., 2003; Gordon et al., 2003). Here, I found that both increased velocity and lengthened migration distance reduced calf growth. Velocity is a cubed-term when calculating transport costs, and as such any rise in velocity resulting from increases in behavioural activity, will have a non-linear impact on energy use and growth rates. Displacement of humpback whales from their normal migration path also incurred costs to energy use and calf growth. Further, it delayed the arrival of the whales to the foraging grounds, potentially reducing their subsequent energy gain during feeding. Therefore, regardless of whether a whale is disturbed or displaced, changes to optimal migration patterns will result in higher energy demands, using a larger proportion of blubber reserves, and reallocating energy away from growth in calves. Early growth is an important life-stage for an animal, and reduced nutrition here can affect long-term attributes, such as a lower adult body size, and shortened lifespan (Metcalfe & Monaghan, 2001). Disturbance to calf growth during migration may therefore have long-term cross-generational implications to its health and reproductive competitiveness. While a female could offset the changing calf
demands by supplying a greater amount of milk, this will add to the depletion of her own energy reserves.

Disturbance to migrating whales can affect energy use and calf growth. However the question remains as to whether current or predicted levels of disturbance present a significant threat to this population of humpback whales. Approximately one third of the migration journey (approximately 2,850 km) occurs along the west Australian coastline. The whale migration route would therefore need to be diverted approximately 500 km further offshore to extend the journey distance to the point where calf growth would be reduced by 10%, and a level of human activity causing this level of displacement is unlikely. Thus, likely increases in migration distance from human activities along the coast may have a minimal impact to whales. However, altering behavioural activity may be a more relevant consideration for whale energetics. A whale that spends 30 days resting at 0.5 m s\(^{-1}\), would be travelling at 1.6 m s\(^{-1}\) for the remaining 60 days to complete the 8,500 km distance. If, for example, swimming speed in resting areas was increased to velocities comparable to travelling (1.6 m s\(^{-1}\)), then calf growth would be reduced by approximately 5%. This may be a more realistic scenario, given the evidence of human activity in changing the behavioural state and activity level of humpback whales (Baker & Herman, 1989; Au & Green, 2000; McCauley et al., 2000). Another possible repercussion of disturbance to resting behaviour is the reduced opportunity for nursing. The maximum amount of milk a calf can receive is limited by the rate of delivery from the mother and the time available for feeding. Reduced resting time, and hence feeding time, means the rate of milk delivery must increase to maintain ideal growth rates. If resting time is reduced to the point where the maximum rate of milk delivery is exceeded, calf growth will be compromised. Assuming maximum milk delivery rate is 70 kg day\(^{-1}\), reducing resting time by 7 days would result in 20% less milk delivered to the calf.

Carry-over effects are an important consideration when assessing the impact of disturbance, as changes to an animal’s condition can affect future performance (Harrison et al., 2011). For example, foraging success in capital breeders determines body condition, which then influences reproductive success (Derocher & Stirling, 1990; Bowen et al., 2001a, 2006; Wheatley et al., 2006). Therefore, while the implications of disturbance to the energy balance of migrating whales may seem minor in a short-term context, these changes in energy may have long-term knock-on effects to reproductive investment. For example, breeding females are required to increase body weight by 65% to fuel migration and breeding, as opposed to approximately 50% for other non-breeding whales (Lockyer, 1981). These high energy demands in female baleen whales can necessitate a ‘rest’ year from breeding if stores are not replenished over the foraging season (Lockyer, 1986; Williams et al., 2013). Additional migratory energy demands for the female could lengthen the
replenishment period. A lower annual calving rate will have implications for population growth rates. Additionally, the body condition of humpback whales fluctuates with annual changes in food abundance (Braithwaite et al., subm.b), influencing the initial capital able to be invested for migration. In food poor years, whales will therefore be migrating on lower energy stores, and disturbances to energy expending during migration will have a greater effect on the proportion of stores used. Extension of the model developed here to include both variations in initial body condition, and measures of fecundity, would enable the investigation of carry-over effects between seasons and year.

Another component to energy use not considered in this model is hydrodynamic condition, which may factor into the energetic repercussion of course diversion. Both the flow direction and strength of water affects the drag force experienced by a whale, and swimming velocity will need to be adjusted accordingly to maintain a particular ground speed (McElroy et al., 2012). The hydrodynamic conditions encountered by a whale can therefore have either a positive and negative influence to the cost of transport, depending on whether they are swimming with or against the flow of water, and the strength of flow encountered. Migrating anadromous fish, for instance, select paths up river that are significantly less energetically demanding than random path conditions, a behaviour interpreted to conserve transport costs and allow for more energy to be invested into reproduction (McElroy et al., 2012). Likewise, birds exploit favourable wind conditions to economise energy use (Liechti, 2006). Indeed, extreme bird migrations across the Pacific Ocean use a wind-assisted corridor resulting from global atmospheric circulation in order to travel these large distances (around 10,000 km) without stopping (Gill et al., 2009). It may be that migrating humpback whales also utilising energy conserving paths in the hydrodynamic environment to reduce transport costs. Therefore, while a small diversion off-course has a seemly minimal impact to energy use in terms of extra distance to travel, it may divert whales to less hydrodynamically favourable conditions, increasing the amount of energy expenditure.

6.6.3 Model sensitivity and uncertainty

The absence of empirical information regarding humpback whale physiology meant that some assumptions were made regarding migration energetics and parameter estimation. First, I measured the energy expended for all physical activity in the cost of transport equation. Humpback whales display a variety of behaviours, ranging from passively lying at the surface, to more active tail slapping and breaching (Corkeron, 1995). These behaviours will have different energetic costs to a constant swimming motion that are not captured by this model. As unsteady movement pattern incurs extra energy expenditure (Daniel, 1985; Fish, 1994), I am likely to be underestimating the energy used for increased behavioural
activity. However, as active behaviours typically involve more physical movement than passive behaviours, grouping all activity to the cost of transport provides a general indicator of how changes to behavioural activity will affect the energy use of increased movement.

A second assumption made was the linear rate of growth in a calf. Growth is generally a curved function, beginning relatively fast and slowing towards maturity (von Bertalanffy, 1938), and large whales are no exception (Lockyer, 1981). To my knowledge, humpback whales growth curves have only been calculated in regard to length, rather than mass, so I was unable to integrate a mass growth rate function into this model. However, curves for body length show growth to be relatively constant for the initial months, not slowing greatly until closer to one year of age (Stevick, 1999). I therefore assumed that uncertainty from the use of a linear growth model is minimal, however any extension of this model to include growth beyond weaning will need to account for a curved growth function in calves.

Thirdly, energy provided from lactation was assumed to be constant in this model although the proportion of milk constituents in cetaceans changes over time (Oftedal, 1997). In humpback whales, for example, the proportion of fat increases over the first few months of lactation, before decreasing again towards weaning (Oftedal, 1997). As I used the 4-7 month average proportion of constituents, the energetic value of milk would be greater than that of early months, and thus the total amount of milk required to support ideal growth will be an underestimate. Consequently, the amount of resting time, as predicted by milk transfer rates, will also be underestimated.

Fourthly the states of resting, waiting, and travelling were categorised by velocity, set respectively at 0.5, 1.5, and 1.1 m s\(^{-1}\). However, velocity was defined as a cubed-term when calculating energetic cost of transport. As such, model outputs regarding energy used for cost of transport will be sensitive to small changes in these set velocity parameters. I used conservative velocity estimates, at the lower end of estimated resting and foraging speeds, so the cost of transport calculated by this model will likely be an underestimate. However, obtaining and integrating telemetry data into the model analysis would be beneficial to obtain better estimates of velocity values in different behavioural states.

Many parameters are not well defined for humpback whales in the literature, and values for other species were used instead, adding to the uncertainty of model outputs. Where possible, I obtained parameter values for large cetacean baleen whale species to minimise this uncertainty. Tortuosity was one parameter that had not been defined for cetacean species. I included tortuosity to account for the raised transport costs associated with not travelling in a straight line, using a value of 5\%. However, without information on how much a whales’ path deviates from a straight line, this is purely an estimate and adds uncertainty
to the model. Again, analysis of telemetry data would be advantageous to defining this parameter, so that the cost of transport can be better estimated.

### 6.7 Conclusion

Whales migrate large distances on a limited energy budget, and managing this energy budget optimally is important to ensure survival over the migration route, and maximise reproductive output. The theoretical model developed in this study demonstrated that an optimal migration strategy exists in which energy use is minimised through managing both swimming velocity and the time spent resting. At each end of the scales, greater than available reserves were required, which would lead to the exhaustion of stores before migration was completed. Observed swimming velocities of migrating whales were comparable to those predicted by the model, suggesting that minimising energy use during migration may be a contributing factor to the evolution of observed migration patterns. Furthermore, human disturbance along the migration route has the potential to alter the energy budgets of these animals by increasing the total energy required and reducing the amount available to be invested in calf growth. Resting areas are particularly vulnerable to disturbance, as disruption to resting behaviour can impede both the amount of milk transferred to the calf, and how the proportion of this milk allocated towards growth. While further developments are necessary to determine the long-term repercussions of migration disturbance to reproductive outcomes and population growth rates, this model provided initial insights into the energy trade-offs associated with migrating and breeding for baleen whales.

### 6.8 Acknowledgements

JE Braithwaite would like to acknowledge the University of Western Australia for providing a PhD scholarship.
Chapter 7

General Discussion

Energy is important to migratory animals, directly influencing their ability to complete migration and reproduce successfully. The aim of this thesis was to assess the conservation requirements of a threatened migratory species, the humpback whale, by determining the value of habitat to their energy balance. Identifying important habitats for conservation is challenging for cetaceans due to their highly mobile, wide ranging, and cryptic nature, requiring the integration of several types of data and approaches (Chapter 2). Here, I linked separate analyses to migration energetics to assess the importance of habitat to humpback whales. I found that energy was an important influencer of small- and large-scale migration behaviour. Resting area habitat use was driven by energy conserving behaviours (Chapters 3 and 4), while energy acquisition was linked to food abundance in foraging habitat (Chapter 5). Overall, migration patterns of humpback whales conformed to those predicted to be theoretically optimal for efficient energy use, suggesting evolutionary fitness, and the conservation of energy is potentially an important aspect determining humpback whale migration patterns (Chapter 6). Human disturbance to valuable habitats, or to their patterns of migration, therefore has implications for the energy balance of migrating whales, directly affecting survival, reproductive investment, and calf growth. An energetics approach to assessing habitat importance is beneficial to understanding the influence of habitat on animal physiology, and predicting consequences to population demographics if habitat use is disturbed. Management can therefore address the specific conservation requirements of a species by identifying areas of value, and the necessary steps to protect this habitat from adverse effects to changes in energy use, and thus long-term population trends.
7.1 Migration energetics

7.1.1 Energy conservation

Both spacing behaviour and habitat use indicated that resting behaviour is associated with energy conservation. Humpback whales consistently occupied the majority of Exmouth Gulf, regardless of abundance (Chapter 3), suggesting that, in general, the sheltered environmental conditions of the Gulf create suitable resting habitat for these whales. Within the Gulf, humpback whale groups were found to maintain a distance of approximately 2 km from each other while resting, likely driven by social behaviour (Chapter 3). Male harassment in whale breeding areas has been associated with increased energy expenditure of females (Cartwright & Sullivan, 2009), and reduced calf survival due to mother-calf separation by other individuals (Elwen & Best, 2004). Thus, the large average distance between humpback whale resting groups found here could reflect females with calves avoiding social stimulation, particularly with male competitive groups, thereby reducing social energy costs. Resting whales were also found to aggregate towards the calmer waters of the western side of the Gulf, conditions favourable for energy conservation, and showed a spatial preference for more temperature stable waters (Chapter 4). The association with energy conserving habitat is consistent with findings for breeding humpback whales in the West Indies (Whitehead & Moore, 1982) and Ecuador (Felix & Botero-Acosta, 2011), where females with calves frequented calmer, more sheltered environments. The influence of temperature on habitat selection was less clear. It is intuitive to theorise that warmer temperatures are advantageous for calf growth, as thermoregulatory costs would be less than existing in cold waters with less blubber for insulation (Clapham, 2001). However, Lavigne et al. (1990) demonstrated that the lower critical temperature limit of large baleen whales is far below polar water temperatures, even for calves, indicating that residing in warmer waters holds no thermoregulatory advantage for calf growth. Nevertheless, globally, humpback whales migrate to breed in waters between 21.1-28.3°C irrespective of latitude (Rasmussen et al., 2007), and this general temperature selection suggests an as yet unknown importance of temperature to these populations.

Migrating animals employ a variety of behavioural strategies for efficient energy use during their journey (Alerstam et al., 2003). Such strategies include refuelling (Alerstam et al., 2003; Sawyer et al., 2009; Silva et al., 2013), taking advantage of favourable wind conditions (Liechti, 2006; Gill et al., 2009), and travelling at speeds to maximise distance per unit power (Hedenstrom & Alerstam, 1995; Pennycuick, 1997). By maintaining a favourable energy balance, the risk of mortality is reduced, and reproductive output maximised (Drent et al., 2003; Smith & Moore, 2003; Newton, 2006), and in migrating bird species that use stopover
sites for refuelling *en route*, habitat quality is an important factor to site selection and residency time (Alerstam & Lindström, 1990; Alerstam, 2011). I propose that the preference for energy conserving habitat when resting is an important and newly identified strategy in humpback whale migration to promote the growth of calves during the journey. The high proportion of mother-calf pairs observed in Exmouth Gulf (McCauley et al., 2000, Chapter 3) suggest this is a nursery area, so mothers are likely to be feeding calves during this time. For a calf, surplus energy intake, i.e. anything that is not used for maintenance and activity, can be allocated towards storage and growth. Thus, the quality of resting habitat lies in how efficiently the energy intake of a calf can be allocated towards growth. For humpback whales, residency time in resting areas is limited, in order to keep transport costs when travelling low (Chapter 6). Therefore, the total amount of milk transferred is restricted by the existence of maximum feeding rates (Lockyer & Brown, 1981). Selecting high quality resting habitat, where energy expenditure towards activity and locomotion can be conserved, is advantageous to maximising the proportion of ‘surplus’ energy from milk intake, and thus promoting the growth of calves.

### 7.1.2 Energy acquisition

The effects of foraging habitat quality on the energetic condition of migrating humpback whales was quantified, for the first time, in this thesis. I found that the body condition of migrating humpback whales was linked with food availability in their Southern Ocean foraging habitat (Chapter 5), and hence the initial energy store of a whale upon commencing migration is likely to be subject to fluctuations in foraging habitat conditions. Humpback whales are capital breeders, relying entirely on stored energy to fuel migration and breeding. In capital breeders, fecundity is highly linked to maternal body condition. Females of lower mass are less likely to become pregnant (Boyd, 2000; Williams *et al.*, 2013), have reduced foetal growth (Lockyer, 1986), diminished lactation length and delivery (Crocker *et al.*, 2001; Wheatley *et al.*, 2006), and smaller offspring (Derocher & Stirling, 1990; Bowen *et al.*, 2001a, 2006; Wheatley *et al.*, 2006). As the capital of energy available for migration is dependant on energy gain, the quality of foraging habitat will influence their reproductive viability and offspring fitness of humpback whales. Large baleen whales exhibit threshold foraging behaviour, only targeting patches with high densities of prey (Piatt & Methven, 1990). This selection of dense prey patches is thought to be an important factor in offsetting the high energetic cost of ‘lunge-feeding’ (Kenney & Winn, 1986; Goldbogen *et al.*, 2008, 2011), the main foraging technique used by baleen whales (Heithaus & Dill, 2009). Low food abundances could therefore lead to fewer dense prey patches, and more time spent searching for these patches, thereby lowering the net gain of energy. As energy intake for
migration is limited to summer foraging in the Southern Ocean, an overall reduction in prey abundance here cannot be compensated for elsewhere. Thus, decreased feeding efficiency in low food years would reduce the rate of energy storage, resulting in whales migrating in poorer body condition.

7.1.3 Optimal migration

There are many factors that contribute to migration patterns across taxa, such as migrant size, travel speed, stopovers, and wind regimes (Alerstam et al., 2003; Alerstam, 2011). For humpback whales, I found that the optimal migration strategy to minimise energy use included both average swimming velocity and time spent resting (Chapter 6). Travel speed is an important component to seasonal migrations, as it influences the timing of arrival to the destination, and energy expended to get there (Alerstam et al., 2003). In birds, it has been hypothesised that optimal migration speed will change depending on whether arrival time or energy use is the most important factor to successful migration outcomes: a faster velocity will benefit arriving early to breeding grounds, while slower velocities will conserve transport costs when energy gain is scarce (Hedenstrom & Alerstam, 1995). A similar trade-off was found for humpback whales, where slow velocities minimised energy for transport while fast velocities reduced travel time. However, the seasonality of food occurrence means there is no advantage for whales arriving early at the foraging grounds, benefitting a slower speed to reduce the cost of transport. Yet, travelling too slow was also a disadvantage, due to the increased daily maintenance costs of a longer travel time. This study is the first to identify the importance of travel speed for humpback whales in managing the energy costs associated with the timing of migration. The theoretical prediction of optimal speed (1.1 ms\(^{-1}\)) was similar to observations documented in the literature (1.4 - 1.8 ms\(^{-1}\); Chittleborough 1953), indicating the speed of humpback whale migrations likely reflect an energy-selected strategy.

It has long been known that humpback whales migrating along the western Australian aggregate in coastal areas to rest (Chittleborough, 1953; Jenner et al., 2001), however the reason for these periods of resting is still unknown. The high proportion of females with calves found in the Gulf (McCauley et al., 2000, Chapter 3) indicate that nursing is likely to be a component to resting behaviour and the results of the bioenergetic model support this theory. Stopping to rest yielded no energetic benefit in terms of total transport costs, as travelling the migration route at a continual slow speed minimised energy use (Chapter 6). However, factoring in the milk transfer rates required for different lengths of resting time to ensure ideal calf growth revealed a minimum resting period would be needed to transfer milk within the bounds of maximum feeding rates. While further research is needed to
validate model predictions against actual resting times, the link between feeding rates and optimal resting time supports the idea that nursing is likely to be an important factor in resting for migrating whales.

### 7.2 Implications of disturbance

Habitats for migrating humpback whales appear to hold energetic value to assist in regulating energy balance. Resting habitats conserve energy and provide efficient feeding conditions for calves, and foraging habitat supplies energy capital to support the costs of migration and breeding. As such, the energy balance of migrating whales will be impacted by any changes to these habitats through both natural and human causes, with implications for mortality and reproductive success.

The ocean is shared space, and in coastal areas, whale migration routes overlap with increasingly concentrated human activities. These activities can disturb the normal behaviour of whales, causing, for example, increases in swim speed (e.g. Baker & Herman, 1989; Au & Green, 2000), entanglement (e.g. Cassoff et al., 2011; Meyer et al., 2011), and longer singing times (Miller et al., 2000). Such changes to behavioural activity counteract the benefit of these areas for conserving energy, essentially degrading the quality of resting habitat for migrating whales. Reductions in the amount of habitat suitable for resting may cause whales to aggregate in higher densities to accommodate the condensed resting space. Smaller distances between whale groups will incur an energetic cost through more frequent social interactions and male harassment (Cartwright & Sullivan, 2009). High levels of continued disturbance can lead to habitat displacement in marine mammals (Bejder et al., 2006b; Becker et al., 2011). If humpback whales are displaced from preferred resting habitat they will be required to use less suitable areas, generating greater energy expenditure. Disturbance that reduces resting habitat quality, or displaces whales elsewhere, will therefore lead to increased energy use over the migration journey.

Modelling the energetics of migrating whales revealed the effect of energetic disturbance to the use and allocation of energy resources (Chapter 6). For a calf, energy gain is limited by milk intake, and a greater proportion of energy expended through behavioural activity (modelled as increase in average migration speed) reduced growth rates. While the long-term repercussion of slower growth in whale calves is unknown, other animals have shown costs to health and reproductive competitiveness when maturity is reached (Metcalf & Monaghan, 2001). A female could compensate for reduced growth by providing more milk, however this will drain her own energy reserve. Disturbance would therefore have a double impact on females, expending energy for her own increased activity level, and that of
her calf. Breeding females require a large amount of energy stores to support lactation costs, accumulating 15% more blubber stores than a non-breeding adult before embarking on migration (Lockyer, 1981). Longer recovery periods may be needed to replenish energy stores (Williams et al., 2013), reducing long-term calving rates and population growth.

Changes to the quality of foraging habitat in the Southern Ocean will also affect the energetics of a whale. Food availability was linked to the average body condition across a large sample of whales each year, derived from whaling records (Chapter 5), suggesting a population-wide response to fluctuations in prey. Krill abundances are strongly associated with environmental conditions, most notably sea ice (e.g. Siegel & Loeb, 1995; Loeb et al., 1997; Atkinson et al., 2004), thus the population trends of humpback whales are indirectly affected by large-scale environmental fluctuations in the polar regions, such as those associated with climate change (van Ommen, 2013; King, 2014). In addition, krill fisheries are growing in the Southern Ocean (Nicol et al., 2012), and the potential expansion of this fishery into humpback whale foraging areas may create competition between fisheries and whales, particularly in years when krill abundances are low.

### 7.3 Benefit of energetics approach to conservation science

A variety of approaches can be employed to assess the importance of habitat use to a species, each offering a unique perspective on species-habitat relationships (Chapter 2). Linking knowledge of habitat use across different data types and analyses through a common currency, such as energy, can reveal more fundamental habitat relationships as driven by animal physiology. For example, in humpback whale resting habitat, an analysis of spacing behaviour suggested a social aspect to resting (Chapter 3), and statistical modelling of spatial distribution patterns indicated a habitat preference for particular environmental conditions (Chapter 4). The association of both these studies to energy conservation, however, revealed the underlying importance of resting habitat to migration whales, and thus the focus of conservation effort. Protecting the energy conserving qualities of resting habitat is a key factor in enabling the successful migration of whales. Thus, connecting different assessments of habitat use through energy can both improve our understanding of species-habitat relationships, and provide priorities for conservation management.

An important question for conservation management is how different habitats contribute to long-term population persistence of threatened species (Hoekstra et al., 2002). Understanding physiological animal-habitat associations can provide answers here, as these cause-and-effect relationships enable the carry-over effects between habitat areas and seasons to be quantified, and then translated into long-term population-level outcomes.
In humpback whales, discrete habitat is used for different activities, foraging in the Southern Ocean and resting in lower latitude coastal areas. However, an energy currency between the two allows for an assessment of the carry-over effects between habitats, and how this may affect survival and reproductive rates. Food abundance in foraging habitat was linked to the body condition of whales (Chapter 5), essentially determining the capital of energy for migration, while the conditions in resting habitat was associated with conserving the rate of energy expended (Chapter 3 and 4). Thus, the conditions encountered in one habitat will have implications to the physical state of whales while occupying the other. For instance, reduced initial energy stores from poor foraging will constrain migration expenditure allowances, and the use of energy conserving habitat will be vital to ensure stores are not exhausted en route. The assessment of such carry-over effects are particularly important for migrating animals, where reproductive success is contingent on arriving at breeding grounds in good condition (Newton, 2006; Castro-Santos & Letcher, 2010; Cooke et al., 2012), which, in turn, depends on the cumulative influence of habitats encountered along the route (Norris, 2005). Fecundity in migrating baleen whales has been shown to be influenced by body condition (Lockyer, 1986; Williams et al., 2013). As such, changes to energy balance through encountered habitat conditions will affect reproductive rates, and thus, the population growth, of whales. This thesis demonstrates that defining habitat associations in terms of a physiological measure enables the carry-over effects between discrete habitats to be assessed in terms of demographic outcomes.

Data collection for wide-ranging, highly mobile species can be logistically challenging, costly, time consuming, and complex to analyse (Chapter 2). In some circumstances, bioenergetic modelling can provide a viable alternative to exploring data-intensive research questions, as demonstrated here. The existence of universal rules of energy use across all animals, or groups of animals (e.g. mammals, reptiles) (Kleiber, 1975; Schmidt-Nielsen, 1997), means theoretical models can be developed without the necessity of data collection, and tailored towards specific species as more data become available. These models can then be used to quantitatively estimate, for example, individual and population food requirements (Kenney et al., 1986; Williams et al., 2011; Fortune et al., 2013), and energy allocation at different life stages (Winship et al., 2002). In this thesis, developing a bioenergetic model enabled me to investigate the energy use of migrating humpback whales in varying conditions, which would otherwise be impractical using in situ techniques for measuring body condition, such as photogrammetry (Perryman & Lynn, 2002; Miller et al., 2012) and ultrasound (Moore et al., 2001), or ethically inappropriate destructive sampling. However, bioenergetic models are only simplified representation of real life, and accuracy relies on how closely assumptions made reflect reality. For example, there was a lack of information regarding some
physiological parameters for humpback whales, and more research is needed to better define these parameters and improve model predictions. Nevertheless, this model revealed insights into those characteristics important for minimising total energy use, such as average swim velocity and the amount of resting and travel time, and highlighted the implications of disturbance to migration in terms of survival and reproductive success. Bioenergetic models can therefore be a useful tool for addressing knowledge gaps where empirical research is challenging.

Quantifying the physiological link between animals and their habitats provides a method to predict population outcomes under a range of scenarios. Bioenergetic models have been used to evaluate the potential impacts of disturbance to anadromous fish migration (Castro-Santos & Letcher, 2010) and killer whale food supply (Williams et al., 2011), predict the consequences of climate change on species distributions (Humphries et al., 2004), and assess the contribution of inadequate foraging habitat conditions to the slow recovery of North Atlantic right whales (Kenney et al., 1986; Fortune et al., 2013). Here, modelling migrating whale energetics showed that the total energy expended by a whale over the migration journey increases in order to accommodate the additional cost of encountering disturbances en route (Chapter 6). These changes to energy use were translated to the possibility of producing fewer calves (longer recovery period for females), producing smaller calves, and increased vulnerability to energy exhaustion during migration. Lower reproductive rates coupled with a greater mortality risk will have long-term impacts on the persistence of this threatened migratory population. The capacity of energetic models to predict population-level outcomes to changing conditions can therefore provide advantages to identifying those factors where animals are more vulnerable to energetic disturbance, and for implementing a proactive approach to conservation.

Climate change also has the capacity to alter habitat conditions encountered by animals, with potential repercussions to population demography (Humphries et al., 2004). Current theories on the impact of climate change to baleen whales speculate that alterations to the physical environment in polar regions, such as sea ice dynamics, will affect food abundances in baleen foraging habitat (Nicol et al., 2008; Leaper & Miller, 2011). Previous studies have found body conditions and reproductive viability of baleen whale species to be associated with prey availability (Lockyer, 1986; Leaper et al., 2006; Williams et al., 2013). In turn, krill abundances, a key prey species, have been connected to sea ice dynamics on a range of scales (Nicol et al., 2000; Brierley et al., 2002; Atkinson et al., 2004), likely due to sea ice microbial communities (Siegel & Loeb, 1995; Loeb et al., 1997; Quetin et al., 2007; O’Brien et al., 2011). My analysis of historical whaling data (Chapter 5) provides evidence to support this theory, by linking annual changes of body condition of humpback whales to changing sea ice dynamics, and then sea ice to krill abundance in the same region of the Southern
Ocean. These findings strongly suggest that winter sea ice dynamics affect summer krill abundance, which in turn affects the energy stores of migrating humpback whales. However, due to the nature of these data, more research is needed to corroborate this finding. The quantified energetic link between baleen whales and their prey, as found here, means any long term changes to sea ice dynamics in the Southern Ocean, such as those associated with climate change (Brierley & Kingsford, 2009), will have long term implications to the persistence of this humpback whale population.

### 7.4 Future directions

The research presented here demonstrates that energy conservation was an important component to the use of resting areas by the population of humpback whales that migrate along the west Australian coast. If the use of energy conserving habitat during migration has been selected for through evolutionary processes, due to the advantage of having greater energy stores for survival and reproduction, then similar behaviours across other humpback whale populations, and other species of baleen whales that seasonally feed in order store blubber before migration over long-distances for breeding purposes, would be expected. Applying the analyses used here to other resting and breeding areas would reveal whether energy conserving behaviours, such as habitat selection and social spacing, are paralleled across humpback and other baleen species, and whether differences occur between species that store blubber for migration, like humpback whales, or more regularly feeding during migration, such as blue and fin whales (Silva et al., 2013).

To investigate the relationship between foraging habitat and humpback whale energetics, I used an indirect method based on sea ice, due to the temporal mismatch between available data on whale body condition and krill abundance. While this method revealed an association between sea ice, krill, and body condition, validation is needed based on more direct data. For example, data on krill abundance could be collected through acoustic surveys (Brierley et al., 2002; Hewitt, 2003). However, the research effort for this scale of data collection is substantial, as population-level data on body condition across years is needed, along with concurrent data on krill in a large area of the Southern Ocean. Yet, the link found in my study suggests that humpback whales are vulnerable to changes in prey availability in the Southern Ocean, and thus validation is important to understand the implications of climate change to baleen whales.

Modelling the bioenergetics of migrating whales revealed that velocity was influential to energy use, due to its affect on drag. As drag is a function of the strength and direction of water flow encountered, hydrodynamic conditions will be an important factor to humpback
whale energy use. Wall et al. (2006b) introduced the idea of an ‘energy-scape’, mapping the spatial variation to the energy use of elephants in relation to topographical conditions. A similar energy-scape could be created for humpback whales, by integrating hydrodynamic data into the bioenergetic model developed here, to determine regions of high and low energy use. A map of energy use would highlight areas that whales could be utilising to conserve energy use, such as resting areas or migratory corridors, and thus would be useful for identifying those habitat requiring protection from any energetic disturbances to migrating whales.

7.5 Concluding remarks

The conservation of threatened species requires the identification of areas essential to long-term persistence. In a heterogeneous environment, animals encounter a range of habitat conditions that can impact their current and future fitness, and subsequent resource allocation decisions. In many migratory species, reproductive success is contingent on arriving at breeding grounds in good condition, which, in turn, can depend on the cumulative influence of habitats encountered along the route. This thesis demonstrated the benefit of a conservation physiology approach to identifying those habitats important for population persistence in migrating humpback whales, by relating habitat use to energy balance, both in terms of energy use and energy gain. Furthermore, establishing these energetic associations allowed for the assessment of long-term impacts to populations in response to changing habitat conditions due to human disturbance and climate change. The conservation of humpback whales should therefore concentrate on maintaining the energy conserving qualities of habitat along the coast to ensure its continuing recovery.
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