Global Change Biology
April 2019, Volume 25 Issue 4 Pages 1466-1481
https://doi.org/10.1111/gcb.14563
https://archimer.ifremer.fr/doc/00860/97179/

Whales in warming water: Assessing breeding habitat diversity and adaptability in Oceania's changing climate

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Abstract :

In the context of a changing climate, understanding the environmental drivers of marine megafauna distribution is important for conservation success. The extent of humpback whale breeding habitats and the impact of temperature variation on their availability are both unknown. We used 19 years of dedicated survey data from seven countries and territories of Oceania (1,376 survey days), to investigate humpback whale breeding habitat diversity and adaptability to climate change. At a fine scale (1 km resolution), seabed topography was identified as an important influence on humpback whale distribution. The shallowest waters close to shore or in lagoons were favored, although humpback whales also showed flexible habitat use patterns with respect to shallow offshore features such as seamounts. At a coarse scale (1 degrees resolution), humpback whale breeding habitats in Oceania spanned a thermal range of 22.3-27.8 degrees C in August, with interannual variation up to 2.0 degrees C. Within this range, both fine and coarse scale analyses of humpback whale distribution suggested local responses to temperature. Notably, the most detailed dataset was available from New Caledonia (774 survey days, 1996-2017), where encounter rates showed a negative relationship to sea surface temperature, but were not related to the El Nino Southern Oscillation or the Antarctic Oscillation from previous summer, a proxy for feeding conditions that may impact breeding patterns. Many breeding sites that are currently occupied are predicted to become unsuitably warm for this species (>28 degrees C) by the end of the 21st century. Based on modeled ecological relationships, there are suitable habitats for relocation in archipelagos and seamounts of southern Oceania. Although distribution shifts might be restrained by philopatry, the apparent plasticity of humpback whale habitat use patterns and the extent of suitable habitats support an adaptive capacity to ocean warming in Oceania breeding grounds.

Keywords : climate change, habitat modeling, humpback whales, Oceania, prediction, sea surface temperature, seamounts, species distribution

INTRODUCTION

In recent decades, evidence for global climate change has spurred ecologists and conservationists to increase research efforts to better understand species-climate relationships. In marine ecosystems, changes in average temperatures around the world are affecting species throughout all trophic levels (Doney et al., 2012; Hoegh-Guldberg & Bruno, 2010; Poloczanska et al., 2013; Sydeman, Poloczanska, Reed, & Thompson, 2015), yet the impact of climate change on marine megafauna, including cetaceans, is considered a 'big unknown' (Clapham, 2016; Thomas, Reeves, & Brownell, 2015). Distribution shifts are expected to occur at various geographic scales (Hazen et al., 2013; Kaschner, Watson, Trites, & Pauly, 2006; Macleod, 2009) and resulting population impacts are expected to vary across species, depending notably on the vulnerability and extent of their critical habitats (Macleod, 2009; Simmonds & Eliott, 2009; Sydeman et al., 2015). Yet, current knowledge remains insufficient to estimate the adaptive plasticity of most species to thermal changes, which is one of the key elements needed to predict the impact of climate change on marine ecosystems (Macleod, 2009; Silber et al., 2017; Sydeman et al., 2015). In recent years, Species Distribution Models (SDMs) have become a popular tool to predict distribution changes in response to climate change (Hazen et al., 2013; Legrand et al., 2016; Morán-Ordóñez, Lahoz-Monfort, Elith, & Wintle, 2017; Torres et al., 2013), but limited long-term empirical data exist to calibrate and validate these models of long-lived marine species such as cetaceans (Silber et al., 2017).

Humpback whales (*Megaptera novaeangliae*) may be impacted by global ocean warming in both polar and tropical ecosystems, as they spend summers feeding in polar areas and seasonally migrate toward tropical breeding grounds where they fast during winter (Chittleborough, 1958). The reasons for such extensive migrations are still debated but could be linked to increased calf fitness in warmer waters of the tropical and subtropical breeding grounds (Clapham, 2000). Although this hypothesis suggests a direct link between humpback whale life history and water temperature, it remains unclear how sea surface temperature (SST) drives distributions within breeding latitudes, as studies have shown both strong relationships (Bortolotto, Danilewicz, Hammond, Thomas, & Zerbini, 2017; Guidino, Llapapasca, Silva, Alcorta, & Pacheco, 2014; Rasmussen et al., 2007; Smith et al., 2012) and weak or no effects of this variable (Trudelle et al., 2016; Dulau et al., 2017). SST is dynamic, with complex changes through time as it fluctuates on multiple temporal scales (monthly, seasonally, annually) and follows patterns that may be stochastic, cyclic (e.g., El Niño Southern Oscillation, Pacific Decadal Oscillation, Antarctic Oscillation) or continuous (climate change). Models studying the effect of temperature on species' distribution should explicitly reflect these variations (Fernandez, Yesson, Gannier, Miller, & Azevedo, 2017; Mannocci, Boustany, et al., 2017; Scales et al., 2017). Hence, datasets collected over large temporal and spatial scales are necessary to understand the effect of SST on the distribution of wide-ranging and long-lived species such as humpback whales.

Industrial whaling decimated humpback whales during the 20th century (Rocha, Clapham, & Ivashchenko, 2015). Since the mid-1980s, populations have shown variable signs of recovery across the globe. The Oceania humpback whale population, which encompasses humpback whales wintering in the South Pacific Islands, is still classified as 'endangered' (Childerhouse et al., 2009) because of its small size and slow recovery rate (Constantine et al., 2012; Jackson et al., 2015). Compared to other breeding regions of the world, Oceania encompasses a remarkably large extent of potential breeding habitat (Valsecchi, Corkeron, Galli, Sherwin, & Bertorelle, 2010). It covers thousands of islands and reefs that offer the conditions usually regarded as preferred for humpback whale breeding and nursing behaviour: sheltered, shallow and warm waters (Bortolotto et al., 2017; Cartwright et al., 2012; Derville, Torres, Iovan, & Garrigue, 2018; Lindsay et al., 2016; Rasmussen et al., 2007; Smith et al., 2012; Trudelle et al., 2016).

In Oceania, humpback whales are structured into geographically separated sub-populations (Childerhouse et al., 2009; Garland et al., 2015; Olavarría et al., 2007) that show varying degrees of connectivity (Garland et al., 2011; Garrigue et al., 2011; Steel et al., 2017). Hence, the International Whaling Commission (IWC) recognizes several breeding stocks and sub-stocks across Oceania with limited exchange (IWC, 2005). Across this vast ocean basin, social factors and culture likely play a large role in humpback whale distribution (Clapham & Zerbini, 2015; Garland et al., 2011; Rendell & Whitehead, 2001), specifically through natal philopatry (Baker et al., 2013) and lek attraction (Herman, 2017). Social aggregation is a proposed hypothesis to explain distribution dynamics (Clapham & Zerbini, 2015), but the effect of environmental drivers has never been explored at a basin scale.

Using a compilation of humpback whale survey data across the South Pacific, this study aims to describe the environmental drivers of humpback whale distribution on breeding grounds, with particular focus on the influence of SST and topography. Variation in SST is hypothesized to influence both current and predicted habitat availability in the context of warming ocean temperatures. Patterns of space use in relation to SST are estimated from coarse scale encounter rates (with spatial resolutions of 0.25° to 1°) and fine scale sampling of used versus available environmental conditions (with a spatial resolution of one kilometre). This study contributes to broad efforts to understand the temporal and spatial scales at which highly mobile marine megafauna species may respond to climate change.

MATERIALS AND METHODS

Study regions and data collection

A database was compiled from dedicated surveys for cetaceans conducted throughout Oceania by several research teams (Table 1), in austral winter and shoulder seasons months (May-December) between 1999 and 2017. Surveys were conducted in various study sites located in

New Caledonia, Vanuatu, Tonga, Niue, Samoa, American Samoa and French Polynesia (Fig. 1). Study sites were grouped in study regions based on their geographic location and affiliation to IWC definitions (Fig. 1): the “western region” (New Caledonia, Vanuatu), the “central region” (Tonga, Niue, Samoa, American Samoa), and the “eastern region” (French Polynesia). This grouping was specifically chosen to reflect genetically differentiated stocks or management units, while still producing relatively homogeneous samples in terms of survey effort and latitudinal SST gradients.

Non-systematic surveys were conducted in a closing-mode (i.e., cetaceans were approached after detection), as the primary objective for most research teams was to locate humpback whales for the purposes of photo-identification and/or genetic sampling. Though field protocols and equipment varied among surveys (e.g., vessel type, number of observers), the following variables were consistently recorded by all teams: 1) whale observations, 2) duration of survey effort, and 3) spatial extent of survey effort. At each whale observation, group size, time of day, GPS position (WGS84 latitude-longitude), and social group types (Singleton, Pair, Mother-calf, Mother-calf-escort, Competitive group, Mother-calf-competitive group) were recorded.

In most surveys, the spatial extent of search effort was precisely recorded with a GPS trackline at a sampling frequency varying from 1 position.hour^{-1} to 2 positions.min^{-1} (84 % survey days). In the remaining 16 % of survey days, search effort was concentrated in small and well-defined areas that could be spatially bounded into georeferenced polygons drawn by the data suppliers (Appendix S1). Four polygons were manually produced in a QGIS graphical interface around the study sites of Hao (Gambier Islands), Huahine and Moorea (Society Islands), and Niue (covering 362 to 2,360 km^2). Finally, for 93 % of the survey days, the time at the beginning and end of the effort was recorded, enabling a daily time on effort to be deduced. When this information was lacking, the time on effort was deduced from the distance travelled along the boat GPS trackline and the average speed calculated over all surveys (estimated at 12.8 km.h^{-1}). Daily times on effort included the time spent to search for whales, plus the time spent with whale groups (during which observers are less likely to detect other whales). Land-based observers were employed to help the boat-based team detect nearshore humpback whales in the South Lagoon of New Caledonia (Derville, Torres, & Garrigue, 2018). This additional observer effort was not accounted for as it only moderately contributed to the group detections. Data processing and statistical analysis were performed with R (version 3.4.4, R Core Team, 2016) and QGIS (version 2.18.3, QGIS Development Team, 2016).

Coarse scale encounter rate analyses

The variation in humpback whale encounter rates, specifically whale encounter rate per survey day, was analysed in relation to coarse scale SST patterns. This measure of SST, referred to as "SST_{coarse}", was based on daily measurements from Reynolds NCEP Level 4 Optimally Interpolated SST with a spatial resolution of 0.25° of latitude-longitude, equivalent to approximately 28 km resolution (https://www.ncdc.noaa.gov/oisst).

Current SST range over Oceania - The average SST_{coarse} from 1999 to 2017 was estimated for each archipelago included in the study, during the month of August to reflect SST at the peak of the breeding season (Rasmussen et al., 2007). As breeding season is reported later in some breeding sites (American Samoa; Munger, Lammers, Fisher-Pool, & Wong, 2012; French Polynesia; Poole, 2002), the average SST_{coarse} in October was also estimated. SST_{coarse} was extracted and averaged at several reference points centred in the main known breeding aggregations or study sites (see Appendix S2 for exact positions). To approximate the surface area of these main breeding grounds and match the rest of the coarse scale encounter rate analysis, the average SST_{coarse} over a 1° radius was used to describe conditions surrounding the reference points.

***Future predicted SST range over Oceania* -** The future SST conditions for the end of the 21st century were assessed under the Representative Concentration Pathway 8.5 (RCP 8.5) of aerosols and greenhouse gases scenario, commonly used as a pessimistic baseline if no climate change mitigation is achieved (Moss et al., 2010). The future SST was computed with a "pseudo- global warming approach" (Kimura & Kitoh, 2007; Knutson, Sirutis, Garner, Vecchi, & Held, 2008; Walsh, 2015; Appendix S3). Here, the pseudo-global warming approach was based on an ensemble of Coupled Model Intercomparison Project models (CMIP5; Taylor, Stouffer, & Meehl, 2012). The CMIP5 models are climate model simulations employed to detect anthropogenic effects in the climate record and project them into the future. The pseudo-global warming approach allowed the production of a raster of future SST conditions for 2080-2100 at 0.25° resolution in Oceania (see modelling details in Appendix S3). Isotherms at 21 °C and 28 °C corresponding to the breeding range described in Rasmussen et al., (2007) were estimated from 1) the current observed August SST_{coarse} (1999-2017), and 2) the projected future August SST_{coarse} for the end of the 21st century (2080-2100).

***Local and regional coarse scale encounter rate models* -** The encounter rate per survey day, in number of whales per hour of survey (whales.h^{-1}) was computed by dividing the total number of whales observed (number of groups multiplied by group size) by the total time on effort per day. Daily encounter rates were modelled with a Generalized Additive Model (GAM, Hastie & Tibshirani, 1990) applied with a Gaussian log link as a function of year, day of year and SST_{coarse}. Variables were modelled with penalized thin-plate regression splines optimized with a Restricted Maximum Likelihood and basis size limited to 5 to prevent overfitting (Wood, 2017). Two separate GAMs were produced: the first, M_{OC}, estimated the effect of SST_{coarse} on encounter rate through space at the regional Oceania scale, and the second, M_{NC}, estimated the local effect of SST_{coarse} and periodic climatic fluctuations at a specific study site, the New Caledonia South Lagoon. This site was chosen as a case study as it provides the most consistent and prolonged survey effort in Oceania (1996 - 2017).

In M_{NC}, SST_{coarse} was extracted at the centre of the New Caledonia South Lagoon (167°E, 22.5°S). This location and the resolution of SST_{coarse} were considered to produce a representative estimate of temperatures in the study site, which had a core survey area of about 20 km wide. For this model, encounter rates were calculated for study days from 1996 to 2017 (Garrigue et al., 2001, Appendix S4). Also, in place of using SST_{coarse} as a predictor of encounter rate in M_{NC}, two variables reflecting conditions during the previous feeding season were also tested. Indeed, Pacific Ocean conditions change in relation to periodic climatic fluctuations such as the El Niño Southern Oscillation phenomenon (ENSO, McPhaden, Zebiak, & Glantz, 2006), the strength of which is measured by the Southern Oscillation Index (SOI). The Antarctic Oscillation (AAO) also affects the Southern Ocean and is measured by the Southern Annular Mode (SAM) index. Consequently, changes in migration length, timing or path can be hypothesized as a result of environmental variability in the Southern Ocean, and in turn could be reflected in humpback whale encounter rates measured at the breeding grounds. In order to assess the effect of the conditions in the feeding grounds and migratory corridors on humpback whale presence in the South Lagoon breeding ground, SAM was obtained from the British Antarctic Survey and SOI was obtained from the National Oceanographic and Atmospheric Administration (Appendix S4). SAM and SOI monthly indexes were averaged between November and April each year to reflect the summer feeding conditions of humpback whales prior to the following breeding season in Oceania (Bengtson Nash et al., 2018).

In M_{OC}, SST_{coarse} was extracted at the centre of each 1° grid cell in which daily encounter rates were calculated. In order to account for spatial autocorrelation in this large scale model across breeding regions, projected geographical coordinates were added as covariates in the M_{OC}

model. These terms corresponded with an isotropic smoother of x- and y-coordinates at which the encounter rates were estimated. Smoothing was performed with a Gaussian process model parametrized with a power exponential correlation function of range based on Kamman & Wand (2003) and basis size 50.

The performance of models was assessed through the computation of the proportion of deviance explained (Guisan & Zimmermann, 2000). Partial dependence plots were produced to visualize the effect of one variable while all others were held constant at their mean (Friedman, 2001). When predicting fitted responses in the M_{OC} model, latitude and longitude were held constant to a fixed position in the South Lagoon (167°E, 22.5°S) to ensure comparability with the M_{NC} predictions.

Fine scale habitat use model

Habitat preferences of humpback whales were modelled based on a binomial response variable comparing ‘used’ to ‘available’ environmental conditions. Indeed, non-systematic cetacean surveys were not designed to record true presence-absence data, but included some information about the area surveyed and time on-effort. In this context, constraining the available background space is known to improve model performance (Engler, Guisan, & Rechsteiner, 2004; Phillips et al., 2009) and can be informed by the extent of survey effort at sea (e.g., Torres, Read, & Halpin, 2008). Following the method in Derville, Torres, Iovan et al., (2018), the area surrounding GPS survey tracklines was used to approximate available environment where background points were sampled. Daily survey track strip-width spanning 10 km to each side of the tracklines were generated to reflect areas surveyed, resulting in daily background areas of 125 to 4,463 km^2. The 10 km width of the background sampling area reflected the maximum detection distance of a humpback whale surface activity, calculated with the geometrical horizon distance for observers standing in a small survey boat (less than 1 m high, as mostly used in Oceania study sites). In the few cases where tracklines were not recorded, background areas were approximated in small polygons enclosing the survey sites (Appendix S1). Background points were sampled randomly within these areas, with a minimum distance of 2 km from each other and independently of presence locations. The number of background points was proportional to the number of hours of effort per day (on average 4 points per hour of survey).

Humpback whales in Pacific tropical breeding grounds have been shown to associate with small seabed and reefs features ranging a few dozen meters to kilometres (model resolution: 50 m, Cartwright et al., 2012; 100 - 150 m, Lindsay et al., 2016; 4.8 km, Smith et al., 2012). Given this potential to select habitat at very fine scale, the effect of topography and SST on habitat suitability within each region of Oceania was assessed at a resolution of 1 km. Moreover, seasonally predictable and persistent SST conditions were assumed to be important factors for humpback whales seeking breeding and nursing habitats; therefore, climatological estimates of SST and its temporal variability were used in this model (Mannocci, Boustany, et al., 2017). Hence, the variable “SST_{fine}” was obtained from a climatology averaging SST from 2003 to 2014 at a daily scale based on the Multi-scale Ultra-high Resolution SST with a fine spatial resolution of 1 km (https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1). The variable “$SST_{fine.CV}$” was derived as the coefficient of variation (in %) of SST_{fine} at a given day of the year over 11 years. Furthermore, bathymetric charts at 1 km resolution (“*DEPTH*”, in meters) were obtained from the General Bathymetric Chart of the Oceans (GEBCO). Seabed slope (“*SLOPE*”, in degrees) was calculated from bathymetry using the raster R package (version 2.6-7; Hijmans, 2017). Coastlines were obtained from the OpenStreetMap dataset (http://openstreetmapdata.com/data/coastlines) and coral reef contours were obtained from the UNEP World Conservation Monitoring Centre (UNEP-WCMC, WorldFish-Centre, WRI, & TNC, 2010). A raster of the distance to the closest shallow reef (emerging at low tide) or coastline (“*DISSURF*”, in km) was calculated.

Environmental variables were extracted at presence and background locations. *DEPTH*, *SLOPE* and *DISSURF* were log-transformed to prevent an inflated influence of outliers as recommended by Wood, (2006). *DEPTH* and *DISSURF* showed a medium to strong correlation depending on the region (Spearman coefficient > 0.7) in the presence-background dataset (Appendix S5). Collinearity among explanatory variables is known to affect a model's stability and capacity to assess the relative influence of each variable (Dormann et al., 2013). Sequential regression was used to correct for collinearity (Graham, 2003). A linear regression between *DEPTH* and *DISSURF* at the points of presence and background was developed (Appendix S5). The residuals of this regression ("$DISSURF_{RES}$") were subsequently used instead of *DISSURF* as they represent the contribution of *DISSURF* after accounting for *DEPTH*. For instance, high $DISSURF_{RES}$ values represent waters 'abnormally' shallow considering how far they are from land or reef (e.g. an offshore shallow seamount).

GAMs were used to model the presence-background response as a function of *DEPTH*, *SLOPE*, $DISSURF_{RES}$, SST_{fine}, $SST_{fine.CV}$, day of year, and year. The smoothed effect of each of these variables, except for year, was assessed as an interaction with the region (i.e., western, central, or eastern Oceania, Fig. 1) in order to capture potentially contrasting habitat selection patterns across regions. Variables were modelled with penalized thin-plate regression splines optimized with a Restricted Maximum Likelihood and basis size limited to 5 to prevent overfitting (Wood, 2017). Finally, local differences in humpback whale prevalence were accounted for by including an isotropic Gaussian process smoother on projected latitude and longitude coordinates similar to that used in M_{OC}.

Stratified Monte Carlo cross-validation was used to assess the significance of predictors' contributions. Models were produced over 50 training subsets containing presence and background points from 90 % randomly selected survey days per region (Derville, Torres, Iovan, et al., 2018), and the proportion of runs with p-values less than 0.001 or 0.05 was reported (Hazen et al., 2016). Partial dependence plots were produced for each significant environmental predictor/region combination. Fitted responses for each region were estimated while holding the latitude and longitude to a fixed location central to the main study site per region, namely: the New Caledonia South Lagoon for the western region (167.00°E, 22.50°S), American Samoa for the central region (170.74°W, 14.29°S) and the Society Islands for the eastern region (149.48°W, 17.54°S). Finally, humpback whale habitat suitability with respect to *DEPTH*, *SLOPE*, $DISSURF_{RES}$, SST_{fine} and $SST_{fine.CV}$ was predicted over 1 km resolution maps. Day of year was fixed to its mean per region dataset, and year was fixed to 2017. Areas where environmental conditions strayed outside the model training ranges by region were dashed out on the final predicted maps relative to each region respectively, as they should be considered with caution (Mannocci, Roberts, Miller, & Halpin, 2017).

In order to account for habitat-associated sampling bias between regions – particularly the dominant tendency in eastern and central Oceania to survey near islands instead of pelagic waters – a predicted map of habitat suitability was also produced for eastern Oceania using the fitted habitat use trends from the western region, where survey effort occurred both near and off shore. However, the SST_{fine} range in the eastern region was largely above that of the western region. To ensure model transferability and prevent environmental extrapolation, predictions were produced with fixed values of SST_{fine} and $SST_{fine.CV}$ (22°C and 0.9 respectively; the preferred SST_{fine} conditions for humpback whales in the western region). As a result, predictions reflected potentially suitable seabed topography, without regard to temperature. Areas where topographic variables strayed outside the training range observed in the western region were removed from the predicted map.

RESULTS

A total of 1,376 days of survey were compiled over years from 1999 to 2017 (for years of survey per country see Table 1). The majority of surveys were conducted in August (36 %), September (33 %), October (16 %) and July (12 %). Overall, 8 % of survey days were conducted more than 10 km off shore. From all survey effort, 6,454 humpback whales were observed (Table 1).

Coarse scale encounter rate and SST

The mean encounter rate per day of survey at the Oceania scale was 0.69 whales.h^{-1} (SD ± 0.90). Averaged in 1° grid cells, the highest encounter rates were recorded southwest of New Caledonia, over the Antigonia seamount (2.4 whales.h^{-1} ± SD 1.6) and Orne bank (2.0 whales.h^{-1} ± SD 0.9), followed by Tutuila (American Samoa, 1.5 whales.h^{-1} ± SD 1.1), Vava'u (Tonga, 1.3 whales.h^{-1} ± SD 0.9) and Rurutu (Austral Islands, French Polynesia, 1.3 whales.h^{-1} ± SD 3.1; Fig. 2). Antigonia showed significantly higher encounter rates than the other four top sites (Kruskal-Wallis test: $X^2 = 13.4$, $p < 0.001$). The lowest encounter rates were recorded in pelagic offshore waters (e.g., French Polynesia, Fig. 2) and in nearshore waters of the Marquesas, Samoas, northwestern New Caledonia, and some of the Tuamotus.

SST_{coarse} measured in each reference point in August (n = 12, Appendix S2) from 1999 to 2017 varied from 22.3 to 27.8 °C. SST_{coarse} fluctuated by 1.1 to 2.0 °C between years at a given site, with the larger annual anomalies recorded in the Tonga (2.0 °C), Niue (1.9 °C), Vanuatu (1.8 °C), and the Gambier islands (1.8 °C). SST_{coarse} measured in October was warmer at all sites (Appendix S2), even those with a breeding season peak reported later in the year (e.g., American Samoa: mean SST_{coarse} Aug = 27.7 °C vs mean SST_{coarse} Oct = 28.2 °C).

The map of mean encounter rate at 1° resolution was overlaid with current and future isotherms estimated from SST_{coarse} with a 0.25° resolution (Fig. 2). Following the climate change predictions for the end of the 21st century, an average SST of 28 °C or greater in August is expected at the northern parts of Vanuatu and Tonga (Vava'u), Niue, Samoa, American Samoa and the northern part of French Polynesia (Society, Tuamotu and Marquesas Islands).

At the Oceania scale between 1999 and 2017, in the M_{OC} model, 1,376 daily encounter rates showed a significant increase with year, particularly between 2003 and 2012 (Fig. 3a). The day of year also affected encounter rates, which followed a bell-shaped trend with a peak around the end of August. After accounting for spatial autocorrelation using an interaction covariate between latitude and longitude (edf = 22.8, F = 10.6, p-value < 0.001), encounter rates showed a decreasing trend with increasing SST_{coarse}, but the relationship was slightly non-significant (F = 0.6, p = 0.06, Fig. 3a). The deviance explained by the model reached 41.4 %.

Similar trends were found in the New Caledonia South Lagoon M_{NC} model of encounter rates between 1996 and 2017 (n = 774 days of survey, Fig. 3b). Encounter rates showed a decreasing trend with increasing SST_{coarse}. Encounter rate also increased with year and reached a peak in 2012 - 2013. The seasonal peak was estimated to occur around the end of August. The deviance explained by the model reached 25.4 %, including 1.1 % that could be attributed to SST_{coarse}. The alternative models of M_{NC} that replaced SST_{coarse} with the SOI or SAM from the previous summer led to slightly lower deviance explained (24.7 % and 24.5 % respectively, Appendix S4), and both variables had no significant effect on encounter rate in the New Caledonia South Lagoon (SOI: F = 0.5, p-value = 0.08; SAM: F = 0.0, p-value = 0.86).

Fine scale habitat use

The fine scale humpback whale habitat preference model explained 21.7 % of the deviance in the presence-background dataset counting 46,426 data points (including 2,872 presences) over a spatial extent of 192,500 km^2.

Depth was a main predictor of fine scale distribution (n-significant = 50; Table 2). The relationship between humpback whale presence and shallow depth was similar between the three regions (Fig. 4), although favouring deeper waters in eastern (mean depth at whale presence positions = 360 m ± SD 480) and central Oceania (mean = 198 m ± SD 296), compared to western Oceania (mean = 43 m ± SD 89; Anova: $F_{(2,\ 2869)} = 523$, $p < 0.001$). In contrast, the relationship with $DISSURF_{RES}$ differed between regions. The trend was significant and positive in western Oceania (Table 2; Fig. 4), indicating a preference for shallow waters away from surfacing reefs or coasts, such as offshore seamounts and banks. This trend was reflected in predicted habitat suitability maps for the region, where the seamounts of the Norfolk and Loyalty Ridges were particularly suitable (Fig. 5b). On the contrary, in both central and eastern Oceania, the trend between humpback whale presence and $DISSURF_{RES}$ was mostly negative (and less robust to cross-validation in the central region; Table 2), indicating that whales were found in waters closest to coasts or reefs and also relatively deep. In the eastern region, steep slopes were more represented and favoured by whales (Fig. 4). Again, these relationships manifested in the predicted habitat suitability maps, which emphasized the importance of the external slope of fringing/barrier reefs and coastal waters of high islands such as Tutuila (Fig. 5c), Tahiti (Fig. 5e) or Niue (Fig. 5f).

The western region had the highest amount of offshore survey effort. Hence, transferring the western fitted trends to eastern Oceania revealed potentially suitable habitats in offshore seamounts located south of the Society archipelago and in the southeastern part of the Austral archipelago (Fig. 6). Based on these predictions, when comparing the areas of highest habitat suitability (values > 0.9 quantile) in the French Polynesia Economic Exclusive Zone (EEZ) with current and predicted future 21°C and 28°C isotherms, it appeared that 90.1 % of the EEZ suitable habitats are currently included in this preferred SST_{coarse} range, against 48.9 % by the end of 21st century.

Temperature and its variability affected fine scale humpback whale distribution less consistently and significantly than topography. Indeed, SST_{fine} ranges were different from one region to the other (the western region displayed the coldest temperatures and the central region the warmest, Fig. 4), and the relationships to SST_{fine} among the regions were generally weak. In eastern Oceania, neither SST_{fine} nor $SST_{fine.CV}$ significantly affected distribution within the region (Table 2). In central Oceania, humpback whale presence was positively correlated to SST_{fine}, as many whales were observed in the warmest site of American Samoa (Fig. 4). In western Oceania, a marginal preference for cooler SST_{fine} was found, as well as a stronger relationship with $SST_{fine.CV}$ (Table 2). Humpback whale presence increased in waters with low $SST_{fine.CV}$, reflecting a preference for persistent temperature conditions across years in western Oceania (Fig. 4).

DISCUSSION

This study describes the relationship between humpback whale habitat use and SST on the breeding grounds of Oceania, using a large-scale dedicated survey dataset collected over almost two decades. At a fine scale, topography was an important driver of humpback whale distribution, and their habitat use patterns geographically varied with respect to shallow waters in islands, reefs, and seamounts. At a coarse scale, humpback whales displayed local responses to SST spatio-temporal variations. Overall, within the average 22.3 to 27.8 °C SST breeding range of Oceania humpback whales, breeding habitat appears to be primarily driven by topography, but is locally influenced by SST temporal variations that affect the predictability of suitable conditions. Global warming is predicted to impact habitat suitability in a great part of current breeding grounds in Oceania, based on shifting isotherms towards higher latitudes.

All of the study sites in Oceania exhibited current SST values within the 21 - 28°C range, suggesting tolerance to SST variations within the relatively narrow temperature range that has previously been established for humpback whale breeding grounds (Rasmussen et al., 2007). However, there may also be differential temperature preferences both within and among breeding ground sites; a pattern that is to be expected from ecological theory describing species thermal niches (Beaugrand & Kirby, 2016). Indeed, the sites with the highest encounter rates in Oceania exhibited both some of the lowest and the highest average SST values for the region. American Samoa was a preferred site in Oceania and was at the high end of the known acceptable breeding ground temperature range (27.7°C). In contrast, the site with highest encounter rates (New Caledonia) was at the lower end (22.3°C) and long-term observations in the South Lagoon suggested slightly greater encounter rates when water temperatures were cooler (< 22°C). Moreover, in the western region, the local predictability of these preferred conditions was also identified as a factor of suitability for humpback whales. Waters that showed low SST_{fine} variability across years were preferentially selected. However, SST conditions were no more or less anomalous in the western region compared to the rest of Oceania. Hence, if SST variability had a similar effect in the latter, it could have been masked by temporally uneven survey effort over the years. Nonetheless, these results suggest that humpback whales may have locally acquired specific responses to water temperature. As seabed topography appears to primarily drive breeding ground distribution within the acceptable temperature range of 21 - 28 °C, local temperature responses could have emerged as by-products of sub-population philopatric structure in Oceania. Hence, when visiting its traditional breeding region, a whale driven by the need to find mating opportunities and/or a suitable calving ground could be targeting preferred topographic conditions and secondarily associate locally with predictable appropriate temperatures. It remains to be seen whether sub-populations will keep visiting their historical breeding grounds in the future, even if the temperature rises above what is currently locally optimal.

In the New Caledonia South Lagoon, where survey effort was most consistent over a long time period, temporal fluctuation of SST was found to affect humpback whale presence. The potentially delayed impact of basin wide climatic phenomena was investigated to explain the changes in encounter rate, but these signals did not seem to covary. The climatic fluctuations of ENSO and the Antarctic Oscillation are known to interact and affect sea-ice concentration in the Antarctic (Curran, van Ommen, Morgan, Phillips, & Palmer, 2003; Meehl, Arblaster, Bitz, Chung, & Teng, 2016), which in turn impacts biological productivity (Zhang et al., 2014) and potential humpback whale foraging success (Bengtson Nash et al., 2018). Although varying feeding conditions in the Antarctic could influence northbound migration, this study suggests that climatic phenomena affecting humpback whale habitats basin wide could not solely explain the variability of humpback whale presence observed at a given breeding site. Encounter rates estimated through time in the South Lagoon were influenced by local SST conditions rather than wider climatic variations.

Distribution shifts are considered the most likely response of large mobile cetaceans to climate change (Silber et al., 2017; Sydeman et al., 2015). History has shown that humpback whale distribution can change on the scale of a few decades, particularly in cases of over-exploitation and local extirpation. For instance, humpback whales historically visited Fijian waters in great numbers but relatively few currently do so (Dawbin, 1959; Gibbs, Childerhouse, Paton, & Clapham, 2006; Miller, Batibasiga, & Solomona, 2015; Paton & Clapham, 2002). By contrast, whales seem to have appeared rather recently in other breeding grounds such as Hawaii (Herman, 1979) and French Polynesia (Olavarría et al., 2007; Poole, 2002). Social aggregation is thought to be a key factor influencing humpback whale breeding ground use of otherwise suitable habitats (Clapham & Zerbini, 2015). Male songs may play a role in attracting conspecifics towards breeding spots as they form (Clapham, Aguilar, & Hatch, 2008; Herman, 2017), but their propagation range is limited (~20 km; Garland et al., 2015). Hence, humpback whales might not disperse to areas with suitable environmental conditions that may have been erased from the cultural memory of individuals (Clapham et al., 2008) or that may be too remote.

To be successful, distribution shifts of humpback whales therefore require the availability of suitable habitats in proximity to the previously occupied ranges. In Oceania, climate change scenarios suggest a shift of the 28°C surface isotherm by several degrees of latitude south by the end of the 21st century (in the high CO2 emission scenario RCP 8.5; Moss et al., 2010). It must be noted that other more optimistic scenarios of climate change, such as the RCP 4.5 (Moss et al., 2010), would have likely predicted a weaker southward shift of the 28°C isotherm. Nonetheless, to follow this shift and remain in a 21 - 28 °C range, humpback whales would need to relocate their breeding and nursing activities, either to shallow waters currently considered as part of the migratory corridors, such as the Kermadec Islands (Riekkola et al., 2018), Cook Islands (Hauser, Peckham, & Clapham, 2000), Norfolk Island (Constantine, Russell, Gibbs, Childerhouse, & Baker, 2007), and Pitcairn Island (Horswill & Jackson, 2012), or to already existing breeding grounds such as New Caledonia, southern Vanuatu, or the Austral Islands. Considering that the sub-populations of Oceania are still well below their pre-exploitation numbers (< 50 % recovered, Jackson et al., 2015), carrying capacity limitations may not be a factor on the southernmost breeding grounds, if some sub-populations were to relocate there in response to climate change.

Survey effort biased towards nearshore waters has likely underestimated the extent of suitable breeding and nursing habitat in Oceania. Offshore shallow banks and seamounts surveyed in western Oceania have revealed the highest encounter rates (Antigonia seamount > 2 whales.h^{-1}). This unexpected preference for unsheltered offshore shallow waters contradicts the paradigm that humpback whales obligatorily seek shelter for breeding and nursing. In central and eastern Oceania, humpback whales were mainly observed in waters closest to islands or on the external slope of fringing and barrier reefs (see also Gannier, 2004; Poole, Albertson, & Oremus, 2014). However, the surveys in these regions have focused on waters surrounding islands, with only occasional transits through offshore deep waters separating archipelagos. Hence, humpback whale presence on offshore shallow seamounts could have gone undetected. Transferred predictions using the ecological relationships fitted in western Oceania support the potential for suitable seamount habitats in French Polynesia. These predictions are sustained by a few anecdotal observations over the President Thiers Bank (19 m), Arago seamount (28 m), and Neilson Reef (3 m, Fig. 6) in the southeastern Austral Islands (Gannier, Bourreau, & Casacci, 2000). Such previously undescribed suitable habitats constitute potential areas for relocation in response to climate change. Further research into offshore shallow habitats is warranted to build a more comprehensive assessment of present and future humpback whale distribution at basin scale.

This study suggests that a great part of the currently occupied breeding sites in Oceania might become unsuitably warm for humpback whales by the end of the 21st century. The thermal tolerance displayed by humpback whales in Oceania, combined with flexible patterns of habitat use and the great extent of available suitable habitats, suggest an adaptive capacity of these sub-populations on their breeding grounds. Sensitive breeding habitats lying at the northern “thermal edge” of the Oceania range should be the focus of future monitoring to clarify the acceptable temperature range of breeding humpback whales, and their organismal response to climate change. Finally, with growing anthropogenic pressure on both coastal and offshore habitats in Oceania and worldwide, whales are potentially facing cumulative stressors (Avila, Kaschner, & Dormann, 2018), which need to be included in future efforts to model distribution dynamics. In response to global warming, humpback whales risk relocating to areas where other threats are currently unidentified and deserve investigation. In this context, understanding and predicting the distribution of suitable habitats for whales is an important step to support the implementation of appropriate conservation measures.

ACKNOWLEDGMENTS

This research benefited from collaboration and data-sharing agreements among members of the South Pacific Whale Research Consortium (SPWRC), the Groupe d'Etude des Mammiferes Marins (Rangiroa) and the Groupe de Recherche sur les Cetaces (Antibes). Funding for the SPWRC was provided by the International Fund for Animal Welfare (IFAW), the Fond Pacifique, the US National Marine Mammal Laboratory, the Australian Department of Water, Heritage and Arts RNHP Fund, and the International Whaling Commission Scientific Committee. Financial support for data analysis was provided by the French Ministry for Europe and Foreign Affairs (Fond Pacifique grant), under collaboration with the Secretariat of the Pacific Regional Environment Programme (SPREP). Additional acknowledgments per study sites are reported in Appendix S1.

REFERENCES

Avila, I. C., Kaschner, K., & Dormann, C. F. (2018). Current global risks to marine mammals: Taking stock of the threats. *Biological Conservation*, *221*, 44–58.

Baker, C. S., Steel, D., Calambokidis, J., Falcone, E., González-peral, U., Barlow, J., … Yamaguchi, M. (2013). Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Marine Ecology Progress Series*, *494*, 291–306.

Beaugrand, G., & Kirby, R. R. (2016). Quasi-deterministic responses of marine species to climate change. *Climate Research*, *69*, 117–128.

Bengtson Nash, S. M., Castrillon, J., Eisenmann, P., Fry, B., Shuker, J. D., Cropp, R. A., …

Mclagan, D. (2018). Signals from the south; humpback whales carry messages of Antarctic sea-ice ecosystem variability. *Global Change Biology*, *24,* 1500–1510.

Bortolotto, G. A., Danilewicz, D., Hammond, P. S., Thomas, L., & Zerbini, A. N. (2017). Whale distribution in a breeding area: spatial models of habitat use and abundance of western South Atlantic humpback whales. *Marine Ecology Progress Series*, *585*, 213–227.

Cartwright, R., Gillespie, B., Labonte, K., Mangold, T., Venema, A., Eden, K., & Sullivan, M. (2012). Between a Rock and a Hard Place : Habitat Selection in Female-Calf Humpback Whale (*Megaptera novaeangliae*) Pairs on the Hawaiian Breeding Grounds. *PLOS One*, *7*, e38004.

Childerhouse, S., Jackson, J., Baker, C. S., Gales, N., Clapham, P. J., & Brownell, R. J. (2009). *Megaptera novaeangliae* (Oceania subpopulation) In: IUCN 2009 IUCN Red List of Threatened Species Version 2009 2. Retrieved from www.iucnredlist.org

Chittleborough, R. G. (1958). The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). *Marine and Freshwater Research*, *9*, 1–18.

Clapham, P. J. (2000). Why do Baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science*, *17*, 432–436.

Clapham, P. J. (2016). Managing leviathan: Conservation challenges for the great whales in a post-whaling world. *Oceanography*, *29*, 214–225.

Clapham, P. J., Aguilar, A., & Hatch, L. T. (2008). Determining spatial and temporal scales for management: Lessons from whaling. *Marine Mammal Science, 24,* 183–201.

Clapham, P. J., & Zerbini, A. N. (2015). Are social aggregation and temporary immigration driving high rates of increase in some Southern Hemisphere humpback whale populations? *Marine Biology, 162,* 625–634.

Constantine, R., Jackson, J. A., Steel, D., Baker, C. S., Brooks, L., Burns, D., … Garrigue, C. (2012). Abundance of humpback whales in Oceania using photo-identification and microsatellite genotyping. *Marine Ecology Progress Series, 453,* 249–261.

Constantine, R., Russell, K., Gibbs, N., Childerhouse, S., & Baker, C. S. (2007). Photo-identification of humpback whales (*Megaptera novaeangliae*) in New Zealand waters and their migratory connections to breeding grounds of Oceania. *Marine Mammal Science, 23,* 715–720.

Curran, M. A. J., van Ommen, T. D., Morgan, V. I., Phillips, K. L., & Palmer, A. S. (2003). Ice core evidence for Antarctic sea ice decline since the 1950s. *Science, 302*, 1203–1206.

Dawbin, W. H. (1959). New Zealand and South Pacific Whale marking and recoveries to the end of 1958. *Norsk Hvalfangsttid, 5,* 214–238.

Derville, S., Torres, L. G., & Garrigue, C. (2018). Social segregation of humpback whales in contrasted coastal and oceanic breeding habitats. *Journal of Mammalogy, 99,* 41–54.

Derville, S., Torres, L. G., Iovan, C., & Garrigue, C. (2018). Finding the right fit: Comparative cetacean distribution models using multiple data sources and statistical approaches. *Diversity and Distribution, 24,* 1657–1673.

Doney, S. C., Ruckelshaus, M., Duffy, E. J., Barry, J. P., Chan, F., English, C. A., … Talley, L. D. (2012). Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science, 4,* 11–37.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36,* 027–046.

Dulau, V., Pinet, P., Geyer, Y., Fayan, J., Mongin, P., Cottarel, G., … Cerchio, S. (2017). Continuous movement behavior of humpback whales during the breeding season in the southwest Indian Ocean: on the road again! *Movement Ecology*, *5*, 11.

Engler, R., Guisan, A., & Rechsteiner, L. (2004). An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, *41*, 263–274.

Fernandez, M., Yesson, C., Gannier, A., Miller, P. I., & Azevedo, J. M. N. (2017). The importance of temporal resolution for niche modelling in dynamic marine environments. *Journal of Biogeography*, *44*, 2816–2827.

Friedman, J. H. (2001). Greedy Function Approximation: A gradient boosting machine. *The Annals of Statistics*, *29*, 1189–1232.

Gannier, A. (2004). The large-scale distribution of humpback whales (*Megaptera novaeangliae*) wintering in French Polynesia during 1997-2002. *Aquatic Mammals*, *30*, 227–236.

Gannier, A., Bourreau, S., & Casacci, C. (2000). Preliminary results on the distribution of wintering humpback whales (*Megaptera novaeangliae*) in French Polynesia 1997-1999. *Report to the Scientific Committee of the International Whaling Commission, SC/52/1A.*

Garland, E. C., Goldizen, A. W., Lilley, M. S., Rekdahl, M. L., Garrigue, C., Constantine, R., … Noad, M. J. (2015). Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. *Conservation Biology*, *29*, 1198–1207.

Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Hauser, N. D., … Noad, M. J. (2011). Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Current Biology*, *21*, 687–691.

Garrigue, C., Constantine, R., Poole, M., Hauser, N., Clapham, P. J., Donoghue, M., … Baker, C. S. (2011). Movement of individual humpback whales between wintering grounds of Oceania (South Pacific), 1999 to 2004. *Journal of Cetacean Research and Management, 3*, 275–281.

Garrigue, C., Greaves, J., & Chambellant, M. (2001). Characteristics of the New Caledonian Humpback whale population. *Memoirs of the Queensland Museum*, *47*, 69–75.

Gibbs, N., Childerhouse, S., Paton, D., & Clapham, P. J. (2006). Assessment of the current abundance of humpback whales in the Lomaiviti Island group of Fiji and a comparison with historical data. *Report to the Scientific Committee of the International Whaling Commission, SC/A06/H34*.

Graham, M. (2003). Confronting multicollinearity in ecological multiple regression. *Ecology*, *84*, 2809–2815.

Guidino, C., Llapapasca, M. A., Silva, S., Alcorta, B., & Pacheco, A. S. (2014). Patterns of spatial and temporal distribution of humpback whales at the southern limit of the Southeast Pacific breeding area. *PLOS One*, *9*, e112627.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*, 147–186.

Hastie, T. J., & Tibshirani, R. J. (1990). Generalized Additive Models. In *Monographs on statistics and Applied Probability* (p. 352). London: Chapman and Hall/CRC.

Hauser, N., Peckham, H., & Clapham, P. (2000). Humpback whales in the southern Cook islands, South Pacific. *Journal of Cetacean Research and Management*, *2*, 159–164.

Hazen, E. L., Jorgensen, S., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., … Block, B. A. (2013). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, *3*, 234–238.

Hazen, E. L., Palacios, D. M., Forney, K. A., Howell, E. A., Becker, E., Hoover, A. L., … Bailey, H. (2016). WhaleWatch : a dynamic management tool for predicting blue whale density in the California Current. *Journal of Applied Ecology*, *54*, 1415–1428.

Herman, L. M. (1979). Humpback whales in Hawaiian waters: A study in historical ecology. *Pacific Science*, *33*, 1–15.

Herman, L. M. (2017). The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: Review, evaluation, and synthesis. *Biological Reviews*, *92*, 1795–1818.

Hijmans, R. J. (2017). *raster: Geographic analysis and modeling with raster data. R package version 2.6-7. https://CRAN.R-project.org/package=raster*.

Hoegh-Guldberg, O., & Bruno, J. (2010). The Impact of Climate Change on the World’s Marine Ecosystems. *Science*, *328*, 1523–1528.

Horswill, C., & Jackson, J. A. (2012). Humpback whales wintering at Pitcairn Island, South Pacific. *Marine Biodiversity Records*, *5*, 1–5.

IWC. (2005). Report of the sub-committee on other Southern Hemisphere whale stocks. *Journal of Cetacean Research & Management*, *7*, 235–244.

Jackson, J. A., Ross-Gillespie, A., Butterworth, D., Findlay, K., Holloway, S., Robbins, J., … Zerbini, A. (2015). Southern Hemisphere Humpback Whale Comprehensive Assessment - A synthesis and summary: 2005-2015. *Report to the Scientific Committee of the International Whaling Commission*, *SC/66a/SH/*, 1–38.

Kamman, E. E., & Wand, M. P. (2003). Geoadditive models. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, *52*, 1–18.

Kaschner, K., Watson, R., Trites, A. W., & Pauly, D. (2006). Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. *Marine Ecology Progress Series, 316*, 285–310.

Kimura, F., & Kitoh, A. (2007). Downscaling by Pseudo Global Warning Method Fujio. *Report of the Research Institute for Humanity and Nature (RIHN), Kyoto, Japan. Accessed 19 October 2018*.

Knutson, T. R., Sirutis, J. J., Garner, S. T., Vecchi, G. A., & Held, I. M. (2008). Simulated reduction in Atlantic hurricane frequency under twenty-first-century warming conditions. *Nature Geoscience*, *1,* 359–364.

Legrand, B., Benneveau, A., Jaeger, A., Pinet, P., Potin, G., Jaquemet, S., & Le Corre, M. (2016). Current wintering habitat of an endemic seabird of Réunion Island, Barau's petrel *Pterodroma baraui*, and predicted changes induced by global warming. *Marine Ecology Progress Series*, *550*, 235–248.

Lindsay, R., Constantine, R., Robbins, J., Mattila, D. K., Tagarino, A., & Dennis, T. (2016). Characterising essential breeding habitat for whales informs the development of large-scale Marine Protected Areas in the South Pacific. *Marine Ecology Progress Series, 548,* 263–275.

Macleod, C. D. (2009). Global climate change, range changes and potential implications for the conservation of marine cetaceans: A review and synthesis. *Endangered Species Research*, *7,* 125–136.

Mannocci, L., Boustany, A. M., Roberts, J. J., Palacios, D. M., Dunn, D. C., Halpin, P. N., … Winship, A. J. (2017). Temporal resolutions in species distribution models of highly mobile marine animals: Recommendations for ecologists and managers. *Diversity and Distributions*, *23,* 1098–1109.

Mannocci, L., Roberts, J. J., Miller, D. L., & Halpin, P. N. (2017). Extrapolating cetacean densities to quantitatively assess human impacts on populations in the high seas. *Conservation Biology*, *31*, 601–614.

McPhaden, M. J., Zebiak, S. E., & Glantz, M. H. (2006). ENSO as an integrating concept in earth science. *Science*, *314*, 1740–1745.

Meehl, G. A., Arblaster, J. M., Bitz, C. M., Chung, C. T. Y., & Teng, H. (2016). Antarctic sea-ice expansion between 2000 and 2014 driven by tropical Pacific decadal climate variability. *Nature Geoscience*, *9*, 590–595.

Miller, C., Batibasiga, A., & Solomona, P. (2015). Very Low Numbers of Endangered Oceania Humpback Whales Seen in Fijian Waters. *The South Pacific Journal of Natural and Applied Sciences*, *33*, 39–45.

Morán-Ordóñez, A., Lahoz-Monfort, J. J., Elith, J., & Wintle, B. A. (2017). Evaluating 318 continental-scale species distribution models over a 60-year prediction horizon: what factors influence the reliability of predictions? *Global Ecology and Biogeography*, *26*, 371–384.

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., van Vuuren, D. P., … Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, *463*, 747–756.

Munger, L. M., Lammers, M. O., Fisher-Pool, P., & Wong, K. (2012). Humpback whale (*Megaptera novaeangliae*) song occurrence at American Samoa in long-term passive acoustic recordings, 2008-2009. *Journal of the Acoustical Society of America*, *132*, 2265–2272.

Olavarría, C., Baker, C. S., Garrigue, C., Poole, M., Hauser, N., Caballero, S., … Russell, K. (2007). Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series*, *330*, 257–268.

Paton, D., & Clapham, P. J. (2002). Preliminary analysis of humpback whale sighting survey data collected in Fiji, 1956-1958. *Report to the Scientific Committee of the International Whaling Commission*, *SC/54/ H7*.

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J. R., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, *19*, 181–197.

Poloczanska, E., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., … Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*, 919–925.

Poole, M. M. (2002). Occurrence Of Humpback Whales (*Megaptera novaeangliae*) in French Polynesia 1988-2001. *Report to the Scientific Committee of the International Whaling Commission*, *SC/54/H14*, 16.

Poole, M. M., Albertson, G. R., & Oremus, M. (2014). Expedition Austral Islands : Photo-identification, song recording, and biopsy sampling of humpback whales (*Megaptera novaeangliae*) in southern French Polynesia. *Report to the Scientific Committee of the International Whaling Commission*, 1–8.

QGIS Development Team. (2016). QGIS Geographic Information System. Open Source Geospatial Foundation Project. *Version 2.18 La Palma*. Retrieved from http://qgis.osgeo.org

R Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.r-project.org/.

Rasmussen, K., Palacios, D. M., Calambokidis, J., Saborío, M. T., Dalla Rosa, L., Secchi, E.

R., … Stone, G. S. (2007). Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biology Letters*, *3*, 302–5.

Rendell, L., & Whitehead, H. (2001). Culture in Whales and Dolphins. *Behavioral and Brain Sciences*, *24*, 309–382.

Riekkola, L., Zerbini, A. N., Andrews, O., Andrews-Goff, V., Baker, C. S., Chandler, D., … Constantine, R. (2018). Application of a multi-disciplinary approach to reveal population structure and Southern Ocean feeding grounds of humpback whales. *Ecological Indicators*, *89*, 455–465.

Rocha, J. R. C., Clapham, P. J., & Ivashchenko, Y. (2015). Emptying the Oceans: A Summary of Industrial Whaling Catches in the 20th Century. *Marine Fisheries Review*, *76*, 37–48.

Scales, K. L., Hazen, E. L., Jacox, M. G., Edwards, C. A., Boustany, A. M., Oliver, M. J., & Bograd, S. J. (2017). Scale of inference: On the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. *Ecography*, *40*, 210–220.

Silber, G. K., Lettrich, M. D., Thomas, P. O., Baker, J. D., Baumgartner, M., Becker, E. A., … Waples, R. S. (2017). Projecting Marine Mammal Distribution in a Changing Climate. *Frontiers in Marine Science*, *4*, 413.

Simmonds, M. P., & Eliott, W. J. (2009). Climate change and cetaceans: concerns and recent developments. *Journal of the Marine Biological Association of the United Kingdom*, *89*, 203–210.

Smith, J., Grantham, H., Gales, N., Double, M., Noad, M., & Paton, D. (2012). Identification of humpback whale breeding and calving habitat in the Great Barrier Reef. *Marine Ecology Progress Series*, *447*, 259–272.

Steel, D., Anderson, M., Garrigue, C., Olavarría, C., Caballero, S., Childerhouse, S., … Baker, C. S. (2017). Migratory interchange of humpback whales (*Megaptera novaeangliae*) among breeding grounds of Oceania and connections to Antarctic feeding areas based on genotype matching. *Polar Biology, 3,* 1–10.

Sydeman, W. J., Poloczanska, E. S., Reed, T. E., & Thompson, S. A. (2015). Climate change and marine vertebrates. *Science, 350,* 171–193.

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society, 93,* 485–498.

Thomas, P. O., Reeves, R. R., & Brownell, R. L. (2015). Status of the world's baleen whales. *Marine Mammal Science, 32,* 682–734.

Torres, L. G., Read, A. J., & Halpin, P. (2008). Fine-scale habitat modelling of top marine predator: Do prey data improve predictive capacity? *Ecological Applications, 18,* 1702–1717.

Torres, L. G., Smith, T. D., Sutton, P., MacDiarmid, A., Bannister, J., & Miyashita, T. (2013). From exploitation to conservation: habitat models using whaling data predict ditribution patterns and threat exposure of an endangered whale. *Diversity and Distribution, 19,* 1138–1152.

Trudelle, L., Cerchio, S., Zerbini, A. N., Geyer, Y., Mayer, F., Jung, J., … Charassin, J.-B. (2016). Influence of environmental parameters on movements and habitat utilization of humpback whales in the Madagascar breeding ground. *Royal Society Open Science, 3,* 160616.

UNEP-WCMC, WorldFish-Centre, WRI, & TNC. (2010). Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 2.0. Includes contributions from IMaRS-USF and IRD (2005), IMaRS-USF (2005) and Spalding et al. (2001). *Cambridge (UK): UN Environment World Conservation Monitoring*. Retrieved from http://data.unep-wcmc.org/datasets/1

Valsecchi, E., Corkeron, P., Galli, P., Sherwin, W., & Bertorelle, G. (2010). Genetic evidence for sex-specific migratory behaviour in western South Pacific humpback whales. *Marine Ecology Progress Series*, *398*, 275–286.

Walsh, K. (2015). Fine resolution simulations of the effect of climate change on tropical cyclones in the South Pacific. *Climate Dynamics*, *45*, 2619–2631.

Wood, S. N. (2006). *Generalized Additive Models: An introduction with R*. Chapman and Hall/CRC.

Wood, S. N. (2017). *Generalized Additive Models: An introduction with R* (second edi). CRC press.

Zhang, H. S., Han, Z. B., Zhao, J., Yu, P. S., Hu, C. Y., Sun, W. P., … Vetter, W. (2014). Phytoplankton and chlorophyll a relationships with ENSO in Prydz Bay, East Antarctica. *Science China Earth Sciences*, *57*, 3073–3083.

TABLES

Table 1: Survey effort and observations of humpback whales in Oceania between 1999 and 2017 that were used for this study. The total number of groups and number of whales observed is reported per country (#) and overall.

Region	Country	Survey years[a]	Effort (days)	Effort (hours)	# groups	# whales
western Oceania	New Caledonia	2003-2017[b]	702	5,145	1,589	3,801
	Vanuatu	2003	8	56	10	15
	Total		7,10	5,201	1,599	3,816
central Oceania	Tonga	2000, 2001, 2003-2005	88	453	274	593
	Niue	2010, 2011, 2014, 2016	44	259	54	78
	American Samoa	2003-2011, 2014-2017	113	745	495	1167
	Samoa	2012	8	77	3	4
	Total		253	1,534	826	1,842
eastern Oceania	French Polynesia	1999-2002, 2007, 2008, 2010-2014	413	2432	447	796
Total			1,376	9,167	2,872	6,454

[a] These numbers are not an exhaustive estimate of research in the region, but only represent the surveys that could be included in this study.

[b] Additional data from 1996 to 2002 was used in the M_{NC} model of encounter rate but could not be used in the whole study because boat GPS tracklines were not recorded.

Table 2: Summary of the fine scale model of humpback whale habitat use in Oceania. Approximate significance of smooth terms is reported for variables in interaction with region (western, central or eastern Oceania) or with no interaction (year and projected coordinates X * Y). Edf = estimated degrees of freedom. *N-significant* correspond to the number of cross-validation runs (out of 50) where the variables were significant with P-values less than 0.001 or 0.05.

	Western					**Central**					**Eastern**				
	edf	**Chi^2**	**P-value**	***n-significant***		**edf**	**Chi^2**	**P-value**	***n-significant***		**edf**	**Chi^2**	**P-value**	***n-significant***	
				<0.001	**<0.05**				***<0.001***	**<0.05**				***<0.001***	***<0.05***
DEPTH	3.5	240	<0.001	50	50	3.9	449	<0.001	50	50	3.8	66	<0.001	50	50
DISSURFres	3.6	132	<0.001	50	50	2.0	26	<0.001	23	41	3.5	170	<0.001	50	50
SLOPE	3.1	28	<0.001	49	50	0	0	0.562	0	3	3.3	61	<0.001	50	50
SST_{fine}	1.0	5	0.011	2	30	1.7	9	0.003	42	45	0	0	0.322	0	0
$SST_{fine.CV}$	3.0	15	<0.001	8	49	0	0	1	0	1	0	0	0.856	0	0
day of year	2.1	25	<0.001	48	48	2.0	10	0.004	43	44	2.3	30	<0.001	43	50
year	Edf = 1.9, Chi^2 = 19, p-value <0.001, *n-significant* < 0.001 = 50 ; <0.05 = 50														
*X * Y*	Edf = 40.2, Chi^2 = 916, p-value <0.001, *n-significant* < 0.001 = 50 ; <0.05 = 50														

FIGURES

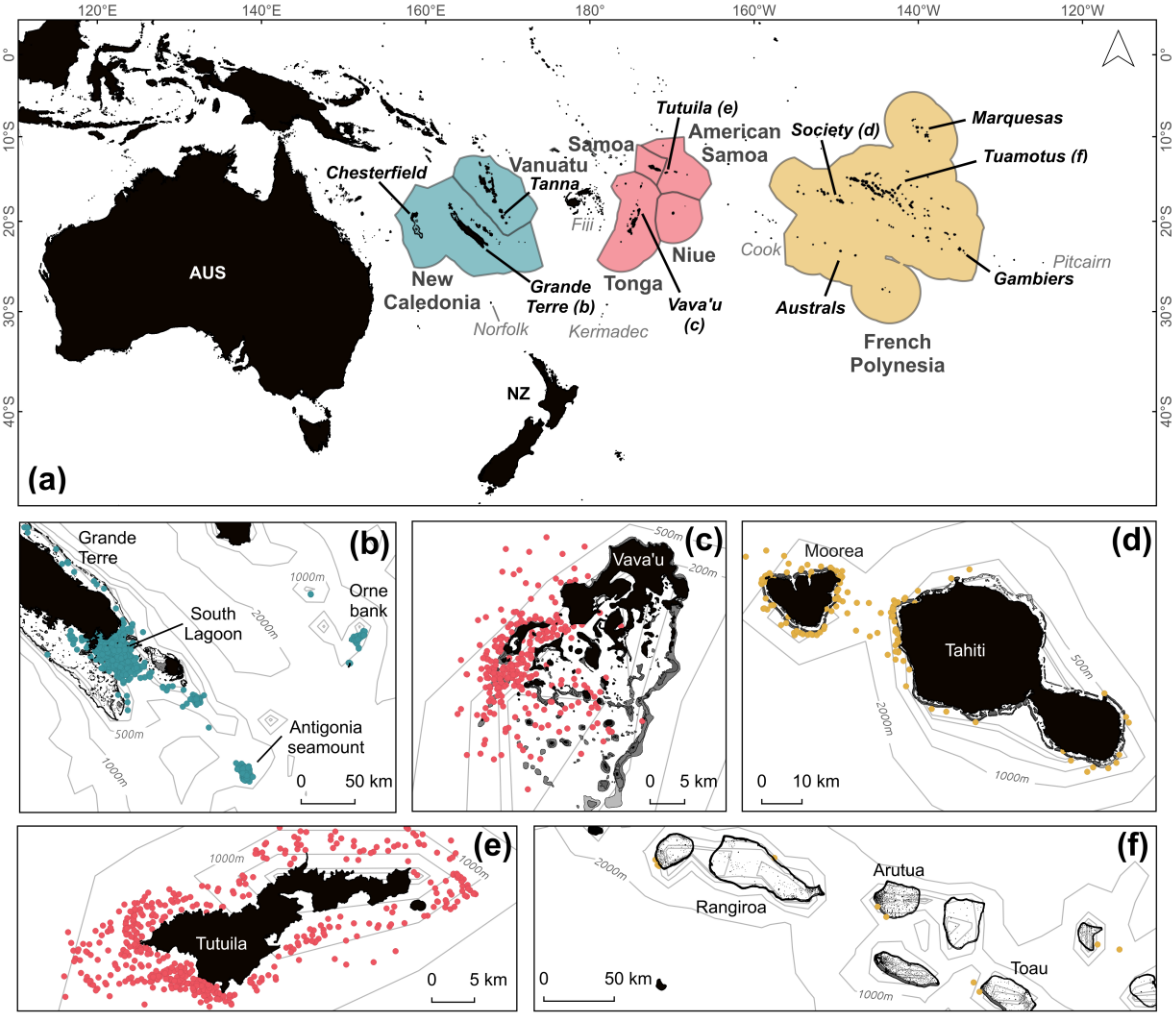

Figure 1: Humpback whale breeding grounds and study sites of Oceania. a) Overview of Oceania with Economic Exclusive Zones included in the study represented by coloured polygons (from left to right: western, central and eastern regions). Country names are shown in bold, localities are shown in italics. Other panels zoom in on specific study sites, with land in black, reefs in grey and presence locations in colour: b) the southern New Caledonia area; c) Vava'u archipelago in Tonga; d) Tahiti and Moorea Islands in the Society archipelago of French Polynesia; e) Tutuila island in American Samoa; f) Rangiroa atoll in the Tuamotu archipelago of French Polynesia. Isobaths are represented with grey lines.

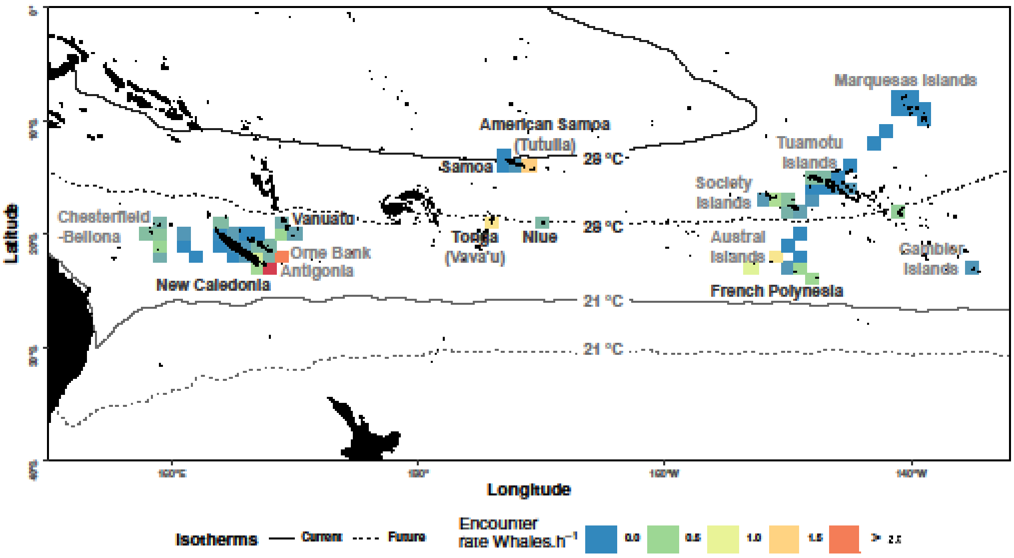

Figure 2: Coarse scale gridded encounter rate of humpback whales (whales.h^{-1}) averaged in 1° cells in Oceania between 1999 and 2017 (n = 1,376 days of survey, from the months of May to December). The map is overlaid with average August SST_{coarse} isotherms at 28 °C and 21 °C in the current (solid line: average August SST from Reynolds NCEP Level 4 Optimally Interpolated dataset, between 1999 and 2017) and future period (dashed line: 2080-2100, prediction based on CMIP5 models and RCP 8.5 scenario using the method by Kimura & Kitoh, 2007). Lands and islands are represented in black.

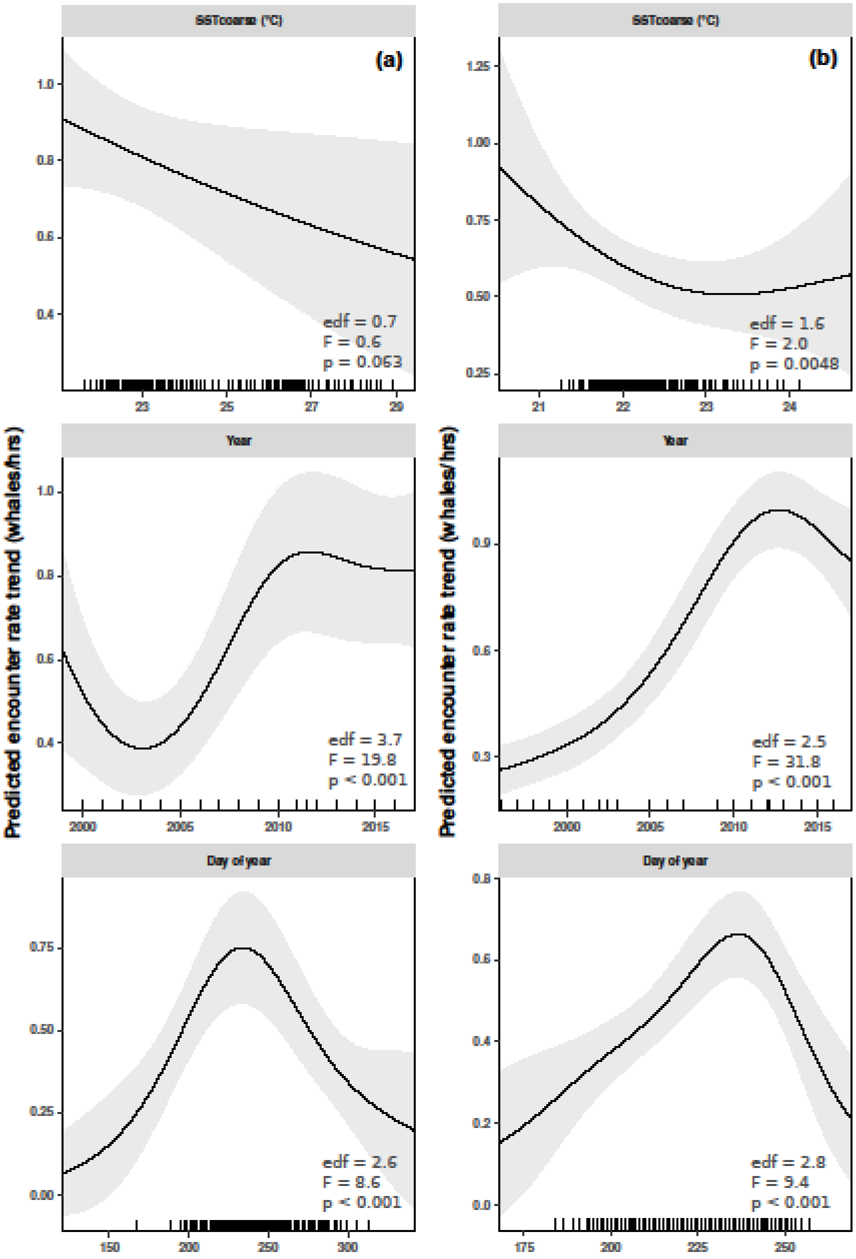

Figure 3: Coarse scale humpback whale encounter rate trends from, a) model M_{OC} at Oceania scale between 1999 and 2017 (n = 1,376), and b) model M_{NC} in the New Caledonia South Lagoon between 1996 and 2017 (n = 774). Solid lines represent the marginal effect of each variable relative to encounter rate. Rug plots show the distribution of values for each predictor. Shaded areas represent approximate 95% confidence intervals.

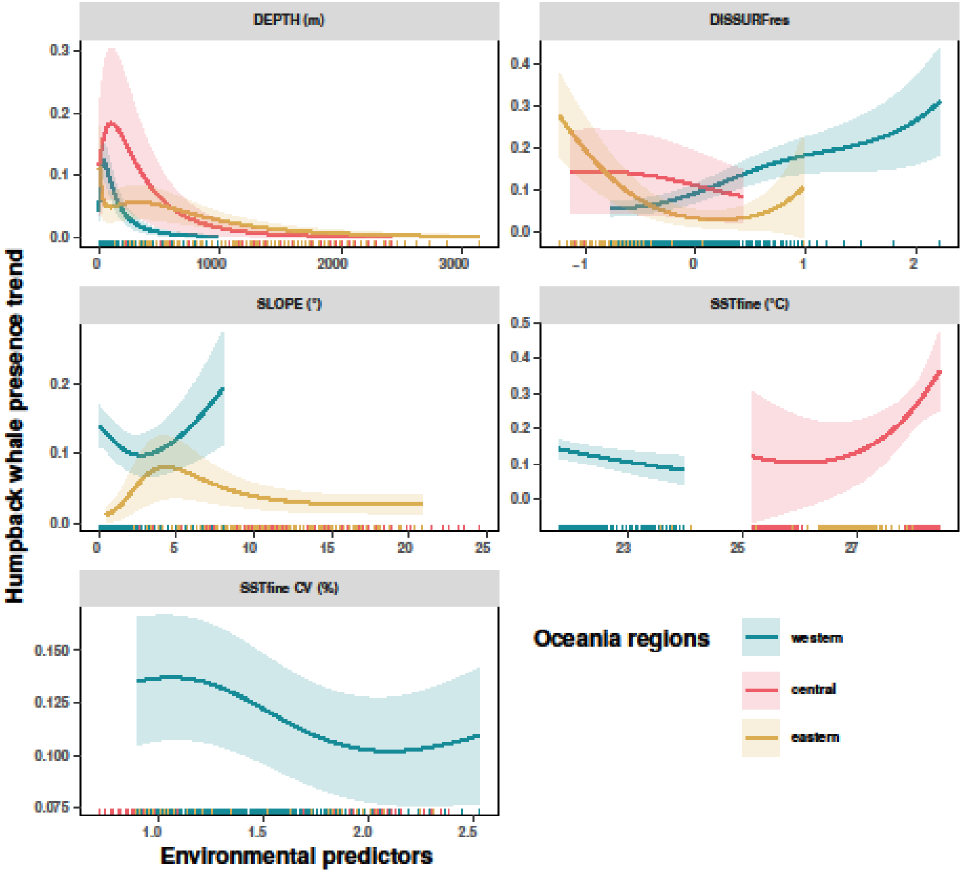

Figure 4: Functional response curves from fine scale GAM between humpback whale presence and significant environmental predictors: seabed depth in meters (*DEPTH*), residual distance to coast/reef accounting for depth ($DISSURF_{RES}$: larger values indicate regions that are shallower than what would be expected considering their distance to closest coast/reef, no unit), seabed slope in degrees (*SLOPE*), SST climatology at fine resolution in °C (SST_{fine}) and its coefficient of variation in % ($SST_{fine.CV}$). Predictors relative to time and space (year, day of year and spatial covariates) were held constant during predictions and are not represented. The y-axis indicates the effect of the smooth function of each predictor upon the trend in humpback whale presence; with higher values indicating increased presence. Regional smooth estimates are shown with different colours. Solid lines represent the marginal effect of each significant variable (with p-value < 0.05) relative to humpback whale presence. Rug plots show the distribution of values per region for each predictor. Shaded areas represent approximate 95% confidence intervals.

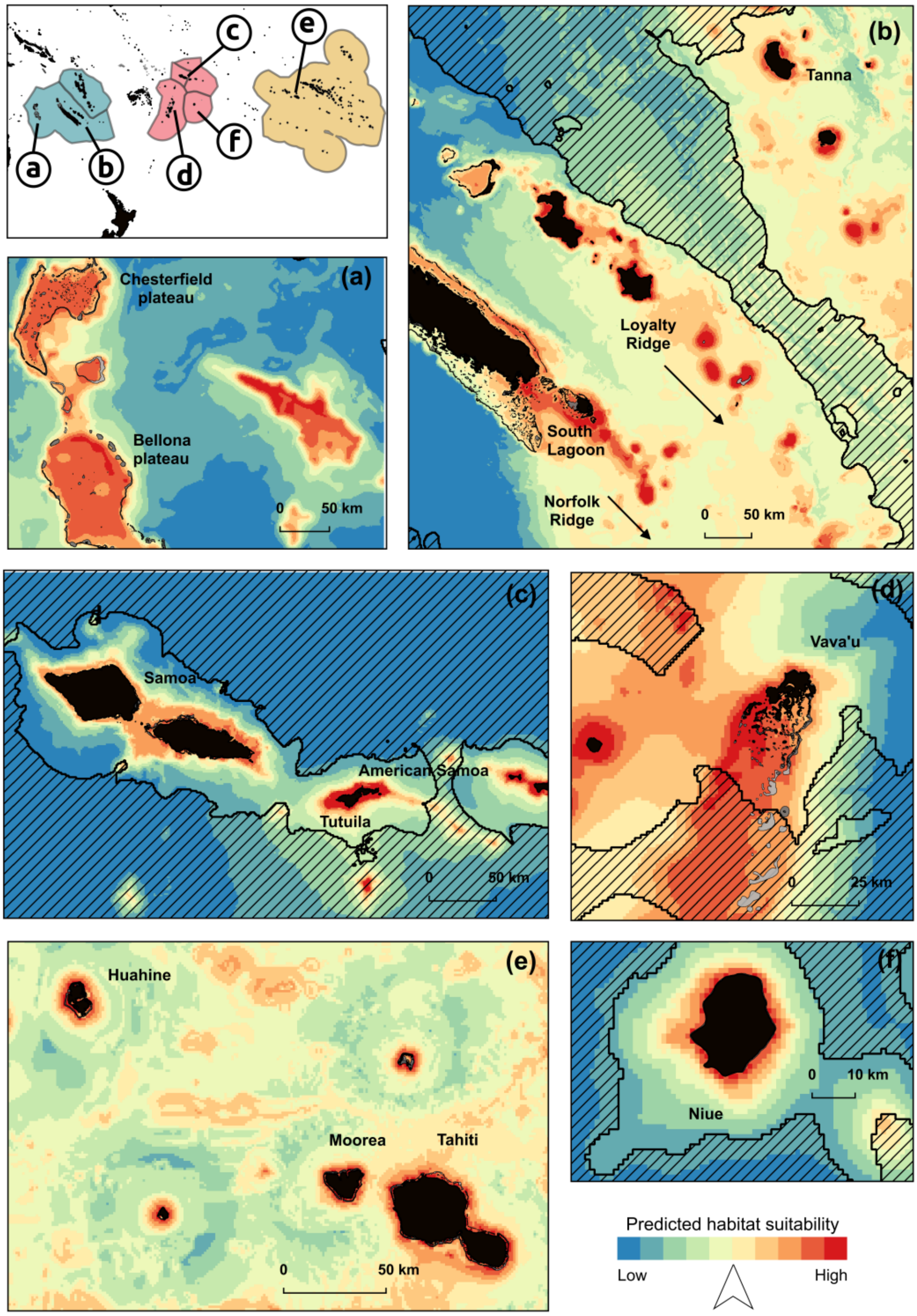

Figure 5: Maps of humpback whale habitat suitability predicted from a fine scale presence-background GAM based on surveys conducted in Oceania from 1999 to 2017. Habitat suitability is shown on a coloured log-scale. Dashed areas represent where the model extrapolated at least one environmental variable beyond the range observed in the training datasets of that region. Land is represented in black and reefs in grey.

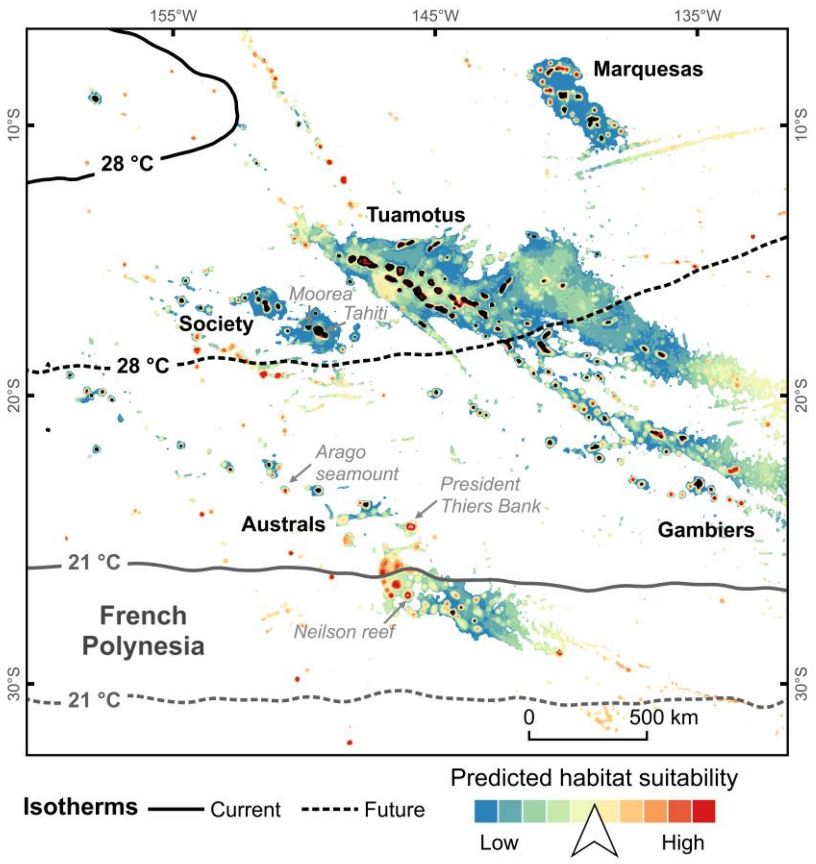

Figure 6: Map of humpback whale habitat suitability predicted from fitted responses for western Oceania and transferred to eastern Oceania. Predictions are based on seabed topography only (*DEPTH*, *SLOPE* and $DISSURF_{RES}$). The map is overlaid with average August SST_{coarse} isotherms at 28 °C and 21 °C in the current (solid line: average August SST from Reynolds NCEP Level 4 Optimally Interpolated dataset, between 1999 and 2017) and future period (dashed line: 2080-2100 prediction based on CMIP5 models and RCP 8.5 scenario using the method by Kimura & Kitoh, 2007). Habitat suitability is shown on a coloured log-scale. White areas represent where the model extrapolated at least one environmental variable beyond the range observed in western Oceania surveys. Islands and reefs are represented in black. Moorea and Tahiti are labelled to allow the comparison with the predictions for the eastern region in Fig. 5e.

SUPPLEMENTARY INFORMATION

S1: Effort and observation summaries per country

S2: Sea Surface Temperature Oceania humpback whale breeding range

S3: Predicting future SST conditions associated to climate change

S4: Effect of the Southern Oscillation Index and the Southern Annular Mode on encounter rates

S5: Dealing with predictor collinearity in habitat models