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Historical and contemporary habitat use of sperm whales around the Galápagos Archipelago: Implications for conservation

Ana Eguiguren[1] | Enrico Pirotta[2,3] | Kristina Boerder[1] | Maurício Cantor[4,5,6,7,8] | Godfrey Merlen[9] | Hal Whitehead[1]

[1]Department of Biology, Dalhousie University, Halifax, NS, Canada

[2]Department of Mathematics and Statistics, Washington State University, Vancouver, WA

[3]School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

[4]Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Constance, Germany

[5]Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil

[6]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[7]Centro de Estudos do Mar, Universidade Federal do Paraná, Pondal do Paraná, Brazil

[8]Centre for the Advanced Study of Collective Behavoiur, University of Konstanz, Constance, Germany

[9]Sea Shepherd, Puerto Ayora, Santa Cruz Island, Galápagos, Ecuador

Correspondence
A. Eguiguren, Department of Biology, Dalhousie University, Halifax, NS B3h 4R2, Canada.
Email: anaeguibur@gmail.com

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Abstract

1. Sperm whales have occupied the waters off the Galápagos Islands, Ecuador, for at least the past 200 years. During the 19th century, they were the target of intensive whaling that severely depleted the population. In recent times, after commercial whaling ended, sperm whales in the region remain vulnerable to multiple threats, especially potential entanglement in fishing gear, which may hinder their ability to recover from the whaling era.
2. As a highly mobile, long-lived species, long-term analysis of the habitat use of sperm whales is necessary to establish effective conservation and management strategies. Here, contemporary (1985–2014) and historical (1830–1850) sperm whale habitat use off the Galápagos Islands was analysed and contrasted to the extent of the Galápagos Marine Reserve (GMR). Contemporary habitat use and its variability over time were modelled as a function of geographic, oceanographic, and topographic variables using generalized additive models.
3. The fine-scale habitat (<50 km) used by sperm whales was associated with topographic (i.e. depth and slope) and oceanographic characteristics (i.e. relative sea surface temperature and standard deviation of sea surface temperature), but these preferences varied over time.
4. While historical and contemporary data indicate that sperm whale habitat primarily occurred within the boundaries of the GMR, in recent years, whales were found up to 30.1% of the time outside the GMR, potentially overlapping with commercial fisheries operating in the area.

5. The dynamic nature of the relationship of this nomadic species with its habitat highlights the need of large-scale conservation efforts across the Eastern Tropical Pacific region, including the wide-scale enforcement of regulations requiring the use of Automatic Identification System in fishing vessels, the promotion of on-board fisheries observer programmes, the development of adaptive management strategies, and international collaboration to identify and mitigate threats.

KEYWORDS
conservation, fisheries, habitat modelling, marine reserve, sperm whale

1 | INTRODUCTION

Habitat models elucidate how species interact with the environment, providing key knowledge on their use of space over time to support and inform conservation efforts. For instance, habitat models can help identify critical areas for a given population, quantify exposure to human activities, and characterize temporal changes in distribution – information that can guide the appropriate design of spatially oriented protection measures (Austin, 2007; Cañadas et al., 2005; Hooker & Gerber, 2004; Scales et al., 2017; Torres et al., 2013). Habitat models are rooted in niche theory and assume implicitly or explicitly that the occurrence of a species depends on local physical constraints, resource availability, predation, and competition (Aristotle, 344AD; Grinnell, 1917; Hutchinson, 1957). However, in highly mobile species, observed distribution patterns do not always reflect resource availability (Fretwell & Lucas, 1969; Sutherland, 1983), due to imperfect individual information on the quality of resource patches and the energetic costs of moving from one patch to another (Kennedy & Gray, 1993; Bernstein, Auger & Poggiale, 1999).

Sperm whales (*Physeter macrocephalus*) are one of the most widely distributed marine species. While males occupy all oceans from the tropics to the polar ice edges (Whitehead, 2003; Mizroch & Rice, 2013), females and juveniles remain in tropical and subtropical waters (Rice, 1989) where they live in long-term social units (Christal, Whitehead & Letteval, 1998). Female sperm whales are highly nomadic and can range over more than 1,000 km a year, occasionally even exceeding 3,000 km (Whitehead et al., 2008). Their movements are responses to fluctuations in the abundance of their prey (Whitehead, 1996; Rendell, Whitehead & Escribano, 2004; Whitehead & Rendell, 2004) – primarily mesopelagic and bathypelagic cephalopods (such as *Dosidicus gigas*, *Histiotheutis* spp., *Ancistrocheirus lesueurii*) that have highly patchy distributions (Clarke, 1996; Smith & Whitehead, 2000; Jaquet & Gendron, 2002; Markaida, 2006). The biomass and distribution of these cephalopods is linked to large-scale oceanic processes, such as the El Niño Southern Oscillation and climate change, and the intensity of upwelling processes that influence productivity and hatching conditions (Taipe et al., 2001; Waluda, Yamashiro & Rodhouse, 2006; Zeidberg & Robison, 2007).

Since direct observations of sperm whale prey are rare (Davis et al., 2007 but see Benoit-Bird, Moline & Southall, 2017), their habitat has previously been described through environmental proxies associated with prey-aggregating processes, such as upwelling, fronts, and mesoscale eddies (Jaquet & Whitehead, 1996; Praca et al., 2009; Pirotta et al., 2011; Wong & Whitehead, 2014; Pirotta et al., 2020). The degree to which sperm whale distribution correlates with these variables depends on the spatial scale. Over large spatial scales (>600 km) sperm whales tend to be associated with highly productive waters along shelf breaks (Jaquet & Whitehead, 1996), but this association is less clear at finer scales (∼5–100 km) (Cañadas, Sagarminaga & García-Tiscar, 2002; Praca & Gannier, 2007; Pirotta et al., 2011).

Consuming a biomass comparable to that captured by contemporary human fishing fleets (Whitehead, 2003), sperm whales play a significant ecological role in mesopelagic food webs, in nutrient cycling and as carbon sinks (Lavery et al., 2010; Roman & McCarthy, 2010; FAO, 2020). However, for the past three centuries, interactions with humans have threatened their survival. Sperm whales were hunted intensively during the early 19th century in the Eastern Tropical Pacific (ETP) (Starbuck, 1878; Hope & Whitehead, 1991) and in Peruvian waters until 1981 (Ramírez, 1989). Currently, sperm whales are globally threatened by the cumulative effects of anthropic activities, but most evidently by fisheries. Off the coasts of Ecuador and Chile (ca. 1,000 km and 2,900 km away from the Galápagos, respectively), sperm whale mortality is most often associated with entanglements in gillnets, and long-lines (Félix et al., 1997; Hucke-Gaete, Moreno & Arata, 2004; Félix, Samaniego & Haase, 2007; Galletti-Vernazzany & Cabrera, 2007). Gillnets and industrial fisheries are prohibited within the Galápagos Marine Reserve (GMR), which extends ca. 74 km off the Archipelago (Comisión Técnica Pesquera de la Junta de Manejo Participativo, 2009; Ley Orgánica del Régimen Especial de la Provincia de Galápagos, 2015). Additionally, the waters 320 km off the Archipelago have been a Whale Sanctuary since 1991, and the International Maritime Organization declared waters within the GMR as a Particularly Sensitive Sea Area and waters surrounding the GMR as an Area to be Avoided by all vessels over 500 tons (Resolution MEPC. 135(53), 2005). Given the, at least inferred, reduced risk of entanglement in fishing gear within the GMR, the reserve potentially provides a refuge for sperm whales within the ETP.

Nevertheless, industrial fisheries often operate along the GMR reserve boundaries (Boerder, Bryndum-Buchholz & Worm, 2017) and, on occasions, violate its limits (Camhi, 1995; Carr et al., 2013; Schiller et al., 2014; Alava & Paladines, 2017). Moreover, in the past decades, an artisanal (i.e. carried out primarily through manually-operated fishing gear) oceanic longline fishing fleet has developed in Ecuador, which operates near GMR borders with the help of mother-ships (7.6–25.9 m) that deploy up to 12 small fiberglass fishing boats each (Martínez-Ortiz et al., 2015; Ley Orgánica para el Desarrollo de la Acuicultura y Pesca – Título Preliminar, 2020).

In this study, the degree to which sperm whale habitat is protected by the GMR is investigated by modelling the species' contemporary and historical distribution and habitat use in the Galápagos region. Contemporary distribution is analysed using data from observational surveys over the past 3 decades (1985–2014) and habitat use is modelled with respect to geographic, topographic, and oceanographic variables. These results are compared to data from whalers' logbooks of the 19th century whaling period (1830–1850) to determine whether the current areas of high sperm whale occurrence are similar to historically documented areas, and how habitat use patterns change over years, decades, and centuries.

2 | METHODS

2.1 | Modelling contemporary sperm whale habitat

2.1.1 | Data collection and processing

Sperm whales off the Galápagos Archipelago (93°W–88°W; 2°N–3°S) were surveyed between January and June of seven years (1985, 1987, 1989, 1991, 1995, 2013 and 2014) from the 10-m and 12-m research sailboats *Elendil* and *Balaena* (Table S1 in Supporting Information 1) covering water depths >1,000 m. Survey transects were not systematic but intended to maximize coverage of the study area. Whales were surveyed acoustically during day and night by monitoring a towed hydrophone every 15–60 min. The hydrophone can detect sperm whale echolocation clicks up to about 7 km away (Whitehead, 2003). During daylight hours, whales were also surveyed visually within a range of 0.2–2.0 km, depending on weather conditions.

Periods during which whales were within visual or acoustic contact are referred to as *encounters*, and periods during which no whales were found are referred to as *search periods*. Encounters started when whales were first detected and ended when visual/acoustic contact was lost for >6 h. During encounters and search periods, the geographic position of the vessel, and thus the approximate position of the whales, was estimated by linear interpolation from SATNAV fixes recorded every 3 hr before 1993, and from GPS fixes recorded every 1–5 min afterwards (Whitehead & Rendell, 2004). The encounters with lone males or small groups of males were omitted from the analyses because breeding and non-breeding males may have different habitat requirements to females and juveniles.

Because geographic positions were collected at uneven intervals across decades, they were linearly interpolated to be available approximately every hour within search periods and encounters in the 1980s and 1990s, and subsampled so that they were available every hour in the 2010s. Only data points collected where the number of geographic positions collected in a 0.10° was at least equal to the lower 30th percentile for that decade (for further details, see Supplement 2 in Supporting Information).

Ethical approval was obtained from the Committee on Laboratory Animals of Dalhousie University to study sperm whales in the field. Research permits to survey waters off the Galápagos Islands were granted by Parque Nacional Galápagos (PC-10-13; PC-12-14), Ministerio de Defensa Nacional (005-2013; 002-14), and Ministerio de Ambiente del Ecuador (IC-FAU-DNB/MA002-12; 009-13).

2.1.2 | Modelling approach

Sperm whale presence at each location was modelled as a function of oceanographic and topographic variables using generalized additive models (GAMs), a flexible approach that allows data to drive the shape of estimated relationships (Hastie & Tibshirani, 1987; Wood, 2006; Pirotta et al., 2011). Presence of whales recorded during encounters were coded as ‘1’, and absence of whales recorded during search periods, as ‘0’. To account for spatial and temporal autocorrelation of the residuals within each encounter or search period, generalized estimating equations (GEEs) were used to fit GAMs (GEE-GAMs) (Yan & Fine, 2004; Højsgaard, Halekoh & Yan, 2006; Pirotta et al., 2011). GEE-GAMs were fitted incorporating splines through the *geepack* R package (Yan, 2002; Yan & Fine, 2004; Højsgaard, Halekoh & Yan, 2006; R Core Team, 2019). A working independence model was used to provide robust estimates of uncertainty, accounting for the observed autocorrelation within each encounter or search period (McDonald, 1993; Pan, 2001; Eguiguren et al., 2019).

Separate models were fitted to the data collected in the 1980s, 1990s, and 2010s to explore decadal variation in habitat use patterns. Interactions between environmental variables and year were also included to explore annual variations. Additionally, a full model including all study years was fitted to gain an overview of sperm whale habitat over the three decades.

2.1.3 | Variables

Four topographic and oceanographic habitat variables that are associated with the distribution of sperm whale prey were included (Jaquet, 1996; Praca et al., 2009): depth, seabed slope, and relative mean and standard deviation of sea surface temperature (relSST and sdSST, respectively; Table 1). Additionally, geographical variables (latitude and longitude) were included to account for unexplained spatial variation. SST and sdSST were obtained for each geographic

TABLE 1 Description of environmental variables used to model sperm whale presence

Variable	Unit	Description	Source	Spatial scale	Temporal scale
Depth	m	Ocean depth	General Bathymetric Chart of the Oceans http://www.gebco.net/data_and_products/gridded_bathymetry_data/	0.88 km	
Slope	%	Seabed slope	Calculated from depth data in ArcGIS	0.88 km	
SST	°C	Sea surface temperature	- Prior to 2010s: Pathfinder 5.0 & 5.1, collected by the Advanced Very High-Resolution Radiometer - 2010s onward: Aqua-MODIS satellite images distribute d by NOAA CoastWatch Program and NASA's Goddard Space Flight Center - Accessed in R through rerddapXtracto (Mendelssohn, 2019)	4 km	weekly
sdSST		Standard deviation of SST with respect to neighbouring cells	- Prior to 2010s: Pathfinder 5.0 & 5.1, collected by the Advanced Very High-Resolution Radiometer - 2010s onward: Aqua-MODIS satellite images distributed by NOAA CoastWatch Program and NASA's Goddard Space Flight Center - Accessed in R through rerddapXtracto (Mendelssohn, 2019) - Derived from SST over a 4 × 4 cell matrix (corresponding to a 0.10° scale) using rerddapXtracto. Due to missing values, may be calculated over 6–16 raster cells.	1.6 km	weekly

position using the rerddapXtracto R package (Mendelssohn, 2019). RelSST was used instead of actual SST to account for annual variations in temperature and was calculated as the difference in SST in a given geographic position and the mean SST of the whole Galápagos region for the corresponding month (Pirotta et al., 2011). Thus, relSST values were intended to indicate the cold upwelling that drives most of the productivity off the Galápagos Islands. SdSST is the standard deviation of SST calculated within a 4 × 4 matrix (ca. $\sim$16 km^2), and is intended to indicate the presence of oceanic fronts, near which pelagic prey tend to aggregate (Olson et al., 1994; Zhou et al., 2020). Geographic positions that occurred <5 km from shore were excluded due to the inaccuracy of SST reported in remotely sensed datasets (NOAA, 2009).

To avoid correlation between explanatory variables in the models, alternative initial models were fitted, in which correlated ($|r| > 0.4$) variables were excluded. This threshold was chosen after visual inspection of correlation plots showed that, in some cases, using a correlation threshold of 0.5 did not capture non-linear relationships between variables (Figures S5–S8, Supporting Information 3). Generalized variance inflation factors (GVIFs) were calculated for all initial models to ensure that there was no multicollinearity (GVIF < 3) among continuous terms and year (Pirotta et al., 2013). Explanatory variables were standardized by subtracting the mean and dividing by the standard deviation to facilitate model convergence.

2.1.4 | Model selection

Model selection was carried out using the quasi-likelihood criterion (QIC) calculated using the MuMIn R package (QIC; Pan, 2001; Bartoń, 2019). Initial candidate models included uncorrelated geographic, topographic, and oceanographic variables, year as a categorical factor, and interactions between topographic and oceanographic variables and year. Geographic, topographic, and oceanographic variables were included as either linear terms or cubic B-splines, and the best combination of independent variables was selected for each spatio-temporal resolution. This resulted in four initial candidate models for the 1980s, four for the 1990s, and eight for the 2010s (Tables S9–S11, Supplement 4 in Supporting Information). Using backwards selection, the model with the lowest QIC was selected. Preliminary analyses indicated that the QIC tended to favour complex models that, in some cases, had poorer predictive accuracy than simpler models. For this reason, model selection was repeated starting with candidate models that did not include interactions with the variable year. Ultimately, the model that had lowest QIC through either of these approaches was selected. For the full habitat model, including all study years, initial candidate models did not include interactions, which resulted in three initial models (Table S12, Supplement 4 in Supporting Information).

2.1.5 | Validation – model fit and predictive accuracy

To validate final models for each study period, goodness-of-fit (GOF) and predictive accuracy (PA) were assessed. GOF was calculated as the percentage of data points that a model correctly identified as presences and absences (Fielding & Bell, 1997). PA was computed through leave-one-out cross-validation, where we calculated the percentage of correctly assigned geographic positions from each encounter or search period when that encounter or search period was excluded from the dataset (Hastie, Tibshirani & Friedman, 2009). Predicted probabilities were transformed into binary assignments using a threshold (henceforth referred to as the presence threshold) that maximized the distance between the receiver operating characteristic curve and a 1:1 line using the R package ROCR (Sing et al., 2005). GOF and PA of the final models for each study period were compared to a null model that included only latitude, longitude, and year. Null models were intended to capture variation in habitat use that was not associated with the available oceanographic or topographic variables.

2.1.6 | Maps of predicted distribution

Maps of predicted sperm whale distribution were produced based on final decadal and overall models at 0.12° resolution (as in Pirotta et al., 2011). For this, a grid of equally spaced geographic positions was generated, and oceanographic and topographic data were extracted for each position. For oceanographic variables (sdSST and relSST), which change over time, an annual average was used. Next, the probability of sperm whale presence at each position was predicted based on final models and rasterized with the R package 'raster' (Hijmans, 2019). Probability of sperm whale presence was predicted only for cells within 20 km of monitored areas, which represents the upper limit of the range over which sperm whales may be heard and sighted within close proximity (Jaquet, 1996; Whitehead, 2003), and where waters were deeper than 1,000 m.

To quantify the variability in habitat-use between regions of the Galápagos Archipelago, the *prevalence* of sperm whale presence was calculated for the north, west, and south regions of the Archipelago (Figure 1). Prevalence in each region was calculated as the percentage of raster cells of that region in which sperm whales were predicted to occur (i.e. where the probability of sperm whale presence exceeded the presence threshold calculated for the relevant model, as described above). Likewise, the *habitat extent* in the entire Archipelago was measured as the percentage of raster cells in which sperm whales were likely to occur.

To assess the relative level of protection that the GMR may provide to sperm whales, the proportion of time that the research vessel (i.e. in contemporary data) spent following whales outside the GMR jurisdiction was calculated. Additionally, maps of habitat overlap were produced, which showed the number of contemporarily surveyed years over which the predicted probability of sperm whale presence fell above the presence threshold (modified from Derville et al., 2019).

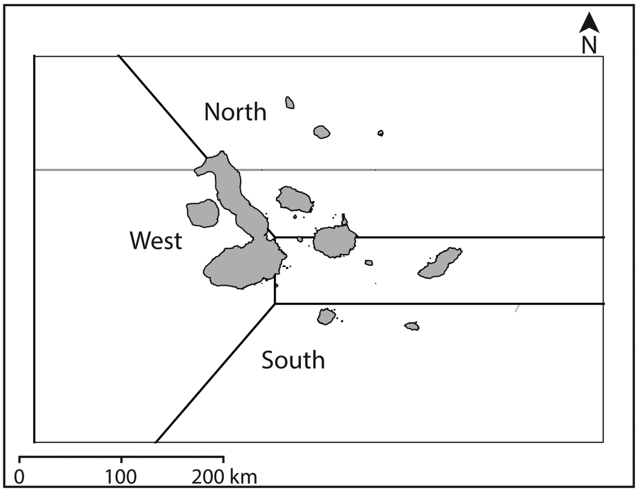

FIGURE 1 North, west, and south oceanic regions off the Galápagos Islands

2.2 | Comparing contemporary habitat to historical distribution

Sperm whale distribution data between 1830 and 1850 were obtained from microfilm copies of the logbooks of whaling vessels that hunted within the Galápagos region (93°W–88°W; 2°N–3°S). While whaling operations often targeted males for their higher oil yield, whalers captured primarily adult females in the 19th century around the Galápagos, as these were predominant in the region (Hope & Whitehead, 1991). These logbooks represent 80% of those available for the region and record activity for 7% of the whalers active within the Galápagos (Hope & Whitehead, 1991). Sighting locations were obtained from logbooks as latitude and longitude annotations, from directional distances to landmarks around the Archipelago, or from interpolation when positions were available the day before and after reported sightings (Hope & Whitehead, 1991). A map of point kernel density of sightings for the entire period (1830–1850) was created using ArcGIS (ESRI, 2011). To make full and decadal sighting densities comparable, kernel densities were scaled by dividing sighting densities in each cell by the maximum sighting density of the corresponding decade. A map showing the absolute difference between scaled decadal sighting densities (i.e. the scaled sighting density in the 1830s minus the scaled sighting density in the 1840s) was produced to show decadal variability in historical habitat use.

3 | RESULTS

3.1 | Contemporary sperm whale habitat

Contemporary assessment of sperm whale habitat included data from 1985 to 2014. During this period, 342 days were spent searching and following female and juvenile sperm whales off the Galápagos Islands (Figure 2), totalling 75 encounters that lasted between 1 h and 9 d (average 39 hr). This resulted in 4,875 geographic positions, 2,680 collected during search periods (absences) and 2,195 collected during encounters (presences). Individual encounters contained 1–261 geographic positions (median 18), and search periods contained 1–218 (median 8). In the decadal habitat models (Table 2), interactions between year and oceanographic and topographic variables were retained in some but not all final models (for annual and decadal effects: Figure S13, Supplement 5 in Supporting Information). Generally, decadal models had better goodness-of-fit and predictive accuracy than the full habitat model including all data (Table 2). Moreover, the model selection procedure favoured models in which relationships with geographic, topographic, and oceanographic variables were non-linear (Table 2). While environmental variables improved model performance in the 1990s and 2010s, the final models for the 1980s and for the full dataset selected through QIC performed worse in terms of GOF and PA accuracy compared to models only including latitude and longitude (Table 2). The inclusion of interactions with year in all models resulted in wide confidence intervals complicating the interpretation of annual patterns.

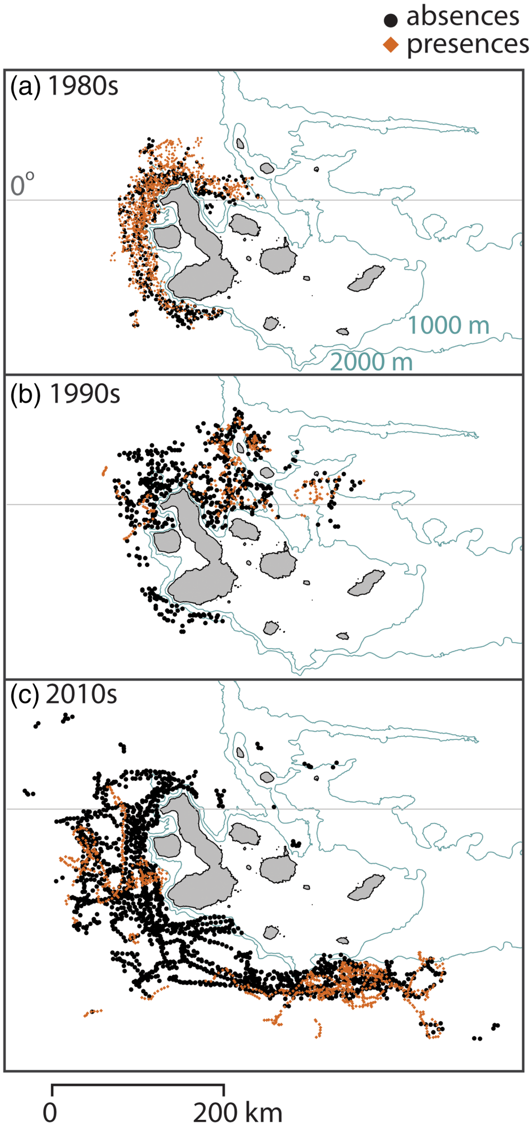

FIGURE 2 Presence and absence positions of sperm whales off the Galapagos Islands in (a) 1980s, (b) 1990s, and (c) 2010s as observed from the research vessels

Throughout the entire study period, the probability of sperm whale presence was highest in waters west of 92°W, off the steep slopes of Isabela Island, and around 89°W along the Marchena Channel that separates Pinta, Marchena, and Genovesa islands from the others (Figures 3a and 4a). Despite annual and decadal changes in habitat distribution, a high probability of sperm whale presence off the western flanks of Isabela was predicted in nearly all surveyed years (Figure 5a). The probability of sperm whale presence was highest in waters of around 3,250 m depth (Figure 3b) and increased with decreasing relative mean SST (Figure 3c). Sperm whale presence was also associated with relatively low sdSST throughout the study period (Figure 3d).

The spatial distribution of sperm whales off the Galápagos Islands varied through the decades, as indicated by the results of the decadal models. The probability of whale presence was higher in the 1980s (mean predicted probability = 0.81, *SD* = 0.11) than in following decades (1990s mean predicted probability = 0.30, *SD* = 0.15; 2010s mean predicted probability = 0.22, *SD* = 0.19; Figure 3e). In the 1980s, during which El Niño and La Niña events occurred consecutively, sperm whale habitat distribution shifted (Figure 4e–d). While high likelihood of sperm whale presence west of the Archipelago occurred in most years (Figure 5a), in 1985 and 1989 – during which colder than normal conditions were documented – whales were more likely to be found directly west of the Archipelago (Figure 4b,d; Table 3), contrasting with the northward shift during the warm El Niño event of 1987 (Figure 3c; Table 3). The extent of sperm whale habitat in 1985 and 1987 was similar but contracted within the west region in 1989 (Figure 4d, Table 3).

Compared to the 1980s, in the 1990s sperm whale habitat shifted to the northern region of the Archipelago and habitat extent was contracted (Figure 4e, Table 3). There was little overlap in the areas where whales were likely to be found in this decade compared to the rest of the study period (Figure 5b). In the 2010s, whales were more likely to be found off the south of the Archipelago (Figure 4f,g), with notably low sperm whale presence in the western flanks in 2014 (Figure 4g). Only in the 2010s, when the southern waters were sufficiently surveyed, was there a high likelihood of sperm whale occurrence in this area (Figure 5d). While habitat extent covered most of the surveyed area in 2013, it was restricted primarily in the south region in 2014 (Table 3).

3.2 | Historical sperm whale distribution

There were 357 sightings available from 19th century whaling logbooks, 97 in the 1830s and 260 in the 1840s. In the 1830s, the

TABLE 2 Final models selected for each decade using quasi-likelihood criterion (QIC; lower QIC indicates a better fit)

Decade	Model type	Selected models	ΔQIC[a]	GOF[b]	PA[c]
1980s	best QIC score	s (latitude) + s (depth) × year + s (relSST) × year + sdSST × year + year	−212.36	0.66	0.40 ± 0.05
	null	s (latitude) + longitude + year	0	0.68	0.58 ± 0.05
1990s	best QIC score	s (longitude) + slope + relSST + sdSST	−107.11	0.78	0.53 ± 0.06
	null	latitude + s (longitude) + year	0	0.73	0.47 ± 0.07
2010s	best QIC score	s (latitude) + depth × year + s (relSST) + s (sdSST) × year + year	−388.67	0.81	0.61 ± 0.06
	null	s (latitude) + longitude + year	0	0.73	0.59 ± 0.06
Full model	best QIC score	s (longitude) + s (depth) + relSST + s (sdSST) + year	179.72	0.75	0.54 ± 0.03
	null	longitude + b (latitude) + year	0	0.73	0.58 ± 0.04

Note: Null models are included for comparison, and ΔQIC is calculated with respect to the null model. Predictive ability (PA) and goodness-of-fit (GOF) are shown. Terms included as cubic splines are indicated as 's()', and interactions between terms are indicated by an ×.

[a] ΔQIC measures the difference between a model's QIC and the null model.

[b] GOF measures how well a model fits the data (see details in Supporting Information 4).

[c] PA measured through leave-one-out cross-validation ± standard error (see details in Supporting Information 4).

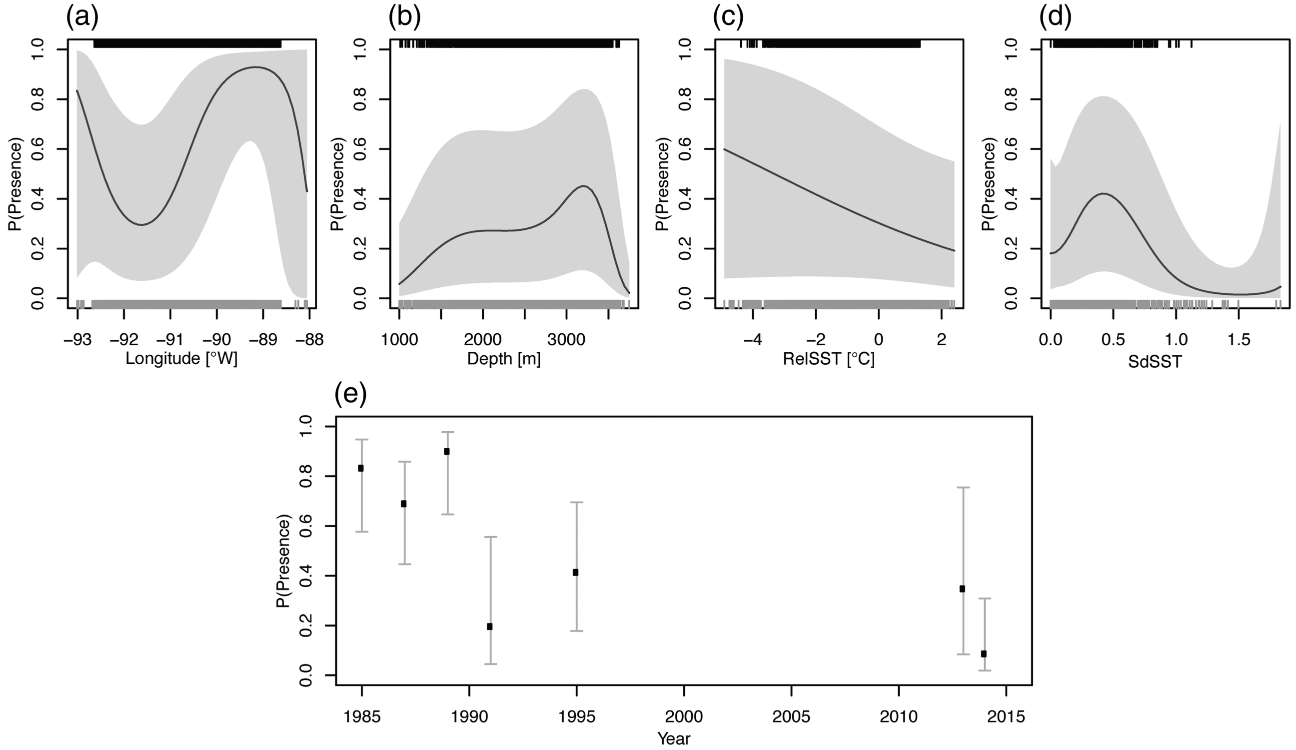

FIGURE 3 Modelled effect of geographic, topographic, and oceanographic variables on sperm whale presence for the 1985–2010s study period. Sperm whale presence was modelled as a function of (a) longitude, (b) depth, (c) relative sea surface temperature (relSST), (d) standard deviation of SST (sdSST), and (e) year. Rug plots of observed values are shown in black for presence positions, and in grey for absence positions

mean sighting density was 0.005 (*SD* = 0.015) and in the 1840s, mean sighting density was 0.015, (*SD* = 0.028). It should be noted that different sighting numbers per decade primarily reflect differences in data availability, as sighting rates significantly decreased throughout this period (Hope & Whitehead, 1991). The contemporary sperm whale distribution remarkably resembled historical areas of high sighting density derived from whaling logbooks. The areas with highest sighting densities occurred west of Isabela Island and to the south of the 1,000-m depth contour around the Archipelago (Figure 6). During 1830–1850, the relative density of whales close to the Archipelago varied slightly between decades but was more stable in offshore waters (Figure 7).

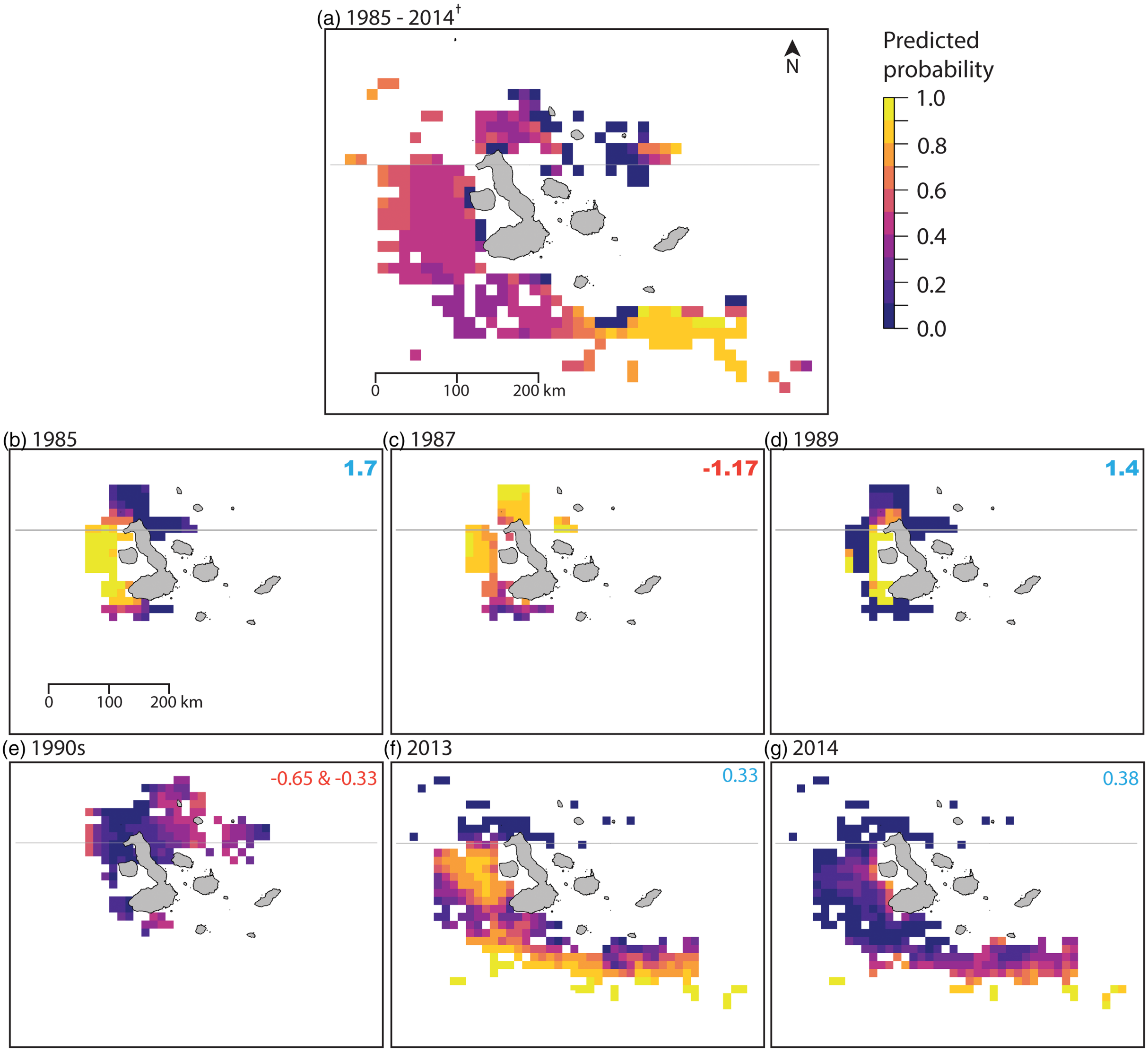

FIGURE 4 Predicted annual probability (0–1) of sperm whale presence as a function of geographic, topographic, and oceanographic variables for all decades (a) 1980s (b-d), 1990s (e) and 2010s (f, g) from final models. Southern Oscillation Index annual averages – obtained from https://www.cpc.ncep.noaa.gov/data/indices/soi – are shown in red (El Niño) and blue (La Niña). Bold numbers indicate strong El Niño and La Niña conditions. Includes data collected in 1985, 1987, 1989, 1995, 2013, and 2014

3.3 | Sperm whale habitat use and the GMR

Although sperm whales were most often sighted within the GMR (Figures 4 and 6), they were also frequently found outside – 41.2% of recorded sightings in the 1830s and 58.1% in the 1840s occurred outside the area later covered by the GMR. In contemporary surveys, whales were observed outside of the GMR boundaries 2.5% of the time in the 1980s, 0.6% of the time in the 1990s, and 30.1% of the time in the 2010s (Figure 4). However, these values probably underestimate sperm whale occurrence outside the GMR as most of the modern survey effort occurred within the GMR: unlike the 19th century whalers, all modern survey was based on the ports in the centre of the GMR and areas outside the reserve were surveyed only in the 2010s.

4 | DISCUSSION

This study shows that the geographical distribution of sperm whale habitat off the Galápagos Islands remained broadly consistent over long temporal scales (>100 years), but with noticeable changes over finer temporal scales of years to decades. Large-scale persistence and finer-scale variation in sperm whale habitat have important implications for conservation of this highly mobile predator. Although both historical and contemporary sperm whale habitat was concentrated within the GMR boundaries, in some years whales mostly occurred outside the reserve, posing challenges for the effective management of human activities in the region.

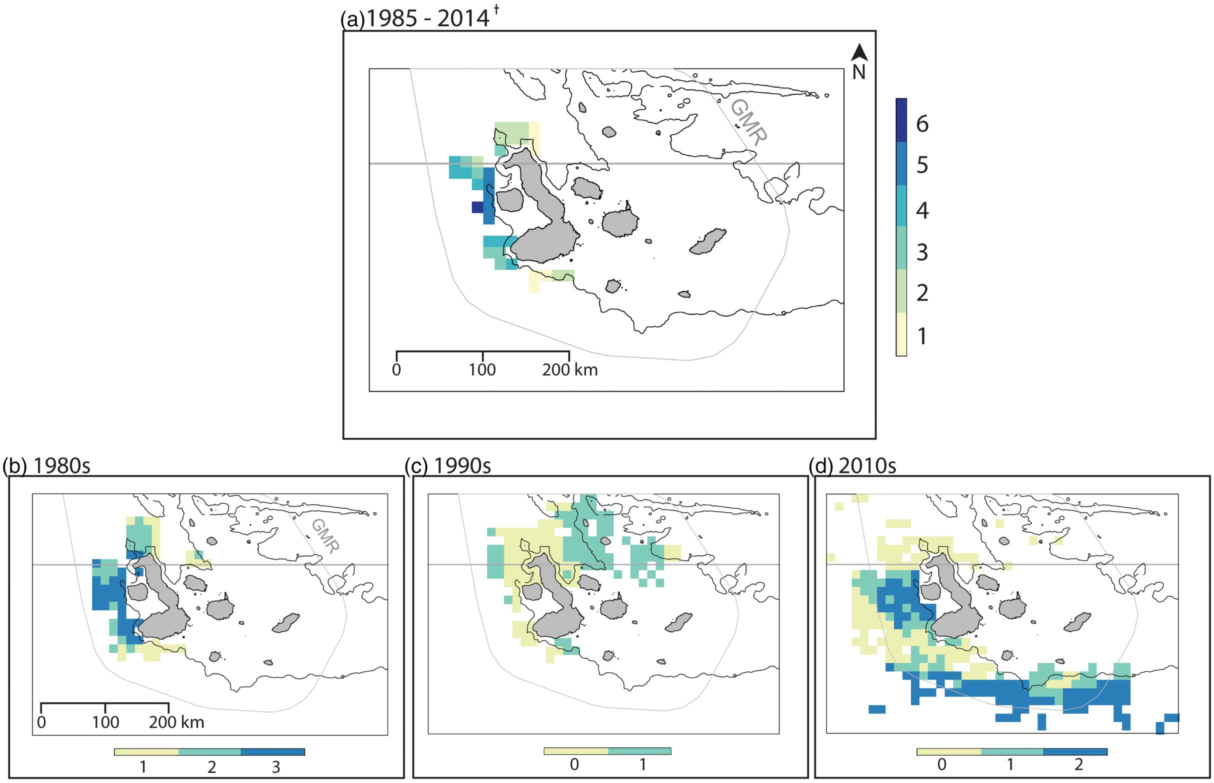

FIGURE 5 Sperm whale habitat overlap across contemporary survey years for the overall study period (a), the 1980s (b), the 1990s (c) and the 2010s (d). The colour scheme represents the number of years over which the probability of sperm whale presence fell above the presence threshold. In the 1990s, the colour scheme shows whether the probability of sperm whale presence fell above the presence cut-off value, because year was not included as a predictor variable. The 2000-m depth contour and the Galapagos Marine Reserve (GMR) are shown for reference

TABLE 3 Sperm whale regional prevalence and overall habitat extent for each year and the entire contemporary period (full)

Year	North	West	South	Overall
1985	2.08	65.00	0.00	41.09
1987	89.29	20.63	0.00	41.30
1989	2.04	38.75	0.00	24.62
1990s[t]	22.95	17.84	0.00	17.84
2013	0.00	67.53	77.24	66.67
2014	0.00	10.42	56.10	26.41
full	34.62	74.56	88.03	29.67

Note: Prevalence in the north, west, and south regions was calculated as the percentage of cells (0.12° × 0.12°) in each region where the predicted probability of sperm whale presence exceeded the presence threshold (calculated as the threshold that maximized the distance between the ROC and 1:1 line for the corresponding model). Overall habitat extent was calculated as the percentage of cells in the overall Galápagos Islands region where the predicted probability of sperm whale presence exceeded the presence threshold.

[t] As the 1990s model did not include year as a variable, regional prevalence and habitat extent are shown for the entire decade.

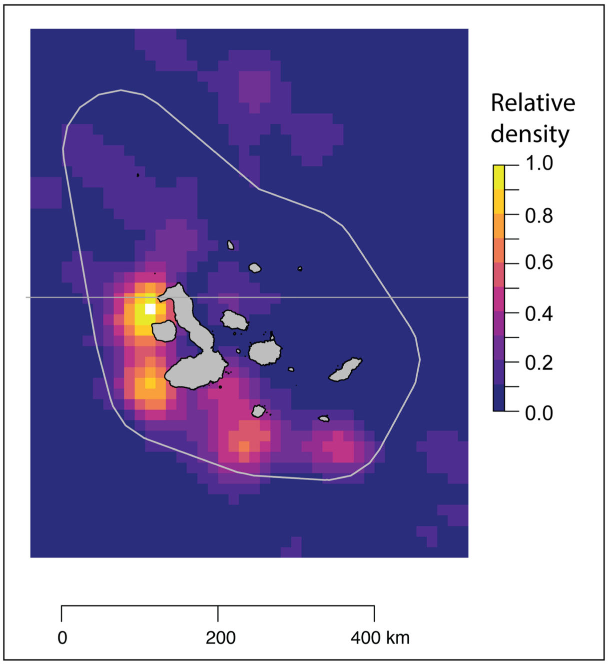

FIGURE 6 Kernel density of sperm whale sightings recorded by whaling vessels' logbooks off the Galápagos Islands between the 1830s and 1850s. An outline of the Galápagos Marine Reserve is shown in the map for the whaling era

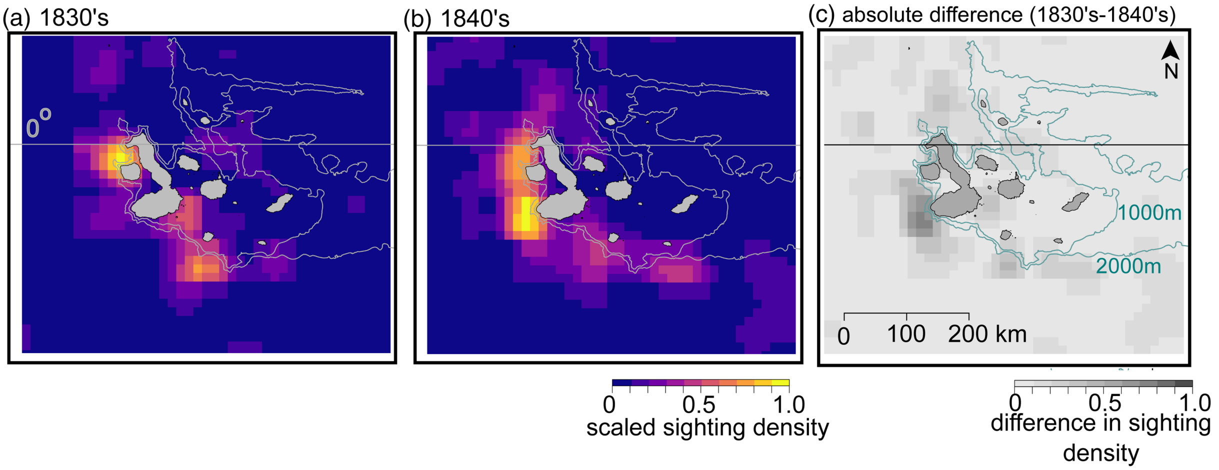

FIGURE 7 Scaled kernel density maps of sperm whale sightings recorded in whaling vessels' logbooks off the Galápagos Islands in (a) the 1830s, (b) the 1840s, and (c) absolute differences between the 2 decades. Historic data were compiled by Hope & Whitehead (1991). The equator is shown for reference

4.1 | Sperm whale habitat over centuries, decades, and years

Over centuries and across the Galápagos Archipelago, sperm whales were consistently found in deep, relatively cool waters off the western flanks of the continental shelf (Hope & Whitehead, 1991; Whitehead & Hope, 1991), where highly productive waters are sustained by topographically-induced upwelling of the Equatorial Undercurrent (Houvenaghel, 1978; Palacios et al., 2006). Sperm whales have shown an affinity for highly productive areas and steep slopes of oceanic islands at large spatiotemporal scales across the Pacific (Gaskin, 1973; Jaquet, 1996; Rendell, Whitehead & Escribano, 2004), Caribbean (Milligan, 2013) and the Mediterranean (Pirotta et al., 2020). In this study, whales were found in waters deeper than in the Gulf of California (Jaquet & Gendron, 2002), where the maximum depths are about 1,500 m, but at similar depths of over 3,000 m as observed in the Mediterranean (Pirotta et al., 2020).

Over a finer spatio-temporal scale, sperm whale distribution and habitat use around Galápagos varied across decades and years, as observed in other places such as the Mediterranean (Pirotta et al., 2020). While during the 1980s sperm whales were found throughout the study area over a wide range of oceanographic conditions, their distribution shifted northward to the shallow and steep waters of the Marchena Channel in the 1990s, and in the 2010s it shifted southward of the islands, where bottom topography is deeper and flatter. Likewise, the probability of encountering whales also varied across decades, with more likely whale sightings in the 1980s than the 1990s and 2010s (Cantor et al., 2017). Decadal shifts in habitat use were also apparent in the 1800s; while in the 1830s sperm whales occurred west and south of the Archipelago, in the 1840s sperm whale sightings were also common in the northern Marchena Channel. It is possible that some of the changes in distribution observed between the 1830s and 1840s resulted from whaling pressure, which removed an estimated 10,000 whales between 1830 and 1850 (Hope & Whitehead, 1991). However, while whaling severely depleted the local populations, habitat shifts in the 19th century were not drastically different from those observed between the 1980s and 2010s, which may suggest that whaling was not the only cause for variation in habitat use. It should be noted that the comparison of habitat among contemporary and historical distribution may be limited by the fact that the historical maps were constructed using presences only (i.e. not accounting for effort), while contemporary distribution maps were built using presence and absence data.

The observed differences at finer spatio-temporal scales probably reflect changes in sperm whale cephalopod prey (Jaquet & Whitehead, 1996; Cantor et al., 2017), whose distribution and biomass have been shown to vary dramatically in response to El Niño oscillations in the eastern Pacific and are substantially driven by productivity and water temperature, especially during early development (Taipe et al., 2001; Nevárez et al., 2002; Waluda, Yamashiro & Rodhouse, 2006). Our research suggests that sperm whales respond to El Niño-induced changes in prey abundance, as the density of whales around Galápagos was reduced during warmer years (1987, 1990s). In the 1980s, sperm whale habitat expanded north and south during the strong 1987 El Niño event, which contrasts with the contraction of sperm whale habitat off the western flanks of the Islands in the mild La Niña conditions of 1989 (Figure 4). The weakened upwelling of the Equatorial Undercurrent to the west of the Islands during La Niña events could result not only in less overall productivity, but also in a more homogeneous distribution of prey throughout the region. Similarly, in the Gulf of California, the distribution and aggregative behaviour of sperm whales was found to change in relation to shifts in catch rates of the jumbo squid, *Dosidicus gigas*, following a strong El Niño event (Jaquet & Gendron, 2002). In that case also, the distribution of sperm whales during the El Niño year was more widespread than in the following, cooler year (Jaquet & Gendron, 2002). However, across decades and over weaker El Niño Southern Oscillation conditions, these patterns are not consistent, and sperm whale habitat use may contract or expand in response to other environmental conditions. Variability in the apparent response to decreased prey availability and in topographic and oceanographic preferences could result from the ability of sperm whales to endure long periods of time (ca. 3 months) without access to food (Whitehead, 1996; Whitehead, 2003). Over short periods (ca. <3 months), sperm whales may remain in areas of poor habitat quality (Whitehead, 1996), if the cost of travelling across oceanic regions in search for prey of uncertain abundance outweighs the potential benefits. Even within regions, the abundance of sperm whales does not always correlate with density of squid aggregations (Jaquet & Gendron, 2002). For instance, off the Galápagos Islands, sperm whales were as abundant during the 1987 El Niño year as they were in 1985, although their feeding rate roughly halved in 1987 (Cantor et al., 2017). Thus, they may occupy unsuitable habitat over weeks or even months, suggesting that presence alone is not a good indicator of habitat preferences and quality (Johnson, 1980; Morrison, Marcot & Mannan, 2006).

Sperm whale habitat use in the region could also be influenced by the risk of predation by killer whales. The effect of killer whale predation on habitat use of other cetaceans has been documented in the Arctic; bowhead whales (*Balaena mysticetus*) and narwhals (*Monodon monoceros*) move inshore towards dense ice when killer whales are nearby (Breed et al., 2017; Matthews et al., 2020). Killer whale predation on sperm whales is prevalent in the Eastern Pacific and is hypothesized to shape key aspects of sperm whale social behaviour (Pitman et al., 2001; Whitehead, 2003; Whitehead et al., 2012). Off the Galápagos, killer whale sightings are most common in the Bolívar Channel, between Isabela and Fernandina but also occur in offshore waters (Merlen, 1999). Therefore, killer whales may affect habitat use of sperm whale in the region, but the nature and magnitude of this effect is unknown.

The different regional, topographic, and oceanographic habitat use patterns across decades could also reflect a cultural turnover, such that one observed in this region between the 1990s and 2010s (Cantor et al., 2016; Eguiguren et al., 2019). Female sperm whales are organized into large clans in which members share several behavioural similarities, from acoustic communication to social norms and movement patterns (Whitehead & Rendell, 2004). In the ETP, where four or five clans have been identified over the last 30 years (Rendell & Whitehead, 2003), different clans use some of the same areas at different times. The waters around the Galápagos underwent a population turnover over the past 30 years: the clans commonly seen in the 1980s were replaced by others the 2010s (Cantor et al., 2016). Moreover, when members from different clans co-occurred around the Galápagos, they tended to occupy distinct areas (Eguiguren et al., 2019). Furthermore, differences in feeding success, movement patterns, and sensitivity to El Niño events suggest that whales of different clans use different resources and/or foraging strategies (Whitehead & Rendell, 2004), which could lead to clan-specific selection of topographic and oceanographic conditions. Hence, regional changes in population composition across decades, and the behavioural shift that followed, potentially mirror the habitat use variation we detected.

4.2 | Implications for conservation

Temporal variability in marine mammal distribution is a challenge for place-based conservation efforts with fixed boundaries, such as marine reserves (Reeves, 2000; di Sciara et al., 2016; Pirotta et al., 2020). This study illustrates the value of using long-term studies to identify critical habitats (Gerber et al., 2003; Hooker & Gerber, 2004), as well as the importance of a dynamic and adaptive approach to the conservation of highly-mobile, long-lived marine mammals (Hyrenbach, Forney & Dayton, 2000; Hobday & Hartmann, 2006; Wedding et al., 2016). While regions where sperm whales were most commonly sighted 200 years ago and in modern times occurred within the boundaries of the reserve, historically and contemporarily, whales also used the waters outside of the reserve. This was particularly apparent in the distribution of sperm whales in 2013 and 2014, during which 30% of time spent following whales was outside GMR boundaries. Since survey effort outside the GMR boundaries was restricted to the 2010s, future research should focus on understanding sperm whale distribution outside the protection of the GMR, particularly in the southern flanks of the Archipelago.

The persistent presence outside the GMR boundary – where 'hotspots' of industrial tuna purse-seiners and artisanal oceanic longliners have been identified Martínez-Ortiz et al., 2015; (Boerder, Bryndum-Buchholz & Worm, 2017) – poses an unquantified risk for sperm whales. This risk could be exacerbated by the presence of illegal longline vessels dedicated to shark finning within and near the GMR borders (Carr et al., 2013; Schiller et al., 2014). While there are no reports of sperm whale mortality associated with purse-seines, there are reports of longline fatalities (Félix et al., 1997; García-Godos et al., 2013). Moreover, sperm whales have been documented to predate on fish caught by longlines in temperate waters (demersal and pelagic), which can result in death from entanglement (Hucke-Gaete, Moreno & Arata, 2004; Richard et al., 2019). This interaction has not been reported in the Eastern Pacific Ocean, but, given sperm whales' ability to learn new behaviours, its occurrence would not be unexpected.

There is currently a proposal under revision by the Ecuadorian legislative body to expand the boundaries of the GMR. In theory, this could provide greater protection for sperm whales and other vulnerable species in the region from interactions with fisheries. However, for this extension to be effective, systematic surveillance and enforcement will be crucial. While surveillance systems are rapidly improving through the use of automatic identification system, vessel monitoring system, and satellite imagery to detect illegal activities (e.g. Park et al., 2020), the capacity for enforcement in the distant waters of the GMR borders is lagging. Strengthening enforcement will require political will and funding, and may be more attainable through international cooperation among ETP nations.

Ultimately, ETP sperm whales are likely to face more urgent and intense threats outside the protected waters of the Galápagos region. Individuals from Galápagos waters have been re-sighted over the last decades in the deep waters off México, Panamá, mainland Ecuador, Perú, and Chile (Cantor et al., 2016). In continental Ecuador and Perú, all reports of sperm whale strandings associated with entanglements have been caused by artisanal gillnets (Félix et al., 1997; García-Godos et al., 2013; Castro & van Waerebeek, 2019), and there is one report of a dead sperm whale used opportunistically as an artisanal fish aggregating device (Castro et al., 2020). Gillnets are also associated with high rates of by-catch of other cetaceans throughout the western waters of South America (Mangel et al., 2010; Reeves, McLellan & Werner, 2013; Alava et al., 2019). However, most available bycatch data are obtained from coastal artisanal fisheries (through landings or fisheries observer programmes) and little is known about interactions with recently developing oceanic artisanal long-liners. Moreover, sperm whales are likely to face other threats as they travel across the ETP Ocean, including vessel traffic and contamination (Galletti-Vernazzany & Cabrera, 2007; Alava et al., 2014).

Moving forward, there is a need to determine the degree to which sperm whales may be threatened by different fisheries and other anthropogenic activities – for example by evaluating the spatial overlap between sperm whales and oceanic fisheries within the Galápagos region and throughout the Eastern Pacific. To this purpose, active monitoring of fishing activities (both industrial and artisanal) will be key. This could be achieved through widespread and compulsory use of satellite monitoring systems in all fisheries. In February 2020, the Ecuadorian government passed a new Law for the Development of Aquaculture and Fisheries, in which all Ecuadorian artisanal fishing boats are required to carry an operating vessel monitoring system throughout the entirety of their trip (Ley Orgánica para el Desarrollo de la Acuicultura y Pesca, 2020). This will contribute to a better picture of where oceanic artisanal fishing occurs near and within the GMR. Active enforcement on landing ports, mostly in continental Ecuador, will also be important to prevent vessels from ‘going dark’ when undertaking unregulated activities (Malarky & Lowell, 2018).

Furthermore, a sustained on-board fisheries observer programme has been deemed crucial for quantifying the incidence of bycatch (Mangel et al., 2010; Reeves, Mclennan & Werner, 2013; Alava et al., 2019). A fisheries observer programme exists for industrial tuna fisheries through the Inter-American Tropical Tuna Commission but has yet to be implemented in artisanal fisheries (Alava et al., 2019). While in traditional small-scale fisheries the lack of space onboard complicates the implementation of such a programme, this may be overcome in oceanic artisanal operations where the larger ‘mother-ships’ (ranging 7.6–25.9 m) (Martínez-Ortiz et al., 2015) may allow for an additional crew member. Nonetheless, budget constraints may hinder the frequent presence of on-board observers. We suggest that passive acoustic monitoring systems can be implemented at lower cost, either on larger vessels or directly on fishing gear, to collect data on sperm whales' and other marine mammals' presence, as a means to assess the extent to which they overlap with fishing activities. This technology has recently been tested to monitor interactions between longline fisheries and false killer whales in Hawai'i, but has not been implemented at a broad scale (Bayless et al., 2017).

Finally, as recently highlighted by the Concerted Action for Sperm Whales of the ETP (Convention on Migratory Species, 2020), the wide ranges of ETP sperm whales will require internationally coordinated and enforced management policies and conservation efforts. Newly generated data on the distribution of oceanic fisheries should be incorporated into existing and accessible platforms, such as Global Fishing Watch. Other technologies, such as satellite tagging and long-term passive acoustic monitoring, would help clarify the factors that drive large scale movements within the Pacific, as well as provide valuable information for basin-wide fisheries management and conservation efforts. We emphasize that, given the large spatial and temporal scale over which sperm whale movements occur (1000s km; years–decades), these efforts will need to be sustained over similar scales.

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ORCID

Ana Eguiguren https://orcid.org/0000-0001-7651-8189
Enrico Pirotta https://orcid.org/0000-0003-3541-3676
Kristina Boerder https://orcid.org/0000-0002-8304-5647
Maurício Cantor https://orcid.org/0000-0002-0019-5106

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SUPPORTING INFORMATION

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