


TELEMETRY CASE REPORT

Open Access



A week in the life of a pygmy blue whale: migratory dive depth overlaps with large vessel drafts

Kylie Owen^{1*} , Curt S. Jenner², Micheline-Nicole M. Jenner² and Russel D. Andrews^{1,3}

Abstract

Background: The use of multi-sensor tags is increasingly providing insights into the behavior of whales. However, due to limitations in tag attachment duration and the transmission bandwidth of the Argos system, little is known about fine-scale diving behavior over time or the reliability of assigning behavioral states based on horizontal movement data for whale species. How whales use the water column while migrating has not been closely examined, yet the strategy used is likely to influence the vulnerability of whales to ship strike. Here we present information from a rare week long multi-sensor tag deployment on a pygmy blue whale (*Balaenoptera musculus breviceauda*) that provided a great opportunity to examine the fine-scale diving behavior of a migrating whale and to compare the occurrence of feeding lunges with assigned behavioral states.

Results: The depth of migratory dives was highly consistent over time and unrelated to local bathymetry. The mean depth of migratory dives (~13 m when corrected for the tag position on the whale) was just below the threshold depth (12 m) that blue whales are predicted to travel below to remove the influence of wave drag at the surface. The whale spent 94 % of observed time and completed 99 % of observed migratory dives within the range of large container ship drafts (<24 m). Areas of high residence identified using the horizontal movement data (FastLoc GPS) did not reflect where lunge feeding occurred.

Conclusions: The lack of correspondence between areas of high residence inferred from horizontal movement data and the locations where the whale performed feeding lunges highlights the need for further research to determine whether movement models can accurately detect whale feeding areas or only areas of prey searching. While migrating, the whale made dives to a depth that is likely to allow it to avoid wave drag and maximize horizontal movement. Although this strategy may reduce energy expenditure during migration, it also placed the whale at greater risk of ship strike for a much longer period than currently thought. If other whales have similar diving behavior to this animal during migration, many whale species may spend much longer periods than currently estimated within the parts of the water column where the risk of ship strike is high.

Keywords: Area-restricted search, Accelerometer, *Balaenoptera musculus breviceauda*, Biotelemetry, Diving, Feeding, Migration, Residence time, Ship strike, Wave drag

Background

Annual migrations involve a large input of energy from an animal in order to travel successfully between alternately favorable environments [1]. Some of the longest migrations of any mammal species are completed

by baleen whales that make annual migrations between high-latitude feeding grounds and low-latitude breeding grounds [2–4]. The large majority of research effort on whale behavior has focused on their feeding and breeding grounds, with comparatively less known about their behavior while migrating. In order to make migration successful, whales should have evolved ways to reduce energy expenditure while migrating between feeding

*Correspondence: kylieo@alaskasealife.org

¹ Alaska SeaLife Center, Seward, AK 99664, USA

Full list of author information is available at the end of the article

and breeding sites. Morphological adaptations such as a streamlined body shape to reduce drag, and the use of oscillatory propulsion allowing for thrust generation on both the upward and downward stroke reduce energy expenditure and increase propulsion efficiency [5]. In addition to these morphological adaptations, behavioral adaptations have also been shown in many marine mammals, such as the use of energy-efficient stroke and glide behavior while diving [6].

When swimming close to the surface, the production of wave drag can increase the drag force felt by an animal by 2.5–5 times that of an animal moving at depth [7–9]. The impact of wave drag decreases with depth until it becomes negligible at depths of greater than three times the body diameter of the animal [10]. When swimming deeper than this threshold at a given speed, the drag forces acting on a whale remain constant with increasing depth [10]. Given that whales are an air-breathing mammal, the most efficient and energy-conserving place for a whale to swim might be just below this depth threshold, removing the influence of wave drag, while remaining in close proximity to the surface to reduce the travel distance to their air supply. As a result, the depth that different species of whales are predicted to swim at while migrating should vary between species based on variation in body diameter (Table 1).

However, an alternate or combined strategy is that whales also use gliding descents during migration, converting potential energy from their negative buoyancy to kinetic energy as a result of lift generated from their pectoral fins [11]. However, in a theoretical model for elephant seals (*Mirounga angustirostris*) it has been suggested that there is little to no energetic advantage of gliding descents over horizontal swimming at a depth of three times their body diameter when transiting to foraging areas [12]. In addition, one study of North Atlantic right whales (*Eubalaena glacialis*) on their feeding grounds suggested that traveling dives between foraging

bouts reached a depth just deeper than that predicted to be required to remove wave drag based on their body diameter [13]. Studies have shown that cetaceans regularly intersperse shallow dives between their foraging dives [14–16], and while it has been recognized that continuous swimming along the surface of the ocean is rarely completed by aquatic mammals [17, 18], there have been limited data available to determine whether the dive depths of migrating whales are optimized, i.e., consistently just below the depth threshold where wave drag has minimal influence or whether whales utilize other parts of the water column while migrating. If whales do optimize their travel depths while migrating, then based on measures of body diameter, it is likely that many species of whales may be spending a significant amount of time within the depth range where the risk of ship strike is high.

The use of biotelemetry and biologging devices to record the behavior of whales has been rapidly expanding in recent years. The majority of data describing the diving depths of whales come from feeding grounds, with whales shown to target the shallowest section of the densest patch of prey [19], and increase the amount of feeding lunges completed per dive when prey is deeper to account for the increase in travel time required to reach the prey [19–21]. However, when considering migratory behavior, the vast majority of studies focus on the horizontal movement of whales in an attempt to delineate population connectivity and the location of unknown breeding or feeding areas, e.g., [22–25]. Very little information is available on the diving behavior of whales while migrating. In addition, models of horizontal movement are also used to infer potential behavioral states, based on the assumption that periods of slow travel speed and high turning angles represent area-restricted search (ARS) behavior and likely foraging areas [26–29]. However, it is unknown whether these areas accurately reflect where lunge feeding behavior occurs for whale species. Given

Table 1 The depth threshold that various baleen whale species should swim below in order to avoid the impact of wave drag close to the surface

Species	Length (m)	N	Girth max (m)	Diameter (m)	Wave drag depth threshold (m)	Wave drag depth-rounded threshold (m)
Blue whale (<i>Balaenoptera musculus</i>)	24.72	3	12.19	3.88	11.64	12
Humpback whale (<i>Megaptera novaeangliae</i>)	13.5	29	10.08	3.21	9.63	10
Gray whale (<i>Eschrichtius robustus</i>)	12.29	5	6.86	2.18	6.54	7
North Atlantic right whale (<i>Eubalaena glacialis</i>)	15.02	10	10.3	3.28	9.84	10
Antarctic minke whale (<i>Balaenoptera bonaerensis</i>)	8.36	2872	4.28	1.36	4.08	4

Data on the girth of whale species were taken from [73] (Antarctic minke whales) and [74] (all other species). Diameter is calculated from girth by assuming a circular shape. The wave drag depth-rounded threshold is calculated to represent the level of accuracy of the pressure sensor in the biotelemetry device used in this study

the increase in evidence of whales feeding while migrating [30–33], and suggestions that some species such as blue whales (*Balaenoptera musculus*) may feed year-round [27, 34], understanding whether ARS behavior is likely to indicate where lunge feeding occurs is necessary.

The ability to describe migratory behavior in detail has been largely constrained due to limitations in tag attachment methods and the transmission bandwidth of the available telemetry systems. In order to provide a long temporal scale, the amount of data that are collected by a tag needs to be reduced. In addition, the high-resolution data required to determine when lunge feeding behavior occurs and to examine fine-scale diving behavior are too large to be transmitted, requiring retrieval of the tag, which usually limits the sampling duration. For cetaceans, the sampling duration is typically 1 day or less because high-resolution, multi-sensor tags are normally attached with suction cups (e.g., [35]). Here we present data from a rare week long deployment of a multi-sensor tag attached with small barbed darts to a pygmy blue whale (*Balaenoptera musculus breviceauda*) that provided highly accurate information on the horizontal movement of the whale (using FastLoc GPS), as well as the dive profile and fine-scale movement data collected by a three-axis accelerometer. Although our sample size is only one animal, it is rare for comparisons of the behavioral states inferred from horizontal movement data and the actual location of lunge feeding behavior to be able to be made for whale species, due to a lack of accelerometer data at the broad temporal scales required to designate behavioral states. Our aim was to describe the behavior of the whale over the week, in order to (1) determine whether the depth of migratory dive behavior matches the predictions made of optimal swimming depth, (2) determine whether areas identified as ARS using a behavioral classification method from horizontal movement data match areas where lunge feeding behavior occurred and (3) investigate the environmental factors that may result in a whale completing exploratory dives and increasing ARS behavior while migrating.

Methods

Tagging operations

A Whale Lander tag (Wildlife Computers, Redmond, WA, USA) was deployed onto a pygmy blue whale from a 5.5-m rigid-hulled inflatable using a handheld 6.5-m carbon fiber pole. The Whale Lander tag (8.9 cm diameter, 6.5 cm tall) was anchored to the dermis with three titanium darts, similar to the darts on the compact double dart satellite tag [36] that we now call the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) system, except that these darts were

designed to only penetrate 4.5 cm into the tissue, and there was only one row of three backward facing barbs, each 10 mm long by 4 mm wide. The tag contained a three-axis accelerometer and a three-axis magnetometer, each sampled at 16 Hz, a pressure sensor (accuracy ± 1 m) and a wet-dry sensor sampled at 4 Hz and a light level sensor and fast-response thermistor sampled at 2 Hz. The tag included a FastLoc GPS receiver (Wildtrack Telemetry Systems Ltd, Leeds, UK) and was satellite-linked, programmed to transmit diving and position information via the Argos system. However, the high-resolution data were obtained upon recovery of the floating tag.

Identifying lunge feeding behavior

In order to determine when feeding lunges occurred throughout the deployment, the minimum specific acceleration (MSA) was calculated using the norm of the acceleration vector in all three axes (x , y and z) and subtracting the influence of gravity [37]. The rate of change in the MSA signal, ‘jerk,’ was also calculated [37]. Although these two parameters are calculated from the same sensor, jerk is likely to provide a stronger signal of rapid changes in the forces acting on a whale at the tag location, such as those that occur when the mouth opens during a feeding lunge [37]. Peaks in MSA have been shown to be a reliable indicator of lunge feeding behavior by humpback whales (*Megaptera novaeangliae*), with MSA found to be two to seven times greater during lunges than during descents or ascents [37]. However, inspection of the data recorded in this study revealed that the MSA during descents was often higher than that of lunges (Fig. 1a), making automatic detection difficult. Instances of lunges could be easily identified by eye using the MSA and jerk signal, with lunges having a distinct rise in MSA and jerk as a result of the gradual increase in acceleration, followed by rapid deceleration and drop in both MSA and jerk when the mouth opens (Fig. 1a) [38]. In contrast, periods of fluking had a diamond- or round-shaped jerk signal, and both MSA and jerk often had a much lower magnitude than during lunges (Fig. 1b, c). As a consequence, the entire tag record was inspected by eye to identify times when feeding lunges occurred. The depth at which each lunge occurred was also determined. Due to the impact that wave drag can have on the whale and on the accelerometer signals expected during lunge feeding at the surface [39], any potential lunges shallower than 10 m were excluded from the analysis.

Diving behavior

A zero offset correction of the pressure sensor data was completed using the ‘filter’ method within the *diveMove*

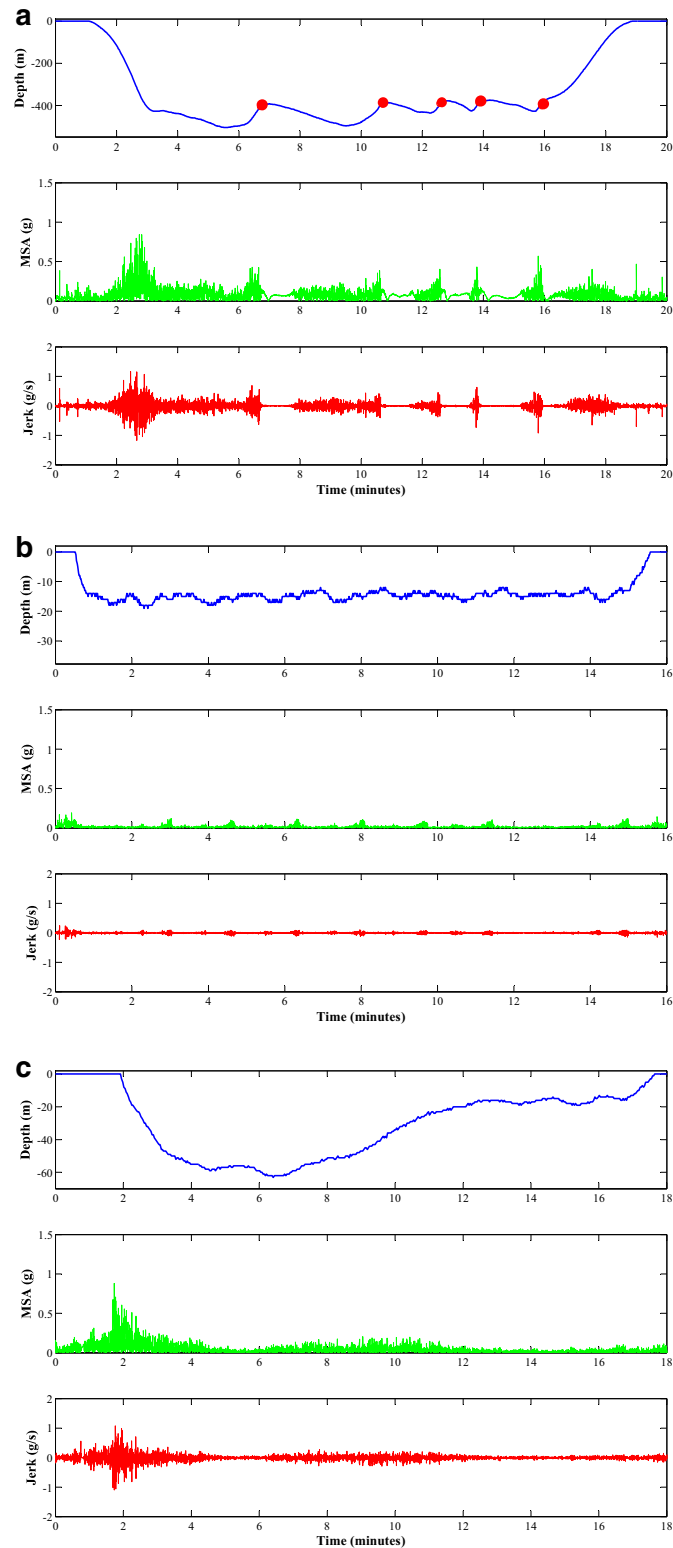


Fig. 1 Dive profiles, minimum specific acceleration (MSA) and jerk of the three dive types (**a** feeding dive, **b** migratory dive and **c** exploratory dive) completed by a pygmy blue whale off the southwest coast of Australia. Lunges (*red dots*) were identified by looking for periods of increasing MSA and jerk, followed by a rapid drop in both parameters

package [40] in R [41] with a minimum depth of 5 m set as the definition of a dive. This package was also used to produce a series of statistics for each dive including the maximum dive depth and mean bottom depth, which is the mean dive depth of the whale from the end of the descent to the beginning of the ascent. Each dive was categorized into one of three dive types (1) feeding dives = dives containing a lunge, (2) migratory dives = dives containing no lunge and varying in depth less than 15 m from the mean of the maximum depth of the 10 surrounding dives (five dives before and five after), (3) exploratory dives = dives containing no lunge that were more than three times deeper than the mean of the maximum depth of the 10 surrounding dives.

Residence time

The FastLoc GPS data were filtered to remove any positions with a residual value >30 [42]. A speed filter set to 25 km/h was then applied to the data to remove any additional positions that were likely to be erroneous. The retained positions were interpolated to provide a position of the whale once every hour. The residence time for each position was calculated using the method described by Barraquand and Benhamou [43] in the *adehabitatLT* package [44] in R [41]. This method builds on the first passage time method [45] by measuring the time spent in the vicinity of each location. The mean distance moved each hour was determined for the whole trajectory and three times the mean distance per hour was then used as the radius for the circle within which residence time was calculated [43]. The animal was allowed to move outside of the circle for a maximum of 1 h before any re-entry into the circle was not included in the residence time calculation for each position data point. The method of Lavielle [46, 47] was used to partition the trajectory based on the residence time of the whale [43]. To do this, the function 'lavielle' within the *adehabitatLT* [44] package in R [41] was used to generate a contrast matrix that allowed for the identification of the optimal number of segments that the trajectory should be broken into based on the residence time. This was completed by identifying the number of segments where a sharp break in the value of the contrast function occurs, identifying the number of segments required before any further increase in the number of segments does not significantly reduce the value of the contrast function. The best location for the segmentation to occur based on the residence time was then calculated and given as a time of the switch from one segment to the next. Segments with high residence times were considered periods of 'area-restricted search (ARS);' and segments with low residence time were considered periods of 'transit.'

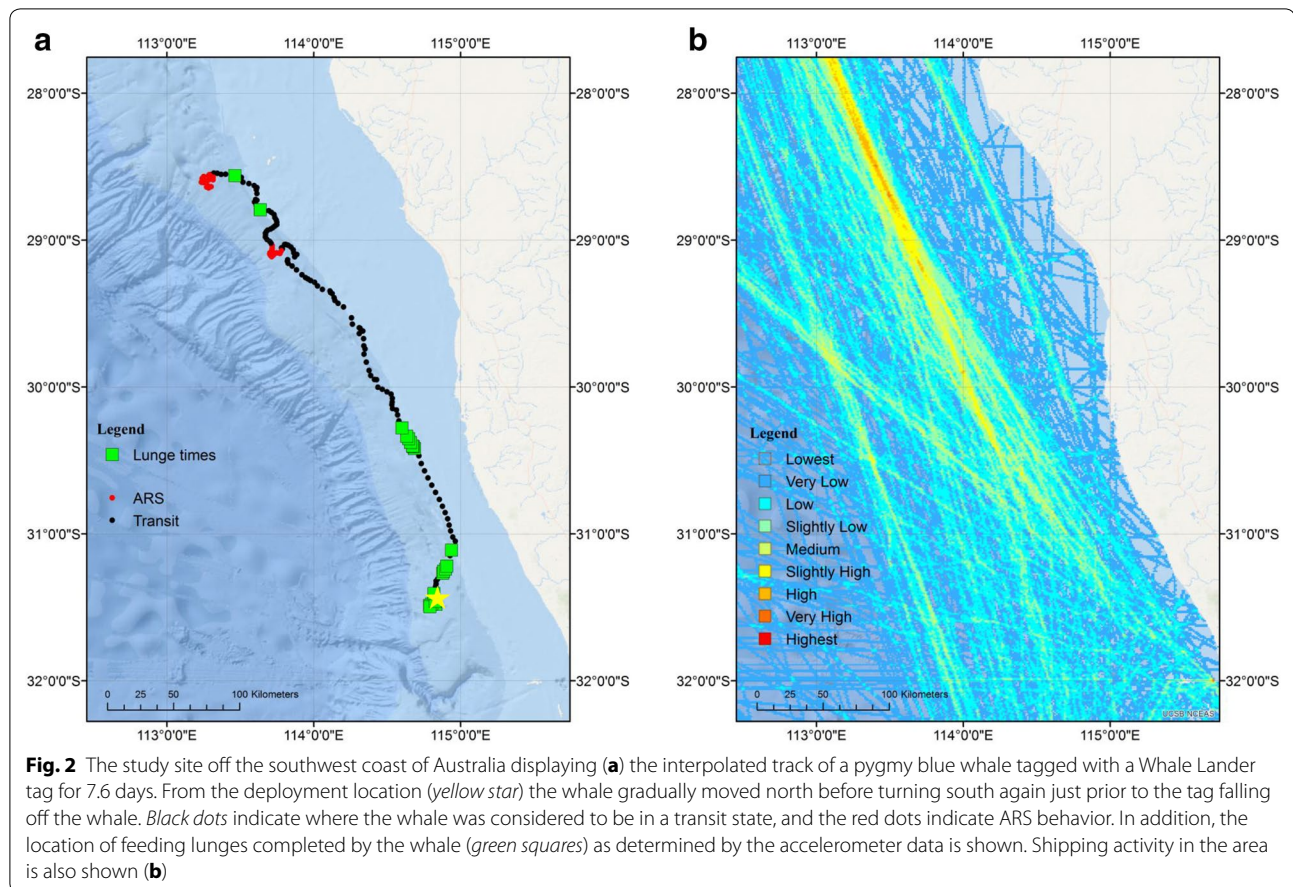
Environmental factors influencing exploratory dives and residence time

The FastLoc GPS positions were annotated with environmental data using a bilinear interpolation method through the EnvDATA system of Movebank [48]. Bathymetry data used were the ETOPO1 topography and bathymetry grid [49], and the chlorophyll a and sea surface temperature (SST) data (both 8 day temporal resolution and 4 km spatial resolution) were sourced from the MODIS Ocean dataset from NASA's OceanColor Web [50]. These data were used to visually determine whether any patterns existed between the environmental conditions and when the whale was determined to be in an ARS state using the horizontal movement data (FastLoc GPS). In addition, patterns in the timing of exploratory dives in relation to environmental parameters were also examined visually. Due to the small sample size, no statistical analyses of habitat associations were completed. All data are presented as mean \pm standard deviation.

Results

A pygmy blue whale was tagged with a Lander tag at 14:23 (local time) on April 30, 2014, at 31.48°S 114.84°E, approximately 35 nautical miles north of the Perth Canyon, Western Australia (Fig. 2a). The tag was positioned approximately 1 m down from the centerline of the dorsal ridge, in line with midline of the pectoral fins. After tagging, the whale moved north, with the tag remaining attached for 7.6 days, falling off at 04:53 (local time) on May 8, 2014, off the coast of Geraldton, Western Australia (Fig. 2a). During that time the whale covered a total distance of 506.3 km, with a mean speed of 2.8 ± 2.2 km/h. Movement from the Perth Canyon region to Geraldton represents approximately 20 % of the total migration distance of this population of pygmy blue whales toward Indonesia [34], and so for this reason, the whale is assumed to have been migrating during the deployment.

The whale completed a total of 37 lunges, 35 of which were within the first 30 h after deployment. Depth of the lunges ranged from 13 to 414 m (mean 167 m). For the first 3–4 h after deployment the whale fed deep within the water column (mean 328 m, minimum 213 m, maximum 414 m) during the afternoon, before switching to shallow surface feeding early the following morning and afternoon (mean 16 m, minimum 13 m, maximum 25 m) (Fig. 3). Inspection of the accelerometer record revealed that exclusion of the upper 10 m of the water column due to the potential influence of surface effects on accurate lunge detection is only likely to have influenced the number of lunges determined to be completed during these two surface feeding bouts and not the overall location of



where lunge feeding occurred. After completing these feeding bouts, the whale migrated north, only lunging two more times throughout the remaining 6 days of the deployment (151.5 h) (Fig. 3).

Diving behavior

The whale completed a total of 1677 dives over the duration of the tag attachment, with 86.1 % classified as either feeding, migratory or exploratory dives. The maximum dive depth was 506 m, which, to the best of our knowledge, is deeper than any previously published dive by a blue whale. This dive had a duration of 14.8 min and was completed during the bout of deep feeding; however, from inspection of the accelerometer data, no lunge was completed during this dive. A total of 21 feeding dives were identified, with a mean maximum depth of 129 ± 183 m (range 13–505 m) and mean dive duration of 7.6 min (maximum 17.5 min). During the bout of deep feeding, mean dive duration was 11.4 min, with the duration of feeding dives shortening during the bout of shallow feeding to a mean of 5.2 min.

A total of 81.8 % of the dives were classified as migratory dives, with a mean dive duration of 5.2 min (maximum

26.7 min). The consistency in the depth of migratory dives throughout the duration of the tag deployment was unrelated to sea floor depth, with the mean bottom depth of migratory dives being 14 ± 4 m. When taking into consideration that the tag was positioned ~ 1 m below the dorsal midline of the whale, the mean depth of the back of the whale was ~ 13 m, just below the predicted 12-m depth threshold that blue whales should swim under to avoid the impact of wave drag (Fig. 3). The whale spent 94 % of its time within the upper 24 m of the water column, and 99 % of migratory dives had a mean depth shallower than 24 m.

A total of 51 exploratory dives were completed, with a mean time between exploratory dives of 3.3 ± 3.4 h. Although these dives were deeper than surrounding dives, review of the accelerometer record confirmed that no feeding lunges were performed (Fig. 1c). The mean maximum depth of exploratory dives (107 ± 81 m, range 23–320 m) was similar to the mean maximum depth of feeding dives (129 m) and did not appear to be related to sea floor depth. Mean dive duration of exploratory dives was 8.6 min (maximum 22.05 min).

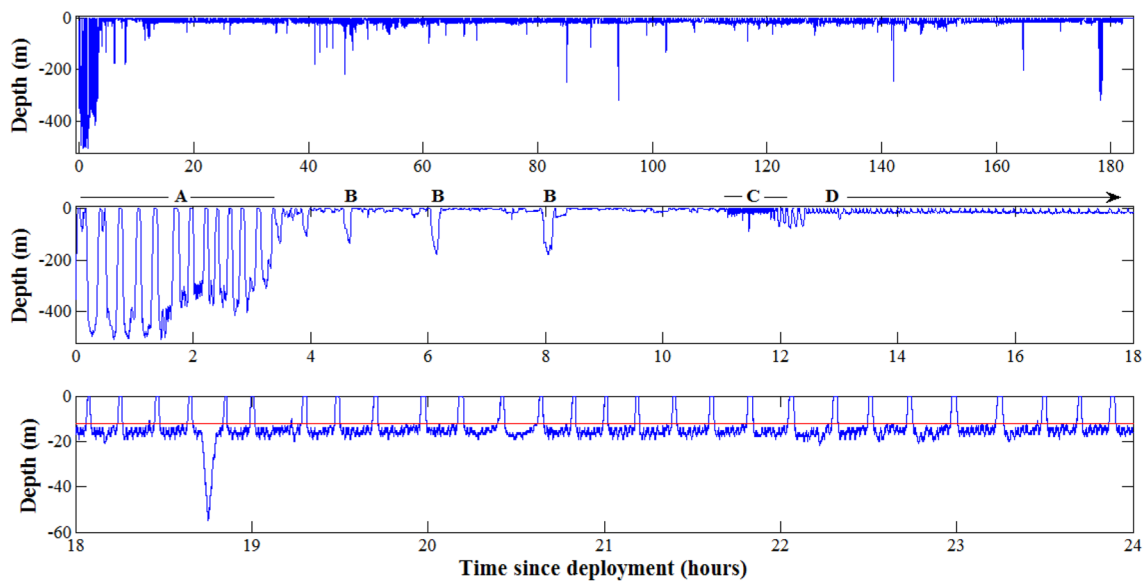


Fig. 3 The dive profile of the tagged pygmy blue whale for (top) the entire week of the deployment, (middle) the first 18 h after deployment and (bottom) 6 h after the whale commenced its northward movement. Letters above the middle panel mark when the whale initially performed feeding behavior at depths below 300 m (a), when it switched to a series of exploratory dives (b) and then shallow feeding behavior (c). After this time, the whale began to migrate (d) and continued this behavior for the majority of the remaining 6 days (151.5 h) of the deployment, as well as some additional exploratory dives. The mean bottom depth of migratory dives was often just below the predicted depth threshold (12 m, red line in bottom panel) that the whale should swim below in order to avoid wave drag

Residence time

A total of 481 FastLoc GPS positions were retained after filtering, with a mean time between positions of 23 ± 22 min. When interpolated to estimate the position once every hour, the track had a mean distance between positions of 2.8 km. Based on this step length, a radius of 8.4 km was assigned to calculate the residence time around each position. Inspection of the contrast matrix revealed that four segments were the optimal number of breaks in the residence time that allowed for a lower contrast function value. Two distinct patches of ARS behavior were located using the FastLoc GPS data, with the whale spending up to 37 h in these ~ 220 km² circular areas (Fig. 4). Locations of ARS behavior identified with the FastLoc GPS data did not correspond to areas of lunge feeding behavior as identified by the accelerometer data (Fig. 2a).

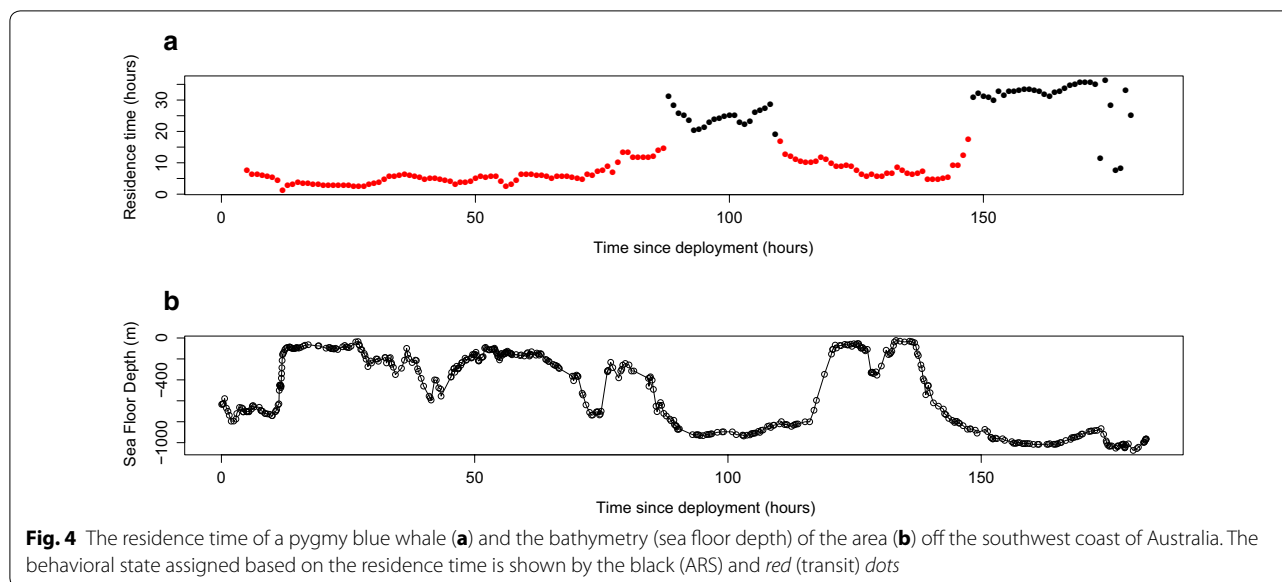
Environmental factors influencing exploratory dives and residence time

The whale appeared to complete ARS behavior in deep (~ 1000 m) areas and transit in more shallow areas (~ 200 m) (Fig. 4). In addition, while the number of exploratory dives completed in a 10-h period was highest upon concluding a lunge feeding bout, the number of exploratory dives also appeared to increase within these deep areas. Comparisons with environmental parameters

revealed that switching into an ARS state by the whale did not appear to be correlated with either SST or chlorophyll a concentration.

Discussion

The mean bottom depth of migratory dives completed by the pygmy blue whale was just below the depth threshold where wave drag is likely to have an influence on the whale. This depth remained consistent over the entire week of the deployment, regardless of bottom bathymetry. By swimming just below the depth where surface drag is predicted to be removed, the whale likely placed itself in an area where it was able to minimize the drag it had to overcome and still remain close to the air supply at the surface, potentially saving energy while migrating. The amount of vertical travel completed by the whale was minimized, allowing for an increase in the horizontal distance covered by the animal in each dive. This potential energy-saving strategy used by the whale is different to that of some other air-breathing divers that have been shown to complete gliding descents to depths much greater than three times their body diameter while traveling [6, 11, 51, 52]. It is possible that factors such as predation risk or foraging along route may play a role in driving differences in the diving behavior of migrating animals [12]. Future research should investigate this pattern further, in order to determine whether other



individuals show a similar pattern in their diving behavior, and whether variation between species is a function of body diameter or migratory strategy.

While reducing drag is likely to reduce energy expenditure and increase travel speed, the use of this depth range also placed the pygmy blue whale at a greater risk of ship strike. During a recorded week of travel and feeding, the pygmy blue whale spent 94 % of its time and completed 99 % of its migratory dives within the possible depth range of large container ship drafts (<24 m). While most container ships have drafts of ~8 m (e.g., Panamax) (the average in the Perth Canyon region is 9 m, maximum 15 m), the draft of some container ships is as deep as 24 m (e.g., Chinamax). Modeling of the hydrodynamic zone of influence of ships on whales suggests that even when a whale is two times the depth of the ships draft, propeller suction will still have a significant impact on the whale, drawing it toward the hull [53]. The lethal zone for whales was shown to extend to over three times the depth of the ships draft when the whale was directly below the ship [53], so even when only considering container ships with moderate drafts (8 m), use of the upper 24 m of the water column for extended periods is likely to have increased the risk of ship strike for this whale. The migratory paths of pygmy blue whales along the Western Australian coast largely overlap with the main shipping routes through the area [34] (Fig. 2b). When responding to oncoming ships, blue whales have been shown to complete a response dive with a slow decent and a lack of movement away from the ship [54]. While in shallow sections of the water column, the Lloyd mirror effect can dramatically influence the ability of a whale to determine both the direction and distance of a ship [55, 56].

In addition, given that the migratory path of the whales and shipping traffic lanes off Western Australia are parallel [34], and not perpendicular (Fig. 2b), it is also possible that shadowing of ship noise by the bow of a ship may impact on a whale's ability to detect a vessel presence [56]. Mortality due to ship strike is thought to be a factor limiting the recovery of some whale populations from past exploitation [57]; however, documenting how often whales are hit by ships is difficult [58]. It has been estimated that the number of whale deaths related to ship strike is likely to be higher than documented numbers due to unrecorded or unrecognized events, and difficulties with assigning the cause of death of stranded animals to ship strike postmortem [58]. The Conservation Management Plan for blue whales in Australia [59] highlights that the risk of ship strike is greatest for calves or feeding animals that are thought to spend the greatest amount of time at the surface. However, if other whales exhibit similar behavior to the whale in this study and optimize their migratory depth to save energy, then many whales may spend a much larger proportion of their time within the danger zone for ship strikes than currently thought.

The consistency of the shallow migratory depths also has implications for programming of satellite-linked dive depth-transmitting tags placed onto whales. These devices require that a dive be defined as submergence below some minimum depth to limit the amount of dive information necessary to compress for transmission through the very limited Argos bandwidth. In many cases, the definition of a dive is set to be potentially deeper than the predicted depth for efficient travel. For example, if predictions hold for each species, Antarctic minke whales (*Balaenoptera bonaerensis*) need to swim

just below 4 m to avoid wave drag (Table 1). Indeed as predicted, inspection of dives referred to as 'shallow non-feeding dives' by Antarctic minke whales in another study appeared to occur at approximately 5 m depth [16], shallower than the depth threshold set for defining dives in many studies [37, 60–62]. If other whales also optimize their dive depths and this is not taken into account when setting dive definition thresholds, then it is possible that migratory dives may not be recorded by these devices and a biased picture of the depth ranges used by species could be produced.

Typically, studies obtaining horizontal movement data lack information on the actual behavioral state of the animal and infer it from track metrics [27, 63–65]. Although the one whale in this study did not lunge feed to a great extent, it provided an opportunity to address the likelihood that the location of lunge feeding behavior by the whale matched areas identified as ARS, and potential foraging locations inferred from horizontal movement data. For this whale, the behavioral states inferred from FastLoc GPS data did not accurately match the locations where lunge feeding occurred. The method used to infer behavior was based on an assumption that areas of low speed and high turning angles result in higher residence time which is likely to be indicative of foraging behavior; a common assumption in many behavioral models applied to both FastLoc GPS and Argos data [26–29]. However, on a fine-scale whales have been shown to feed while still maintaining relatively straight trajectories with low turning angles [33]. Other studies have looked at how well behavior inferred from horizontal movement data overlaps with presumed feeding in other taxa with mixed conclusions. In southern elephant seals (*Mirounga leonina*), increases in body condition, and likely foraging success, have been used to show that the foraging behavior detected in horizontal movement data is a good proxy for foraging success [66]. However, in migratory tuna it was found that periods of high residence can also be associated with periods of fasting [67], as was observed in this study. It is possible that for species that spend their entire lives in the marine environment, periods of residency are also likely to be associated with periods of resting, behavior that is often completed on land for species that can haul out. More research is needed in this area to determine whether the behavioral states identified from horizontal movement data are reflective of the location of feeding by baleen whales.

However, when examining the periods of ARS behavior by the tagged pygmy blue whale it is possible to speculate that the animal was indeed searching for prey during these times when no lunges were observed. Off Western Australia, pygmy blue whales are known to feed along the edges of deep water canyons [68]. The two periods of ARS

observed both occurred over deep water areas, with an increase in exploratory diving behavior suggesting potential prey searching. Therefore, deep canyons around the southwest coast of Australia may provide suitable feeding habitat for blue whales. However, depending on the timing of local conditions with the arrival of a whale, some areas may have varying success as a feeding area year to year. Lunge feeding is an energetically expensive strategy with prey density needing to be above a certain level to induce feeding behavior by a whale [69, 70]. If an animal enters an area where they have reliably fed previously, then they may initiate ARS behavior to assist with searching for prey, and spend longer in the area, yet not lunge feed if dense prey is not located successfully [71, 72]. Therefore, while horizontal movement data were not able to successfully locate areas where lunge feeding occurred, they may still provide information on potential foraging sites of whales.

Conclusions

The migratory dive depth of a pygmy blue whale was found to be highly consistent over the week of observation, with the whale appearing to optimize its travel depth to reduce the impact of wave drag near the surface, yet remain close to the surface where it must return regularly to breathe. While this strategy may reduce energy expenditure during migration, it also placed the whale at greater risk of ship strike for a much longer period than currently thought. In addition, periods of ARS identified using horizontal movement data did not accurately reflect where lunge feeding behavior occurred for this animal, but may still highlight some foraging areas. This suggests that the core assumptions of movement models should be further tested in relation to fine-scale accelerometer data, as the behavioral states obtained may not accurately reflect the feeding behavior of whales. Further development of methods for recognizing actual lunge feeding events by the tag software and subsequent transmission of that information over longer time periods will also assist with the identification of whale feeding areas.

Abbreviations

ARS: area-restricted search; LIMPET: Low Impact Minimally Percutaneous External-electronics Transmitter; MSA: minimum specific acceleration; SST: sea surface temperature.

Authors' contributions

KO developed ideas, completed data analyses, wrote the manuscript, RDA developed ideas, collected data, assisted with manuscript preparation, MNJ collected data, assisted with manuscript preparation, and CSJ collected data, assisted with manuscript preparation. All authors read and approved the final manuscript.

Author details

¹ Alaska SeaLife Center, Seward, AK 99664, USA. ² Centre for Whale Research (WA Inc), Fremantle, WA 6959, Australia. ³ School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

Acknowledgements

The authors would like to thank the crew of the Whale Song and especially Simon Kenion for retrieving the tag. This research was completed under Commonwealth permit number 2013-00012.

Competing interests

The authors declare that they have no competing interests.

Availability of data and material

The dataset supporting the conclusions of this article is available in the Movebank repository [A week in the life of a pygmy blue whale, https://www.movebank.org/panel_embedded_movebank_webapp].

Ethics approval

Ethical approval for this study was provided by the Western Australian Department of Parks and Wildlife (number 2013/45).

Funding

Funding for this research was provided by the Centre for Whale Research (Western Australia). The funding body assisted with data collection and manuscript preparation. The Whale Lander tag was developed by Wildlife Computers and RDA with funding from the Office of Naval Research and the DOD Small Business Technology Transfer (STTR) program.

Received: 2 April 2016 Accepted: 1 August 2016

Published online: 12 August 2016

References

- Alerstam T, Hedenstrom A, Akesson S. Long-distance migration: evolution and determinants. *Oikos*. 2003;103:247–60.
- Rasmussen K, Palacios DM, Calambokidis J, Saborio MT, Dalla Rosa L, Secchi ER, Steiger GH, Allen JM, Stone GS. Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biol Lett*. 2007;3:205–302.
- Robbins J, Rosa LD, Allen J, Mattila D, Secchi ER, Friedlaender AS, Stevick P, Nowacek D, Steel D. Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: a seasonal migration record. *Endang Species Res*. 2011;13:117–21.
- Mate BR, Ilyashenko VY, Bradford AL, Vertyankin VV, Tsidulko GA, Rozhnov VV, Irvine LM. Critically endangered western gray whales migrate to the eastern North Pacific. *Biol Lett*. 2015;11:20150071.
- Fish FE. Transitions from drag-based to lift-based propulsion in mammalian swimming. *Am Zool*. 1996;36:628–41.
- Williams TM, Davis RW, Fuiman LA, Francis J, Le Boeuf BJ, Horning M, Calambokidis J, Croll DA. Sink or swim: strategies for cost-efficient diving by marine mammals. *Science*. 2000;288:133–6.
- Goldman JA. Effects of the free water surface on animals that jump out of the water. Ph.D. thesis, Duke University, Durham, NC; 2001 p. 256
- Vennell R, Pease D, Wilson B. Wave drag on human swimmers. *J Biomech*. 2006;39:664–71.
- Blake RW. Biological implications of the hydrodynamics of swimming at or near the surface and in shallow water. *Bioinspir Biomim*. 2009;4:1–9.
- Hertel H. Structure, form, movement. New York: Reinhold Publishing Co; 1966.
- Gleiss AC, Norman B, Wilson RP. Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Func Ecol*. 2011;25(3):595–607.
- Davis RW, Weihs D. Locomotion in diving elephant seals: physical and physiological constraints. *Philos Trans R Soc Lond B Biol Sci*. 2007;362(1487):2141–50.
- Nousek-McGregor AE. The cost of locomotion in North Atlantic right whales, *Eubalaena glacialis*. PhD thesis. Duke University; 2010.
- Tyack PL, Johnson M, Aguilar Soto N, Sturlese A, Madsen PT. Extreme diving of beaked whales. *J Exp Biol*. 2006;209:4238–53.
- Watwood S, Miller PJO, Johnson M, Madsen PT, Tyack P. Deep diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J Anim Ecol*. 2006;75:814–25.
- Friedlaender AS, Goldbogen JA, Nowacek DP, Read AJ, Johnston D, Gales N. Feeding rates and under ice foraging strategies of smallest lunge filter feeder, the Antarctic minke whale (*Balaenoptera bonaerensis*). *J Exp Biol*. 2014;217:2851–4.
- Fish FE. Aquatic locomotion. In: Tomasi TE, Horton TH, editors. *Mammalian energetics: interdisciplinary views of metabolism and reproduction*. Ithaca: Cornell University Press; 1992. p. 34–63.
- Williams TM. Swimming by sea otters: adaptations for low energetic cost locomotion. *J Comp Physiol A*. 1989;164(81):5–24.
- Goldbogen JA, Calambokidis J, Croll DA, Harvey JT, Newton KM, Oleson EM, Schorr G, Shadwick RE. Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *J Exp Biol*. 2008;211:3712–9.
- Tershry B, Acevedo-Gutiérrez A, Breese D, Strong C. Diet and feeding behavior of fin and Bryde's whales in the Central Gulf of California, México. *Rev Invest Cient*. 1993;1(1):31–7.
- Doniol-Valcroze T, Lesage V, Giard J, Michaud R. Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behav Ecol*. 2011;22:880–8.
- Heide-Jørgensen MP, Laidre KL, Jensen MV, Dueck L, Postma LD. Dissolving stock discreteness with satellite tracking: bowhead whales in Baffin Bay. *Mar Mam Sci*. 2006;22(1):34–45.
- Zerbini AN, Andriolo A, Heide-Jørgensen MP, Pizzorno JL, Maia YG, Van-Blaricum GR, DeMaster DP, Simões-Lopes PC, Moreira S, Bethlam C. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Mar Ecol Prog Ser*. 2006;313:295–304.
- Garrigue C, Zerbini AN, Geyer Y, Heide-Jørgensen MP, Hanaoka W, Clapham P. Movements of satellite-monitored humpback whales from New Caledonia. *J Mamm*. 2010;91(1):109–15.
- Mate BR, Best PB, Lagerquist BA, Winsor MH. Coastal, offshore, and migratory movements of South African right whales revealed by satellite telemetry. *Mar Mam Sci*. 2011;27(3):455–76.
- Jonsen ID, Mills Flemming J, Myers RA. Robust state space modeling of animal movement data. *Ecology*. 2005;86:2874–80.
- Bailey H, Mate BR, Palacios DM, Irvine L, Bograd SJ, Costa DP. Behavioural estimation of blue whale movements in the Northeast Pacific from state-space model analysis of satellite tracks. *Endanger Species Res*. 2009;10:93–106.
- Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J. State-space models of individual animal movement. *Trends Ecol Evol*. 2008;23:87–94.
- Patterson TA, Basson M, Bravington MV, Gunn JS. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *J Anim Ecol*. 2009;78:1113–23.
- Best PB, Sekiguchi K, Findlay KP. A suspended migration of humpback whales *Megaptera novaeangliae* on the west coast of South Africa. *Mar Ecol Prog Ser*. 1995;118:1–12.
- Stockin KA, Burgess EA. Opportunistic feeding of an adult male humpback whale (*Megaptera novaeangliae*) migrating along the coast of south eastern Queensland, Australia. *Aquat Mamm*. 2005;31(1):120–3.
- Visser F, Hartman KL, Pierce GJ, Valavanis VD, Huisman J. Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. *Mar Ecol Prog Ser*. 2011;440:267–79.
- Owen K, Warren JD, Noad MJ, Donnelly D, Goldizen AW, Dunlop RA. Effect of prey type on the fine-scale feeding behaviour of migrating east Australian humpback whales. *Mar Ecol Prog Ser*. 2015;541:231–44.
- Double MC, Andrews-Goff V, Jenner KCS, Jenner MN, Laverick SM, Branch TA, Gales NJ. Migratory movements of pygmy blue whales (*Balaenoptera musculus brevicauda*) between Australia and Indonesia as revealed by satellite telemetry. *PLoS One*. 2014;9(4):e93578.
- Johnson MP, Tyack PL. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J Ocean Eng*. 2003;28(1):3–12.
- Andrews RD, Pitman RL, Ballance LT. Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biol*. 2008;31:1461–8.
- Simon M, Johnson M, Madsen PT. Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *J Exp Biol*. 2012;215:3786–98.
- Goldbogen JA, Calambokidis J, Shadwick R, Oleson EM, McDonald MA, Hildebrand JA. Kinematics of foraging dives and lunge-feeding in fin whales. *J Exp Biol*. 2006;209:1231–44.

39. Owen K, Dunlop RA, Monty JP, Chung D, Noad MJ, Donnelly D, Goldizen AW, Mackenzie T. Detecting surface-feeding behavior by rorqual whales in accelerometer data. *Mar Mamm Sci.* 2016;32(1):327–48.
40. Luque SP. Dive analysis and calibration. R Package version 1.3.9. CRAN. 2015. R-project.org/package = diveMove; 2015.
41. R Development Core Team. R: A language and environment for statistical computing, reference index version 3.1.3. R Foundation for Statistical Computing, Vienna, Austria. 2015. URL <http://www.Rproject.org>.
42. Witt MJ, Åkesson S, Broderick AC, Coyne MS, Ellick J, Formia A, Hays GC, Luschi P, Stroud S, Godley BJ. Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. *Anim Behav.* 2010;80:571–81.
43. Barraquand F, Benhamou S. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology.* 2008;89(12):3336–48.
44. Calenge C. Analysis of Animal Movements in R: the adehabitatLT Package. 2015. R Package version n 0.3.20. CRAN. R-project.org/package = adehabitatLT. 2015.
45. Fauchald P, Tveraa T. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology.* 2003;84(2):282–8.
46. Lavielle M. Detection of multiple changes in a sequence of dependent variables. *Stoch Proc Appl.* 1999;83:79–102.
47. Lavielle M. Using penalized contrasts for the change-point problem. *Signal Process.* 2005;85:1501–10.
48. Dodge S, Bohrer G, Weinzierl R, Davidson SC, Kays R, Douglas D, Cruz S, Han J, Brandes D, Wilkelski M. The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Mov Ecol.* 2013;1:3.
49. Amante C, Eakins BW. ETOPO1 1 Arc-minute global relief model: procedures, data sources and analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data Center, NOAA. 2009. doi:10.7289/V5C8276M. Accessed 1 Oct 2015.
50. NASA Ocean Biology (OB.DAAC). Sea-viewing wide field-of-view sensor (SeaWiFS) ocean color data, 2014.0 Reprocessing. NASA OB.DAAC, Greenbelt, MD, USA. doi:10.5067/ORBITVIEW-2/SEAWIFS_OC.2014.0. Accessed 01 Dec 2015.
51. Davis RW, Fuiman LA, Williams TM, Le Boeuf BJ. Three-dimensional movements and swimming activity of a northern elephant seal. *Comp Biochem Physiol A.* 2001;129:759–70.
52. Sato K, Mitani Y, Cameron MF, Siniff DB, Naito Y. Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J Exp Biol.* 2003;206:1461–70.
53. Silber GK, Slutsky J, Bettridge S. Hydrodynamics of a whale/ship collision. *J Exp Mar Biol Ecol.* 2010;391:10–9.
54. McKenna MF, Calambokidis J, Oleson EM, Laist DW, Goldbogen JA. Simultaneous tracking of blue whales and large ships demonstrates limited behavioral responses for avoiding collision. *Endanger Species Res.* 2015;27:219–32.
55. Urlick RJ. Principles of underwater sound. New York: McGraw-Hill; 1983.
56. Terhune JM, Verboom WC. Right whales and ship noise. *Mar Mamm Sci.* 1999;15:256–8.
57. Irvine LM, Mate BR, Winsor MH, Palacios DM, Bograd SJ, Costa DP, Bailey H. Spatial and temporal occurrence of blue whales off the US West Coast, with implications for management. *PLoS One.* 2014;9(7):e102959.
58. Laist DW, Knowlton AR, Mead JG, Collet AS, Podesta M. Collisions between ships and whales. *Mar Mamm Sci.* 2001;17(1):35–75.
59. Conservation Management Plan for the Blue Whale—A Recovery Plan under the Environment Protection and Biodiversity Conservation Act 1999, Commonwealth of Australia 2015.
60. Croll DA, Acevedo-Gutiérrez A, Tershy BR, Urban-Ramirez J. The diving behaviour of blue and fin whales: Is dive duration shorter than expected based on oxygen stores? *Compar Biochem Physiol A.* 2001;129:797–809.
61. Heide-Jørgensen MP, Laidre KL, Wiig Ø, Jensen MV, Dueck L, Maiers LD, Schmidt HC, Hobbs RC. From Greenland to Canada in ten days: tracks of bowhead whales, *Balaena mysticetus*, across Baffin Bay. *Arctic.* 2003;56(1):21–31.
62. Nielsen NH, Laidre K, Larsen RS, Heide-Jørgensen MP. Identification of potential foraging areas for bowhead whales in Baffin Bay and adjacent waters. *Arctic.* 2015;68(2):169–79.
63. Forester JD, Ives AR, Turner MG, Andersen DP, Fortin D, Beyer HL, Smith DW, Boyce MS. State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecol Monograph.* 2007;77(2):285–99.
64. Heithaus MR, Frid A, Wirsing AJ, Dill LM, Fourqurean JW, Burkholder D, Thomson J, Bejder L. State-dependent risk-taking by green sea turtles mediates top-down effects of tiger shark intimidation in a marine ecosystem. *J Anim Ecol.* 2007;76(5):837–44.
65. Jonsen ID, Myers RA, James MC. Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Mar Ecol Prog Ser.* 2007;337:255–64.
66. Dragon A, Bar-Hen A, Monestiez P, Guinet C. Comparative analysis of methods for inferring successful foraging areas from Argos and GPS tracking data. *Mar Ecol Prog Ser.* 2012;452:253–67.
67. Bestley S, Patterson TA, Hindell MA, Gunn JS. Feeding ecology of wild migratory tunas revealed by archival tag records of visceral warming. *J Anim Ecol.* 2008;77:1223–33.
68. Rennie S, Hanson CE, McCauley RD, Pattiaratchi C, Burton C, Bannister J, Jenner C, Jenner MN. Physical properties and processes in the Perth Canyon, Western Australia: Links to water column production and seasonal pygmy blue whale abundance. *J Mar Syst.* 2009;77:21–44.
69. Piatt JF, Methven DA. Threshold foraging behavior of baleen whales. *Mar Ecol Prog Ser.* 1992;84:205–10.
70. Hazen EL, Friedlaender AS, Goldbogen JA. Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Sci Adv.* 2015;1(9):e1500469.
71. Weimerskirch H. Are seabirds foraging for unpredictable resources? *Deep Sea Res.* 2007;54:211–23.
72. Thums T, Bradshaw CJA, Hindell MA. In situ measures of foraging success and prey encounter reveal marine habitat-dependent search strategies. *Ecology.* 2011;92(6):1258–70.
73. Konishi K, Tamura T, Zenitani R, Bando T, Kato H, Walløe L. Decline in energy storage in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. *Polar Biol.* 2008;31:1509–20.
74. Woodward BL, Winn JP, Fish FE. Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *J Morphol.* 2006;267:1284–94.

Submit your next manuscript to BioMed Central and we will help you at every step:

- We accept pre-submission inquiries
- Our selector tool helps you to find the most relevant journal
- We provide round the clock customer support
- Convenient online submission
- Thorough peer review
- Inclusion in PubMed and all major indexing services
- Maximum visibility for your research

Submit your manuscript at
www.biomedcentral.com/submit

