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Habitat use of culturally distinct Galápagos sperm whale *Physeter macrocephalus* clans

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

KEY WORDS: Habitat preference · Cetacean · Culture · Generalized additive model · GAM · Generalized estimating equation · GEE · Galápagos

1. INTRODUCTION

Traditionally, ecological niche and habitat use have been defined at the species level (Hutchinson 1957, Leibold 1995). However, mounting evidence for individuals of the same population having low niche overlap reminds us that conspecifics are not always ecologically equivalent (Bolnick et al. 2003). To date, most of the theoretical work on individual niche variation has focussed on intrinsic sources of variation, such as morphological, physiological, and ontogenic traits (Van Valen 1965, Roughgarden 1972, Svanbäck & Persson 2004). Less attention has been given to social learning as a mechanism for individual niche

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variation (but see Galef 1976, Laland et al. 2000, Slagsvold & Wiebe 2007, Sargeant & Mann 2009).

When behavioural traits are socially learned and shared among groups of individuals, there is culture (Boyd & Richerson 1996, Laland & Hoppitt 2003). Culture, as so defined, can play an important role in the divergence of resource and space use among individuals, especially in species in which foraging strategies and habitat selection are socially transmitted (e.g. Laland & Galef 2009, Whitehead & Rendell 2014). Notable cases include apes and monkeys that learn to use different tools to exploit nuts and termites (Whiten et al. 1999, van Schaik et al. 2003, Ottoni & Izar 2008), birds that learn about feeding areas and prey sizes from their parents' choices (Slagsvold & Wiebe 2011), female mountain sheep retaining the home ranges of their social groups (Geist 1971), dolphins using the same foraging tactics and areas of their mothers and/or peers (Mann & Patterson 2013, Cantor et al. 2018), and sea otters using foraging tools to meet their matrilineally transmitted dietary preferences (Estes et al. 2003). These and other foraging techniques and habitat use patterns are socially acquired behavioural traits that result in different resource use patterns, and so reduce trophic niche overlap among subsets of individuals within the same population (Jaeggi et al. 2010, Slagsvold & Wiebe 2011, Allen et al. 2013).

However, it is not always straightforward to disentangle culture from other underlying causes of foraging behaviour variation. Both genetic and ecological factors are explanatory candidates for behavioural divergence, especially in allopatric populations (e.g. Laland & Galef 2009, Koops et al. 2013). One way to overcome this issue is excluding all sources of noncultural behavioural variation (Whiten et al. 1999), but this has proved problematic (Laland & Janik 2006). Alternatively, by studying resource-use variation among sympatric groups of genetically similar individuals, one can account for such environmental and genetic mechanisms. Two particularly well-known marine examples are killer whales *Orcinus orca* and Indo-Pacific bottlenose dolphins (*Tursiops* sp.). Mammal-eating and fish-eating killer whales use the same waters off British Columbia, Canada, but feed exclusively on very different prey (Ford et al. 1998). Off Shark Bay, Australia, part of a bottlenose dolphin population uses marine sponges as tools to forage on the seafloor for prey that are hard to access otherwise, leading to distinct social communities of 'sponging' and 'non-sponging' dolphins that coexist in the same habitat (Mann et al. 2012). Neither case can be explained by genetic variation alone (Krützen et al. 2005, Mann et al. 2012, Riesch et al. 2012).

Over much wider spatial scales, there is the case of sympatric cultural divergence among female sperm whales *Physeter macrocephalus* into clans. While males lead mostly solitary lives in high latitudes, females and immatures live in tightly knit social units, containing few matrilines, in tropical and subtropical waters (Best 1979, Christal et al. 1998). Social units form temporary larger groups (Whitehead et al. 1991), but they do so with other units with which they share a large proportion of their acoustic repertoire, thus delineating a higher social level: the 'vocal clan' (Rendell & Whitehead 2003, Whitehead et al. 2012, Gero et al. 2016). Sperm whale clans of the Eastern Tropical Pacific are genetically indistinct (Rendell et al. 2012) and sympatric (Rendell & Whitehead 2003). Members of different clans can encounter one another easily, in theory. However, they not only maintain distinct vocal dialects over time (Rendell & Whitehead 2005), but also differ in movement and social behaviour, reproductive and foraging success, and diet composition (Whitehead & Rendell 2004, Marcoux 2005, Marcoux et al. 2007a, Cantor & Whitehead 2015). These divergences suggest that sperm whales belonging to culturally distinct but sympatric clans may use different habitats, but this has not yet been studied directly.

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

Here, we evaluated whether sympatric sperm whale clans differ in habitat use by investigating the spatial, oceanographic, and topographic characteristics of the waters they occupy off the Galápagos Islands. Specifically, we compared the relative habitat use of 2 vocal clans that were particularly common in the area in the 1980s (Rendell & Whitehead 2003), and of 2 other clans that have recently replaced them in the 2010s (Cantor et al. 2016).

2. MATERIALS AND METHODS

2.1. Field methods

We studied sperm whales off the Galápagos Archipelago (3° N–3° S, 93°–88° W) aboard dedicated research sailboats (10–12 m) between January and June, in 1987, 1989, 2013, and 2014 (Table 1). We searched for whales acoustically, monitoring hydrophones that could detect sperm whale clicks up to about 7 km away every 15–60 min (Whitehead 2003). During daylight hours, we also searched for whales visually within a range of 0.2 to 2.0 km, depending on weather conditions. Upon finding a group of sperm whales, we approached it cautiously to photograph their flukes for individual identification (Arnbom 1987). We refer to the periods during which we had continuous (within <6 h) visual and/or acoustic contact with the same group of females as 'encounters'.

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

Field procedures for approaching, photographing, and recording sperm whales were approved by the Committee on Laboratory Animals of Dalhousie University.

2.2. Clan identification

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

We assigned clan memberships to all groups of whales that were photo-identified together and had their acoustic repertoire sufficiently sampled (see Rendell & Whitehead 2003, Cantor et al. 2016). Geographic positions within a day were assigned to a corresponding clan because: (1) typically only 1 group of

Table 1. Summary of time spent following female and juvenile sperm whales during the 1980s and 2010s surveys off the Galápagos Islands. Encounters were defined as consecutive geographic positions that were assigned to the same clan and occurred within <6 h of each other. Clan types are 'Regular' (typically producing regularly-spaced clicks), 'Plus-One' (typical codas with an extended pause before the last click), 'Short' (typical codas with fewer than 5 clicks), and 'Four-Plus' (typical codas with a basis of 4 regular clicks)

Year	Surveyed period	Days spent following whales	Encounters with females and immatures[a]	'Regular' encounters	'Plus-One' encounters	'Short' encounters	'Four-Plus' encounters
1985[b]	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)[c]	Apr 9–Apr 12	4	9	0	0	3	2
2013[c] (Western)[c]	Jan 3–Feb 21	10	2	0	0	0	2
2014 (Southern)[c]	Jan 23–May 22	24	11	0	0	2	3
2014[b] (Western)[c]	Jan 13–Feb 10	2	1	0	0	0	1
	Total	152	72	32	11	7	9

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

[b] Data from these survey periods were used for external cross-validation only

[c] Southern regions consist of areas south of 1.3° S and Western regions are north of 1.3° S (Fig. 1)

whales was tracked per day; (2) whales of the same group belong to the same clan; (3) groups from different clans are typically found some days apart (Whitehead & Rendell 2004). However, in 4 multiple-day encounters, more than 1 clan was identified, likely due to the replacement of the tracked group by one of another clan during the night. Since we could not determine the time the new group of whales was found, for these encounters, we used only geographic positions that were recorded in daylight (06:00–18:00 h), during which photo-identifications were available (see Whitehead & Rendell 2004).

2.3. Environmental descriptors

As topographical variables, we used depth from the General Bathymetric Chart of the Oceans (www.gebco.net/data_and_products/gridded_bathymetry_data/) and percentage of slope incline, calculated with Spatial Analysis tools in ArcGIS. As oceanographic variables, we used relative mean sea surface temperature (relSST) as a proxy for upwelling, and standard deviation of SST (sdSST) as a proxy for frontal activity from the Pathfinder Version 5.0 & 5.1 dataset collected by the Advanced Very High Resolution Radiometer (AVHRR) and processed by the NOAA National Oceanographic Data Center for 1980s data points, and Aqua-MODIS satellite images distributed by the NOAA CoastWatch Program and NASA's Goddard Space Flight Center for 2010s data points (see Griffin 1999, Praca et al. 2009, Pirotta et al. 2011). We calculated relSST as the difference between SST at a geographic position and the mean SST over the entire Galápagos region (defined as 2° N–2° S, 93°–88° W for the 1980s period and 1.5° N–2° S, 93°–88° W for the 2010s period) for the corresponding month. We also considered chlorophyll *a* (chl *a*) concentration as a measure of primary productivity for the 2013–2014 survey period, which was not available for the earlier studies. We obtained these data from NOAA CoastWatch Program Aqua MODIS satellite images. Since the sperm whales' cephalopod prey are themselves predatory, there is an expected temporal lag of about 3–4 mo between primary productivity peaks and increases in cephalopod biomass (see Jaquet 1996, Pirotta et al. 2011). Thus, we considered the monthly chl *a* concentration averaged over the 3 mo prior to the encounter date. We note that while relSST, sdSST, and chl *a* reflect processes that affect primary productivity at the surface, these values may not reflect high productivity hundreds of metres below the surface, which is where sperm whale prey is found (Volkov & Moroz 1977). However, an association between surface and subsurface waters is suggested by the significant correlation between sperm whale feeding success and surface conditions (Smith & Whitehead 1993). Finally, we used latitude and longitude to account for spatial variation unexplained by oceanographic and topographical variables.

We linked values of depth and slope to geographic positions using the raster package in R (R Development Core Team 2016). We obtained SST and chl *a* values for each geographic position using the rerddapXtracto R package (Mendelssohn 2016). Topographic and oceanographic variables were extracted at 0.10° resolution, to reflect the distances over which sperm whales could be detected visually and acoustically. Oceanographic variables were weekly averages. In the case of chl *a*, we used the monthly mean averaged over 3 mo, starting from 3 mo prior to recorded geographic positions. During analysis, we found that models fitted using environmental variables extracted at coarser spatial and temporal scales did not produce substantially different results (see Supplement 1 at www.int-res.com/articles/suppl/m609p257_supp.pdf).

2.4. Modelling differences in habitat use

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

We analysed data collected in the 1980s and in the 2010s separately, because different clans were sighted during each of these periods (Table 1; see also Cantor et al. 2016): predominantly Plus-One and Regular in the former; Short and Four-Plus in the latter. For the 1980s analysis, we included only sightings with Plus-One and Regular clans as there was only 1 encounter with each of the Short and Four-Plus clans over this period (Table 1). We binarized records in each period (i.e. assigning '0' to one clan, '1' to the other). We used individual geographic positions as our unit of analysis and encounters with single clans as the blocking variable, because each encounter represented 1 group of whales. All locations within each encounter were included within a block. Autocorrelation function plots of residuals from individual encounters for the final models (see below) rapidly converged to 0, indicating that encounter was an appropriate blocking variable (Scott-Hayward et al. 2013; see Figs. S3 & S4 in Supplement 2). We tested whether latitude and longitude were best entered as linear terms or cubic spline smooths (see below), while other variables were treated as linear terms, because we assumed that relationships between habitat use and oceanographic and topographic variables would be monotonic.

Habitat use can be influenced by behavioural states in cetacean species (Cañadas & Hammond 2008, Palacios et al. 2013) but we did not include behavioural information in our analyses. Sperm whales have 2 very distinct behavioural states — they forage for about 75% of the time and socialize during the rest (Whitehead & Weilgart 1991). While socializing, sperm whales tend to move slowly and in more variable directions (Whitehead & Weilgart 1991), so that at the spatial scales of this study (>10 km), positions collected during socializing would not be much different, if at all, from those recorded at the end and beginning of the foraging bouts respectively preceding and following the period of socializing. Therefore, in this case, habitat use records will largely be determined by foraging behaviour.

We subsampled or interpolated geographic positions so that they were available approximately every hour and retained only geographic positions collected in areas that were sufficiently surveyed during both study periods (for further details, see Supplement 3). To identify and avoid collinearity, we calculated correlation coefficients for all pairs of explanatory variables (Tables S2 & S3 in Supplement 4). When variables were collinear ($|r| > 0.4$), we fit alternative initial models that included only uncorrelated variables.

2.5. Model selection

To select the most parsimonious combination of uncorrelated variables and the best form (linear or smooth) in which latitude and longitude should be included, we used the quasi-likelihood under independence model criterion (QIC) — an adaptation of Akaike's information criterion (AIC) for GEEs (Pan 2001, Cui & Qian 2007) available in the MuMIn R package (Barton 2018). First, we fitted alternative initial models using uncorrelated predictors, in which latitude and longitude were entered as either linear terms or cubic splines, and then used QIC to select the best shape at which these should be entered. Next, we used backwards stepwise selection to determine which variables to include.

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

2.6. Prediction maps

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

2.7. Validation

To validate the final models, we analysed the following 3 aspects of predictive performance. First, we used goodness of fit (GOF) — a measure of how well the final models fit the data — by generating confusion matrices to assess the models' accuracy in predicting the data used to fit the models (Fielding & Bell 1997).

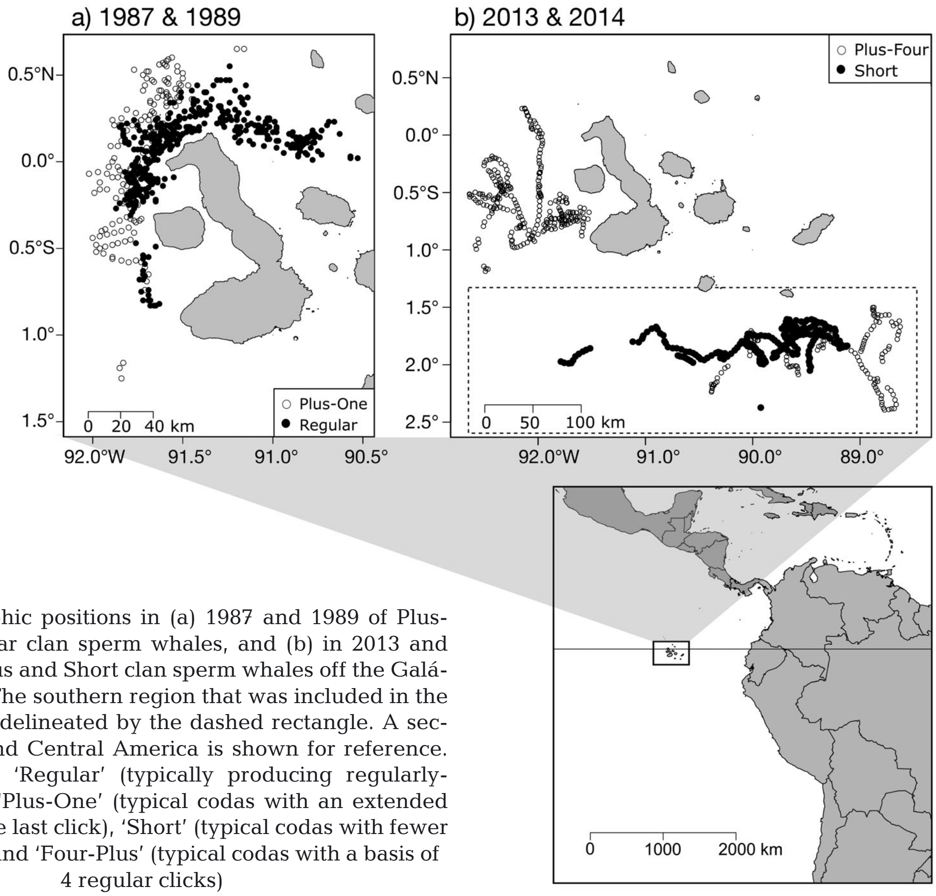

Fig. 1. Geographic positions in (a) 1987 and 1989 of Plus-One and Regular clan sperm whales, and (b) in 2013 and 2014 of Four-Plus and Short clan sperm whales off the Galápagos Islands. The southern region that was included in the 2010s period is delineated by the dashed rectangle. A section of South and Central America is shown for reference. Clan types are 'Regular' (typically producing regularly-spaced clicks), 'Plus-One' (typical codas with an extended pause before the last click), 'Short' (typical codas with fewer than 5 clicks), and 'Four-Plus' (typical codas with a basis of 4 regular clicks)

To build confusion matrices, we estimated the predicted probability that locations during encounters indicated a given clan. We transformed predicted probability values into a binary assignment using a cut-off that maximized the distance between the receiver operating characteristic (ROC) curve and a 1:1 line using the ROCR package in R (Fielding & Bell 1997, Sing et al. 2005). Second, we used leave-one-out (LOO) cross validation to quantify how accurately a model predicted clan identity for an encounter when that encounter was iteratively removed from the data used to fit the model. In each encounter, we calculated the percentage of geographic positions for which clan identity was correctly assigned (Hastie et al. 2009). Finally, we used external cross-validation, i.e. assessed how accurately models predicted clan identity in data that were not used in the model fitting and selection process. We calculated the accuracy in predicting clan identity for whales found in 1985 for the 1980s models, and for whales found in the western region during 2013 and 2014 for the 2010s models. For each study period, we compared these 3 aspects of performance of the final models to those of corresponding null models.

3. RESULTS

3.1. 1980s period

We analysed 596 geographic positions collected between 1987 and 1989. Of these, 168 positions were collected while following the Plus-One clan whales and 479 while following Regular clan whales. Most encounters occurred in the west and northwest of the archipelago (Fig. 1a), and lasted between 1 h and 6 d, averaging 1.6 d (SD = 1.4 d). We fitted 2 alternative initial models (Table S4 in Supplement 6). Our final model included latitude and longitude as cubic splines and slope and weekly sdSST as linear terms (GOF = 85.2%) (Table S5 in Supplement 6).

Most of the variation among the clans was explained by geographic variables. Whales of the Plus-One clan were more likely to be found north of 0.25° N, although uncertainty in predicting clan identity in that region was high (Fig. 2a). This is consistent with the observed latitudinal distributions of the Plus-One and Regular clans north of the Equator, but not with their distributions in the southern limits of the study region where only Plus-One clan whales were

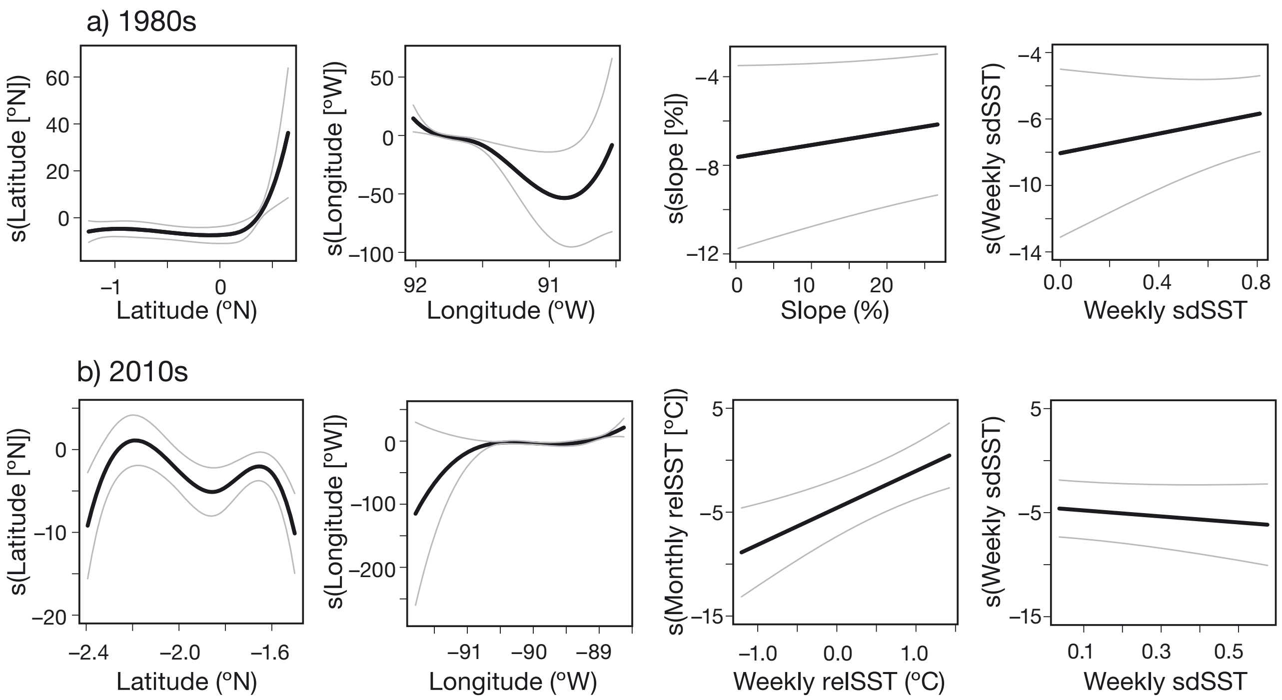

Fig. 2. Partial plots of $\log_e$(odds) of female and juvenile sperm whales found off the Galápagos Islands belonging to (a) the Plus-One clan in the 1980s study period and (b) the Four-Plus clan in the 2010s study period. Clan types are defined in Fig. 1. In the 1980s, clan identity = Plus-One is modelled as a function of latitude, longitude, slope incline, and weekly standard deviation of SST (sdSST). In the 2010s, clan identity = Four-Plus is modelled as a function of latitude, longitude, weekly relative mean SST (relSST), and weekly sdSST. Grey lines represent 95% confidence intervals

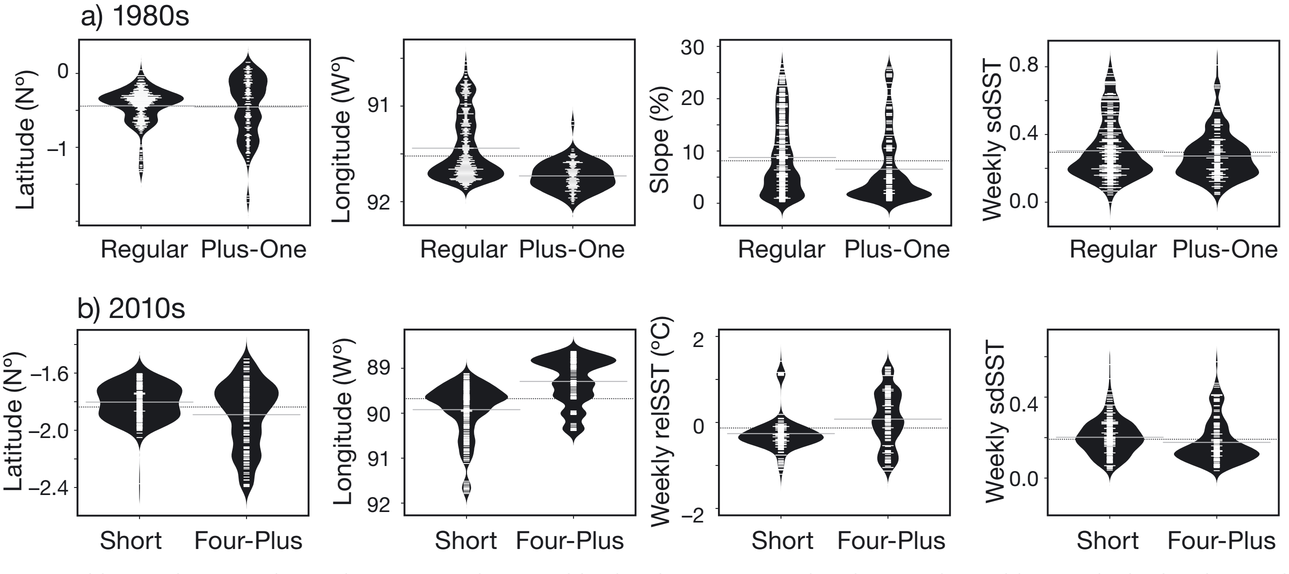

Fig. 3. Observed geographic and oceanographic variables by clan. (a) 1980s distribution of variables in which Plus-One and Regular clan whales were found off the Galápagos Islands: latitude, longitude, slope incline, and weekly standard deviation of sea surface temperature (sdSST). (b) 2010s distribution of variables in which Four-Plus and Short clan sperm whales were found: latitude, longitude, weekly relative mean SST (relSST), and weekly sdSST. Clan types are defined in Fig. 1

found (Fig. 3a). Plus-One whales were also found predominantly in more western waters, but uncertainty in predicting clan identity increased east of the archipelago (91° W; Fig. 2a). This was consistent with the observed distribution of Plus-One whales throughout study years, which was restricted to areas west of 91.5° W, and with the distribution of Regular clan whales, which occurred throughout the longitudinal range of sperm whale distribution (Fig. 3a). High uncertainty in predicting clan identity in the east likely

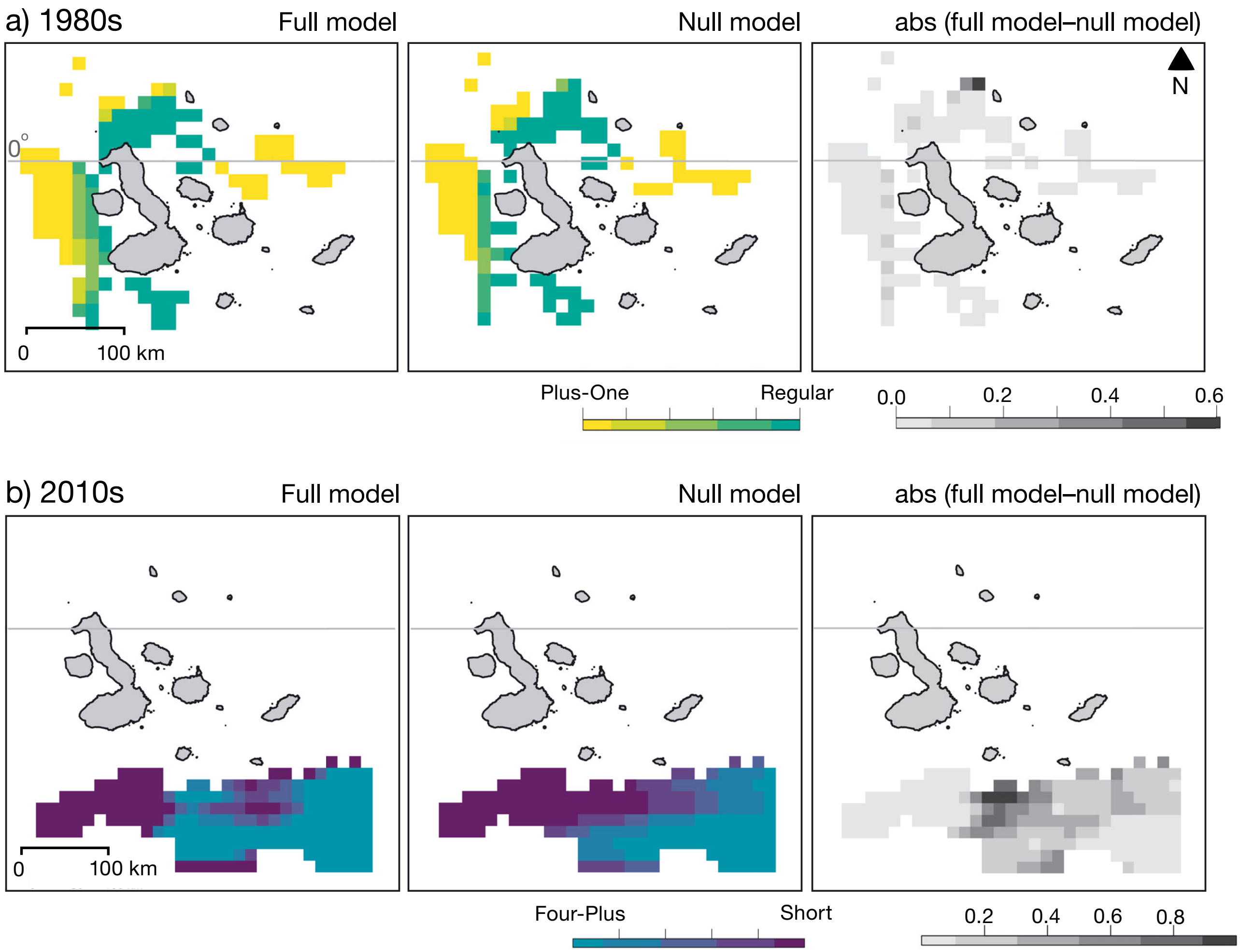

Fig. 4. Predicted probability of sperm whales belonging to different clans off the Galápagos Islands mapped at 0.12° resolution. (a) Sperm whales of the Plus-One and Regular clans in 1987 and 1989 as a function of the full model, the null model (latitude and longitude only), and the absolute difference between the full and null models. (b) Sperm whales of the Short and Four-Plus clans in 2013 and 2014 as a function of the full model, the null model (latitude and longitude only), and the absolute difference between the full and null models. Clan types are defined in Fig. 1

resulted from the small number of encounters that occurred in that area (Fig. 3a). Although our final model included slope and weekly sdSST (Figs. 2a), response curves did not reflect the observed slope, and sdSST at which the clans were found (Fig. 3a).

The predominant effects of geographic variables in differentiating clan identity were also apparent from the similarity between predictive maps generated using the final model and the null model (Fig. 4a). These 2 models predicted identical clan distributions in areas both close to and far from the Galápagos Islands, where there was little spatial overlap among the Plus-One and Regular clans, but more dissimilar distributions in regions of higher spatial overlap between the clans (Fig. 4a).

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

3.2. 2010s period

Between 2013 and 2014, we analysed 370 geographic positions to the south of the Galápagos Islands (Fig. 1b). Of these, 226 positions were collected while following the Short clan whales and 144 while following Four-Plus clan whales. Encounters lasted between 1 h and 8 d, and averaged 1.3 d (SD = 2.3 d). We fitted 6 initial candidate models (Table S6 in Supplement 6). The best final model included latitude and longitude as cubic splines, and weekly relSST and sdSST (Table S7 in Supplement 6; GOF = 87%).

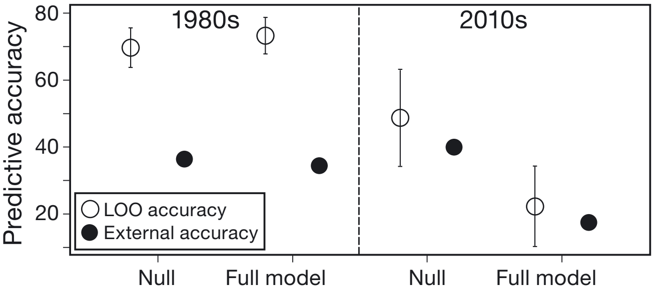

Fig. 5. Predictive accuracy (%) of null models (fit with latitude and longitude only) and full models of clan identity of sperm whales off the Galápagos Islands in the 1980s (1987 and 1989) and 2010s (2013 and 2014). Predictive accuracy was measured through leave-one-out (LOO) and external cross-validation.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

The variation in clan distribution during this period was explained by geographic and oceanographic variables. We found that Four-Plus whales were most likely to occur at around 2.2° and 1.8° S, and least likely to occur over latitudinal ranges between these values (Fig. 2b). Four-Plus whales were also more likely to occur east of 90.5° W, but uncertainty in predicting clan identity was high further west, where there was only 1 encounter (with Short clan whales; Fig. 2b). This predicted geographic distribution reproduced the observed distribution of clans during the 2010s study period (Fig. 3b). Four-Plus whales were also more likely to occur in areas of higher weekly relSST (Fig. 2b) and lower weekly sdSST (Fig. 2b). The modelled relationships between weekly relSST and sdSST and clan identity were consistent with the oceanographic conditions measured during the 2010s study period (Fig. 3b). However, we note that the relSST mean is skewed towards lower temperatures by an encounter with Short clan whales that consistently covered colder waters.

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

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

4. DISCUSSION

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

4.1. Spatial partitioning

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

Previous analysis has shown that, over days up to a few weeks, areas on the scale at which we can survey from a small vessel are predominantly occupied by groups of whales of a single clan (Whitehead & Rendell 2004). Social units may group to forage together. Individuals may benefit from eavesdropping on group members' echolocation clicks and locate prey more easily, or use other social information on prey location (Whitehead 1989, Whitehead et al. 1991). At daily to weekly scales, we hypothesise that social units could benefit from remaining in an area where other clan members are found and/or avoiding areas dominated by social units of other clans. In this sense, the distribution of sperm whales could be affected by the distributions of fellow clan members as well as by members of other clans. The reactions of sperm whales to encounters with other clans have not been documented, but active avoidance of members of different cultural entities has been proposed for transient and resident killer whales (Bigg 1979, Baird & Dill 1995). We note, however, that because these killer whale ecotypes have very different diets, social avoidance could be entangled with different spatial use driven by prey distribution, whereas diet differences are likely much subtler among sperm whale clans (Marcoux et al. 2007b), making social avoidance more evident.

We found that the spatial partitioning among sperm whale clans over few days and weeks was consistent throughout the months over at least 2 yr. This was most remarkable in the 1980s, during which the overall distribution of the clans was maintained despite variation in environmental conditions and sperm whale feeding success between 1987 — a strong El Niño year — and 1989 — a normal year (Whitehead & Rendell 2004). During the 1987 El Niño, temperatures were 4°C higher than in 1989 (Whitehead & Rendell 2004). Increased temperatures during El Niño events are associated with decreased marine production, which affects the fitness of species across taxa (Trillmich & Dellinger 1991, Schaeffer et al. 2008, Wolff et al. 2012). Feeding rates of both Regular and Plus-One sperm whales were significantly lower in 1987 than in 1989 (Whitehead & Rendell 2004). While there is no direct information on sperm whale prey abundance off the Galápagos Islands, decline in the biomass of the squid *Dosidicus gigas*, an important prey of sperm whales in the region (Clarke et al. 1988, Clarke & Paliza 2001), has been documented across the eastern Pacific during strong El Niño years (Taipe et al. 2001, Markaida 2006). The distribution of clans remained relatively constant across 2 highly different years, suggesting that site fidelity over the annual temporal scale may be maintained if social units rely on the presence of other clan members as a cue for habitat selection. Thus, while sperm whale clans are often described as sympatric at a regional scale — for example, around the Galápagos Archipelago, off the Coast of Chile, and in the Caribbean (Rendell & Whitehead 2003, Gero et al. 2016) — spatial partitioning was apparent at a finer spatial scale (less than 10 km).

Studies that span greater temporal and spatial scales indicate that clan-specific habitat use patterns become diluted. Our study focussed on a window of up to 3 yr around the Galápagos and was restricted to the months between January and June, which are mostly representative of the warm season. This represents a snapshot of a female sperm whale's lifespan of 60–70 yr (Rice 1989) and covers only a portion of the home range of such nomadic animals, i.e. at least 2000 km across the Eastern Pacific (Whitehead et al. 2008, Mizroch & Rice 2013, Cantor et al. 2016). Throughout the decades, the clan composition in the Galápagos Islands shifted abruptly from being dominated by the Regular and Plus-One clans in the 1980s, to the Regular clan in the 1990s, and to the Short and Four-Plus clans in the 2010s (Cantor et al. 2016). This shift may have resulted from movements triggered by environmental changes and fluctuation in prey availability over large scales (Cantor et al. 2016, 2017). Additionally, patterns of habitat use for the same clans in other areas were less discrete (Whitehead & Rendell 2004). Off the Chilean coast in the year 2000, Regular, Short, and Plus-One clan ranges overlapped more than off the Galápagos (Whitehead & Rendell 2004). Movement patterns of Regular clan whales off Chile were also significantly more convoluted than those of Regular clan whales off the Galápagos (Whitehead & Rendell 2004).

4.2. Oceanographic variation

Whether oceanographic conditions drive variation in clan space use remains uncertain. During the 1980s, oceanographic variables did not contribute to discriminating the space use of Plus-One and Regular clans. However, 3 lines of evidence suggest that oceanic conditions were different in the areas occupied by the Plus-One and Regular clans. First, the relative species composition of sperm whale diet varied regionally, as described by the analysis of faecal samples off the Galápagos Islands (Smith & Whitehead 2000). Second, Regular clan whales in this period had a higher carbon-13 (^{13}C) isotope signature compared to Plus-One clan whales (Marcoux et al. 2007b). Higher ^{13}C signatures are characteristic of less turbulent habitats, and have been suggested to reflect the difference in oceanic flow conditions between the more inshore habitat of the Regular clan and the oceanic habitat of Plus-One clan whales (France 1995, Marcoux et al. 2007a). Third, Regular and Plus-One clan whales had significantly different movement patterns and foraging success rates during this period (Whitehead & Rendell 2004). Thus, different conditions between the areas in which the clans were found could have existed but may have not been captured by the oceanographic variables we included in the present analysis. However, it remains uncertain whether observed behavioural differences in Regular and Plus-One clans were a consequence of different habitat conditions or if these behaviours caused different habitat selection patterns among the clans (Whitehead & Rendell 2004).

In the 2010s, Four-Plus clan whales were found in warmer waters and areas of higher variation in SST than Short clan whales. These differences may have arisen if these clans were directly tracking different environmental cues to find their prey or if the prey they preferred was found in association with different environmental conditions. Alternatively, these differences might also be a by-product of the spatial segregation described above. In addition, these patterns were described based on a limited number of unevenly represented encounters, and models that captured these patterns performed poorly through cross-validation (although they fit well to the data). Thus, our sample may not be sufficient to accurately represent the habitat of the Short and Four-Plus clans during this period.

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

5. CONCLUSIONS

Our study reveals fine-scale spatial partitioning among clans around the Galápagos Islands that suggests another layer of complexity in the cultural lives of sperm whales. We show that clans differ in fine-scale space use, in addition to vocal repertoire (Rendell & Whitehead 2003), movement patterns (Whitehead & Rendell 2004), fitness (Marcoux et al. 2007a), diet (Marcoux et al. 2007b), and social behaviour (Cantor & Whitehead 2015). Taken together, these findings suggest that the niche of sperm whale clans is constructed on the basis of both social and environmental information, both of which interact over different spatial and temporal scales (see also Boyd & Richerson 1988, Whitehead 2007, van der Post & Hogeweg 2009). The potential ability of sperm whales to balance socially acquired traditions with environmental cues likely plays a part in their ecological success in such a highly dynamic, mesopelagic environment (see also Laland et al. 2000, Whitehead 2007).

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

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