



# Evidence of likely foraging by pygmy blue whales in the Timor Trough during the late austral winter and early austral spring

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**ABSTRACT:** Understanding the behavioural context of wildlife movement patterns is imperative to the conservation of migratory species like cetaceans. The traditional model of baleen whale migration entails uninterrupted journeys performed throughout extended periods of fasting, during which individuals sustain the enormous costs of travelling from the poles to the tropics only from energy reserves acquired prior to departure. However, this 'feast and famine' paradigm is being challenged by increasing observations of supplemental feeding events along whale migratory routes. In this context, identifying the location of migratory stopovers is key to managing cetacean populations, particularly in data-poor ecosystems subject to changing ocean conditions. We report on likely foraging activity by migrant pygmy blue whales *Balaenoptera musculus brevicauda* in the Timor Trough (ca. 9.5° S, 126° E), a deep-water habitat south of the species' presumed breeding grounds. Using photo-identification and generalised additive modelling, we analysed visual sightings collected aboard seismic vessels operating off Timor-Leste in 2007–2008 and demonstrate that (1) whales engage in surface behaviours suggestive of active feeding, (2) some individuals remain within the region for more than 1 d, and (3) whale presence is significantly associated with predictably high chlorophyll *a* concentrations. Despite previous efforts to examine pygmy blue whale movements at low latitudes using long-term satellite telemetry, knowledge of the species' behavioural ecology in the tropics remains limited. Our results lend support to previously untested hypotheses about the possible use of the Timor Trough as a foraging site by eastern Indian Ocean pygmy blue whales during the late austral winter and early austral spring.

**KEY WORDS:** Feeding behaviour · Migration · Cetacean habitat modelling · Platform of opportunity · Indonesia

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## 1. INTRODUCTION

Every year, billions of animals—from small insects to large vertebrates—travel across continents and ocean basins to exploit seasonally available resources and seek favourable conditions that will

enhance their survival prospects and maximise their fitness (Alerstam & Bäckman 2018). Despite huge variations in the nature of movement decisions both within and among taxa, a common challenge faced by all migrants is that of maintaining energy balance and offsetting the colossal metabolic demands asso-

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ciated with journeys that may span thousands of kilometres and last several months (Bowlin et al. 2010). ‘Staging’ migrants, such as numerous species of income-breeding birds, insects, and mammals, do so by repeatedly suspending migration to forage at discrete stopover sites where they can replenish their energy stores, given adequate food resources (Sawyer & Kauffman 2011). Optimal migration theory predicts that the extent of stopover behaviour will dictate total migration speed and thus potential reproductive success, as early arriving individuals may benefit from enhanced opportunities to find mates, establish territories, and breed (Weber & Houston 1997, Smith & Moore 2005, Rotics et al. 2018). Previous studies have also shown that both extrinsic (e.g. prevailing environmental conditions, day of year, migration distance) and intrinsic (e.g. fuelling rate, individual body condition) factors influence the duration of stays and the timing of departures (e.g. Anderson et al. 2019). By contrast, capital breeding species de-couple reproduction and feeding, sustaining themselves and their offspring by relying exclusively on reserves acquired during bouts of intense foraging performed in advance of migration. Amongst mammals, this strategy is mostly observed in large-bodied species like bears, true seals, and cetaceans, whose body mass allows individuals to withstand the costs of migration throughout prolonged periods of fasting (Irvine et al. 2017).

In baleen whales, this ‘feast and famine’ hypothesis is supported by multiple strands of evidence, including (1) records of animals caught with empty stomachs at low latitudes (Chittleborough 1965), (2) expectations that prey abundance is reduced outside polar and subpolar feeding grounds and may not be sufficient to meet the costs of energetically expensive foraging behaviours like lunge-feeding (Goldbogen et al. 2011), and (3) no indication of characteristic multi-day prey searching in tracking data from some populations (Modest et al. 2021). These observations have long cemented the belief that most baleen whales rarely feed along their migratory corridors, or only do so opportunistically (Stockin & Burgess 2005). However, recent studies have revealed a stronger degree of feeding plasticity than previously understood (Eisenmann et al. 2016), and increasing reports of feeding events in temperate waters are starting to challenge the classical model of baleen whale migration for several species, including humpback *Megaptera novaeangliae* (e.g. García Cegarra et al. 2021), blue *Balaenoptera musculus* (e.g. Silva et al. 2013, Lesage et al. 2017), and fin *B. physalus* whales (e.g. Silva et al. 2013).

The ability to forecast foraging stopovers is critical for understanding the impacts of human pressures on whale populations, as any interruptions to feeding activity in response to disturbance may have long-term demographic consequences (Pirota et al. 2021a). In particular, gestating and lactating females invest considerable resources into their offspring and therefore must carefully regulate their energy budgets during migration. Previous research has shown that females experience significant declines in body condition throughout this time (e.g. Bradford et al. 2012), which corroborates reports that feeding events are especially prevalent during the post-parturition phase of migration (i.e. on the southbound [northbound] journey for Southern [Northern] Hemisphere breeding stocks, respectively) (e.g. Stockin & Burgess 2005, Silva et al. 2013, Pirota et al. 2021b). As a result, stressors that lead to habitat avoidance or cessation of foraging may impair the acquisition of energy that is essential for calf growth and female reproduction (Braithwaite et al. 2015). This is of particular concern for cetaceans, which are subject to increasing anthropogenic pressures in the forms of vessel traffic, noise pollution, entanglements, or changing climatic conditions (Nelms et al. 2021), and for which even brief disturbance events may result in dramatic reductions in net energy gains. For instance, Pirota et al. (2021a) estimated that blue whales would lose their entire daily energy intake following a 30 min exposure to military sonar. Similarly, Guilpin et al. (2020) showed that repeated vessel interactions over a period of only 3–10 h could lead to energy losses of up to 85%. In this context, the delineation of biologically important areas (BIAs) and important marine mammal areas (IMMAs) is key to the conservation of threatened whale species (Van Parijs et al. 2015). Although not a blueprint for conservation designations, BIAs and IMMAs provide a useful foundation for marine spatial planning that can lead to the siting of protected areas or the implementation of special management regulations (Agardy et al. 2019).

Pygmy blue whales *Balaenoptera musculus brevicauda* (hereafter PBWs) undertake long-range migrations between temperate or subtropical feeding grounds and presumed breeding grounds in Indonesian waters (Double et al. 2014, Möller et al. 2020, Thums et al. 2022), although both the timing of breeding and the geographic boundaries of breeding habitats remain largely unknown (Fig. 1). Feeding aggregations of the eastern Indian Ocean subpopulation have been documented off southern and western Australia during the austral summer, with 2 high-use foraging BIAs (i.e. the Perth Canyon, ca. 31.8° S,

114.5° E and the Bonney upwelling, ca. 38° S, 140° E) characterised by strong pulses of primary productivity (Rennie et al. 2009, Gill et al. 2011, Garcia-Rojas et al. 2018). In the tropics, the confluence of strong ocean currents dominated by the Indonesian throughflow (ITF) is also likely to create favourable foraging conditions for PBWs, particularly across the southern shelf of Timor-Leste, where seasonal upwelling stimulates elevated levels of surface chlorophyll *a* (chl *a*) (Fig. 1) (Alongi et al. 2013). Furthermore, 31 species of euphausiids (i.e. krill) have been documented in the Banda Sea, with densities peaking during the south-east monsoon (July to September) (van Couwelaar 1994). PBW occurrence has previously been linked with upwelling events and high euphausiid biomass (Gill et al. 2011, Priyadarshana et al. 2016, McCauley et al. 2018), and chl *a* is known to be a key proxy of blue whale presence in other parts of the world, including California (Croll et al. 2005), southern Australia (Gill et al. 2011), southern Chile (Buchan & Quiñones 2016) and the Sub-Tropical Convergence (Garcia-Rojas et al. 2018). Despite this, little is known about PBW habitat use within Indonesian waters. The eastern Indian Ocean (pygmy) blue whale migratory route IMMA (<https://www.marinemammalhabitat.org/portfolio-item/eastern-indian-ocean-blue-whale-migratory-route/>) encompasses a large swath of ocean from Cape Naturaliste in Western Australia to Timor-Leste. This area is based on the pygmy blue whale biologically important area (BIA) designated in the Australian Government's Conservation Values Atlas and adds an area to the west and north-west (i.e. Banda and Timor Seas; Fig. 1), where tagged individuals have been shown to engage in area restricted search (ARS) behaviour over periods of several weeks (Double et al. 2014, Möller et al. 2020). However, state-space models fitted to these data were unable to differentiate potential breeding from resting and/or feeding behaviours (Möller et al. 2020, Thums et al. 2022), and recent studies suggest that areas of high residency inferred from horizontal movement data (e.g. using FastLoc GPS) do not necessarily reflect where lunge-feeding occurs (Owen et al. 2016). Thus, there is a need for additional data on PBW behaviour and space use to facilitate the identification of BIAs at low latitudes.

Here, we provide multiple lines of evidence suggesting the existence of a foraging hotspot for PBWs off Timor-Leste. We do this by (1) examining the habitat preferences of PBWs using generalised additive models (GAMs) and (2) assessing patterns in the animals' residency time and diving behaviour from

photographic identification data. Our analyses harness visual sightings made aboard seismic survey vessels operating south of Timor throughout the late winter and early spring of 2007–2008 and highlight the benefits of capitalising on platforms of opportunity to conduct informative assessments of cetacean distribution and behaviour in data-poor ecosystems. The identification of BIAs for PBWs has important implications for the management of this recovering subpopulation in the eastern Indian Ocean.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study area covers approximately 20 000 km<sup>2</sup> to the south of The Democratic Republic of Timor-Leste (Fig. 1), a small island state situated on the eastern side of the Island of Timor, ca. 600 km to the north-west of Darwin in northern Australia. Timor Island is a geographic part of the eastern islands (Lesser Sunda Islands) of Indonesia and is bounded by the Timor Sea to the south and the Savu and Banda Seas to the north. The ITF creates a complex system of water inflows from the Pacific Ocean, which mix within the Banda Sea and are exported into the eastern Indian Ocean through 3 main deep-water passages: the Ombai Strait, the Lombok Strait, and the Timor Trough (Gordon 2005), a 150-km wide, 3000 m deep seafloor depression bordered by a narrow continental margin. Seasonal variation in the strength and direction of the ITF is driven mainly by wind and tidal forces, with the south-east monsoon providing cooling and wind-induced upwelling in the Timor Passage during the austral winter (June–August) (Gordon 2005). Of the 6 submarine canyons found in the area (Harris & Whiteway 2011), only the westernmost incises the continental shelf (see Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m718p099\\_supp.pdf](http://www.int-res.com/articles/suppl/m718p099_supp.pdf)) and is therefore likely to confer higher 'habitat potential' for pelagic species like cetaceans (Huang et al. 2018).

### 2.2. Data collection

Field observations took place between September and December 2007 and between July and September 2008 from vessels undertaking seismic surveys for hydrocarbons in the Timor Trough that were used as platforms of opportunity (Fig. 1). In 2007, data were collected from the 'Geco Eagle', a large 3D seismic vessel

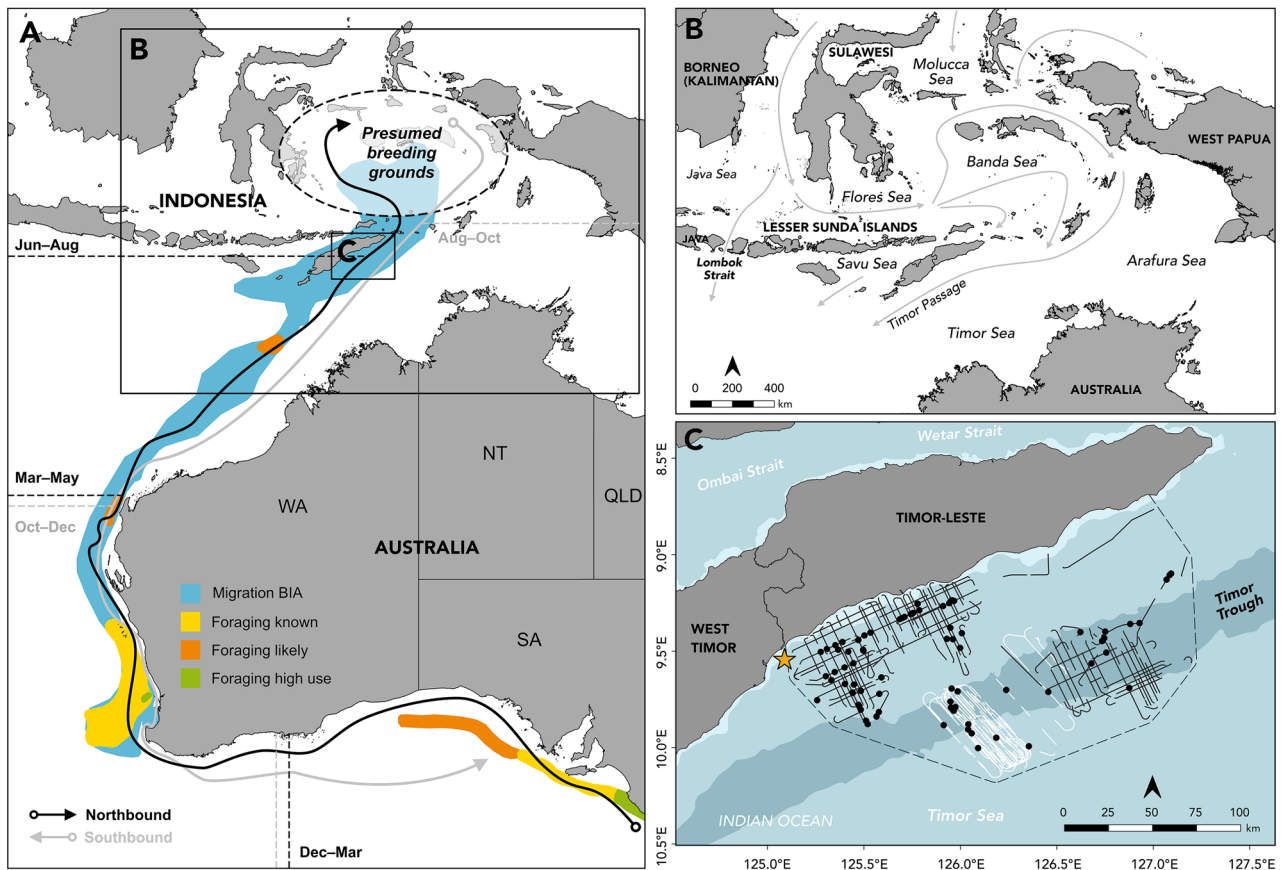


Fig. 1. (A) Approximate migration route and timing for the eastern Indian Ocean population of pygmy blue whales *Balaenoptera musculus brevicauda*. Pygmy blue whales feed in productive temperate ecosystems during the austral summer before travelling north to the Indonesian archipelago, where they are assumed to reproduce in hitherto unmapped breeding habitats. The (pygmy) blue whale migratory route biologically important area (BIA) is shown in blue and overlaps known foraging grounds (yellow) off Western Australia (WA) and South Australia (SA), including areas of seasonally high use such as the Perth Canyon (ca. 31.8° S, 114.5° E) and the Bonney upwelling (ca. 38° S, 140° E) (green). Sites where foraging is likely to occur (i.e. western Great Australian Bight, Ningaloo Reef, Scott Reef) appear in orange. Arrival times during northbound and southbound movements are generalised from the findings of Möller et al. (2020) and McCauley & Jenner (2010) but remain uncertain and are likely to vary across individuals. NT: Northern Territory; QLD: Queensland. (B) The Indonesian Seas, highlighting the primary circulation pathways of the Indonesian Throughflow (ITF) (solid arrows). Boxed inset: location of the study area within the overall region. (C) Visual detections of pygmy blue whales (filled circles) made during opportunistic surveys conducted aboard seismic exploration vessels off Timor-Leste. Solid lines: vessel tracks during observer effort in 2007 (white) and 2008 (black), shown relative to both the continental shelf (light blue, 200 m contour) and the Timor Trough (dark blue, 2000 m contour). Yellow star: location of the only shelf-incising submarine canyon found in the area, as classified by Harris & Whiteway (2011). Dashed line: boundaries of the study area

with 18.5 m eye height and an airgun array of 3147 cubic inches (0.052 m<sup>3</sup>). In 2008, data were collected from the 'Pacific Titan', a 2D vessel with 11.0 m eye height and an airgun array of 3000 cubic inches (0.0492 m<sup>3</sup>) (see Table 1). Both vessels travelled at an average speed of 4–5 knots along predetermined survey lines designed to accommodate the requirements of geophysical survey work. This resulted in uneven coverage of the area, with sampling effort confined to finite blocks that extended perpendicularly to bathymetric contours, covering a range of shallow (<200 m) to very

deep (>2500 m) habitats in the Timor Trough, approx. 1–50 km south of Timor-Leste. Observations were made in accordance with Joint Nature Conservation Committee protocols (JNCC 2010). Trained marine mammal observers were on-effort throughout daylight hours and in all weather conditions on each day at sea. A single observer visually monitored the ocean surface in an arc of approximately 240° in front and abeam of the vessel for indications of the presence of cetaceans. Visual cues used to locate whales included splashes, blows, surfacings, as well as the presence of flocking

seabirds. Reticle binoculars (Fujinon 7×50) were used for species identification and distance estimation; these were calibrated prior to survey commencement using the ship's radar. Observers were tasked with strictly monitoring each whale when at the surface (i.e. during an individual breathing sequence leading to a dive), as required by seismic survey shutdown protocols, and to record whether they believed a sighting was a repeat encounter of an animal that had been previously seen. This was a subjective, yet informed, assessment made based on the location of the animal, its behaviour and direction of travel, the time since last sighting, and the ship's speed. Observer effort was recorded daily in terms of both hours and distance travelled, using a hand-held GPS unit (Garmin GPS 76).

When a cetacean was detected, a GPS waypoint was marked to record the date, time, and coordinates of the vessel at the time of encounter (Derville et al. 2018). Data were logged into a mobile FileMaker database stored on a hand-held Palm device (Palm Tungsten T3 PDA), which included information on species, estimated group size and composition, behaviour (i.e. travelling, milling, potential foraging), and direction of movement. Notes were also taken when an encounter was deemed likely to be a resight of a previously encountered animal. Where possible, whales were photographed to confirm identification using a Canon DSLR camera fitted with a 100–400 mm Canon telephoto zoom lens. Contextual data including Beaufort Sea State, wind direction and speed, visibility, and swell height were also recorded upon shift start and end as well as in association with each sighting.

### 2.3. Photographic identification

Photographic identification (Photo-ID) is a widespread method for assessing the abundance and movements of marine wildlife (including blue whales and other cetacean species) and for estimating residency times in areas of interest (Calambokidis et al. 2009). Body and fluke images of PBWs were entered into an Adobe Lightroom® photo-ID database held by the first author (C.B.) and were initially scrutinized to remove images with no obvious elements useful in identification. As per Barlow et al. (2018), photographs were reviewed and grouped by individual within each sighting event (consecutive pod numbers were used for each day) and later compared between events. Photographs were graded on quality using a nominal scale of 1–4 (poor, fair, good, and

excellent), which considered image sharpness, viewing angle, and the number and distinctiveness of identification features, including the shapes of the animals' dorsal fins, the size and location of fluke notches, the presence or absence of a blaze (i.e. a small area of white pigmentation at the base of the dorsal fin, which appears to be prevalent in this population), any obvious scars and bite marks from cookiecutter sharks *Isistius brasiliensis*, as well as the unique patterns of lateral body pigmentation visible within a minor portion of the flank adjacent to the dorsal fin (Gendron & De La Cruz 2012). Photograph quality was completely determined by the animals' distance, movements, swimming directions, and orientations relative to the ship at the time of encounter, as no attempt was made to approach individuals. Photographs of quality 1–2 were discarded to minimise identification errors (Barlow et al. 2018). Images were examined by 2 experienced reviewers, who independently searched for resights.

### 2.4. Behavioural observations

One of the dominant species of krill in the eastern Indian Ocean, *Euphausia recurva*, is known to be an important food source for PBWs (Jenner et al. 2002), although the diet of PBWs varies regionally (Gill 2002) and may also extend to epibenthic species such as sergestid shrimp (de Vos et al. 2018). Many euphausiids (including *E. recurva*) exhibit pronounced diel vertical movements, ascending from depths of ca. 200–500 m during the day to <100 m at night (Werner & Buchholz 2013). Daytime feeding, therefore, necessitates deep foraging dives, which animals typically initiate by 'fluking up', i.e. lifting their tail flukes above the surface (Gill 2002). Fluke-up dives (FUDs) allow individuals to flip vertically to orient their bodies in a way that minimises pressure drag and enables faster acceleration while gliding on descent (Goldbogen et al. 2006). FUDs are frequently observed on foraging grounds (e.g. the Bonney Upwelling of southern Australia) (Gill 2002, Gill et al. 2011) but are also common in the northern Indian Ocean, where they can make up to 55–70% of terminal dives (Ilangakoon & Sathasivam 2012, de Vos et al. 2013). Although the diving behaviour of migrating PBWs has been the focus of limited research to date, unlike in other parts of the world (COSEWIC 2002), there is currently no evidence of behavioural idiosyncrasy in any Indian Ocean sub-population (de Vos et al. 2013). To our knowledge, Owen et al. (2016) is the only study that has reported on the depths

reached by a tagged PBW in different behavioural modes (i.e. feeding, migratory, or exploratory dives). Throughout the duration of the tag deployment in that study, the animal reached a maximum depth of 506 m, which is deeper than any previously published dive by a blue whale. This dive was associated with a feeding bout, as were 20 others within the tag record (mean max. depth:  $129 \pm 183$  m; range: 13–505 m). By contrast, migratory dives had a mean depth of 13 m, which is half the average body length of the species (Branch et al. 2007) and just below the predicted 12 m depth threshold that blue whales should swim under to avoid the impact of wave drag (Owen et al. 2016). FUDs are therefore unlikely to be associated with migratory behaviour (e.g. oriented travel) in our study area; rather, we believe they plausibly reflect deep daytime foraging. This is consistent with observations made off the coast of Sri Lanka, where FUDs are often followed by steep dives and associated with defecation events (Alling et al. 1991, Priyadarshana et al. 2016). In this context, we reviewed photographs and field notes to assess the prevalence of FUDs as a conservative indicator of possible foraging behaviour. FUDs were defined as terminal dives (i.e. last breath in a surfacing sequence), whereby animals revealed their full tail flukes, not simply an arched tail stock (Buchan & Quiñones 2016). Note that multiple short-duration dives (1–2 min, similar to Gill 2002) performed successively were recorded as part of the same sighting event, such that the number of FUDs per sighting may be greater than one.

## 2.5. Spatial modelling

All analyses described in this section were conducted in R v.4.2.1 software (R Core Team 2022). PBW distribution was modelled using binomial (i.e. presence–absence) GAMs built with a logit link function in the ‘mgcv’ package. The resultant models describe the probability of PBW presence as a function of selected environmental variables (see below for details). GAMs are popular in cetacean research due to their ability to trade off good predictive performance with high ecological intelligibility (Derville et al. 2018), and there is an expanding body of literature documenting their successful applications to the modelling of cetacean data collected under a variety of scenarios (e.g. Redfern et al. 2017, Sutton et al. 2018). Our focus was on the late austral winter (i.e. July–August) and early austral spring (i.e. September), which was the only period during which PBWs were detected (see Table 1). Repeated encounters of

the same presumed individual within a survey day were discarded to maximise independence between sighting events (Stingle 2012). Similarly, ad hoc (off effort) observations without associated measures of effort (i.e. GPS tracks) were excluded from the analysis.

As per Fiedler et al. (2018) and Correia et al. (2021), periods of continuous effort with no sightings were treated as absences. However, these were in the form of strip transect areas as opposed to discrete locations, so absence points were generated to produce the denominator of the logit function that underpins inference in binomial GAMs (Torres et al. 2008). This was done by adapting the methods of Derville et al. (2018) and selecting absences from subsets of survey tracks that had no sightings of the species (i.e. the ‘observed absence’ scenario described in Fiedler et al. 2018). This is similar to splitting survey tracks into segments as in density surface modelling (Bouchet et al. 2020), except that survey segments are polygons instead of lines (Fig. S2). Point selection proceeded as follows. First, GPS tracks were split into segments based on temporal proximity; whenever consecutive GPS positions occurred more than 5 min apart, a new sub-track was created. Extremely short (<250 m) segments were removed, and spatial buffers of 3 km on either side of the vessel track lines were then drawn. This distance is commensurate with the average effective strip width reported during visual line-transect surveys of blue whales (and other large mysticetes) undertaken aboard vessel platforms of comparable dimensions to ours (e.g. Calambokidis & Barlow 2004, Williams et al. 2011, Baines et al. 2017, Kavanagh et al. 2019). Second,  $n = 1000$  absence points were sampled within track buffers. Doing so accounted for uneven survey coverage and has been shown to alleviate the biases that would otherwise arise from random point selections throughout the broader study region (Fiedler et al. 2018). It is worth noting that there is no consensus on the best strategy to select absence locations and that method choice can strongly affect model outcomes (Jarnevich et al. 2017). A total of 1000 points is broadly comparable to the number of sightings typically obtained during large-scale dedicated cetacean surveys (Fiedler et al. 2018) and was deemed adequate to capture habitat variability in areas where whales were absent without artificially introducing spatial autocorrelation. Although GAMs are somewhat insensitive to prevalence, their predictive accuracy is known to improve when absences are given a total (summed) weight equal to that of presences (Barbet-Massin et al. 2012, Guisan et al. 2017, Iturbide et al. 2018, Liu et al. 2019,

Grimmett et al. 2020). Using functions from the 'biomod2' package, presence and absence points were thus weighted inversely proportionally to their relative fraction on the total sample size (Guisan et al. 2017). Absence points were allocated to each daily survey segment in proportion to the time spent on-effort (in hours) that day and were also constrained to lie outside a 3 km exclusion zone around presences to avoid sampling locations too similar to those already representing presence data (O'Toole et al. 2021). Lastly, presence points were also randomly jittered within a 3 km buffer centred around the position of the vessel at the time of sighting. This was done to better reflect survey conditions, as animals are unlikely to be seen exactly on the trackline of an operating seismic survey vessel (Fig. S2).

GAMs included a suite of static and dynamic explanatory variables chosen according to their putative influence on blue whale distribution, as reported in previous modelling studies (Croll et al. 2005, Gill et al. 2011, Bedriñana-Romano et al. 2018, Garcia-Rojas et al. 2018, González García et al. 2018). Static variables included bathymetric depth, seabed slope, and distance to the nearest shelf-incising or slope-confined submarine canyon (see Fig. S3). Depth (in m) was obtained from the 2022 General Bathymetric Chart of the Oceans (<https://www.gebco.net/>) at 15 arc-second resolution (GEBCO Compilation Group 2022). Seabed slope was calculated from the GEBCO grid as the 'rise over run' (in degrees) using the 'slope' function in the 'SDMTools' package. The location and classification of submarine canyons followed Harris & Whiteway (2011); the heads of 'blind' (i.e. slope-confined) submarine canyons terminate on the continental slope, whereas 'shelf-incising' canyons incise into the continental shelf and may have bathymetric connections to river systems. Euclidean distances to the nearest canyon features were calculated using the 'gDistance' function in the 'rgeos' package. Dynamic environmental variables included remote-sensed chl *a* concentration (in  $\text{mg m}^{-3}$ ) and sea surface temperature (SST, in °C). Chl *a* was derived from Aqua MODIS satellite imagery (<https://oceandata.sci.gsfc.nasa.gov/>) at 4 km resolution. SST was extracted from NASA's multi-scale ultra-high resolution data set ([https://podaac.jpl.nasa.gov/Multi-scale\\_Ultra-high\\_Resolution\\_MUR-SST](https://podaac.jpl.nasa.gov/Multi-scale_Ultra-high_Resolution_MUR-SST)) as an analysed product available at 1 km resolution. Gridded data for both variables were accessed directly using bespoke routines adapted from the 'rerddap' R package. Any gaps (e.g. due to cloud cover) were interpolated with inverse distance weighting using the 'rfillspgaps' function from the 'meteo' R package.

Many mobile marine species interact with ephemeral oceanographic processes that may fluctuate over timescales ranging from seconds to decades (Mannocci et al. 2017a). Therefore, the selection of an appropriate temporal grain is essential to cetacean distribution modelling (Fernandez et al. 2017, 2018). Recent studies have indicated that models based on daily or weekly timeframes are preferable when dynamic variables constitute important components of habitat preference, whereas associations with persistent oceanographic features are best captured using longer-term synoptic products (i.e. climatologies) (Mannocci et al. 2017a, Fernandez et al. 2018). The Timor Trough is a seasonally variable but inter-annually stable oceanic system (Fig. S4), making the latter a more adequate choice (Mannocci et al. 2017a). Therefore, bespoke R functions were written to build 7 d climatologies for both SST and chl *a* from the RERDDAP data. Climatologies spanned a period of 10 yr, centred on 2007. From these, mean weekly SST, mean weekly chl *a*, and maximum weekly chl *a* were obtained for each pixel in the study area. The relationship between wind-driven vertical mixing and biological production in upwelling zones is highly variable around the world, with evidence that phytoplankton blooms can precede the arrival of larger predators such as blue whales by 2 wk to 4 mo (Croll et al. 2005, Visser et al. 2011, Bedriñana-Romano et al. 2018, Barlow et al. 2021, Buchan et al. 2021). To test for a similar temporal mismatch in our study system, we also considered 2 time-lagged chl *a* covariates at lags of 2 and 4 wk. All variables were resampled to the same resolution as the bathymetry data using bilinear interpolation, and chl *a* values were  $\log_{10}$  transformed prior to analysis. Finally, the mean chl *a* climatology was used to calculate values of the frequency of chlorophyll peak index (FCPI), an integrative measure of productivity that quantifies the frequency with which chl *a* anomalies exceed the mean signal of a region-wide model (Suryan et al. 2012). As such, the FCPI provides a metric of long-term deviation from the temporal trend in chl *a* surface concentrations.

Model fitting proceeded by testing all possible combinations of explanatory variables, according to the information-theoretic approach implemented in the 'FSSgam' package (Fisher et al. 2018). Thin-plate regression splines were used for all smooth terms, capping the maximum number of uncorrelated ( $|\rho| < 0.25$ ) predictors to 3 in each candidate model. To model simple density-environment relationships and mitigate overfitting, the basis size of each smooth was restricted to  $k = 4$  (Mannocci et al. 2017b).

Restricted maximum likelihood was also used as the criterion for estimating smooth parameters, as it penalises over-fitting and leads to more pronounced optima (Wood 2011). The best model was elected as the one minimising Akaike's information criterion corrected for small sample sizes (AICc) (Fisher et al. 2018). Model checking was performed using standard residual diagnostics plots as returned by the 'gam.check' function, and residual autocorrelation was assessed using variograms from the 'geoR' and 'gstat' packages. Following Pirota et al. (2011), goodness-of-fit was evaluated by using both the percentage of deviance explained and confusion matrices, the latter of which compares binary predictions to observed values and reports rates of true and false positives or negatives. Model performance was also measured using a stratified cross-validation approach (Roberts et al. 2017, Derville et al. 2018), whereby data were split into 100 pairs of training and testing sets (by days, at a ratio of 0.75/0.25 respectively) and models fitted to each training partition. Performance metrics included the area under the curve of the receiver operating characteristic (ROC-AUC), the true statistic skill (TSS), the Sørensen index of similarity, and sensitivity (i.e. the percentage of sightings correctly predicted as presences) (Torres et al. 2008, Pirota et al. 2011). All R code for reproducing analyses is available at <https://github.com/pjbouchet/timorbw>. An overview, data, model, assessment, and prediction (ODMAP) protocol (Zurell et al. 2020) is also included in Text S1 in the Supplement to ensure transparency and reproducibility.

### 3. RESULTS

Surveys took place in the austral spring and early austral summer (September–December) of 2007 and in the late austral winter (July–August) of 2008, covering 5772 km and totalling 73 d of effort (at an aver-

age  $\pm$  SD of  $8.9 \pm 1.57$  h d<sup>-1</sup>). No detections of PBWs were made between mid-October and mid-December 2007 (1259.6 km over 16 d); however,  $n = 100$  cetacean encounters were recorded on-effort during the rest of the sampling period (4512.4 km over 57 d spread across the 2 yr) (Fig. 1, Table 1). These consisted of 322 individuals from a minimum of 6 identified species: the common dolphin *Delphinus delphis*, false killer whale *Pseudorca crassidens*, Fraser's dolphin *Lagenodelphis hosei*, short-finned pilot whale *Globicephala macrorhynchus*, striped dolphin *Stenella coeruleoalba*, and PBWs (Table S1). PBWs were the most prevalent species, comprising 77% ( $n = 77$ ) of all detections and 29.5% ( $n = 95$ ) of individuals. Due to equipment failure, one record of 2 individuals in September 2008 had no associated GPS track and was discarded from the spatial analysis, bringing the sample size down to 76 sightings ( $n = 94$  individuals) for modelling.

#### 3.1. Photo-ID

A total of 38 of the 77 sighting events had accompanying photo-ID data. Within these, 62 photographs were deemed of sufficient quality for matching. Review of these photographs identified 21 individual PBWs, including 2 animals for which both right-side and left-side photographs were obtained, 34 left-side-only IDs, and 24 right-side-only IDs. Two individuals were resighted respectively 1 and 4 d apart within the 2008 season, consistent with the intervals between intra-seasonal resights reported in other studies of baleen whales at oceanic stopover sites (Grove et al. 2023). No individuals were resighted between years. An ad hoc comparison made with 3 Australian PBW photo-ID catalogues—respectively maintained by Western Whale Research, the Blue Whale Study, and the Centre for Whale Research WA—yielded no matches.

Table 1. Survey effort and pygmy blue whale *Balaenoptera musculus brevicauda* sightings (including calves) made by dedicated marine mammal observers during visual surveys conducted opportunistically aboard seismic vessels operating in the Timor Trough and surrounding waters in 2007 and 2008. Values are only reported for effort days during which whales were encountered and for sightings with associated effort (i.e. GPS tracks). Note that no pygmy blue whale detections were made in 16 d of survey effort (totalling 1260 km) between mid-October and mid-December 2007

Vessel	Year	Period	Effort (days)	Effort (km)	Depth (m)	No. of sightings	No. of individuals	No. of calves
Geco Eagle	2007	1–22 Sep	21	1476.6	115–2950	16	18	1
Pacific Titan	2008	25–31 Jul	7	525.2	1460–2940	8	14	3
Pacific Titan	2008	1–31 Aug	29	2510.6	10–2950	52	62	4
Total			57	4512.4		76	94	8



### 3.2. Behavioural observations

PBW were frequently observed engaging in steep diving behaviour suggestive of foraging, with 22.1% ( $n = 17$ ) of PBW encounters involving one or more FUDs (Table S2). On several occasions, PBWs were also recorded swimming in a circular trajectory and repeatedly resurfacing in the same location after a series of short-duration (1–2 min) dives (C. Burton pers. obs.). There was evidence that FUDs occurred over shallower seabed depths (Kruskal-Wallis  $\chi^2 = 5.738$ ,  $p = 0.017$ ) and closer to the area's only shelf-incising canyon (Kruskal-Wallis  $\chi^2 = 4.802$ ,  $p = 0.028$ ) than other non-FUD dives. No defecation events were recorded; however, a juvenile PBW was observed lunging at the surface upside down with its jaw agape and ventral pleats showing, indicating potential foraging (Fig. 2).

### 3.3. Habitat preferences

Several covariates were correlated (Fig. S5), leading to a total of 45 candidate model formulations. Statistical support (according to the AICc) was greatest for the model that included maximum weekly chl *a*, seabed slope, and distance to the nearest shelf-incising canyon (Table S3). All terms were significant ( $p < 0.001$ ; Table 2) and

together explained 80.1% of the deviance. Chl *a* made the largest contribution, alone explaining 66.3% of the deviance. By contrast, distance to shelf-incising canyon and slope had much lower contributions (11.5 and 2.3%, respectively). Overall, the probability of PBW presence was found to increase in areas of elevated productivity (i.e. higher maximum weekly chl *a*), in proximity to shelf-incising canyons (ca. 0–150 km), and over flatter seabed slopes (Fig. 3). The cut-off for the construction of the confusion matrix was chosen as the threshold that maximised sensitivity and specificity, at a value of 0.63. The model exhibited excellent fit to the data and correctly classified 94.7% of the presences and 94.8% of the absences (ROC-AUC: 0.984; TSS: 0.896; Sørensen similarity index: 0.72). The model also maintained high predictive performance when applied to withheld data (mean  $\pm$  SD cross-validated score: ROC-AUC:  $0.973 \pm 0.02$  [min.–max.: 0.851–0.998]; TSS:  $0.850 \pm 0.089$  [0.473–0.988], Sørensen index:  $0.632 \pm$

Table 2. Summary of the best-fitting generalised additive model relating the probability of pygmy blue whale *Balaenoptera musculus breviceauda* presence to static and dynamic environmental variables. EDF: effective degrees of freedom. Approximate significance levels (p-values) are also given. \*\*\* $p \leq 0.001$

Variable	EDF	$\chi^2$	p	Significance
Weekly maximum chl <i>a</i>	2.935	234.47	$p < 0.0001$	***
Distance to incising canyon	2.906	154.84	$p < 0.0001$	***
Seabed slope	2.939	31.84	$p < 0.0001$	***

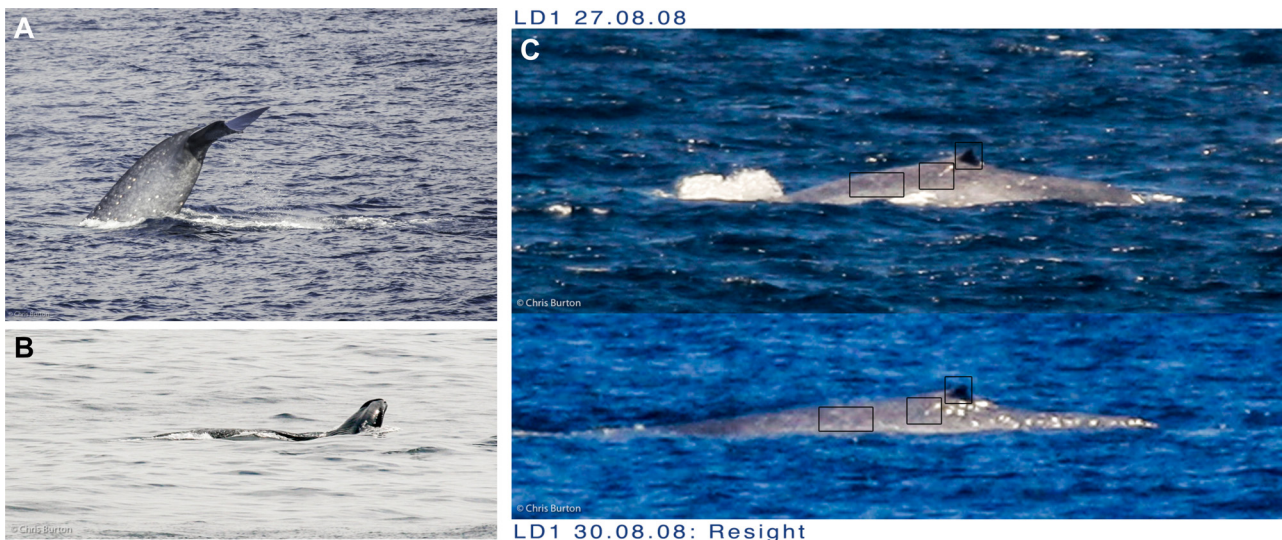


Fig. 2. Photographic evidence of pygmy blue whale *Balaenoptera musculus breviceauda* residency and likely foraging behaviour off Timor-Leste. (A) A fluke-up dive, which typically indicates the onset of a steep foraging dive. (B) Lateral lunge by a pygmy blue whale calf, revealing ventral pleats. (C) Example identification photographs from an individual resighted 4 d after first encounter. Areas delimited by the boxes indicate matching features. Image copyrights: Chris Burton

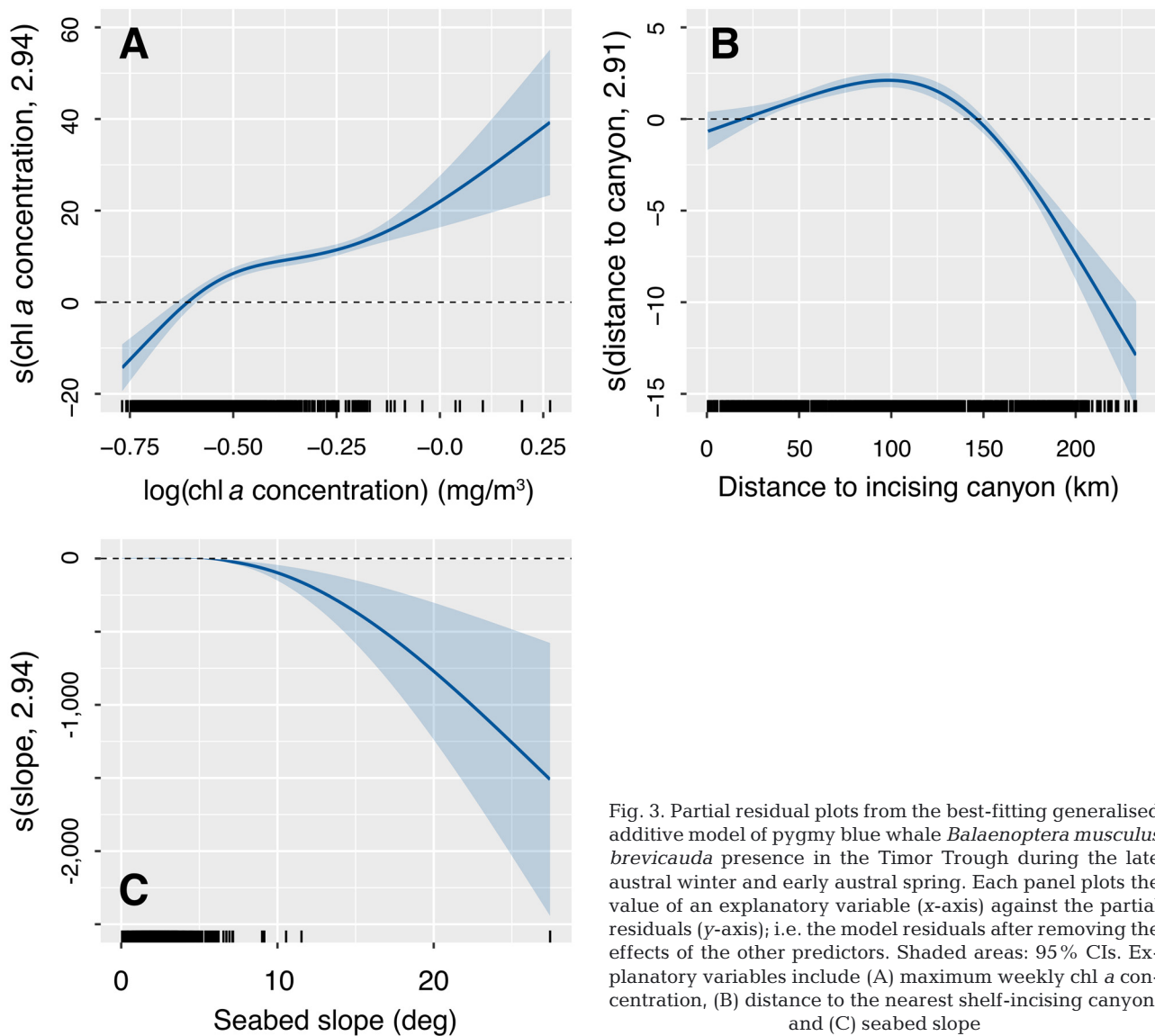


Fig. 3. Partial residual plots from the best-fitting generalised additive model of pygmy blue whale *Balaenoptera musculus brevicauda* presence in the Timor Trough during the late austral winter and early austral spring. Each panel plots the value of an explanatory variable (x-axis) against the partial residuals (y-axis); i.e. the model residuals after removing the effects of the other predictors. Shaded areas: 95% CIs. Explanatory variables include (A) maximum weekly chl a concentration, (B) distance to the nearest shelf-incising canyon, and (C) seabed slope

0.158 [0.192–0.958], true positive rate:  $0.925 \pm 0.048$  [0.75–1]; Fig. S6), providing further assurance that it was not overfitted. Variograms showed no indication of residual autocorrelation (Fig. S7).

#### 4. DISCUSSION

Migratory marine species are among those most at risk from anthropogenic change (Lascelles et al. 2014), yet research examining the movement ecology and fine-scale behaviours of whales during transit between summer and wintering grounds is exceedingly rare (Modest et al. 2021). In the Indian Ocean, animal-borne telemetry and acoustic monitoring studies suggest that the tropical waters of

northern Western Australia and eastern Indonesia provide important habitats for migrating PBWs (Double et al. 2014, Gavrilov et al. 2018, Thums et al. 2022). For instance, 21 animals have been tracked using satellite tags since 2009 as they travelled north from the Perth Canyon (ca. 31.8° S, 114.5° E) and from the North West Cape (21.9° S, 114.1° E) towards Indonesia. Of these, 2 reached West Timor before the tags ceased transmitting, while another 5 moved through the Timor Trough and the Ombai Strait into the Banda Sea (Double et al. 2014, Möller et al. 2020, Thums et al. 2022). The latter showed prolonged residency times (ca. 2 mo) over a large swath of ocean currently presumed to be breeding grounds (Double et al. 2014, Möller et al. 2020). Although ARS behaviour was inferred in both the Timor and Banda

Seas, state–space models were unable to confidently detect feeding activity (Möller et al. 2020, Thums et al. 2022) because slow sinuous movements as derived from positional estimates are insufficient to discriminate between feeding and other time-intensive behaviours such as unsuccessful search, social interactions, mating, or resting (Owen et al. 2016, Torres et al. 2017). In addition, few attempts have been made to validate predictions of ARS with empirical measurements of prey capture (Palacios et al. 2019) and therefore no ‘foraging’ BIAs are currently recognised for PBWs within Indonesian waters (Department of the Environment 2015).

Our study builds upon these efforts to highlight the likely significance of the Timor Sea for migrating PBWs, adding to a growing body of literature documenting the presence of blue whales in productive, low-latitude upwelling zones during the winter (e.g. Gill 2002, Hucke-Gaete et al. 2004, Torres 2013). Until recently, little information existed on PBW distribution in Indonesian waters. Historical whaling data indicate low levels of sampling effort and relative catches in this area (Branch et al. 2007), although isolated strandings dating back to 1916 have been described within the Indonesian Archipelago and anecdotal sightings have also been logged in the Savu Sea to the northwest of Timor since 1979 (Rudolph et al. 1997, Mustika 2006, Kahn 2007, Dethmers et al. 2012). Our observations confirm that the Timor Trough attracts some PBWs during the late austral winter and early austral spring; to our knowledge, this is the first account of PBW occurrence south of Timor-Leste during at-sea surveys (Dethmers et al. 2012). Importantly, we recorded a small number of animals ( $n = 2$ ) residing in the area for periods of 1–4 d and engaging in steep dives suggestive of deep daytime foraging. One calf was also seen performing a lateral lunge at the surface (Fig. 2). Similar lines of evidence have been used in tandem to characterise the incidence of foraging activity in nearby eco-regions (Barlow et al. 2018). In blue whales, prey depth and prey density strongly interact to define habitat quality and dictate the bioenergetics of foraging (DFO 2018). Indeed, kinematic data from digital tags have revealed that blue whales modulate feeding effort to optimize net caloric intake in response to the 3-dimensional characteristics of the preyscape (i.e. vertical distribution, accessibility, and density of krill swarms) (Goldbogen et al. 2011, Hazen et al. 2015). Blue whales are known to perform lunges anywhere between the surface and 250–300 m (Doniol-Valcroze et al. 2011, Torres et al. 2020); yet, a single surface lunge is estimated to be

2.5 times less energetically costly than multiple successive lunges at depth (Acevedo-Gutiérrez et al. 2002, Guilpin et al. 2019). To offset the metabolic costs of diving and oxygen consumption, a blue whale should, accordingly, only feed at depth when relative krill density exceeds surface density by a factor of 3 or more (Goldbogen et al. 2011). The prevalence of FUDs in our study area suggests that this may be the case here, much like it is in other ecosystems where krill follow strong diurnal cycles and aggregate in large numbers around the thermocline (e.g. southern California) (Goldbogen et al. 2011). By contrast, surface feeding is far more common in New Zealand and southern Australia (Torres et al. 2020), where PBWs target a coastal euphausiid, *Nyctiphanes australis*, that often swarms in the upper part of the water column (Gill 2002). Hourly variation in foraging effort has also been noted in several populations, with feeding depth increasing in the morning and shallow foraging occurring predominantly at night (Doniol-Valcroze et al. 2011, Guilpin et al. 2019). Here, any nocturnal surface feeding events would have been missed by onboard observers constrained to surveying during daylight hours. It is also possible that we underestimated the extent of foraging activity by focusing solely on FUDs and disregarding other indicators of deep diving (e.g. arched tail stocks; Buchan & Quiñones 2016). Clearly, there is a need to better characterise the diet and prey selection strategies of PBWs in the face of diel, seasonal, and geographical plasticity in foraging behaviour throughout the species’ range. It is also difficult to determine the exact nature of foraging decisions made by PBWs in the Timor Trough, as there is scant information on planktonic communities offshore of Timor-Leste, and some heterogeneity in foraging efficiency is apparent amongst individual whales of different sex, age, and reproductive status (Guilpin et al. 2019). Faecal sampling would be useful to characterise PBW diet in the tropics but will necessitate dedicated focal follows from small-vessel platforms, which were not possible here. Future studies should leverage high-resolution biologging and hydro-acoustics to elucidate relationships between diving behaviour, feeding manoeuvres, and prey availability. Ultimately, the minimum prey density needed to fulfil the energy requirements of migrating PBWs will vary as a function of the energy content of the targeted prey species, and the duration of migratory stopovers is also likely influenced by seasonal productivity and prey availability (Owen et al. 2015). Previous research has shown that North Atlantic blue whales spend as little as 16 h in areas

where ARS behaviour has been identified (Silva et al. 2013), and the intervals we report between resights made within the same year are well within the range of other baleen whale studies (e.g. Grove et al. 2023). How much energy PBWs can replenish by pausing migration offshore of Timor Leste is currently unknown; however, recent studies indicate that baleen whale prey consumption has long been underestimated (Savoca et al. 2021), and bioenergetic models of blue whales suggest that even a single day of feeding on low-density krill patches may be sufficient to offset an animal's average daily energetic costs several times over (Pirodda et al. 2021a).

Modelling cetacean–environment relationships at stopover sites can help contextualise the mechanisms underlying foraging decisions in long-range migrants. Our best GAM model highlighted 3 covariates (2 static, 1 dynamic) as significant predictors of PBW presence in the Timor Trough, and indicates a preference for more productive oceanic habitats associated with shelf-incising submarine canyons, consistent with previous studies of both blue whales and other cetacean species in offshore systems (Hucke-Gaete et al. 2004, Croll et al. 2005, Salgado Kent et al. 2020). In recent decades, there has been mounting recognition of the role that abrupt seafloor features can play in facilitating benthic–pelagic coupling through upwelling and nutrient enrichment (Genin 2004, Cotté & Simard 2005, Bouchet et al. 2015); this includes the south Timorese coast, where intrusions of ITF water along the continental margin during the winter monsoon season have been shown to stimulate phytoplankton production and benthic metabolism (Alongi et al. 2013, Muskananfolo et al. 2021). Shelf-incising submarine canyons also have high upwelling potential compared to slope-confined ('blind') canyons and typically act as krill hotspots that confer reliable foraging opportunities for many species of fishes, seabirds, and marine mammals (Croll et al. 2005, Huang et al. 2018, Santora et al. 2018, Salgado Kent et al. 2020). Wind forcing is the primary mechanism responsible for enhanced productivity in these systems (Croll et al. 2005), and significant variation in observed time lags between plankton and blue whale aggregations has been linked to variation in wind input over the preceding 30 d (Barlow et al. 2021). Specifically, wind surges in already well-mixed waters may concentrate zooplankton on shorter time scales (i.e. shorter lags) and make prey more readily available immediately following upwelling (Benoit-Bird et al. 2019, Ryan et al. 2022), whereas longer time lags may be required to spur productivity in a more stratified water column

(Barlow et al. 2021). Several studies have noted similar short-term synchrony with phytoplankton biomass, reporting rapid shifts from low to peak surface chl *a* concentrations in a matter of 2–3 d (e.g. Shang et al. 2004, Walker et al. 2005, Wilkerson et al. 2006, McPhee-Shaw et al. 2011, Lucas et al. 2014, Carranza & Gille 2015, Broullón et al. 2023). Water sampling along the south coast of Timor-Leste indicates a good degree of surface mixing (Alongi et al. 2013), which may therefore explain why time-lagged chl *a* was not retained in our top-ranking model. The relationship between PBW presence and seabed slope is more ambiguous. The traditional paradigm is that blue whales tend to aggregate in areas of steep terrain (e.g. Croll et al. 2005, Lesage et al. 2017, Nickels et al. 2019), and slope has indeed been identified as a good proxy of PBW habitat suitability throughout the wider Indonesian archipelago (Jak 2020). However, deep (>50 m) lunge-feeding has been reported over flat bottoms at certain times of the day or year in other areas (Doniol-Valcroze et al. 2012), highlighting heterogeneity in the use of different seascapes at varying temporal scales. More importantly, global bathymetric data have been shown to significantly underestimate seabed slopes (Costello et al. 2010), which may lead to biases in estimates of species–habitat associations. A 2-fold increase in the resolution of the GEBCO depth products in the last few years (from 30 to 15 arc-second) was accompanied by a 4-fold increase in the maximum slope values reported for our study area (from 10 to 40°; see Fig. S3). Concerted efforts to refine maps of the world's seafloor (e.g. the Nippon Foundation—GEBCO Seabed2030 project) are poised to further our understanding of the way PBWs utilise slope habitats in the future. Until then, we advise caution in interpreting our results for the slope covariate.

Recent studies have proposed that eastern North Pacific blue whales rely on spatial memory and multiple individual or collective sensory cues (e.g. long-distance acoustic signals from conspecifics) to track long-term average oceanographic conditions and synchronise their migrations with the expected availability of food in inter-annually stable foraging habitats (Abrahms et al. 2019). Although significant flexibility in the timing of transitions from foraging to breeding migrations has been demonstrated (Oestreich et al. 2022), the need to match arrival with periods of peak prey abundance implies that animals may struggle to adapt to future changes in foraging conditions resulting from long-term climatic shifts, particularly if these occur outside the realm of the

animals' sensory perception (Abrahms et al. 2019, Oestreich et al. 2020). For instance, Hazen et al. (2013) estimated that blue whale habitat will shrink by up to 20% over the next century, following alterations to preyscapes caused by temperature-driven deepening of the thermocline, increases in water column stratification, and changes in the composition of plankton communities. While PBWs are morphologically adapted for efficient travel and may be able to exploit additional resources throughout the wider Indonesian archipelago in years of low food supply, recent simulations demonstrate that they are likely to face considerable energy deficits if krill density fluctuates by more than 5% (Guilpin et al. 2020). This is of concern, as reproductive success is inherently linked to energy intake in blue whales; for instance, a 50% reduction in mean swarm density during a feeding season of 120 d is predicted to lead to an 80% drop in calving rate (Wiedenmann et al. 2011). Several calves were encountered in the Timor Trough across our 2 survey years ( $n = 8$ ; Table 1), and PBW mother–calf pairs have been monitored moving southward down the coast of Western Australia between October and December. Therefore, it is expected that mating, calving, and the early development of newborns occurs during the south-east monsoon between July and September. The timing of PBW occurrence in Timorese waters matches this period and what is currently known of the species' annual reproductive cycle, suggesting that the breeding grounds of PBW may extend as far south as the Timor Sea. However, more research is needed to determine the importance of the Timor Trough as a potential reproductive habitat.

Pinpointing the mechanisms that shape animal migration can inform our expectations of how wildlife will respond to the challenges brought forth by the Anthropocene (Abrahms et al. 2019, Doherty et al. 2021). Australian and Indonesian waters along the PBW migratory route face rising pressures from human activities, including oil and gas exploration, shipping traffic, commercial fishing, tourism, and noise pollution (Nelms et al. 2021). Exposure to these stressors can impair individual vital rates (Pirota et al. 2021a) and may further undermine the already uncertain conservation status of PBWs at both species and population levels. Whilst several items of marine mammal legislation exist in Indonesia, practical actions for implementation and enforcement are unclear, leaving considerable protection gaps (Sahri et al. 2020). Of the approximately 180 Indonesian marine protected areas currently in place, only 2 have been formally designated for marine mammals

despite mandates to include the migration paths of marine biota in regional zoning plans (Sahri et al. 2020). Our findings provide a foundation for charting the future course of PBW management in Indonesian Seas and suggest that (1) the inclusion of the Timor Trough in future updates to Indian Ocean BIAs and (2) the expansion of the Savu Sea and Surrounding Areas IMMA under criteria B2 and C2 may be warranted. South Timorese waters have already been earmarked as an 'area of interest' for consideration in the IMMA framework; yet, full IMMA status with defined boundaries cannot be achieved until the formal expert regional workshop, which is convened only once every decade (Agardy et al. 2019). Highlighting candidate important habitats in the intervening years, as we do here, can however be useful to guide effective conservation of vulnerable species in the interim (Agardy et al. 2019), especially given predictions of weakened upwelling systems throughout the Banda Sea due to more frequent weather events (e.g. El Niño) (Wirasatriya et al. 2021). Given increasing reports of emaciated female PBWs in the tropics (K. Edyvane pers. comm.), ongoing monitoring of the species in the Timor Trough is essential to keep track of changing conditions that might necessitate revision of the management focus provided by IMMA designation (Agardy et al. 2019).

In petroleum development areas, geophysical seismic survey vessels can be used as platforms of opportunity to assess spatial and temporal patterns in cetacean occurrence, species diversity, and density (Stack & Currie 2022). The number of publications making use of non-systematic cetacean sighting records collected during seismic surveys has been growing steadily in recent years, with each study often making important contributions to our understanding of species occurrence and relative abundance, particularly in remote and poorly accessible offshore regions where dedicated field sampling remains rare (e.g. de Boer 2010, Baines & Reichelt 2014, Holst et al. 2017, Peters & Stockin 2022). Seismic survey ships provide key advantages for scientific data collection, considering that (1) vessels are typically large, with high and comfortable observation platforms, (2) surveys usually last several weeks or even months, allowing sustained periods at sea in all seasons of the year, (3) data of sufficient quality for modelling can be obtained if observers are adequately trained and adhere to strict protocols, and spatio-temporal coverage captures habitat variability (Redfern et al. 2006, Baines & Reichelt 2014, Stack & Currie 2022). However, these benefits come at the cost of limited flexibility in survey design, potential

spatial biases, and lower resolution in some data streams. For instance, vessels are set to follow a pre-determined course with little regard for weather conditions and no option to reduce speed or divert from the track. This can compromise the collection of accurate information (e.g. photo-ID) on all individuals encountered, and undermine confidence in species determination (Peters & Stockin 2022). It is possible that the same individuals were seen on several occasions over multiple days during our surveys, but that our photo-ID data were not adequate to confirm repeat encounters. Such repeat sampling, if it occurred, would violate the assumption of statistical independence between observations and lead to misleading inference about the significance of covariate smooths. It also means that the residency times we report should be taken as minimum estimates. Another issue is that cetacean behaviour can be affected by the emission of noise when airguns are active. At present, it is unclear whether or how PBWs respond to seismic exploration activity, particularly as the impacts of impulsive sounds are heavily species- and context-dependent (Bain & Williams 2006, Stone et al. 2017). For example, Kavanagh et al. (2019) showed an 88% (82–92%) decrease in baleen whale sightings in the northeast Atlantic during periods of active firing, likely as a result of temporary displacement. By contrast, Dunn & Hernandez (2009) found no correlation between blue whale vocalizations or movements and airgun activity in the north-eastern Pacific. Our own experience of monitoring PBWs on Australian foraging grounds suggests that PBWs may continue to feed in the vicinity (<2.5 km) of operating seismic vessels if resources are abundant enough to outweigh the physical and energetic costs of acoustic disturbance (Morrice et al. 2004). More research is needed to contextualise the effects of petroleum exploration on migrating PBWs.

In conclusion, this study provides novel information on the behavioural ecology of a threatened whale population within a part of its geographical range where limited data exist. Although the prevalence of FUDs does not in itself constitute direct evidence of foraging activity, our results contribute to growing support for the hypothesis that the Timor Trough is an area of biological importance that provides feeding (and potentially breeding) habitat for the eastern Indian Ocean subpopulation of PBWs during the late austral winter and early austral spring. While platforms of opportunity are valuable for addressing knowledge gaps in data-poor tropical ecosystems, dedicated line-transect surveys that adhere to rigorous sam-

pling designs are required to further elucidate patterns in PBW habitat use and facilitate robust estimates of abundance. This information is essential for supporting population recovery as well as mitigating the potential consequences of increasing regimes of anthropogenic disturbance. We propose that spatial management of the Timor Trough as a foraging BIA may offer an opportunity for effective conservation of a charismatic yet little-known ocean migrant.

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