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**WHALES IN WARMING WATER: ASSESSING BREEDING HABITAT DIVERSITY AND
ADAPTABILITY IN OCEANIA'S CHANGING CLIMATE**

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

Whales in Oceania warming waters

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Primary Research Article

43 **Abstract**

44 In the context of a changing climate, understanding the environmental drivers of marine
45 megafauna distribution is important for conservation success. The extent of humpback whale
46 breeding habitats and the impact of temperature variation on their availability are both
47 unknown. We used 19 years of dedicated survey data from 7 countries and territories of
48 Oceania (1,376 survey days), to investigate humpback whale breeding habitat diversity and
49 adaptability to climate change. At a fine scale (one kilometre resolution), seabed topography
50 was identified as an important influence on humpback whale distribution. The shallowest
51 waters close to shore or in lagoons were favoured, although humpback whales also showed
52 flexible habitat use patterns with respect to shallow offshore features such as seamounts. At a
53 coarse scale (one degree resolution), humpback whale breeding habitats in Oceania spanned a
54 thermal range of 22.3 to 27.8 °C in August, with inter-annual variation up to 2.0 °C. Within
55 this range, both fine and coarse scale analyses of humpback whale distribution suggested local
56 responses to temperature. Notably, the most detailed dataset was available from New
57 Caledonia (774 survey days, 1996 - 2017), where encounter rates showed a negative
58 relationship to sea surface temperature, but were not related to the El Niño Southern
59 Oscillation or the Antarctic Oscillation from previous summer, a proxy for feeding conditions
60 that may impact breeding patterns. Many breeding sites that are currently occupied are
61 predicted to become unsuitably warm for this species (> 28 °C) by the end of the 21st century.
62 Based on modelled ecological relationships, there are suitable habitats for relocation in
63 archipelagos and seamounts of southern Oceania. Although distribution shifts might be
64 restrained by philopatry, the apparent plasticity of humpback whale habitat use patterns and
65 the extent of suitable habitats support an adaptive capacity to ocean warming in Oceania
66 breeding grounds.

67 INTRODUCTION

68 In recent decades, evidence for global climate change has spurred ecologists and
69 conservationists to increase research efforts to better understand species-climate relationships.
70 In marine ecosystems, changes in average temperatures around the world are affecting species
71 throughout all trophic levels (Doney et al., 2012; Hoegh-Guldberg & Bruno, 2010;
72 Poloczanska et al., 2013; Sydeman, Poloczanska, Reed, & Thompson, 2015), yet the impact
73 of climate change on marine megafauna, including cetaceans, is considered a 'big unknown'
74 (Clapham, 2016; Thomas, Reeves, & Brownell, 2015). Distribution shifts are expected to
75 occur at various geographic scales (Hazen et al., 2013; Kaschner, Watson, Trites, & Pauly,
76 2006; Macleod, 2009) and resulting population impacts are expected to vary across species,
77 depending notably on the vulnerability and extent of their critical habitats (Macleod, 2009;
78 Simmonds & Elliott, 2009; Sydeman et al., 2015). Yet, current knowledge remains insufficient
79 to estimate the adaptive plasticity of most species to thermal changes, which is one of the key
80 elements needed to predict the impact of climate change on marine ecosystems (Macleod,
81 2009; Silber et al., 2017; Sydeman et al., 2015). In recent years, Species Distribution Models
82 (SDMs) have become a popular tool to predict distribution changes in response to climate
83 change (Hazen et al., 2013; Legrand et al., 2016; Morán-Ordóñez, Lahoz-Monfort, Elith, &
84 Wintle, 2017; Torres et al., 2013), but limited long-term empirical data exist to calibrate and
85 validate these models of long-lived marine species such as cetaceans (Silber et al., 2017).

86 Humpback whales (*Megaptera novaeangliae*) may be impacted by global ocean warming in
87 both polar and tropical ecosystems, as they spend summers feeding in polar areas and
88 seasonally migrate toward tropical breeding grounds where they fast during winter
89 (Chittleborough, 1958). The reasons for such extensive migrations are still debated but could
90 be linked to increased calf fitness in warmer waters of the tropical and subtropical breeding
91 grounds (Clapham, 2000). Although this hypothesis suggests a direct link between humpback

92 whale life history and water temperature, it remains unclear how sea surface temperature
93 (SST) drives distributions within breeding latitudes, as studies have shown both strong
94 relationships (Bortolotto, Danilewicz, Hammond, Thomas, & Zerbini, 2017; Guidino,
95 Llapapasca, Silva, Alcorta, & Pacheco, 2014; Rasmussen et al., 2007; Smith et al., 2012) and
96 weak or no effects of this variable (Trudelle et al., 2016; Dulau et al., 2017). SST is dynamic,
97 with complex changes through time as it fluctuates on multiple temporal scales (monthly,
98 seasonally, annually) and follows patterns that may be stochastic, cyclic (e.g., El Niño
99 Southern Oscillation, Pacific Decadal Oscillation, Antarctic Oscillation) or continuous
100 (climate change). Models studying the effect of temperature on species' distribution should
101 explicitly reflect these variations (Fernandez, Yesson, Gannier, Miller, & Azevedo, 2017;
102 Mannocci, Boustany, et al., 2017; Scales et al., 2017). Hence, datasets collected over large
103 temporal and spatial scales are necessary to understand the effect of SST on the distribution of
104 wide-ranging and long-lived species such as humpback whales.

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

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

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

136 **MATERIALS AND METHODS**

137 **Study regions and data collection**

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

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

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

157 In most surveys, the spatial extent of search effort was precisely recorded with a GPS
158 trackline at a sampling frequency varying from 1 position.hour⁻¹ to 2 positions.min⁻¹ (84 %
159 survey days). In the remaining 16 % of survey days, search effort was concentrated in small
160 and well-defined areas that could be spatially bounded into georeferenced polygons drawn by
161 the data suppliers (Appendix S1). Four polygons were manually produced in a QGIS
162 graphical interface around the study sites of Hao (Gambier Islands), Huahine and Moorea
163 (Society Islands), and Niue (covering 362 to 2,360 km²). Finally, for 93 % of the survey days,
164 the time at the beginning and end of the effort was recorded, enabling a daily time on effort to
165 be deduced. When this information was lacking, the time on effort was deduced from the

166 distance travelled along the boat GPS trackline and the average speed calculated over all
167 surveys (estimated at 12.8 km.h⁻¹). Daily times on effort included the time spent to search for
168 whales, plus the time spent with whale groups (during which observers are less likely to
169 detect other whales). Land-based observers were employed to help the boat-based team detect
170 nearshore humpback whales in the South Lagoon of New Caledonia (Derville, Torres, &
171 Garrigue, 2018). This additional observer effort was not accounted for as it only moderately
172 contributed to the group detections. Data processing and statistical analysis were performed
173 with R (version 3.4.4, R Core Team, 2016) and QGIS (version 2.18.3, QGIS Development
174 Team, 2016).

175 **Coarse scale encounter rate analyses**

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

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

191 ***Future predicted SST range over Oceania*** - The future SST conditions for the end of the 21st
192 century were assessed under the Representative Concentration Pathway 8.5 (RCP 8.5) of
193 aerosols and greenhouse gases scenario, commonly used as a pessimistic baseline if no
194 climate change mitigation is achieved (Moss et al., 2010). The future SST was computed with
195 a “pseudo- global warming approach” (Kimura & Kitoh, 2007; Knutson, Sirutis, Garner,
196 Vecchi, & Held, 2008; Walsh, 2015; Appendix S3). Here, the pseudo-global warming
197 approach was based on an ensemble of Coupled Model Intercomparison Project models
198 (CMIP5; Taylor, Stouffer, & Meehl, 2012). The CMIP5 models are climate model simulations
199 employed to detect anthropogenic effects in the climate record and project them into the
200 future. The pseudo-global warming approach allowed the production of a raster of future SST
201 conditions for 2080-2100 at 0.25° resolution in Oceania (see modelling details in Appendix
202 S3). Isotherms at 21 °C and 28 °C corresponding to the breeding range described in
203 Rasmussen et al., (2007) were estimated from 1) the current observed August SST_{coarse} (1999-
204 2017), and 2) the projected future August SST_{coarse} for the end of the 21st century (2080-2100).

205 ***Local and regional coarse scale encounter rate models*** - The encounter rate per survey day,
206 in number of whales per hour of survey (whales.h⁻¹) was computed by dividing the total
207 number of whales observed (number of groups multiplied by group size) by the total time on
208 effort per day. Daily encounter rates were modelled with a Generalized Additive Model
209 (GAM, Hastie & Tibshirani, 1990) applied with a Gaussian log link as a function of year, day
210 of year and SST_{coarse} . Variables were modelled with penalized thin-plate regression splines
211 optimized with a Restricted Maximum Likelihood and basis size limited to 5 to prevent
212 overfitting (Wood, 2017). Two separate GAMs were produced: the first, M_{OC} , estimated the
213 effect of SST_{coarse} on encounter rate through space at the regional Oceania scale, and the
214 second, M_{NC} , estimated the local effect of SST_{coarse} and periodic climatic fluctuations at a

215 specific study site, the New Caledonia South Lagoon. This site was chosen as a case study as
216 it provides the most consistent and prolonged survey effort in Oceania (1996 - 2017).

217 In M_{NC} , SST_{coarse} was extracted at the centre of the New Caledonia South Lagoon (167°E,
218 22.5°S). This location and the resolution of SST_{coarse} were considered to produce a
219 representative estimate of temperatures in the study site, which had a core survey area of
220 about 20 km wide. For this model, encounter rates were calculated for study days from 1996
221 to 2017 (Garrigue et al., 2001, Appendix S4). Also, in place of using SST_{coarse} as a predictor of
222 encounter rate in M_{NC} , two variables reflecting conditions during the previous feeding season
223 were also tested. Indeed, Pacific Ocean conditions change in relation to periodic climatic
224 fluctuations such as the El Niño Southern Oscillation phenomenon (ENSO, McPhaden,
225 Zebiak, & Glantz, 2006), the strength of which is measured by the Southern Oscillation Index
226 (SOI). The Antarctic Oscillation (AAO) also affects the Southern Ocean and is measured by
227 the Southern Annular Mode (SAM) index. Consequently, changes in migration length, timing
228 or path can be hypothesized as a result of environmental variability in the Southern Ocean,
229 and in turn could be reflected in humpback whale encounter rates measured at the breeding
230 grounds. In order to assess the effect of the conditions in the feeding grounds and migratory
231 corridors on humpback whale presence in the South Lagoon breeding ground, SAM was
232 obtained from the British Antarctic Survey and SOI was obtained from the National
233 Oceanographic and Atmospheric Administration (Appendix S4). SAM and SOI monthly
234 indexes were averaged between November and April each year to reflect the summer feeding
235 conditions of humpback whales prior to the following breeding season in Oceania (Bengtson
236 Nash et al., 2018).

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

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

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

250 **Fine scale habitat use model**

251 Habitat preferences of humpback whales were modelled based on a binomial response
252 variable comparing ‘used’ to ‘available’ environmental conditions. Indeed, non-systematic
253 cetacean surveys were not designed to record true presence-absence data, but included some
254 information about the area surveyed and time on-effort. In this context, constraining the
255 available background space is known to improve model performance (Engler, Guisan, &
256 Rechsteiner, 2004; Phillips et al., 2009) and can be informed by the extent of survey effort at
257 sea (e.g., Torres, Read, & Halpin, 2008). Following the method in Derville, Torres, Iovan et
258 al., (2018), the area surrounding GPS survey tracklines was used to approximate available
259 environment where background points were sampled. Daily survey track strip-width spanning
260 10 km to each side of the tracklines were generated to reflect areas surveyed, resulting in daily
261 background areas of 125 to 4,463 km². The 10 km width of the background sampling area
262 reflected the maximum detection distance of a humpback whale surface activity, calculated
263 with the geometrical horizon distance for observers standing in a small survey boat (less than
264 1 m high, as mostly used in Oceania study sites). In the few cases where tracklines were not

265 recorded, background areas were approximated in small polygons enclosing the survey sites
266 (Appendix S1). Background points were sampled randomly within these areas, with a
267 minimum distance of 2 km from each other and independently of presence locations. The
268 number of background points was proportional to the number of hours of effort per day (on
269 average 4 points per hour of survey).

270 Humpback whales in Pacific tropical breeding grounds have been shown to associate with
271 small seabed and reefs features ranging a few dozen meters to kilometres (model resolution:
272 50 m, Cartwright et al., 2012; 100 - 150 m, Lindsay et al., 2016; 4.8 km, Smith et al., 2012).
273 Given this potential to select habitat at very fine scale, the effect of topography and SST on
274 habitat suitability within each region of Oceania was assessed at a resolution of 1 km.
275 Moreover, seasonally predictable and persistent SST conditions were assumed to be important
276 factors for humpback whales seeking breeding and nursing habitats; therefore, climatological
277 estimates of SST and its temporal variability were used in this model (Mannocci, Boustany, et
278 al., 2017). Hence, the variable “ SST_{fine} ” was obtained from a climatology averaging SST from
279 2003 to 2014 at a daily scale based on the Multi-scale Ultra-high Resolution SST with a fine
280 spatial resolution of 1 km (<https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1>).
281 The variable “ $SST_{fine.CV}$ ” was derived as the coefficient of variation (in %) of SST_{fine} at a given
282 day of the year over 11 years. Furthermore, bathymetric charts at 1 km resolution (“ $DEPTH$ ”,
283 in meters) were obtained from the General Bathymetric Chart of the Oceans (GEBCO).
284 Seabed slope (“ $SLOPE$ ”, in degrees) was calculated from bathymetry using the raster R
285 package (version 2.6-7; Hijmans, 2017). Coastlines were obtained from the OpenStreetMap
286 dataset (<http://openstreetmapdata.com/data/coastlines>) and coral reef contours were obtained
287 from the UNEP World Conservation Monitoring Centre (UNEP-WCMC, WorldFish-Centre,
288 WRI, & TNC, 2010). A raster of the distance to the closest shallow reef (emerging at low tide)
289 or coastline (“ $DISSURF$ ”, in km) was calculated.

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

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

311 Stratified Monte Carlo cross-validation was used to assess the significance of predictors'
312 contributions. Models were produced over 50 training subsets containing presence and
313 background points from 90 % randomly selected survey days per region (Derville, Torres,
314 Iovan, et al., 2018), and the proportion of runs with p-values less than 0.001 or 0.05 was

315 reported (Hazen et al., 2016). Partial dependence plots were produced for each significant
316 environmental predictor/region combination. Fitted responses for each region were estimated
317 while holding the latitude and longitude to a fixed location central to the main study site per
318 region, namely: the New Caledonia South Lagoon for the western region (167.00°E, 22.50°S),
319 American Samoa for the central region (170.74°W, 14.29°S) and the Society Islands for the
320 eastern region (149.48°W, 17.54°S). Finally, humpback whale habitat suitability with respect
321 to *DEPTH*, *SLOPE*, *DISSURF_{RES}*, *SST_{fine}* and *SST_{fine.CV}* was predicted over 1 km resolution
322 maps. Day of year was fixed to its mean per region dataset, and year was fixed to 2017. Areas
323 where environmental conditions strayed outside the model training ranges by region were
324 dashed out on the final predicted maps relative to each region respectively, as they should be
325 considered with caution (Mannocci, Roberts, Miller, & Halpin, 2017).

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

337 **RESULTS**

338 A total of 1,376 days of survey were compiled over years from 1999 to 2017 (for years of
339 survey per country see Table 1). The majority of surveys were conducted in August (36 %),

340 September (33 %), October (16 %) and July (12 %). Overall, 8 % of survey days were
341 conducted more than 10 km off shore. From all survey effort, 6,454 humpback whales were
342 observed (Table 1).

343

344 **Coarse scale encounter rate and SST**

345 The mean encounter rate per day of survey at the Oceania scale was 0.69 whales.h⁻¹ (SD ±
346 0.90). Averaged in 1° grid cells, the highest encounter rates were recorded southwest of New
347 Caledonia, over the Antigonua seamount (2.4 whales.h⁻¹ ± SD 1.6) and Orne bank (2.0
348 whales.h⁻¹ ± SD 0.9), followed by Tutuila (American Samoa, 1.5 whales.h⁻¹ ± SD 1.1), Vava'u
349 (Tonga, 1.3 whales.h⁻¹ ± SD 0.9) and Rurutu (Austral Islands, French Polynesia, 1.3 whales.h⁻¹
350 ± SD 3.1; Fig. 2). Antigonua showed significantly higher encounter rates than the other four
351 top sites (Kruskal-Wallis test: $X^2 = 13.4$, $p < 0.001$). The lowest encounter rates were recorded
352 in pelagic offshore waters (e.g., French Polynesia, Fig. 2) and in nearshore waters of the
353 Marquesas, Samoas, northwestern New Caledonia, and some of the Tuamotus.

354 SST_{coarse} measured in each reference point in August (n = 12, Appendix S2) from 1999 to
355 2017 varied from 22.3 to 27.8 °C. SST_{coarse} fluctuated by 1.1 to 2.0 °C between years at a
356 given site, with the larger annual anomalies recorded in the Tonga (2.0 °C), Niue (1.9 °C),
357 Vanuatu (1.8 °C), and the Gambier islands (1.8 °C). SST_{coarse} measured in October was
358 warmer at all sites (Appendix S2), even those with a breeding season peak reported later in
359 the year (e.g., American Samoa: mean SST_{coarse} Aug = 27.7 °C vs mean SST_{coarse} Oct = 28.2
360 °C).

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

365 American Samoa and the northern part of French Polynesia (Society, Tuamotu and Marquesas
366 Islands).

367 At the Oceania scale between 1999 and 2017, in the M_{OC} model, 1,376 daily encounter rates
368 showed a significant increase with year, particularly between 2003 and 2012 (Fig. 3a). The
369 day of year also affected encounter rates, which followed a bell-shaped trend with a peak
370 around the end of August. After accounting for spatial autocorrelation using an interaction
371 covariate between latitude and longitude (edf = 22.8, $F = 10.6$, p -value < 0.001), encounter
372 rates showed a decreasing trend with increasing SST_{coarse} , but the relationship was slightly
373 non-significant ($F = 0.6$, $p = 0.06$, Fig. 3a). The deviance explained by the model reached 41.4
374 %.

375 Similar trends were found in the New Caledonia South Lagoon M_{NC} model of encounter rates
376 between 1996 and 2017 ($n = 774$ days of survey, Fig. 3b). Encounter rates showed a
377 decreasing trend with increasing SST_{coarse} . Encounter rate also increased with year and
378 reached a peak in 2012 - 2013. The seasonal peak was estimated to occur around the end of
379 August. The deviance explained by the model reached 25.4 %, including 1.1 % that could be
380 attributed to SST_{coarse} . The alternative models of M_{NC} that replaced SST_{coarse} with the SOI or
381 SAM from the previous summer led to slightly lower deviance explained (24.7 % and 24.5 %
382 respectively, Appendix S4), and both variables had no significant effect on encounter rate in
383 the New Caledonia South Lagoon (SOI: $F = 0.5$, p -value = 0.08; SAM: $F = 0.0$, p -value =
384 0.86).

385

386 **Fine scale habitat use**

387 The fine scale humpback whale habitat preference model explained 21.7 % of the deviance in
388 the presence-background dataset counting 46,426 data points (including 2,872 presences) over
389 a spatial extent of 192,500 km².

390 Depth was a main predictor of fine scale distribution (n-significant = 50; Table 2). The
391 relationship between humpback whale presence and shallow depth was similar between the
392 three regions (Fig. 4), although favouring deeper waters in eastern (mean depth at whale
393 presence positions = 360 m \pm SD 480) and central Oceania (mean = 198 m \pm SD 296),
394 compared to western Oceania (mean = 43 m \pm SD 89; Anova: $F_{(2, 2869)} = 523$, $p < 0.001$). In
395 contrast, the relationship with *DISSURF_{RES}* differed between regions. The trend was
396 significant and positive in western Oceania (Table 2; Fig. 4), indicating a preference for
397 shallow waters away from surfacing reefs or coasts, such as offshore seamounts and banks.
398 This trend was reflected in predicted habitat suitability maps for the region, where the
399 seamounts of the Norfolk and Loyalty Ridges were particularly suitable (Fig. 5b). On the
400 contrary, in both central and eastern Oceania, the trend between humpback whale presence
401 and *DISSURF_{RES}* was mostly negative (and less robust to cross-validation in the central
402 region; Table 2), indicating that whales were found in waters closest to coasts or reefs and
403 also relatively deep. In the eastern region, steep slopes were more represented and favoured
404 by whales (Fig. 4). Again, these relationships manifested in the predicted habitat suitability
405 maps, which emphasized the importance of the external slope of fringing/barrier reefs and
406 coastal waters of high islands such as Tutuila (Fig. 5c), Tahiti (Fig. 5e) or Niue (Fig. 5f).
407 The western region had the highest amount of offshore survey effort. Hence, transferring the
408 western fitted trends to eastern Oceania revealed potentially suitable habitats in offshore
409 seamounts located south of the Society archipelago and in the southeastern part of the Austral
410 archipelago (Fig. 6). Based on these predictions, when comparing the areas of highest habitat
411 suitability (values > 0.9 quantile) in the French Polynesia Economic Exclusive Zone (EEZ)
412 with current and predicted future 21°C and 28°C isotherms, it appeared that 90.1 % of the
413 EEZ suitable habitats are currently included in this preferred *SST_{coarse}* range, against 48.9 %
414 by the end of 21st century.

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

426

427 **DISCUSSION**

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

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

463 populations will keep visiting their historical breeding grounds in the future, even if the
464 temperature rises above what is currently locally optimal.

465 In the New Caledonia South Lagoon, where survey effort was most consistent over a long
466 time period, temporal fluctuation of SST was found to affect humpback whale presence. The
467 potentially delayed impact of basin wide climatic phenomena was investigated to explain the
468 changes in encounter rate, but these signals did not seem to covary. The climatic fluctuations
469 of ENSO and the Antarctic Oscillation are known to interact and affect sea-ice concentration
470 in the Antarctic (Curran, van Ommen, Morgan, Phillips, & Palmer, 2003; Meehl, Arblaster,
471 Bitz, Chung, & Teng, 2016), which in turn impacts biological productivity (Zhang et al.,
472 2014) and potential humpback whale foraging success (Bengtson Nash et al., 2018). Although
473 varying feeding conditions in the Antarctic could influence northbound migration, this study
474 suggests that climatic phenomena affecting humpback whale habitats basin wide could not
475 solely explain the variability of humpback whale presence observed at a given breeding site.
476 Encounter rates estimated through time in the South Lagoon were influenced by local SST
477 conditions rather than wider climatic variations.

478 Distribution shifts are considered the most likely response of large mobile cetaceans to
479 climate change (Silber et al., 2017; Sydeman et al., 2015). History has shown that humpback
480 whale distribution can change on the scale of a few decades, particularly in cases of over-
481 exploitation and local extirpation. For instance, humpback whales historically visited Fijian
482 waters in great numbers but relatively few currently do so (Dawbin, 1959; Gibbs,
483 Childerhouse, Paton, & Clapham, 2006; Miller, Batibasiga, & Solomona, 2015; Paton &
484 Clapham, 2002). By contrast, whales seem to have appeared rather recently in other breeding
485 grounds such as Hawaii (Herman, 1979) and French Polynesia (Olavarría et al., 2007; Poole,
486 2002). Social aggregation is thought to be a key factor influencing humpback whale breeding
487 ground use of otherwise suitable habitats (Clapham & Zerbini, 2015). Male songs may play a

488 role in attracting conspecifics towards breeding spots as they form (Clapham, Aguilar, &
489 Hatch, 2008; Herman, 2017), but their propagation range is limited (~20 km; Garland et al.,
490 2015). Hence, humpback whales might not disperse to areas with suitable environmental
491 conditions that may have been erased from the cultural memory of individuals (Clapham et
492 al., 2008) or that may be too remote.

493 To be successful, distribution shifts of humpback whales therefore require the availability of
494 suitable habitats in proximity to the previously occupied ranges. In Oceania, climate change
495 scenarios suggest a shift of the 28°C surface isotherm by several degrees of latitude south by
496 the end of the 21st century (in the high CO₂ emission scenario RCP 8.5; Moss et al., 2010). It
497 must be noted that other more optimistic scenarios of climate change, such as the RCP 4.5
498 (Moss et al., 2010), would have likely predicted a weaker southward shift of the 28°C
499 isotherm. Nonetheless, to follow this shift and remain in a 21 - 28 °C range, humpback whales
500 would need to relocate their breeding and nursing activities, either to shallow waters currently
501 considered as part of the migratory corridors, such as the Kermadec Islands (Riekkola et al.,
502 2018), Cook Islands (Hauser, Peckham, & Clapham, 2000), Norfolk Island (Constantine,
503 Russell, Gibbs, Childerhouse, & Baker, 2007), and Pitcairn Island (Horswill & Jackson,
504 2012), or to already existing breeding grounds such as New Caledonia, southern Vanuatu, or
505 the Austral Islands. Considering that the sub-populations of Oceania are still well below their
506 pre-exploitation numbers (< 50 % recovered, Jackson et al., 2015), carrying capacity
507 limitations may not be a factor on the southernmost breeding grounds, if some sub-
508 populations were to relocate there in response to climate change.

509 Survey effort biased towards nearshore waters has likely underestimated the extent of suitable
510 breeding and nursing habitat in Oceania. Offshore shallow banks and seamounts surveyed in
511 western Oceania have revealed the highest encounter rates (Antigonia seamount > 2 whales.h⁻¹
512 ¹). This unexpected preference for unsheltered offshore shallow waters contradicts the

513 paradigm that humpback whales obligatorily seek shelter for breeding and nursing. In central
514 and eastern Oceania, humpback whales were mainly observed in waters closest to islands or
515 on the external slope of fringing and barrier reefs (see also Gannier, 2004; Poole, Albertson, &
516 Oremus, 2014). However, the surveys in these regions have focused on waters surrounding
517 islands, with only occasional transits through offshore deep waters separating archipelagos.
518 Hence, humpback whale presence on offshore shallow seamounts could have gone
519 undetected. Transferred predictions using the ecological relationships fitted in western
520 Oceania support the potential for suitable seamount habitats in French Polynesia. These
521 predictions are sustained by a few anecdotal observations over the President Thiers Bank (19
522 m), Arago seamount (28 m), and Neilson Reef (3 m, Fig. 6) in the southeastern Austral Islands
523 (Gannier, Bourreau, & Casacci, 2000). Such previously undescribed suitable habitats
524 constitute potential areas for relocation in response to climate change. Further research into
525 offshore shallow habitats is warranted to build a more comprehensive assessment of present
526 and future humpback whale distribution at basin scale.

527 This study suggests that a great part of the currently occupied breeding sites in Oceania might
528 become unsuitably warm for humpback whales by the end of the 21st century. The thermal
529 tolerance displayed by humpback whales in Oceania, combined with flexible patterns of
530 habitat use and the great extent of available suitable habitats, suggest an adaptive capacity of
531 these sub-populations on their breeding grounds. Sensitive breeding habitats lying at the
532 northern “thermal edge” of the Oceania range should be the focus of future monitoring to
533 clarify the acceptable temperature range of breeding humpback whales, and their organismal
534 response to climate change. Finally, with growing anthropogenic pressure on both coastal and
535 offshore habitats in Oceania and worldwide, whales are potentially facing cumulative
536 stressors (Avila, Kaschner, & Dormann, 2018), which need to be included in future efforts to
537 model distribution dynamics. In response to global warming, humpback whales risk relocating

538 to areas where other threats are currently unidentified and deserve investigation. In this
539 context, understanding and predicting the distribution of suitable habitats for whales is an
540 important step to support the implementation of appropriate conservation measures.

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821 **TABLES**

822 Table 1: Survey effort and observations of humpback whales in Oceania between 1999 and
 823 2017 that were used for this study. The total number of groups and number of whales
 824 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

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

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

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

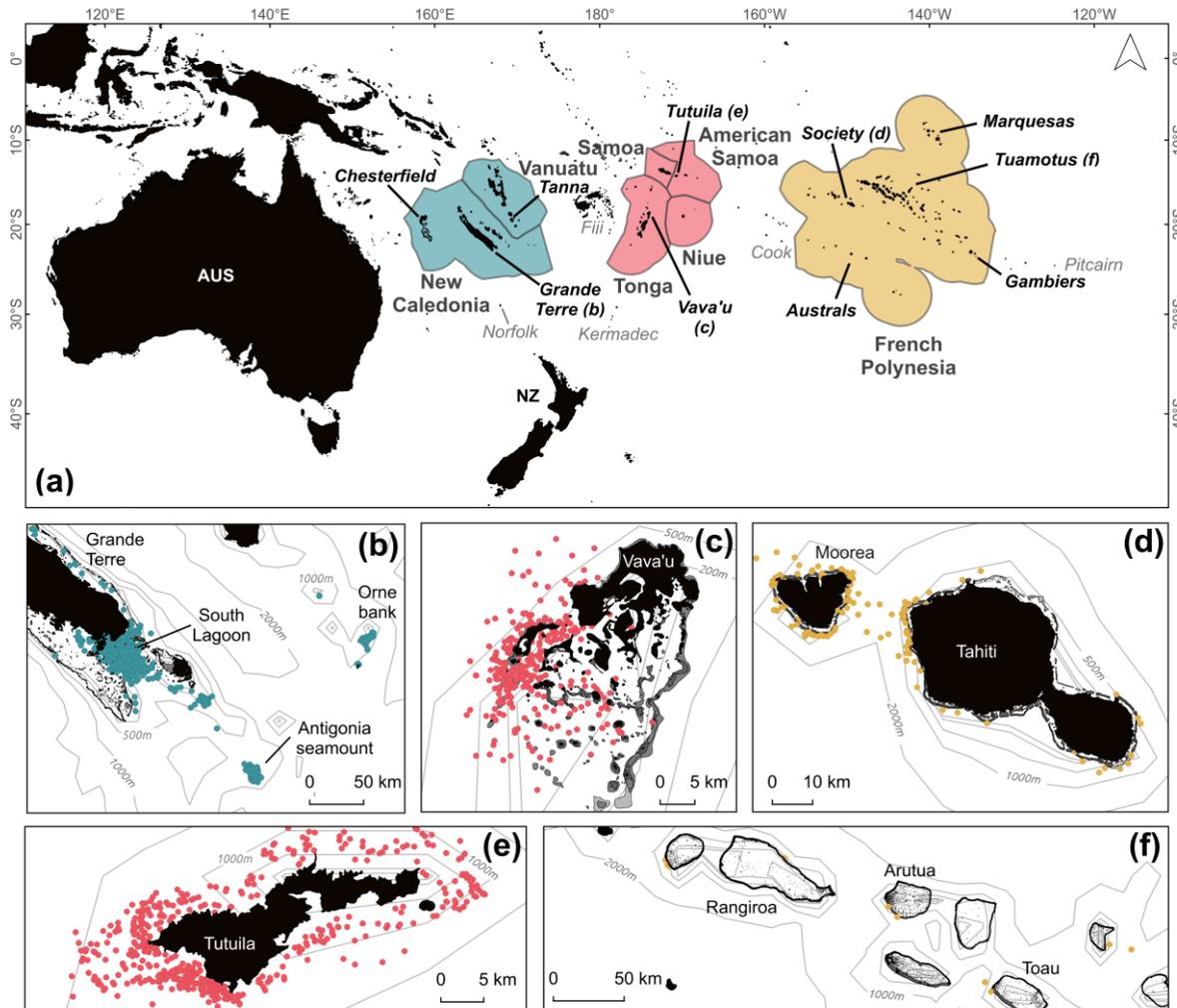
	Western					Central					Eastern				
	edf	Chi ²	P-value	<i>n-significant</i>		edf	Chi ²	P-value	<i>n-significant</i>		edf	Chi ²	P-value	<i>n-significant</i>	
				<0.001	<0.05				<0.001	<0.05				<0.001	<0.05
<i>DEPTH</i>	3.5	240	<0.001	50	50	3.9	449	<0.001	50	50	3.8	66	<0.001	50	50
<i>DISSURFres</i>	3.6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

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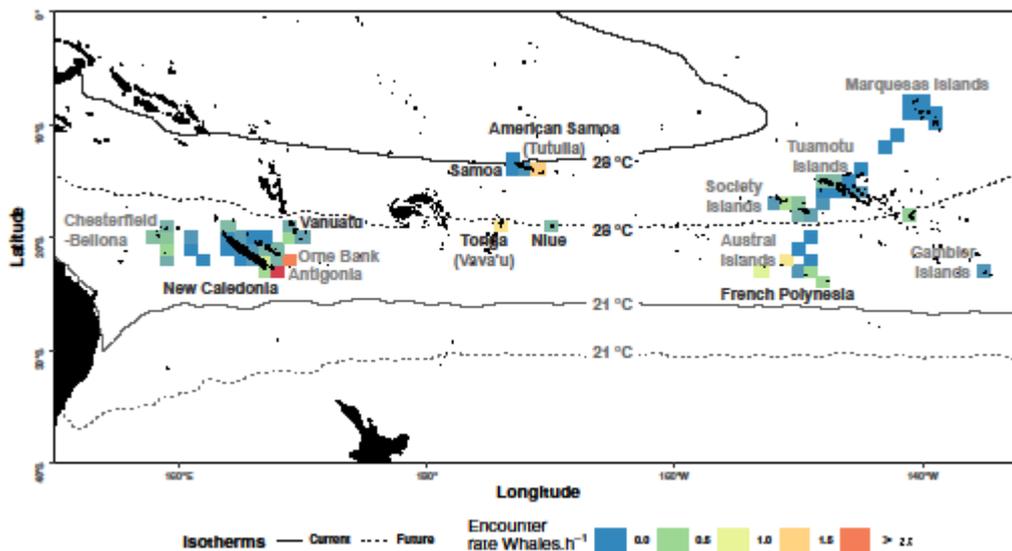


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846 Figure 1: Humpback whale breeding grounds and study sites of Oceania. a) Overview of
 847 Oceania with Economic Exclusive Zones included in the study represented by coloured
 848 polygons (from left to right: western, central and eastern regions).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

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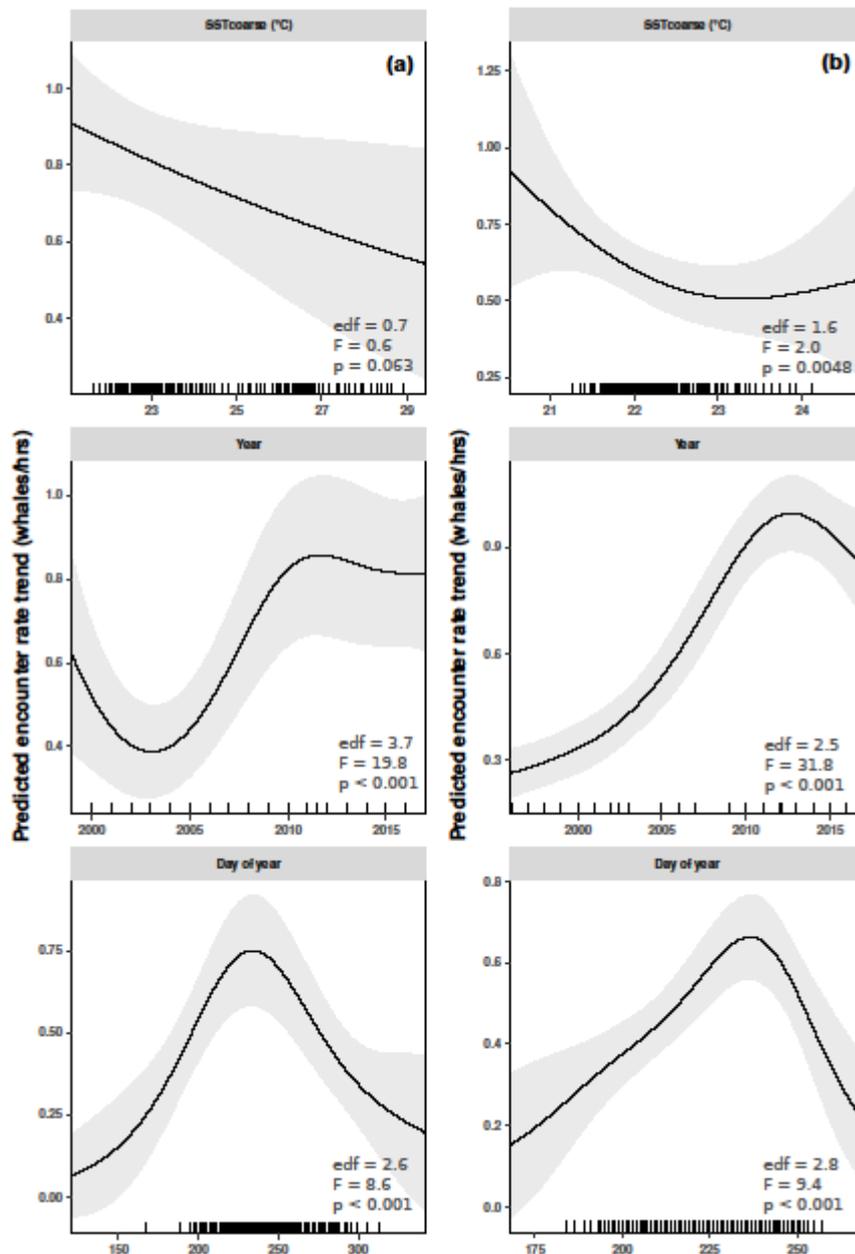
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857 Figure 2: Coarse scale gridded encounter rate of humpback whales (whales.h⁻¹) averaged in 1°
858 cells in Oceania between 1999 and 2017 (n = 1,376 days of survey, from the months of May
859 to December). The map is overlaid with average August *SST_{coarse}* isotherms at 28 °C and 21
860 °C in the current (solid line: average August SST from Reynolds NCEP Level 4 Optimally
861 Interpolated dataset, between 1999 and 2017) and future period (dashed line: 2080-2100,
862 prediction based on CMIP5 models and RCP 8.5 scenario using the method by Kimura &
863 Kitoh, 2007). Lands and islands are represented in black.

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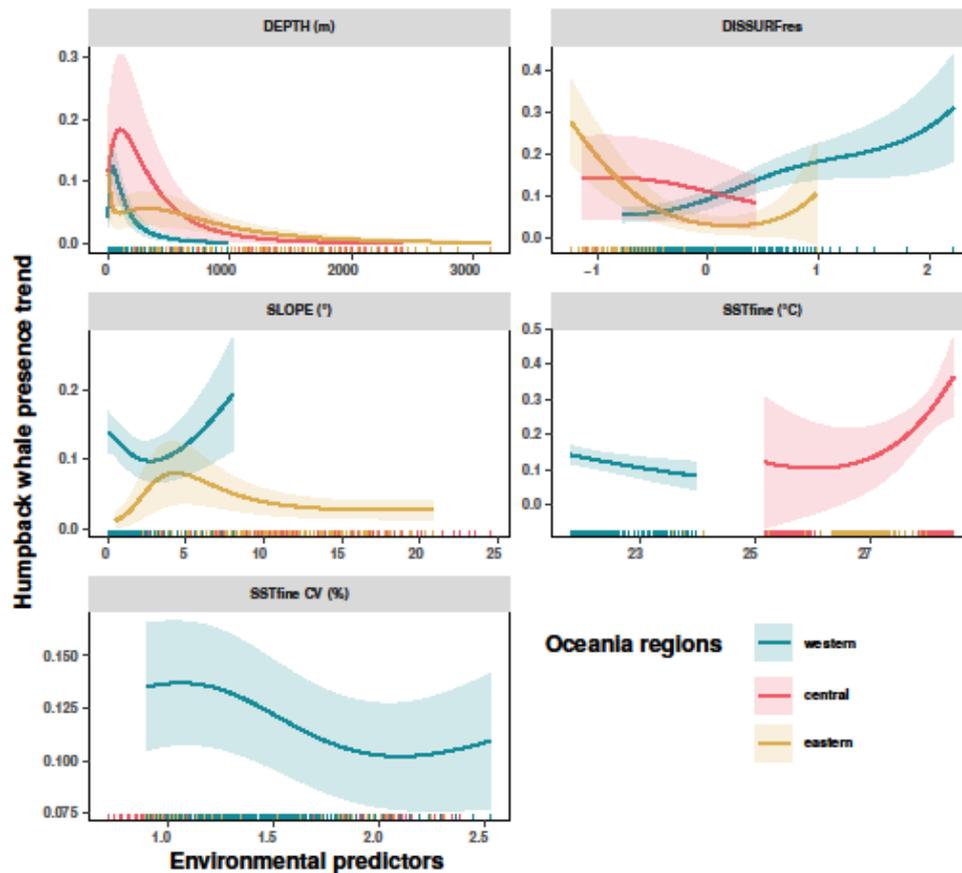


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866 Figure 3: Coarse scale humpback whale encounter rate trends from, a) model M_{OC} at Oceania
 867 scale between 1999 and 2017 ($n = 1,376$), and b) model M_{NC} in the New Caledonia South
 868 Lagoon between 1996 and 2017 ($n = 774$). Solid lines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

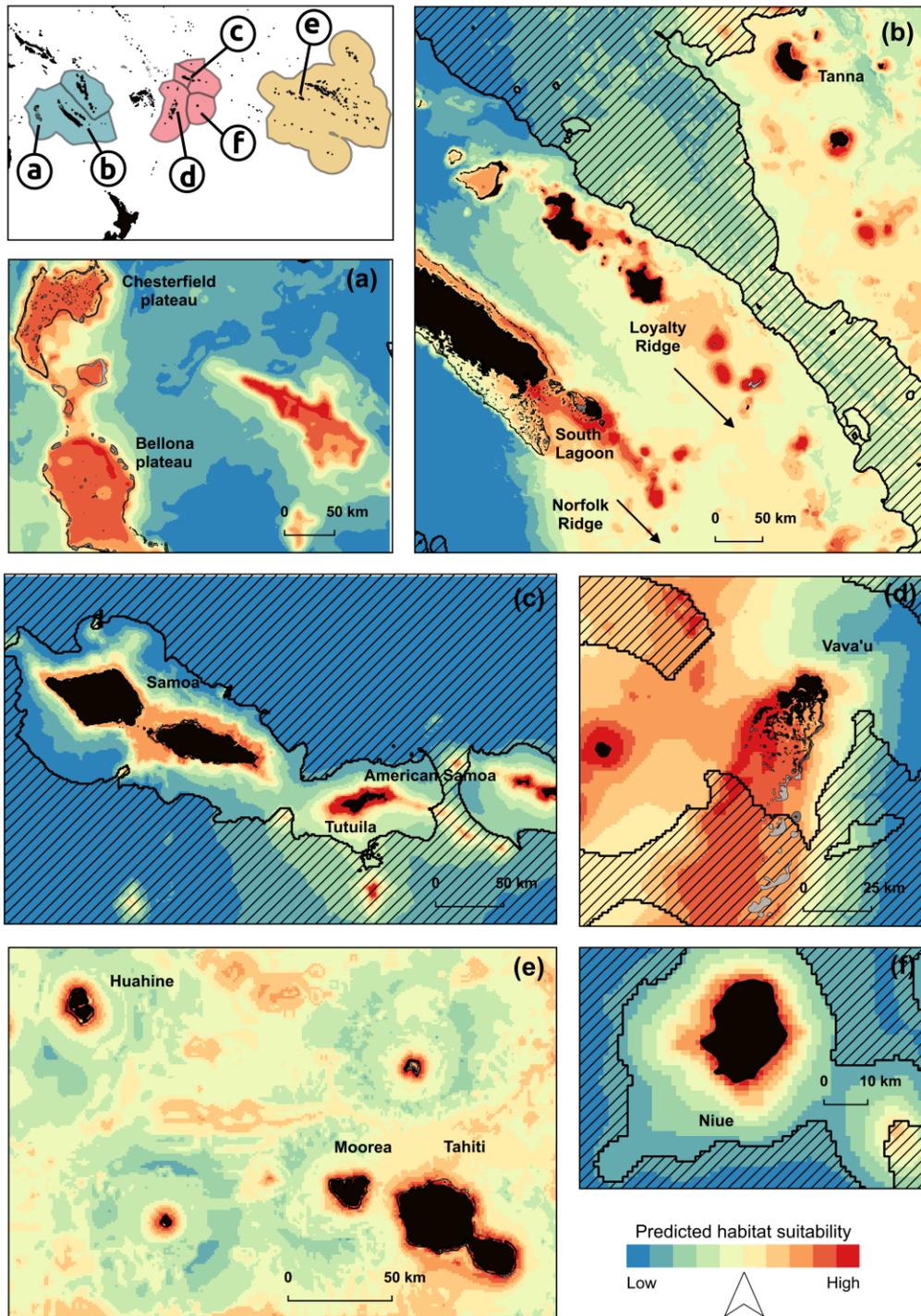
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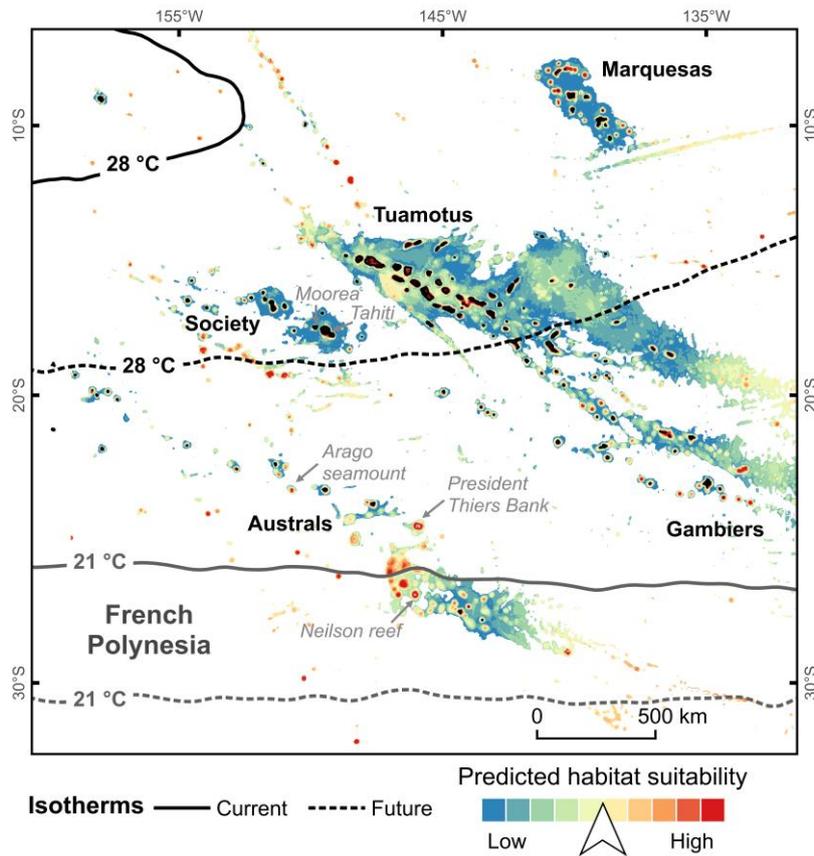
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874 Figure 4: Functional response curves from fine scale GAM between humpback whale
 875 presence and significant environmental predictors: seabed depth in meters (*DEPTH*), residual
 876 distance to coast/reef accounting for depth (*DISSURF_{RES}*: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



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



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

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907 **SUPPLEMENTARY INFORMATION**

908 S1: Effort and observation summaries per country

909 S2: Sea Surface Temperature Oceania humpback whale breeding range

910 S3: Predicting future SST conditions associated to climate change

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

912 rates

913 S5: Dealing with predictor collinearity in habitat models