THE UNIVERSITY OF QUEENSLAND
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# The feeding behaviour of humpback whales while on migration: methods, driving factors and its importance to whale ecology

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# Abstract

Many migratory species use stopover sites to reduce the cost of transport or increase energy intake. In terrestrial taxa, the quality of prey at these sites is linked to future survival and reproductive success with animals spending more time feeding when prey quality is high. The humpback whale (*Megaptera novaeangliae*) makes annual migrations between high latitude feeding grounds and low latitude breeding grounds, with historical data indicating that whales fast while migrating. However, there is growing evidence of whales feeding while on migration, yet little research describing or understanding this behaviour. The aim of this thesis was to develop appropriate methods to study the feeding behaviour of whales while on migration, determine factors that elicit feeding, and, from these results, infer the potential importance of feeding at migratory stopovers to whale ecology. Data were collected off the coast of Eden, NSW, Australia for three weeks in 2011 and five weeks in 2012, during the southward migration of the whales towards feeding grounds. Behavioural data were collected using group surveys ($n = 82$), digital tag (DTAG) deployments ($n = 9$) and focal follow sampling ($n = 18$). Data on the prey type and density available to the whales was also collected concurrently. First, a method was developed to detect both surface-feeding lunges and lunges at depth using accelerometer data from the DTAG. The lunges detected from the DTAGs were then used to determine the amount of time spent feeding and the rate of energy intake in relation to the prey species available.

Given that whales in the east Australian population feed predominantly on krill on their main feeding grounds, it was hypothesised that the availability of krill along the migratory route would provide an opportunity for whales to consume a familiar prey item and begin to accumulate energy reserves prior to reaching feeding grounds. It was assumed that if the feeding behaviour observed was important to whale ecology, the behaviour of whales would be more similar to the behaviour described on main feeding grounds and different from the behaviour of whales during migration. When fish were available, whales had relatively straight track lines as well as group sizes and compositions that were similar to those of whales on migration. In contrast, when krill were available, whales regularly looped back through the same area and had group sizes and compositions that were more similar to those on the main feeding grounds. Additionally, individual whales spent a significantly greater amount of time feeding and a larger proportion of the groups observed were determined to be feeding when krill, rather than fish, were available. Therefore, feeding behaviour on migration may be more important to whale ecology than previously thought and is likely influenced by the type of prey available. Given this observation, the influence of prey type, and prey depth on the rate of energy intake was investigated. Whales lunged at a significantly higher rate when feeding on krill compared to when feeding on fish, consuming prey at a rate of up to 3.7 times their energetic requirements. Therefore, feeding on migration may contribute more to annual energy budgets than previously thought and allow whales to begin to restore their energy supplies prior to reaching the Antarctic.

As changes in the prey species available influenced the behaviour of whales while on migration, a technique to determine the diet of migrating whales is required. Whales often feed underwater and migrate through remote areas, which can make the observation of feeding during migration difficult. This thesis tested whether stable isotope analysis of the skin of the whales would reflect the short-term dietary changes that occur on migration. Stable isotope analysis of skin was not a suitable technique as the skin still displayed historical dietary signatures of Antarctic prey. Therefore, further development of a technique to determine the most recent diet of whales is required in order to determine the diet of whales while on migration.

This study is the first to investigate the factors that influence the fine-scale feeding behaviour of whales while migrating. The results suggest that a change in the type of prey that is available at migratory stopovers influences behavioural characteristics of whales such as the amount of time spent feeding and the rate at which energy is consumed. Future research should focus on determining how often feeding occurs over larger spatial and temporal scales, and whether the rate of energy intake observed is sustained for longer periods. This will assist in determining the contribution of feeding behaviour while on migration to the annual energy budgets of humpback whales.

# Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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## Publications during candidature

*Peer reviewed publications*

Miller BS, Barlow J, Calderan S, Collins K, Leaper R, Olson P, Ensor P, Kelly N, Peel D, Donnelly D, Andrews-Goff V, Olavarria C, Owen K, Rekdahl M, Schmidt N, Wadley V, Gedamke J, Gales N, Double MC (In Press) Validating the reliability of passive acoustic localisation: a novel method for encountering rare and remote Antarctic blue whales. Endangered Species Research.

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## Contributions by others to the thesis

All four data chapters outlined below have been prepared for submission to relevant journals but are yet to be submitted or accepted for publication.

*Owen K, Dunlop R, Monty J, Chung D, Donnelly D, Noad M, Goldizen A, Mackenzie T (In Review)* ***Breaking the surface: a method to detect surface-feeding behaviour of whales in accelerometer data.*** *Prepared for submission to Marine Mammal Science.*

TM assisted with MATLAB programming to develop the algorithm code, and along with JM and DC provided guidance on the interpretation of the data with respect to the physics influencing the data. DD assisted with data collection. DD, RD and MN were responsible for obtaining the project funding. DD, RD, JM, DC, TM, AG and MN all assisted with editing the final manuscript. KO developed the research concept, collected and processed the data, completed the data analysis, interpreted the results, wrote the manuscript.

*Owen K, Donnelly D, Warren J, Noad M, Goldizen A, Dunlop R (2014)* ***Is feeding by humpback whales during migration a 'quick snack' or more important to their ecology?*** *Prepared for submission to Marine Ecology Progress Series.*

DD assisted with data collection and RD, DD and MN were responsible for obtaining the funding for the project. JW assisted with data collection and processed the prey availability data. RD assisted with development of the research concept. RD, DD, JW, MN and AG all assisted with editing the final manuscript. KO developed the research concept, collected and processed the data, analysed the data, interpreted the results and wrote the manuscript.

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DD assisted with data collection and RD, DD and MN were responsible for obtaining the funding for the project. RD and JW assisted with development of the research concept. AK assisted with the data analysis. JW assisted with data collection and processed the prey availability data. RD, AK, DD, JW, AG and MN all assisted with editing the final manuscript. KO developed the research concept, collected and processed the data, analysed the data and interpreted the results, wrote the manuscript.

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RT provided guidance on the methodology and interpretation of the data. DD assisted with sample collection. DD, RD and MN were responsible for obtaining the project funding. RD, RT, DD, AG, and MN assisted with editing the final manuscript. KO collected the samples, processed and analysed the samples, completed the data analyses, interpreted the results and wrote the manuscript.

## Statement of parts of the thesis submitted to qualify for the award of another degree

None

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# List of abbreviations

| | |
|---|---|
| ANOVA | analysis of variance |
| $Av_{LR}$ | average lunge rate |
| BMR | basal metabolic rate |
| $C_{efficiency}$ | capture efficiency |
| DNA | deoxyribonucleic acid |
| DTAG | digital acoustic recording tag |
| $E_{volume}$ | engulfment volume |
| EXA | excess x-acceleration |
| FMR | field metabolic rate |
| GLMM | generalised linear mixed model |
| GPS | global positioning system |
| HC | hourly consumption |
| I | ingestion rate |
| L | length |
| LDA | lunge detecting algorithm |
| LMM | linear mixed model |
| M | mass |
| MSA | minimum specific acceleration |
| NEA | net energy acquisition |
| NSW | New South Wales |
| $P_{density}$ | prey biomass density |
| PC | prey consumed |
| PQL | penalized quasi-likelihood |
| ROC curve | receiver operator characteristic |
| SIA | stable isotope analysis |
| TS | target strength |
| VGB | ventral groove blubber |
| VHF | very high frequency |

*Photo: A vertical lunge by a humpback whale feeding off the coast of Eden, NSW (photo by David Donnelly)*

# Chapter 1

## Introduction

# 1

# Introduction

## 1.1 Thesis overview

This thesis investigates the feeding behaviour of humpback whales (*Megaptera novaeangliae*) while on migration. Traditionally, it has been believed that the feeding behaviour of humpback whales is confined to high latitude feeding grounds. However, there is increasing documentation of humpback whales feeding during migration. Feeding on migratory stopovers is important to other migratory animals, with the quality and quantity of prey available on migration routes impacting on individual survival and reproductive success. Despite this, little research has focused on understanding what factors elicit this behaviour in whale populations and the importance of this behaviour to humpback whale ecology. Given the pressures of a changing climate and a growing krill fishery in the Southern Ocean, understanding the contribution of feeding while on migration to the annual energy budgets of humpback whales will assist with the conservation of this species. In addition, increasing the understanding of the feeding behaviour of the whales during migration will allow for the identification and protection of important feeding sites along the migratory route.

This chapter introduces various areas of research discussed in this thesis including optimal foraging theory, the ecology of animals on migratory stopovers, and baleen whales' feeding morphology and behaviour. The study species is then introduced to provide information on what is currently known about the ecology and feeding behaviour of humpback whales. Finally, a thesis outline is provided to explain how the following chapters contribute to knowledge gaps on the migratory ecology and feeding behaviour of humpback whales.

## 1.2 Foraging ecology

Optimal foraging theory predicts that foraging animals will behave in a way that maximises their net energy gain per unit time (MacArthur & Pianka 1966; Krebs 1977). As such, this theory proposes that the strategies animals use to search for, capture, and handle prey, as well as the characteristics of ingestion and digestion should be optimised. The behavioural characteristics of foraging are expected to be under natural selection, meaning that over time the most efficient foraging strategies will become more dominant. An example of optimal foraging involves crows (*Corvus caurinus*) feeding on whelks (*Thais lamellose*). Crows drop the whelks from a height to break the shell (Zach 1979) and have been shown to select larger whelks that have a higher energy content and break more readily compared to other size classes (Zach 1979). The crows also minimise the amount of energetically expensive ascending flight required by dropping the whelks from an optimal height. Whelks are also dropped onto rock to increase the likelihood of the shell breaking (Zach 1979). Therefore, the crow is able to increase the amount of energy it takes in, while keeping its energy expenditure as low as possible during foraging.

An additional aspect of optimal foraging relates to the behaviour of an animal in relation to the patches of prey that are available. In predator-prey systems, the distribution of a predator often shows a sigmoidal or threshold response in relation to the availability of prey (Holling 1965), suggesting that the distribution of animals is likely to be influenced by the distribution of prey species. The ideal free distribution states that the resource intake of an animal will decreases as the number of animals in the patch increases (Fretwell & Lucas 1970). This theory is based on many assumptions including that the number of animals remains constant and that all animals are equal competitors that are free to settle in any patch (Fretwell & Lucas 1970; Krivan *et al.* 2008). It also makes the assumption that there are no travel costs between patches and that the animals are aware of the environmental quality in each patch which is also assumed to be constant (Fretwell & Lucas 1970; Krivan *et al.* 2008). Consequently, animals should distribute themselves to increase their resource intake with the resulting distribution being referred to as the ideal free distribution. Similar to this theory is the marginal value theorem which states that when the expected net gain from continued foraging in a patch drops to the same level as the expected gain from travelling to a new patch, an animal should leave the current patch (Charnov 1976). Therefore, animals should distribute themselves in areas that allow for the highest intake of energy.

While the idea of optimal foraging was well developed theoretically, it was not well developed for easy testing. A major criticism of the optimal foraging theory and other associated theories (such as the marginal value theorem) has been the assumption that animals have prior knowledge or information about the quality of surrounding prey (Pyke 1984). While in some cases animals base their foraging behaviour on learned information on patch quality or their previous catch rate in a patch (Asmyhr *et al.* 2013), most animals are naive to the quality and availability of surrounding prey (McNamara & Houston 1985). More recently, methods from statistical physics, such as random walks, have assisted with incorporating the ignorance of animals about their surroundings into foraging models (Viswanathan *et al.* 2000; Bartumeus *et al.* 2005). In addition, the currencies that animals should maximise were also unclear and these needed to be parameterised before any tests of the theory could be completed. This included determining factors such as the rate of prey intake, the nutritional quality of the prey, and the cost of prey intake in terms of energy usage to capture the prey (Pierce & Ollason 1987). Once the definitions of these parameters had been developed, tests of the theory could be completed.

There are many examples of animals following what would be predicted to be an ‘optimal strategy’ while foraging. Eurasian beavers (*Castor fiber*) that are central place foragers have been shown to decrease their foraging intensity and become more selective about the size of the food they target as they move further away from their central place (Haarberg & Rosell 2006). In the marine environment, air-breathing predators such as blue whales (*Balaenoptera musculus*) have been shown to increase their time feeding as the depth of the prey increases to compensate for the additional time taken to travel between the air and prey (Doniol-Valcroze *et al.* 2011). In other air-breathing predators such as king penguins (*Aptenodytes patagonicus*), the transit time between prey and air has also been shown to be minimised as foraging activity increases, potentially to allow for more time to be spent feeding when prey is readily available (Hanuise *et al.* 2013). Therefore, the use of optimal foraging strategies has been observed across many taxa living in different environments.

In recent years the importance of trade-offs between optimal foraging and factors such as predation risk, risk of injury and the condition of the forager have been highlighted. Such trade-offs suggest that the optimal strategy may vary both temporally and between individuals (Houston and McNamara 2014). The risk of predation can influence the behaviour of animals, which are likely to forage more in a patch with a lower predation risk, even when the food quality in that patch is lower than other patches (Brown *et al.* 1992). In addition, vigilance for, or hiding from a predator can reduce the rate at which an animal feeds (Fraser & Gilliam 1987). As well as facing the threat of predation, a forager may also be injured by its prey (Berget-Tal *et al.* 2009). An injured predator may not be capable of catching prey until healed and may starve to death while recovering (Brown

& Kotler 2004). As a consequence, the risk of injury is likely to play a role in the decisions of a predator, with the cost of foraging on dangerous prey being higher, even if the nutritive value of the prey is high. The risk that an animal is willing to take has also been shown to be influenced by the hunger state or body condition of the animal, with animals becoming more risk prone when their condition is poor (Murray 2004). When taking into consideration all of the factors that may influence a forager, optimal foraging theory provides a useful framework within which to study the foraging decisions made by animals.

## 1.3 Animal migration

Migration is movement that takes an individual out of its home range and does not cease for a period of time, until the animal reaches an area where resources are favourable (Dingle & Drake 2007). This type of movement occurs as a product of animals tracking changes in resource availability. At an individual level, it has been defined as movement that is undistracted, persistent and direct or the relocation of an animal on a much greater scale both spatially and temporally than would occur during normal activities (Dingle and Drake 2007). On a population level, it is described as movements between regions of asynchronously favourable conditions or movements resulting in the redistribution of a population spatially (Dingle and Drake 2007). Migration is a phenomenon observed in many different animal taxa. The most well-known type is ‘to-and-fro’ migration, which describes the movement of whole species or populations between two alternately favourable resource-rich areas (Dingle & Drake 2007). One example of this is wildebeest (*Connochaetes taurinus*) in the Serengeti that make annual migrations between wet and dry season ranges to track changes in rainfall and plant nutritional gradients (Holdo *et al.* 2009). ‘Round trip’ migrations are similar to ‘to-and-fro’ movements except that animals may move between more than two areas of resource richness but always return to the same breeding area (Dingle & Drake 2007). ‘Vertical migrations’ involve the daily movement of organisms from deep to shallow parts of the water column (Lampert 1989). Similarly, ‘altitudinal migrations’ occur between different elevations in terrestrial environments, such as those made by deer (*Odocoileus hemionus*) tracking areas of high forage availability (Sawyer & Kauffman 2011). ‘One way migrations’ often occur as a part of the life cycle of many marine larvae (Dingle & Drake 2007). Similarly, ‘diadromous migrations’ occur between fresh and salt water as a part of the lifecycle of many fish species (McDowall 1992). Therefore, migratory movement occurs over many different temporal and spatial scales.

As well as variation in the type of movement, the degree to which movement occurs can also vary. Animals can be ‘obligate migrants’, meaning that an individual must migrate, or ‘facultative migrants', meaning that an individual can make a choice about whether to stay or go depending on the conditions encountered (Dingle & Drake 2007; Newton 2012). This distinction then leads to different categories that describe the proportion of the population that migrates. 'Complete migration' relates to movement that is undertaken by an entire population, whereas 'partial migration' occurs when only some of a population migrates (Dingle & Drake 2007). The Yellowstone pronghorn (*Antilocapra americana*) is an example of a facultative migrant, with the proportion of the population that migrates each year ranging from 20% to 80% (White *et al.* 2007). 'Differential migration' occurs when the choice to complete migration or the pattern of migration is influenced by either the age, and likely reproductive status, or gender of the individual (Drake & Dingle 2007). Variation in the migratory pattern with the sex of the animal is often associated with species that have high levels of sexual dimorphism. For example, male northern elephant seals (*Mirounga angustirostris*) are much larger than the females and they begin to migrate to different areas compared to the females to access prey once they reach puberty (Stewart 1997). Therefore, variation exists between species and individuals in the extent to which migration occurs.

In many cases, migration away from an area of declining resources to a new area of resource availability occurs prior to resources becoming limited. For migratory animals, resources can relate to either the availability of food, or access to nesting territories or mating opportunities. Arriving early into areas of increasing resource availability provides advantages by allowing an animal to establish a territory or utilise a resource before it becomes diminished (Dingle & Drake 2007). In contrast, arriving late often means higher levels of competition to establish access to resources. Animals that arrive late are also often the last to feed at a previous area where resources were diminishing. This places the animal at risk of running out of resources, which may limit its ability to successfully raise offspring to independence and to store enough energy to complete the migration (Dingle & Drake 2007). Since animals cannot rely on obvious cues such as a sudden shortage of food to cue the timing of migration, selection has favoured the evolution of the ability to recognise cues that relate to an impending shortage of resources and the need to move to a new area (Gwinner 1996; Ramenofsky & Wingfield 2007). One example of this is the use of circadian rhythms, which have been shown to control the timing of migrations in butterflies (Sauman *et al.* 2005) and birds (McMillan 197; Bartell & Gwinner 2005). Therefore, the evolution of mechanisms to predict the need for migration can be beneficial to individuals.

An important aspect of the definition of migratory movement compared to other types of movement is that migration is 'undistracted' (Dingle 1996). Migrants have been shown to switch off 'station keeping' responses at the initiation of migration (Kennedy 1985). This response allows an animal to move past an area that may have a useful resource at that time, but is likely to quickly deplete. The individual can then continue moving until it reaches an area outside of its home range where resources will remain available for a longer period. However, in some cases, species are able to switch on and off ‘station keeping’ responses throughout the migratory route, and swap between periods of foraging and periods of migrating (Kennedy 1985). The areas in which migratory animals feed while on migration have been termed ‘migratory stopovers’ and the ecology of migrants in these areas can often provide insight into the motivation and requirements for successful migration within the species (Sawyer & Kauffman 2011).

## 1.4 The ecology of animals on migratory stopovers

Seasonal migration requires long distance movement and hence a large input of energy from the animal (Alerstam *et al.* 2003). The storage of enough energy supplies to successfully complete migration can have large impacts on the cost of transport for animals, particularly flying animals (Akesson & Hedenstrom 2007). For this reason, some species have adapted to relying on migratory stopovers to allow for refuelling and resting along the migratory path (Newton 2006; Fusani *et al.* 2009). Resource availability at stopover sites has been shown to influence the behaviour of individuals, as well as their future survival and reproductive success.

The quality of a stopover site can influence both the initial decision of an animal to stop and the amount of time spent feeding (Newton 2006; McLaren *et al.* 2013). In migratory birds, individuals in poorer body condition spend more time on migratory stopovers (Fusani *et al.* 2009). The choice to depart a stopover site has been linked to both the current fuel load of the individual and the rate of fuel deposition at the site (Beekman *et al.* 2002; McLaren *et al.* 2013). Migrants are more likely to spend less time at migratory stopovers when the rate of fuel deposition is relatively low or relatively high (Schaub *et al.* 2008). To increase the rate of fuel deposition, migratory animals have also been shown to change their diet while migrating. For example, European populations of flycatchers (*Ficedula hypolueca* and *Muscicapa striata*) that are insectivorous on their breeding and wintering grounds have been shown to consume fruit during their migrations (Hernandez 2009). They specifically target fruit with a high lipid content, which is believed to be important for fattening in long distance migrations (Hernandez 2009). Individual migrants in both bird and terrestrial mammal species have been shown to have high fidelity to stopover sites (Cantos & Telleria 1994; Sawyer & Kauffman 2011). Therefore, the use of migratory stopovers is important for fuel deposition along the migratory route.

As well as being important for the accumulation of fuel reserves, migratory stopovers have also been shown to be important for the overall fitness of individuals. For example, in garden warblers (*Sylvia borin)*, low food availability on migratory stopovers leads to slower testicular recrudescence and hence a likely poorer reproductive success in the breeding season (Bauchinger *et al.* 2008). For many bird species, individuals who are in better body condition on migratory stopovers, or arrive to breeding sites in better body condition, are more likely to produce young (Ebbinge and Spaans 1995; Madsen 1995; Prop and Black 1998; Drent *et al.* 2003), lay their eggs earlier (Krapu 1981; Pattenden and Boag 1989; Bety *et al.* 2003; Smith and Moore 2003) and have larger clutch sizes and offspring (Krapu 1981; Pattenden and Boag 1989). Therefore, the conditions encountered on migratory stopovers can have a significant influence on the future reproductive success of an individual.

The overwhelming majority of research into the importance of migratory stopovers to the ecology of seasonal migrants has focused on bird species despite evidence for the use of migratory stopovers by other taxa. In terrestrial mammals such as deer (*Odocoileus hemionus*), it has been shown that the use of migratory stopovers is important to allow for an increased energy intake during migration. This energy intake is more important to the deer than the speed of the migration (Sawyer & Kauffman 2011). Migrating monarch butterflies (*Danaus plexippus*) have also been shown to rely on stopover sites, with the number of butterflies using the stopover sites varying as a function of wind direction, temperature and cloud cover (Meitner *et al.* 2004). Therefore, stopover use by non-avian migratory animals may be more common than currently thought and is potentially important to the ecology of many migratory taxa (Sawyer & Kauffman 2011).

The study of migratory ecology in the marine environment is particularly challenging due to the remoteness of likely stopover sites and the occurrence of feeding behaviour underwater. However, the use of stopover sites as potential feeding areas by marine animals has been demonstrated across many taxa including fish (Sims *et al.* 2009), marine reptiles (Broderick *et al.* 2007; Cuevas *et al.* 2008) and marine mammals (Cacchione *et al.* 1987; Stamation *et al.* 2007; Silva *et al.* 2013). Hawksbill turtles (*Eretmochelys imbricata*) have been shown to use stopover sites while migrating from breeding areas to feeding areas, which may indicate that turtles feed while migrating (Broderick *et al.* 2007; Cuevas *et al.* 2008). Sunfish (*Mola mola*) have also been shown to spend long periods of time in small areas with movements consistent with foraging during long distance movements (Sims *et al.* 2009). While the identification of potential stopover sites in the marine environment has occurred, very little is known about the importance of migratory stopovers to the ecology of marine species. Is the use of stopover sites purely opportunistic, or, similarly to bird species, is this more essential to the ecology of marine species than currently understood?

## 1.5 Feeding during migration by baleen whales

Understanding the behaviour of animals along the migratory route is important for species conservation. For long-lived migratory animals, such as many baleen whales species, the survival rate of individuals outside of the breeding season may have a strong influence on the size of the population (Calvert *et al.* 2009). Often, very little is known about the behaviour of whales while migrating and what impact this behaviour may have on subsequent survival and reproductive success. The shortage of information on the behaviour of whales while on migration is likely a consequence of the difficulty in studying whales while they migrate across ocean basins. Many baleen whale species make seasonal migrations between low latitude breeding grounds and high latitude feeding grounds and were historically thought to fast while breeding and migrating (Dawbin 1966; Lockyer & Brown 1981a; Baraff *et al.* 1991). The low rate of feeding while outside of the feeding grounds has been attributed to the low availability of prey in breeding areas and the observation that whales on migration captured by whalers often had empty stomachs (Dawbin 1966; Lockyer 1981b). However, the large majority of whales were caught during the migration from feeding grounds to breeding grounds as this time represented the period when the whales had the highest oil or fat content (Dawbin 1966). As a consequence, there is very little information available on the stomach contents or behaviour of whales during the migration from breeding grounds back towards feeding grounds.

There is growing evidence that some baleen whale species feed during migration. This includes indirect evidence of area-restricted search patterns from the satellite tracks of blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*) (Silva *et al.* 2013) and humpback whales (*Megaptera novaeangliae*) (Gales *et al.* 2009), as well as the occurrence of scratch marks on the ocean floor indicative of bottom-feeding by gray whales (*Eschrichtius robustus*) (Cacchione *et al.* 1987). Feeding behaviour has been observed in humpback whales in many different migratory locations around the world (Best *et al.* 1995; Gill *et al.* 1998; Stockin & Burgess 2005; Stamation *et al.* 2007; Visser *et al.* 2011). The large majority of these observations have occurred during the migration from breeding grounds back towards feeding grounds (Best *et al.* 1995; Gill *et al.* 1998; Stamation *et al.* 2007; Visser *et al.* 2011), which coincides with the time that whales have completed mating, and for females, are likely to have given birth. As a consequence, whales are likely to experience depleted energy reserves. Despite this evidence, the importance of feeding behaviour while on migration to the ecology of baleen whales and the factors that drive this behaviour are currently unknown.

## 1.6 Baleen whale feeding behaviour

Feeding in an aquatic environment can pose difficulties for organisms for many reasons. First, sea water is more dense and viscous than air, which has shaped the morphology and physiology of the organisms in the ocean differently to those on land (Connell & Gillanders 2007). In addition, changes in light levels, salinity, pressure and temperature with depth produces depth-related gradients in the ocean (Carr *et al.* 2003). These gradients combined with variation in the bathymetry and movement of water masses result in patchy and ephemeral areas of productivity that impact on the ecology of animals living in the ocean (Croll *et al.* 2008). This patchiness often leads to the presence of swarms of communities of animals such as krill, plankton and small fish and has led to the evolution of filter feeding mechanisms to take advantage of these swarms (Raffaelli *et al.* 2005). Filter feeding allows organisms to take in many individual prey items in a single feeding event (Croll *et al.* 2008) or to obtain food passively as seen in many sessile organisms (Stuart & Klumpp 1984; Riisgard *et al.* 1993). It is a feeding mode that has evolved in many different animal groups in the ocean, including, but not limited to, sponges (Riisgard *et al.* 1993), crustaceans (Stuart & Klumpp 1984), fish (Blaber 1979), and marine mammals such as leopard seals (*Hydrurga leptonyx*) (Hocking *et al.* 2013) and baleen whales (Croll *et al.* 2008).

The order Cetacea is divided into two branches of species that are distinct from each other based on the morphology of their feeding apparatus. These two branches are the toothed whales (Odontocetes) that use teeth to feed and the baleen whales (Mysticetes) that use keratinised baleen plates hanging from the upper jaw to filter small prey items from the water column (Demere *et al.* 2008). These baleen plates grow continuously throughout the life of the whale and are fringed on the inner edge to allow for filtration (Lambertsen 1983). By filter feeding, baleen whales are able to consume adequate food supplies to support their large body mass, including that of the largest animal to have ever lived, the blue whale (Alexander 1998).

To filter the prey, baleen whales use one of three strategies: ram feeding, suction feeding, or lunge feeding (Werth 2000). Lunge feeding is a behaviour used by rorqual whales including species such as the blue whale (Acevedo-Gutierrez *et al.* 2002) and the humpback whale (Jurazs & Jurasz 1979; Goldbogen *et al.* 2008). It involves the whale swimming at speed towards a patch of prey and engulfing large quantities of prey-laden water (Jurasz & Jurasz 1979). Rorqual whale species have ventral pleating called ventral groove blubber (VGB) that expands in an accordion-like fashion allowing vast quantities of prey-laden water to be held temporarily (Potvin *et al.* 2010). The morphology of the VGB allows for controlled expansion while feeding and contraction back against the body of the whale to maintain the streamlined shape required for efficient locomotion (Shadwick *et al.* 2013). Consequently, lunge feeding is considered to be the "largest biomechanical action in the animal kingdom" (Brodie 1993).

The morphology of rorqual whales is highly specialised to enable the engulfment of prey-laden water. When a rorqual whale lunges it opens its mouth to an angle of nearly 90° (Field *et al.* 2010). This increased area exposed to flow greatly increases the drag acting on the animal and forces water into the mouth, which expands the VGB. Unlike other baleen whales, the tongue of rorqual whales is flexible and is forced back into a ventral cavity called the cavum ventral between the muscle and skin layer (Potvin *et al.* 2010). The tongue essentially acts as a balloon to hold the water that is engulfed (Lambertsen 1983). In addition, the jaw bones and joints of rorqual whales are different from those of other mammals. The rostral connection of the mandibles is not fused as it is in the majority of mammals but connected by a fibrocartilage disc that contains a jelly-like core (Brodie, 1993; Lambertsen *et al.* 1995; Pivorunas 1977). This connection allows for outward rotation of the mandibles to increase the mouth volume. The mandibles are extremely long (approximately 25% of the total body length) and are not connected to the skull by a synovial joint as seen in other mammals (Field *et al.* 2010). Instead, the bones are embedded in a pad-like structure comprised of connective tissue infiltrated with oil (Brodie 1993; Lambertsen *et al.* 1995; Field *et al.* 2010). It is this connection that increases the rotation of the joint and allows rorqual whales to achieve such large gape angles while lunge feeding. In addition, the mineral density distribution and shape of the mandibles allow for the bending forces encountered during lunge feeding (Field *et al.* 2010). Therefore, the morphology of rorqual whales is highly evolved to allow for efficient lunge feeding in the marine environment.

Lunge feeding is an energetically expensive feeding strategy. This high cost is likely due to the increase in drag that lunge feeding creates and the repeated acceleration of an animal from a near stop that is required while feeding (Goldbogen *et al.* 2008; Simon *et al.* 2012). In addition, blue whales and fin whales have shorter dive times while foraging than expected based on body size and oxygen stores (Croll *et al.* 2001; Acevedo-Gutiérrez *et al.* 2002). The shorter times submerged are attributed to the high cost of lunge feeding (Acevedo-Gutiérrez *et al.* 2002) and are also likely to be associated with the whales requiring time at the surface to recover from the anaerobic catabolism that occurs during a lunge (Potvin *et al.* 2012). These high energetic constraints have also been demonstrated in intermediate sized rorqual whales including the humpback whale (Goldbogen *et al.* 2008). Given this high energetic cost, whales are likely to display a foraging threshold for prey density, above which it becomes energetically worthwhile for a whale to feed. A foraging threshold has been demonstrated previously in Newfoundland, Canada, where whale numbers were low when prey densities were low and high when prey densities exceeded a certain threshold (Piatt & Methven 1992). This threshold level for baleen whale feeding has also been shown to change from year to year, depending on the overall mean abundance of prey (Piatt & Methven 1992). Therefore, given the high energy demands of lunge feeding, areas of high prey availability are likely to be important to whales in order to increase their net energy gain while foraging.

Many different techniques have been used to understand the prey species and densities targeted by whales. Traditionally, whales' diets were determined by either direct observation of feeding behaviour (Jurasz & Jurasz 1979; Hain *et al.* 1982; D'Vincent *et al.* 1985), or the examination of stomach contents (Haug *et al.* 1994; Flinn *et al.* 2002). For feeding behaviour at depth, echosounders have been used to determine the prey targeted (Dolphin 1987; Friedlaender *et al.* 2009b). More recently, diet has also been studied using DNA collected from faeces (Jarman *et al.* 2002). However, all of the techniques currently available potentially bias the interpretation of whales' diets (Bowen and Iverson 2013). Determining the diet of marine mammals is often difficult because much of the feeding behaviour is completed underwater (Walker & Macko 1999). In addition, some prey items are digested more quickly than others, leading to an overestimation of the importance of prey items with hard parts to the diet of marine mammals (Tollit *et al.* 1997; Yonezaki *et al.* 2003). As a consequence, studies often use chemical signatures in the tissue of whales and prey to determine diet. Techniques including stable isotope analysis (Todd *et al.* 1997; Lesage *et al.* 2001; Newsome *et al.* 2010; Witteveen *et al.* 2011) and fatty acid analysis (Borobia *et al.* 1995; Hooker *et al.* 2001; Iverson *et al.* 2004) can provide insight into the diet of whales over many different time scales depending on the tissue analysed (Tieszen *et al.* 1983). Understanding the diet of whales is important for assisting with protecting important prey species, interpreting variation in the feeding behaviour observed, and locating important feeding grounds.

Previously, gaining an understanding of the feeding behaviour of baleen whales was difficult due to an inability to observe underwater behaviours (Baumgartner & Mate 2003). The invention of digital tags that record data on underwater movement has increased our understanding of whale behaviour. The tags can record the three-dimensional orientation, acceleration, depth, turning angle and sounds produced by the animal they are attached to, as well as other sounds produced around the animal (Johnson & Tyack 2003). This has allowed for the detection of underwater feeding behaviour and provided detailed insight into previously undescribed behaviours such as barrel rolls by blue whales (Goldbogen *et al.* 2013). It has also enabled an understanding of the role of buoyancy in the diving behaviour of marine mammals (Miller *et al.* 2004), shown the use of bottom-feeding techniques (Friedlaender *et al.* 2009a), and provided a greater understanding of the energetic costs of feeding behaviours (Goldbogen *et al.* 2008; Potvin *et al.* 2009). Therefore, valuable insights into the underwater behaviours exhibited by whales can be provided by digital tags.

## 1.7 The humpback whale

### 1.7.1 Migratory ecology

Humpback whales are found world-wide and make one of the largest seasonal migrations of any mammal species on the planet (Stone *et al.* 1990). These annual migrations are from high latitude feeding grounds to low latitude breeding grounds (Chittleborough 1965; Dawbin 1966). The species is divided into several populations globally that all migrate and show high fidelity to particular feeding and breeding areas (Darling & McSweeney 1985; Calambokidis *et al.* 2001; Boye *et al.* 2010). An exception to this is a population that appears to be resident to the Arabian Sea (Mikhalev 1997). The east Australian population makes annual migrations between winter breeding areas in the Coral Sea and summer feeding grounds in the Antarctic (Figure 1.1) (Chittleborough 1965; Dawbin 1966). In the Antarctic, summer feeding grounds have been divided into distinct areas (Area I – VI) (IWC 2005; IWC 2006), with the east Australian population currently believed to rely on area V. Potential reasons for this migration include an optimisation of energetic budgets by avoiding less productive and colder polar waters over winter (Brodie 1975), a vestigial migratory behaviour from a past era when continents were closer together (Evans 1987), improved calf survival and growth in warmer waters (Norris 1967), and avoidance of predation on calves by killer whales (*Orcinus orca*) (Corkeron & Connor 1999). Therefore, the reason that humpback whales migrate is still highly debated.

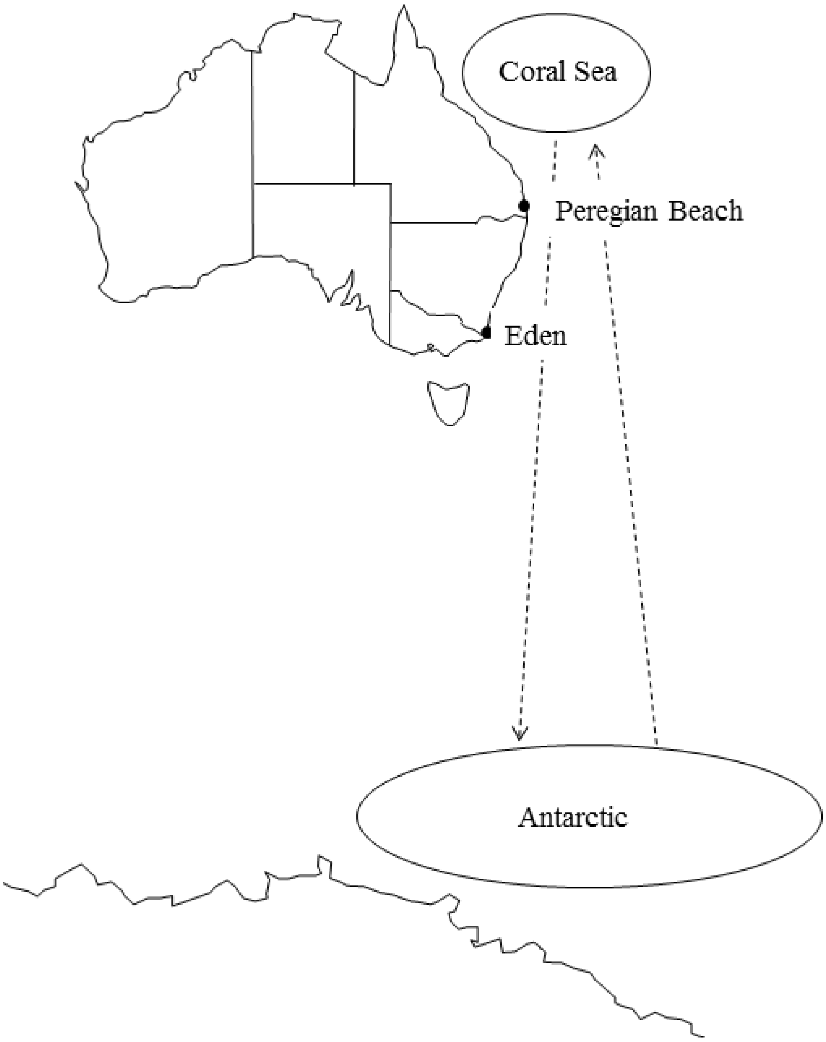

**Figure 1.1:** The relative location of the feeding grounds in the Antarctic and breeding grounds in the Coral Sea for the east Australian population of humpback whales. The locations of the two migratory sites referred to in this study, Eden and Peregian Beach, are also displayed.

The timing of migrations by humpback whales is segregated based on the gender and reproductive status of the individual (Chittleborough 1965; Dawbin 1966). Sexual maturity is believed to be reached between the ages of three to six years (Chittleborough 1965) and gestation is approximately 11 months, with females then lactating for 10.5 months on average (Chittleborough 1958). This implies that females that become pregnant, or begin lactating during one breeding season are pregnant, or lactating for both directions of the migration and the time on the feeding grounds. Females and calves are thought to separate after approximately one year when back on the breeding grounds (Clapham and Mayo 1990). The migration of humpback whales is segregated with mature, newly pregnant females being the first to reach the feeding grounds followed by the males and then lastly the newly lactating females with calves (Chittleborough 1965; Dawbin 1966). The lactating females with calves are the first to leave the feeding grounds, even though they were the last to arrive. Consequently, the lactating females spend less time on the feeding grounds compared to other whales (Chittleborough 1965; Dawbin 1966; Brown *et al.* 1995a), even though lactation is energetically demanding (Oftedal 2000). Humpback whales are sexually dimorphic, with females being slightly larger, and this difference is thought to have evolved to compensate for the higher cost of lactation and pregnancy (Clapham & Mead 1999). However, while on migration and on the breeding grounds, humpback whales have a male-biased sex ratio (Brown & Corkeron 1995b; Schmitt *et al.* 2014). The higher occurrence of males at this time suggests that not all females migrate each year, with some females possibly remaining in polar or temperate waters to continue feeding (Brown *et al.* 1995a). Therefore, continuing to feed in temperate areas would allow females to make up for the shorter time spent feeding during reproductive periods and avoid experiencing the extreme temperatures and lower food supply at the poles over winter.

### 1.7.2 Feeding behaviour

Humpback whales have evolved many morphological adaptations that make them fast and manoeuvrable predators including a low aspect ratio tail and high aspect ratio pectoral fins (Woodward *et al.* 2006). The aspect ratio of a limb relates to the length of the limb in relation to its area (Woodward *et al.* 2006). A low aspect ratio tail provides a large area to push against the water to generate propulsion which increases speed (Woodward *et al.* 2006a). In addition long, high aspect ratio pectoral fins reduce drag and allow exceptional manoeuvrability in the water column (Fish & Battle 1995). The shape of the pectoral fins generates lift, and tubercles along the leading edge assist with maintaining lift at high angles of attack, to allow for more efficient feeding lunges and sharp turning within the water column (Fish *et al.* 2008). In addition, humpback whales have large spacing between their vertebrae that increases the manoeuvrability of this species compared to other baleen whales (Woodward 2006b). This specialised morphology allows for a range of fine-scale feeding behaviours and the successful capture of many prey species. While Southern Hemisphere populations of humpback whales mainly target krill, particularly Antarctic krill (*Euphausia superba*) (Chittleborough 1965; Dawbin 1966; Friedlaender *et al.* 2006; Friedlaender *et al.* 2009b), opportunistic feeding on small fish has been observed outside of the feeding grounds (Stockin & Burgess 2005; Stamation *et al.* 2007; Alves *et al.* 2009). In the Northern Hemisphere, humpback whales have a broader diet targeting fish such as herring (*Clupea harengus*), capelin (*Mallotus villosus*) and sand lance (*Ammodytes* spp.) on their main feeding grounds, as well as krill species and other small crustaceans (Jurasz & Jurasz 1979; Dolphin 1987; Hain *et al.* 1982; Friedlaender *et al.* 2009a). Therefore, there is variation in the diet and prey species targeted by humpback whale populations around the world.

To capture prey, humpback whales complete feeding lunges in many different orientations in relation to the water surface. ‘Vertical lunges’, where the whale swims straight up perpendicular to the surface, are often used to target fish (Jurasz & Jurasz 1979). ‘Lateral lunges’ along the surface appear to be used when targeting slower moving zooplankton (Jurasz & Jurasz 1979; Kieckhefer 1992). There is a lot of variation in the terminology used to define the different lunge orientations. For example, ‘lateral lunges’ have been referred to as ‘horizontal lunges at the surface’ (Wenzel *et al.* 1988), ‘feeding on their sides’ (Stewart and Leatherwood 1985), and ‘side feeding’ (Watkins and Schevill 1979; Edds and Macfarlane 1987). In a recent review, Kot (2009) compared all of the terminology in the literature and summarised it into six lunge orientations. These include: 1) Oblique lunge (Type I): forward trajectory at angles of between 10 and 70 degrees to the sea surface without any roll. 2) Right side lateral lunge (Type IIa): forward trajectory at low angles to the sea surface with the right flank of the animal facing down, 3) Left side lateral lunge (Type IIb): forward trajectory at low angles to the sea surface with the left flank of the animal facing down, 4) Clockwise ventral lunge (Type IIIa): forward trajectory that occurs from an inverted position at a low angle to the sea surface before an axial clockwise roll, 5) Counter clockwise ventral lunge (Type IIIb): forward trajectory that occurs from an inverted position at a low angle to the sea surface before an axial counter clockwise roll, and 6) Vertical lunges (Type IV): Near vertical trajectory to the sea surface (Kot 2009). Humpback whales have been observed to use all of these lunge types except for Type IIIa, however it is suspected that this is also used at times (Kot 2009).

Prior to lunging in an area, many different prey corralling techniques have been observed to be used by humpback whales. One example is flick feeding, which involves the whale diving until its tail is almost submerged and then flicking its tail to create a suction force that condenses the prey (Jurazs & Jurasz 1979). The whale then quickly surfaces again, lunging in the same area. The use of bubbles to trap and corral prey has evolved in a number of populations (Jurasz & Jurasz 1979; Friedlaender *et al.* 2009a; Acevedo *et al.* 2011). Bubble clouds are formed by small (< 2 cm), uniformly sized bubbles that extend into large bubble clouds 4-7 m in diameter (Hain *et al.* 1982). Bubble columns are comprised of larger varying sizes of bubbles (> 2 cm) forming 1-1.5 m diameter columns (Hain *et al.* 1982). The bubbles are produced in a number of shapes, including the formation of complete circles or bubble nets (Jurasz & Jurasz 1979; Hanser 2009; Wiley *et al.* 2011). Bubble nets assist by trapping the prey, which actively avoid swimming through walls of bubbles (Sharpe 2001; Leighton *et al.* 2004). Whales have been shown to increase the turning angle of the spiral they swim in while blowing bubbles to produce the bubble net, which is hypothesised to corral prey into a tighter ball (Wiley *et al.* 2011). In addition to the use of bubbles, it is thought that the white ventral surface of the pectoral fins may also assist in corralling prey. This is due to the observation that when exposed to downwelling light, the white surface of the fins reflects a large amount of light (Brodie 1977). The reflected light may then present two light bars with a dark patch at the mouth that prey may flee towards (Brodie 1977). In an experiment using modelled pectoral fins, fish were found to swim away from the white side, suggesting that the white pectoral fins could help to lead the prey closer to the mouth (Sharpe 2001). This finding is similar to the prey corralling techniques used by other cetacean species such as dusky dolphins (*Lagenorhyncus obscurus*), that have been shown to flash their white flanks or abdomen at their prey (Wursig *et al.* 1990). Another prey corralling method used by humpback whales involves circular swimming or thrashing techniques which involves the whale swimming in a circle while thrashing its flukes from side to side. The whale then lunges in the centre of the circle. It is possible that the thrashing tail generates turbulence that works to trap prey in a similar way to that of a bubble net. This technique is believed to be uncommon but has been observed off eastern North America (Hain *et al.* 1982) and in Norway (Ingebrigtsen 1929). Finally, bottom-feeding, which involves whales removing fish from the sediment by skimming along the bottom, is also used by humpback whales (Hain *et al.* 1985; Friedlaender *et al.* 2009a; Ware *et al.* 2014). Therefore, there is variation in the prey corralling techniques used in different populations.

It is likely that each of these strategies evolved to target different prey species or varying densities and manoeuvrability of the targeted prey (Jurasz & Jurasz 1979; Hain *et al.* 1982). For slow prey found in high densities, lunge feeding may be sufficient. However, if the density of the prey becomes too low then a method that condenses the prey may evolve, such as flick feeding. In addition, for fast moving prey, more complex strategies such as bubble nets may prevent prey escaping capture. Humpback whales have also been shown to switch the feeding behaviour used in relation to the diurnal ecology of targeted prey. An example of this is humpback whales feeding on sand lance, with the whales using bubble nets to trap the prey when it is in the water column during the day and then switching to bottom-feeding when the prey is in the sediment at night (Friedlaender *et al.* 2009a). Therefore, even within a population, whales may modify their behaviour to increase the efficiency of foraging on different prey species or in different parts of the water column.

In addition to the prey corralling techniques described, humpback whales also often feed in cooperative groups. Group feeding can assist with prey capture in a three-dimensional environment (Norris & Schilt 1988). Cooperative behaviour is defined as any behaviour by two or more individuals where all individuals in the group benefit. Cooperative group behaviour while feeding usually evolves when the result of feeding together outweighs the outcome of feeding alone (Packer *et al.* 1990). This behaviour is expected in some cetacean species since they often form pods that are comprised of close kin. For example, the killer whale (*Orcinus orca*) forms matriarchal pods and is an example of a cooperative hunter in which individuals work together to coral prey (Simila & Ugarte 1993), take it in turns to share the labour of an attack (Tarpy 1979), and share catches with other members of the pod (Hoelzel 1991). However, humpback whales are polygynous (Cerchio *et al.* 2005), have short mother/offspring associations, and feeding groups have been confirmed not to comprise of close kin (Sharpe 2001). Despite this, stable feeding associations of predominantly male/female and female/female pairs have been observed on the feeding grounds (Ramp *et al.* 2010; Weinrich & Kuhlberg 1991). While associations between male/female pairs only lasted within a single feeding season, associations between female/female pairs were observed to last up to six feeding seasons in the Gulf of St. Lawrence (Ramp *et al*. 2010). Females forming stable pairs appeared to have the highest reproductive output and it was hypothesised that this could be due to cooperative feeding even though surface-feeding was not observed (Ramp *et al*. 2010). However, whether these pairs are genetically related still remains unknown (Ramp *et al.* 2010). Close associations between females have also been documented both within and between feeding seasons in the Gulf of Maine (Weinrich & Kuhlberg 1991). This was hypothesised to be due to the benefit of cooperative feeding given the extra energetic requirements of females, particularly when pregnant (Weinrich & Kuhlberg 1991). Male/male associations were only very brief (Ramp *et al.* 2010) and it has been hypothesised that males may not associate on the feeding grounds, since cooperation while feeding may only support the survival of a potential competitor in the following breeding season (Weinrich & Kuhlberg 1991). It has also been suggested that group feeding in some animals evolved to assist in monopolising food patches (Wrangham 1980). However, the lack of observations of group dominance or aggression by humpback whales on feeding grounds has led to this idea being rejected as a likely cause of group feeding in this species (Clapham 1993b; Clapham 2000). The lack of dominance hierarchies in humpback whales is thought to be the result of prey availability being variable both spatially and temporally (Steele 1976), making prey patches not worth defending. Therefore, cooperative group feeding behaviour is more likely to provide an energetic or prey corralling benefit to the individuals, rather than assisting with the defence of prey patches.

Group feeding by humpback whales often involves the whales working in synchrony. For example, bubble netting by humpback whales in Alaska and northwest British Columbia involves large groups of whales lunging at the same time to capture herring (Jurasz & Jurasz 1979; Sharpe 2001; Leighton *et al.* 2004; Hansen 2009; Wiley *et al.* 2011). Hypotheses for the occurrence of this behaviour include cooperation (D'Vincent *et al.* 1985) and interference competition for prey

(Watkins & Schevill 1979). It involves one whale swimming in a circle blowing bubbles while another whale emits a loud feeding call. It is unclear whether the function of this feeding call is to startle the herring (Sharpe 2001) or to coordinate the behaviour of the whales (D'Vincent *et al.* 1985), though it may serve both functions concurrently. Within a group of bubble netting humpback whales the same individual always blows the bubbles, while another emits the feeding call (Hanser 2009). When the bubble net is complete, up to twelve individual whales lunge synchronously in the bubble net. The consistent surfacing orientation of the whales involved (D'Vincent *et al.* 1985) and the role specialisations within the group suggest that the behaviour is cooperative. Similar to this, whales off the northeast coast of North America have been seen feeding in groups of two to three animals while using bubble clouds and columns (Hain *et al.* 1982; Wiley *et al.* 2011). However, in this area, the lack of bubble production by some whales has been hypothesised to be a form of 'cheating', with some whales taking advantage of the efforts of others (Wiley *et al.* 2011). Therefore, synchronised group behaviour by humpback whales is common and is often likely to represent a form of cooperative behaviour.

Humpback whales have been observed to lunge synchronously in groups of two to four animals in echelon formation (Jurarsz & Jurasz 1979). Echelon feeding occurs when each whale lunges offset from the next so that the first whale is slightly ahead of the second and the second whale is slightly ahead of the third and so on. This formation has also been observed during feeding of other rorqual whales such as blue whales and fin whales (Croll *et al.* 2008) and in ram feeding species such as bowhead whales (Wursig *et al.* 1984). It has also been hypothesised to assist with foraging efficiency in other pelagic species such as Atlantic bluefin tuna (*Thynnus thynnus*) (Partridge *et al.* 1983). Echelon formation is believed to assist in funnelling prey items that are missed or flee capture by the first animal into the mouth of the second animal, or to prevent prey from being able to flee to the side (Wursig *et al.* 1984). This may act to increase the density of the prey fed upon by the second animal, assuming that it is lunging in an area of similar prey density as the first animal, which would allow for more effective exploitation of prey patches than if feeding alone (Wursig *et al.* 1984). It is also potentially used as an energy saving strategy based on similar principles to those of cetacean calves who hitch a ride with their mothers (Noren *et al.* 2008) and birds in flying V formation (Weimerskirch *et al.* 2001). Therefore, echelon feeding may also provide both an energetic and prey condensing benefit to humpback whales, however, whether this is a cooperative strategy or an example of one whale taking advantage of another remains unknown.

### 1.7.3 Feeding while on migration

Historically, the feeding behaviour of humpback whales has been thought to be confined to the summer months spent on the high latitude feeding grounds, with most whales thought to fast or feed at a very low rate while breeding and migrating (Lockyer & Brown 1981a). However, there is growing evidence that humpback whales feed while on the breeding grounds and on migration. Feeding on breeding grounds has been observed off Brazil (Alves *et al.* 2009; Danilewicz *et al.* 2009), Hawaii (Salden 1989), and the Dominican Republic (Baraff *et al.* 1991). In these instances, the whales appeared to be juveniles or sub-adults and were seen to be feeding on small fish. Feeding by migrating whales has been observed off South Africa (Best *et al.* 1995), Bermuda (Stone *et al.* 1987), the Azore Islands (Visser *et al.* 2011), New Zealand (Dawbin 1966), and the east coast of Australia (Gill *et al.* 1998; Stockin & Burgess 2005; Stamation *et al.* 2007). Feeding outside of known feeding grounds has often been dismissed as rare or opportunistic behaviour that is unlikely to contribute anything substantial to the energy budget of humpback whales, despite a shortage of research to determine whether or not this is the case.

Accounts of humpback whales feeding while migrating appear to be more common in the Southern Hemisphere. Whales are generally larger in the Southern Hemisphere (Brodie 1975) and it is possible that feeding along the migratory route has evolved as a way to support their large body size. It has been suggested based on the observed energy stores of humpback whales in the Antarctic, that feeding outside of the main feeding season is likely to be more important than currently realised, unless whales have a much lower metabolic rate than would be predicted for animals of their size (Leaper & Lavigne 2007). In the Southern Hemisphere, whales also generally have a shorter feeding season compared to the Northern Hemisphere populations (approximately three-four months compared to six months) (Brodie 1975). Feeding predominantly on Antarctic krill, they also have access to a lower diversity of prey items compared to the Northern Hemisphere populations that feed on both fish and krill (Jurasz & Jurasz 1979; Hain *et al.* 1982; Friedlaender *et al.* 2009b). However, it is also possible to speculate that feeding along the migratory route may have supported the evolution of the larger body size in these populations. It is therefore likely that feeding while on migration may be important, particularly in Southern Hemisphere populations, in order for whales to meet their energy demands.

The area off Eden, New South Wales (NSW), Australia (Figure 1.1) has recently been highlighted as a potentially important feeding area for migrating humpback whales (Stamation *et al.* 2007). In this area whales have been seen to feed to a varying extent each year during the southward migration towards Antarctic feeding grounds (Stamation *et al.* 2007; Silva *et al.* 2010). Accounts of whales feeding in the area, taken from historical newspapers and journal entries from whalers, date back to the early 1900s prior to industrial whaling. Additionally, humpback whales satellite tagged off Eden appeared to delay migration to spend time in many productive temperate areas, such as off the coast of Eden, the east coast of Tasmania, and the west coast of New Zealand (Gales *et al.* 2009). The east Australian population of humpback whales has one of the best documented cases and fastest recovery from whaling world-wide (Noad *et al.* 2010). It also has one of the highest numbers of accounts of feeding behaviour while on migration of any whale population. Given the impact of feeding behaviour while on migration on the reproductive success of other migratory taxa (Newton 2006), understanding the importance of this behaviour to humpback whales may assist with understanding the recovery of different whale populations post whaling. Therefore, gaining an understanding of the importance of feeding while on migratory stopovers to humpback whales and the factors that influence their decision to stop and feed may assist in conserving this species and add greatly to our knowledge of its ecology.

## 1.8 Thesis outline

This thesis investigates the feeding behaviour of humpback whales while on migration. In order to achieve this, a method to study the surface-feeding behaviour of whales is developed and tested. The factors that may drive feeding behaviour while on migration in this species and to what extent the prey consumed during migration may contribute to the whales' energy budgets was also examined. The suitability of stable isotope analysis as a method to determine the most recent diet, and therefore the diet of whales on migration is also tested. Following this introduction there are four data chapters, which utilise data collected from two field seasons off the coast of Eden, NSW, Australia.

All current methodologies available for detecting feeding lunges in accelerometer data do not apply to surface-feeding behaviour due to the different forces acting on an animal at the surface compared to at depth. In Chapter 2, the performance of an existing methodology at detecting surface-feeding behaviour is tested and the development of a new methodology with a novel acceleration parameter to detect feeding lunges at the surface is described. The potential influence of wave drag and a lowering of propulsive efficiency at the surface on the detection of whale feeding behaviour is discussed.

Very little research has focused on the behaviour of whales feeding while on migration and as a result the current understanding of this behaviour is that it is rare or opportunistic and of little importance to whale ecology. In Chapter 3, the factors that may influence feeding behaviour are investigated by comparing the behaviour of whales feeding on different prey types while on migration to published accounts of whales' behaviour both on migration and on the feeding grounds. The results are discussed in relation to the impact of changes in prey availability on the importance of migratory feeding to humpback whales.

A complete understanding of the importance of feeding while on migration requires information about the amount of prey consumed on migration compared to annual energy budgets. Chapter 4 investigates the impact of both prey species and prey depth on the amount of feeding behaviour exhibited by the whales. Using the observed feeding rates and density of prey in the area, the likely amounts of energy consumed by humpback whales are determined in order to place migratory feeding in the context of the energy requirements of humpback whales.

Given that a change in the prey species available can influence whale behaviour, a method to determine the diet of whales while migrating is required. While stable isotope analysis is often used as a technique to study the diet of whales on main feeding grounds, very little is known about the turnover rate of baleen whale skin and whether this technique is suited to determining the most recent diet. In Chapter 5, the suitability of stable isotope analysis of skin as a technique to determine the most recent diet of whales and therefore the diet of whales on migration is investigated.

In Chapter 6, an explanation of how the thesis has furthered our knowledge of the techniques used to study whale feeding behaviour and the migratory ecology of humpback whales is provided. In addition, other factors that may influence feeding behaviour of whales while on migration and the potential importance of this behaviour to whale ecology is discussed. Finally, directions for future research, building on the research completed as a part of this thesis, are proposed.

*Photo: A right side lateral lunge by a humpback whale feeding off the coast of Eden, NSW (photo by Scott Sheehan)*

# Chapter 2

## Breaking the surface: a method to detect surface-feeding behaviour of whales in accelerometer data

*The use of accelerometer data to study the feeding behaviour of whales is becoming more common. The large majority of baleen whale species have been observed to lunge feed at the surface. Despite this, the methodologies that exist to detect lunge feeding behaviour in accelerometer data do not apply to lunges that occur once a whale breaks the surface. In this Chapter a new methodology is developed to detect surface-feeding behaviour by baleen whales, that takes into consideration the differing forces acting on a whale at the surface. It has been prepared for submission to Marine Mammal Science.*

# 2

# Breaking the surface: a method to detect surface-feeding behaviour of whales in accelerometer data

## 2.1 Abstract

Accurate detection of feeding behaviour in biotelemetry data is essential for determining feeding sites and prey preferences of species, particularly in the marine environment. For animals feeding at the surface, wave drag and a lowering of propulsive efficiency may restrict the movement of an animal. Lunge feeding is a feeding behaviour used by rorqual whale species that involves a whale accelerating towards prey and engulfing large quantities of prey-laden water. Many rorqual whale species lunge feed at the surface, yet the existing methodologies for detecting lunges in accelerometer data have not been applied to surface-feeding behaviour. The aim of this study was to develop a method that used accelerometer data to detect lunges completed at the surface and to determine whether wave drag is likely to have an influence on the detection of surface-feeding behaviour. A new acceleration parameter is described, that takes into consideration the forward acceleration of the animal in relation to the pitch of the animal. This parameter more successfully distinguished between lunges at the surface and other times when the whale surfaced to breathe, than an existing acceleration parameter initially developed for lunges at depth that considers the acceleration in all three axes to detect lunges. The new parameter, along with information on the deceleration and pitch angle of the animals, was then used in a lunge detecting algorithm that detected approximately 70% of the lunges observed to be completed by the whales at the surface during focal follow sampling, and had a false detection rate of approximately 8%. The forward acceleration of lunges was found to significantly decrease with increasing proximity to the surface. This lower acceleration at the surface is likely to influence the ability to detect lunge feeding behaviour close to the surface. Future research should attempt to determine the cause of this relationship which may be the result of wave drag and lower propulsive efficiency influencing the energetics of surface-feeding whales, or due to behavioural flexibility by the whales that may reduce the propulsion applied to a lunge at the surface to lower the drag encountered. Such a strategy may allow whales to save energy while foraging on slow moving prey trapped against the surface.

**Keywords:** drag, DTAG, foraging effort, humpback whale, lunge, minimum specific acceleration

## 2.2 Introduction

Knowing the rate at which predators attempt to capture prey allows for a more accurate estimation of the energy expenditure allocated to foraging by an animal (Stephens & Krebs 1986). In the marine environment, direct observation of feeding behaviour is not always possible; as a consequence, the use of biotelemetry devices such as accelerometers to detect feeding behaviour has become more common. In some instances, patterns in the data recorded by a biotelemetry device can be confirmed to reflect a specific behaviour using concurrent video recordings or photographs. For example, the head movements recorded by accelerometer tags attached to chinstrap penguins (*Pygoscelis antarcticus*) and gentoo penguins (*Pygoscelis papua*) were confirmed to coincide with prey capture attempts using images taken by a back-mounted camera (Kokubun *et al.* 2011). In other instances, particularly where behaviours cannot be easily detected in other ways, detection of feeding behaviour relies on assumptions being made about the patterns in accelerometer data that are likely as a result of the kinematics of the behaviour. Therefore, it is possible that inaccurate assumptions about the kinematics of feeding behaviour could result in incorrect detection of feeding behaviours and misjudgements about important feeding sites and the prey requirements of a species.

Kinematic parameter values are likely to vary with depth, irrespective of the kinematics of the behaviour, due to changes in the forces that act on an animal at the surface compared to at depth. Many marine animals feed near, or at, the surface. This is due to the surface providing an interface between the water and the air that many animals need to breathe, or to prey species being distributed in the upper water column. As an animal breaks the surface, any changes in buoyancy, pressure drag or friction drag that occur become dominated by wave drag, which is a force that is generated by an object moving near the surface. Wave drag is caused by the interaction of two different wave formations generated by the motion of the animal near the surface (Hertel 1966). Studies have shown that an animal moving at the surface is likely to experience a drag force between 2.5 and 5 times higher than an animal moving at depth, with wave drag contributing up to 50% of the drag component depending on the speed of the animal (Goldman 2001; Vennell *et al.* 2006; Blake 2009). Wave drag is highest at the surface and gradually decreases with depth until it is negligible at a depth equal to two to three times the diameter of the animal's body (Hertel 1966). In addition to an increase in wave drag, the propulsive efficiency of whales is likely to be reduced at the surface due to the use of oscillatory propulsion in an up and down motion, which displaces water near the surface and limits the forward motion generated by a kick (Fish 1996). Therefore, it is most likely that animals feeding at the surface experience a higher resistance to movement and less efficient propulsion than animals feeding at depth, even if they have not broken the surface.

Rorqual whales are a group of baleen whales that have ventral pleating that allows for the expansion of the oral cavity while feeding (Orton & Brodie 1987). Lunge feeding is a feeding mode used by rorqual whales that involves an animal swimming at speed towards a patch of prey and engulfing large quantities of prey-laden water (Goldbogen *et al.* 2007). The large majority of rorqual whale species have been observed to lunge feed at the surface (Jurasz & Jurasz 1979; Watkins & Schevill 1979; D'Vincent *et al.* 1985; Hoelzel *et al.* 1989; Schoenherr 1991; Kot 2005; Wiseman 2008; Friedlaender *et al.* 2009). Despite this, studies of the detailed kinematics of lunge feeding and assessment of the energetic requirements of this behaviour have been restricted to studies focusing on feeding behaviour at depth (10-260 m) (Acevedo-Gutierrez *et al.* 2002; Goldbogen *et al.* 2006; Goldbogen *et al.* 2011; Simon *et al.* 2012; Ware *et al.* 2011). This is most likely due to limitations in the methods available for detecting lunge feeding behaviour in biotelemetry data when the whale breaks the surface.

The most common method used to detect a lunge in biotelemetry data is to measure changes in the level of flow noise recorded by a digital tag attached to the animal, as flow noise increases with the speed of the animal (Goldbogen *et al.* 2006; Goldbogen *et al.* 2011; Simon *et al.* 2012; Ware *et al.* 2011). The use of this technique is unlikely to be reliable for detecting lunges near the surface due to the spike in noise level expected as the whale and the tag break the surface, irrespective of whether the whale lunged or surfaced to breathe. Other techniques look for changes in the accelerometer signal to identify a lunge (Ware *et al.* 2011; Simon 2010; Simon *et al.* 2012), but these studies often explicitly exclude the upper section of the water column due to the changes in buoyancy and drag that occur when a whale breaks the surface (Simon *et al.* 2012). Despite the exclusion of the upper water column in the use of this method, a peak in minimum specific acceleration has recently been put forward as a reliable cue for detecting lunge feeding that would allow for satellite transmission of data on feeding behaviour over longer time periods to provide information on energy budgets (Simon *et al.* 2012). However, to the best of our knowledge, the suitability of this method for detecting surface-feeding behaviour has never been tested. Given the observations of whales feeding at the surface, the exclusion of data from the surface layer is likely to result in inaccurate calculations of feeding rates and energy budgets.

While a method for detecting feeding behaviour at depth is clearly required, it is often assumed that a method for detecting feeding behaviour at the surface is less important due to the potential to visually observe behaviour at the surface. However, even when whales are observed, determining the occurrence of lunges by visual observation alone is likely to result in an underestimation of the number of lunges actually completed due to an observer potentially missing lunges, particularly when the group size is large. In addition, whales cannot be visually observed at night or in bad weather, so data from archival tags are the only data available during these times. Using velocity data from archival tags, the rate of feeding by blue whales (*Balaenoptera musculus*) has been shown to be approximately twice as high at night compared to during daylight hours (Doniol-Valcroze *et al.* 2011). This indicates that the ability to detect feeding behaviour overnight and at other times when a whale cannot be observed is essential to understanding activity budgets and energetic requirements. Some studies have used biotelemetry data to successfully study feeding behaviour of rorqual whales near or at the surface. Ware *et al.* (2011) successfully detected shallow lunges by humpback whales using accelerometer data, but only included lunges that occurred deeper than 10 m (Ware *et al.* 2011) that were likely to be outside of the zone where wave drag will have an influence. Additionally, a consistent pattern in the feeding behaviour of the animals has been used to determine the occurrence of loops while blowing a bubble-net preceding a lunge to the surface by humpback whales (Friedlaender *et al.* 2009). However, not all populations or species of rorqual whales use bubble-nets while feeding and there is also often large variation in the roll angles that can occur during lunges (Kot 2009). This suggests that a consistent pattern in feeding behaviour that can be used to detect lunges may rarely be present. Speed can be estimated using paddlewheels (Baird *et al.* 2005), which have been successfully used to determine when surface-feeding has occurred in blue whales (Doniol-Valcroze *et al.* 2011), but speed data are not recorded by accelerometers. Orientation-corrected depth rate can also be used to calculate speed (Miller *et al.* 2004). Although, it becomes less accurate to calculate speed when the whale is at a shallow pitch angle (Ware *et al.* 2011) while feeding near the surface. Therefore, the methods that are currently available for detecting lunges are not always applicable for detecting surface-feeding behaviour from accelerometer tag data.

The aims of this study were to 1) test whether an existing method of using peaks in minimum specific acceleration to detect feeding behaviour at depth can be used to detect lunges in the surface-feeding behaviour of humpback whales (*Megaptera novaeangliae*), 2) develop a new method to assist with detecting lunges in surface-feeding behaviour from accelerometer data and, 3) determine the potential influence of wave drag on the acceleration of lunges completed near the surface and therefore the potential influence of this force on the detection of feeding behaviour.

## 2.3 Materials and methods

### 2.3.1 Data collection

Data were collected off the coast of Eden, New South Wales, Australia (37.07° S, 149.90° E) in an area where humpback whales stop to feed while on their southward migration back towards Antarctic feeding grounds (Stamation *et al.* 2007). High resolution digital tags (DTAGs) (Johnson & Tyack 2003) were attached to the dorsal surface of whales approximately halfway between the blow holes and dorsal fin using a 6 m long carbon-fibre pole. DTAGs are small, light-weight tags that contain a 3-axis accelerometer (± 2 g range) and 3-axis magnetometer that record data on the 3-dimensional movement and acceleration of the animal (Johnson & Tyack 2003). In addition, a pressure sensor records the dive profile of the animal (accuracy of ± 0.5 m). The sampling rate of the sensors was 50 Hz and these data were decimated to 5 Hz during calibration. While other studies have relied on 25 Hz (Simon *et al.* 2012) or 50 Hz data (Goldbogen *et al.* 2013), these studies often aim to describe the fine-scale kinematics of lunges, such as the frequency of fluking prior to a lunge. Many previous studies have successfully detected the presence of lunges at depth using 1 Hz to 5 Hz accelerometer data (Goldbogen *et al.* 2006; Doniol-Valcroze *et al.* 2011, Ware *et al.* 2011). Given that the aim of this study was to detect the presence of a potential lunge, not to describe it in detail, 5 Hz data were used to ease computations and data manipulation. The time scale of a lunge is approximately 10 seconds, and as a consequence, this sampling rate is unlikely to have created any issues associated with aliasing.

The tag was attached to the whale using four silicon suction cups and was programmed to release from the whale after two to three hours, depending on weather conditions. The tag contained a VHF transmitter that was used to track the whale while the tag was attached. Once off the whale, the tag floated to the surface and was collected. The data were then downloaded via infrared transmission.

A focal follow was completed on each tagged animal. This involved using a pre-defined ethogram (Appendix 2) to record every surface-behaviour of the tagged animal (Mann 1999). When surface-feeding lunges occurred, the orientation of the lunge was noted using previously described definitions of lunge types (Kot 2009). These lunge types included 1) Oblique lunges (Type I): forward trajectory at pitch angles of between 10 and 70 degrees without any roll, 2) Right side lateral lunges (Type IIa): forward trajectory at low pitch angles with the right flank of the animal facing down, 3) Left side lateral lunges (Type IIb): forward trajectory at low pitch angles with the left flank of the animal facing down, 4) Clockwise ventral lunges (Type IIIa): forward trajectory that occurs from an inverted position at a low pitch angle before an axial clockwise roll, 5) Counter clockwise ventral lunges (Type IIIb): forward trajectory that occurs from an inverted position at a low pitch angle before an axial counter clockwise roll, and 6) Vertical lunges (Type IV): Near vertical trajectory (Kot 2009). The data were recorded vocally by an observer using a H1 Zoom acoustic recorder and later transcribed. All focal follows were completed by a single observer (KO) to reduce inter-observer reliability issues (Mitchell 1979). The length of a focal follow was determined by the length of the tag deployment. Focal follows and DTAG data were time synchronised using a hand held GPS (Garmin GPSmap 78SC). Only lunges that broke the surface, where the whale was seen to be collecting water with an open mouth, were recorded by the observer.

### 2.3.2 Testing the existing method

Searching for peaks in minimum specific acceleration (MSA) in accelerometer data is a method that was developed to detect lunges by humpback whales feeding at depth (Simon *et al.* 2012). MSA is calculated by using the norm of the acceleration vector in all three axes (x, y and z) and subtracting the influence of gravity. This gives a MSA value for every sampling point throughout the tag deployment. Simon *et al.* (2012) focused on feeding behaviour by humpback whales at depth and excluded the upper 40 m of the water column. It was stated that this method may not be suitable once the whale breaks the surface due to changes in buoyancy and drag forces (Simon 2010).

Whales at the surface have been recorded to lunge at speeds of approximately 2.5 $ms^{-1}$ (Jurasz & Jurasz 1979). This is similar to the average speeds recorded for whales lunging at depth (Goldbogen *et al.* 2007; Goldbogen *et al.* 2008; Simon *et al.* 2012). Given that the drag force is likely to be higher at the surface due to wave drag, more propulsion would be required by the animal to reach these similar speeds. This should result in similar net acceleration values for whales lunging at depth and whales lunging at the surface. Therefore, it seemed plausible that this method of searching for peaks in MSA could work for detecting the lunges at the surface. It should be noted that Simon *et al.* (2010; 2012) also used other lines of evidence, including flow noise, to assist with determining whether a spike in MSA was the result of a lunge. However, as mentioned previously, flow noise is unlikely to be a reliable indicator of a feeding lunge for surface-feeding whales.

A receiver operator characteristic curve (ROC curve) was produced to test the suitability of MSA as a potential parameter for separating ‘true lunges’ from ‘false lunges’. ‘True lunges’ were defined as the times when the whale was visually observed to lunge at the surface, with water filling an open mouth. ‘False lunges’ were defined as times when the whale broke the surface but was observed to breathe, mouth closed and did not lunge. For all cases, the maximum value of MSA within ± 5 seconds of the time of the observed behaviour was used in the analysis. A ROC curve displays the relationship between the sensitivity and specificity of a test at different threshold levels of a given parameter (in this case, MSA) (Metz 1978; Faraggi & Reiser 2002). Sensitivity relates to the probability of a positive result, or in this case, the probability of detecting a 'true lunge' at each threshold. Specificity relates to the probability of a negative result and is visualised on the curve as 1-specificity (Metz 1978; Faraggi & Reiser 2002). The area under the curve is equal to the probability that a 'true lunge' has a higher value for the given parameter than a 'false lunge' (Faraggi & Reiser 2002). In the case of MSA, the ROC curve revealed that this parameter is only a fair predictor of 'true lunges' vs. 'false lunges' with an area under the curve of 0.73 (Figure 2.1). As a consequence, a new parameter that more accurately discriminates between 'true lunges' and 'false lunges' at the surface was required.

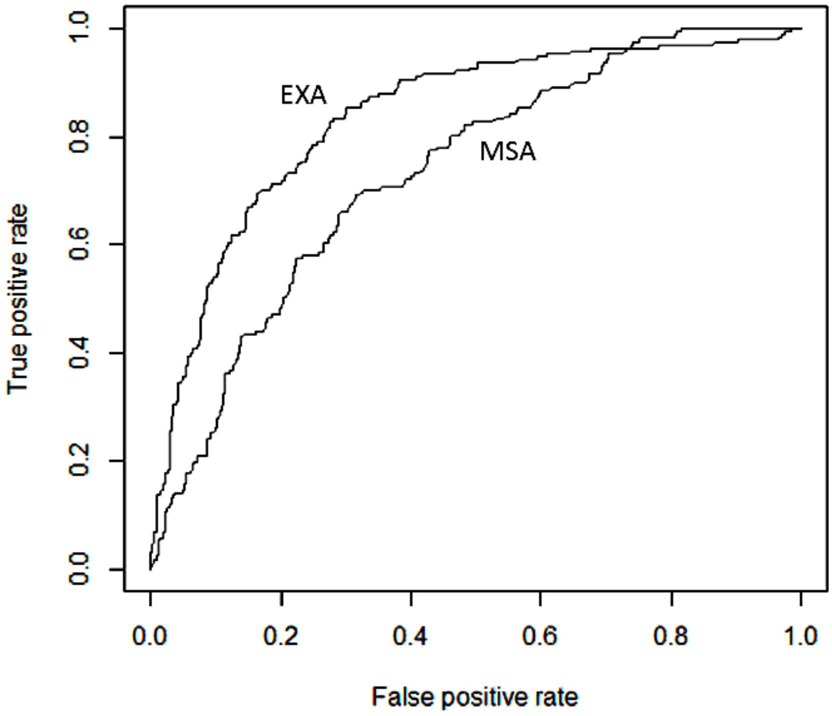

**Figure 2.1:** Receiver operator characteristic curve (ROC curve) comparing the true positive rate to the false positive rate for different thresholds of both minimum specific acceleration (MSA) (used in the existing method) and excess x-acceleration (EXA) (used in the new method).

### 2.3.3 Development of a new technique for detecting surface-feeding lunges

Given that lunge feeding involves an animal accelerating towards prey, acceleration in the forward direction is likely to indicate the presence of a potential lunge. Consequently, the acceleration in the x- axis in 'whale-frame' (see Johnson & Tyack 2003) was chosen for use given that it represents the forward acceleration of the whale. Although acceleration in the other two axes in ‘whale-frame’ is still likely to occur during a lunge (Simon *et al.* 2012), the amount of acceleration in these axes is likely to vary as a function of the amount of roll completed by the animal and the amount of lift generated by movement of the pectoral fins. Given the variability expected in these two axes, the acceleration signals in these directions were excluded.

In ‘whale-frame’, the acceleration in all three axes is still influenced by gravity (see Johnson & Tyack 2003; equation (3)). This is accounted for in the MSA method by subtracting 1 g from the magnitude of the measured acceleration. In the x-axis in ‘whale-frame’, this influence is likely to vary as a function of the pitch of the animal given that gravity acts in the vertical plane (Figure 2.2).

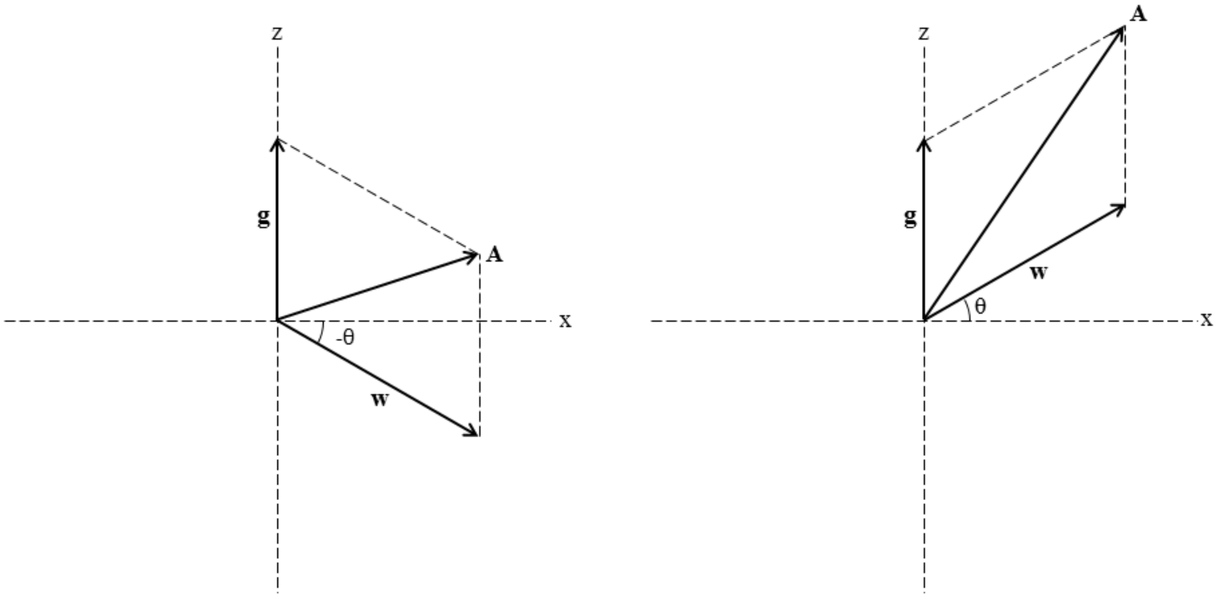

**Figure 2.2:** Vector diagram displaying the magnitude of acceleration recorded by the tag (A) for descending (left) and ascending (right) pitch angles of the whale (θ). Even when the force applied by the whale (w) is constant, the magnitude of the force recorded by the tag (A) will vary in relation to the pitch angle (θ) as a result of the influence of gravity (g) shown in the vertical direction as recorded by the accelerometer.

Therefore, as the animal ascends or descends, gravity is likely to have a stronger influence on the x-acceleration signal than when the animal is moving in the horizontal plane. To compensate for this, the influence of gravity was subtracted from the x-acceleration signal as follows (Figure 2.3):

$$\boldsymbol{EA} = \boldsymbol{A_w} - \boldsymbol{G}$$

$$\begin{bmatrix} EXA \\ EYA \\ EZA \end{bmatrix} = \begin{bmatrix} a_{w,x} \\ a_{w,y} \\ a_{w,z} \end{bmatrix} - g \begin{bmatrix} \sin(\theta) \\ 0 \\ \cos(\theta) \end{bmatrix}$$

$$EXA = a_{w,x} - g\sin(\theta)$$

$$EXA = a_{w,x} - g\sin(\theta)$$

where θ is the pitch angle of the whale as defined by Johnson and Tyack (2003). This produced excess x-acceleration (EXA) values that were representative of the forward acceleration by the animal regardless of its pitch angle (Figure 2.3).

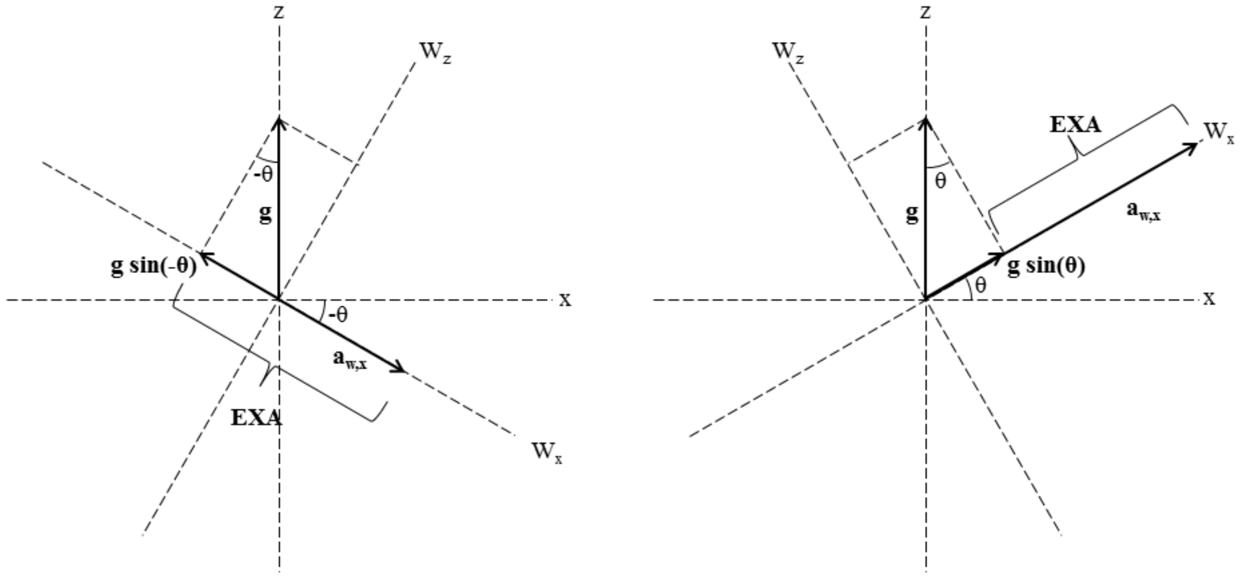

**Figure 2.3:** Vector diagram displaying how excess x-acceleration (EXA) was calculated based on the forward acceleration of the whale ($A_{w,x}$) corrected for the pitch angle (θ) of the whale. The scenarios displayed represent the influence of gravity on the recorded forward acceleration of the whale when the whale is diving (left) and when the whale is ascending towards the surface (right). In both scenarios, the forward acceleration of the whale ($A_{w,x}$) is adjusted for the influence of gravity (g) by subtracting the magnitude of the gravity vector multiplied by sin(θ).

In order to test whether EXA represented a more reliable parameter than MSA for separating ‘true lunges’ from ‘false lunges’, a ROC curve was produced. EXA was shown to be a good predictor of ‘true lunges’ vs. ‘false lunges’ at the surface, with the area under the curve being equal to 0.84

(Figure 2.1). Therefore, the EXA parameter distinguished between lunges at the surface and other times when the whale surfaced to breathe more effectively than MSA, regardless of the threshold or level of MSA chosen to detect lunges. Based on the ROC curve, the EXA threshold of 0.02 g was chosen to detect lunges as it represented the best balance between the true positive and false positive rate (Figure 2.4A).

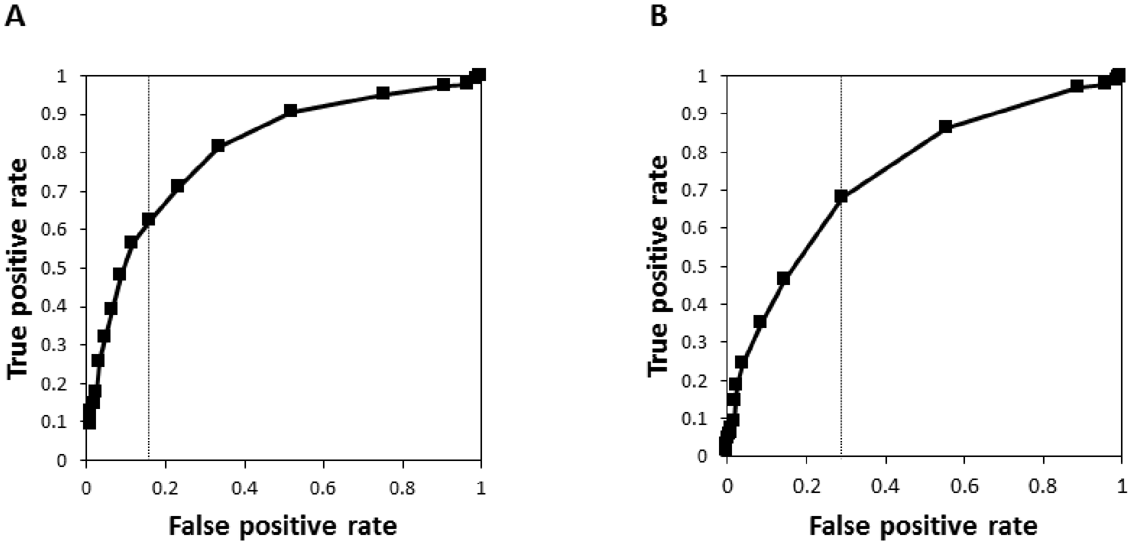

**Figure 2.4:** Receiver operator characteristic curves (ROC curves) for both excess x-acceleration (EXA) (A) and EXA jerk (B). Each black square displays the true positive rate and false positive rate for a different threshold of each parameter. The thresholds set for the EXA (0.02 g) and EXA jerk (-0.01 g/sample) in the lunge detecting algorithm are displayed by the vertical grey lines and represent the best balance between a high true positive rate and low false positive rate with the aim being to increase the number of true lunges detected, while minimising the increase in the false detection rate.

It is common for detection methods to rely on more than one parameter to detect the presence of a lunge. For example, a combination of speed and deceleration (Doniol-Valcroze *et al.* 2011) or acceleration and flow noise (Simon *et al.* 2012) have previously been successfully used to confirm the presence of lunges. By relying on multiple parameters likely to represent the kinematics of the behaviour in question, detections made by a method are more likely to be truly representative of the behaviour. Although EXA was able to distinguish between lunges and other times when the whale surfaced to breathe, it was possible that peaks in EXA would occur in association with other behaviours. To ensure that detections were more likely to represent lunges, rather than surges in forward acceleration associated with social interactions, two additional parameters were chosen for use in the lunge detecting algorithm. Another feature of feeding lunges is the rapid deceleration of the animal during the lunge due to the increased drag associated with the mouth opening (Goldbogen *et al.* 2006). A jerk is a rate of change in acceleration, with a highly negative jerk indicating a rapid deceleration of the animal. Therefore, the EXA jerk (the rate of change in EXA) was calculated. A ROC curve was produced to test the performance of EXA jerk as a parameter to separate ‘true lunges’ from ‘false lunges’. The area under the curve was equal to 0.75 and given the shape of the curve, -0.01 g/sample was set as the threshold for EXA jerk (Figure 2.4B).

A lunge-detecting algorithm (LDA) (Appendix 1) was created to determine times when EXA was greater than 0.02 g and the EXA jerk dropped below -0.01 g/sample within two seconds after the time of maximum EXA. In addition, whales feeding near the surface typically approach prey from below in an attempt to trap prey against the surface (Kot 2009), meaning that whales feeding at the surface typically have positive pitch angles. As a consequence, pitch angle was included in the LDA to only output times when the data met all three requirements: the EXA was greater than 0.02 g, the pitch angle was positive, and EXA jerk was less than -0.01 g/sample within two seconds after the peak in EXA. These threshold levels were determined based on lunges completed at the surface, and given that drag is likely to be higher at the surface, the acceleration thresholds set were less likely to miss a lunge with increasing depth. As a consequence, the LDA was run over the entire data set with the above thresholds for each of the tag deployments, regardless of depth. The times where the data met all three requirements of the algorithm were output as detection times. The times of detections were then compared to the times of visually observed lunges to determine the proportion of visually observed lunges that were detected and missed by the algorithm. For each of the lunges missed by the algorithm, the maximum EXA of the visually observed lunge was determined.

### 2.3.4 Application of a TrackPlot filter

Studies often rely on the use of human visual systems to validate that the detections made by an automated lunge detector are likely to represent a lunge (Friedlaender *et al.* 2009; Ware *et al.* 2011; Tyson *et al.* 2012). The data collected by accelerometers on digital tags near the surface can be quite noisy due to the tag breaking the surface. To account for this, and to ensure that a conservative indication of lunges was obtained, a process of visual validation was used to ensure that each of the detections made by the algorithm were likely to represent lunges. To achieve this, the DTAG data were entered into the visualisation software TrackPlot (Ware *et al.* 2006) to provide a 3-dimensional view of the movement of the tagged individual. This program uses the process of dead-reckoning to produce a pseudo-track of the whale’s movement in three-dimensions but makes an assumption of constant speed throughout the tag deployment (Ware *et al.* 2006). Although the assumption of constant speed is unrealistic for whale behaviour, over the short time scale of a lunge (approximately 10 seconds), the three-dimensional picture produced by TrackPlot is still likely to provide an accurate indication of the orientation of the whale. Once the tag data were entered into TrackPlot, the pseudo-track produced was compared to the visual observations of surface-behaviour to ensure that the orientations of the whale as shown by TrackPlot at various times matched the observed orientations of the whale during the focal follow.

For each of the detections made by the LDA, the movement of the animal in TrackPlot at that time was observed to determine if the time corresponded with a lunge-like movement. Only times that coincided with lunge-like movement were considered to represent detections of a lunge. A lunge-like movement was defined based on the previously described definitions of lunge types (described above) completed by rorqual whales to incorporate the likely variation in roll and pitch angle that occurs in lunges (Kot 2009). This helped to exclude any behaviours by the whale that met the requirements of the LDA but were not likely to be lunges. Each of the detection times considered to be a lunge using the TrackPlot filter were compared to the times of visually observed lunges in the focal follow to categorise each of the detected lunges as a visually-observed or a non-visually observed lunge. The detection times considered unlikely to represent a lunge were divided into times likely to represent another form of surface-active behaviour (such as a breach where the whale jumps out of the water or a peduncle slap where the entire fluke and peduncle is raised clearly out of the water and forcibly slapped against the water surface) and times likely to represent a false detection by the LDA. This enabled the proportion of detections that represented both lunge types, and the proportion that represented false detections to be determined. The total false detection rate was defined as:

$$Total\ false\ detection\ rate = \frac{Surface\ active\ behaviour\ detections\ +\ False\ detections}{Total\ number\ of\ detections}$$

However, given this number is likely to be inflated depending on the amount of other surface-active behaviours completed by a whale, a corrected false detection rate was determined based on:

$$Corrected\ false\ detection\ rate = \frac{False\ detections}{Total\ number\ of\ detections}$$

### 2.3.5 Influence of wave drag on the detection of surface feeding behaviour

A linear mixed model (LMM) was used to determine whether the proximity of a lunge to the surface had an influence on the magnitude of the acceleration of the lunge, and therefore on the potential to detect the lunge. EXA was used as the response variable, with depth as the explanatory variable. Given that the location of tag placement can affect the magnitude of the acceleration signal recorded, and that multiple lunges completed by the same animal are not independent, the whale identity was used as a random effect in the model. The nlme package (Pinheiro *et al.* 2013) in R (R development core team 2013) was used with significance level set a $p < 0.05$. In order to meet the assumption of normality made by the model, the data were log transformed. Outliers were defined as any data points outside 1.5 times the interquartile range above the upper quartile and below the lower quartile of the data. Given that outliers have a stronger influence on the outcome of a model than other data points, the model was run with outliers (n = 5, 1.9% of the data points) removed. The residuals were checked for homoscedasticity and were normally distributed. Given the nature of the data collection of an individual over time, the model was also checked for the presence of temporal autocorrelation using the Auto- and Cross- Covariance and -Correlation Function Estimation (acf) in R (R development core team 2013). The degrees of freedom were determined based on the number of tagged animals, minus the number of parameters in the model. All means are presented as mean ± standard error.

## 2.4 Results

### 2.4.1 Observed surface-feeding behaviour

Nine humpback whales were tagged off the coast of Eden, NSW, Australia but only three of these animals were observed during the focal follows to lunge feed at the surface (96, 20 and 74 times, respectively) (Table 2.1). It was determined from visual observations that all three animals were feeding on krill (*Nyctiphanes australis*). Many different lunge types were observed to be completed by each whale including oblique lunges, right side lateral lunges, left side lateral lunges, and vertical lunges. An example of the kinematic pattern of each of the lunge types observed is displayed in (Figure 2.5).

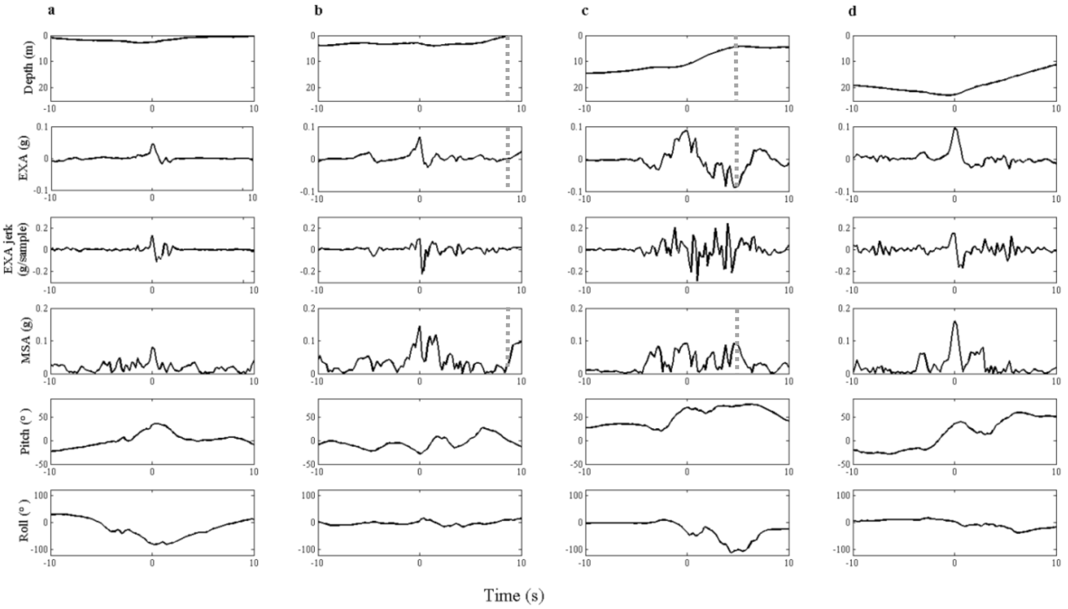

**Figure 2.5:** Kinematic diagrams displaying the details of four different lunge types including a) a right side lateral lunge, b) an oblique lunge, c) a vertical lunge at the surface, and d) a vertical lunge at depth. Left side lateral lunges had a similar pattern to right side lateral lunges for all parameters except for roll which occurred in the opposite direction. Changes in depth (m), excess x-acceleration (EXA) (g), EXA jerk (g/sample), minimum specific acceleration (MSA) (g), pitch (degrees) and roll (degrees) are displayed. Time zero is the time of maximum EXA for each lunge. The grey dotted lines (in (b) and (c)) represent the time the whale was observed to break the surface following the lunge.

### 2.4.2 Detecting surface-feeding behaviour with the new method

The LDA detected approximately 70% of the visually observed lunges (Table 2.1). After the TrackPlot filter was applied, the detection rate of the visually observed lunges remained the same (Table 2.1). This implies that approximately 30% of the observed lunges were missed by the new method, regardless of whether the TrackPlot filter was applied or not. This also indicates that the TrackPlot filter was successful at determining whether a detected time represented a lunge or not as 100% of the observed lunges that were detected were determined to represent a lunge using the filter. The average EXA of the missed lunges was found to be 0.007 g which is below the 0.02 g threshold set in the LDA, with some observed lunges having an EXA very close to 0.0 g.

**Table 2.1:** Performance of the lunge detecting algorithm (LDA) displayed in two parts: 1) The success of the LDA at detecting visually observed lunges (VO lunges) and 2) The detections made by the algorithm when applied to the whole data set. The results are shown as both the detections made purely by the LDA and as the detections with the TrackPlot filter applied (TP filter).

**Visually observed lunges**

| Whale number | 1 | 2 | 3 | Overall |
|---|---|---|---|---|
| Tag number | mn11_258b | mn11_259a | mn11_260a | |
| Number of VO lunges | 96 | 20 | 74 | 190 |
| VO lunges detected by the LDA (%) | 64 | 65 | 74 | 68 |
| VO lunges detected by the LDA (TP filter) (%) | 64 | 65 | 74 | 68 |
| VO lunges missed by the LDA (TP filter) (%) | 37 | 35 | 26 | 32 |
| EXA of missed VO lunges (g) (average ± se) | 0.008 ± 0.001 | 0.005 ± 0.007 | 0.007 ± 0.006 | 0.007 |

**Whole data set**

| Whale number | 1 | 2 | 3 | Overall |
|---|---|---|---|---|
| Total number of detections by the LDA | 138 | 72 | 120 | 330 |
| Number of detections by the LDA (TP filter) | 126 | 28 | 108 | 262 |
| Detections that were VO lunges (%) | 44.2 | 18.1 | 45.8 | 39.1 |
| Total false detections (TP filter) (%) | 8.7 | 61.1 | 10.0 | 20.6 |
| Number of SA behaviours visually observed | 13 | 39 | 14 | 66 |
| False detections confirmed to be SA behaviour (%) | 41.7 | 79.5 | 25.0 | 63.2 |
| False detections when SA behaviours removed (%) | 5.1 | 12.5 | 7.5 | 7.8 |
| Number of non-VO lunges detected (TP filter) | 65 | 15 | 53 | 133 |
| Detections that were non-VO lunges (%) | 47.1 | 20.8 | 44.2 | 40.3 |
| Depth of non-VO lunges (m) (average ± se) | 8.0 ± 1.0 | 5.8 ± 1.9 | 7.6 ± 1.0 | 7.6 |

When applied to the whole data set, the LDA made a total of 330 detections (Table 2.1). Without applying a further filter, all 330 detections would have been considered to represent lunges by the whales. However, when the TrackPlot filter was applied to each of the detections the number of detected lunges was reduced to 262 (Table 2.1). Examples of the lunge-like movements that were observed in TrackPlot to validate that the detected times were likely to represent a lunge is provided in Figure 2.6. After applying the TrackPlot filter, 39.1% of the total detections by the LDA were determined to represent visually observed lunges and 40.3% were of non-visually observed lunges (Table 2.1). Of the non-visually observed lunges, 27.1% were confirmed to be lunges by comparison to the focal follow where the observer had seen a lunge but could not identify whether the focal animal was the individual lunging. Given the average depth of the non-visually observed lunges was 7.6 m (Table 2.1) it is likely that the remaining lunges occurred underwater, out of sight of the observer.

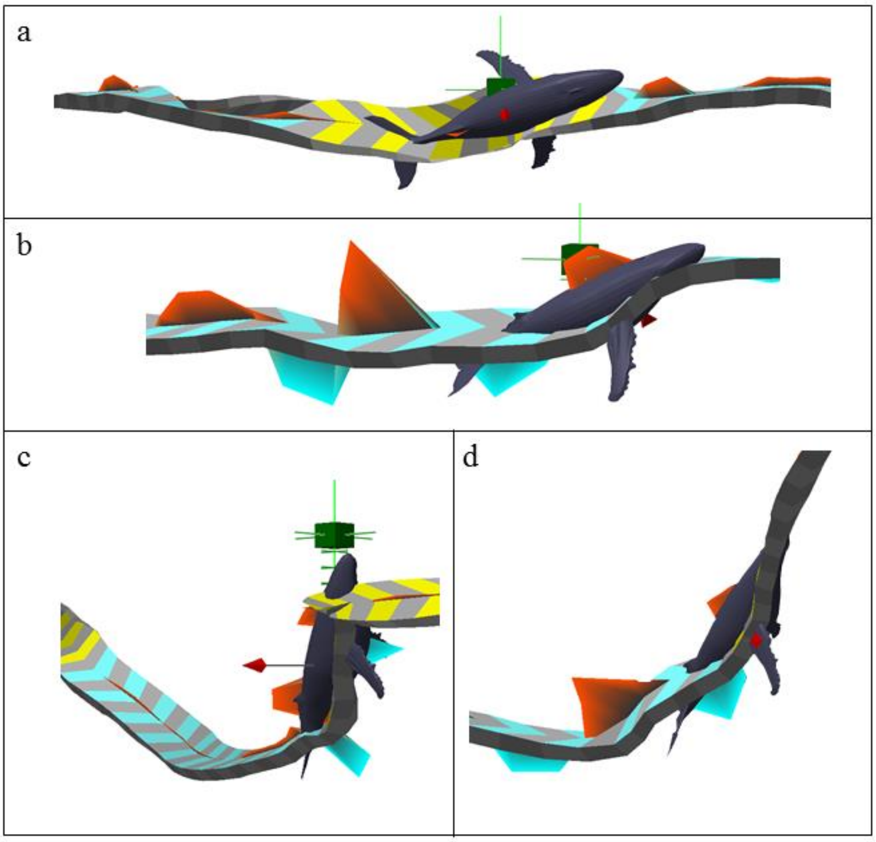

**Figure 2.6:** An example of the lunge-like movements for each of the lunge types as shown in TrackPlot. The lunge types shown include a) a right side lateral lunge, b) an oblique lunge, c) a vertical lunge at the surface, and d) a vertical lunge at depth. The lateral view of all four lunge types is displayed.

The total false detection by the LDA was 20.6% and represented times that did not correspond to a lunge-like movement (Figure 2.7). Of the detections not corresponding to a lunge-like movement, 63.2% were determined likely to represent another form of surface-active behaviour (such as breaches and peduncle slaps) and 36.8% were determined likely to be false detections. Of the detection times determined to be likely to be due to another surface-active behaviour using the TrackPlot filter, 100% were confirmed to be the result of a surface-active behaviour when compared to the focal follows. Animal 2 had the largest number of surface-active behaviours observed throughout the focal follow (Table 2.1) and this resulted in a larger total error for that animal (61% of detections were considered to not represent a lunge-like movement after the TrackPlot filter was applied). Given this, the impact of surface-active behaviours on the error rate of the LDA was removed by only considering false detections. This resulted in a corrected error rate of 7.8% for the new method (Figure 2.8).

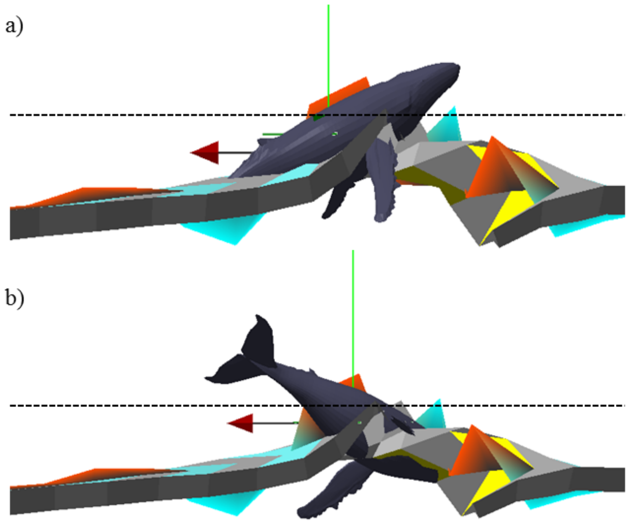

**Figure 2.7:** Example of a detection that did not represent a lunge-like movement. The reason for the detection by the lunge detecting algorithm is displayed in (a) with the whale accelerating towards the surface at a positive pitch angle, approximately one second prior to a high jerk as the animal flicks its tail out of the water (b) to complete a peduncle slap. Such movement at this time distinguishes it as another surface-active behaviour, rather than a lunge-like movement. The black dashed line indicates the water surface.

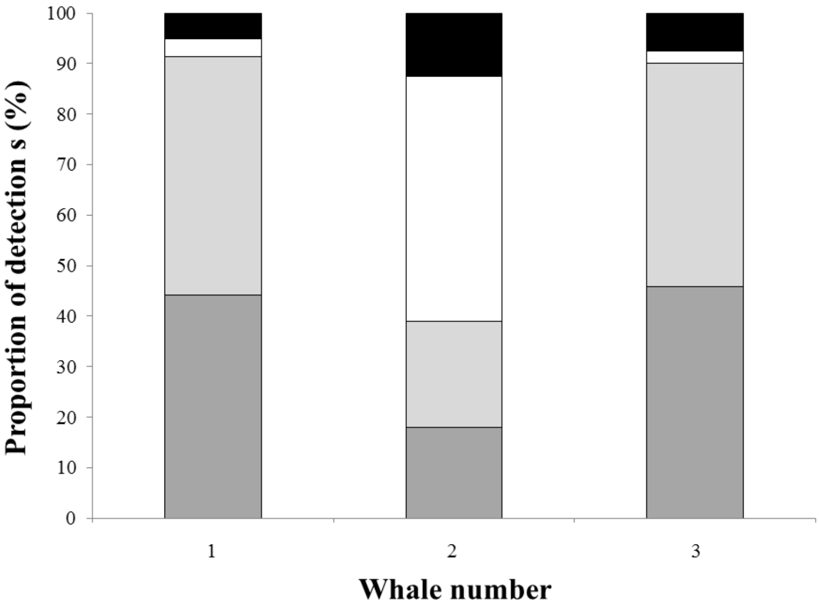

**Figure 2.8:** Comparison of true vs. false detections by the lunge detecting algorithm (LDA) for the three tag deployments as determined by the TrackPlot filter and comparisons to the focal follow record. Colours represent the proportion of detections made by the LDA that were visually observed lunges (dark grey), non-visually observed lunges (light grey), surface-active behaviours (white) and false detections (black). Total error for the LDA is a combination of the surface-active behaviours (white) and false detections (black). Corrected error for the LDA is only the false detections (black).

### 2.4.3 Influence of wave drag on the detection of surface feeding behaviour

The depth of maximum EXA for the detected lunges (visually observed and non-visually observed) ranged from 0 m to 49 m with a mean of 5.4 m ± 3.5 m. The depth of the lunge was found to have a significant influence on the acceleration signals with EXA found to significantly decrease as the depth of the lunge decreased (LMM, df = 1, t = 4.58, $p < 0.0001$) (Figure 2.9). This implies that the LDA is less likely to miss a lunge at depth than it is at the surface when using the defined thresholds that were set based on lunges at the surface. It also suggests that feeding behaviour at the surface may be unable to be detected successfully due to the extremely low acceleration of some lunges.

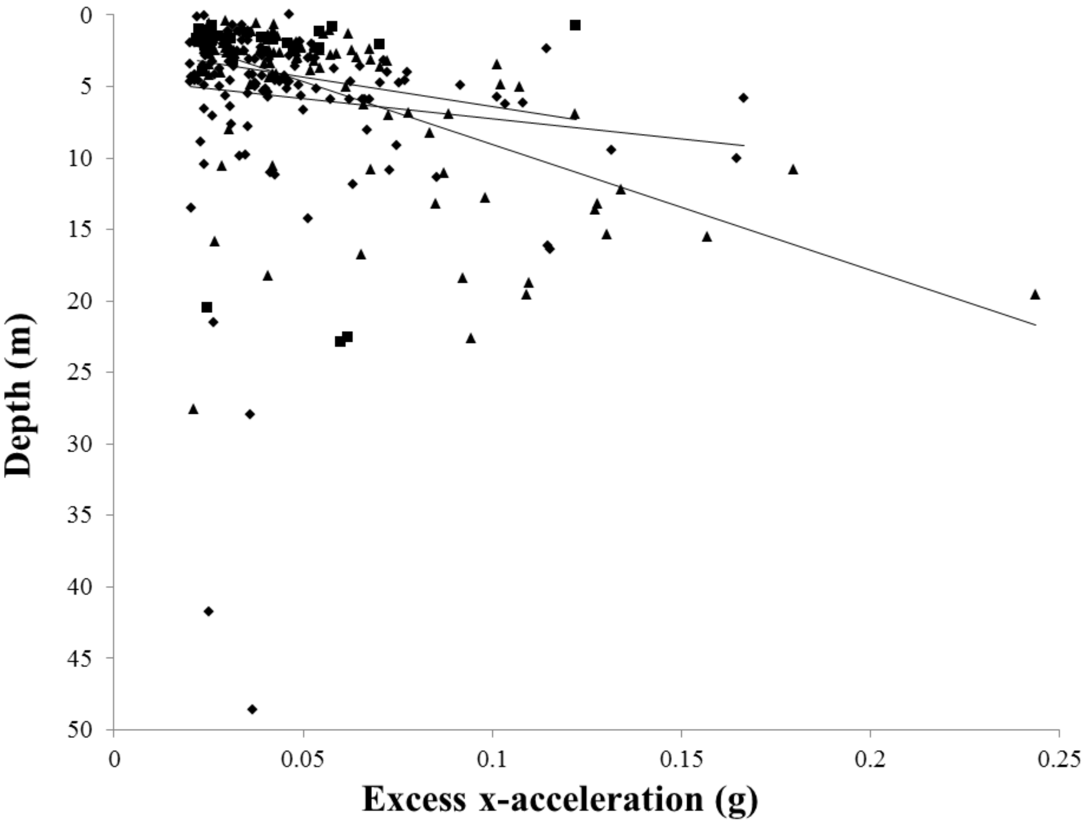

**Figure 2.9:** The relationship between excess x-acceleration (EXA) (g) and depth (m) of the detected lunges (visually observed and non-visually observed). Each dot represents one lunge, with the different symbol representing the three tag deployments. The line of best fit through the data points for each animal is also included.

### 2.5 Discussion

To the best of our knowledge, the method described here represents the first method to detect surface-feeding behaviour by whales in accelerometer data. The new parameter, EXA, more successfully distinguished between lunges at the surface and other times that the whale surfaced to breathe than an existing parameter, MSA, developed for feeding behaviour at depth. The new method detected approximately 70% of the visually observed lunges, and only 7.8% of the detections made by the algorithm were determined to be false detections after applying the TrackPlot filter. The TrackPlot filter allowed each detection to be labelled with 100% accuracy as either a lunge, another surface-active behaviour, or as a false detection. The results of this study also suggest that the accelerometer signal is likely to vary as a function of the depth of the animal. The visually observed lunges not detected by the algorithm were found to have an average EXA much lower than the threshold set, however, lowering the threshold any further to detect these lunges was likely to inflate the number of false detections. Given the relationship between EXA and depth, it is likely that the amount of lunges missed by the algorithm decreases with increasing depth. Detection thresholds should take into consideration the proximity of animals to the surface and the influence of the forces acting on an animal at the time. That the acceleration signal decreases with proximity to the surface suggests that the high levels of acceleration expected during lunge feeding may not always be observed in biotelemetry data when whales are surface-feeding.

Given that both EXA and MSA are computed from the same sensor, EXA is inherently related to MSA. MSA was initially developed as a method to detect lunges at depth and has been shown to be a reliable indicator of lunges when whales are feeding deeper in the water column (Simon *et al.* 2012). In this study, the depth of lunges was relatively shallow (less than 50 m). For lunges occurring at depth, both EXA and MSA appeared to be a reliable indicator of when a lunge occurred (see Figure 2.5d). This suggests that at depth, both parameters may be reliable to indicate the presence of a lunge. However, the use of acceleration in all three axes, as is the case with MSA, was found to be more variable at the surface, with a similar signal produced regardless of whether a whale lunged or surfaced to breathe. This can be seen in Figure 2.5b and Figure 2.5c where MSA peaks as the whale surfaces (as indicated by the grey lines) to a similar level as what it does when the whale lunges (at time 0). EXA is therefore more likely to be able to successfully distinguish between lunges and other times that the animal surfaces to breathe than MSA when close to the water surface. The success of the new parameter at identifying lunges at or close to the surface is likely attributed to the focus on orientation-corrected forward acceleration, and not on acceleration in the other two axes. Wave drag has been shown to be negligible at a depth equal to two to three times the diameter of the animal’s body (Hertel 1966). Therefore, it is suggested that studies searching for feeding lunges within this region use the EXA signal as a parameter. Future studies should attempt to determine the reliability of both MSA and EXA over a range of depths by comparing the detections made by both parameters to that of video recordings from back mounted cameras that can potentially confirm whether lunges have occurred at depth.

One potential reason for the lower acceleration signals closer to the surface may be that the higher wave drag near the surface and lower propulsive efficiency may limit the net acceleration of the animals, even when similar levels of propulsion are applied by the whale. This would imply that for the same energy usage per lunge, whales feeding at the surface reach lower speeds, which could limit the volume of water engulfed. In addition, when feeding along the surface at least some of the oral cavity would be filled with air, and not water, which would again limit the volume of water engulfed. Feeding near the surface provides advantages for whales because of the reduced distance between prey and air supplies (Doniol-Valcroze *et al.* 2011) and the loss of escape routes for prey that are pinned against the sea surface (Kot 2009). The reduced travel time between prey and air would allow for an increased lunge rate per unit time during foraging at the surface compared to feeding at depth (Doniol-Valcroze *et al.* 2011). However, if wave drag acts to reduce the prey intake per lunge, then the increase in the number of lunges near the surface may only act to balance out the rate of prey intake over time. In addition, if each lunge uses the same amount of energy, but more lunges are required by surface-feeding whales to take in the same amount of prey, then it is possible that feeding at shallow depths where wave drag has an influence may actually be more energetically expensive than feeding just below this depth threshold.

However, engulfment of large volumes of water during a lunge may still be possible even when whales lunge at lower speeds (Goldbogen *et al.* 2011). It is possible that the lower lunge accelerations near the surface found in this study could also be the result of whales choosing to put less propulsion into each lunge whilst surface-feeding. Prey often becomes trapped against the surface which may reduce the area available for particular prey species to escape an approaching predator (Kot 2009). Reduced escape abilities of the prey may then allow the predator to approach with less acceleration and still successfully capture the prey. However, previous calculations found that whales would require speeds of approximately 3 $ms^{-1}$ to inflate the ventral groove blubber (Orton & Brodie 1987). It is thought that whales contract the muscles of the ventral groove blubber against the engulfed water as a way of transferring momentum to the engulfed water mass, which would reduce deceleration of the animal (Potvin *et al.* 2009). However, simulations have shown that similar volumes of water should be able to be engulfed with differing lunge speeds (Goldbogen *et al.* 2011). The amount of water engulfed is likely to be dependent on the amount of force the whale applies back against the engulfed water by contracting muscles of the ventral groove blubber (Potvin *et al.* 2009; Goldbogen *et al.* 2011). This implies that whales that accelerate less may still engulf large volumes of water by reducing muscle contraction (Shadwick *et al.* 2013). They would then benefit by reducing the energy required to accelerate for each lunge and reducing the energy needed to contract their muscles. Video recordings have shown that the ventral groove blubber of humpback whales expands even during extremely slow bottom feeding (Ware *et al.* 2014). Therefore, future research should attempt to determine whether whales may modify their behaviour while feeding on surface-orientated prey as a way to reduce drag and save energy.

Previous studies have suggested that there is variation in the speed at which lunges are completed between lunge types (Kot 2009). This suggests that the acceleration of the whales varying as a function of depth may also be a result of the variation in pitch angle of the lunges observed. In this study, the lunge types varied from lateral lunges with low pitch angles of approximately 10 degrees, through to vertical lunges with high pitch angles of close to 90 degrees. Calculations of the impact of wave drag near the surface are determined based on an object or an animal moving horizontally along the surface at low pitch angles (Hertel 1966). However, when whales lunge vertically the high pitch angles may reduce the impact of wave drag and allow propulsive efficiency to remain high by keeping the flukes away from the surface. Vertical lunges are often used to target fish near the surface at much faster speeds than observed in this study (Jurasz & Jurasz 1979). Therefore, future research should investigate whether variation in the pitch angle of lunges at the surface may potentially be a tactic used by whales to allow for faster lunges when prey conditions require speed that avoid the influence of wave drag and a lowering of propulsive efficiency.

To the best of our knowledge, this study presents the first technique for detecting lunges by surface-feeding whales in accelerometer data. The lunge detecting method described here is a flexible method in which the thresholds set can be adjusted depending on the species or behaviour observed. It is recommended that this method be used when searching for lunges in the upper section of the water column where wave drag is likely to have an influence on the animal. The results of this study suggest that the high amounts of acceleration expected during lunge feeding may not always occur due to the presence of wave drag or due to behavioural adaptations by the animals. As a consequence, setting acceleration thresholds that are too high may lead to an underestimation of feeding rates. This may in turn lead to incorrect calculations of energy budgets and result in feeding on certain prey types or densities by whales not being detected from biotelemetry data. Future research should focus on determining whether whales modify their feeding behaviour when feeding at the surface as a way to lower the potential impact of wave drag on feeding energetics or whether the lunges are just as energetic but the higher wave drag and lowering of propulsive efficiency results in a lower net acceleration achieved by the whales. Although deep lunges were detected in this study, the applicability of this method should also be further tested for deeper feeding animals. This will assist with the development of a unified method that is capable of detecting lunges in biotelemetry data irrespective of depth. Development of such a technique would allow for a more accurate transmission of data reflecting potential feeding behaviour via satellite. This would allow for calculations of time and energy budgets that are more representative of the foraging behaviour of animals over longer time periods than those calculated while excluding surface-behaviour.

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*Photo: Humpback whales lunging in echelon while feeding off the coast of Eden, NSW (photo by Scott Sheehan)*

# Chapter 3

## Is feeding by humpback whales during migration a 'quick snack' or more important to their ecology?

*The new methodology developed in Chapter 2 is utilised in this Chapter to detect the presence of feeding behaviour by whales while on migration. It is currently assumed that feeding behaviour by whales while on migration is rare or opportunistic and of little importance to whale ecology, despite very little research describing this behaviour. This Chapter investigates whether a change in the prey species available on migration influences the feeding behaviour of the whales. It has been prepared for submission to Marine Ecology Progress Series.*

# 3

# Is feeding by humpback whales during migration a ‘quick snack’ or more important to their ecology?

## 3.1 Abstract

For terrestrial migrants, feeding at migratory stopover sites is important, with prey quality being linked to future survival and reproductive success. However, the importance of this behaviour to marine species is largely unknown. The humpback whale (*Megaptera novaeangliae*) is a marine migrant that has historically been believed to fast while migrating. Feeding behaviour during migration has not been studied in detail, and the rarity of observations has led to the belief that it is not important to the ecology of whale species. The aim of this study was to describe the fine-scale feeding behaviour of humpback whales while on migration to provide insight into some of the factors that may influence this behaviour. Given that whales in the east Australian population are believed to feed predominantly on krill on their main feeding grounds, it was hypothesised that the availability of krill on migration would be more important to whales than the availability of other prey types such as fish species. As a consequence, migrating whales would spend more time feeding on krill than other prey types. In addition, their behaviour while doing so would be more similar to that observed on main feeding grounds and different from typical migratory behaviour. Digital acoustic recording tags (DTAGs) and focal follows of individual whales encountering different prey types while migrating off southeast Australia were used to examine 1) the amount of time spent feeding, 2) the linearity of the tracks of feeding whales, 3) the size and composition of feeding groups, and 4) the occurrence of cooperative or synchronous behaviour between animals within the group. Whales feeding on fish only spent a small percentage of time feeding and behaved similarly to non-feeding whales on migration, with relatively straight tracks and small groups that were male dominated. However, whales feeding on krill spent a significantly greater amount of time feeding and behaved more similarly to whales on feeding grounds, with tracks with high turning angles, and large, female-biased groups. The results of this study suggest that when prey availability is favourable, in this case when krill is abundant, animals may dedicate time to consuming prey along the migratory route. That whales dedicate time to feeding suggests that this behaviour may be of more importance to the ecology of some whales than previously thought.

**Keywords:** Area-restricted search, lunge, migration, marine, *Megaptera novaeangliae*, state-space modelling

## 3.2 Introduction

Seasonal migrations involve the movement of individuals between geographically distinct breeding and non-breeding areas (Dingle & Drake 2007). Successful completion of migration is largely dependent on the availability of energy reserves to fuel locomotion (Alerstam *et al.* 2003). The storage of enough energy to complete migration without stopping would greatly increase the cost of transport and reduce the travel speed for many animals, particularly for flying animals such as birds (Akesson & Hendenstrom 2007). Migratory speed has been shown to be of importance to many bird species that have evolved the use of stopover sites to allow for refuelling along the way (Alerstam & Hedenstrom 1998; Dingle & Drake 2007; Newton 2008). It is thought that the use of stopover sites minimises the cost of transport and the time required to complete migration (Akesson & Hendenstrom 2007). This allows birds to reach breeding areas early, establish nesting territories, and find a mate before competition intensifies (Weber & Houston 1997). In contrast, in non-avian taxa that walk or run, such as terrestrial mammals, increased migratory speed has been found to be of little importance. Instead, species such as mule deer (*Odocoileus hemionus*) have been found to take much longer periods than would be expected to complete migration, by feeding at high quality forage sites along the migratory route (Sawyer & Kauffman 2011). In this case, the speed of migration and use of stopover sites has been linked to the phenology of plants, with the deer tracking forage availability to increase energy intake during the season of highest plant growth (Sawyer & Kauffman 2011). Therefore, migratory strategies and the importance of stopover sites to the ecology of a species are likely to vary between taxa.

The overwhelming majority of studies of the importance of migratory stopovers to seasonal migrants have focused on avian taxa, with a small number of studies focusing on other terrestrial migratory species. The availability of resources at migratory stopover sites has been linked to the subsequent survival and reproductive success of individuals and the migratory strategy used by animals is thought to have evolved to maximize both of these parameters (Newton 2006; Sawyer & Kauffman 2011). However, the migratory strategies of swimming animals in the marine environment are likely to be different from those of the terrestrial environment. It has been suggested for swimming animals that if there is selection for increased migratory speed, an increase in the size of the animal should occur (Hedenstrom 2003). In addition, the cost of transport is usually lower for swimming animals compared to running or flying animals, meaning that an increased fuel load may have a lower impact on the cost of transport for marine animals (Schmidt-Nielsen 1972) which may make storage of enough energy supplies to complete migration without feeding possible. In the marine environment, the ephemeral distribution of resources often leads to a reduced reliance on territoriality to secure mating and feeding opportunities, particularly in wide-ranging species such as baleen whales (Clapham 1996), which may reduce the importance of migratory speed. A lower reliance on migratory speed and an increased ability to store sufficient fuel may reduce the reliance on migratory stopover sites in the marine environment. However, the use of migratory stopover sites as potential foraging areas in the marine environment has been highlighted in fish (Sims *et al.* 2009), marine reptiles (Broderick *et al.* 2007; Cuevas *et al.* 2008) and marine mammals (Stamation *et al.* 2007; Barendse *et al.* 2010; Visser *et al.* 2011; Silva *et al.* 2013). Despite this, very little is understood about the role that these stopover sites may provide to the ecology of marine species.

Most baleen whale species are examples of migratory marine animals. Historically it was thought that intensive feeding behaviour during summer in high latitude feeding grounds enabled baleen whales to store enough energy supplies to successfully complete migration while fasting, or feeding at a very low rate (Lockyer 1981; Clapham 1996). This idea was partially based on the low abundances of available prey in low latitude breeding grounds and the fact that whales caught on migration by whalers often had empty stomachs (Chittleborough 1965; Lockyer 1981). The large majority of whaling efforts were completed during the migration from feeding grounds to breeding grounds when the whales had the highest fat and oil content (Dawbin 1966), and as a consequence, there is little information on the stomach contents of whales migrating back towards feeding grounds. More recently there has been an increasing amount of evidence that suggests that some baleen whale species feed during migration, particularly during the migration from breeding to feeding grounds when body reserves may be more depleted (Best *et al.* 1995; Gill *et al.* 1998; Stamation *et al.* 2007; Barendse *et al.* 2010; Visser *et al.* 2011). This evidence ranges from assumed feeding as a result of gouges along the ocean floor that are believed to be the result of bottom feeding by gray whales (*Eschrichtius robustus*) while migrating (Cacchione *et al.* 1987), to satellite tracks of many baleen whale species that have revealed the presence of potential foraging behaviour along the migratory route (Gales *et al.* 2009; Silva *et al.* 2013). In addition, there are many brief observations of whales feeding in areas of productivity while migrating, including the identification of potentially important migratory stopover sites (Best *et al.* 1995; Stamation *et al.* 2007; Barendse *et al.* 2010; Visser *et al.* 2011). Therefore, it appears that whales feed while migrating, however whether this feeding behaviour is opportunistic or an important component of their migratory ecology remains unknown.

For avian species, migratory stopover sites are often in terrestrial locations which make the location of sites and observation of animals at these sites easier than in the marine environment. Despite this challenge, some information is known about the ecology of whales on migratory stopover sites. Individual whales have been observed to spend up to twenty days in the same area while on migration (Best *et al.* 1995; Visser *et al.* 2011) suggesting that animals may at times delay the completion of migration to feed. Many of the records of whales feeding while migrating are reported to be of juvenile animals that potentially rely on the sites as a result of their smaller body size and reduced ability to store sufficient energy reserves to complete migration (Salden 1989; Swingle *et al.* 1993; Gill *et al.* 1998; Alves *et al.* 2009; Silva *et al.* 2010). In addition, a female-bias in the composition of groups at one previously identified stopover site suggests that the behaviour may also be important for females (Barendse *et al.* 2010). However, the impact that changes in the prey type available along the migratory route may have on the amount of time and effort dedicated by an individual whale to feeding while migrating have not been investigated.

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species that makes annual migrations between high latitude feeding grounds and low latitude breeding grounds. The species is divided into several populations with the east Australian population migrating between Antarctic feeding grounds and breeding grounds in the Coral Sea off the north east coast of Australia. The area off Eden, New South Wales, on the south east coast of Australia, has recently been highlighted as a potentially important feeding area for this population of humpback whales while on migration (Stamation *et al.* 2007). This is due to the regular observations of whales feeding on both krill and fish during the southward migration from breeding grounds back towards feeding grounds (Stamation *et al.* 2007). The aims of this study were to determine how the type of prey available at a migratory stopover site influenced 1) whether whales were observed to feed or not, and 2) the fine-scale feeding behaviour of individual humpback whales. Given that the east Australian population of humpback whales is believed to feed predominantly on krill on their main feeding grounds in the Antarctic (Matthews 1937), it was hypothesised that the availability of krill at the migratory stopover site would lead to more whales feeding and whales behaving more similarly to that of whales on the main feeding grounds, compared to when fish were available. The behaviour of whales on main feeding grounds is different from that of whales on migration in many ways, including 1) the amount of time spent feeding, 2) the linearity of their tracks, 3) their group sizes and compositions, and 4) the occurrence of cooperative or synchronous behaviour. For whales determined to be feeding, these aspects of the behaviour of the whales were compared to concurrent information on the type of prey that was available to the whales at the time of observation. It was hypothesised that when krill were relatively abundant, more whales would feed and individual whales would spend more time feeding and behave similarly to whales on main feeding grounds. In contrast, when fish were relatively abundant and krill were not, fewer whales would feed, and individual whales would spend less time feeding, and behave similarly to non-feeding whales on migration.

## 3.3 Methods

### 3.3.1 Study site

Data were collected off the coast of Eden, New South Wales, Australia (37.07° S, 149.90° E) from the 9th of September to the 2nd of October 2011 and the 9th of September to the 19th of October 2012. This time corresponded to the southward migration of the whales back towards Antarctic feeding grounds. The study site included the area out to approximately 20 km offshore and 20 km to the north and south of Eden.

### 3.3.2 Behavioural data collection

Regardless of their size, composition or apparent behaviour, groups of whales sighted were approached and a boat-based survey of the group was conducted from a distance of approximately 100 m for a period of up to 20 minutes (Mann 1999). During this time an assessment was made about whether or not the whales in the group were likely to be feeding. For surface-feeding animals/groups this was determined by the observation of a feeding lunge, which was confirmed by the observation of the whale engulfing water and prey into an open mouth. For animals feeding at depth, this was determined by considering a combination of factors: the presence/absence of prey in the area, the surface movement pattern of the whale over the short time period of the observations, and the presence/absence of other predatory species e.g. short-tailed shearwaters (*Puffinus tenuirostris*), Australasian gannets (*Morus serrator*), and common dolphins (*Delphinus delphis*). Whales that were determined to be feeding were generally found in areas where patches of prey were present in the water column in the same area the whale was observed. This was determined either by direct observation of the group within a patch of prey visible at the surface or from echosounder data with the whale being observed to dive into an area where prey were available (prey sampling methods described below). Feeding whales also showed no fine-scale trend in the direction of travel over the short time observed, and were located within 100 m of one or more other predatory species. In contrast, whales that were determined to not be feeding had a consistent direction of travel and surfacing intervals over the short time observed, and were located in areas where very little prey were available. This sampling method was used to identify whether each group was feeding or not, and what prey type was available to each group at the time of observation.

For some of the groups that were determined to be feeding, a digital acoustic recording tag (DTAG) (Johnson & Tyack 2003) was deployed onto the back of one of the whales between the blow holes and dorsal fin using a 6 m long carbon-fibre pole. Four silicon suction-cups were used to attach the DTAG to the back of the whale. The DTAG contained a 3-axis accelerometer, a 3-axis magnetometer, and a pressure sensor (accuracy of ± 0.5 m) and was programmed to release after two to three hours, depending on weather conditions. All sensor data were collected at a sampling rate of 50 Hz. The DTAG also contained a VHF transmitter that allowed the whale to be tracked when at the surface. All data collected by the tag were archived and downloaded via infrared transmission upon retrieval of the tag.

Once a tag was deployed, behavioural data collection commenced. The tagged individual was chosen as the focal animal so that a complete account of behaviour at and below the surface could be collected. When tag deployment was not successful, a focal individual was selected randomly from the group. The follow protocol used was an individual-follow with a continuous sampling method (Mann 1999). A pre-defined ethogram (Appendix 2) was used to record all observed surface behaviours by the focal whale. Behavioural records were made by speaking into an audio recorder (Zoom H1 recorder) to provide a time-stamped record of the behaviour. The same observer (KO) completed every focal follow to avoid inter-observer reliability issues (Jones *et al.* 2001; Kaufman & Rosenthal 2009). Both the DTAG and the audio recorder were time synchronised using a handheld GPS (Garmin GPSmap 78SC).

As well as recording the individual-follow, continuous incident sampling was conducted by the same observer on the remaining animals in the focal individual’s group (Mann 1999). A group was defined as any animals with a similar movement and surfacing pattern within 50 m of each other. Incident sampling involved recording the time of any observed lunge feeding behaviour by any animals in the group and whether the lunge was completed in synchrony with other animals. Synchronous lunging behaviour was defined as lunging behaviour by two or more individuals where the individuals lunged within two seconds of each other less than one body length apart. Synchronously feeding whales use one of two formations when feeding together. The first is ‘echelon formation’ where one animal lunges slightly behind the second, and the second lunges slightly behind the third, and so on (Jurasz & Jurasz 1979). The second type is ‘side-by-side formation’ where all animals lunge synchronously in a line beside each other. When synchronous lunges occurred, the formation type was noted, as well as which individuals completed the lunge. Individuals were identified visually using lateral pigmentation and dorsal fin shape (Katona & Whitehead 1981). In cases where the group split during a focal follow, the continuous incident sampling data continued to be collected only from animals that remained in the same group as the focal individual. This helped to reduce bias in selecting a group post-split. An additional observer collected data every 10 minutes on the current group size.

In order to determine the sex of the animals, a biopsy sample was collected. This was completed using the Paxarms system, which involved firing a biopsy dart from a modified .22 rifle (Krutzen *et al.* 2002). When a group was small (less than five), an attempt was made to biopsy sample all individuals in the group. However this was often limited by weather conditions or permit restrictions. When the group was large, only focal animals and individuals seen to have had a close association with the focal animal were biopsied. For some tagged individuals, skin was collected from the suction cups of the DTAG. Biopsy samples were stored in a -20° C freezer prior to processing. Sex determination was completed by the Australian Marine Mammal Centre at the Australian Antarctic Division (sex determination methods explained in Morin *et al.* 2005).

Due to the nature of the tagging effort, dedicated surveys to determine mark-recapture rates could not be completed. However, photo identification images were taken during every sighting. This allowed for comparisons of the individuals between sightings to give an indication of how many were re-sighted by chance throughout the course of the study.

### 3.3.3 Determining the prey type available to the whales

In 2011, the prey type available to the whales was determined based on 1) surface observations of the prey type in close proximity to the whale throughout the duration of the observations, 2) dropping a camera over the side of the vessel to a depth of 2 m every 20 minutes throughout the duration of the focal follows, and 3) prey sampling for species identification. Prey sampling was completed by towing a 200 µm plankton net with a 40 cm aperture behind the vessel for two minutes in areas where the whales had been observed to lunge. One net tow was completed per focal follow during the course of the focal follow. The prey sampling was used purely for species identification and no attempts were made to determine density or abundance of krill or fish using this method. Observations of prey at the surface, aligned with surface feeding behaviour by the whales, allowed to the predominant prey type to be determined for each surface-feeding whale. While the use of these methodologies provided an understanding of the prey available to the whales near the surface, it is acknowledged that it provides no understanding of the prey available to the whales at depth in 2011.

The method used to determine the type of prey available to the whales differed between years of sampling. This was due to no echosounder being available in 2011. While not ideal, given that the aim of the prey sampling was to determine the predominant prey type available to the whales, rather than detailed information on prey density and abundance, this is not thought to have influenced the accuracy of the assignment of predominant prey type information to each group or individual.

In 2012, a dual frequency (38 and 200 kHz) echosounder (ES60, Simrad/Kongsberg) was used to provide information on the availability of fish and krill. The echosounder was deployed off the starboard side of the vessel using a small towfish which held it at a depth of approximately 50 cm. For both frequencies, the echosounder had a ping rate of 0.5 Hz, depth bins of 10 cm, pulse length of 256 µs, and a power setting of 2000 W. The system was calibrated using a standard 38.1 mm Tungsten carbide sphere (Foote *et al.* 1987) at the beginning of the 2012 surveys. The sphere was lowered to between 10 and 20 m beneath the echosounder in a location with little biological scattering and a water depth of 26 m. Backscatter values for the standard target were less than 0.5 dB different from theoretical predictions.

In order to identify prey patches, the backscatter was thresholded at 38 and 200 kHz at -80 dB re 1 $m^{-1}$. A dB-differencing method (Reiss *et al*. 2008; Warren & Demer 2010) was used to identify scattering aggregations as either krill or fish depending on the value of the difference in volume backscattering strength ($D_{dB}$ = Sv at 200 kHz – Sv at 38kHz). Theoretical target strength (TS) models were used to determine likely backscatter values for monospecific aggregations of krill (Conti & Demer 2006). Aggregations were identified as krill when 2 dB < $D_{dB}$ < 30 dB. These values result from an estimated krill length distribution of 5 mm to 60 mm, which was based on net tow data from 2011 and visual observations of surface krill aggregations in 2012. Aggregations were identified as fish when -100 dB < $D_{dB}$ < -20 dB. These values result from estimates of acoustic backscatter from fish that ranged in length from 10 to 40 cm, including species with (Weber *et al.* 2009; Simmonds & MacLennan 2005) and without (Gorska *et al.* 2005) swim-bladders. These parameters (i.e. species and length) were based on visual observations of surface schools in 2012 and discussions with local fisherman about the typical sizes of baitfish in this region at the time of the survey.

Echosounder data were collected continuously throughout the entire focal follow at locations near the focal whale by following the path of the focal whale in a zig-zag pattern. Typically, a 50-200 m distance was maintained, although occasionally larger separations of up to 500 m would occur between the location of the focal whale and where the echosounder data were collected. Scattering aggregations that were encountered near the whale were used to categorise the dominant prey available for each whale as either krill or fish.

### 3.3.4 Data processing and analysis

*Data analyses*

All data analyses were completed in R (R Development Core Team 2013) with significance levels set a $p < 0.05$. A number of models were developed in order to test the influence of the prey type available on the behaviour of the whales. Detail of the type of models and packages used are provided in the sections to follow. However, all models were checked for the presence of temporal autocorrelation, homoscedascity, and that the residuals were normally distributed. The identity of the whales was used as a random effect in all of the models to account for the repeated measures nature of the data collection. Degrees of freedom were determined based on the number of random effects (whale identity) minus the number of parameters in the model.

*Time spent feeding*

All tag data were calibrated and decimated to 5 Hz using the methods described in Johnson and Tyack (2003). Given that the orientation of the tag on the whale can vary both between and within deployments, the data collected by the tag were corrected for the orientation of the tag on the whale (Johnson & Tyack 2003). For tagged individuals, the times when presumed feeding lunges were completed were determined using the lunge detecting algorithm with the TrackPlot filter applied as described in Chapter 2. Any lunges that were observed but not detected by the algorithm were also used in the analysis. Given that some feeding behaviour occurred underwater and out of sight of the observer, only tagged individuals were used for the analysis of the time spent feeding.

For tagged whales, focal observations were divided into 10 minute time bins. The duration of the time bins was chosen based on the length of the focal follow, the desire to model behavioural states as opposed to behavioural events, and the likelihood of each bin containing a lunge. It was assumed that each dive by a humpback whale was unlikely to be longer than approximately 10 minutes, so a 10 minute bin would possibly contain a foraging dive, and the next 10 minute time bin could contain a non-foraging dive. Each time bin was assigned as either containing a lunge (‘feeding’), or not containing a lunge (‘not feeding’). Using the glmmadmb package (Fournier *et al.* 2012; Skaug *et al.* 2013,) in R (R Development Core Team 2013), this parameter was then used as a binomial response variable in a generalised linear mixed model (GLMM) to compare the amount of time spent feeding on different prey types (krill vs. fish).

### *Linearity of the track*

In order to assess the linearity of the movement of the whale, the heading data collected by the DTAG were used. The collection of heading data relies on a 3-axis magnetometer to assess the orientation of the tag in relation to the magnetic field of the earth. These data are then corrected for the pitch and roll of the animal to determine the heading of the whale in the horizontal frame, similar to the measurements of a compass (Johnson & Tyack 2003). Therefore, the heading data represent a two-dimensional indication of the direction of travel by the whale. If a track is linear, it is expected that over the course of the track the changes in heading from one point in time to the next should be small. In a track that is not linear, the changes in heading over time should be larger. The heading for each animal was determined every five minutes. Variation in turning angle is likely to be higher while the animals are feeding. It was therefore assumed that by looking at the change over 10 minutes (as was done when looking at behavioural states) this variation within a potential behavioural state may be missed. As a consequence, the time bin for this analysis was halved to five minutes in the hope of detecting the variation that occurs while feeding, while still adequately displaying the lack of variation while not feeding.

As the bearings are collected in a continuous 360°, there are always two solutions to the change in heading. As a result, an assumption was made that whales were unlikely to have changed more than 180° in a given time step and the smaller angle was always used as the change in heading. Heading data were collected by the tag from -180° to 180°. Given that the direction of the change in heading is less relevant than the magnitude of the change, the absolute value of the change in heading for each time step was calculated. This produced a series of changes in heading values for each whale. The change in heading data were then used as a response variable in a linear mixed model (LMM) to determine whether the prey type targeted had an influence on the linearity of the track of the whales. In order to meet the assumption of normality made by the model, the square root of the data was used. The nlme package (Pinheiro *et al.* 2013) in R (R Development Core Team 2013) was used for the analysis.

Given that the direction of migratory movement has been shown to vary among individuals migrating through Eden, NSW (with some individuals migrating south towards Tasmania and others migrating south east towards New Zealand) (Gales *et al.* 2009), the heading data for each individual were then corrected so that the most common (mode) movement direction of each animal was centred on zero degrees. The data for all whales were then pooled to produce a radial rose for whales feeding on krill and an additional radial rose for whales feeding on fish. These radial roses provide a visual comparison of the variability in the direction of movement by the whales when feeding on the two prey types.

### *Group size and composition*

For each focal animal, the size of the group it was feeding in was recorded every 10 minutes. A generalised linear mixed model (GLMM) was completed to compare the group sizes of animals feeding on fish to those of animals feeding on krill. The data were modelled using the glmmadmb package (Fournier *et al.* 2012; Skaug *et al.* 2013) in R (R Development Core Team 2013) with a truncated Poisson distribution to account for the lack of zero values.

The east Australian population of humpback whales has been shown to have a male-biased sex ratio during migration with approximately two males for every female (male: female sex ratio of 2.1: 1 in whaling records and 2.4: 1 off southern Queensland (Brown *et al.* 1995a) and 1.6: 1 off Eden and Tasmania, NSW (Schmitt *et al.* 2014)). This assumed average sex ratio during migration of two males per female was used to compare to the observed sex ratio of feeding groups in both 2011 and 2012. The numbers of males and females biopsied each year were determined to calculate the observed sex ratio for 2011 and 2012. For each year, the observed sex ratio was compared to the sex ratio expected based on the results of other studies. Due to the small sample size, for each year, a Chi Squared analysis with 1000 permutations was completed in R (R Development Core Team 2013) with significance level set to $p < 0.05$. Similar to this, to determine which animals fed synchronously together, synchronous pairs were determined to be either male-male (MM), male-female (MF), or female-female (FF). An additional Chi Squared analysis with 1000 permutations to account for the small sample size was completed in R (R Development Core Team 2013) to determine if the observed proportion of different pair types matched those predicted by the described sex ratio while on migration. Significance level was set to $p < 0.05$.

## 3.4 Results

### 3.4.1 Observed feeding behaviour

A total of 82 groups of whales were approached to determine the likelihood that the group was feeding and what type of prey were available to the group of whales at the time. Across the two years, of the groups observed to encounter krill (n = 24), 71% were presumed to be feeding and only 29% were determined to be not feeding at the time of observation. In contrast, of the groups that were observed to encounter fish (n = 58), only 21% were determined to be feeding with 79% determined to be unlikely to be feeding during the survey. In 2011 when krill were abundant, five individuals were re-sighted on multiple days, with three of these animals spending at least eight to ten days in the area (Table 3.1). However, in 2012, there were no re-sights of individuals despite more groups being seen in that year.

**Table 3.1:** Re-sighting data for individual whales observed to feed across multiple days on the migratory stopover site off the coast of Eden, NSW.

| Date first observed | Date last observed | Number of days in Eden |
|---|---|---|
| 13 September 2011 | 15 September 2011 | 3 |
| 13 September 2011 | 17 September 2011 | 5 |
| 14 September 2011 | 21 September 2011 | 8 |
| 17 September 2011 | 26 September 2011 | 10 |
| 17 September 2011 | 26 September 2011 | 10 |

For eighteen of the groups approach, a focal follow was completed on the whales (Table 3.2). Nine of these focal follows involved a tagged individual (Table 3.2). The methods used to determine the predominant prey type in 2011 limited the ability to determine what prey were available at depth. No fish were observed at the surface in 2011. However, it is possible that some of the lunges completed by whales at depth in 2011 were targeting fish. Camera drops completed throughout the focal follows in 2011 revealed that the krill was often distributed in the upper 5 – 10 m of the water column suggesting that a number of the non-visually observed lunges were also likely to have been targeting krill below the surface. Given that more than half of the total lunges completed by the whales in 2011 were visually-observed to have been targeting krill (Table 3.3), krill was determined to be the predominant prey type targeted for all three tagged animals in 2011. In contrast, in 2012, no surface lunges were observed to be completed by tagged animals (Table 3.3). However, based on the echosounder data for all of these animals the lunges were determined to be completed in areas where schools of fish were present in the water column (Table 3.3). As a consequence, the predominant prey type for all six tagged whales in 2012 was determined to be fish. Schools of fish were regularly observed at the surface in 2012.

**Table 3.2:** Details of the focal follows completed off Eden, NSW. Total lunges could only be determined for animals with a DTAG given the potential for underwater feeding behaviour. Surface-lunges relates to the number of lunges observed at the surface for the whole group throughout the focal follow.

| Date | **DTAG** | **Tag ID** | **Sex** | **Start time** | **Duration (hh:mm)** | **Prey** | **Group size (min)** | **Group size (max)** | **Individual lunges/hour** | **Surface-lunges/hour** |
|---|---|---|---|---|---|---|---|---|---|---|
| 13/09/2011 | no | - | F | 8:14 | 2:00 | krill | 2 | 5 | - | 170 |
| 14/09/2011 | no | - | M | 8:18 | 2:01 | krill | 1 | 3 | - | 156 |
| 15/09/2011 | yes | 1 | F | 9:45 | 2:10 | krill | 1 | 9 | 82 | 204 |
| 16/09/2011 | yes | 2 | M | 12:29 | 2:13 | krill | 1 | 3 | 23 | 9 |
| 17/09/2011 | yes | 3 | F | 8:29 | 2:13 | krill | 2 | 12 | 70 | 157 |
| 21/09/2011 | no | - | M | 12:57 | 2:01 | krill | 1 | 2 | - | 5 |
| 22/09/2011 | no | - | F | 8:29 | 1:29 | krill | 2 | 4 | - | 6 |
| 24/09/2011 | no | - | F | 10:09 | 2:04 | krill | 2 | 2 | - | 0 |
| 26/09/2011 | no | - | - | 9:26 | 1:10 | krill | 3 | 8 | - | 48 |
| 1/10/2011 | no | - | F | 8:15 | 2:05 | krill | 2 | 3 | - | 27 |
| 16/09/2012 | yes | 4 | M | 10:08 | 3:27 | fish | 2 | 3 | 3 | 0 |
| 17/09/2012 | yes | 5 | F | 14:06 | 1:19 | fish | 1 | 1 | 2 | 0 |
| 18/09/2012 | no | - | M | 10:40 | 3:59 | krill | 1 | 3 | - | 3 |
| 2/10/2012 | yes | 6 | M | 10:04 | 2:47 | fish | 2 | 3 | 11 | 0 |
| 4/10/2012 | yes | 7 | F | 8:54 | 3:09 | fish | 1 | 2 | 6 | 0 |
| 6/10/2012 | yes | 8 | - | 9:36 | 3:06 | fish | 2 | 3 | 6 | 0 |
| 9/10/2012 | yes | 9 | M | 12:50 | 2:47 | fish | 1 | 1 | 1 | 0 |
| 16/10/2012 | no | - | - | 1150 | 0:59 | fish | 1 | 1 | - | 0 |

**Table 3.3:** Prey type targeted by each of the tagged whales in both years. The proportion of visually-observed (VO) lunges where the whale was observed to feed on both prey types is presented, as is the prey targeted during the non-visually observed lunges. Due to the prey sampling methods used in 2011, it is unknown (U) what prey type was targeted by whales for the non-visually observed lunges. No lunges were visually-observed by a tagged whale at the surface in 2012.

| Year | Whale number | Total lunges (n) | VO lunges (n) | VO lunges on krill (%) | VO lunges on fish (%) | Non-VO lunges (n) | Non-VO lunges on krill (%) | Non-VO lunges on fish (%) |
|---|---|---|---|---|---|---|---|---|
| 2011 | 1 | 161 | 96 | 100 | 0 | 65 | U | U |
| | 2 | 35 | 20 | 100 | 0 | 15 | U | U |
| | 3 | 127 | 74 | 100 | 0 | 53 | U | U |
| 2012 | 4 | 3 | 0 | NA | NA | 3 | 0 | 100 |
| | 5 | 1 | 0 | NA | NA | 1 | 0 | 100 |
| | 6 | 53 | 0 | NA | NA | 53 | 0 | 100 |
| | 7 | 9 | 0 | NA | NA | 9 | 0 | 100 |
| | 8 | 11 | 0 | NA | NA | 11 | 0 | 100 |
| | 9 | 2 | 0 | NA | NA | 2 | 0 | 100 |

### 3.4.2 Fine-scale feeding behaviour individual humpback whales

*Time spent feeding*

Tagged whales that were feeding on krill fed during significantly more of the 10 minute time bins during the focal follows than did whales that were feeding on fish (average of 92% of the 10 min time bins during the focal follow compared to 28%) (GLMM, df = 7, z = 3.47, p = 0.0005).

*Linearity of the track*

Two of the three animals feeding on krill were observed to regularly loop back through the same area whereas all six animals feeding on fish displayed a more obvious direction of movement (Figure 3.1). The mean change in heading was found to be significantly larger for animals feeding on krill compared to animals feeding on fish, which had a more consistent heading with occasional deviation (86° ± 6° vs. 45° ± 3°) (LMM, df = 6, t = 4.50, p = 0.004) (Figure 3.2).

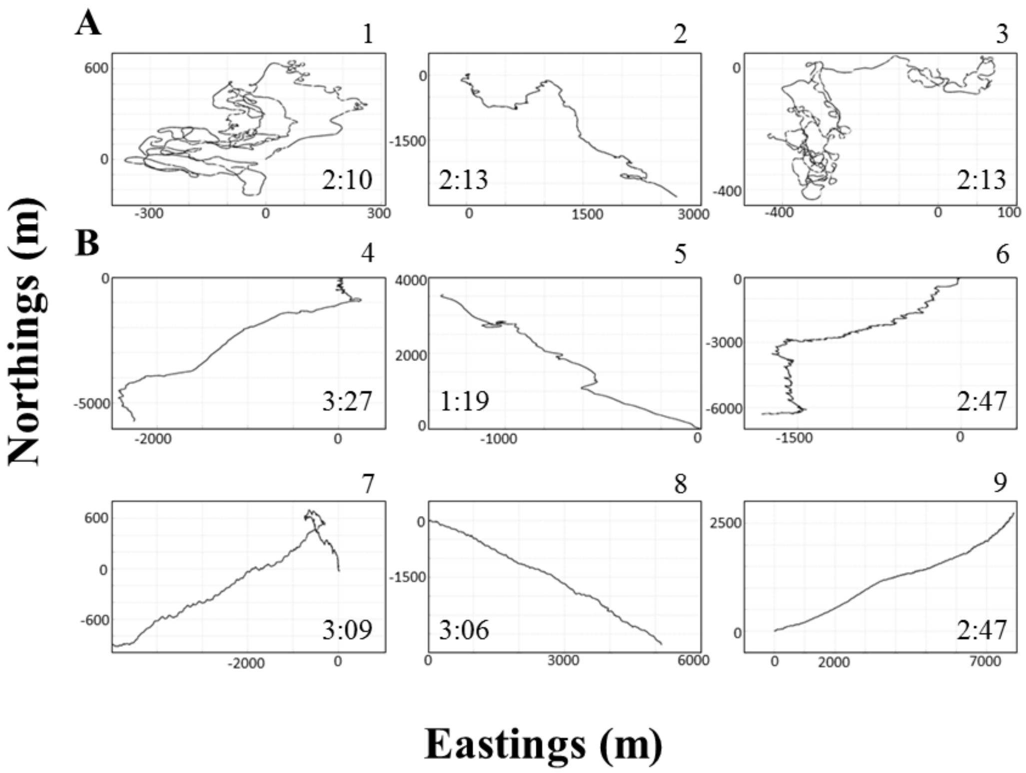

**Figure 3.1:** Pseudo tracks of tagged whales feeding on krill (A) and fish (B). The tag ID of each animal is provided in the top right corner of each window. Track duration is displayed in the bottom corner of each window (hours: mins). The scales of the windows vary in order to better display the variation in the pattern of each track.

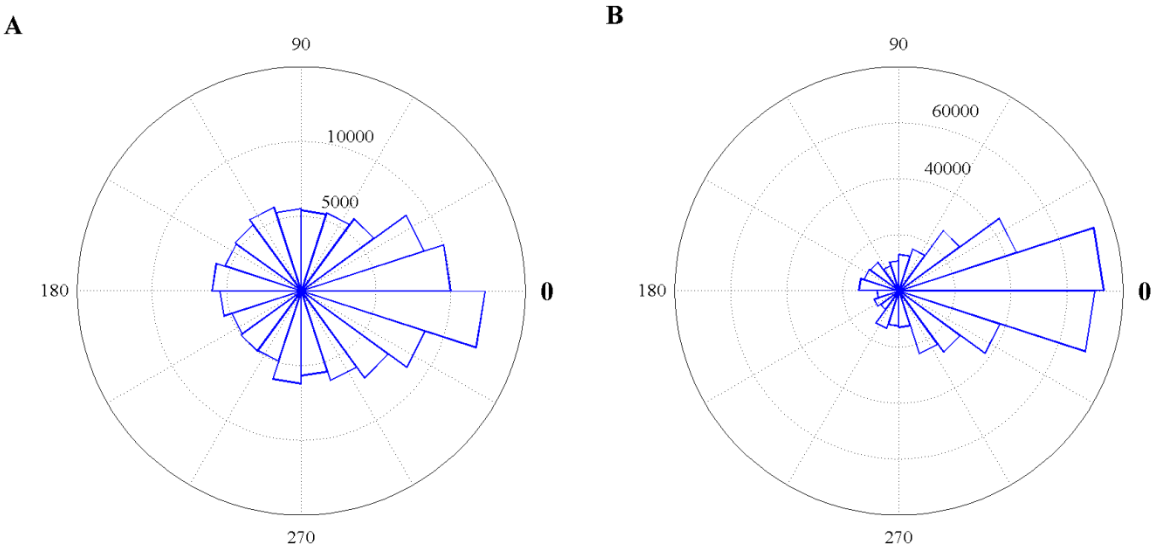

**Figure 3.2:** Radial rose histograms of the heading data for whales feeding on krill (A) and whales feeding on fish (B). Data were corrected so that the mode direction of travel for each whale was centred on zero degrees. Circles within the radial rose represent the number of samples where the whale was heading in the given direction.

### *Group size and composition*

Whales had significantly larger group sizes when feeding on krill (ranging from 1 to 12 individuals with an average of 3.4) compared to when feeding on fish (ranging from 1 to 4 with an average of 1.7) (GLMM, df = 14, z = 2.85, p = 0.004). When krill were available, groups were female dominated with 12 out of the 19 animals biopsied being female (Table 3.4). This is a significantly greater proportion of females than expected by chance given the male-biased sex ratio of the population while migrating reported in other studies (Brown *et al.* 1995a; Schmitt *et al.* 2014) (Chi squared permutation test, $X^2 = 7.6$, $p = 0.0087$). Conversely, when fish were available, groups were male dominated with only 7 out of 20 animals biopsied being female, consistent with the expected sex ratio of this population while migrating (Chi squared permutation test, $X^2 = 0.025$, $p = 0.9999$). When feeding on krill, individual animals within the groups formed close associations and were observed to feed synchronously as pairs over the majority of the focal follow. Such close associations were observed in nine of the eleven focal follows completed on animals feeding on krill across both years. In addition to the synchronisation of lunges, all other surface behaviours of the individuals and their directions of movement were also highly synchronised. Of the five re-sighted animals when krill were available mentioned above, two of them (sex unknown) were observed to feed together on the 17th of September, and again, 10 days later, on the 26th of September (Table 3.1). Synchronous pairs were comprised of 1/3 FF pairs (5 of 15 individual pairs) and 2/3 MF pairs (10 of 15 individual pairs). No MM pairs were observed, which is significantly fewer than expected compared to the expected ratios predicted based on published sex ratios of the population while migrating (Chi squared, $X^2 = 22.4887$, $p = 0.0004$). In contrast, in 2012, although no surface-feeding behaviour was observed, there was also no synchronous behaviour evident at the surface. The exception to this is the one group observed to feed on krill in 2012 which was observed to be surface-feeding with synchronous lunges by pairs of animals also observed.

**Table 3.4:** Group size and composition of each of the groups of humpback whales sampled on the migratory stopover site off Eden, New South Wales, Australia. Group size is presented as the maximum group size throughout the duration of the observations. The sum of the number of males and females is larger than the number of males and females used in the analyses due to re-sightings of the same individuals in multiple groups.

| Date | Group size | Number of males | Number of females | Number with unknown sex |
|---|---|---|---|---|
| **Krill** | | | | |
| 12 September 2011 | 4 | 0 | 1 | 3 |
| 12 September 2011 | 3 | 1 | 0 | 2 |
| 13 September 2011 | 5 | 1 | 4 | 0 |
| 14 September 2011 | 3 | 1 | 2 | 0 |
| 15 September 2011 | 9 | 2 | 3 | 4 |
| 16 September 2011 | 1 | 1 | 0 | 0 |
| 17 September 2011 | 12 | 1 | 4 | 7 |
| 21 September 2011 | 1 | 1 | 0 | 0 |
| 22 September 2011 | 2 | 0 | 1 | 1 |
| 24 September 2011 | 2 | 1 | 1 | 0 |
| 1 October 2011 | 2 | 1 | 1 | 0 |
| 18 September 2012 | 3 | 1 | 0 | 2 |
| **Fish** | | | | |
| 16 September 2012 | 2 | 2 | 0 | 0 |
| 17 September 2012 | 1 | 0 | 1 | 0 |
| 2 October 2012 | 2 | 1 | 0 | 1 |
| 4 October 2012 | 2 | 0 | 2 | 0 |
| 9 October 2012 | 1 | 1 | 0 | 0 |
| 14 October 2012 | 1 | 0 | 1 | 0 |
| 15 October 2012 | 3 | 1 | 0 | 2 |
| 15 October 2012 | 2 | 0 | 1 | 1 |
| 15 October 2012 | 5 | 3 | 0 | 2 |
| 16 October 2012 | 2 | 1 | 0 | 1 |
| 16 October 2012 | 1 | 1 | 0 | 0 |
| 18 October 2012 | 3 | 1 | 1 | 1 |
| 18 October 2012 | 2 | 0 | 1 | 1 |
| 18 October 2012 | 3 | 2 | 0 | 1 |

## 3.5 Discussion

To provide information for marine conservation strategies, most research focuses on understanding and protecting species' breeding areas, and in some cases, feeding areas (Calvert *et al.* 2009). For animals that are long-lived, survival of individuals during the non-breeding season can have a substantial impact on population growth (Saether *et al.* 1996; Heppell *et al.* 2000). The majority of accounts of humpback whales feeding while on migration have described this as rare or opportunistic behaviour (Baraff & Clapham 1991; Gendron & Urban 1993; Stockin *et al.* 2005; Alves *et al.* 2009). However, several lines of evidence in this study suggest that feeding while on migration may be more important to humpback whales than currently believed and that when prey conditions are suitable, some individuals may delay migration and dedicate time to feeding.

Differences in the amount of time spent feeding on the two prey types suggest that changes in the prey type available on migration may influence the duration of stay at stopover sites by humpback whales. In migratory bird species, the duration of stay at migratory stopover sites has been shown to be linked to the quality of the resources available, with stopover duration being longer if the resource quality is high and required by the animal (Newton 2006). In this study, when krill were available, it was much more likely that a group of whales encountered were observed to be feeding. In contrast, when fish were available, the majority of groups encountered were observed to be migrating through the area. When a group was determined to be feeding on fish, the amount of time spent feeding by each individual was low. Individual whales dedicated more time to consuming krill than they did to consuming fish. In addition, several individual whales were re-sighted up to 10 days apart feeding on krill within the study site. Previous accounts of humpback whales feeding on fish while on migration have documented whales feeding for periods ranging from minutes (Stockin *et al.* 2005; Alves *et al.* 2009) to many days (Swingle *et al.*1993). In contrast, accounts of whales feeding while on migration on krill have described individuals feeding from many hours to up to 20 days in the same location in both the Northern and Southern Hemispheres (Best *et al.* 1995; Visser *et al.* 2011). Therefore, variation in the availability of different prey types may influence the amount of time dedicated to feeding by whales while on migration.

There were a number of differences in the behaviour of the whales feeding on the two prey types, with whales that were feeding on krill behaving more like whales on main feeding grounds and differently from that of non-feeding whales on migration. One difference was the variation in the linearity of the tracks of the animals which showed that two out of three animals feeding on krill looped back frequently and dedicated more effort to feeding in the area. When feeding on krill on the main feeding grounds, the tracks of humpback whales have been shown to include lots of turns and regular movements through the same area as animals exploit prey patches (Ware *et al.* 2011). In contrast, none of the six tagged whales feeding on fish in this study looped back through the same area. The difference in linearity could be the result of the higher mobility of the fish, making lunging in the same area not as profitable for this type of prey. However, higher turning angles in the tracks of animals are often used to determine that an animal is likely foraging, regardless of the prey type targeted (Gales *et al.* 2009; Silva *et al.* 2013). In contrast to this, migrating humpback whales have been shown to swim in very straight lines at a broad-scale over large distances (Horton *et al.* 2011). It is possible that the straighter tracks of animals feeding on fish may be a strategy that allows whales to combine migrating with a small amount of feeding instead of delaying migration to feed when the prey quality is low. This is also supported by the observation that the direction of travel in these cases was typically in a south or south-east direction which is consistent with the typical direction of the migratory movement at the study site during the southward migration towards feeding grounds (Gales *et al.* 2009). Given that whales migrate through remote ocean areas, variation in turning angles is often used to detect potential foraging behaviour at a broader scale in satellite tag data using state-space modelling (Gales *et al.* 2009; Silva *et al.* 2013). However, determining whether whales feed along the migratory route using state-spaced modelling may be difficult as even whales that were observed to feed in this study still had reasonably straight tracks. Satellite tag data typically transmits a location of the animal only a small number of times daily (Zerbini *et al.* 2006; Gales *et al.* 2009; Gales *et al.* 2010). Given this, the presence of the fine-scale feeding behaviour observed in this study would be missed by state-space modelling of satellite tag data. Therefore, this method may only be sensitive to detecting larger-scale feeding behaviour. As a consequence, straight tracks from satellite tag data without area restricted search behaviour do not necessarily indicate a lack of feeding behaviour by migrating whales. In addition, the straighter tracks of whales feeding on fish while on migration suggest that this prey type may not be as important to whales as krill while on migration.

Another difference in the behaviour of groups feeding on krill and groups feeding on fish was the size of the group. The larger group sizes observed while feeding on krill may be a result of the whales using different strategies to target the two prey types. Humpback whales have been shown to change their feeding behaviour in response to a change in prey species or prey distribution (Jurasz & Jurasz 1979; Friedlaender *et al.* 2009). On the main feeding grounds, when feeding on Antarctic krill (*Euphausia superba*), humpback whales often feed alone or in small groups of two to three (Kasamatsu *et al.* 1996; Gill *et al.* 1998). Group sizes in this population are also small while on migration, with the mean group size during the southward migration towards feeding grounds being approximately two and group sizes only rarely observed to be above four (Brown *et al.* 1995b). Large group sizes similar to those observed in this study have been recorded on feeding grounds in the North Pacific where humpback whales feed in groups of up to twelve individuals on fish species (Jurasz & Jurasz 1979; D'Vincent *et al.* 1985; Sharpe 2001). To the best of our knowledge, the large group sizes observed in this study have not been documented while whales feed on krill on the main feeding grounds. Humpback whales feeding on krill while migrating off the coast of South Africa have also been observed to feed in large group sizes of up to 15 animals (Best *et al.* 1995; Barendse *et al.* 2010). Group size may also be influenced by the size of the prey patch (Whitehead 1983); thus the large group sizes may be a product of the size of the krill patch available. However, given that there is often an overabundance of krill and large patch sizes in the Antarctic, and that humpback whales in the Antarctic feed in smaller group sizes, this explanation appears less likely. Therefore, the aggregation of large group sizes feeding on krill may indicate that many animals are drawn to this resource, which may be limited along the migratory route, suggesting that the availability of krill may be valuable to whales while migrating.

There was also variation in the sex composition of groups feeding on krill compared to groups feeding on fish. On the breeding grounds, humpback whales have a male biased sex ratio (Brown *et al.* 1995a) and form male-dominated groups that compete for access to lone females (Baker & Herman 1984; Clapham *et al.* 1992). While on the southern migration from breeding grounds to feeding grounds, the east Australian population of humpback whales has a sex ratio and group compositions that are most similar to those found on breeding grounds (Brown *et al.* 1995b). In contrast, on the feeding grounds humpback whales form female dominated groups, with females forming stable pairs, which are believed to be a way for females to optimize their energy gain and potentially increase their reproductive output (Weinrich 1991; Ramp *et al.* 2010). A female bias has also been observed during the southern migration of humpback whales from breeding grounds to feeding grounds off the coast of South Africa, an area where whales have been observed to feed while on migration (Barendse *et al.* 2010). The observation of female-dominated groups feeding on krill while on migration from breeding grounds to feeding grounds in this study provides further support for the observation that whales feeding on krill behaved similarly to whales on main feeding grounds. In contrast, when feeding on fish, whales on the migratory stopover were still in male dominated groups similar to what has been described for whales on migration. This suggests that females may be more likely to take advantage of feeding opportunities while migrating, particularly when krill are available.

One potential reason for the female bias in groups feeding on krill is the higher energy demands on females as a result of reproductive activity. In humpback whales, pregnancy begins on the breeding grounds and last for approximately 11 months with females giving birth upon their return to the breeding grounds the following year (Chittleborough 1958). Females then begin lactating for approximately 10.5 months, weaning the calf on the subsequent return to breeding grounds Chittleborough 1958). As a consequence, sexually mature females on migration can either be pregnant, lactating, or recovering from previous reproductive activity. Both pregnancy and lactation are energetically demanding (Oftedal 2000). Despite this, lactating females with a calf spend the least amount of time on the feeding grounds each summer (Dawbin 1966; Brown *et al.* 1995a), suggesting that they have a lower energy intake during a period of higher energy expenditure. The possibility that not all females complete the migration from the feeding grounds each year as a way to recover from this energy investment has been proposed as an explanation for the male bias on breeding grounds and on migration (Brown *et al.* 1995a). It is also possible that some females still migrate but rely on migratory stopover sites as a way to recover from the energy investment of reproduction. However, it is unknown whether the females observed in this study had completed the entire migration all of the way to the breeding grounds, or remained in productive temperate areas close to the stopover site to feed that year. Although animals are found in groups while migrating, very little close association between individuals is observed outside of the feeding grounds (Clapham 1996). Similar to on the main feeding grounds, the cooperative feeding between pairs of individuals, particularly between females, also suggests that whales may rely on migratory stopover sites to increase their energy gain and reproductive output. Therefore, the importance of feeding behaviour while on migration may vary between different sexes of whales and assist with optimising energy budgets.

The east Australian population of humpback whales has made one of the best documented and quickest recoveries from whaling worldwide (Noad *et al.* 2010). In addition, accounts of whales feeding while on migration are higher in this population than any other population (Dawbin 1966; Gill *et al.* 1998; Stockin *et al.* 2005; Stamation *et al.* 2007; Silva *et al.* 2010). Given that the use of migratory stopover sites and the quality of prey available at these sites has been linked to population demographics in other taxa (Newton 2006), this correlation deserves more attention. The high occurrence of observations may either be the result of the whales being more accessible while migrating along the coast, or of the whales having access to many different upwelling processes along the coast of Australia (Connell & Gillanders 2007). Such differences in upwelling and therefore, potentially the availability of prey while migrating, may assist in understanding the difference in recovery rates of whale populations post whaling. For example, the South Pacific populations have only shown a slight recovery and are still a long way from estimates of pre-exploitation population sizes (Gibbs *et al.* 2006). These populations are likely to migrate through remote areas of open-ocean and may therefore not have access to the same feeding opportunities that the east Australian population does. Future research should focus on determining whether there is any link or causal relationship between population recovery rates and the extent to which whales feed while on migration.

The results of this study suggest that migratory feeding may be of differing importance to whales depending on both the type of prey available and the sex of the whale. Given that east Australian population of humpback whales are thought to feed predominantly on krill while on the main feeding grounds, a preference for feeding on krill over fish is expected. In order to fully understand the potential importance of feeding behaviour while on migration, an understanding of the amount of feeding and energy intake that occurs on migratory stopover sites is required. It may be that this behaviour is beneficial to some individuals when prey conditions are favourable and allows for a higher reproductive rate or success, which in turn would result in an increase in population growth. While the current migratory strategy of humpback whales is thought to be one of ‘feast and famine’ with whales feeding extensively over summer, and very little for the rest of the year, it may be that there are biological limitations that influence the ability of certain individuals to store sufficient energy to complete migration. As a consequence, the availability of the right type of prey in sufficient quantities along the migratory route may assist with increasing the success of migration by humpback whales.

## 3.6 Acknowledgements

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*Photo: A right side lateral lunge by a humpback whale feeding off the coast of Eden, NSW (photo by Scott Sheehan)*

# Chapter 4

## Potential energy gain by whales outside of the Antarctic: prey preferences and consumption rates of migrating humpback whales

*In the previous Chapter, a change in the prey species available was found to influence the feeding behaviour of humpback whales while on migration. However, it is unclear as to whether this behavioural variation was driven by a change in the prey species or a difference in the depth distribution of the prey. Therefore, the influence of both prey species and prey depth on the rate of lunge feeding behaviour by humpback whales while on migration and the amount of energy consumed was investigated in this Chapter. It has been prepared for submission to Polar Biology.*

# 4

# Potential energy gain by whales outside of the Antarctic: prey preferences and consumption rates of migrating humpback whales

## 4.1 Abstract

The humpback whale (*Megaptera novaeangliae*) is an Antarctic predator that makes annual migrations from Antarctic feeding grounds to tropical breeding grounds. The extent to which it feeds during migration is unknown but thought to be very low. However, whether an animal feeds during migration is likely to depend not only on the availability of prey but also on the ease with which it can capture the available prey. This study measured how changes in the type of prey available and the depth of the prey influenced the lunge feeding rates and the amount of energy consumed by humpback whales during their southward migration from breeding grounds towards feeding grounds off the south east coast of Australia. The type of prey available significantly influenced feeding rate in that whales that targeted krill lunged at significantly higher rates compared to whales that targeted fish. Depth of the prey was not found to be a significant factor. The observed lunge rates when feeding on krill, to the best of our knowledge, are higher than any previously reported rates of whales feeding. Estimates of the energetic content of the prey ingested revealed that whales may consume between 1.4 and 3.7 times their daily energy requirements per day while feeding on krill during migration, but less when feeding on fish. This suggests that whales may begin to restock energy supplies prior to reaching the Antarctic. Determining how often this high rate of energy intake occurs along the migratory route will assist with understanding the contribution of migratory energy intake to annual energy budgets.

**Keywords:** lunge feeding, krill, *Megaptera novaeangliae*, migratory stopover, Southern Ocean

## 4.2 Introduction

The large majority of top predators in the Southern Ocean rely either directly or indirectly on the presence of Antarctic krill (*Euphausia superba*) (Hunt *et al.* 1992; Croxall *et al.* 1999; Nicol *et al.* 2008) which is currently thought to be one of the most abundant species in the world (Vestheim & Jarman 2008). However, factors such as climate change and a growing krill fishery threaten to reduce the availability of krill to Antarctic predators (Nicol & Foster 2003; Flores *et al.* 2012; Nicol *et al.* 2012). Management of this ecosystem requires an understanding not only of the amount of krill present but also of the amount of krill required by each predatory species. As a consequence, determining the consumption rates of predators has become an aim of current Southern Ocean research (Childerhouse 2013). Some predators, such as crabeater seals (*Lobodon carcinophagus*), are believed to be Antarctic krill specialists that rely almost entirely on the presence of this prey item to fulfil their annual energy budgets (Laws 1984; Lowry *et al.* 1988). Other animals, such as many whale species, are migratory and spend only part of their time feeding in the Antarctic (Dawbin 1966; Lockyer 1981). Such animals may therefore supplement their energy budgets with feeding effort in other areas. The current understanding of feeding outside of Antarctic waters by migratory whales is that the rate of feeding is extremely low (Mackintosh & Wheeler 1929; Matthews 1937; Gambell 1968; Lockyer 1981). Despite this, based on data on the energy stores of whales, it has been suggested that it is unlikely that feeding outside of Antarctica is limited, unless whales have much lower field or basal metabolic rates than predicted for animals of their size (Leaper & Lavigne 2007). However, a lack of data on the feeding behaviour of whales while migrating outside of the Antarctic has limited our understanding of the potential contribution of this behaviour to energy supplies.

Feeding during migration has been shown to play an important role in the ecology and survival of many animals (Newton 2006). During migration, animals are constrained to feeding on the prey that is available along the migratory route. As a consequence of environmental heterogeneity, prey availability and quality along a migratory route may vary between years. Variation in prey quantity and quality means that migratory animals are faced with a trade-off between the benefit of stopping to feed on the available prey and the benefit of continuing migration and reaching high quality feeding grounds earlier. In bird species, prey quantity and quality on the migratory route has been shown to influence factors such as the timing of migrations, future breeding success, survival of individuals, and population size increases or declines (Newton 2006). Terrestrial mammals have also been shown to time their migrations according to the likely availability of food while migrating

(Sawyer & Kauffman 2011). To the best of our knowledge, the factors that influence the amount of feeding completed while on migration by marine mammals have never been investigated.

Baleen whales are an example of a group of marine mammals that have been reported to feed while migrating. For many species, feeding behaviour during migration has been identified through potential foraging behaviour in the tracks of satellite tag data (Gales *et al.* 2009; Silva *et al.* 2013) or via direct (Stone *et al.* 1987; Best *et al.* 1995; Gill *et al.* 1996; Stockin & Burgess 2005; Visser *et al.* 2011; Chapter 3) and indirect (Cacchione *et al.* 1987) observations of feeding behaviour. Feeding during migration has been observed most often by humpback whales (Stone *et al.* 1987; Best *et al.* 1995; Gill *et al.* 1996; Stockin & Burgess 2005; Visser *et al.* 2011). Off the south east coast of Australia, humpback whales have been observed to feed regularly in spring during the southward migration towards Antarctic feeding grounds on both krill (*Nyctiphanes australis*) and small baitfish species (Stamation *et al.* 2007), despite the population being believed to feed predominantly on krill on their main feeding grounds (Matthews 1937). The amount of feeding that is observed has varied among years (Silva *et al.* 2010), but it is unknown whether this is due to the animals not feeding during migration in some years, or feeding at depth out of sight of observers. Therefore, while feeding behaviour during migration has regularly been observed, the factors that influence the extent of this behaviour remain largely unknown.

The choice of an animal to delay the completion of migration in order to feed is likely to be dependent on the ease with which it can find and capture prey while migrating. Humpback whales are rorqual baleen whales that lunge feed (Jurasz & Jurasz 1979). This behaviour involves the whale swimming at speed towards a patch of prey and engulfing a large quantity of prey-laden water (Goldbogen *et al.* 2008). Compared to other rorqual whale species, the humpback whale has evolved morphological adaptions that make it an efficient predator, including long pectoral fins that assist with turning and generating lift, and a large, low-aspect ratio tail that provides propulsion (Woodward *et al.* 2006). These adaptations enable humpback whales to accelerate quickly and maneuver at high speeds (Woodward *et al.* 2006), which allows them to target a number of prey types ranging from small zooplankton through to schooling fish (Clapham & Mead 1999). Different prey types have differing movement and predator avoidance abilities, which may result in whales needing to expend different amounts of energy to successfully capture them. Given that humpback whales are an air breathing mammal, the depth of prey is also likely to influence the energy required to capture the prey. The deeper the prey, the greater the travel distance between the surface and the prey and the longer the recovery time necessary at the surface (Houston & Carbone 1992). This means that less time can be spent consuming prey per unit time during foraging, with whales often increasing the amount of lunges completed in deeper water to account for the increase in travel time to the prey at depth (Tershy *et al.* 1993; Croll *et al.* 2001; Doniol-Valcroze *et al.* 2011). Similarly, blue whales have been shown to have a higher feeding rate near the surface (Doniol-Valcroze *et al.* 2011) with the animals potentially combining recovery time at the surface with purging of the water engulfed during the lunges (Goldbogen *et al.* 2011). Consequently, variation in both the type of prey available and the depth at which they occur should affect the energy required to capture prey, which in turn could influence the choice of a whale to feed during migration.

The aim of this study was to determine whether the type of prey and/or prey depth influenced the amount of feeding by humpback whales outside of their Antarctic feeding grounds. In addition, the study aimed to determine the amount of energy acquired while feeding during migration in relation to the energy requirements of whales over the same time period. Given that krill is a slow prey item which likely requires less energy to catch than fish, and that the whales in the population studied feed predominantly on Antarctic krill on their main feeding grounds, it was hypothesised that whales would lunge at a higher rate on krill compared to fish. It was also hypothesised that the whales would feed at a higher rate on shallow prey compared to deep prey given the close proximity to the surface and reduced travel time to access shallow prey. In order to make the choice to delay migration to feed worthwhile, it was hypothesised that humpback whales should either meet their energy requirements for the period of time spent feeding or have a higher rate of energy intake.

## 4.3 Materials and methods

### 4.3.1 Behavioural data collection

The east Australian population of humpback whales makes annual migrations from the Antarctic where they feed over summer, to low latitude waters off the north east coast of Queensland, Australia where they breed over winter (Chittleborough 1965; Dawbin 1966). Data were collected off Eden, NSW, on the south east coast of Australia (37.07° S, 149.90° E) (Figure 4.1) during spring, from the 9th of September to the 2nd of October 2011 and the 9th of September to the 19th of October 2012. This time coincided with the southward migration of the whales towards Antarctic feeding grounds. Groups of whales were located opportunistically and approached by a 5.5 m (2011) or 8.5 m (2012) rigid-hulled inflatable boat (RHIB) for tagging. A 6 m long, carbon-fibre pole was used to deploy digital acoustic recording tags (DTAGs) (Johnson & Tyack 2003) onto the backs of humpback whales between the blow holes and dorsal fin. The DTAGs were attached using four silicon suction-cups and were programmed to release after two to three hours, depending on weather conditions. DTAGs are small, lightweight, and pressure resistant tags that contain a 3-axis accelerometer, a 3-axis magnetometer, and a pressure sensor (accuracy of +/-0.5m) (Johnson & Tyack 2003). All data were collected at a sampling rate of 50 Hz. The DTAGs contain a VHF antenna which allowed the whale to be tracked and the tag to be collected when detached. The data collected by the tag were downloaded via infrared transmission.

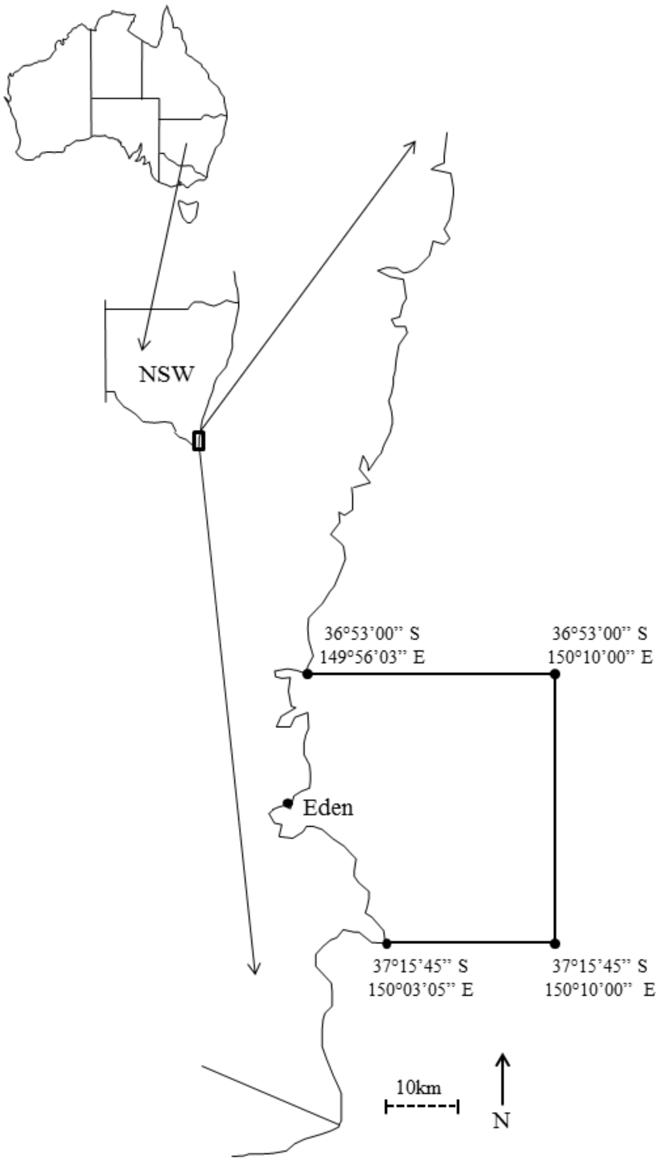

**Figure 4.1:** Location of the study site, Eden, New South Wales (NSW), Australia.

A continuous focal follow was completed on the tagged individual at approximately 50 to 200 m distance depending on the sea state. This involved using a pre-defined ethogram (Appendix 2) to record every behaviour of the animal while at the surface (Altmann 1974; Mann 1999), including the occurrence of feeding lunges as well as respirations. The data were collected vocally using a H1 Zoom audio recorder and later transcribed. Focal follow and DTAG data were time synchronised using a hand-held GPS (Garmin GPSmap 78SC). All focal follows were completed by a single observer (KO) to avoid inter-observer reliability issues (Mitchell 1979).

### 4.3.2 Identification of prey type and density

In 2011, the prey type targeted by the whales was determined using a combination of methods including 1) direct visual observation of whales engulfing the prey at the surface, 2) camera drops to determine the likely vertical distribution of the prey, and 3) collection of prey samples for species identification. Prey samples were collected to identify the prey species targeted, not to determine the density of the prey. To collect the prey, a 200 µm plankton net was towed at approximately 2 m depth behind the vessel travelling at a speed of 5 knots in areas where the whales had been observed to lunge feed at the surface. No attempts were made to catch fish species using this method. The collected prey species were then identified under the microscope using various identification keys. As a consequence of these methods, no consistent information was available on the prey type present at depth in 2011, although all camera drops assisted with visualisation of prey in the upper 10 m. It is therefore assumed that the prey type targeted at depth in 2011 was the same as the prey type observed to be targeted at the surface.

In 2012, a dual frequency (38 and 200 kHz) echosounder (ES60, Simrad/Kongsberg) was used to provide information on the availability of fish and krill. The echosounder was deployed off the starboard side of the vessel using a small towfish that held the echosounder at a depth of approximately 50 cm below the surface. For both frequencies, the echosounder had a ping rate of 0.5 Hz, depth bins of 10 cm, pulse length of 256 µs, and a power setting of 2000 W. The system was calibrated using a standard 38.1 mm Tungsten carbide sphere (Foote *et al.* 1987) at the beginning of the 2012 surveys. The sphere was lowered to between 10 and 20 m beneath the echosounder in a location with little biological scattering and a water depth of 26 m. Backscatter values for the standard target were less than 0.5 dB different from theoretical predictions.

Prey patches were identified by thresholding the backscatter at 38 and 200 kHz at -80 dB re 1 $m^{-1}$. A dB-differencing method (Reiss *et al.* 2008; Warren & Demer 2010) was used to identify scattering aggregations as either krill or fish depending on the value of the difference in volume backscattering strength ($D_{dB}$ = Sv at 200 kHz – Sv at 38kHz). Target strength (TS) values for krill were obtained using theoretical models for monospecific aggregations of krill (Conti & Demer 2006). Krill lengths were determined based on net tow data from 2011, visual observations of surface krill aggregations in 2012, and the largest possible size of krill that might be in this region (although most of the krill observed had lengths of 5 to 20 mm). An estimated krill length range of 5 mm to 60 mm was used and aggregations were identified as krill when $2 \text{ dB} < D_{dB} < 30 \text{ dB}$. Similarly, the species and length of fish were based on visual observations of surface schools in 2012 and discussions with local fisherman about the typical size of baitfish in this region at the time of the survey. Aggregations were identified as fish when $-100 \text{ dB} < D_{dB} < -20 \text{ dB}$. These values result from estimates of acoustic backscatter from fish ranging in length from 10 to 40 cm, including species with (Weber *et al.* 2009; Simmonds & MacLennan 2005) and without (Gorska *et al.* 2005) swim-bladders. Measured TS values from a study of similar baitfish (e.g. pilchards) were also used (Lynam *et al.* 2004).

During the focal follows of tagged whales in 2012, echosounder data were collected continuously at locations near to, and in the wake of the tagged whale. Data collected in the wake of the whale were collected by following the whale in a zig-zag pattern. Typically a 50 to 200 m distance was maintained, although occasionally larger separations up to 500 m would occur between the location of the tagged whale and the echosounder data. Scattering aggregations that were encountered during the focal follow of the whale were used to categorise the dominant prey type available during the tag deployment for each whale as either fish or krill.

### 4.3.3 Lunge rate calculations

DTAG data were decimated from 50 Hz to 5 Hz. Given that the orientation of the tag on the whale can vary both between and within a deployment (due to the tag slipping on an animal), the data were corrected for the orientation of the tag on the whale (methods explained in Johnson & Tyack 2003). The times when presumed feeding lunges were completed were determined using the lunge detecting algorithm with a TrackPlot filter applied, as described in Chapter 2, which looks for peaks in excess x-acceleration (forward acceleration minus the influence of gravity), along with a positive pitch angle and a highly negative level of jerk in the EXA signal (rate of change in forward acceleration), which is indicative of strong deceleration by the animal. Any lunges that were observed during the focal follow but were not detected by the algorithm were also included in the analyses. To determine lunge rates, the number of lunges every 10 minutes was calculated. The depth of a lunge was defined as the depth of maximum excess x-acceleration (see Chapter 2). To determine the influence of prey depth on the lunge rate, the average depth of the lunges completed in each 10 minute time bin was calculated and used as a proxy for the targeted prey depth. Any time bins with no lunges in them were excluded as the animal did not feed in that time interval. All means are presented as mean ± standard error.

### 4.3.4 Determining the impact of prey type and prey depth on lunge rate

A generalised linear mixed model (GLMM) was used to determine the influence of prey type and prey depth on the lunge rate of the whales. The model was run using the glmmADMB package (Fournier *et al.* 2012; Skaug *et al.* 2013) in R (R Development Core Team 2013). This package uses Laplace approximation to estimate the parameters of the model. Laplace approximation is more appropriate than PQL approximation for Poisson data where the mean number of counts per treatment is less than five, and is better for inference because it uses true likelihood rather than quasi-likelihood (Bolker *et al.* 2008). The individual whale was used as a random effect to account for the lack of independence of the multiple lunge rates determined for each individual over time. A zero-truncated distribution was used given the skewed nature of the data towards low lunge rates and the lack of zero values. Any data points outside 1.5 times the interquartile range above the upper quartile and below the lower quartile of the data were defined as outliers in the data. As outliers are likely to have a stronger influence on the outcome of a model than other data points, the model was run with outliers removed (n = 2, 3% of the data points). The residuals were checked for homoscedasticity and were normally distributed. Degrees of freedom were calculated based on the number of random effects (number of whales), minus the number of parameters in the model (in this case three: prey type, depth, and whale). Wald tests were completed to determine the z-values and p-values for each of the model parameters to assist with hypothesis testing, with significance levels set at $p < 0.05$.

### 4.3.5 Calculations of energy consumption

Many different methods have been proposed to determine the amount of prey and energy consumed by large baleen whales. Direct observations of consumption (Baumgartner & Mate 2003; Beardsley *et al.* 1996; Kenney *et al.* 1986), variation in the volume of stomach contents of captured animals (Vikingsson 1997), respiratory rates (Lockyer 1981; Blix & Folkow 1995), and changes in the energy stores of individuals have previously been used (Brodie 1975; Lockyer 1981). However, the most commonly used method relies on a relationship between the body mass of the animal and the estimated energy required to sustain metabolic rates. For many homeotherms, the basal metabolic rate (BMR) can be calculated based on the mass of the animal using the following equation:

$$BMR = 293.1M^{0.75}$$

where $M$ is the mass of the animal in kg (Kleiber 1975). However, due to the large size of baleen whales they are often an outlier in these models, and, as a consequence, there is still much debate over whether this equation accurately describes whales' metabolic rates. Many different estimates of the values of model parameters have been proposed. This has resulted in large variations in the estimated energy requirements of baleen whales, which in many cases are not supported by empirical data (Leaper & Lavigne 2007). It has been suggested that models that raise the mass of the animal to a power of greater than 0.75, and therefore greater than the BMR of the animal, are unlikely to represent true consumption given that the cost of thermal homeostasis and locomotion decrease with mass (Leaper & Lavigne 2001; Barlow *et al.* 2008). In a recent review, Leaper and Lavigne (2007) suggest that given many of the challenges in determining model inputs for baleen whales, the best way forward in calculating consumption would be to use separate models to provide an indication of the likely upper and lower limits of consumption. Based on a review of available methods they recommend the model by Innes *et al.* (1986) to represent an upper limit of the likely consumption rate, which is expressed as follows:

$$I = 0.42M^{0.67}$$

where $M$ is the mass of the whale in kg (assumed to be 26924 kg for humpback whales (Reilly *et al.* 2004)) and $I$ is the daily ingestion rate (given as kg/day). In addition, Leaper and Lavigne (2007) recommend an equation proposed by Boyd (2002) as an appropriate model to represent the likely lower limit of consumption by whales, which has the following form:

$$FMR = 2529.2M^{0.524}$$

where $FMR$ is the field metabolic rate of the whale expressed in kJ/day. Using these two equations, the average daily requirements of whales were calculated as a lower limit and upper limit of likely consumption. However, one of these equations represents the requirements of whales in terms of energy and the other represents it as the mass of food. Given that the prey types consumed during this study are likely to have different energy contents, the mass of prey was converted to an energy requirement. No information on the actual energetic value of the prey targeted in this study was available. As a consequence, the energetic content of the prey types was assumed to be 3900 kJ/kg for krill and 5450 kJ/kg for fish. These values have been used in many studies to provide an indication of the energetic content of crustaceans and fish (Leaper & Lavigne 2007). However, future studies should attempt to measure this parameter directly.

In order to calculate the consumption of prey by whales while on migration, estimates of a number of parameters were required. The first of these was an estimate of the numerical density of the prey (number of animals / $m^3$) and biomass density (g wet weight / $m^3$) available to the whales. For both krill and fish, echosounder data collected in 2012 were used to estimate prey density. Although krill swarms were visually observed more frequently in 2011 than in 2012, there were no echosounder data from 2011, so the 2012 krill density values were assumed to be similar to the prey density available to whales migrating through Eden in 2011. Given the large, visibly higher density swarms observed at the surface in 2011, this was likely to be a conservative approach, resulting in lower krill density values than actually encountered by whales in 2011.

Thresholded echosounder data (volume backscattering strength, $S_v$) were identified as being from krill or fish using the method detailed previously. The numerical density of the prey (number of animals / $m^3$) was calculated for each voxel (grid cell in three-dimensional space) in the swarm using an average TS value (at 200 kHz) for a single individual of -83.45 dB for krill and -52 dB for fish (Simmonds & MacLennan 2005). We selected two krill swarms and two fish schools for the analysis. Despite the wide range of volumes for the aggregations of the prey types, the numerical densities for the krill swarms were similar, as were the numerical densities of the fish schools (Table 4.1). Therefore these patches were assumed to be representative of the average biomass density of the prey available to the whales. To convert the numerical density (number of animals / $m^3$) into a biomass density (g wet weight / $m^3$), an equation was required for both krill and fish to translate body size into a weight. No data were available on the size/weight relationship of the specific prey species fed upon by the whales. To account for this, information from the literature on similar sized prey species for each prey type was used and assumed to be representative of the relationship between size and weight for the prey types targeted. It is thought that any error associated with this assumption is unlikely to have had a large influence on the calculated energy consumptions. In this study, the equation developed for Antarctic krill (*Euphausia superba*) by Wiebe *et al.* (2004) was used to convert the size of the krill into a wet weight.

$$krill\ wet\ weight\ (g) = (5.5 * 10^{-6}) * L^{3.2059}$$

where $L$ is the length of the krill (mm). The sizes of the krill collected during plankton tows were found to range between 5 and 20 mm in length. A mean krill length of 15 mm was assumed for these calculations as that was the length used in the conversion of the acoustic data to biological information.

To determine the sensitivity of this method to animal length, separate runs were completed using lengths of 10 mm and 20 mm, which resulted in biomass densities (g wet weight / $m^3$) that differed only by 15 to 20% (this is because larger animals scatter more sound so they produce a smaller numerical density estimate). For fish, the following equation was used:

$$fish\ wet\ weight\ (g) = \ 0.0044 * L^{3.1843}$$

where L is the length (cm) of the fish (FAO 1994). It was assumed that the fish were approximately 15 cm in length based on observations of fish near the surface and discussions with local fisherman about the average size of fish present in the study area at the time. The calculated wet weight per individual was then multiplied by the numerical density to provide an estimate of the biomass density (g wet weight /$m^3$).

The engulfment volume of humpback whales has been calculated to be 28 $m^3$ (Goldbogen *et al.* 2011). However, this volume likely represents a maximum engulfment volume and it is unlikely that humpback whales would regularly completely expand the oral cavity while feeding, especially when feeding near the surface when air may fill some of the cavity. In addition, the engulfment volume varies with the size of the animal, a factor that was not measured as part of this study and is difficult to measure accurately in the field. Given this, a more conservative value of 14 $m^3$ (half of the maximum) was used in the calculations. The amount of prey consumed in each lunge (PC) (g) was determined by:

$$PC = E_{volume} * P_{density} * C_{efficiency}$$

where $E_{volume}$ is the engulfment volume of the whale ($m^3$), $P_{density}$ is the average biomass density of the targeted prey (g wet weight / $m^3$) and $C_{efficiency}$ is the capture efficiency of the lunge (%). Capture efficiency relates to the proportion of the patch of prey that is actually caught in the mouth of the whale as opposed to fleeing during the approach by the whale. Very few data exist on the capture efficiencies of humpback whales targeting different prey types. However, it is likely to be influenced by the size and mobility of the prey (Mayo *et al.* 2001). As a consequence, the capture efficiencies by the whales for the two prey types were estimated for the purposes of this study based on observations of whales feeding on both prey types in various locations around the world. It was assumed that whales targeting krill would have a higher capture efficiency than that of whales targeting fish (80% compared to 60%), as krill are slower and therefore less likely to be able to flee capture. In order to complete the calculations, an additional assumption was made that the size of the prey patches was big enough to completely fill the mouth of the whale. This assumption appears justified given the extensive swarms of krill observed in 2011 and the size of the schools of fish detected by the echosounder (Table 4.1).

The average lunge rate ($Av_{LR}$) (number lunges / hour) was taken from data collected during this study. To determine the hourly consumption rate of prey (HC) (g) by whales on migration the following equation was used:

$$HC = Av_{LR} * PC$$

To convert this to an estimate of the energy provided by the prey, the HC was multiplied by the energetic content of the prey type (3900 kJ/kg for krill and 5450 kJ/kg for fish) and the assimilation efficiency (%), which is the amount of energy that becomes available to the whales from the prey ingested. Assimilation efficiency was assumed to be 80% for both krill and fish (Lockyer 1981; Innes *et al.* 1986; Kenney *et al.* 1997; Leaper & Lavigne 2007). The average energy content of prey consumed daily was then determined by extrapolating the HC. The durations of the focal follows in this study were only 2 to 3 hours. Given that very little is known about how much time humpback whales dedicate to feeding during migration, it is difficult to know the validity in extrapolating the feeding rate outside of the observed time, even though the whales observed in this study were often feeding prior to tagging, and were often still actively feeding at the end of the focal follow. To avoid extrapolating outside of the observed time, HC during the focal follows was also compared to the hourly energy intake rate required by the whales to meet their FMR. To determine the rate of energy intake required per hour by a whale, the daily energy requirement of humpback whales was divided by 24. However, it has been suggested that humpback whales do not spend 24 hours per day feeding in the Antarctic, potentially as a result of diel changes in prey distribution (Friedlaender *et al.* 2013). Consequently, the daily energy requirements were also divided into an hourly energy intake rate based on an assumption that whales only feed for 12 hours a day. The energy intake rate of whales on migration on various time scales (daily/hourly) was then compared to the required energy intake rate of humpback whales in the Antarctic to maintain their FMR (daily, hourly assuming 24 hours of feeding, hourly assuming 12 hours of feeding) using the following equation:

$$NEA = \frac{energy\ intake\ on\ migration\ (in\ x\ time\ frame)}{energy\ intake\ required\ by\ whale\ to\ maintain\ FMR\ (in\ x\ time\ frame)}$$

where *NEA* is the net energy acquisition by the whales. The comparison provided an indication of the likelihood that whales either lose or gain energy while feeding on migration.

## 4.4 Results

Nine individual whales were tagged off the coast of Eden, NSW, Australia (three in 2011 and six in 2012). Lunges were detected in all nine of the tag deployments. It was determined by visual observations at the surface that all three animals in 2011 were feeding on krill (*Nyctiphanes australis*) (Chapter 3). For the purposes of this study, it was assumed that these three animals were feeding on krill regardless of the depth of the lunge. This assumption was based on the observation from camera drops of krill being distributed within the upper 5 – 10 m of the water column throughout the focal follows and the lack of observation of schools of fish at any stage in 2011 (Chapter 3). Using echosounder data, all six animals in 2012 were determined to be feeding on schools of baitfish (Chapter 3). The baitfish species targeted likely included species such as jack mackerel (*Trachurus declivis*), pilchards (*Sardinops neopilchardus*), and redbait (*Emmelichthy nitidus*) that were regularly observed at the surface during the focal follows in 2012.

The lunge rates for animals assumed to be feeding on krill ranged from 1 to 21 lunges per 10 minutes, with an average of 9.50 ± 0.82. This corresponds to an average lunge rate of 57 lunges per hour. In comparison, animals that fed on fish had lunge rates that ranged from 1 to 5 lunges per 10 minutes, with an average of 2.47 ± 0.27, corresponding to an average lunge rate of 14.8 lunges per hour. The depths of lunges completed by whales assumed to be feeding on krill ranged from 1.4 m to 22.6 m with an average of 5.4 m ± 0.8 m compared to those of animals feeding on fish, which ranged from 4.1 m to 47.7 m with an average of 22.0 m ± 1.6 m. The lunge rate was significantly higher (GLMM, df = 6, z = 3.28, p = 0.001) for whales assumed to be feeding on krill compared to fish (Figure 4.2). However, the depth of the prey did not have a significant influence on the lunge rates of the animals (GLMM, df = 6, z = -1.20, p = 0.229) (Figure 4.2).

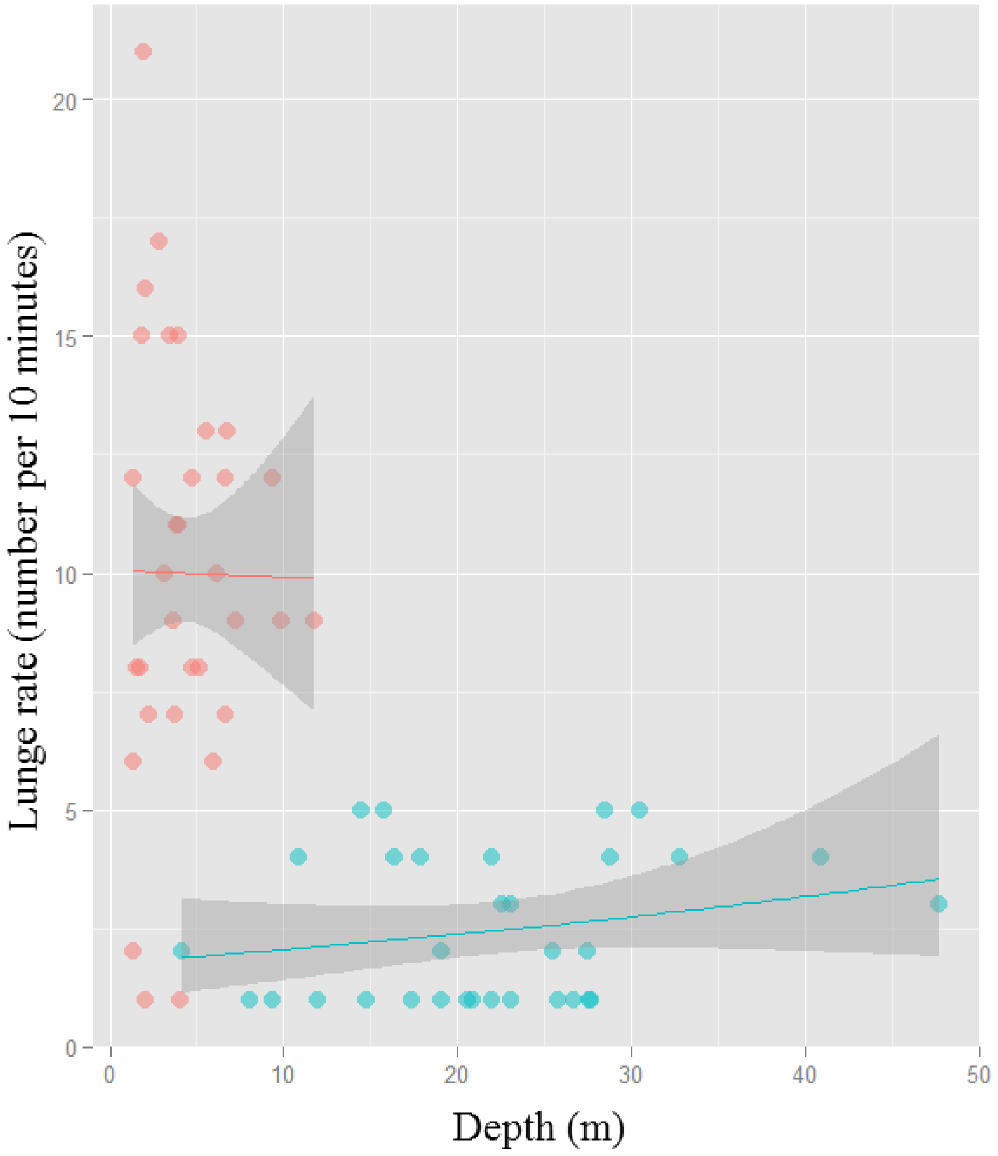

**Figure 4.2:** Changes in lunge rate (number per 10 minutes) with depth (m) as a function of prey type (krill (red dots) and fish (blue dots)). The coloured lines indicate the line of best fit for the prey type with the dark grey sections indicating the confidence intervals.

The biomass densities of the prey observed in the study site are provided in Table 4.1. It was determined that a humpback whale requires between 530 and 1522 MJ per day in order to meet the demands of their FMR. This corresponds to an hourly energy intake rate of between 22 and 63 MJ assuming that whales feed for 24 hours, or 44 and 127 MJ assuming that they only feed for 12 hours. While feeding on krill on migration, whales were estimated to have an average hourly energy intake of 86 MJ (Table 4.2). In contrast, when feeding on fish on migration, whales had an average hourly energy intake of 38 MJ (Table 4.2). This corresponds to whales feeding on krill while on migration consuming between 1.4 and 3.7 times their required daily energy intake rate if they fed for 24 hours per day, or 0.7 to 2.0 times their hourly required energy intake rate assuming whales only feed for 12 hours per day (Table 4.3). In contrast, whales feeding on fish while on migration are estimated to have only consumed between 0.6 and 1.7 times their required daily energy intake rate if they fed for 24 hours and between 0.3 and 0.8 times their hourly required energy intake rate when assuming whales only feed for 12 hours per day (Table 4.3).

**Table 4.1:** Details of the example prey patches that were representative of the prey available to the whales while on migration. All of the prey patches were being fed upon by whales, except for krill patch number 2.

| | Krill | | Fish | |
|---|---|---|---|---|
| Patch number | 1 | 2 | 1 | 2 |
| Size of patch ($m^3$) | 78540 | 29 | 760 | 60 |
| Mean prey numerical density of patch (number of animals / $m^3$) | 1300 | 1400 | 4 | 2 |
| Maximum prey numerical density of patch (number of animals / $m^3$) | 80000 | 48100 | 370 | 48 |
| Mean biomass density of patch (g wet weight / $m^3$) | 42 | 45 | 88 | 5 |
| Maximum biomass density of patch (kg wet weight / $m^3$) | 2.6 | 1.5 | 9 | 1.2 |

**Table 4.2:** Consumption of prey by humpback whales feeding on krill and fish while on migration. Values are expressed as mean (maximum) values.

| | Krill | Fish |
|---|---|---|
| Mean biomass density of prey (kg wet weight / $m^3$) | 0.043 (1.5) | 0.069 (5.1) |
| Whale engulfment volume ($m^3$) | 14 | 14 |
| Prey consumed per lunge (kg) | 0.49 (16.8) | 0.58 (42.8) |
| Average lunge rate (number / hour) | 57 | 14.8 |
| Capture efficiency (%) | 0.8 | 0.6 |
| Assimilation efficiency (%) | 0.8 | 0.8 |
| Energy content of the prey (kJ/kg) | 3900 | 5450 |
| Hourly migratory energy intake (MJ) | 86 (2988) | 38 (2765) |
| Daily energy intake (assuming 24 hours feeding) (MJ) | 2064 (71712) | 912 (66360) |

**Table 4.3:** Net energy acquisition of the whales feeding during migration given as a proportion of the energy needed to sustain field metabolic rates.

| | Krill | Fish |
|---|---|---|
| Upper daily | 1.4 | 0.6 |
| Lower daily | 3.7 | 1.7 |
| Upper hourly (24 hours feeding) | 1.4 | 0.6 |
| Lower hourly (24 hours feeding) | 3.7 | 1.7 |
| Upper hourly (12 hours feeding) | 0.7 | 0.3 |
| Lower hourly (12 hours feeding) | 2.0 | 0.8 |

## 4.5 Discussion

The consumption rate of prey by predators is an important input into models created for ecosystem-based management that aim to determine the impact of fisheries on ecosystems (Wiedenmann *et al.* 2011). Such models for the Southern Ocean are often based on the assumption that consumption by predators comes predominantly from Antarctic prey sources and not from prey consumed during migration. Models that vary the amount of food intake during migration show that fluctuations in migratory feeding could result in significant influences on the birth rates of whale populations (Wiedenmann *et al.* 2011). Despite this, little is known about what factors may lead to fluctuations in food intake by whales and the rates at which energy may be assimilated while migrating (Leaper & Lavigne 2007; Wiedenmann *et al.* 2011). The results of this study reveal that whales may change the rate at which they feed and the amount of energy that is consumed on migration, depending on the type of prey that is available. Humpback whales on migration were found to lunge feed at a high rate on krill and consume a greater amount of energy per unit time than required to maintain their FMR. Despite the hypothesis that the depth of the prey would influence the rate of feeding while on migration, there was no pattern in lunge rate as a function of the depth of the prey. However, this may be due to the relatively shallow distribution of prey encountered in this study. The results suggest that when prey conditions are favourable, feeding while on migration may allow whales to begin to refuel energy reserves prior to reaching Antarctic feeding grounds.

It is assumed that whales on migration feed less than they do on the feeding grounds (Lockyer 1981). Accounts of whales feeding while on migration typically describe an extremely brief feeding period (minutes to a few hours) (Salden 1989; Swingle *et al.* 1993; Gill *et al.* 1996; Stockin & Burgess 2005; Stamation *et al.* 2007; Alves *et al.* 2009) and whaling records also indicated that the large majority of animals had empty stomachs while migrating (Mackintosh & Wheeler 1929; Matthews 1937; Gambell 1968; Lockyer 1981). Whaling data has also been used to estimate that the rate of feeding while on migration is approximately 10% or less of that on the Antarctic feeding grounds (Lockyer 1981). However, whaling was often carried out during the migration of the animals from the feeding grounds towards breeding grounds (in the case of the east Australian population, during the northward migration) and as a consequence, there is little information on the stomach contents of animals migrating from breeding grounds to feeding grounds (Dawbin 1966). The results of this study suggest that whales may consume energy at a much higher rate (1.4 to 3.7 times their daily requirements) while migrating than previously believed. This is likely due to the whales lunge feeding at a higher rate on average than previously documented in the Antarctic. On the main feeding grounds, the lunge rate of humpback whales has been reported to be up to approximately 30 to 40 lunges an hour (Ware *et al.* 2011; Tyson *et al.* 2012). To the best of our knowledge, the lunge rate observed by animals feeding on krill while on migration in this study (average rate of 57 lunges per hour) is higher than any published account of humpback whales feeding world-wide. This high rate of energy intake, combined with other evidence that individual whales may spend up to 10 days feeding in the area off Eden (Chapter 3) suggests that the amount of energy intake during migration may be higher than previously thought. In addition, satellite tracks of whales migrating from the east coast of Australia towards the Antarctic revealed the presence of potential foraging by whales in several productive temperate areas (Gales *et al.* 2009). If individuals consume prey at such high rates and feed multiple times during migration, feeding while on migration may contribute a large amount to some humpback whale populations' energy budgets.

The rate of energy intake by whales feeding on fish was lower than that of whales feeding on krill, mainly as a result of the lower lunge rate when fish were available. Despite this, the energy intake rate by whales feeding on fish was still likely to be high enough to allow whales to essentially break-even (0.6 to 1.7 times their daily energy requirements assuming whales feed for 24 hours). In this case, when fish are available, whales may be able to balance their energy intake with energy expenditure, while still making progress southwards on migration towards feeding grounds (Chapter 3). In contrast, when krill were available, whales gained energy and were observed to delay migration and dedicate a significantly greater amount of time to feeding (Chapter 3). Therefore, when the prey conditions encountered enable whales to have a net energy gain per unit time foraging, whales may choose to delay migration to feed.

The difference in the lunge rate of the whales when targeting krill or fish is possibly due to differences in the speed of the prey types. Compared to krill species, schooling fish are more mobile and thus present a more difficult and energetically demanding prey target for humpback whales (swimming speeds of 67 to 159 cm/s for sardines (*Sardinops sagax*) (Misund *et al.* 2003) compared to 10 to 20 cm/s for krill species (*Nyctiphanes australis* and *Euphausia superba*) (Sidhu *et al.* 1970; Hamner 1984; Reinhardt & Van Vleet 1986; O'Brien 1988). In addition to the lower rate of lunges observed when feeding on fish, only 20% of the groups observed in the area were determined to be feeding when fish were available compared to 70% when krill were abundant (Chapter 3). Given the high availability of krill on the main Antarctic feeding grounds (Tarling *et al.* 2009; Nowacek *et al.* 2011), and the potential for animals to encounter slower prey further south on migration (Gill *et al.* 1996), the energy expenditure required to capture fish successfully may not be worth the delay in migration and the potential energy return for the majority of individuals. Therefore, the speed of the prey may influence the amount of energy required to capture the prey and impact on the decision to feed while migrating.

Despite the higher speed of fish, humpback whales have been observed to feed on fish species in many parts of the world (Jurasz & Jurasz 1979; Friedlaender *et al.* 2009; Acevedo *et al.* 2011). The morphology of humpback whales enables them to be a manoeuvrable predator that is capable of catching many different species of prey (Woodward *et al.* 2006). However, the efficient capture of fish often requires the use of various prey corralling techniques (Jurasz *et al.* 1979; Friedlaender *et al.* 2009; Acevedo *et al.* 2011). For example, bubble columns and clouds are often used in many different ways to corral and trap fish and reduce their escape abilities (Wiley *et al.* 2011). The east Australian population of humpback whales is believed to feed predominantly on Antarctic krill on the main feeding grounds (Matthews 1937). Although echelon feeding was observed by whales feeding on krill in this study, no evidence of prey corralling was observed while the whales fed on fish (Chapter 3). Due to the short amount of time spent on migratory stopovers, exposure to the potential prey species available on migration is also brief. The spread of new feeding behaviour through a population of humpback whales has been shown to take several decades, even though the whales may spend months feeding on the prey (Allen *et al.* 2013). Therefore, it is possible that given the short encounter time of the east Australian population of humpback whales with fish species as potential prey items, the population may not have yet evolved optimally efficient strategies for capturing fish. Although the east Australian population has been observed to feed on fish while on migration (Stockin & Burgess 2005; Stamation *et al.* 2007; Chapter 3), the efficiency of this behaviour may not be sufficient to make a large energy investment worthwhile.

The differing lunge rates on the different prey types could also be influenced by the nutritional quality of the prey. Migrating animals have been shown to choose prey items that contribute to the energy supplies required. For example, migratory birds have evolved the use of fatty acids in adipose tissue as a fuel and therefore benefit by consuming a diet high in lipids (McWilliams *et al.* 2004). Birds that typically feed on insects have been shown to switch to feeding on fruit during migration which has a lower protein to calorie ratio, which assists with fattening (Bairlein 1987; Bairlein & Gwinner 1994; Parrish 1997). In mammals, fats are only important as fuel during rest and low intensity exercise (Weber & Haman 2004; Guglielmo 2010). Whales making long distance migrations have the option to swim more slowly or use prevailing currents (Baker *et al.* 1981) to reduce the intensity of the exercise and increase their reliance on fat reserves. Although fish have a higher energetic content per gram than krill, based on % weight, temperate pelagic fish species are likely to have lower protein (~20% vs. ~50%) and similar or lower lipid content than krill (*Nyctiphanes australis*) depending on the season (~1 to 20% vs. ~10 to 20%) (Dunstan *et al.* 1988; Virtue *et al.* 1995; Bunce 2001; Zotos & Vouzanidou 2012). Therefore, if the whales consume the same weight of either krill or fish prey, they are likely to be able to replenish fat reserves more quickly by feeding on krill. This suggests that the lipid content of the available prey may also play a role in the decision of a whale to feed while on migration.

Whether or not migratory feeding is opportunistic or an essential part of the annual energy acquisition of whales, the results of this study suggest that changes in the prey type available on migration significantly influence the lunge rate of whales and the rate of energy intake. If changes in prey type can influence the amount of feeding while on migration, an understanding of what environmental variables may drive changes in prey availability is required. Future research should also focus on determining what other factors, such as prey density or whale body condition, may influence feeding behaviour and how frequently feeding behaviour occurs along the migratory route. This will assist with increasing knowledge of the extent to which whales rely on feeding during migration to meet their energy demands or assist with energy gain. Comparisons of the factors that influence feeding behaviour while on migration between populations that target different prey on their main feeding grounds will also assist in understanding whether or not the lower rate of feeding on fish compared to krill is the result of fish being an unfamiliar prey item for this population. The factors that influence the amount of feeding while on migration should also be incorporated into models to predict the impacts of climate change and krill fisheries on Antarctic predators, as fluctuations in migratory feeding could influence the extent to which humpback whales rely on the Antarctic ecosystem each year.

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*Photo: Humpback whales lunging in echelon while feeding off the coast of Eden, NSW (photo by Scott Sheehan)*

# Chapter 5

## Is stable isotope analysis of skin a suitable method for determining the diet of whales on migration?

*A change in the prey species available along the migratory route was found to have a significant impact on the behaviour of the whales and their rate of energy intake. As a consequence, a method to detect the most recent diet of whales was required. While direct observations in conjunction with echosounder data were used in this study, these methodologies may not always be suitable for use when sampling a large number of animals to determine if whales have fed while migrating. This Chapter aimed to determine whether stable isotope analysis of whale skin could be used to determine the most recent diet of whales, and therefore, the diet of whales while on migration. This chapter has been prepared for submission to Marine Mammal Science and as a consequence, has American spelling.*

# 5

# Is stable isotope analysis of skin a suitable method for determining the diet of whales on migration?

## 5.1 Abstract

Many whale species have been observed to feed while migrating, yet little is understood about the migratory diet and role of stopovers in whale ecology. This study investigated whether stable isotope analysis of skin is a suitable method to determine the diet of whales on migratory stopovers. The carbon isotope signatures of food webs vary across different latitudes, with polar food webs often having lower signatures than those of temperate or tropical food webs. Stable isotope analysis was completed on the skin of humpback whales (*Megaptera novaeangliae*) collected off the east coast of Australia while the whales were migrating south from breeding grounds to feeding grounds. The two sites of sample collection included a sub-tropical area where very little to no feeding is observed, and a temperate area that had previously been described as an important migratory stopover site for feeding by the east Australian population of humpback whales. At both sites, the carbon signature of the skin of the whales was still consistent with consuming Antarctic krill (*Euphausia superba*) in polar regions. At the temperate site, the whales were observed to feed on krill (*Nyctiphanes australis*) in 2011 and baitfish species in 2012, which occupy a higher trophic position than the krill. However, the nitrogen signature of the whales at the temperate site was significantly higher in 2011 compared to 2012, which would be indicative of the whales having fed at a higher trophic position in 2011. This suggests that stable isotope analysis of skin does not accurately reflect the observed diet or trophic position of the whales while on migration. However, in both years the isotope signatures at the temperate site were elevated compared to the sub-tropical site. The elevation of the signatures towards the expected isotope signatures on the migratory route suggests that the prey consumed may still have some impact on the isotope signatures of whale skin. The degree to which the signatures are influenced may be affected by the amount of feeding completed which could bias interpretation of tropic position. Further methodological developments are required in order to determine the potential impact of fluctuations in prey availability along the migratory route on whale populations.

**Keywords:** fasting, feeding, humpback whale, *Megaptera novaeangliae*, migratory stopover, skin, trophic position

## 5.2 Introduction

Migrations from feeding grounds to breeding grounds or between seasonal areas of resource availability are common in many animal taxa. During migration some animals are believed to fast, whilst others supplement their diet at migratory stopover sites (McLaren *et al.* 2013; Sawyer *et al.* 2013). The diet of animals on migratory stopovers is often different from the diet on their main feeding grounds. These changes may be due to differences in the availability of prey sources or to changes in the nutritional requirements of the species while migrating. For example, species of songbirds that feed on insects on the main feeding grounds change to feeding on fruit during migration which has a lower protein to calorie ratio that assists with fattening (Bairlein 1987; Bairlein & Gwinner 1994; Parrish 1997). The role of migratory stopovers for the ecology of animals is best understood for bird species where food availability at migratory stopovers has been shown to influence the timing of migrations, future breeding success, survival of individuals, and population size increases or declines (Newton 2006). Stopover use by non-avian taxa may be more common than currently believed (Sawyer & Kauffman 2011) with studies of stopover ecology in terrestrial mammals revealing that migrations are often timed to plant phenology so that animals can maximize their energy intake while migrating (Sawyer & Kauffman 2011). The role of migratory stopovers to the ecology of many other migratory species is poorly understood, particularly for whale species. A change in the type of prey available on migration has been shown to influence the behavior of whales while migrating (Chapter 3) and the rate at which energy is consumed which could impact on the degree to which whales depend on prey at high latitude feeding grounds each year (Chapter 4). However, in order to quantify the influence of changes food availability on migratory stopovers and its impact on ecological parameters, an understanding of the diet of animals during migration is required.

Understanding the diet of animals that live in the marine environment is challenging compared to determining the diet of terrestrial animals. In the marine environment, feeding occurs underwater and so it is not always possible to make direct observations of diet (Walker & Macko 1999). Advances in the development of accelerometer tags have allowed interpretation of underwater behavior of marine mammals in three-dimensions and the detection of presumed feeding attempts (Chapter 2; Goldbogen *et al.* 2008; Ware *et al.* 2011). However, alignment of presumed feeding attempts with areas of prey availability does not provide an understanding of the success of the prey capture attempt, and such short term observations may not provide an accurate representation of the whole diet (Deb 1997). Analysis of diet is often completed using stomach content analysis; although informative, this technique is often biased given that prey items are assimilated at different rates (Tollit *et al.* 1997; Bowen & Iverson 2013). In addition, for some animals, particularly large marine taxa, access to stomach contents is only possible from dead animals that were likely sick or injured prior to death and as a consequence, the stomach contents sampled may not represent the normal diet of a healthy animal. However, for many animals access to small tissue samples through non-invasive sampling methods is possible. As a result, many studies have turned to the use of chemical signatures to provide information on the diet of marine mammals (Iverson *et al.* 2004; Newsome *et al.* 2010; Bowen & Iverson 2013).

Stable isotope analysis is a method commonly used to gain information on the diet of marine mammals by comparing the isotope ratios of the tissues of predators to that of potential prey (Newsome *et al.* 2010). The difference between the isotopic composition of a predator and its prey is referred to as the trophic discrimination factor (Martinez del Rio *et al.* 2009) and the magnitude of this difference can vary as a function of prey quality, predator physiology and body condition, and differences in the metabolism of dietary components (lipids, carbohydrates, and proteins) (Newsome *et al.* 2010). The ratio of the two stable isotopes of nitrogen ($^{14}$N and $^{15}$N, referred to hereafter as $\delta^{15}$N) provide information on the trophic position of the animal as a result of the lighter isotope, $^{14}$N, being metabolised and excreted preferentially by organisms leading to an accumulation of the heavier $^{15}$N with each trophic step (DeNiro & Epstein 1981). The trophic discrimination factor for nitrogen has been shown to range from approximately 2‰ to 5‰ per trophic step across a range of taxa and food webs (DeNiro & Epstein 1981; Kelly 2000; Vanderklift & Ponsard 2003). Unlike nitrogen, the trophic discrimination factor of the ratios of carbon isotopes ($^{12}$C and $^{13}$C, referred to hereafter as $\delta^{13}$C) between trophic steps is small, allowing carbon isotopes to be used to identify the source of primary production in the food web (DeNiro & Epstein 1978). In the marine environment, $\delta^{13}$C varies between inshore and offshore environments, benthic and pelagic food webs, and temperate, tropical and polar areas (Clementz & Koch 2001). However, the pattern in which $\delta^{13}$C varies across these environments is often quite variable (McMahon *et al.* 2013). In some cases, the combination of $\delta^{13}$C and $\delta^{15}$N can allow food webs to be constructed based on isotope values and the likely diet or source of energy for a predator to be determined.

Stable isotope analysis is often used to determine the trophic position and diet of baleen whales while on their main feeding grounds (Schell *et al.* 1989; Best & Schell 1996; Hobson & Schell 1998; Witteveen *et al.* 2011; Gavrilchuk *et al.* 2014). Determining the diet of whales on migratory stopovers presents additional challenges given that the period of time that feeding occurs may be extremely short and that the amount of feeding may be small. In order to determine the prey consumed recently by a predator, access to a tissue with a high turnover rate is required as the turnover rate of the tissue being analyzed influences the period of time that the isotope signatures represent (Abend & Smith 1995). In terrestrial environments, stable isotope analysis of tissues with a high turnover rate such as blood plasma, feces and feathers have been used to describe diet during migration (Podlesak *et al.* 2005). The carbon dioxide exhaled in the breath of polar bears (*Ursus maritimus*) has also been used in an attempt to determine the contribution of the consumption of berries during fasting to polar bear energetics (Hobson *et al.* 2009). In whales, access to internal tissues such as baleen plates or fluids such as blood is limited to that of deceased or captive animals. Although the amount of feeding completed during migration is thought to be low, fluctuations in stable isotope values along baleen plates that grow continuously throughout the lifetime of a whale have been proposed to be the result of whales feeding in different isoscapes while migrating (Schell *et al.* 1989; Aguilar *et al.* 2014). This suggests that analyses of a tissue with a fast turnover rate, such as skin, may provide insight into the diet of whales while on migration. The turnover rate of the skin of baleen whales is unknown (Gavrilchuk *et al.* 2014) but is often assumed to be similar to that of other cetacean species such as belugas (*Delphinapterus leucas*) and bottlenose dolphins (*Tursiops truncatus*) where skin turnover rate has been shown to be approximately 70 days (Hicks *et al.* 1985; St. Aubin *et al.* 1990). However, some whale species such as the humpback whale (*Megaptera novaeangliae*) slough their skin regularly (Amos *et al.* 1992) meaning that it is possible that the skin of this species has a higher turnover rate than other cetacean species. Skin has the additional benefit that it is easily collected from live free-ranging whales (Krutzen *et al.* 2002). Therefore, given that skin is likely to have the highest turnover rate of the tissues accessible from live whales, and the ease with which this tissue type can be collected in the field, skin provided the best chance of determining whether dietary changes had occurred during migration in baleen whales.

The east Australian population of humpback whales feeds during the summer months on Antarctic feeding grounds where they are believed to consume predominantly Antarctic krill (Matthews 1937) (Figure 5.1). Krill in the Antarctic has previously been shown to have $\delta^{13}$C signatures ranging from -25‰ to -30‰ (Quillfeldt *et al.* 2010). At the end of summer, the whales migrate north for the winter months towards tropical breeding grounds in the Coral Sea off the north coast of Queensland, Australia (Figure 5.1). From previous studies, zooplankton sampled on the breeding grounds of this population has been shown to have $\delta^{13}$C signatures of approximately -18‰ (Frisch *et al.* 2014). At the end of winter, the whales then migrate south along the east coast of Australia towards feeding grounds, migrating through the two sites where whales were sampled as a part of this study. The first of these sites is Peregian Beach, Queensland (26.47° S, 153.08° E) (hereafter referred to as the sub-tropical site), followed by Eden, New South Wales (37.07° S, 149.90° E) (hereafter referred to as the temperate site) (Figure 5.1), which is a known migratory stopover site (Stamation *et al.* 2007). Based on calculations from known swim speeds of humpback whales on migration (Noad *et al.* 2007) it was estimated that it takes approximately three weeks for a humpback whale to move from Peregian Beach to Eden (likely longer for cow/calf pairs). During migration, humpback whales in this population have been observed to feed during both the northern (Stockin *et al.* 2005) and southern migration; however accounts of feeding behaviour are most common during the southern migration from breeding grounds back towards Antarctic feeding grounds (Gill *et al.* 1998; Stamation *et al.* 2007; Silva *et al.* 2010; Chapter 3). In this area and other similar migratory stopover sites around the world, whales have been observed to spend periods of up to 10-20 days in the one place feeding in temperate areas while on migration (Chapter 3; Best *et al.* 1995). In addition, there are many accounts of humpback whales feeding on breeding grounds from around the world (Salden 1989; Baraff *et al.* 1991; Alves *et al.* 2009; Danilewicz *et al.* 2009). The aim of this study was to determine the suitability of stable isotope analysis of skin for determining the diet of whales on migratory stopovers. Given the difference in the likely turnover rate of the skin in relation to the timing of migration and extent of feeding it was hypothesized that the chance of stable isotope analysis being a suitable technique to detecting the diet of the whales on migration was likely to be low.

If stable isotope analysis of the skin of the whales was able to be used to determine the diet during migration it was hypothesised that 1) the $\delta^{13}C$ signatures of the skin of the humpback whales at the temperate site would be similar to the $\delta^{13}C$ signatures of the prey available to the whales at the temperate site, or to that of tropical to sub-tropical carbon sources closer to the breeding grounds, 2) the $\delta^{15}N$ signature of whales on the temperate site would be higher than the prey items sampled at the same site, and 3) the $\delta^{15}N$ signature of whales at the temperate site in 2012 would be higher than the $\delta^{15}N$ signature of the whales in 2011, due to an observed shift in the predominant prey type available at the temperate site from krill (*Nyctiphanes australis*) in 2011 to baitfish species in 2012 (Chapter 3). It was also hypothesised that while the isotope signature of the skin may not have altered enough to accurately determine diet, input from prey sources consumed on migration are likely to have shifted the mean isotope values of the skin at the temperate site compared to that of the sub-tropical site in the direction of the lower latitude prey consumed while migrating.

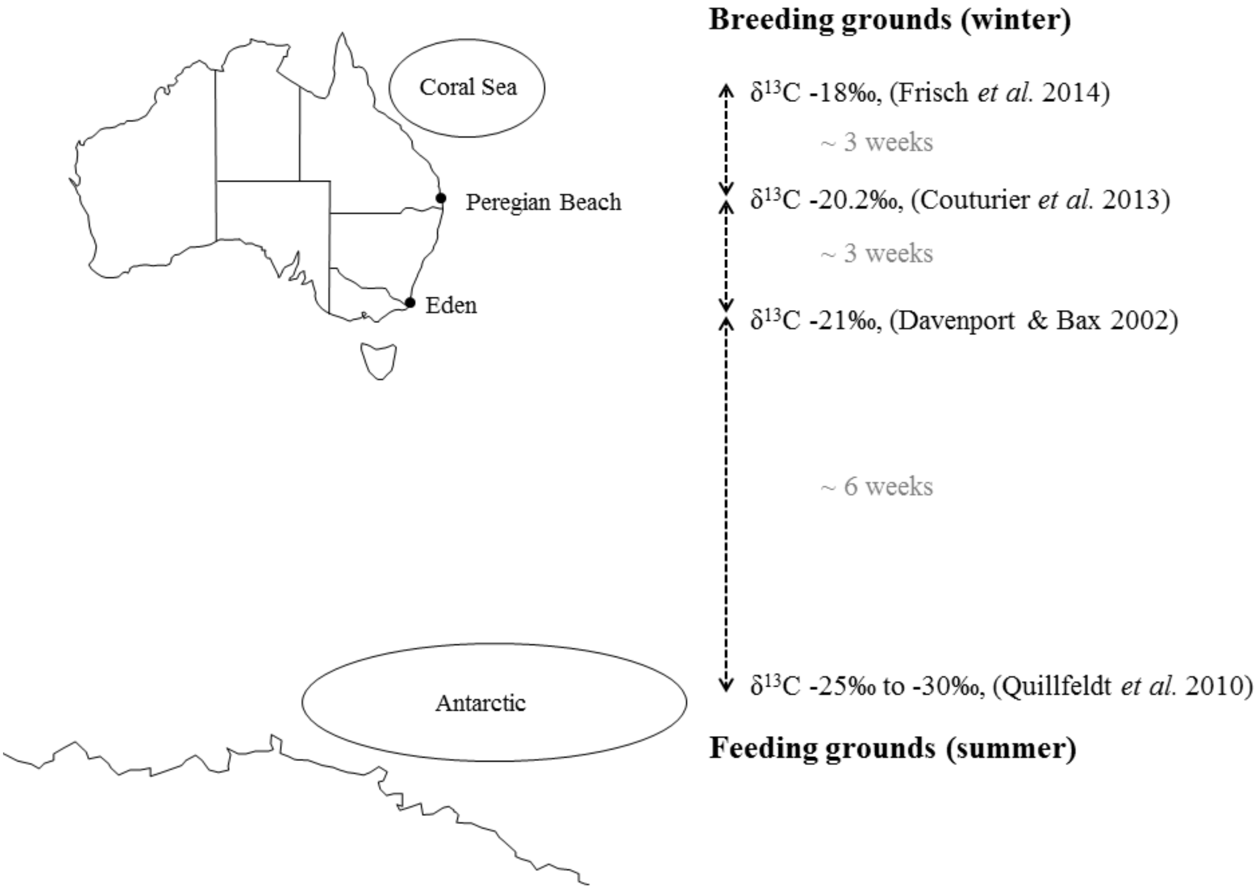

**Figure 5.1:** A map showing the relative location of the temperate site (Eden) and the sub-tropical site (Peregian Beach) in relation to the location of the feeding grounds in the Antarctic and breeding grounds in the Coral Sea. The expect $\delta^{13}C$ (‰) values for zooplankton at each location based on previously published studies is displayed, along with the estimated duration taken for whales to migrate between the locations.

## 5.3 Methods

### 5.3.1 Sample collection

The majority of humpback whale skin samples were collected using the PAXARMS biopsy system (Krutzen *et al.* 2002). This system uses a modified .22 rifle to fire a small, hollow dart at the animal. The dart collects a small sample of skin and blubber tissue (approximately 2.0 cm x 0.5 cm) and floats to facilitate collection. Samples were collected at the temperate site (Eden, NSW) between the 9th of September and the 2nd of October 2011 (n = 19) and the 9th of September and the 19th of October 2012 (n = 18). In addition, one sample was collected from the suction cups of a digital acoustic recording tag (DTAG) (Johnson & Tyack 2003) deployed onto an animal observed to be feeding at the temperate site in 2012 (n = 1). In 2011, all of the animals sampled had been observed to feed on krill (*Nyctiphanes australis*) at the surface and krill was the predominant prey type available to the whales that year (Chapter 3 & 4). None of the animals sampled in 2012 were observed to feed at the surface. When feeding at depth, animals were determined to be likely to be feeding based on the observation of animals having no consistency to their direction of movement, and being located within 100 m of one or more other predatory species. For some individuals, data collected by DTAGs deployed onto the whales and concurrent echosounder data in the area revealed that feeding behavior had occurred (Chapter 3 & 4). Based on echosounder data, whales at the temperate site in 2012 were determined to be feeding at depth on schools of baitfish (Chapter 3 & 4). Biopsy samples were also collected at the sub-tropical site (Peregian Beach, QLD) which is further north on the migratory route between the 17th of September and 29th of October 2011 (n = 20) and the 8th of October and 20th of October 2012 (n = 8). Using the same methodology previously described, no animals at the sub-tropical site were determine to be feeding. Where possible, all samples were taken from the mid-lateral section of the animal. Variation in the location of sample collection in cetaceans has been shown to have no influence on the stable isotope signature of skin (Williams *et al.* 2008). All biopsy samples were frozen at -20 ºC prior to analysis.

Krill (*Nyctiphanes australis*) were collected at the temperate site in 2011 and 2012 as a potential prey item by towing a 200 µm net behind the vessel when surface swarms were observed, in areas where the sampled whales were feeding. The krill were fixed and stored in 70% ethanol. In 2012, the krill were removed from the ethanol within four weeks of fixing, however the krill collected in 2011 remained in ethanol for just over 12 months. Once removed from the ethanol krill samples were rinsed in distilled water and frozen at -20 ºC prior to analysis. Storage in ethanol has been shown to influence the $\delta^{13}$C and $\delta^{15}$N signatures zooplankton by up to 1‰ (Feuchtmayr & Grey 2003; Syvaranta *et al.* 2008). The direction of the influence of ethanol storage on zooplankton samples is highly variable with some studies indicating an increase in both $\delta^{13}$C and $\delta^{15}$N signatures (Feuchtmayr & Grey 2003) while others observed a decrease in $\delta^{15}$N values (Syvaranta *et al.* 2008). This variation in response to the influence of ethanol makes correcting for storage in this solution difficult. However, the potential influence of storage in ethanol on the results obtained for the krill samples collected was considered when interpreting the results of this study. Australian sardines (*Sardinops sagax*) (n = 6) were also collected in 2012 from local fishermen at the temperate site as another potential prey item (Stamation *et al.* 2007) and were also frozen at -20 ºC prior to analysis. Although other species of baitfish are found at the study site (e.g. jack mackerel (*Trachurus declivis*), pilchards (*Sardinops neopilchardus*), or redbait (*Emmelichthys nitidus*)), these species are not caught commercially and no collection permit for baitfish was available, and as a consequence, other species were unavailable for analysis. We therefore use the isotope signature of Australian sardines as representative of the other baitfish species present at the study site given that the majority of these species are zooplankitvorous and are likely to have similar diets and as a consequence, isotope signatures. This assumption is supported by the findings of a previous study on the isotope signatures of baitfish in south eastern Australia that were found to be similar across species of zooplanktivorous fish ($\delta^{15}$N of 10.2 to 12.6‰; $\delta^{13}$C of -18.3 to -20.6‰) (Davenport & Bax 2002).

### 5.3.2 Stable isotope analysis

For each fish collected, a section of muscle approximately 1 $cm^3$ was cut from the dorsal surface. A selection of individual krill from each sample were combined and homogenized for use in the analysis (approximately 50 individual krill per sample) (2011 n = 6, 2012 n = 6). Each humpback whale biopsy sample had the blubber removed using a scalpel, so that only skin was analyzed as these tissue types have differing turnover rates (Abend & Smith 1995).

Each sample was freeze dried for five days. Once dried, the samples were ground in a mortar and pestle and approximately 0.1 mg of dried tissue powder was weighed into tin capsules. Analysis of the samples was completed at the Water Studies Centre at Monash University on an ANCA GSL2 elemental analyzer interfaced to a Hydra 20-22 continuous-flow isotope ratio mass-spectrometer (Sercon Ltd., UK). The elemental analysis had a precision of 0.5 µg for both C and N (n = 5 for both C and N). The precision of the stable isotope analysis was ± 0.1‰ for $^{13}$C and ± 0.2‰ for $^{15}$N (SD for n = 5 for both C and N). Stable isotope data are expressed in the delta notation ($\delta^{13}$C and $\delta^{15}$N), relative to the stable isotopic ratio of Vienna Pee Dee Belemnite standard ($R_{VPDB}$ = 0.0111797) for carbon and atmospheric $N_2$ ($R_{Air}$ = 0.0036765) for nitrogen. Isotope values are expressed as:

$$\delta(‰) = \left(\frac{Rsample}{Rstandard} - 1\right)1000$$

### 5.3.3 Lipid normalisation of stable isotope data

Lipid extraction has been shown to influence the $\delta^{15}$N signature of the skin of Balaenopterid whales in unpredictable ways (Ryan *et al.* 2012). As a consequence, all samples in this study were prepared for stable isotope analysis without lipid extraction. However, due to the depletion of $^{13}$C in lipids relative to proteins (DeNiro & Epstein 1977), analysis of samples without lipid extraction can influence the interpretation of trophic ecology (Murray *et al.* 2006). To account for this, models were applied to the stable isotope data to adjust for the impact of lipid on the samples. For prey samples, the lipid normalisation method described by Post *et al.* (2007) was applied to the isotope analysis results. This model was developed based on a large number of both terrestrial and aquatic animals and normalises the data using the following equation:

$$\delta^{13}\mathrm{C}_{\boldsymbol{corrected}} = \delta^{13}\mathrm{C} - 3.32 + (0.99 \times \mathrm{C{:}N})$$

where C:N is the carbon to nitrogen ratio of the sample which is positively correlated to the lipid content of the sample (Post *et al.* 2007). However, for the whale skin samples, a model that was developed by McConnaughey & McRoy (1979) (see also McConnaughey 1978) was used:

$$L = \frac{93}{1 + [0.246 \times (C{:}N) - 0.775]^{-1}}$$

$$\delta^{13}\mathrm{C}_{\boldsymbol{corrected}} = \delta^{13}\mathrm{C} + \mathrm{D} \times \left(I + \frac{3.90}{1 + 287/L}\right)$$

where *D* defines the slope of the curve, and *I* is a constant. Parameter values for both *D* (6.219) and *I* (-0.002) that were calculated by Lesage *et al.* (2010) were used in the calculations as these values were determined by specifically considering the impact of lipids on the $\delta^{13}$C values of Balaenopterid skin, which is most likely to represent the influence of lipids on the $\delta^{13}$C of the humpback whales sampled in this study. All data analyses were then completed using the lipid normalised data.

### 5.3.4 Data analysis

All statistical analyses were completed using R Statistical Program (R Core Development Team 2013). The isotope values of the whales from the temperate site were compared to those of krill (*Nyctiphanes australis*) and baitfish collected at the temperate site using two factorial ANOVAs, one for $\delta^{13}$C and one for $\delta^{15}$N. Helmert contrasts with type III sum of squares were applied to account for the uneven sample sizes. In both cases, a Tukey's test was carried out *post hoc* to determine which pairwise interactions in the ANOVA were significant. This test adjusts the p-value given to account for the large number of pairwise comparisons to keep the type I error low. An additional two factorial ANOVAs were completed, one for $\delta^{13}$C and one for $\delta^{15}$N, to determine the differences in the $\delta^{13}$C and $\delta^{15}$N signatures of the whales between years (2011, 2012) and locations (the temperate site, the sub-tropical site) with the same *post hoc* corrections to pairwise p-values. The whales at the sub-tropical site were not compared to the prey items sampled at the temperate site since the whales sampled had not yet reached the temperate latitudes where the prey items were sampled. Results are presented as F values with associated degrees of freedom (df). Significance was set at $p < 0.05$.

Antarctic krill (*Euphausia superba*) are believed to be the predominant dietary item of the Southern Hemisphere populations of humpback whales while on their main feeding grounds in the Antarctic (Matthews 1937). Given that no Antarctic krill were available for analysis, isotope values of the whales were compared visually to published data on the isotopic signature of Antarctic krill (Cherel 2008; Tierney *et al.* 2008). No statistical analyses were completed to compare the published values for Antarctic krill to the whales sampled as a part of this study due to the small sample size of the Antarctic krill data available.

## 5.4 Results

The results of the stable isotope analysis for the whales and the prey are presented in Table 5.1. There were significant differences in the $\delta^{13}C$ signature of the whales at the temperate site compared to the potential prey items sampled (Factorial ANOVA, df = 2, F = 686.9, $p < 0.0001$) (Figure 5.2); however, the year of sampling did not have a significant influence on the $\delta^{13}C$ signatures (Factorial ANOVA, df = 1, F = 0.371, p = 0.546). In both years, the whales had a significantly lower $\delta^{13}C$ than that of the krill sampled which suggests that the $\delta^{13}C$ signatures of the whales are unlikely to be representative of the diet of the whales during migration (Tukey's test; 2011, $p < 0.0001$; 2012, $p < 0.0001$). Although the krill had been stored in ethanol, the use of this preservative is only likely to have caused an approximate 1‰ difference in the $\delta^{13}C$ signatures of the krill (Feuchtmayr & Grey 2003; Syvaranta *et al.* 2008). The difference between the whales and krill was 6.8‰ in 2011 and 6.9‰ in 2012, which suggests that storage in ethanol was unlikely to have influenced the conclusions drawn. The whales sampled in both years had $\delta^{13}C$ signatures more similar to that of zooplankton sampled in polar regions on the main feeding grounds of the population (Figure 5.3). In contrast, the krill had $\delta^{13}C$ signatures that were close to previously published values of zooplankton at similar latitudes. There was no significant difference between the $\delta^{13}C$ of the krill sampled in 2011 and 2012 (Tukey's test, p = 0.99), or between the $\delta^{13}C$ of the krill and fish sampled in 2012 (Tukey's test, p = 0.99). The whales in 2012 also had a $\delta^{13}C$ signature that was significantly lower than that of the fish sampled in 2012 (Tukey's test, $p < 0.0001$).

**Table 5.1:** The mean (± SE) $\delta^{13}C$, lipid normalised $\delta^{13}C$ ($\delta^{13}C_{corrected}$), $\delta^{15}N$, and C:N of the whales and prey items sampled at both the temperate site and the sub-tropical site in the two years (2011 and 2012).

| Species | Location | Year | N | $\delta^{13}C$ (‰) | | $\delta^{13}C_{corrected}$ (‰) | | $\delta^{15}N$ (‰) | | C:N | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | mean | SE | Mean | SE | mean | SE | mean | SE |
| **Humpback whale** | | | | | | | | | | | |
| | Temperate | 2011 | 19 | -25.6 | 0.28 | -25.1 | 0.25 | 9.2 | 0.15 | 3.9 | 0.08 |
| | Temperate | 2012 | 19 | -25.6 | 0.15 | -25.2 | 0.17 | 8.1 | 0.17 | 3.8 | 0.08 |
| | Sub-tropical | 2011 | 22 | -27.0 | 0.30 | -26.0 | 0.17 | 8.0 | 0.09 | 4.3 | 0.17 |
| | Sub-tropical | 2012 | 8 | -26.4 | 0.33 | -25.9 | 0.20 | 7.4 | 0.16 | 3.9 | 0.14 |
| **Fish** | | | | | | | | | | | |
| | Temperate | 2012 | 6 | -18.7 | 0.25 | -18.8 | 0.25 | 12.0 | 0.07 | 3.3 | 0.02 |
| **Krill** | | | | | | | | | | | |
| | Temperate | 2011 | 6 | -19.6 | 0.48 | -18.3 | 0.15 | 7.9 | 0.08 | 4.7 | 0.34 |
| | Temperate | 2012 | 6 | -18.9 | 0.04 | -18.5 | 0.02 | 8.3 | 0.05 | 3.8 | 0.02 |

Similar to the $\delta^{13}C$ signatures, there were also significant differences between the $\delta^{15}N$ signatures of the whales at the temperate site and the prey sampled (Factorial ANOVA, df = 2, F = 144.93, $p < 0.0001$). In 2012, the $\delta^{15}N$ signature of the whales was not significantly different from that of the krill sampled (Tukey's test, $p = 0.43$). In contrast, in 2011, the whales at the temperate site had a significantly higher $\delta^{15}N$ signature than that of the prey items by 1.05‰ (Tukey's test, $p = 0.0003$). Given that the krill had been stored in ethanol, which has been shown to influence the isotope signatures of zooplankton by up to 1‰ (Feuchtmayr & Grey 2003; Syvaranta *et al.* 2008), it is difficult to determine the cause of this difference. In contrast, the $\delta^{15}N$ signature of the whales sampled at the temperate site was higher than that of published $\delta^{15}N$ values for Antarctic krill by 4.94‰ in 2011 and 3.84‰ in 2012. At both the temperate site and the sub-tropical site the whales had $\delta^{15}N$ signatures that were consistent with the whales having consumed prey in polar regions (Figure 5.4) There was also a significant difference between the whales in 2012 and the fish sampled (Tukey's test, $p < 0.0001$); however, the fish sampled had a higher $\delta^{15}N$ signature than the whales, the opposite to what would be expected if the whales consuming the fish had influenced the isotope signatures (Figure 5.2). The fish sampled had a significantly higher $\delta^{15}N$ signature than the krill by 3.71‰ (Tukey's test, $p < 0.0000$), which is consistent with the fish species sampled being zooplankivorous. There was no significant difference between the $\delta^{15}N$ signature of the krill sampled in both years (Tukey's test, $p = 0.65$).

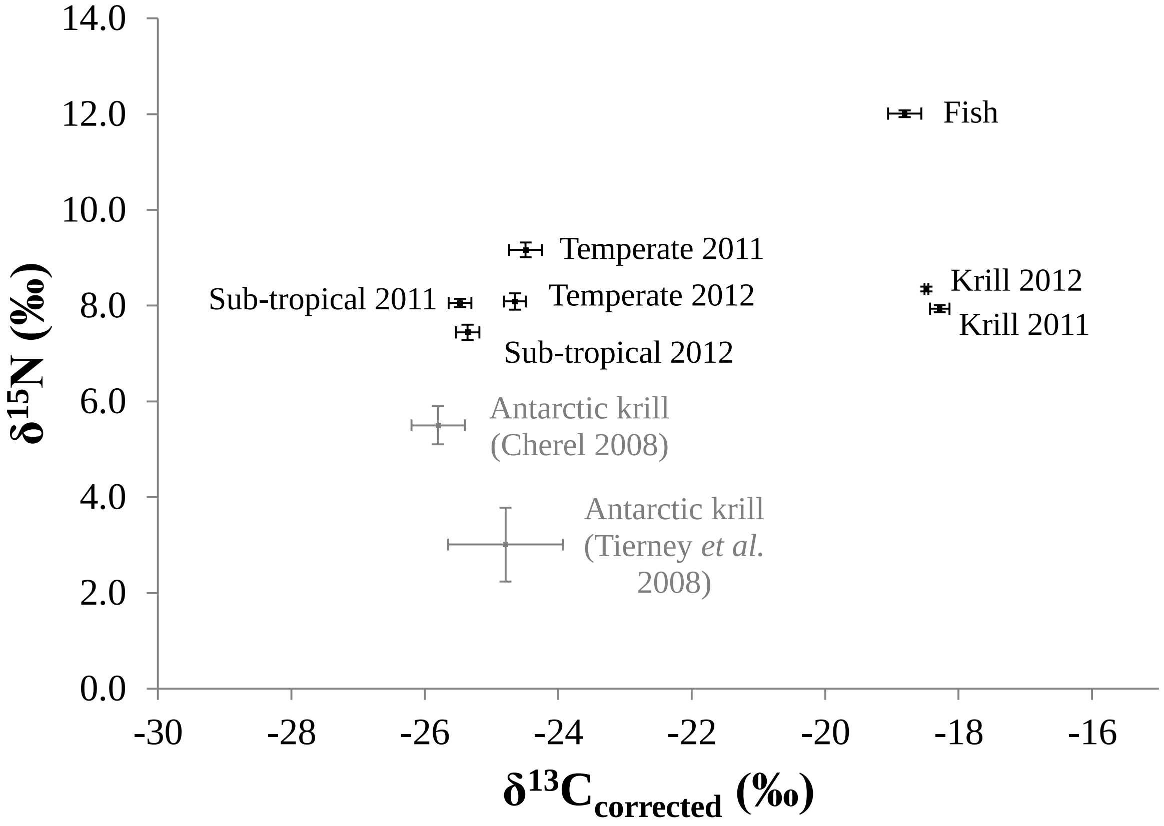

**Figure 5.2:** The mean (± SE) $\delta^{13}C_{corrected}$ (‰) and $\delta^{15}N$ (‰) of the skin of humpback whales sampled at a sub-tropical site and a temperate site while migrating south from breeding grounds to feeding grounds in two years (2011/2012). Isotope signatures of the prey items sampled at the temperate site are also provided. Values for Antarctic krill (grey) were taken from the literature.

The $\delta^{13}C$ signature of the whales also varied between locations (Factorial ANOVA, $df = 1$, $F = 12.347$, $p = 0.0008$); however post hoc comparisons revealed that this was mainly due to the $\delta^{13}C$ signature of the whales sampled at the temperate site being significantly higher than the whales sampled at the sub-tropical site in 2011 (Tukey's test, $p = 0.02$) (Figure 5.2). In contrast, the whales sampled at the sub-tropical site and the temperate site did not differ in the $\delta^{13}C$ signature in 2012 (Tukey's test, $p = 0.34$). There were no significant differences in the $\delta^{13}C$ signature between the whales sampled at the temperate site in 2011 and 2012 (Tukey's test, $p = 0.99$), or between whales sampled at the sub-tropical site in 2011 and 2012 (Tukey's test, $p = 0.98$) (Figure 5.2).

Similar to δ$^{13}$C signatures, the δ$^{15}$N signature was also influenced by the location of sampling (Factorial ANOVA, df = 1, F = 19.607, $p < 0.0001$) but was also influenced by the year of sampling (Factorial ANOVA, df = 1, F = 44.081, $p < 0.0001$). At both locations, the δ$^{15}$N signature was higher in 2011 compared to 2012 (Tukey's test; temperate site, $p < 0.0001$; sub-tropical site, p = 0.02). There was no significant difference between the δ$^{15}$N signature of whales sampled at the sub-tropical site and the temperate site in 2012 (Tukey's test, p = 0.11). However, the δ$^{15}$N signature of the whales sampled at the temperate site in 2011 was significantly higher than that of the whales sampled at the sub-tropical site in the same year (Turkey's test, $p < 0.0001$).

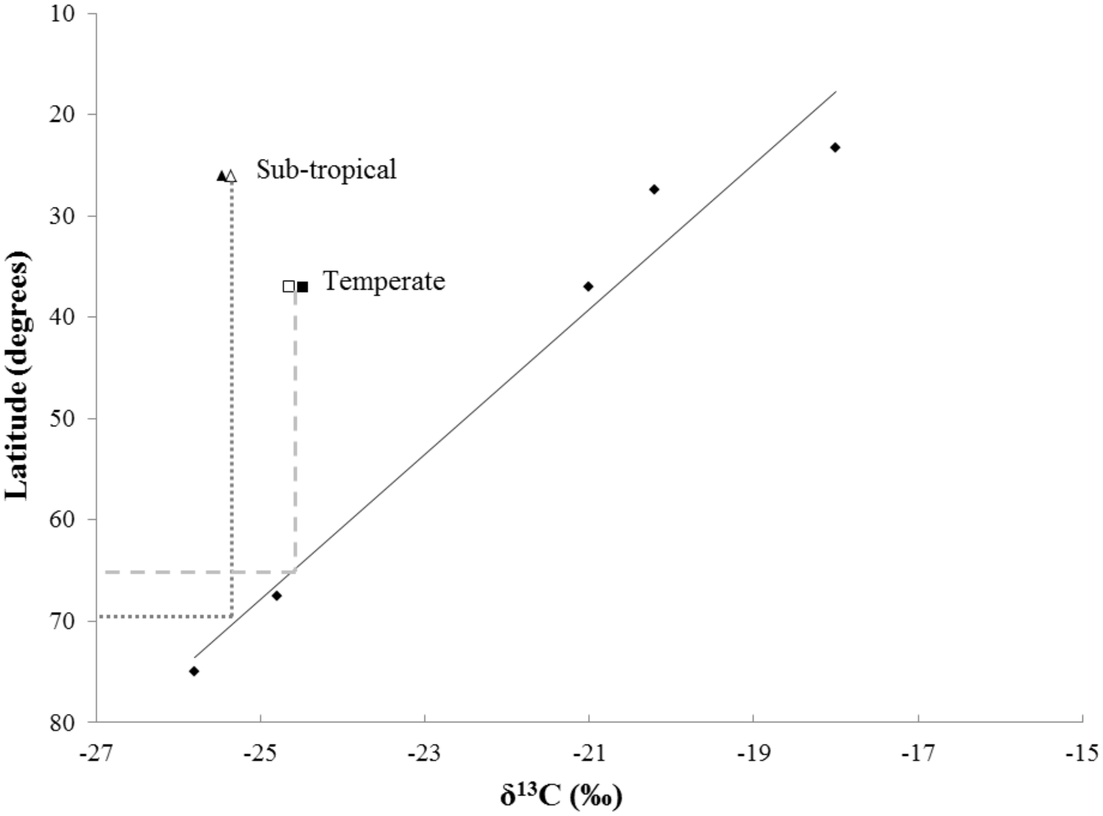

**Figure 5.3:** Relationship between published δ$^{13}$C values for zooplankton at various latitudes over the migration range of the east Australian population of humpback whales. The line of best fit between the published values (closed diamonds) is displayed. The δ$^{13}$C of the skin of the whales recorded at the sub-tropical site (triangles) and the temperate site (squares) in both years (2011= black, 2012 = white) do not match the relationship between latitude and δ$^{13}$C observed in other studies. The latitude that the δ$^{13}$C of the whales at both sites corresponds to is shown with the dashed light grey line (temperate site) and the dotted dark grey line (sub-tropical site). For both locations δ$^{13}$C values appear to be closest to Antarctic or polar latitudes.

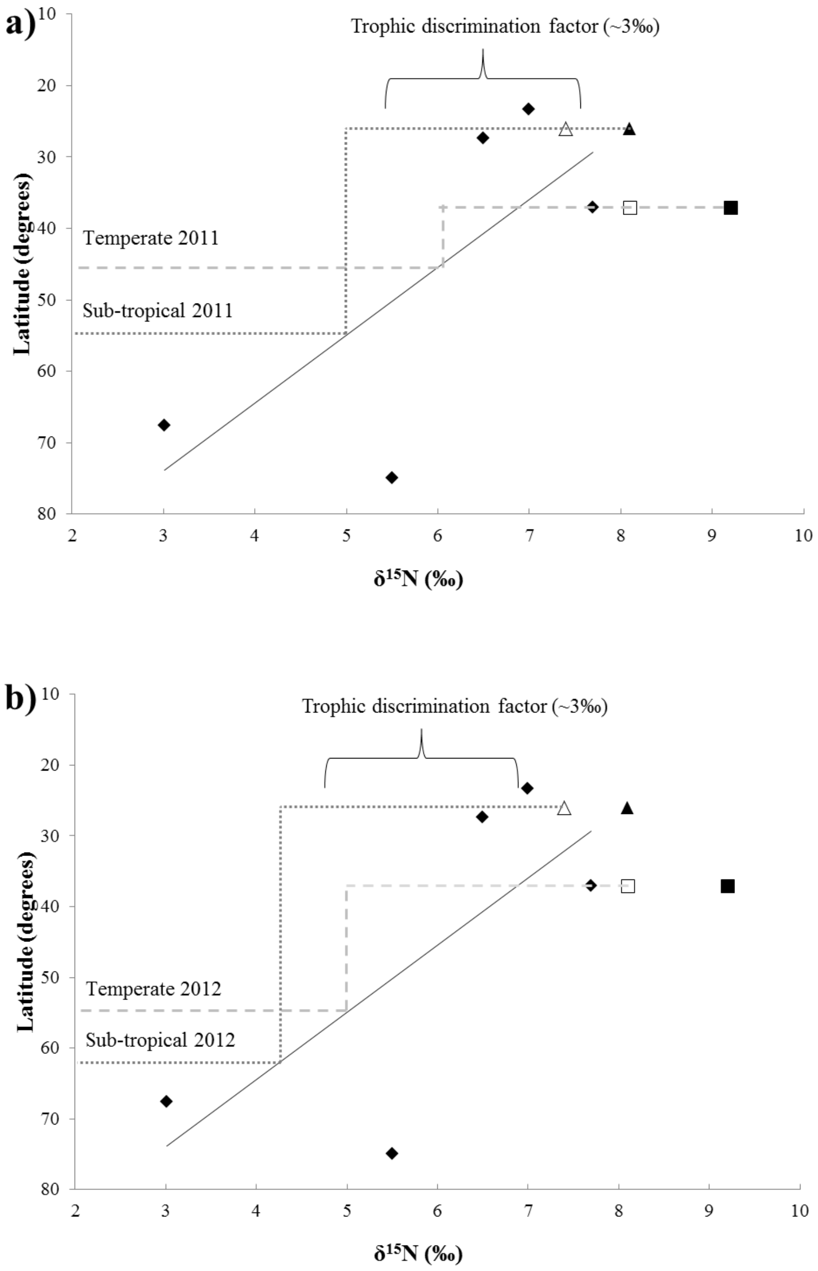

**Figure 5.4:** Relationship between published $\delta^{15}$N values for zooplankton at various latitudes over the migration range of the east Australian population of humpback whales. The line of best fit between the published values (closed diamonds) is displayed. When taking into consideration a trophic discrimination factor of approximately 3‰, the $\delta^{15}$N of the skin of the whales recorded at the sub-tropical site (triangles) and the temperate site (squares) in both years (a) 2011 (black shapes) and (b) 2012 (white shapes), do not match the relationship align with consuming prey in temperate or sub-tropical waters. The latitude that the $\delta^{15}$N of the whales at both sites corresponds to is shown with the dashed light grey line (temperate site) and the dotted dark grey line (sub-tropical site). For both locations $\delta^{15}$N values appear to be closest to Antarctic or polar latitudes, with the whales sampled at the temperate site having $\delta^{15}$N signatures closer to that expected in lower latitudes than the whales sampled at the sub-tropical site.

## 5.5 Discussion

Comparisons of the stable isotope signatures of the skin of whales sampled at a temperate site on the migratory route that is a known migratory stopover site, to that of potential temperate prey items revealed that the signatures observed most likely represented historical diet from Antarctic feeding grounds and not the diet on the migratory stopover site. The $\delta^{13}C$ signatures of whales at the temperate site were most similar to Antarctic krill $\delta^{13}C$ signatures and significantly different from the $\delta^{13}C$ signatures of potential temperate prey. In addition, the $\delta^{15}N$ signature of the whales in 2011 was significantly higher than that of the whales in 2012, in contrast to the prediction that the whales in 2012 would have a higher $\delta^{15}N$ signature due to the observation of the whales feeding at a higher trophic position. Consequently, our results suggest that stable isotope analysis of skin may not be an appropriate method for determining the diet or trophic position of whales on migratory stopovers.

There are a number of reasons why stable isotope analysis of skin may not be successful in detecting the diet of whales on migratory stopover sites. Firstly, it is likely that the quantity of food that humpback whales consume during migration is relatively low in comparison to the amount consumed on the main feeding grounds (Lockyer 1981). As a result, the observed stable isotope signatures are likely to represent a mix of historical polar prey and a small input of recent temperate or tropical prey consumed on migration or on the breeding grounds. In both 2011 and 2012, the $\delta^{13}C$ and $\delta^{15}N$ signature of the whales at the temperate site shifted towards the expected lower latitude signatures, compared to the whales sampled at the sub-tropical site (Figure 5.3 and Figure 5.4). Fasting has previously been shown to have little to no impact on the carbon signature of animals (Hobson *et al.* 1993), suggesting that the shift towards higher $\delta^{13}C$ signatures found in this study is likely to be the result of the metabolism of prey sources consumed while migrating or on the breeding grounds. While in many animals fasting has been shown to lead to an elevation in $\delta^{15}N$ (Hobson *et al.* 1993; Polischuk *et al.* 2001; Fuller *et al.* 2005; Hobson *et al.* 2009; Lee *et al.* 2012), it has recently been suggested that the opposite may occur in whales, with $\delta^{15}N$ declining during periods of fasting (Aguilar *et al.* 2014). This difference in nitrogen enrichment in relation to other fasting taxa was hypothesized to be due to the low use of body proteins as a source of energy by migrating whales (Aguilar *et al.* 2014), a factor believed to be responsible for an elevation in $\delta^{15}N$ in other fasting animals (Hobson *et al.* 1993). In addition, unlike most terrestrial taxa, whales obtain water from their prey (Costa 2009) and so a period of fasting also corresponds to a period of reduced water intake, with blubber becoming the source of both water and energy during this time (Aguilar *et al.* 2014). As a consequence, whales are likely to reduce the amount of urine produced during periods of fasting, meaning that less nitrogen$^{14}$ is excreted, reducing any further depletion of nitrogen$^{14}$ and subsequent increase in $\delta^{15}$N (Aguilar *et al.* 2014). When whales begin feeding, they return to protein anabolism and reduce lipid catabolism, and as a result, an increase in $\delta^{15}$N is likely to be observed (Aguilar *et al.* 2014). Therefore, the higher $\delta^{15}$N signature of the whales at the temperate site compared to the sub-tropical site is also likely indicative of feeding while migrating.

However, this shift towards isotopic signatures expected if feeding in lower latitudes for both $\delta^{13}$C and $\delta^{15}$N was only significant in 2011, which suggests that in some years a shift towards the isotope values of prey sources consumed on the migratory route may not be observed in the skin, even if the whales have fed while on migration. A possible reason for the difference observed in the amount of change between the sub-tropical site and the temperate site in the two years is a difference in the rate of energy intake. On the temperate site off Eden, the whales were observed to feed at a higher rate with a higher energy intake in 2011 when feeding on krill compared to 2012 when feeding on fish (see Chapter 4). This differing rate of food intake may explain why the isotope signatures of whales in 2011 had shifted significantly towards low latitude isotope signatures for both $\delta^{13}$C and $\delta^{15}$N but did not in 2012. In 2012, the whales may not have yet taken in sufficient food to significantly influence isotope signatures. It is rare for studies to have information on both the rate of energy intake on various prey types and the isotope signature of animals at that time. In 2011, whales were observed to feed on surface swarms of krill, a prey type that occupies a lower trophic position than the baitfish species consumed by the whales in 2012. However, comparisons of the $\delta^{15}$N signature of the whales at the temperate site in 2012 to the whales in 2011 showed that $\delta\,^{15}$N signatures were lower in 2012 (Figure 5.2), which is indicative of a lower trophic position of feeding. This pattern in $\delta\,^{15}$N between the years is different from that observed in the krill collected on the temperate site that did not vary between years, suggesting that the difference in $\delta^{15}$N of the whales between years was more likely the result of an increased intake of temperate prey items as described above, and not the result of a shift in basal isotope values. However, analysis of these isotope values without information on the actual diet of the whales would have led to the conclusion that whales fed at a slightly higher trophic position in 2011, which is likely not the case. Therefore, it is possible that differences in the rate of energy intake may influence the analysis of trophic position from whale tissue.

Another reason why the diet of whales on migratory stopover sites cannot be determined correctly from stable isotope analysis is that the turnover rate of the skin may not be fast enough to allow the signature representing the most recent diet to be incorporated into the tissue. To avoid this issue, samples should be taken from animals further along their migratory route allowing a longer period of time for the dietary signature to incorporate into the tissue. In the case of the east Australian population of humpback whales, sampling skin tissue from sites further south on the migratory route, such as off the coast of Tasmania, or close to the Antarctic at the onset on the main feeding season, may enable migratory diet signatures to be measured. The turnover rate of the tissues of animals can only be accurately determined using controlled feeding studies (Tieszen *et al.* 1983) which are not possible for the larger species. For this reason, the turnover rate for baleen whales is assumed to be similar to that of other cetacean species in captivity, but the accuracy of this assumption is unknown. It is therefore difficult to judge how far along the migratory route sampling should occur. In addition, for many whale populations the migratory paths are not fully understood (Hauser *et al.* 2010) nor are the locations where feeding occurs during migration. The diet could also change along the migratory corridor depending on available prey species. Therefore, it may often be difficult to determine a suitable sampling location to ensure that isotope signatures of recent diet have had time to incorporate into the tissue.

The development of methodologies for accessing a tissue type with a faster turnover rate than skin from live whales would also improve the chance of detecting isotope values that represent recent diet. While accessing blood and liver from live whales is not feasible, accessing carbon dioxide ($CO_2$) from breath may be possible. Although initially developed as a tool in human medicine (Schoeller & Klein 1979), the use of $CO_2$ from breath to determine recent carbohydrate intake in the diet has been completed in birds (Podlesak *et al.* 2005) and mammals (Hobson *et al.* 2009). When whales exhale they release 'blow' which is expired air with droplets of mucus mixed with sea water (Hunt *et al.* 2013) which has been used to detect hormones (Hogg *et al.* 2009), pathogens (Acevedo-Whitehouse *et al.* 2010) and to collect DNA (Frere *et al.* 2010). However, these studies involve catching mucous residue and not the gaseous sample needed to analyze the $CO_2$ being exhaled. Collection of the breath of whales may be difficult in the field and further development of this technique is required (Hunt *et al.* 2013). In addition, this technique would only work to determine $\delta^{13}C$, not $\delta^{15}N$, therefore information on trophic position would still be unavailable. Despite this, as this technique allows for the detection of the metabolism of recently ingested carbohydrates (Hobson *et al.* 2009), development of this technique would allow for the detection of potential feeding sites along the migratory route. This would also prove valuable in other foraging studies by enabling the detection of the most recent diet of whales and other cetaceans.

The success of stable isotope analysis of skin to determine migratory diet will depend on the turnover of the tissue in the species of concern and the amount of feeding that occurs on migration. Given that the $\delta^{15}N$ signatures may not only be representative of trophic position of foraging but also of the amount of energy intake, it is important that studies using stable isotope analysis have a basic understanding of the ecology of the species they target before analyzing results. Fluctuations in $\delta^{15}N$ signatures could easily be interpreted as fluctuations in the trophic position of foraging or prey switching when in fact they could be displaying a period of feeding fluctuating with a period of fasting or lower energy intake. If skin is the only tissue available, collection of skin samples should occur in areas where dietary signatures will have had time to incorporate into the tissue, not necessarily in areas where the highest amount of feeding occurs. Future research should focus on increasing our understanding of the turnover rate of different whale tissues, and developing non-invasive techniques to access tissues or fluids with a faster turnover rate. This will assist in increasing our understanding of the diet of whales on migratory stopovers and will allow for better protection of important areas on the migratory route. Once the diet of animals on migration is understood, the impact of fluctuations in prey availability on migration on the ecological parameters of individuals and populations can be investigated.

## 5.6 Acknowledgments

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*Photo: An oblique lunge by a humpback whale feeding off the coast of Eden, NSW (photo by Scott Sheehan)*

# Chapter 6

## Discussion

# 6

# Discussion

## 6.1 Summary

This thesis investigated the feeding behaviour of humpback whales while on a migratory stopover site. Digital acoustic recording tags (DTAGs) were deployed onto whales with the aim of determining what factors may elicit this behaviour, and from these results, suggesting the potential importance of this behaviour to this population of humpback whales and also potentially to the species. In order to achieve this, a new method was developed to assist with detecting feeding behaviour at the surface in accelerometer data. The use of this method highlighted the potential for wave drag and a lowering of propulsive efficiency to potentially impact on the detection of feeding behaviour of whales at the surface. Using this method to determine the occurrence of lunge feeding behaviour, the influence of a shift in prey type (krill to fish) on the behaviour of the whales was examined. Whales feeding on fish had low lunge rates, only spent a short amount of time feeding, had relatively straight tracks and were in small, male dominated groups, similar to the behaviour of non-feeding animals on migration. In contrast, whales feeding on krill spent significantly greater amounts of time feeding, lunged at significantly higher rates (higher than any previously documented feeding rate for humpback whales), had tracks with high turning angles, and formed large female dominated groups, more similar to what is observed on the main feeding grounds. In addition, when feeding on krill, close associations between females were observed and five animals were found to spend between eight to ten days in the area off Eden feeding. Calculations of the consumption rates by whales feeding on krill suggest that whales feeding while on migration may consume prey at a rate of up to 3.7 times their energetic requirements. This suggests that whales may begin to replenish energy reserves prior to reaching the Antarctic. Given that individual whales were observed to feed continuously for a couple of hours, that some individuals spent up to 10 days in the area, and the previous identification of potential feeding sites in many productive temperate areas along the migratory route (Gales *et al.* 2009), the results of this study suggest that the feeding behaviour observed on migration may contribute more to energy budgets than previously thought. This behaviour may be of particular importance for some animals, such as females that have a higher energy demand due to pregnancy and lactation. If feeding along the migratory route is of importance then effort should be placed on attempting to determine what other factors may influence the degree to which whales rely on migratory stopover sites, and the impact that prey quality may have on the future fitness of individuals.

In the following pages the findings of the thesis are further discussed in relation to the potential for individual whales to modify their feeding behaviour in response to prey characteristics. In addition, the factors that may drive feeding behaviour by whales while on migration, and the likely importance of this behaviour to whale ecology is also discussed. Finally, directions for future research are proposed that will build on the findings of the thesis and assist with further increasing our understanding of the significance of feeding while on migration to humpback whales.

## 6.2 Lunge feeding energetics

Lunge feeding is thought to be a highly stereotyped and energetically expensive feeding strategy (Simon *et al.* 2012). However, the results of this study suggest that whales may not always achieve similar levels of acceleration across multiple feeding lunges. Variation in the speed or acceleration of lunges has previously been documented between different species of rorqual whales (Kot 2009; Goldbogen *et al.* 2011a), and within a species or individual (Jurasz & Jurasz 1979; Goldbogen *et al.* 2008; Kot 2009; Ware *et al.* 2011; Doniol-Valcroze *et al.* 2011; Goldbogen *et al.* 2011b). However, the factors that influence this have not been investigated thoroughly. One factor that has been found to influence lunge speed between species is the size of the animal with larger animals lunging faster compared to smaller animals (Goldbogen *et al.* 2011a). However, this difference was found to be scaled to the size of the animal with the speed being similar when expressed as body lengths over time (Goldbogen *et al.* 2011a). While this may explain the difference in speed between animals of different sizes, it does not explain the variation in lunge speed observed within an individual.

The correlation between lunge acceleration and depth of the lunge observed in this study suggests that the proximity of the animal to the surface may be a factor that could influence the maximum acceleration of a lunge achieved by an individual whale. However, whether the lower acceleration near the surface is the result of the whales encountering higher levels of drag closer to the surface, or of the whales modifying the amount of propulsion applied to reduce the impact of drag remains unclear. By lowering the force applied and therefore the likely speed of the lunge, a whale reduces the drag encountered. Based on simulation data, it has been proposed that by lowering the speed of a lunge whales could save energy while feeding (Goldbogen *et al.* 2011a). Feeding near the surface may allow animals to use the surface as a barrier to lower the escape abilities of prey (Kot 2009) rather than relying on acceleration to successfully capture prey. This may particularly be the case when feeding on slow moving prey that are less able to flee capture. It has also been suggested that for surface-feeding animals, differences in the orientation or pitch angle of each lunge may result in differing speeds by individual whales (Kot 2009). Wave drag has a strong effect on animals moving along the surface, which may limit the acceleration of lateral lunges at low pitch angles, compared to that of vertical lunges at high pitch angles. Whales may therefore modify the pitch angle of a lunge in order to reduce the impact of wave drag and change the level of acceleration achieved with the same energy input. When higher speed is required (i.e. to catch fast prey such as fish species) high pitch angles may be more effective, compared to when prey is slow and distributed along the surface layer and slow lateral lunges may be efficient. Therefore, further research is required to determine whether there is a difference in the pitch angle of the lunge used in relation to the escape ability of the prey or distribution of the prey and the amount of acceleration achieved.

Despite the proximity to the surface being found to correlate to the acceleration of a lunge, variation in the speed of a lunge has also been observed at depth (Goldbogen *et al.* 2008; Ware *et al.* 2011; Doniol-Valcroze *et al.* 2011; Goldbogen *et al.* 2011b). This implies that there are likely to be other factors that may also influence the amount of energy put into lunges, such as the escape ability or the quality of the prey. Optimal foraging theory predicts that animals should attempt to reduce their energy expenditure while foraging (MacArthur & Pianka 1966; Krebs 1977). It may be that regardless of depth, for slow moving prey such as krill, whales do not need to accelerate as much in order to successfully capture the prey. In addition, when prey density is really low or really high, putting lower amounts of acceleration into lunges may be beneficial to whales. When prey density is low, a minimal amount of prey capture with low energy expenditure may be more profitable than not feeding. Conversely, when prey density is extremely high, the chances of a whale not capturing at least some of the prey may make the use of a large amount of energy inefficient. Therefore, differences in the density of the prey targeted may also influence the amount of energy applied to a lunge by a whale and future research into this hypothesis is required.

## 6.3 Determining minimum foraging thresholds of whales

In predator-prey systems, sigmoidal or threshold responses of predator aggregations usually occur in response to increasing prey density (Holling 1965). The minimum foraging threshold of an animal is the minimum density of prey required by a species to elicit feeding behaviour (Piatt & Methven 1992). Determining this threshold level is of particular importance in some areas such as the Southern Ocean where factors such as climate change and a growing krill fishery threaten to reduce the availability of prey items to many predators (Flores *et al.* 2012; Nicol *et al.* 2012).

Whales are large Southern Ocean predators that use an energetically expensive feeding technique (Acevedo-Gutiérrez *et al.* 2002; Goldbogen *et al.* 2008). As a consequence, the energy requirements of whales and the minimum amount of prey required to induce feeding behaviour in whale species is likely to be higher than that of other Antarctic predators. Therefore, determining the minimum foraging threshold of whales may provide an indication of the minimum amount of prey required to sustain many Antarctic species.

A threshold response by baleen whales to prey availability has previously been documented (Piatt & Melven 1992). However, current studies of the relationship between rorqual whale feeding behaviour and prey density come from main feeding grounds (Piatt & Methven 1992; Goldbogen *et al.* 2008; Friedlaender *et al.* 2009b; Hazen *et al.* 2009) where the whales are increasing their energy stores in preparation for migration. In addition, feeding grounds are in highly productive high latitude waters where there is often an overabundance of prey available to the whales (Hamner *et al.* 1983; Tarling *et al.* 2009; Nowacek *et al.* 2011) which may make determining minimum foraging thresholds difficult. Therefore, to determine minimum foraging thresholds, an area where prey is likely to be limited is required.

When reaching the area off Eden, the whales have been fasting for approximately six months since leaving Antarctic feeding grounds. The prey they encounter off Eden is likely to be some of the first prey they have had the opportunity to forage on since the end of the previous summer. The hunger level of a predator has been shown to influence foraging decisions in a number of taxa (Akre & Johnson 1979; Pastorok 1990; Wallin & Ekbom 1994). However, the influence of hunger on the feeding behaviour and foraging thresholds of whales is currently unknown. It is possible that hunger drives whales to feed on lower prey densities than that observed on main feeding grounds. Determining the differences or similarities between the prey density thresholds of whales on migration compared to whales on main feeding grounds could provide insight into the influence of hunger on whale behaviour and potential further insight into the minimum foraging threshold of humpback whales. This information could then be input to models that predict the impact of fluctuations in krill availability to determine the likelihood that krill densities will fall below this threshold and the areas in which this could occur. Predictions could then be made about the likely impact of a reduction in krill availability by factors such as climate change (Flores *et al.* 2012) and krill fisheries (Nicol *et al.* 2012) on whale populations. This would further provide an indication of which populations of whales may be most at threat from declines in krill abundance.

## 6.4 Factors eliciting feeding behaviour by whales while on migration

To the best of our knowledge, this study is the first to investigate the factors that may drive feeding behaviour by whales while on migration. Previous studies had speculated that the feeding behavior occurred because animals had encountered an area of productivity on the migratory route (Baraff *et al.* 1991; Best *et al.* 1995; Gendron & Urban 2006; Alves *et al.* 2009), although what exactly had driven the whale to feed remained unknown. In addition, it had also been noted that feeding behaviour by whales while on migration appeared to be more common in sub-adult or juvenile animals (Salden 1989; Swingle *et al*. 1993; Gill *et al.* 1998; Alves *et al.* 2009; Silva *et al.* 2010) or that a female bias was observed for a period during the migration towards feeding grounds (Barendse *et al.* 2010). No previous research had focused on how changes in the prey characteristics would influence the fine-scale behaviour of individual whales.

Prey quality on migratory stopover sites has been shown to influence the amount of feeding completed, and the duration of stay at these sites by other migratory taxa (Beekman *et al.* 2002; Schaub *et al.* 2008; McLaren *et al.* 2013). In this study it was found that abundant supplies of krill resulted in longer periods of feeding behaviour and higher feeding rates, compared to fish, which suggests that krill may be a higher quality prey for the whales in this population. This is not surprising, given that the whales in the population studied feed predominantly on krill while on their main feeding grounds in the Antarctic (Matthews 1937). As a consequence, the whales may not have evolved efficient strategies to capture fish. In addition, the escape abilities of krill are likely to be lower than that of fish making them an easier prey target. For other migratory taxa, prey quality has also been linked to nutritive content with animals changing their diet while migrating to target specific nutrients (Hernandez 2009). In the case of humpback whales, krill are likely to have higher lipid content than the fish species available (see Chapter 4) and therefore be of better nutritive value for whales when compared to fish. Despite krill being distributed in shallower waters than the fish, the results of this study suggest that the depth of the prey may not influence the extent to which whales feed. Therefore, the type of prey that is available appears to influence whether a whale feeds on migration; however what aspect of the prey characteristics drive this decision remains unknown.

As well as a shift in the type of prey that is available on the migratory route, there are other factors that may influence whether or not a whale feeds while on migration. One of these factors is the amount of prey that is available. Other migratory taxa, such as birds and terrestrial mammals, concentrate in areas where food supply is greatest along the migratory route (Newton 2006; Sawyer

& Kauffman 2011). When food is abundant birds have been shown to be more likely to stay at stopover sites and also move on when food is scarce (Bibby & Green 1981; Spina & Bezzi 1990; Ottick & Dierschke 2003). The quantity and quality of prey available to whale species is likely to be influenced by both the density and size of the prey patch (Dolphin 1988; Piatt & Methven 1992; Goldbogen *et al.* 2008). Whales will only begin to feed once prey density reaches a certain threshold (Piatt & Methven 1992), likely as a result of lunge feeding being an energetically expensive feeding strategy (Acevedo-Gutiérrez *et al.* 2002; Goldbogen *et al.* 2008). The influence of prey density on the behaviour of the whales was not thoroughly investigated as a part of this study due to a lack of prey density data in 2011. However, it is still possible to consider whether the variation in behaviour of the whales was likely to be driven by differences in the density of the two prey types. The schools of fish observed to be available to the whales were higher in density, in terms of wet weight, than the patches of krill, assuming that their relative densities were similar in 2011. If this is the case, whales may have fed at a higher rate and spent longer feeding on krill to account for the lower density of the prey. However, despite the lower density of the krill, calculations of the amount of energy consumed when feeding on the two prey types revealed that whales consumed more energy per unit time foraging while feeding on krill. Therefore, the difference in feeding rate by the whales over compensates for the difference in density, which suggests that another factor may have driven the behavioural change. In addition to the density of the patch, the size of the patch may also influence whale behaviour (Whitehead 1983), meaning that the large swarms of krill in 2011 may have resulted in the high amount of feeding. Only one large swarm of krill was observed in 2012, and this swarm was being fed on by a group of three whales. However, the whales were not observed to feed on any of the other small patches of krill observed in 2012. Therefore, it is possible that variation in the size of the patches of krill available on migration may also influence the behaviour of the whales.

An additional factor that could elicit feeding behaviour by whales while on migration is variation in the energy requirements of individuals. Stopover sites provide a mechanism for animals to refuel along the migratory route in cases where insufficient energy is stored to successfully complete migration (Dingle & Drake 2007). Similar to many species, female whales have higher energetic costs than males due to the demands of pregnancy and lactation (Oftedal 2000). In addition, the segregated migration of humpback whales means that lactating females with calves spend the shortest amount of time on the feeding grounds compared to other whales (Chittleborough 1965; Dawbin 1966). As a consequence, females may be unable to store sufficient energy reserves to complete migration without feeding. It has been suggested that the sexual dimorphism of humpback whales, with females being slightly larger than males, may have evolved to account for this additional energy cost (Ralls 1976; Clapham 1996). However, the observation of a high number of females feeding on krill while on migration in this study and others (Barendse *et al.* 2010), suggests that the additional costs of reproduction may not be completely accounted for by the larger body size. Therefore, feeding while on migration may be a mechanism that allows females to account for a higher energetic cost and to complete the migration successfully.

Similar to female animals, juveniles and sub-adults are also unlikely to be able to store sufficient energy to complete migration due to their smaller body size. Although juvenile whales are typically fatter than adults for their size (Lockyer 1981b), smaller animals are unable to store the same amount of energy reserves as larger animals (Lindstedt & Boyce 1985). In addition, smaller animals also have a higher mass-specific cost of transport than larger animals (Garland 1983). These differences in energy storage and cost of transport may explain why feeding on migration has been observed to be more prevalent in juvenile animals (Salden 1989; Swingle *et al*. 1993; Gill *et al.* 1998; Alves *et al.* 2009; Silva *et al.* 2010). While direct measures of body size were not completed in this study, observations off Eden revealed that the majority of animals observed to feed were juveniles or sub-adults. This observation has also been suggested for the area off Eden previously (Silva *et al.* 2010). If size influences an animal's ability to store sufficient energy, this factor may also lead to differences in the importance of feeding behaviour while on migration between different species of baleen whales. It is then possible that feeding behaviour while on migration may be more important to smaller baleen whales such as Antarctic minke whales (*Balaenoptera bonaerensis*), and less important to larger baleen whale species such as blue whales (*Balaenoptera musculus*). In addition, it is possible that the high occurrence of juveniles feeding while on migration is linked to an inability to compete on the breeding grounds due to their small size. Body size has been shown to be of importance in competitions between male humpback whales attempting to access a female (Spitz *et al.* 2002). Given this, it would be more beneficial for juveniles to stay in higher latitudes and continue feeding to increase their growth. This would allow the animals to reach a size where they may be successful in competing for access to females sooner. Therefore, feeding while on migration may be important for smaller animals, either as a mechanism to allow for successful migration or to allow for faster growth and access to reproductive opportunities.

The reliance of an animal on feeding opportunities along the migratory route may also be influenced by variation in the energy requirements of populations and the amount of time available to feed. For example, fin whales (*Balaenoptera physalus*) in the Southern Hemisphere are thought to only spend approximately 120 days on the main feeding grounds in the Antarctic (Lockyer

1981b) which is a substantially shorter time than the estimated six months in the North Pacific populations (Brodie 1975). In one population of humpback whales, juvenile animals have been shown to migrate a shorter distance and feed in lower latitude areas over summer compared to the adults, potentially as a way to reduce the energy required to complete migration (Swingle *et al.* 1993). Therefore, differences in the length of the migratory route and the amount of time spent on the main feeding grounds each year between species and populations may play a role in determining the extent to which an animal relies on feeding while on migration.

Variation in the size or energy requirements of individuals may also lead to variation in the body condition of the whales which could influence whether a whale feeds while migrating. There is some evidence to suggest that individual birds that arrive to migratory stopover sites in poor body condition stay longer to replenish fuel loads (Bairlein 1985; Biebach 1985; Biebach *et al.* 1986; Fusani *et al.* 2009). Assessing the body condition of baleen whales is understandably difficult given that the animal cannot be easily weighed or measured (Croll *et al.* 1998). While direct measurements of whale body condition were not completed as a part of this study, anecdotal evidence from observations of the whales in the two years suggest that the whales appeared to be in worse body condition in 2011 compared to 2012, with more obvious bones protruding and a higher occurrence of skin lesions. In addition, anecdotal data collected on the quantity of strandings or mortality of whales in both years revealed that there was a total of fifteen recorded deaths in 2011 and eight in 2012 across coastal Victoria (David Donnelly, unpublished data) and Tasmania (Department of Primary Industries, Parks, Water and Environment, unpublished data). However, stranding data is potentially biased due to differences in currents that may change the frequency that carcasses wash up and variation in the effort put towards documenting mortality (Coughran *et al.* 2013). Additionally, the large majority of stranded animals in this area were too decomposed to provide any information on the cause of death, and others appeared to be in good body condition (Department of Primary Industries, Parks, Water and Environment, unpublished data). It is therefore difficult to determine any link between changes in the feeding behaviour of animals, and changes in body condition and the mortality rate of animals at this stage. However, it is possible to speculate that the whales feeding at a higher rate for longer periods on krill in 2011 may have been the result of whales being in poorer body condition and in greater need of nutrition that year.

Poorer body condition in whales while on migration and on the breeding grounds has been linked to changes in access to prey resources the previous summer feeding season which in turn has been linked to lower calving success (Perryman & Lynn 2002; Leaper *et al.* 2006). This suggests that the body condition of the animals off Eden is likely influenced by the availability of prey in the

Antarctic the previous summer. The Antarctic ecosystem is incredibly complex with changes in sea ice characteristics and ocean currents shown to influence the abundance and distribution of krill and potentially baleen whales (Nicol *et al.* 2008). Changes in the timing of sea ice advancement or retreat in relation to the timing of whale migrations is likely to influence the ability of whales to access prey. Additionally, the El Niño-Southern Oscillation Index (ENSO) has been shown to influence the availability of krill in some parts of the Southern Ocean (Atkinson *et al.* 2004; Murphy *et al.* 2007). The most recent El Niño period peaked from May 2009 to March 2010 (Australian Bureau of Meteorologyhttp://www.bom.gov.au/climate/enso/enlist/index.shtml). In addition, one of the strongest La Niña events on record peaked between late 2010 and early 2011 (Australian Bureau of Meteorology http://www.bom.gov.au/climate/enso/lnlist/) when the whales would have been in the Antarctic feeding the season prior to the 2011 migration. It has been suggested that krill abundance may be lower in areas after periods of El Niño given that it is usually associated with low ice cover which reduces food availability for Antarctic krill (Atkinson *et al.* 2004; Murphy *et al.* 2007). The availability of krill may therefore have been low in the 2010/2011 summer prior to whales feeding at high rates while on migration. Low krill abundance also forces the whales to travel over larger distances to find prey, potentially increasing the energetic requirements of the whales that year. ENSO has been linked to declines in other krill predators in the Antarctic such as Antarctic fur seals (*Arctocephalus gazelle*) (Croxall *et al.* 1999). It is therefore also possible that ENSO influences the ability of whales to meet their energy needs and their dependence on feeding while on migration. Therefore, linking the behaviour of whales and the rate of prey intake on migration to the conditions experienced the previous summer in the Antarctic could provide valuable insight into the drivers of feeding behaviour by whales while on migration.

## 6.5 The contribution of feeding while on migration to annual energy budgets

One of the main difficulties in determining the importance of feeding behaviour while on migration is establishing whether or not whales have been feeding and how frequently whales feed along the migratory route. Whales often migrate through remote areas of ocean basins and may complete a lot of their feeding behaviour underwater. Currently, determining the occurrence of potential foraging behaviour by whales while on migration often relies on state-space modelling of the tracks of whales collected by satellite tags (Gales *et al.* 2009; Silva *et al.* 2013). State-space modelling identifies potential foraging behaviour by looking for periods with slow travel speeds and high turning angles (Gales *et al.* 2009). However, the results of this study suggest that feeding behaviour can occur with the whales still maintaining relatively straight track lines. This indicates that feeding behaviour may not be detected by state-space modelling which could lead to an underestimate of the amount of feeding that occurs on migration. Additionally, the use of tagging technologies is expensive and it is not easy to gain a large sample size to compare across individuals, genders and age groups. As a consequence, this study also tested whether the use of stable isotope analysis of skin could be used to determine the current diet of an animal and therefore, whether or not an animal had been feeding while migrating. The results suggest that the turnover rate of the skin of baleen whales may not be sufficient to correctly determine the diet of whales feeding while on migration or even reliably determine whether temperate prey has been consumed. Therefore, detecting the occurrence and amount of feeding by whales while on migration still represents a significant challenge when attempting to determine the importance of this behaviour to whale energy budgets and ecology.

Most accounts of humpback whales feeding while on migration describe the behaviour as opportunistic or rare, with whales briefly taking advantage of a fleeting moment of productivity (Baraff *et al.* 1991; Best *et al.* 1995; Gendron & Urban 2006; Alves *et al.* 2009). It has been suggested that feeding outside of the Antarctic may contribute approximately 17% to the annual energy budget of whales (Lockyer 1981b). However, based on the energy stores of whales, it has been proposed that whales either have a much lower metabolic rate than would be predicted for their size, or a much larger proportion of their annual energy budget comes from sources outside of the Antarctic than currently believed (Leaper & Lavigne 2007). In addition, satellite tracks of migrating whales have revealed potential foraging behaviour in several productive areas along the migratory route (Gales *et al.* 2009; Silva *et al.* 2013). Observations of whales feeding while on migration in this thesis and other studies have shown that some individuals may spend extended periods feeding in productive areas (Best *et al.* 1995; Visser *et al.* 2011). In addition, the results of this study indicate that while feeding during migration, whales may consume prey at a rate of between 1.4 and 3.7 times their energetic requirements. This suggests that whales may begin to restock energy supplies prior to reaching the Antarctic. If this rate of energy intake is maintained for the extended periods of time that whales have been observed to feed, it is possible that feeding behaviour while on migration may be more common than currently believed and contribute a substantial amount to their energetic budgets.

## 6.6 The migratory strategy of humpback whales

The migratory strategy of an animal relates to the behaviour of an animal during migration which has often evolved to optimise a certain parameter, such as the speed of migration or the rate of energy intake (Erni *et al.* 2002; Sawyer & Kauffman 2011). For example, birds are thought to have a time-minimisation strategy, using migratory stopover sites to decrease the cost of transport and therefore, the time taken to complete migration (Alerstam & Hedenstrom 1998; Akesson & Hedenstrom 2007). Increased speed allows birds to reach breeding grounds earlier and establish nesting territories (Weber & Houston 1997). In addition, birds that use high quality stopover sites arrive to breeding grounds in better condition which has been shown to influence breeding success (Krapu 1981; Pattenden and Boag 1989; Ebbinge and Spaans 1995; Madsen 1995; Prop and Black 1998; Drent *et al.* 2003). In contrast, the migratory strategy of terrestrial mammals has been shown to be one of energy maximisation, with animals taking much longer to complete migration than predicted while tracking changes in resource availability (Sawyer and Kauffan 2011). However, the migratory strategy of baleen whales and the potential role that stopover sites may play in this strategy has been given very little attention.

Unlike birds, the migratory strategy of humpback whales, and many other baleen whale species, has historically been thought to be one of ‘feast and famine’ with whales feeding extensively over summer and fasting for the remainder of the year (Dawbin 1966; Lockyer & Brown 1981a; Baraff *et al.* 1991). The high occurrence of feeding behaviour in high latitudes and the low occurrence of this behaviour in the low latitudes has supported this conclusion (Chittleborough, 1965; Dawbin, 1966). In addition, whaling records indicate that many whale species had empty stomachs when caught in low latitude areas which further supported this idea (Dawbin 1966; Lockyer 1981b). While feeding behaviour has more recently been observed to occur on migration, the potential role that feeding along the migratory route could play to either migratory speed or energy maximisation is unknown.

In the case of humpback whales, the choice to feed while on migration will influence the timing of arrival to feeding grounds. Whales are not thought to be territorial (Clapham 1993b; Tyack 1981), and the ephemeral distribution of their prey does not make protection of prey patches worthwhile (Clapham 1996). As a consequence, increasing the likelihood of completing migration successfully and delaying arrival to the feeding grounds is unlikely to limit a whale’s ability to access high quality prey. However, a subsequent delay in the storage of sufficient energy reserves to depart the feeding grounds may delay their arrival to breeding grounds. The mating system of humpback whales has been described as a ‘floating lek’ with males competing for access to females without defending territories (Clapham 1996). Since newly pregnant females are often the first to leave the breeding grounds (Chittleborough 1965; Dawbin 1966), the late arrival of males to the breeding grounds may reduce their ability to access a high number of fertile females which could limit their reproductive success. Alternatively, the results of this study suggests that whales that feed on migration may actually begin the deposition of energy reserves sooner, and, as a consequence, may have stored sufficient energy to leave the feeding grounds earlier. This implies that these animals may be capable of reaching breeding grounds sooner, which may increase the amount of time available to dedicate to mating opportunities. In many migratory bird species, early arrival to breeding grounds has been linked to reproductive success (Weber & Houston 1997; Newton 2006). Similar to terrestrial mammals, whales may time their migrations and use of stopover sites as a way to track areas of productivity. A correlation between the timing of whale migrations in relation to the North Atlantic spring bloom has been shown in the Azores (Visser *et al.* 2011). That whales may migrate to track areas of productivity has also been suggested for right whales (*Eubalaena australis*) (Payne 1995). Therefore, whales may time their migrations to track areas of productivity to maximise energy intake while migrating and begin the migration from feeding grounds to breeding grounds sooner which may influence mating success. The influence that feeding while on migration has on the arrival time of whales to breeding grounds deserves more attention.

Another important factor to consider when attempting to conserve migratory species is the timing of migrations in relation to the availability of prey both on the main feeding grounds, and for animals that rely on them, migratory stopover sites (Viser & Both 2005; Sawyer & Kauffman 2011). In many cases, the timing of the peaks in prey availability as well as the type of prey available at both of these sites may be influenced by a warming climate (Visser & Both 2005). In order to determine the potential influence of shifts in the timing of prey availability in relation to the timing of animal migrations, an understanding of the cues that animals rely on to determine when to migrate is required. Many bird species are cued by endogenous biological rhythms (Ramenofsky & Wingfield 2007), whereas ungulate species appear to be cued by changes in forage condition (Garrot *et al.* 1987). This likely makes ungulate species less susceptible to climate influences on prey seasonality (Sawyer & Kauffman 2011). However, very little is known about what cues whales rely on to time their migrations. It is therefore difficult to determine the potential influence of a changing climate on the ability of whales to access prey either on migration or on the main feeding grounds. It has been proposed that changes in day length may cue whales to migrate, and that given variation in the timing of females initiating migration depends on their reproductive status, there may also be a hormonal aspect to the control (Dawbin 1966). If this is the case, then it is possible that humpback whales are susceptible to the potential negative influence of a warming climate on the availability of their prey in relation to their migratory timing. The most northerly point of consistent observations of whales feeding while on migration off the east coast of Australia is off Montague Island, NSW. It is therefore possible that once whales reach certain latitudes where productivity is high enough to provide suitable quantities of prey, whales begin to feed. However, if climate change results in shifts in the latitude where appropriate prey conditions occur, it may result in a reduced amount of time available for whales to access prey. Therefore, understanding the cues that whales rely on to begin migration or start feeding while migrating will allow for a better understanding of the potential impact of a warming climate on the ability of whales to meet their energy budgets.

## 6.7 Cooperative feeding as a mechanism to dominate prey patches

The use of cooperative feeding behaviour by humpback whales has been well documented (Jurasz & Jurasz 1979; D'Vincent 1985; Wiley *et al.* 2011). Despite this, the reason for this behaviour and the benefit it provides to individual whales is often unclear. Feeding in echelon, as observed in this study, is likely to provide energetic benefits to the whales by allowing them to lunge in forward flowing water or by funnelling prey items into the mouth of the second whale (Fish *et al.* 2013). However, an additional purpose for this behaviour may be to assist whales with defending a prey patch. Humpback whales are not thought to be territorial, likely as a result of the ephemeral distribution of their prey (Clapham 1993b; Tyack 1981). As a consequence, prey patches are unlikely to be worth defending. Therefore, the idea that whales may feed cooperatively to dominate prey patches is often dismissed.

Despite the belief that humpback whales are not territorial, observations of likely territorial behaviour by humpback whales were observed during this study. On many occasions, individual whales appeared to be clearly pushed off a patch of prey by a pair of whales. This behaviour was most obvious on three occasions where two whales were feeding cooperatively for a period of time, lunging either in echelon or side-by-side formation, and were approached by a third animal. When the third animal approached, it was observed to begin to lunge in synchrony with one or both of the whales. It was noted, that at this time there was an increase in the number of vocal blows completed by one or both of the original pair of animals. Shortly after the initiation of vocal blows, the third animal would quickly separate from the pair and continue feeding within a couple of hundred meters of the pair for a period of approximately twenty to thirty minutes. After this time, it was not uncommon to see the third animal re-approach the pair and the same behavioural and vocal response to occur. On two of these occasions, the third animal was a found to be a male approaching a pair of females, and in the third case the sex was unknown. On all three occasions, the animals were feeding on krill which the results of this study suggest is a valuable prey source to migrating humpback whales. Whether these observations represent animals competing for access for the opportunity to feed cooperatively with another whale and gain an energetic advantage or whether it is animals' competing for access to a prey patch remains unclear.

Although it has never been observed, it has been suggested that when the availability of prey becomes limiting relative to the number of whales present, some sort of ranking hierarchy should be expected in whales (Clapham 1996). It is possible that the prey conditions, plus the likely high hunger level of whales on migratory stopover sites may elicit such behaviour. Therefore, further observations of this behaviour and the sex of individuals involved are required in order to determine whether these observations represent a form of territoriality in humpback whales. If results find that animals do become territorial and cooperate to defend patches of prey encountered on migration, this would provide further evidence that the availability of prey on migration may be important to whales and worth defending.

## 6.8 Future directions

Whales are long lived species that inhabit incredibly complex environments. It is therefore very difficult to determine causal relationships between factors over short time periods. The application of digital tags to study the underwater behaviour of animals, aligned with concurrent data on prey availability provided valuable insight into the ecology of whales feeding while on migration. This has highlighted the importance of the prey type available as a potential driver of feeding behaviour by whales while on migration and the likely importance of this behaviour to females. However, the mechanism through which shifts in prey type may influence whale behaviour and the potential influence of other factors on this behaviour still remains unknown.

Many features of the different prey types encountered by whales over the two study years were identified as the potential cause for the shift in whale feeding behaviour. Determining which of these factors may have been responsible for this shift should be a direction of future research. Measuring the nutritive content of the prey available to whales in terms of the lipid content and caloric value would assist with determining what benefits each prey type may provide to whale energy gain. In addition to the nutritive content, fish are also a relatively novel or unfamiliar prey item for the whales in the east Australian population. As a consequence, studies of the behaviour of whales feeding while on migration in a population that consumes fish on the main feeding grounds may assist with determining whether krill were fed upon by whales as a result of them being a familiar prey item or whether there was some other benefit provided by the prey. One example of a potential location for this research is off the Azores. In this area, multiple baleen whale species' have been observed to feed while migrating, mainly on krill (Visser *et al.* 2011). Determining how this population responds to shifts in the availability of different prey types will assist with determining whether similar features of prey are selected by migrating whales, regardless of their diet on the main feeding grounds. Another approach could be to compare the capture efficiency of the east Australian population while feeding on fish compared to Northern Hemisphere populations that feed on fish on the main feeding grounds. If the capture efficiencies are similar, then it is unlikely that fish were fed upon to a lesser extent due to an inability to capture the prey effectively. Therefore, differences in the feeding behaviour of populations may provide insight into the characteristic of the prey types that drove the shift in whale behaviour.

There are also other factors that potentially drive migratory feeding behaviour that were not examined as a part of this study. The initiation of a long-term monitoring study that records information on both the whale and prey characteristics would greatly assist with further developing our understanding of the factors that may influence feeding behaviour of whales while on migration. Dedicated transects over larger spatial scales to determine the spatial extent of feeding behaviour in relation to the type and amount of prey available between years should also be completed. This would also assist with clarifying whether the shifts observed were the result of the small spatial scale of this study with large amounts of feeding behaviour possibly occurring elsewhere in 2012. Biopsy sampling of individual whales in the area would allow for comparisons of the gender and potentially reproductive status of the animals, providing insight into the demographics of animals observed to feed, compared to animals observed to be migrating through the area. These biopsy samples, along with photogrammetry, could also allow for a comparison of the body condition of animals that choose to feed in relation to those that do not feed. Photogrammetry may also assist with determining the size or age class of the animal to determine whether this parameter also influences the feeding behaviour of whales while on migration. One difficulty is determining whether an animal that is not feeding at the current time has indeed been feeding previously or will feed in the near future. This issue may potentially confound analyses that compare metrics of feeding and non-feeding animals. Therefore, there are many factors that should be further investigated as a part of longer term monitoring studies that will assist with disentangling which factors play the most important role in driving feeding behaviour by whales while on migration.

Whether or not feeding behaviour while on migration is opportunistic or a learnt behaviour is currently unknown. Humpback whales have been shown to have a high fidelity to main feeding grounds where the same individuals have been observed to feed together over multiple feeding seasons (Clapham & Mayo 1987; Clapham *et al.* 1993a; Katona & Beard 1990; Calambokidis *et al.* 2001; Ramp *et al.* 2010). It would therefore be of interest to determine whether the same individuals and associations between individuals are found on migratory stopovers inter-annually. Other migratory species have been shown to use the same migratory stopover sites from year to year (Cantos & Telleria 1994; Alerstam *et al.* 2006; Sawyer & Kauffman 2011). It is likely that data sets and photographs of individuals already exist that could assist with addressing this question. This would help with determining whether the feeding behaviour by whales while on migration occurs through opportunism or by travelling through known areas where conditions are likely to be favourable. While whales may learn about areas of productivity by accidently migrating through productive areas and remembering them, it is also possible that whales learn the location of migratory stopover sites from their mothers, as seen off the coast of South Africa (Barendse *et al.* 2013). Investigating whether there is a maternal linkage between animals using a particular stopover site compared to the rest of the population could also be completed using the biopsy samples. This would assist in determining the mechanism by which this behaviour may be passed within and between generations of whales.

Given that shifts in prey availability influence whale feeding behaviour, determining the environmental factors that may result in this shift is important. Correlations between the number of whales observed to feed off Eden and remote sensed data suggest that cold water, and therefore potentially increased upwelling, may promote a larger number of animals feeding in the area (Silva *et al.* 2010). It has also been suggested that during periods of La Nina such as what occurred in 2011 and 2012, an influx of warm water may reduce the availability of krill off south east Australia (Harris *et al.* 1991; Young *et al.* 1993), despite high abundances of krill being observed in 2011 during this study. It is therefore unclear as to what exactly drove the abundance of krill off the coast of Eden in 2011. The potential influence of lag times between environmental conditions and the timing of whale migrations should also be taken into consideration (Visser *et al.* 2011). In addition, links between the feeding behaviour of whales while on migration and the conditions in the Antarctic in the previous summer should also be investigated. By determining what environmental features result in favourable feeding conditions, other potential migratory stopover sites can also be identified. It is also important to determine what prey features are required by whales while on migration in order to determine the likelihood of a mismatch in the availability of prey on migration and in the Antarctic. If similar conditions are likely to result in a reduction in both the availability of Antarctic krill and the availability of prey on the migratory route, it is possible that the survival and reproductive success of whales may be influenced.

Humpback whale populations in the Southern Hemisphere are currently believed to rely on the presence of Antarctic krill as their primary dietary item and source of the majority of their annual energy supplies (Matthews 1937). This places humpback whales under threat from factors that may influence the availability of Antarctic krill such as climate change and a growing krill fishery in the Southern Ocean (Flores *et al.* 2012; Nicol *et al.* 2012). However, it is difficult to determine the influence of these factors on humpback whales, without first understanding the actual extent to which humpback whales rely on feeding in the Antarctic, compared to feeding while on migration. One of the main factors preventing the interpretation of the importance of feeding behaviour while on migration and the amount that it contributes to the annual energy budgets of humpback whales is the ability to determine how often whales feed while migrating. Given that the results of this study suggest that feeding or foraging behaviour may not always be detected in satellite tag data, the development of digital tags that transmit more fine-scale behaviour over longer time periods would be beneficial. There are two aspects of tag development that could assist with determining the frequency of feeding behaviour along the migratory route. The first is development of tags that can transmit more fine-scale locational data, potentially using GPS technology, which would provide a more accurate location of the animal as often as possible. The second would be development of tags that transmit information of the time of potential feeding lunges (Simon *et al.* 2012), possibly using a lunge detecting algorithm such as the one developed as a part of this study. Therefore, development of new digital tags to transmit fine-scale feeding behaviour over long time periods may assist with determining how frequently whales feed while on migration.

Prior to the development of new tags, some information may be gained on the importance of feeding behaviour while on migration by comparing the feeding rates observed in this study to that of the speed of migratory movement recorded in satellite tag data, and not to potential ARS behaviour. Satellite tags deployed onto whales off the coast of Eden revealed the presence of potential foraging behaviour by whales in several productive temperate areas along the migratory route (Gales *et al.* 2009). This data could be used to determine the duration of stay in various areas, which could be compared to the duration of stay expected given the average migratory speed of whales (Noad *et al.* 2007). This would provide an indication of the amount of days whales potentially delay migration for to feed. Combining this duration with the rate of energy intake observed in this study, could provide the ability to test whether current estimates of the contribution of feeding outside of feeding grounds to annual energy budgets are accurate. One downfall of this method would be the issue associated with whales feeding while still maintaining close to the average migratory speed, as seen when feeding on fish in this study. In this case, the duration of feeding would be assumed to be very low. One way to overcome this would be to correlate the rate of energy intake while migrating to the migratory speed of whales moving through Eden and extrapolating this over the rest of the length of migration until whales reach their Antarctic feeding grounds. Therefore, prior to tag development, it may still be possible to gain a stronger understanding of the potential for feeding behaviour while on migration to contribute whale energy budgets. However, given the patchiness of resources along the migratory route and the lack of information on whether the feeding rates observed in this study occur over extended periods, this representation may not be completely accurate.

In many cases, determining the appropriate area to examine the feeding behaviour of whales while on migration may be difficult unless some baseline understanding of the likelihood that animals are feeding is provided. The results of this study suggest that stable isotope analysis of skin is not suitable to determine the diet of an animal while on migration, however, shifts in the isotopic signature in comparison to a sub-tropical site, may still provide an indication of whether an animal has fed while on migration. Future research should determine if it is possible to detect recent consumption of prey in the breath of whales using stable isotope analysis. The gaseous sample exhaled by animals has been used previously to provide information on the diet of other mammals such as polar bears (*Ursus maritimus*) (Hobson *et al.* 2009). Although the gaseous sample provides valuable information on carbon isotope signatures of potential prey, given that it involves analysing the $CO_2$ exhaled, it does not provide any insight into nitrogen isotopes or the trophic level of the animals (Podlesak *et al.* 2005; Hobson *et al.* 2009). While collection of the exhaled breath of baleen whales is associated with many logistical challenges (Hunt *et al.* 2013), if possible, it may be able to provide insight into whether temperate prey has been recently ingested. Therefore, further development of the techniques used to access tissues or fluids with a high turnover rate from whales may also assist in determining whether feeding occurs while on migration in many species.

The ultimate aim of research into the importance of feeding behaviour while on migration would be linking changes in the amount and quality of prey consumed to the future survival and reproductive success of the individual. This in turn could then be linked to differences in the growth rate of populations. Feeding behaviour while on migration has been shown to influence these parameters in migratory birds (Newton 2006). However, determining the impact of fluctuations in ecological parameters to survival and reproductive success of cetacean species is extremely challenging (Croll *et al.* 1998; Goldbogen *et al.* 2013). It is very difficult to track individuals for long periods and to determine reproductive success and survival of that animal. Most satellite tags on baleen whales only last for a few months (Gales *et al.* 2009; Garrigue *et al.* 2010; Silva *et al.* 2013), tracking the movement of an animal from a migratory stopover site to the feeding ground at best. Therefore, relocating that same individual on the breeding ground to determine whether it has successfully reproduced is extremely difficult (Croll *et al.* 1998). However, the east Australian population of humpback whales has one of the best documented cases of recovery from whaling (Noad *et al.*

2010). In addition, it also has one of the highest noted occurrences of feeding behaviour while migrating (Gill *et al.* 1998; Stockin *et al.* 2005; Stamation *et al.* 2007; Silva *et al.* 2010). While it is impossible to draw a causal link between these two observations, given the relationship between the quality of the prey available on the migratory route and individual survival and reproductive success in other migratory taxa, the possible correlation between these two observations deserves more attention. Many whale species and populations have undergone severe declines as a result of commercial whaling activities, with many yet to recover (Baker & Clapham 2004; Magera *et al.* 2013). As a consequence, understanding whether feeding behaviour of whales while on migration has contributed to the recovery of some populations could assist with identifying other areas that need to be addressed for populations that are yet to recover and potentially highlight the protection of migratory stopover sites as a conservation priority.

The findings of this thesis suggest that the mechanisms that drive feeding behaviour by whales while on migration may be more complex and important to whale ecology that previously thought. The main goal of future research should be to further attempt to determine the importance of factors that may elicit this behaviour. In addition, studies into the amount of feeding behaviour that occurs while on migration will assist with understanding how much this behaviour could contribute to annual energy budgets and the reliance by humpback whales on Antarctic krill abundance. Finally, linking fluctuations in this behaviour to the future reproductive success and survival of whale populations will provide the ultimate explanation of the importance of this behaviour to whale ecology. Only by linking the variation in this behaviour to these population parameters will the full significance of this behaviour to whale ecology be understood.

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# Appendix 1

## Lunge detecting algorithm MATLAB script

```
function [ Output ] = LDA(Aw, pitch, start_time, end_time, p, Observed)
%Lunge Detecting Algorithm:
% An algorithm used to detect lunges of surface-feeding whales using DTAG
% data, as referenced in "Owen et al., Breaking the surface: a method
% to detect surface-feeding behaviour of whales in accelerometer data".
%
% A lunge is defined as a time when acceleration in the x-direction in
% whale frame data is above 'mag_accel', pitch is above 'mag_pitch' within
% 'time_margin_pitch' and jerk is below 'mag_jerk' within
% 'time_margin_jerk'
%
%   Inputs:
%       Aw - Acceleration matrix in whale frame [g]
%       pitch - pitch vector [radians]
%       start_time - detection start time [s]
%       end_time - detection end time [s]
%       p - depth profile vector [m]
%       Observed - Vector of observed lunge times [s]
%
%   Outputs:
%       Column 1 - Time [s] of the peak acceleration in Awx
%       Column 2 - Magnitude of peak acceleration [g] in Awx
%       Column 3 - Depth [m] at the time of peak acceleration in Awx
%       Column 4 - Equivalent value of Minimum Specific Acceleration [g]
%           at the time of peak acceleration in Awx

% Input threshold levels for each parameter to define a lunge.
mag_accel = input('Input acceleration threshold [g]: ');
mag_pitch = input('Input pitch threshold [radians]: ');
mag_jerk = input('Input jerk threshold [g/sample]: ');

% Sample rate of data [Hz]
fs = 5;

% LDA will look for a pitch matching the defined threshold
% 'time_margin_pitch' seconds after the time of peak acceleration in Awx
time_margin_pitch = 2;

% LDA will look for a jerk matching the defined threshold
% 'time_margin_jerk' seconds after the time of peak acceleration in Awx
time_margin_jerk = 2;

% Isolate accelerometer signal in the x-direction of whale frame (Aw) data
% and remove the influence of gravity.
Awx = Aw(:,1) - sin(pitch);

% Find the peaks in the x-direction of the whale frame acceleration (Awx)
acc_values = PeakFinder(Awx,start_time,end_time,mag_accel,fs);

% Set up output matrix shape
Output = zeros(1,4);
```

```
% Calculate the jerk. Jerk is the rate of change of the Awx signal.
jerk = zeros(length(Awx),1);
for i = 1:length(Awx)-1
   jerk(i+1) = Awx(i+1) - Awx(i);
end

% Set found flag
found_lunge = 0;

% Set initial value of counter
k=1;

% Step through found peak acceleration values
for i=1:length(acc_values)
   % Test if pitch goes above 'mag_pitch' within 'time_margin_pitch'
   % seconds after the peak in acceleration
   for j = 0 : time_margin_pitch*fs
      if pitch(acc_values(i,1)*fs + j) >= mag_pitch && found_lunge == 0
         % Test if jerk goes below 'mag_jerk' within 'time_margin_jerk'
         % seconds after the peak in acceleration
         for l = 0 : time_margin_jerk*fs
            if jerk(acc_values(i,1)*fs + l) <= mag_jerk && found_lunge == 0
               % FOUND A LUNGE!!
               % Record Data
               Output(k,:) = [acc_values(i,:) p(acc_values(i,1)*fs) norm(Aw(acc_values(i,1)*fs,:))-1];
               k = k+1;
               found_lunge = 1;
               break
            end
         end
      end
   end
   found_lunge = 0;
end

fprintf('\n')
% Compare detected lunges against observed lunges within +/- 't' seconds

% Input time margin to allow for time lag between detected peak
% acceleration and observed lunge at the surface
t = input('Input time margin allowed between detected and observed lunge lists [s]: ');

% Initialise found count
found = 0;

% Take detected lunge times
Detected = Output(:,1);

% Step through each Observed time
for i = 1:length(Observed)
   % Step through each detected lunge time
   for j = 1:length(Detected)
```

```
        % Test if Observed time is within detected lunge time +/- margin
        if Observed(i) >= Detected(j)-t && Observed(i) <= Detected(j)+t
            %Found lunge time on list, increase count
            found = found + 1;
            break
        end
    end
end
fprintf( '\n')
fprintf( 'Found %d out of %d observed lunges\n', found, length(Observed))
fprintf( 'Missed %d out of %d observed lunges\n', length(Observed)-found, length(Observed))
fprintf( 'Detected %d additional unobserved lunges\n', length(Detected)-found)
fprintf('\n')
end

function [values] = PeakFinder(X,start_time,end_time,mag,fs)
% PEAKFINDER Finds peaks in data, outputs x-value in time and y-value
% start and end times are input in seconds, finder will find peak values
% above the threshold value 'mag'

% convert seconds to sample number
start_sample = start_time * fs + 1;
end_sample = end_time * fs;

% set initial values of peak finding flags
n1 = 0;
n2 = 0;

%set initial counter value
j = 1;

for i=start_sample:end_sample
    % find a start point, where X goes +ve
    if n1 == 0 && X(i) > 0;
        n1 = i;
    end
    % with a start point, find the end point where the X goes -ve
    if n1 ~= 0 && X(i) < 0;
        n2 = i;
    end
    % with a start and end point, find the max X value within the two
    % points and the position
    if n1 ~= 0 && n2 ~= 0
        % if the peak value is above the magnitude,
        if max(X(n1:n2)) > mag
            % record the value
            [values(j,2) values(j,1)] = max(X(n1:n2));
            % record the sample
            values(j,1) = values(j,1) + n1 - 1;
            j = j+1 ;
        end
        % reset flags
```

```
        n1 = 0;
        n2 = 0;
    end
end
% convert output sample to time in seconds
values(:,1) = values(:,1)/fs;
end
```

# Appendix 2

## Ethogram of humpback whale behaviours

**Table A2.1:** The ethogram for humpback whale behaviour used during all focal follows completed during this study.

| Behaviour Recorded | Definition |
|---|---|
| **Blow** | Visible plume of water vapour exhaled by the whale upon surfacing. It is assumed that the back of the whale is also seen. |
| **Oblique lunge** | Forward trajectory at angles of between 10 and 70 degrees to the sea surface without any roll, with mouth open |
| **Right side lateral lunge** | Forward trajectory at low angles to the sea surface with the right flank of the animal facing down, with mouth open |
| **Left side lateral lunge** | Forward trajectory at low angles to the sea surface with the left flank of the animal facing down, with mouth open |
| **Clockwise ventral lunge** | Forward trajectory that occurs from an inverted position at a low angle to the sea surface before an axial clockwise roll, with mouth open |
| **Counter clockwise ventral lunge** | Forward trajectory that occurs from an inverted position at a low angle to the sea surface before an axial counter clockwise roll, with mouth open |
| **Vertical lunge** | Near vertical trajectory to the sea surface, with mouth open. |
| **Echelon feeding** | When multiple whales lunge side by side with the animals slightly offset from each other so that one is slightly ahead of the next. |
| **Straight line feeding** | When multiple whales lunge side by side with the animal's side by side in a line. |
| **Pec Slap** | The left or right pectoral is raised out of the water and forcibly slapped with their ventral surface against the water; the whale is usually positioned on its side. |
| **Inverted Pec Slap** | The left or right pectoral is raised out of the water and forcibly slapped with the dorsal surface against the water; the whale is usually positioned on its back (i.e. belly up). |

| Behaviour Recorded | Definition |
|---|---|
| **Bilateral Pec Slap** | Both pectorals are raised out of the water and forcibly slapped with their dorsal surface against the water; the whale is positioned on its back. |
| **Pec Wave** | The lifting of the pectoral fin clear of the water, without a violent slapping motion. |
| **Peduncle Slap** | The entire fluke and peduncle is raised clear out of the water and forcibly slapped against the water surface; more energetic than a tail slap. |
| **Peduncle Throw** | The throwing of the entire fluke and peduncle out of the water in a lateral motion. No initial lifting from the water as in a peduncle or tail slap, just a single high scything motion; high energy behaviour. |
| **Fluke Slap** | The fluke, and little of the peduncle, is raised out of the water and forcibly slapped against the water surface; less energetic than peduncle slap. |
| **Inverted Fluke Slap** | Whilst the whale is belly up in the water, the fluke is lifted clear of the water and slapped, dorsal surface down, against the water's surface. |
| **Round out** | A dive where the peduncle is arched upward out of the water but the flukes are not lifted from the water. Usually heralds a deep dive by the whale. Same as a 'peduncle arch dive' or a 'high arch dive'. |
| **Fluke Down Dive** | A dive where a peduncle arch is followed by the fluke lifted from the water as the whale dives, the fluke is not lifted far from the water, it remains parallel to the water and its ventral surface cannot be seen from behind. |
| **Fluke Up Dive** | A dive where a peduncle arch is followed by the fluke lifted from the water as the whale dives, the fluke is held vertically so that its ventral surface can be seen from behind. |
| **Splash / Surface Activity** | An undetermined behaviour that resulted in a splash, usually recorded when the whale is far away. |

| Behaviour Recorded | Definition |
|---|---|
| **Spy Hop** | A vertical lifting of the head (usually exposing the entire rostrum and head) above the water surface. Usually a single low-energy bobbing motion. |
| **Sailing** | The whale is balancing head down in the water with its fluke above the water, for extended periods of time, without slapping motions. |
| **Footprint** | Upwelling of water causing circular ripples on the surface caused by underwater upward fluke stroke. |
| **Underwater blow** | A full exhalation underwater, producing a sudden large cloud of bubbles. More forceful and bigger than ‘bubble blowing’. |
| **Body impact** | The (usually violent) collision of two or more whales. |
| **Surface vocalisation** | Noise made by whale after surfacing, may sound like trumpeting or tonal blow. |
| **Vocal Blow** | Blow accompanied by a loud vocalization. |
| **Belly Up** | The whale floating in the water with its ventral side / belly up. |
| **Bubble Blowing** | When the whale blows a stream of bubbles underwater. Less forceful and more gradual than an underwater blow. |
| **Logging** | Where the whale is lying on the waters surface with very little activity. |
| **Milling** | When the whale is moving slowly in various directions within a similar area. |
| **Roll** | Surface or underwater roll in any direction or plane. |
| **Tail Swish** | Movement of tail through water in sideways motion. |
| **Slip under** | A flat, gentle submergence as opposed to normal rounding out dive. |

| **Behaviour Recorded** | **Definition** |
|---|---|
| **Fluke Wave** | The lifting of the fluke clear of the water and waving around, without a violent slapping motion, fluke not still as in sailing. |

# Appendix 3

## Seaweed Interactions by Humpback Whales (*Megaptera novaeangliae*): A Form of Object Play?

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# Short Note

## Seaweed Interactions by Humpback Whales (*Megaptera novaeangliae*): A Form of Object Play?

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Cetaceans have been shown to use a range of natural and manmade objects such as kelp, bubbles, sponges, coconuts, nets, rope, and even other animals for a potential number of reasons that are yet to be properly investigated. The function of the use of these objects has been proposed to range from tool use (Smolker et al., 1997; Parra, 2007), to socio-sexual displays (Martin et al., 2008), epimeletic behaviour (Fertl & Fulling, 2007), and object play (Payne, 1972; Würsig et al., 1989; Bloom, 1991; Miles & Herzing, 2003). However, the function of object use in cetaceans is often difficult to determine given the sporadic occurrence of such behaviour and difficulties in observing behaviour under water.

Reports of object use by cetaceans are far more prevalent for odontocetes than for mysticetes. For example, sticks, branches, and clumps of grass are believed to be used as a socio-sexual display in Amazon River dolphins (*Inia geoffrensis*) (Martin et al., 2008). Additionally, bottlenose dolphins (*Tursiops* sp.) in north Western Australia have been shown to use sponges on their rostrum as a form of tool use to assist with foraging in the sand (Smolker et al., 1997), and there is some evidence that Indo-Pacific humpback dolphins (*Sousa chinensis*) may do the same (Parra, 2007). Many dolphin species have been shown to use seaweed as a form of object play, passing the seaweed between their melon, pectoral fins, and tail flukes and even between members of a pod (Würsig & Würsig, 1979, 1980; Bloom, 1991; Miles & Herzing, 2003; Kuczaj & Yeater, 2007).

Unpublished anecdotal observations of humpback whales (*Megaptera novaeangliae*) interacting with seaweed appear to be relatively common, yet there is no attention paid to the function and characteristics of this behaviour in the literature. Consequently, the reason for such behaviour is not yet fully understood. Herein, the authors present what is believed to be the first published account of three instances of humpback whales interacting with seaweed. These observations provide the basis for the first discussion of the likely reason for this behaviour in this species.

All observations were made opportunistically off the coast of Eden, New South Wales, Australia by two of the authors (KO and DD) while conducting research on humpback whale feeding behaviour during their southward migration between the Great Barrier Reef breeding grounds and the Antarctic feeding grounds. The observations were made from a 5.5-m rigid hulled inflatable boat. Photographs were taken using digital SLR cameras and an underwater housed GoPro video camera mounted on a ski pole, which was held off the side of the vessel to collect underwater images of the behaviour. Observations were made by the naked eye, through the camera lens, and through the review of underwater video footage.

The first observation was made on 16 September 2011. In this case, the animal involved was a subadult humpback whale that had a D-tag attached to it prior to the observations and, as a consequence, was the subject of a focal follow lasting just over 2 h. The tag was on the animal at the time observations were made. At the time of tag deployment (approximately 1230 h), the whale was part of a group of three whales feeding on krill. The focal animal split from the group approximately 15 min after tagging and continued feeding alone until 1312 h. At 1333 h, it was noted that there was an Australian fur seal (*Arctocephalus pusillus*) close to the focal animal which the whale appeared to start to follow. By 1338 h, it was noted that the seal often surfaced just in front of the whale's rostrum. By this point, the whale's behaviour was very surface-orientated, with repeated rolling and spy hopping observed. At 1347 h, the whale spy hopped and rotated 360° with rostrum out and vertical in the water column. A piece of seaweed (*Phyllospora comosa*) was sighted in the water beside the whale. At 1348 h, the authors noticed the whale had the seaweed in its mouth (exterior to the baleen plates), and it began to roll and made snake-like movements at the surface before draping the seaweed across its head. After 3 min, the whale dropped the seaweed and moved directly towards another piece of seaweed which it again grasped in its mouth. This was quickly followed by a spy hop with the seaweed draped over the head of the whale. The whale then rolled and dropped the seaweed, only to retrieve it on its pectoral fin and dive with it draped over the fin. After another 2 min of interacting with the seaweed, the whale dropped it and appeared to swim away but then turned around and came back to the seaweed. It continued to grab the seaweed in its mouth and logged at the surface with it draped over its back. During this time interacting with the seaweed, the whale made a number of trumpeted (tonal) blows. The last time the whale was seen interacting with the seaweed was 1400 h, and the interaction lasted 12 min. By 1406 h, the whale was back to feeding alone. No other whales were in visual range at the time of these observations. The focal whale was determined to be a male by visual inspection of the genital region during rolling behaviour at the surface, confirming the absence of a hemispherical lobe immediately anterior to the genital slit as is present in females (Glockner, 1983).

Two additional observations were made on 22 September 2011. The first of these was a short observation during a focal follow. In this instance, the animal was a nontagged subadult whale. The animal had been observed feeding with another whale for half an hour on patches of krill. At 0914 h, 12 min after the last feeding lunge was observed, the whale picked up a piece of seaweed (species was also *P. comosa*) in its mouth and manipulated the seaweed at the surface. It then dropped the seaweed in a position that allowed it to slide down its back. The two animals then continued to travel east further offshore. No change in the behaviour of the second whale was evident as a result of the first whale picking up the piece of seaweed. The sex of both whales is unknown.

Later that day, at 1054 h, we observed another whale interacting with seaweed (species was again *P. comosa*) with no other whales in visual range. This whale was identified to be a subadult male (from visual inspection of the genital region), and he had been observed feeding at 0900 h, 1 h and 54 min prior to being observed interacting with the seaweed. This whale exhibited similar behaviour to the two previous whales with the animal swimming around with the seaweed on its pectoral fin (Figure 1 A), picking up the seaweed in its mouth (Figure 1 B & C), and draping the seaweed over its back (Figure 1 D). We left the whale when it moved away from the seaweed at 1123 h—almost half an hour after we encountered the whale already interacting with the seaweed.

Our observations are very similar to those made by Payne (1972) of southern right whales (*Eubalaena australis*) interacting with seaweed: the whales lifting the seaweed with their heads, sliding the seaweed along their backs, and manipulating the seaweed with their pectoral fins. Other mysticete species have also been reported to interact with objects. Bowhead whales (*Balaena mysticetus*) in the Beaufort Sea have been seen to interact with logs up to 10 m long (Würsig et al., 1989). During these interactions, the whales nudged the logs, lifted them with their back, and even laid belly up with the log clasped between their pectoral fins. In both of these interactions, this behaviour was deemed to be object play behaviour.

To the best of our knowledge, there are no currently published reports of humpback whales interacting with seaweed. However, humpback whales have been reported to interact with objects other than seaweed. For example, in Hawaii, a juvenile female humpback whale was observed for over an hour to be passing a piece of cargo netting between her pectoral fin and rostrum. She then continued this behaviour with a piece of rope (Deakos et al., 2010). This behaviour has similarities to the behaviour described herein with an object being passed between the mouth and pectoral fins. Also in Hawaii, a humpback whale has been observed to lift a bottlenose dolphin (*Tursiops truncatus*) completely out of the water. This observation was concluded to be the result of social play by the dolphins and a form of object play by the whale (Deakos et al., 2010). A humpback whale was also observed overturning a turtle that appeared to be suffering from buoyancy issues. This interaction was hypothesised to be a form of epimeletic or care-giving behaviour by the whale (Fertl & Fulling, 2007). It seems that a regular conclusion drawn from mysticetes interacting with objects is that for them it is play behaviour.

Play behaviour has been observed in a number of different animal phyla and is prevalent within mammals. In a recent review, play was defined as behaviour that is (1) not obviously functional; (2) voluntary, spontaneous, and self-rewarding in nature; (3) different structurally or temporally from other obviously functional behaviours; (4) repeated during the life span of the animal; and (5) initiated when the animal is in a favourable situation (well-fed, safe from predators). It can be divided into three different types: (1) locomotor play (leaping, running), (2) social play (directed towards another living animal), and (3) object play (directed towards an inanimate object) (Burghardt, 2005).

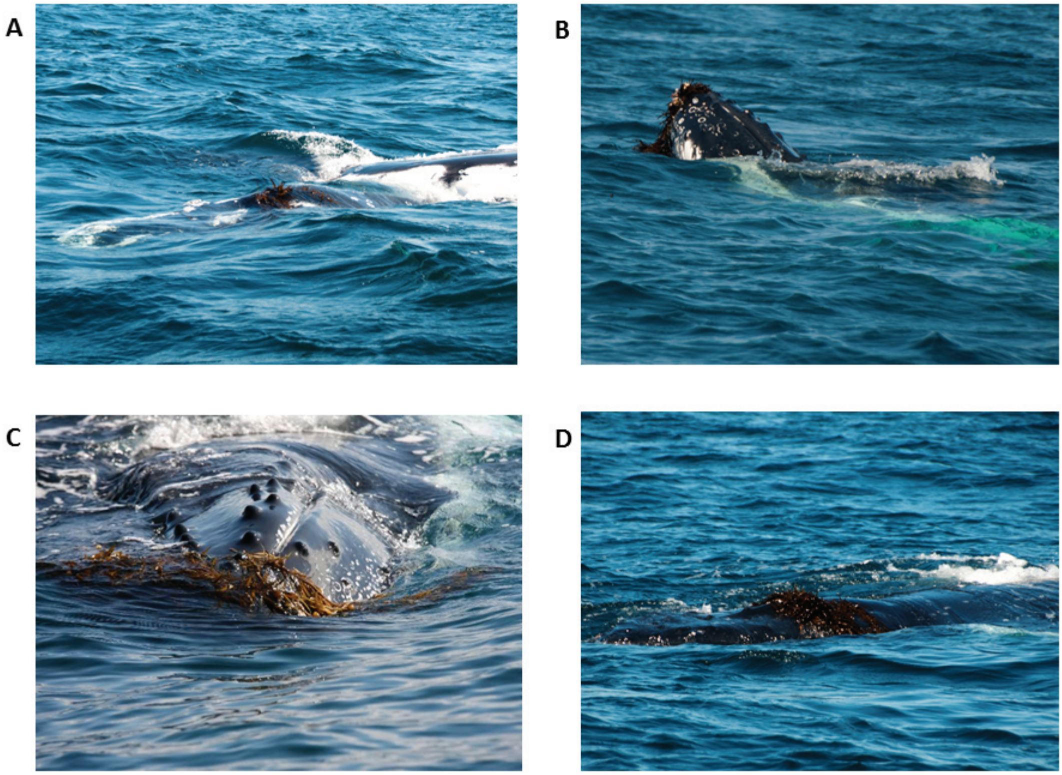

**Figure 1.** Seaweed interactions by humpback whales. (A) The whale dives with the seaweed on its left pectoral fin; (B) the whale raises its head out of the water with the seaweed in its mouth; (C) the whale pushes the seaweed around while swimming with the seaweed in its mouth; and (D) the whale drops the seaweed and rises below it so that the seaweed is placed on top of its head.

This definition fits well with the observations described herein of seaweed interactions in humpback whales. During these interactions, there appeared to be no obvious functional gain (e.g., prey capture, mating success, or communication benefits) that the whale could be receiving from the interaction. Additionally, the behaviour started with no other obvious prompt other than the whale locating a piece of seaweed. The fact that two of our three observations occurred when no other whales were in visual range suggests that this behaviour was self-rewarding and was not used as a form of social display as there were no conspecifics around to witness the display. Additionally, in the one instance where a second whale was present, no change in behaviour was observed in the second animal. While interacting with the seaweed, the animal stayed in the one location, and no feeding lunges were observed, suggesting that seaweed interactions were distinct from other observed behaviours such as feeding and travelling. In all three instances, the animal had been observed feeding prior to the seaweed interaction (36 min, 12 min, and 1 h 54 min, respectively). In the study area the main predation threats towards humpback whales come from killer whales (*Orcinus orca*) and, given the presumably low population size of this predator, predation levels on humpback whales in this area are believed to be relatively low. Consequently, it is likely that the animals were all in favourable situations (well-fed and safe from predators) at the initiation of the behaviour. All of our observations came from subadult animals, so it is difficult to comment on the likelihood that this behaviour occurs at different life stages of individual animals. However, a calf has been observed interacting with seaweed (also *P. comosa*) for approximately 1 h in the same area as these observations with very similar behaviour to what was observed in the subadults (D. Donnelly, pers. comm., 29 March 2012) (Figure 2). It is therefore possible that this behaviour does occur throughout different stages of the individual humpback whales' lives. We therefore conclude that object play appears to be the most likely explanation for seaweed interactions in humpback whales.

**Figure 2.** A humpback whale calf interacting with seaweed off Eden, New South Wales, Australia

However, whether or not these interactions are determined to be play behaviour does not provide us with information on the specific function of the behaviour. Given that *play behaviour* is thought to provide a mechanism for animals to perfect motor skills (Paulos et al., 2010), is it possible that the whales interact with the seaweed to learn how to manipulate objects? If so, what function does this level of object manipulation serve to the humpback whales' later life stages?

Another possible explanation for the play behaviour is that the whales interact with the seaweed because they enjoy the sensation of the seaweed on their skin similar to killer whales rubbing themselves on pebble beaches (Ford, 1989). Additionally, cow/calf pairs of many whale species often make physical contact, and the fact that only subadults and a calf were observed interacting with seaweed may suggest that young animals could be seeking out tactile stimulation that is no longer provided by a conspecific. Mysticete whales are believed to have a well-developed sense of touch, with many vibrissae and dermal receptors located around the lower jaw and head area and a smaller amount located in other parts of the body (Tinker, 1988). It is therefore possible that objects such as seaweed are interacted with for the sensation they create. In addition to tactile stimulation, the seaweed may be used to assist with shedding skin and ectoparasites similar to belugas (*Delphinapterus leucas*) in northern Canada that use rocky estuaries as a place to rub on the bottom (Smith et al., 1992). Perhaps the unsuitable bottom type present in some locations means that whales have to seek out floating objects to elicit the same sensation or result.

These observations are believed to represent the first published description of humpback whales interacting with seaweed. While a likely reason for this behaviour appears to be object play, the function of such behaviour still remains unknown, and future research documenting the age class, gender, and situations in which this behaviour is observed is recommended. Additionally, potential correlations between feeding behaviour and seaweed interactions should be investigated further as should similarities between the tactile stimulation provided by seaweed and that of humpback whale cows to their calves. Such studies will assist in increasing our understanding of the function of interactions with seaweed and other objects in humpback whales.

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