

Potential energy gain by whales outside of the Antarctic: prey preferences and consumption rates of migrating humpback whales (*Megaptera novaeangliae*)

Kylie Owen¹ · Ailbhe S. Kavanagh¹ · Joseph D. Warren² · Michael J. Noad¹ · David Donnelly³ · Anne W. Goldizen⁴ · Rebecca A. Dunlop¹

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Abstract The humpback whale (*Megaptera novaeangliae*) makes annual migrations from Antarctic feeding grounds to tropical breeding grounds. The extent to which it feeds during migration is unknown, but thought to be very low. Whether an animal feeds during migration is likely dependent on prey availability and on the ease with which it can capture the available prey. This study used digital tags (DTAGs) and concurrent prey sampling to measure how changes in the depth and type of prey influenced the lunge feeding rates and the amount of energy consumed by migrating humpback whales. Whales targeting krill lunged at significantly higher rates than whales targeting fish; however, the depth of the prey did not influence lunge rate. The observed lunge rates when feeding on krill, to the best of our knowledge, are higher than any previously reported rates of whales feeding. Estimates of the energetic content of the prey ingested revealed that whales may consume between 1.2 and 3.4 times their daily energy requirements per day while feeding on krill during migration, but less when feeding on fish. This suggests that whales may begin to restock energy supplies prior to reaching the Antarctic.

Determining how often this high rate of energy intake occurs along the migratory route will assist with understanding the contribution of migratory energy intake to annual energy budgets.

Keywords Energy budget · Lunge feeding · Krill · *Megaptera novaeangliae* · Migratory stopover · Southern Ocean

Introduction

The large majority of top predators in the Southern Ocean rely either directly or indirectly on the presence of Antarctic krill (*Euphausia superba*) (Hunt et al. 1992; Croxall et al. 1999; Nicol et al. 2008) which is currently highly abundant (Vestheim and Jarman 2008). However, factors such as climate change and a growing krill fishery threaten to reduce the availability of krill (Nicol and Foster 2003; Flores et al. 2012; Nicol et al. 2012). Management of this ecosystem requires an understanding of the amount of krill present but also of the amount of krill required by predators. As a consequence, determining the consumption rates of predators has become an aim of current Southern Ocean research (Childerhouse 2013). Some predators, such as crabeater seals (*Lobodon carcinophagus*), are Antarctic krill specialists that rely almost entirely on this prey item to fulfil their annual energy budgets (Laws 1984; Lowry et al. 1988). Other animals, such as many whale species, are migratory (Dawbin 1966; Lockyer 1981) and may supplement their energy budgets with feeding effort in other areas. The current understanding of feeding outside of Antarctic waters by migratory whale species, based on whaling data (Mackintosh and Wheeler 1929; Matthews 1937; Gambell 1968; Lockyer 1981), is that the rate of

✉ Kylie Owen
kylie.owen@uqconnect.edu.au

¹ Cetacean Ecology and Acoustics Laboratory, School of Veterinary Science, The University of Queensland, Gatton, QLD 4343, Australia

² Acoustic Laboratory for Ecological Studies, School of Marine and Atmospheric Sciences, Stony Brook University, Southampton, NY 11968, USA

³ Australian Orca Database, 8 Campbell Parade, Box Hill South, VIC 3128, Australia

⁴ Behavioural Ecology Research Group, School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

feeding is extremely low (Friedlaender et al. 2009a; Stimpert et al. 2012; Friedlaender et al. 2013; Curtice et al. 2015). Despite this, based on data on the energy stores of whales, it has been suggested that feeding outside of Antarctica is likely to occur more frequently than currently understood, unless whales have much lower field or basal metabolic rates than predicted for animals of their size (Leaper and Lavigne 2007). However, a lack of data on the feeding behaviour of whales while migrating outside of the Antarctic has limited our understanding of the potential contribution of this behaviour to energy supplies.

Feeding during migration plays an important role in the ecology and survival of many bird species (Newton 2006) and terrestrial mammals (Sawyer and Kauffman 2011). During migration, animals are constrained to feeding on the prey that is available along the migratory route, which may vary between years as a consequence of environmental heterogeneity. Migratory animals may be faced with a trade-off between the benefit of stopping to feed on the available prey, and the benefit of continuing migration and reaching high-quality feeding grounds while prey quality is optimal. In bird species, prey quantity and quality on the migratory route influences factors such as the timing of migrations, future breeding success, survival of individuals, and population size increases or declines (Newton 2006). In addition, terrestrial mammals time their migrations according to the likely availability of food while migrating (Sawyer and Kauffman 2011). To the best of our knowledge, the factors that influence the amount of feeding completed while on migration by baleen whale species have never been investigated.

Feeding behaviour during migration by baleen whale species has been identified through potential foraging behaviour in the tracks of satellite tag data (Gales et al. 2009; Silva et al. 2013) or via direct (Stone et al. 1987; Best et al. 1995; Gill et al. 1996; Stockin and Burgess 2005; Visser et al. 2011; Owen et al. 2015) and indirect (Cacchione et al. 1987) observations of feeding behaviour. The species most frequently documented to feed while migrating is the humpback whale (*Megaptera novaeangliae*) (Stone et al. 1987; Best et al. 1995; Gill et al. 1996; Stockin and Burgess 2005; Visser et al. 2011; Owen et al. 2015). Off the south-east coast of Australia, humpback whales feed regularly in spring during the southward migration towards Antarctic feeding grounds on both krill (*Nyctiphanes australis*) and small baitfish species (Stamation et al. 2007; Owen et al. 2015), despite the population being believed to feed predominantly on krill on their main feeding grounds (Matthews 1937). The amount of feeding that is observed has varied among years (Silva et al. 2010), but it is unknown whether this is due to the animals not feeding during migration in some years, or feeding at depth out of sight of observers. Therefore, while feeding

behaviour during migration has regularly been observed, the factors that influence the extent of this behaviour remain largely unknown.

The choice of an animal to delay the completion of migration to feed is likely dependent on the ease with which it can find and capture prey. Many whale species make annual migrations between high-latitude feeding grounds and low-latitude breeding grounds. Rorqual whales (Balaenopteridae) are a group of species that are characterised by long ventral grooves in the blubber that allow for the expansion of the buccal cavity and the use of a filter-feeding strategy called lunge feeding (Jurasz and Jurasz 1979; Lambertson 1983). This behaviour involves the whale swimming at speed towards a patch of prey and engulfing a large quantity of prey-laden water (Goldbogen et al. 2008). The action of opening the mouth at speed greatly increases the drag forces acting on the animal and the amount of energy required to lunge feed (Goldbogen et al. 2008, 2011). As a result, rorqual whales display a threshold foraging response, where it only becomes profitable for an animal to feed when prey density is above a certain level (Piatt and Methven 1992). Compared to other rorqual whale species, the humpback whale has several morphological adaptations that make it an efficient predator, including long pectoral fins that assist with turning and generating lift, and a large, low aspect ratio tail that provides propulsion (Woodward et al. 2006). These adaptations enable humpback whales to accelerate quickly and manoeuvre at high speeds (Woodward et al. 2006), which allows them to target a number of prey types ranging from small zooplankton through to schooling fish (Clapham and Mead 1999). Different prey types have differing movement and predator avoidance abilities, which may result in whales needing to expend different amounts of energy to successfully capture them. Therefore, changes in the prey type available on the migration route could influence the extent to which humpback whales feed.

Given that humpback whales are an air-breathing mammal, the depth of prey is also likely to influence the energy required to capture the prey. Deeper prey results in a greater travel distance to the surface, a longer recovery time at the surface (Houston and Carbone 1992), and less time-consuming prey while foraging. Whales often increase the amount of lunges completed in deeper water to account for the increase in travel time to the prey at depth (Tershy et al. 1993; Croll et al. 2001; Doniol-Valcroze et al. 2011). This suggests that the feeding rate of an animal may not be influenced by depth or may even increase with depth. However, blue whales (*Balaenoptera musculus*) have been shown to have a higher feeding rate near the surface than at depth (Doniol-Valcroze et al. 2011), potentially as a result of the animals being able to combine recovery time at the surface with purging of the water

engulfed during the lunges (Goldbogen et al. 2011). Therefore, the depth of the prey is likely to influence the balance between energy gained and energy spent by a feeding whale. Consequently, prey depth may also affect the choice of a whale to feed during migration.

The aims of this study were to (1) determine whether the depth and type of prey influenced the amount of feeding by humpback whales outside of their Antarctic feeding grounds, and (2) estimate the amount of energy acquired while feeding during migration. It was hypothesised that whales would lunge at a higher rate on krill compared to fish, given that krill is a slow prey item likely requiring less energy to catch, and is the main prey type of the east Australian population of humpback whales on their main feeding grounds (Matthews 1937). It was also hypothesised that the whales would feed at a higher rate on shallow prey compared to deep prey given the close proximity to the surface. To make the choice to delay migration to feed worthwhile, it was hypothesised that humpback whales should either meet their energy requirements for the period of time spent feeding or have a higher rate of energy intake.

Materials and methods

Behavioural data collection

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

A continuous focal follow (Altmann 1974; Mann 1999) was completed on the tagged individual at approximately 50–200 m distance depending on the sea state. This involved using a pre-defined ethogram (Owen et al. 2015) to record every behaviour of the animal while at the surface, including the occurrence of feeding lunges. The data were collected using a H1 Zoom audio recorder and later transcribed. Focal follow and DTAG data were time-synchronised using a hand-held GPS (Garmin GPSmap 78SC). All focal follows were completed by a single observer (KO) to avoid interobserver reliability issues (Mitchell 1979).

Identification of prey type

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

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

were less than 0.5 dB different from theoretical predictions. Collected backscatter data were corrected for this offset before subsequent processing.

Prey patches were identified by thresholding the volume backscattering strength (Sv) data at 38 and 200 kHz at -80 dB re 1 m^{-1} . A dB-differencing method (Reiss et al. 2008; Warren and Demer 2010; Ressler et al. 2015) was used to identify scattering aggregations as either krill or fish depending on the value of the difference in Sv ($\Delta_{\text{dB}} = \text{Sv at 200 kHz} - \text{Sv at 38 kHz}$). Target strength (TS) values for krill were obtained using theoretical models for monospecific aggregations of krill (Conti and Demer 2006). Krill lengths were determined based on the net tow data from 2012, visual observations of surface krill aggregations in 2012, and the largest possible size of krill that might be in this region (although most of the krill observed had lengths of 5–20 mm). An estimated krill length range of 5–60 mm was used, and aggregations were identified as krill when $2 \text{ dB} < \Delta_{\text{dB}} < 30 \text{ dB}$. Similarly, the species and length of fish were based on the visual observations of surface schools in 2012 and discussions with local fisherman about the typical size of baitfish in this region at the time of the survey. Aggregations were identified as fish when $-100 \text{ dB} < \Delta_{\text{dB}} < -20 \text{ dB}$. These values result from estimates of acoustic backscatter from fish ranging in length from 10 to 40 cm, including species with (Simmonds and MacLennan 2005; Weber et al. 2009) and without (Gorska et al. 2005) swim bladders. Measured TS values from a study of similar baitfish (e.g. pilchards (*Sardinops ocellatus*)) were also used (Lynam et al. 2004).

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

Lunge rate calculations

DTAG data were decimated from 50 to 5 Hz. Given that the orientation of the tag on the whale can vary both between and within a deployment (due to the tag slipping on an animal), the data were corrected for the orientation of the tag on the whale (methods explained in Johnson and Tyack 2003). The detection of lunge feeding behaviour often involves the use of flow noise data

(Goldbogen et al. 2006) or acceleration parameters that are likely to be influenced by surface dynamics (Ware et al. 2011; Simon et al. 2012). As a consequence, the upper 10–40 m of the water column is often excluded from studies describing whale feeding behaviour from biotelemetry devices (Ware et al. 2011; Simon et al. 2012). Given that exclusion of the upper sections of the water column would likely underestimate feeding rates, the times when presumed feeding lunges were completed were determined using the lunge detecting algorithm with a TrackPlot filter applied, as described in Owen et al. (2016). This method was specifically designed to allow for the detection of lunge feeding behaviour regardless of depth. It identifies lunges by finding peaks in excess x-acceleration (forward acceleration minus the influence of gravity), along with a positive pitch angle and a highly negative level of jerk in the EXA signal (rate of change in forward acceleration), which is indicative of strong deceleration by the animal. The use of the TrackPlot filter allowed for the removal of any false detections by the algorithm (Owen et al. 2016). Using this method, 70 % of the lunges observed during the focal follows were detected, with the method less likely to miss lunges at depth due to the lower drag forces at depth (Owen et al. 2016). Any lunges that were observed during the focal follow but were not detected by the algorithm were also included in the analyses of lunge rate.

Sub-sampling of continuous behavioural data sets into discrete time bins is a common practice used to enable the calculation of behavioural rates and to assign behavioural states (Mann 1999). In order to calculate lunge rates, the data were divided into 10-min time bins and the number of lunges completed in each time bin was counted. The length of the time bins was chosen to allow for adequate variation in lunge rate and lunge depth among time bins. Longer time bins would likely have reduced statistical power, and shorter time bins would have reduced variation and impacted on the ability of models comparing the lunge rate between prey types to converge. Any time bins with no lunges in them were labelled as non-feeding periods by the whales and were excluded from the analysis of feeding rates. This was due to the significant difference in the amount of time spent in a feeding state between animals feeding on krill and animals feeding on fish (Owen et al. 2015), which would have likely biased the comparison of the rates at which the whales fed when consuming the two different prey types. The depth of a lunge was defined as the depth of maximum excess x-acceleration. To determine the influence of prey depth on the lunge rate, the average depth of the lunges completed in each 10-min time bin was calculated and used as a proxy for the targeted prey depth. All means are presented as mean \pm standard error.

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

A generalised linear mixed model (GLMM) was used to determine the influence of prey type and prey depth on the lunge rate of the whales (Lunge rate \sim Prey type + Prey depth + (1| Whale identity)). The model was run using the `glmmADMB` package (Fournier et al. 2012; Skaug et al. 2013) in R (R Development Core Team 2013). This package uses Laplace approximation to estimate the parameters of the model. Laplace approximation is more appropriate than PQL approximation for Poisson data where the mean number of counts per treatment is less than five and is better for inference because it uses true likelihood rather than quasi-likelihood (Bolker et al. 2008). The individual whale was used as a random effect to account for the lack of independence of the multiple lunge rates determined for each individual over time. A zero-truncated distribution was used given the skewed nature of the data towards low lunge rates and the lack of zero values. Any data points outside 1.5 times the interquartile range above the upper quartile and below the lower quartile of the data were defined as outliers in the data. As outliers are likely to have a stronger influence on the outcome of a model than other data points, the model was run with outliers removed ($n = 2, 3$ % of the data points). Degrees of freedom were calculated based on the number of random effects (number of whales), minus the number of parameters in the model (in this case three: prey type, depth, and whale). Wald tests were completed to determine the z values and p values for each of the model parameters to assist with hypothesis testing, with significance levels set at $p < 0.05$.

Calculations of energy consumption

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

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

where M is the mass of the animal in kg (Kleiber 1975). However, due to the large size of baleen whales, they are often an outlier in these models, and, as a consequence,

there is still much debate over whether this equation accurately describes whales' metabolic rates. Many different estimates of the values of model parameters have been proposed, resulting in large variations in the estimated energy requirements of baleen whales (Leaper and Lavigne 2007). It has been suggested that models that raise the mass of the animal to a power of greater than 0.75, and therefore greater than the BMR of the animal, are unlikely to represent true consumption given that the cost of thermal homeostasis and locomotion decrease with mass (Leaper and Lavigne 2001; Barlow et al. 2008). In a recent review, Leaper and Lavigne (2007) suggest that given many of the challenges in determining model inputs for baleen whales, the best way forward in calculating consumption would be to use separate models to provide an indication of the likely upper and lower limits of consumption. Based on a review of available methods, they recommend the model by Innes et al. (1986) to represent an upper limit of the likely consumption rate, which is expressed as follows:

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

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

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

where FMR is the field metabolic rate of the whale expressed in kJ/day. Using these two equations, the average daily requirements of whales were calculated as a lower limit and upper limit of consumption. However, one of these equations represents the requirements of whales in terms of energy, and the other represents it as the mass of food. Given that the prey types consumed during this study are likely to have different energy contents, the mass of prey was converted to an energy requirement. No information on the actual energetic value of the prey targeted in this study was available. As a consequence, the energetic content of the prey types was assumed to be 3.9 MJ/kg for krill and 5.4 MJ/kg for fish, values that have been used in many studies to provide an indication of the energetic content of crustaceans and fish (Leaper and Lavigne 2007).

In order to calculate the consumption of prey by whales while on migration, estimates of a number of parameters were required. The first of these was an estimate of the numerical density of the prey (number of animals/m³) and biomass density (kg wet weight/m³) available to the whales. For animals feeding on fish in 2012, the echosounder data collected in 2012 were used to estimate density. In 2011 when the whales were consuming krill, no

echosounder data were available, so the echosounder data collected for krill patches in 2012 were used to estimate krill density. In 2011, krill were observed at the surface as incredibly dense swarms that appeared to carpet the surface. In contrast, in 2012 the low number of krill swarms observed were noticeably smaller and less dense. This suggests that the use of density values from 2012 is likely to have considerably underestimated the density of krill being consumed by the whales in 2011. This conservative approach is likely to have resulted in lower estimates of consumption rates than the actual rates experienced by the whales feeding on krill in 2011.

Thresholded echosounder data (volume backscattering strength, S_v) were identified as being from krill or fish using the method detailed previously. The numerical density of the prey (number of animals/m³) was calculated for each voxel (grid cell in three-dimensional space) in the swarm using an average TS value (at 200 kHz) for a single individual of -83.45 dB for krill and -52 dB for fish (Simmonds and MacLennan 2005). We selected two krill swarms and two fish schools for the analysis. These four aggregations were selected to represent the range of prey aggregations available to the feeding whales (one large and one small for each prey type). Despite the wide range of volumes for the aggregations of the prey types, the mean numerical densities for the krill swarms were similar, as were the mean numerical densities of the fish schools (Table 1). Therefore, these patches were assumed to be representative of the average biomass density of the prey available to the whales. To convert the numerical density (number of animals/m³) into a biomass density (kg wet weight/m³), an equation was required for both krill and fish to translate body size into a weight. No data were available on the size/weight relationship of the specific prey species fed upon by the whales. To account for this, information from the literature on similar-sized prey species for each prey type was used and assumed to be representative of the relationship between size and weight for the prey types targeted. It is thought that any error associated with this assumption is unlikely to have had a large influence on the calculated energy consumptions. In this study, the equation developed for Antarctic krill (*E. superba*) by Wiebe et al. (2004) was used to convert the size of the krill into a wet weight.

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

where L is the length of the krill (mm). The sizes of the krill collected during plankton tows were found to range between 5 and 20 mm in length. A mean krill length of 15 mm was assumed for these calculations as that was the length used in the conversion of the acoustic data to biological information. To determine the sensitivity of this method to animal length, separate runs were completed

using lengths of 10 and 20 mm, which resulted in biomass densities (kg wet weight/m³) that differed only by 15–20 % (this is because larger animals scatter more sound so they produce a smaller numerical density estimate). For fish, the following equation was used:

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

where L is the length (cm) of the fish (FAO 1994). It was assumed that the fish were approximately 15 cm in length based on the observations of fish near the surface and discussions with local fisherman about the average size of fish present in the study area at the time. The calculated wet weight per individual was then multiplied by the numerical density to provide an estimate of the biomass density (kg wet weight/m³).

The engulfment volume of humpback whales has been calculated to be 28 m³ (Goldbogen et al. 2011). However, this volume represents a maximum engulfment volume, and it is unlikely that humpback whales would regularly completely expand the oral cavity while feeding, especially when feeding near the surface when air may fill some of the cavity. In addition, the engulfment volume varies with the size of the animal, a factor that was not measured as part of this study and is difficult to measure accurately in the field. Given this, a more conservative value of 14 m³ (half of the maximum) was used in the calculations (7 m³ was used in a sensitivity analysis calculation). The amount of prey consumed in each lunge (PC) (g) was determined by:

$$PC = E_{\text{volume}} \times P_{\text{density}} \times C_{\text{efficiency}}$$

where E_{volume} is the engulfment volume of the whale (m³), P_{density} is the average biomass density of the targeted prey (kg wet weight/m³), and $C_{\text{efficiency}}$ is the capture efficiency of the lunge. Capture efficiency relates to the proportion of the patch of prey that is actually caught in the mouth of the whale as opposed to fleeing during the approach by the whale. Very few data exist on the capture efficiencies of humpback whales targeting different prey types. However, it is likely to be influenced by the size and mobility of the prey (Mayo et al. 2001). As a consequence, the capture efficiencies by the whales for the two prey types were estimated for the purposes of this study based on the observations of whales feeding on both prey types in various locations around the world. It was assumed that whales targeting krill would have a higher capture efficiency than that of whales targeting fish (0.8 compared to 0.6), as krill are slower and therefore less likely to be able to flee capture (0.5 was used for both prey types as a part of a sensitivity analysis). In order to complete the calculations, an additional assumption was made that the size of the prey patch was big enough to completely fill the mouth of the whale. This assumption appears justified given the threshold foraging response of whales [that only begin to

Table 1 Details of the example prey patches that were representative of the prey available to humpback whales (*Megaptera novaeangliae*) while on migration. All of the prey patches were being fed upon by whales, except for krill patch number 2

Patch number	Krill		Fish	
	1	2	1	2
Size of patch (m ³)	78,540	29	760	60
Mean prey numerical density of patch (number of animals/m ³)	1300	1400	4	2
Maximum prey numerical density of patch (number of animals/m ³)	80,000	48,100	370	48
Mean biomass density of patch (kg wet weight/m ³)	0.042	0.045	0.088	0.050
Maximum biomass density of patch (kg wet weight/m ³)	2.6	1.5	9	1.2

feed when prey density is above a certain threshold, which allows the energy consumed to match or exceed the high energy demands of their lunge feeding strategy (Piatt and Methven 1992)], and the extensive swarms of krill observed in 2011 and the size of the schools of fish detected by the echosounder in 2012 (Table 1).

The average lunge rate (AV_{LR}) (number lunges/hour) was taken from data collected during the focal follows in this study. In order to provide an indication of the lunge rates of the animals over time, the total number of lunges completed by an animal was divided by the length of the focal follow (including any periods during which no feeding lunges occurred). This method allows for an incorporation of the differences in the amount of time spent feeding by the whales when targeting the two different prey types (Owen et al. 2015). To determine the hourly consumption rate of prey (HC) (kg) by whales on migration, the following equation was used:

$$HC = AV_{LR} \times PC$$

To convert this to an estimate of the energy provided by the prey, the HC was multiplied by the energetic content of the prey type (3.9 MJ/kg for krill and 5.4 MJ/kg for fish) and the assimilation efficiency (%), which is the amount of energy that becomes available to the whales from the prey ingested. Assimilation efficiency was assumed to be 80 % for both krill and fish (Lockyer 1981; Innes et al. 1986; Kenney et al. 1986; Leaper and Lavigne 2007). The average energy content of prey consumed daily was then determined by extrapolating the HC. Given that the calculation of HC included periods of no feeding by the whales, this extrapolation is likely to be valid. The daily energy intake rate of whales on migration was then compared to the required daily energy intake rate of humpback whales in the Antarctic to maintain their FMR using the following equation:

$$NEA = \frac{EM}{EFMR}$$

where EM is the daily energy intake on migration, EFMR is the daily energy intake required by the whale to maintain FMR, and NEA is the net energy acquisition by the whales. The comparison provided an indication of the likelihood

that whales either lose or gain energy while feeding on migration.

Results

Nine individual whales were tagged off the coast of Eden, NSW, Australia (three in 2011 and six in 2012). Details of the deployment durations, number of lunges, and prey type targeted are provided in Table 2. Tag deployment durations were the same as the focal follow durations. Lunges were detected in all nine of the tag deployments. It was determined by visual observations at the surface that all three animals in 2011 were feeding on krill (*N. australis*) (Owen et al. 2015). For the purposes of this study, it was assumed that these three animals were feeding on krill regardless of the depth of the lunge. This assumption was based on the observation from camera drops of krill being distributed within the upper 10 m of the water column throughout the focal follows and the lack of observation of schools of fish at any stage in 2011 (Owen et al. 2015). Using echosounder data, all six animals in 2012 were determined to be feeding on schools of baitfish (Owen et al. 2015). The baitfish species targeted likely included species such as jack mackerel (*Trachurus declivis*), pilchards (*Sardinops neopilchardus*), and redbait (*Emmelichthy nitidus*) that were regularly observed at the surface during the focal follows in 2012. Therefore, the whales observed were either feeding in the presence of krill ($n = 3$) or in the presence of fish ($n = 6$).

The lunge rates for animals assumed to be feeding on krill ranged from 1 to 21 lunges per 10 min (average of 10 ± 1 per 10 min). In comparison, animals that fed on fish had lunge rates that ranged from 1 to 5 lunges per 10 min (average of 3 ± 1 per 10 min). When considering all of the lunges completed by each whale and the total length of each focal follow (including times when the whales were not feeding), whales feeding on krill had an average lunge rate of 49/hour, whereas whales feeding on fish had an average lunge rate of 5 lunges per hour (Table 2). The depths of lunges completed by whales assumed to be feeding on krill ranged from 1.4 m to 22.6 m with an average of $5.4 \text{ m} \pm 0.8 \text{ m}$ compared to

Table 2 Details of the nine focal follows of humpback whales (*Megaptera novaeangliae*) completed while migrating off the coast of Eden, NSW, Australia. The prey type refers to the predominant prey type encountered by the whales during the focal follow. Lunge rate was calculated as the total number of lunges divided by the focal follow duration

Date	Focal follow duration (hh:mm)	Sex	Prey type	Number of lunges visually observed	Total number of lunges	Lunge rate (lunges/hour)	Average lunge depth (m) (mean \pm SD)	Echosounder data collected
2011								
15 September 2011	2:10	F	Krill	96	161	75	4.7 \pm 6.1	No
16 September 2011	2:13	M	Krill	20	35	16	3.4 \pm 5.9	No
17 September 2011	2:13	F	Krill	74	127	57	4.6 \pm 5.4	No
				Average	Average	49	4.2	
2012								
16 September 2012	3:27	M	Fish	0	3	1	11.9 \pm 13.5	Yes
17 September 2012	1:19	F	Fish	0	1	1	19.1	Yes
2 October 2012	2:47	M	Fish	0	53	19	25.2 \pm 14.4	Yes
4 October 2012	3:09	F	Fish	0	9	3	25.1 \pm 5.1	Yes
6 October 2012	3:06	Unknown	Fish	0	11	4	17.7 \pm 9.0	Yes
9 October 2012	2:47	M	Fish	0	2	1	10.7 \pm 1.9	Yes
				Average	Average	5	18.3	

those of animals feeding on fish, which ranged from 4.1 m to 47.7 m with an average of 22.0 m \pm 1.6 m. The lunge rate was significantly higher (GLMM, $df = 6$, $z = 3.28$, $p = 0.001$) for whales assumed to be feeding on krill compared to fish (Table 2). However, the depth of the prey did not have a significant influence on the lunge rate of the animals (GLMM, $df = 6$, $z = -1.20$, $p = 0.229$) (Table 2).

The biomass densities of the prey observed in the study site are provided in Table 1. It was determined that a humpback whale requires between 530 and 1522 MJ per day in order to meet the demands of their FMR. While feeding on krill on migration, whales were estimated to have an average hourly energy intake of 74.6 MJ (Table 3). In contrast, when feeding on fish on migration, whales had an average hourly energy intake of 11.6 MJ (Table 3). This corresponds to whales consuming between 1.2 and 3.4 times their required daily energy intake while feeding on krill during migration (Table 3). In contrast, whales feeding on fish while on migration are estimated to have only consumed between 0.6 and 1.7 times their required daily energy intake rate (Table 3). While it is felt that the values used in the calculations are conservative values likely to represent the consumption rate of the whales, a sensitivity analysis completed revealed that even when some parameters are lowered to extremely conservative values, whales consuming krill while on migration may still just exceed their required daily energy intake rate (Table 3).

Discussion

The consumption rate of prey by predators is an important input into models created for ecosystem-based management that aim to determine the impact of fisheries on ecosystems (Wiedenmann et al. 2011). Such models for the Southern Ocean are often based on the assumption that consumption by predators comes predominantly from Antarctic prey sources and not from prey consumed during migration. Models that vary the amount of food intake during migration show that fluctuations in migratory feeding could result in significant influences on the birth rates of whale populations (Wiedenmann et al. 2011). Despite this, little is known about what factors may lead to fluctuations in food intake by whales and the rates at which energy may be assimilated while migrating (Leaper and Lavigne 2007; Wiedenmann et al. 2011). The results of this study reveal that whales may change the rate at which they feed and the amount of energy that is consumed on migration depending on the type of prey that is available. Humpback whales on migration were found to lunge feed at a high rate on krill and consume a greater amount of

Table 3 Consumption of prey by humpback whales (*Megaptera novaeangliae*) feeding on krill and fish while on migration. Average lunge rate was calculated by dividing the total number of lunges completed by the whale by the duration of the focal follow. The net energy acquisition (NEA) is the daily migratory energy intake divided

by the amount of energy required to sustain field metabolic rates (both the upper and lower limits calculated for FMR). Values are shown for both prey types (krill and fish) as well as for a sensitivity analysis (SA) where the estimates of certain parameters were made extremely conservative

	Krill	Krill SA	Fish	Fish SA
Mean biomass density of prey (kg wet weight/m ³)	0.04	–	0.07	–
Whale engulfment volume (m ³)	14	7	14	7
Capture efficiency	0.8	0.5	0.6	0.5
Prey consumed per lunge (kg)	0.49	0.15	0.58	0.24
Average lunge rate (number/hour)	49	–	5	–
Assimilation efficiency (%)	0.8	–	0.8	–
Energy content of the prey (MJ/kg)	3.9	–	5.4	–
Hourly energy intake (MJ)	74.6	23.3	11.6	4.8
Daily migratory energy intake (MJ)	1791.2	559.8	279.0	116.2
NEA (assuming upper limit of FMR)	1.2	0.4	0.6	0.1
NEA (assuming lower limit of FMR)	3.4	1.1	1.7	0.2

energy per unit time than required to maintain their FMR. Despite the hypothesis that the depth of the prey would influence the rate of feeding while on migration, there was no pattern in lunge rate as a function of the prey depth. However, this may be due to the relatively shallow distribution and the lack of contrast in the vertical structure of the prey encountered by whales in this study. The results suggest that when prey conditions are favourable, feeding while on migration may allow whales to begin to refuel energy reserves prior to reaching Antarctic feeding grounds.

It is assumed that whales on migration feed less than they do on the feeding grounds (Lockyer 1981). Accounts of whales feeding while on migration typically describe an extremely brief feeding period (minutes to a few hours) (Salden 1989; Swingle et al. 1993; Gill et al. 1996; Stockin and Burgess 2005; Stamation et al. 2007; Alves et al. 2009) and whaling records also indicated that the large majority of animals had empty stomachs while migrating (Mackintosh and Wheeler 1929; Matthews 1937; Gambell 1968; Lockyer 1981). Whaling data have also been used to estimate that the rate of feeding while on migration is approximately 10 % or less of that on the Antarctic feeding grounds (Lockyer 1981). However, whaling was often carried out during the migration of the animals from the feeding grounds towards breeding grounds (in the case of the east Australian population, during the northward migration), and as a consequence, there is little information on the stomach contents of animals migrating from breeding grounds to feeding grounds (Dawbin 1966). The results of this study suggest that whales may consume energy at a much higher rate (1.2–3.4 times their daily requirements) while migrating than previously believed.

This is likely due to the whales lunge feeding at a higher rate on average than previously documented in the Antarctic. On the main feeding grounds, the lunge rate of humpback whales has been reported to be up to approximately 30–40 lunges an hour (Ware et al. 2011; Tyson et al. 2012). To the best of our knowledge, the lunge rate observed by animals feeding on krill while on migration in this study (average rate of 49.1 lunges per hour; maximum of 75) is higher than any published account of humpback whales feeding worldwide. This high rate of energy intake, combined with other evidence that individual whales may spend up to 10 days feeding in the area off Eden (Owen et al. 2015) suggests that the amount of energy intake during migration may be higher than previously thought. In addition, satellite tracks of whales migrating from the east coast of Australia towards the Antarctic revealed the presence of potential foraging by whales in several productive temperate areas (Gales et al. 2009). If individuals consume prey at such high rates and feed multiple times during migration, feeding while on migration may contribute a large amount to some humpback whale populations' energy budgets.

The rate of energy intake by whales feeding on fish was lower than that of whales feeding on krill, mainly as a result of the lower lunge rate when fish were available and less time spent actively feeding (Owen et al. 2015). When fish are available, whales may be able to balance their energy intake with energy expenditure, while still making progress southwards on migration towards feeding grounds (Owen et al. 2015). In contrast, in 2011 when krill were available, whales gained energy and were observed to delay migration and dedicate a significantly greater amount of time to feeding (Owen et al. 2015). Therefore, when the

prey conditions encountered enable whales to have a net energy gain per unit time foraging, whales may choose to delay migration to feed.

The difference in the lunge rate of the whales when targeting krill or fish is possibly due to differences in the speed or patch sizes of the prey types. Compared to krill species, schooling fish are more mobile and thus present a more difficult and energetically demanding prey target for humpback whales (swimming speeds of 67–159 cm/s for sardines (*Sardinops sagax*) (Misund et al. 2003) compared to 10–20 cm/s for krill species (*N. australis* and *E. superba*) (Sidhu et al. 1970; Hamner 1984; Reinhardt and Van Vleet 1986; O'Brien 1988). In addition to the lower rate of lunges observed when feeding on fish, only 20 % of the groups observed in the area were determined to be feeding (based on the surface observations of movement patterns, diving behaviour, and lunge feeding, as well as the presence of prey and other predatory species) when fish were available compared to 70 % when krill were abundant (Owen et al. 2015). Due to the high availability of krill on the main Antarctic feeding grounds (Tarling et al. 2009; Nowacek et al. 2011), and the potential for animals to encounter slower prey further south on migration (Gill et al. 1996), the energy expenditure required to capture fish successfully may not be worth the delay in migration and the potential energy return for the majority of individuals. Given that the sizes of the prey patches observed of both prey types varied from very large patches (much greater than the engulfment volume of a whale) to smaller patches (about the same size as the engulfment volume of a whale), it seems unlikely that the patch sizes influenced the differences in lunge rates observed between the two prey types. Therefore, the speed of the prey may influence the amount of energy required to capture the prey and impact on the decision to feed while migrating.

Despite the higher speed of fish, humpback whales have been observed to feed on fish species in many parts of the world (Jurasz and Jurasz 1979; Friedlaender et al. 2009b; Acevedo et al. 2011). The morphology of humpback whales enables them to be a manoeuvrable predator that is capable of catching many different species of prey (Woodward et al. 2006). However, the efficient capture of fish often requires the use of various prey corraling techniques (Jurasz and Jurasz 1979; Friedlaender et al. 2009b; Acevedo et al. 2011). For example, bubble columns and clouds are often used in many different ways to corral and trap fish and reduce their escape abilities (Wiley et al. 2011). The east Australian population of humpback whales is believed to feed predominantly on Antarctic krill on the main feeding grounds (Matthews 1937), and no evidence of prey corraling was observed while the whales fed on fish. Due to the short amount of time spent on migratory stopovers, exposure to the potential prey species available on

migration is also brief. The spread of a new feeding behaviour through a population of humpback whales has been shown to take several decades, even though the whales may spend months feeding on the prey (Allen et al. 2013). Therefore, it is possible that given the short encounter time of the east Australian population of humpback whales with fish species as potential prey items, the population may not have yet evolved optimally efficient strategies for capturing fish. Although the east Australian population has been observed to feed on fish while on migration (Stockin and Burgess 2005; Stamation et al. 2007; Owen et al. 2015), the efficiency of this behaviour may not be sufficient to make a large energy investment worthwhile.

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

Whether or not migratory feeding is opportunistic or an essential part of the annual energy acquisition of whales, the results of this study suggest that changes in the prey type available on migration significantly influenced the lunge rate of whales and the rate of energy intake. If changes in prey type can influence the amount of feeding while on migration, an understanding of what environmental variables may drive changes in prey availability is required. Future research should also focus on determining what other factors, such as prey density or whale body condition, may influence feeding behaviour and how frequently feeding behaviour occurs along the migratory route. This will assist with increasing knowledge of the

extent to which whales rely on feeding during migration to meet their energy demands or assist with energy gain. Comparisons of the factors that influence feeding behaviour while on migration between populations that target different prey on their main feeding grounds will also assist in understanding whether or not the lower rate of feeding on fish compared to krill is the result of fish being an unfamiliar prey item for this population. The factors that influence the amount of feeding while on migration should also be incorporated into models to predict the impacts of climate change and krill fisheries on Antarctic predators, as fluctuations in migratory feeding could influence the extent to which humpback whales rely on the Antarctic ecosystem each year.

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