Riekkola Leena (Orcid ID: 0000-0002-9653-7106)

Title page

Title: Longer migration not necessarily the costliest strategy for migrating humpback whales

Authors: Leena Riekkola[1,*], Virginia Andrews-Goff[2], Ari Friedlaender[3], Alexandre N. Zerbini[4, 5, 6], Rochelle Constantine[1, 7]

Author affiliations:

1. School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand.
2. Australian Marine Mammal Centre, Australian Antarctic Division, 203 Channel Hwy, Kingston, TAS 7050, Australia.
3. Institute of Marine Sciences, University of California – Santa Cruz, 115 McAllister Way, Santa Cruz, CA 95060, USA.
4. Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA.
5. Cascadia Research Collective, 218 1/2 W 4th Ave., Olympia, WA 98501, USA.
6. Marine Ecology and Telemetry Research, 2468 Camp McKenzie Tr NW, Seabeck, WA, 98380, USA.
7. Institute of Marine Science, University of Auckland, Private Bag 92019, Auckland, New Zealand.

* corresponding author: Leena Riekkola. lrie003@aucklanduni.ac.nz. +64(0)212922551.

Abstract

1. Long-distance migration is a demanding physical activity, and how well animals manage the associated costs will have important implications for their fitness.
2. The Oceania humpback whale (*Megaptera novaeangliae*) population is recovering from past exploitation markedly slower than the neighbouring east Australian whales. The reasons for this are unknown, however, higher energetic costs of longer migratory distances could be a possible explanation. Studying the energy expenditure of these large animals requires methods that do not rely on capture, such as bioenergetic models.
3. A state-space model was fitted to satellite data to infer behavioural states for southern migrating whales. Travel speeds and behavioural states were used in a bioenergetic model to estimate the energetic cost of the migration phase. Relative differences in average duration, distance and energetic costs were compared between migratory routes and distances.
4. Total energy used during migration was a trade-off between cost of transport (determined by travel speed) and daily maintenance (determined by daily basal metabolic costs). Oceania whales migrating to the Amundsen and Bellingshausen Seas travelled fastest and furthest, 15% and 21% further than whales migrating to the d'Urville Sea (east Australian whales) and Ross Sea, respectively. Therefore, they had the highest cost of transport, 25% and 85% higher than for d'Urville Sea and Ross Sea whales, respectively. However, energy saved in terms of daily maintenance by using fewer days to complete a longer migration resulted in only a 6-7% increase in total energetic cost.
5. The results highlight that travelling further does not necessarily translate into an increase in total energy expenditure for migratory whales, since they can compensate for longer distance by

travelling faster. Further research on the energetics of different whale populations could provide insight into the productivity of Southern Ocean feeding regions and help understand the environmental and anthropogenic effects on the whales' energy budgets.

Keywords

Cetacean, energetic cost, humpback whale, migration, modelling, population recovery

1. Introduction

Migration has evolved among many different animal groups and is primarily a behavioural adaptation to spatio-temporal variation in resources, habitats, predation and competition (Alerstam, Hedenström & Åkesson, 2003; Dingle & Drake, 2007). Long-distance migrations are outstanding physical behaviours and typically occur between geographically separated key habitats required for different life history stages and functions for animals (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; Alestram et al., 2003; Alexander, 1998). A critical aspect of long-distance migration is the need to balance available energy reserves between processes such as basal metabolism, storage, growth, activity and reproduction (Karasov, 1992; Kooijman, 2010; 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 utilize currents and tidal stream transport (Lambardi, Lutjeharms, Mencacci, Hays &

Luschi, 2008; Parker & McCleave, 1997) while flying animals such as birds take advantage of thermal updrafts and favourable air currents to save energy (Bohrer et al., 2012; Egevang et al., 2010).

There are two general strategies for meeting the energetic demands of reproduction: income and capital breeding (Jönsson, 1997; Stephens, Boyd, McNamara & Houston, 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 (Dingle & Drake, 2007; Jönsson, 1997). 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, and they may in some cases be susceptible to exhausting their energy reserves before reaching the feeding grounds (Braithwaite, Meeuwig & Hipsey, 2015; Jönsson, 1997).

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, although a considerable amount is also stored in muscle, intra-abdominal fat and organs (Lockyer, 1986, 1987; Lockyer, McConnell, & Waters, 1985). Many whale species rely on these energy stores for several months out of the year to cover the cost of their long-distance migration as well as that of breeding and lactation (Brodie, 1975; Dawbin, 1966). 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.

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 (Christiansen et al., 2018; Goldbogen et al., 2013; Williams & Noren, 2009). 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 (Christiansen et al., 2018; Fortune, Trites, Mayo, Rosen & Hamilton, 2013). 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, Schwarz, Sumich & Costa, 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 (Dodge et al., 2014; Mandel, Bildstein, Bohrer & Winkler, 2008; Nathan et al., 2008).

Commercial whaling during the 20th century heavily exploited all Southern Hemisphere humpback stocks (Clapham & Ivashchenko, 2009; Ivashchenko & Clapham, 2014). The Oceania humpback whales, comprising whales from multiple breeding ground subpopulations from the South Pacific Islands (Figure 1), are estimated to be <50% of pre-exploitation numbers (Childerhouse et al., 2008; Constantine et al., 2012; International Whaling Commission, 2015). Furthermore, this population is recovering slower than the neighbouring east Australian population (International Whaling Commission, 2015) which could be indicative of differences in available energy resources and/or use between these populations. A recent satellite tracking study has revealed the migratory paths of Oceania humpback whales travelling to their Southern Ocean feeding grounds (Riekkola et al., 2018; Figure 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 1). A longer migration distance might incur a higher energetic cost, as suggested by recent models of migratory whales (Braithwaite et al., 2015; Villegas-Amtmann, Schwarz, Gailey, Sychenko & Costa 2017), and could therefore have consequences on population recovery rates.

The aim of this study was to use satellite tracking data of humpback whales to build a bioenergetic model for estimating the cost of transport across different migration routes and distances, and to investigate the relative differences between whales migrating to different Southern Ocean feeding grounds. Comparisons were made within the Oceania humpback whale population, where individual whales migrated to one of two feeding ground destinations, as well as between Oceania whales and humpbacks from a neighbouring population (east Australia). Whales using a similar route to migrate to the same feeding ground destination are referred to here as 'cohorts'. The closely neighbouring Oceania and east Australian populations have different migratory routes and behaviours, and they are recovering from the effects of whaling at very different rates. Given the difficulty of studying the energy requirements and expenditure of these animals in the field, this study makes use of newly available telemetry data to examine whether a longer migration distance incurs a markedly higher energetic cost to the whales, consequently playing a role in the differential rates of population recovery.

2. Methods

2.1 Satellite tag deployment and hierarchical state-space model for Oceania and East Australian humpback whales

This study used existing humpback whale telemetry data for southern migrating humpback whales reported in Riekkola et al. (2018). Adult humpback whales (n=25; Table 2a) were fitted with location-only SPOT-5 satellite transmitters (Wildlife Computers, Redmond, USA) at the Kermadec Islands (Figure 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).

A hierarchical Bayesian state-space model (SSM; Jonsen, Flemming & Myers 2005; Jonsen, Myers & James, 2006) at a 6-h time-step was used to estimate locations via an observational model, and to infer behavioural states via a movement model, either 'transiting' or 'area restricted search' (indicative of foraging). 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 3.3.2, R Core Team, 2018) using the software JAGS (Plummer, 2013) and the R packages rjags (Plummer, 2016) and bsam (Jonsen, Luque, Winship & Pedersen, 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 independent 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. A conservative approach (Jonsen, Myers & James, 2007) was used 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’.

To make comparisons with the neighbouring east Australian populations existing satellite tracking data reported in Andrews-Goff et al. (2018) were used. Location-only SPOT-5 satellite transmitters were deployed on adult humpback whales (Table 2a) 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.

2.2 Data preparation

Swimming speed was calculated between consecutive locations for each whale using the SSM data. Distance between consecutive locations was calculated using a great circle distance (trip package, function trackDistance, Sumner, 2016). 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, each track required to have a data point every 6 hours. Any data gaps were therefore filled by generating new time points spaced at 6-h intervals (note that no locational data were associated with these points, only time and speed). The speed of each newly generated point within the data gap was assigned to be the speed across the entire gap (i.e. the speed between the last SSM location before the gap and the 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, specific start and end points were defined for the migratory phase, which was considered to begin when the animals crossed 30°S (Figure 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). Therefore, the migration phase was considered 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). Within the Oceania population the whales had two migratory destinations: Ross Sea or Amundsen and Bellingshausen Seas (Figure 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 1), and their migratory destination will therefore be referred to as the d'Urville Sea.

2.3 Energetic cost of transport & basal metabolic rate:

The energetic cost for the migration phase was only calculated for those animals whose tags transmitted north of 30°S and lasted until at least 60°S. Following Braithwaite et al. (2015) the energy expenditure of all activities for a migrating humpback whale were grouped 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 (Fish, 1994; Sumich, 1983). The energetic cost of transport in Watts (W) was calculated for each SSM derived location (6-hr time step) 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 for an actively swimming animal (Hind & Gurney, 1997), ε_A is aerobic efficiency, ε_P is propulsive efficiency, ρ is the density of sea water (kg m^{-3}), S is the wetted surface area (m^2) calculated for a marine mammal (Ryg et al., 1993), C_D is the drag coefficient, and V is the swimming speed for that time step. All model parameters and their sources are summarized in Table 1. Estimates for aerobic and propulsive efficiencies are generic values for cetaceans, which are lift-based swimmers (Fish, 1996). The value for drag coefficient was estimated for humpback whales by Braithwaite et al. (2015) based on values for other cetacean species. To help maintain consistency between studies, the whale mass for the model was set at 30 000kg as per Braithwaite et al. (2015), which was derived from the length-to weight relationship of Lockyer (1976) for a humpback whale of 13m. All E_{COT} values were summed for each whale for the entire migratory period. As the aim of this study was to compare the energetic costs of different migration distances, all other variables (e.g. sex, age, size) were kept constant, and therefore the energetic cost of e.g. growth or lactation were not estimated.

Basal metabolic rate (BMR) is the energy required by an organism to maintain vital bodily functions at rest (Schmidt-Nielsen, 1997). 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). The BMR value was multiplied by the migration length (days) for each individual whale (for total BMR cost) and added to the summed E_{COT} value to obtain the total migratory cost. The migration distance, duration and the energetic costs were compared by calculating the relative (or percentage) differences between cohort averages.

3. Results

For the Oceania cohort, 8 whales (out of the 25 originally tagged) had tracks covering the full migration from 30°S to the observed change in behaviour south of 60°S (Ross Sea n=5, Amundsen & Bellingshausen Seas n=3; Figure 1,Table 2a). Only two whales from east Australia had migration data across the same spatial range. Three whales from the Oceania cohort whose tracks covered the full migration had large data gaps resulting in a large proportion (>13%) of generated data points and speeds during the migration phase. As the accuracy of the generated sections could not be fully trusted, these tags were not included in the final comparisons between cohorts (Table 2b), however the available data outside the data gaps were used to examine travel speeds (Table 3).

The whales that migrated to the Amundsen & Bellingshausen Seas covered the longest migration distance (in km), 21% and 15% longer than for the Ross Sea and d'Urville Sea migratory cohorts respectively (Table 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 2b). Sample sizes were too small to permit a statistical comparison between cohorts. The average migratory speed for each cohort varied throughout the migration phase (Table 3). Apart from the very beginning 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 (Table 3). The whales migrating to the Ross Sea comprised both mother-calf pairs and adults without calves, and although the swimming speed for each class varied across the migration phase neither class was consistently faster than the other (Table 3).

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, Overdijk & Piersma, 2015), and monarch butterflies (*Danaus plexippus*) infected with protozoan parasites were not able to migrate as far as uninfected individuals (Altizer, Hobson, Davis, De Roode & Wassenaar, 2015). This study 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 might minimize the immediate energy expenditure of moving though water, 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 longer 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 utilizing favourable environmental conditions or stopover sites, to reduce migration costs (Bohrer et al., 2012; Lambardi et al., 2008; Sawyer & Kauffman, 2011). A faster migration speed may therefore be a behavioural adaptation through which the whales travelling to the Amundsen and Bellingshausen Seas minimize 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, Stanley & Stutchbury, 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} (Table 3), 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 minimizes 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). Whales migrating to the Ross Sea swam slightly slower than Amundsen and Bellingshausen Sea whales (Table 3), and out of the Ross Sea whales half where mother-calf pairs, which have been reported to swim slower than adults without calves (e.g. Andriolo et al., 2014; Noad & Cato, 2007). However, the dataset used in this study, albeit small, shows that mother-calf pairs migrating to the Ross Sea had comparable speeds to adults without calves, and were in fact faster in some sections of the migration phase (Table 3).

Even a small annual energetic deficit could have a big impact on migrating animals. For example, Klansjcek, Nisbet, Caswell, and Neubert (2007) found that a 16% reduction in energy intake was enough to inhibit reproduction in North Atlantic right whales (*Eubalaena glacialis*), while Villegas-Amtmann et al. (2015) estimated that a 4% loss in the annual energy budget of a female gray whale (*Eschrichtius robustus*) during pregnancy could prevent the successful production and weaning of a calf. Such energetic impacts may not necessarily compromise a healthy individual, but could interact with other factors, such as entanglement, which was estimated to add up to 8% to the 4-year energy budget of a female North Atlantic right whale (van der Hoop, Corkeron, & Moore, 2016). A bioenergetics 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 2-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 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, it is currently unknown 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 satellite tagged at the Kermadec Islands migrated to the more distant feeding grounds of Amundsen and Bellingshausen Seas (Riekkola et al. 2018). 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 (Fortune et al., 2013; Worthy, 1987), and may therefore be more vulnerable to nutritional stress during the migration or fasting period than mature individuals (Irvine, Thums, Hanson, McMahon, & Hindell, 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, Béchet, Germain, Johnson, & Pradel, 2012). However, considering calves in other humpback whale populations successfully complete long-distance migrations (Rasmussen et al., 2007; Stevick, Øien & Mattila, 1999) there is no reason to assume that young calves 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 (Gittleman & Thompson 1988; Lockyer, 1986), and in capital breeding humpback whales this cost occurs during the fasting period. It might therefore be hypothesized that the preference for a closer feeding ground by lactating females 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 (Alves et al., 2013; Newton, 2004). 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 (Hellessey et al., 2018; Murase, Matsuoka, Ichii, & Nishiwaki, 2002), as well as the availability of sufficiently dense krill swarms (e.g. Hazen, Friedlaender, & Goldbogen, 2015). Furthermore, future environmental change and anthropogenic disturbances on the whales’ feeding grounds could significantly impact their energy acquisition (Pirotta et al., 2019). Some humpback whale populations have shifted their habitat use, switched prey type and foraging strategies in response to environmental change (e.g. Fleming, Clark, Calambokidis, & Barlow, 2016; Hain et al., 1995; Neilson & Gabriele, 2019; Owen et al., 2015). Although such changes can be beneficial, displacement might affect resource and niche partitioning between humpbacks and other recovering whale populations, as seen around the Antarctic Peninsula (Friedlaender, Lawson, & Halpin, 2009; Friedlaender et al., 2011; Herr et al., 2016) but of which our understanding is lacking in most other Antarctic regions. For conservation purposes it may be important to ensure that intense anthropogenic activities (e.g. tourism, fisheries) do not occur in critical feeding areas. An increase in tourism pressures is of concern (see Schuler et al., 2019), especially around the Antarctic Peninsula where tourism is focused and predicted to grow (Bender, Crosbie, & Lynch, 2016). The Antarctic krill fishery has grown in the recent decade (Commission for the Conservation of Antarctic Marine Living Resources, 2018), and there are concerns regarding how the spatial overlap between fishery efforts and Antarctic krill predators might negatively impact these species and the marine ecosystem (Smith et al., 2011; Weinstein, Double, Gales, Johnston, & Friedlaender, 2017). However, the Antarctic krill fishery is currently focused on the South Atlantic sector and around the Antarctic Peninsula and is therefore not a primary concern for the Oceania humpback whale population. Feeding grounds that have a higher proportion of mothers with calves, such as the Ross Sea region (Riekkola et al., 2018) may be more sensitive to disturbances and to lost foraging opportunities (Pirotta et al., 2019). Additionally, females in poorer condition produce smaller calves, which is expected to affect the calf's chance of survival (Christiansen et al., 2016, 2018; McMahon, Burton, & Bester, 2000). The establishment of marine protected areas may provide an opportunity to protect whales from potential anthropogenic impacts, but changes in prey availability due to climate change effects on productivity will be more difficult to control (e.g. Constable et al., 2014; Tulloch, Plagányi, Brown, Richardson, & Matear, 2019).

Migratory animals 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 (Andrews-Goff et al., 2018; Owen et al., 2017). 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 be associated with the opportunistic additional energy intake by the east Australian whales, rather than the energetic costs associated with different migration distances, 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, such as strengthening of westerly winds (Langlais et al., 2015), increasing wave action and deep ocean temperatures (Dobrynin et al., 2012; Gille, 2002), a pole-ward shift of major ocean fronts (Rudeva & Simmonds, 2015), as well as changes in the extent, duration and thickness of sea ice (Deppeler & Davidson, 2017; Stewart et al., 2019; Turner et al., 2015). 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).

4.1 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 (Christiansen et al., 2018; Goldbogen et al., 2013; Williams & Noren, 2009). Additionally, small errors or changes in parameter measurements can have large impacts on the final results (Jeanniard-du-dot, Trites, Arnould, & Guinet, 2017). Therefore, the aim of this paper was not to attempt to obtain exact values, but instead to only estimate 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) all activity was grouped as 'cost of transport'. Even though this likely underestimated the exact energetic costs by not including different high energy behaviours (such as breaching, a frequent behaviour for humpback whales; Clapham, Palsbøll, & Mattila, 1993) all cohorts would be expected 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 this study, it provides valuable insight into the migratory ecology of these animals. The work also highlights an opportunity for more detailed model development, for example specific models for pregnant and lactating females (e.g. Pirotta et al., 2019; Villegas-Amtmann et al., 2015), 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 utilized 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).

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 can manage the energy used by balancing swimming velocity and the time taken to complete the migration. Although there are other factors that may also be of influence in some cases, such as the presence of a calf, and the fact that the whales do not always swim straight but meander (e.g. Riekkola et al., 2018). 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.

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Tables

Table 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)
Aerobic 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)	$0.054M^{0.696}$	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}, also see Table 3)

Table 2. a) Summary of satellite tag data used for calculating energetic cost of migration. ID = unique tag number, M = male, F = female, MC = mother-calf pair, U = animal of unknown sex but travelling without a calf, E_{cot} = energetic costs of transport (in Watts (W)), BMR = basal metabolic rate. b) Relative difference of energetic cost metrics between migration destinations. Comparisons were done excluding individuals with a large proportion of generated data points (see Methods and Results for details).

(a)

Migratory destination	ID	Sex/reproductive class	Migration length		Migration E_{cot} (W)	Migration BMR (W)	Total migratory cost (W)
			days	km			
Amundsen and Bellingshausen Seas	102218	M	63	5,564	176,236	487,116	663,352
	131182	F	56	6,161	244,925	434,925	679,850
	131187	F	53	5,025	161,722	411,729	573,451
	Average		58	5,583	194,294	444,590	638,884
Ross Sea	88727	MC	37	3,709	108,495	286,084	394,579
	112722	U	87	5,487	100,112	670,751	770,863
	131178	MC	95	5,517	101,592	732,607	834,199
	131188	MC	48	4,202	118,562	367,270	485,832
	131190	MC	55	4,127	95,866	427,193	523,059
	Average		64	4,609	104,926	496,781	601,707
d'Urville Sea	64235	M	39	4,158	195,069	301,548	496,617
	98129	MC	76	5,579	115,968	583,766	699,734
	Average		57	4,869	155,519	442,657	598,176

(b)

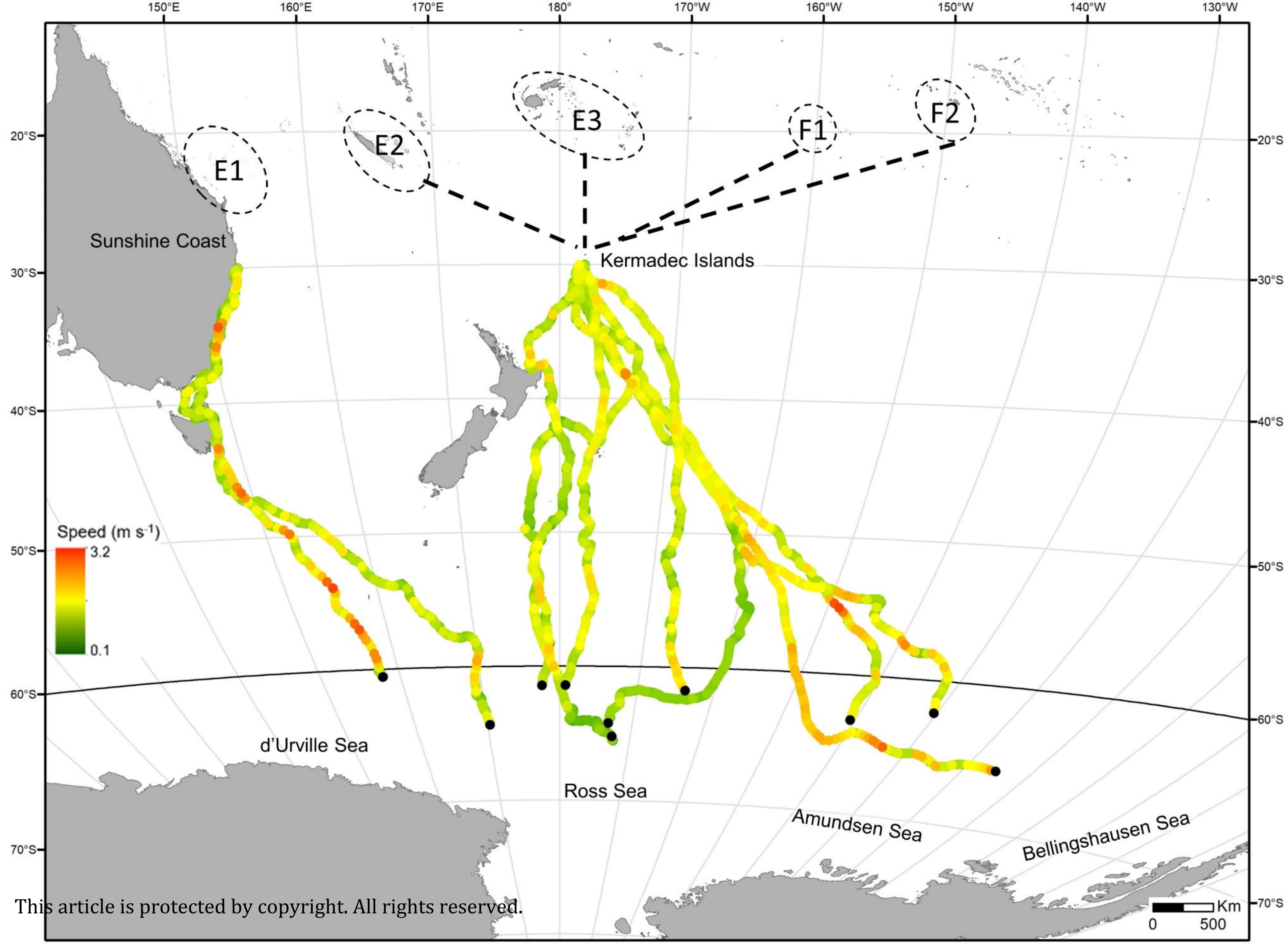
Comparison	Migration length		Migration E_{cot} (W)	Migration BMR (W)	Total migratory cost (W)
	days	km			
Amundsen & Bellingshausen Seas *relative to* Ross Sea	-11%	21%	85%	-11%	6%
Amundsen & Bellingshausen Seas *relative to* d'Urville Sea	0%	15%	25%	0%	7%
Ross Sea *relative to* d'Urville Sea	12%	-5%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

Table 3. Average speed (m s^{-1}) for whales in different migratory destination cohorts, and of different reproductive classes for Ross Sea (Adult n=3, MC = mother with a calf, n=4). AB Seas = Amundsen and Bellingshausen Seas, n=4, d’Urville Sea, n=2. For individuals whose satellite tagging data included data gaps (AB Seas n=1, Ross Sea – Adult n=2) only actual data outside of the data gaps were used in the table.

	Latitude band (S°)							
	30	35	40	45	50	55	60	Average
AB Seas	0.5	1.0	1.1	1.1	1.1	1.4	1.0	1.0
Ross Sea	0.8	0.9	1.0	1.0	0.8	0.9	1.0	0.9
Adult	0.7	0.8	1.2	1.0	1.0	0.8	0.9	0.9
MC	0.9	1.0	1.0	1.0	0.7	1.0	1.2	0.9
d'Urville Sea	0.9	0.9	0.8	1.0	1.2	1.2	1.0	1.0

Figure legends

Figure 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, East Australian population), Ross Sea (n=5, Oceania population), Amundsen and Bellingshausen Seas (n=3, Oceania population). Note that only those tags that covered the 'full migration phase' (30°-60°S) and without large data gaps were included in the analyses (see Methods and Results for details). 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.


150°E
160°E
170°E
180°
170°W
160°W
150°W
140°W
130°W
20°S
30°S
40°S
50°S
60°S
70°S
E1
E2
E3
F1
F2
Sunshine Coast
Kermadec Islands
Speed (m s-1)
3.2
0.1
d'Urville Sea
Ross Sea
Amundsen Sea
Bellingshausen Sea
Km
0
500