Migratory timing in southern right whales on their breeding grounds: what are the key factors stimulating migration?

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Declaration

I, Shane Dickeson, declare that to the best of my knowledge and belief this thesis contains no material

previously published by any other person except where due acknowledgment has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma

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Date: 22nd October 2018

Abstract

Migrations are key events in the annual life cycle for many animal species, including baleen whales. Despite having some of the longest migrations among mammals, relatively little is known about what triggers migration behaviour in baleen whales, and how intrinsic and extrinsic factors influence the timing of migrations. This study investigated the timing of migration in southern right whales (*Eubalaena australis*) and whether the probability of departure of individuals from winter breeding and calving grounds is determined by intrinsic (maternal body condition and calf size) or extrinsic variables (day length, temperature). Unmanned aerial vehicles were used to record data on the body size (length and width) of right whale mother and calves between the June 24 and September 25, 2016, providing repeated measurements of 40 mother-calf pairs. I used the time interval between sightings of individuals to determine the departure date of whales from the breeding grounds. Generalised linear models were used to determine which variable (maternal body condition, calf size, day length and sea surface temperature) was the best predictor of the departure time of the whales from the breeding grounds. Diurnal period was found to be the best predictor of migration for southern right whales, followed by calf size (i.e. body volume and length), sea surface temperature and maternal body condition. Hence it seems like migration in this population of right whales is determined by calves reaching a large enough body size to facilitate migration, rather than mothers pushing themselves energetically to their lower limit. Apart from improving our understanding of migratory behaviour in large whales, the findings of this study will help determine residency times of southern right whales on their breeding and calving grounds, which can be used to identify key times for protection (e.g. temporary exclusion periods for fisheries) during the winter breeding and calving season.

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1. Introduction

Animals across different taxa undertake long-distance migrations to exploit favourable foraging opportunities, habitat conditions and a higher probability of reproduction (Dingle, 1996). Animal migration consists of multi-level interactions on an individual migrant including intrinsic factors and aspects of the surrounding environment (Dingle & Drake, 2007). Research on many migratory species has helped build a better foundation for understanding the underlying behaviours, and factors stimulating migration and has facilitated the development of general models about the ecology and physiology of migrating animals (Dingle & Drake, 2007; Bowlin et al., 2010). Further research on how, why, where and what triggers individuals to migrate will aid further in our conceptual understanding the mechanism and function of migration at both individual and population levels (Dingle & Drake, 2007; Cote et al., 2017). Failure to understand the importance of intrinsic and extrinsic factors that trigger life-history events in migratory species may lead to erroneous assumptions on the timing of migratory behaviour (Monteith et al., 2011). Baleen whale migration is one of the great wonders of nature, with most species undertaking annual migrations between high-latitude feeding grounds in summer and low-latitude breeding grounds in winter (Corkeron & Connor, 1999). Much of the current literature on baleen whale migration pays attention to the movement patterns, and the costs-benefits of migration. However, factors that trigger the timing of the migration have rarely been investigated and remain poorly understood.

1.1 Mammal migration

Migration is a common life-history strategy in mammals that differs noticeably from invertebrate, bird, fish, amphibian and reptilian migrations. Migratory mammals are already highly mobile and long-distance migration in most mammals generally requires minimal

physiological modifications prior to starting their migration (Fryxell & Sinclair, 1988; Avgar et al., 2013). Terrestrial mammal migrations are some the greatest events seen in nature, where many large-bodied ungulates embark on lengthy migrations to avoid unsuitable habitats and to seek new foraging grounds (Fryxell & Sinclair, 1988; Briscoe et al., 2017). These animals are able to maintain the intake of food and increase fecundity and survival by seasonal movements between geographic locations (Fryxell & Sinclair, 1988; Berger, 2004; Holdo et al., 2009). Terrestrial ungulates, such as wildebeest (*Connochaetes taurinus*) in Africa, travel hundreds of kilometres at a time to avoid unsuitable environmental conditions and to take advantage of distant, high quality foraging sites after rain events (Hays & Scott, 2013).

In the marine realm, marine mammals travel great distances annually between breeding and/or calving areas and productive foraging areas. For example, elephant seals (*Mirounga* spp.) complete a double migration annually, travelling vast distances (~21,000 km for males and ~18,000 km for females; Le Boeuf et al., 2000) between rookeries in offshore islands and open ocean foraging areas along the edge of the continental shelf (Brillinger & Stewart, 1998; Avgar et al., 2013). Baleen whales (Mysticeti), such as humpback whales (*Megaptera novaeangliae*), right whales (*Eubalaena spp.*) and gray whales (*Eschrichtius robustus*), travel enormous distances (> 9,000 km in one direction) during their seasonal migration to and from summer feeding grounds in high latitudes to shallow winter coastal breeding and calving grounds in low latitudes (Baker & Herman, 1981; Rasmussen et al., 2007; Hays & Scott, 2013). Others, such as the bowhead whale (*Balaena mysticetus*), move relatively shorter distances (~1,000 km) along diffuse migratory pathways that can vary from year to year between feeding and breeding grounds, depending on environmental conditions. While Bryde's whales (*Balaenoptera brydei*) rarely migrate and are thought to undertake feeding and breeding in

warm tropical waters (Bannister, 2002; Hucke-Gaete, Osman, Moreno, Findlay, & Ljungblad, 2004; Ford & Reeves, 2008).

1.2 The benefits of migration

The benefits of animal migration involve an individual's ability to exploit the spatial-temporal variation in foraging sites, environmental conditions, managing risk of predation and/or a combination of these factors (Boyle & Conway, 2007; Shaw & Couzin, 2012; Avgar et al., 2013). The annual cycle of the changing seasons brings with it contrasting differences in duration of the solar day and the energy received and absorbed into the atmosphere (Nebel, 2010). Migratory species have adapted to exploit short-term favourable habitats and foraging conditions that arise across geographical distinct sites through movement (Alexander, 1998). Different life stages may require access to resources found at different locations and migratory individuals within an animal population may gain an advantage for survival and reproduction by moving between locations (Nebel, 2010; Cote et al., 2017). Individuals that remain sedentary during winter conditions may suffer greatly, as they may not find enough food if environmental conditions become adverse (Alexander, 1998; Avgar et al., 2013). The costs and benefits of animal migration can be assessed under the following categories: energy intake, energy expenditure, predation risk and reproduction.

1.2.1 Energy intake

Migrating to areas that support higher productivity (quantity) and quality of food results in an increased energy intake for migrants (Fryxell & Sinclair, 1988; Alerstam et al., 2003; Avgar et al., 2013). Food quantity is likely a limiting factor for migrants synchronizing migration during a narrow window where resources briefly undergo a favourable seasonal increase in abundance. (Fryxell, 1991; Avgar et al., 2013; Cherry et al., 2013). Migrants need to time their

movement with the prevailing spatio-temporal patterns in food abundance and quality. By tracking the favourable environmental conditions, a migrating animal can obtain a continuous foraging opportunities and high-quality energy intake (Alerstam et al., 2003; Avgar et al., 2013). Further, migrants that show high site fidelity (e.g., long-distant migratory birds; Cotton, 2003) in systems with a predictable resource renewal can synchronize and direct their migratory movements as distinct from nomadic movements. To maximise energy intake, migrants aim to depart their current location while foraging conditions are favourable and arrive at next destination just prior to peak foraging conditions (Alerstam et al., 2003; Cote et al., 2017; Keogan et al., 2018).

1.2.2 Energy expenditure

Migration is a very demanding process in terms of both energy expenditure and the time required for migration by many species. Nevertheless, migration can still serve as a strategy that individuals can employ to reduce their annual energy expenditure through efficient thermoregulation and avoiding or shedding ectoparasites to reduce a migrant's parasite load (Alerstam et al., 2003; De La Hera, Díaz, Pérez-Tris, & Luis Tellería, 2009). For endotherms, maintaining a body temperature equilibrium can be energetically very costly, especially when the difference between the temperature of the body and the surrounding environment is very large (Avgar et al., 2013). By migrating to warmer areas where conditions are more favourable for thermoregulation, endotherms can obtain thermal benefits that greatly exceed the costs of the migration itself (Fryxell et al., 1988; Avgar et al., 2013). Parasites inflict a severe metabolic cost on the host, via the direct consumption of nutrients, or as in some ectoparasites, disrupting the host's potential time available for foraging or resting (Hughes, Albon, Irvine, & Woodin, 2009). Terrestrial ungulates, such as elk (*Cervus canadensis*) and

caribou (*Rangifer tarandus*) with high ectoparasite loads will spend time ear flapping and tail wagging, reducing their time spent replenishing or conserving energy (Avgar et al., 2013). By migrating, the host animals can both get rid of ectoparasites, which consequently reduce their energy expenditure, and reduce future infection risk by leaving a habitat where ectoparasites may be more prevalent (Altizer et al., 2011; Avgar et al., 2013).

1.2.3 Predation risk

Migration can reduce the risk of predation in certain populations (e.g., Serengeti herbivore migrants such as wildebeest; *Connochaetes taurinus*), as constant movement provides a refuge for a population being regulated by predators (Fryxell & Sinclair, 1988; Avgar et al., 2013). Typically, predators are unable or unwilling to extend past their home ranges to follow prey over the entire annual migratory cycle. Predators may also be physically unable to follow prey on migratory routes due to metabolic and anatomical adaptations for short-range hunting, which means that they are not able to cover long distances efficiently (Fryxell & Sinclair, 1988; Dingle & Drake, 2007; Avgar et al., 2013). Hence, temporal refuge can reduce predation risk and total mortality for a migratory population compared to a sedentary resident population (Fryxell & Sinclair, 1988; Avgar et al., 2013). Further, local predator populations are often limited in size because they need to rely on an alternate resident prey for most of the year and may consequently be unable to respond to a short-term/temporary overabundance of a migrant prey population.

The combination of temporal refuge and decoupling of predator abundance from the abundance of migrants suggests that the migratory population is likely to be subject to lower predation risk compared to resident populations (Fryxell & Sinclair, 1988). However, migrants may be exposed to a higher risk of predation along migratory routes when travelling in

between seasonal ranges through narrow corridors in high density. For example, the populations of Serengeti migrant species are forced through a bottleneck at select river crossings where they are exposed to significant predation by Nile crocodiles (*Crocodylus niloticus*) (Avgar et al., 2013; Middleton et al., 2013).

1.2.4 Reproduction

Migration is often associated with seasonal fidelity to familiar areas (Anderson et al., 2013). The reproductive benefits arise when the energetic costs incurred from staying in the same habitat outweigh those incurred from migrating to more suitable habitat (Chapman et al., 2012). The ability to exploit more suitable habitats (e.g. optimal thermal regime) through habitat relocation allow energy stores to be focused on behaviours (e.g., establishing mating territories or leks; Wiley, 1978) that are likely to increase the probability of reproductive success (Chapman et al., 2012; Avgar et al., 2013). In the marine environment, males aggressively compete with other males for the opportunity to mate with females through dominant displays or advertisement (Tyak, 1981). For example, dominant male pinnipeds aggressively defend small territories of breeding beaches for the opportunity to mate with individuals occupying his territory (Riedman, 1990). In some baleen whale species, it is thought that lone males sing complex songs to attract a reproductive female for mating. The presence of an additional male has been described as a floating lek and they compete for the opportunity to mate with the individual female. This is opposed to the classical lek (Wiley, 1978), where males compete for, and defend a specific territory, for the opportunity to mate with females that aggregate within the territory (Tyack, 1981; Clapham, 1996). Breeding habitats are typically used repeatedly with populations returning to locations frequented by the migrant population (Anderson et al., 2013; Cherry et al., 2013). High density aggregations

of conspecifics within an area, contrast with sparse aggregations outside the breeding season, increasing the probability of selecting a mate (Avgar et al., 2013). Migratory mammals have relatively long gestation periods and may not reproduce every year (e.g., the bowhead whale reproduces on average every 3-4 years; George et al., 1999) and the ability to migrate to aggregation points for mate finding and successful reproduction crucial for maintaining population fecundity (Avgar et al., 2013).

1.3 The importance of internal state and environmental factors to migration

1.3.1 What factors drive migration?

The motivation for animals to move stems from the basic biological need to replenish energy stores and maximise survival and reproductive success in the annual cycle (Fryxell & Sinclair, 1988). The influence of intrinsic and extrinsic factors such as habitat suitability, predation risk, competition and food availability often form the foundations of why animals move (Nathan et al., 2008). While migration is often the adaptive behavioural response to spatio-temporal patterns in these factors, it is often difficult to identify a single factor as the stimulus for migratory behaviour (Avgar et al., 2013; Jachowski & Singh, 2015).

1.3.1.1 Intrinsic factors (reproduction, physiology)

The internal state of an animal has been identified as a major factor in determining what stimulates animals to move. This may override extrinsic factors that are commonly thought to explain animal movements and ultimately migration behaviour (Cooke, 2008; Nathan et al., 2008; Jachowski & Singh, 2015).

Reproduction

Mate seeking and reproduction are innate traits and two of the key underlying drivers of migratory behaviour in many species, especially in populations where seasonal aggregations coincide with females being sexually receptive (Fryxell & Sinclair, 1988; Dingle & Drake, 2007). Males and females differ in their ecological and physiological needs and in populations that aggregate as family groups, a single sex (e.g. males) may range outside the family group during migration to breeding sites to seek potential mates (Fryxell & Sinclair, 1988; Avgar et al., 2013). This separation has been documented in both terrestrial (e.g. African elephants (*Loxodonta africana.*; Hollister-Smith et al., 2007) and marine environments (e.g. long-finned pilot whales (*Globicephala melas*; Amos, Barrett, & Dover, 1991).

Physiology

Physiology plays an integral and fundamental role in animal migration, as travelling long distances between habitats requires adaptations for efficient energy use (Lennox et al., 2016). Endogenous mechanisms prime and regulate physiological processes that impact migration behaviour such as timing, locomotion and synchronicity of migration (Dingle & Drake, 2007). The accumulation of energy reserves is an essential mechanism that supports migration behaviour and translates physiologically into animal endurance (Lennox et al., 2016). Recent studies that have monitored the internal state of free-moving ungulates in the wild have discovered direct linkages between the internal physiological state of animals and their movement behaviour (Bowlin et al., 2010; Jachowski & Singh, 2015). For example, in male African elephants, measuring testosterone levels enables researchers to identify when individuals are in must and thus provide an indicator of when movement behaviours are likely to be observed (Poole, 1987; Jachowski & Singh, 2015). However, the motivation to migrate may vary among different demographic groups within the population, depending on

physiological state of different age and sex classes. These intrinsic factors, interacting with the prevailing extrinsic factors, have the potential to influence the migratory strategies adopted by individuals differently (Alerstam et al., 2003; Cote et al., 2017). Ongoing studies in physiological energetics, with a focus on free-ranging organisms, aim to further understand the physiological limits of an organism combined with external environmental factors and their impacts on animal movement and migration (Jachowski & Singh, 2015). For example, tracking studies of invertebrate (e.g., locus) and avian movement suggest correlations of the time of movement with periods of optimal wind direction/speed, migratory movement and the associated energetic benefits of these conditions (Jachowski & Singh, 2015).

1.3.1.2 Extrinsic factors (abiotic factors, resource availability, competition and predation)

Extrinsic factors represent all aspects of the abiotic and biotic environment influencing animal movement (Fryxell & Sinclair, 1988). Movement in space and time requires an ability to sense and respond to information about the spatio-temporal dynamics of the environment, including the distribution and abundance of other individuals (Dingle, 1996; Nathan et al., 2008).

Abiotic factors

Migratory behaviour is often driven by shifting environmental gradients as seasons change, where populations are stimulated to move in response to changing abiotic conditions or resource availability (Avgar et al., 2013; Hauser et al., 2017). In pelagic systems, currents and oceanographic features (e.g., upwellings, eddies, fronts, filaments, changes in vertical mixing) are the major factors influencing environmental variability over intra-annual time scales that may have a direct impact on migratory behaviour (Briscoe et al., 2017). Seasonal changes in water temperature can influence migratory behaviour, especially in endotherms that need to

remain in warm tropical waters year around. For example, the West Indian manatee (*Trichechus manatus*) and the more southern populations of Australian dugong (*Dugong dugon*) move to warmer waters during cooler winter months (Gales et al., 2004; Avgar et al., 2013). Conversely, populations of dugongs at lower latitudes are influenced more by changes in water depth and the hydrological cycle than water temperature (Gales et al., 2004; Avgar et al., 2013).

Changes in the physical environment influence migratory behaviour (Fryxell & Sinclair, 1988; Cherry et al., 2013). In the Arctic, migration can be directly linked to the fluctuating seasonal sea ice dynamics. For example, polar bears (*Ursus maritimus*), wait for complete ice melt in Hudson Bay before migrating south (Cherry et al., 2013). Some mammalian species carry heavy ectoparasite loads (e.g. whale lice: *Cyamus spp.*), such as baleen whale species (e.g. humpback whales; Clapham, 2000; Altizer et al., 2011) and migration in some species has been suggested to be a behavioural mechanism to reduce such loads, with the parasites unable to adjust to the change in temperatures experienced (Alerstam et al., 2003; Altizer et al., 2011). Such hosts are able to shed the majority of unwanted ectoparasites during these migrations and return to feeding grounds and tolerate parasites that may be prevalent in that habitat (Alerstam et al., 2003; Altizer et al., 2011). However, little evidence is available to demonstrate links between the prevalence of ectoparasites as a significant threat to the health of individuals and as a motivating force for migratory behaviour (Clapham, 2000).

Resource availability

Resources that vary in quality across spatio-temporal gradients are often thought to be a fundamental factor in some animal migrations. This is commonly seen in the movements of marine megafauna between regions, where suitable conditions for breeding and foraging are

potentially located in different areas and seasonal migrations are therefore required for reproduction and foraging (e.g., elephant seals; Le Beouf et al., 2000) (Alerstam et al., 2003; Block et al., 2011; Hays et al., 2016). Populations may migrate to take advantage of optimal foraging times and enter dormancy during times of scarce resource availability as a strategy for survival. Migrants that are unable to time migration to take advantage across time and space when resources are abundant will lower their liklihood of breeding and reproductive success (Dingle, 1996; Alerstam et al., 2003; Dingle & Drake, 2007).

Competition

Within a population, migration behaviour may differ across age and sex classes (Cote et al., 2017). Typically, juveniles and females may be more likely tomigrate further than males of the same species (Fryxell & Sinclair, 1988). Competition is often thought to explain such differential migration patterns within a population, either as intra- or inter-competition among populations (Alerstam et al., 2003). In general, for some species dominant individuals will displace subordinates, and will move to migration areas further from breeding and optimal foraging ranges. For example, synchronous breeding in older migrant seabirds within small areas and already established nest sites forced younger birds to nest further away from the main colony in isolation (Coulson, 2001). Additionally, juveniles typically seek areas away from parents to avoid competition for resources and/or potential inbreeding during breeding migration (Alerstam et al., 2003; Dingle & Drake, 2007). High density populations may potentially impact the timing of migration of different age classes within a population to ensure that unnecessary competition for resources is avoided (Fryxell & Sinclair, 1988). However, competition will work in combination with other extrinsic factors such as suitable habitat, resource productivity and the intrinsic factor associated to reduce the cost of migration (Alerstam et al., 2003).

Predation

Predation pressure has been identified as an important selective factor in species anti-predator adaptation, one of those being migration (Ford & Reeves, 2008; Avgar et al., 2013). Research has shown that in microscopic oceanic organisms, such as zooplankton, predation has been linked as a main factor in the evolution of diel vertical migration (Zaret & Suffern, 1976). However, in larger migratory species, less is understood of how predation risk influences seasonal migrations (Fryxell & Sinclair, 1988; Avgar et al., 2013). It has been hypothesised that predation on neonates drives migration during the calving season in both terrestrial and marine systems (Avgar et al., 2013). Examples of such predation are well documented in bighorn sheep (*Ovis canadensis*); (Festa-Bianchet, 1988), caribou (*Rangifer tarandus*); (Bergerud, Ferguson, & Butler, 1990; Heard, Williams, & Melton, 1996) and baleen whales (Corkeron & Connor, 1999; Connor & Corkeron, 2001; Ford & Reeves, 2008). However, it is particularly difficult to isolate the potential impact of predation from other extrinsic and intrinsic factors as a main driver of migratory behaviour. Predation pressure may play a role in shaping behaviour and may in fact act in combination with other known factors (Fryxell & Sinclair, 1988).

1.3.2 What factors trigger migration timing?

The abiotic and biotic triggers for migration can be difficult to identify and often combine with external and internal drivers for migration to further complicate migration behaviour. It can be the onset of an annual environmental events or other distinct seasonal changes that trigger individuals to migrate to exploit alternate habitats (Nebel, 2010; Li, Zhang, & Yin, 2014; Briscoe et al., 2017).

1.3.2.1 Intrinsic Factors

Gene expression and the endocrine system are now known to play a role in controlling migration (Nebel, 2010; Liedvogel et al., 2011). Analyses of the DNA of migratory species have identified genes and networks of genes that contain a 'migratory gene package' that have been used to characterise and track the genotypic and phenotypic expression of a migratory individual (Liedvogel et al., 2011). In migratory species, such as birds, fish and insects, specific hormones within the endocrine system regulate physiological functions within the body associated with responding to the external environment and movement (Jachowski et al., 2015). For example, releasing stress hormones becomes the physiological mechanism that drives a behavioural response (e.g., movement) to an environmental stressor (Nebel, 2010; Jachowski et al., 2015). However, further research is required to understand the role of the endocrine system in movement ecology across different taxa and key life history transitions (Nebel, 2010; Jachowski et al., 2015).

1.3.2.2 Extrinsic factors

For some migratory populations, migratory behaviour may be triggered by a specific change in environmental conditions or onset of a seasonal event. The migration of anadromous Pacific salmon (*Oncorhynchus* spp.), juveniles downstream and adults upstream, relies on temperature cues in combination with photoperiod length to initiate migration (Scheuerell et al., 2009; Anderson et al., 2013). Furthermore, salmon migrations are triggered by a combination of environmental factors such as sea surface and air temperature, sea ice cover, currents and photoperiod length (Anderson et al., 2013; Hays et al., 2016). The link between photoperiod and migration onset have be correlated in many bird species (e.g. garden warblers, *Sylvia borin*; Gwinner, 1996) in conjunction with specific seasonal environmental changes. Some bird species will alter migration in response to changes of certain triggers,

such as climate (Nebel, 2010; Cherry et al., 2013). However, the extrinsic or intrinsic triggers for mammals are much less known and which have potential influence on the seasonal migrations (Cherry et al., 2013).

1.4 Factors influencing migration in cetaceans

Migration is a common behaviour in both toothed (Odontoceti) and baleen whales (Mysticeti), where this behaviour is thought to be determined by a seasonal trade-off between optimal environmental conditions for breeding and feeding. This results in most migratory cetaceans routinely returning to distinct breeding and feeding grounds, particularly for baleen whales that maintain predictable migratory routes (Gaskin, 1982; Corkeron & Connor, 1999; Avgar et al., 2013). However, migratory patterns in toothed whales are generally less predictable than those of baleen whales with shorter distances travelled at irregular intervals (Gaskin, 1982; Durban & Pitman, 2012; Avgar et al., 2013).

1.4.1 Odontoceti (toothed whales)

Migrations of toothed whales between breeding and feeding grounds occur, however their migratory patterns appear to be quite unpredictable (Gaskin et al., 1982). Killer whales (*Orcinus orca*) in sub-Antarctic regions are thought to migrate into subtropical waters during winter months to shed diatom parasites that inhabit the colder waters and allow the skin to regenerate in the absence of these parasites (Ford & Reeves, 2008; Durban & Pitman, 2012). This behaviour may also be seen in other toothed whales, such as the beluga whale (*Delphinapterus leucas*), and this helps maintain thermal integrity through repairing and replacing a damaged external skin layer (Durban & Pitman, 2012). Whether such factors act as primary or secondary drivers of migration in toothed whales are yet to be determined, as

obtaining nutrition and reproduction have been suggested to be the two major factors that influence migrations (Ford & Reeves, 2008; Durban & Pitman, 2012).

The ice-adapted beluga whale (an odontocete) is distributed throughout the Arctic. Though some populations remain sedentary throughout the year, many populations adopt large-scale migratory movements annually (Bailleul et al., 2012). This migratory behaviour is generally thought to be an adaptation to resource availability that fluctuates spatio-temporally from year to year (Tynan & DeMaster, 1997; Bailleul et al., 2012). Belugas use environmental cues such as ocean temperature, prey distribution and quantity to adjust the timing of their migrations and ensure optimal foraging opportunities (Bailleul et al., 2012). As water temperatures fluctuate in cooler months, most marine endotherms need to seek warmer temperatures through migration. However, small odontocetes have evolved efficient thermoregulation strategies that permit them to remain in cooler waters to give birth to young and take advantage of the abundance of the ectothermic fish they prey on before migrating (Dingle, 1996; Corkeron & Connor, 1999; Bailleul et al., 2012). In contrast, bowhead whale, which has the thickest blubber of any whale (up to 50 cm deep), remain in arctic waters almost all year (Nerini, Braham, Marquette, & Rugh, 1984). The largest of the toothed whales, the sperm whale (*Physeter macrocephalus*), undergo migrations but not as predictably as other whale species (Whitehead, 2003). This species is distributed globally through tropical and subtropical waters, but the social organization of populations result in seasonal segregation by reproductive class, age and sex (Best, 1979). Females and immature males maintain tropical and subtropical distributions year-round, while sexually mature males become solitary during the summer months (Christensen, Haug, & Øien, 1992). Males undertake migrations towards high latitude polar regions, possibly in a north-south manner

where they may stay for several winter seasons before returning to tropical waters to breed (Lyrholm et al., 1999; Whitehead, 2003).

1.4.2 Mysticeti (baleen whales)

Most baleen whales make seasonal migrations between productive high-latitude feeding grounds in summer and low-latitude oligotrophic breeding grounds in winter (Baker & Herman, 1981; Corkeron & Connor, 1999; Rasmussen et al., 2007). Polar regions are the preferred habitat during spring and summer months as they see a substantial increase in food production at this time (Gaskin 1982; Corkeron & Connor, 1999; Avgar et al., 2013). During winter months, baleen whales generally will not feed while migrating to breeding grounds in sub-tropical and tropical waters that are ideal for calving (Rasmussen et al., 2007; Rizzo & Schulte, 2009). Humpback whales (Clapham, 2009), fin whales (*Balaenoptera physalus*; Mizroch et al., 2009), gray whales (Killingley, 1980), blue whales (*Balaenoptera musculus*; Mate et al., 1999) and right whales (Bannister, 1990) are examples of baleen whales that perform such seasonal migrations and may travel up to 9,000 km in one direction (Rasmussen et al., 2007; Avgar et al., 2013). Other baleen species, such as sei whales (*Balaenoptera borealis*; Baumgartner & Fratantoni, 2008) and bowhead whales (Laidre et al., 2008) embark on relatively shorter-distance migrations that vary with fluctuating environmental conditions (Hucke-Gaete et al., 2004; Ford & Reeves, 2008).

The major hypotheses proposed as stimuli for baleen whale migration include; thermoregulatory and energetic benefits of warmer waters on breeding grounds during winter (Brodie, 1975), calmer waters to increase calf survival on breeding grounds (Clapham, 1996), s strategy to avoid predators by maternal females and calves (Corkeron & Connor, 1999), greater opportunities for males to compete for reproductive females (Clapham, 2001)

and to reduce the parasite load on an individual (Altizer et al., 2011). The warmer coastal waters of low-latitude breeding grounds provide optimal calm surface conditions that minimise energy consumption and heat loss during winter months when food availability is low in the high-latitude regions (Brodie, 1975; Cartwright et al., 2012; Taber & Thomas, 1982). The energetic costs for female baleen whales are high during gestation/lactation, as they rely primarily on their stored energy resources when fasting until returning to feeding grounds to complete the annual migratory cycle (Chittleborough, 1958; Lockyer, 2007; Christiansen et al., 2016; Christiansen et al., 2018). The warmer, calm waters of the low latitudes benefit the growth and development of newly born calves (Craig, Herman, Gabriele, & Pack, 2003). Physiologically, the benefits to neonate calves of these conditions are that energy that would be used for heat production in polar regions is, instead, used for growth in warmer waters (Clapham, 1996; Corkeron & Connor, 1999).

Neonates are highly susceptible to predation pressure from killer whales, and group migratory behaviour is considered to be an anti-predator strategy for mothers and calves (Corkeron & Connor, 1999; Ford & Reeves, 2008; Cartwright et al., 2012). Although, predator pressure is an important source of mortality, whether predation is a primary migration stimulus is a topic of debate (Clapham, 2001; Ford & Reeves, 2008). After leaving the breeding and nursing grounds and migrating towards natal feeding grounds, maternal females and calves experience predatory pressure from killer whales (Mehta et al., 2007). Calf survival (Chittleborough, 1958) and swimming ability (Ford & Reeves, 2008) increases with calf body size, which is influenced by the energy budget of the maternal female-calf pair, as the stored fat of the female is the sole source for nutrition for both mothers and calves (Chittleborough, 1958; Cartwright et al., 2012).

1.5 Gaps in scholarly knowledge

It is evident that animal migration is a well-studied topic across the different phyla and that a thorough understanding of the underlying drivers of such movements is needed to enhance the management and conservation of the species. However, research on the intrinsic and extrinsic factors that stimulate or combine to stimulate the timing of migration of individuals is still largely lacking. Here I have investigated the cues for migration in a model migratory species, the southern right whale, and aim to further contribute to scholarly knowledge on the factors that influence the migratory timing of this species.

1.6 Project aims

The overall aim of this project is to determine the relationship between migratory timing in southern right whales and intrinsic and extrinsic variables on their breeding grounds. More specifically, it is hypothesised that the probability of departure of maternal individual right whales is determined by their body condition rather than by calf size or by environmental variables such as water temperature and diurnal period. This study is the first to our knowledge to test predictors of migration for baleen whales on a winter breeding ground and it aims to further build a better foundation for understanding the underlying stimuli that initiates migration and facilitate the further development of models about the ecology and physiology of migrating individuals. This study develops an understanding of factors influencing the residency time and migratory cues for southern right whales found in the coastal regions of Australia during the winter months.

2. Materials and methods

2.1 Study species and study area

Southern right whales are distributed throughout the Southern Hemisphere latitudes from 16 ºS to 65 ºS and seasonally migrate between productive high-latitude feeding grounds in summer and low-latitude oligotrophic breeding grounds in winter (Bannister, 2001). Separate, genetically distinct, breeding populations exist in Australia (Bannister et al., 1997), New Zealand (Patenaude et al., 2001), South Africa (Best et al., 1993), western South America (Chile and Peru; Vernazzani, Cabrera, & Brownell, 2014) and eastern South America (Argentina and Brazil, Rosenbaum et al., 2000; Patenaude, Todd, & Stewart, 2001). The seasonal population of southern right whales in Australian waters are divided into an eastern (*n=257*) and a western *(n=2,200)* sub-population through genetic differentiation (Carroll et al., 2018) and individual photo identification determined the differing population sizes and reproduction rates (Bannister, 2017). Compared to a ~7% per annum rate of increase for the South African population (Best, Brandão, & Butterworth, 2001), the western Australian sub-population increased by ~ 5.6 % annually from 1991 to 2016, while the eastern sub-population has shown no signs of growth during the same period (Bannister, 2017; Charlton, 2017). During May to October, the western sub-population is distributed in waters off southern Western Australia and South Australia, while the eastern sub-population is distributed in waters off Victoria, Tasmania and New South Wales (Bannister, 2017).

The Head of Bight (HoB), South Australia, is an important winter aggregation and calving ground within the coastal waters of the Great Australian Bight Commonwealth Marine Reserve (Figure 1). It is estimated that up to 48% of the western sub-population of southern right whales in Australia use this aggregation area during the breeding season at peak times

between late May and early September (Burnell & Bryden, 1997; Charlton, 2017). Southern right whales tend to migrate to coastal, shallow-water calving areas where neonates can be protected from rough weather and defended from attacks by predators (Pirzl, Patenaude, Burnell, & Bannister, 2009). Female right whales become sexually mature from around 5 years of age (mean age of first calf in HoB is 9.1 yrs; Burnell, 2008) and produce a single calf on average every 3-4 years (Burnell, 2008). This inter-calving interval consists of 1 yr gestation (Best et al., 2001), 1 yr lactation (Tormosov et al., 1998) and 1 yr for the whale to recover and replenish energy reserves (Brandão et al., 2010; Cooke et al., 2001).

The study site at HoB (31° 29' S, 131° 08' E) is situated within the Great Australian Bight (GAB) on the western edge of South Australia and 300 km west of Ceduna (Figure 1). It is situated within the coastal waters of the GAB Commonwealth Marine Reserve and Marine Mammal Protection Zone, which extends over an area of ~ 9,000 km^2. The study site habitat consists of shallow (5-20 m), gently sloping sandy bays, with cliffs on the western edge providing some protection from the dominant south-westerly winds and swell. Whales are generally seen along these cliffs and sandy bay within the study site within 50-2,000 m of shore (Charlton, 2017), providing opportunities to observe and collect data with an unmanned aerial vehicle (UAV).
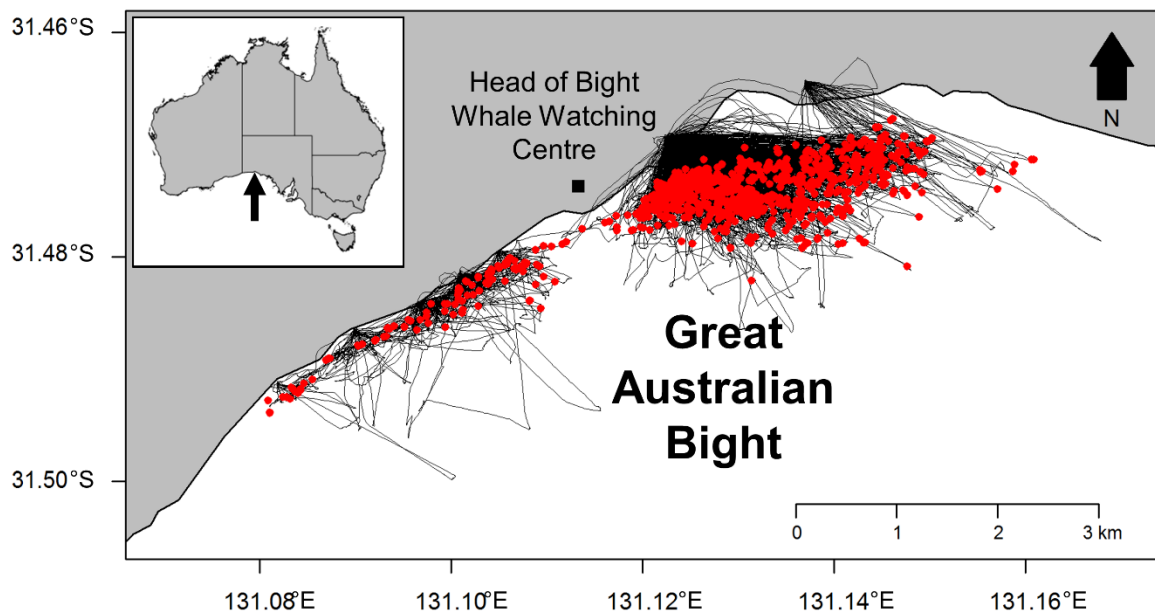
Figure 1. Head of Bight study area in South Australia, displaying the unmanned aerial vehicle flight tracks (solid lines) during the study period (24 June to 25 September 2016) and the positions of the photographed southern right whale females and calves (red points) used in the analyses. n = 1118 measurements (from Christiansen et al., 2018).

2.2 Data collection

Aerial photographs of southern right whale mother and calves were taken at HoB between 24 June and 25 September 2016 coinciding with the peak times of the breeding migration. A DJI Inspire 1 Pro quadcopter UAV (56 cm diameter, 3.5 kg) was flown (mean flight time = 13 min) from land and out to sea at altitudes of 5 to 120 m, within 2 km of the coast. The UAV was equipped with a 16 megapixel DJI Zenmuse X5 micro four-thirds camera and an Olympus M.Zuiko 25 mm f1.8 lens and polarized filter for capturing images. A gimbal was used to provide stability during operation and account for pitch and roll of the UAV. It also allowed the camera to be remotely rotated and positioned vertically by the pilot on shore in preparation for image capture. While photographing a whale, the UAV was positioned to hover directly above the animal for up to a maximum time of 10 min, at altitudes of between 20 and 50 m, until adequate photographs were obtained.

Photographs ideal for sampling were considered those of a whale situated flat at the surface, dorsal side facing up, with straight body axis and peduncle that was non-arching (Figure 2) (Christiansen et al., 2016a, 2018). The UAV operator was able to remotely view and correct the position of the UAV above a whale. They were also able to ensure adequate quality of the images via a video live feed from the UAV camera, streamed through an iPad Air tablet attached to the UAV remote control. The UAV was retrofitted with a Lightware SF11/C laser range finder (Lightware Optoelectronics, weight: 35 g), mirroring the setup used by Christiansen et al. (2018) to measure the altitude of the UAV above sea level during flight. Downward facing sensors were attached at the rear of the UAV to provide the range finder with an altitude accuracy within 0.1 m, measurement resolution of 1 cm and record distance 20 times per second with a 15-mW laser. The pitch and roll of the UAV during operation were recorded with a compass and tilt sensor that were connected to the range finder. During operation, the altitude (*H*, in meters) of the UAV above sea level was calculated by adjusting for the pitch and roll of the UAV and multiplied by the distance (Dist) measured by the range finder (Christiansen et al. 2018):

$$H = cos(pitch) \times cos(roll) \times Dist \tag{1}$$

where pitch and roll are given in radians and distance is given in meters. During post-flight processing, the range finder data were matched to the vertical photographs of the whales using the GPS time stamps of the range finder attached to the UAV.
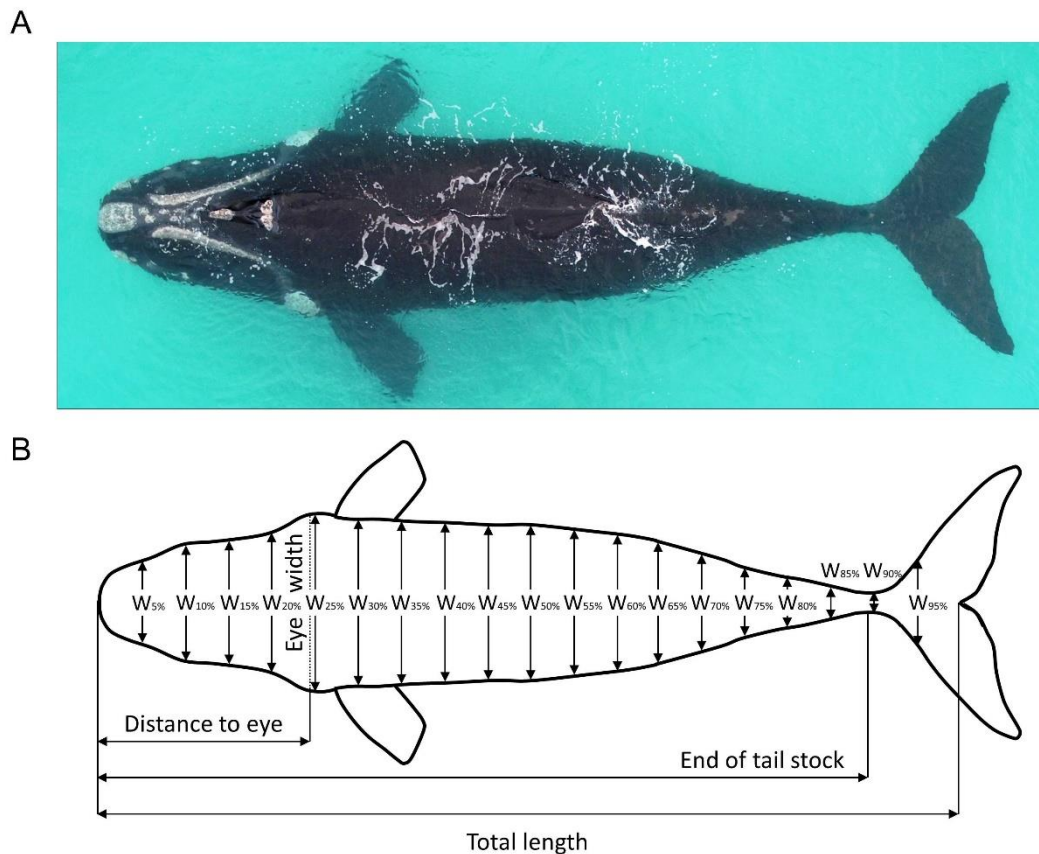
Figure 2. (A) Example aerial photograph of a southern right whale used to measure body volume. Only photographs in which the whale was lying flat at the surface, with its dorsal side up and with a straight body axis and non-arching peduncle, were used in the. *(B)* Positions of measurement sites used in the study. The dotted line indicates the location of the eye width measurement, located at 25 and 20% body length from the rostrum for lactating females and calves, respectively. W: width (from Christiansen et al., 2018).

2.3 Determining departure times of individuals

Individual southern right whales were identified through high-quality photographs taken from the UAV while hovering vertically above an animal. The UAV was positioned to take images focused on the dorsal surface of the head, where the unique callosity patterns (keratinised skin patches colonised by cyamid spp.) allow individuals to be identified. These unique markings persist throughout the life of juvenile and adult right whales and are present on the dorsal surface of the rostrum, lip line of lower jaw and posterior to the blowhole (Payne et

al., 1983). By repeatedly sampling the same whales through the breeding season, we were able to create a catalogue of sightings histories for individual whales.

The first and last sighting of each whale was extracted from the individual sighting histories. It is possible that animals sighted at the beginning of the field season may have been present prior to the start of sampling. Similarly, animals still present in the study area at the end of the field season, might not have departed until later. To avoid this edge effect, we calculated the number of days between sightings of individual whales. A cumulative density distribution was then created to represent the probability of resighting an individual whale as a function of days since the last sighting (Figure 3). The 95% threshold for this distribution was determined, which represents the number of days needed to resight an individual whale present in the study area with 95% probability (*n = 18*; Table 1). A departure threshold date was then calculated based on this threshold, with animals sighted after this threshold being removed from further analyses. The remaining animals represented individuals for which we knew the departure date into the study area with 95% certainty.
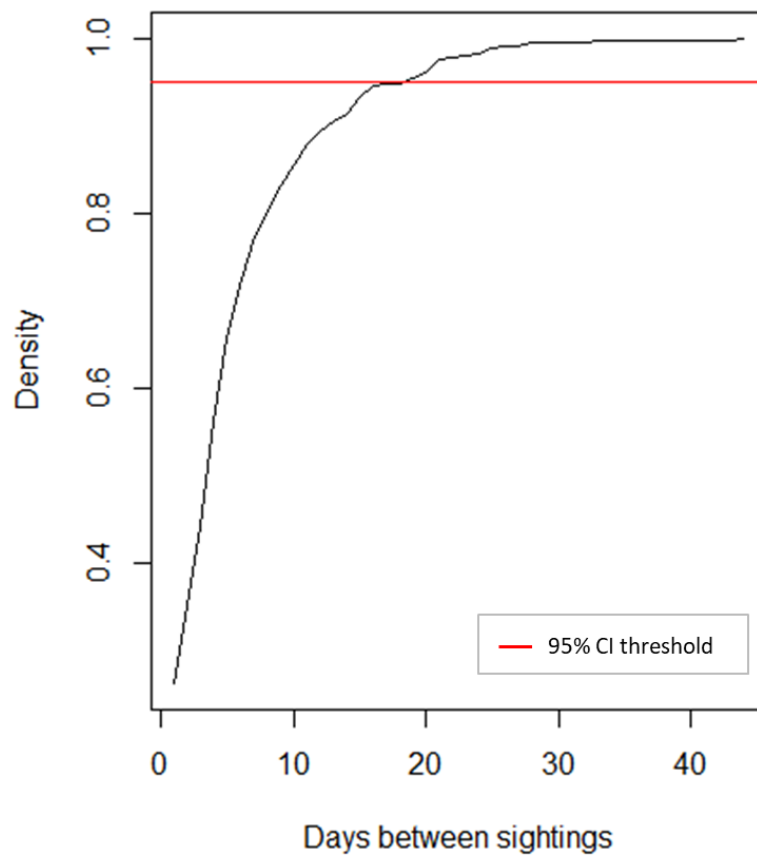
Figure 3. Cumulative density distribution of days between last sightings of southern right whale mother-calf pairs with an 18-day (95% confidence interval) threshold (shown by the red horizontal line) applied

2.4 Variables influencing departure time

2.4.1 Intrinsic variables

Body condition: Aerial photogrammetric methods were used to determine morphometric measurements from the best vertical photographs obtained of whales, following the approach of Christiansen et al. (2016a, 2018). During post-flight processing the best images of identified individual whales for each flight were selected (both body condition and ID) and graded. Key attributes such as; camera focus, body straightness, body roll, body arch, body pitch (vertically), body length measurability and body width measurability were given a

quality score of 1 (good), 2 (medium) or 3 (poor) for each (for details, see Christiansen et al. 2018). Any photographs that were given a quality score of 3 were removed from further analyses. Furthermore, photographs that were given a quality score of 2 for both arch and pitch, pitch and roll or arch and roll were also removed from further analyses. From the selected photographs, the body length of the whale (from the tip of the rostrum along the axis of the whale down to the notch of the tail stock) and the body width (W) (at 5% length intervals along the entire body length of the whale, i.e. 19 measurements in total) were measured (in pixels) (Christiansen et al. 2016a, 2018), using a custom written script in R. To convert the pixel measurements to actual size (in meters), the relative size of the whale in each photograph was estimated based on the known resolution of the image (4698 x 3456 pixels). This proportion was then converted to meters using the known size of the camera sensor (17.3 x 13.0 mm) and scaled to the size of the whale in meters by multiplying it with the scale factor *C*:

$$C = \frac{H}{f} \qquad (2)$$

where *H* is the altitude (m) of the UAV above the water surface during operation and *f* is the focal length (25 mm = 0.025 m) of the camera lens. Following the methods described by Christiansen et al. (2018) and assuming a circular cross-section shape of the whales, the body volume of each whale was calculated by first estimating the radius at each width measurement site (r = W/2), from which the body volume (m³) of each segment (V_s) was calculated:

$$V_s = \frac{1}{3} \pi h (r^2 + rR + R^2) \qquad (3)$$

where h is distance (m) between 2 adjacent body width measurements along the body axis (h = 0.05 x total length), r is the radius of the smaller girth section while R is radius of the larger girth section. The total body volume (V_{total}) could then be estimated;

$$V_{total} = \sum_{s=1}^{s} V_s$$
(4)

where s is the total number of segments along the length of the body from the rostrum that were measured. In adult and maternal females, the estimated body volume included only those body segments between the position of the eyes to the end of the tail, which has been shown to be the metabolically active areas in baleen whales (Christiansen et al. 2016a, 2018).

Following the methods of Christiansen et al. (2014, 2016a), body condition (BC) was then calculated for each individual whale:

$$BC_i = \frac{BV_{Obs,i} - BV_{Exp,i}}{BV_{Exp,i}} = \frac{\epsilon_i}{BV_{Exp,i}}$$
(5)

where $BV_{Obs,i}$ and $BV_{Exp,i}$ are the observed (measured) and expected (predicted) body volume of the individual whale i. BV_{Exp} was estimated for each individual from the linear log-log relationship between BV and body length, fitted using linear models in R (Figure 4). Hence $BV_{Exp,i}$ represent the expected (predicted) body volume of individual i given its known body length. A positive BC is an indication that an individual is in relatively better than average condition, a negative BC indicates that an individual is in relatively poorer than average condition. This body condition index allows the body condition of individual whales of different sizes (lengths) to be compared as it accounts for variation in body length between individual whales.

Calf size: The body volume and condition of calves was estimated in a similar way to that described above for adults. Southern right whale calves increase in relative body width as they grow, also across their head region (Christiansen et al. 2018). The body volume of calves was therefore estimated for the entire body from the tip of the rostrum to end of the tail stock, with exception of only the fins and fluke. Similarly, the length of calves was obtained by measuring from the tip of the rostrum along the axis of the whale to the end of the tail stock.

2.4.2 Extrinsic variables

Diurnal period

Data on diurnal (day) period were obtained for the study site at HoB (31° 29' S, 131° 08' E, 9.5 h east of Greenwich UTC) throughout sampling during the field season for 2016 from the U.S. Naval Observatory Astronomical Applications Department (Washington, DC; http://aa.usno.navy.mil/data/docs/Dur_OneYear.php).

Sea surface temperature

Sea surface temperatures (SST) were obtained from the Australian Ocean Data Network (AODN; https://portal.aodn.org.au/search) for the field season. These data come from a combined Integrated Marine Observing System (IMOS) and CSIRO Oceans and Atmosphere SST dataset using a SRS Satellite (MODIS Ocean Colour and SST), with a 1-day composite average with a point series (31° 40' 12'' S, 131° 7' 48'' E) spatial resolution. Sea surface temperature data were not available for each day of sampling, with measurements available every four days on average. To account for the missing data, linear interpolation in Excel was used to predict missing SST data between two known measurements.

2.5 Data analyses

To determine the relationships between whale departure time from the study site (the probability that a specific sighting was the last one sampled for an individual for the season), i.e. the response variable, and the explanatory variables (body condition, calf size, diurnal period and SST), separate binomial generalised linear models (GLMs) with logit link functions (whale presence and absence data) were developed in R Studio (Version 1.1.423 – © 2009-2018 R Studio, Inc.). For each individual whale, two values of each explanatory variable were extracted: one at the last measurement occasion (the last day a specific individual was sampled), representing the observed departure state of the animal, and one on a random day through the sampling period for that individual (from all sightings prior to the departure day), representing the presence state of the animal. By selecting a single presence measurement for each individual, potential issues with temporal auto-correlation, from using multiple samples of the same individual in time, were avoided.

To assure that our random selection of presence data points was robust, bootstrapping resampling methods were used, where the process of randomly selecting presence data points (the departure data point was always the same) was repeated 1,000 times, and each model was refitted. The resampling process resulted in a density distribution around each parameter value (1,000 values for each parameter) for each model. Model selection, using Akaike's Information Criterion (AIC), was then performed to determine which explanatory variable was the best predictor of the departure time of the whales from the breeding grounds. The selection was based on the mean AIC value for each model from the bootstrap output (1,000 AIC values for each model).

Model validation tests were undertaken to ensure identification of any violations of assumptions for the models tested. This included examining scatter plots of the residuals and fitted values and residuals and each explanatory variable fitted in the model. Normality of residuals was tested with Quantile-Quantile (QQ) plots and residual histograms (Figure 4). We also tested for influential points and outliers using leverage and Cook's distance. Collinearity between the explanatory variables was investigated by estimating the variance inflation factor, using a threshold of 3 to indicate collinearity between variables. Collinearity was further investigated by fitting linear models between each explanatory variable. If two explanatory variables were found to be significantly correlated, the one with the lowest AIC score was kept in the analyses.
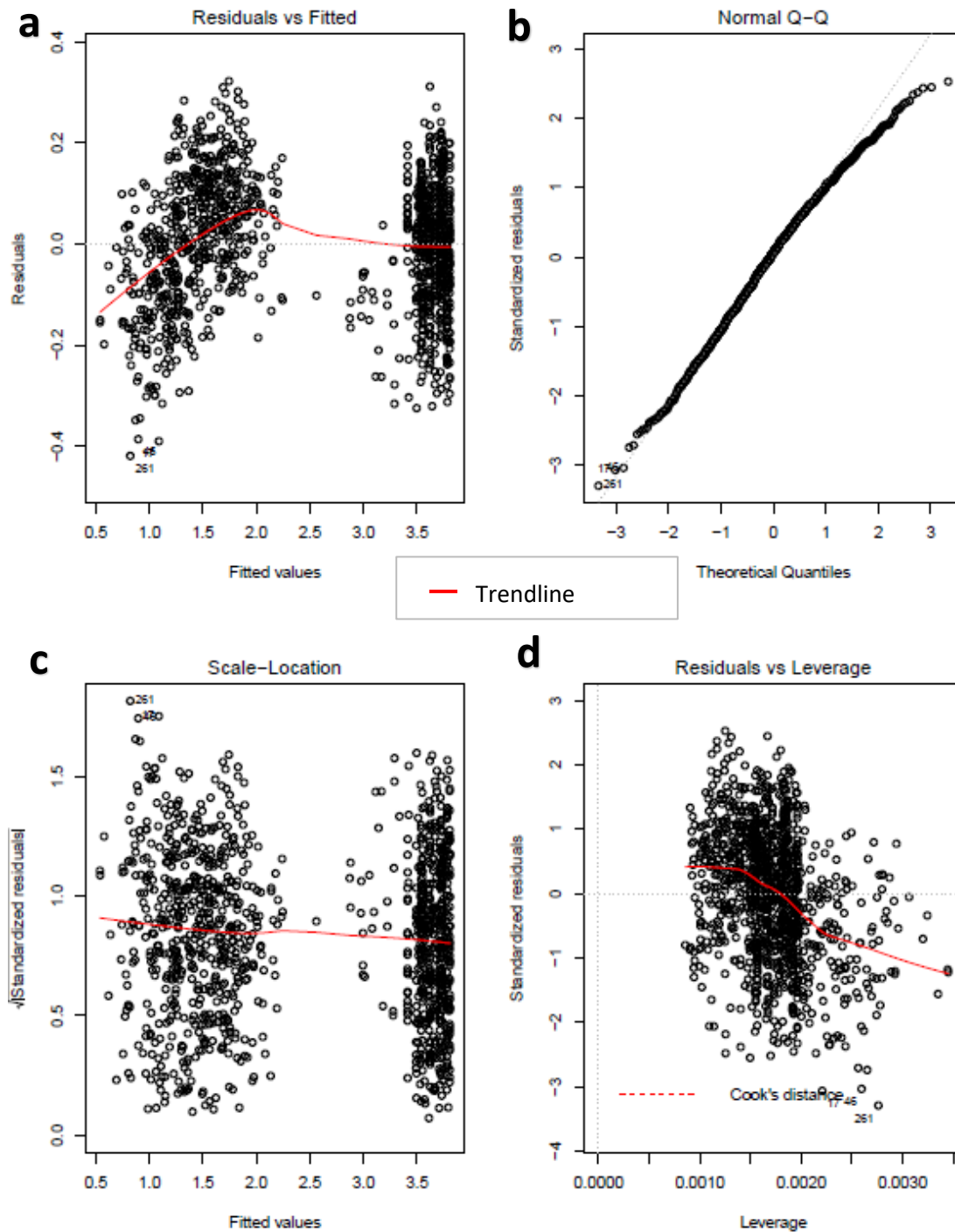
Figure 4. Model validation tests were undertaken to ensure identification of any violations of assumptions for the models tested. Heteroscedasticity in residuals was tested with (a) scatter plot of the residuals versus fitted values and (c) standardized residuals versus fitted values. (b) normality of residuals was tested with Quantile-Quantile (Q-Q) plots. (d) Influential points and outliers were tested using leverage and Cook's distance.

3. Results

Fieldwork was carried out between June 24 and September 25, 2016, a duration of 93 days. During this time, a total of 878 UAV flights (175.5 h) were completed on 49 days (52.7%). A total of 3,354 aerial photographs of whales were taken (average of 4 individual whales per flight), of which 2,890 (86.2%) could be used to measure body condition. Filtering the aerial photographs by picture quality resulted in 1,118 images remaining from 40 mother and calf pairs, each sampled over periods ranging from 40 to 89 days (Table 1).

Table 1. Mother-calf pairs (*n=40*) remaining after image filtering process with Julian Day final measurement provided for individuals, days until last day of 2016 season and maternal body condition recorded on last day of measurement. Shaded individuals indicate animals that were removed from analysis because they were below the 18-day (95% CI) threshold (*n=22*) applied, additionally individuals with above average body condition in bold (*n=2*) at departure from breeding grounds were classified as transient individuals and removed from analysis.

#	Mother ID No.	Last Day Measured (Julian Day)	Last Day of Season (Julian Day)	Days Until End of Season	Maternal Body Condition
1	3	223	268	45	-0.113
2	**21**	**223**	**268**	**45**	**0.045**
3	13	224	268	44	-0.064
4	**6**	**225**	**268**	**43**	**0.046**
5	14	225	268	43	-0.006
6	5	226	268	42	-0.268
7	11	226	268	42	-0.074
8	19	228	268	40	-0.106
9	8	229	268	39	-0.109
10	7	234	268	34	-0.207
11	10	235	268	33	-0.028
12	12	238	268	30	-0.256
13	27	238	268	30	-0.118
14	22	241	268	27	-0.116
15	4	243	268	25	-0.204
16	2	247	268	21	-0.148
17	36	247	268	21	-0.072
18	9	248	268	20	-0.138
19	18	253	268	15	-0.243
20	25	253	268	15	-0.220
21	28	253	268	15	-0.007
22	32	253	268	15	-0.088
23	17	254	268	14	-0.054

24	34	254	268	14	0.036
25	1	258	268	10	-0.171
26	15	258	268	10	-0.249
27	23	258	268	10	-0.071
28	29	258	268	10	-0.097
29	35	258	268	10	-0.170
30	16	264	268	4	-0.013
31	30	264	268	4	-0.094
32	24	265	268	3	-0.092
33	20	268	268	0	-0.051
34	26	268	268	0	-0.212
35	31	268	268	0	-0.103
36	33	268	268	0	-0.193
37	37	268	268	0	-0.021
38	38	268	268	0	-0.103
39	39	268	268	0	-0.224
40	40	268	268	0	-0.039

There was a significant linear relationship between body volume (BV) and body length (BL) per segment on the log-log scale (ANOVA: $F_{1,1168}=92484$, $P < 0.001$, $R^2=0.99$), with body volume of individual whales (i) being predicted from the relationship: $\log(BV_i) = -3.89 + 2.85 \times \log(BL_i)$ (Figure 5). The mean of the last maternal body condition was -0.11 and that of the last calf length was 7.58 m. The mean SST and diurnal length at the time of the last observations were 14.6 °C and 11.6 h respectively.
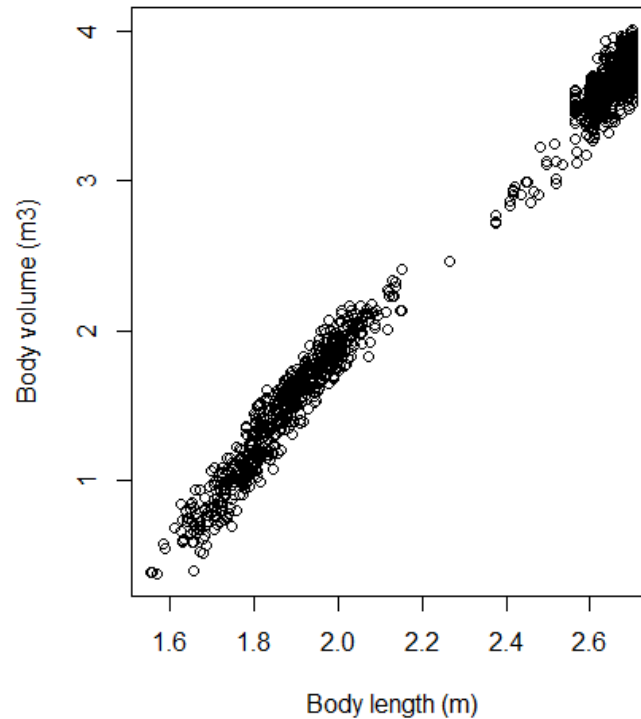
Figure 5. Linear log-log relationship between body volume (m³) and body length (m) per segment of individual southern right whales, *Eubalaena australis*.

3.1 Departure times of individuals

Migratory individuals were identified as individuals with a body condition below the average (*n = 16*; Table 1), while transient individuals were classified as those individuals with above average body condition (*n= 2*; Table 1) at the time of departure and were excluded from analyses.

3.2 Variables influencing departure time

There was significant collinearity between maternal body condition and both calf length (Figure 6) and calf volume (Figure 7). Maternal body condition decreased when calf length and volume increased during the season. This collinearity resulted in each being modelled separately. The model selection process showed that photoperiod was the best predictor of

departure time in southern right whale mother-calf pairs (AIC = 24.464, Table 2, Figure 8f). The probability of departure increased with photoperiod increasing during the breeding season. The second-best predictor of departure time from the breeding grounds was calf body volume (AIC = 32.271, Table 2, Figure 8d). The probability of departure increased with increasing calf volume. The third-best predictor of departure from the breeding grounds was absolute calf body length (AIC = 35.698, Table 2, Figure 8b). The probability of departure increased with increasing calf length. Absolute calf body length was a better predictor of departure than relative body length (AIC = 38.159, Table 2, Figure 8c). The fifth best predictor of departure from the breeding grounds was SST (AIC = 39.009, Table 2, Figure 8e). The probability of departure increased with decreasing surface temperature. The sixth best predictor of departure from the breeding grounds was maternal body condition (AIC = 43.366, Table 2, figure 8a). The probability of departure increased as maternal body condition decreased during the season.

Figure 6. The relationship between maternal body condition and calf length, with body condition decreasing with increased calf length (ANOVA: $F_{1,444}=307.4$, P<0.001). The red solid line represents the fitted (predicted) regression line from a linear model.

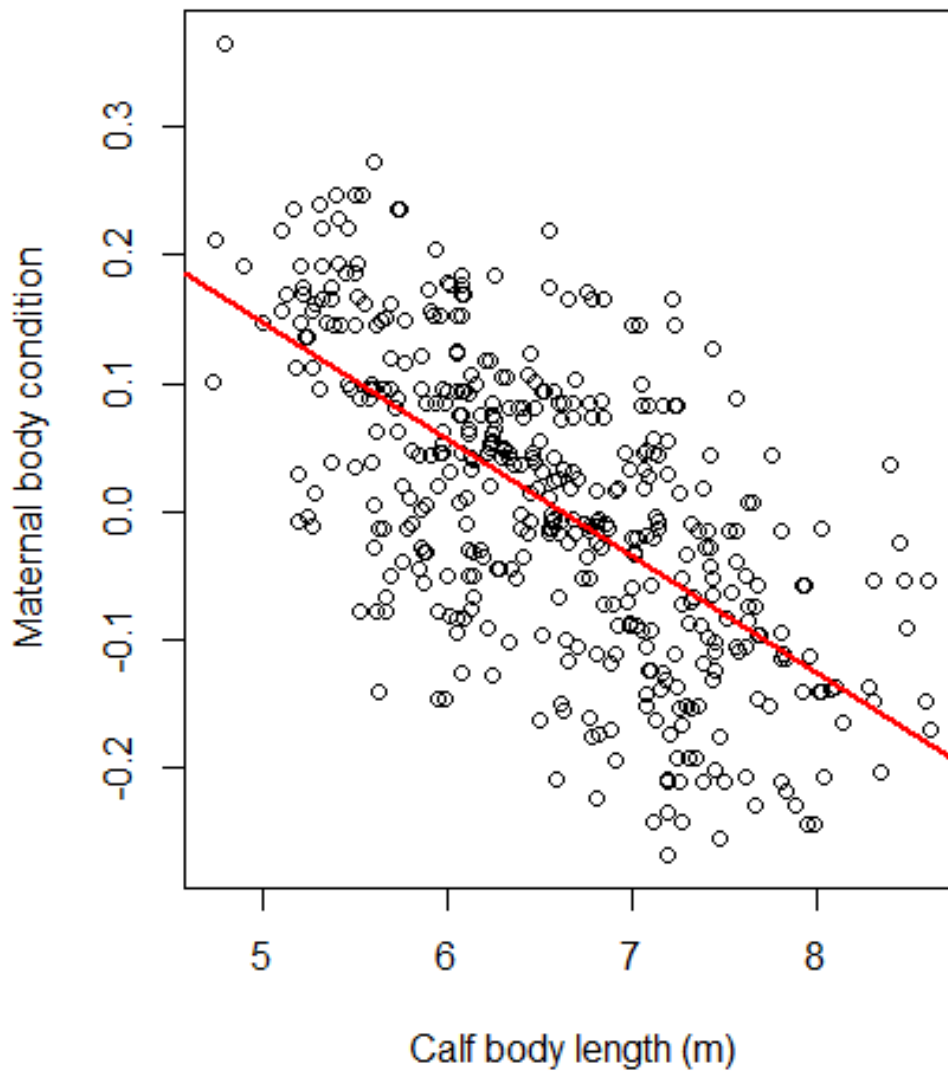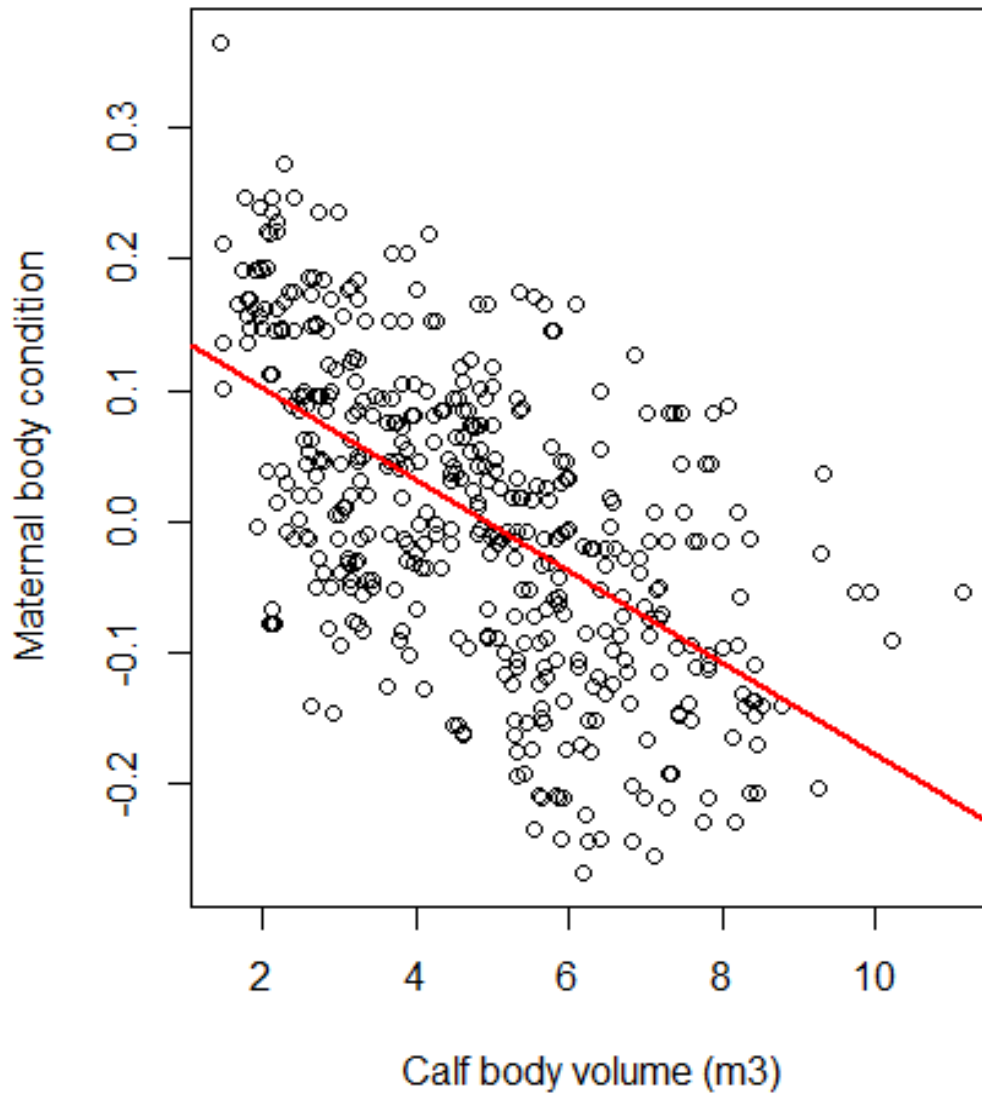*Figure 7.* Significant collinearity between maternal body condition and calf volume, with body condition decreasing with increased calf volume (ANOVA: $F_{1,444}$=227.6, P<0.001). The red solid line represents the fitted (predicted) regression line from a linear model.

Table 2. Result of the model selection process of identifying which explanatory variable best predicted the departure time of southern right whale mother-calf pairs from their breeding grounds. The table is organized with the best fitting model at the top. Predicted = values of the explanatory variable were derived (i.e. predicted) from a model. Observed = values of the explanatory variable were derived directly from the raw data.

Model	Variable	AIC	Distribution	Link Function
GLM	Diurnal period	25.464	Binomial	Logit
GLM	Calf body length (predicted)	29.228	Binomial	Logit
GLM	Calf body volume (predicted)	29.713	Binomial	Logit
GLM	Calf body volume (observed)	32.271	Binomial	Logit
GLM	Calf relative body length (predicted)	33.173	Binomial	Logit
GLM	Calf body length (observed)	35.698	Binomial	Logit
GLM	Calf relative body length (observed)	38.159	Binomial	Logit
GLM	Sea Surface Temperature	39.009	Binomial	Logit
GLM	Maternal body condition (observed)	43.366	Binomial	Logit
GLM	Maternal body condition (predicted)	44.711	Binomial	Logit
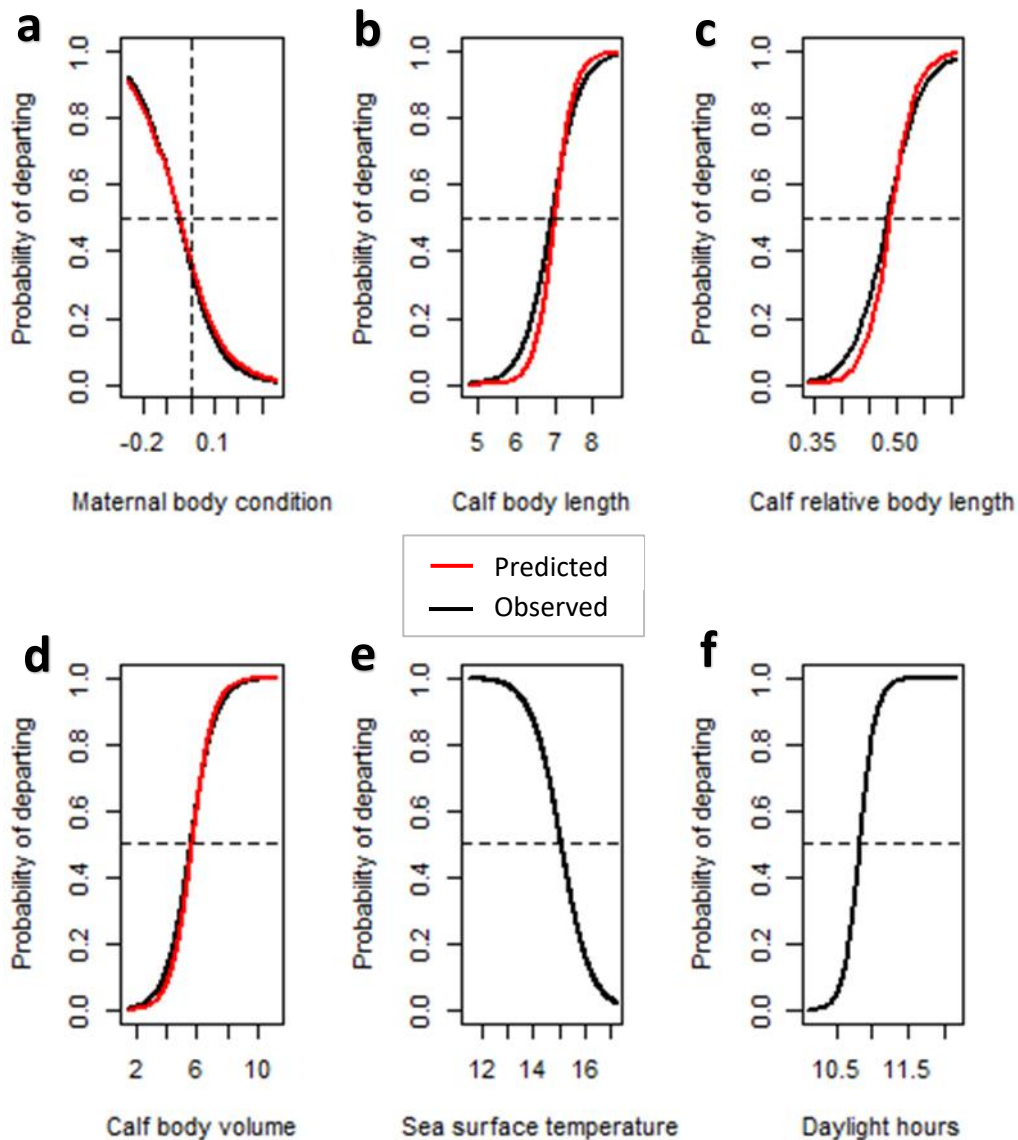
Figure 8. The probability of departure of southern right whale mother-calf pairs from their breeding grounds as a function of (a) maternal body condition, (b) calf absolute body length (m), (c) calf relative body length, (d) calf body volume (m^3), (e) sea surface temperature (° C) and (f) daylight hours (h). The solid lines in each sub-figure represent the fitted regression line of the best fitting Binomial GLM for each explanatory variable. The red and black colour of the lines indicates if the model was fitted to the predicted or observed data, respectively. For sea surface temperature (e) and daylight hours (f), models were fitted to observed data only. The horizontal dashed lines represent the 50% threshold, at which there is a 50% change that an individual departs the breeding grounds.

4. Discussion

The relationships between the migratory timing in southern right whales and intrinsic (maternal body condition and calf size) and extrinsic (sea surface temperature and diurnal period) variables on their breeding grounds were investigated. While there are numerous studies on migration in baleen whales, few studies have investigated the factors influencing the timing of migration. Migratory timing in southern right whales was best predicted by diurnal period followed by calf size (both body length and volume), while SST and maternal body condition explained much less of the variation in timing of migration.

4.1 Effect of diurnal period

Diurnal period (photoperiod) was the best predictor of migration timing of southern right whales from their winter breeding grounds. Most mother-calf pairs departed the winter breeding grounds at a mean day length of 11.6 h (Table 1). Photoperiod is a known "zeitgeber" and stimulus for migratory behaviour. This is especially visible in long-lived mammals that inhabit seasonally changing environments where photoperiod is often used to predict timed events such as migration, reproductive activities and optimum periods of resource productivity (Immelmann, 1973; Gwinner, 2003; 2012). In migratory marine mammals, including the majority of baleen whales, summer migrations to polar regions coincide with foraging opportunities on feeding grounds when the photoperiod length and productivity is at its greatest (Dawbin, 1966; Alerstam et al., 2003; Cote et al., 2017). Hence, photoperiod length is potentially the initiating cue during different stages of the annual migration for these species. Some baleen whale species (e.g., humpback whales) exhibit variation in migratory timing between reproductive classes, and thus it is possible that this initiating cue for migration may differ between reproductive classes (Dawbin, 1966; Baker et al., 1986; Stern,

2009). In other taxa, such as anadromous fish species (e.g. Pacific salmon, *Oncorhynchus* spp.*;* Scheuerell et al., 2009), bird species (e.g. garden warblers, *Sylvia borin*; Gwinner, 1996) and invertebrates (e.g. monarch butterflies, *Danaus plexippus*; Froy et al., 2003) (Berthold, 1996) It has been shown that important life history stages in some animals are organized and controlled by endogenous circannual rhythms. Throughout nature these rhythms are often synchronized by the seasonal changes in photoperiod (Gwinner, 2012). Further research into the migratory timing of different reproductive classes in relation to diurnal period would help determine this.

4.2 Effect of calf size

Calf size (calf length and volume equally) was the second-best predictor of migration timing of southern right whales from their winter breeding grounds. This finding supports the anti-predation hypothesis relating to baleen whale migration which predicts that larger calves are less susceptible to predatation than smaller calves (Fryxell et al., 1988; Corkeron & Connor, 1999; Cartwright et al., 2012). The mean length of the southern right whale calf measured during this study at the time of emigration from the breeding and calving grounds was 7.63 ±0.036 m. Neonate calves are highly susceptible to predation from larger marine predators and the survival of the calf increases with larger body size and increased swimming ability (Chittleborough, 1958; Corkeron & Connor, 1999; Ford & Reeves, 2008). Additionally, longer periods spent by calves on the breeding grounds allows them to build up greater muscle mass and improve their swimming ability before they migrate towards their summer feeding grounds (Chittleborough, 1958; Nielsen, 2018). As the swimming ability of calves increases, so will their chances of surviving the arduous journey of their first southern migration. Thus, it could be beneficial for mothers to remain on the winter breeding grounds until their calf

has reached a certain size before starting the migration south. Similarly, the first year survival of pinnipeds increases with weaning mass of the pups (Northern fur seals, *Callorhinus ursinus,* Baker et al., 1992; Southern Elephant Seals, *Mirounga leonina,* McMahon, Burton & Bester 2000; grey seals, *Halichoerus grypus,* Hall, McConnell & Barker 2008) and a positive relationship exists between first year survival and larger weaning mass of pups (Noren et al., 2004).

It has been suggested that warmer waters at lower latitudes are a potential driver for maternal females to migrate from higher latitudes for calving during winter due to potential thermoregulation benefits for the calves (Brodie, 1975). Due to the high surface area to volume ratio of neonates, calves benefit from warmer waters during early development to minimise heat loss and maximise energy use for growth. As the calves grow in size, their surface area to volume ratio reduces, which aides in the reduction of heat loss. Thus, calf survival is likely to increase the longer the mother remains on the calving grounds prior to migrating south (Chittleborough, 1958). The fact that absolute calf size was a considerably better predictor than relative calf size adds further support to this hypothesis.

4.3 Effect of sea surface temperature

Sea surface temperature (SST) was a relatively poor predictor of migration timing of southern right whales from their winter breeding grounds. This was expected, since the temperature changes experienced by the whales on their breeding grounds at the Head of Bight are very small, only from 11.5 °C to 20.0 °C. Since the temperature range experienced may vary from year to year by a few degrees (Table 3), SST is unlikely to be a reliable cue to initiate the southern migration. Diurnal period, on the other hand, is constant between years and may therefore have evolved as a beneficial environmental cue to initiate migration. Further,

Dawbin (1966) argues that the temperature differences experienced by pregnant, lactating and non-lactating humpback whale adults on their breeding grounds are minimal and hence unlikely to act as a cue to initiate migration. While SST does not seem to play an important role in the migratory timing of southern right whales, it is correlated with the distribution of baleen whales on both breeding and feeding grounds (Moses et al., 1997; Keller et al., 2006). Sea surface temperature has been used to identify areas of high primary productivity and upwelling events in the feeding grounds (Simard et al., 1986). Also, it has been documented in other marine taxa such as pelagic fish (Atlantic bluefin tuna, *Thunnus thynnus*; Humston et al., 2002; Southern bluefin tuna, *T. maccoyii;* Murphy and Majkowski*, 1981*) and cephalopods (veined squid, *Loligo forbesi*; Sims et al., 2001) to be a factor to potentially drive spawning migrations. Additionally, SST may influence the locations of offshore, foraging migrations in adult northern elephant seals (*Mirounga angustirostris*) as their prey distribution (give species or general taxa of prey) on the feeding grounds is influenced by ambient changes of SST (Hakoyama et al., 1994; Bost et al., 2008).

Table 3. Seven-year record of sea surface temperature (range and average) during peak breeding season (1 May - 31 Oct) at Head of Bight (31° 29' S, 131° 08' E) within the Great Australian Bight.

Year	Max (^oC)	Min (^oC)	Δ ^oC	Avg. (^oC)
2010	19.91	11.09	8.82	16.5
2011	20.71	15.01	5.7	16.95
2012	19.95	12.67	7.28	16.6
2013	21.08	12.4	8.68	17.4
2014	19.83	14.3	5.53	16.8
2015	19.15	12.63	6.52	16.41
2016	19.96	11.47	8.49	16.31

4.4 Effect of maternal body condition

Amongst the variables investigated in this study, maternal body condition was the poorest predictor of migration timing of southern right whales from their winter breeding and calving grounds. This was unexpected, since mothers have limited energy stores whilst on the grounds (Chittleborough, 1958; Lockyer, 2007; Christiansen et al., 2018), which will limit the time they spend there. Lactating southern right whale females at the Head of Bight lose, on average, 25% of their initial body volume during the season (Christiansen et al., 2018). Additionally, a relationship between maternal energy reserves and fasting times was demonstrated in a study of northern elephant seal pups. Fasting times varied among individual pups before heading to offshore feeding grounds, however, it was found across all individuals that energy reserves were negatively correlated with individual fasting times (Noren et al., 2004). Although it is logical to assume that southern right whale mothers in the current study should begin the southern migration at a point where their body reserves have reached a lower critical level, this was not found to be the case. It may be that this population of right whales is, on the whole, in good condition, meaning that females are unlikely to ever push themselves energetically to this lower body condition threshold. To confirm this assumption further research would be required involving comparisons of body condition of individuals from this population with those in other populations where individual females have poorer body condition.

4.5 Departure time relationship of combined environmental factors

Environmental variables are often suggested as triggers for migration behaviour, however it is often a combination of multiple environmental variables and/or climatic events that are thought to influence such behaviour (Smith et al., 1984; Fryxell et al., 1988). Although this

study was limited to testing only two environmental variables, potentially other variables, such as salinity, pH, turbidity, bathymetry, ocean currents or atmospheric pressure, may influence the migratory timing of the whales. In fact, more than one of the variables tested for this study (diurnal period, calf volume, calf length) were shown to be relatively good predictors (AIC values; Table 1) of migration timing of maternal female southern right whales. However, due to collinearity it was difficult to separate individual effects. For instance, decreasing maternal body condition is directly related to increasing calf size due to the calf being reliant on the energy stores of the female for growth (Chittleborough, 1958; Lockyer, 2007). Similarly, environmental variables are generally linked (e.g., photoperiod length, ocean temperatures) and changes across the entire environment will generally simultaneously impact individual variables making it difficult to separate individual effects (Dawbin, 1966). The timing of migration and cues that potentially initiate it are likely to be intricately linked and complex. In previous studies across different migratory taxa, multiple environmental and intrinsic variables were thought to possibly initiate migratory behaviour (Cagnacci et al., 2011). For example, a combination of photoperiod and SST has been shown to trigger the offshore spawning migration of tautog wrasse (*Tautoga onitis*), a temperate fish species in the western North Atlantic Ocean (Olla et al., 1980). Additionally, multiple environmental cues, including photoperiod length and air temperature, coincided to trigger the annual long-distance migration in greater snow geese (*Anser caerulescens atlantica*) in North America (Smith et al., 1984). It is possible that the annual migration cycle of southern right whales may have an initial starting point that requires environmental cues, (such as a certain day length) to initiate the migration and that the remaining annual migratory cycle occur regardless of intrinsic and environmental influences. Such a mechanism has been suggested to initiate

humpback whale migration in the polar regions where differences in photoperiod is at its greatest (Dawbin, 1966; Stern, 2009).

4.6 Limitations, assumptions and sources of error

A limiting factor in this study was the fact that the dataset constitutes only a single year. This restricted my ability to detect trends or differences in explanatory variables across multiple years. Additional sampling years will allow a better test of the migratory predictors that may fluctuate considerably from year to year. For example, SST potentially will fluctuate (e.g., across days/months) and predicting timing of migration from the breeding grounds may further prove to be an unreliable from year to year. Conversely, this study only investigated the relationship these variables had with mother-calf pairs, thus limiting observation of potential variability across the different age, sex and reproductive classes. It is evident that the different reproductive classes of whales (juveniles, adults, pregnant/lactating females) have differing energy requirements, which could influence their individual migration behaviour. Any future research would ideally incorporate these classes to gain a more complete picture of how these cues influence individuals differently within a population. Potential sources of error in the measured variables occur during measurement of individual whales for body condition estimates and assessing picture quality during post-processing. Further to the sources of error and biases identified in Christiansen et al. (2018), errors in body condition measurements may introduce additional variance and to some degree obscure the patterns of the timing of migration for individual whales. During analysis, identification of migratory individuals and transient individuals that have departed the sampling location was required. A body condition threshold was utilised, where departing individuals identified to be above the observed average body condition was designated to

identify transient individuals moving to other areas. Whereas departing individuals with a body condition threshold below the observed average were designated to identify migrating individuals. If errors occurred in body condition measurements, this would potentially result in the incorrect body condition threshold designation and, subsequently the classification of departing individuals. Another limitation of this study was that it did not consider endogenous variables. In other taxa, migratory behaviour is controlled by endogenous circannual rhythms and hormones that are synchronized by environmental cues (e.g. warblers, *Sylvia spp.,* Gwinner, 2003; 2012). Unfortunately, there are few direct studies that link hormone concentrations with animal movement (Jachowski et al., 2015). Further research is required to fully understand if environmental cues regulate the migratory behaviour of southern right whales through hormone production, such as measuring hormone levels throughout the breeding and calving season leading up to migration.

4.7 Management implications

Understanding which variables influence the migratory timing, and hence the residency time of southern right whales on their breeding and calving grounds, has important management implications. For example, knowledge of when animals arrive and depart into an area can be used to identify key times for protection during the winter breeding season. Similarly, failure to understand the importance of intrinsic and extrinsic factors that trigger life-history events in migratory species may lead to erroneous assumptions in regard to timing of migratory behaviour (Monteith et al., 2011). Understanding the factors that drive migration are important in developing efficient strategies that would aim protect the species during key migration periods, especially in face of global climate change. Failure has the potential to inadvertently lead to the inadequate derivation and application of such strategies and

potentially mismanage threats (e.g. area usage) (Holdo, Holt, & Fryxell, 2009; Anderson, et al., 2013). Climate influences a variety of ecological processes, especially in the marine environment through sea temperature, wind conditions and northern and southern oscillations (NAO, ENSO). Changes to these processes has potential disruption to species that synchronize with cyclical events for survival. Long distance migratory species (e.g. baleen whales) that undertake migrations to polar regions to feed are particularly vulnerable to detrimental impacts of climate change to food productivity on their feeding grounds (Stenseth et al., 2002; Robinson et al., 2009).

4.8 Conclusions

Photoperiod was the best predictor of the migration timing of southern right whales from their breeding and calving ground. Similar findings have been documented across other migratory taxa to be triggered by this environmental cue (Gwinner, 1996; Froy et al., 2003; Scheuerell et al., 2009). Diurnal period is a consistent variable from year to year and it is hence logical for taxa to synchronise endogenous rhythms and key life history stages to this predicable environmental cue. However, future research needs to determine if any intrinsic variables, such as hormone levels and endocrine function, are triggered by photoperiod synchronisation that combine to influence timing of migration. Further, it would be worthwhile to compare a similar body condition dataset with a population considered to be not in the same condition to determine if the similar triggers still adhere. The finding of the relationship between photoperiod and migration timing is an important step towards unravelling the underlying mechanics of the migratory behaviour of large whales. With better understanding of the variables that influence the timing of migration, and by testing this

across multiple baleen whale species, it will help to improve the protection and conservation

of these important species.

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