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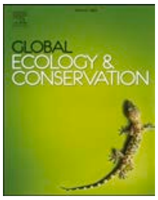

Original research article

Tracking pygmy blue whale diving behaviour and validation of foraging areas defined from horizontal movement data

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ABSTRACT

Foraging in large vertebrates is often inferred from horizontal movement behaviour from satellite tracking data, but the strength of this inference has not been adequately verified. Here, nine pygmy blue whales (*Balaenoptera musculus brevicauda*) were tagged with satellite tracking tags and pop-up archival tags (PATs) providing depth and accelerometry time series to determine where actual foraging occurs during migration. Four PATs were recovered, providing depth and accelerometry data at 1 Hz, and the remaining tags transmitted 75 s sample-rate data for up to 40 days. The depth time series allowed us to distinguish foraging dives, with accelerometry data key to distinguishing lunge-feeding. Despite a weak temporal relationship between putative (inferred from a movement model) and actual foraging, there was generally good spatial overlap detected, predominantly in high use areas, while more opportunistic foraging areas with lower use were less likely to be detected by the model. More opportunistic foraging occurred off north-west Australia where foraging dives were shallower, horizontal travel rates faster, and there was an absence of a diurnal pattern in diving. This suggests a reliance on more ephemeral prey than off south-west Australia where whales have high residency. Foraging/feeding occurred every 1–10 days at a rate of 4 hours (median) per day (range 0.1 – 12) and occurred during migration, providing support for use of a mixed breeding strategy (income and capital) in this sub-species. Our test of movement models to define foraging is extremely useful given its common usage in ecology and our spatial delineation of foraging areas assists with conservation management.

1. Introduction

Many migratory animals exhibit spatially and temporally distinct phases in their movement behaviour related to various needs such as breeding, foraging, or specific thermal requirements (Dingle, 1996). Movements to meet these needs pose energetic challenges, especially for long distance migrants (Evans and Bearhop, 2022). Some animals adapt by relying on stored energy reserves (Irvine et al., 2017, Russell et al., 2024a), others meet their energy needs by feeding during migration (Stephens et al., 2014, Guilpin et al.,

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2019), or by adopting a combined strategy which may be dependent on food availability (Busquets-Vass et al., 2021).

Many of these strategies are evident in the rorqual whales (Balaenopteridae) that lunge feed on krill or fish in the water column (Geijer et al., 2016). During lunge feeding, rorquals approach a school of prey at high speed then open their mouths to engulf and filter their prey (Potvin et al., 2012). It is thought that patches of prey need to be sufficiently dense or of a certain biomass to be profitable (Guilpin et al., 2019, Torres et al., 2020). As such, many rorqual species focus their foraging activities in specific areas of high prey density that are somewhat predictable in time and space, as has been suggested from studies of blue whales *(Balaenoptera musculus)* in California and Mexico (Goldbogen et al., 2011, 2015). In many cases these reliable foraging areas are seasonal and/or are distant from breeding grounds (Geijer et al., 2016). For species with less capacity to store excess energy as fat deposits, opportunistic feeding on ephemeral prey encountered during migration may be necessary. This is possibly the case for Eastern Indian Ocean (EIO) pygmy blue whales (*Balaenoptera musculus brevicauda*), as intermittent feeding has been reported for this subspecies and a number of other rorquals during migration (Silva et al., 2013, Owen et al., 2016, Owen et al., 2017). While some major feeding hotspots of EIO pygmy blue whales have been identified (Double et al., 2014; Gill, 2002; Möller et al., 2020; Rennie et al., 2009; Thums et al., 2022; Garcia-Rojas et al., 2018), there is a paucity of data for individual reliance on additional, smaller feeding areas between aggregation grounds. Especially since many of these may be ephemeral and dynamic in nature (Goldbogen et al., 2015). As pygmy blue whale populations are unlikely to have recovered from whaling (Branch et al., 2018, McCauley et al., 2018b) and individuals are exposed to various anthropogenic threats along their long (1000's of km) migratory route (Sahri et al., 2022, Ferreira et al., 2023), understanding the presence and location of all foraging areas is important to effectively manage potential impact to this sub-species and protect critical habitats.

In the Eastern Indian Ocean, pygmy blue whales aggregate in the austral summer to feed in the Subtropical Convergence Zone and the Great Australian Bight Coastal Upwelling System (Branch et al., 2007, Garcia-Rojas et al., 2018) from as far west as 77° E (Samaran et al., 2013, Torterotot et al., 2020) and east to Bass Strait (~146E, between the Australian states of Victoria and Tasmania) (Balcazar et al., 2015, McCauley et al., 2018a). As autumn approaches, whales start migrating north and are known to aggregate along the continental shelf west of Australia, particularly the Perth Canyon (Rennie et al., 2009). Feeding areas along the west coast of Australia in between areas off the Ningaloo coast and Rowley Shoals have recently been identified as whales migrate further north towards Indonesia for the winter months (Thums et al., 2022). These spatially non-continuous foraging areas are used by pygmy blue whales prior to or during their migration north in the austral winter to Indonesian waters, predominantly to the Banda, Molucca, Savu, and Timor Seas (Double et al., 2014, Möller et al., 2020). These seas are considered the northern terminus of the migration and possibly represent the breeding and calving grounds, but probably also act as feeding areas (Kahn, 2007, Double et al., 2014, Burton et al., 2023).

These known foraging areas are being increasingly well documented and recognised by management agencies (e.g., through designation as Biologically Important Areas) (Commonwealth of Australia, 2015). However, some evidence suggests that foraging also occurs outside these areas (Thums et al., 2022). Outputs from a movement model applied to satellite tag location data showed that the migrations (high move persistence; relatively fast and straight) of EIO pygmy blue whales were interspersed with relatively short periods (a few days) of low move persistence (slow and tortuous movement), which is commonly inferred to be foraging behaviour (Double et al., 2014, Möller et al., 2020, Thums et al., 2022). Low move persistence is also referred to as area-restricted search (ARS) and in cetaceans, milling. There is a theoretical basis for assigning putative foraging behaviour along animal tracks based on such analyses of location estimates from satellite tags (Kareiva and Odell, 1987; Zollner and Lima, 1999). However, one study on an EIO pygmy blue whale found poor association with foraging movement behaviour (ARS) via residency time calculated from GPS data and lunging feeding events, but not foraging behaviour (Owen et al., 2016). As foraging occurs while the animals are diving, having data from the vertical dimension is important for validation of these metrics. Although valuable, the tags used by Owen et al. (2016) had to be recovered, as the high-resolution depth and accelerometry data used in their study to identify feeding events could not be transmitted via satellite due to bandwidth limitations of the Argos animal tracking satellite systems. As tag recovery is difficult (and expensive) on these animals since they move 10's to 100's of kilometres in a day (Mate et al., 2017), tags with high resolution depth and accelerometry data are usually only programmed to have short (days to weeks) attachment periods as a way of facilitating tag and therefore data recovery, though successful tag recovery from some longer deployments have been achieved with implantable tags (up to 30 days, Mate et al., 2017) and tags with LIMPET style darts (Szesciorka et al., 2016, Fahlbusch et al., 2022). As such, fine scale diving data for weeks to months for blue whales is relatively rare, as are studies that can validate the outputs of movement models.

Obtaining feeding data for greater spatial and temporal extents than is reliable with recoverable tags has been attempted with tags that transmit summarised depth data and outputs of onboard event detectors (Mate et al., 2017, Heerah et al., 2019, Palacios et al., 2022). Such tags can collect higher resolution data (usually ≥ 1 Hz depth and accelerometry) that is processed while still attached to the animal and trained to identify feeding events using known signatures in these time-series (Heerah et al., 2019). Counts of feeding events, locations, and summaries of the depth time-series (time-at-depth histograms, dive profiles, or other dive statistics) are then transmitted via the satellite network (Palacios et al., 2022). These methods may be able to provide more directed outputs, such as the locations and times of feeding events, but this comes at the cost of continuous time-series data that gives a more holistic view of animal behaviour.

Pop-up satellite archival tags (PSAT) are potentially one solution to obtaining depth use data over longer temporal scales (weeks to months). PSATs were designed to track large-scale movements and depth use of fish and other animals that do not spend enough time at the surface to allow the use of real-time Argos satellite tags (Hussey et al., 2015). PSATs are a combination of archival and satellite tag technology, with depth (± 0.5 m), light (for geolocation) and temperature (± 0.05 °C) collected at 1 s intervals and summarised (user defined, at best is 75 s intervals) for transmission and archived (at 1 s intervals) on board the tag. At programmed release from the animal, the tag floats up to the surface and transmits the summarised data. If the tag is recovered, the archived, higher resolution time series data on board can also be downloaded. Such tags have been a boon for understanding the movement behaviour of many pelagic fish species (Block et al., 2002; Hussey et al., 2015) but are not commonly used on air breathing animals. More recently, PSATs have been equipped with sensors that record acceleration at 8 Hz for calculation of a filtered proxy for overall dynamic body acceleration (ODBA) known as Mobility (archived on board the tag) and an 'activity-time series' (ATS, summarised from Mobility to be suitable for transmission through the Argos satellite network), which is a count of high activity/mobility events relative to overall activity/mobility (see Skubel et al., 2020 for details). During feeding lunges, pygmy blue whales undergo considerable variation in their activity patterns, resulting from speeding up to engulf prey and then coming to a near complete stop due to deceleration caused by drag of the huge open mouth. These feeding lunges have been detected using peaks in accelerometry data collected at a resolution of 1 Hz (e.g., Mate et al., 2017).

To characterise and track pygmy blue whale dive behaviour in known foraging areas and along their migratory paths, we deployed Fastloc GPS satellite tags with PSATs that provided time-series of depth and Mobility. Specifically we aimed to 1) determine whether depth and summarised accelerometry time series data obtained from PSATs deployed on pygmy blue whales could be used to differentiate the range of dive types known in pygmy blue whales and especially lunge feeding, 2) determine what temporal resolution is required for accurate detection of foraging and lunge feeding behaviour, 3) depict the spatial and temporal patterns in foraging behaviour, and 4) use the location and timing of the occurrence of actual foraging (foraging and lunge feeding dives) to validate putative foraging behaviour inferred by a movement model. Accurately defining the location and spatial extent of pygmy blue whale foraging and feeding behaviour is key to assess overlap between the whales' foraging areas and anthropogenic activities to inform impact assessment and mitigation and conservation management.

2. Methods

2.1. Tag deployment

To collect data on pygmy blue whale dive behaviour, we deployed PSATs (miniPATs, Wildlife Computers; Redmond, Washington, USA) on nine pygmy blue whales (Table 1). The PSATs were connected by a braided stainless-steel tether (~10 cm long) to a titanium dart and the dart embedded using a handheld 6 m long carbon fibre tagging pole to the upper shoulder area, below the ridge of the spine (see Supplementary Methods for details). This technique was modified in 2022 to allow for a biopsy sample to be collected simultaneously by adding a standard whale tissue biopsy punch (5 mm diam × 10 mm long) to the end of the tagging pole. DNA was extracted from the tissue samples using a salting-out method, and the sex of the whales determined by PCR-amplification of fragments of the ZFX and SRY genes (Gibson and Mace, 2003) (Table 1).

The PSATs recorded depth (± 0.5 m), light (for geolocation), temperature (± 0.05 °C), and acceleration along the x, y, and z axes (Ax, Ay and Az) at 8 Hz. The data are processed for calculation of Mobility and an 'activity time-series' (ATS). After release from the animal, Mobility is calculated by the tag every 1 s as the mean standard deviation of summed acceleration (x, y, and z) over a 3-second sliding window of 8 Hz values. ATS is a count of high activity events relative to overall activity/ mobility during the summary period (75 s) identified by the outliers in the tail of the Mobility distribution (for more details see (Skubel et al., 2020). Mobility and Az are archived on board the tag at 1 s intervals, along with the raw depth, temperature, and light data. ATS, depth, temperature and light are transmitted through Argos at a sampling rate selected by the user. Here the highest possible sampling interval of 75 s was selected. The tags were programmed to detach from the whales after 30 days (2021) or 40 days (2022 and 2023). At release, the tags are designed to float to the surface and transmit their data through Argos until the batteries are depleted. Four tags were recovered after release (Table 1), with three of those washing up on beaches (Hopetoun, Mindarie, and Augusta, WA) and a fourth recovered in the Perth Canyon, using a directional VHF receiver to orient the search to the signals emitted by the tag. Upon retrieval, archived 1 s sampled data stored on the tag were downloaded from the device and for the tags not recovered (n = 5) data transmitted through Argos were downloaded from the Wildlife Computers Portal.

As only two geolocation estimates per day can be calculated from the PSATs and the location data are far less accurate than satellite

Table 1
Deployment details for each of the tagged pygmy blue whales. LIMPET and PSAT duration is the period of time that the tag provided data/was attached. Recovered PSATs are noted with an asterisk. Data recovery is the percentage of data received from each tag, i.e. was transmitted through the Argos satellite network, which can be affected by sea state and battery limitations with recovered PSATs yielding 100 %. The first two whales were only instrumented with PSATs.

ID (PSAT ID)	Deployment date	Location	LIMPET duration (d)	PSAT duration (d)	Data recovery (%)	Dives (n)	Whale length (m)	Sex
214432	27/04/2021	Perth	NA	30 *	100	11331		
214430	27/04/2021	Perth	NA	30	56	3058		
233088	24/04/2022	Perth	11	12 *	100	2125	19.9	F
214431	30/04/2022	Perth	11	6 *	100	1042		M
233091	01/05/2022	Perth	77	29	39	1159	19.8	F
233095	07/05/2022	Perth	98	27	55	1601		M
233102	08/05/2022	Perth	39	41	82	1441	21.2	F
233101	09/05/2022	Perth	9	5 *	100	1200	18.4	F
233096	23/07/2023	Ningaloo	44	4	100	632	21.7	F

location estimates, after 2021 we simultaneously instrumented each pygmy blue whale with a Wildlife Computers LIMPET (Low Impact Minimally Percutaneous Electronic Transmitters, type: SPLASH10-F-333) using a Dan-Inject CO_2 rifle (Table 1) (See supplementary Materials and Thums et al. 2022 for details).

Video of surfacing pygmy blue whales were digitally recorded using Remotely Piloted Aircraft (RPA); a DJI Phantom 4 Pro UAV, which had an integrated camera sensor and an attached laser range finder to obtain the UAV altitude which was used to obtain measurements of the whales (Russell et al., 2024b) (See Supplementary Methods for details) based on the methods of Christiansen et al. (2016, 2020).

2.2. *Data analysis*

2.2.1. *Location data*

The movement paths of two whales where PSATs were deployed without LIMPETs, were determined using the Wildlife Computers geolocation processing software (GPE3) using observations of twilight, temperature, along with corresponding reference data on sea surface temperature and bathymetry to provide two location estimates per day (at dawn and dusk).

To account for location error and standardise the location estimates at set intervals (calculated from the average number of raw location estimates per day), a correlated random walk model was applied to all the location estimates received from the LIMPETs including Argos (location classes 3, 2, 1, 0, A, and B with estimated error of <250 m, 250 – 500 m, 500 – 1500 m, >1500 m, and unknown, respectively) and Fastloc GPS using the R (R Core Team, 2022) package *foieGras* (Jonsen et al., 2020). Then, a move persistence model (*mpm*) (Jonsen et al., 2020) was applied to provide an objective behavioural index (g) along the track. The index, known as move persistence, is a continuum ranging between 0 (decrease in speed and directionality = low move persistence) and 1 (increase in speed and directionality = high move persistence). Segments of relatively low move persistence are generally indicative of foraging, but could also represent resting and/or breeding (Bailey et al., 2009), while segments of relatively high move persistence are related to migration or transit behaviour (Jonsen et al., 2019). Tracks with large gaps (>7 days) were split and each portion of data analysed separately. All models were checked for convergence.

Move persistence was also summarised into a binary measure, based on the threshold move persistence (g) of 0.8 developed by Thums et al., (2022). Putative foraging was inferred where satellite location points along the track had $g < 0.8$ and transit/migration was inferred for those points with $g \geq 0.8$ as Thums et al. (2022).

2.2.2. *Dive data*

2.2.2.1. Dive definition. The depth time–series were analysed in R (R Core Team, 2022) using the library *diveMove* (Luque and Guinet, 2007) to define dives, dive phases and summary statistics (see Supplementary methods for details) according to a minimum depth threshold of 1.5 m and a minimum dive duration of 10 s. We also calculated the number of lunges on feeding dives and the number of wiggles (large undulations in depth on the bottom portion of foraging dives) in each dataset, using custom algorithms to detect spikes in Mobility and ATS as lunges and large undulations in depth as wiggles. These combined dive statistics (these and those produced by *diveMove,* Table A1) were then used to develop supervised dive classification algorithms.

2.2.2.2. Visual dive classification. The depth and Mobility/ATS -time series of all dives were visualised for each dive in turn by two scientists independently, for each of the recovered (1 s sampling interval) and the transmitted datasets (75 s sampling interval) using custom code written in R. Each dive was classified as one of ten types (Table 2), which were agreed *a-priori*. The seven dive types were

Table 2
The classified dive types and their description, in each of the 75 s (transmitted) and 1 s (recovered) time series datasets from pygmy blue whales. Some dive types were not able to be discerned in the transmitted tag dataset (type 1, 3, and 7) due to low temporal resolution, and three additional categories had to be added.

Dive type #	1 s data	75 s data	Dive behaviour	Description
0	Y	Y	Other/ unknown	Does not fit any other category
1	Y	N	Inter-blow	Shallow (0 – 4 m) and short (< 1 min), usually part of a surfacing sequence
2	Y	Y	Travel	Square-ish or round shaped (usually < 40 m depth)
3	Y	N	Resting	Similar to travel dives, but very shallow (< 12 m) and very low Mobility (< 40)
4	Y	Y	Exploratory	V-shape with no/minimal bottom time
5	Y	Y	Foraging	Square-ish and deep (> 40 m but often hundreds of metres), wiggles present or absent
6	Y	Y, but only when ATS data were available	Lunge feeding	As for foraging but containing depth wiggles and spikes in Mobility/ATS associated with wiggles
7	Y	N	Porpoising	Very high mobility, generally shallow and short, rapid depth undulations
8	N	Y	Unknown	Incomplete dives (occurs as not all data are transmitted)
9	N	Y	Too short	Too little information as only one data point in 'dive'
10	N	Y	Surface active	Like porpoising, (< 12 m), spikes in ATS but insufficient temporal resolution to classify as porpoising

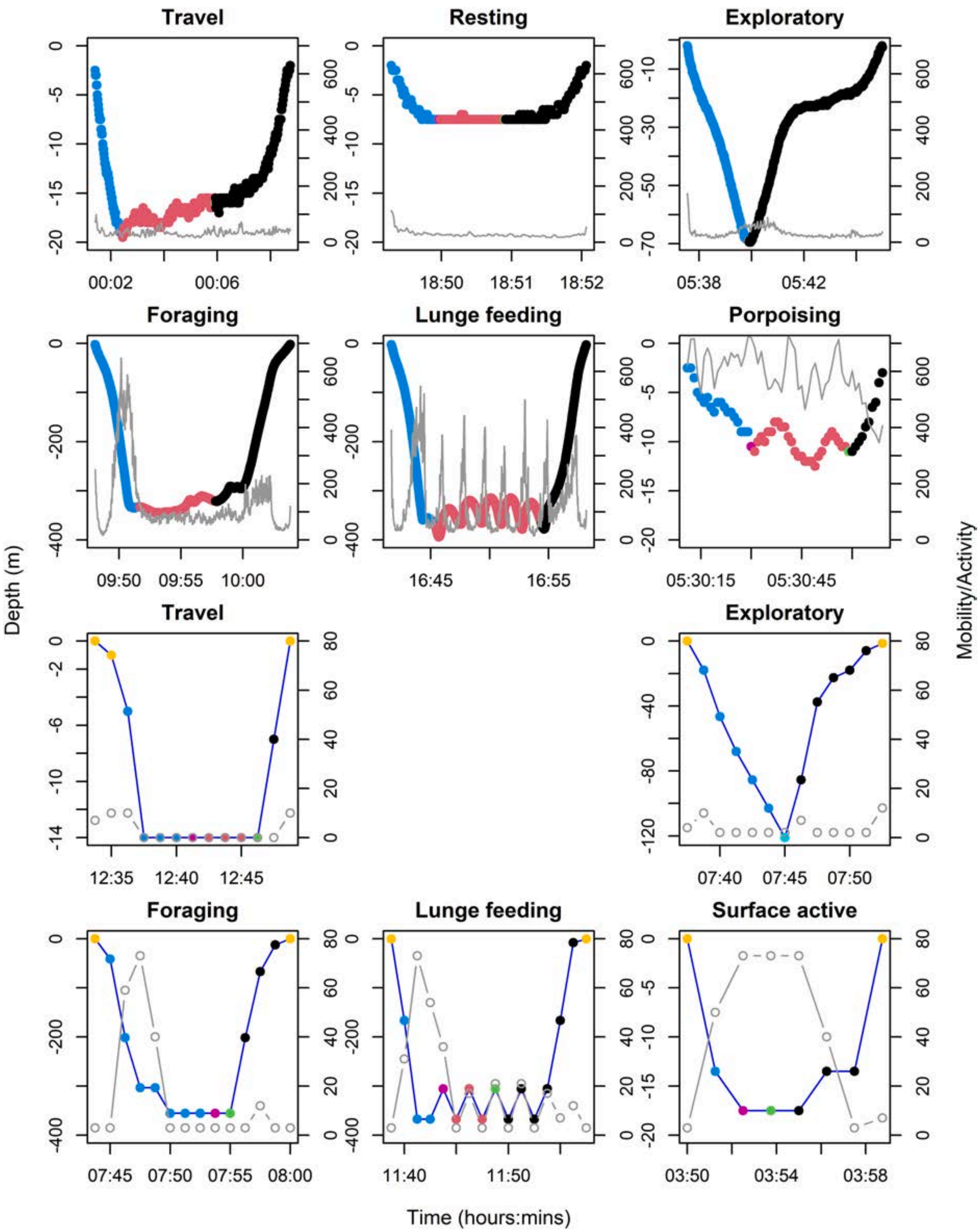


Fig. 1. Representative time-depth and -Mobility/ATS profiles of each of the dive types detected in the recovered (top 6 plots) and transmitted (bottom 6 plots) tag data. Colours represent phases of the dives (descent in blue, end of the descent/ start of the bottom period in pink, bottom of the dive in red, end of the bottom period/start of the ascent in green, ascent in black). Mobility (grey line); the filtered proxy for overall dynamic body acceleration, is plotted on the opposite y-axis for the recovered tag data. Activity (grey line) is plotted in the opposite y-axis for the transmitted data. Activity is the summarised (for transmission through the Argos satellite network) version of Mobility and refers to the number of high Mobility events relative to overall mobility during the summary period (75 s).

decided based on previously described dive types for pygmy blue whales (Davenport et al., 2022), eastern North Pacific blue whales (Oleson et al., 2007), fin whales (Fonseca et al., 2022) and other diving vertebrates (e.g., Schreer et al., 2001) (Fig. 1). Among these we classified lunge feeding dives as distinct from foraging dives. Although both comprise foraging behaviour, the former are foraging dives where prey was detected and prey capture was attempted as indicated by the Mobility/ATS metrics in the form of lunging. Whereas those classified as ‘foraging’ indicate searching for prey but prey capture was not attempted, likely because prey were not present or at high enough density for it to be initiated. We calculated the agreement between the dive classifications of the two scientists to check the error associated with visual classification, first assuming scientist 1 was correct and again assuming that scientist 2 was correct.

Gaps occurred in the transmitted tag data (depth and/or ATS) due to high sea state interrupting transmission and battery capacity. If ATS data were absent, the dive was classified as a foraging dive, even if wiggles were present because a whale may search vertically through the water column without encountering sufficient prey density.

2.2.2.3. Training dataset for supervised dive classification. To objectively classify the dives into different types (Table 2, excluding types 0, 8 & 9), we developed a supervised diving classification algorithm using the methods of Thums et al. (Thums et al., 2008). In supervised classification algorithms, a data subset must be provided that has dives already classified, and this data subset is known as the training dataset. The algorithm can then use the classified dives in the training dataset to pick up patterns that maps the input variables (Table A1) to the output (provided classifications) and uses this pattern to predict values with new datasets. Two training datasets were made; one for each of the transmitted and recovered data. Only the dives where the visual classification from both scientists agreed were used. Many of the predictor variables were collinear and thus we removed those with correlation coefficient higher than 0.7. A slightly different and smaller set of variables were calculated for the transmitted tag dataset as Mobility was not available and was replaced by ATS (Table A1).

2.2.2.4. Supervised dive classification. We used the Random Forest model (Breiman, 2001) to develop the supervised classification algorithms using the R package *randomForest* (Liaw and Wiener, 2002). In Random Forest models, an unbiased estimate of error is calculated internally and known as the ‘out-of-bag’ (OOB) error estimate (Breiman, 2001) (see Supplementary Methods). We developed three Random Forest classification algorithms, one for the recovered tag data (Algorithm 1) and two for the transmitted tag data; one with ATS variables (Algorithm 2) and another without them (Algorithm 3) to determine the importance of ATS in dive classification.

2.3. Diving and foraging behaviour of pygmy blue whales

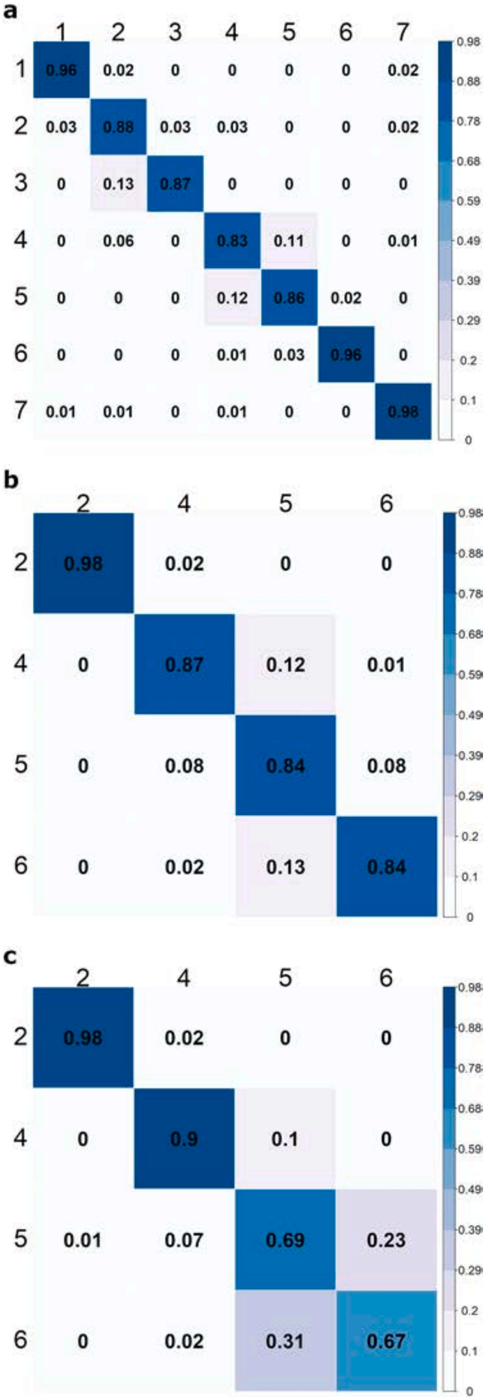
We used Random Forest algorithm 1 to classify all the dives in the entire record for each of the recovered datasets. Although Algorithm 3 was to be used to classify the dives for the transmitted dataset, the Random Forest error rate was high for foraging and lunge feeding dives and in contrast, the error rates of the visual classifications by the scientists were equal or better. Thus, all further analyses and plotting were done using the visual classifications for the transmitted dataset and the Random Forest classifications for the recovered dataset. An exception was the summary statistics (max depth, dive duration, etc) calculated for each dive type for each whale. These were done on the visually classified dives where both classifiers agreed. In addition, we calculated the number of dives in a bout for each dive type, where a bout was a consecutive run of the same dive type and bout ending was identified where there was a switch to another dive type. The classified dives were merged (by timestamp) with the location estimates and plotted spatially and temporally to determine where and when important behaviours (such as foraging) occurred. The location estimates (latitude and longitude; 2D) received from the LIMPETs had to be interpolated at the sampling interval of the PSAT data (depth at 1 or 75 s; 2D) to facilitate the merge. This was achieved using the R package *move* (Kranstauber et al., 2024) and the interpolated 2D track was then merged with the PSAT dataset by the time stamp to add an interpolated location point (latitude and longitude) to every value of depth. The merged datasets were then plotted in 3-dimensional (3D) space to produce interactive plots using the R package *rayshader* (Morgan-Wall, 2024). Underlying bathymetry data for the 3D interactive plots were obtained either from the Australian Bathymetry and Topography Grid 250 m 2023 (Bearman, 2023) or the General Bathymetric Chart of the Oceans 2024 grid (GEBCO Compilation Group, 2024) depending on the spatial extent of each track. In many cases the LIMPET duration was longer than the PSAT duration (Table 1, Fig. 3a & b), thus we could only geolocate the dives for which we had corresponding location data, and the 3D satellite tracks presented were cropped to the duration of the PSAT data (Table 1). The merged dataset was used to calculate horizontal travel rate for the parts of the track where foraging and feeding dives occurred.

2.4. Comparison of putative foraging with actual foraging

We calculated the mean g value (move persistence) each day of the tag deployment and the total number of hours spent on foraging and feeding dives per day per whale. We fit a generalised linear mixed model on the combined recovered and transmitted datasets, with number of hours spent foraging as the response variable, mean daily g as the predictor, and whale ID as a random effect. We compared the AICc of this model to the AICc of the NULL model. We also used the dataset produced from the calculation of the number of hours spent on foraging and feeding dives per day to calculate the median and range of hours spent feeding per day and feeding occurrence on a day scale.

We plotted the points to determine the concordance between the spatial distribution of foraging and lunge feeding dives (actual foraging) and where the move persistence model indicated foraging (g < 0.8, putative foraging). As the diving and location datasets came from different tags with differing durations (tags were shed/failed at different rates), we excluded location data where corresponding dive data was unavailable and *vice versa* in the comparison.

Summary statistics are means and standard deviation unless otherwise stated.



a

	1	2	3	4	5	6	7
1	0.96	0.02	0	0	0	0	0.02
2	0.03	0.88	0.03	0.03	0	0	0.02
3	0	0.13	0.87	0	0	0	0
4	0	0.06	0	0.83	0.11	0	0.01
5	0	0	0	0.12	0.86	0.02	0
6	0	0	0	0.01	0.03	0.96	0
7	0.01	0.01	0	0.01	0	0	0.98

b

	2	4	5	6
2	0.98	0.02	0	0
4	0	0.87	0.12	0.01
5	0	0.08	0.84	0.08
6	0	0.02	0.13	0.84

c

	2	4	5	6
2	0.98	0.02	0	0
4	0	0.9	0.1	0
5	0.01	0.07	0.69	0.23
6	0	0.02	0.31	0.67

Fig. 2. The out-of-bag estimate of error from the Random Forest dive classification algorithms for each dive type (1 = inter-blow, 2 = travel, 3 = resting, 4 = exploratory, 5 = foraging, 6 = lunge feeding, and 7 = porpoising) showing results for Algorithm 1 (a) for the recovered pygmy blue whale tag dataset, Algorithm 2 (b) with and without (Algorithm 3 (c) variables associated with ATS. The rows represent the true dive types and the columns represent predicted dive types. Values on the centred diagonal from top-left to bottom-right represent the proportion of dives where the prediction matched the true dive type. Values in the other cells represent the proportion of dives that were misclassified by the algorithm.

3. Results

Deployment durations of the seven LIMPETS ranged from 9 – 98 d (Table 1). Four of the nine PSATs deployed came free of the whales and went to the surface and started transmitting prior (4 – 12 d) to the programmed release date (30 d from deployment) being reached (Table 1). Four of the PSATs were recovered (Table 1). For the other five PSATs not recovered, 39 – 100 % of the depth data was transmitted via satellite and available for analysis (Table 1). Tissue samples were obtained from seven of the tagged whales, with five genetically sexed as females, and two as males (Table 1).

3.1. Visual dive classification

The number of dives from each whale ranged from 632 – 11331 with variability related to deployment duration, whether the tag was recovered, and how much of the on-board data was transmitted (Table 1). The percentage of each dive type in the record in both number and time are as shown in Appendix Table 1 (See Supplementary for more details).

The overall agreement rate between the visual dive classifications of the two scientists was 93 ± 3 % for the transmitted tag data and 92 ± 6 % for the recovered tag data. The agreement for the main dive types (2, 4, 5, and 6) was generally higher (88 – 97 %) for the transmitted tag data compared to the recovered tag data (77 – 98 %) (Appendix Table 1).

3.2. Supervised dive classification

The overall out-of-bag classification error rate was 9 % for the recovered tag dataset (Algorithm 1), 14 % for the transmitted tag dataset with ATS variables included (Algorithm 2), and 19 % without ATS variables (Algorithm 3). For the recovered tag dataset, the lowest classification error rates were achieved for the type 1 (inter-blow, 4 %), 6 (lunge feeding, 4 %), and 7 (porpoising, 2 %) dives, with greater error on the remaining dives (12–17 %) (Fig. 2a). Type 2 (travel) dives were most misclassified as type 3 (resting) dives (13 %) and type 4 (exploratory) dives were misclassified as type 5 (foraging) dives and vice-versa in 11 – 12 % of cases (Fig. 2a).

Using algorithm 2 for the transmitted tag dataset, travel dives had the lowest classification error (2 %), while exploratory, foraging, and lunge feeding dives had the highest (13, 16, and 15 % respectively) (Fig. 2b). Without variables associated with ATS (Algorithm 3), the error rate improved a little or remained the same for travel and exploratory dives, while the error rate was near or more than double for the foraging and lunge feeding dives (Fig. 2c). Foraging dives were misclassified as lunge feeding dives in 31 % of cases and lunge feeding dives were misclassified as foraging dives in 23 % of cases (Fig. 2c).

3.3. Distinctive characteristics of dive types

For the recovered tag data, the top three ranked predictors were the mean of Mobility calculated across the entire dive, the maximum depth, and the descent duration (Figure A1a). For the transmitted tag data (Algorithm 2), maximum depth was by far the most important variable, followed by the maximum first derivative of ATS on the bottom of the dive, and the minimum ascent rate (Figure A1b). Without variables associated with ATS (Algorithm 3), the most important variables were maximum depth, minimum ascent rate, and 3rd quartile of the bottom rate (Figure A1c, Table A1). Maximum depth was the highest ranked or second ranked variable for all algorithms, with type 1 dives (inter-blow) the shallowest (3.5 ± 0.5 m), followed by type 2 (travel), type 3, (resting) and type 7 (porpoising) at 13 ± 6 m, 10 ± 2 m, and 14 ± 5 m, respectively, for the recovered and transmitted tag data combined (Table 3, see Table A3 for calculations done per dataset). The foraging and lunge feeding dives were deepest at 250 ± 89 and 290 ± 101 m, respectively and the exploratory dives intermediate depth (118 ± 37) (Table 3, A3). For the foraging (237 ± 120 m) and lunge feeding dives (241 ± 131 m) found in the transmitted tag data, the depth values were not as deep and more variable compared with those dive types in the recovered tag data (267 ± 37 m and 338 ± 15 m respectively) (Table A3). The number of lunges, number of wiggles and total vertical distance covered during the bottom phase on the lunge feeding dives for the recovered dataset were 2.6 ± 0.3, 2.7 ± 0.3 and 325 ± 33 m respectively and for the transmitted dataset was 0.9 ± 0.3, 1 ± 0.3 and 84 ± 39 m respectively.

3.4. Spatial and temporal overview of foraging

The majority of the whales tagged in Perth Canyon (6 of 8) had foraging and lunge feeding dives between Perth Canyon and Cervantes/Jurien Bay (~30°S) (Fig. 3b, A2 & A3, also see HTML files). For three of these, their deployment was restricted to this area over the 5–12 days the tags provided data. For those tagged at Perth Canyon with data north of this area (233091, 214430, 233095, 233102) (Figure A3 & HTML files) foraging and feeding dives also occurred at/near the shelf edge between Geraldton and Shark Bay (Fig. 3b). For those tags that continued providing data northwards of Shark Bay (214430, 233102) and for the one whale (233096) tagged at Ningaloo (Figure A3), foraging and feeding dives occurred off the shelf of the Ningaloo region up to NW of the Montebello Islands (See HTLM for 233096, Fig. 3b, Figure A3). Only one whale provided data north of the Montebello Islands (233102, 40 day duration tag) and travel dives then dominated, interspersed with foraging and exploratory dives while migrating between ~-15°S and the Savu Sea where foraging and lunge feeding dives occurred (See HTLM for 233102, Fig. 3b, A3).

Unlike all the other whales, one whale (214432) headed south after spending eight days in the Perth Canyon on foraging, lunge feeding and resting dives among others (See HTML file for 214432, Fig. 3b). This whale exhibited foraging dives to around 200 m at the shelf break offshore of Cape Naturaliste (See HTML file for 214432, Fig. 3b) and intermittently at the shelf edge in the canyons offshore of the Bremer Bay region until tag release. In between foraging dives, the whale performed predominantly travel and exploratory dives

Table 3

Summary statistics for each dive type (1 = inter-blow, 2 = travel, 3 = resting, 4 = exploratory, 5 = foraging, 6 = lunge feeding and 7 = porpoising) for 4 whales with recovered (1 s) and 5 whales with transmitted (75 s) data combined (See Table A3 for statistics calculated per dataset) as classified visually where both scientists agreed. All means (Calculated as the mean per animal for each dive, then the mean of each dive type across all whales) are followed by the standard deviation.

Dive type	Absolute max dive depth (m)	Max dive depth (m)	Dive duration (min)	Post-dive surface interval (min)	Descent rate (m s^{-1})	Bottom rate (m s^{-1})	Ascent rate (m s^{-1})	Bottom time (min)	Median n dives per ID	Range n dives per ID	Number of IDs in sample
1	14.5	3.5 ± 0.5	0.3 ± 0	0.9 ± 0.6	0.3 ± 0.1	0.2 ± 0	−0.3 ± 0.1	0.1 ± 0	326	174–5464	4
2	82	12.8 ± 5.3	7.9 ± 4.1	2.5 ± 2.1	0.1 ± 0.1	0.1 ± 0.1	−0.1 ± 0.1	2.1 ± 1.3	693	62–4263	9
3	28.5	10.1 ± 1.7	4.2 ± 1.4	1.3 ± 0.3	0.2 ± 0	0.2 ± 0	−0.1 ± 0	1.9 ± 0.3	110.5	0–1027	2
4	464	117.7 ± 37	9.1 ± 1.9	3.9 ± 5.3	0.5 ± 0.2	0.3 ± 0.1	−0.4 ± 0.2	1.9 ± 1.2	51	35–549	9
5	483	250.2 ± 89.1	13.8 ± 3	3.2 ± 2	0.9 ± 0.4	0.4 ± 0.1	−0.8 ± 0.3	4.2 ± 1.5	73	16–147	9
6	498	289.4 ± 100.8	13.5 ± 1.7	3.4 ± 1.2	1.3 ± 0.7	0.6 ± 0.3	−1.1 ± 0.5	4.9 ± 1.8	75	0–212	8
7	72.5	13.5 ± 5.2	0.5 ± 0.1	0.3 ± 0.1	1.1 ± 0.3	0.5 ± 0.1	−1 ± 0.3	0.2 ± 0.1	74.5	29–147	4
5 & 6	498	273.4 ± 92.8	14.1 ± 2.7	3.5 ± 1.5	1.1 ± 0.6	0.5 ± 0.2	−0.9 ± 0.4	5 ± 1.1	141	16–294	9

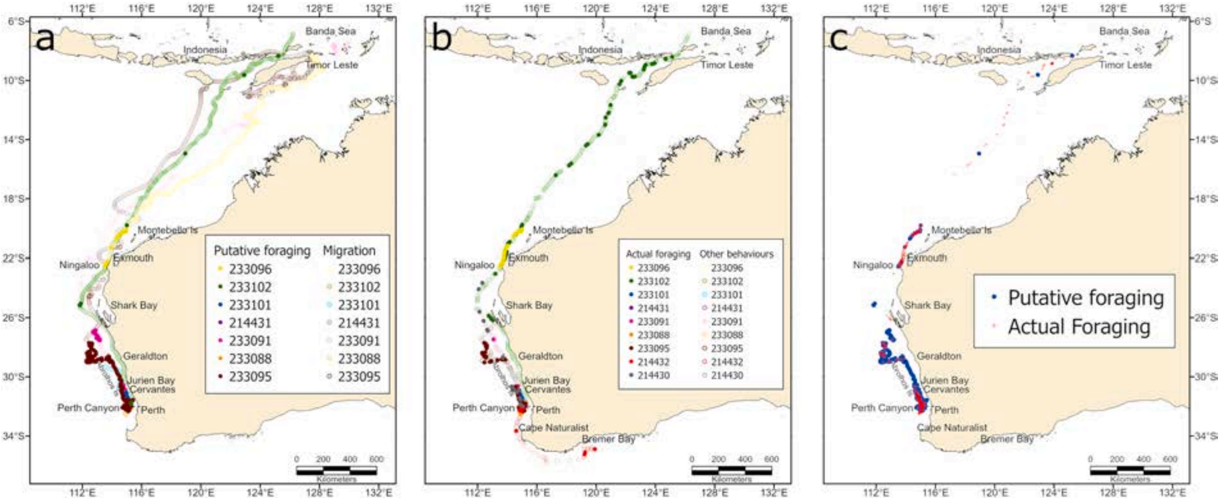


Fig. 3. Pygmy blue whale state-space modelled (SSM) location points where putative foraging; move persistence (g) < 0.8 is indicated by darker colours and non-foraging; move persistence (g) > 0.8 is indicated by lighter colours a) and where foraging (type 5) and lunge feeding (type 6) dives (actual foraging) occurred (b) plotted in darker colours and in lighter colours for points where non-foraging/feeding dive behaviours occurred. Location points (c) of putative and actual foraging/feeding for the periods of each whale's double tag deployment where both tags were providing data. Note that the two tags were shed at different rates within and among individual whales.

(See HTML files, Figure A2, Figure A3).

Foraging/ feeding dives occurred every 1 – 10 d. This was the same when considering the recovered dataset only and using this dataset, the median number of hours spent foraging/feeding per day was 247 mins (4.11 hours) with a range of 7–745 mins (0.1–12 hrs).

3.5. *Location of foraging and feeding dives*

Three main foraging areas were found based on the location points where foraging and feeding dives occurred: 1) from Perth Canyon to offshore of Jurien Bay; 2) adjacent to Geraldton and the Abrolhos Islands (noting $n_{whales} = 1$ here); and 3) offshore of Ningaloo, extending from near Coral Bay to offshore of the Montebello Islands (~19°S) (Fig. 3b). There were three other smaller areas detected with $n_w = 1$ in each: 4) off Dirk Hartog Island (adjacent to Shark Bay) (~ 26°S), 5) offshore of Bremer Bay and 6) in the Savu Sea (Indonesian waters). There was also some foraging and feeding dives that occurred outside of these six areas, specifically while 233102 was migrating between the Ningaloo area and the Savu Sea, far off the continental shelf adjacent to the Kimberley region of Western Australia (10 – 17°S).

Median (range also reported) travel rate of foraging and lunge feeding dives were slowest in the Bremer (1.20 km/h, 0.30 – 1.93 km/h), Perth (1.51 km/h, 0.28 – 15.8 km/h), and Geraldton (1.90 km/h, 0.18 – 10.83 km/h) areas. Travel rates were highest in the Ningaloo (4.49 km/h, 0.64 – 9.62 km/h) and offshore Kimberley regions (3.92 km/h, 0.61 – 5.13 km/h), with the Savu Sea area being intermediate (2.80 km/h, 0.30 – 7.76 km/h) (Fig. 6a). Maximum dive depth of foraging and lunge feeding dives were deeper in the Perth (321 m, 31 – 540 m) and Geraldton (338 m, 64 – 483 m) regions, followed by Savu Sea (176 m, 42 – 259 m), with Ningaloo being the shallowest (99 m, 39 – 306 m) (Fig. 6b). These patterns were not due to the animals being bathymetrically constrained as shown in Fig. 6c. Whales in the Ningaloo and Perth areas foraged in the shallowest bathymetry at 731 m (89 – 1221 m) and 603 m (65 – 2975 m) respectively, while in the Savu Sea and far off the Kimberley coast, foraging occurred in water depths of 3197 m (957 – 3345 m) and 3871 m (2123 – 5739 m) respectively (Fig. 6c).

3.6. *Comparison of putative foraging with actual foraging (test of move persistence models)*

Three of the whales (233101, 233091 and 233095) had reasonable agreement between the occurrence of foraging and feeding dives and when move persistence (g) indicated putative foraging (g < 0.8) (Fig. 4, A2, A3, A4). However, for the remaining whales, foraging and lunge feeding occurred both when g > 0.8 and g < 0.8 (Fig. 4, A2, A5). When considering the statistical relationship between number of hours spent on foraging and feeding dives per day and the mean daily move persistence (Fig. 4), the model with move persistence was supported (AICc = 889) over the null (AICc = 901), however there was only a weak relationship (R2 = 11 %) (Fig. 5). Putative foraging occurred in the three main areas where actual foraging occurred, however areas 1 and 2 were linked by the putative foraging points of one whale (233095) (Fig. 3c). Putative foraging was not detected in the area offshore of Shark Bay where actual foraging occurred. While the putative foraging points matched the area where actual foraging occurred offshore between Exmouth and the Montebello Islands, many instances of actual foraging in between Exmouth and the Montebello Islands did not have matching putative foraging points. Similarly, very few putative foraging points were detected on migration between the Montebello

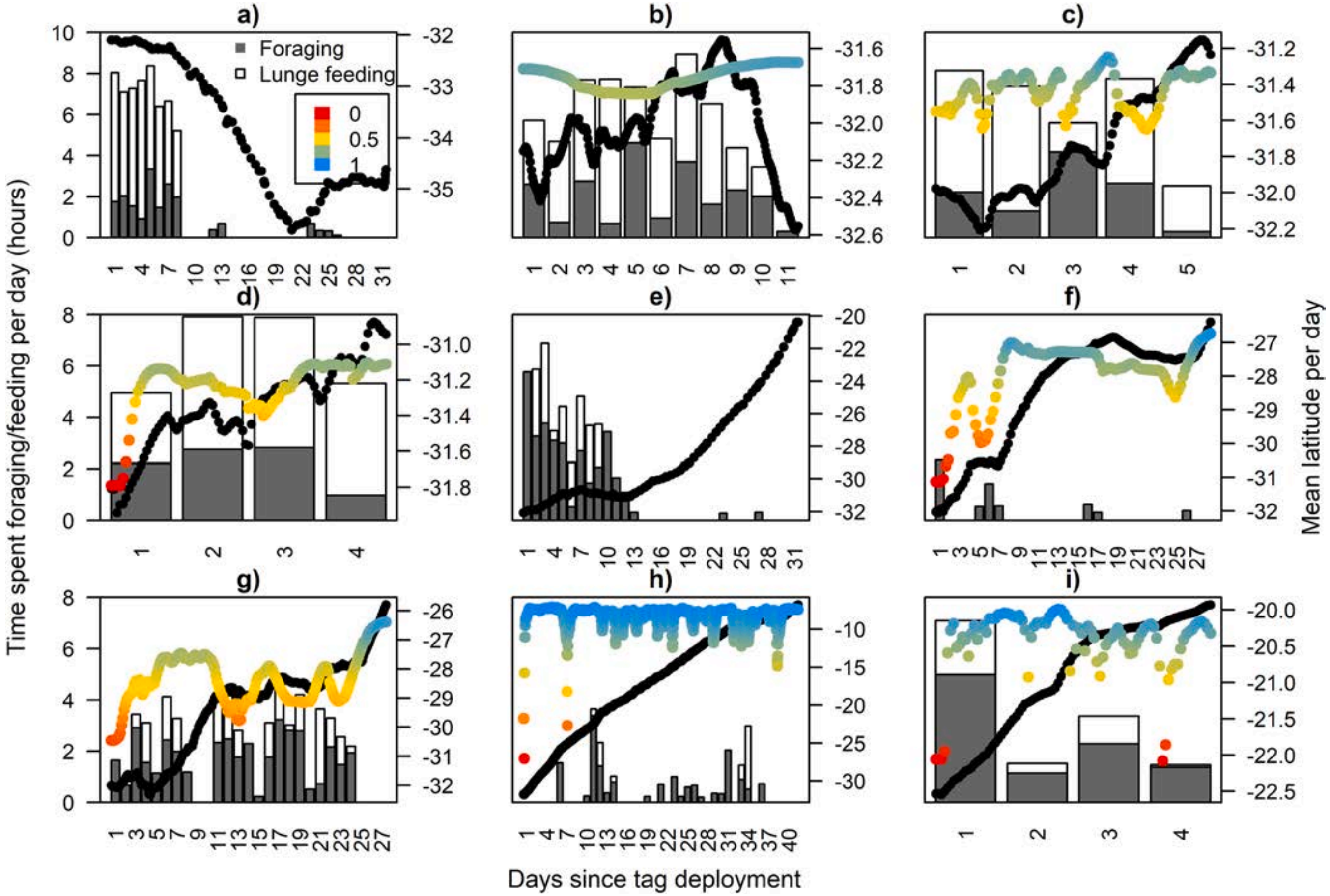


Fig. 4. Time spent on foraging and feeding dives per day for four whales based on the recovered tag data, for a) 214432, b) 233088, c) 214431, and d) 233101 and five whales based on the transmitted data for e) 214430, f) 233091, g) 233095, h) 233102, and i) 233096. Move persistence (g) is overlaid on the plots, colour coded from high (blue) to low (red) with 0.8 (green) as the threshold below which putative foraging is inferred. Also plotted is the mean latitude per day (24 h) in black. Move persistence is not shown for 214432 and 214430 as these whales were not double tagged and thus had no adequate location data to be modelled by the SSM.

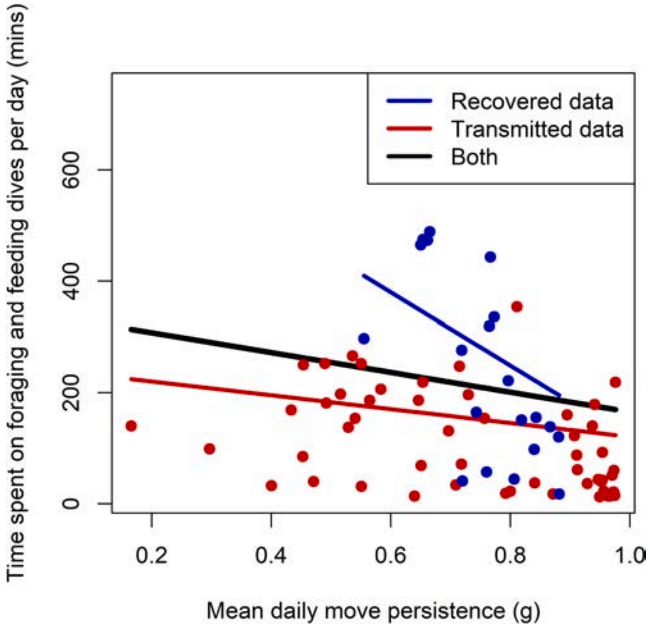


Fig. 5. Relationship between time spent foraging and feeding per day and move persistence (g). The fitted line is shown for each dataset (recovered in blue and transmitted, in red) separately and combined (black bold line).

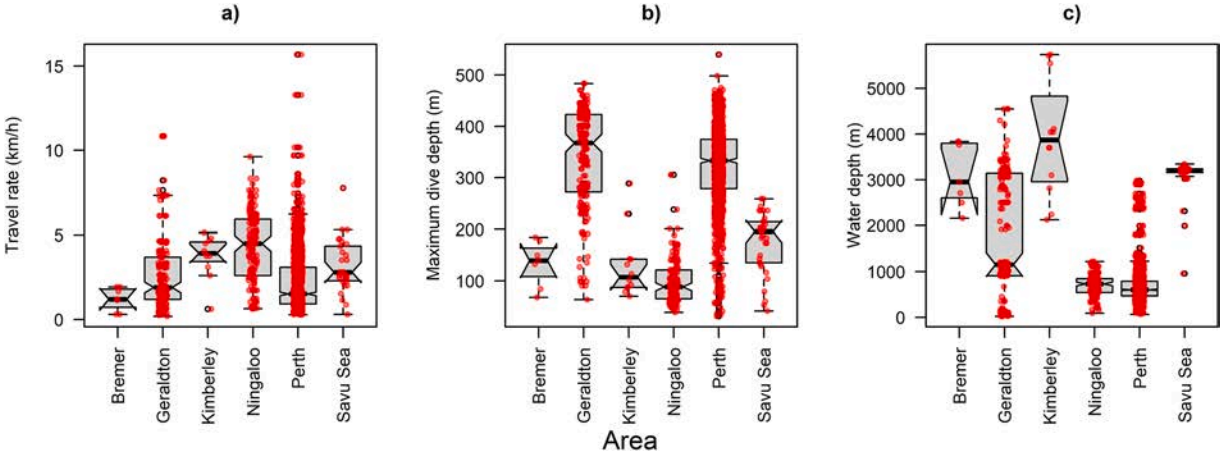


Fig. 6. Boxplots of foraging (type 5) and lunge feeding (type 6) dives combined per area, showing travel rate (a), maximum dive depth (b) and water depth (c). The notch in the box represents the 95 % confidence interval for the median. Where notches do not overlap, there is strong evidence that the medians differ. Note some notches went outside the end of the box due to small sample size (most notable for Bremer). Overlaid in red are the jittered points (each point is a dive) used to construct the boxplot in order to see the number and spread of points. Sample size: Bremer = 1, Geraldton = 1, Kimberley = 1, Ningaloo = 2, Perth = 6 and Savu Sea = 1.

Islands and Indonesia/Timor Leste compared to the actual foraging points (Fig. 3c).

A diel signal in foraging/lunge feeding and resting dives could be observed, especially earlier in the trip (Figures A4, A5 and A6) when the majority (8 out of 9) were in the Perth or the Geraldton area. At this time the lunge feeding and foraging dives occurred in the daytime only. This was also the case for foraging dives at Bremer. At Ningaloo, Kimberley and Savu Sea foraging dives occurred day and night, while lunge feeding was observed day and night at Ningaloo, only during the day in the Savu Sea, and not at all in the Kimberley (Fig. 7, A6).

4. Discussion

Combining dive data from the PSATs with satellite location data transmitted from LIMPETs simultaneously deployed on the same individuals, this study characterised and tracked the vertical movement behaviours of EIO pygmy blue whales along Western Australia,

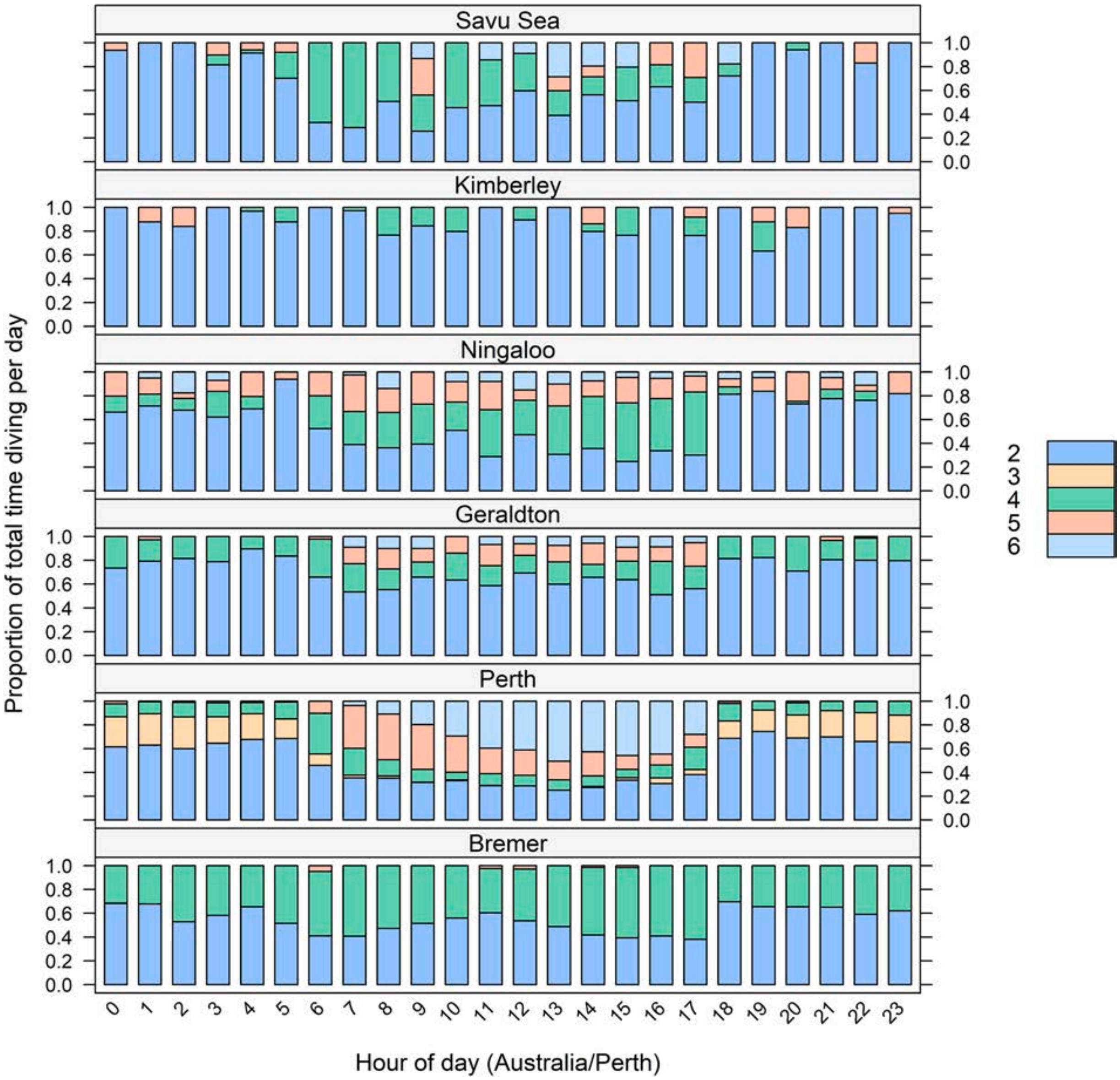


Fig. 7. Time spent diving per dive type (2 =travel, 3 =resting, 4 =exploratory, 5 =foraging and 6 =lunge feeding) per hour as a proportion of the total time spent diving per dive type per day for each of the main dive types for each broad region defined in Fig. 6. Whale sample size in each region noted in Fig. 6 caption.

Indonesia and Timor Leste, identified their foraging areas and compared inferred foraging behaviour from movement models. The results demonstrated that PSAT depth and accelerometry time-series data at low (75 s depth and ATS) and high (1 s depth and Mobility) resolution can reveal pygmy blue whale diving behaviour over temporal scales that encompass the migration. In the recovered tag dataset (1 s depth and Mobility), we used visual and statistical methods to classify pygmy blue whale diving behaviour indicative of resting, porpoising, lunge feeding, foraging, exploration, and travelling. It was only possible to distinguish the four latter dive types in the transmitted tag dataset (75 s depth and ATS), but with higher statistical misclassification rates for foraging and lunge feeding dives. This was especially the case when the ATS was unavailable, showing accelerometery data is key to separate these two dive types with acceptable error. Daily average move persistence decreased (low move persistence = putative foraging) as the daily average of time spent on foraging and feeding dives increased, but this relationship was only weak. Despite the weak relationship, when the data were aggregated, there was generally a good spatial match between the areas where foraging and feeding dives occurred and the areas where putative foraging occurred, except for foraging that occurred outside the known foraging areas during migration. The use of PSATs to transmit depth and accelerometry time-series negates the need for difficult and costly tag recoveries and has produced the longest of such time-series collected to date for blue whales. Our study provides an understanding of the strengths and limitations of defining areas of importance for marine vertebrates using the outputs of movement models and information needed for conservation management for this threatened sub-species.

This study is the first to record prey capture attempts (foraging lunges) for multiple animals of this sub-species across a cumulative 184 days of data, and with it we present the first calculation of foraging/feeding rate for this population, at a median of 4 hours per day (range: 0.1 – 12). Foraging/feeding occurred every 1–10 days and occurred outside of the main foraging area in Western Australia (Perth Canyon) during migration to Indonesia. These results support the use of a mixed breeding strategy (income and capital) like blue whales in the northeast Pacific (*Balaenoptera musculus musculus*) (Busquets-Vass et al., 2021). However a larger sample size is needed to compare rates of energy acquisition among the main foraging grounds like Perth Canyon and the other areas foraging occurred. It would appear that supplemental foraging during migration is important to this species and points to the importance of warm-water productive ecosystems for the health and recovery of this population. In support of recent evidence (Burton et al., 2023), we also show that foraging and feeding occurred in Indonesian/Timor Leste waters, an area thought to be associated mainly with breeding (and potentially foraging (Double et al., 2014, Kahn, 2007)). This highlights that if breeding is occurring there, it is not to the exclusion of foraging.

Location estimates are only able to be obtained when the whales are at the surface, whereas, the depth time series is obtained at 1 s or greater, as programmed by the user (with 75 s being the highest sample rate for transmission). Thus, our 3D representations of the pygmy blue whale movement paths relied on interpolations of latitude and longitude for each depth record in the dive datasets. These interactive (can zoom, etc) plots are extremely useful for visualising pygmy blue whale movement behaviour in 3D space. We note that the interpolation introduces some error in the fine scale spatial area at which the dives occur, however this research was not focussed at fine scales of movement behaviour and 3-axis accelerometers are required for such a study. However, as noted in the introduction, deployment of these type of devices is usually restricted to short time periods (a few days).

For most individuals, the timing on the scale of hours of putative foraging behaviour based on satellite location data were not strongly aligned with the timing of actual foraging/ feeding dives. The mismatch in the scales of sampling – kilometres and hours for the satellite location data, and metres and seconds for the dive data likely influenced this result. On a daily scale, a weak relationship existed between move persistence and time spent foraging. Potentially contributing to this weak result is that the transmitted data potentially missed some foraging/feeding dives, given not all the data were transmitted, with only one whale's tag transmitting the full archive and the others transmitting 39 – 82 % of the dive data on board. This is supported by the weaker relationship found for the transmitted data compared to the recovered dataset. However, the relationship fitted with the recovered dataset may also have some bias as most of the data is from the area between Perth Canyon and Cervantes, where whales are known to have high residency for feeding (Double et al., 2014, Thums et al., 2022). A previous study on high-resolution tag data from a pygmy blue whale also found a lack of correspondence between lunge feeding and area-restricted search (ARS) behaviour (defined using residence time). However, the authors concluded that foraging could have occurred without feeding lunges (Owen et al., 2016) and suggested that ARS could have been related to resting. We did find an association between the areas where resting dives occurred and lower move persistence for two pygmy blue whales who exhibited resting dives (233088 and 214431). It is also worth noting that a later analysis of the dataset of Owen et al. (2016) found less lunge feeding events, which may have impacted their analysis of the relationship between lunge feeding and ARS (Davenport et al., 2022). Some other studies on other species have found associations between foraging/feeding indices and ARS (Heerah et al., 2019; Thums et al., 2011; Iorio-Merlo et al., 2022), whereas others have not (Florko et al., 2023) or had mixed results (Thums et al., 2011).

Despite the weak temporal relationship, the main areas where foraging and lunge feeding dives occurred for all whales combined (Perth to Cervantes and Ningaloo to the Montebello Islands) had a good spatial overlap with areas inferred to be putative foraging grounds from a move persistence model. The differences were that the putative foraging points linked the Perth-Cervantes area with the foraging area off Geraldton. The absence of actual foraging dives between these areas may have been due to missing data from whale 233095 (55 % data recovery – Table 1). However, the move persistence model did not detect much of the actual foraging detected between Ningaloo and the Montebello Islands and while migrating between the Montebello islands and Indonesia/Timor Leste. There was generally higher alignment between foraging areas defined by actual and putative foraging points in southern Western Australia compared to northern Western Australia, which may be explained by the greater resolution of dive data (mostly 1 s sample rate in the south), increased sample size, and the more clustered location data indicative of a foraging aggregation area. In comparison, the lower sample size and sample rate of dive data in northern Western Australia may have impeded the alignment of foraging areas, which was likely exacerbated by a more opportunistic feeding strategy in this area, which is not as easily detected by a move persistence model. Therefore, for the purposes of allocating spatial areas of importance, areas of low move persistence can be a good predictor of foraging behaviour in pygmy blue whales when data from individual whales are aggregated, but are more likely to accurately predict foraging areas where sample size is adequate and foraging areas are known to be high use.

One of the whales (214432) travelled south instead of north, highlighting that not all EIO pygmy blue whales undertake the northward migration to Indonesian waters every year. This whale foraged at the shelf edge off Bremer Bay, an area where one whale tagged in South Australia also appeared to forage (Möller et al., 2020). Blue whales are known from this area with reports of predation on them by killer whales (Totterdell et al., 2022).

As found elsewhere for blue whales (e.g., Mate et al. (2017) in Californian waters), there was a diel pattern in the diving behaviour with foraging and lunge feeding dives occurring in the day and travel and resting dives predominantly at night. This pattern was not evident for whales at Ningaloo, with foraging and lunge feeding dives occurring day and night. Shallow foraging has previously been reported to occur predominantly at night for north Atlantic blue whales (Guilpin et al., 2019), humpback whales (Friedlaender et al., 2013), and minke whales (*Balaenoptera bonaerensis*) (Cade et al., 2023) following the diel vertical prey migration (Caruso et al., 2021). Surface feeding during daylight hours has also been reported for pygmy blue whales in the South Taranaki Bight, New Zealand (Torres et al., 2020) and Great Australian Bight Coastal Upwelling System (Gill, 2002). The foraging and feeding whales at Ningaloo (and

Kimberley) had much shallower maximum dive depths (median = 100 m), compared to Perth (320 m) and Geraldton (340 m). This suggests that the highest prey density at Ningaloo is nearer to the surface than the seafloor, similar to the South Taranaki Bight (Torres et al., 2020). This suggests that krill density in surface waters at Ningaloo is sufficiently high to support feeding there over diving to deeper waters and /or that deeper waters do not have higher krill density. Feeding at depth is thought to only be energetically efficient if krill density at depth is three times higher than in surface waters (Goldbogen et al., 2011). These results match visual observations of lunge feeding whales seen at the surface at Ningaloo (Thums et al., 2022), but surface feeding has not been reported at the Perth Canyon despite hundreds of hours of observations (Jenners pers comm.). A shallower dive depth combined with the faster travel rate and lack of a diel pattern suggest that foraging and feeding behaviour at Ningaloo is quite different from that in the other regions examined here, particularly at Perth and Geraldton, which are known high use foraging areas where pygmy blue whales exhibit high residency (Double et al., 2014, Möller et al., 2020, Thums et al., 2022). Pygmy blue whales at Ningaloo and further north, may forage opportunistically on ephemeral prey more than in the Perth and Geraldton regions, where prey may be more predictable and at higher densities (Rennie et al., 2009) enabling more intensive foraging behaviour. However, we still have a limited sample size for the Ningaloo area, to understand the diversity of diving behaviour in this region.

From transmitted PSAT data, the Random Forest model could only distinguish foraging from lunge feeding dives with the inclusion of ATS data. When ATS was unavailable, foraging was incorrectly classified as lunge feeding in 23 % of cases and vice versa in 31 % of cases. However, foraging behaviour in general (searching for food regardless of whether prey is detected and feeding lunges occur) was accurately predicted in the Random Forest model in 90 % of cases (10 % of foraging dives were classified as exploratory dives). Given that Mobility/ATS was key to distinguishing lunge feeding dives, our manual classification of lunge feeding dives in the transmitted dataset is likely an underestimate given it was not always available (see Supplementary material for more details).

Travel dives comprised most of the record for the transmitted tag data (~60 % in number and time spent), while the proportion of travel dives in the recovered dataset was lower (30 % in number and ~40 % of time spent). This may be due to resting dives (a similar dive profile, 20 – 40 % time) being classified in the recovered tag data, and when the time budget is combined with travelling dives, it constituted a similar proportion to travelling dives only in the transmitted dataset. Although the time-depth profiles of the travel and resting dives appear similar (Fig. 1), the time-Mobility profile was different, usually with very low Mobility on resting dives. This was the main distinguishing feature between the two dives, but travel dives sometimes also had low Mobility and resting dives were often (but not always) shallower (11 ± 2 m) than travel dives (15 ± 5 m). The shallow depth we report for resting dives is just below the predicted depth of 12 m that pygmy blue whales could avoid wave drag while swimming (Owen et al., 2016). Resting dives have been reported in pygmy blue whales before (Davenport et al., 2022) (albeit classified using fluking rates), and in fin whales (*Balaenoptera physalus)* (Fonseca et al., 2022). It seems, 1 s depth time series data is necessary for distinguishing between low-activity behaviours such as travelling, resting, and potentially others such as nursing.

Many of the PSATs detached earlier than expected. We found no evidence of tag malfunction nor predation attempts on the recovered tags (i.e. teeth marks). It is possible that it was caused by whales rubbing against each other during courtship behaviours or aggression between conspecifics (see Supplementary material for more details). Alternatively, the whale skin condition may contribute to attachment duration, whereby heavily scarred individuals are more likely to have tags implanted in dense scar tissue and assisting tag retention.

5. Conclusions

This study has tracked the diving behaviour of the elusive and threatened EIO pygmy blue whale by combined GPS tag and dive logger deployments, characterising diving behaviour (aim 1) to determine where and when pygmy blue whales forage (aim 3), determining the type and resolution of depth and accelerometry data needed to characterise pygmy blue whale diving behaviour, especially foraging and feeding (aim 2) and compared timing and areas of putative foraging inferred from movement models to foraging timing and areas defined by areas where foraging and lunge feeding dives occurred (aim 4).

Accelerometry data was key to distinguish between foraging and lunge feeding although foraging behaviour in general (foraging and lunge feeding dives combined) could be classified with acceptable error using transmitted (75 s) data. A depth time series with 1 s resolution appears to be necessary for distinguishing between low-activity behaviours such as travelling and resting.

Intermittent feeding combined with the regular foraging observed during migration provides evidence that this sub-species exhibits some traits of the income breeding strategy, potentially indicating that their breeding strategy is placed somewhat central on the capital-income breeding spectrum.

On temporal scales of hours or a day, putative foraging behaviour based on satellite location data were not strongly aligned with the actual foraging/ feeding dives due to the mismatch in the scales of sampling, but spatially, when all whales were combined, the match between core areas of use based on putative foraging and actual foraging/ feeding dives was good, especially for areas of high use and where sample size is not limited (e.g. Perth Canyon to Cervantes).

Importantly, the inference of behaviour from movement models on satellite tracking data cannot conclusively infer foraging, as low move persistence can also be a result of resting or breeding behaviours. However, the diving profiles provide more conclusive evidence of a particular behaviour type and the important characteristics that go along with it (e.g., dive depth), that are useful for understanding overlap between pygmy blue whales and threats below the surface (e.g., noise disturbance).

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e03362.

Data availability

Data will be made available on request.

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