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Telemetry-based home range and habitat modelling reveals that the majority of areas important for pygmy blue whales are currently unprotected

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ABSTRACT

Marine migratory species tend to be overlooked in marine spatial planning due to limited knowledge of their habitats and migration pathways, resulting in a disconnect between animal migration ecology and spatial management decision making. The aim of this study was to predict the migratory corridors, suitable habitats and use of marine reserves by pygmy blue whales and overlap with marine traffic. Firstly, based on available telemetry data, we analysed the home ranges, core-use areas and migratory corridors using Brownian Bridge Movement Models. Secondly, we predicted suitable habitat by modelling telemetry data against environmental predictors using Maximum Entropy modelling; and lastly we geometrically overlaid home ranges and suitable habitats with designated migration lanes, marine protected areas and marine traffic. Consistent movement of pygmy blue whales from Western Australia to the Banda and Molucca Seas in Indonesia demonstrated a high level of connectivity between the two regions. There is a discrepancy between the designated migration lanes for large whales in Indonesian marine spatial planning and migration routes suggested by this study. The home range analysis and habitat models revealed that large areas of the migration corridors, core-use, and suitable habitats are currently not protected, particularly along international waters and within the Banda and Molucca Seas. The results can aid marine conservation planning by delineating the important areas and areas with high marine traffic density to optimise migratory species protection.

1. Introduction

Identifying movement patterns, distribution, and habitat use of highly migratory marine species represents a vital component for their effective conservation management (Costa et al., 2012; Schuster et al., 2019). Conservation management including area-based management such as Marine Spatial Planning (MSP) and Marine Protected Areas (MPAs) (Garrigue et al., 2015) provides spatial protection for species from anthropogenic threats (Scales et al., 2017). Our understanding of oceanic species movement is limited (Rosenbaum et al., 2014), yet it is imperative for determining the extent of habitat connectivity since species movement usually encompasses large geographical ranges, both within and beyond national waters (Dunn et al., 2019), and varies depending on different species life stages (Dulau et al., 2017). Unfortunately, due to limited knowledge, marine migratory species tend to be overlooked in conservation management (Hooker et al., 2011), which enables a disconnect between animal movement science and conservation policy and decision-making (McGowan et al., 2017). A key issue for the conservation of migratory species is the identification of important habitats throughout the annual cycle, including 'core-use areas' where individuals spend a lot of time and 'corridors' used during migration.

Information on cetacean species around Indonesia was primarily

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based on whaling operations (Sahri et al., 2020b; Townsend, 1935), strandings (Mustika et al., 2009), and incidental sightings (Rudolph et al., 1997). Only recently have cetacean monitoring programs been conducted at several sites in Indonesia (Kreb, 2004; Ender et al., 2014). Recent cetacean records are mainly collected by coastal boat surveys, particularly with platforms of opportunity or incidental observations (Sahri et al., 2020c), as well as limited-coverage aerial surveys, and telemetry data is lacking. Achieving a more detailed understanding of cetacean movement has been difficult, because they are elusive species and highly mobile (Horton et al., 2017). Boat and aerial surveys are restricted to areas and seasons where the surveys occur (Olsen et al., 2018), meaning data on movements across the ocean basin and in remote areas are extremely limited. Alternatively, telemetry data, as in the current study, provides movement data over large distances and long-time spans (Costa et al., 2012) for individual animals (Riekkola et al., 2019) that spend most of their lives away from direct observation (Harrison et al., 2018), with reasonable resolution and accuracy (Irvine et al., 2014).

A satellite tagging study of a marine migrant, the pygmy blue whale (*Balaenoptera musculus brevicauda*, hereafter PBW), which passes Indonesian waters, revealed basin-scale oceanic migrations and full latitude range of the Indian Ocean from West Australia to the Banda and Molucca Seas, Indonesia (Double et al., 2014). Like other baleen whales, the seasonal movement patterns of pygmy blue whales are traditionally thought to occur between productive high-latitude cold feeding areas in summer to oligotrophic, tropical or sub-tropical warm calving and mating areas in the winter (Bailey et al., 2010). Double et al. acquired many telemetry records, although the data have not yet been used for home range analysis and habitat modelling. There are only a few publications describing PBW's migration routes, seasonal distribution patterns and environmental variables determining the species distribution (Möller et al., 2020; Thums et al., 2021). Therefore, the current study provided the potential for improved knowledge on PBW ecology, mainly regarding its home range (core-use areas and migration corridors), spatial distribution, potential habitat, and seasonal preference.

PBW is one of the least known whale species, and in the early 1960s the PBW was recognized as a subspecies separated from Antarctic blue whales (Branch et al., 2007a; Kato et al., 1995; LeDuc et al., 2007). Historically, PBW occurred mainly north of 52° S (Branch et al., 2007a; Kato et al., 1995). The whales were commercially exploited in the 20th century and their status is currently listed as 'Data Deficient' in the IUCN Red List of Threatened Species (Garcia-Rojas et al., 2018). The number of individuals reduced from a possible 12,000–13,000 animals in the pre-whaling era to very low levels during the whaling era, before increasing again due to the whaling moratorium (~4000 animals in the early 1970s), although the current population is still unknown (Branch et al., 2004). Their original abundance was probably lower than that of Antarctic blue whales, but is likely less depleted at present (Branch et al., 2007b). Since the whales pass through many areas, their exposure risk is higher, mainly from human activities such as hydrocarbon exploration and oil/gas infrastructure (Di Iorio and Clark, 2010), shipping traffic (Priyadarshana et al., 2016), fisheries (Read et al., 2006), and pollution (Vegter et al., 2014).

To adequately conserve whales, including PBW, entire migration routes should be managed. Indonesian regulations mandate incorporating marine biota migration routes as lanes in provincial MSP establishment and their critical habitats in MPA designation (Ministry of Marine Affairs and Fisheries, 2008; Sahri et al., 2020a). However, hitherto there is no scientifically accepted method in determining these lanes. The representation of the species distribution and movement in management areas is not well known and their efficiency in providing proper habitat protection needs to be evaluated. This study, therefore, investigates how to better perform lane allocation in an MSP and the zoning system design of an MPA. Next, spatial assessments are necessary to evaluate whether species critical habitats are already protected by the managed areas (MSP and MPAs) (de Castro et al., 2014). Still, assessing the extent of coverage offered by these reserves is important to unveil the extent of the overlap. Until now, the use of MPAs in Indonesia by migratory species has not been studied, which makes it unclear how much of the important seasonal habitats are protected, as these habitats have never been identified.

This study aimed to assess the relevance of current MPAs for PBW protection by identifying their overlap with PBW home ranges and suitable habitats. Home ranges include migratory corridors and core-use areas of species individuals and suitable habitats will be identified using available telemetry data. Our results can be used to guide conservation and management planning efforts for PBW in Indonesia and can serve as a model for assessing the representativeness of protected areas for whales in other parts of the world where telemetry data are available.

2. Materials and methods

2.1. Study area

The study area ranges from Western Australia to East Indonesian waters from 1° N–36° S and 109–132° E (Fig. 1). The area has a diverse and complex submerged topography; a wide continental shelf extends from the Australian shorelines with deep waters occurring far offshore; in contrast, a narrower continental shelf is found in East Indonesia with water depth increasing abruptly from the shelf edge relatively close to the shoreline. Both Indonesian waters and Western Australia are situated in an upwelling system with high productivity (Steinke et al., 2014; Rennie et al., 2009).

2.2. Telemetry data

We used the telemetry dataset published in Double et al., 2014, which describes the movements of eleven pygmy blue whales that were tagged in the Perth Canyon, Australia in 2009 and 2011 (Table S1). Erroneous locations had been filtered from this dataset based on speed, distance and angle (Freitas et al., 2008). Our focus was the migration of the whales from Australia to Indonesia. Thus, a subset of positions ($n = 95$) from one individual (tag 98,135) in southern Australia was excluded, since it did not migrate in that direction. The tag of this individual whale previously experienced a three-month signal pause in which locations were not transmitted from the last reported location in the Banda Sea, Indonesia (Double et al., 2014).

2.3. Home range analysis

We used a Brownian Bridge Movement Model (BBMM), an advanced kernel method that takes into account: (i) the level of uncertainty of the recorded locations, (ii) the trajectory in between reported locations, and (iii) minimizes temporal and spatial autocorrelation of the tracking data (Horne et al., 2007). The BBMM requires the sequence of time-specific location data, the estimated error associated with the location data, and grid-cell size for the output (Horne et al., 2007). The error of locations was assigned by the Argos system (Argos, 2016), and for our dataset it ranges between 0.25 and >1.5 km (Double et al., 2014). We chose 5 km for the error value, which was a reasonable estimate for our Argos dataset, and a cell size of 10 km, as a compromise of desired spatial resolution and computing time. We used 90% probability for migration corridors (higher probabilities can include more extraneous or transitory locations [Börger et al., 2006]); and 50% probability for core-use areas. Home ranges were assessed per individual and were combined by overlaying the areas for each probability and count the number of individuals per area. From these arrangements the overall merged home ranges based on migration corridors and core-use areas were constructed representing population-level space use (Pagès et al., 2013). We used bathymetry (0 m depth) as a mask to prevent home ranges being estimated over land. BBMMs were calculated in R package using the 'brownian.bridge' function (https://www.rdocumentation.

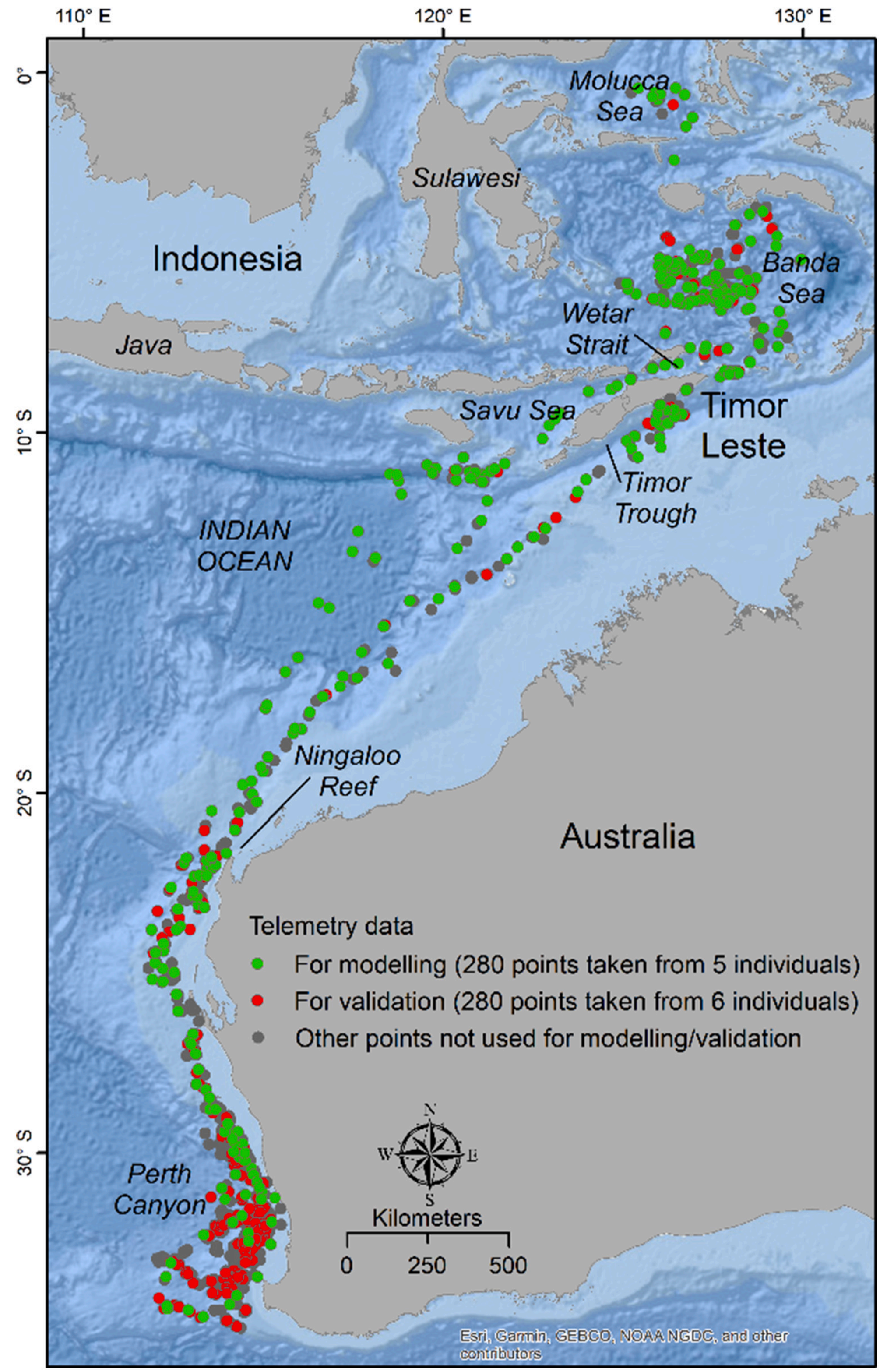


Fig. 1. Pygmy blue whale telemetry study area ranging from the western Australian to the eastern Indonesian waters. The different colours of the telemetry data points indicate how these are used in the habitat modelling. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

org/packages/BBMM/versions/3.0/topics/brownian.bridge).

For home range analysis, data from all eleven animals was used, except the data subset that was excluded in Section 2.2. We used all individual tracks, including those of incomplete migrations (e.g. whales that only occur around West Australia), because we deem all trajectories to contribute important information about the migration ecology of the species.

2.4. Habitat suitability modelling

Maximum entropy model (Maxent) was applied to assess PBW habitat preference and spatial distribution. Maxent is a powerful predictive modelling method when there are presence-only data and no absence data (Phillips et al., 2006), with small and unbalanced sample sizes (Elith et al., 2006), and when data are prone to positioning errors (Graham et al., 2008), all of which is often true for satellite telemetry data. Maxent coupled with proper data sub-sampling in cases where a small number of individuals have been tracked (Edrén et al., 2010) makes it a forceful tool for the investigation of species-habitat relationships.

We performed the habitat modelling using Maxent software version 3.4.1 (https://biodiversityinformatics.amnh.org/open_source/maxent). For the Maxent settings, we followed Sahri et al., 2021. For the Maxent modelling, only data from five individuals was used (Table S1). The telemetry data per individual is sequentially correlated, therefore we used the following steps for sampling the whales' positions with the aim of reducing spatio-temporal autocorrelation. Firstly, we removed all positions from the first 2 days after tagging to further reduce the spatial and temporal influence of the release site (Edrén et al., 2010). Secondly, only one position (the best location class) per animal per day was selected manually (Mikkelsen et al., 2016). Lastly, we rarefied the positions by excluding positions that were located <10 km apart using SDMtoolbox (Brown et al., 2017). These steps reduced the number of location data points from the original 1378 locations to 280 locations.

We split the telemetry data into seasonal strata. We explored different models i.e. 'all year' model (n = 280 locations) and two separate seasonal models: Inter-monsoonal/Transition 1 season (T1 season, March–May, n = 140 locations) coinciding with the Austral autumn, and SE monsoon season (June–August, n = 140 locations) coinciding with the Austral winter. Because our focus was on the broad-scale habitat use of PBW, we decided not to run separate models by individual whale, but rather to run one model for all individuals.

Eleven submerged topographic predictors and three oceanographic predictors were initially prepared based on the expected ecological relevance to PBW habitats in the study area (Table S2). The rationale of the selected predictors, sources and derivation process of the predictors are given in Table S2. Prior to modelling, we checked the multicollinearity among candidate predictors which could potentially overshadow the effect of a particular predictor. Only predictors with Spearman's correlation values ≤0.7 were used in habitat modelling (Table S2). Four predictors were finally selected for 'all year' and T1 season models, i.e. slope, distance to −1000 m isobaths, distance to shelf, and sea surface temperature. The same predictors, and in addition the chlorophyll-a concentration, were selected for the SE monsoon model.

The performance of our Maxent models were assessed using multiple model evaluation matrix due to none are perfect when true absence data is not available (Sahri et al., 2021). They are the Area Under Curve (AUC) of the receiver-operating-characteristics (ROC) (Phillips et al., 2006), True Skill Statistic (TSS) (Allouche et al., 2006), sensitivity and specificity (Raes and ter Steege, 2007).

2.5. Overlap of areas important for PBWs with marine reserve use, designated migration lanes and shipping traffic

To evaluate the use of existing MPAs by PBWs, we calculated the areas (size and proportion) used by the PBW (i.e., home range [including migration corridors and core-use areas from BBMM], and suitable habitats from Maxent, together as areas important for PBW) that fell within existing MPAs versus unprotected areas. The area calculation was performed in ArcGIS 10.6.1. Boundary data of MPAs in Indonesia were obtained from the Ministry of Marine Affairs and Fisheries, while the data for Australia were downloaded from the UNEP-WCMC website (https://www.protectedplanet.net/country/AU). To assess the suitability of designated migration lanes for large whales within Indonesian MSP and potential conflict with marine traffic, we overlaid the lanes with the migration corridors from the BBMM and shipping density. The discrepancies between both spatial functions were then investigated. The designated migration lane map encompassing the Savu, Flores and Banda Seas was obtained from the Authority of National Aquatic Conservation Areas (BKKPN) Kupang, Indonesia. Shipping density data were obtained from a global map of shipping traffic (Halpern et al., 2008).

3. Results

3.1. Analysis of movement patterns of pygmy blue whales

All individuals in Australian waters in the Perth Canyon traveled northward within 100 km of each other (Figs. 1 and 2). Individual whales separated over a greater distance (>500 km apart) from each other from the Ningaloo Reef, particularly in Indian Ocean international waters. Whales used two different routes, across the Savu Sea and the Timor Trough, respectively. The tagged whales showed relatively high residency in the Banda Sea, which they occupied for >3 months through the SE monsoon season, coinciding with Austral winter. One individual even dispersed to the Molucca Sea. Interestingly, PBWs followed nearly similar migration paths within and between years, mainly along the Western Australian coastline, reflecting a fidelity of migratory paths.

3.2. Home ranges (migration corridors and core-use areas)

Migratory corridors and core-use areas between the Western Australia and Indonesian waters were clearly identifiable from the BBMM home range analysis (Fig. 2). The individual home ranges varied greatly (4-fold) in size, as did core-use areas (40-fold) (Table 1). In addition, the shape of home ranges was highly variable among individuals, and differed in degree of overlap (Fig. 2a, b). The overlapping individual home ranges represent areas that were used by several individuals during migration. Ten out of eleven whales had overlapping home ranges (Fig. 2a) and eight whales had overlapping core-use areas (Fig. 2b), both mainly around the Western Australian continental shelf.

The combined home ranges of the eleven whales covered most of the Australian EEZ, all Timor Leste EEZ, and a part of the east Indonesian waters (Fig. 2a, c). The combined home ranges (BBMM 90%) that also function as migratory corridors comprised ~2.2 million km^2 (Table 3). The core-use areas (BBMM 50%) of all combined individuals consist of five smaller aggregation areas located in the Western Australian waters, three localised areas in Indian Ocean international waters (counted as 1), and the Timor Trough, Banda Sea, and Molucca Sea (Figs. 2b). The combined core-use areas comprise ~0.8 million km^2 (Table 3), accounting for 36.6% of the total home ranges.

3.3. Habitat suitability models

The performance metrics of the Maxent modelling generated using both internal and external validation data (Table 2) indicate good predictive power and model robustness with AUC and sensitivity values > 0.75 and TSS values > 0.4. Model sensitivity for 'all year' and two seasons was higher than its model specificity (Table 2), indicating that the model performed well in predicting where whales occurred (Thorne et al., 2019).

The predicted spatial distribution of PBWs for 'all year' and two seasonal models were visually dissimilar, indicating clear seasonal movement patterns (Fig. 3). The distribution in the 'all year' model aligned quite well with telemetry data, except for a small part in the Perth Canyon and Indian Ocean (Fig. 3a). The 'all year' model also predicted highly suitable habitats in areas where telemetry data were not recorded, such as in the southern Java and southern Sulawesi Seas (Fig. 3a).

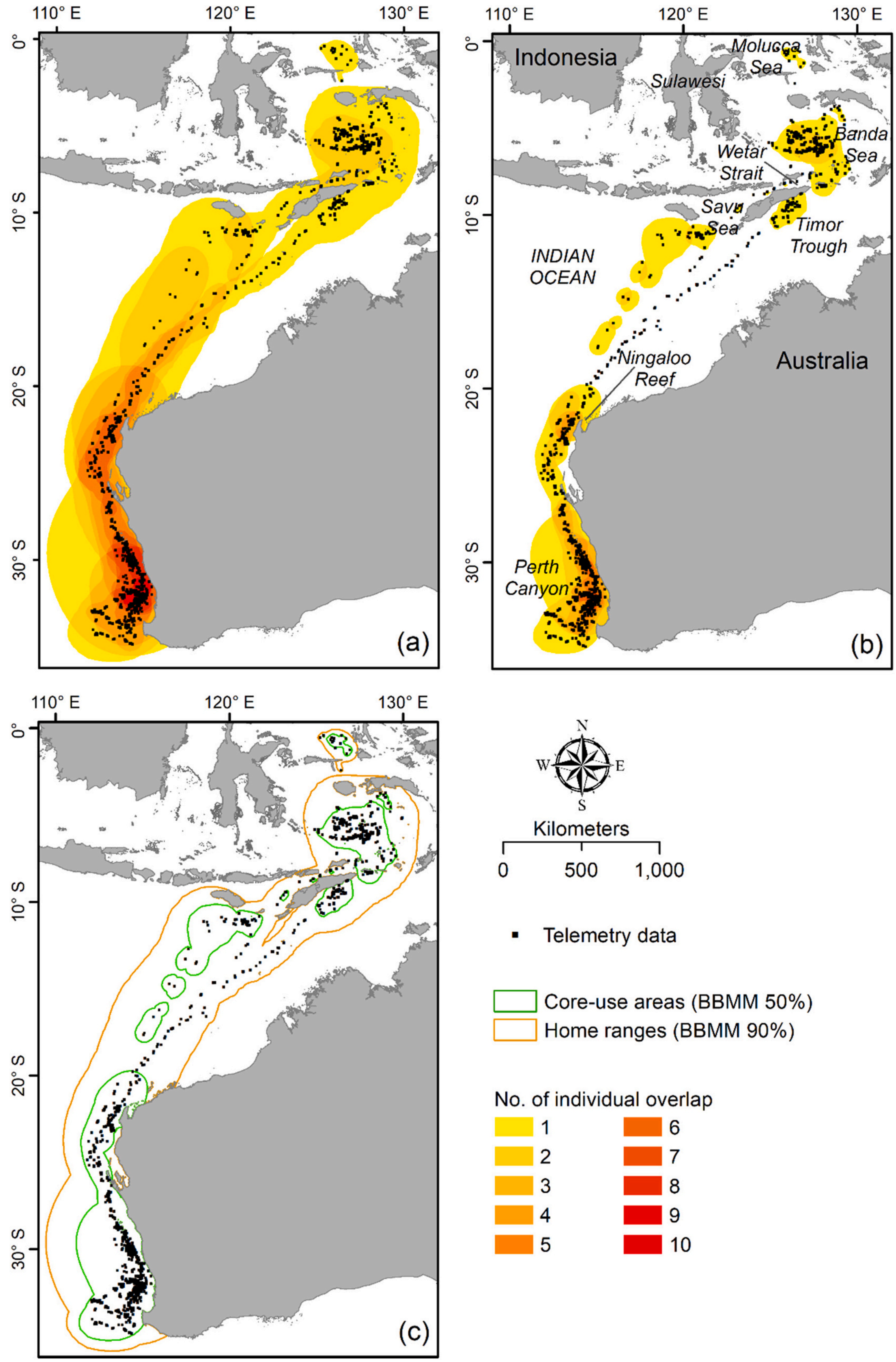


Fig. 2. The number of overlapping areas of individual whales in (a) home ranges (including migration corridors) and (b) core-use areas indicated by gradual colours from yellow to red. The combined home ranges (c) (Brownian Bridge Movement Model-BBMM 90% isopleths, orange polygons) and core-use areas (BBMM 50% isopleths; green polygons) of 11 satellite-tracked pygmy blue whales in the study area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Area (km^2) of individual Pygmy blue whale home ranges (migration corridors and core-use areas).

#	Tag ID	Area of individual home range (km^2)	
		Migration corridors (BBMM 90%)	Core-use areas (BBMM 50%)
1	53734	77,385	16,394
2	53791	627,523	248,358
3	88731	35,756	8948
4	88739	623,759	131,126
5	88740	99,380	31,577
6	98106	755,396	318,291
7	98108	1,286,448	328,466
8	98115	180,083	43,085
9	98134	244,392	76,997
10	98135	964,815	188,238
11	98141	39,143	11,317
Mean		448,553	127,527
SE		129,226	37,401
Max		1,286,448	328,466
Min		35,756	8948

BBMM — Brownian Bridge Movement Model.

Table 2
Maxent model performance metrics (mean ± SD).

Seasons	Metrics	Internal validation (test data)	External validation
All	AUC	0.853 ± 0.015	0.832 ± 0.039
	TSS	0.506 ± 0.039	0.473 ± 0.097
	Sensitivity	0.877 ± 0.037	0.899 ± 0.001
	Specificity	0.628 ± 0.024	0.574 ± 0.097
T1	AUC	0.881 ± 0.013	0.902 ± 0.038
	TSS	0.484 ± 0.054	0.583 ± 0.163
	Sensitivity	0.848 ± 0.096	0.900 ± 0.001
	Specificity	0.637 ± 0.069	0.683 ± 0.163
SE	AUC	0.953 ± 0.006	0.951 ± 0.010
	TSS	0.720 ± 0.050	0.779 ± 0.037
	Sensitivity	0.874 ± 0.017	0.900 ± 0.001
	Specificity	0.845 ± 0.058	0.879 ± 0.037

Abbreviations: All — all year, T1 — Transition 1 season (March–May); SE — Southeast monsoon season (June–August), AUC — Area Under Curve of receiver-operating-characteristic, TSS — true skill statistics.

The seasonal shift in telemetry records to the north was also reflected in the seasonal model outputs. During the T1 season, a strong presence of PBWs was predicted in the Western Australian waters (Fig. 3b). In the Indian Ocean, an absence of distribution was predicted between Australia and Indonesia, while telemetry records still occurred there (Fig. 3b), bordered by a narrow distribution with moderate predicted values in the south of Indonesian islands. During the SE monsoon, the predicted whale distribution was concentrated in Indonesian waters, mainly in the Banda Sea, which aligned well with the telemetry presence data (Fig. 3c).

Sea surface temperature (SST) and distance to shelf were the most important predictors in determining environmental niches for the PBWs in all model outputs, with a permutation importance of >0.457 and >0.227 respectively (Fig. 4). Slope (0.130) and chlorophyll-a concentration (Chl-a, 0.107) were subsequently also the next important predictors for the 'all year' model and SE model (Fig. 4). The shape of the response curves of SST and slope in all models was different, while that of the distance to shelf and distance to the −1000 m isobath was generally similar (Fig. 4). The 95% confidence intervals in the response curves based on the 10 bootstrapped replicates are narrow (less vary among replicates) for all predictors except slope.

The predicted suitability of PBW habitats increased with low SST (∼25 °C) in the T1 season, and with higher SST (∼28 °C) in the SE monsoon season (Fig. 4b, c); this is reflected in the 'all year' model (Fig. 4a) as a bimodal distribution with a low (23 °C) and high (29 °C) SST. In the 'all year' and SE models, the predicted habitat suitability increased with an increasing distance to a shelf (∼100 km), while for the T1 model a closer distance of only ∼30 km was found (Fig. 4d–f). For both the 'all year' and SE models the optimal slope reaches ∼10% which relates to the complex deep seafloor. However, it was close to ∼1% in the T1 model which relates to the gentle undulating continental shelf (Fig. 4g–i). In the 'all year' and two seasonal models, the predicted suitability was negatively associated with distance to the −1000 m isobath, with high predicted whale occurrence closer to this feature at a distance of ∼30 km (Fig. 4j–l). Finally, for the SE model the high predicted suitability occurred in offshore waters with low Chl-a (∼0.3 mg m^{-3}), although most of the Chl-a at the study area was in fact low, and the few very high Chl-a areas only occurring near coastlines that were unfavoured by the whales.

3.4. Overlap with MPAs, designated migration lanes, and marine traffic

Overall, <20% of the PBW's migration corridors and core-use areas, and < 13% of the suitable habitats identified in this study are currently protected in MPAs, mainly in Australia (Table 3, Fig. 5a). Further, none of the migration corridors, core-use areas, and suitable habitats in international waters were located within MPAs. The majority (>80%) of migration corridors and core-use areas are currently not protected by existing MPAs, mainly in Australia (∼40%) and Indonesia (∼35%). A large area (60%) of suitable habitats within the Indonesian waters, mainly in the Banda Sea and southern Java, is likewise unprotected by existing MPAs. Moreover, almost 10% of the migration corridors are in international waters beyond national jurisdiction.

The designated migration lanes for large whales in Indonesian marine spatial planning (MSP) slightly deviate from migration routes found in this study, revealing that they do not match for PBW (Fig. 5b, c). For instance, the migration routes in the Wetar Strait, Timor Trough and Molucca Sea are not currently included in the designated migration lanes in Indonesia, although migration corridors occurred there (Fig. 5b, c; purple circles). The home ranges, core-use areas, suitable habitats, migration routes and designated migration lanes also overlap with some of the busiest shipping routes (>60 routes/km^2/yr) in the region (Fig. 5b, c).

4. Discussion

The current knowledge on movement patterns, distribution and habitat use of marine migrants is very limited, yet crucial for effective conservation management. In this study, we have successfully demonstrated the utility of telemetry data in identifying migration corridor width, home range, potentially suitable habitat, and seasonal environmental preferences for PBW migrating from Western Australia to east Indonesian waters. Using both home range and habitat modelling approaches, we unveiled that much of the PBW habitats across the study area were outside of the marine reserve systems. Here, we first discuss the PBW home ranges and habitats, then asses their overlap with conservation areas, designated migration lanes and potential conflicts with marine traffic to optimise protecting the whale habitats. The caveats and limitations of the data and methods used in this study and their potential biases were also discussed.

4.1. Home range

We detected individual route preferences among whales during the migration in the Indian Ocean, but they ultimately converged towards the north along a wide corridor exceeding 500 km. This behavior was also recognized in other baleen whale studies, and is suggested to be related to prey availability in relation to the dynamic environmental characteristics of different areas (Dunn et al., 2019; Riekkola et al., 2019). Whether this also is the case for PBW needs further investigation. When entering Indonesian waters, the whales utilized two adjacent separate migration corridors: one to the Savu Sea, and another to the Timor Trough. Therefore, corridor width is important when defining

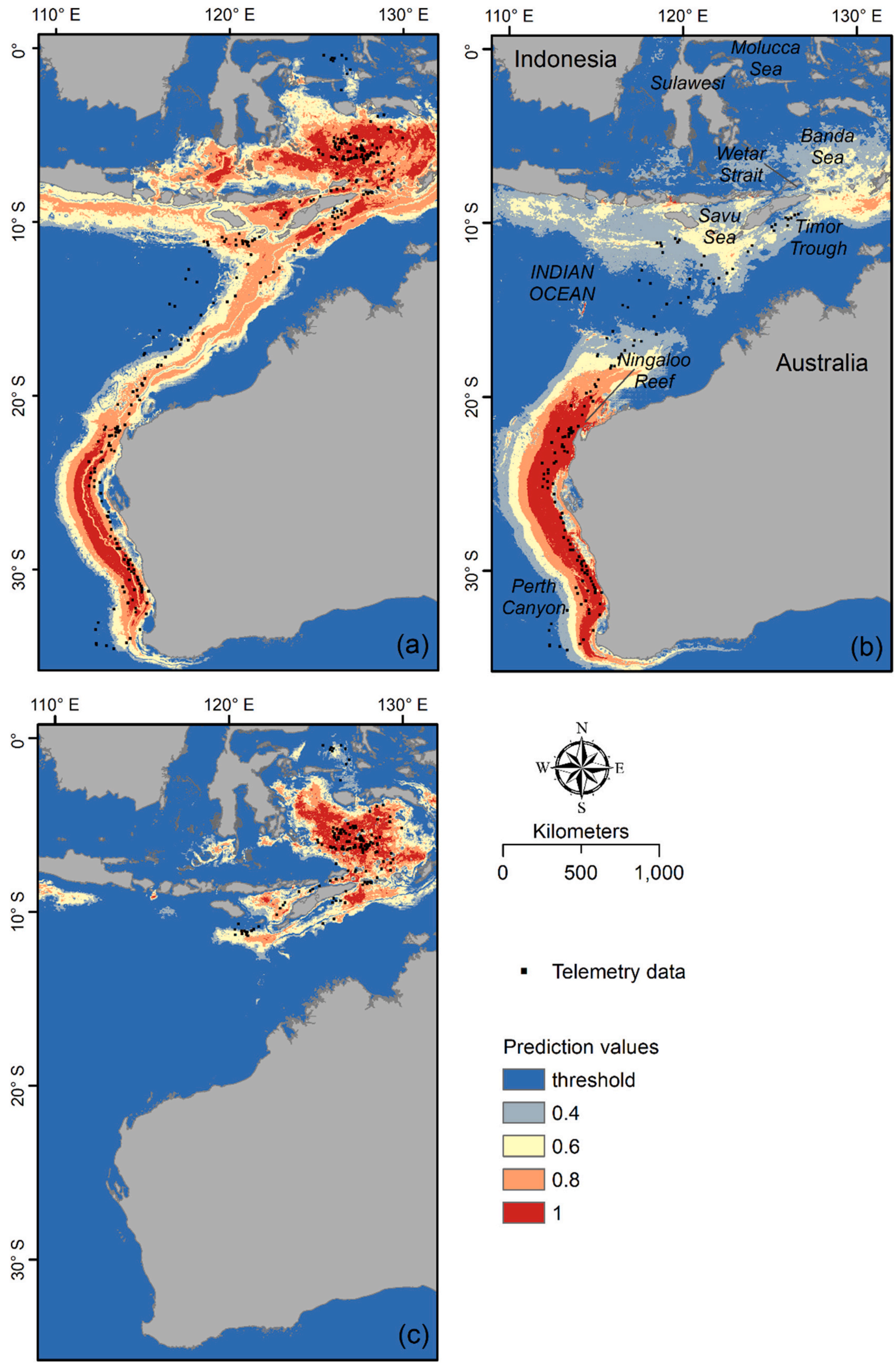
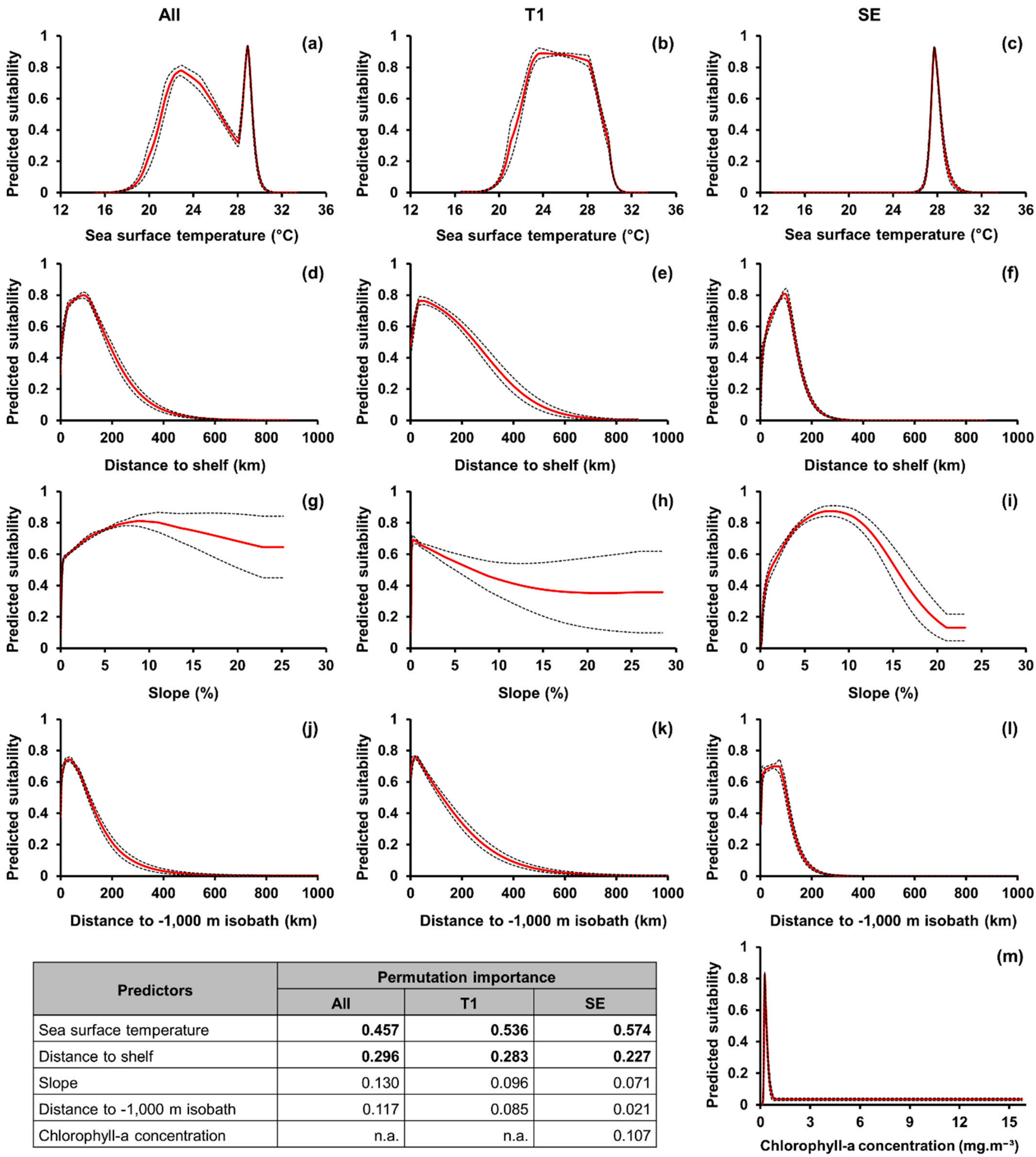


Fig. 3. Pygmy blue whale distributions as predicted by Maxent modelling for (a) all year and per season: (b) T1 — Transition 1 season (March–May) and (c) SE — Southeast monsoon season (June–August). The value of the predictions are classified into five classes ranging between 0 and 1. The 10th percentile training presence threshold indicates unsuitable habitats (dark blue areas). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Predictors	Permutation importance		
	All	T1	SE
Sea surface temperature	**0.457**	**0.536**	**0.574**
Distance to shelf	**0.296**	**0.283**	**0.227**
Slope	0.130	0.096	0.071
Distance to -1,000 m isobath	0.117	0.085	0.021
Chlorophyll-a concentration	n.a.	n.a.	0.107

Fig. 4. Response curves of the predicted suitability of pygmy blue whale habitats across the range of values for different environmental predictors. Red lines represent the mean response curve from 10 bootstrapped Maxent model replicates, while the dashed black lines represent 95% confidence intervals. Different response curves are presented for all year model (All, left panels) and per season: T1 — Transition 1 season (March–May; middle panels) and SE — Southeast monsoon season (June–August; right panels). The table presents the relative importance of each predictor in Maxent model outputs. In bold the two most important predictors that determine pygmy blue whale habitats. The relative importance value is rescaled to sum 1. n.a. — not available. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Overlapping area (km^2) and proportion (%) between home ranges (migration corridors & core-use areas) and Maxent-predicted suitable habitats against marine protected areas (MPAs).

	Home ranges (BBMM)		Suitable habitats (Maxent)
	Migration corridors (90%)	Core-use areas (50%)	
Within MPAs:	430,521 km^2 (19.3%):	151,124 km^2 (18.6%):	294,742 (12.9%):
– Indonesia	37,703 km^2 (1.7%)	3921 km^2 (0.5%)	59,889 km^2 (2.6%)
– Australia	391,860 km^2 (17.6%)	147,177 km^2 (18.1%)	234,008 km^2 (10.3%)
– Timor Leste	958 km^2 (<0.01%)	26 km^2 (<0.01%)	845 km^2 (<0.01%)
Outside MPAs*:	1,797,203 km^2 (80.7%):	663,143 km^2 (81.4%):	1,983,942 km^2 (87.1%):
– Indonesia	790,047 km^2 (35.5%)	272,692 km^2 (33.5%)	1,366,995 km^2 (60.0%)
– Australia	714,353 km^2 (32.1%)	332,290 km^2 (40.8%)	557,651 km^2 (24.5%)
– Timor Leste	75,076 km^2 (3.4%)	26,190 km^2 (3.2%)	57,760 km^2 (2.5%)
– International waters	217,732 km^2 (9.8%)	31,972 km^2 (3.9%)	1536 km^2 (0.1%)
Total	2,227,725 km^2 (100%)	814,267 km^2 (100%)	2,278,684 km^2 (100%)

Abbreviations: MPAs — Marine Protected Areas; BBMM — Brownian Bridge Movement Model.

* Areas outside MPAs are areas that fall within the EEZ waters of each country and international waters. The International waters are high seas beyond EEZ boundaries. The EEZ boundaries were obtained from the VLIZ Maritime Boundaries Geodatabase (Flanders Marine Institute, 2019); some boundaries are disputed.

migratory corridors in MSP and MPA designation.

Indonesian waters are potentially the winter breeding grounds for PBW populations (Double et al., 2014), although further investigation is needed. The seasonal latitudinal migrations of blue whales between winter breeding and foraging grounds at higher latitudes are also reported in the eastern North Pacific of the northern hemisphere (Bailey et al., 2010; Irvine et al., 2014). In our study, the PBWs show relatively high residency in the Banda Sea by wandering this localised area for >3 months during the SE monsoon season which coincides with the Austral winter. The wandering behavior and high residency in this putative breeding habitat may enhance individual reproductive success (Dulau et al., 2017) and is therefore relevant in possible temporal conservation management strategies for specific MPAs. The long residence periods of blue whales in certain areas also reflect foraging habitats (Etnoyer et al., 2006). The PBW migration routes were characterized by a series of core-use areas where whales travel slowly, connected by movement corridors through which whales travel quickly. The slow travel speed areas probably represent foraging areas (Bailey et al., 2010; Owen et al., 2016). Far-ranging movement between alternate foraging habitats is a favoured ecological strategy for blue whales in the North Pacific (Mate et al., 1999), which also are non-fasting animals with large energy requirements (Goldbogen et al., 2013). It is highly likely that their migration pathways are directed by the occurrence of multiple alternate feeding areas as well, but this has not been studied yet.

Our analysis showed that PBW individual home ranges and core-use areas vary greatly in size and shape, while the overlapping core-use areas clearly show relatively small aggregation areas where the tracked population as a whole spent quite a lot of time. Larger variations in movement trajectories and increases in the scale of movement from local to ocean-basin driven by species' behavioural differences will result in changes in BBMM variance (Horne et al., 2007).

The BBMM showed that most of the indicated core-use areas were typically situated over the continental shelf in Western Australia and in deep waters in the Indian Ocean, Timor Trough, Banda Sea and Molucca Sea. Extended periods of time spent in those areas indicate that whales are using these habitats extensively for other activity such as foraging (Sawyer et al., 2009), breeding or nursing grounds, although further research is needed to clarify this correspondence (Owen et al., 2016). Because some core-use areas and migration corridors were used by more individuals than others, this could be used to steer conservation prioritisation (Fig. 2b).

4.2. Habitat modelling

Our habitat suitability results (Fig. 3) indicated a distinct PBW seasonal movement pattern. The 'all year' model predicted a distribution with a high suitability of PBW habitat, also in several areas where telemetry data used in our study was not recorded such as in southern Java and southern Sulawesi. Subsequently, the occupancy of PBW in southern Java was proved by Möller et al. (2020). Given that a limited number of tagged PBW were used in our model, and that they represent a very small proportion of the population, it is possible that the model predicts distribution where there was no telemetry data recorded (Thorne et al., 2019). The suitable habitats could stay unoccupied due to anthropogenic disturbances, a matter that deserves to be further explored. Habitat models thus may provide more comprehensive information than telemetry recorded points alone for incorporating into area-based management tools such as MPA and MSP.

Unlike the SE season model output that predicted distribution closely related to the presence data, the T1 season model predicted a discontinuity in distribution in the deep waters of the Indian Ocean while there were some presence data recorded there. The environmental conditions (Table S3) of this relatively small sample size (n < 10% of total samples) that falls within these restricted areas are significantly different from that of the majority of the other records. This may explain why the Maxent model did not detect these relationships and subsequently predicted no occurrence. It is also possible that the whales react differently to their environment in stages of their migration so using the same relationships in the entire area may not match the actual situation (Guisan and Thuiller, 2005). Therefore, their unique environmental preferences were not recognized as the suitable habitat from the Maxent model outputs. This could occur because Maxent will give a higher habitat suitability score to an area that has similar environmental conditions as the majority of the training samples (Elith et al., 2011). The discontinuity in distribution could also be due to the absence of other predictors that better represent the habitat preferences of the species but are not accounted for in our models.

The key environmental predictor in explaining PBW distribution in all models was sea surface temperature (SST) (Fig. 4). The second most important predictor in predicting PBW distribution was distance to shelf, followed by slope and chlorophyll-a concentration (Chl-a). Further discussion on how each environmental predictor determine PBW distribution can be found in the Appendix Text S2.

4.3. Overlaps

Our results revealed gaps in PBW protection over large important areas including PBW's migration corridors, core-use areas and suitable habitats. The fact that (i) <20% of the PBW's important areas are currently protected by MPAs, and (ii) >80% of migration corridors and core-use areas, as well as (iii) 60% of suitable habitats in Indonesian waters, are located outside MPAs, demonstrates an obvious shortcoming of the MPA network for this migratory whale in Western Australia and Indonesia (Table 3). In addition, it is advisable to add the three important areas [points (i)–(iii); Table 3] that are not yet protected and the additional 10% of the migration corridors outside MPAs in international waters to the PBW protection framework of MPAs (Table 3). It is crucial, since hitherto Indonesia does not yet have a deep-sea and offshore (>12 nm) MPA. The size and shape of MPAs are a crucial feature for conservation management, with larger MPAs being relevant for protecting the

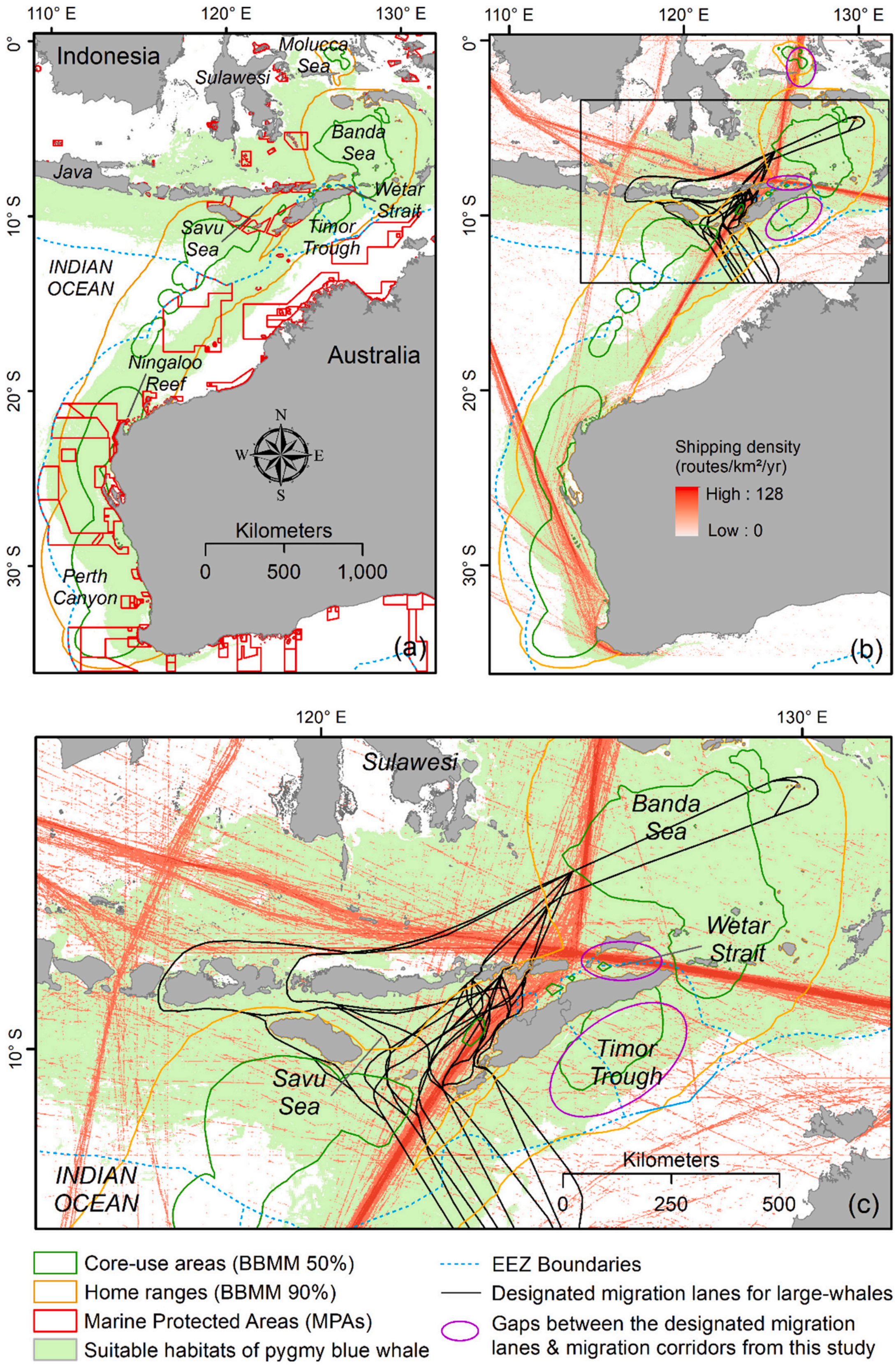


Fig. 5. The areal overlaps between home ranges (migration corridors), core-use areas and Maxent-predicted suitable habitats against: (a) marine protected areas (MPAs), and (b) designated migration lanes for large-whales in Indonesia, and marine traffic. Panel (c) is the zoom-in area of the black box in the panel (b). The exclusive economic zone (EEZ) boundaries were obtained from the VLIZ Maritime Boundaries Geodatabase (Flanders Marine Institute, 2019); some boundaries are disputed. Purple circles indicate important unprotected PBW migration routes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

migratory species (Lambert et al., 2017), although there has long been debate about the effectiveness of large MPAs for these species (Pala, 2013).

Ideally, data on the distribution of individuals throughout their life cycle would be available to allow MPA network design to include important breeding, foraging and migration corridors (Game et al., 2009; Hooker et al., 2011), therefore properly delineating spatial and temporal boundaries around important habitats (de Castro et al., 2014). Not all parts of the PBW life cycle (e.g. the return migration) were represented in our models because of absence of full life cycle telemetry data. A greater sample size that also covers full species life cycle is needed to more precisely identify the mismatches and to refine our insights about this migratory species. The initial design of an MPA should be informed by the movements and core-use habitats of the target species, to ensure that it covers sufficient critical habitats over its full biological cycle (Costa et al., 2012; Lambert et al., 2017). MPA networks consisting of small and large MPAs may increase their usefulness, although the level of restriction and associated enforcement in particular determine the efficacy of MPAs (Edgar et al., 2014).

We revealed clear discrepancies between the designated migration lanes for large-whales in Indonesia and actual migration routes as suggested by this study (Fig. 5b, c). For instance, migration corridors in the Wetar Strait, Timor Trough and Molucca Sea (Fig. 5b, c; purple circles) are not currently included within the designated migration lanes. This is important information for managers for improving future migration lanes for large whales and optimizing whale protection.

Since PBWs migrate seasonally, their foraging and migratory habitats often overlap with multiple anthropogenic threats at different times of the year. This would require mitigation measures over their entire range. For instance, the migratory corridors of PBWs along the Western Australia and Savu Sea largely overlap with the main shipping routes (Fig. 5b, c), since ships follow their habitual routes passing through MPAs in these areas. Mortality due to ship strikes is an important factor hindering the recovery of some whale populations from past overexploitation (Irvine et al., 2014). Our results on spatiotemporal distribution of PBW in relation to marine traffic could inform improved management protocols (e.g. time-area closures or traffic adjustment) to reduce ship-collision in areas where there is currently a lack of observer coverage and enforcement (Harrison et al., 2018).

4.4. Caveats and limitations of the used data and methods

Due to telemetry data availability, we used relatively small sample size in our study, thus more sample size would enhance the future research in reducing potential biases of model outputs (Hays et al., 2019). The methods used in our study (BBMM and Maxent) were chosen based mainly on data type and availability (Edrén et al., 2010; Horne et al., 2007), therefore comparing more methods (Elith et al., 2006) is a matter that deserves to be fully explored. The full explanation of the limitations of using telemetry data for home range analysis and habitat modelling can be found in the Supplementary Text S1.

4.5. Future perspectives and implication for management

Wide-ranging animals like PBW travel through the waters of multiple nations as well as in the areas beyond national jurisdiction (ABNJ) during different times of the year. This makes their conservation a challenge, requiring a coordinated action through multinational or international collaboration (Harrison et al., 2018; Hooker et al., 2011). The conservation of PBW is crucial, since the species was part of the commercial whaling hunt, the degree to which they have recovered is unknown, and their IUCN Red List status is not evaluated (Data Deficient). The PBW habitats and home ranges in this study, on the other hand, fall almost entirely within the EEZs of Indonesia, Timor Leste and Australia, making management for this species more straightforward through MPA establishment within EEZs. Such protection, however, is practically non-existent in most ABNJ or high seas, including several migration paths, where the lack of legal frameworks for making and enforcing MPA designations (Ardron et al., 2008) still hampers conservation efforts for marine migratory species.

Several international and regional initiatives regarding management of marine mammals are already established, and important steps forward can be made as discussed in Sahri et al. (2020a). This includes the recommendation for Indonesia to involve itself in regional collaborations and to be a full member of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and the International Whaling Commission (IWC). For some species or populations, collaboration among just a few countries stemming from local or regional collaborations could help conserve specific, especially resident, marine mammal populations (Harrison et al., 2018). The PBW habitats and home ranges revealed in this study have recently been recognized to be important for conservation by an ongoing international conservation initiative, namely the Important Marine Mammal Areas (IMMAs) (IUCN-MMPATF, 2019). IMMAs are recognized for their importance but do not receive any formal protection, unless declared as such by a national authority. This recognition highlights the need for protecting these important yet vulnerable areas through management measures following science-informed consideration.

Static area-based management approaches such as MPAs may still be unable to contribute sufficiently to migratory marine species conservation (Lewison et al., 2015) while still impacting the interests of marine stakeholders, although political, economic and social feasibility are always taken into account as well (Game et al., 2009). Recently, new dynamic management approaches have been proposed such as time-dependent area closures or dynamic MPA networks, as a compromise between human and animal interests (Hooker et al., 2011; Lewison et al., 2015). An example of this approach is the Whale Watch program, which although not established as an MPA, fulfils the criteria in terms of spatial protection of blue whales from ship strikes (Hazen et al., 2017). Dynamic MPAs that target predictable habitat traits, such as temperature fronts to delineate migration corridors of loggerhead turtles in the central Pacific, may be more appropriate for management (Hooker et al., 2011). Spatially explicit measures advised by real time surveys and tracking, e.g. right whale sightings and acoustic detections to inform shipping slow-speed zones in the eastern US (Van Parijs et al., 2009), are also another good example of dynamic spatial conservation. By applying these techniques, protective measures could therefore entail dynamic spatiotemporal boundaries, with seasonally implemented protection and adaptive coordinates for protection, representing an improvement over conventional MPAs (Sequeira et al., 2019). Limitations of dynamic MPAs do exist however, especially if they are implemented in situations with poor monitoring capacity and limited law enforcement.

Ethics statement

Ethical approval was not required for the current study because the data were obtained from existing biotelemetry programs. The original biotelemetry program was conducted strictly according to the Australian law (see Double et al., 2014).

Data statement

The original telemetry dataset is publicly available and can be downloaded via: https://data.aad.gov.au/metadata/records/AAS_2941_blue_whale_Argos_sda_filter_tracks.

CRediT authorship contribution statement

Achmad Sahri: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. **Charlotte Jak:** Data curation, Methodology, Formal analysis, Validation, Visualization. **Mochamad Iqbal Herwata Putra:** Conceptualization, Formal analysis, Investigation, Methodology, Resources, Validation, Visualization, Writing – review & editing. **Albertinka J. Murk:** Conceptualization, Methodology, Writing – review & editing. **Virginia Andrews-Goff:** Data curation, Formal analysis, Investigation, Methodology, Resources, Validation, Writing – review & editing. **Michael C. Double:** Data curation, Resources. **Ron J. van Lammeren:** Conceptualization, Investigation, Methodology, Validation, Writing – review & editing.

Declaration of competing interest

Authors declare no competing interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109594.

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