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Characterising essential breeding habitat for whales informs the development of large-scale Marine Protected Areas in the South Pacific

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ABSTRACT: There are significant challenges associated with mapping critical habitat for large, migratory species. The humpback whales of Oceania in the South Pacific are no exception, with their winter breeding grounds spanning >4000 km of ocean basin. This subpopulation is listed as endangered, but there are few systematic spatial data with which to prioritise specific areas for additional research or conservation. A few sites in Oceania have been the focus of long-term, non-systematic population surveys. Using the maximum entropy algorithm, we developed predictive habitat models for 2 such sites: American Samoa 2003–2010 (n = 300) and Tonga 1996–2007 (n = 475), using sightings of whale groups and environmental factors hypothesised to influence their space-use patterns. At both sites, shallow water was the best predictor of the spatial distribution of mother–calf pairs. In contrast, access to deep water was important for adult groups, and seafloor slope and rugosity influenced habitat suitability for males engaged in acoustic breeding displays. Our study illustrates the value of predictive modelling for identifying habitat partitioning for specific sub-groups of a wider population. Similarities between habitat requirements predicted in our study to those identified for other populations suggest that the slow recovery of Oceania humpback whales cannot be attributed to unusual breeding-habitat needs; instead, there may be other factors influencing the slow increase in population size. We recommend that the modelling techniques utilised here be used to identify other breeding sites within Oceania for future research and conservation efforts across the South Pacific region.

KEY WORDS: Habitat · Maximum Entropy Modelling · Humpback whale · MPA · *Megaptera novaeangliae*

INTRODUCTION

Knowledge of the environmental factors that influence the geographic distribution of species is essential for understanding the processes that drive population dynamics, as well as for the development of effective conservation and management strategies (Guisan & Thuiller 2005). Identification of key areas is especially pertinent for endangered animals because the availability of suitable habitat is considered a critical component of population viability (Oviedo & Solís 2008, Bailey & Thompson 2009, Goetz et al. 2012). Cetaceans present particular challenges to investigations of spatial distribution and critical habi-

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tats owing to their mobile nature and the fact that only a fraction of their lives is spent at the surface where they are observable.

The humpback whale *Megaptera novaeangliae* is a cosmopolitan and migratory species that typically inhabits mid- to high-latitude seas for summer feeding and the waters surrounding tropical islands for winter breeding. The breeding grounds of Oceania (South Pacific; Fig. 1) extend from New Caledonia in the west through to French Polynesia in the east and span thousands of islands and coral-reef systems over a large expanse of ocean. The majority of research to date has focused on a few discrete breeding sites within this range, and these studies have provided an understanding of site fidelity (Garrigue et al. 2002), the extent of regional interchange (Garrigue et al. 2011), and abundance (Constantine et al. 2012). Humpbacks in Oceania were subjected to years of intense exploitation (Clapham & Ivashchenko 2009) and are presently only at 37% of historical levels (International Whaling Commission 2014), with overall low levels of population increase despite decades of protection (Constantine et al. 2012). Oceania humpbacks are one of only 2 subpopulations in the world that remain classified as Endangered by the International Union for Conservation of Nature (IUCN) (Childerhouse et al. 2008), but the cause of their slow recovery remains unknown. Because of the low number of humpbacks in this region and their wide-ranging movements, large areas throughout the South Pacific have been designated as sanctuaries where the whales are free from the threat of hunting (SPREP 2008). However, further research is needed to identify specific areas of importance to the whales.

Investigations into fine-scale patterns of habitat use have been conducted on humpback breeding grounds globally, revealing that the whales have a strong affiliation with the shallow waters of tropical islands and coral reefs. Water temperature, distance to shore, water depth, sea-floor slope, and rugosity have all been identified as influential factors for explaining the spatial distribution of humpback whales during the winter (Herman & Antinoja 1977, Whitehead & Moore 1982, Martins et al. 2001, Rasmussen et al. 2007, Oviedo & Solís 2008, Cartwright et al. 2012, Smith et al. 2012). Habitat-use patterns may further vary due to behavioural class or repro-

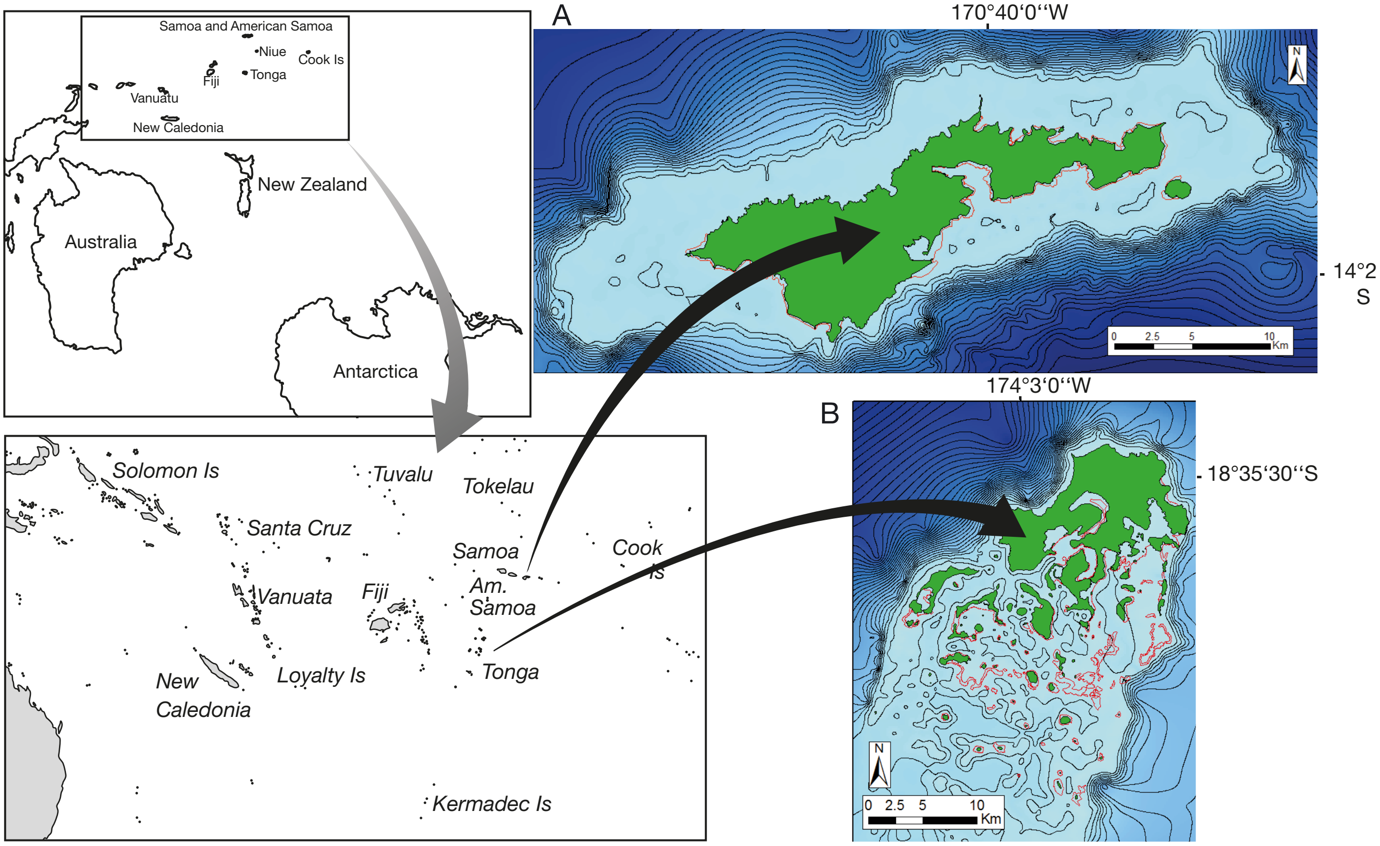

Fig. 1. Location of (A) Tutuila, American Samoa, and (B) Vava'u, Tonga, within Oceania (South Pacific). Contour lines in the right panels represent 50 m intervals. Red lines denote coral reefs

ductive state (Smultea 1994, Frankel et al. 1995, Martins et al. 2001, Craig et al. 2003, Ersts & Rosenbaum 2003).

Over the last 2 decades, there have been improvements in the analytical techniques available to quantify habitat use in marine ecosystems (Guisan & Thuiller 2005, Redfern et al. 2006). Species distribution models (SDMs) are a popular, cost-effective means of describing and understanding patterns of habitat-use and potential geographic distributions of organisms (Franklin 2006). Techniques for modelling species′ distributions and their associations with environmental factors have traditionally relied on the collection of presence/absence data, by way of systematic surveys conducted along line transects. Analysis of such data commonly involves regression-based generalised additive models (GAMs), generalised linear models (GLMs), boosted regression trees, climatic envelopes, or multivariate regression splines (Elith et al. 2011). However, many datasets exist as a set of presence locations that originate from multiple platforms of opportunity or limited coverage studies. Such data have driven the development of distribution modelling techniques that do not require systematic sampling or true absences to be included. One such method that has shown to perform with high predictive accuracy over a wide range of circumstances is maximum entropy modelling (MaxEnt) (Phillips et al. 2006). This technique relates environmental covariates associated with organismal occurrences to those associated with randomly selected pseudo-absences over the extent of the study domain. The result is the generation of a probability surface of habitat suitability that is as unconstrained as possible with respect to the environmental attributes associated with the locations of organisms (Elith et al. 2011). The highly mobile and often cryptic nature of cetaceans presents obvious challenges for the collection of true absence data. Therefore, through utilisation of a modelling technique that requires presence information to be compared with randomly sampled pseudo-absences, this concern is eliminated (Elith et al. 2011). Whilst acknowledging that marine ecosystems present particular challenges to habitat modelling owing to their dynamic nature (Redfern et al. 2006, Robinson et al. 2011), application of predictive habitat modelling to seascape ecosystems using MaxEnt is becoming increasingly prevalent (e.g. Moura et al. 2012, Smith et al. 2012, Thorne et al. 2012).

We used data from non-systematic boat-based surveys at 2 sites in Oceania to better understand and predict the breeding habitat requirements of endangered humpback whales. Our specific objectives were (1) to investigate whether the spatial distribution of preferred habitat for humpback whales varies with key reproductive states and breeding-ground behaviours and (2) to identify the oceanographic characteristics that best predict the geographic distribution of suitable habitat among key breeding classes.

MATERIALS AND METHODS

Study sites

Fine-scale habitat use by humpback whales was assessed at 2 discrete breeding grounds of the South Pacific: Tutuila, American Samoa (Fig. 1A) and Vava′u, Tonga (Fig. 1B). These areas were selected because they represent areas where surveys of humpback whales have been conducted for several years, providing a detailed dataset.

Tutuila, American Samoa

The island territory of American Samoa is situated at 14° 20′ S, 170° 00′ W. Tutuila, the largest of 5 rocky, volcanic islands that constitute this region, has an area of 142 km^2 and consists of rugged peaks surrounded by fringing coral reefs (Fig. 1A). The continental shelf extends up to 9 km around Tutuila, where the average water depth is 60 to 80 m, before dropping off steeply into depths exceeding 500 m approximately 3 to 8 km offshore.

Vava′u, Tonga

The Tongan archipelago is a series of volcanic islands and coral atolls extending from 15 to 23° S and 173 to 177° W. A northern cluster of 55 low-lying coral islands in this region is collectively known as Vava′u (Fig. 1B) with a combined land area of 121 km^2. The low and irregular southern coastline of the main island Vava′u Lahi merges into a complex network of channels, bays, and smaller islands, surrounded by waters of 60 to 80 m in depth.

Sighting data

Non-systematic winter surveys conducted from small vessels ~5 to 7 m in length were undertaken in the waters of Vava′u, Tonga (1996 to 2007) and Tutuila, American Samoa (2003 to 2010). The primary objectives of these surveys were to collect fluke photographs of humpback whales for individual identification and skin samples for genetic analysis. Location data were also collected, and group composition was classified based on the number of associated individuals and their behaviour. Due to the non-systematic nature of the surveys, we were unable to account for detection bias, but the surveys were conducted in a similar manner, with broad coverage of the study sites (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m548p263_supp.pdf). Here, we focused on occurrences of 3 categories of groups: mother-calf pairs, singing males, and adult-only groups. Calves were identified by their length, which was half of or less than half of the adult whale with which it was closely associated (most likely the mother) (Clapham & Mayo 1987). Singers are adult males who perform an acoustic display while on their breeding ground; it has been theorised that aspects of the surrounding environment may affect how the song is propagated or perceived (e.g. Mercado & Frazer 1999). Singing was confirmed with the aid of an underwater hydrophone. The locations of groups were documented, through either marking the position on a map (1996 in Vava′u) or obtaining the coordinates from a handheld Global Positioning System (GPS) receiver (1998 to 2007 in Vava′u and 2003 to 2010 in Tutuila). Only the initial geographic position for each pod was used for analysis (see Fig. S2).

Environmental factors

Eight environmental layers encompassing the Tutuila and Vava′u regions were created in ArcMap v.10.1 (Esri) and used for prediction of suitable habitat for humpback whales: depth, sea-floor slope, sea-floor rugosity, distance to nearest shore, distance to nearest coral reef, and distance to the 100 m, 200 m, and 1000 m bathymetric contours. Selection of environmental factors was informed through comparable habitat-use studies of humpback whales in other breeding grounds (e.g. Martins et al. 2001, Ersts & Rosenbaum 2003, Oviedo & Solís 2008). Extensive investigation of global bathymetric datasets revealed spatial resolution that was too coarse (Gebco08; Spatial Resolution 30 arc-sec) for use in our study. Accordingly, geo-referenced nautical charts of Vava′u (Land Information New Zealand, chart NZ822; 1:50 000) and Tutuila (National Oceanic and Atmospheric Administration, chart 83484; 1:60 000) were digitised in ArcMap v.10.1 to create a bathymetric raster. The cell size for the environmental rasters was determined by the distance between the bathymetric contours provided on the nautical charts and was set at 100 m × 100 m for Tutuila and 153 m × 153 m for Vava′u. A projected coordinate system, WGS 1984 Universal Transverse Mercator, was used for both the Tonga (Zone 1S) and American Samoa (Zone 2S) regions. The slope of the terrain at both sites was generated using ArcGIS v.10.1 Spatial Analyst extension. Rugosity provided a measure of sea-floor roughness and was constructed using the default settings in the ArcGIS Benthic Terrain Modeller extension (Wright et al. 2005). Dynamic factors such as sea-surface temperature (SST) and wind/swell data were considered as potential variables to be included in model development but were unavailable at a sufficiently fine spatial scale for our study sites. Raster surfaces representing the closest distances to shore, coral reef, and the contour lines were generated using the 'Euclidean distance' tool in ArcMap. The area covered by the non-systematic boat surveys, the location of humpback sightings, and the extent of information provided on the nautical charts determined the spatial domain of the study area at both sites. All humpback sightings at Tutuila were located within the demarcated study area. In Vava′u, there were 18 humpback sightings (3 singers and 15 adult-only groups) that fell outside of the extent of bathymetric information and thus were not included in model development. Raster layers of all environmental factors were clipped to the same extent, and areas of land were masked prior to analysis.

We assessed the extent of multicollinearity among explanatory variables by determining the correlation coefficient between layers using the Band Collection Statistics tool (Spatial Analyst extension) in Arcmap v.10.1. We adopted the classification system as used by Katz (2006), whereby 2 variables that possessed a correlation coefficient >0.75 were considered to be highly correlated, between 0.5 and 0.75 moderately correlated, and those <0.5 were considered to have low correlation. We ensured that only low to moderately correlated variables were entered into the same model by excluding one of a pair of highly correlated variables (see Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m548p263_supp.pdf).

Predictive habitat-suitability models

Probability surfaces of habitat suitability were generated for the regions of Tutuila and Vava′u using the software Maximum Entropy (MaxEnt v.3.3.3). The MaxEnt method involves comparing the values of environmental factors associated with animal occurrences with environmental values throughout the entire study area, to predict locations that likely provide favourable habitat. Initially, an equal probability of habitat suitability is assigned over the entire study area. A deterministic algorithm then works to optimise the probability surface to improve model fit, resulting in an increase in probability of habitat suitability in locations that possess similar environmental conditions to those associated with the presence sightings (Phillips et al. 2006). Of all possible surfaces that satisfy these requirements, the one that is closest to uniform (i.e. that of maximum entropy) is generated. Separate habitat models were developed for the humpback group types (mother−calf pairs, adult-only groups, and singers) for comparison of differences in key habitat characteristics.

Regularisation parameters were used to constrain the models to avoid over-fitting (i.e. matching too closely to the observed locations of whales and not generalising to the entirety of the study area); these function similarly to Akaike's information criterion as selection criteria in terms of reducing model complexity (Merow et al. 2013). A regularisation parameter of 1 was selected, based on prior optimisation of this value (Phillips & Dudik 2008). The predictive habitat models were executed for 5000 iterations, to provide sufficient time for model convergence; 15 replicates of each model were run in total (Young et al. 2011), and the average of these was selected. MaxEnt predictions can be sensitive to spatial biases of input data (Peterson et al. 2007). We addressed the issue of sample-selection bias by converting the available survey tracks into a raster surface of track density and incorporated this information during model development. Inclusion of the survey-bias file constrained the selection of background samples from known surveyed locations.

Threshold-independent measures of predictive accuracy were used to assess model performance. Bootstrapping analysis was undertaken, where 25% of the sighting data were randomly selected per replicate to be used as independent test data. This procedure provided an estimation of uncertainty for the 'area under the curve' (AUC) score of the receiver operating characteristic (ROC). The ROC curve involved plotting sensitivity values (true positives) on the *y*-axis, with the fractional predicted area on the *x*-axis. The AUC value is the probability that the cell containing a randomly selected occurrence has a habitat suitability score that is higher than a randomly selected background (pseudo-absence) cell (Phillips et al. 2006). This value provides a single measure of overall accuracy and thus is useful for comparison between models. Higher AUC values indicate greater ability for models to discriminate between suitable and unsuitable habitat; an AUC score of 0.5 indicates a model that can predict no better than randomly. The relative ability of each environmental variable to predict suitable habitat was assessed via jackknife tests as part of the MaxEnt procedure. This procedure involved running the models with each environmental factor individually.

RESULTS

Overview

The locations of a total of 475 groups of humpback whales in Vava'u and 300 groups in Tutuila informed the development of the spatial habitat models (Table 1). Three environmental surfaces were highly correlated with other layers (see Tables S1 & S2 in the Supplement and subsequently were excluded, resulting in 5 environmental factors that were retained for development of the predictive habitat models at both study areas. These factors were water depth, distance to nearest coral reef, distance to 200 m bathymetric contour, sea-floor rugosity, and sea-floor slope.

Outputs of predictive habitat models

Areas identified as preferential habitat for humpback whales varied among group types. Shallow, near-shore waters were most suitable for mother−calf pairs at both breeding sites. In Tutuila, a few areas were particularly suitable for mother−calf pairs, including the region south of Pago Pago harbour, around the island of Aunuu, the Taputimu area, and the waters surrounding Pola Island (Fig. 2A). In Vava'u, suitable habitat for mother−calf pairs was

Table 1. Number of humpback whale groups by group type used for development of spatial habitat models at the 2 research sites in the South Pacific

Group type	Vava'u	Tutuila
Mother−calf pairs	109	61
Adults only	334	221
Singers	32	18

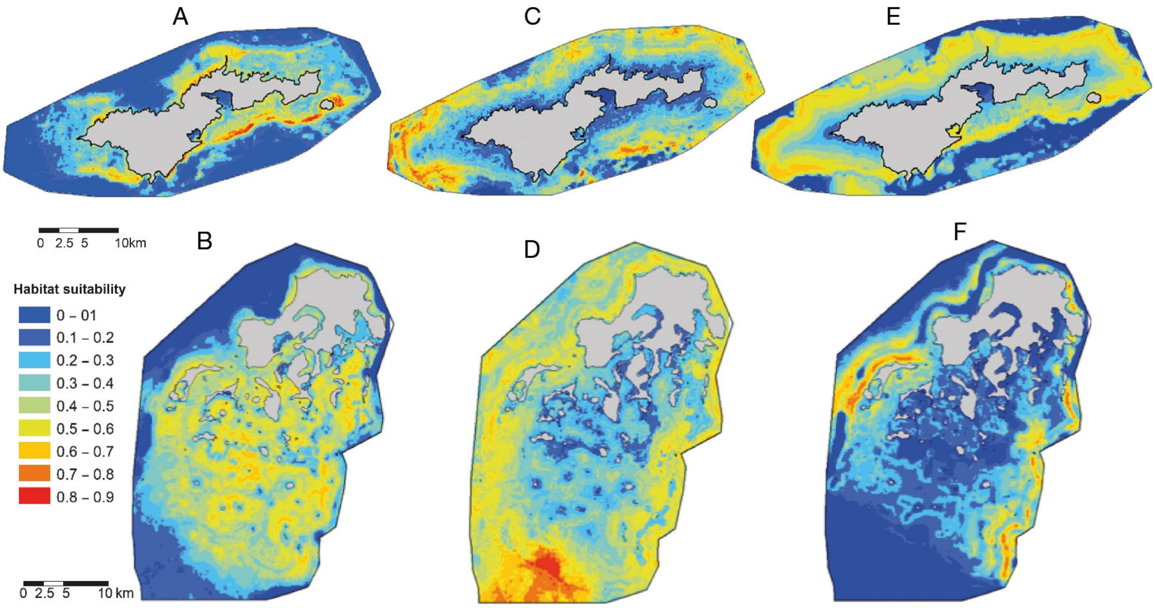

Fig. 2. Predicted habitat-suitability surfaces for (A,B) mother–calf pairs, (C,D) adults only, and (E,F) singers in (A,C,E) Tutuila and (B,D,F) Vava'u. Yellow and red indicate areas predicted by the MaxEnt models to provide suitable habitat for humpback whales

more broadly distributed around the majority of smaller islands and coral reefs (Fig. 2B). At both breeding sites, prediction of suitable habitat for adult-only groups indicated a contrasting pattern to that of mother–calf pairs. Adult groups favoured deeper-water areas around the periphery of Tutuila and Vava'u near the seaward edge of the continental shelf (Fig. 2C,D). Lalalomei Bank (10 km south of Vava'u) was also predicted to be highly suitable habitat for adult groups (Fig. 2D), despite the fact that no surveys have yet been performed there. Predicted suitable habitats for singers in Tutuila and Vava'u were consistent with that for adult groups, but were more spatially restricted (Fig. 2E,F). Bootstrapping analysis indicated that all models performed with good-to-excellent discriminatory power (Hosmeret al. 2013); the AUC of the ROC ranged from 0.71 to 0.88 (Fig. 3).

The influence of environmental factors on the predictive accuracy of our habitat models varied between group types and between islands. For mother–calf pairs at Tutuila, water depth had the highest predictive accuracy when run in isolation (Fig. 4A). Similarly in Vava'u, water depth was important, but the distance to the coral reef had the highest predictive accuracy (Fig. 4D). For mother–calf pairs at both sites, the predictive accuracy of the models was improved when distance to the 200 m contour line covariate was excluded, suggesting that proximity to deep water provided little or no information in determining suitable mother–calf habitat. Conversely, distance to the 200 m contour had the highest predictive accuracy when run in isolation for discriminating suitable adult-only habitat in Tutuila (Fig. 4B) and Vava'u (Fig. 4E). At both sites, slope and sea-floor rugosity were influential in predicting suitable habitat for singing males (Fig. 4C,F). Distance to the 200 m contour line was also informative for discerning suitable singing habitat in Tutuila and Vava'u.

DISCUSSION

Using presence-only data to develop predictive habitat models, our study identified preferred areas among humpback whale group types at 2 South Pacific breeding sites (Tutuila and Vava'u). These differences likely reflect the particular environmental characteristics favoured by different groups for breeding. Furthermore, our study revealed that habitat preference in the vast and geographically diverse region of the South Pacific is similar to that of many breeding areas of humpback whales elsewhere. This finding suggests that the slow recovery of Oceania humpback whales following the cessation of hunting cannot be attributed to their unusual breeding-habitat needs.

Consistent patterns of suitable habitat among group types were revealed between Tutuila and Vava'u. Water depth was an informative variable for

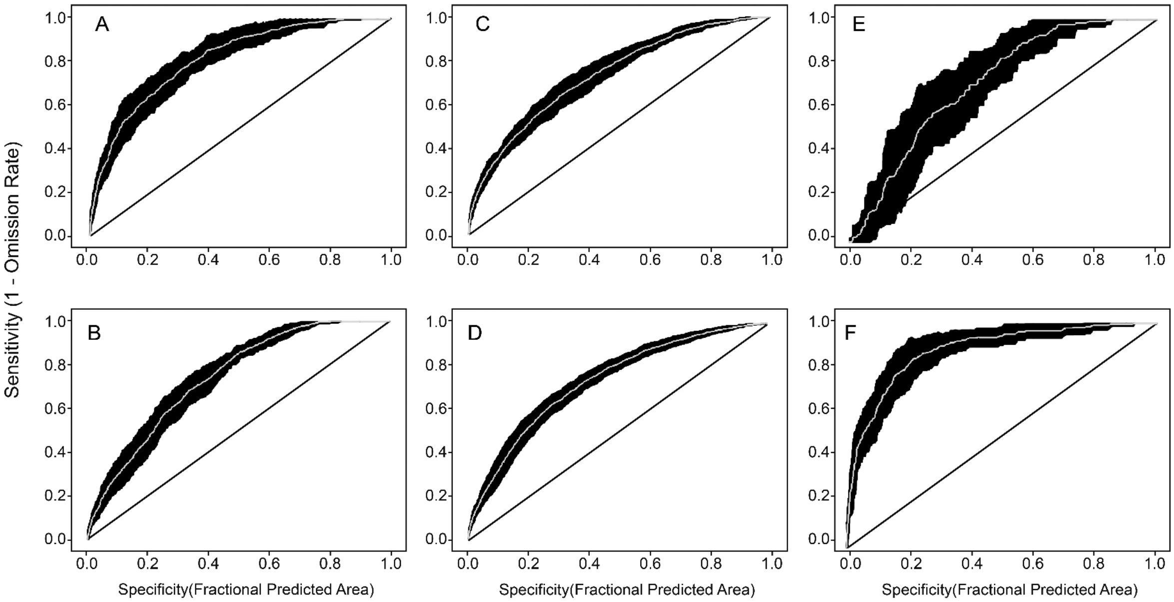

Fig. 3. Mean receiver operating characteristic scores (white line) ± 1 SD for assessing the predictive accuracy of suitable habitat for mother–calf pairs in (A) Tutuila AUC = 0.81 and (B) Vava'u AUC = 0.73, adult-only groups in (C) Tutuila AUC = 0.73 and (D) Vava'u AUC = 0.73, and singers in (E) Tutuila AUC = 0.71 and (F) Vava'u AUC = 0.88. A score of 0.5 — indicating a prediction no better than random — is denoted by the black line

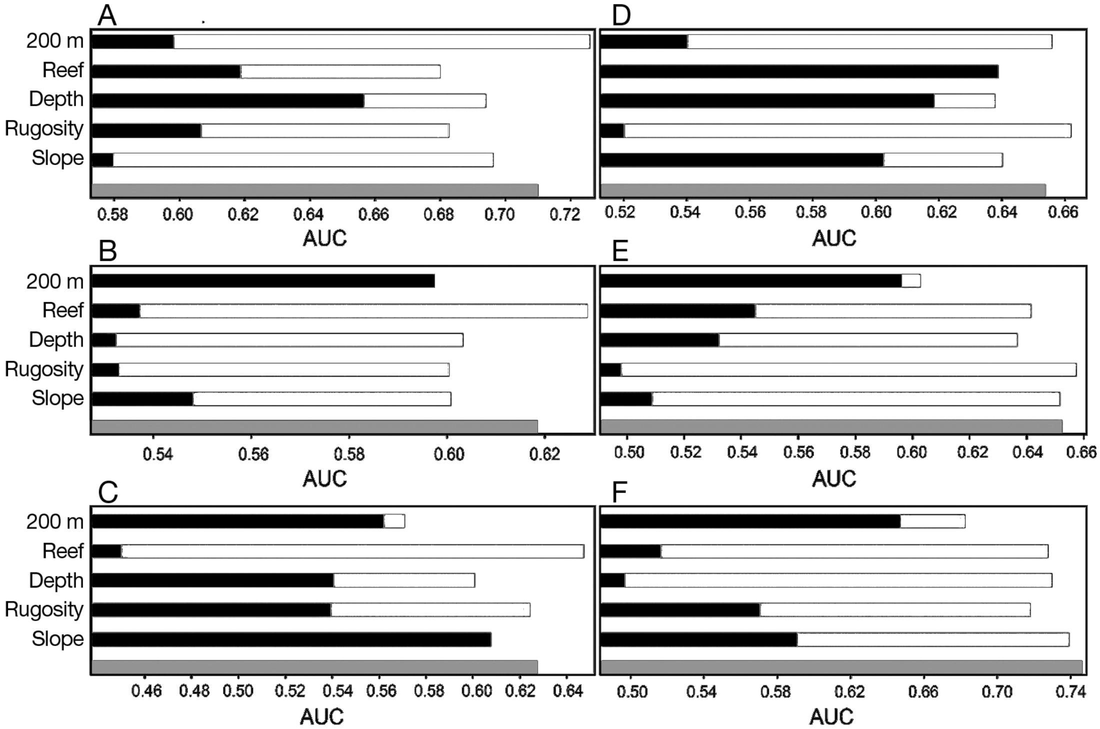

Fig. 4. Jackknife tests for assessing the predictive ability of environmental factors for (A,D) mother–calf pairs, (B,E) adults only, and (C,F) singers in (A–C) Tutuila and (D–F) Vava'u. Models were run with each variable in isolation (black bars) and with each variable excluded (white bars). The grey bar indicates the model run with all variables included. '200m' and 'reef' denote distance to 200 m bathymetric contours and distance to nearest coral reef, respectively

determining suitable habitat for mother–calf pairs at both sites, and suitability decreased as water depth increased (Figs. 5A & 6A). In Tutuila, the region of Taema Bank, which is shallow but not adjacent to the coast, was predicted to be highly suitable, suggesting that water depth is the most important factor for

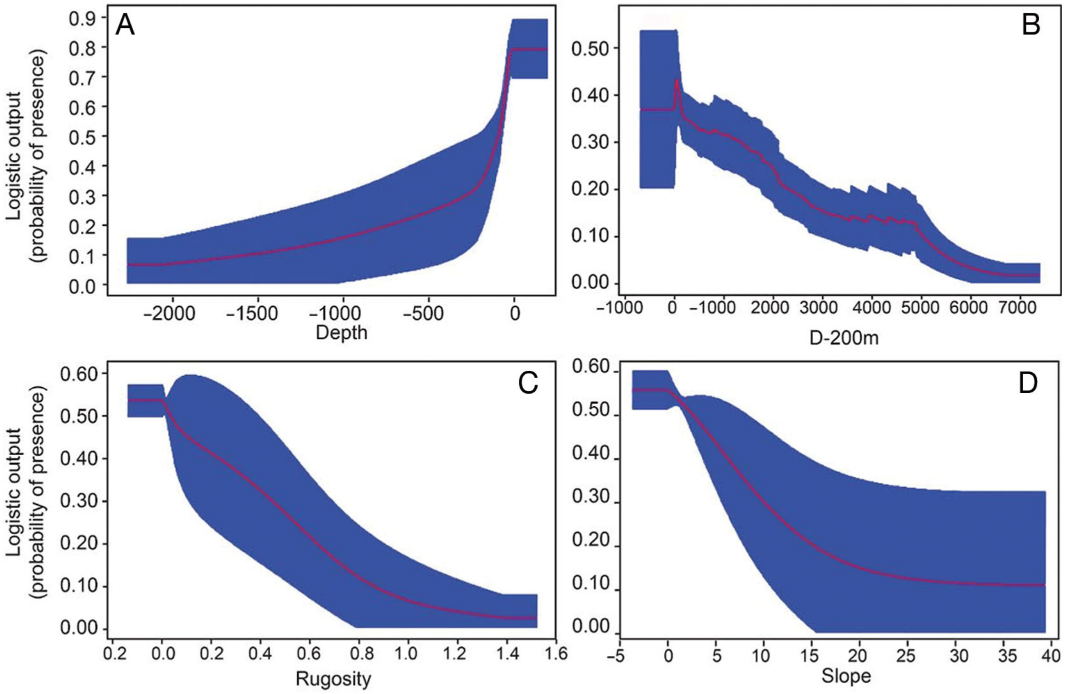

Fig. 5. MaxEnt response curves of informative environmental variables for predicting suitable habitat in Tutuila, American Samoa: (A) Depth (m) for mother–calf pairs, (B) distance to the 200 m contour line for adults (D-200m), (C) rugosity for singers, and (D) slope for singers

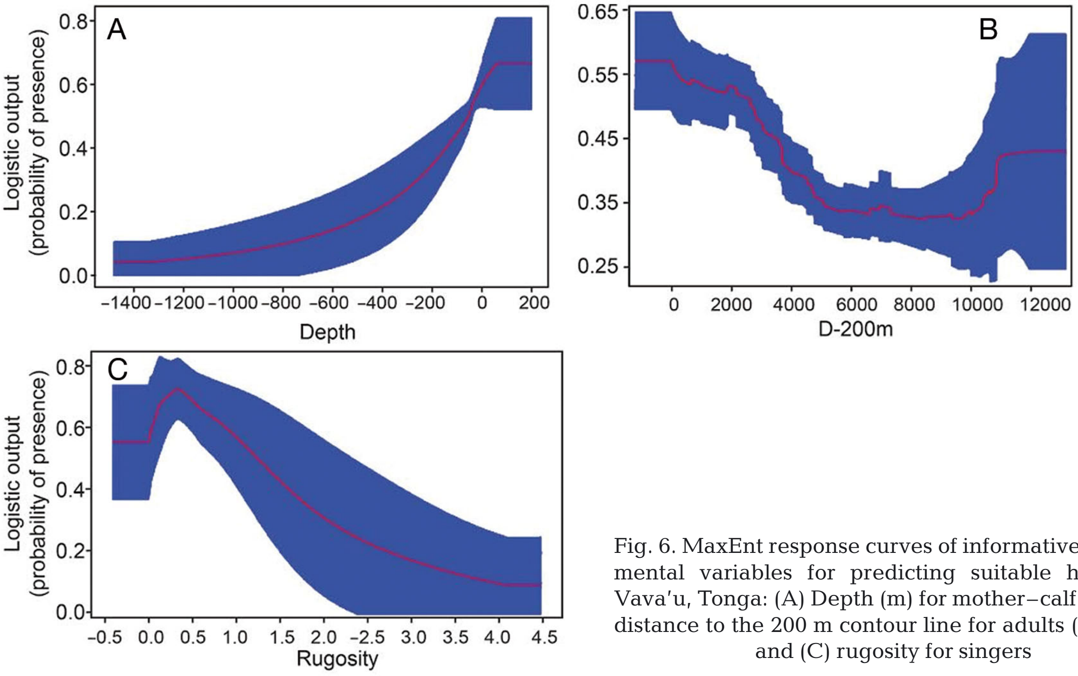

Fig. 6. MaxEnt response curves of informative environmental variables for predicting suitable habitat in Vava'u, Tonga: (A) Depth (m) for mother–calf pairs, (B) distance to the 200 m contour line for adults (D-200m), and (C) rugosity for singers

mother–calf pairs. Shallow water may provide shelter from predators, such as killer whales *Orcinus orca* (Smultea 1994, Mehta et al. 2007). Distance to the nearest coral reef was more influential for predicting mother–calf habitat in Vava'u than Tutuila. However, this finding may be an artefact of habitat type: there are fewer coral reefs in Tutuila than in Vava'u, and they generally form a shallow fringe around the coastline that may affect the importance of this variable for the whales. Occupancy of areas closer to coral reefs may provide protection from prevailing winds and rough water, and consequently, such areas may be beneficial for behaviours such as nursing and for energy conservation (Martins et al. 2001).

Areas predicted to be suitable for adult groups at both breeding grounds encompassed deeper water farther offshore, compared to that of mother–calf pairs. We used the distance to the 200 m contour line as a proxy for access to deep water; this was the most informative variable for predicting habitat for adult humpback groups at both sites. As the distance (predominantly inshore distance due to the extent of the study domains) from the 200 m contour increased, habitat suitability decreased at both Tutuila and Vava'u (Figs. 5B & 6B). An association between courtship activities and deep water has been observed in other breeding ground regions (e.g. Félix & Haase 2001, Ersts & Rosenbaum 2003). In Vava'u, Lalalomei Bank, 10 km south of the islands, was predicted to be highly suitable habitat for adult groups. This may help explain why the individual response curve of adult groups in Vava'u showed an increase in habitat suitability approximately 10 km from the 200 m contour (Fig. 6B). However, additional data are required to understand the importance of this area for humpback whales during the winter breeding season throughout the South Pacific (Garrigue et al. 2015).

In both Tutuila and Vava'u, slope and rugosity of the sea floor were more informative for prediction of habitat for singing whales than for other group types. Higher sea-floor rugosity resulted in lower habitat suitability at both sites (Figs. 5C & 6C). In Tutuila, as the slope of the sea floor increased, habitat suitability for singers decreased (Fig. 5D), suggesting that flat sea beds are more suitable for singing. This finding may reflect an environmental influence of these bathymetric characteristics on song propagation. Flat ocean floor may result in less scattering of sound waves than a rough bottom (Whitehead & Moore 1982). However, whilst the effect of environmental variables on propagation of humpback song has been described using a theoretical approach (Mercado & Frazer 1999), field testing of these effects have yet to be undertaken.

The predictive models developed in our study for identifying areas of important habitat in 2 remote regions within Oceania have utilised valuable datasets that were not originally collected for the purpose of habitat analysis, providing a cost-effective alternative to systematically surveying these regions. Such an approach potentially can reveal important unknown habitats, such as Lalalomei Bank south of Vava'u. Identification of potentially suitable habitats is important in Oceania, where population monitoring has only been performed at select sites and/or for which there remain questions regarding population status. The results of our study in the South Pacific may facilitate the design of future systematic surveys for abundance or validation of distributional patterns, through identifying where survey effort should be focused (Johnston et al. 2007). Discrimination of key habitat also may help elucidate the social factors driving humpback aggregations. High densities of whales in a particular location likely attract more whales (Clapham & Zerbini 2015).

Whilst the benefits of habitat model development make it an attractive choice for analysis, it is important to recognise several inherent limitations. In our study, the MaxEnt outputs are predictive maps of 2 small island chains that depict areas humpbacks are more likely to use, based on the oceanographic characteristics of the region. However, only through empirical confirmation of model outputs with additional field observations can the accuracy and validity of the models truly be quantified.

The choice of environmental variables used to characterise the preferred habitat of a species clearly dictates model outputs. We did not use SST in our model due to the low spatial resolution of available data (5 km × 5 km). However, whilst acknowledging that SST is likely to be influential for humpback whales at an ocean-basin scale (Rasmussen et al. 2007), during the winter breeding season, SST is relatively homogenous throughout humpback breeding grounds in Oceania; such a finding is consistent with that of Rasmussen et al. (2007), who observed that humpbacks are found in wintering areas above 21.1°C, regardless of latitude.

If model explanatory variables are highly co-linear, caution must be exercised when interpreting individual response curves because the importance of highly correlated variables may be inflated (Phillips et al. 2006). Collinearity among environmental variables is common, owing to the complex nature of ecological data (Graham 2003). We attempted to reduce the influence of collinearity in our model by excluding variables that were highly correlated and utilising only those with a low-to-moderate correlation (Katz 2006). Furthermore, jackknife testing facilitated assessment of the individual contributions of variables to the predicted geographic distributions, allowing comparisons among variables (Baldwin 2009). Our habitat models therefore identify areas that are likely to be of importance to whales, rather than explicitly evaluating the significance of environmental predictors.

Sample size has been shown to influence the outputs of SDMs; small numbers of location observations (<30) tend to result in less robust and poorer-performing models (Wisz et al. 2008). In our study, there were fewer singing males at both sites (n = 32 and 18) than the number of mother–calf pairs (n = 109 and 61) and adult groups (n = 334 and 221; Table 1). Models performed with small sample sizes are better suited for exploratory predictions, rather than testing specific range limits of a species (Pearson et al. 2007). For this reason, our predictions of the locations of singing habitat should be interpreted with caution. However, it should be noted that when assessed against other SDMs, MaxEnt has been shown to outperform alternative methods when sample sizes are small (Hernandez et al. 2006, Pearson et al. 2007, Baldwin 2009).

We assessed performance of our SDMs through use of the threshold-independent AUC (Phillips & Dudik 2008). The primary goal of this technique is to evaluate the discriminatory ability of the model; the method is particularly suitable for comparison of models involving the same species and the same study regions (Radosavljevic & Anderson 2014). Our study focused on the distributional patterns of habitat suitability among different social classes of humpbacks in 2 different breeding areas. However, in some circumstances, a binary presence-absence predictive map may be preferable, such as for estimating biodiversity hotspots (Cumming 2000). In such cases, threshold-dependent measures of predictive accuracy such as kappa, or the True Skill Statistic (Allouche et al. 2006), should be used in place of, or in addition to, the AUC.

Humpback whales throughout the Southern Hemisphere are recovering from decades of intense whaling pressure (Clapham & Ivashchenko 2009, Constantine et al. 2012, International Whaling Commission 2014). To help protect Oceania's endangered humpback whales, large whale sanctuaries covering millions of square kilometres of ocean have been established (SPREP 2008). Although no South Pacific Island nation currently hunts whales, other threats include disturbance from whale watching, ship strikes, entanglement, and habitat degradation. Whilst habitat is an integral component of population viability (Goetz et al. 2012), and we have shown the importance of particular habitats to humpback whales in our study, reasons for the slow recovery of Oceania's whales are not completely understood. Although we have examined habitat use of humpbacks on their breeding grounds, these grounds represent only part of the whales' total habitat; it may be that factors associated with the migratory route and/or feeding grounds may play a greater role in the recovery of whales in Oceania. Investigations in the North Pacific suggest that as populations of humpback whales increase, their geographic distributions may extend into formerly occupied or previously unoccupied areas (Johnston et al. 2007). Within the South Pacific, humpbacks are now observed in areas where they had not previously been recorded, such as the Pitcairn Islands, west of French Polynesia (Horswill & Jackson 2012).

The majority of member states of the Pacific Regional Environment Programme have declared their waters as whale sanctuaries to aide conservation endeavours and have committed to a Memorandum of Understanding for the Convention of Cetaceans and their habitats in the Pacific Island region under the International Convention on Migratory Species. Whilst these initiatives provide crucial protection for whales over a large geographic scale, identification of important habitats at fine spatial scales is also required. Such efforts will assist with targeting protection in local areas and indicating the geographical extent required for effective management actions. During recent years, concern has been raised over the impacts that unregulated whale-watching may have on humpback populations (Schaffar et al. 2013), particularly by encroaching on resting areas (Kessler & Harcourt 2012); however, one long-term study on humpbacks and tourism failed to show a population-level effect (Weinrich & Corbelli 2009). Whale watching is a significant economic activity for many South Pacific Islands, such as Vava'u (Orams 2002). Our finding that near-shore areas are important for mother–calf pairs, and deep water is important for adult groups, is consistent with studies of humpback breeding grounds elsewhere (e.g. Smultea 1994, Martins et al. 2001, Ersts & Rosenbaum 2003). Mother–calf pairs inhabit easily accessible coastal waters and are generally recognised as the most vulnerable individuals to disturbance from human activities such as tourism and vessel strikes (e.g. Schaffar et al. 2013). We therefore recommend that conservation measures in the South Pacific prioritise mother–calf breeding areas, by incorporating them into protection measures for whales in the region (SPREP 2008), for example, by restricting the number of whale-watching licences or implementing zoning schemes for no-go areas (Kessler & Harcourt 2012, Schaffar et al. 2013).

Conducting comprehensive systematic surveys for whales throughout the vast expanse of Oceania is logistically and financially problematic. Through use of methods such as species distribution modelling based on presence data, areas of important habitat for wide-ranging species such as humpbacks may be revealed. In some cases, specific habitat requirements may be a limiting factor for recovering populations. Our study found that the requirements of Oceania humpback whales for breeding habitat are generally consistent with those of populations elsewhere and are unlikely to be the cause of the slow rate of recovery in Oceania. Humpbacks have been resighted in the extreme eastern and western breeding regions of Oceania both within and between years (Garrigue et al. 2002, 2011), suggesting that protection should be provided for the species at all breeding grounds to aid recovery of all sub-populations. Such protection will be facilitated through identification of remaining key habitats within the South Pacific basin. Accordingly, we recommend that investigations of habitat use in breeding grounds should be extended to more regions within the South Pacific.

Currently, there is a global trend toward implementation of large-scale reserve networks to protect all marine organisms and their habitat (e.g. Toonen et al. 2013). The expansive Marine Mammal Protected Areas declared by many Pacific island nations provide a valuable platform for South Pacific-wide protection for Oceania humpback whales and other cetaceans. Our study clearly identifies important habitat requirements for different sub-groups of humpback whales in Oceania and addresses concerns raised about broad-scale MPA approaches to conservation efforts for marine mammals (Kaschner et al. 2012, Williams et al. 2014). Future work should include further modelling of key habitats within the South Pacific, with a focus on identifying the major factors that influence whale aggregation behaviours (Clapham & Zerbini 2015). This may resolve issues associated with large-scale ecosystem approaches (e.g. Pompa et al. 2011) often used in spatial planning efforts to protect individual species. With conservation efforts by South Pacific island nations, including protecting critical habitat through more effective MPA design (see Williams et al. 2014), our study provides robust evidence of exactly what type of oceanographic features are required for these endangered whales on their breeding grounds.

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