Effect of prey type on the fine-scale feeding behaviour of migrating east Australian humpback whales

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ABSTRACT: For terrestrial migrants, feeding at migratory stopover sites is important, with prey quality linked to future survival and reproductive success. In contrast, the importance of this behaviour to marine species is unknown. The humbpack whale *Megaptera novaeangliae* is a marine migrant that is thought to fast while migrating; however, recent studies suggest that feeding may occur during this time. The aims of this study were to determine how the prey type available on a migratory route off Eden, New South Wales, Australia, influenced whether whales fed or not, and to study the fine-scale behaviour of the whales. Digital acoustic recording tags (DTAGs) and focal follows were used to record whale behaviour. A larger proportion of groups were determined to be feeding when krill was observed at the surface. Whales encountering fish spent a small percentage (28%) of time feeding, behaving similarly to non-feeding whales on migration, with small groups, a higher proportion of males sampled, and relatively straight tracks. In contrast, whales encountering surface swarms of krill spent significantly more time feeding (92%) and behaved similarly to whales on feeding grounds, with larger groups, more females sampled, and tracks with high turning angles. Therefore, changes in the available prey type influenced the amount of time spent feeding and the social dynamics of groups. Given the link between the amount of feeding completed on migration and the future survival and reproductive success of individuals in terrestrial species, the impact of such fluctuations on marine species such as the humbpack whale deserves more attention.

KEY WORDS: Area-restricted search · Humbpack whales · Krill · Fish · Feeding behaviour · Migration · Prey type · Stopover site

INTRODUCTION

Seasonal migrations involve the movement of individuals between geographically distinct breeding and non-breeding areas (Dingle & Drake 2007). Successful completion of migration is largely dependent on the availability of energy reserves to fuel loco-motion (Alerstam et al. 2003). However, the storage of enough energy to complete the entire migration would greatly increase the cost of transport and reduce the speed of travel for many animals, particularly for flying animals such as birds (Åkesson & Hedenström 2007). Migratory speed has been shown to be of importance to many bird species that receive

fitness benefits by reaching breeding areas early, establishing nesting territories, and finding a mate before competition intensifies (Weber & Houston 1997). Refuelling at migratory stopover sites allows birds to reduce their cost of transport and decrease the amount of time taken to reach their destination (Alerstam & Hedenström 1998, Dingle & Drake 2007, Newton 2008). In contrast, in non-avian taxa that walk or run, such as terrestrial mammals, migratory speed has been shown to be of less importance. Instead, species such as mule deer *Odocoileus hemionus* take much longer periods than would be expected to complete migration if they travelled continuously. This is attributed to the large amount of time spent feeding at high quality forage sites along the migratory route (Sawyer & Kauffman 2011). In this case, variation in the speed of migration has been linked to the phenology of plants, with the deer tracking prey availability to increase energy intake during the season of highest plant growth, which delays their arrival at their destination (Sawyer & Kauffman 2011). Therefore, migratory strategies and the importance of stopover sites to the ecology of a species are likely to vary between taxa.

The overwhelming majority of studies on the importance of migratory stopover sites to seasonal migrants have focused on avian taxa, with a small number of studies on other terrestrial species. Resource availability at these sites has been linked to the subsequent survival and reproductive success of individuals, and the migratory strategy used by animals is thought to have evolved to maximize both of these parameters (Newton 2006, Sawyer & Kauffman 2011). The migratory strategy of animals in the marine environment is likely to be different from that of terrestrial species as the cost of transport is lower for swimming animals (Schmidt-Nielsen 1972). Consequently, an increased fuel load has a lower impact on the energetics of marine animals (Schmidt-Nielsen 1972) that may be able store enough energy reserves to complete migration without feeding, which would increase migratory speed. It has been suggested that if there is selection for increased migratory speed in swimming animals, an increase in the size of the animal should occur (Hedenstrom 2003). However, the importance of migratory speed may be reduced in the marine environment due to the ephemeral distribution of resources that reduces reliance on territoriality to secure mating and feeding opportunities, particularly in wide-ranging species such as baleen whales (Clapham 1996). The use of migratory stopover sites as potential foraging areas in the marine environment has been highlighted in fish (Sims et al.

2009), marine reptiles (Broderick et al. 2007, Cuevas et al. 2008) and marine mammals, including many baleen whale species (e.g. humpback whales *Megaptera novaeangliae*, Stamation et al. 2007, Barendse et al. 2010, Visser et al. 2011; blue whales *Balaenoptera musculus*, Visser et al. 2011, Silvia et al. 2013; and fin whales *B. physalus*, Visser et al. 2011, Silvia et al. 2013). Despite this, very little is understood about the role that these stopover sites may provide to the ecology of marine species.

Most baleen whale species are migratory. Historically it was thought that intensive feeding during summer on high latitude feeding grounds enabled baleen whales to store enough energy to complete migration while fasting, or feeding at a very low rate (Lockyer 1981, Clapham 1996). This idea was based on the low abundance of available prey on low latitude breeding grounds and the fact that whales caught on migration by whalers often had empty stomachs (Chittleborough 1965, Lockyer 1981). However, most whaling was conducted during the migration toward breeding areas when whales had the highest fat and oil content (Dawbin 1966); thus, little information exists on stomach contents of whales migrating back towards their feeding grounds. There has been an increasing amount of evidence suggesting that some baleen whale species feed during migration, particularly during the migration toward feeding grounds, when body reserves may be depleted as a result of breeding activities and nursing (Best et al. 1995, Gill et al. 1998, Stamation et al. 2007, Barendse et al. 2010, Visser et al. 2011). This evidence ranges from assumed bottom feeding by migrating gray whales *Eschrichtius robustus* (Cacchione et al. 1987) to numerous satellite tracks of several baleen whales species assumed to forage during migration (Gales et al. 2009, Silva et al. 2013). In addition, there are direct observations of migrating whales feeding in areas of high productivity (Baraff & Clapham 1991, Gendon & Urban 1993, Best et al. 1995, Stockin & Burgess 2005, Stamation et al. 2007, Barendse et al. 2010, Visser et al. 2011). Many of the records of whales feeding during migration are reported to be of juvenile animals, perhaps due to their smaller body size and reduced ability to store sufficient energy reserves (Salden 1989, Swingle et al. 1993, Gill et al. 1998, de Sá Alves et al. 2009, Silva et al. 2010). A female bias at one previously identified stopover site suggests that feeding while migrating may also be important for females (Barendse et al. 2010). Individual whales have been observed spending up to 20 d in the same area while migrating towards feeding grounds (Best

et al. 1995, Visser et al. 2011), indicating that animals may at times delay arrival at high latitude feeding grounds in order to feed at productive sites along the migratory route. Whether these delays to feed are an integral aspect of the migratory strategy of baleen whales has received little attention in the literature. Given that prey quality influences the feeding behaviour of terrestrial species while migrating (Newton 2006, Sawyer & Kauffman 2011), changes in the prey encountered (in terms of prey type, density, quantity, and energetic content) along the migratory route may also influence whale behaviour. Yet, the impact that changes in the prey type available has on the amount of time and effort spent by whales to feeding while migrating has not been investigated.

The east Australian population of humpback whales makes annual migrations between Antarctic feeding grounds and breeding grounds in the Coral Sea off the north east coast of Australia. The area off Eden, New South Wales, on the south-east coast of Australia, has recently been suggested as a potentially important feeding area for this population, with whales observed to feed on both krill and fish while migrating towards Antarctic feeding grounds (Stamation et al. 2007). The aims of this study were to determine how the prey type available at this migratory stopover site influenced whether whales fed and the fine-scale feeding behaviour of individual humpback whales.

MATERIALS AND METHODS

Study site

Data were collected off the coast of Eden, New South Wales, Australia (37.07°S, 149.90°E) (Fig. 1) from 9 September to 2 October 2011 and from 9 September to 19 October 2012. This time corresponded to the southward migration of the whales back towards Antarctic feeding grounds. The study site included the area out to approximately 20 km offshore and 20 km to the north and south of Eden.

Determining the prey type available to the whales

In 2011, the potential prey type available to the whales was determined based on surface observations of prey in close proximity to the whales, by dropping a camera (GoPro Hero 2, resolution 11 megapixels) over the side of the vessel to a depth of 2 m every 20 min throughout the duration of a focal follow, and prey sampling. Prey sampling was completed by towing a 200 μm plankton net with a 40 cm aperture behind the vessel at a depth of between 1 and 5 m for 2 min in an area where the whales had been observed to lunge feed. One net tow was completed per focal follow within 2 min of the whales being observed to lunge in the area. The prey sampling was used purely for krill species identification, and no attempts were made to determine density or abundance of krill or fish using this method, due to net avoidance capabilities. In addition, due to the net avoidance abilities of fish, it was not possible to collect any fish species using this sampling method. For each lunge completed at the surface, the prey type (krill vs. fish) targeted could be directly observed and recorded. While the use of these methodologies provided an understanding of the prey available
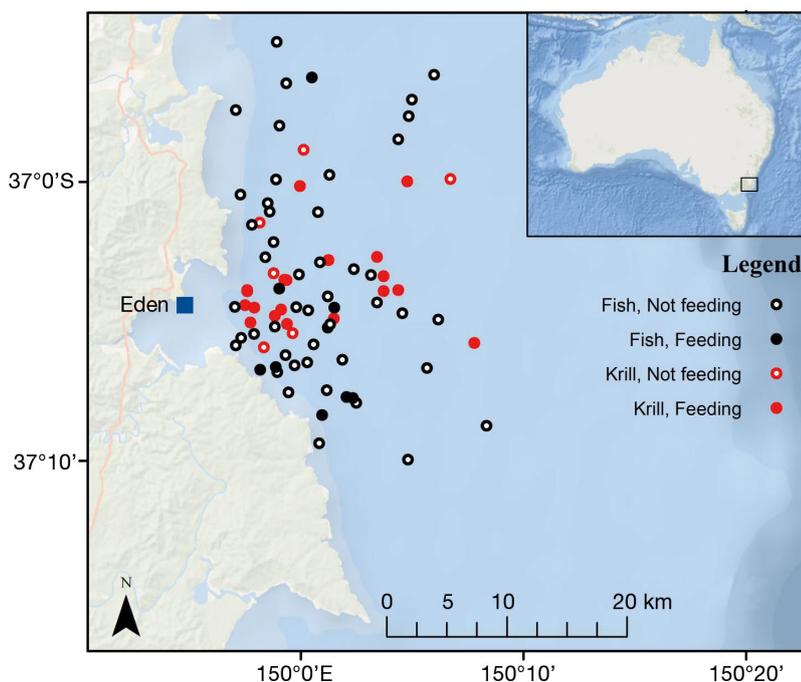

Fig. 1. Study site off Eden, NSW, Australia, showing the location of the groups of humpback whales encountered during group surveys. Prey type encountered by each group is displayed as red for krill and black for fish. Behaviour of the group during the survey is indicated by closed circles (feeding) and open circles (not feeding)

to the whales near the surface, it is acknowledged that it provided no information on the prey available to the whales at depth in 2011.

In 2012, a dual frequency (38 and 200 kHz) echosounder (ES60, Simrad/Kongsberg) was used to provide information on the availability of fish and krill. The echosounder was deployed off the starboard side of the vessel using a small towfish, which held it at a depth of approximately 50 cm. For both frequencies, the echosounder had a ping rate of 0.5 Hz, depth bins of 10 cm, pulse length of 256 μs, and a power setting of 2000 W. The system was calibrated using a standard 38.1 mm Tungsten carbide sphere (Foote et al. 1987) at the beginning of the 2012 surveys. The sphere was lowered to between 10 and 20 m beneath the echosounder in a location with little biological scattering and a water depth of 26 m. Backscatter values for the standard target were less than 0.5 dB different from theoretical predictions. A camera was also dropped off the side of the vessel to a depth of 2 m every 20 min throughout the duration of a focal follow, and net tows were also completed as above in order to provide a comparison to the 2011 methods.

In order to identify prey patches, the backscatter was thresholded at 38 and 200 kHz at −80 dB re 1 m^{-1}. A dB-differencing method (Reiss et al. 2008, Warren & Demer 2010) was used to identify scattering aggregations as either krill or fish depending on the value of the difference in volume backscattering strength (Δ_{dB} = Sv at 200 kHz − Sv at 38 kHz). Theoretical target strength (TS) models were used to determine likely backscatter values for monospecific aggregations of krill (Conti & Demer 2006). Aggregations were identified as krill when 2 dB < Δ_{dB} < 30 dB. These values result from an estimated krill length distribution of 5 to 60 mm, which was based on net tow data from 2012 and visual observations of surface krill aggregations in 2012. Aggregations were identified as fish when −100 dB < Δ_{dB} < −20 dB. These values result from estimates of acoustic backscatter from fish that ranged in length from 10 to 40 cm, including species with (Simmonds & MacLennan 2005, Weber et al. 2009) and without (Gorska et al. 2005) swim-bladders. These parameters (i.e. species and length) were based on visual observations of surface schools in 2012 (as no fish were caught as a part of the present study) and on discussions with local fisherman about the typical sizes of baitfish in this region at the time of the survey.

Echosounder data were collected continuously throughout the entire focal follow at locations near the focal whale by following behind the path of the focal whale in a zig-zag pattern. Typically, a 50–

200 m distance from the feeding whale was maintained, although occasionally larger separations of up to 500 m would occur between the location of the focal whale and where the echosounder data were collected. Scattering aggregations that were encountered near the whale were used to categorise the dominant prey available for each whale as either krill or fish.

Sampling of behavioural data

In order to determine the behaviour of humpback whales, 2 different behavioural sampling protocols were used. The first was a 20 min survey of the groups of whales encountered to determine the likelihood that they were feeding. Secondly, continuous focal follows of individual whales determined to be feeding were completed.

Surveys of group behaviour

For each group of humpback whales sighted, a boat-based survey (Mann 1999) was conducted from a distance of approximately 100 m for a period of up to 20 min. A group was defined as any animals with a similar movement and surfacing pattern within 50 m of each other. During the survey an assessment was made about whether or not the whales in the group were likely to be feeding. Surface-feeding events were confirmed by the observation of a lunge, which involved a whale engulfing water and prey into an open mouth, and the group was then recorded as a feeding group. For animals feeding at depth, a combination of factors was considered. (1) The presence/absence of prey in the area: feeding whales were found in areas where prey patches were present in the water column. This was determined either by direct observation of the whales within a patch of prey visible at the surface (2011 and 2012) or from echosounder data with the whale being observed to dive into an area where prey were available (2012) (prey sampling methods described above). (2) The surface movement pattern of the whale over the 20 min: feeding whales showed no fine-scale trend in the direction of travel. In contrast, non-feeding whales had a consistent direction of travel and surfacing intervals. (3) The presence/absence of other predatory species (e.g. short-tailed shearwaters *Puffinus tenuirostris*, Australasian gannets *Morus serrator*, and/or common dolphins *Delphinus delphis*): feeding whales were located within 100 m of one or

more other predatory species. For groups where no surface lunge was observed, the group had to meet at least two of these criteria to be recorded as a feeding group.

Focal follows of individual whales

For some of the groups that were determined to be feeding, a digital acoustic recording tag (DTAG) (Johnson & Tyack 2003) was deployed onto the back of one of the whales between the blow holes and dorsal fin using a 6 m carbon-fibre pole. Four silicon suction-cups were used to attach the DTAG to the back of the whale. The DTAG contained a 3-axis accelerometer, a 3-axis magnetometer, and a pressure sensor (accuracy of ± 0.5 m) and was programmed to release after 2 to 3 h. All sensor data were collected at a sampling rate of 50 Hz. The DTAG also contained a VHF transmitter that allowed the whale to be tracked when at the surface. All data collected by the tag were archived and downloaded via infrared transmission upon retrieval of the tag.

Once a tag was deployed, behavioural data collection commenced. The tagged individual was chosen as the focal animal so that a complete account of the tagged whale's behaviour at and below the surface could be collected. When tag deployment was not successful, a focal individual was selected randomly from the group. Focal follow duration ranged from 2 to 3 h. The follow protocol used was an individual-follow with a continuous sampling method (Mann 1999). A pre-defined ethogram (Table S1 in the Supplement; www.int-res.com/articles/supp/m541p231_supp.pdf) was used to record every observed surface behaviour by the focal whale throughout the duration of the focal follow. Behavioural records were made using an audio recorder (Zoom H1 recorder) to provide a time-stamped record of the behaviour. The same observer (K.O.) completed every focal follow to avoid inter-observer reliability issues (Jones et al. 2001, Kaufman & Rosenthal 2009). Both the DTAG and the audio recorder were time synchronised using a handheld GPS (Garmin GPSmap 78SC).

As well as recording the individual focal follow, incident sampling was conducted by the same observer on the remaining animals in the focal individual's group (Mann 1999). Incident sampling involved recording the time of lunge feeding behaviour by any whale in the group and determining whether the lunge was completed in synchrony with other group members. Synchronous lunging behaviour was defined as lunging behaviour by 2 or more individuals where the individ-

uals lunged within 2 s of each other, in the same direction, less than one body length apart. The identity of individuals completing each synchronous lunge was noted. Individuals were identified visually using lateral pigmentation and dorsal fin shape when possible (Katona & Whitehead 1981). In cases where the group split during a focal follow, we continued to collect incident sampling data only from animals that remained in the same group as the focal individual. This helped to reduce bias in selecting a group post-split. The group size was recorded every 10 min.

A biopsy sample was collected where possible to determine the sex of the animals observed. This was completed using the Paxarms system, which involved firing a biopsy dart from a modified .22 rifle (Krützen et al. 2002). When a group was small (less than 5), an attempt was made to collect a sample from all individuals in the group with the priority for sampling being the tagged individual. For some tagged individuals, skin was collected from the suction cups of the DTAG. Biopsy samples were stored in a −20°C freezer prior to processing. Sex determination was completed by the Australian Marine Mammal Centre at the Australian Antarctic Division (sex determination methods explained in Morin et al. 2005).

Comparisons of the individuals identified between sightings were made using photographic-identification techniques to give an indication of how many were re-sighted by chance throughout the course of the study. Only high quality photographs where markings and dorsal fin/fluke shape could be easily observed were used for comparisons. The matches made were confirmed by an independent observer.

Data processing and analysis

Data analyses

All data analyses were performed in R (R Development Core Team 2013) with significance levels set at $p < 0.05$. A number of models were developed in order to test the relationship between the prey type and whale behaviour (for specifics of which behaviours, the type of models, and packages used see the sections below). All models were checked for temporal autocorrelation, homoscedascity, and whether the residuals were normally distributed. The identity of the whales was used as a random effect (intercept) in all of the models to account for the repeated measures. Degrees of freedom were determined based on the number of random effects (whale identity) minus the number of parameters in the model.

Time spent feeding

All tag data were calibrated and decimated to 5 Hz using the methods described in Johnson & Tyack (2003). Given that the orientation of the tag on the whale can vary both between and within deployments, the data collected by the tag were corrected for the orientation of the tag on the whale. This included accounting for any changes in the orientation of the tag throughout each deployment (Johnson & Tyack 2003). For tagged individuals, the times when presumed feeding lunges were completed were determined using a lunge-detecting algorithm (that relied on orientation-corrected forward acceleration, jerk, and pitch angle) with the TrackPlot Visual Classification Method applied as described in Owen et al. (2015). Any lunges that were observed but not detected by the algorithm were also used in the analysis. Given that some feeding behaviour occurred underwater and out of sight of the observer, only tagged individuals were used for the analysis of the time spent feeding.

For tagged whales, observations were divided into 10 min time bins. The duration of the time bins was chosen based on the lengths of the focal follows, the desire to model behavioural states as opposed to behavioural events, and the likelihood of each bin containing a lunge. Each time bin was assigned as either containing a lunge ('feeding'), or not containing a lunge ('not feeding'). This parameter was then used as a binomial response variable in a generalised linear mixed model (GLMM) (feeding behaviour ~ prey type, random = ~1|whale identity), using the glmmadmb package (Fournier et al. 2012, Skaug et al. 2013) in R (R Development Core Team 2013) to compare the amount of time spent feeding on different prey types (krill and fish).

Linearity of the track

The heading data collected by the DTAGs were used to assess the linearity of the movement of the whales (Johnson & Tyack 2003). The heading data represent a 2-dimensional indication of the direction of travel by the whale. The temporal changes in heading should be greater in non-linear tracks compared with linear tracks. Although the heading data were available at a 5 Hz sampling rate, such fine-scale changes in heading are not necessary to delineate changes in the linearity of the track. Therefore, the heading of animals was subsampled every 5 min.

As the bearings are collected in a continuous 360°, there are always 2 solutions to the change in heading.

An assumption was made that whales were unlikely to have changed more than 180° in each 5 min time step, and the smaller angle was always used as the change in heading. Heading data were collected by the tag from −180° to 180°, so the absolute value of the change in heading for each time step was calculated. This produced a series of changes in heading values for each whale that were then used as a response variable in a linear mixed model (LMM) to determine whether the prey type targeted had an influence on the linearity of the track of the whales (change in heading ~ prey type, random = ~1|whale identity). The heading data were square root-transformed in order to meet the normality assumption. The nlme package (Pinheiro et al. 2013) in R (R Development Core Team 2013) was used for the analysis.

Given that the direction of migratory movement has been shown to vary among individuals migrating through Eden, NSW, Australia (with some individuals migrating south towards Tasmania, Australia, and others migrating south-east towards New Zealand) (Gales et al. 2009), the heading data for each individual were corrected so that the most common (mode) movement direction of each animal was centred on zero degrees. The data from all whales were then pooled to produce a radial rose for whales feeding on krill and for whales feeding on fish. These radial roses provide a visual comparison of the variability in the direction of movement by whales feeding on the 2 prey types.

Group size and composition

A GLMM was completed to compare the group sizes of animals feeding on fish to those of animals feeding on krill (group size ~ prey type, random = ~1|whale identity). The group size data utilised were those collected every 10 min throughout the duration of the focal follows. The data were modelled using the glmmadmb package (Fournier et al. 2012, Skaug et al. 2013) in R (R Development Core Team 2013), as this package is able to model a truncated Poisson distribution that allowed for the lack of zero values in the group size data.

RESULTS

Feeding behaviour

A total of 82 groups of whales were approached to determine whether the group was feeding and what

Table 1. Details of the individual focal follows of humpback whales completed off Eden, NSW, Australia. Total number of lunges and mean lunge depth could only be determined for animals with a digital acoustic recording tag (DTAG) given the potential for underwater feeding behaviour. −: information that is unknown due to a lack of tag data; VO lunges: visually observed lunges at the surface. Sex was determined using the genetic methods explained in Morin et al. (2005). Prey type was determined using visual and net tow techniques (2011) and by echosounder surveys (2012)

Date	Focal follow start time (local time, h:min)	Focal follow duration (h:min)	Sex	DTAG number	Prey type	Total no. of lunges	Lunge depth (mean ± SD)	No. of VO lunges	VO lunges (%)
2011									
13 Sep	8:14	2:00	F	−	Krill	−	−	81	
14 Sep	8:18	2:01	M	−	Krill	−	−	147	
15 Sep	9:45	2:10	F	1	Krill	161	4.7 ± 6.1	96	59.6
16 Sep	12:29	2:13	M	2	Krill	35	3.4 ± 5.9	20	57.1
17 Sep	8:29	2:13	F	3	Krill	127	4.6 ± 5.4	74	58.3
21 Sep	12:57	2:01	M	−	Krill	−	−	10	
22 Sep	8:29	1:29	F	−	Krill	−	−	5	
24 Sep	10:09	2:04	F	−	Krill	−	−	0	
26 Sep	9:26	1:10	−	−	Krill	−	−	−	
1 Oct	8:15	2:05	F	−	Krill	−	−	16	
2012									
16 Sep	10:08	3:27	M	4	Fish	3	11.9 ± 13.5	0	0
17 Sep	14:06	1:19	F	5	Fish	1	19.1	0	0
18 Sep	10:40	3:59	M	−	Krill	−	−	5	
2 Oct	10:04	2:47	M	6	Fish	53	25.2 ± 14.4	0	0
4 Oct	8:54	3:09	F	7	Fish	9	25.1 ± 5.1	0	0
6 Oct	9:36	3:06	−	8	Fish	11	17.7 ± 9.0	0	0
9 Oct	12:50	2:47	M	9	Fish	2	10.7 ± 1.9	0	0
16 Oct	11:50	0:59	−	−	Fish	−	−	0	0

prey type was available at the time. Based on the survey data, a total of 24 groups were observed to encounter krill at the surface (average group size of 4), with 71% of these groups considered likely to be feeding. In contrast, only 21% of the groups encountering fish (fish species details given below) were considered likely to be feeding (n = 58, average group size 2). In 2011, when krill were visually observed to be abundant at the surface, 5 individuals were resighted on multiple days (3, 5, 8, 10 and 10 d apart, respectively). However, in 2012 when fish were the most common prey type available (as determined via the echosounder data and lack of krill swarms observed at the surface), there were no re-sights of individuals despite more groups being approached in that year (n = 23 groups in 2011, 59 groups in 2012).

The methods used to identify the predominant prey type in 2011 limited the information available about the prey type at depth. For an average of 58.3% of the lunges completed by the 3 tagged whales determined to be feeding on krill, the whales were actually observed to be targeting krill *Nyctiphanes australis* at the surface (Table 1) (Fig. 2). Camera drops completed throughout the focal follows in 2011 revealed that krill were often distributed in the upper

5–10 m of the water column, with no fish observed in these camera drops. In addition, the average depth of lunges completed by the tagged whales targeting krill was 5.4 ± 0.8 m, within the depth range observed by the camera and sampled by the net tows. This suggests that a number of the non-visually observed lunges also likely involved whales targeting krill below the surface. However, while the majority of lunges appeared to relate to krill, it is still possible that some of the lunges completed were whales targeting fish at depth. For this reason, the results presented from here on represent comparisons between the behaviour of whales encountering krill at the surface (and potentially fish at depth; hereafter referred to as 'targeting krill') and that of whales only encountering fish at depth with no krill available (hereafter referred to as 'targeting fish'). The depths of lunges completed by whales feeding on fish were deeper (22.0 ± 1.6 m), and no surface lunges by these animals were visually observed (Table 1). However, based on the echosounder data for all of these animals, the lunges were determined to have occurred in areas where schools of fish were present (Table 1). As a consequence, the predominant prey type for all 6 tagged whales in 2012 was fish. The baitfish spe-

Fig. 2. Three different east Australian humpback whales feeding on krill *Nyctiphanes australis* in 2011 using various lunge orientations (A,B,C) while migrating. The krill can be seen to be attempting to escape capture by the whale as the small droplets on the water surface within the gape of the whale

cies targeted likely included species such as jack mackerel *Trachurus declivis*, pilchards *Sardinops neopilchardus*, and redbait *Emmelichthy nitidus*, which were regularly observed at the surface during the focal follows in 2012. Humpback whales have previously been observed to feed on these fish species at the study site (Stamation et al. 2007).

Fine-scale feeding behaviour of individual humpback whales

Focal follows were completed on 18 individual whales (Table 1). Nine (50%) of these follows in-volved a tagged individual (Table 1). The tagged whales encountering krill spent significantly (GLMM, n = 9, df = 7, z = 3.47, p = 0.0005) more time feeding (92% of the 10 min time bins were classified as 'feeding') than the whales encountering fish (28%). Two of the 3 animals feeding on krill regularly looped back through the same area, whereas all 6 animals feeding on fish displayed a more consistent (less turning) direction of movement (Fig. 3). The mean change in heading was significantly larger for animals feeding on krill compared to animals feeding on fish (86° ± 6° vs. 45° ± 3°) (LMM, n = 9, df = 7, t = 4.50, p = 0.004) (Fig. 4).
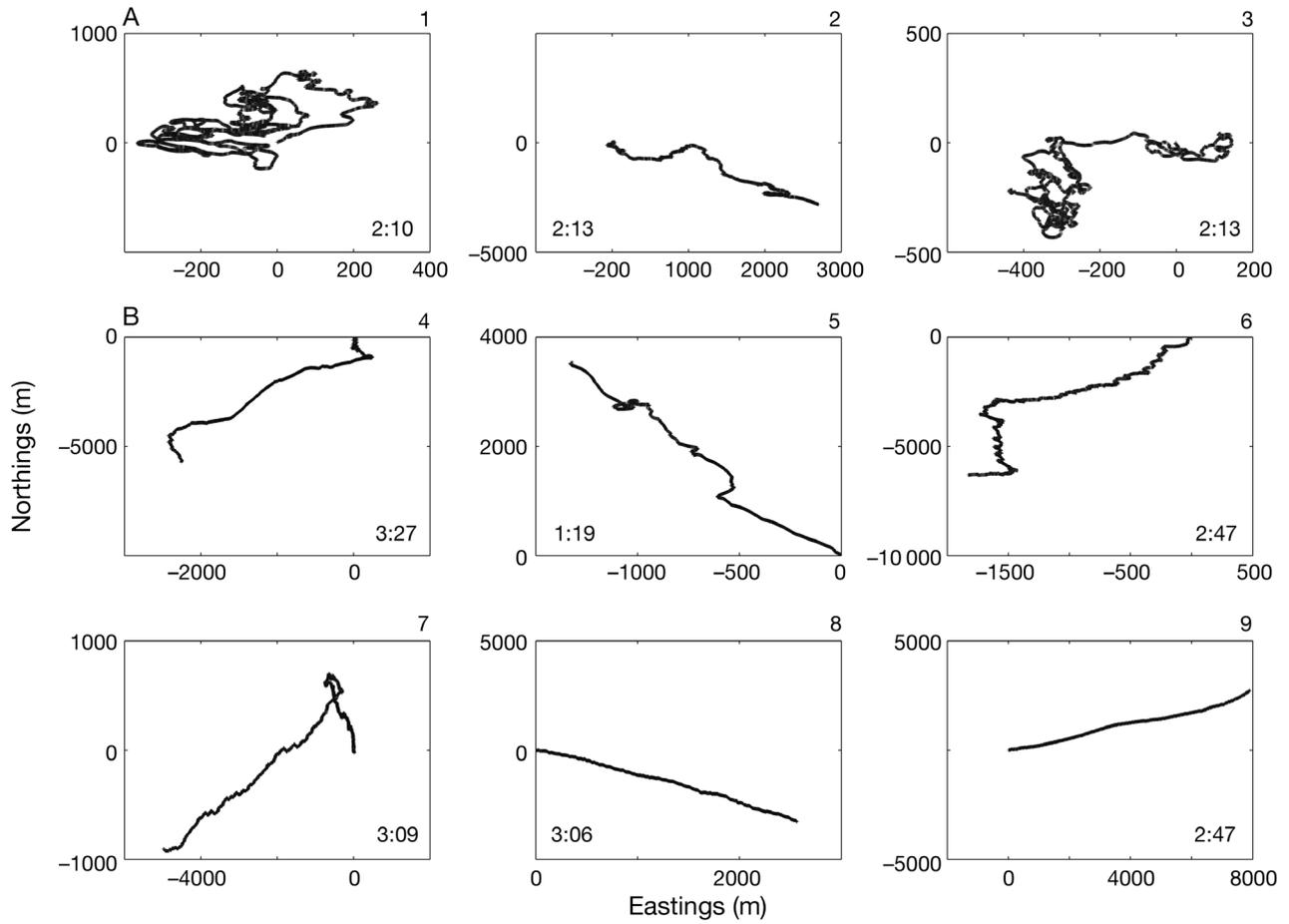
Fig. 3. Pseudo tracks of tagged whales feeding on (A) krill and (B) fish. Tag identification of the animal is provided in the top right corner above each panel; track duration is in the bottom corner (h:min). Scales of the panels vary in order to better display the variation in the pattern of each track
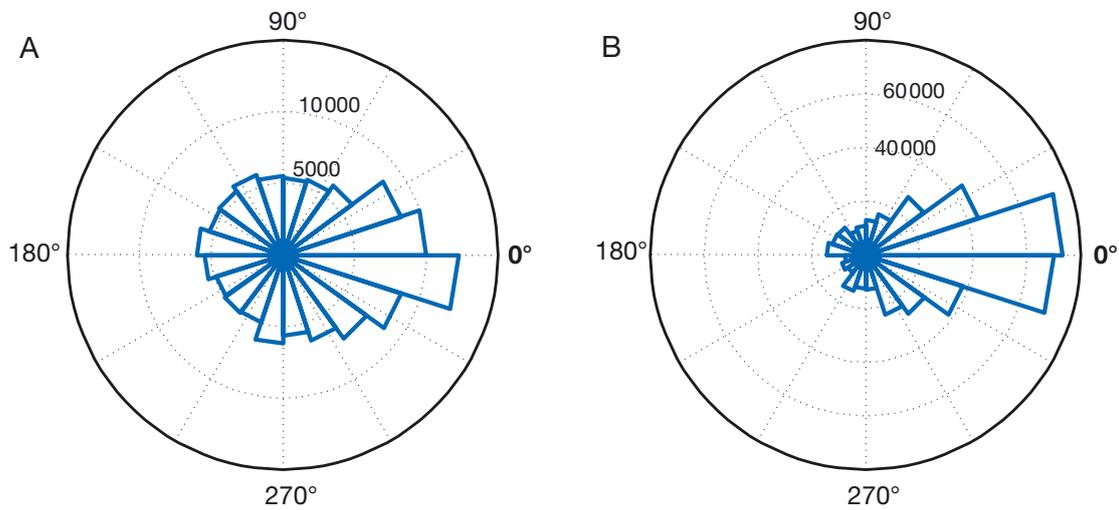

Fig. 4. Radial rose histograms of the heading data for whales feeding on (A) krill and (B) fish. Data were corrected so that the mode direction of travel for each whale was centred on zero degrees. Circles within the radial rose represent the number of samples of whales heading in the given direction

The average maximum group size that the focal individual was observed to be in was 4 (targeting krill = 5.1, targeting fish = 2.1) (Table 2). Throughout the focal follows the group size changed regularly. This made it difficult to assign a group composition. Only 3 cow/calf pairs were observed throughout the study, and none of these groups were observed to be feeding. When considering all of the group size changes throughout the focal follows, whales were in significantly larger groups when feeding on krill (mean = 3.4; SD = 2.4; range = 1 to 12) compared to fish feeding groups (mean = 1.7, SD = 0.7, range 1 to 4) (GLMM, n = 16, df = 14, z = 2.85, p = 0.004) (Table 2).

Of the biopsied whales encountering krill, 63% were female. Conversely, when fish were available, only 35% of the animals biopsied were female. When feeding on krill, $32.7 \pm 6.9\%$ of the lunges observed to be completed by the focal animals were completed as synchronous lunges. In 6 of the 8 focal follows where the group size exceeded 2 animals, the focal animal was observed to lunge primarily with one other individual in the group throughout the focal follow duration. In addition to the synchronisation of lunges, all other surface behaviours (such as blows and fluke up dives) of the individuals and their directions of movement were also highly synchronised. Close associations were also observed between other individuals within the group that did not involve the focal animal. These associations were monitored for a shorter period (due to the fluidity of the groups), and so it is difficult to quantify their duration. Synchronous pairs observed were comprised of 1/3 female/female (FF) pairs (5 of 15 individual pairs) and 2/3 male/female (MF) pairs (10 of 15 individual pairs). No MM pairs were observed. Of the 5 animals re-sighted in 2011, 2 of them (sex unknown) were observed to feed synchronously together on 17 September and again, 10 d later, on 26 September. Although little surface-feeding behaviour was observed in 2012, one pair of animals (sex unknown) was observed to feed synchronously on krill.

Table 2. Incident sampling data collected on the group behaviour of humpback whales off Eden, NSW, Australia. Data were collected during a focal follow of an individual whale within the group. Minimum and maximum group sizes represent the changes in the group size in which the focal individual was observed throughout the focal follow. VO lunges: visually observed lunges at the surface. Prey type: predominant prey type determined to be fed upon by the whales throughout the focal follow determined using visual observations and net tow techniques (2011) and echosounder surveys (2012)

Date	Duration of obs. (h:min)	Prey type	Min. obs. group size	Max. obs. group size	Total VO lunges
2011					
13 Sep	2:00	Krill	2	5	340
14 Sep	2:01	Krill	1	3	315
15 Sep	2:10	Krill	1	9	443
16 Sep	2:13	Krill	1	3	20
17 Sep	2:13	Krill	2	12	349
21 Sep	2:01	Krill	1	2	10
22 Sep	1:29	Krill	2	4	8
24 Sep	2:04	Krill	2	2	0
26 Sep	1:10	Krill	3	8	56
1 Oct	2:05	Krill	2	3	57
2012					
16 Sep	3:27	Fish	2	3	0
17 Sep	1:19	Fish	1	1	0
18 Sep	3:59	Krill	1	3	19
2 Oct	2:47	Fish	2	3	0
4 Oct	3:09	Fish	1	2	0
6 Oct	3:06	Fish	2	3	0
9 Oct	2:47	Fish	1	1	0
16 Oct	0:59	Fish	1	1	0

DISCUSSION

To provide information for marine conservation strategies, most research focuses on understanding and protecting species' breeding areas, and in some cases, feeding areas (Calvert et al. 2009). For animals that are long-lived, survival of individuals during the non-breeding season influences population growth (Saether et al. 1996, Heppell et al. 2000). In our study, a larger proportion of groups were feeding, and individual whales dedicated more time to feeding when krill, as opposed to fish, were available. In addition, several whales were re-sighted up to 10 d apart feeding on krill within the study site, suggesting that some individuals spent an extended period of time in the area feeding to take advantage of this prey type. In contrast, when fish were available, the majority (79%) of groups encountered were travelling, and there were no re-sights of individuals, despite the fact that whales have been observed to feed on the species of fish present at this study site (Stamation et al. 2007). This difference in the number of re-sightings could be driven by potential differences in the density of whale groups between the 2 years; however, this appears unlikely given the larger number of groups encountered in 2012, when the number of re-sights was low. Therefore, similar to bird species, the duration of stay at migratory stopover sites by humpback whales appears to be influenced by changes in the prey type available, which may pro-

vide an indication of the prey quality or nutritional requirements of the animals while migrating.

In addition to changes in the amount of time dedicated to feeding, the whales displayed prey type-dependent foraging behaviour; krill-feeding whales displayed a more 'random walk like' movement in the same area, similar to humpback whales feeding on krill on the main feeding grounds (Ware et al. 2011), whereas the 6 fish-feeding whales displayed a more consistent movement (more directional displacement). Migrating (i.e. non-feeding) animals, including turtles (Jonsen et al. 2007), sharks (Weng et al. 2008), seals (Breed et al. 2009) and whales (Gales et al. 2009, Silva et al. 2013), swim in straight lines at a broad-scale over large distances (Horton et al. 2011). The relatively straight tracks of whales feeding on fish in this study suggest that straight tracks may not always indicate a lack of feeding behaviour by migrating marine animals. The difference in linearity when targeting different prey may be due to the higher mobility of fish, which could make repeated lunging in the same area less profitable. Alternatively, straighter tracks may allow whales to combine migrating with a small amount of feeding when the prey quality is lower. This possibility is supported by the general direction of travel by the whales when feeding on fish, which was typically in a south or south-east direction (Fig. 3), consistent with the direction of migration towards feeding grounds (Gales et al. 2009).

The social dynamics of humpback whales on migration were also observed to change depending on the prey type encountered. On the main feeding grounds, the east Australian population of humpback whales feed alone or in small groups of 2 to 3 (Kasamatsu et al. 1996, Gill et al. 1998). Group sizes of this population are also small during the migration towards the feeding grounds, with a mean of approximately 2 individuals (Brown & Corkeron 1995). While feeding on krill, group sizes were larger, ranging up to a maximum of 12 individuals compared to a maximum of 3 when feeding on fish. Large groups have been observed for humpback whales feeding on fish at the main feeding grounds in the North Pacific (Jurasz & Jurasz 1979, D'Vincent et al. 1985, Sharpe 2001) and feeding on krill while migrating off the coast of South Africa (Best et al. 1995, Barendse et al. 2010). Group size can be influenced by the size of the prey patch (Whitehead 1983); thus, the large group sizes may have been a product of the large patches of krill. However, this explanation is unlikely given the small group sizes (Kasamatsu et al. 1996, Gill et al. 1998) feeding on large patch sizes in the Antarctic (Hamner

et al. 1983, Tarling et al. 2009, Nowacek et al. 2011). While the sample size in this study is small, the aggregation of large groups feeding on krill suggests that many individuals may be drawn to patches of krill, which may be limited along the migratory route.

The east Australian population of humpback whales has been shown to have a male-biased sex ratio during migration with an average of approximately 2 males for every female (average calculated from a male:female sex ratio of 2.1:1 in whaling records, 2.4:1 off southern Queensland [Brown et al. 1995] and 1.6:1 off Eden and Tasmania, NSW [Schmitt et al. 2014]). The larger proportion of males biopsied when feeding on fish (65%) matches the sex compositions expected for migrating whales (Brown et al. 1995, Schmitt et al. 2014). In contrast, the higher proportion of females sampled (63%) while feeding on krill deviates from the expected composition of migrating whales. A female bias has also been observed by humpback whales feeding on krill during their southward migrating off South Africa towards Antarctic feeding grounds (Best et al. 1995, Barendse et al. 2010). Humpback whales often form female-dominated groups and stable pairs on the main feeding grounds that may help to optimize their energy gain and potentially increase their reproductive output (Weinrich 1991, Ramp et al. 2010). While migrating, females are typically either pregnant or lactating, which are both energetically demanding (Oftedal 2000). The use of synchronous behaviour by whales in this study, in particular by females, may assist the whales with meeting the energy demand of migration. Although none of the females feeding in this study were lactating (as determined by the presence of a dependent calf), females with calves have been observed to feed off Eden in the past (Stamation et al. 2007). Lactating females tend to migrate later than newly pregnant females and males (Chittleborough 1965, Dawbin 1966). However, the timing of sampling in this study was similar in both years, suggesting that this factor was unlikely to have introduced bias to the different proportion of females observed when feeding on the 2 prey types. There is also the potential for male and female humpback whales to use slightly different migratory routes (Valsecchi et al. 2010). Given the similarity in the study site between years and the difference in sex composition at this location, this factor also appears unlikely to have influenced the variation observed. The sample size of this study was small, so further research into this topic is required to determine whether feeding along the migratory route is of particular importance to females.

The results of this study provide preliminary evidence that the feeding behaviour of whales during migration may be influenced by both the prey type available and the energetic demands of the individual. There are many reasons why krill may be a preferred prey type for this population, including differences in the energetic content, ease of capture, or familiarity with the prey type, given that Antarctic krill *Euphausia superba* is the predominant prey type of this population on the main feeding grounds (Matthews 1937). In addition, other factors such as prey density or depth, access to prey resources in the previous summer feeding season, or whale body condition may have also influenced the differences in behaviour observed across the 2 years, and these factors deserve more attention in future research. In order to fully understand the potential importance of feeding behaviour while migrating, an estimate of the frequency of feeding and energy intake during these events is required. Given that the use of migratory stopover sites and the quality of available prey at these sites has been linked to population demographics in other taxa (Newton 2006), the potential for feeding along the migratory route to contribute to annual energy supplies needs further investigation. While the current migratory strategy of humpback whales is thought to be one of 'feast and famine', with whales feeding extensively over summer, and very little for the rest of the year, it may be that there are biological limitations that influence the ability of certain individuals to store sufficient energy to complete migration. Future research should focus on determining whether this is also the case for other marine species completing migrations.

LITERATURE CITED

Åkesson S, Hedenström A (2007) How migrants get there: migratory performance and orientation. Bioscience 57: 123–133

Alerstam T, Hedenstrom A (1998) The development of bird migration theory. J Avian Biol 29:343–369

Alerstam T, Hedenstrom A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103: 247–260

Baraff LS, Clapham PJ (1991) Feeding behaviour of a humpback whale in low latitude waters. Mar Mamm Sci 7: 197–202

Barendse J, Best PB, Thornton M, Pomilla C, Carvalho I, Rosenbaum HC (2010) Migration redefined? Seasonality, movements and group composition of humpback whales *Megaptera novaeangliae* off the west coast of South Africa. Afr J Mar Sci 32:1–22

Best PB, Sekiguchi K, Findlay KP (1995) A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. Mar Ecol Prog Ser 118: 1–12

Breed GA, Jonsen ID, Myers RA, Bowen WD, Leonard ML (2009) Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. Ecology 90:3209–3221

Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and overwintering of sea turtles. Proc R Soc Biol 274:1533–1538

Brown M, Corkeron P (1995) Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the East Australian coast. Behaviour 132:163–179

Brown MR, Corkeron PJ, Hale PT, Schultz KW, Bryden MM (1995) Evidence for a sex-segregated migration in the humpback whale (*Megaptera novaeangliae*). Proc R Soc Biol 259(1355):229–234

Cacchione DA, Drake DE, Field ME, Tate GB (1987) Seafloor gouges caused by migrating gray whales off northern California. Cont Shelf Res 7:553–560

Calvert AM, Walde SJ, Taylor PD (2009) Nonbreeding-season drivers of population dynamics in seasonal migrants: conservation parallels across taxa. Avian Conserv Ecol 4:5

Chittleborough RG (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). Aust J Mar Freshw Res 16:33–128

Clapham PJ (1996) The social and reproductive biology of humpback whales: an ecological perspective. Mammal Rev 26:27–49

Conti SG, Demer DA (2006) Improved parameterization of the SDWBA for estimating krill target strength. ICES J Mar Sci 63:928–935

Cuevas E, Abreu-Grobois FA, Guzmán-Hernández V, Liceaga-Correa MA, van Dam RP (2008) Post-nesting migratory movements of hawksbill turtles *Eretmochelys imbricate* in waters adjacent to the Yucatan Peninsula, Mexico. Endang Species Res 10:123–133

D'Vincent CD, Nilson RM, Hama RH (1985) Vocalizations and coordinated feeding of the humpback whale in Southeastern Alaska. Sci Rep Whales Res Inst 36: 41–47

Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In: Norris KS (ed) Whales, dolphins and porpoises. University of California Press, Berkeley, CA, p 145–170

de Sá Alves LCP, Andriolo A, Zerbini A, Pizzorno JLA, Clapham P (2009) Record of feeding by humpback whales (*Megaptera novaeangliae*) in tropical waters off Brazil. Mar Mamm Sci 25:416−419

Dingle H, Drake VA (2007) What is migration? Bioscience 57:113−121

Foote KG, Knudsen HP, Vestnes G, MacLennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimates: a practical guide. ICES Coop Res Rep 144. International Council for the Exploration of the Sea, Copenhagen

Fournier DA, Skaug HJ, Ancheta J, Ianelli J and others (2012) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim Method Softw 27:233−249

Gales N, Double MC, Robinson S, Jenner C and others (2009) Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. Paper SC/61/SH17 presented at the International Whaling Commission Scientific Committee, Madeira, Portugal

Gendron D, Urban R (1993) Evidence of feeding by humpback whales (*Megaptera novaeangliae*) in the Baja California breeding ground, Mexico. Mar Mamm Sci 9:76−81

Gill PC, Evans KJ, Wapstra H (1998) Feeding by humpback whales in Tasmanian waters. Queen Victoria Museum and Art Gallery 107:1−5

Gorska N, Ona E, Korneliussen R (2005) Acoustic backscattering by Atlantic mackerel as being representative of fish that lack a swimbladder. Backscattering by individual fish. ICES J Mar Sci 62:984−995

Hamner WM, Hamner PP, Strand SW, Gilmer RW (1983) Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling and molting. Science 220: 433−435

Hedenstrom A (2003) Optimal migration strategies in animals that run: a range equation and its consequences. Anim Behav 66:631−636

Heppell SS, Caswell H, Crowder LB (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654−665

Horton TW, Holdaway RN, Zerbini AN, Hauser N, Garrigue C, Andriolo A, Clapham PJ (2011) Straight as an arrow: humpback whales swim constant course tracks during long-distance migration. Biol Lett 7:674−679

Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. IEEE J Oceanic Eng 28:3−12

Jones AE, Ten Cate C, Bijleveld CCJH (2001) The interobserver reliability of scoring sonagrams by eye: a study on methods, illustrated on zebra finch songs. Anim Behav 62:791−801

Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Mar Ecol Prog Ser 337:255−264

Jurasz CM, Jurasz VP (1979) Feeding modes of the humpback whale *Megaptera novaeangliae* in southeast Alaska. Sci Rep Whales Res Inst 31:69−83

Kasamatsu F, Joyce GG, Ensor P, Mermoz J (I996) Current occurrence of baleen whales in Antarctic waters. Rep Int Whaling Comm 46:293−304

Katona SK, Whitehead HP (1981) Identifying humpback whales using their natural markings. Polar Rec (Gr Brit) 20:439−444

Kaufman AB, Rosenthal R (2009) Can you believe my eyes? The importance of interobserver reliability statistics in observations of animal behaviour. Anim Behav 78: 1487−1491

Krützen M, Barré LM, Möller LM, Heithaus MR, Simms C, Sherwin BW (2002) A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* spp. Mar Mamm Sci 18:863−878

Lockyer C (1981) Growth and energy budgets of large baleen whales from the Southern Hemisphere. FAO Fisheries Series No. 5 (Mammals in the seas) 3: 379−487

Mann J (1999) Behavioral sampling for Cetaceans: a review and a critique. Mar Mamm Sci 15:102−122

Matthews LH (1937) The humpback whale, *Megaptera nodosa.* Discov Rep 17:7−92

Morin PA, Nestler A, Rubio-Cisneros NT, Robertson KM, Mesnick SL (2005) Interfamilial characterization of a region of the ZFX and ZFY genes facilitates sex determination in cetaceans and other mammals. Mol Ecol 14: 3275−3286

Newton I (2006) Can conditions experienced during migration limit the population levels of birds? J Ornithol 147: 146−166

Newton I (2008) The migration ecology of birds. Elsevier, San Diego, CA

Nowacek DP, Friedlander AS, Halpin PN, Hazen EL and others (2011) Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. PLoS ONE 6(4):e19173

Oftedal OT (2000) Regulation of maternal reserves and effects on lactation and the nutrition of young animals: use of maternal reserves as a lactation strategy in large mammals. Animal Nutrition and Metabolism Group Symposium. Proc Nutr Soc 59:99−106

Owen K, Dunlop RA, Monty JP, Chung D and others (2015) Detecting surface-feeding behavior by rorqual whales in accelerometer data. Mar Mamm Sci, doi:10.1111/mms. 12271

Pinheiro J, Bates D, Debroy S, Sarkar D, Team RDC (2013) nlme: linear and nonlinear mixed effects models. R package version 3.1-111

R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna; www.r-project.org

Ramp C, Hagen W, Palsbell P, Berube M, Sears R (2010) Age-related multi-year associations in female humpback whales (*Megaptera novaeangliae*). Behav Ecol Sociobiol 64:1563−1576

Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996−2006. ICES J Mar Sci 65:497−508

Saether BE, Ringsby TH, Roskaft E (1996) Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. Oikos 77:217−226

Salden DR (1989) An observation of apparent feeding by a sub-adult humpback whale off Maui, Hawaii. Abstracts. Eighth Biennial Conference on the Biology of Marine Mammals. Pacific Grove, CA, p 58

Sawyer H, Kauffman MJ (2011) Stopover ecology of a migratory ungulate. J Anim Ecol 80:1078−1087

Schmidt-Nielsen K (1972) Locomotion: energy cost of swimming, flying, and running. Science 177:222−228

Schmitt NT, Double MC, Jarman SN, Gales N and others (2014) Low levels of genetic differentiation characterize Australian humpback whale (*Megaptera novaeangliae*) populations. Mar Mamm Sci 30:221–241

Sharpe FA (2001) Social foraging of the southeast Alaskan humpback whale, *Megaptera novaeangliae*. PhD thesis, Simon Fraser University, Burnaby

Silva IF, Kaufman GD, Hutsel A, Macie A, Maldini D, Rankin R (2010) Mid-migration humpback whale feeding behavior off Eden, NSW, Australia. Report to the International Whaling Commission. Report No. SC/63/SH12, International Whaling Commission

Silva MA, Prieto R, Jonsen I, Baumgartner MF, Santos RS (2013) North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? PLoS ONE 8:e76507

Simmonds J, MacLennan D (2005) Fisheries acoustics: theory and practice, 2nd edn. Blackwell Science, Oxford

Sims DW, Queiroz N, Humphries NE, Lima FP, Hays GC (2009) Long-term GPS tracking of ocean sunfish *Mola mola* offers a new direction in fish monitoring. PLoS ONE 4:e7351

Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B (2013) Generalized linear mixed models using AD model builder. R package version 0.7.5

Stamation KA, Croft DB, Shaughnessy PD, Waples KA (2007) Observations of humpback whales (*Megaptera novaeangliae*) feeding during their southward migration along the coast of southeastern New South Wales, Australia: identification of a possible supplemental feeding ground. Aquat Mamm 33:165–174

Stockin KA, Burgess EA (2005) Opportunistic feeding of an adult male humpback whale (*Megaptera novaeangliae*) migrating along the coast of southeastern Queensland, Australia. Aquat Mamm 31:120–123

Swingle WM, Barco SG, Pitchford TD, McLellan WA, Pabst DA (1993) Appearance of juvenile humpback whales feeding in the nearshore waters off Virginia. Mar Mamm Sci 9:309–315

Tarling GA, Klevier T, Fielding S, Watkins J and others (2009) Variability and predictability of Antarctic krill swarm structure. Deep-Sea Res I 56:1994–2012

Valsecchi E, Corkeron PJ, Galli P, Sherwin W, Bertorelle G (2010) Genetic evidence for sex-specific migratory behaviour in western South Pacific humpback whales. Mar Ecol Prog Ser 398:275–286

Visser F, Hartman KL, Pierce GJ, Valavanis VD, Huisman J (2011) Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. Mar Ecol Prog Ser 440:267–279

Ware C, Friedlaender AS, Nowacek DP (2011) Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. Mar Mamm Sci 27:587–605

Warren JD, Demer DA (2010) Abundance and distribution of Antarctic krill (*Euphausia superba*) nearshore of Cape Shirreff, Livingston Island, Antarctica, during six austral summers between 2000 and 2007. Can J Fish Aquat Sci 67:1159–1170

Weber TP, Houston AI (1997) Flight costs, flight range and the stopover ecology of migrating birds. J Anim Ecol 66:297–306

Weber TC, Pena H, Jech JM (2009) Consecutive acoustic observations of an Atlantic herring school in the Northwest Atlantic. ICES J Mar Sci 66:1270–1277

Weinrich MT (1991) Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. Can J Zool 69:3012–3019

Weng KC, Foley DG, Ganong JE, Perle C, Shillinger GL, Black BA (2008) Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distance ecoregions. Mar Ecol Prog Ser 372:253–264

Whitehead H (1983) Structure and stability of humpback whale groups off Newfoundland. Can J Zool 61:1391–1397