Movement Ecology of Humpback Whales in the South Pacific

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Abstract

Determining the distribution, movements and habitat use of animals is fundamental to understanding their ecology and the development of effective conservation measures. However, studying animals that migrate thousands of kilometres and inhabit remote and inaccessible areas is extremely difficult, especially in the marine environment. The Oceania humpback whale (*Megaptera novaeangliae*) population has been slow to recover from the effects of commercial whaling, and our understanding of what may influence this slow recovery has been limited by a lack of knowledge about the whales outside of their tropical breeding grounds. The aim of this thesis was to investigate the migratory movements, patterns of Antarctic feeding ground habitat use and energetics of Oceania humpback whales as they migrated from the South Pacific to the Southern Ocean.

Satellite tags were deployed on 25 humpback whales on their southern migration past the Kermadec Islands, New Zealand, in September and October 2015. Photo-identification and genetic data were collected to assign breeding ground origins and to determine the pregnancy rate and age-profile of the population. The whales' migratory paths and behavioural states were investigated by applying a hierarchical state-space model to the satellite telemetry data. These data were used in linear mixed-effect models to elucidate ecological relationships between whale behaviour and the environment within the remote Southern Ocean feeding grounds. The tag data, and data from two whales tagged in east Australia, were also used to inform a bioenergetic model to estimate the relative energetic cost of different migratory routes and distances.

The Kermadec Islands were an important aggregation point for Oceania's humpback whales from a range of breeding grounds spanning ~3,500 km of ocean, almost the entire breeding ground range, as they migrated south to their Southern Ocean summer feeding grounds. The age profile of the whales (mean = 14 years) and a high (57%) pregnancy rate indicated a recovering population. The whales migrated to two key feeding areas, the Ross Sea and the Amundsen and Bellingshausen Seas (~2,000 km apart), the choice of which was influenced by the presence of a calf, as mothers with calves migrated a shorter distance to the Ross Sea region. There were marked differences in the environmental features between the two areas (e.g. oceanic *vs* near continental shelf) and consequently the whales used these areas differently. Overall, time lagged ice-edge dynamics were identified as a key environmental feature influencing the whales' foraging behaviour, along with season and sea surface height. Whales with the longest migration distance migrated the fastest (97 km/day *vs* 71 km/day) and had the highest cost of transport, but this was offset by energy savings in terms of daily maintenance costs by using 11% fewer days to complete the migration, suggesting that migration distance alone is not a limiting factor to population recovery.

Whilst there is no doubt that a complex set of variables is affecting the Oceania humpback whale population recovery, the findings of this thesis have improved our understanding of the whales and their movement ecology once they depart from their breeding grounds. Furthermore, understanding the movement patterns and habitat use of this large predator also improves our knowledge of the remote Southern Ocean ecosystem and the changes occurring within it as a result of climate change. With such a wide geographic longitudinal range of feeding grounds (~4,000 km span) behavioural plasticity may play a critical role in the whales' ability to adapt to the environmental changes, therefore affecting the species' future recovery. This work further highlights the value of bio-logging in providing opportunities to advance ecological research.

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Chapter 1

General Introduction

1.1. Spatial ecology in conservation

In nature, resources are not distributed uniformly in space and time, but instead they form spatial gradients and aggregations (Legendre & Fortin, 1989; Wiens, 1989). This heterogeneity plays a key role in the lives of mobile organisms as it forces them to move through their landscape in search of suitable habitat, mates and food, thus creating habitat use and distribution patterns for individual organisms and populations (Kareiva, 1990; Wiens et al., 1993; Ims, 1995).

Understanding how animals select resources and utilise habitats is a central topic in animal ecology (Johnson, 1980; Sutherland et al., 2013). Studies on the spatial ecology of animals generally investigate the distribution and habitat use of organisms in respect to the spatial characteristics of their environment (Turner et al., 1995; Nathan & Muller-Landau, 2000). The term 'movement ecology' has been recently used as a unifying paradigm for studying the movement patterns of living organisms and how these are influenced by both internal and external factors (Nathan, 2008; Nathan et al., 2008; Spiegel et al., 2017). The external (environmental) factors affecting animal movement can operate at multiple spatial and temporal scales. For example, at fine scales (tens of meters; hours to days) animals may track suitable ephemeral food patches, while at broad scales (hundreds to thousands of kilometres; years to decades) animals select habitats based on predictable environmental patterns (Mayor et al., 2009; Mannocci et al., 2017; Abrahms et al., 2019).

Studying the spatial ecology of individuals or species is a popular means of investigating their distribution, habitat use patterns and identifying areas of importance for the animals, and this information can be used for conservation purposes (Shuter et al., 2011; Runge et al., 2014; Allen & Singh, 2016). In fact, conservation and management efforts are more reliable when informed by data on the movements of animals and their critical habitats (Noss et al., 1997; Wells et al., 2018). Spatial ecology studies have been used in many cases, for example to mitigate the impacts of infrastructure developments on migratory animals (Bastille-Rousseau et al.,

2018) and to discover population home ranges to properly inform conservation measures (López-López et al., 2016; Wells et al., 2018). Accurate information on species' movements and interactions with the habitat therefore allows for the development of spatially explicit conservation management strategies. Changes in the spatial distribution of resources, habitats or environmental barriers over time can affect distribution and movement patterns of individuals (e.g. Laidre et al., 2008). Continued monitoring to identify changes in habitat use over time may therefore be vital in some cases when making management decisions (Hartel et al., 2014).

1.2. Migration and capital breeding as life history strategies

Many different animal groups in all major branches of the animal kingdom, including insects (Williams, 1917), fish (Jones, 1968), birds (Baird, 1867) and mammals (Lockyer & Brown, 1981), display migratory behaviour through air, water and/or land (Dingle & Drake, 2007). Migration occurs primarily in response to the spatiotemporal variation in resources, habitats, predation and competition, as well as the animal's requirements at different life history stages and at different times of the year (Southwood, 1962; Alerstam et al., 2003). For example, the highly conspicuous seasonal movement of many bird species is perhaps one of the most recognised forms of migration between discrete summer and winter areas (Dingle, 1996). Migration between geographically separate key habitats following pulses in resource availability and abundance has a key role in the spatial distribution of mobile populations (Taylor & Taylor, 1977; Dingle & Drake, 2007).

Migration utilises both time and energy (Alexander, 1998), hence there is always an element of trade-off between the benefits of moving (e.g. access to better habitats, increased food availability), and the costs associated with moving (e.g. energetic cost of transport, risk of mortality; Alexander, 1998; Alestram et al., 2003). The animal's ability to balance available energy reserves is therefore a critical aspect of migration (Blem, 1980; Piersma & Jukema, 1990). All animals need to allocate the energy they gain from food between maintaining bodily processes (e.g. basal metabolism, respiration, thermoregulation), daily activities (e.g. moving, feeding), growth, energy storage and reproduction (Karasov, 1992). How much energy gets allocated to each process will depend on the sex and the life stage of an individual, as well as on food availability and the environmental conditions (Kooijman, 2010). For example, an individual with limited access to food would likely prioritise energy allocation to vital survival functions over reproduction (Martin, 1987; Taylor et al., 2005).

In general, there are two strategies of resource use to facilitate the energetic demands of reproduction: income and capital breeding (Jönsson, 1997; Stephens et al., 2009). Income breeders increase their energy intake during the breeding season in response to a higher resource demand, while capital breeders rely on endogenous or exogenous energy reserves acquired prior to the breeding season (Jönsson, 1997; Stephens et al., 2009). The capital breeding strategy often involves periods of intensive feeding in areas of temporarily abundant food resources, followed by periods of fasting in habitats more suited for reproduction (Jönsson, 1997; Alerstam et al., 2003; Dingle & Drake, 2007). Capital breeders that perform long-distance migrations between these spatially and temporally separated key habitats must have sufficient energy stores to cover the cost of migration as well as the cost of reproduction during a period of fasting (Lockyer, 1987a; Plot et al., 2013). Therefore, the link between body condition and reproductive success is particularly strong in those capital breeders that meet the cost of reproduction using endogenous energy reserves (Festa-Bianchet et al., 1998; Bonnet et al., 2002). Although capital breeders may run the risk of exhausting their energy reserves before reaching suitable foraging grounds, in an unpredictable environment where food resources are limited and patchily distributed, being able to store and utilise energy reserves can be beneficial (Jönsson, 1997; Braithwaite et al., 2015).

1.2.1. Baleen whales: migratory capital breeders

Many species of baleen whales (mysticetes) undertake seasonal migrations, often across thousands of kilometres, between their low-latitude (winter) breeding grounds and high-latitude (summer) feeding grounds (Lockyer & Brown, 1981; Corkeron & Connor, 1999). Baleen whales perform these long-distance migrations in response to the need for warm waters for breeding and calving, and cold, nutrient-rich waters for feeding, however, the exact reasons for these migration patterns are still unclear (Corkeron & Connor, 1999; Bannister, 2018; Stern & Friedlaender, 2018).

Most baleen whales are capital breeders that rely heavily on their stored energy reserves (mainly blubber) during the fasting period lasting for several months when they migrate and reproduce within the less productive warmer waters (Lockyer, 1987b, 2007). During the feeding season baleen whales build up the energy reserves required to support energetically costly migratory behaviour as well as their large body size by filter feeding, whereby they strain small prey items (typically zooplankton such as euphausiids and copepods, or small schooling fish) from the water. To do this baleen whales use multiple plates made of keratin that hang down from the upper jaw. Filter feeding allows baleen whales to efficiently exploit lower trophic levels with higher biomass and therefore have more energy available for consumption (Werth, 2000; Goldbogen et al., 2017). The evolutionary transition of baleen whales from life on land to the life in water included a dramatic increase in size and foraging techniques that enabled exploitation of small prey, ultimately leading to successful expansion throughout the world's oceans (Pyenson, 2017).

1.3. Humpback whale ecology

Humpback whales (*Megaptera novaeangliae*) have a cosmopolitan distribution and are found in all major oceans of the world, however populations from the Northern and Southern Hemispheres do not typically intermingle (Johnson & Wolman, 1984; Clapham & Mead, 1999). During winter, humpback whales aggregate close to islands and reef systems in the tropics to breed (Chittleborough, 1965; Dawbin, 1966; Clapham & Mead, 1999). The inter-calf interval for females is around 2-3 years (Chittleborough, 1958; Clapham & Mayo, 1990; Gabriele et al., 2017), although annual calving does occur (Clapham & Mayo, 1990; Glockner-Ferrari & Ferrari, 1990; Robbins, 2007). Humpback whales typically do not feed during the winter breeding season, but instead they typically spend spring through to autumn at discrete foraging grounds in mid- or high-latitude waters (Chittleborough, 1965; Dawbin, 1966; Lockyer, 1981). Humpback whales are generalist predators and in the Southern Hemisphere the whales feed mainly on euphausiids (krill) as well as on various species of small schooling fishes (Kawamura, 1994). The prey base for Northern Hemisphere whales is even more diverse and includes multiple species of krill (*Thysanoessa* spp., *Euphausia pacifica*) and fish such as Pacific herring (*Clupea pallasii*), juvenile salmon (*Oncorhynchus* spp.), capelin (*Mallotus villosus*), Pacific sandlance

(*Ammodytes hexapterus*), juvenile walleye pollock (*Theragra chalcogramma*), eulachon (*Thaleichthys pacificus*) and myctophids (*Stenobrachius leucopsarus*; Krieger & Wing, 1986; Neilson & Gabriele, 2008; Witteveen et al., 2008; Chenoweth et al., 2017), and the whales' diet can vary by location, season and possibly individual preference (Witteveen et al., 2011). Many humpback whale populations exhibit natal breeding ground fidelity (i.e. whales will return to the breeding grounds where they were born), and in some cases also strong maternally inherited feeding ground fidelity, where the calf learns the migration path from their mother during the first year of life (Clapham & Mayo, 1987; Baker et al., 1990, 2013; Acevedo et al., 2006).

Globally, humpback whales undertake annual migrations between their winter breeding and summer feeding grounds (Clapham, 2000). An exception to this is the non-migratory population in the Arabian Sea that is resident year-round (Mikhalev, 1997; Pomilla et al., 2014). Additionally, some humpbacks may refrain from migrating every year, and instead overwinter on the feeding grounds (Brown et al., 1995; Van Opzeeland et al., 2013; Magnúsdóttir & Lim, 2019). Humpback whales navigate across thousands of kilometres between their feeding and breeding grounds, however the exact cues they use to do this remain unresolved (Horton et al., 2011, 2017). As capital breeders, humpback whales rely on stored energy reserves (blubber) acquired during the summer feeding season to support the energetic costs of basal metabolic activity, growth, reproduction as well as their annual migration (Lockyer, 1981). Traditionally the incidence of feeding outside the feeding grounds was considered to occur at very low levels, with only a few cases of feeding during migration or on the breeding grounds initially reported (Lockyer, 1981; Baraff et al., 1991). However, in recent times there is increased evidence of feeding during migration, which could in fact play an important role in the whales' annual energy budgets (Danilewicz et al., 2009; Barendse et al., 2010; Owen et al., 2017; Andrews-Goff et al., 2018).

1.3.1. Humpback whales of the South Pacific and Oceania

In the Southern Hemisphere, for management purposes the International Whaling Commission (IWC) recognises seven geographically separate breeding populations, labelled as breeding stocks A to G (IWC, 1998), and six distinct Antarctic feeding grounds (previously used as IWC management areas) labelled as Areas I-VI (Donovan, 1991). In summer, the whales from the South Pacific breeding stocks between Australia and South America (stocks E-G) migrate to high latitude feeding grounds in the Southern Ocean around Antarctica (Areas V-VI, I).

Within the South Pacific, the humpback whale breeding populations that winter around the Pacific Islands of Oceania include the whales of New Caledonia (sub-stock E2), Tonga (sub-stock E3), the Cook Islands and French Polynesia (sub-stock F; IWC, 2014; Figure 1.1). Although these Oceania sub-populations are genetically distinct (Olavarría et al., 2007) there is some degree of connectivity throughout the region (Garland et al., 2011; Garrigue et al., 2011), and some areas (e.g. the Cook Islands) function mainly as migratory corridors rather than designated breeding grounds (Hauser et al., 2010; Garrigue et al., 2011). Apart from mainland New Zealand, there are no major land masses between the tropical breeding and Antarctic feeding grounds of the Oceania whales, especially when compared to breeding stocks D and E that migrate along the coasts of Australia, and stock G that migrates along the west coast of South America (Chittleborough, 1959a; Dawbin, 1966; Gales et al., 2010; Guzmán & Félix, 2017). Until now there has been relatively little research on the movements of the Oceania population (Dawbin, 1964; Garrigue et al., 2010, 2015; Hauser et al., 2010; Robbins et al., 2011; Steel et al., 2018). Apart from earlier thoughts that the whales travelled due north and south between their breeding grounds and Southern Ocean feeding grounds, as determined from the historical *Discovery* tag data (Chittleborough, 1965; Dawbin, 1966), very little is still known about their long-distance migratory behaviour.

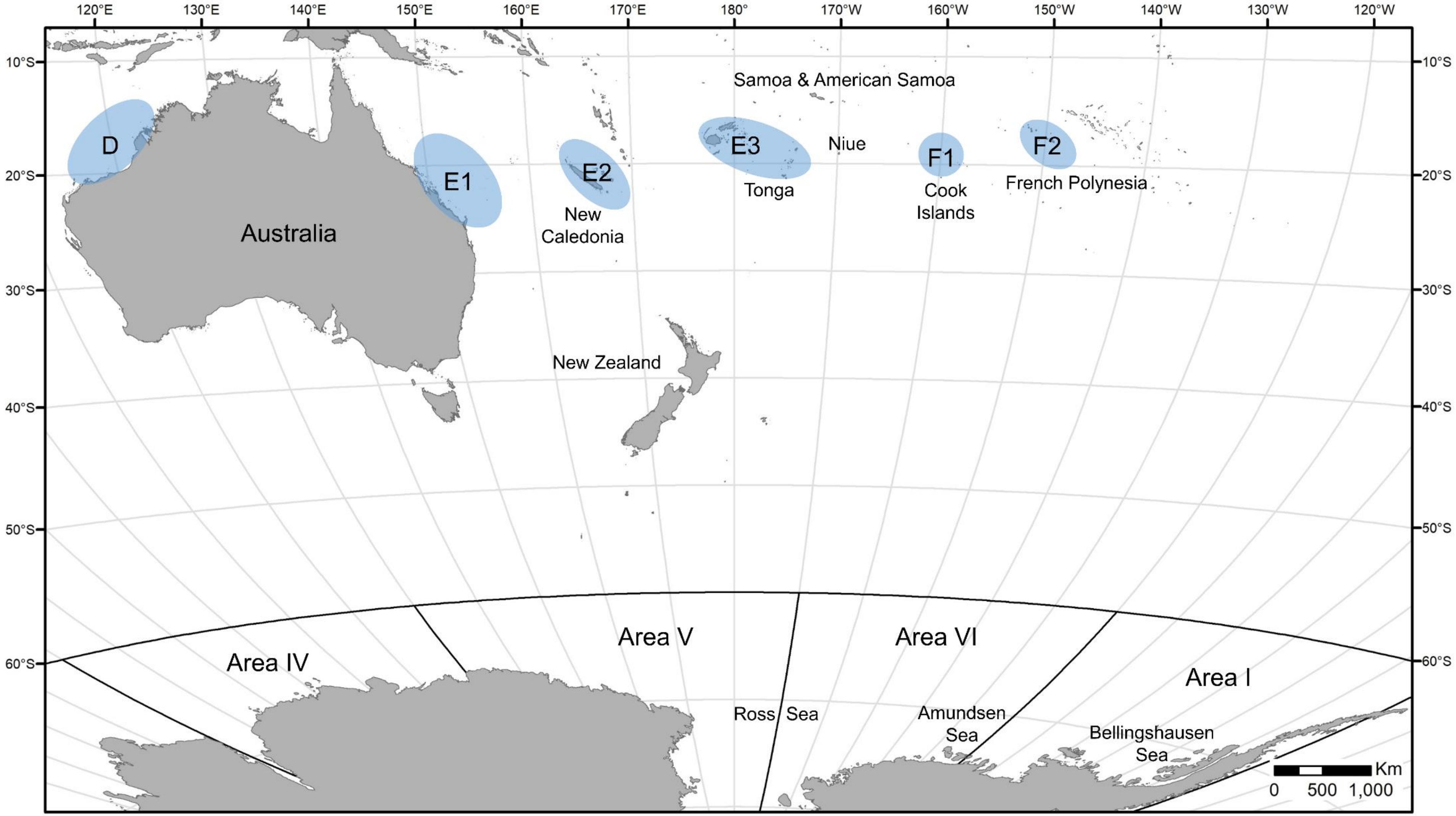

Figure 1.1 Breeding (blue circles) and feeding grounds (International Whaling Commission management areas IV-VI, I) of South Pacific humpback whales. Oceania population comprises breeding grounds E2, E3, F1 and F2. Southern Ocean is denoted by black line at 60°S

1.3.2. Southern Ocean ecosystem

The remote Southern Ocean is a large, circumpolar ecosystem, semi-enclosed to the north by the Polar Front. The Southern Ocean has a strikingly rich and diverse biodiversity with high levels of spatial variation and community patchiness from the deep sea to pelagic and benthic communities (Clarke, 1990; Clarke & Johnston, 2003; Rogers et al., 2012). The patchy distribution of primary productivity is driven by a range of physical, chemical and biological factors, particularly light, mixed depth layer, sea ice dynamics, micronutrients and grazing (Sakshaug & Holm-Hansen, 1984; Petrou et al., 2016). Low levels of primary production are generally found in oligotrophic (iron deficient) open waters, while high concentrations are associated with coastal areas, oceanic fronts, polynyas and the marginal ice zone (Moore & Abbott, 2000; Knox, 2006). The key area of interest for this study are the waters south of the South Pacific, around the Ross Sea region (Figure 1.1). The ocean circulation and surface properties in this area are dominated by the wind-driven Ross Sea gyre and it is one of the most biologically productive regions of the Southern Ocean (El-Sayed et al., 1983; Gouretski, 1999; Dinniman et al., 2003; Arrigo et al., 2008).

The circumpolar distribution of herbivorous zooplankton follows that of primary productivity. The predominant herbivores are the euphausiids (*Euphausia superba*, the Antarctic krill, and *E. crystallorophias*, the crystal krill), which can form large aggregations (O'Brien, 1987; Knox, 2006; Nowacek et al., 2011). The Southern Ocean krill-based ecosystem provides the primary food source for a diverse group of large predators, including fish, birds, and marine mammals (Knox, 2006). The peak in productivity in the Southern Ocean is concentrated in late spring and summer, during which many migratory animals come to the region to take advantage of the seasonally available and abundant food resource (Dawbin, 1966; El-Sayed, 1988; Arrigo et al., 1998; Boyd et a., 1998; Egevang et al., 2010).

The Southern Ocean is currently undergoing rapid climate-related changes. These include trends such as strengthening of westerly winds, increasing deep ocean temperatures, and a pole-ward shift of major ocean fronts (Gille, 2002; Fahrbach et al., 2011; Langlais et al., 2015; Rudeva & Simmonds, 2015). Some areas, such as the Amundsen and Bellingshausen Seas are experiencing significant decreases in the winter sea ice extent and duration, and while other regions, such as the Ross Sea, are experiencing increasing sea ice extent (Parkinson & Cavalieri, 2012; Hobbs et al., 2016) the ice cover itself may be thinning (e.g. Stewart et al., 2019). Another major trend in the Southern Ocean over the last decades has been the regional decline in Antarctic krill densities (mainly within the Southwest Atlantic sector) and the increase of salps (mainly *Salpa thompsoni*) in the southern part of their range (Atkinson et al., 2004; Hill et al., 2019).

By identifying changes in the population sizes or demographic parameters of long-lived top predators, such as marine mammals, these species can serve as indicators of the ecosystem status (Hindell et al., 2003; Weimerskirch et al., 2003; Taylor et al., 2007). Although our current knowledge of the ecosystem role of large baleen whales is still lacking, baleen whales have been hypothesised to play a critical role in the recycling of iron in the surface waters of the Southern Ocean, thereby affecting phytoplankton productivity and ecosystem function (Nicol et al., 2010; Lavery et al., 2014; Ratnarajah et al., 2014). To understand the extent to which recovering whale populations may increase phytoplankton productivity in the iron-limited Southern Ocean through their role in the biochemical cycling of iron, we must first have a better understanding of their spatial distribution, habitat use and projected population recovery.

1.3.3. Whaling in the South Pacific

Humpback whale hunting began in the 19th century following the decline in southern right whale (*Eubalaena australis*) stocks (Townsend, 1935; Wray & Martin, 1983). However, it was the 20th century that brought about a revolution in whaling with technological advancements and inventions enabling more efficient hunting (Clapham & Ivashchenko, 2009; Clapham & Baker, 2018). Additionally, the industry expanded geographically as whalers discovered the rich whaling grounds around Antarctica that had until then remained largely unexplored (Clapham & Ivashchenko, 2009; Clapham & Baker, 2018).

During the 20th century, humpback whales of the South Pacific were overexploited and hunted to near extinction, with illegal Soviet whaling playing a key role late in the whaling era when stocks were already heavily depleted (Clapham et al., 1999a; Clapham & Ivashchenko, 2009; Clapham & Baker, 2018). Over 25,000 whales were taken in just two seasons (1959-1961) primarily in the Antarctic management areas IV, V, and VI located south of Australia and New Zealand (Figure 1.1) contributing to the collapse of whale populations and the closure of whaling operations on land and at sea (Clapham et al., 2009; Ivashchenko et al., 2011). By the time commercial whaling (both legal and illegal) ended, more than 200,000 Southern Hemisphere humpback whales had been killed (Clapham & Ivashchenko, 2009; Rocha et al., 2014), reducing the South Pacific stocks to <10% of pre-exploitation levels (Jackson et al., 2015).

Since the end of commercial whaling Southern Hemisphere humpback populations have exhibited different recovery trajectories, with some populations recovering more slowly than others (Best, 1993; Clapham et al., 1999a; Jackson et al., 2015). While the neighbouring populations of east Australia and Oceania were subjected to similar whaling pressures (although this is complicated by the difficulty of allocating precise Antarctic whale catches to the correct breeding grounds) these populations have contrasting patterns of recovery (Chittleborough 1957, 1962; Jackson et al., 2015). The Oceania population (which consists of a number of sub-populations) is currently listed as Endangered by the IUCN, estimated to be <50% of pre-exploitation numbers and recovering markedly slower than the almost fully recovered neighbouring east Australian population (Childerhouse et al., 2008; Constantine et al., 2012; IWC, 2015; Jackson et al., 2015). The reason for this slow recovery rate is currently unknown. Suitable breeding habitat throughout Oceania does not appear to be a limiting factor (Garrigue et al., 2015; Lindsay et al., 2016; but see Derville et al., 2019), but low numbers post-whaling and social factors may have played a part driving some whales to move to more populated areas (Clapham & Zerbini, 2015). Alternatively, the slow recovery may be explained by factors related to the whales' feeding grounds and/or the long-distance migration.

1.4. Bio-logging in conservation

Many aspects of animal ecology, such as distribution, behaviour and physiology are traditionally and most accurately studied through direct observations and measurements. However, in many cases obtaining such data for highly mobile and wide-ranging species, both terrestrial and marine, is often difficult especially for migratory animals that travel long distances across multiple ecosystems and habitats (Jacoby et al., 2012; Goldbogen et al., 2013; Chin et al., 2017). The conservation of such migratory species therefore presents a unique challenge that requires innovative solutions (Runge et al., 2014).

The advancements made in telemetry and bio-logging techniques and the miniaturisation of animal-borne tags seen in recent decades allow us to study the behaviour, space use, energetics and physiology of even the most remote of species (Cooke, 2008; Hussey et al., 2015). Data on animal locations, movements as well as their environment can now be collected at high spatial and temporal resolutions using radio telemetry, electronic archival tags, ARGOS and Global Positioning System satellite tags (Cooke, 2008; Rutz & Hays, 2009; Labrousse et al., 2018). These tools have been used to track everything from the movements and behaviour of birds (e.g. Weimerskirch et al., 2000; Hahn et al., 2004) and free ranging terrestrial mammals (e.g. Morales et al., 2004; Singh & Ericsson, 2014), to the long-distance migration and foraging of large pelagic animals (e.g. Godley et al., 2008; Bestley et al., 2010; Galuardi et al., 2010).

An important complement to the advancement of technology and the increase in the amount of spatial data are increasingly sophisticated analytical methods and models (Morales et al., 2004; Van Moorter et al., 2010; Gregr et al., 2013). For example, movement models can be used to identify underlying behavioural states, such as foraging, in remotely collected movement data (Morales et al., 2004; Jonsen et al., 2005, 2006; Michelot et al., 2017), and statistical models can be further used to examine the relationships between animal locations or behavioural states and the environment (e.g. Mandel et al., 2008; Jonsen et al., 2019). Furthermore, modelling also allows us to study physiological processes and the energetic consequences of disturbances in animals that cannot be studied in captive settings (Fortune et al., 2013; New et al., 2013; Braithwaite et al., 2015; Villegas-Amtmann et al., 2015).

These technological and analytical advancements have many applications in addressing management questions, and scientists are increasingly relying on these tools in conservation research (Hays et al., 2016). Bio-logging has been used to inform conservation of many taxa, from reptiles such as snakes and turtles (Baxter-Gilbert et al., 2015); to eagles (López-López et al., 2016), songbirds (Bisson et al., 2008), moles (Jackson et al., 2009), elephants (Bastille-Rousseau et al., 2018), rays and sharks (Graham et al., 2012; Wells et al., 2018), and large whales (McKenna et al., 2015).

1.4.1. Bio-logging as a tool to study humpback whales

While advancements in technology once allowed for more efficient hunting of whales, now, technological improvements are allowing us to remotely study whales and better understand their movements and ecology. Directly observing the migration routes, behaviour and habitat use of humpback whales is logistically and financially challenging as they travel thousands of kilometres across open-oceans and often inhabit remote high-latitude locations (Clapham, 2000). Obtaining physiological and metabolic measurements is equally difficult due to the whales' fully aquatic lives which prevent capture and studying them in laboratory settings (Williams & Noren, 2009; Goldbogen et al., 2013; Christiansen et al., 2018). For this reason, most of our knowledge on the physiology of these animals is limited to findings during the commercial whaling era (e.g. Bannister, 1964; Chittleborough, 1958). For pinnipeds and seabirds that periodically come to land, more creative methods can be deployed. For example, Kooyman (1967) captured Weddell seals (*Leptonychotes weddellii*) and transported them to a man-made ice hole surrounded with a tent and laboratory equipment. Due to its distance from any other breathing holes, the seals were constrained to return to the site allowing repeated measurements to be taken. Similarly, an Automated Penguin Monitoring System was set up by Kerry et al. (1993) whereby tagged penguins returning to the colony were made to walk over a weighing station.

The first limited information on humpback whale movements and migration came from expeditions in the 1950s-60s where *Discovery* tags implanted into the whales were recovered after the individuals were killed (Chittleborough, 1959b; Dawbin, 1964). More recently photo-identification (e.g. Robbins et al., 2011; Stevick et al., 2011) and genotyping (e.g. Steel et al., 2018) provided non-lethal ways of investigating migratory paths, however, like the *Discovery* tags these methods only provided information on single endpoint locations, omitting detailed movement information between sampling and re-sighting locations. The development of satellite telemetry and bio-logging tools has therefore been crucial in allowing us to study whale movements and habitat use in the most remote parts of the world at resolutions not previously possible (Dalla Rosa et al., 2008; Curtice et al., 2015).

Satellite telemetry has so far been successfully used to study humpback whale migration routes and destinations (e.g. Hauser et al., 2010; Zerbini et al., 2011; Félix & Guzmán, 2014; Kennedy et al., 2014a), behavioural and habitat use patterns (e.g. Mate et al., 1998; Dalla Rosa et al., 2008; Kennedy et al., 2014b), and to discover novel habitats (Garrigue et al., 2015). Given the lack of knowledge on the Oceania populations, satellite telemetry and bio-logging provide an opportunity to study the whales' migration routes, behaviour and habitat use patterns. These are important for understanding not only the whales' ecology, but also may reveal why whales from this region are recovering so slowly, as well as guiding future conservation and management efforts.

1.5. Thesis structure

The main aim of this thesis is to examine the migratory movements and energetics as well as the patterns of feeding ground habitat use of the endangered Oceania humpback whale population. This research will contribute to understanding the link between these factors and the population's slow recovery rate. This aim is addressed in three data chapters, each of which deals with a key objective of this research. This thesis is formatted as a single body of work with a single reference list at the end. However, each data chapter is written as an independent scientific manuscript that has been published or submitted for publication. Consequently, there may be some overlap or repetition between the chapters. A brief overview of each chapter is presented below.

Chapter 1. A general introduction to the topic. This chapter contains background information relating to the themes of this thesis, e.g. spatial ecology, migration and conservation, followed by an overview of the study species, the study area and the broad tools discussed in this thesis.

Chapter 2. This chapter examines the broad-scale movements and population demographics of the humpback whales of Oceania. Using a multidisciplinary dataset and innovative analytical tools the objective was to comprehensively assess the population structure of these whales, to identify their migratory paths and behaviour, and to reveal their Antarctic feeding ground destinations. This chapter has been published as: Riekkola, L., et al. (2018). Application of a multi-disciplinary approach to reveal population structure and Southern Ocean feeding grounds of humpback whales. *Ecological Indicators*, 89, 455-465.

Chapter 3. In this chapter the fine-scale habitat use patterns and behaviour of Oceania humpback whales are investigated within the Southern Ocean feeding grounds using satellite telemetry data, movement models and statistical models. The objective of this chapter was to identify underlying behaviour from movement data, and to investigate the relationship between whale behaviour and environmental variables between animals using different regions of the Southern Ocean. This chapter has been published as: Riekkola, L., et al. (2019). Environmental drivers of humpback whale foraging behaviour in the remote Southern Ocean. *Journal of Experimental Marine Biology and Ecology*, 517, 1-12.

Chapter 4. This chapter examines the energetic cost of long-distance migration. Using satellite telemetry data to inform a bioenergetic model the objective of this chapter is was to estimate the relative differences in the energetic cost of different migratory routes and distances to determine whether migration distance is a factor in the slow population recovery rate of the Oceania humpbacks. This chapter has been provisionally accepted as: Riekkola, L., et al. Estimating the energetic cost of long-distance migration in satellite tagged humpback whales. *Aquatic Conservation: Marine and Freshwater Ecosystems*.

Chapter 5. A general discussion which draws together the thesis findings and provides future research directions.

Chapter 2

Application of a multi-disciplinary approach to reveal population structure and Southern Ocean feeding grounds of humpback whales

2.1. Introduction

Using animal-borne loggers to monitor the movement and behaviour of wide-ranging predators such as marine mammals can provide valuable information on the environmental conditions in extreme habitats such as the Southern Ocean (e.g. Aarts et al., 2008; Hindell et al., 2016). Additionally, cross-discipline collaborations can be helpful in identifying patterns in animal movements that are often important when designing conservation strategies (Hays et al., 2016). Therefore, it is increasingly important to collect a suite of data when undertaking field studies in remote sites, or when examining species that are rare, elusive or unable to be caught. Studying migratory animals across their full range poses logistical and operational challenges, particularly for studies of large animals in the complex marine environment (e.g. Heupel et al., 2015). Yet, migration is important for many marine animals, including for baleen whales which undertake some of the longest documented annual movements (e.g. Robbins et al., 2011; Stevick et al., 2011), and is therefore an important research area.

The humpback whale (*Megaptera novaeangliae*) requires specific habitats for major life functions: warm waters for breeding and calving, and cold, nutrient-rich waters for feeding. Most humpback populations undertake annual migrations between low-latitude (winter) breeding grounds and high-latitude (summer) feeding grounds (Chittleborough, 1965; Dawbin, 1966; Clapham & Mead, 1999). In the Southern Hemisphere, studying humpbacks within their breeding grounds near continental mainland or islands is logistically attainable.

However, within their Antarctic feeding grounds discrete populations of these whales collectively span large areas of open ocean that are largely inaccessible (Amaral et al., 2016).

Commercial whaling heavily exploited all Southern Hemisphere humpback stocks (Clapham & Ivashchenko, 2009; Ivashchenko & Clapham, 2014) and the Oceania whales, that feed in Areas V and VI around Antarctica (Figure 2.1) are still estimated to be <50% of their pre-exploitation numbers. Their recovery is considerably slower than the neighbouring east Australian population and the reasons for this remain unknown (Constantine et al., 2012; IWC, 2015). The migratory movements of the Oceania humpback whales as they travel across open ocean to their remote Southern Ocean feeding grounds are poorly described, and have typically involved single individual movement data. *Discovery* tag data from the 1950s–60s provided the first limited information on the movements of a few individuals, suggesting that these whales likely moved directly north to south between their breeding and feeding grounds (e.g. Chittleborough, 1959b; Dawbin, 1964). Later, matches of photo-identified (Robbins et al., 2011) and genotyped individuals (Steel et al., 2018) provided alternate, non-lethal methods of investigating the migratory destinations of this population. However, like *Discovery* tags, these methods provided only endpoint locations, omitting detailed movement information between sampling and re-sighting locations.

The advancement of satellite telemetry has provided the opportunity to study migratory animals, such as humpback whales, continuously for several months. Telemetry has been an effective tool for describing migration routes and destinations (e.g. Zerbini et al., 2006, 2011; Garrigue et al., 2010; Félix & Guzmán, 2014), behaviour and habitat use patterns (Kennedy et al., 2014b; Curtice et al., 2015; Weinstein et al., 2017), and for discovering novel habitats (Zerbini et al., 2006; Garrigue et al., 2015). However, most tag deployments on Oceania humpbacks have occurred on the breeding grounds (Garrigue et al., 2010, 2015; Hauser et al., 2010) and have not been fully integrated with other research tools.

Large whales are challenging to study as they can be difficult to approach and cannot be captured or handled during tag deployment and sample collection. The development of remote biopsy sampling techniques allowed the relatively easy collection of tissue samples from wild cetaceans (Lambertsen, 1987). These tissue samples (containing skin and sometimes blubber) can be used for several analyses that can inform us about the whales' life history patterns. Genetic methods can for example be used to obtain the genotype and sex of individuals (Lambertsen et al., 1988; Baker et al., 1991), as well as investigating the relatedness between whales (Steeves et al., 2001; LeDuc et al., 2002). Adequate sampling of the source populations and a sufficient number of genetic markers are required for accurate relatedness estimations (Kalinowski, 2004; Thomas, 2005), however many of the growing whale populations may not be sampled frequently enough to obtain this, and if too much time lapses between sampling events the historic data can become less robust for understanding population genetics. New approaches such as genome by sequencing, skim-sequencing and restriction site-associated DNA sequencing may provide a way of obtaining greater population level genomic information for highly mobile marine mammals (e.g. Cammen et al., 2016; Lah et al., 2016; Lal et al., 2016). Another life history trait that can be obtained from tissue samples is epigenetic aging (Polanowski et al., 2014; Jarman et al., 2015). However, there are still uncertainties associated with the precision of this method for measuring the age of long-lived animals such as humpback whales. In particular, in young populations a variance of +/-3 years for an age estimate can influence the interpretation of the results (Polanowksi et al., 2014). We can also gain information on the diet and foraging location of sampled individuals through isotope and fatty acid analyses (Todd et al., 1997; Clark et al., 2016). Such dietary studies are hindered for example by accurate data on the distribution of carbon and nitrogen isotopes in the Southern Ocean food webs across different regions. It is also important to understand the variability in tissue types used for isotopic diet analyses as they can differ in their metabolic activity.

Tissue biopsies are often small (~10-20 mm), as obtaining larger samples may lead to ethical considerations, and blubber samples may be needed for multiple analyses, such as pregnancy assignment (Mansour et al., 2002; Kellar et al., 2006) and toxicology (Borrell, 1993; Metcalfe et al., 2004). Challenges associated with pregnancy assignment from blubber hormones includes the lack of historic controls, and as large whales cannot be managed in captive settings long-term datasets on contemporary populations are required. One such population exists in the Gulf of Maine and has been used to calibrate recent pregnancy assignment models (Pallin et al., 2018a), but such long-term consistent data is sparse in the Southern Hemisphere. Another use for blubber samples is toxicology analyses of lipophilic compounds. Biopsies typically sample the superficial blubber layer yet the vertical distribution of contaminants through the blubber layer may vary (Waugh et al., 2014). Also, the timing of sampling is an important factor due to the mobilisation of toxins in metabolically active blubber and the fluctuations in body energy stores across the year during feeding and fasting phases, which may influence the results (Bengtson Nash et al., 2013). Although these tools provide us with the opportunity to investigate different aspects of whales' lives, the technologies are changing and being developed at different rates. However, by combining oceanic movement patterns, life history and relatedness markers we can integrate several research techniques to answer complex questions about whale populations and their relationship with the Southern Ocean ecosystem.

In this multi-disciplinary study, we combined satellite tagging, genotyping, epigenetic markers, photo-identification and hormone analysis to undertake the most extensive assessment of a highly mobile baleen whale, and of their southern migration to their Antarctic feeding grounds. The movement, behaviour and population demographics of these whales are used as indicators of important habitats within the Southern Ocean ecosystem.

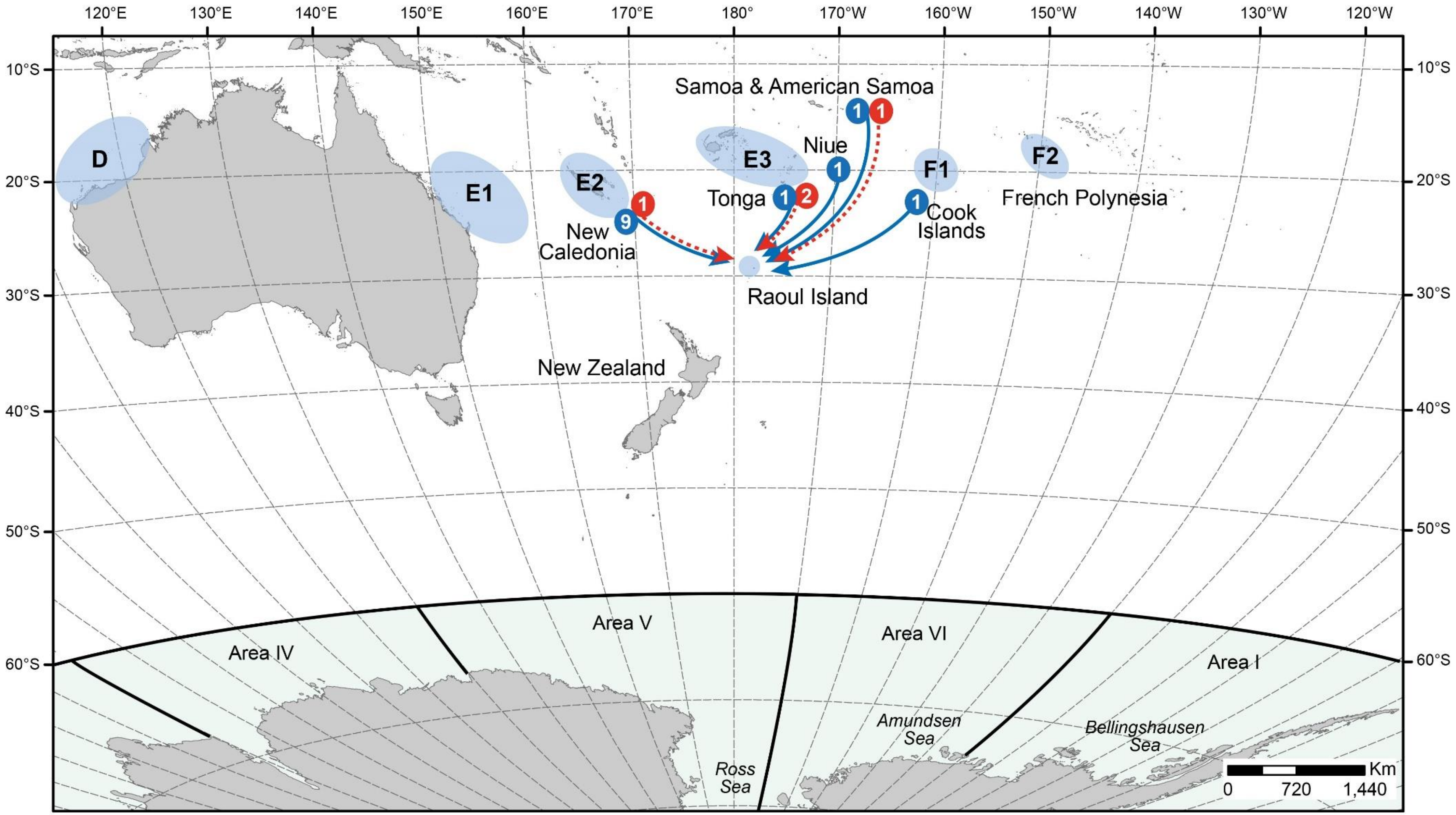

Figure 2.1 Breeding (blue areas) and feeding grounds (International Whaling Commission management areas; green areas) of Southern Hemisphere humpback whales. Oceania population comprises breeding grounds E2, E3, F1 and F2. Note that only breeding grounds D-F, and feeding grounds IV, V, VI and I are shown. Arrows denote photo-identification (solid blue) and genotype matches (dashed red) in the current study between various breeding grounds of the Oceania humpback whales and the study site (Raoul Island, Kermadec Islands) in 2015.

2.2. Methods

2.2.1. Data collection

Data were collected off Raoul Island (29°16'S, 177°55'W), Kermadec Islands, New Zealand, from 29th September to 11th October 2015. Land-based observations since 2008 have indicated large numbers of southbound whales passing the Kermadec Islands between mid-September to mid-November (Brown, 2010; Gibson, 2014). We used two rigid-hulled vessels to conduct non-systematic surveys, recording the position, number, and age-class (adults/calves; Clapham et al., 1999b) of whale pods. The pods were approached for photo-identification, biopsy sampling, and/or satellite tag deployment; detailed descriptions below.

2.2.2. Photo-identification

We used digital SLR cameras with 100–400 mm lenses to photograph the ventral surface of whale flukes to identify individuals (Katona et al., 1979). Following methods used in previous studies on the Oceania population (Constantine et al., 2012) the fluke photographs were quality scored from 1 (highest) to 5 (lowest) on each of five features (proportion of the fluke visible, vertical angle, lateral angle, focus/sharpness, and exposure) according to standards developed for North Pacific humpback whale research and required for mark-recapture (Friday et al., 2000; Calambokidis et al., 2001). Only high-quality images, irrespective of distinctiveness of the fluke, were reconciled to create the Kermadec Islands catalogue of whales. The catalogue consisted of 124 photos collected during this study and 12 opportunistic photos from 2007–2015. The images were entered into Fluke Matcher, a computer assisted matching program (Kniest et al., 2010) and compared to catalogues from the Oceania breeding grounds, the migratory corridors of east Australia, New Zealand and Norfolk Island, and Antarctica (Appendix A Table A.1). Due to the large size of some of the catalogues, this was a preliminary matching effort focusing on the most likely matches; as such, our results do not represent all possible matches.

2.2.3. Genetics

Biopsy samples were collected using a modified veterinary capture rifle or a crossbow equipped with 7 × 10 mm or 7 × 20 mm surgical stainless-steel cutting tips. Samples were processed by separating the blubber from the epidermis, with the blubber used for pregnancy assignment. The blubber was frozen at -20°C, and the epidermis was stored in 70% ethanol. Sloughed skin samples were opportunistically collected from the sea surface.

Total genomic DNA was extracted using standard proteinase K digestion and phenol/chloroform methods (Sambrook et al., 1989), as modified for small samples by Baker et al. (1994). Each sample was used for individual identification and stock analysis by DNA profiling, consisting of sex identification, mitochondrial DNA (mtDNA) control region haplotype (470 bp). Up to fifteen microsatellite loci (EV1, EV14, EV21, EV94, EV96 and EV104; Valsecchi & Amos, 1996; GATA28 and GATA417; Palsbøll et al., 1997; RW18, RW31, RW410 and

RW48; Waldick et al., 1999; GT23, GT211 and GT575, Bérubé et al., 2000) were generated following methods previously described by Olavarría et al. (2007) and Constantine et al. (2012).

MtDNA control region sequences were identified to haplotype using Sequencher v4.7 (Genecodes) and all variable sites were visually inspected. Microsatellite alleles were sized with Genemapper v4.0 (Applied Biosystems) and all automated calling was confirmed by visual inspection (Bonin et al., 2004). As a precaution against poor DNA quality, only those samples that amplified at a minimum of 11 microsatellite loci were retained for further analyses (Quality Control dataset). Arlequin v3.1 (Excoffier & Lischer, 2010) was used to test for differentiation in mtDNA haplotype frequency between the Kermadec Islands population, the migratory corridors of east Australia and New Zealand, and the winter breeding grounds in Oceania. The significance of this differentiation was tested with 10,000 random permutations within Arlequin. Replicate genotypes within the Kermadec Islands samples were identified using Cervus v3.0 (Kalinowski et al., 2007). Individuals identified within the Kermadec Islands samples were compared with a curated database of DNA profiles from 2,262 humpback whales sampled in three breeding grounds of Oceania (New Caledonia/stock E2, Tonga/stock E3, American Samoa-Samoa-French Polynesia/stock F), two databases from the east Australian migratory corridor (Anderson et al., 2010; Schmitt, et al., 2014a), a database from the New Zealand migratory corridor (Steel et al., 2014), and Antarctic data.

To investigate the origins of whales migrating through the Kermadec Islands we conducted a mixed-stock analysis of mtDNA using SPAM (v.3.7, Alaska Department of Fish and Game, 2003; Debevec et al., 2000). We considered three breeding grounds within Oceania, and the migratory corridor of east Australia as likely source populations and calculated maximum likelihood estimates of contributions from these sources to the Kermadec Islands population using similar methods to Schmitt et al. (2014b). We included the east Australian migratory corridor as a proxy in the absence of breeding ground data. Whales sampled on the Tongan breeding grounds include whales passing the Cook Islands (Garrigue et al., 2011) and are considered a similar stock. The whales of east Oceania (American Samoa, Samoa and French Polynesia) are genetically similar (Albertson et al., 2018) and considered one stock.

2.2.4. Pregnancy assignment

To assign pregnancy status to sampled whales, progesterone concentrations were quantified from a blubber subsample (Mansour et al., 2002; Kellar et al., 2006). Progesterone was extracted from the blubber using a multitube homogeniser, followed by a series of ethanol, ethanol: acetone, and ethyl ether washes. The resulting lipid residue was separated from the sex-steroid hormones using a biphasic mixture of acetonitrile and hexane. The progesterone concentrations from the steroid pellets were quantified using a progesterone enzyme immunoassay (EIA, ADI-900-011, ENZO Life Sciences). Pregnancy status was assigned for sampled female humpbacks by predicting the probability of being pregnant across a logistic model developed from a series of humpback progesterone control samples of females of known reproductive status (Pallin, 2017).

2.2.5. Epigenetic age estimation

We used the Humpback Epigenetic Age Assay (HEAA) method developed by Polanowski et al. (2014) to estimate whale age based on changes in DNA methylation levels at three age-informative CpG sites in three loci: TET2 (ten eleven translocation 2), CDKN2A (cyclin dependent kinase inhibitor 2A), and GRIA2 (glutamate receptor Ia2/AMPA2). Age estimates for whales in our study were based on the calibration used in Polanowski et al. (2014). The overall precision of HEAA (estimated as the standard deviation of the mean difference between known and estimated ages) is 2.991 years, with similar variance throughout the range of ages assayed, although the method generally slightly overestimates the age of young whales and slightly underestimates the age of older whales. Whales with an age estimate of <2 years (i.e. calves, n = 7) were excluded due to the uncertainty within the method (Polanowski et al., 2014), and as calves could be visually identified in the field by size.

2.2.6. Satellite tagging and telemetry data analysis

Satellite tags (n = 25) were deployed on adult whales, high on the body near the dorsal fin (Gales et al., 2009) using a modified version of the Air Rocket Transmitter System (Heide-Jørgensen et al., 2001) at 10–12 bar pressure. We used transdermal-implantable, location-only SPOT-5 satellite transmitters (Wildlife Computers, Redmond, USA) housed in stainless-steel cylinders, and sterilised with a chlorhexidine-methylated spirits mixture prior to deployment.

Tags were duty cycled to transmit for 21 h each day to maximise the time with overhead Argos satellites. The maximum number of transmissions per day was set to 600 at a repetition rate of 45 s. Observed locations and estimated errors were calculated by the Argos System when multiple uplinks from a tag were received by a satellite, and raw locations were assigned a location class in a descending order of accuracy: 3, 2, 1, 0, A, B and Z. Location classes A and B have no accuracy estimation and Z is an invalid location.

A hierarchical version of a Bayesian switching state-space model (SSM; Jonsen et al., 2005, 2006) was fitted to the data to estimate locations and behavioural states at a 12-h time-step. We used a SSM as it simultaneously solves for observational and movement models (Jonsen et al., 2005), yielding more accurate estimates of the locations and the associated uncertainty than raw tracking data (Jonsen et al., 2005, 2006). The SSM was fitted in R (R Core Team, 2016) using the software JAGS (Plummer, 2013) and the R packages *rjags* (Plummer, 2016) and *bsam* (Jonsen et al., 2015).

Two Markov chain Monte Carlo (MCMC) chains were run in parallel, each for a total of 90,000 simulations. The first 50,000 samples were discarded as a ’burn-in’, and the remaining samples were thinned, retaining every 50th sample to reduce autocorrelation. The final 1,600 samples were used to compute the posterior distribution of the model parameter estimates. The behavioural modes (*b*) were inferred from the means of the MCMC samples, ranging between 1 and 2. We used a conservative approach (Jonsen et al., 2007) for classifying behavioural modes, with mean estimates of $b<1.25$ labelled as ‘transiting’, and mean estimates of $b>1.75$ labelled as ‘area restricted search’ (ARS), indicative of foraging, resting or breeding behaviour. Locations with a mean *b* estimate between 1.25 and 1.75 were classified as uncertain in the final dataset.

Total track distance was calculated for each whale as Great Circle distances. Based on visual inspection of tracks and bearings between consecutive locations, the whales began migration at ~30°S, when the tracks took on a linear south or south-easterly direction. Whales reached the Antarctic feeding grounds (60°S) when their tracks became more sinuous. The state-space modelled data were used to calculate speeds between consecutive locations for each whale. To determine whether there were differences in travel speed during migration (30°–60°S) and non-migration (<30°S, >60°S) between females with calves and adults without calves, we conducted a Welch two-sample t-test. The data were log-transformed prior to statistical testing, and results were considered significant at p≤0.05.

2.3. Results

2.3.1. Research effort

Over 13 days we non-systematically surveyed 1,480 km around Raoul Island. We encountered 127 pods of humpback whales, containing a cumulative total of 235 adults and 37 calves.

2.3.2. Photo-identification

A total of 136 individual whales were included in the Kermadec Islands humpback whale catalogue. A total of thirteen individuals were matched to whales from the breeding grounds of New Caledonia (n = 9), Tonga (n = 1), Niue (n = 1), American Samoa (n = 1) and the Cook Islands (n = 1; Figure 2.1).

2.3.3. Biopsy samples and genotype identification

A total of 84 tissue samples were collected (70 biopsy and 14 sloughed skin). Three samples did not amplify due to insufficient quantities of extracted DNA, and one failed to pass Quality Control (QC11) criteria of amplification at a minimum of 11 microsatellite loci. From the remaining 80 samples, we genetically identified 72 individuals (27 males: 45 females).

There were four genotype matches to whales previously sampled on the breeding grounds: New Caledonia (female with a calf, sampled as a calf in 1999), American Samoa (male, 2009 sample), and Tonga (two females, 2003 and 2005 samples; Figure 2.1) both of which were satellite tagged in the current study (PTT112721 and PTT111866, respectively). The female matched to New Caledonia was the only whale identified both genetically and photographically.

2.3.4. Population differentiation and mixed-stock analysis

Review of mtDNA control region sequences identified 33 haplotypes from 71 individuals with confirmed sequence; one individual did not give a clean sequence. The humpbacks migrating past the Kermadec Islands had no 1:1 relationship with any single breeding ground population and were significantly different to all other populations at $p = 0.05$, reflecting the diversity of genotype matches to the Oceania breeding grounds and migratory corridors (Table 2.1a). We identified one haplotype (EC007, Genbank No. HQ241485) that was previously unknown from the Oceania or east Australia regions. The mixed stock analysis assigned probable breeding ground origins of whales to New Caledonia (49%), Tonga (36%), American Samoa – Samoa – French Polynesia (12%), east Australia (1%) and an unknown stock (2%; Table 2.1b).

Table 2.1 a) Pairwise comparisons for mtDNA haplotype diversity (F_{ST}) between humpback whales sampled at Raoul Island, Kermadec Islands (n = 71 with sequence), the migratory corridors of east Australia and New Zealand, and breeding grounds of Oceania (see Figure 2.1). The number in brackets is the number of individuals with sequence used for each population. b) Results of the SPAM mixed stock analysis assigning probability of breeding ground for the humpback whale samples at the Kermadec Islands.

(a)

Sampling site (n)		F_{ST}	p-value
East Australia (316)	Migratory corridor	0.012	0.000
New Zealand (151)	Migratory corridor	0.009	0.001
New Caledonia (953)	Breeding ground	0.004	0.011
Tonga (337)	Breeding ground	0.005	0.009
French Polynesia - American Samoa - Samoa (292)	Breeding ground	0.020	0.000

(b)

Population	Estimate	S.E.	C.V
East Australia	0.0007	0.0031	4.7
New Caledonia	0.4941	0.1153	0.23
Tonga	0.3641	0.1444	0.40
French Polynesia - American Samoa - Samoa	0.1212	0.1006	0.83
Unknown	0.0200		

2.3.5. Pregnancy assignment

Progesterone levels were analysed from 38 blubber samples, including samples from three males and four calves as controls (all classified as not-pregnant). Progesterone levels for one adult female could not be determined. Concentrations, reported as nanograms of progesterone per gram of blubber (ng/g P4), ranged between 1.28 and 5.26 for non-pregnant, and between 25.81 and 352.68 for pregnant individuals (Appendix B Table B.1). Seventeen out of 30 females (56.7%) were classified as pregnant. This included five out of 11 (45.5%) females that were accompanied by a calf at the time of sampling, and six out of 11 (54.5%) females, for which we had satellite tag data.

2.3.6. Epigenetic age estimation

Epigenetic age was estimated for 81 sampled whales, including eight whales sampled twice, and three samples for which age could not be determined (due to poor DNA quality). Thus, 78 age estimates were obtained from 70 individuals to generate an age profile for the sampled population. The mean observed age estimate was 13.8 years (median = 11.6, range = 2.1–67.5, n = 71, excludes whales estimated as <2 years, Figure 2.2).

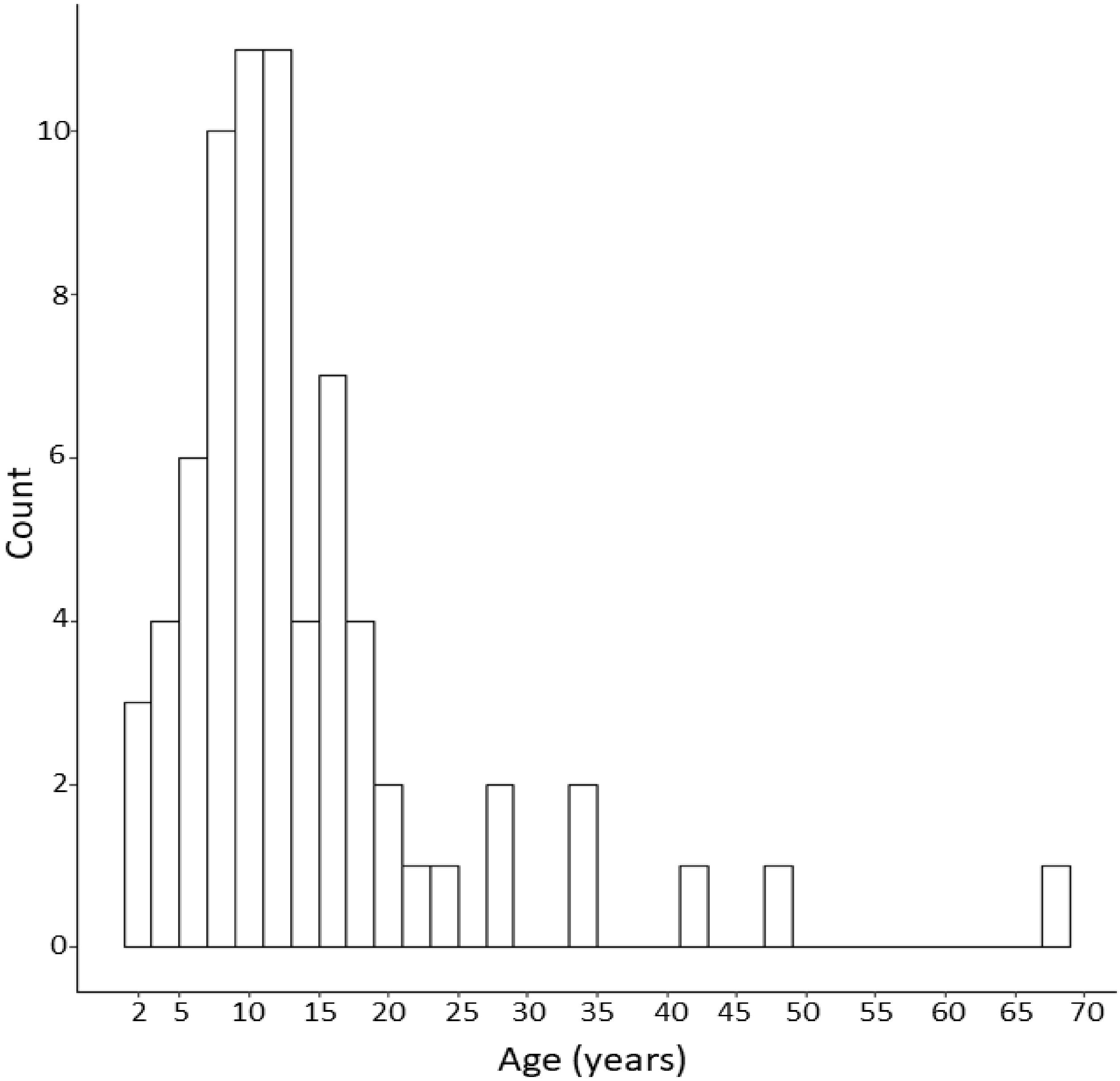

Figure 2.2 Population age distribution estimated with the HEAA (Humpback Epigenetic Age Assay) method for n = 71 humpback whale samples collected at Raoul Island, Kermadec Islands in 2015. Ages are grouped into bins of two years. Whales with an age estimate of <2 years were excluded.

2.3.7. Satellite tag deployment

Of 25 tags, six failed to transmit. One tag (PTT131172) transmitted inconsistently for five days, during which the whale never left Raoul Island. Due to insufficient migration data, this tag was excluded from further analyses. The remaining 18 whales comprised 5 females without calves, 6 females with calves, 5 males, and 2 of unknown sex (PTT102211 – no sample, PTT112722 – molecular sex identification unsuccessful). These whales were tracked for an average of 105 days (range = 12–254, Table 2.2, Figure 2.3). Four tags did not transmit for an extended period after deployment (range = 32–66 days), including two that began transmissions after reaching the Antarctic feeding grounds south of 60°S.

2.3.8. Migratory behaviour and destinations

The average migration duration between the Kermadec Islands (30°S) and the Southern Ocean (60°S) was 51 days (range = 35–67, n = 11). This excluded tags that stopped before 60°S (n = 4), or those for which the first transmission occurred south of 30°S (n = 3). The longest tag transmission duration was 254 days with a total track distance of 13,113 km, including the beginning of the return (northbound) migration (Table 2.2).

The average speed (± SD) of all whales used for the SSM was significantly different between migration (3.3 ± 1.6 km/h) and non-migration (1.8 ± 1.6 km/h; Welch two-sample t-test, $p<0.01$, $t = 29.8$, 95% CI for difference between means: 0.46–0.53; Table 2.3). The average speed of females with a dependent calf during migration (3.1 ± 1.5 km/h), and non-migration (1.5 ± 1.4 km/h) was significantly different from the average speed of adults without calves both during migration (3.4 ± 1.7 km/h) and non-migration (1.8 ± 1.7 km/h; Welch two-sample t-test, $p = 0.038$, $t = 2.0746$, 95% CI for difference between means: 0.003–0.100, and $p = 0.002$, $t = 3.14$, 95% CI for difference between means: 0.036–0.157, respectively; Table 2.3).

The SSM tracks show the occurrence of different behavioural states throughout the whales' southern migration (Figure 2.4a). The model distinguished between transiting ($b<1.25$, 86% of locations) and ARS ($b>1.75$, 4% of locations), with the behavioural mode of the remaining 10% of locations categorised as uncertain ($1.25<b<1.75$). The range of b-values varied along the migration path with a general shift towards higher b-values at 60°S (Figure 2.4b). The satellite tracks show that the whales migrated to feeding grounds spanning ~4,500 km from eastern Ross Sea to eastern Bellingshausen Sea. Of those individuals whose tags transmitted the entire migration to the feeding grounds, all females with a calf (n = 4) migrated to the Ross Sea region, while 70% of adults without calves (n = 4 females, n = 3 males) migrated to the Amundsen and Bellingshausen Seas. The remaining three adults (one male, two of unknown sex) migrated to the Ross Sea region.

Table 2.2 Summary of satellite tracking data from 18 humpback whales tagged at Raoul Island, Kermadec Islands in 2015. F = female, M = male, calf refers to a young-of-year animal, and * denotes a pregnant female. Whales of unknown sex: PTT102211 - no sample, PTT112722 - molecular sex identification unsuccessful. All dates are in UTC. Tracking duration = from first to last transmission. Data days = number of days when one or more locations were received. Track distance is calculated using state-space modelled data.

Tag PTT number	Sex – behaviour class	Deployment date	First transmission	Last transmission	Tracking duration (d)	Data days (d)	Track distance (km)
88727	F + calf	08 Oct 15	08 Oct 15	14 Jan 16	99	99	5,369
102211	Unknown	10 Oct 15	11 Oct 15	19 Dec 15	70	57	5,124
102218	M	10 Oct 15	11 Oct 15	20 Jun 16	254	249	13,113
111866	F*	04 Oct 15	06 Nov 15	15 Mar 16	131	130	5,877
111871	F	08 Oct 15	09 Oct 15	04 Nov 15	27	26	2,359
112718	M	05 Oct 15	05 Oct 15	13 Nov 15	40	40	3,234
112721	F + calf	09 Oct 15	10 Nov 15	28 Nov 15	19	19	752
112722	Unknown	10 Oct 15	11 Oct 15	03 Apr 16	176	174	8,307
112723	F* + calf	06 Oct 15	07 Oct 15	18 Oct 15	12	12	500
131173	M	30 Sep 15	30 Sep 15	08 Apr 16	192	184	10,174
131175	M	04 Oct 15	04 Oct 15	18 Jan 16	107	97	6,395
131178	F* + calf	08 Oct 15	09 Oct 15	17 Jan 16	101	101	5,524
131179	M	02 Oct 15	07 Dec 15	22 Mar 16	107	84	2,844
131182	F*	01 Oct 15	02 Oct 15	02 Apr 16	184	150	10,497
131185	F*	02 Oct 15	27 Nov 15	06 Jan 16	41	41	1,900
131187	F	30 Sep 15	01 Oct 15	02 Jan 16	94	94	7,303
131188	F* + calf	29 Sep 15	30 Sep 15	11 Dec 15	73	73	4,749
131190	F + calf	08 Oct 15	08 Oct 15	20 Mar 16	165	90	6,755

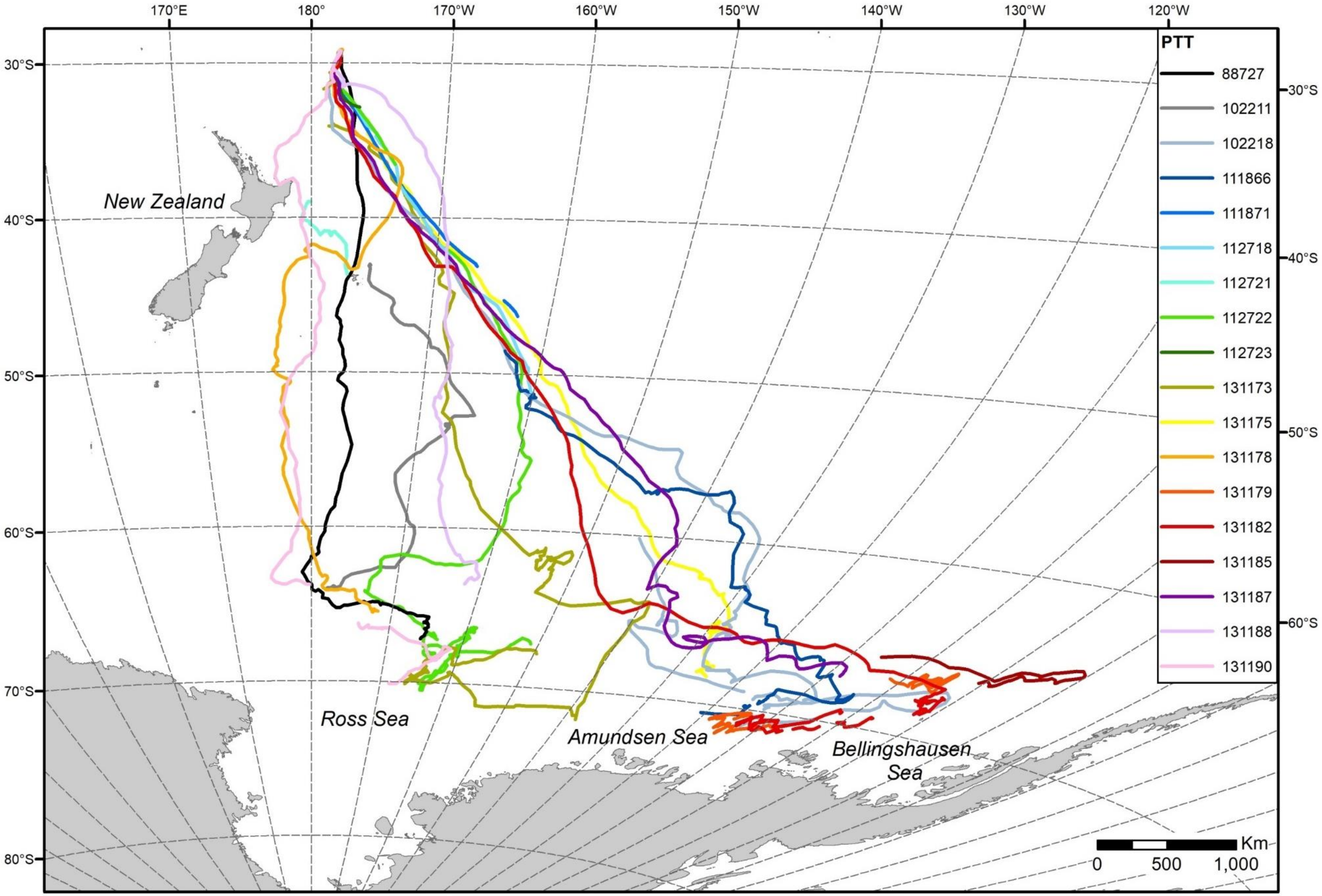

Figure 2.3 Tracks for 18 humpback whales satellite tagged at Raoul Island, Kermadec Islands in 2015

Table 2.3 Average and median (± SD) travel speeds (km/h) for humpback whale adults without (w/o) calves and females with (w/) a young-of-year calf during migration (30-60°S), and non-migratory (<30°S, >60°S) phases. The number of individual whales and the number of data points used to calculate speeds and conduct t-tests are shown. Calculations were done using state-space modelled data from the tags of 18 whales (note that some tags only transmitted during the migration, or non-migration phase).

	During migration				Non-migration			
	Average	Median	SD	Individuals (data points)	Average	Median	SD	Individuals (data points)
Adult w/o calf	3.4	3.5	1.71	10 (889)	1.8	1.2	1.66	12 (1730)
Female w/ calf	3.1	3.1	1.48	6 (452)	1.5	0.9	1.44	5 (323)
All whales	3.3	3.3	1.64	16 (1341)	1.8	1.2	1.63	17 (2053)

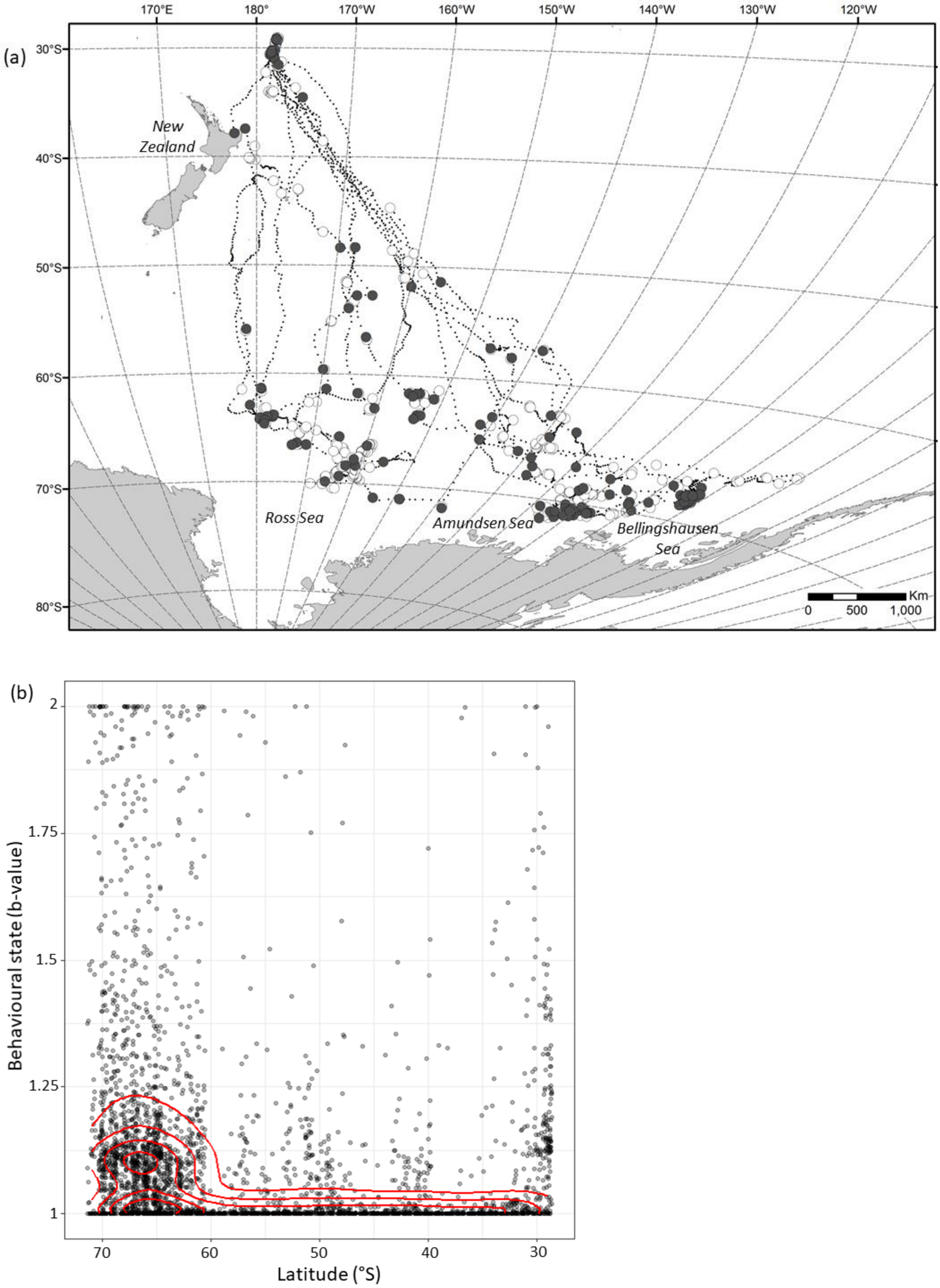

Figure 2.4 a) State-space modelled tracks of 18 humpback whales showing behavioural states identified by the model at each location (dot = transit, open circle = uncertain, filled in circle = area restricted search, and b) distribution of *b*-values (denotes behavioural state) from the state-space model by latitude (*b*<1.25 = transit, 1.25<*b*<1.75 = uncertain, *b*>1.75 = area-restricted search). Red line represents a 2D density plot (kernel density estimation) of the data.

2.4. Discussion

Obtaining direct measurements to characterise the functioning of a complex system such as the Southern Ocean marine ecosystem can be challenging due to its large size, the complex interactions within the system and the difficulty and cost involved in accessing the region (Girardin et al., 1999). Advances in satellite tracking technology and the miniaturisation of animal-borne loggers have enabled the use of animals as tools to collect information about the ecosystem in remote and inaccessible environments (e.g. Aarts et al., 2008; Hindell et al., 2016). Here we combined multiple research and analytical tools to obtain a comprehensive understanding of the population demography, life history differences and space use of Oceania humpback whales over their large spatial range. We reveal a young population of whales indicating recovery from exploitation, from winter breeding grounds spanning ~3,500 km, with high pregnancy rates not reflected in the rate of population recovery. The whales had different migratory trajectories depending on their reproductive state and spread across ~4,500 km of Antarctic waters to feed during the productive summer months.

2.4.1. Differential dispersal to feeding grounds

Our findings suggest that Oceania humpback whales may migrate to different feeding grounds based on their life history stage. All tagged females with calves tracked through their full migration travelled to the Ross Sea region, whereas most adults without calves travelled east to the Bellingshausen Sea. This pattern, whereby the presence of a calf may influence the choice of feeding ground destination for female humpbacks, was also reflected in historical whaling catch data (Appendix C, Figure 5.1).

Differential habitat use occurs in some mammals and may be a result of differences in energetic requirements, environmental conditions, social mechanisms or risk of predation (e.g. Main et al., 1996; Loe et al., 2006). Humpback whales exhibit some age- and sex-linked differences, most notably the staggered time of departure and arrival at breeding and feeding grounds (Chittleborough, 1965; Dawbin, 1966, 1997). Also, small-scale habitat use patterns vary on the breeding grounds depending on sex and reproductive status (Smultea, 1994; Craig & Herman, 2000; Lindsay et al., 2016). However, the large-scale division based upon reproductive status that we observed in this study has not, to our knowledge, been reported across feeding grounds. Although differences in the spatial distribution of some sex or age classes have been observed within feeding grounds such as the Gulf of Maine in the North Atlantic (Clapham & Mayo, 1987; Robbins, 2007), our study is on a much larger scale (distances of 2,000 km+ vs ~400 km).

Humpbacks have been found to show natal fidelity to feeding grounds, where the calf learns the migration path from their mother during the first year of life (e.g. Clapham & Mayo, 1987; Baker et al., 1990, 2013; Acevedo et al., 2006). Our findings however suggest a possible deviation from the traditional view of maternally inherited migration routes and feeding ground destinations. Calves may migrate to the Ross Sea during their first year, and to either the Ross Sea or the Amundsen and Bellingshausen Seas later in life. The utilisation of the region north of the Ross Sea for feeding, especially by females with dependent calves, may be used as an indicator of the ecological resources available in the marine environment, and highlights the conservation importance of this area.

Our satellite tracking shows several adult humpback whales migrating towards the broader Amundsen and Bellingshausen Sea area, which has remained poorly studied (e.g. Kaiser et al., 2009; Griffiths, 2010; Munilla & Soler-Membrives, 2015). Humpback whales have huge energetic demand and their presence in the Amundsen and Bellingshausen Seas region could be taken as an indicator of the quality and suitability of this habitat to satisfy their energetic needs. This region must be able to support sufficient amounts of krill (*Euphausia superba*), the whales' main prey, to provision for the (slowly) recovering whale population. Comparisons with future tracking studies of these whales' distribution will be informative in assessing changes in prey availability in this region.

It is worth noting how in our case, the additional information on the reproductive status of the animals was key to interpreting the distribution data. Knowledge of the reproductive status of individuals using different regions for feeding could be relevant in the future when examining fluctuations in their distribution patterns, as one reproductive class might respond more strongly to changes in the environment or prey availability. Future research should now aim to validate these findings of different migratory destinations in the Oceania population and distinguish whether such division is due to life history related requirements, differences in productivity between feeding habitats or the energetic cost associated with migration distance. Within the Southern Ocean, this dispersal pattern could result in different exposure to threats (e.g. fisheries, climate change effects) by life history stage, with potentially complex implications for the management and conservation of this population.

2.4.2. Migration behaviour

Baleen whales undertake some of the longest migrations known, and the Kermadec Islands humpbacks crossed ~50° of latitude, and ~110° of longitude, one way, between their breeding and feeding grounds. The straight-line distances from breeding grounds (with photo-identification or genetic matches) to Kermadec Islands ranged from ~900 km (Tonga) to ~2,000 km (Cook Islands), and from Kermadec Islands to the Antarctic feeding grounds from ~4,500 km (Ross Sea) to ~6,000 km (Amundsen and Bellingshausen Seas). Reported extreme long-distance movements (>7,000 km) between feeding and breeding grounds (Stone et al., 1990; Stevick et al., 1999, 2011; Rasmussen et al., 2007; Robbins et al., 2011) have mainly involved a single or a few individuals and were generally considered exceptional. Our simultaneous tracking of several individuals highlights that long-distance migration from Oceania to the Amundsen and Bellingshausen Seas region is not exceptional, and confirms previous single records (Hauser et al., 2010; Robbins et al., 2011). The energetic costs of the different migration distances (Ross Sea *vs* Amundsen and Bellingshausen Seas), the effects on the fitness and reproductive potential of individuals of different life history stages, and the consequences of climate change on krill availability in these areas should be investigated.

The travel speeds we report are comparable to previous studies (Lagerquist et al., 2008; Kennedy et al., 2014b; Rosenbaum et al., 2014; Garrigue et al., 2015). Females with calves were slower than other adults, however, due to a large sample size this difference, while statistically significant, may not be biologically meaningful. Other baleen whales have been shown to have similar speed differences: for example, North Atlantic right whale (*Eubalaena glacialis*) females with calves were slower than adults without calves (Hain et al., 2013). Andriolo et al. (2014) tagged pairs of humpbacks within larger groups, and a mother-calf pair was found to move slower than the adult female associated with them when they were tagged. Within the Oceania population, slower travel speeds by mother-calf pairs could be linked to the feeding ground destination. Females with calves could be theorised to migrate to the Ross Sea as this is a shorter and more direct route to the feeding grounds from Kermadec Islands, with possibly a lower energetic cost for the young calf or the lactating mother.

The SSM identified different behavioural modes in the data, with the high number of transiting points reflecting the long migration. The shift in whale behaviour at ~60°S, at which point the whales began to move more sinuously, presumably in search of prey, roughly coincided with the locations of the Antarctic Circumpolar Current (ACC) fronts (the placement of which fluctuate from year-to-year; Kim & Orsi, 2014). Some of the fronts of the ACC have been associated with productivity (e.g. Tynan, 1998; Bost et al., 2009). The change in whale behaviour may therefore be due to the whales encountering productive conditions and possibly the first patches of krill. Future northward or southward movement in the shift from migratory behaviour to feeding could serve as an indicator of changes in krill availability and distribution. Humpback whales occasionally feed outside Antarctic waters and during their southern migration, e.g. off south-eastern Australia (Stockin & Burgess, 2005; Stamation et al., 2007; Owen et al., 2015), and possibly off south-western New Zealand (Gales et al., 2009). In some areas this may be important in the annual energy budget. In our study, nine whales exhibited ARS behaviour outside the feeding grounds, accounting for 1.7% of all modelled locations during migration. This ARS behaviour may have been opportunistic feeding, or a collection of behaviours that have similar movement characteristics (e.g. resting, socialising, mating). Future studies should quantify the role of supplementary feeding for the Oceania humpbacks that will allow comparisons with the rapidly increasing east Australian whales. Additionally, increase in the feeding activity during migration might serve as an indicator of the Southern Ocean ecosystem in that the energetic requirements of the whales aren’t fully met during the summer feeding season.

2.4.3. Age distribution and pregnancy

The age profile of whales migrating past the Kermadec Islands is an indicator of a recovering Oceania population. With an average age of 14 years the profile was similar to an epigenetic-based estimate of the adjacent east Australian population (Polanowski et al., 2014). Both populations had a high proportion of younger individuals and a relatively low proportion of older individuals. Comparison of the east Australian age estimates with the population’s expected pre-exploitation age structure was suggestive of high fecundity in the population (Polanowski et al., 2014). Given the adjacency of the areas, we assume that the pre-exploitation age structure for Oceania humpbacks was comparable. Determining population age structure can be a powerful tool for ascertaining the impact of exploitation on populations of long-lived animals (Jones et al., 2018).

Over half (57%) of all sampled females were pregnant. This is similar to earlier studies (Chittleborough, 1965; Baker et al., 1987; Clark et al., 2016), and to a recent estimate of 58% from the Western Antarctic Peninsula (Pallin, 2017). However, our findings may not be representative of the population. Although the field work was conducted at the peak of the southern migration past the Kermadec Islands, and we aimed to sample all possible whales, there is a chance of bias. Humpbacks stagger their departure from their breeding grounds by life history stage (Chittleborough, 1965; Dawbin, 1966, 1997). Due to a short sampling period at the Kermadec Islands, we may have captured uneven proportions of these migration cohorts. Additionally, we do not have an accurate estimate of the proportion of sampled females that were not sexually mature at the time of sampling. The average age at sexual maturity in humpback whales is known to range from ~5 to 10 years (Chittleborough, 1965; Clapham, 1992; Gabriele et al., 2007; Zerbini et al., 2010), and although likely to be similar, this has not been estimated for the Oceania population.

Almost half of the females with new-born calves were also pregnant, suggesting a higher rate of annual pregnancies than expected. Female humpbacks generally have an inter-calf interval of ~2–3 years (e.g. Chittleborough, 1958, 1965; Clapham & Mayo, 1990; Gabriele et al., 2017), with annual pregnancies less common (e.g. Clapham and Mayo, 1990; Glockner-Ferrari & Ferrari, 1990; Barlow & Clapham 1997; Robbins, 2007). However, most of the information has come from Northern Hemisphere whales. Recent work in New Caledonia has estimated a 1.4-year inter-calf interval (Chero, 2017).

The high pregnancy rates observed in the Oceania population is in contrast to the estimated low population size and relatively slow recovery rate (Constantine et al., 2012; IWC, 2015). This discrepancy could be due to calf loss, possibly in the form of foetal resorption, or early termination of pregnancy that can occur in mammals in response to changing environmental conditions or stressors (e.g. Conaway et al., 1960; Huck et al., 1988). The sampling for our study occurred soon (~6–8 weeks) after the peak of the breeding season (Chittleborough, 1958, 1965; Garrigue et al., 2001) and the whales may not have experienced conditions resulting in foetal loss. However, similar rates of pregnant females (58%) and annual pregnancies (52%) were reported from the Western Antarctic Peninsula ~5–8 months into the 12-month gestation period (Pallin, 2017). We currently do not have an estimate of foetal and neonatal mortality for the Oceania population, nor of the recruitment rate of calves into the population. Such inference would require resightings of previously sampled females to ascertain the fate of the pregnancy. The high pregnancy rate could indicate that the foraging areas are able to support a high proportion of females with increased energetic need due to gestation. Future monitoring of the pregnancy rates could serve as an indicator of the energetic gain females obtain during the summer feeding season.

2.5. Conclusions

Here we show how combining new techniques and different analysis methods can be an efficient approach for investigating a key ecological species, and its environment, that may otherwise be hard to access. For the Oceania humpback whale population, this work represents the most comprehensive study on the population demography, life history differences and space use patterns over their large spatial range. The life history stage of the whales may have influenced their choice of two Antarctic feeding regions. This is important when informing conservation and management planning as whales may be exposed to very different climate change and anthropogenic pressures. This highlights the need for sufficient knowledge of the dispersal patterns and population demography for understanding how individuals and populations respond to future environmental change. Sampling and satellite tagging whales further north, closer to their breeding grounds, was a cost-effective alternative to expensive and logistically difficult voyages to the remote Southern Ocean. Comparisons with future re-sampling and satellite tagging could provide valuable insight into changes in the distribution of the whales' main prey (krill) as well as into possible factors affecting the whales' future recovery.

Chapter 3

Environmental drivers of humpback whale foraging behaviour in the remote Southern Ocean

3.1. Introduction

Many animal behaviours, such as movement and habitat use, are driven by responses to internal cues as well as the external conditions experienced by the animal (Nathan et al., 2008). Understanding how the physical environment shapes the behaviour and distribution of animals as they try to satisfy their resource requirements is a fundamental topic in behavioural ecology (e.g. Ballance et al., 2006; Aarts et al., 2008; Davies et al., 2012). A wide range of animals from moths to caribou (*Rangifer tarandus*) migrate between critical habitats following pulses in resource availability and abundance (Jiang et al., 2011; Le Corre et al., 2017). In many terrestrial and aquatic taxa the decision to depart for a new habitat is often controlled by variables such as photoperiod, temperature, snow fall and severe weather at the initial location, at which point the animals cannot predict the habitat conditions at the end destination (Jonsson & Ruud-Hansen, 1985; Vøllestad et al., 1986; Cotton, 2003; Balbontín et al., 2009; Jiang et al., 2011; Rivrud et al., 2016). Memory of long-term average conditions may also play a role in directing migrants to their destination (Bracis & Mueller, 2017; Abrahms et al., 2019). Upon arrival at a new location resources, such as prey, are often patchily distributed throughout space and time, at which point animals initiate search strategies to locate and secure prey (Benhamou, 1992; Boyd,1996; Sims et al., 2008; Humphries et al., 2010; Carroll et al., 2017). In marine systems specifically, biological productivity can be highly variable due to the heterogeneity of the many physical processes in the environment (Haury et al., 1978). This results in some habitats being more productive than others, which in turn influences prey availability and predator behaviour. To forage efficiently predators must move through their dynamic environment in search of prey while maximising time spent foraging in the most productive areas (Stephens & Krebs, 1986; Fauchald & Tveraa, 2006). In patchy environments individuals may even adjust aspects of their foraging behaviour depending on the external environmental conditions (Weimerskirch, 2007; Sebastiano et al., 2012; Kirchner et al., 2018).

Obtaining direct observations of movement and behaviour in wide-ranging predators can be challenging, and more indirect techniques, such as animal-borne transmitters and data loggers, are often required to detect and identify behaviour. Advancements in satellite telemetry and tagging technology have improved the ability to remotely collect animal movement data at high spatial and temporal resolutions (Hussey et al., 2015; Gurarie et al., 2016; Chimienti et al., 2017). Different movement models can be applied to these remotely collected data to identify underlying behavioural states such as foraging (Morales et al., 2004; Jonsen et al., 2005, 2006; Michelot et al., 2017). Various statistical models can then be used to link animal locations and behaviour with ecological variables. Such models are useful tools for explaining spatial distribution patterns of highly mobile animals, for identifying critical habitats, and they have many applications including addressing management and conservation questions (Mandel et al., 2008; Gregr et al., 2013; Guisan et al., 2013).

In the Southern Hemisphere, humpback whales (*Megaptera novaeangliae*) migrate thousands of kilometres annually from the tropics to the Southern Ocean to feed on their main prey, the Antarctic krill (*Euphausia superba*; Kawamura, 1994; Murase et al., 2002). The endogenous and exogenous cues used by the whales to navigate to the feeding grounds and to search for prey remains unresolved (Horton et al., 2011, 2017; Torres, 2017). Directly observing the foraging behaviour and characterising the foraging habitat of large marine predators, such as humpback whales, in the Southern Ocean is notoriously difficult due to the logistical challenges associated with accessing this remote and vast area (Griffiths, 2010). Therefore, our knowledge of the fine-scale behaviour and patterns of habitat use by humpback whales in this region remains limited, compared to for example the more accessible Antarctic Peninsula (e.g. Friedlaender et al., 2013, 2016).

During the commercial whaling era, Southern Hemisphere humpback whale stocks were highly overexploited and hunted to near extinction (Ivashchenko & Clapham, 2014; Clapham & Baker, 2018). Since being granted protection from whaling, humpback populations have shown variable recovery. The Oceania humpback whales, comprising whales from multiple breeding ground subpopulations from the Pacific Islands (spanning New Caledonia to French Polynesia) are estimated to be <50% of pre-exploitation numbers and recovering more slowly than the neighbouring east Australian population (Childerhouse et al., 2008; Constantine et al., 2012; IWC, 2015). To date there has been little information available on the Oceania humpback whales within the Southern Ocean feeding grounds, and we only recently revealed their migration paths and location of the feeding grounds (Riekkola et al., 2018 - Chapter 2). As a consequence, we do not know whether the feeding behaviour and patterns of habitat use by these humpback whales could be linked to the different population recovery rates (IWC, 2015).

Here we applied a movement model to satellite tagging data of humpback whales on their Southern Ocean feeding grounds to infer underlying behavioural states: transiting and area restricted search (ARS), a behaviour indicative of foraging (Weinstein et al., 2017; Andrews-Goff et al., 2018). We expected that aspects of whale foraging behaviour would change throughout the feeding season. For example, we hypothesised that there would be an increase in foraging effort as prey becomes more abundant with the onset of spring and summer. We then used a statistical model to investigate the relationship between the inferred behavioural states (specifically the occurrence of ARS-foraging) and different environmental variables. We expected the whales' behaviour to be affected by different environmental factors, and that behavioural differences would exist between animals utilising different regions of the Southern Ocean. By linking whale movement data and behavioural changes to the conditions of their foraging habitat, this study ultimately contributes to a better understanding of the behaviour of wide-ranging predators.

3.2. Methods

3.2.1. Satellite tag deployment

Wildlife Computers (Redmond, WA, USA) SPOT 5 Platform Transmitting Terminals (PTTs) were attached to 25 adult humpback whales during the peak of their southern migration past the Kermadec Islands, New Zealand, between September and October 2015 (Figure 3.1). The tags were deployed using a modified version of the Air Rocket Transmitter System (Heide-Jørgensen et al., 2001) at a pressure of 10-12 bars. Observed locations were calculated by the Argos System using the Doppler Effect on transmission frequency when multiple messages from a tag were received by a satellite. An estimated error and a location class (in descending order of accuracy: 3, 2, 1, 0, A, B, Z) were assigned to each location (see Argos user’s manual, 2016). Location classes A and B have no accuracy estimation and Z is an invalid location. The tags were duty cycled to transmit for 21 hours each day to maximise the time with overhead Argos satellites. The maximum number of transmissions per day was set to 600 at a repetition rate of 45 s. Reproductive status (mother with a calf, or adult) of the tagged whales was inferred in the field based on the presence of a calf closely associated with the satellite tagged animal (Clapham et al., 1999b). Molecular sex identification was conducted using tissue samples collected at the time of tagging (Riekkola et al., 2018 - Chapter 2).

3.2.2. Data processing and hierarchical state-space model

Raw Argos locations were speed filtered using the R package *argosfilter* (Freitas et al., 2008) at a conservative maximum speed of 36 km/h to remove only highly erroneous and unrealistic locations. We used a hierarchical version of a Bayesian state-space model (SSM; Jonsen et al., 2005, 2006) to estimate locations (via an observational model) and behavioural states (via a movement model). We used a 6-h time-step in the model to provide detailed whale movement data. Obtaining whale data on an even finer scale was not necessary given the low resolution of some of the environmental covariates (see section ‘Explanatory variables for statistical model’ and Table 3.1). The SSM was fitted in R (version 3.5.1, R Core Team, 2018) using the software JAGS (Plummer, 2013) and the R packages *rjags* (Plummer, 2016) and *bsam* (Jonsen et al., 2015). Where a gap of >1 day existed in the satellite data transmission, the individual track was split and ran as segments to avoid interpolating over long periods of time with no data. Two Markov chain Monte Carlo (MCMC) chains were run in parallel, each for a total of 200,000 simulations. The first 100,000 samples were discarded as a ’burn-in’, and the remaining samples were thinned, retaining every 100th sample to reduce autocorrelation. The final 2,000 samples were used to compute the posterior distribution of the model parameter estimates: the mean turning angles, and movement persistence (i.e. the autocorrelation in speed and direction). The behavioural mode estimate (*b*), ranging between 1 and 2, was inferred from the means of the MCMC samples. A behavioural mode close to 1 (*b* <1.25) indicates transiting behaviour, which is persistent and highly directional movement with low turning angles (near 0°). Animals are expected to be in transiting mode during migration or when traveling between favourable locations (e.g. prey patches). A behavioural mode close to 2 (*b* >1.75) indicates area-restricted search (ARS) behaviour, a more variable movement with large turning angles (near 180°) and increased rate of turning. ARS is generally considered to be indicative of foraging, resting or breeding behaviour (e.g. Weinstein et al., 2017; Andrews-Goff et al., 2018). Locations with a mean *b* estimate between 1.25 and 1.75 were treated as 'uncertain'.

3.2.3. Explanatory variables for statistical model

We used both static and dynamic variables estimated at each state-space modelled location as explanatory variables to identify those that had most effect on the whales' behavioural mode (specifically the occurrence of ARS-foraging). We selected environmental variables which, based on prior knowledge, are likely to be biologically relevant (e.g. Friedlaender et al., 2011; Bombosch et al., 2014; Trudelle et al., 2016; Andrews-Goff et al., 2018; Table 3.1), and that were available for the entire spatial extent of location data.

Daily sea ice concentration data were obtained from the National Snow and Ice Data Center (NSIDC, https://nsidc.org/data). Distance to the ice edge was calculated from the daily ice concentration as the minimum distance between whale locations and the 15% sea ice concentration contour (e.g. Gloersen et al., 1993; Stammerjohn & Smith, 1997). One month and two-month lags were calculated as the distance of each SSM-estimated whale location to where the ice edge was one month and two months prior. It takes approximately one to two months after ice melt for productivity to peak in the marginal ice zone (Lehodey et al., 1998; Arrigo et al., 2008; Dalpadado et al., 2014). Altimeter derived daily sea surface heights (SSH) and daily sea surface current velocity data were obtained using E.U. Copernicus Marine Service Information (http://marine.copernicus.eu). SSH and sea surface current velocity gradients can be used to trace the locations of the Antarctic Circumpolar Current fronts, and therefore by using these variables we could account for possible interactions with the fronts (e.g. Sokolov & Rintoul, 2009). Sea surface current velocity was log transformed prior to analysis. Data on sea ice, SSH, and sea surface current velocity were obtained through the Australian Antarctic Data Centre and extracted using the R package *raadtools* (Sumner, 2016a).

Bathymetry was obtained from the International Bathymetric Chart of the Southern Ocean (IBCSO) digital bathymetric model of the circum-Antarctic waters (Arndt et al., 2013). IBCSO is a regional mapping project of the General Bathymetric Chart of the Oceans (GEBCO) and the digital bathymetric model is publicly available (www.ibcso.org). Slope was derived from the IBCSO digital bathymetric model using the '*slope'* tool in ArcGIS (version 10.5, Esri, Redlands, CA, USA) and was log transformed prior to analysis.

Month for each point was obtained from the SSM estimated locations. We chose to include month as a continuous variable in the model. Therefore, November, the first month for which there were data within the feeding grounds, was labelled '0' (followed by December = 1 through to June = 7) in order to set November as the baseline and to maintain chronological order.

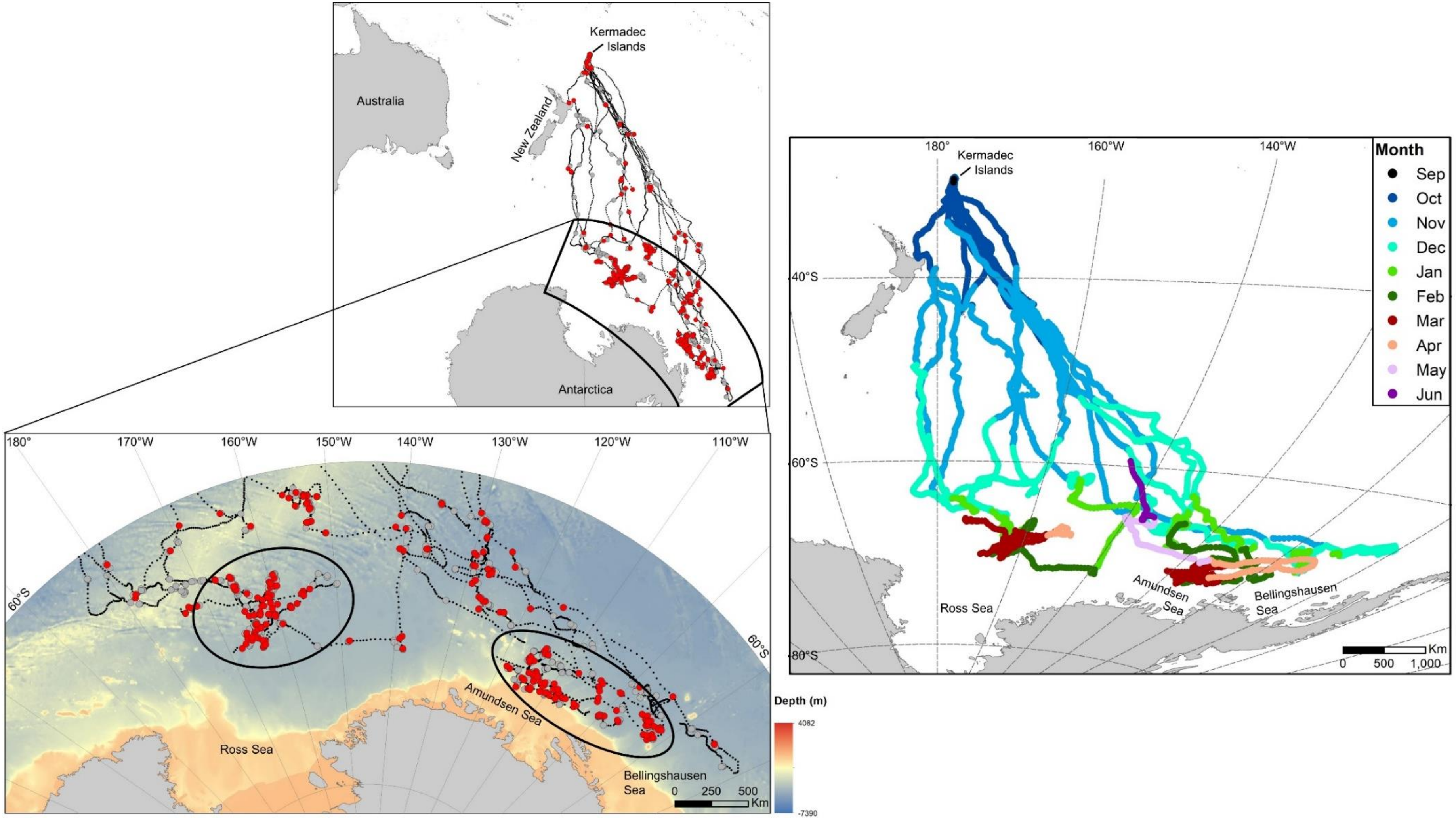

Figure 3.1 Migration pathways for 18 Oceania humpback whales satellite-tagged at the Kermadec Islands, New Zealand. Left column: State-space model estimated behavioural states: red dot = area restricted search (ARS; inferred foraging); black dot = inferred transit; grey dot = uncertain behavioural mode. Bottom left: Tracks of 14 whales whose tags transmitted on their Southern Ocean feeding grounds with circles denoting the approximate locations of the two key foraging grounds. The background colour scale indicates the bathymetric depth (derived from the International Bathymetric Chart of the Southern Ocean (IBCSO) digital bathymetric model of the circum-Antarctic waters). Right column: Satellite tracks colour coded by month.

Table 3.1 The unit of measure, source and resolution of the environmental predictor variables used to construct the species distribution models.

Variable		Definition and unit	Source	Resolution	
				Spatial	Temporal
Dynamic					
	Ice concentration (ice conc)	Percentage of ocean area covered by sea ice	National Snow and Ice Data Center (NSIDC)	25 x 25km	Daily
	Distance to ice edge (dist ice)	Distance of whale location to ice edge (15% ice concentration; km) on the same day	Derived from ice concentration	25 x 25km	Daily
	Distance to ice edge – 1-month lag (dist ice lag 1)	Distance of whale location to where the ice edge was 1 month prior	Derived from ice concentration	25 x 25km	Daily
	Distance to ice edge – 2-month lag (dist ice lag 2)	Distance of whale location to where the ice edge was 2 months prior	Derived from ice concentration	25 x 25km	Daily
	Sea surface height (SSH)	Sea surface height (m)	E.U. Copernicus Marine Service Information (CMEMS)	0.25 x 0.25°	Daily
	Sea surface current velocity (current)	Surface current velocity (m/s)	Derived from SSH	0.25 x 0.25°	Daily
Static					
	Bathymetry (bathy)	Depth (m)	International Bathymetric Chart of the Southern Ocean (IBCSO)	500 x 500m	
	Slope	Topographic gradient (degrees)	Derived from bathymetry	500 x 500m	
Other					
	Month	Month	SSM estimated locations		
	Region	Ross Sea or Amundsen and Bellingshausen Seas (cut-off at 130°W)	SSM estimated locations		

Prior analysis of the satellite tags had revealed that the whales diverged to two broad feeding regions (Riekkola et al., 2018 - Chapter 2). To make comparisons between these feeding areas, each location was assigned a 'region' based on whether it occurred west (Ross Sea) or east (Amundsen and Bellingshausen Seas) of the 130°W meridian (Figure 3.1). Studies have identified regional trends in the Antarctic sea ice variability, with increasing sea ice extent occurring in the Ross Sea region, and contrasting decrease in sea ice extent occurring in the Amundsen and Bellingshausen Seas region (e.g. Zwally et al., 2002; Turner et al., 2009). Future ocean and sea-ice changes are also projected to affect the growth rates of krill (the whales' main prey), with modelled high potential growth rates in Ross Sea, and low or negative potential growth rates in the Amundsen and Bellingshausen Seas (Murphy et al., 2017).

3.2.4. Environmental drivers of behaviour

To assess the influence of the explanatory variables on the SSM estimated behavioural modes, we fitted a series of linear mixed-effect models (LMMs) by maximum likelihood (ML) using the R software package *nlme* (Pinheiro et al., 2018). Similar to previous studies, we adjusted the behavioural mode (*b*) to range between 0 and 1 (by subtracting 1 from each value), after which the variable (continuous) was logit transformed (O'Toole et al., 2015; Cerchio et al., 2016). We dealt with sample proportions equal to exactly zero or one by adding the smallest non-zero proportion (ε) to the numerator and denominator of the logit function (i.e. $\log(y+\varepsilon\ /1\text{-}y+\varepsilon)$) as per Warton & Hui (2011). Individual whales (i.e. unique tag numbers/PTTs) were fitted as a random effect to account for individual variation, and a first order AR(1) autocorrelation structure for each individual whale was assumed. We first built LMMs with the full data set using region as a factorial variable, and then split the data to build region specific models.

The remotely sensed variables SSH and sea surface current speed included missing values ($n = 31$ and $n = 35$ respectively, representing 0.9% of the data), most likely due to sea ice coverage. To maintain the same number of observations between models, the rows including missing values were removed from the data set prior to model fitting. The variables sea surface current velocity and slope were log transformed prior to analysis. A quadratic term was included for month and the different 'distance to ice edge' candidate variables following examination of the relationships visually. All continuous variables were tested for pairwise correlation (Appendix D Figure D.1). SSH and log transformed sea surface current velocity had a Spearman correlation of 0.66. All other variables showed a Spearman correlation of ≤ 0.5.

As the different 'distance to ice edge' candidate variables represent the same environmental process, we included each of these terms sequentially during the model building (Table 3.2). Several model combinations of the different main effects and various interaction terms were run (Table 3.2). For model selection we explored both backward selection following Zuur et al. (2009; starting with a full model with all explanatory variables included, dropping individual variables one by one until all remaining variables are significant) and automated model selection (function *dredge* in R package *MuMIn*; Bartoń, 2018) to check for all possible variable combinations. We used the Akaike Information Criterion (AIC) to select the most parsimonious (lowest AIC value) model as the criterion penalises for the use of more variables (Burnham & Anderson, 2002; Burnham et al., 2011). The best model based on AIC was then run using restricted maximum likelihood (REML) to obtain the final parameter estimates (as per Zuur et al., 2009). The normality of residuals was checked graphically.

Table 3.2 Model selection results of the best linear mixed-effect models to explain the effects of different variables on humpback whale behavioural mode (*b*).

Variables	K	AIC	ΔAIC
Comparison of different ice distance variables			
Month + Month^2 + Region + dist ice lag 2 + dist ice lag 2^2 + Ice conc + SSH + bathy + slope(log)	13	18471.5	
Month + Month^2 + Region + dist ice lag 1+ dist ice lag 1^2+ Ice conc + SSH + bathy + slope(log)	13	18475.2	3.7
Month + Month^2 + Region + dist ice + dist ice^2 + Ice conc + SSH + bathy + slope(log)	13	18475.6	4.1
Comparison of different interaction terms			
All models have the same base: Month + Month^2 + Region + dist ice lag 2 + dist ice lag 2^2 + Ice conc + SSH + bathy + slope(log)			
+ Region*Month + Region*Month^2	15	18449.9	
+ Region*SSH	14	18468.9	19.0
+ Region* dist ice lag 2 + Region* dist ice lag 2^2	15	18471.2	21.3
Reduced version of the best model			
Month + Month^2 + Region + dist ice lag 2 + dist ice lag 2^2 + SSH + Region*Month + Region*Month^2	12	18447.5	

All models include the individual whale (unique tag number, PTT) fitted as a random effect. For each candidate model we report the Akaike's Information Criterion (AIC) and the change in AIC (ΔAIC) compared to the best model of each scenario. K = number of parameters. The best overall model is bolded.

3.3. Results

3.3.1. Whale movement and behaviour

Out of 25 tags deployed, 18 transmitted sufficient data for the SSM analysis (Table 3.3). This included five females without calves, six females with calves, five males and two individuals of unknown sex (PTT102211 had no tissue sample; molecular sex identification for PTT112722 was unsuccessful). Ten tags had data gaps of >1 day (range = 2-76 d), excluding those tags that did not begin transmission straight after deployment. The average number of location fixes per day received from a tag was 22 (range = 10-42).

The tags of 14 individual humpback whales transmitted data within the feeding grounds south of 60°S, covering a temporal period from November 2015 to June 2016 and a spatial range from 175°E to 80°W. The number of active tags transmitting data varied between months (range = 1-14; Table 3.4). The SSM distinguished well between the two behavioural states (Appendix E Table E.1) and classified 6.3% of locations as ARS-foraging, and 79.3% of locations as transiting behaviour, with the remaining 14.4% classified as uncertain (Figure 3.1). The average behavioural mode (i.e. likelihood of ARS-foraging behaviour) increased as the feeding season progressed, peaking in March (February-March for whales on the Ross Sea region only; Figure 3.2a). Overall, the whales on the Ross Sea region were consistently farther away from the continental shelf break (Figure 3.1) and from the ice edge than the whales in the Amundsen and Bellingshausen Seas region (Figure 3.2b). In general, the whales' distance from the ice edge increased between December and January (December-February for Ross Sea whales) and decreased between January and April (February-May for Ross Sea whales; Figure 3.2b).

3.3.2. Environmental drivers of behaviour

Out of the highly correlated variables SSH was identified as being a more important predictor than log transformed sea surface current speed and was therefore kept in the model. Examination of the different 'distance to ice edge' scenarios resulted in two-month lag being identified as the most relevant, and out of several trials with different interaction terms interaction between month (representing time) and region was found to be most significant (Table 3.2). The most parsimonious model identified month, two-month lag in the distance to the ice edge, SSH and the interaction between region and month as important predictors of the behavioural state of humpback whales within their Southern Ocean feeding grounds (Table 3.2, Table 3.5). Non-linear relationships indicated that the whales were more likely to exhibit ARS-foraging behaviour during the middle of the summer feeding season, and near where the marginal ice-edge had been two months prior. Humpback whales were also more likely to exhibit ARS-foraging behaviour at lower SSH values, and there was a significant interaction between region and month (Table 3.5, Figure 3.3). The model provided some indication of possible differences between regions. The variable 'region' was marginally significant (F-test $p = 0.06$), although the coefficient estimate was not significantly different from zero (t-test $p = 0.36$). Dredge automated model selection identified region to be a significant variable in 70% of 1,664 model variations.

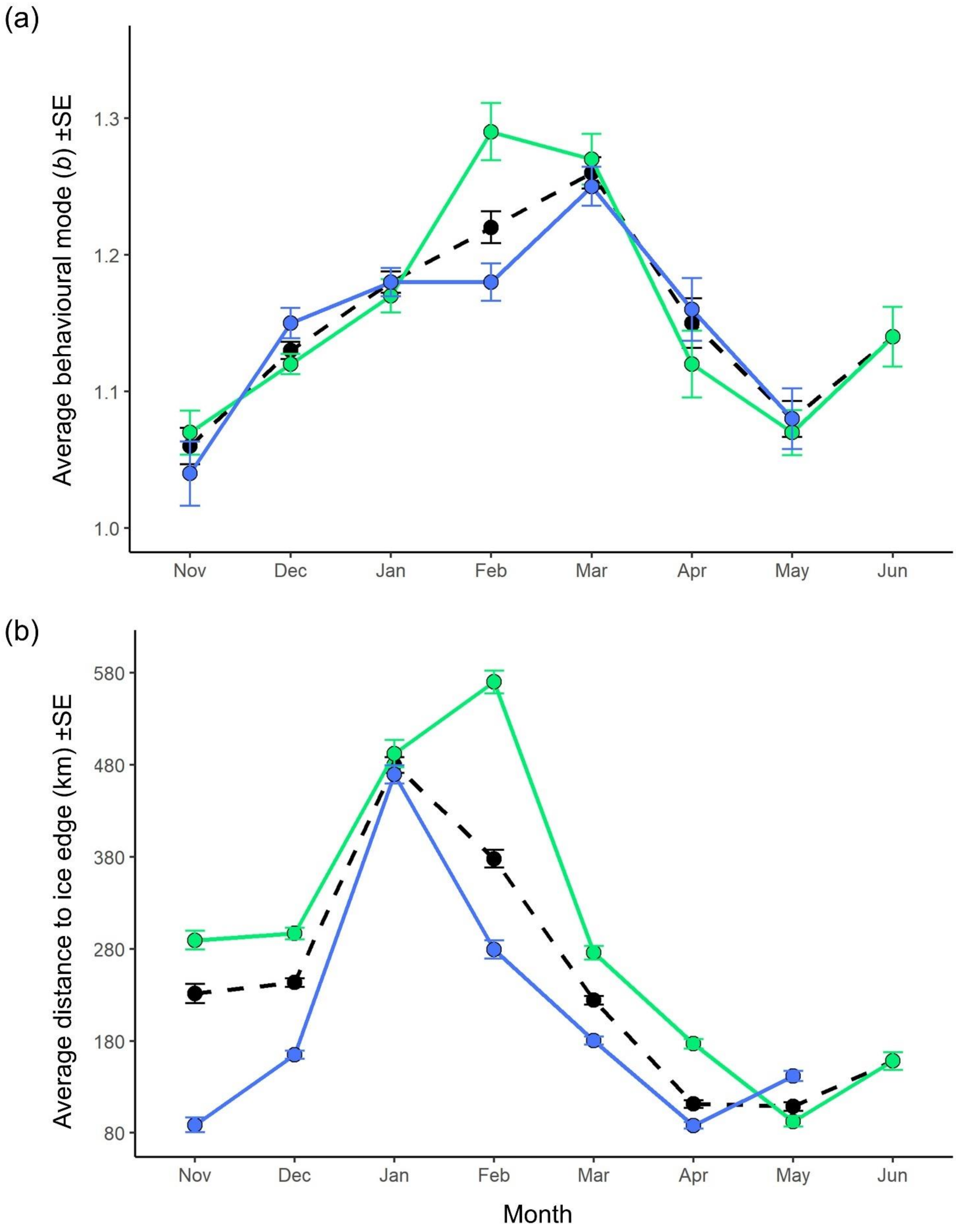

Figure 3.2 a) Average behavioural mode (*b*) by month. Values closer to 1 indicate transiting behaviour and values closer to 2 indicate ARS-foraging behaviour, and b) distance to ice edge (km; all locations) by month. Black dashed = all whales, green = Ross Sea, blue = Amundsen & Bellingshausen Seas.

Table 3.3 Summary of satellite tag deployments and tracking data for 18 humpback whales used in the state-space model.

PTT	Transmitted south of 60°S	Sex (*=with calf)	Deployment date	First location	Last location	Transmitting days	Data gaps (d_1,d_2,d_n)	No. of locations	Mean no. locs/day (± SE; range)	% Argos location class							Mean time (h) between locs (± SE)
										3	2	1	0	A	B	Z	
88727	Yes	F*	08-Oct-15	08-Oct-15	14-Jan-16	99		2,665	27 (±1.3; 1-64)	3.3	6.1	7.0	2.0	16.3	64.9	0.3	0.9 (±0.02)
102211	Yes	U	10-Oct-15	11-Oct-15	19-Dec-15	57	14	594	10 (±0.9; 1-26)	0.2	0.2	0.0	0.2	4.7	94.1	0.7	2.8 (±0.57)
102218	Yes	M	10-Oct-15	11-Oct-15	20-Jun-16	249	2,4	8,659	33 (±1.1; 1-85)	4.1	10.1	12.2	3.8	15.1	54.7	0.0	0.7 (±0.02)
111866	Yes	F	04-Oct-15	06-Nov-15	15-Mar-16	130	2	3,820	29 (±1.1; 4-65)	2.1	4.3	5.7	2.2	13.5	72.1	0.1	0.8 (±0.02)
112722	Yes	U	10-Oct-15	11-Oct-15	03-Apr-16	174	2,2	6,390	37 (±1.0; 3-71)	12.8	17.0	11.4	2.5	18.9	37.4	0.0	0.7 (±0.02)
131173	Yes	M	30-Sep-15	30-Sep-15	08-Apr-16	184	8,2	5,925	32 (±1.1; 2-70)	2.9	7.9	11.1	3.9	16.7	57.5	0.1	0.8 (±0.04)
131175	Yes	M	04-Oct-15	04-Oct-15	18-Jan-16	97	11	2,077	21 (±1.1; 4-47)	0.7	1.7	1.7	1.1	11.2	83.4	0.2	1.2 (±0.13)
131178	Yes	F*	08-Oct-15	09-Oct-15	17-Jan-16	101		2,167	21 (±1.1; 2-58)	0.8	1.7	4.7	1.6	14.4	76.7	0.2	1.1 (±0.03)
131179	Yes	M	02-Oct-15	07-Dec-15	22-Mar-16	84	23,2	1,785	21 (±0.9; 6-50)	0.3	0.6	1.6	0.3	6.2	90.9	0.2	1.4 (±0.30)
131182	Yes	F	01-Oct-15	02-Oct-15	02-Apr-16	150	30,5,2	6,264	42 (±1.2; 11-90)	10.0	27.9	22.0	5.8	12.1	22.1	0.0	0.7 (±0.12)
131185	Yes	F	02-Oct-15	27-Nov-15	06-Jan-16	41		886	22 (±1.4; 1-44)	0.1	0.3	1.0	0.2	6.2	91.6	0.5	1.1 (±0.06)
131187	Yes	F	30-Sep-15	01-Oct-15	02-Jan-16	94		1,876	20 (±0.9; 6-51)	1.4	1.6	2.6	0.9	10.5	82.9	0.0	1.2 (±0.04)
131188	Yes	F*	29-Sep-15	30-Sep-15	11-Dec-15	73		1,310	18 (±0.7; 8-37)	1.0	2.8	2.3	0.8	13.4	79.7	0.0	1.3 (±0.04)
131190	Yes	F*	08-Oct-15	08-Oct-15	20-Mar-16	90	76	2,334	26 (±0.9; 1-45)	5.8	13.5	13.4	4.4	18.4	44.5	0.0	1.7 (±0.78)
111871	No	F	08-Oct-15	09-Oct-15	04-Nov-15	26	2	308	12 (±1.1; 1-20)	1.9	4.5	4.2	1.0	14.0	74.4	0.0	2.1 (±0.20)
112718	No	M	05-Oct-15	05-Oct-15	13-Nov-15	40		562	14 (±0.6; 2-21)	2.1	3.4	3.4	0.9	14.4	75.4	0.4	1.7 (±0.08)
112721	No	F*	09-Oct-15	10-Nov-15	28-Nov-15	19		224	12 (±1.1; 5-24)	0.4	1.3	1.3	0.0	6.3	90.2	0.4	2.0 (±0.16)
112723	No	F*	06-Oct-15	07-Oct-15	18-Oct-15	12		204	17 (±1.7; 2-24)	2.5	2.9	4.9	2.9	18.1	68.6	0.0	1.3 (±0.08)

All tags were deployed at Raoul Island (Kermadec Islands, New Zealand). PTT = unique tag number. Only whales whose tags transmitted data south of 60°S were used in the linear mixed-effect model.

F = female, M = male, U = unknown sex, and * denotes animals that had a calf. All dates are in UTC. Transmitting days = number of days when one or more locations were received.

Data gaps = any gaps in data transmission >1 day in length, data gap length is in days, multiple data gaps for the same animal are separated with a comma.

Percent of locations belonging to each of the seven Argos service provider assigned location classes. Location classes in a descending order of accuracy: 3, 2, 1, 0, A, B and Z. See Argos user’s manual, 2016.

Table 3.4 Number of unique tags transmitting in any given month, and the number of state-space modelled data points (in brackets) within the feeding grounds (south of 60°S).

Year	Month	Ross Sea	A&B Seas	Total
2015				
	November	4*(119)	2*(48)	5 (167)
	December	11†(717)	6†(487)	14 (1204)
2016				
	January	5‡(373)	7‡(453)	11 (826)
	February	2 (187)	4 (365)	6 (552)
	March	3 (323)	4 (378)	7 (701)
	April	2 (45)	2 (127)	4 (172)
	May	1§(80)	1§ (39)	1 (119)
	June	1 (77)	0 (0)	1 (77)

In total, the tags of 14 individual whales transmitted data within the feeding grounds.

A&B seas = Amundsen and Bellingshausen Seas.

* PTT131182 travels through both regions during the month of November

† PTT102218, PTT131175 and PTT131187 travel through both regions during the month of December

‡ PTT131175 travels through both regions during the month of January

§ PTT102218 travels through both regions during the month of May

Table 3.5 Results of the best linear mixed-effect model, with logit transformed behavioural state (*b*) as a response variable and individual whales as a random effect. Higher *b*-values indicate an increasing likelihood of whales exhibiting ARS-foraging behaviour.

Parameter	Estimate	SE	DF	t-value	p-value
Intercept	-9.49	1.10	3796	-8.61	**<0.001**
Region_Ross Sea	-0.55	0.58	3796	-0.96	0.34
Month	1.91	0.38	3796	4.99	**<0.001**
Month^2	-0.35	0.06	3796	-5.40	**<0.001**
dist ice lag 2	0.00	0.00	3796	0.26	0.80
dist ice lag 2^2	-0.00	0.00	3796	-3.55	**<0.001**
SSH	-4.92	1.08	3796	-4.57	**<0.001**
Region_Ross Sea*Month	-0.93	0.48	3796	-1.95	0.05
Region_Ross Sea*Month^2	0.24	0.08	3796	3.16	**<0.01**

Estimates are in log-odds scale. During model selection all models were fitted using maximum likelihood for comparing models with different fixed effects. The best model was then fitted with restricted maximum likelihood to obtain final parameter estimates. Variables with a significant parameter estimate (<0.05) are in bold.

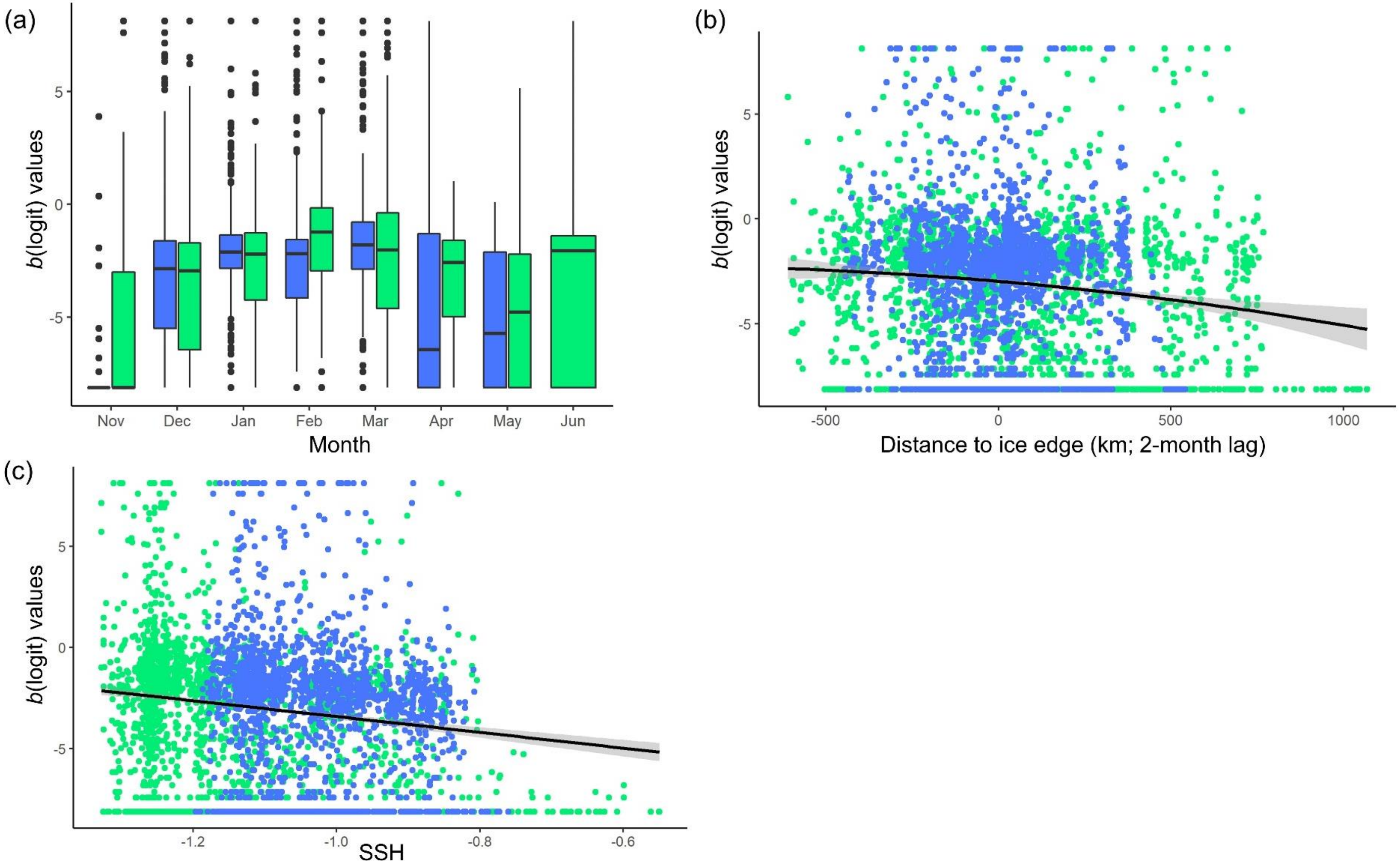

Figure 3.3 The relationship between significant explanatory variables a) month, b) distance to the ice edge (2-month lag) and c) SSH (sea surface height) and the logit transformed behavioural mode (*b*). Green = Ross Sea, Blue = Amundsen and Bellingshausen Seas. Higher predicted *b*(logit) values indicate an increasing likelihood of whales exhibiting ARS-foraging behaviour. A negative value for 'distance to ice edge' indicates that the whale has moved past the point where the ice edge was two months prior. Simplified univariate regression lines from the mixed-effect model analysis (without random effects and autocorrelation structure) were added to b) and c) to highlight the overall trend in the data for the sample population.

3.4. Discussion

Humpback whales foraging in the Southern Ocean changed their ranging behaviour and habitat use patterns throughout the summer feeding season suggesting that behavioural plasticity is important for this large predator. The changes were related to the environmental features of the different habitats, in particular to an important lag effect in the ice edge dynamics, and consequently the whales ended up utilising these areas very differently. Similar to other long-distance migrants that move between critical habitats for different life functions (Both & Visser, 2001; Le Corre et al., 2017), these whales time their arrival at their feeding grounds to exploit the habitat optimally without knowing the precise habitat conditions when beginning their migration ~7,000km north. The large-scale sensitivity to environmental cues enabling prediction of conditions in another geographic location is key to the success of migratory animals, e.g. barn swallow (*Hirundo rustica* L.; Balbontín et al., 2009), caribou (Le Corre et al., 2017).

3.4.1. Characterising whale movement and behaviour on the Southern Ocean feeding grounds

The SSM results revealed two important resource sites for Oceania humpback whale foraging; one within the Amundsen and Bellingshausen Seas and one north of the Ross Sea, ~2,000 km west (Figure 3.1). The majority of ARS-foraging locations for the whales within the Amundsen and Bellingshausen Seas occurred near the continental shelf break (within ~200km) where high densities of krill are expected to be found due to life history related movement (e.g. Pauly et al., 2000; Nicol, 2006; Davis et al., 2017), as well as near the ice edge (~210 km on average) where ice melt stimulates primary production which in turn supports elevated concentrations of higher trophic level organisms (e.g. Brierley et al., 2002; Nicol, 2006; Meyer et al., 2017). In contrast, the main aggregation of ARS-foraging locations north of the Ross Sea did not occur near the shelf break (>500 km away; Figure 3.1) nor the ice edge (~370 km on average; Figure 3.2b). However, the ARS-foraging locations of the Ross Sea whales occurred in a reported hotspot, with increased chlorophyll *a* as an indicator of primary production (Schine et al., 2016). The observed differences between the foraging regions suggest that humpback whales utilise different environmental cues, with some cues being of greater importance for whales in one area than the other.

Although we were not able to confirm ARS behaviour identified by our SSM as foraging, both previous studies and the general knowledge about humpback whale behaviour south of 60°S suggest that ARS behaviour identified by the SSM is largely foraging (Chittleborough. 1965; Weinstein et al., 2017; Andrews-Goff et al., 2018). With this assumption in mind, the high overall amount of transiting behaviour south of 60°S might serve as an indicator of prey distribution, whereby whales may have to move quite long distances between prey patches. For instance, the Amundsen and Bellingshausen Seas reportedly have generally low chlorophyll *a* concentration with only isolated pockets of high productivity (e.g. Constable et al., 2003; Stambler, 2003). This could result in smaller prey aggregations that are highly spread out, increasing the whales' need to transit between foraging patches.

Humpback whales in the Northern Hemisphere have been shown to exhibit strong maternally inherited feeding ground fidelity (Palsbøll et al., 1995; Stevick et al., 2006; Baker et al., 2013). In contrast, humpback whales from discrete Oceania breeding grounds do not show such clear patterns of feeding ground fidelity (Rosenbaum et al., 2017). Additionally, as satellite tagged Oceania mothers with calves migrated to the Ross Sea and given that whales still also migrate to the Amundsen and Bellingshausen Seas (Riekkola et al., 2018-Chapter 2), these whales may not have maternally inherited feeding grounds. Knowing the approximate location of profitable foraging areas and consistently returning to them may increase foraging success and individual fitness, which could be highly advantageous for the slowly recovering Oceania population. Memory of long-term average conditions may be more important for cetaceans than previously thought (Abrahms et al., 2019), and some marine species in the Southern Ocean have been found to consistently return to foraging areas that may have arisen as a consequence of predictable oceanographic conditions (Weimerskirch, 2007; McIntyre et al., 2017; Sztukowski et al., 2018). Data on the Oceania whales across multiple years could help identify persistent patterns in the whales' behaviour to determine the role of memory, and assess the stability of the two feeding areas over time, especially given the predicted future changes in ice dynamics due to climate change (de la Mare, 1998; Turner et al., 2009). Changes in global oceanographic events are becoming more common, for example they are likely to have disrupted the long-term feeding ground fidelity of humpback whales in southern Alaska (Neilson & Gabriele, 2019).

3.4.2. Environmental effects on whale movement and behaviour on the Southern Ocean feeding grounds

Because large baleen whales have very high energetic demands (Lockyer, 1981), we expect that humpback whale behaviour on the feeding grounds is largely driven by the distribution and availability of krill; especially given they effectively undertake all foraging during the ~five months they spend in the Southern Ocean. Previous studies have linked the behaviour and distribution of humpback whales to krill abundance and distribution (e.g. Friedlaender et al., 2006, 2011, 2013; Curtice et al., 2015). However, as obtaining reliable data on krill abundance and distribution for the large temporal and spatial extent covered by our satellite telemetry data is all but impossible, we examined how the behaviour of these whales was affected by more easily recorded, remotely sensed environmental parameters. In the absence of easily obtained prey field data understanding how marine top predators, such as whales, pinnipeds and seabirds, respond to more easily recorded variables (which act as proxies for prey availability) is often the only approach available (Raymond et al., 2015; Reisinger et al., 2018).

The best LMM indicated that the inferred behavioural states of humpback whales within the Southern Ocean feeding grounds were most affected by timing within the feeding season (month), where the marginal ice edge was two months prior, SSH, and to some extent the region (Table 3.5, Figure 3.3). All these variables are thought to be linked to krill availability and distribution associated with local and regional scale oceanographic features. By targeting and favouring areas with environmental conditions that are associated with increased prey availability, large marine predators, such as humpback whales, can improve their foraging opportunities (Heerah et al., 2017). In the absence of prior knowledge regarding potential prey locations, whales might use environmental cues to place themselves in likely profitable foraging areas.

As the feeding season progressed the likelihood of adopting ARS-foraging behaviour increased, peaking in February-March (Figure 3.2a). This was expected as the whales would be finding sufficient prey to feed on after several months of fasting, and as productivity should increase following the spring/summer ice melt (Lehodey et al., 1998; Arrigo et al., 2008; Dalpadado et al., 2014). After the peak, the likelihood of ARS-foraging behaviour decreased likely in response to productivity declining in late summer-autumn months, however data for the last two months came from only one whale (Table 3.4).

The results indicated that foraging behaviour was more likely to occur near where the ice edge was two months prior. As the sea ice melts, the ice-free waters promote phytoplankton blooms which in turn trigger grazers such as krill to aggregate at the sea ice edge (Nicol, 2006; Arrigo et al., 2008). This link between humpback whales and the ice indicates that the whales do not actively track the ice edge itself, but instead the productivity that occurs following ice melt (i.e. after a time lag). Organisms do not always respond immediately to changes in the physical or biotic environment. Animal population trends respond to fluctuations in the environment after appropriate time lags (e.g. Baker et al., 2007; Walker et al., 2013), however distribution and foraging behaviour can also show lagged responses to environmental conditions (Pinaud & Weimerskirch, 2005). Our findings therefore support the importance of including time-lagged variables when modelling the relationships between animals and their environment, which is applicable to both aquatic and terrestrial species across a broad array of ecosystems.

The humpback whales were also more likely to exhibit ARS-foraging behaviour at lower SSH values. Lower (more negative) SSH values are linked to meso-scale eddies, which stimulate productivity near the surface through vertical mixing of deep nutrient rich waters, and trap aggregations of buoyant and weekly swimming plankton and fish (Olson & Backus, 1985; Nel et al., 2001; Hyrenbach et al., 2006). However, whether the whales can detect changes in SSH and relate them to krill presence is unknown. As noted above, areas with lower SSH are generally linked to productivity and prey, and SSH is therefore functioning as a proxy for prey in our model.

There was some evidence that the behavioural mode of the whales was affected by the feeding region they were in, and the interaction between region and month suggests that the whales behave differently in the different regions during different points of the season (Figure 3.2a). Animals are expected to strive to maximise foraging success while minimising the associated effort and costs (MacArthur & Pianka, 1966; Schoener, 1971). Predators foraging in complex and patchy environments should therefore adjust their movements and foraging behaviour according to prey availability (and density) to maximise foraging efficiency. They might for instance employ distinct foraging strategies in different habitats (Arthur et al., 2016). We expect that the observed regional foraging behaviours by the humpback whales are the result of region-specific decisions made in response to the dynamic characteristics of the environment in each habitat, suggesting that there is behavioural plasticity in this population. Many ecological studies have treated conspecific individuals as ecological equivalents, but the existence of intraspecific plasticity in foraging behaviour (in the form of dietary differences, variation in habitat use or foraging strategies for example) is widespread among taxonomic groups and can be ecologically important (Bolnick et al., 2003; Ceia & Ramos, 2015; McHuron et al., 2018). The predicted climate change induced spatial variability in factors that influence krill populations, such as sea ice characteristics and seasonal dynamics, are likely to result in region-specific responses in the whales' main prey (e.g. Constable et al., 2014), which might necessitate region-specific foraging strategies in the future.

In order to respond dynamically to sensory cues from the dynamic environment whales likely use multimodal sensory systems (Carroll et al., 2017; Torres, 2017). Additionally, species-habitat relationships are often scale dependent, and different environmental parameters may have a stronger influence on animals at different scales (Ballance et al., 2006; Redfern et al., 2006). For example, during long distance migration to the feeding grounds (thousands of kilometres) humpback whales, as well as other cetaceans, use large-scale oceanographic patterns and features to navigate (Horton et al., 2017; Torres, 2017). Once near or within the feeding grounds the whales are expected to change their movement to a smaller-scale prey search pattern, and will likely utilise different, finer-scale environmental cues (Ballance et al., 2006; Doniol-Valcroze et al., 2007; Torres, 2017; Kirchner et al., 2018). It is therefore important to use temporal and spatial scales that are appropriate for the main objectives of the analysis and relevant for the ecology of the target species (e.g. Ballance et al., 2006; Redfern et al., 2006; Fernandez et al., 2017). Unfortunately, the temporal and spatial scale used is often determined by the availability of the environmental data. We were not immune to this problem, yet we aimed to use resolutions closest to our modelled data to best capture the whales' behaviour patterns. Using different movement/behavioural modelling techniques (e.g. McClintock et al., 2015; McClintock & Michelot, 2018) it can be possible to further improve the accuracy of the animal locations. In our case, due to the low resolution of many of the environmental covariates (raster data), improving the whale location estimates would have likely resulted in us sampling from the same environmental raster cell. In studies covering a smaller study area and having higher quality environmental data increasing the accuracy of the animal locations would be more paramount. Despite some caveats, using the available remotely sensed data and spatial modelling techniques enabled us to uncover the behavioural patterns of these whales spread over 4,000 km across the Southern Ocean largely devoid of distinct land mass features, apart from the Antarctic continent. The whales' ability to detect and use environmental cues to locate patchily distributed prey in this vast ocean environment is remarkable and identifying the key variables for these animals will help us better understand their behaviour and how they might respond to changes in their environment.

In many animal taxa (including insects, birds and mammals) the decision to begin migrating from one critical habitat to another often occurs in response to environmental conditions, social cues or sexual hierarchy, and is highly affected by individual variation (Chittleborough, 1965; Gunnarsson et al., 2006; Balbontín et al., 2009; Jiang et al., 2011; Rivrud et al., 2016; Berdahl et al., 2017). Climate change has a variety of effects on the critical habitats of different animals, for example by altering the distribution and seasonal availability of food as well as the size of suitable breeding areas (Fitter & Fitter, 2002; Walther et al., 2002; Derville et al., 2019). If the timing of migration relies on endogenous cues that are not affected by climate change (compared to e.g. weather cues), the migration of such species will not advance even though they need to arrive earlier on their breeding or feeding grounds (Both & Visser, 2001). It is yet unclear whether climate change will influence whale arrival at the Southern Ocean feeding grounds, and whether this would have a positive or a negative effect on their fitness. Waiting for krill to become available could incur an energetic cost due to the wait time, yet the whales might adapt and prey switch to forage more on already available prey; this has been documented in different humpback whale populations (e.g. Weinrich et al., 1992; Fleming et al., 2016).

3.5. Conclusions

Here we used spatial modelling techniques to identify underlying behavioural states from movement data for a wide-ranging marine predator inhabiting a remote area and related those behaviours with environmental conditions. We identified two important Southern Ocean feeding areas for humpback whales and observed differences in behaviour, likely related to decisions made about the local environmental variation between the two adjacent habitats. Behavioural plasticity is critical to survive in environments that are unpredictable and changing (Stien et al., 2010; Wong & Candolin, 2015; Courbin et al., 2017). This could therefore be of advantage to whales in a changing Southern Ocean, especially as the two feeding areas are experiencing different responses to climate change; sea ice increase in the Ross Sea, sea ice retreat in the Amundsen and Bellingshausen Seas (e.g. Zwally et al., 2002; Turner et al., 2009) and regional differences in food web structure (e.g. Murphy et al., 2012; Constable et al., 2014). Environmental changes may therefore elicit different behavioural and demographic responses for populations inhabiting different, yet adjacent, regions of the Southern Ocean. Having whales of the same population being subject to different environmental conditions provides an opportunity to study changes in their distribution and behaviour within and between circum-Antarctic regions, which in turn can be used as indicators of change in the ecosystem (e.g. prey distribution) for all marine predators (Raymond et al., 2015). The phenomena of range shifts and behavioural adaptations in response to environmental change are currently better understood in the Northern Hemisphere where such events are more apparent (Both & Visser, 2001; Post et al., 2009).

Chapter 4

Estimating the energetic cost of long-distance migration in satellite tagged humpback whales

4.1. Introduction

The way in which animals allocate energy to different activities and behaviours has important implications for their fitness and population demography (Nathan et al., 2008; Morales et al., 2010). Migration has evolved among many different animal groups and is primarily a behavioural adaptation to spatiotemporal variation in resources, habitats, predation and competition (Alerstam et al., 2003; Dingle & Drake, 2007). Long-distance migrations are outstanding physical achievements and typically occur between geographically separated key habitats required for different life history stages and functions (Dingle & Drake, 2007).

Migration requires both time and energy (Alexander, 1998), hence there needs to be a balance between the benefits of moving (e.g. access to better habitats, increased food availability), and the costs associated with the migratory process (e.g. energetic cost of movement, risk of mortality; Alexander, 1998; Alestram et al., 2003). Migrants moving through different media use various modes of locomotion, either running, swimming or flying, each with their own associated energetic cost (Schmidt-Nielsen, 1972; Alexander, 1998). For same-sized animals swimming has the lowest cost of transport, three and ten times lower than for flying and running, respectively (Schmidt-Nielsen, 1972), and hence long-distance migrations should only be worthwhile for flyers and endothermic swimmers (Alexander, 1998; Alerstam et al., 2003). For example, the longest terrestrial migration, <2,000 km round trip by the caribou (*Rangifer tarandus*; Alerstam & Bäckman, 2018) pales in comparison to those reported for swimming (22,000 km round trip, gray whale, *Eschrichtius robustus*, Mate et al., 2015) and flying animals (81,000 km round trip, Arctic tern, *Sterna paradisaea*, Egevang et al., 2010).

A critical aspect of long-distance migration is the need to balance available energy reserves (Blem, 1980; Piersma & Jukema, 1990). Many animals therefore use different strategies to reduce their locomotory costs during migration. Aquatic animals such as eels, fish and sea turtles utilise currents and tidal stream transport

(Parker & McCleave, 1997; Lambardi et al., 2008) while flying animals such as birds take advantage of thermal updrafts and favourable air currents to save energy (Egevang et al., 2010; Bohrer et al., 2012). Another strategy to facilitate long-distance migration involves the use of stopover sites along the migration route to feed and refill energy stores (Alerstam et al., 2003; Sawyer & Kauffman, 2011). Since carrying large and heavy energy reserves, usually stored in the form of fat (Downer & Matthews, 1976; Jenni & Jenni-Eiermann, 1998), increases locomotion cost, the best strategy for minimising energy expenditure may be to travel as light as possible and to use all potential feeding sites along the migratory route (Alerstam et al., 2003). However, this is more relevant for smaller aerial and terrestrial migrants, as due to allometric scaling the large body size of some oceanic migrants, such as marine mammals, allows for greater fasting capabilities (Boyd, 2004). For time-minimising migrants on the other hand it may be better to by-pass poor quality stopover sites and only stop at those of high enough quality (Beekman et al., 2002). Insufficient access to feeding sites can exhaust the animals' energy reserves before migration is completed, or influence future reproductive success and survival (Newton, 2006; Braithwaite et al., 2015). Feeding during migration is therefore important for many bird species and terrestrial mammals, whereas due to the low cost of transport swimming migrants can go for a longer time without stopping to refuel (Newton, 2006; Sawyer & Kauffman, 2011; Alerstam & Bäckman, 2018).

There are two general strategies for meeting the energetic demands of reproduction: income and capital breeding (Jönsson, 1997; Stephens et al., 2009). While income breeders continue to feed throughout the reproductive period, capital breeders meet the cost of reproduction using previously accumulated endogenous or exogenous energy stores (Jönsson, 1997; Stephens et al., 2009). The capital breeding strategy generally involves periods of intensive feeding in habitats of temporarily abundant food resources, followed by periods of fasting in environments more suited for reproduction (Jönsson, 1997; Dingle & Drake, 2007). This spatial and temporal decoupling of feeding and breeding activities brings about the need to move between the two habitats. Capital breeders undertaking long-distance migrations between these key habitats must therefore have sufficient energy stores to cover the cost of migration as well as the cost of reproduction during the period of fasting. If the animals cannot replenish their energy stores during the breeding season or during migration, they may be susceptible to exhausting their energy reserves before reaching the feeding grounds (Jönsson, 1997; Braithwaite et al., 2015).

Obtaining direct measurements of energy requirements and expenditure for free-ranging migratory baleen whales is challenging due to their large size and fully aquatic lives, which prevents capture and studying them in laboratory settings (Williams & Noren, 2009; Goldbogen et al., 2013; Christiansen et al., 2018). Compared to sea birds and pinnipeds that periodically come ashore, data on the metabolic rates of fully aquatic large whales are limited as most standard methods (e.g. caloric intake, respirometry, doubly labelled water) generally used for marine species in the field or in captive settings cannot be applied (Fortune et al., 2013; Christiansen et al., 2018). As an alternative tactic, mathematical and bioenergetic models can be used to estimate energy needs and to quantitatively assess how animals acquire and allocate their energy resources (Fortune et al., 2013; Villegas-Amtmann et al., 2015). The developments made in satellite tracking technology in recent years coupled with the discipline of movement ecology provides further opportunity for studying physiological processes and energy use and acquisition of hard to access long-distance migrants (Mandel et al., 2008; Nathan et al., 2008; Dodge et al., 2014).

Humpback whales (*Megaptera novaeangliae*), like other baleen whales (mysticetes), are capital breeders that migrate annually between their breeding grounds in the tropics and feeding grounds in higher latitudes (Stern & Friedlaender, 2018). During the summer feeding season surplus energy is stored mainly as fat tissue in the blubber (Lockyer et al., 1985; Lockyer, 1986). Many whale species rely on these energy stores for six to eight months out of the year to cover the cost of their long-distance migration as well as that of breeding and lactation (Dawbin, 1966; Brodie, 1975). Maternal body condition has been linked to reproductive success in migratory baleen whales, with females in poorer condition and insufficient energy stores sometimes foregoing reproduction during years of low food availability (Lockyer, 2007; Seyboth et al., 2016). How the whales balance their energy reserves during the migratory cycle may therefore affect individual survival, reproductive success and ultimately the population dynamics.

Commercial whaling during the 20th century heavily exploited all Southern Hemisphere humpback stocks (Clapham & Ivashchenko, 2009; Ivashchenko & Clapham, 2014) and the Oceania humpback whales, comprising whales from multiple breeding ground sub-populations from the South Pacific Islands (Figure 4.1), are estimated to be <50% of pre-exploitation numbers (Childerhouse et al., 2008; Constantine et al., 2012; IWC, 2015). Furthermore, this population is recovering slower than the neighbouring east Australian population (IWC, 2015) which could be indicative of differences in energy reserves and/or use between these populations. A 2015-2016 satellite tracking study has revealed the migratory paths for a sample of Oceania humpback whales that migrate to their Southern Ocean feeding grounds (Riekkola et al., 2018 - Chapter 2; Figure 4.1). The Oceania whales migrating to the Amundsen and Bellingshausen Seas have a longer migratory distance than satellite tracked east Australian whales (Andrews-Goff et al. 2018; Figure 4.1).

The aim of this study was to build a model to estimate the cost of transport for a long-distance marine migrant across different migration routes and distances. We use satellite tracking data of humpback whales to investigate the relative difference in the energetic costs of whales migrating to different Southern Ocean feeding grounds. We compare two cohorts of whales from the same population (Oceania) with two different routes and destinations, as well as between a third migratory cohort from a neighbouring population (east Australia). The neighbouring humpback whale populations of Oceania and east Australia have different migratory routes and behaviours, and they are recovering from the effects of whaling at very different rates. We therefore examine whether migratory energetics play a role in the differential rates of population recovery. In addition, studying the physiology of these animals in the field is highly difficult, yet necessary for accurate conservation management. Therefore, they represent an ideal system for examining the cost of transport and migration energetics by using a mathematical model, which can be applied to other migrating organisms.

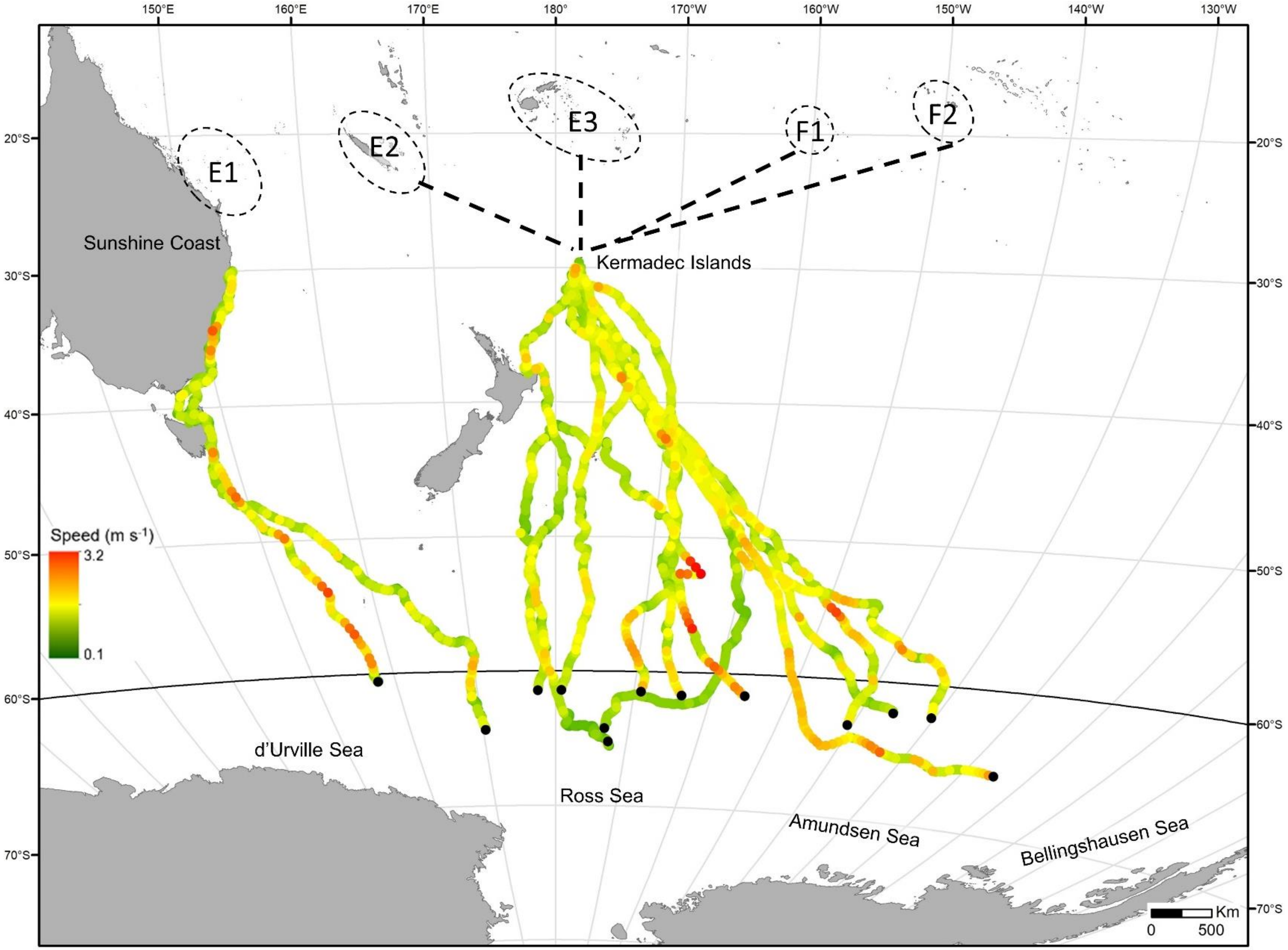

Figure 4.1 Satellite tracks with speed (m s^{-1}) used to calculate the energetic cost of migration for three cohorts of humpback whales: d'Urville Sea (n = 2), Ross Sea (n = 7), Amundsen and Bellingshausen Seas (n = 4). Black dots denote the end of migration phase for each track. Dashed circles denote International Whaling Commission designated population breeding grounds; the Oceania population comprises breeding grounds E2, E3, F1 and F2. Dashed lines from Oceania breeding grounds denote straight-line paths to the Kermadec Islands tagging location. Southern Ocean is denoted by black line at 60°S.

4.2. Methods

4.2.1. Satellite tag deployment and hierarchical state-space model

4.2.1.1 Oceania humpback whale data

We used existing humpback whale telemetry data reported in Riekkola et al. (2018 - Chapter 2). Adult humpback whales (n = 25) were fitted with location-only SPOT-5 satellite transmitters (Wildlife Computers, Redmond, USA) at the Kermadec Islands (Figure 4.1), New Zealand, between September and October 2015. Observed locations were calculated by the Argos System using the Doppler Effect on transmission frequency when multiple messages from a tag were received by a satellite. Further details on the study site, deployment techniques and duty cycles are reported in Riekkola et al. (2018 - Chapter 2).

We used the hierarchical version of a Bayesian state-space model (SSM; Jonsen et al., 2005, 2006) at a 6-h time-step to estimate locations (via an observational model) and behavioural states (via a movement model). The SSM provides more accurate estimates of the locations and the associated uncertainty than raw tracking data (Jonsen et al., 2005, 2006). The model was fitted in R (version 3.5.1, R Core Team, 2018) using the software JAGS (Plummer, 2013) and the R packages *rjags* (Plummer, 2016) and *bsam* (Jonsen et al., 2015). Where a gap of >1 day existed in the raw satellite transmission data the individual track was split and ran as separate segments to avoid interpolating over long periods of time. Two Markov chain Monte Carlo (MCMC) chains were run in parallel, each for a total of 200,000 simulations. The first 100,000 samples were discarded as a 'burn-in', and the remaining samples were thinned, retaining every 100th sample to reduce autocorrelation. The final 2,000 samples were used to compute the posterior distribution of the model parameter estimates. The behavioural mode estimates (*b*), ranging between 1 and 2, were inferred from the means of the MCMC samples. We used a conservative approach (Jonsen et al., 2007) for classifying behavioural modes, with mean estimates of $b<1.25$ labelled as 'transiting', and mean estimates of $b>1.75$ labelled as 'area restricted search' (ARS), indicative of foraging. Locations with a mean *b* estimate between 1.25 and 1.75 were classified as 'uncertain'.

4.2.1.2 East Australian humpback whale data

To make comparisons with the neighbouring east Australian populations we used existing satellite tracking data reported in Andrews-Goff et al. (2018). Location-only SPOT-5 satellite transmitters were deployed on adult humpback whales along the east coast of Australia near Eden between October and November 2008, and off the Sunshine Coast during October 2010. Further details on the study site, deployment techniques and duty cycles are reported in Andrews-Goff et al. (2018). The tracks were entered into a separate hierarchical switching state-space model using the same settings as for the Oceania data.

4.2.2. Data preparation

We calculated speed between consecutive locations for each whale using the SSM data. Distance between consecutive locations were calculated using a great circle distance (*trip* package, function *trackDistance*, Sumner, 2016b). Where the raw satellite track for an individual whale was run as two or more separate segments in the SSM (Oceania dataset only) this resulted in data gaps in the final SSM tracks. For the tracks to be comparable between whales we were required to have a data point every 6 hours. We therefore filled the data gaps by generating new time points spaced at 6-h intervals (note that no locational data were associated with these points, only time and speed). For each newly generated point within the data gap we assigned the speed to be the speed across the entire gap (i.e. the speed between last SSM location before the gap and first SSM location after the gap). There were no gaps in the east Australian tracks and generating new points was not required.

In order to keep the tracks comparable between whales we specified the start and end points for the migratory phase for which we the energetic cost of transport. The migration phase began when the animals crossed 30°S (Figure 4.1). Using a set latitude as the end for the migration phase was not appropriate as the whales do not stop migrating at an arbitrary human-defined latitude (Andrews-Goff et al., 2018; Riekkola et al., 2018 - Chapter 2). Therefore, we considered the migration phase complete at the first sign of behavioural change after entering the feeding grounds (south of 60°S). This behavioural change was defined as the first occurrence of ARS behaviour as identified by the SSM, or three or more consecutive locations classified as 'uncertain' behaviour (PTTs 131178 where the model identified no ARS, and 131190 that had a data gap south of 60°S). This meant that the energetic cost for the migration phase was only calculated for tagged animals whose tags transmitted north of 30°S and lasted until at least 60°S. Within the Oceania population the whales had two migratory destinations: Ross Sea or Amundsen and Bellingshausen Seas (Figure 4.1). The migratory destination for each whale was assigned based on a visual grouping of the tracks on either side of 150°W. The east Australian whales migrated to a region between western Ross Sea and d'Urville Sea (Figure 4.1), and their migratory destination will therefore be referred to as the d'Urville Sea.

4.2.3. Energetic cost of transport and basal metabolic rate

Following Braithwaite et al. (2015) we grouped the energy expenditure of all activities for a migrating humpback whale as the energetic cost of transport (E_{COT}). The power required by a swimming animal to overcome the hydrodynamic drag forces (D) is proportional to the cube of swimming velocity (V), and therefore the energetic cost of swimming increases exponentially with speed (Sumich, 1983; Fish, 1994). The energetic cost of transport in Watts (W) was calculated using the formula from Hind & Gurney (1997):

$$E_{COT} = \frac{\lambda}{\varepsilon_A(V)\varepsilon_P}\frac{\rho S C_D V^3}{2}$$

where λ is the ratio of active to passive drag, ε is aerobic efficiency, ρ is the density of sea water (kg m^{-3}), S is the wetted surface area (m^2), and C_D is the drag coefficient. All model parameters and their sources are summarised in Table 4.1. As we aimed to compare the energetic costs of different migration distances, we kept all other variables (e.g. sex, age, size) constant, and therefore did not estimate the energetic cost of e.g. growth or lactation.

Basal metabolic rate (BMR) is the energy required by an organism to maintain vital bodily functions at rest. BMR was estimated as:

$$BMR = \frac{4186.8}{86400}[70M^{0.75}]$$

where M is mass (kg). The term in brackets is the allometric relationship between BMR and body mass among animals (kcal d^{-1}; Kleiber, 1975), and the first term converts this to W (as per Baumgartner & Mate, 2003).

4.3. Results

For the Oceania cohort, 11 whales had tracks covering the full migration from 30°S to the observed change in behaviour south of 60°S (Ross Sea n = 7, Amundsen & Bellingshausen Seas n = 4; Table 4.2a). Only two whales from east Australia had migration data across the same spatial range. Three whales from the Oceania cohort (PTTs 131175, 102211, 131173; Table 4.2a) had large data gaps resulting in a large proportion (>13%) of generated data points and speeds during the migration phase. As we could not be fully confident in the accuracy of the generated sections, we excluded these whales from the final comparisons (Table 4.2b).

The whales that migrated to the Amundsen & Bellingshausen Seas covered the farthest migration distance (in km), 21% and 15% longer than for the Ross Sea and d'Urville Sea migratory cohorts respectively (Table 4.2b). The Ross Sea whales migrated for 12% longer (in days) than the d'Urville Sea and Amundsen & Bellingshausen Seas whales. The Amundsen & Bellingshausen Seas whales had 85% and 25% higher energetic cost of transport than the Ross Sea and d'Urville Sea whales, respectively. The total energetic cost of migrating (cost of transport and BMR) to the Amundsen & Bellingshausen Seas was 6% and 7% higher than for the Ross Sea and d'Urville Sea migratory cohorts, respectively (Table 4.2b). The average migratory speed for each cohort varied throughout the migration phase (Figure 4.2). Apart from the early stages of the migratory phase, the Amundsen & Bellingshausen Seas whales migrated in general at a faster velocity than the Ross Sea and d'Urville Sea whales (Figure 4.2).

Table 4.1 Model parameters and values used to calculate energetic cost of transport.

Parameter	Unit	Value	Source
Ratio of active to passive drag	λ	0.7	Hind & Gurney (1997)
Assimilation efficiency	ε_A	0.2	Fish (1996)
Propeller efficiency	ε_P	0.8	Fish (1996)
Density of fluid	ρ (kg m$^{-3)}$	1,027	Standard for seawater
Surface area	S (wetted, m^2)	$0.045M^{0.696}$	Ryg et al. (1993)
Mass	M (kg)	30,000	Lockyer (1976); value held constant between whales
Drag coefficient	C_D	0.003	Estimated for humpback whale by Braithwaite et al. (2015)
Swimming velocity	V (m s^{-1})	Dynamic variable	SSM data, this study (range: 0-3.2 m s^{-1})

Table 4.2 a) Summary of satellite tag data used for calculating energetic cost of migration. PTT = unique tag number, % generated points = points generated to fill data gaps (‘na’ denotes cases with no data gaps), M = male, F = female, MC = mother-calf pair, U = animal of unknown sex, E_{COT} = energetic costs of transport (in Watts (W)), BMR = basal metabolic rate. b) Relative difference of energetic cost metrics between migration destinations. Note that the comparisons were done excluding individuals with >5% generated points.

(a)

Migratory destination	PTT	% generated points	Sex/reproductive class	Migration length		Migration E_{COT} (W)	Migration BMR (W)	Total migratory cost (W)
				days	km			
Amundsen and Bellingshausen Seas	102218	na	M	63	5,564	176,236	487,116	663,352
	131175	16.1	M	66	4,504	108,810	512,245	621,055
	131182	na	F	56	6,161	244,925	434,925	679,850
	131187	na	F	53	5,025	161,722	411,729	573,451
	Average			60	5,313	172,923	461,504	634,427
Ross Sea	88727	na	MC	37	3,709	108,495	286,084	394,579
	102211	24.9	U	55	3,208	158,587	427,193	585,780
	112722	2.0	U	87	5,487	100,112	670,751	770,863
	131173	13.5	M	57	4,192	143,866	442,657	586,523
	131178	na	MC	95	5,517	101,592	732,607	834,199
	131188	na	MC	48	4,202	118,562	367,270	485,832
	131190	na	MC	55	4,127	95,866	427,193	523,059
	Average			62	4,349	118,154	479,108	597,262
d’Urville Sea	64235	na	M	39	4,158	195,069	301,548	496,617
	98129	na	MC	76	5,579	115,968	583,766	699,734
	Average			57	4,869	155,519	442,657	598,176

(b)

Comparison	Migration length		Migration E_{COT} (W)	Migration BMR (W)	Total migratory cost (W)
	days	km			
Amdundsen & Bellingshausen Seas *relative to* Ross Sea	-11%	21%	85%	-11%	6%
Amdundsen & Bellingshausen Seas *relative to* d'Urville Sea	0%	15%	25%	0%	7%
Ross Sea *relative to* d'Urville Sea	12%	-5%	-33%	12%	1%

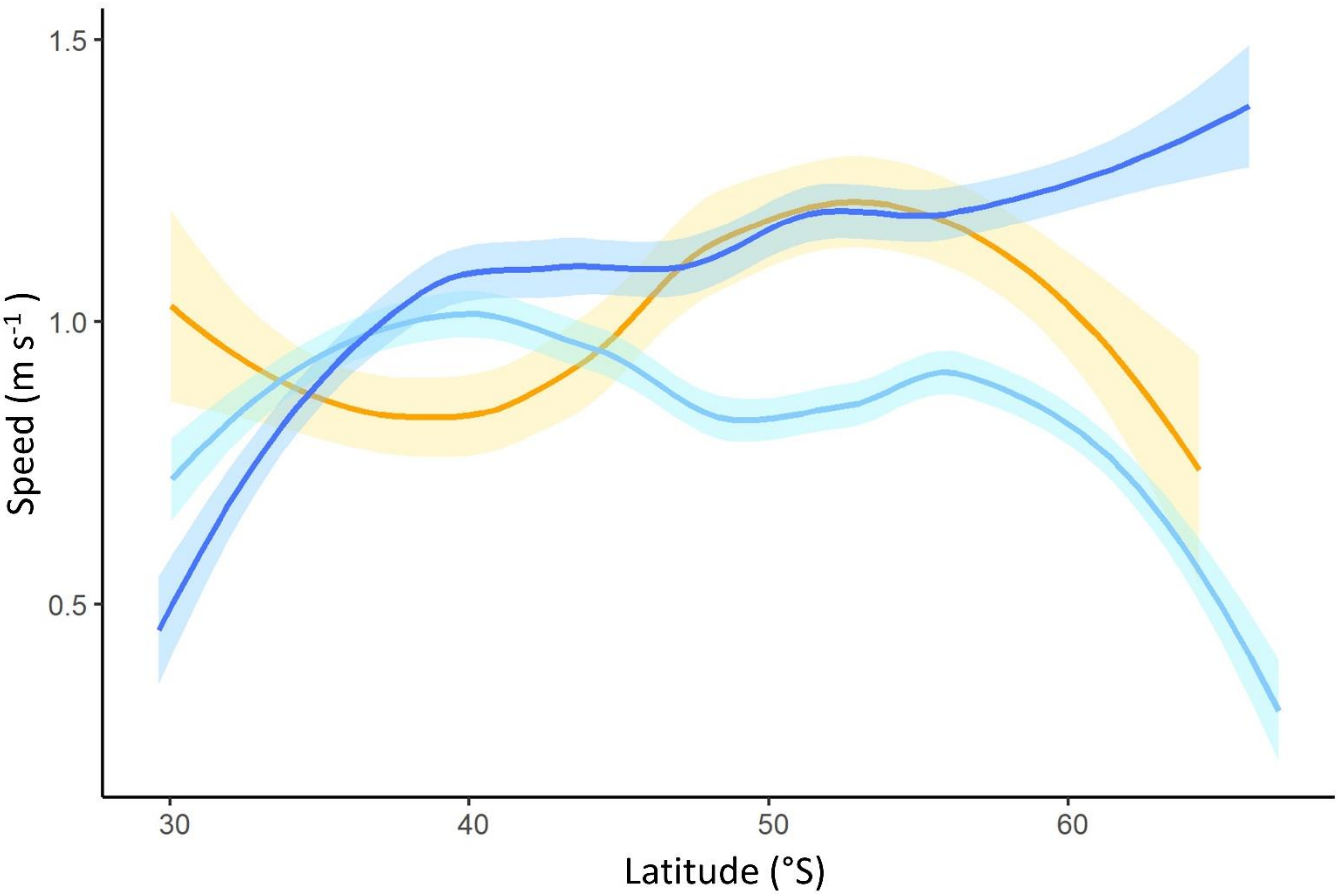

Figure 4.2 Swimming speed (m s^{-1}) by latitude during the migration phase (30°-60°S). Orange = d'Urville Sea, light blue = Ross Sea, dark blue = Amundsen and Bellingshausen Seas. Shaded areas represent LOESS smoother functions applied to whales of the same cohort.

4.4. Discussion

Animals need to balance their energy reserves during long-distance migration, and additional costs incurred during the migratory cycle can have consequences on individual survival and breeding success. For example, mortality during spring migration was highest in Eurasian spoonbills (*Platalea leucorodia leucorodia*) with the longest migration distance (Lok et al., 2015), and monarch butterflies (*Danaus plexippus*) infected with protozoan parasites were not able to migrate as far as uninfected individuals (Altizer et al., 2015). Here we estimated migratory costs for humpback whales with different migration routes and distances to their Southern Ocean feeding grounds. The total energetic cost of migration was a trade-off between cost of transport (speed) and daily maintenance costs (BMR). While migrating slowly minimises the energetic cost of transport, the extended travel time accrues a higher cost in terms of daily maintenance. In this case, while the cost of transport was highest for the Amundsen and Bellingshausen Seas whales due to the longest migration distance and their faster speed of travel, the energy saved in BMR costs by using fewer days to migrate to the feeding grounds resulted in only a small (6-7%) increase in the total energetic cost compared to the two shorter migration routes.

Migratory animals often employ different strategies, such as using favourable environmental conditions or stopover sites, to reduce migration costs (Lambardi et al., 2008; Sawyer & Kauffman, 2011; Bohrer et al., 2012). A faster migration speed may therefore be a behavioural adaptation through which the whales travelling to the Amundsen and Bellingshausen Seas minimise the costs associated with daily BMR, thus reducing the total energetic cost. Migratory wood thrushes (*Hylocichla mustelina*) for example adjust their travel speed as a migratory strategy, whereby individuals that departed later from their non-breeding habitats migrated faster and for fewer days to compensate for the delayed departure (McKinnon et al., 2015). Many marine mammals regardless of size routinely swim at slow speeds, ranging from 1.0 to 3.6 m s^{-1} (Williams, 2009), which is similar to the estimated range of optimal swimming velocities for baleen whales (Kshatriya & Blake, 1988). Throughout much of the migration phase the average speed of whales migrating to the Amundsen and Bellingshausen Seas was around 1.1 m s^{-1} (Figure 4.2b), which was identified in simulation models by Braithwaite et al. (2015) to be the most optimal speed for migrating humpback whales. This suggests that the whales likely migrate near the optimal speed that minimises cost of transport, at which point the total cost of long-distance migration is not expected to be significantly different from moving around in one location (Costa & Maresh, 2018).

Even a small annual energetic deficit can have a big impact on migrating animals. For example, a 4% loss in the annual energy budget of a female gray whale during pregnancy can prevent the successful production and weaning of a calf (Villegas-Amtmann et al., 2015). A bioenergetic modelling approach revealed that a 25% increase in the migration length, as well as higher metabolic rates at foraging grounds, resulted in ~11% greater energy requirements during a two-year breeding cycle for the western gray whale population compared to the eastern population (Villegas-Amtmann et al., 2017). However, the small extra cost during migration that we identified here for humpback whales does not necessarily equal to a net loss in the animals' annual energy budget. As detailed data on the energy usage and gain for these whale cohorts on the feeding grounds does not exist, we do not know whether the whales that use more energy during migration also gain more during the feeding season, or if the extra cost is balanced out in some other way during the year. Such data, as well as a more detailed model will be required to quantitatively estimate all annual energy costs and gains and to determine whether a 6-7% extra cost during migration could be significant to all, or some individuals in the population dependent on their life-history stage and natural variation in body size and condition.

None of the Oceania females with a dependent calf tagged at the Kermadec Islands migrated to the more distant feeding grounds of the Amundsen and Bellingshausen Seas (Riekkola et al., 2018 - Chapter 2). While a ~6% extra cost during migration might not affect the energy balance of adult whales, the added cost may have more of an impact on individuals that also have to bear the cost of growth or lactation. Immature and growing individuals require more energy than adults due to the energetic costs associated with body growth and high mass-specific metabolic demand (Worthy, 1987; Fortune et al., 2013), and may therefore be more vulnerable to nutritional stress during the migration or fasting period than mature individuals (Irvine et al., 2017). For example, long-distance migration to wintering grounds was found to be costlier for young and inexperienced greater flamingos (*Phoenicopterus roseus*) compared to adults (Sanz-Aguilar et al., 2012). However, considering calves in other humpback whale populations successfully complete long-distance migrations (Stevick et al., 1999; Rasmussen et al., 2007) we have no reason to assume that they would not be physically capable of migrating to the Amundsen and Bellingshausen Seas. Lactation on the other hand is one of the most energetically costly physiological process in mammals (Lockyer, 1986; Gittleman & Thompson, 1988), and in capital breeding humpback whales this cost occurs during the fasting period. We might therefore hypothesise that the preference for a closer feeding ground by lactating females (Riekkola et al., 2018 - Chapter 2) may indicate that they are more conservative with their energy expenditure, and therefore less likely to migrate to the Amundsen and Bellingshausen Seas. As stated above, more detailed data on the physiology of these animals are required for testing such hypotheses.

Because life is a balance between energy gain and use, the energetic costs of a given migratory route and distance is only one part of the equation. To maintain a positive energy balance, the energy acquired by capital breeding animals during the feeding season must exceed the energy required during the year. Experiencing favourable conditions at either end of the migratory range has been linked to better survival and breeding success in migrant animals, including many bird species (Newton, 2004; Alves et al., 2013). Therefore, the extra 6-7% migratory cost of a longer migration distance in humpback whales may not have a negative net effect as long as prey of sufficient quantity and quality is consumed during the feeding season. Future studies could therefore focus on evaluating the quality of the various Antarctic feeding grounds, for example by measuring lipid content in krill (*Euphausia superba*), the whales' main prey (Murase et al., 2002; Hellessey et al., 2018), as well as the availability of sufficiently dense krill swarms (e.g. Hazen et al., 2015).

The whales can also help balance their annual energy budget by feeding at stopover sites during migration, a strategy that is important for many bird species and terrestrial migrants (Newton, 2006; Sawyer & Kauffman, 2011). Due to the low cost of transport for swimming, aquatic migrants can go for a long time without stopping to refuel (Alerstam & Bäckman, 2018). Therefore, although humpback whales might not need to stop to forage during migration, supplementary feeding has been recorded in the east Australian population (Owen et al., 2017; Andrews-Goff et al., 2018). While humpback whales mostly rely on energy gained during the summer feeding season, opportunistic feeding during migration could in fact be an important contribution to the whales' annual energy budgets (Owen et al., 2017). The difference in the recovery rate between the Oceania and east Australian humpback whale populations might therefore be less due to energetic costs associated with different migration distances and more due to the extra energy gained by the east Australian whales, or perhaps a compounding effect of the two. It remains to be seen how these differences might affect the two populations in coming years given the expected ecosystem changes occurring on the Southern Ocean feeding grounds (e.g. Deppeler & Davidson, 2017). Various consequences of climate change on long-distance migrants, such as increased migration distances due to shifts in breeding ranges and temporal mismatches between food availability and migrant arrival, have already been recorded (e.g. Both et al., 2009; Doswald et al., 2009).

4.4.1. Caveats of the model

All models are inherently constrained by their input parameters. It is therefore crucial to use the most accurate and reliable data available, however obtaining estimates of energetic expenditure for large whales measured in absolute caloric value is highly difficult. Many of the variables required for such calculations cannot be reliably measured for free-living whales (Williams & Noren, 2009; Goldbogen et al., 2013; Christiansen et al., 2018). Additionally, small errors or changes in parameter measurements can have large impacts on the final results (Jeanniard-du-dot et al., 2017). We therefore did not attempt to obtain exact values and were instead interested only in the relative energetic costs between different migration routes and distances. Nonetheless, many of the factors in the model were likely over-simplified due to the lack of data on the physiology of large migratory whales. For example, an estimate for the drag coefficient does not exist for humpback whales, and the parameter used in our model was estimated based on values for other species (Braithwaite et al., 2015). Following Braithwaite et al. (2015) we grouped all activity as ‘cost of transport’. Even though we likely underestimated the exact energetic costs by not including different high energy behaviours (such as breaching, a frequent behaviour for humpback whales; Clapham et al., 1993) we expect all cohorts to display these behaviours equally and therefore that the ratios of total energetic costs between the cohorts (and populations) would remain similar. Despite the various limitations and the small sample size of our study, we provide valuable insight into the migratory ecology of these animals. The work also highlights an opportunity for more detailed model development, as well as the need to obtain better parameter estimates for hard to study marine migrants and to account for uncertainty and variability in these estimates. Our modelling approach utilised currently available biological knowledge and it can be adapted to incorporate new information or to include more detail on movement, environment, or other costs (e.g. lactation).

4.5. Conclusions

For capital breeding humpback whales that complete long-distance migrations the ability to balance limited energy reserves will have consequences on migratory performance as well as on individual survival and breeding success. The model developed in this study demonstrates that long-distance migrants manage energy used by balancing swimming velocity and the time taken to complete the migration. Our approach represents an example of using satellite tracking data to better inform energetic models and is therefore applicable to other organisms where similar data are available.

The whales studied here migrated at speeds near to those estimated to be optimal, suggesting that even extreme long-distance migration does not take a heavy toll on the animals, as much as we might be inclined to believe the opposite. However, the high additional energetic cost of lactation might limit the migration ability of mothers with a suckling calf.

Based on the energetic calculations done here, it seems that migration distance alone is not enough to explain the slow recovery rate for the Oceania population. However, models of the full annual energy budgets are required to fully determine whether energy gained during the feeding season is enough to outweigh all migratory costs, as well as to discern the role of stopover sites and supplementary feeding. Such insight will increase our ability to conserver these whale populations, especially given the changing environment. While more detailed data and models are required, our model provides valuable insight into the migratory energetics of humpback whales and into the differences between the two neighbouring populations.

Chapter 5

General discussion

5.1. New findings about Oceania humpback whale ecology

Prior to the research presented in this thesis, we had a rudimentary understanding of the migratory movements and the Antarctic feeding ground distribution patterns of Oceania humpback whales. Our knowledge was mainly limited to imprecise individual movement data from whales tagged with *Discovery* tags during the commercial whaling era, and more recently to whales identified through fluke matching or genetics at the end points of their migratory range (e.g. Chittleborough, 1959b; Dawbin, 1964; Robbins et al., 2011; Steel et al., 2018). Unlike the Northern Hemisphere, the area where most of our knowledge about humpback whales comes from (e.g. Clapham, 1992; Smith et al., 1999; Gabriele et al., 2007; Calambokidis et al., 2008), the Southern Ocean has no terrestrial geographic boundaries. This opens the possibility for whales to move great distances across their feeding grounds to other breeding grounds (e.g. Noad et al., 2000; Stevick et al., 2011; Robbins et al., 2011). Through the use of bio-logging tools my research revealed the migratory routes and the vast expanse of Southern Ocean feeding grounds for Oceania's humpback whales.

Humpback whales passing the Kermadec Islands, an area once abundant with whale sightings (Oliver, 1922; Townsend, 1935; Richards, 2009) and the site where satellite tags were deployed for this research, came from a range of breeding grounds spanning ~3,500 km of ocean, almost the entire breeding ground range for the Oceania humpbacks. This challenges previous ideas that most whales migrate from their breeding grounds due north (e.g. Fiji, Tonga; Chapter 2) to the feeding grounds due south (Chittleborough, 1965; Dawbin, 1966). The Kermadec Islands, in particular Raoul Island, is an important stopover location for the Oceania whales ~1,000 km (Tonga) to ~3,000 km (French Polynesia) south of their primary breeding grounds. From mid-September to mid-November, whales from multiple breeding grounds stay for periods of several days (Clark et al., 2017; Lindsay et al., *unpublished manuscript*), resting, engaging in low level social activity including exposure to the song of whales from other breeding grounds (Owen, 2016) before continuing their migration south. The area is the largest aggregation point for Oceania humpback whales in the open waters of the South Pacific once they are on their migration path and is therefore a region of great conservation value.

From the Kermadec Islands the whales migrated to the Southern Ocean (straight-line distances of up to 7,000 km). Apart from one individual that migrated past mainland New Zealand and four others that transited past Chatham Island to the east, all other whales migrated through open ocean waters. The whales' migratory tracks were not straight, but instead were quite sinuous with multiple individuals performing noticeable turns. Without obvious land masses constricting and guiding movement the whales are able to choose their paths, however we still do not fully understand this process (Horton et al., 2011, 2017). With the ever-developing accuracy of satellite tags and remote sensing data this is hopefully a question we can answer in the future.

The Antarctic feeding grounds of Oceania's whales spanned ~4,500 km from the eastern Ross Sea to eastern Bellingshausen Sea. This expanse of Southern Ocean covers regions where our understanding of productivity is quite poor (Siegel & Harm, 1996; Kaiser et al., 2009; Munilla & Soler-Membrives, 2015), compared to areas such as the Antarctic Peninsula (El-Sayed, 1967; Arrigo et al., 2008). Despite such a wide expanse, none of the tagged whales migrated to the west Antarctic Peninsula or the Balleny Islands, primary feeding grounds for humpbacks from western South America (Stevick et al., 2004) and east Australia (Constantine et al., 2014), respectively. Oceania whales have been recorded in both the west Antarctic Peninsula and the Balleny Islands (Robbins et al., 2011; Franklin et al., 2012; Constantine et al., 2014; Albertson et al., 2018) and such sightings are likely to increase in the future as whale numbers increase. However, my work suggests that most Oceania whales are spread in the open, remote Antarctic waters south of South Pacific (175°E-90°W), a region that remains largely under-represented by Antarctic scientists (e.g. Clarke et al., 2007; Griffiths, 2010; McLeod et al., 2010). The Oceania humpback whale telemetry data have helped answer questions about the extent to which stocks mix on the feeding grounds (Valsecchi et al., 2010; Jackson et al., 2015). This will inform the allocation of historical feeding ground whaling catches to individual breeding populations, something that has proven challenging when tracking the recovery of the heavily exploited humpback whales in this region (Clapham & Ivashchenko, 2009; Jackson et al., 2015). The whales' use of the IWC designated Southern Ocean feeding areas were historically informed by *Discovery* tag data when humpback whale populations were larger. Although these assignments may have been relevant at the time, now that the whale populations are recovering in a changing Southern Ocean these feeding areas may not be as representative as they once were, especially when informed by using modern research approaches.

The life history stage of the whales influenced their feeding ground destination, with all fully tracked mothers with a dependent calf migrating to the Ross Sea, and most adults without calves migrating to the Amundsen and Bellingshausen Seas. This appears to be a long-term pattern for these whales, as the same trend was observed in the historical whaling data (Appendix C, Figure 5.1). During their first year of life the calves learn the migration route to the Ross Sea from their mothers (typical for humpback whales; Palsbøll et al. 1995; Stevick et al., 2006; Baker et al., 2013). As the Kermadec Islands are an important social gathering point, young animals may learn the migration route to the Amundsen and Bellingshausen Seas from their mother if she returns to these feeding grounds with her calf after the first year, or possibly from other whales during subsequent years once independent. Of course, this pattern is not strictly adhered to, as all reproductive classes are found in both of the regions, but it is clear that the pattern has been persistent in the Oceania whales both when there were abundant numbers of whales and when numbers are severely reduced. This indicates the importance of culture in humpback whales, which may be the most social species of all rorquals (e.g. Clapham, 1996, 2000; Clapham & Zerbini 2015). There are well documented examples of cultural transmission, i.e. the social learning of information or behaviours from conspecifics, such as natal site fidelity and migration paths (Clapham & Mayo, 1987; Baker et al., 1990; Olavarría et al., 2007; Rosenbaum et al., 2017), feeding strategies (Allen et al., 2013), and song evolution (Garland et al., 2011). The suggested non-maternal inheritance of migratory routes and the lack of maternal fidelity to feeding grounds clearly highlights the difference between Northern and Southern Hemisphere feeding grounds and humpback whale populations.

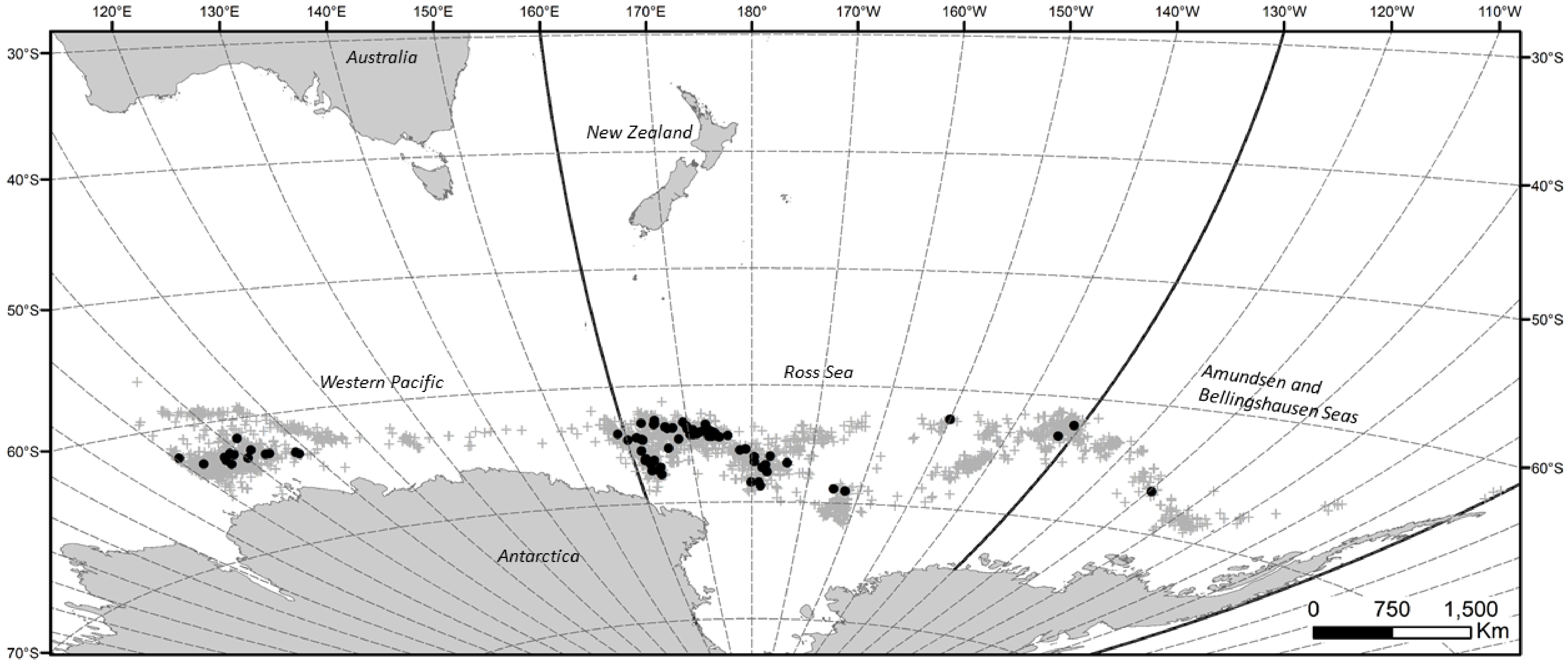

Figure 5.1 Location of humpback whale catches by the Soviet factory ship Yuri Dolgorukiy (1960-1973) within Western Pacific (90°-160°E), Ross Sea (160°E-130°W), and Amundsen and Bellingshausen Seas (130°-60°W); grey plus = adult, black dot = calf (inferred from the recorded length, whales <8.4m in length). Data provided by Dmitry Tormosov.

5.2. How will Oceania whales respond to climate change?

The Southern Ocean, like many other marine ecosystems, is experiencing rapid change (e.g. Turner et al., 2009; Hindell et al., 2017). In Chapter 3 I modelled the whales' behaviour within the feeding grounds and identified two areas within the Ross Sea and the Amundsen and Bellingshausen Seas regions where the whales focused their foraging efforts. There were clear differences in the environmental characteristics of the two key feeding habitats (e.g. depth, sea ice extent and dynamics). This raises the question, how will the Oceania whales respond to climate change, especially if the environmental effects are not the same across this large feeding region? Discerning how cetaceans in general will respond to climate change can be difficult, but some of the possible effects may include changes in their distribution patterns (MacLeod, 2009; Lambert et al., 2014), in the timing and length of migration (Ramp et al., 2015), and in reproductive success, mainly due to variations in prey abundance or distribution (Leaper et al., 2006). Behavioural plasticity is key in enabling individuals and populations to rapidly respond to environmental changes (Sydeman et al., 2015; Hindell et al., 2017). Plasticity in foraging strategies in particular may be important enabling species to better adapt to long-term climate change impacts, for example as seen in wandering albatrosses (*Diomedea exulans*) that successfully shifted their foraging range in response to changes in the Southern Ocean wind patterns (Weimerskirch et al., 2012). In Chapter 3 I identified behavioural plasticity within the Oceania whales, suggesting that these whales have the ability to adapt to the inevitable environmental changes, for example by prey switching or by completely shifting their range and distribution within the Southern Ocean.

The diverse and flexible diet of humpback whales enables them to forage on different available prey, leading to shifts between prey types (Hain et al., 1995; Owen et al., 2015; Fleming et al., 2016) and the exploitation of fully novel prey (Chenoweth et al., 2017). The Southern Ocean food web is already changing, with regional declines in krill stocks (mainly within the Southwest Atlantic sector) and the increase of salps in the southern part of their range (Atkinson et al., 2004; Lee et al., 2010; Constable et al., 2014; Hill et al., 2019). Although traditionally viewed as nutritionally poor, salps have recently been shown to have high levels of protein and carbon, and to be a key part of the Southern Ocean food web and the diets of many predators (Knox, 2006; Dubischar et al., 2012; Henschke et al., 2016). Due to their flexible diet and the apparent behavioural plasticity, we would expect Oceania humpbacks to successfully prey switch from krill to forage more on fish or salps, if necessary. In other regions the diet of baleen whales has been found to contain salps (e.g. Carroll et al., 2019), however whether they provide sufficient energy for a capital breeding whale needs to be assessed. Regardless, flexibility in diet and behaviour are likely to be important for the future survival and recovery of Oceania whales, given that models are predicting declines in those whale species that cannot adapt to the shifting prey base (Tulloch et al., 2019).

Alternatively, Oceania humpback whales might shift their range and distribution within the Southern Ocean. This could be especially relevant for the Amundsen and Bellingshausen Seas regions which have low overall productivity (Siegel & Harm, 1996; Constable et al., 2003), however this region remains poorly studied (Kaiser et al., 2009; Munilla & Soler-Membrives, 2015). If for example the area can no longer support foraging whale populations, or if krill distribution shifts markedly (Atkinson et al., 2019), we might see fewer whales in the Amundsen and Bellingshausen Seas in the future. A situation like this has recently arisen in south-eastern Alaska where a previously important humpback whale feeding ground has seen a drastic reduction in the number of whales (Neilson & Gabriele, 2019). It is unclear whether this reflects a range shift, or increased mortality, but the observed trend seems to be linked to poorer prey availability and/or quality in the Gulf of Alaska ecosystem as a result of a marine heatwave in the North Pacific (Neilson & Gabriele, 2019). Range shifting by Oceania whales would also influence competition with other krill predators, however this is a highly complex subject (Fraser et al.,1992; Clapham & Brownell, 1996; Clapham et al., 2007). Range shifting might also affect resource and niche partitioning between humpbacks and other recovering whale populations, a topic that has been studied around the Antarctic Peninsula (Friedlaender et al., 2009, 2011; Herr et al., 2016) but of which our understanding is lacking in almost all other Antarctic regions.

The observed division to two feeding regions by the Oceania whales could also lead to contrasting responses to environmental change. The physical oceanography fluctuates across the Southern Ocean resulting in a variable distribution and abundance of lower trophic level species (Fraser & Hofman, 2003; Murphy et al., 2007; Southwell et al., 2015). Studies have identified regional trends in the Antarctic sea ice variability, with increasing sea ice extent occurring in the Ross Sea region, and a decrease in sea ice extent occurring in the Amundsen and Bellingshausen Seas region (e.g. Zwally et al., 2002; Turner et al., 2009; but see Stewart et al., 2019 on sea ice thinning in Ross Sea). Due to these regional differences in the food web structure and sea ice dynamics, the environmental changes experienced by populations of the same species inhabiting different parts of the Southern Ocean may not be uniform and may elicit contrasting responses from the animals (Hindell et al., 2016, 2017; Jonsen et al., 2019). For example, differences in habitat quality and in the long-term trends in sea ice conditions across regions have been linked to the different population trends among southern elephant seal (*Mirounga leonina*) colonies (Hindell et al., 2016). For the Oceania whales, the fact that most, if not all, mothers with dependent calves migrate to the Ross Sea feeding grounds is important information for conservation management. This population might be more sensitive to changes occurring in the Ross Sea region as any major anthropogenic impacts, either direct (e.g. increased krill fishery) or indirect (e.g. climate change effects), could have proportionately larger impact on mothers and calves, which is more likely to affect the overall population recovery.

Furthermore, the whales’ world is changing at both ends of their range. Warming waters in the tropics are predicted to result in some of the Oceania breeding sites (such as American Samoa) to become unsuitable for the whales by the end of 21st century (Derville et al., 2019). Plasticity in habitat use patterns may therefore facilitate distribution shifts to more suitable habitats of southern Oceania. Alternatively, some Oceania whales may immigrate to east Australia, something that has been suggested as a possible reason for the high rate of increase in east Australian population (Clapham & Zerbini, 2015; work is underway to answer this question – Steel et al. in progress).

5.3. Oceania population recovery and migratory energetics

One of the main aims of my thesis was to better understand why the Oceania whale population is recovering slower than for example the neighbouring east Australian population, which continuous to grow at a rapid rate and is now considered fully recovered (IWC, 2015; Noad et al., 2019). The Oceania population is recovering, albeit slowly (Constantine et al., 2012; IWC, 2015), and the pregnancy and age analyses (Chapter 2) support this. There was a high proportion of younger whales and a relatively low proportion of older whales, similar to that seen for the east Australian whales a decade ago and indicative of a population recovering from exploitation

(Polanowski et al., 2014; Jones et al., 2018). The 57% pregnancy rate was higher than expected for such a slow recovering population. It is worth noting however, that the last abundance estimate for the Oceania population is 15 years old, and recent estimates show that the New Caledonian sub-population is growing (Garrigue et al., 2012). Furthermore, populations experiencing high levels of exploitation often show a decrease in age and size at sexual maturity, favouring early reproduction (Lockyer, 1984; Proaktor et al., 2007), therefore the high pregnancy rates in the young Oceania populations may be a population level post-whaling response. The high pregnancy rate recorded here was also comparable to the rapidly growing western South American populations of humpback whales feeding in the West Antarctic Peninsula where pregnancy rates ranged from 36% in 2010 to 86% in 2014 (average 63.5% across five years), and between 58% and 72% from summer to autumn across all years (Pallin et al., 2018b). It is possible that the Oceania whales are experiencing a high rate of foetal loss and/or calf mortality, with fewer calves being recruited into the population than in other areas, thus slowing down the overall population recovery. However, we are currently very limited with such information for the Oceania population, with the breeding grounds of New Caledonia the only region where a sufficient long-term dataset exists for us to answer some of these questions (Garrigue et al., 2001; Chero et al., 2017). Such inference would require re-sightings of previously sampled females to ascertain the fate of their pregnancy, as well as re-sightings of the calf to ascertain survival and recruitment success. Obtaining such repeated measures is complicated by low resighting rates within and between breeding grounds (Garrigue et al., 2011; Constantine et al., 2012) largely due to the vast and complex network of atolls, seamounts and islands that offer suitable habitat for these whales within the Oceania region (Oremus & Garrigue, 2014; Garrigue et al., 2015; Lindsay et al., 2016; Derville et al., 2019). Additionally, for a large part of the year these whales migrate through the remote waters of the South Pacific and the Southern Ocean and are not easily observed or sampled.

As the breeding grounds are unlikely to be a limiting factor for humpback whale recovery, my research on the Southern Ocean feeding grounds as well as the migratory routes taken there may provide some explanation for the slower recovery than the neighbouring east Australian whales. Once I determined the migration path and feeding grounds (Chapter 2), I was able to examine whether whales migrating greater distances (to the Amundsen and Bellingshausen Seas) bear a higher energetic cost compared to whales with shorter migration distances (Ross Sea region; Chapter 4). As capital breeders the reproductive success of humpback whales during a period of fasting is related to maternal body condition (Festa-Bianchet et al., 1998; Bonnet et al., 2002; Christiansen et al., 2014). Greater energetic requirements during the ~six to seven month migration and breeding portion of the whales' lifecycle could therefore mean that there is less energy available for successful breeding and weaning of calves. I investigated this question in Chapter 4 where I used the satellite tracking data to inform a bioenergetic model. I found insufficient evidence to support the idea that a greater migration distance alone is the reason for the different recovery rates between Oceania and east Australian humpback whale populations. This is not surprising given how little we know about the fine-scale feeding behaviour of humpback whales and the environmental dynamics in the Southern Ocean, with the exception of the west Antarctic Peninsula (e.g. Ware et al., 2011; Friedlaender et al., 2013; Tyson et al., 2016).

The main reason I was unable to conclude that the slightly higher (7%) total energetic cost for those Oceania whales migrating to the Amundsen and Bellingshausen Seas was the reason behind the slow recovery was that we do not have sufficient information on the energetic gains by the whales throughout the year. Because the life of a capital breeding humpback whale is a balance between energy gain and use, the energetic costs of a given migratory route and distance is only one part of the equation. For example, lunge feeding is energetically costly (e.g. Goldbogen et al., 2007, 2011, 2012; Potvin et al., 2012) and there is no evidence of cooperative feeding by humpbacks in the Southern Ocean, unlike the Northern Hemisphere whales feeding on fish (e.g. D'Vincent et al., 1985; Weinrich & Kuhlberg, 1991; Wiley et al., 2011). Therefore, a key component in building accurate bioenergetic models for these whales will be the acquisition of reliable data on the energy gained and used throughout the feeding season, which will depend on the availability of prey as well as the quality of prey consumed. The use of data archival tags, such as DTAGs, would be a valuable tool to answer such questions.

As with most ecological studies the complex dynamics between behaviour, individual variation and the environment mean there is never a simple answer. For example, the slightly higher energetic cost to Oceania whales migrating to the Amundsen and Bellingshausen Seas likely interacts with other factors, such as a higher energetic gain by east Australian whales due to higher quality prey on the feeding grounds or feeding during migration. Feeding on fish and krill has been recorded in the east Australian population (Stamation et al., 2007; Owen et al., 2017; Andrews-Goff et al., 2018), however, the full extent of its occurrence within the population is unknown and the recorded cases could represent only a small proportion of individuals. Feeding during migration is a critical aspect for some migratory species (Alerstam & Bäckman, 2018; Newton, 2006; Sawyer & Kauffman, 2011) and insufficient access to re-fuelling sites may cause animals to exhaust their energy reserves before migration is completed (Braithwaite et al., 2015; Newton, 2006). Given that feeding during migration could be an important contribution to the whales' annual energy budgets (Owen et al., 2017) future studies should aim to ascertain the energetic importance of re-fuelling sites for migrating humpback whales from all populations.

Large inter-individual variation has been observed in humpback whale body condition (Christiansen et al., 2016; Irvine et al., 2017; Narazaki et al., 2018), yet we do not know what role this plays in their energetics. Like other long-distance migrants, humpback whales cannot predict resource availability and abundance at the end destination when departing from the breeding grounds, whereas for short-distance migrants the conditions at one end of the migratory range may be a better predictor for the optimal arrival time at the other end (Both & Visser, 2001; Cotton, 2003). In general, the timing of arrival is likely to be critical for animals to fully exploit their habitat. By arriving too early the animal may risk facing unfavourable weather conditions or having to wait for resources to become available, whereas late arrival may mean that the best, or all, of the resources (e.g. breeding partners, nesting sites, prey patches) have been locally depleted. For humpback whales, arriving too early, before sea ice melting and prey becoming available, would incur the cost of daily metabolic requirements with little to no foraging success and energetic gain. Such wait could be detrimental for some, perhaps smaller animals in poorer condition. It is also possible that for a capital breeding whale a wait time of few days or even weeks might not make a difference in the overall condition of individuals. It is yet unclear whether climate change will influence the arrival time of Oceania humpbacks at the Southern Ocean feeding grounds, and whether this will have a positive or a negative effect on their fitness. Waiting for krill to become available may drive those individuals with sufficient energy stores to move elsewhere, or the whales might prey switch to forage on already available prey, which has been documented in different humpback whale populations (e.g. Weinrich et al., 1992; Fleming et al., 2016). With baleen whales potentially playing an important role in nutrient cycling in the iron depleted Southern Ocean, understanding the whales' response to ice-related changes in productivity may help prioritise areas of future investigations (Nicol et al., 2010; Ratnarajah et al., 2014, 2016).

5.4. The power of bio-logging and the challenges with cetacean telemetry

By using bio-logging and modelling tools I was able to determine cumulative totals of ~58,000 km of migratory tracks from 18 whales travelling from the Kermadec Islands to the Southern Ocean (60°S), ~47,000 km of movement and behavioural patterns for 14 whales within the Southern Ocean, as well as conducting energetic modelling. All of this was done without having to directly observe the animals (apart from the tag deployment). I would not have been able to achieve all this without bio-logging and modelling methods, as Oceania humpbacks inhabit vast sections of remote oceans that are logistically challenging to access. This is true for most parts of the Southern Ocean, with the exception of the Antarctic Peninsula, where research on the fine-scale behaviour of humpback whales is facilitated by the whales congregating in more sheltered waters close to the coast, often at high densities (e.g. Nowacek et al., 2011; Johnston et al., 2012; Herr et al., 2016). Yet it is worth noting that this region differs from most of the Southern Ocean (Siegel & Harm, 1996; El-Sayed, 1967; Meredith & King, 2005; Arrigo et al., 2008) and findings may not be applicable to whale populations away from the Peninsula.

Tagging of cetaceans (or any other animal for that matter) should not be taken lightly, however, as there are almost certainly costs of some kind to the animal. Implantable satellite tags deployed on large cetaceans penetrate the tissue and anchor into the blubber-muscle interface, thereby causing damage to the tissue (Mate et al., 2007; Moore et al., 2012). Tag deployment sites have been reported to exhibit symptoms such as shallow depressions surrounding the tag and swelling that has persisted over extended periods, leaving permanent indentations and scarring once the tag has been expelled from the body (Mate et al., 2007; Robbins et al., 2013; Best et al., 2015). Such permanent visible damage can even be a sign of remnants of the tag (e.g. splines or petals) being left in the tissue and there have been reported cases of known issues with earlier versions of transdermal tags (Robbins et al., 2013; Best et al., 2015; Gendron et al., 2015). Although in general the negative impacts of tagging have not been found to significantly impact the animals' survival or reproduction there have been relatively few studies on the long-term effects of tagging or the related injuries which have the potential to affect the animals' fitness (Robbins et al., 2013; Baumgartner et al., 2015; Best et al., 2015; Gendron et al., 2015; Moore & Zerbini, 2017).

Less invasive tag attachment methods such as glue and tethering exist, as often used for pinnipeds (Field et al., 2012; Labrousse et al., 2015) and manatees (Deutsch et al., 2003; Aven et al., 2015), however the use of these methods is not possible for baleen whales as they require the capture of the animal, and whales are constantly sloughing skin to remain hydrodynamic. Suction cup attachments have successfully been used on large baleen whales to collect fine-scale information, but these attachments are usually short-lived (e.g. Tyson et al., 2012; Wensveen et al., 2015; Szesciorka et al., 2016; Izadi et al. 2018). Transdermal-implantable tags with longer attachment times are therefore required for long-term movement and behavioural studies for large cetaceans (Best et al., 2015), however even then the tag duration has been highly variable (Lagerquist et al., 2008; Rosenbaum et al., 2014; Garrigue et al., 2015; Riekkola et al., 2018 - Chapter 2), and generally shorter than the battery capacity (Robbins et al., 2013).

Tagging of cryptic and highly mobile animals such as large whales has obvious benefits in gathering information about their distribution, movements, behaviour and physiology. It is therefore necessary to carry out a cost-benefit analysis to carefully assess the conservation need for the tagging study and the ethical considerations of potential negative impacts to the animals so that studies on endangered species do not further exacerbate species decline or hinder their recovery (Cooke, 2008; Weller, 2008). It is important to also carefully consider the number of animals to be tagged in order to sufficiently answer the conservation question on a population level (without having to rely too heavily on extrapolation) while minimising the number of animals being affected by the equipment of tags (Roncon et al., 2018). Furthermore, it is always advisable to maximise opportunities for data collection as well as the data collected. Such was the case with my study, as multiple data were collected to produce a more comprehensive picture than the tagging data alone could have provided, and I was able to answer multiple research questions. The data still has potential to be used further and is being used by other researchers.

5.5. Future research directions

5.5.1. Opportunities with a long-term data set

Given that this tagging study provided the first movement data on the Oceania humpbacks, and only for one season, an obvious future direction will be to collect more data. A longer-term data set would allow us to answer a new array of questions.

Long-term memory of average environmental conditions plays a key role in terrestrial mammalian migration (e.g. Bracis & Mueller, 2017) and has recently also been shown to be important in the long-distance migration of marine megafauna (Hindell et al., 2017; Abrahms et al., 2019). In Chapter 3 I assessed how contemporary environmental cues were driving whale movements and behaviour but could not assess the role of memory with a single sampling season. With multiple years of tracking data, ideally on the same individuals, a logical continuation of this work will be to determine what role memory plays in driving Oceania humpback whale migratory movements. Animals that rely on memory may struggle to respond to rapid deviations from historical mean environmental conditions (Abrahms et al., 2019), therefore knowledge of the role of memory may help us predict how Oceania humpbacks will respond to changes in the Southern Ocean ecosystem. Obtaining a long-term tagging data set for Oceania whales is within our power, but repeatedly finding and tagging the same individuals will be logistically challenging. Additionally, with a population that seems to be recovering slowly, repeated tagging of the same individuals will carry additional ethical concerns.

Due to their long lifespans, marine mammals such as whales can be monitored long-term and they can act as sentinels of the overall ecosystem status and health (Schick et al., 2013; Fleming et al., 2016). Quantifying the distribution and behaviour of large whales can provide information on areas of high and low ocean productivity and how these change over time (Roncon et al., 2018; Neilson & Gabriele, 2019). Previous studies on humpback whales have demonstrated that these animals respond to ecosystem shifts (Fleming et al., 2016; Neilson & Gabriele, 2019), and we should therefore be able to effectively use their distribution and behaviour as indicators of the oceanographic and ecological conditions in the Southern Ocean. This is a useful addition to the well established and valuable studies of pinniped and seabird movements throughout the Southern Ocean (Charrassin et al., 2008; Raymond et al., 2010; Labrousse et al., 2017; Roquet et al., 2017).

5.5.2. Opportunities with tags and models

The tags used in this study (Wildlife Computers SPOT-5) provided a great opportunity to answer multiple questions about the movement and behaviour of Oceania humpback whales in the open ocean, something I would not have been able to achieve otherwise. These tags however provided locational data only, and they had very variable deployment durations, providing data only on the southward part of the migration (with the exception of PTT102218). Although the tagging and modelling approaches used here were useful tools, they were limited in revealing any fine-scale behavioural patterns. There are therefore multiple avenues for improvements.

Given that the current tag design and hardware seem unlikely to last for the full migratory cycle of the Oceania humpback whales, one possible workaround to capture the return (northward) migration would be to deploy tags on the whales at the feeding grounds. This task is unfortunately hindered by the fact that the Southern Ocean feeding areas of the Oceania whales lack clear aggregation points, compared to for example the Kermadec Islands on the way south, or the Balleny Islands as a key feeding ground for east Australian whales (Franklin et al., 2012; Constantine et al., 2014). A possible solution to identify the location of whales in the Southern Ocean could be the use of recent technology such as drones and cameras (Linchant et al., 2015; Werth et al., 2019), gliders (Baumgartner et al., 2013) or high-resolution satellite imagery (Fretwell et al., 2014; Cubaynes et al., 2018). These technologies, especially satellite imagery, could inform research voyage plans to areas of high whale density, monitor and count the presence of whales across different regions of the Southern Ocean and/or to determine whether whales consistently return to the two key feeding areas identified in my thesis. Satellite imagery would not be sufficiently detailed to identify individual humpback whales (by fluke markings) but could confirm the annual presence of whales in specific areas. Using such technology might be more cost effective in geographically isolated regions like the Southern Ocean, especially if we develop advanced algorithms and automate the process of identifying whales in satellite imagery (Fretwell et al., 2014; Cubaynes et al., 2018).

Future tag deployments should also aim to use high resolution dive tags. Fine-scale behaviours within the feeding grounds have been reported for humpback whales within the Antarctic Peninsula (e.g. Nowacek et al., 2011; Friedlaender et al., 2013), but not in my study area. Data on the whales' dive patterns can for example help confirm whether ARS behaviour identified by state-space modelling is truly feeding. Although the energetics work I present in this thesis shows the potential for this kind of quick approach, I acknowledge that there were several caveats and uncertainties with the methods used. DTAGs that record dive data could capture dive depths and durations, metabolic energy expenditure (via respiration rates; Bejder et al., 2019) and 3-axis acceleration data which can be fitted to a hydrodynamic glide model to estimate parameters such as tissue density, drag term and diving gas volume (e.g. Narazaki et al., 2018). Such information can be used to develop more sophisticated and detailed energetic models.

In addition to dive data, cetacean tags could draw inspiration from tags used for example with pinnipeds that also collect other in situ environmental data, such as hydrographic profiles of temperature and salinity, and phytoplankton fluorescence which can be used to calculate chlorophyll *a* (Charrassin et al., 2008; Lander et al. 2015; Labrousse et al., 2018). This approach would allow us to obtain local environmental data at the exact time and location required. The information could also help deal with the problem that remotely sensed data of such variables is often of very high resolution, and may therefore not accurately capture and represent smaller, local scale events in the environment.

There are almost certainly many reasons behind the contrasting recovery rates of Oceania and east Australian humpback whale populations. Considering the energetic costs was not, at least on its own, found to be a clear indicator, the next logical step would be to estimate differences in energetic gain between the populations. Possible approaches to this would be the sampling of krill from the Antarctic feeding grounds and evaluating their energetic quality by measuring lipid content (Hellessey et al., 2018) or by sampling the blubber of the whales as a proxy of their built-up energetic reserves (Waugh et al., 2012; Castrillon et al., 2017). Differences in whales prey and its nutritional content could reveal differences in the energetic gains between regions or cohorts. For example, isotope studies (e.g. Quillfeldt et al., 2008; Eisenmann et al., 2016) enable us to evaluate diet and foraging areas for the whales. Preliminary results of this approach on Oceania whales suggest the males forage on a higher trophic level prey (Constantine, 2016), providing an opportunity for the future to investigate this further.

5.6. Conclusions

This thesis provided the first comprehensive study on the population demographics, migratory movements and energetics, and feeding ground habitat use patterns for the endangered Oceania humpback whales. The results complement our current understanding of humpback whales throughout the Southern Hemisphere, and the methods are broadly applicable to other species and environments. The remoteness of the Southern Ocean feeding grounds makes data collection very difficult, therefore the use of bio-logging technologies and modelling tools were key to studying whales without the need for capture or direct observations. However, our knowledge on the fine-scale behavioural patterns of these whales still remains limited. Understanding the whales’ current status is the first step in determining how these and other whales will respond to a rapidly changing climate. The knowledge I present here will therefore help direct future research questions as well as inform future conservation and management decisions about whales whose lives span the vast expanse of ocean from the tropics to Antarctica.

APPENDIX

Appendix A

Table A.1 Summary of fluke identification catalogues of humpback whales from breeding grounds, migratory corridors and feeding grounds entered in Fluke Matcher and matched to the Kermadec Islands catalogue (n = 136). The photographs from Antarctica are primarily supplied from previous Southern Ocean Research Partnership voyages (Areas V & VI only) and these have been submitted to the Antarctic Humpback Whale Catalogue curated by College of the Atlantic. The east Australia photographs include whales from the northern and southern migration past the Gold Coast, southeast Queensland (SEQ) only.

	Location	**Fluke Matcher catalogue size**	**Years included**
	Kermadec Islands	136	2007, 2008, 2011, 2013, 2015
Breeding grounds			
	American Samoa	265	2003-2011, 2014, 2015
	Cook Islands	98	1999-2008
	Fiji	15	2002, 2003, 2005, 2008, 2011, 2013
	New Caledonia	1200	1995-2015
	Niue	58	2001, 2007-2011, 2014, 2015
	Samoa	15	2001, 2006-2008
	Tonga	141	2007-2012, 2015
	Vanuatu	7	2003, 2007
Migratory corridors			
	East Australia (SEQ)	641	2008-2012
	New Zealand	130	1994-1996, 1998, 2001, 2002, 2004-2013
	Norfolk Island	6	2001, 2002, 2007, 2008
Feeding grounds			
	Antarctica	115	1991, 1999, 2002, 2006, 2008, 2010, 2013, 2015

Appendix B

Table B.1 Progesterone analysis of adult female humpback whales (n = 31) sampled at Raoul Island, Kermadec Islands in 2015. Progesterone concentrations are reported as nanograms of progesterone per gram of blubber (ng/g P4). Females were assigned as pregnant if their probability of being pregnant was greater than 99%, and not-pregnant if the probability was less than 1%, using a logistic regression model. Progesterone analysis of one sample was unsuccessful. Final column indicates if the female was with a dependent calf at the time of sampling.

Sample-ID	ng/g P4	Status	With a calf?
Mno15KI-004	140.937	Pregnant	
Mno15KI-016	74.927	Pregnant	
Mno15KI-018	283.191	Pregnant	
Mno15KI-019	71.735	Pregnant	
Mno15KI-022	25.810	Pregnant	
Mno15KI-023	76.572	Pregnant	
Mno15KI-024	147.229	Pregnant	
Mno15KI-027	352.676	Pregnant	
Mno15KI-031	78.714	Pregnant	
Mno15KI-036	147.532	Pregnant	
Mno15KI-045	63.712	Pregnant	
Mno15KI-062	287.891	Pregnant	
Mno15KI-003	68.878	Pregnant	Yes
Mno15KI-038	26.596	Pregnant	Yes
Mno15KI-049	33.524	Pregnant	Yes
Mno15KI-053	231.240	Pregnant	Yes
Mno15KI-218	87.728	Pregnant	Yes
Mno15KI-009	2.778	Not-pregnant	
Mno15KI-032	5.257	Not-pregnant	
Mno15KI-035	3.404	Not-pregnant	
Mno15KI-047	4.977	Not-pregnant	
Mno15KI-052	1.746	Not-pregnant	
Mno15KI-055	4.037	Not-pregnant	
Mno15KI-221	2.471	Not-pregnant	
Mno15KI-017	1.482	Not-pregnant	Yes
Mno15KI-054	2.006	Not-pregnant	Yes
Mno15KI-056	1.282	Not-pregnant	Yes
Mno15KI-057	3.172	Not-pregnant	Yes
Mno15KI-205	1.305	Not-pregnant	Yes
Mno15KI-216	1.540	Not-pregnant	Yes
Mno15KI-044	na	Unsuccessful	

Appendix C

To investigate whether the observed difference between migratory destinations between mothers with dependent calves and adults without calves was observed during high whale abundance (i.e., during commercial whaling), we examined data from one Soviet factory ship, the *Yuri Dolgorukiy* (data provided by Dmitry Tormosov), operating between the Western Pacific and the Bellingshausen Sea between 1960 and 1973. We found that the proportion of calves taken between the regions differed significantly (Pearson's χ^2, $p = 0.008$), with the highest proportion of calves caught within the Ross Sea region (Table C.1, Figure 5.1). Proportionally the least amount of calves caught occurred in the Amundsen and Bellingshausen Seas sector.

Table C.1 Percentage of humpback whale calves (<8.4m in length) and adults caught by the Soviet whaling ship Yuri Dolgorukiy (1960-1973; data provided by Dmitry Tormosov). Regions: Western Pacific 90°E-160°E, Ross Sea 160°E-130°W, Amundsen and Bellingshausen Seas 130°W-60°W.

	% Total catch	
Region	Calf	Adult
Ross Sea	2.13	97.87
Western Pacific	1.14	98.86
Amundsen & Bellingshausen Seas	0.30	99.70

Appendix D

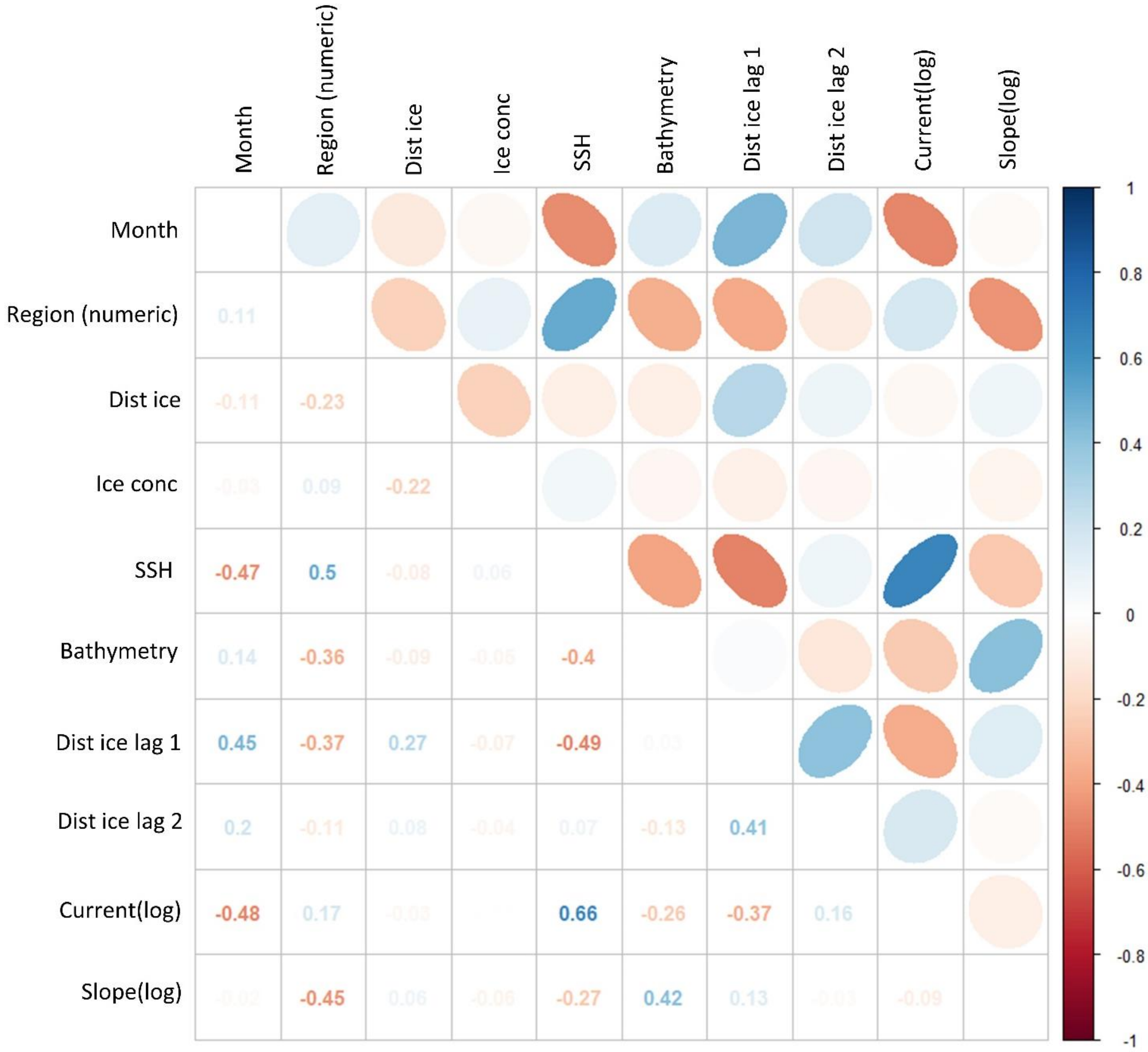

Figure D.1 Spearman correlation matrix of the 10 covariates used in the statistical model.

Appendix E

Table E.1 Posterior sample means and 95% confidence intervals for movement parameters (transit, and area-restricted search; ARS) estimated using a hierarchical state-space model. γ = autocorrelation in speed and direction, θ = turning angles (radians).

	State	Lower 95%	Mean	Upper 95%
γ	ARS	0.0491	0.0497	0.0503
	Transit	0.9545	0.9546	0.9547
θ	ARS	2.9088	2.9156	2.9224
	Transit	0.0042	0.0043	0.0044

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