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1 **Habitat use of culturally distinct Galápagos sperm whale**
2 **(*Physeter macrocephalus*) clans**

3 Running page head: Sperm whale clan habitat

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20 **Abstract**

21 Ecological niche is traditionally defined at the species level, but individual niches can vary
22 considerably within species. Research on intra-specific niche variation has been focused on
23 intrinsic drivers. However, differential transmission of socially learned behaviours can also lead
24 to intra-specific niche variation. In sperm whales (*Physeter macrocephalus*), social transmission
25 of information is thought to generate culturally distinct clans, which at times occur
26 sympatrically. Clans have distinct dialects, foraging success rates, and movement patterns, but
27 whether the niches of clan members are also different remains unknown. We evaluated the
28 differences in habitat use of clans off the Galápagos Islands, using data collected over 63
29 encounters between 1985 and 2014. During encounters, we recorded geographic positions,
30 determined clan identity through analysis of group vocalizations and individual associations, and
31 used topographical and oceanographic variables as proxies of sperm whale prey distribution. We
32 used logistic Generalized Additive Models, fitted with Generalized Estimating Equations to
33 account for spatiotemporal autocorrelation, to predict clan identity as a function of the
34 environment descriptors. Oceanographic variables marginally contributed to differentiating
35 clans. Clan identity could be predicted almost entirely based on geographic location. This fine-
36 scale, within-region spatial partitioning likely derives from whales preferring areas where
37 members of their clans occur over temporal scales of a few months to a few years. By identifying
38 differences in clans' space use, we have uncovered another level of sperm whale life that is
39 likely influenced by their cultural nature.

40 **Key words:** habitat preference, cetacean, culture, GAM, GEE, Galápagos

41

42 **Introduction**

43 Traditionally, ecological niche and habitat use have been defined at the species level (Hutchinson
44 1957, Leibold 1995). However, mounting evidence for individuals of the same population having
45 low niche overlap reminds us that conspecifics are not always ecologically equivalent (Bolnick
46 et al. 2003). To date, most of the theoretical work on individual niche variation has focused on
47 intrinsic sources of variation, such as morphological, physiological, and ontogenic traits (Van
48 Valen 1965, Roughgarden 1972, Svanbäck & Persson 2004). Less attention has been given to
49 social learning as a mechanism for individual niche variation (but see Galef 1976; Laland et al.
50 2000; Slagsvold and Wiebe 2007; Sargeant and Mann 2009).

51 When behavioural traits are socially learned and shared among groups of individuals, there is
52 culture (Boyd & Richerson 1996, Laland & Hoppitt 2003). Culture, as so defined, can play an
53 important role in the divergence of resource and space use among individuals, especially in
54 species in which foraging strategies and habitat selection are socially transmitted (e.g. Laland &
55 Galef, 2009; Whitehead & Rendell, 2014). Notable cases include apes and monkeys that learn to
56 use different tools to exploit nuts and termites (McGrew et al. 1979, Boesch et al. 1994, Whiten
57 et al. 1999, van Schaik et al. 2003, Ottoni & Izar 2008), birds that learn about feeding areas and
58 prey sizes from their parents' choices (Slagsvold & Wiebe 2011), female mountain sheep
59 retaining the home ranges of their social groups (Geist 1971), dolphins using the same foraging
60 tactics and areas of their mothers and/or peers (Mann & Patterson 2013, Cantor et al. 2018), and
61 sea otters using foraging tools to meet their matrilineally transmitted dietary preferences (Estes et
62 al. 2003). These and other foraging techniques and habitat use patterns are socially acquired
63 behavioural traits that result in different resource use patterns, and so reduce trophic niche

64 overlap among subsets of individuals within the same population (Jaeggi et al. 2010, Slagsvold
65 & Wiebe 2011, Allen et al. 2013).

66 However, it is not always straightforward to disentangle culture from other underlying causes of
67 foraging behaviour variation. Both genetic and ecological factors are explanatory candidates for
68 behavioural divergence, especially in allopatric populations (e.g. Laland and Galef 2009; Koops
69 et al. 2013). One way to overcome this issue is excluding all sources of non-cultural behavioural
70 variation (Whiten et al. 1999), but this has proved problematic (Laland & Janik 2006).

71 Alternatively, by studying resource-use variation among sympatric groups of genetically-similar
72 individuals, one can account for such environmental and genetic mechanisms. Two particularly
73 well-known marine examples are killer whales (*Orcinus orca*) and Indo-Pacific bottlenose
74 dolphins (*Tursiops* sp.). Mammal-eating and fish-eating killer whales use the same waters off
75 British Columbia but feed exclusively on very different prey (Ford et al. 1998). Off Shark Bay,
76 Australia, part of a bottlenose dolphin population uses marine sponges as tools to forage on the
77 seafloor for prey that are hard to access otherwise, leading to distinct social communities of
78 “sponging” and “non-sponging” dolphins that coexist in the same habitat (Mann et al. 2012).

79 Neither case can be explained by genetic variation alone (Krützen et al. 2005, Mann et al. 2012,
80 Riesch et al. 2012).

81 Over much wider spatial scales, there is the case of sympatric cultural divergence among female
82 sperm whales (*Physeter macrocephalus*) into clans. While males lead mostly solitary lives in
83 high latitudes, females and immatures live in tightly-knit social units, containing few matrilineal,
84 in tropical and subtropical waters (Best 1979, Christal et al. 1998). Social units form temporary
85 larger groups (Whitehead et al. 1991), but they do so with other units with which they share a
86 large proportion of their acoustic repertoire, thus delineating a higher social level: the *vocal clan*

87 (Rendell & Whitehead 2003, Whitehead et al. 2012, Gero et al. 2016). Sperm whale clans of the
88 Eastern Tropical Pacific are genetically indistinct (Rendell et al. 2012) and sympatric (Rendell &
89 Whitehead 2003). Members of different clans can encounter one another easily, in theory.
90 However, they not only maintain distinct vocal dialects over time (Rendell & Whitehead 2005),
91 but also differ in movement and social behaviour, reproductive and foraging success, and diet
92 composition (Whitehead & Rendell 2004, Marcoux 2005, Marcoux et al. 2007a, Cantor &
93 Whitehead 2015). These divergences suggest that sperm whales belonging to culturally distinct
94 but sympatric clans may use different habitats, but this has not yet been studied directly.

95 Understanding sperm whale niche is hampered by logistical constraints. Their trophic niche, for
96 instance, is known only indirectly. Sperm whales seem to primarily prey on cephalopods, but
97 since they live offshore and feed at great depths (Papastavrou et al. 1989), observations of
98 predation are rare. Moreover, analyses of stomach contents and defecation yield contrasting
99 results regarding the species consumed (see Clarke et al. 1988, Clarke & Paliza 2001, Smith &
100 Whitehead 2000). While many bathypelagic squid have overlapping ranges and niches
101 (Nigmatullin et al. 2001), different age and size classes within single species have different
102 distributions and dietary preferences (Nigmatullin et al. 2001; Markaida 2006). On the other
103 hand, the habitat component of sperm whale niche can be assessed via the environmental
104 variables that influence the distribution of the cephalopods they prey upon (Jaquet & Whitehead
105 1996), such as bottom topography and oceanographic variables that are related to upwelling
106 processes and increased productivity (Jaquet & Whitehead 1996, Pirota et al. 2011, Wong &
107 Whitehead 2014).

108 Here, we evaluate whether sympatric sperm whale clans differ in habitat use by investigating the
109 spatial, oceanographic, and topographic characteristics of the waters they occupy off the

110 Galápagos Islands. Specifically, we compared the relative habitat use of two vocal clans that
111 were particularly common in the area in the 1980's (Rendell & Whitehead 2003), and of two
112 other clans that have recently replaced them in the 2010's (Cantor et al. 2016).

113 **Methods**

114 *Field Methods*

115 We studied sperm whales off the Galápagos Archipelago (93°-88°W; 3°N-3°S) aboard dedicated
116 research sailboats (10-12m) between January and June, in 1987, 1989, 2013, and 2014 (Table 1).

117 We searched for whales acoustically, monitoring hydrophones that could detect sperm whale
118 clicks up to about 7 kilometres away every 15-60 minutes (Whitehead 2003). During daylight
119 hours, we also searched for whales visually within a range of 0.2 to 2.0 km, depending on
120 weather conditions. Upon finding a group of sperm whales, we approached it cautiously to
121 photograph their flukes for individual identification (Arnbom 1987). We refer to the periods
122 during which we had continuous (within less than 6 hours) visual and/or acoustic contact with
123 the same group of females as *encounters*.

124 Groups of females and immatures (identified based on body size and behaviour; Whitehead
125 2003) were followed for as long as possible, during which time the vessel's geographic location
126 was recorded. Until 1993, positions were estimated by interpolation from SATNAV fixes at least
127 every 3 hours; after 1993, positions were recorded every 1-5 min using GPS (as in Whitehead
128 and Rendell 2004). Vessel positions were used as indicators of the whales' locations, which,
129 given the range of acoustic detection, could be up to 7 kilometres away from the vessel.

130 *Clan identification*

131 We assigned clan identity to groups of female and immature sperm whales based on the
132 similarity of their communication sounds, called codas (see Rendell and Whitehead 2003; Cantor
133 et al. 2016). A clan was considered a collection of groups of sperm whales that shared an
134 identifiable part of their coda repertoires (see Rendell & Whitehead 2003). At least four vocal
135 clans were commonly sighted around Galápagos (Rendell & Whitehead 2003, Cantor et al.
136 2016): *Regular* (typically producing regularly-spaced clicks); *Plus-One* (typical codas with an
137 extended pause before the last click), *Short* (typical codas with fewer than 5 clicks), and *Four-*
138 *Plus* clan (typical codas with a basis of 4 regular clicks).

139 We assigned clan memberships to all groups of whales that were photo-identified together and
140 had their acoustic repertoire sufficiently sampled (see Rendell & Whitehead 2003, Cantor et al.
141 2016). Geographic positions within a day were assigned to a corresponding clan because: 1)
142 typically only one group of whales was tracked per day; 2) whales of the same group belong to
143 the same clan; 3) groups from different clans are typically found some days apart (Whitehead &
144 Rendell 2004). However, in four multiple-day encounters, more than one clan was identified,
145 likely due to the replacement of the tracked group by one of another clan during the night. Since
146 we could not determine the time the new group of whales was found, for these encounters, we
147 used only geographic positions that were recorded in daylight (06:00-18:00), during which
148 photo-identifications were available (see Whitehead and Rendell 2004).

149 *Environmental descriptors*

150 As topographical variables, we used depth from the General Bathymetric Chart of the Oceans
151 (http://www.gebco.net/data_and_products/gridded_bathymetry_data/) and percentage of slope
152 incline, calculated with Spatial Analysis tools in ArcGIS. As oceanographic variables, we used
153 relative mean sea surface temperature (relSST) as a proxy for upwelling and standard deviation

154 of SST (sdSST) as a proxy for frontal activity from the Pathfinder Version 5.0 & 5.1 dataset
155 collected by the Advanced Very High Resolution Radiometer (AVHRR) and processed by the
156 NOAA National Oceanographic Data Center for 1980's data points, and Aqua-MODIS satellite
157 images distributed by the NOAA CoastWatch Program and NASA's Goddard Space Flight
158 Center for 2010's data points (see Griffin 1999; Praca et al. 2009; Pirota et al. 2011). We
159 calculated relSST as the difference between SST at a geographic position and the mean SST over
160 the entire Galápagos region (defined as 93°-88°W; 2°N-2°S for the 1980's period and 93°-88°W;
161 1.5°N-2°S for the 2010's period) for the corresponding month We also considered chlorophyll-a
162 concentration (Chla) as a measure of primary productivity for the 2013-2014 survey period,
163 which was not available for the earlier studies. We obtained these data from NOAA CoastWatch
164 Program Aqua MODIS satellite images. Since the sperm whales' cephalopod prey are
165 themselves predatory, there is an expected temporal lag of about 3-4 months between primary
166 productivity peaks and increases in cephalopod biomass (see Jaquet 1996; Pirota et al. 2011).
167 Thus, we considered the monthly Chla concentration averaged over the three months prior to the
168 encounter date. We note that while relSST, sdSST, and Chla reflect processes that affect primary
169 productivity at the surface, these values may not reflect high productivity hundreds of metres
170 below the surface, which is where sperm whale prey is found (Volkov & Moroz 1977; Pierce et
171 al. 2008). However, an association between surface and subsurface waters is suggested by the
172 significant correlation between sperm whale feeding success and surface conditions (Smith &
173 Whitehead 1996). Finally, we used latitude and longitude to account for spatial variation
174 unexplained by oceanographic and topographical variables.

175 We linked values of depth and slope to geographic positions using the raster package in R (R
176 Core Team 2016). We obtained SST and Chla values for each geographic position using the

177 rerddapXtracto R package (Mendelssohn 2016). Topographic and oceanographic variables were
178 extracted at 0.10° resolution, to reflect the distances over which sperm whales could be detected
179 visually and acoustically. Oceanographic variables were weekly averages. In the case of Chla,
180 we used the monthly mean averaged over three months, starting from three months prior to
181 recorded geographic positions. During analysis, we found that models fitted using environmental
182 variables extracted at coarser spatial and temporal scales did not produce substantially different
183 results (Supplement 1)

184 *Modelling differences in habitat use*

185 To examine whether the different clans of sperm whales had different habitat use patterns, we
186 used logistic Generalized Additive Models (GAMs) and Generalized Estimating Equations
187 (GEEs) in which oceanographic and topographic variables were used as predictors of clan
188 identity (following Pirotta et al. 2011). We used GEEs to account for spatiotemporal
189 autocorrelation expected from our continuous method of data collection (Pirotta et al. 2011).
190 This method has previously been used in ecological studies when data were sequentially
191 collected or when measurements were gathered repeatedly from a group of individuals (Dormann
192 et al. 2007, Pirotta et al. 2011, Pirotta et al. 2014, Scott-Hayward et al. 2015). Specifically,
193 sequential data points are grouped into independent blocks and a correlation structure is fitted
194 within blocks (Liang & Zeger 1986). We used a working independence model, which is
195 preferred when the true nature of the correlation is unknown (Liang & Zeger 1986, McDonald
196 1993, Pan 2001). This approach returns more realistic estimates of uncertainty compared with a
197 standard GAM to account for the observed degree of autocorrelation within blocks, but
198 parameter estimates are not affected.

219 We analyzed data collected in the 1980's and in the 2010's separately, because different clans
220 were sighted during each of these periods (Table 1; see also Cantor et al. 2016): predominantly
221 *Plus-One* and *Regular* in the former; *Short* and *Four-Plus* in the latter. For the 1980's analysis,
222 we included only sightings with *Plus-One* and *Regular* clans as there was only one encounter
223 with each of the *Short* and *Four-Plus* clans over this period (Table 1). We binarized records in
224 each period (i.e. assigning "0" to one clan, "1" to the other). We used individual geographic
225 positions as our unit of analysis and encounters with single clans as the blocking variable,
226 because each encounter represented one group of whales. All locations within each encounter
227 were included within a block. Autocorrelation function (ACF) plots of residuals from individual
228 encounters for the final models (see below) rapidly converged to zero, indicating that encounter
229 was an appropriate blocking variable (Scott-Hayward et al. 2013; See Figs. S1 & S2 in
230 Supplement 2). We tested whether latitude and longitude were best entered as linear terms or
231 cubic spline smooths (see below), while other variables were treated as linear terms, because we
232 assumed that relationships between habitat use and oceanographic and topographic variables
233 would be monotonic.

234 Habitat use can be influenced by behavioral states in cetacean species (Cañadas & Hammond
235 2008; Palacios et al. 2013) but we did not include behavioural information in our analyses.
236 Sperm whales have two very distinct behavioural states – they forage for about 75% of the time
237 and socialize during the rest (Whitehead and Weilgart 1991). While socializing, sperm whales
238 tend to move slowly and in more variable directions (Whitehead and Weilgart 1991), so that at
239 the spatial scales of this study (>10 km) positions collected during socializing would not be
240 much different, if at all, from those recorded at the end and beginning of the foraging bouts

221 respectively preceding and following the period of socialising. Therefore, in this case, habitat use
222 records will largely be determined by foraging behaviour.

223 We subsampled or interpolated geographic positions so that they were available approximately
224 every hour and retained only geographic positions collected in areas that were sufficiently
225 surveyed during both study periods (see Supplement 3 for further details). To identify and avoid
226 collinearity, we calculated correlation coefficients for all pairs of explanatory variables (Tables
227 S1-2 in Supplement 4). When variables were collinear ($|r| > 0.4$), we fit alternative initial models
228 that included only uncorrelated variables.

229 *Model selection*

230 To select the most parsimonious combination of uncorrelated variables and the best form (linear
231 or smooth) in which latitude and longitude should be included, we used the quasi-likelihood
232 under independence model criterion (QIC)—an adaptation of Akaike’s information criterion
233 (AIC) for GEEs (Pan 2001, Cui & Qian 2007) available in the MuMIn R package (Barton,
234 2016). First, we fitted alternative initial models using uncorrelated predictors, in which latitude
235 and longitude were entered as either linear terms or cubic splines, and then used QIC to select the
236 best shape at which these should be entered. Next, we used backwards stepwise selection to
237 determine which variables to include.

238 We also fitted null models that included only latitude and longitude, aiming to capture variation
239 in relative habitat preferences that could not be accounted for by any of the oceanographic or
240 topographic variables available and investigate the degree to which oceanographic and
241 topographic variables retained in the model improved predictive ability. All explanatory
242 variables were standardised by subtracting the mean and dividing by the standard deviation.

243 *Prediction maps*

244 To examine the spatial distribution of predicted probabilities of encountering a given clan, we
245 produced prediction maps for each study period within areas where whales were found, using the
246 final models (see Supplement 5). We also generated maps of predicted probabilities under the
247 null models for each study period. To identify regions where predictions from the final and the
248 null model differed the most, we generated a mean difference raster. Specifically, for each study
249 period, we obtained the absolute difference between the calculated probabilities generated from
250 the final best model for each year and those calculated through the null model, and averaged
251 annual differences to create a single raster.

252 *Validation*

253 To validate the final models, we analyzed the following three aspects of predictive performance.
254 First, we used goodness of fit (GOF)—a measure of how well the final models fit the data—by
255 generating confusion matrices to assess the models' accuracy in predicting the data used to fit
256 models (Fielding & Bell 1997). To build confusion matrices, we estimated the predicted
257 probability that locations during encounters indicated a given clan. We transformed predicted
258 probability values into a binary assignment using a cut-off that maximized the distance between
259 the Receiver Operating Characteristic (ROC) curve and a 1:1 line using the ROCR package in R
260 (Fielding & Bell 1997, Sing et al. 2005). Second, we used leave-one-out cross validation (LOO)
261 to quantify how accurately a model predicted clan identity for an encounter when that encounter
262 was iteratively removed from the data used to fit the model. In each encounter, we calculated the
263 percentage of geographic positions for which clan identity was correctly assigned (Hastie et al.
264 2009). Finally, we used external cross-validation, i.e. assessed how accurately models predicted
265 clan identity in data that were not used in the model fitting and selection process. We calculated

266 the accuracy in predicting clan identity for whales found in 1985 for the 1980's models, and for
267 whales found in the western region during 2013 and 2014 for the 2010's models. For each study
268 period, we compared these three aspects of performance of the final models to those of
269 corresponding null models.

270 **Results**

271 *1980's period*

272 We analyzed 596 geographic positions collected between 1987 and 1989. Of these, 168 positions
273 were collected while following the *Plus-One* clan whales and 479 while following *Regular* clan
274 whales. Most encounters occurred in the west and northwest of the archipelago (Fig. 1a), and
275 lasted between an hour and 6 days, averaging 1.6 days (SD = 1.4 days). We fitted two alternative
276 initial models (Table S1 in Supplement 6). Our final model included latitude and longitude as
277 cubic splines and slope and weekly sdSST as linear terms (GOF = 85.2%) (Table S2 in
278 Supplement 6).

279 Most of the variation among the clans was explained by geographic variables. Whales of the
280 *Plus-One* clan were more likely to be found north of 0.25°N, although uncertainty in predicting
281 clan identity in that region was high (Fig. 2a-i). This is consistent with the observed latitudinal
282 distributions of the *Plus-One* and *Regular* clans north of the Equator, but not with their
283 distributions in the southern limits of the study region where only *Plus-One* clan whales were
284 found (Fig. 3a-i). *Plus-One* whales were also found predominantly in more western waters, but
285 uncertainty in predicting clan identity increased east of the archipelago (91° W; Fig. 2a-ii). This
286 was consistent with the observed distribution of *Plus-One* whales throughout study years, which
287 was restricted to areas west of 91.5° W, and with the distribution of *Regular* clan whales, which

288 occurred throughout the longitudinal range of sperm whale distribution (Fig. 3a-ii). High
289 uncertainty in predicting clan identity in the east likely resulted from the small number of
290 encounters that occurred in that area (Fig. 3a-ii). Although our final model included slope and
291 weekly sdSST (Figs. 2a-iii-iv), response curves did not reflect the observed slope, and sdSST at
292 which the clans were found (Figs. 3a-iii-iv).

293 The predominant effects of geographic variables in differentiating clan identity were also
294 apparent from the similarity between predictive maps generated using the final model and the
295 null model (Figs. 4a-i, ii). These two models predicted identical clan distributions in areas both
296 close to and far from the Galápagos Islands, where there was little spatial overlap among the
297 *Plus-One* and *Regular* clans, but more dissimilar distributions in regions of higher spatial overlap
298 between the clans (Fig. 4a-iii).

299 The inclusion of oceanographic and topographic variables in the final model did not significantly
300 improve the goodness of fit or the average predictive accuracy through LOO cross-validation in
301 comparison to the null model (Fig. 5). Moreover, the inclusion of these variables did not improve
302 the null model's poor ability to predict the clan identity of whales found in 1985 (Fig. 5).

303 *2010's period*

304 Between 2013 and 2014, we analyzed 370 geographic positions to the south of the Galápagos
305 Islands (Fig. 1b). Of these, 226 positions were collected while following the *Short* clan whales
306 and 144 while following *Four-Plus* clan whales. Encounters lasted between 1 hour and 8 days,
307 and averaged 1.3 days (SD = 2.3 days). We fitted six initial candidate models (Table S3 in
308 Supplement 6). The best final model included latitude and longitude as cubic splines, and weekly
309 relSST and sdSST (Table S4 in Supplement 6; GOF = 87 %).

310 The variation in clan distribution during this period was explained by geographic and
311 oceanographic variables. We found that *Four-Plus* whales were most likely to occur at around
312 2.2 and 1.8°S, and least likely to occur over latitudinal ranges between these values (Fig. 2b-i).
313 *Four-Plus* whales were also more likely to occur east of 90.5°W, but uncertainty in predicting
314 clan identity was high further west, where there was only one encounter (with *Short* clan whales;
315 Fig. 2b-ii). This predicted geographic distribution reproduced the observed distribution of clans
316 during the 2010's study period (Fig. 3b-i & ii). *Four-Plus* whales were also more likely to occur
317 in areas of higher weekly relSST (Fig. 2b-iii), and lower weekly sdSST (Fig. 2b-iv). The
318 modelled relationships between weekly relSST and sdSST and clan identity were consistent with
319 the oceanographic conditions measured during the 2010's study period (Figs. 3b-iii, iv).
320 However, we note that the relSST mean is skewed towards lower temperatures by an encounter
321 with *Short* clan whales that consistently covered colder waters.

322 The importance of oceanographic variables in differentiating the habitat of *Four-Plus* and *Short*
323 clans was illustrated by the different prediction maps yielded by the final model and null models
324 (Fig. 4b-i, ii). While both the full and null models generated identical probabilities in the
325 easternmost region where only *Short* clan whales were encountered, they differed greatly over
326 the regions where both clans overlapped (Fig. 4b-iii)

327 However, while modelled differences in the oceanographic conditions over which *Four-Plus* and
328 *Short* clans occurred were consistent with observed differences in habitat use between *Four-Plus*
329 and *Short* clans, models that included oceanographic variables performed worse in terms of LOO
330 than the null model (Fig. 5b). The same was true regarding performance measured through
331 external cross-validation (Fig. 5b). Further, the performance measured through LOO and external
332 cross-validation of both null and full model was poor overall (<50%; Fig. 5b).

333 **Discussion**

334 We found that culturally distinct sperm whale clans that are sympatric at the regional scale,
335 around the Galápagos Archipelago, vary considerably in fine-scale habitat use, delineated by
336 spatial partitioning and, to a lesser degree, by oceanographic characteristics. In the 1980's,
337 whales from the *Regular* and *Plus-One* clan used different geographical locations, while in the
338 2010's, *Four-Plus* and *Short* clan whales used waters with different oceanographic features. In
339 the following sections, we discuss how the sociality of this species may influence its space use
340 patterns via social transmission of habitat preferences and foraging behaviours.

341 *Spatial partitioning*

342 We found sperm whale clans used different areas around the Galápagos Archipelago. In the
343 1980's *Plus-One* whales were more common in offshore western waters than *Regular* clans
344 whales—consistent with previous findings (Whitehead & Rendell 2004). In the 2010's period,
345 only the *Four-Plus* clan occurred west of the archipelago and, in the southern region, the areas of
346 overlap with the *Short* clan were limited.

347 Previous analysis has shown that, over days up to a few weeks, areas on the scale at which we
348 can survey from a small vessel are predominantly occupied by groups of whales of a single clan
349 (Whitehead & Rendell 2004). Social units may group to forage together. Individuals may benefit
350 from eavesdropping on group members' echolocation clicks and locate prey more easily, or use
351 other social information on prey location (Whitehead 1989, Whitehead et al. 1991). At daily to
352 weekly scales, we hypothesise that social units could benefit from remaining in an area where
353 other clan members are found and/or avoiding areas dominated by social units of other clans. In
354 this sense, the distribution of sperm whales could be affected by the distributions of fellow clan

355 members as well as by where members of other clans. The reactions of sperm whales to
356 encounters with other clans have not been documented, but active avoidance of members of
357 different cultural entities has been proposed for *transient* and *resident* killer whales (Bigg 1979,
358 Baird & Dill 1995). We note, however, that because these killer whale ecotypes have very
359 different diets, social avoidance could be entangled with different spatial use driven by prey
360 distribution, whereas diet differences are likely much subtler among sperm whale clans
361 (Marcoux et al. 2007), making social avoidance more evident.

362 We found that the spatial partitioning among sperm whale clans over few days and weeks was
363 consistent throughout the months over at least two years. This was most remarkable in the
364 1980's, during which the overall distribution of the clans was maintained despite variation in
365 environmental conditions and sperm whale feeding success between 1987—a strong el Niño
366 year— and 1989—a normal year (Whitehead & Rendell 2004). During the 1987 El Niño,
367 temperatures were 4°C higher than in 1989 (Whitehead & Rendell 2004). Increased temperatures
368 during El Niño events are associated with decreased marine production, which affects the fitness
369 of species across taxa (Trillmich & Dellinger 1991, Boersma 1998, Schaeffer et al. 2008, Wolff
370 et al. 2012). Feeding rates of both *Regular* and *Plus-One* sperm whales were significantly lower
371 in 1987 than in 1989 (Whitehead and Rendell 2004). While there is no direct information on
372 sperm whale prey abundance off the Galápagos Islands, decline in the biomass of the squid
373 *Dosidicus gigas*, an important prey of sperm whales in the region (Clarke et al. 1988, Clarke &
374 Paliza 2001) has been documented across the eastern Pacific during strong El Niño years (Taipe
375 et al. 1991, Markaida 2006). The distribution of clans remained relatively constant across two
376 highly different years, suggesting that site fidelity over the annual temporal scale may be
377 maintained if social units rely on the presence of other clan members as a cue for habitat

378 selection. Thus, while sperm whale clans are often described as sympatric at a regional scale—
379 for example, around the Galápagos Archipelago, off the Coast of Chile, and in the Caribbean
380 (Gero et al. 2016; Rendell & Whitehead 2003)—spatial partitioning was apparent at a finer
381 spatial scale (less than 10 km).

382 Studies that span greater temporal and spatial scales indicate however that clan-specific habitat
383 use patterns become diluted. Our study focused on a window of up to three years around the
384 Galápagos and was restricted to the months between January-June, which are mostly
385 representative of the warm season. This represents a snapshot of a female sperm whale's
386 lifespan—60 to 70 years (Rice 1989)—and a portion of the home range of such nomadic
387 animals—at least 2000 km across the Eastern Pacific (Whitehead et al. 2008, Mizroch & Rice
388 2013, Cantor et al. 2016). But throughout the decades, the clan composition in the Galápagos
389 Islands shifted abruptly from being dominated by the *Regular* and *Plus-One* clans in the 1980's,
390 to the *Regular* clan in the 1990's, and to the *Short* and *Four-Plus* clans in the 2010's (Cantor et
391 al. 2016). This shift may have resulted from movements triggered by environmental changes and
392 fluctuation in prey availability over large scales (Cantor et al. 2016, 2017). Additionally, patterns
393 of habitat use for the same clans in other areas were less discrete (Whitehead & Rendell 2004).
394 Off the Chilean coast in the year 2000, *Regular*, *Short*, and *Plus-One* clans ranges overlapped
395 more than off the Galápagos (Whitehead & Rendell 2004). Movement patterns of *Regular* clan
396 whales off Chile were also significantly more convoluted than those of *Regular* clan whales off
397 the Galápagos (Whitehead & Rendell 2004).

398 *Oceanographic variation*

399 Whether oceanographic conditions drive variation in clan space use remains uncertain. During
400 the 1980's, oceanographic variables did not contribute to discriminating the space use of *Plus-*

401 *One* and *Regular* clans. However, three lines of evidence suggest that oceanic conditions were
402 different in the areas occupied by the *Plus One* and *Regular* clans. First, the relative species
403 composition of sperm whale diet varied regionally, as described by the analysis of fecal samples
404 off the Galápagos Islands (Smith & Whitehead 2000). Second, *Regular* clan whales in this period
405 had a higher carbon-13 isotope signature compared to *Plus-One* clan whales (Marcoux et al.
406 2007b). Higher C-13 signatures are characteristic of less turbulent habitats, and have been
407 suggested to reflect the difference in oceanic flow conditions between the more inshore habitat of
408 the *Regular* clan and the oceanic habitat of *Plus-One* clan whales (France 1995, Marcoux et al.
409 2007a). And third, *Regular* and *Plus-One* clan whales had significantly different movement
410 patterns and foraging success rates during this period (Whitehead & Rendell 2004). Thus,
411 different conditions between the areas in which the clans were found could have existed but may
412 have not captured by the oceanographic variables we included in the present analysis. However,
413 it remains uncertain whether observed behavioural differences in *Regular* and *Plus-One* clans
414 were a consequence of different habitat conditions or if these behaviours caused different habitat
415 selection patterns among the clans (Whitehead & Rendell 2004).

416 In the 2010's, *Four-Plus* clan whales were found in warmer waters and areas of higher variation
417 in SST than *Short* clan whales. These differences may have arisen if these clans were directly
418 tracking different environmental cues to find their prey or if the prey they preferred was found in
419 association with different environmental conditions. Alternatively, these differences might also
420 be a by-product of the spatial segregation described above. In addition, these patterns were
421 described based on a limited number of unevenly represented encounters and models that
422 captured these patterns performed poorly through cross-validation (although they fit well to the

423 data). Thus, our sample may not be sufficient to accurately represent the habitat of the *Short* and
424 *Four-Plus* clans during this period.

425 Some of the uncertainty in characterizing the habitat of the clans arises from the difficulty in
426 measuring sperm whales' habitat accurately, and is further confounded by the lack of detailed
427 information on diving behaviour. Although the oceanographic and topographic variables we used
428 are valid proxies for the distribution of sperm whale prey (Jaquet & Whitehead 1996, Pirotta et
429 al. 2011, Wong & Whitehead 2014), they do not equate to their presence, abundance or quality.
430 Furthermore, our measurements of oceanographic variables describe surface conditions. It is
431 uncertain the degree to which indicators of upwelling or frontal activity at the sea surface
432 represent those in deeper waters, because these features can be displaced or dissipated at greater
433 depths (Jaquet 1996). Our inclusion of mostly surface-level oceanographic variables also likely
434 explains the small contribution that these variables had in predicting clan identity. Recent
435 advances in echosounding technology used to measure composition, biomass, and movements of
436 bathypelagic squid offer a promising way to better characterize the fine-scale habitat of sperm
437 whales (Benoit-Bird et al. 2015, Benoit-Bird et al. 2017). Additionally, we aimed to identify
438 differences in niche traits among the clans but did not evaluate the possibility of niche width
439 varying among the clans, which has been found among killer whale ecotypes (Foote et al. 2009).
440 Thus, our decision to study only linear differences in habitat-use patterns may have restricted our
441 ability to find non-monotonic contrasts in the oceanographic conditions where clans were found.

442 **Conclusions**

443 Our study reveals fine-scale spatial partitioning among clans around the Galápagos Islands that
444 suggests another layer of complexity in the cultural lives of sperm whales. We show that clans
445 differ in fine-scale space use, in addition to vocal repertoire (Rendell & Whitehead 2003),

446 movement patterns (Whitehead & Rendell 2004), fitness (Marcoux et al. 2007a), diet (Marcoux
447 et al. 2007b) and social behaviour (Cantor & Whitehead 2015). Taken together, these findings
448 suggest the niche of sperm whale clans is constructed on the basis of both social and
449 environmental information, both of which interact over different spatial and temporal scales (see
450 also Boyd and Richerson 1988; Whitehead 2007; van der Post and Hogeweg 2009). The
451 potential ability of sperm whales to balance socially acquired traditions with environmental cues
452 likely plays a part in their ecological success in such a highly dynamic, mesopelagic environment
453 (see also Laland et al. 2000; Whitehead 2007).

454 To further understand clan-specific niches of sperm whales, future studies should collect spatial
455 data from other regions of the eastern Tropical Pacific and couple them with detailed diving data
456 using tag technologies and direct measurements of prey availability through echosounding
457 devices (Watwood et al. 2006, Benoit-Bird et al. 2015, Benoit-Bird et al. 2017). Combining such
458 large- and fine-scale spatial data will help clarify whether clans have consistently different
459 foraging strategies or if these behaviours are a response to varying environmental conditions.

460

461 **Ethics statement**

462 Field procedures for approaching, photographing, and recording sperm whales were approved by
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706

707 **Tables**

708 Table 1. Summary of time spent following female and juvenile sperm whales during the 1980's and
 709 2010's surveys off the Galápagos Islands. Encounters were defined as consecutive geographic positions
 710 that were assigned to the same clan and occurred within < 6 hours of each other.

Year	Surveyed period	Days spent following whales	Encounters with females and immatures ^a	<i>Regular</i> clan encounters	<i>Plus-One</i> clan encounters	<i>Short</i> clan encounters	<i>Four-Plus</i> clan encounters
1985 ^c	Jan. 18 – Apr. 22	29	12	10	1	1	0
1987	Jan. 2 – Jun. 30	51	21	12	7	1	0
1989	Apr. 4 – May 22	32	16	10	3	0	1
2013 (Southern) ^b	Apr. 9 – Apr. 12	4	9	0	0	3	2
2013 ^c (Western) ^b	Jan. 3 – Feb. 21	10	2	0	0	0	2
2014 (Southern) ^b	Jan. 23 – May 22	24	11	0	0	2	3
2014 ^c (Western) ^b	Jan. 13 – Feb. 10	2	1	0	0	0	1
	Total	152	72	32	11	7	9

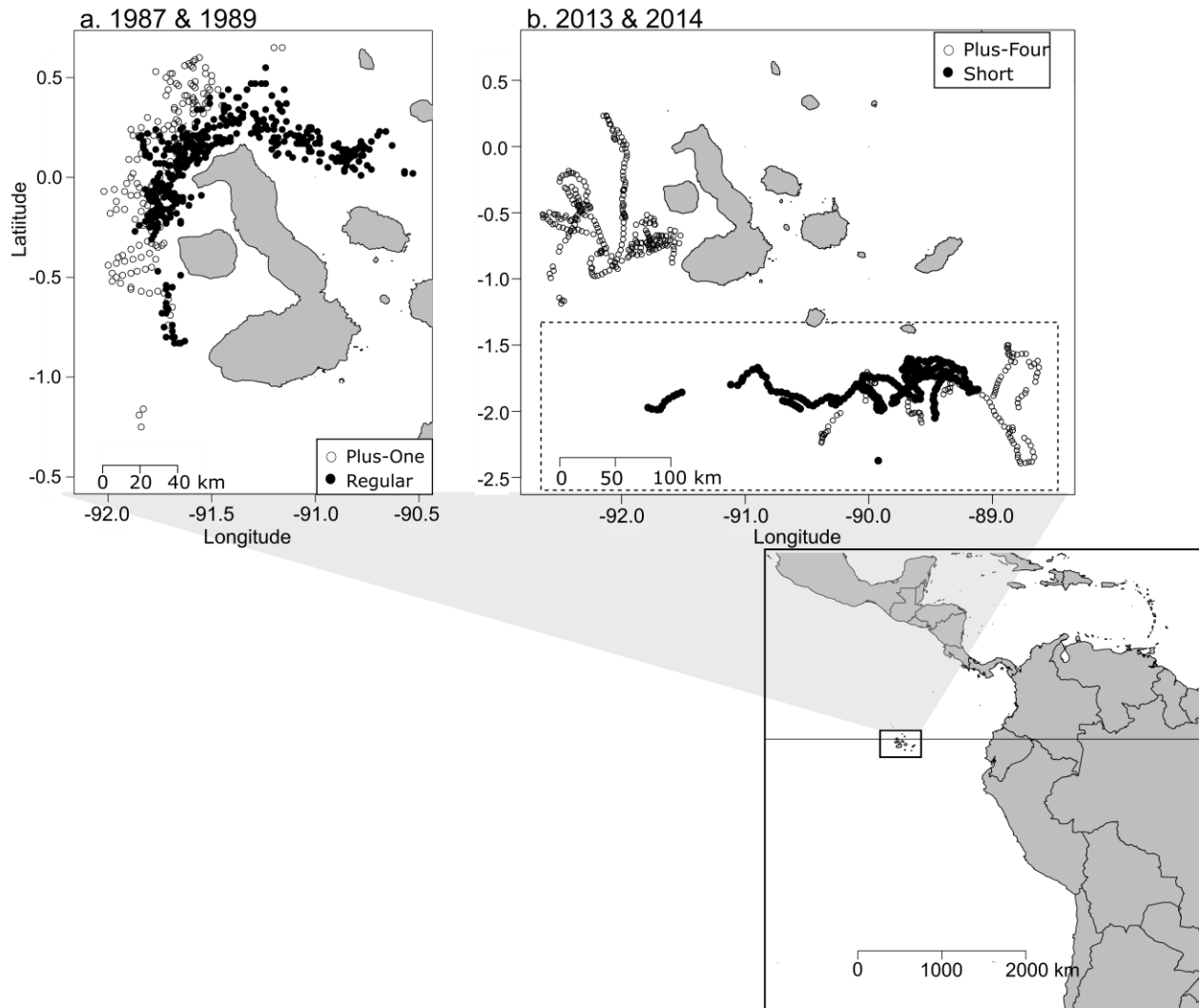
711

712 a. Encounter number includes encounters for which clan identity was not assigned, which is why
 713 this number does not always equal the sum of encounters with each of the clans

714 b. Southern regions consist of areas south of 1.3°S and Western regions are north of 1.3°S (Fig. 1)

715 c. Data from these survey periods were used for external cross-validation only

716 **Figures**



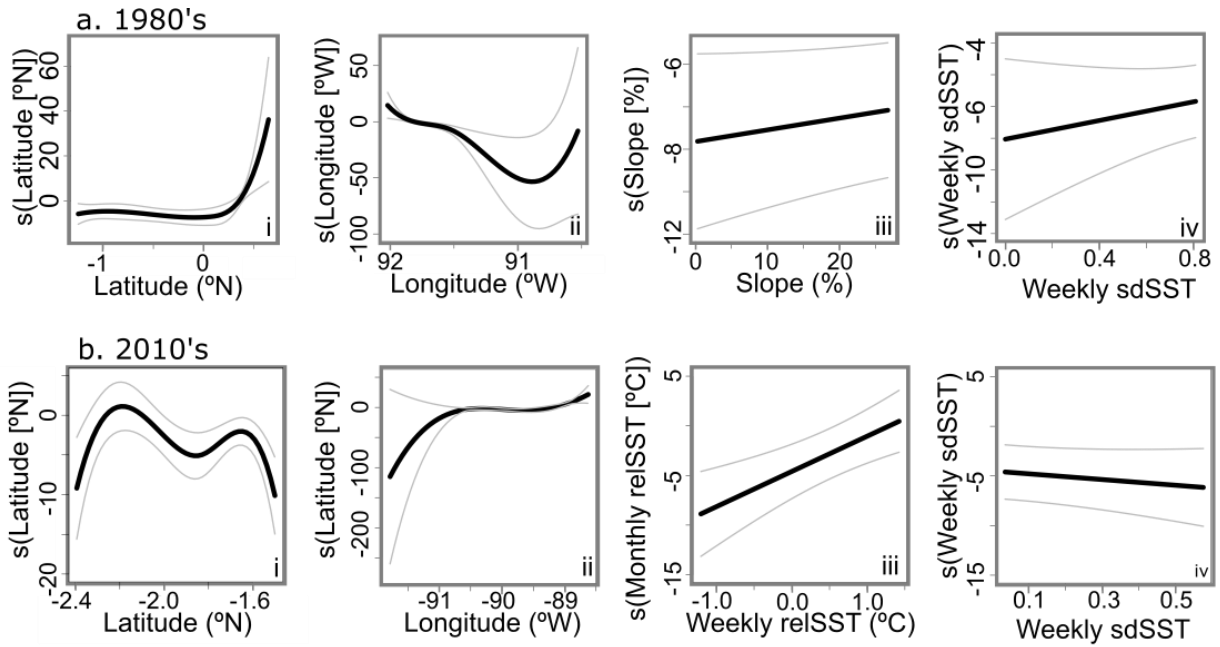
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718 Figure 1. Geographic positions in (a) 1987 and 1989 of *Plus-One* and *Regular* clan sperm whales, and (b)

719 in 2013 and 2013 of *Four-Plus* and *Short* clan sperm whales off the Galápagos Islands. The southern

720 region that was included in the 2010's period is delineated by the dashed rectangle. A section of South

721 and Central America is shown for reference



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723 Figure 2. Partial plots of $\log_e(\text{odds})$ of female and juvenile sperm whales found off the Galápagos Islands

724 belonging to (a) the *Plus-One* clan in the 1980's study period and (b) the *Four-Plus* clan in the 2010's

725 study period. (a) In the 1980's, clan identity = *Plus-One* is modelled as function of (a-i) latitude, (a-ii)

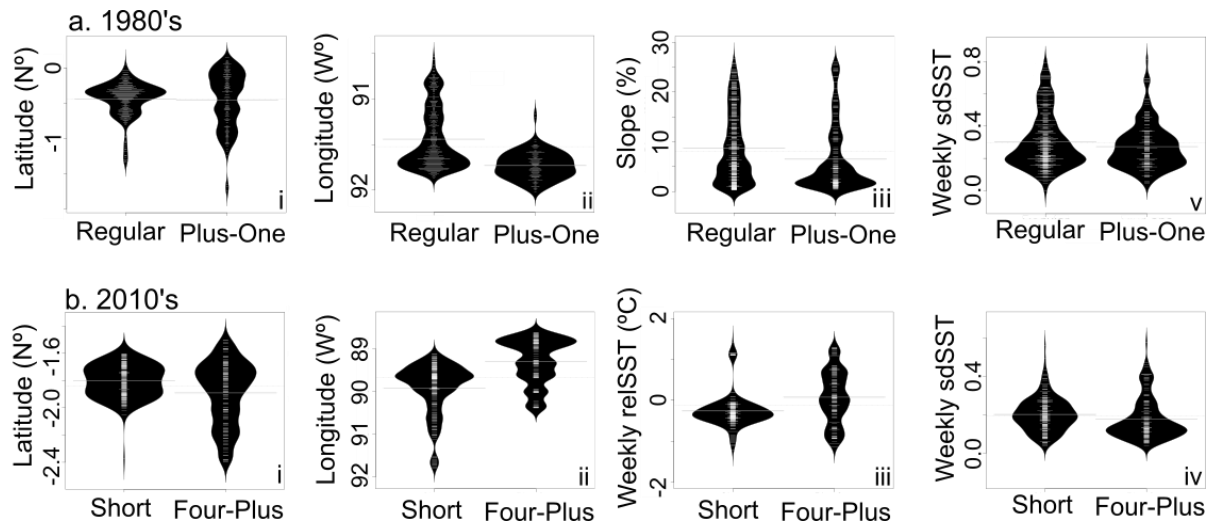
726 longitude, (a-iii) slope incline, (a-iv) weekly standard deviation of SST (sdSST). (b) In the 2010's, clan

727 identity = *Four-Plus* is modelled as a function of (b-i) latitude, (b-ii) longitude, (b-iii) weekly relSST,

728 and (b-iv) weekly sdSST. Grey lines represent 95% confidence intervals.

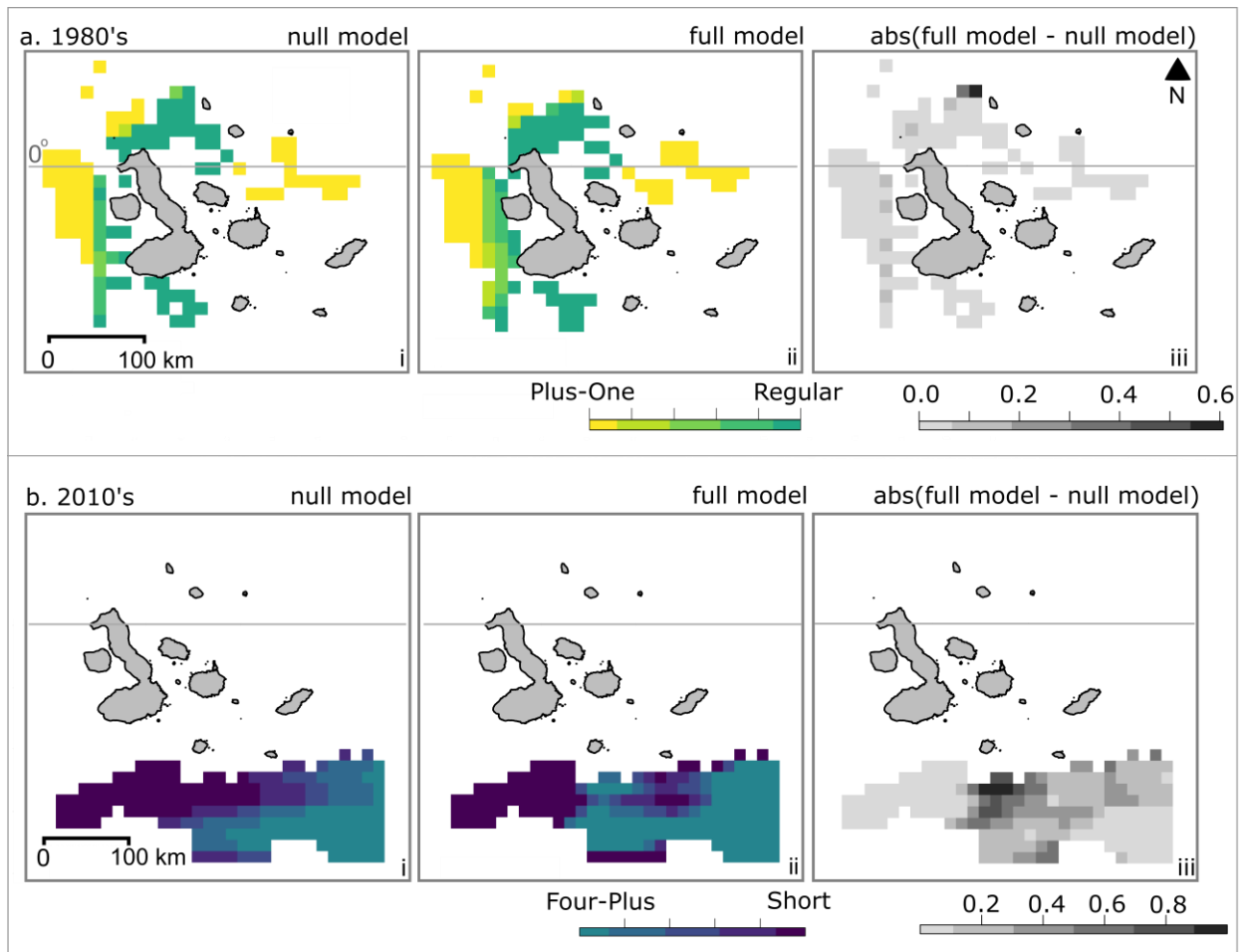
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Figure 3. Bean-plots of observed geographic and oceanographic variables by clan; (a) shows the 1980's distribution of variables in which *Plus-One* and *Regular* clan whales were found off the Galápagos Islands: (a-i) latitude, (a-ii) longitude, (a-iii) slope incline, and (a-iv) weekly standard deviation of sea surface temperature (sdSST); (b) shows the 2010's distribution of variables in which *Four-Plus* and *Short* clan sperm whales were found: (b-i) latitude (b-ii) longitude, (b-iii) weekly relSST, and (b-iv) weekly sdSST.



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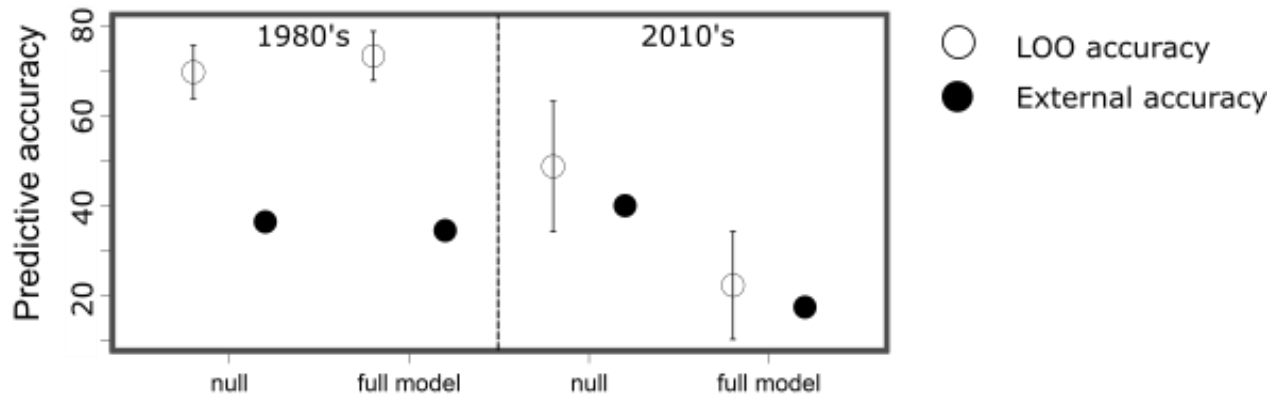
739 Figure 4. Predicted probability of sperm whales belonging to different clans off the Galápagos Islands
 740 mapped at 0.12° resolution. (a) sperm whales of the *Plus-One* and *Regular* clans in 1987 and 1989 as a
 741 function of (a-i) a full model, (a-ii) a null model (latitude and longitude only), and (a-iii) absolute
 742 difference between the full and null models. (b) sperm whales of the *Short* and *Four-Plus* clans in 2013
 743 and 2014 as a function of (b-i) a full model, (b-ii) a null model (latitude and longitude only), and (b-iii)
 744 the absolute difference between the full and null models.

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 750 Figure 5. Predictive accuracy (%) of null models (fit with latitude and longitude only) and full models of
 751 clan identity of sperm whales off the Galápagos Islands in the 1980's (1987 and 1989), and 2010's (2013
 752 and 2014). Predictive accuracy was measured through leave-one-out (LOO) and external cross-validation.
 753 Standard errors are shown for LOO accuracy.

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