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# Pygmy blue whale movement, distribution and important areas in the Eastern Indian Ocean

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ABSTRACT

Pygmy blue whales in the South-east Indian Ocean migrate from the southern coast of Australia to Indonesia, with a significant part of their migration route passing through areas subject to oil and gas production. This study aimed at improving our understanding of the spatial extent of the distribution, migration and foraging areas, to better inform impact assessment of anthropogenic activities in these regions. Using a combination of passive acoustic monitoring of the NW Australian coast (46 instruments from 2006 to 2019) and satellite telemetry data (22 tag deployments from 2009 to 2021) we quantified the pygmy blue whale distribution and important areas during their northern and southern migration. We show extensive use of slope habitat off Western Australia and only minimal use of shelf habitat, compared to southern Australia where use of the continental shelf and shelf break predominates. In addition, movement behaviour estimated by a state-space model on satellite tag data showed that in general pygmy blue whales off Western Australia were mostly engaged in migration, interspersed with relatively short periods (median = 28 h, range = 2 – 1080 h) of low move persistence (slow movement with high turning angles), which is indicative of foraging. Using the spatial overlap of time and number of whales in area analysis of the satellite tracking data (top 50% of grid cells) with foraging movement behaviour, we quantified the spatial extent of pygmy blue whale high use areas for foraging and migration. We compared these areas to the previously described areas of importance to foraging and migrating whales (Biologically Important Areas; BIAs). In some cases these had good agreement with the most important areas we calculated from our data, but others had only low (5%) to moderate (15%) overlap. Month was the most important variable predicting the number of pygmy blue whale units and number of singers (acting as indices of pygmy blue whale density). Whale density was highest in the southern part of the NW Australian coast and whales

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were present there between April-June, and November-December, a pattern also confirmed by the satellite tracking data. Available data indicated pygmy blue whales spent up to 124 days in Indonesian waters (34% of annual cycle). Since this area may also be the calving ground for this population, inter-jurisdictional management is necessary to ensure their full protection.

## 1. Introduction

Many populations of great whales were decimated during the industrial whaling era, with most populations still recovering (Rocha et al., 2015). Due to this, many are classified as threatened or endangered and there are ongoing human pressures that may be impeding their recovery (Bowler et al., 2020; Maxwell et al., 2013) such as anthropogenic noise and vessel disturbance and collisions. For example, expansion of industrial development and shipping traffic elevates ambient noise (from oil and gas drilling, pile driving, vessel movement and seismic air guns) (Cato et al., 2013; Wilcock et al., 2014) and raises ship strike occurrence/risk (Pirotta et al., 2018; Van Waerebeek et al., 2007). For many whale species, we lack quantitative data on movement, distribution and important areas across their ranges, which are required for effective environmental impact assessment. This is largely due to the difficulty of obtaining spatial data on these species, given they are difficult to satellite tag, often occur at low density, range over vast areas far from shore, and are rarely visible from the surface.

The pygmy blue whale (*Balaenoptera musculus brevicauda*) is one of two recognised blue whale subspecies in the Southern Hemisphere. It is listed on the International Union for Conservation of Nature (IUCN) as Not Evaluated (Data Deficient), and under the Australian Environment Protection and Biodiversity Conservation (EPBC) Act as Endangered. The south-east Indian Ocean or Eastern Indian Ocean stock of pygmy blue (henceforth simply referred to 'pygmy blue whale') whales aggregates in the Austral summer to feed at several known locations on or adjacent the Australian continental shelf including: (1) the Perth Canyon and adjacent waters off Western Australia (Rennie et al., 2009); (2) the Great Southern Australian Coastal Upwelling System (Möller et al., 2020), which includes the Bonney Upwelling and other smaller upwelling centres off South Australia, Victoria and Tasmania (Gill, 2002; McCauley et al., 2018; Möller et al., 2020) and (3) further south along the sub-tropical convergence zone (Garcia-Rojas et al., 2018) from as far west as 74° E (Samaran et al., 2013) and east to Bass Strait (between the Australian states of Victoria and Tasmania) (Balcazar et al.,

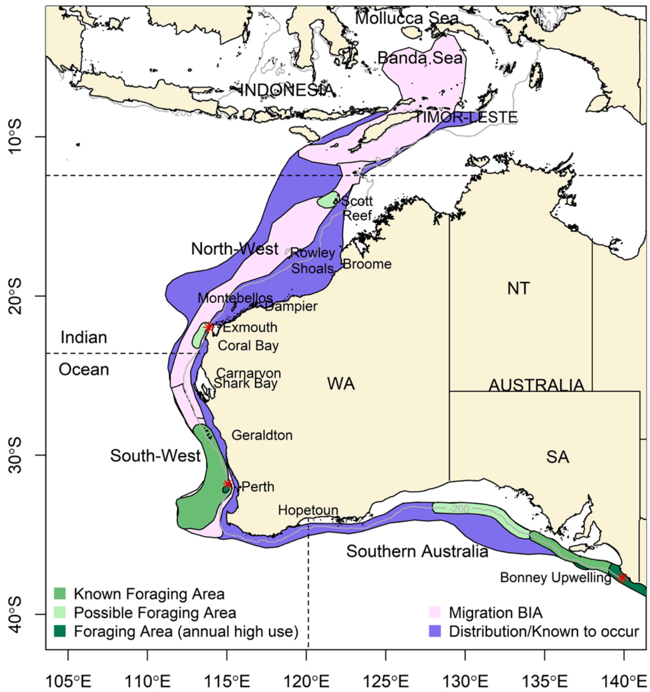


**Fig. 1.** Map showing the Biologically Important Areas (BIA) and satellite tagging locations of the pygmy blue whales used in the study marked with red asterisks: North West Cape off Exmouth (n = 6), Perth Canyon (n = 15) and Bonney Upwelling (n = 1). Also shown are the main regions referred to in text including the North-West Western Australia (WA), South-West WA and Southern Australia. Polygons of the distribution/known to occur area and BIAs identified in the Recovery Plan for the Blue Whale, downloaded from the National Conservation Values Atlas (NCV Atlas) are also overlaid. Note that the Migration BIA is not identified in the Recovery Plan but is identified in the NCV Atlas. Also shown are the other states of Australia including South Australia (SA) and the Northern Territory (NT). The approximate position of the continental shelf is shown by the 200 m contour in grey. Note that the pygmy blue whale distribution is considered to be much larger than depicted here (See Leroy et al., 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2015; McCauley et al., 2018). The stock transits from as far north as the equator (Double et al., 2014) and south to at least 55° S (McCauley et al., 2018). Acoustic and genetic evidence suggests that blue whales feeding at these three sites are part of the same population (Attard et al., 2010; McCauley et al., 2018). A methodology for estimating abundance from acoustic data is currently being refined, following recommendations by the IWC Abundance Steering Group. Mark-recapture analyses based on photo-identification estimated 569–1147 individuals in the Perth Canyon feeding area between 2000 and 2005 (Jenner et al., 2008). This estimate did not account for animals travelling further west into the Indian Ocean (McCauley et al., 2018) and further south into the Southern Ocean.

Visual surveys of whales are logistically challenging and expensive. In some cases, they may not provide adequate sightings for robust statistical analysis, hence efforts to use and combine other techniques for pygmy blue whales. In addition, sub-species identification and population assignment can be difficult without genetic and/or acoustic data. Many populations produce unique and acoustically distinct songs that can often be detected over greater distances than visual detections. Therefore, data from passive acoustic monitoring are now being used for cetacean density and distribution models (Carlén et al., 2018; Marques et al., 2013).

In addition, satellite telemetry, though a challenging technique for cetaceans, can provide otherwise unobtainable data on movement and habitat use when successful. For example, telemetry data from five satellite tags deployed on pygmy blue whales at their southern feeding grounds off southern Western Australia were of durations long enough to reveal that the pygmy blue whales migrate north to winter in Indonesian waters, predominantly to the Banda and Molucca seas (Double et al., 2014; Möller et al., 2020). These seas are considered the northern terminus of the migration and potentially the breeding and calving ground, but may also act as a feeding area (Double et al., 2014; Kahn, 2007). The tagged pygmy blue whales also showed area-restricted search (ARS) behaviour (putative foraging) along the migratory route, e.g. off North West (NW) Cape midway along the Western Australian coast (Double et al., 2014; Möller et al., 2020). This migratory path interspersed with feeding stop-overs may conflict with coastal and offshore activities for hydrocarbon and mineral resource exploitation (e.g. iron ore shipping) off the north-west coast of Australia and in Indonesia. Impact assessment and mitigation of these activities and other pressures in the region are difficult with only a small number of the deployed satellite tags providing information regarding pygmy blue whale use of this area. In addition, passive acoustic monitoring (PAM) has also been used to understand pygmy blue whale use of this area, however much of the PAM data has been collected on behalf of industry for specific projects and has not been published.

The blue whale's conservation listing in Australia makes it subject to a National Recovery Plan under the EPBC Act (Commonwealth of Australia, 2015) and spatial areas of importance to pygmy blue whales have been identified therein, known as Biologically Important Areas (BIA) (https://environment.gov.au/marine/marine-species/bias) (Fig. 1). BIAs are areas where biologically important behaviour occurs such as calving, foraging, resting or migration (Commonwealth of Australia, 2015). The BIAs were defined largely by using the limited empirical data, scientific literature, and personal field experience of experts. The BIA approach is similar in concept to the Ecologically or Biologically Significant Areas (EBSA) approach to identify areas in need of protection and defined by the Convention on Biological Diversity (see Corrigan et al., 2014; Dunn et al., 2014).

**Table 1**
Summary of each pygmy blue whale tag deployment including deployment location name (Perth Canyon, Bonney Upwelling and North West Cape (NWC)) and coordinates. Also shown is date deployed, duration of tag deployment in days (d), median, minimum (min) and maximum (max) rate of movement (speed, in km $hr^{-1}$). Tag type is indicated after ID, with S = SPOT, L = LIMPET and P = PAT.

| ID number | Long (°E) | Lat (°S) | Location | Date | Duration (d) | Median Speed | Min Speed | Max Speed |
|---|---|---|---|---|---|---|---|---|
| 88740 (S) | 114.96 | 31.95 | Perth | 5/04/2009 | 27.5 | 2.4 | 0.1 | 8.2 |
| 88731 (S) | 114.56 | 31.87 | Perth | 8/04/2009 | 7.5 | 2.1 | 0.3 | 7.9 |
| 88739 (S) | 113.77 | 32.17 | Perth | 8/04/2009 | 132.2 | 1.4 | < 0.1 | 9.2 |
| 98115 (S) | 115.10 | 32.02 | Perth | 14/03/2011 | 57.5 | 0.8 | 0.1 | 2.3 |
| 98134 (S) | 114.53 | 31.97 | Perth | 17/03/2011 | 20.0 | 3.1 | 0.1 | 6.2 |
| 53734 (S) | 115.05 | 31.97 | Perth | 18/03/2011 | 31.5 | 1.9 | 0.1 | 5.7 |
| 53791 (S) | 115.06 | 32.01 | Perth | 30/03/2011 | 28.5 | 4 | 0.6 | 6.2 |
| 98108 (S) | 115.04 | 32.02 | Perth | 30/03/2011 | 48.0 | 3.5 | 0.2 | 6.1 |
| 98135 (S) | 114.88 | 31.73 | Perth | 6/04/2011 | 141.0 | 2.2 | < 0.1 | 11.3 |
| 123229 (S) | 139.89 | 37.71 | Bonney | 13/03/2015 | 271.0 | 3.5 | 0.1 | 15.4 |
| Summary | | | | | 76.47 ± 82.3 | 2.3 | < 0.1 | 15.4 |
| 182671 (L) | 113.76 | 21.75 | NWC | 26/06/2019 | 16.8 | 2.8 | 0.4 | 13.5 |
| 182658 (L) | 113.86 | 21.96 | NWC | 29/05/2020 | 82.5 | 2.3 | < 0.1 | 13.9 |
| 182665 (L) | 113.66 | 22.03 | NWC | 2/06/2020 | 14.0 | 4.2 | 0.4 | 8.6 |
| 182657 (L) | 113.77 | 21.76 | NWC | 3/06/2020 | 121.9 | 1.8 | 0.1 | 8.7 |
| 182668 (L) | 113.73 | 21.75 | NWC | 3/06/2020 | 77.8 | 2.8 | 0.1 | 11.5 |
| 182667 (L) | 113.74 | 21.69 | NWC | 4/06/2020 | 28.2 | 2.4 | 0.1 | 13.8 |
| Summary | | | | | 56.9 ± 43.8 | 2.6 | < 0.1 | 13.9 |
| 182660 (L) | 115.15 | 32.06 | Perth | 24/04/2021 | 95 | 2.7 | 0.1 | 11.0 |
| 182669 (L) | 115.15 | 31.97 | Perth | 28/04/2021 | 26 | 2.8 | 0.1 | 9.4 |
| 212705 (L) | 115.16 | 32.06 | Perth | 25/04/2021 | 12 | 2.1 | 0.2 | 8.4 |
| 212712 (L) | 115.17 | 32.04 | Perth | 27/04/2021 | 8 | 2.2 | 0.1 | 8.8 |
| 214430 (P) | 115.15 | 32.04 | Perth | 27/04/2021 | 30 | 2.4 | 0.5 | 9.1 |
| 214432 (P) | 115.15 | 32.05 | Perth | 27/04/2021 | 30 | 1.5 | 0.3 | 11.8 |
| Summary | | | | | 33.3 ± 31.7 | 2.3 | 0.1 | 11.8 |
| Summary all | | | | | 55.5 ± 50.5 | 2.4 | < 0.1 | 15.4 |

The polygons for the BIAs are provided in the Australian National Conservation Values Atlas (NCV Atlas) (Fig. 1). The NCV Atlas is a dynamic tool that allows for up-to-date information to be stored, building on information in the Recovery Plan in an iterative process. These include the Known Foraging Areas for pygmy blue whales mentioned above - the Perth Canyon and adjacent waters off the Western Australian coast and the Bonney Upwelling and other upwelling systems off the southern Australian coast. Off the NW coast of Australia, two other areas are identified BIAs; an area off Ningaloo Reef (a fringing reef along NW Cape) near Exmouth and around the Scott and Seringapatam reefs (a group of atoll-like reefs in the Timor Sea on the edge of Australian continental shelf). These BIAs are identified as "Known Foraging areas' in the NCV Atlas and 'Possible Foraging Areas' in the Recovery Plan. The 'possible' tag exists as the identification of these areas is based on limited data and using qualitative means as mentioned above. In addition, although the available data suggest pygmy blue whales largely use habitat off the shelf in north-western Australia (Branch et al., 2007; Double et al., 2014; Garcia-Rojas et al., 2018; Gavrilov et al., 2018; Möller et al., 2020), the Recovery Plan and NCV Atlas identifies blue whale distribution/area they are known to occur, across the entire continental shelf. Ideally, clarification regarding distribution, habitat use and the appropriateness of the existing BIA extents should be addressed to be able to assess any overlap with anthropogenic activities and improve the prospects of effective management of potential threats to this population.

Here, we made use of pre-existing satellite tag and PAM data sets, and combined them with targeted deployments of satellite tags and noise loggers off Western Australia. We used these data sets to model and map the spatial distribution of pygmy blue whales and define areas of importance for them off Western Australia, with a focus on the NW coast of Australia and Indonesia where data are limited and many anthropogenic threats occur.

## 2. Methods

### 2.1. Satellite telemetry

#### 2.1.1. Data collection

Pygmy blue whale satellite tracks that provided data off Western Australia were compiled from previous tagging studies during the northward migration (Table 1). These included 11 whales tagged at Perth Canyon in March-April 2009 and 2010 (3 males, 3 females and 5 unknown) (Double et al., 2014) and one tagged in the Bonney Upwelling region of South Australia in March 2015 (Möller et al., 2020) (Table 1). Although 13 tags were deployed on pygmy blue whales in the latter study, only one deployment (female) included telemetry data for the focal area. The whales from both studies were tagged with implantable satellite-linked transmitters (Wildlife Computers SPOT; Type C invasive tags; Andrews et al., 2019) that provided Argos satellite location data. The satellite tags from Double et al. (2014) were programmed with a duty cycle of 6 h on, 18 h off with a 30 s repetition rate (the time between two consecutive message transmissions). The data from the single satellite tag used from Möller et al. (2020) had a 45 sec repetition rate (not duty cycled). Further details can be found in Double et al. (2014) and Möller et al. (2020).

As part of this study, Wildlife Computers (WC; Redmond, WA, USA) LIMPETs (Low Impact Minimally Percutaneous Electronic Transmitters, Type A invasive tags (Andrews et al., 2019) (type: SPLASH10-F-333) were deployed on six pygmy blue whales at NW Cape and four pygmy blue whales at Perth Canyon between 2019 and 2021 (Table 1). The LIMPET tags incorporated four sterilised titanium dart anchors 6 mm diameter × 60 mm long with six petals on each dart to assist in retention of the tag to the whale. The repetition interval of LIMPETs deployed in 2019–2020 was 45 s whereas it was 15 s for those deployed in 2021. All were programmed to collect GPS positions every hour. In addition, two WC pop-off archival tags; (miniPAT) were attached to two pygmy blue whales at Perth Canyon, in 2021. The miniPAT tags were connected with a tether (~10 cm long) to a titanium dart.

For the deployments done as part of this study, the RV *Whale Song* (28 m length) was used as a mothership to coordinate tagging operations in open water west of Ningaloo Reef (approx. 22° S), and in the Perth Canyon (approx 32° S) Western Australia. At NW Cape, whales were located using three methods: (1) acoustically triangulating vocalisations radioed to RV *Whale Song* by sonobuoys and purpose designed software; (2) zigzag surveys from the edge of the reef out to around the shelf edge from approximately Coral Bay to NW Cape; and (3) visual detection by observers on the ship. At Perth Canyon, whales were located predominantly using method 3 combined with method 1 on occasion. Once a whale was located, the tagging team was deployed in a 7 m rigid-hull inflatable boat (RHIB) and the team were directed towards whales either by the acoustician or observers on-board RV *Whale Song*, by the pilot in the light aircraft or a combination of both for deployments at NW Cape.

The LIMPETs were deployed using a Dan-Inject $CO_2$ rifle from the RHIB at a range of ~8 m, aiming for a position high on the body, when the whale was at peak emergence from the water during surfacing and perpendicular to the RHIB. The tags were activated automatically by a saltwater switch after deployment on the whales. The darts of the tethered miniPATs were embedded in the side of the whales using a pole, also from the RHIB at ~8 m.

#### 2.1.2. Whale movement model and metrics

A state-space model (SSM) (Jonsen et al., 2005, 2003) was applied to the raw Argos and Fastloc GPS location data from the LIMPETs using the R (R Core Team, 2020) package *foieGras* (Jonsen et al., 2020) to account for location error and provide an objective behavioural index (g) along the track. The index 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). Although resting has not been observed in Western Australia (author observations), it may occur at the northern terminus of the migration in Indonesian waters.

The model was fitted to combined data from multiple individuals with a similar number of average location estimates per day. They were analysed together so that the time step we specified (time step to which locations are predicted) could align with the average number of locations received per day. This included all locations received from all location classes of Argos (3, 2, 1, 0, A & B with estimated error of <250 m, 250–500 m, 500–1500 m, >1500 m and unknown respectively) and Fastloc GPS. Tracks with large gaps (> 7 days) were split and each portion of data analysed separately. For the LIMPET deployments, the model included error ellipse information provided by CLS (Collective Localisation Satellites) to represent the precision of each location including the error semi minor (least error) and major axis (largest error) and the error ellipse orientation. These metrics were not provided by CLS in the earlier deployments. All models were checked for convergence.

Move persistence was summarised into a binary measure, based on the mean move persistence (g) of 0.8 (median = 0.82). This was similar to previous blue whale studies inferring movement behaviour from a SSM, where the continuous value (similar to g) ranged from 1 to 2 and values > 1.75 were considered area-restricted search (Bailey et al., 2009). In our analysis, 54% of SSM position estimates had move persistence $\geq$ 0.8 (Fig. S7). Thus, we designated points along the track with g< 0.8 as foraging/resting/breeding and g $\geq$ 0.8 as migration.

The miniPATs recorded depth ( ± 0.5 m), light (for geolocation), temperature and acceleration along the x, y and z axes at 8 Hz (Skubel et al., 2020). Only the light data were used here, with the remaining data streams for a subsequent analysis. The tags were programmed to detach from the whales after 30 days (the maximum deployment length at the specified sampling frequency of 75 s), and at that point they floated to the surface and transmitted their data through the Argos satellite network. The GPE3 state-space modelling tool in the WC Portal was used to estimate the movement paths of the two whales. The GPE3 tool is based on the geolocation method (see DeLong et al., 1992) which uses the transmitted light data to calculate sunrise and sunset times to provide information on time of midday and day length and combines it with sea surface temperature, dive depth and a movement model to estimate the most likely positions of the whales (see Beck et al., 2002). These are usually less precise than satellite-based estimates and usually only two location estimates can be calculated per day. Mean error calculated for geolocation from double tagging experiments on sharks and sea lions was 0.5 – 1° of longitude (Winship et al., 2012). We were not able to calculate move persistence as for the LIMPET data for these tracks.

We calculated the mean rate of movement (km $hr^{-1}$) for each whale. We present all values as mean ± standard deviation (SD) unless indicated otherwise.

#### 2.1.3. Quantification of spatial distribution and important areas

For this analysis, the data from the majority of the southern coast of Australia for the single Bonney Upwelling deployment was excluded as it had no spatial overlap with the rest of the dataset. Thus, analyses of pygmy blue whale distributions were made from Hopetoun, in southern Western Australia, and north along the west coast up to Indonesia.

To identify spatial distribution and areas of highest use, we overlaid the study area with a 20 × 20 km square grid and calculated the time spent in each grid cell using all the satellite tracks combined from all whales using the R package *trip* (Sumner et al., 2020, 2009) and hereafter referred to as occupancy. To define high use areas indicative of foraging, we ranked all the cells from highest to lowest occupancy. The core foraging area was then defined as the cells encompassing the top 50% of the cumulative frequency distribution based on the method described by Soanes et al. (2013) and after Ford (1979). This is similar in concept to the 50% utilisation distribution (UD); i.e. the minimum area in which the animal has 50% probability of being found (Worton, 1989). We show all commonly represented UDs (25%, 50%, 75% and 100%) for comparison.

As the occupancy distribution is an index of time spent in a grid cell and less time is usually spent when migrating due to relatively fast and directed movement at this time, we also calculated a second metric to determine areas of importance (particularly during migration) by summing the number of whales in each grid cell and then dividing by the total number of whales in the study (and multiplying by 100) to provide the percentage of tagged whales that used each grid cell.

To identify the most important areas of use for foraging/breeding/resting, we overlaid the 50% UDs calculated using gridded time spent (occupancy) and percentage of whales that used a cell, with grid cells where the average (across all whales) move persistence (g) was < 0.8. Grid cells with overlap between all three measures, that is, grid cells with the greatest time spent and largest percentage of whales with lowest move persistence (g), were designated as the most important areas for foraging (and/or resting/breeding). Similarly, to identify the most important areas for migration, we overlaid the 50% UD calculated using percentage of whales in a grid cell with grid cells with high move persistence (g) $\geq$ 0.8. Grid cells with overlap between these two measures were considered the most important areas for migration. Note that the data from the two miniPATs were used to calculate the 50% UDs but we could not calculate move persistence for these datasets as noted above.

To establish whether pygmy blue whale BIAs align with these areas important for foraging (and/or resting/breeding) and migrating, we plotted and calculated the spatial overlap between these areas and each of the BIAs as depicted in the NCV Atlas (National Conservation Values Atlas - Home Page (environment.gov.au)). We also overlaid the 2 min ETOPOv2 bathymetry from the National Geophysical Data Centre of NOAA (National Geophysical Data Center, 2006) and the Australian Marine Park boundaries.

#### 2.1.4. Habitat use

To identify prevailing habitat use of pygmy blue whales, we overlaid the SSM estimated positions onto the GIS dataset for the maximum extent of geomorphic provinces and features for Australia's Exclusive Economic Zone (EEZ) (Heap and Harris, 2008) using the function *over* in the R package *sp* (Bivand et al., 2013; Pebesma and Bivand, 2013). The geomorphic provinces are the four broad divisions of Shelf, Slope, Rise and Abyssal plain/deep ocean floor and the geomorphic features are subsidiary elements superimposed on the provinces (e.g. Canyon, Plateau, Terrace, Ridge, Seamount, etc) (Heap and Harris, 2008). To determine the importance of the continental shelf, we calculated the mean proportion of points per whale falling within each of the four geomorphic provinces that comprise the Australian EEZ. We used the point data rather than the UDs as calculated above, as the relatively large grid cell size used may overlap with more than one province or feature. We also examined the most prevalent geomorphic features within these provinces.

We separated the dataset into three regions: Indonesia, all points north of 12.4°S (the northern extent of Australia's EEZ); north-west Western Australia, between 12.4°S and the southern extent of Ningaloo Reef (23.6°); south-west Western Australia, between the southern extent of Ningaloo Reef and Cape Naturaliste (32°S), and southern Australia, from Cape Naturaliste and along the coast; less than 32° S and greater than 116° E (Fig. 1).

#### 2.1.5. Temporal components of movement

We used the tracking data to calculate the mean time spent in each of the regions and the mean minimum and maximum Julian day, to understand the temporal components of the migration (northern and southern). Mean min and max Julian day were then converted to their corresponding date. There were only two pygmy blue whales that provided data on the southern migration; #123229 (tagged in Bonney Upwelling) and #182657 (tagged at NW Cape). The former whale had a gap in the data record on the southern migration between the Banda Sea and the NW coast of Western Australia (Fig. S4), thus there was no need to impose a transition between northern and southern migration for this whale. To determine when the southern migration started for the latter whale, we selected the date where there was a consistent movement to the south combined with movement behaviour consistent with migration ($g \geq 0.8$).

### 2.2. Passive acoustic data

Analysis of passive acoustic data are outlined in detail in the Supplementary Methods and briefly described here. Passive acoustic data comprised recordings from the north-west of Western Australia between 2006 and 2020 including: (a) moorings (18 deployed instruments); (b) ocean glider missions (three); and (c) ocean bottom seismometers (14 set in a line to the north-west of NW Cape, eight in a line to the north-west from on-shelf west of Broome). Moorings provided up to a five-year time series from several locations.

Mooring data and instruments were as described in McCauley et al. (2017), comprising a seabed mounted CMST-DSTO instrument decoupled from the mooring and thus from mooring noise artefacts. Sample regimes used were 200 or 300 s every 15 min sampled at 6 kHz, with the shorter sample times for the earlier deployments.

To fill spatial gaps in the moorings data, ocean gliders fitted with noise loggers were used as an alternative to expensive manned vessel surveys. Instrumented gliders can be a cost effective method of detecting whale vocalisations (e.g. Baumgartner and Fratantoni, 2008). Glider missions (2019) involved Teledyne Webb Research Slocum gliders that perform repeat, sawtooth-like dives up to 200 m depth over transects of hundreds of kilometres (Pattiaratchi et al., 2017). The gliders were externally fitted with forward and aft facing SoundTraps ST300 instrument (OceanInstruments NZ) attached on the top side (Fig. S1), which were set to sample eight minutes of every 15 min at 48 kHz.

The seismometers were Gürlap instruments from the ANSIR Research Facility for Earth Sounding used in studies of natural seismic events with only the pressure channel used here. The line of seismometers which ran north west of NW Cape provided data for two weeks in December 2014 (although two ran for almost eight weeks) sampling continuously with one hour samples (the instruments write data in one hour blocks) at 250 Hz (as reported by Gavrilov et al., 2018). The line of seismometers which ran in a north westerly direction from west of Broome into the deeper Indian Ocean provided data for 240 days (seven OBS) and 276 days (one OBS) over September 2017 to June 2018, all with one hour samples at 100 Hz.

The pygmy blue whale produces three predominant song types with variants of these (Jolliffe et al., 2019). One song unit (unit-II) is common to all three song types and variants and was the focus of this study. Unit-II was first located using a search algorithm that searched for the 18–25 Hz (fundamental frequency) or 60–70 Hz (harmonic frequency) sweep, as described in Gavrilov and McCauley (2013) with extra noise rejection features added. For the 100 Hz sample rate of the CANPASS data set the detection algorithm only searched for the 18–25 Hz sweep. The detection algorithm as used in Gavrilov and McCauley (2013) had miss-detection and false-detection rates of less than 5%. Manual checking was used to verify the detection algorithm outputs. This process involved: (1) displaying spectrograms in 300–400 s lengths (< 0.5 Hz frequency resolution used) and overlaying detector time stamps for each unit-II component detected; (2) checking the search algorithm unit-II detection time stamps and removing or adding time stamps within samples (mooring and glider data) or sub-sections of samples (seismometers) as appropriate (refer Supplementary Methods for details); and (3) once all search algorithm samples had been checked, we bracketed samples with verified detections by three samples, checked these, added a time stamp for missed units as appropriate and reiterated this until no new detections were found in adjacent samples. Various permutations of the manual checking process were used, with this documented in Supplementary Methods. Once unit times had been identified, the received root mean squared pressure (rms) unit level (dB re 1μPa rms) was calculated from the calibrated waveform. Calculating levels was difficult in certain circumstances due to overlapping natural or man-made noise sources or during periods of high numbers of singing pygmy blue whales when multiple units would overlap.

The inter-song time spacing or increment (ISI), i.e., the space between consecutive units, for unit-II differs between the three song types so the number of unit-II signals per unit time varies depending on the prevalence of song types, which may change due to singer density effects (Jolliffe et al., 2019). The ISI was checked using the 'feature space' method described in the Supplementary Methods of Jolliffe et al. (2019). Once an ISI was established the number of 'instantaneously number of singers' was established by splitting a sample, or 15 min section for the seismometer data, into overlapping windows (0.9 overlap used) of length just less than the two most common song types present. The maximum number of unit-II signals within a *window* was used as the number of individual whales singing in that sample. A checked dataset then comprised a series of 15 min samples, each with a measure of the 'instantaneous' number of individual singing pygmy blue whales and the number of units within a defined sample length.

To estimate the listening area of pygmy blue whales about each receiver and the estimated range of a whale from the receiver, sound propagation modelling for frequencies spanning the unit II dominant frequencies was carried out on a series of headings about a mooring location. A source level was assumed for the pygmy blue whale unit II component and ambient noise in the frequency band of interest was derived for each sample. The estimated transmission of the source level down to ambient noise level, with corrections for the bandwidth of units and the detector thresholds included, gave a range for detection under the prevailing ambient noise conditions on each heading about the receiver. For sample with pygmy blue whale song present, the polygon encompassing the likely detection range given the unit II received level was calculated (details supplied in Supplementary Methods). For the glider sound recorders that were moving and changed depth, the sound propagation modelling was calculated at 26–28 km distances along the glider track at multiple depths. For each sample or unit-II signal, the closest location and glider depth were used to calculate listening area and probable range to source.

### 2.2.1. Pygmy blue whale spatial model

A spatial 10 km × 10 km grid of the study region was established, where two metrics were summed into the appropriate grid cells for each sample, *units/(day•1000 km$^2$)* and *singers/(day•1000 km$^2$)* using the derived counts of units, singers and the listening area estimates. While we calculated probable range to source and probable range ± 3 dB as an estimate of the likely range band the source was in about a receiver, this metric was not presented, as in periods of high density pygmy blue whale calling, vessel or air gun noise, we were not confident that unit levels were measured correctly due to overlapping sources.

This spatial grid was then used to extract environmental variables for each point of the grid. Monthly surface current direction and magnitude were generated from NOAA Ocean Surface Current Analyses Real-time (OSCAR) data 5-day at 1/3° resolution using the Marine Geospatial Ecology Tools (MGET) (Roberts et al., 2010) in ArcGIS 10.8. Remote-sensed data for sea surface temperature (SST), chlorophyll-a (Chl-a) and the euphotic zone depth at 9 km resolution were from NASA Ocean Color (https://oceancolor.gsfc.nasa.gov/). Monthly averaged SST and Chl-a products represent mapped binned data generated from the Moderate Resolution Imaging Spectroradiometer (MODIS), Aqua satellite Level 3. Bathymetry was obtained from the General Bathymetry Chart of the Oceans Gebco15 with 30 arc-second resolution (http://www.gebco.net). Aspect, rugosity and slope were calculated from the bathymetry data using the digital terrain analysis with fixed window sizes in ArcGIS 10.7 with a 1 km resolution. Distance to canyons was calculated in ArcGIS 10.7 using the shapefile of 'shelf' from the GIS dataset discussed above from Heap and Harris (2008).

To further understand pygmy blue whale distribution we developed a spatial model by using the two metrics described above (*units/(day•1000 km$^2$)* and *singers/(day•1000 km$^2$)* as response variables, and examined their relationship with the environmental variables (covariates) outlined above and plotted the predicted relationships in space as an index of pygmy blue whale distribution. Due to high correlation coefficients between some covariates, some were dropped and thus the final covariate set used was: bathymetry, slope, aspect, rugosity, sea surface temperature, chlorophyll a, distance to canyons, current direction, current magnitude and month. All covariates were modelled as numeric continuous variables.

We used Random Forest to model the relationships between the response variables and the predictor variables listed above. Random Forest is a supervised machine learning algorithm where a forest is created by combining multiple decision trees (an algorithm used to classify data and in this case a regression tree) (Breiman, 2001). This approach stabilises model estimates and optimises predictive accuracy. Random Forest models use bootstrapped samples drawn randomly from the original dataset. A regression tree is fitted to a bootstrapped sample and works by recursive portioning of the covariate space to make predictions for these observations. During this partitioning process each node of a tree is associated with a random subset of covariates from the original set of covariates. The Random Forest predicted estimate for each observation is then calculated by aggregating and averaging the results across the collection of all trees. Random Forest modelling is particularly flexible as it is a non-parametric approach and so fewer assumptions about the data need to be met.

The main parameters that need to be optimised are the number of regression trees (*ntree*), the number of input variables per node (*mtry)* and the minimum number of random samples of the full dataset for each node that controls the complexity of trees (*nodesize*). Values from 100 to 500 with intervals of length 100 were tested for *ntree* and values from 2 to 11 were tested for both *mtry* and *nodesize* with interval of 3. The *ntree*, *mtry* and *nodesize* values of 100, 10 and 2 and 100, 10 and 10 were selected for the two metrics (number of units/1000 km$^2$•day and singers/1000 km$^2$·day) respectively. We withheld a random sample of one-third of the data to use for model performance estimates (testing set) and used the remaining two-thirds to train the model (training set).

We used the measure of Increase in Mean Square Error (%IncMSE), that indicates the decrease of accuracy in predictions if the given variable is excluded from the model, as a measure to rank variables based on their predictive importance. However, to identify relevant from irrelevant predictors we applied a variable selection procedure using the *vita* package (Celik, 2015) to reduce the set of predictors to the most important ones. This package employs a method that uses the existing data without any permutations to estimate the null distribution of variable importance scores from the model from which p-values can be calculated (Janitza et al., 2018) and thus p-values $< 0.001$ indicated the most important variables (Celik, 2015). This assessment of p-value indicates the probability of observing an importance score for the variable higher than the importance score calculated by the model (Janitza et al., 2018). Prediction maps of the density of singing whales and density of whale units were created using the final model including only the most important variables.

## 3. Results

### 3.1. Satellite telemetry

#### 3.1.1. Movement behaviour

During the May-June 2020 satellite tagging effort off NW Cape, we encountered 24 pygmy blue whales during the ten-day field trip (either observed from the RHIB or plane). These were confirmed to be distinct from Antarctic blue whales which are also thought to be present off Western Australia from the songs relayed by the sonobuoys. Ten of the 24 whales were directly observed displaying feeding behaviour (Fig. S2) and we deployed tags onto six of the 24 whales with most tagged in the vicinity of the heads of the Cape Range and Cloates Canyons (see Fig. 3 for the positions of these canyons).

The SSM could not be fitted to two of the tagged whales described in Double et al. (2014) due to short tracking durations and poor quality location estimates, so those deployments were not included in the analysis (1 unknown sex and 1 female from 2011). Thus, the final dataset for Western Australia comprised 22 pygmy blue whales (Fig. 2, Figs. S3:S5). The average satellite tag deployment duration (all data combined) was 56 ± 51 days with a maximum of 271 days for implantable SPOT tags (mean = 76 ± 82) and 121 days for LIMPETs (mean = 48 ± 42). The median rate of travel was 2.4 km $hr^{-1}$ (<0.1–15.4 km $hr^{-1}$) and the mean was 2.8 ± 0.8 km $hr^{-1}$ (Table 1). There were only two whales that provided data for the southern migration where pygmy blue whales appeared to travel faster (#182657 = 4.0 km $hr^{-1}$ and #123229 = 5.0 km $hr^{-1}$) than on the northern migration (#182657 =2.5 km $hr^{-1}$ and #123229 = 3.9 km $hr^{-1}$) (no SD as n = 2).

All of the whales travelled north except one. This was one of the two whales tagged with a miniPAT (214432; Fig. S6). After leaving Perth Canyon, whale 214432 headed south around Cape Leeuwin and out to the shelf edge and slope and at programmed release (30 d after deployment) the tag came free around Hopetoun.

Areas of lower move persistence occurred in sections of the coast offshore from Carnarvon (25° S) to the Rowley Shoals (17.5°S), from the southern tip of Western Australia (latitude 35.0°S) to offshore of Geraldton (28°S), and in Indonesian waters, predominantly in the Banda Sea (5° S), but also in the Molucca, Timor and Savu Seas (Figs. 2a, 3g:i and Figs. S3:6). During the northern migration, the tagged whales fanned out extensively after passing the Montebello Islands (~20° S) where move persistence was high (Fig. 2a). Prior to passing the northern tip of the Montebello Islands, the width of the migration path was around 175 km; following that the migration path spread to 690 km, its widest point. After leaving Australia's EEZ, the whales still providing data migrated up to the Banda Sea

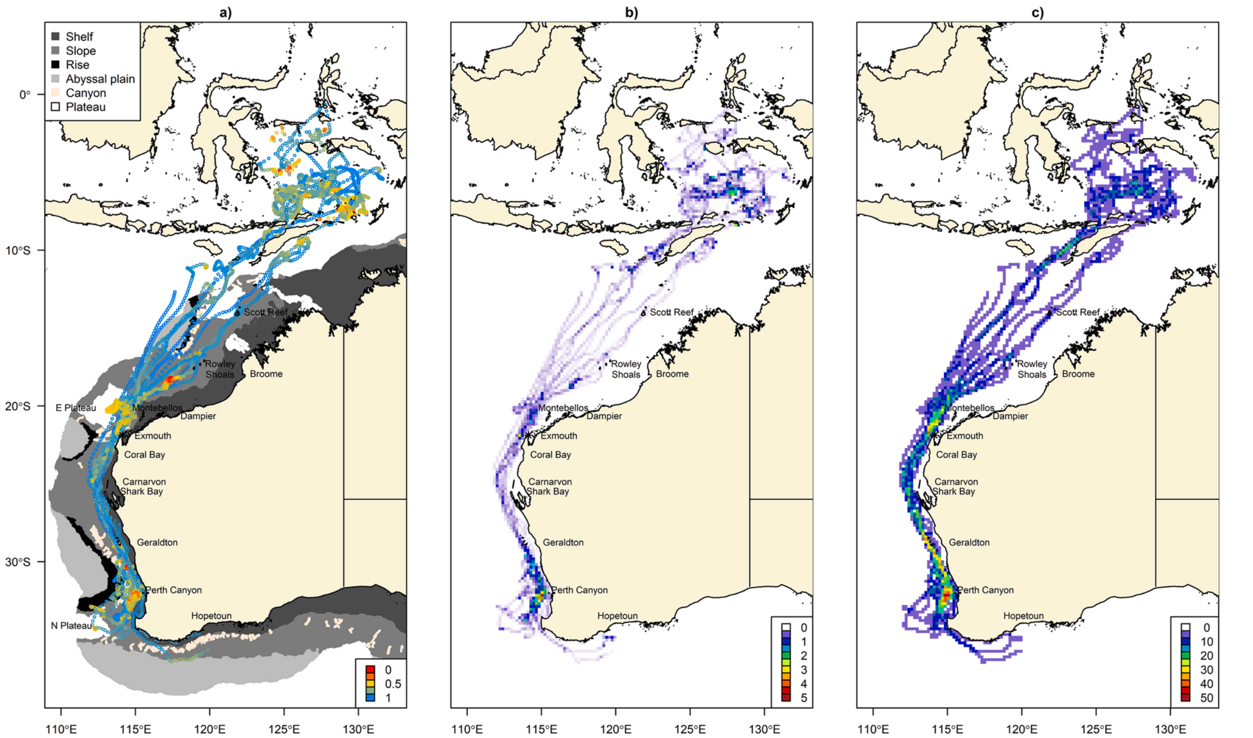


**Fig. 2.** a) Pygmy blue whale (n = 16) state space modelled position estimates are colour coded by move persistence with cooler colours indicating high move persistence (indicative of migration) and warmer colours indicating low move persistence (indicative of foraging, and/or resting/ breeding). b) shows the distributions calculated using the modelled position estimates with occupancy (time spent per grid cell in days), and c) shows percentage of pygmy blue whales per grid cell. Satellite tag deployment locations marked with an asterisk, including NW Cape (n = 6), Perth Canyon (n = 15), Bonney Upwelling, SA (n = 1), noting that only data from Hopetoun WA to Indonesia is shown for the latter deployment. Geomorphic features of the Australian EEZ are also shown, including the Exmouth (E) Plateau and the Naturaliste (N) plateau.

through the Savu or Timor Sea. The median duration of bouts of foraging (and/or breeding/resting) movement behaviour ($g < 0.8$) was 28 h (2 – 1080 h), with calculations also provided per migration and region (Table 2).

### 3.1.2. Whale distribution and important areas

The overall spatial distribution of occupancy (time spent per grid cell) highlighted that the whales spent most of their time in three main areas described in the previous paragraph (Figs. 2b, 3a:c). Occupancy was predictably low outside of these areas due to the relatively higher speed of migratory movements and, consequently, less time spent in individual grid cells (Figs. 2b). Hence, the percentage of whales in a grid cell was more informative for highlighting migratory pathways (Fig. 2c). These three areas were also areas used by most of the whales (Figs. 2c, 3d:f).

The time of year and duration in each of the regions are summarised in Table 2. Time pygmy blue whales spent in north-west Western Australia was 19 ± 6 days on the northern migration (n = 14). For the two deployments that provided a near round trip back to their tagging area (#123229 and #182657), 23 and 10 days, respectively, were spent in this region on the southern migration (Table 2). These two whales spent 124 and 91 days, respectively, in Indonesian waters, whereas the six that had deployment durations long enough to transmit data during their migration to and within the Banda Sea spent 83 ± 25 days in Indonesian waters. The median dates whales were present in north-west Western Australia on the northern migration was from 28 May (range = 12 April – 25 June) to 10 June (range = 27 April to 12 July).

Across all individual whales, 89 ± 9.3% of modelled location estimates were overlying slope waters. The next most used geomorphic province was the abyssal plain (9.2 ± 7.6%), followed by shelf (7 ± 5.4%) and rise (6.5 ± 4.8%) (Fig. 2a, Figs. S3:S6). Shelf use only occurred south of Ningaloo Reef. When considering all the geomorphic features superimposed on the geomorphic provinces, the whale SSM location estimates overlapped with seven geomorphic features, with slope again having the highest overlap (50%) and terrace at 20% and the remaining categories having ≤ 10% overlap. Lower move persistence (foraging movement behaviour) and areas of higher occupancy overlapped with the Perth Canyon and canyons adjacent to it's south and north (un-named but ranging from off Mandurah to off Jurien Bay), the Cape Range Canyon, Cloates Canyon (Figs. 2a, 3, Figs. S3:S6) and the canyons off the south-west coast of WA (Fig. 2a & Fig. 3). Lower move persistence also overlapped with plateau features, including the Naturaliste Plateau and the Exmouth Plateau (Fig. 2a, Figs. S3:S6).

Two whales (#182657 and #123229) had a return trip, southbound, to the tagging site, providing further evidence that the Banda Sea region is the migratory endpoint for this population and thus is potentially its breeding ground (Double et al., 2014) (Fig. S8). The movement behaviour for #123229 is described in Möller et al. (2020) and is also summarised in Table 2 and Fig. S7. The other (#182657) appeared to leave the tagging location off NW Cape directly or soon after tagging on 3 June 2020. It had two periods of low move persistence; first (each around 5 days) along its path to Rowley Shoals (Fig. S3) thereafter (on 24 June 2020) transmissions ceased until the whale arrived in the Banda Sea (straight line distance of ~1400 km) 21 days later on 19 July 2020 (Fig. S7 and S3). Although it is difficult to determine when the southern migration started, a consistent movement to the south combined with movement behaviour consistent with migration began around 14 September 2020. The tag again ceased transmissions on 22 September around 80 km west of the southern tip of the island of Timor. Transmissions began again on 28 September 2020 off the Rowley Shoals, in a similar place to where transmissions ceased on the northward migration (straight line from start to end point of deployment, distance of ~800 km). This pygmy blue whale had a short period (~ 12 h) of likely foraging there, before meeting up with its northward migratory pathway once again (Fig. S7 and S3). The tag stopped transmitting on 3 October 2020 prior to presumably reaching its original tagging location.

**Table 2**
Calculations for the time spent in each of the zones during the period each whale provided satellite tracking data on the northern and southern migration. Zones are: Indonesian waters (all points north of latitude 12.4°S (the northern extent of Australia's EEZ)), north-west Western Australia (NW WA, between latitude 12.4°S and the southern extent of Ningaloo Reef (latitude 23.6°S)), south-west Western Australia (SW WA, between the southern extent of Ningaloo Reef and Cape Naturaliste (latitude 32° S)) and the southern coast of Australia (SA), those points beyond Cape Naturaliste and greater than longitude 116°E). We also calculated the median and range Julian day and converted those to date with year 2020 and the median foraging bout duration (in hours) (continuous sections of track with $g < 0.8$). *one individual only (# 182657) and only one bout as the only other individual that provided data on southern migration (#123229) had no foraging bouts in this region. ** = one individual only (#182657) with 7 foraging bouts, † = one bout only.

| | Indonesia | | NW WA | | SW WA | | SA | |
|---|---|---|---|---|---|---|---|---|
| Detail | Northern migration | Southern migration | Northern migration | Southern migration | Northern migration | Southern migration | Outward migration | Inward migration |
| n | 7 | 2 | 14 | 2 | 10 | 1 | 1 | 1 |
| Mean ± SD time spent (days) | 83 ± 25 | 124,91 | 19 ± 6 | 23, 10 | 21 ± 8 | 9 | 59 | 56 |
| Median & range min date | 9 Jun (15 May–19 Jul) | unknown | 28 May (12 Apr–25 Jun | 30 Oct, 23 Sep | 16 Apr (16 Mar, 10 May) | 3 Nov | 12 Mar | 12 Nov |
| Median & range Max date | 20–Aug (28 Jul-11 Oct) | 11-Oct, 22 Sep | 10 June (27 Apr–12 Jul | 3 Nov, 3 Oct | 12 May (2 Apr–26 May) | 12 Nov | 10 May | 8-Dec |
| Median & range foraging bout length (h) | 22 (2–966) | 8 (4–28)** | 66 h (3–486) | 12* | 30 (3–366) | 12 (3–21) | †1080 h | 45 (6–348) |

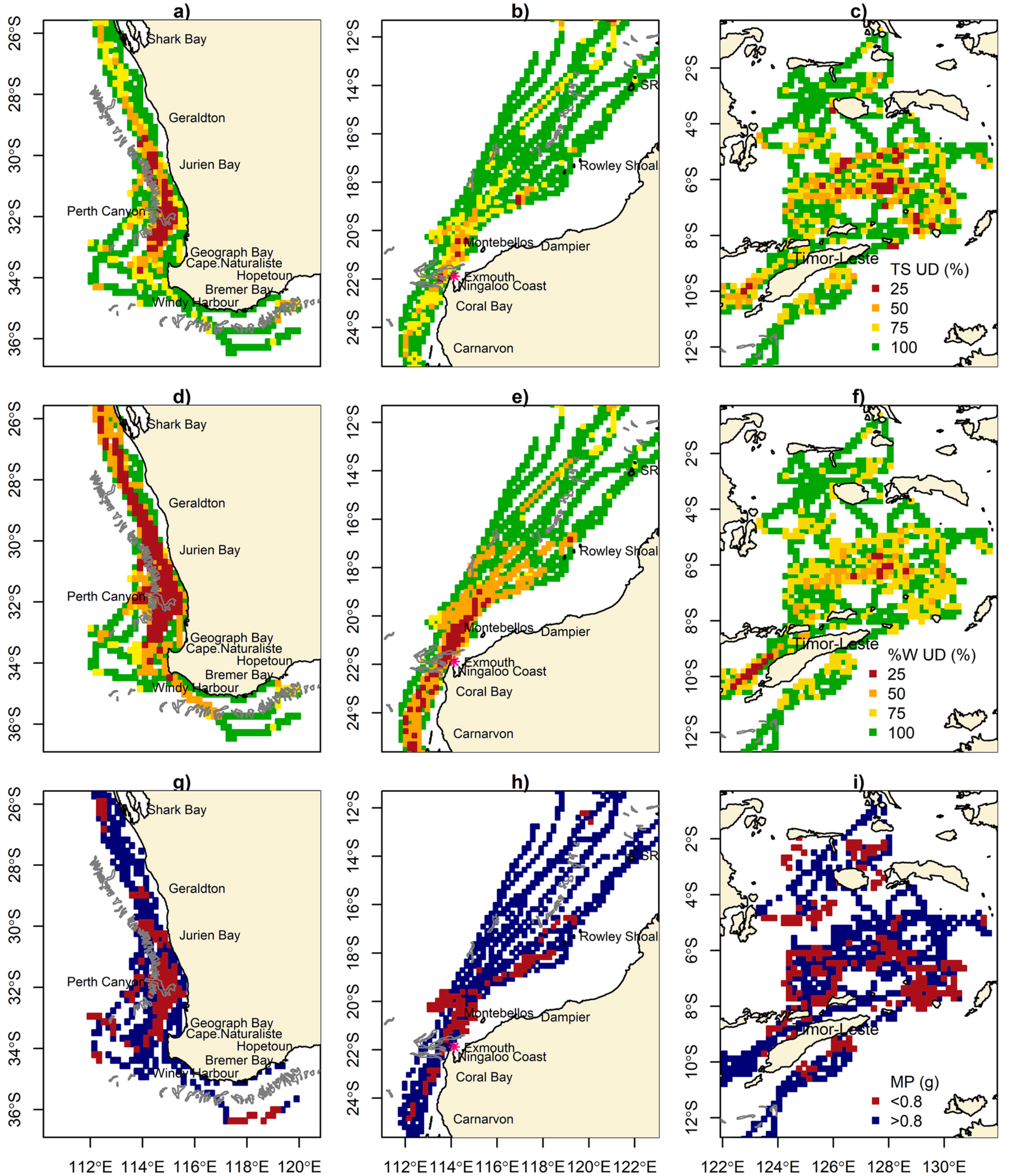


**Fig. 3.** Finer scale plots of each of the three metrics calculated (occupancy, number of whales in a cell and move persistence), showing the 25% UD in red, the 50% UD in orange, 75% UD in yellow and 100% UD in green for the distribution calculated using time spent (occupancy) (a:c) and number of whales in a cell (d:f) and move persistence (MP) (g:i) with $g < 0.8$ indicative of foraging, resting or breeding (red) and $g \geq 0.8$ indicative of migration (blue). Map locations are for south-west Western Australia, (a, d & g), north-west Western Australia (b, e & h) and Indonesian waters (c, f & i). NW Cape is denoted by the red asterisk in b) and SR = Scott Reef. Canyons are shown in grey with Cape Range Canyon (north) and Cloates Canyon (south) shown off the Ningaloo Coast. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 3.1.3. Most important areas

Based on the overlap between the three metrics we calculated using this dataset, we designate the most important foraging (and/or resting/breeding) areas from south to north as 1. The Perth Canyon and vicinity, 2. the shelf edge off Geraldton, 3. the shelf edge from Ningaloo Reef to the Rowley Shoals (not continuous) and including a couple of small areas near the shelf edge off approx. 25°S and 4. the Banda Sea. The Foraging BIA off the south-west of Western Australia encompassed 83% of the most important areas in that region (Fig. 4, Table 3). However, the 'Annual High Use Foraging' BIA within that BIA only encompassed 7% of the most important area (Fig. 4) (Table 3). The Foraging BIAs off NW Cape and Scott Reef also only encompassed a small percentage of the most important foraging areas in the north-west of Western Australia (Fig. 4) at 5% (Table 3), and a moderate overlap with the Australian Marine Parks (14%) (Table 3). Although there are no designated 'Breeding' or 'Foraging' BIAs in Indonesia, the 'Migration' BIA designated in the NCV Atlas encompassed the important breeding/foraging area we calculated in Indonesia, and the most important area we calculated in the Banda Sea had 89% overlap with the 'Migration' BIA (Table 3).

Regarding the overlap between the canyons and the most important areas, 60% of the Perth Canyon was encompassed by the important areas. Only 0.3% of the Cape Range Canyon was encompassed by the important areas and 3% overlap occurred between the Cloates Canyon and the important areas.

The extent of the most important migration areas (overlap between the area used by most whales and areas where migratory movement behaviour occurred) was almost continuous from the bottom the Western Australia to around the latitude of Rowley Shoals

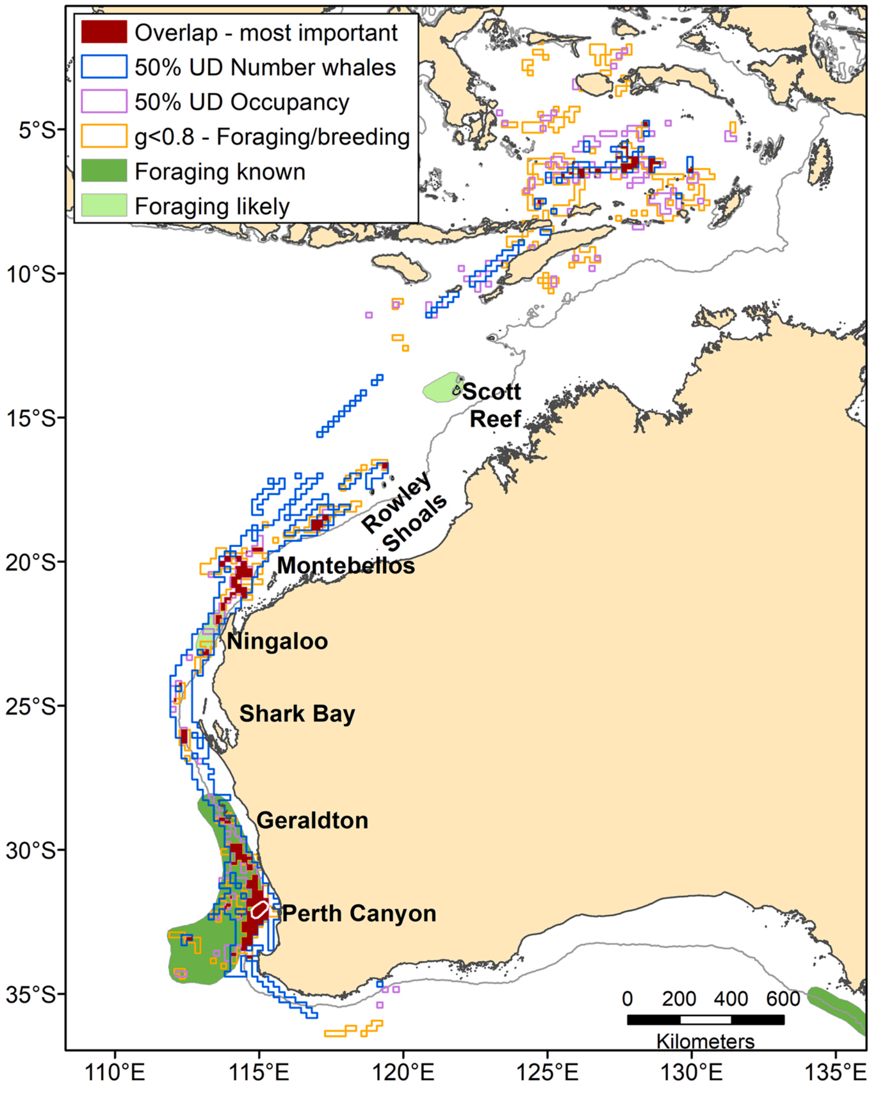


**Fig. 4.** Map showing the 50% UD of occupancy (purple), 50% UD for number of whales in a cell (blue), the grid cells where the average move persistence (g) < 0.8 (orange), and the overlap between these three metrics of pygmy blue whale spatial use (red) representing the most important foraging/breeding areas calculated from this dataset. Green polygons represent the Known and Possible Foraging BIAs delineated in the NCV Atlas and Recovery Plan with the white polygon outline denoting the Annual High Use Foraging BIA. Grey line represents the extent of the shelf.

**Table 3**
Percentage overlap between the most important areas calculated using the pygmy blue whale satellite tracking data, with the Commonwealth of Australia Marine Parks (AMPs) and State Marine Parks, and spatial areas in Western Australia (WA) and extending into Indonesian waters identified in the Blue Whale Recovery Plan and the NVC Atlas. Note that overlap with AMPs and the known to occur/distribution polygon only included the area of the distribution and important areas we calculated within the Australian EEZ.

| Type of area | Most important foraging area | Most important migration area | Entire distribution |
|---|---|---|---|
| Australian Marine Parks | 14 | 22 | 15 |
| State Marine Parks | 0.2 | 0.7 | 0.5 |
| Foraging BIA south-west WA | 83 | NA | NA |
| Foraging BIA north-west WA | 5 | NA | NA |
| Annual High use Foraging BIA | 7 | NA | NA |
| Migration BIA whole | NA | 83 | NA |
| Migration BIA Australia | NA | 82 | NA |
| Migration BIA Indonesia | NA | 89 | NA |
| Known to occur/distribution area | NA | 90 | 56 |

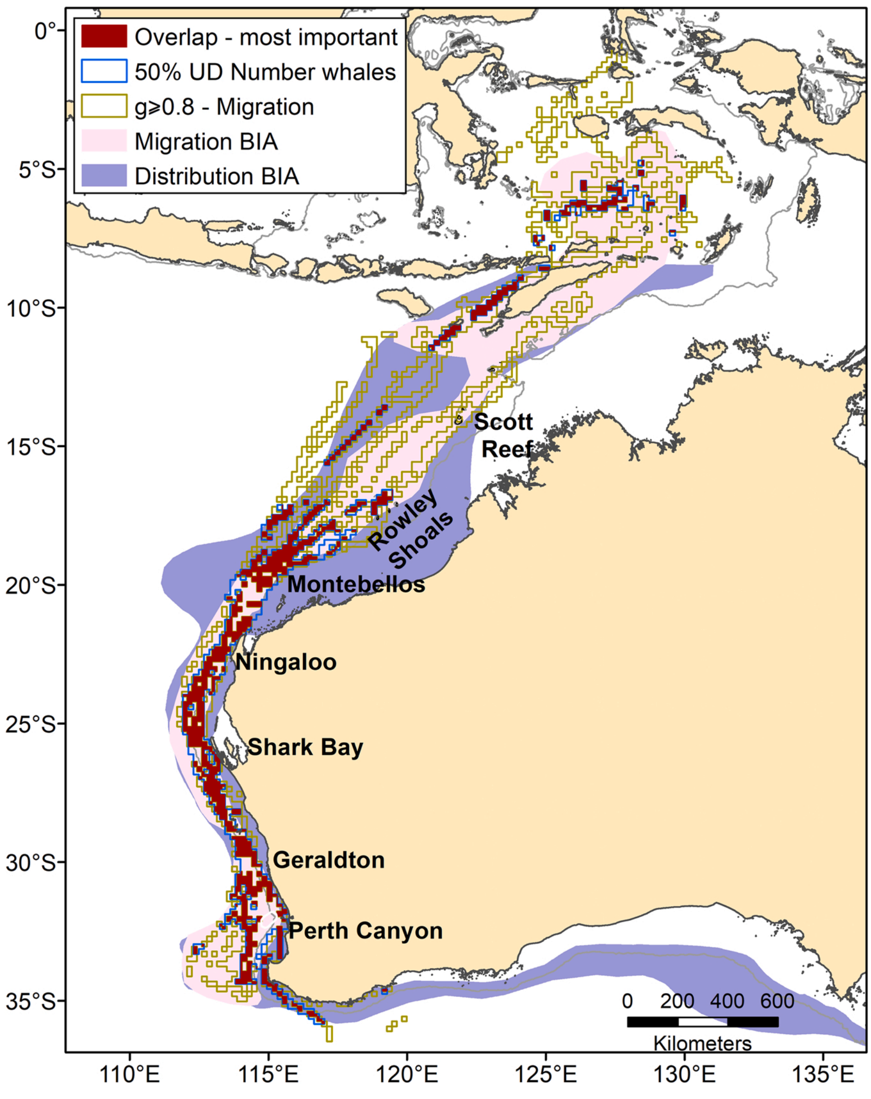


**Fig. 5.** Map showing the 50% UD for number of overlapping whales (blue), the grid cells where the average move persistence (g) was < 0.8 (orange), and the overlap between these two metrics of spatial use representing the most important migratory paths (red) of pygmy blue whales calculated from this dataset. Pink polygons represent the migration BIA delineated in the NCV Atlas and the purple polygon represents the distribution delineated in the Management Plan. Grey line represents the extent of the shelf.

and thereafter was more dispersed. Other important areas were calculated around 15°S, in the Savu Sea, Ombai Strait and Banda Sea (Fig. 5). The most important migration area had 82% overlap with the part of the Migration BIA that occurs in Australia and 83% overlap with the entire Migration BIA (Table 3) (Fig. 5).

The polygon designating the area pygmy blue whales are known to occur (Distribution) identified in the Recovery Plan accounted for 56% of the entire distribution we calculated (100% UD) (Table 3) and 79% when just considering the Australian range.

### *3.2. Passive acoustic monitoring data*

Details of the results of the passive acoustic analysis are outlined in the Supplementary Results and summarised here. The feature space analysis technique of Jolliffe et al. (2019) for inter song interval showed the predominant song types recorded were the *P2* type (see Jolliffe et al., 2019 for song terminology, *P2* is song units II & III repeated every 80–90 s) and the *P3* type (unit I, II & III repeated every 180–200 s). Thus, the number of singers per sample was found from maximum counts of unit II within 60 s windows. Of the 29 data sets that included full manual checking, the mean number of singers was 1.8 $\pm$ 0.94 SD and the median was two although the distribution was skewed to one singer (49% of all 69,695 samples with pygmy blue singing present had one singer, 30% two, 15% three, 4% four while the remaining 2% had five or more with the maximum number of singers 12). There was no trend in mean number of singers at a point in time, across the sampling period (2000–2020).

The estimated receiver sampling areas varied considerably, as can be seen for the area curves of five sites calculated for the maximum area in the 18–28 Hz or 60–75 Hz band at the median ambient noise level of a site, shown overlaid on Fig. S9. These sites were typical, with areas ranging from 15,156 km$^2$ (NW Cape) to 87,866 km$^2$ (west of Broome). The curves along the shelf slope tended to align with the constant depth contour.

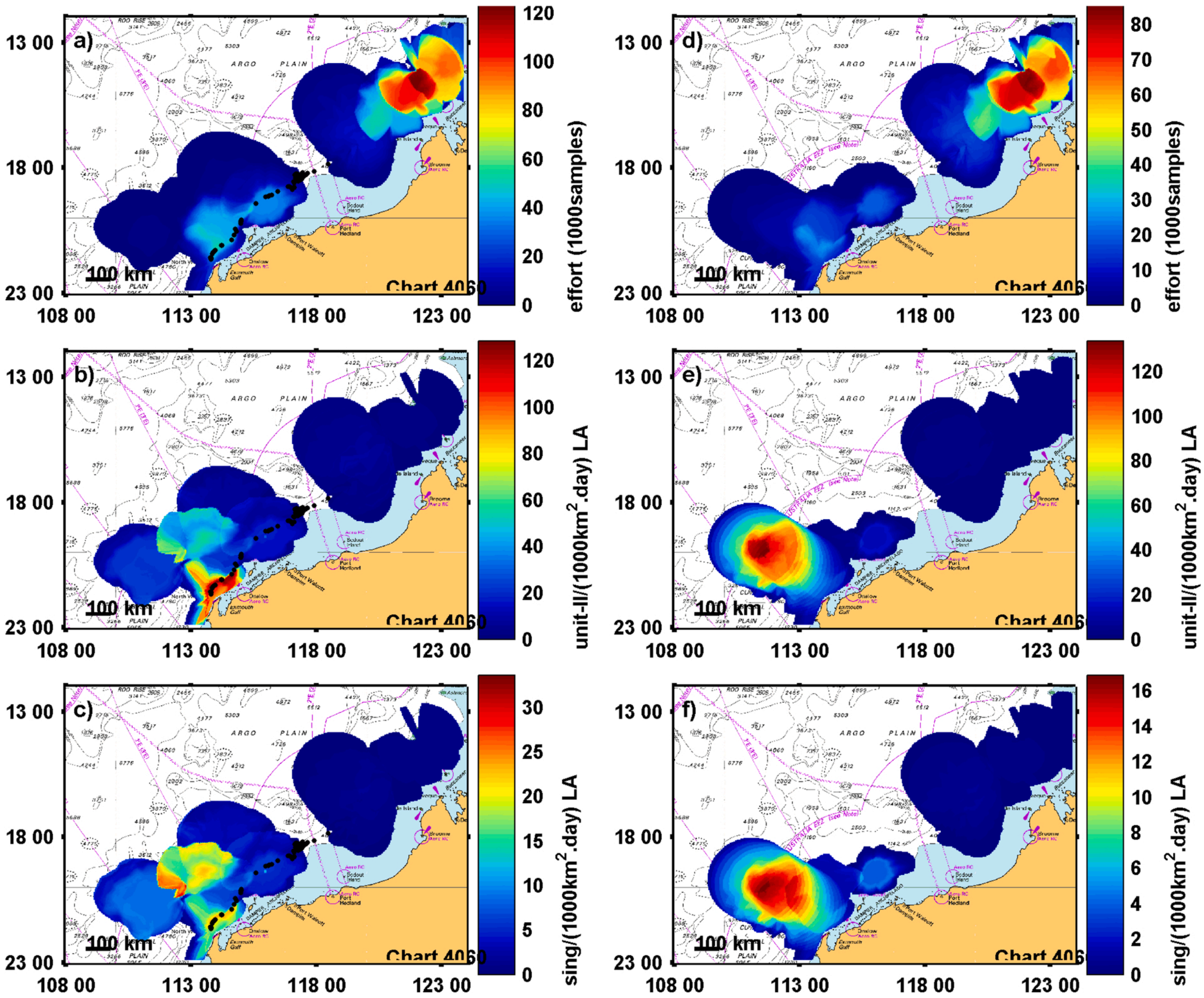


**Fig. 6.** Density plots of units and singers detected on fixed loggers for the northern migration on the left and the southern migration on the right. The top plots (a) show effort, middle plots show number of units/(day• 1000 km$^2$) (b) and the bottom plots shows number of singers/(day•1000 km$^2$) (c). Also plotted (in black points) is the track of pygmy blue whale #182671 for reference.

The highest sampling effort for the fixed loggers was in the northernmost part of the study area, but lowest unit and singer densities were recorded there on the northern and southern migrations (Fig. 6). Highest unit and singer densities occurred in offshore waters between NW Cape and off Dampier (Fig. 6). Unit and singer densities were higher to the west on the southern migration (Fig. 6), as observed by Gavrilov et al. (2018) and during the glider missions (Fig. S10). The density plots made from pygmy blue whales recorded on noise loggers on board gliders (Fig. S9) showed that the highest density was recorded in the most southern and middle glider surveys and the inward leg of the northern most glider survey. The region where the highest density of units was recorded was in offshore waters between Dampier and Ningaloo (Fig. 6 & S9). Pygmy blue whale detections on the noise logger deployed off NW Cape showed pygmy blue whales were heard in that region from April to July (Fig. S9). These dates were in line with the times calculated from satellite tracking data (Table 2).

### 3.2.1. Distribution model

The top ranked predictor variables from the Random Forest modelling for both response variables were month, sea surface temperature and distance to canyons based on %IncMSE. The latter two variables switched when number of units / 1000 km$^2$·day was the response variable. (Fig. S11). The variable selection procedure indicated Month and SST (Fig. S10) as most important ($p < 0.01$ based on the 100 permutations of variable importance measure for singers/1000 km$^2$·day and units/1000 km$^2$·day). The predictions from the top ranked Random Forest models indicated that a greater number of units/1000 km$^2$·day and singers/1000 km$^2$·day were recorded between April and June/July (northern migration), with a secondary peak in November and December (Fig. 7a, c, southern migration). A greater density of singing whales were also associated with an SST of 26.9° with secondary peaks between 25 °C and 26 °C (Fig. 7b). A greater density of units were associated an SST of 28.4 °C with secondary peaks between 25.5 °C and 26.5 °C

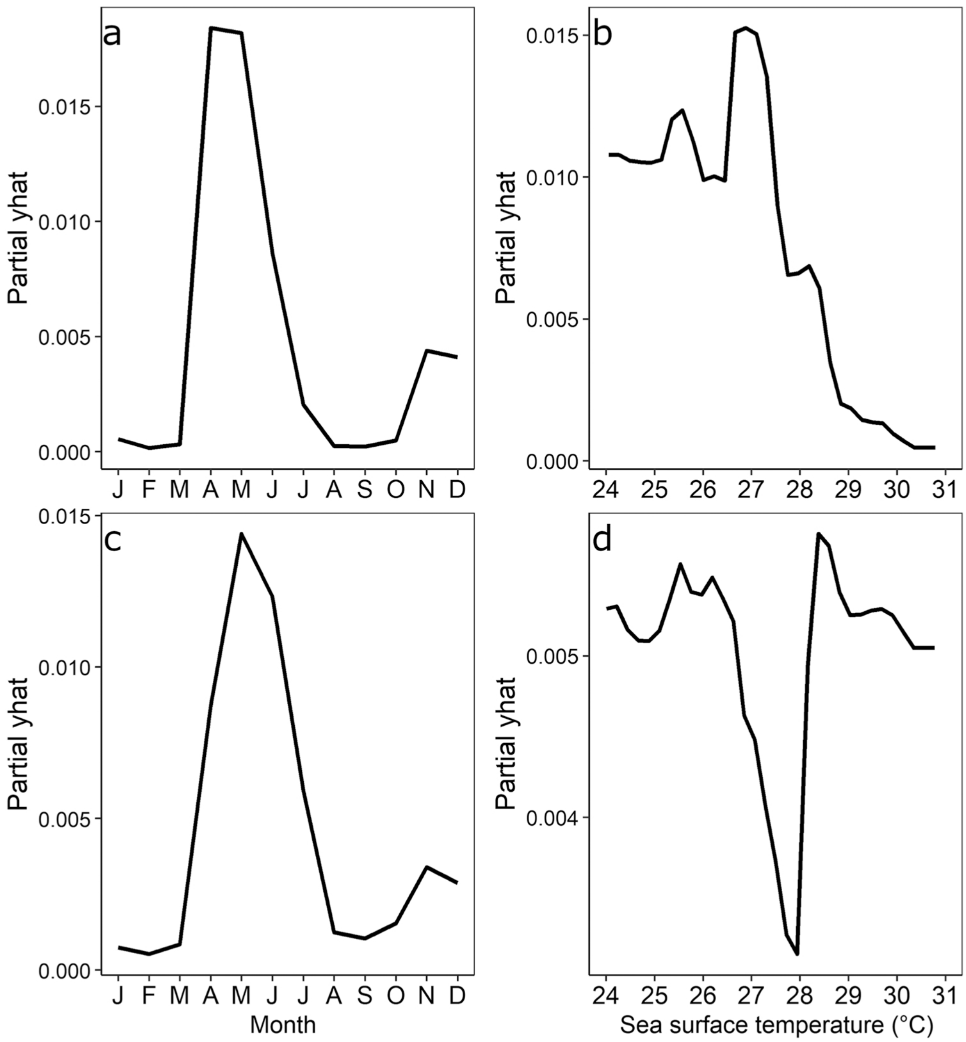


**Fig. 7.** Partial plots from the four most important covariates included in the final random forest model explaining density of singers: month (a) and sea surface temperature (SST, b) and explaining density of whale units for month (c) and SST (d).

(Fig. 7d). Monthly spatial predictions of singing whales also indicated higher density of singing whales during April to July with most pygmy blue whale singer density in the southern extent of the north-west of Western Australia in the months of the northern and southern migration (Fig. 8) with similar but slightly different spatial predictions for the density of pygmy blue whale units (Fig. S13).

## 4. Discussion

This study provides novel information on the spatial ecology of a threatened whale population from a part of its range where there are limited data. With a backdrop of industrial development and activities (e.g. oil and gas exploration and production, commercial

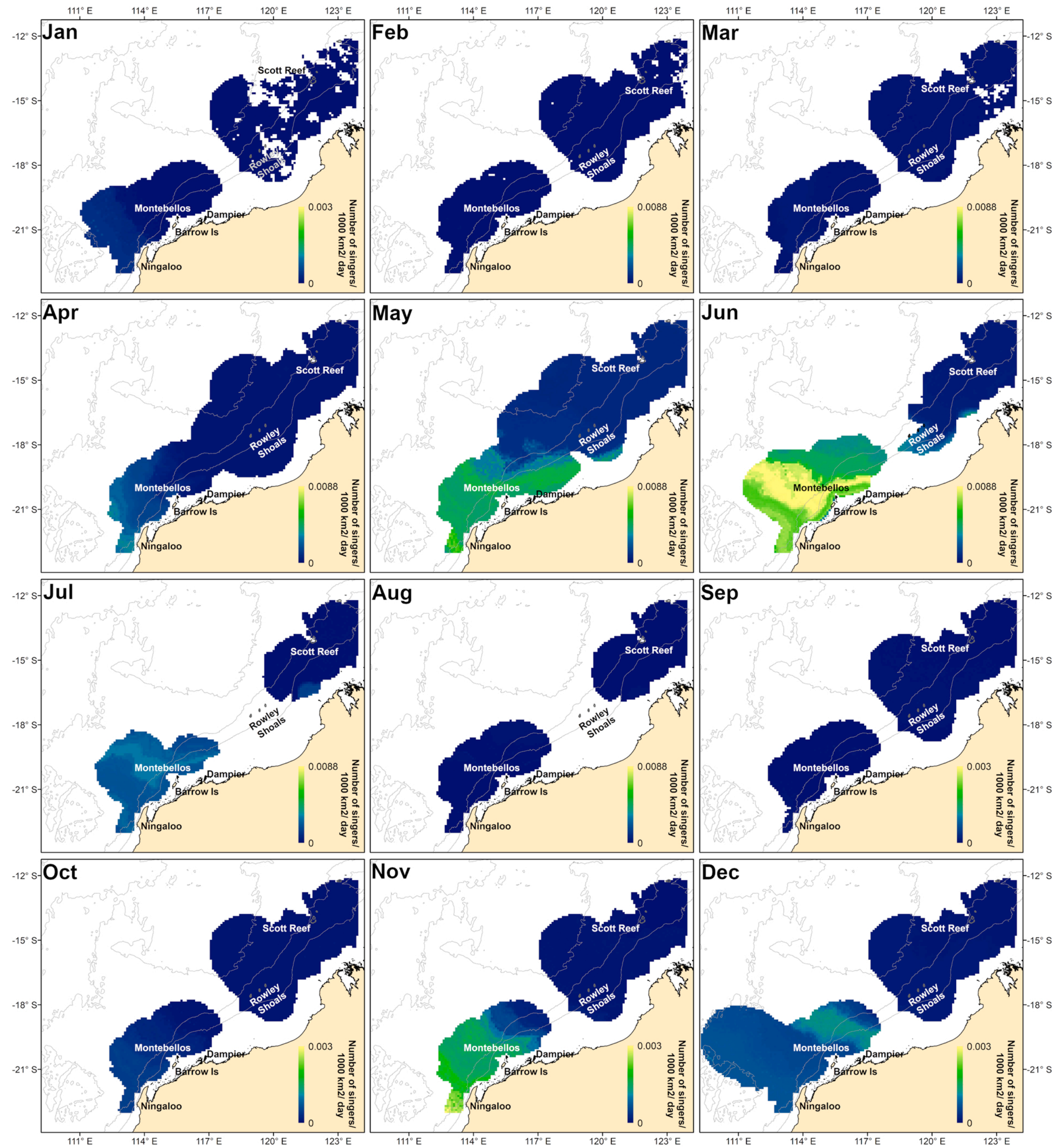


**Fig. 8.** Predicted number of pygmy blue whale singers/1000 km$^2$•day for each month from the top ranked Random Forest model. Note that the northern migration includes the months of February to August and the southern migration includes September to January. Note Fig. S12 shows each month with its own colour scale.

shipping) in this area, there is a fundamental need for accurate spatial data to mitigate threats to the pygmy blue whale's recovery. Our holistic approach of combining passive acoustics with satellite tracking data allowed us to quantify the spatial and temporal components of pygmy blue whale distribution and identify areas of greatest importance for foraging, potential breeding and migration. Pygmy blue whales demonstrated extensive use of slope habitat off Western Australia and only limited use of shelf waters, as previously found (Branch et al., 2007; Double et al., 2014; Garcia-Rojas et al., 2018; Gavrilov et al., 2018; Möller et al., 2020). Pygmy blue whale movement off north-west Western Australia was predominantly relatively fast, directed travel (high move persistence) interspersed with relatively short (median = 28 h) periods of low move persistence indicative of foraging and/or resting/breeding. Pygmy blue whales had high use (both in time and number of whales) and low move persistence along the Ningaloo Coast up to the Rowley Shoals from April to June on their northern migration to the Banda Sea. From November to December, they were present in the north-west of Western Australia, with some periods of high use and low move persistence in similar areas while on their southern migration. The high use and low move persistence we calculated off the Ningaloo Coast, combined with observations of feeding behaviour during tagging there, supports the 'Possible Foraging BIA' identified in the Blue Whale Recovery Plan. The evidence of foraging (both actual and putative) suggests that the 'possible' classification should be reviewed. Furthermore, this BIA currently encompasses only 5% of the pygmy blue whales' most important areas as defined by these analyses. Therefore, our quantification of pygmy blue whale spatial and temporal use of the north-west of Western Australia may be useful for updating the BIA boundaries in this area.

Considering the offshore industrial development and activities off the NW coast of Australia and in the waters of Timor Leste and Indonesia, a critical need exists to understand habitat use along the migration path of the whales in these regions. Only 7% of locations from satellite tagged pygmy blue whales occurred in shelf waters (as defined by Heap and Harris (2008) and shown in Fig. 2), mostly in the southern section of Western Australia (south of Ningaloo). This suggests that the north-west Australian shelf areas may not be the core pygmy blue whale distribution. Our sample size, though improved from previous studies in this area, may not be representative of movements and distribution of the entire pygmy blue whale population and only two satellite tag deployments provided data on the southern migration. This is partly made up for in the passive acoustic data that provided spatial and temporal data on the northern and southern migration for all calling whales in the area. For the northern and southern migration, the acoustic data appears to support limited use of the shelf, with the mapping of pygmy blue whale song mostly occurring in the deeper parts of the shelf along the Ningaloo Coast, towards Barrow Island and off Dampier. However, the spatial resolution of the passive acoustic dataset is very large (whales can be heard over an area of up to 200 km) compared to the satellite tracking data, such that the mapping and estimated density surfaces of pygmy blue whale singers and units likely extend over larger areas than the locations of the whales themselves. Also supporting this argument is that there were several noise loggers deployed on the shelf with no pygmy blue whale singing detected (Fig. S1.1). Given this, our data suggests minor use of the shelf, especially between the area NW of Dampier and Scott Reef. In contrast, pygmy blue whales tagged in the Bonney Upwelling spent most of their time over the continental shelf, but three of the 13 tagged whales tagged there also used continental slope and the deep-sea (Möller et al., 2020). Pygmy blue whale slope and shelf use has also been reported from aerial surveys on the southern coast of Australia (Gill et al., 2011).

Although the majority of the most important migration areas were encompassed by the Migration BIA in Australia, our analysis suggests that it includes a broader north-west distribution and migration extent than that represented there. In fact, most whales migrate much further offshore along the north-west part of the coast, even out to the abyssal plain. This is further supported by McCauley (2011), where 6–40% of pygmy blue whales that pass by the northern end of the Montebello Islands were estimated to pass by Scott Reef. The line of seismometers off Broome analysed here and sonobuoy detections as far west as latitude 110°E during a 2019 voyage on board the RV *Investigator* (C. Jenner, pers comm) also support migration much further west of the shelf edge. Similarly, pygmy blue whales in Indonesian waters have been reported in waters further west of those reported here along the islands of Flores and Komodo (Rudolph et al., 1997) and a satellite tagged whale from Australia travelled to waters as far west as Java (Möller et al., 2020).

The Foraging BIA in the south-west of Western Australia off Perth aligns well with the pygmy blue whale satellite tracking data in this part of their range. However, only low overlap existed (7%) between the 'Foraging - Annual High Use Area' BIA and the most important area calculated here. Although only 10% of whale location estimates overlapped canyon habitat (all canyons), a large part of the Perth Canyon was encompassed by the most important areas used by pygmy blue whales (60%). In contrast, the Cape Range and Cloates Canyon had only a very low percentage of their area encompassed by these UDs (< 3%). Although this suggests only low importance of these canyons, the whales appeared to focus their activities at the canyon heads, which are a small proportion of the overall extent of the entire canyon area. Upon searching the whole length of the Ningaloo Reef for pygmy blue whales to tag, the majority were found at the head of these canyons suggesting it is a focus for the whales, at least over the time period of tagging, and many of these were observed foraging there. The Exmouth Plateau also had relatively high occupancy (overlapping with the 50%UD), but by just one tagged whale. This whale was the westernmost of all tracked whales but the passive acoustic analysis showed high density of pygmy blue whale units and singers in this area on the line of seismometers deployed off NW Cape in 2014, also supported by Gavrilov et al. (2018). However, the sample size of tagged pygmy blue whales is small and they were tagged at sites close to the Australian coast, and largely followed the Australian shelf edge and slope. McCauley and Jenner (2010) suggest many pygmy blue whales may not follow this pattern and may migrate in deeper waters of the Indian Ocean, as evidenced by acoustic detections of pygmy blue in the southern Indian Ocean as far west as 74° E (Samaran et al., 2013). This may also account for the apparent discrepancy between the shelf use calculated from tagged whales and that calculated from the passive acoustic data and suggests more research focus is needed to substantiate our conclusions regarding use of the NW Shelf.

Our analysis of the satellite tracking and acoustic data suggest that pygmy blue whales may not use the area around Scott Reef as intensively as the areas off Perth Canyon and NW Cape, even though a foraging BIA is defined there. However, some limitations of the data and the outputs mean that the relative importance of Scott Reef is still unclear. For example, although the acoustic data underlying our distribution model is at a resolution comparable to the satellite tracking data, i.e. the range from Scott Reef noise loggers to whales were several 10's km, the gridding of the data for modelling densities of singing whales/units that we provide is at a much coarser resolution. In relation to the satellite tracking data, a number of satellite tags stopped transmitting shortly before, or just after, arriving at Scott Reef. One whale tagged off NW Cape (#182665) came to within approximately 100 m of Scott Reef (arriving on 15 June). At this time the tag provided 18 location estimates, 15 of these were Argos class A and B (~10 km accuracy (Hoenner et al., 2012)) and three were fastlocGPS with 4 (n = 1) or 6 (n = 2) satellites used to obtain the fix. Based on the 50th percentile, this equates to 37 m and 18 m accuracy respectively. Although this whale did not exhibit foraging movement behaviour, the time spent off the southern end of Scott Reef was the longest (~half a day) compared to the time spent along the rest of the track. However it did appear to be moving northward after this, but the tag went offline ~18 km north of Seringapatam Reef two days later. As such, it is not clear whether this whale would have spent additional time in the Scott Reef area. Two other tagged whales (#98135 and #123229) passed in the vicinity (within 28 and 44 km, respectively) of Scott Reef. It should be noted that these tags provided Argos locations only (at best < 250 m and at worst > 1500 m (although the SSM accounts for location error)) and in the case of the former, the tag was programmed with a 6-hour duty cycle. In addition, a further two whales (#182657 and #182671) were following a similar pathway to #182665 but stopped transmitting around Rowley Shoals. The presence of pygmy blue whales has been consistently recorded using passive acoustics across seasons in the Scott Reef area and in the 400 m depth channel separating the Scott Reef northern and southern lagoons (McCauley, 2011) and significant quantities of krill have been observed in this channel during the period of the southern migration (Sutton et al., 2019).

As tag deployment duration was variable, our calculations of the 50% UDs and important areas may have resulted in bias towards areas with more data. For example, many of the whales tagged at Perth Canyon only provided data for the SW region, fewer provided data for the NW region and even fewer whales provided data for Indonesia. Our tagging campaign at NW Cape alleviated this issue for the NW region, however there were still fewer whales providing data for the more northern sections of the NW and Indonesian waters. Although there are ways to counteract this bias such as by dividing by deployment duration, this can result in other biases and so was not used here. Thus, with more data, the important areas in Indonesia are likely to be larger than those presented here.

Although here and elsewhere (e.g. Recovery Plan and NCV Atlas), foraging areas are depicted as static, they are probably not entirely stable over time and depend largely on their prey (Pendleton et al., 2020) distribution which in turn depends on dynamic oceanographic features (Santora et al., 2011; Hazen et al., 2017). Thus, these areas are also likely to become more variable into the future with climate change (Hazen et al., 2017, 2013) suggesting a need for dynamic management approaches.

Interestingly, one of the whales tagged in the Perth Canyon travelled south instead of north towards Indonesia. This suggests that not all whales travel north at this time of the year (April/May), however more satellite tracking data are needed to confirm this.

The spatial modelling shows that singing whales are more likely present off the NW coast of Australia from April to July with low/no density occurring during August to October and only low density from October to December. This suggests that pygmy blue whales either: (1) may not sing as much on the southern migration compared to the northern migration (2) travel faster/have shorter residency times on the southern than northern migration; (3) use different migration routes to travel south; or (4) some combination of these factors. There was some suggestion that the whales had a shorter residency time on the southern migration, at least for one of the two whales that provided data on the southern migration (10 days spent compared to the mean of 19 days on the northern migration). We also recorded faster southern travel speeds compared to northern travel speeds, but this has a limited sample size (n = 2), not suitable for statistical comparison.

After month, SST was the next most important predictor of pygmy blue whale unit and singer densities. There was a moderate density of singing whales between 22 and 26 °C with a peak in density at SSTs of ~27 °C and rapidly dropping off around 28 °C with the decline exceptionally steep for unit density with another peak thereafter, again greater for singing whale density. Previous studies have suggested that SST is an important predictor in pygmy blue whale habitat selection (Gill et al., 2011) and foraging behaviour (area restricted search behaviour, ARS) in the Bonney Upwelling region, with ARS associated with SSTs between 14 and 17 °C (Möller et al., 2020). Such cool surface temperatures are not often observed in north-west Western Australia. In addition, our response variable was not movement behaviour (i.e. ARS) but density of singing whales, therefore our prediction may be more related to habitat preference of singing rather than foraging whales.

The spatial patterns in densities of both singers and units were slightly different. This may be related to whales introducing new song types with shorter repetition intervals when more whales are present (Jolliffe et al., 2019). In addition, songs have shorter phrases in higher background noise conditions and in deeper water (Jolliffe et al., 2021). Such changes in the whales' singing behaviour mean that patterns between singer and unit densities may vary in different conditions.

Two satellite tracked whales, both of which completed round trips back to the tagging areas, spent a high proportion of their time in the Banda Sea and outside of Australia's EEZ. In the context of a 365-day annual cycle, this constituted 25% (91 days) and 34% (124 days), respectively. Such high use indicates inter-jurisdictional management with Indonesia and Timor-Leste is necessary to ensure full and adequate protection for pygmy blue whales.

The deployment (whale #182657) that provided data on northern and southern migration ceased to provide position estimates in almost the exact same position on the northern and southern migration – near the Rowley Shoals (Fig. S8). Similarly, tag 182660 stopped transmitting between Geraldton and at NW Cape (Fig. S6). The loss of reception is likely, in part, due to initiation of relatively fast, directed migratory movements with potentially short surface intervals at approximately the same location. Both these tags was also deployed low on the back (~1 m down from the dorsal ridge) so that the tag antennae may not have cleared the water as frequently (average of 4 location estimates per day for #182657 for the whole track whereas the others had 19 ± 5). Fastloc relies on Argos location data to give it seed location data to calculate the position estimate but for this tag, Argos locations were of low quality or absent. The later LIMPETS had a 15 s instead of 45 sond repetition rate, as we hypothesised that it may have played a role in earlier poor performance. However, as tag #182660 had a 15 s interval and also had a period of non-detection, it seems it was more related faster speeds and shorter surface intervals during migration and that these deployments were relatively low on the back. It is noteworthy that these two tags provided the longest durations, suggesting that low tag placement may play a role in extending tag adherence.

After the period of being offline, #182657 (tagged at NW Cape 2020) and #123229 (tagged at Bonney Upwelling 2015) returned to a similar (to each other) location in north-west Western Australia (part of the 50% UD). In addition, they appeared to forage there as evidenced by low move persistence. Both whales then proceeded to follow the same/similar northern migration path suggesting at least, in some sections of the offshore waters of the coast, that they might follow a similar path on the southern and northern migration as previously shown for blue whales in California (Abrahms et al., 2019), and some other populations of mega-fauna (Bradshaw et al., 2004). These issues aside, in some cases the less invasive LIMPETs provided deployment durations equal to, or better than, invasive implantable satellite tags. However, it is noted that implantable satellite tags have since undergone technological improvement (implantable tag data used here was collected 2009–2015).

## 5. Conclusion

This study has generated new satellite tracking and acoustic data which, when combined with the other contemporary tracking and acoustic datasets off the coast of Western Australia, significantly improve our understanding of pygmy blue whale movement in the region. Although we are focussed on the south-east Indian ocean population of pygmy blue whales and the designated protected areas therein, our approach of identifying important areas is transferable to any population and region. The Australian Government may now consider this quantitative assessment of important areas in future reviews of the BIAs. Failure to define these areas effectively may impede the rate of population recovery if anthropogenic activities result in displacement from significant foraging areas. Further pygmy blue whale satellite tag deployments are still required to understand the relative importance of the Foraging BIA off Scott Reef, to define the important areas in Indonesia and those used on the southern migration with more certainty, and to provide data for future monitoring of habitat usage and modelling based on dynamic ocean management approaches.

## 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.

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### *Ethics statement*

Whales were approached and tagged under the following permits issued to CWR: Commonwealth EPBC 2018-0005; Commonwealth Marine Parks #PA2018-00098-1; DBCA AEC Permit 20167-48, DBCA Scientific Permit #TFA 2019-0134, and DPIRD Scientific Licence U 217 / 2020 – 2022. The authors acknowledge the Australian Defence Department, specifically Chris "Daffy" Donald, Wayne Bennett and Steve Cuffe, for making available the opportunities to conduct these studies along with the creators of the *RV Whale Song* acoustic tracking equipment from L3 Oceania and Sonartech Atlas.

*Data statement*

The data collected by this project will be made publicly available on the AIMS data portal. We are not at liberty to share the other datasets provided for use here as we are not the custodian of those datasets.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02054.

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