HABITAT OF GALÁPAGOS SPERM WHALES: A CULTURAL PERSPECTIVE AND IMPLICATIONS FOR CONSERVATION

by

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DEDICATION PAGE

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ABSTRACT

Habitat models elucidate species-environment relationships and inform conservation. But the influence of environmental variables on habitat use is scale-dependent and influenced by behaviour. Sperm whales (*Physeter macrocephalus*) occupy a broad range of spatiotemporal scales and their behaviour is culturally driven. Here, I characterized sperm whale habitat off the Galápagos Islands through time, determined their vulnerability to threats within the Galápagos Marine Reserve (GMR), and investigated the role of culture in shaping habitat use. Over fine spatiotemporal scales (less than a decade, <50 km) sperm whale habitat was associated with environmental conditions, but these varied across time. Over broader scales (between centuries, >100 km) their distribution was associated with productive areas and was encompassed by the GMR, although encounters also occurred outside its boundaries. The cultural identity of sperm whales affected their habitat use. This work contributes to our understanding of processes shaping sperm whale habitat and provides insights for conservation.

LIST OF ABBREVIATIONS USED

ACF	Autocorrelation Function
AIC	Akaike’s Information Criterion
AIS	Automatic Identification System
AVHRR	Advanced Very High-Resolution Radiometer
AVISO	Archiving, Validation, and Interpretation of Satellite Oceanographic data
chla	Chlorophyll-a concentration
d	day
EKE	Eddy Kinetic Energy
GAM	Generalized Additive Models
GEE	Generalized Estimating Equation
GIS	Geographic Information System
GMR	Galápagos Marine Reserve
GOF	Goodness of Fit
GPS	Global Positioning System
hr	hour
km	Kilometres
LOO	Leave-one-out (cross-validation)
m	Metres
nm	Nautical miles
PA	Predictive Ability
PAM	Passive Acoustic Monitoring
QIC	Quasi-likelihood under the independence model criterion
relSST	Relative sea surface temperature
|r|	Correlation coefficient
ROC	Receiver Operator Curve
s	Seconds
SATNAV	Satellite Navigation
sdSST	Standard deviation of sea surface temperature
SSHA	Sea Surface Height Anomaly
SST	Sea surface temperature
yr	year

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CHAPTER 1 – Introduction

1.1 Habitat

A species' habitat is defined by the biotic and abiotic environmental characteristics that allow it to survive (Block and Brennan 1993; Hall *et al.* 1997). In this sense, a species' habitat is a component of a species niche, which can also be defined by the environmental variables that allow presence of a species, as well as the biotic relationships—predation, competition, mutualism—it experiences, and the functional role it occupies in the ecosystem (Grinell 1917; Hutchinson 1957; Block and Brennan 1993). How favourable a habitat is for the survival and reproduction of a species is referred to as its "suitability," and can be measured by the reproductive rate that species can achieve within it (Block and Brennan 1993). Thus, there is selective pressure for species to occupy suitable habitats (Morris 2003). The behaviour by which individuals choose to occupy a particular portion of habitat is defined as *habitat selection* (Johnson 1980; Morris 2003; Morrison *et al.* 2006; Beyer *et al.* 2010). But, because this is an internal behavioural process, it may be difficult to assess through observational studies (Morrison *et al.* 2006).

Alternatively, research may also be focused on *habitat use*—the proportion of time species spend in a subset of habitat—and *habitat preference*—the probability that species will occupy a subset of habitat relative to its availability—as ways of approaching species-habitat relationships (Morrison *et al.* 2006; Beyer *et al.* 2010). According to the "ideal free distribution model," it is expected that individuals of a species will be disproportionately distributed in relatively more suitable habitat as a result of individual choices (Fretwell and Lucas 1969; Sutherland 1983; Morris 2003). However, this expectation is often not met (Sutherland 1983; Whitehead and Hope 1991; Bernstein *et al.* 1999) This is the case when there are barriers to access, when there is intraspecific competitive exclusion, risk of predation, when information regarding habitat quality is imperfect, and when there are significant costs of travelling across resource patches (Whitman 1980; Abrahams 1986; Hugie and Grand 1998; Bernstein *et al.* 1999). Ultimately, these departures mean that while studying habitat use provides valuable information regarding species use of space and resources, often research results do not often not reflect true behavioural habitat selection or habitat preferences (Morrison *et al*. 2006).

Another essential consideration in the study of species-habitat relationships is scale. The degree to which environmental variables are associated with species occurrence is largely scale-dependent (Morris 1987; Levin 1992; Block and Brennan 1993; Mannocci *et al.* 2017). Specifically, different environmental variables and behavioural processes may be associated with a species distribution at geographic scales, among home ranges, and within resource patches (Johnson 1980). Additionally, while species-habitat relationships are typically studied at the population or species level, individual variation in habitat use may often exceed interspecific differences (Bolnick *et al.* 2003; Hatase *et al.* 2006; Palacios *et al.* 2013). Sources of variation in habitat use may be internal drivers such as by physiology, sex, or phenotype (Van Valen 1965; Roughgarden 1974; Svanbäck and Persson 2004). But they may also result from socially acquired differences in behaviour that may result not only in different habitat use patterns but, ultimately, in distinct niches among socially discrete units of a population (Galef 1976; Laland *et al.* 2000; Sargeant and Mann 2009; Palacios *et al.* 2013).

1.2 Why study habitat?

With the advent of computer-based geographic information systems (GIS), habitat models that relate where and when species are found to environmental variables have become a widespread practice in ecology (Guisan and Zimmermann 2000; Guisan and Thuiller 2005). But what can be gained from modelling a species' habitat? And why is it helpful to consider individual variation in habitat use as well as departures from the ideal free distribution assumptions? Habitat models have been used to infer the ecological constrains of species distributions (Torres *et al.* 2008; Elith and Graham 2009; Drew *et al.* 2011; Pirotta *et al.* 2011; Yu *et al.* 2015; Scales *et al.* 2017) and to inform conservation decisions (Angelstam *et al.* 2004; Cañadas *et al.* 2005; Matern *et al.* 2007; Bailey and Thompson 2009; Torres *et al.* 2013). Specifically, habitat models have been used as the basis to create protected areas (e.g., Hooker *et al.* 2002) and to evaluate the degree to which existing ones protect species habitats (e.g., Bailey and Thompson 2009). But, to provide useful information on the ecology of a species as well as to inform policies, habitat models should take into account biological characteristics of species and how these mediate their relationship to their environment, and also consider appropriate spatiotemporal scales (Graf *et al.* 2005; Austin 2007; McPherson and Jetz 2007; Cotté *et al*. 2011; Milligan 2013; Fernandez *et al.* 2017; Mannocci *et al.* 2017).

Specifically, recent advances in animal behaviour suggest that, for species in which social learning and culture are important drivers of behaviour and resource use (e.g., Geist 1971; McGrew *et al.* 1979; Boesch and Boesch 1990; Whiten *et al.* 1999; Slagsvold and Wiebe 2011), including culture in our approach to conservation and as well as our analysis of habitat use may be key (Whitehead *et al.* 2004; Palacios *et al.* 2013).

1.3 Culture

Culture may be defined as information or behaviour that is socially learned and shared among conspecifics (Boyd and Richerson 1996; Laland and Hoppitt 2003). Under this definition, culture has been recognized in birds, primates, and cetaceans (Grant and Grant 1996; Biro *et al.* 2003; van Schaik *et al.* 2003; Whitehead and Rendell 2015). Socially transmitted information does not only influence social behaviour and communication (Ford 1991; Cantor and Whitehead 2015) but can also influence feeding, foraging strategies, and niche preferences (McGrew *et al.* 1979; Ford *et al.* 1998; Estes *et al.* 2003; Slagsvold and Wiebe 2011), all of which can affect a species' distribution and habitat selection, use, and preferences. Additionally, because social transmission of information can occur within a generation, it is typically faster than the transmission of genes, and can be adaptive in highly variable environments (Alvard 2003; Whitehead 2003; van der Post and Hogeweg 2009).

1.4 Study system: the sperm whale

One species whose behaviour is influenced by cultural information and that experiences a wide breadth of spatial and temporal scales is the sperm whale. Sperm whales (*Physeter macrocephalus*) are among the most widely distributed mammals and live over 60 years (Rice 1989). They can be found from the tropics to the polar ice edges (Rice 1989), and, while they usually forage at around 500m below the surface (Papastavrou *et al.* 1989; Drouot *et al.* 2004; Watwood *et al.* 2006), they can dive up to a few thousand metres in search of their cephalopod prey (Watkins *et al.* 1993). The distribution of sperm whales across the ocean however is not homogeneous; males occur from the ice edges to the tropics, but females and juveniles are restricted to tropical and subtropical waters (Rice 1989; Richard *et al.* 1996; Christal *et al.* 1998). And, while males are mostly solitary (Whitehead *et al.* 1992), females spend their lives in long term social units formed of about 13 individuals (Christal *et al.* 1998). Over periods of a few hours to a few days, social units associate to form groups (Christal and Whitehead 2001), which likely facilitate cooperation during foraging through sharing of information on the location of prey, as well as confer protection from predators (Christal and Whitehead 2001). Finally, units do not associate with other units at random, but do so only with other social units of their own clan (Rendell and Whitehead 2003).

Sperm whale clans share, and can be identified on the basis of, common vocal dialects (Rendell and Whitehead 2003; Gero *et al.* 2016). Sperm whale clans were first identified off the Galápagos Islands, where they often occur sympatrically (Rendell and Whitehead 2003). Further research showed that sympatrically occurring clans also have different social behaviours, movement patterns, foraging success rates, and responses to environmental phenomena (Whitehead and Rendell 2004; Marcoux *et al.* 2007; Whitehead *et al.* 2008; Cantor and Whitehead 2015). Differences in how clans move through their habitat and how they respond to similar environmental conditions suggest that sperm whale clans may also differ in their habitat selection behaviours, and possibly their patterns of habitat use, which in turn may reflect different methods of acquiring prey.

However, studying the prey of sperm whales is challenging. Sperm whales feed mostly on meso- and bathypelagic squid (Kawakami 1980; Clarke *et al.* 1993; Clarke 1996; Smith and Whitehead 2000). The diet composition of sperm whales is known mostly through stomach content analysis and is regionally variable (Kawakami 1980). In the eastern Pacific, R. Clarke and colleagues suggested that it is almost exclusively composed of the jumbo squid, *Dosidicus gigas* (R. Clarke *et al.* 1988; R. Clarke and Paliza 2001), but this was disputed by M. Clarke and colleagues (M. Clarke *et al.* 1976; M. Clarke *et al.* 1993). Off the Galápagos, fecal analysis suggests that sperm whale diet is diverse (Smith and Whitehead 2000), but there is some debate regarding whether these apparent differences are due to methodology or actual variation in diet (R. Clarke and Paliza 2001; Smith and Whitehead 2001). However, until recent advances in echosounding technology (Benoit-Bird *et al.* 2015; Benoit-Bird *et al.* 2017), studying the distribution of bathypelagic prey of sperm whales was not feasible (Jaquet 1996). Instead, previous endeavours to describe the sperm whale habitat have used proxies that likely influence prey aggregation, such as indicators of upwelling and oceanic fronts (Jaquet and Whitehead 1996; Praca *et al.* 2009; Pirotta *et al.* 2011; Wong and Whitehead 2014). The degree to which sperm whale presence is associated with these environmental indicators is largely scale dependent; specifically, while over spatial scales beyond a few hundred kms, sperm whale occurrence can be associated more consistently to environmental conditions, over finer spatial scales this association becomes less clear (Jaquet 1996; Jaquet and Whitehead 1996; Jaquet and Gendron 2002; Milligan 2013).

1.4 Sperm whales off the Galápagos Islands

The Galápagos Islands have been recognized as an important area for sperm whales since the open boat whaling years in the 18th and 19th centuries (Townsend 1935). Here, sperm whales often forage and socialize (Cantor *et al.* 2017). During the 19th Century, whaling reduced the population of sperm whales off the archipelago by removing around 5000 individuals between 1830-1850 (Hope and Whitehead 1991). Whales were not hunted off the Galápagos after the late 19th century, but they still suffer from low recruitment rates possibly due to the removal of the majority of large breeding males from the region by intense whaling off Perú between 1957-1981 (Ramirez 1989; Whitehead *et al.* 1997; Whitehead *et al.* 2008; Cantor *et al.* 2016). And, while sperm whales across the world are no longer being commercially hunted, there is little sign of recovery and some populations face ongoing declines (Notarbartolo di Sciara 2014; Gero and Whitehead 2016). Modern threats to sperm whale survival include entanglements with fishing gear, primarily drift gillnets, but also purse seines, (Félix *et al.* 1997; Lewison *et al.* 2004), vessel collisions, acoustic and chemical pollution, and irresponsible tourism (Notarbartolo di Sciara 2014; Gero and Whitehead 2016).

The waters off the Galápagos Islands do not experience a high intensity of these threats. Since 1994, the surrounding waters 40 nautical miles off the archipelago were declared a marine protected area within which only artisanal fisheries, tourism, and research is allowed (LOREG, 2015). However, illegal industrial and artisanal fishing has been documented (Camhi 1995; Carr *et al.* 2013; Schiller *et al.* 2015), and purse-seining for tuna is common near the borders of the Galápagos Marine Reserve (GMR). Thus, while the GMR could provide a safe habitat for South Pacific sperm whales, it is unknown to what degree they are effectively protected from interactions with fisheries.

Additionally, sperm whales off the Galápagos Islands are not permanent residents of the area, but rather travel throughout the continental coasts of the Eastern Tropical Pacific (Whitehead *et al.* 2008; Cantor *et al.* 2016), and perhaps elsewhere. As a result, the whales that were found in the 1980's and 1990's belonged to different clans than those found in the early 2010's (Cantor *et al.* 2016). These large scale movements that occur over the years are thought to be a response to changes in prey abundance (Whitehead 1996; Cantor *et al.* 2017). The waters off the Galápagos Islands for most of the time are highly productive as a result of the topographically induced upwelling of the cold Equatorial counter-current at the west of the Islands (Houvenagher 1978; Palacios 2002; Palacios 2003). However, over fine spatial scales, there is high variability in primary productivity due to the convergence of warm equatorial currents and cool southern currents around the Archipelago (Palacios 2003; Edgar *et al.* 2004; Palacios *et al.* 2006). (Palacios 2003; Edgar *et al.* 2004). At the multiannual scale, the El Niño Southern Oscillation disrupts upwelling, which causes primary productivity to drop (Feldman *et al.* 1984; Schaeffer *et al.* 2008). This drop is associated with increased mortality of animals across taxa and trophic levels (Arntz and Tarazona 1990; Trillmich and Dellinger 1991; Boersma 1998). Off the Galápagos, sperm whales' feeding success, reproductive rates, and sighting rates decreased during the 1987 El Niño (Smith and Whitehead 1996; Whitehead and Rendell 2004).

1.5 Thesis Overview

In this thesis, I investigate the habitat of sperm whales around the Galápagos Islands. I intended to answer the following questions: What are the overall characteristics of sperm whale habitat off the Galápagos Islands (Chapter 2)? Are these variable in time (Chapter 2)? How does the distribution of recent surveys compare to that found two centuries ago

(Chapter 2)? How much of the habitat of Galápagos sperm whales is protected by the GMR (Chapter 2)? Is there overlap between the habitat and satellite-tracked fishing effort (Chapter 2)? And do sympatrically occurring clans have different habitat use patterns (Chapter 3)?

CHAPTER 2 – Habitat of the Galápagos sperm whales through time and implications for conservation

2.1 Abstract

Habitat models can provide insights into the relationship between species and their environments as well as being useful conservation tools. However, relationships to environmental variables are often scale-mediated, so that associations between species' presence and environmental conditions will vary when analyzed over different spatiotemporal scales. Sperm whales experience some of the widest range of spatiotemporal scales; they occur in all ocean basins and may live over 60 years. While sperm whales are no longer the target of commercial whaling, they are currently threatened by interactions with human fisheries, ship strikes, and oceanic pollution. We characterized recent (1985-2014) sperm whale habitat off the Galápagos Islands using Generalized Additive Models fit through Generalized Estimating Equations. We compared recent distributions to those recorded in 19th century whaling logbooks (1830-1850). To assess overlap with fishing effort, we overlaid recent habitat with fishing effort data obtained from Automatic Information System. We found that the over fine spatial scales (<50 km) sperm whale habitat within the Galápagos region was associated with topographic and oceanographic characteristics, but that the conditions over which whales were found were variable over years and decades. Between centuries and at coarse spatial scales (>100 km), we found that sperm whales consistently occupied regions of abrupt topography and high productivity, most of which occurred within the boundaries of the Galápagos Marine Reserve, within which potentially harmful activities are restricted. However, in some years sperm whales occupied regions outside the GMR, where in some cases they could overlap with fishing effort. These results contribute to the understanding of sperm whale habitat selection and provide information for conservation and management efforts.

2.2 Introduction

Habitat models provide insights into the relationship between species and their environment and are useful tools for conservation (Hooker *et al.* 2002; Cañadas *et al.* 2005; Austin 2007; Torres *et al.* 2013; Scales *et al.* 2017). Often, habitat models are rooted in ecological theory, and, implicitly or explicitly, assume that where a species is found depends on local physical constraints, resource availability, predation, and competition (Aristotle 344AD; Grinell 1917; Hutchinson 1957; Austin 2007; Palacios *et al*. 2013). However, the degree to which species respond to environmental conditions is scale-dependent—different processes can determine where a species is found over years and kilometres compared to over days and metres (Levin 1992; Graf *et al.* 2005; Fernandez *et al*. 2017; Mannocci *et al*. 2017). In highly mobile species that disperse among resource patches, distribution often departs from an *ideal free distribution*—where species are predicted to occur disproportionately in habitats of higher resource availability (Fretwell and Lucas 1969; Sutherland 1983)—as a result of imperfect information regarding the quality of a current patch relative to that of alternative distant patches, the distance between patches, and the cost of travel (Gray and Kennedy 1994; Bernstein *et al.* 1999; Shochat *et al.* 2002). This means that occupancy may not always reflect relative habitat quality and active habitat selection (Johnson 1980; Kennedy and Gray 1993; Morrison 2006) (Kennedy and Gray 1993), which influences the type of conclusions that can be made based on models that relate environmental characteristics to a species' habitat-use patterns.

One of the most widely distributed animals in the world is the sperm whale; they can be found in all oceans from the tropics to the ice edges (Whitehead 2003; Mizroch and Rice 2013). However, only mature males occupy the full extent of this distribution; females and juveniles are mostly found in tropical and subtropical waters (Rice 1989), where they live in long-term social units (Christal *et al.* 1998). Social units associate with each other for hours to days forming groups (Whitehead 2003; Whitehead *et al.* 2012), which only occur among units of the same vocal clan (Rendell and Whitehead 2003; Whitehead *et al.* 2012; Gero *et al.* 2016). Across the South Pacific, female sperm whales will frequently move up to 1000 km within a year and occasionally more than 3000 km (Whitehead *et al.* 2008). Both daily and annually, the movements of sperm whales relate to the abundance of their prey (Whitehead *et al.* 1997; Rendell *et al.* 2004; Whitehead and Rendell 2004), bathypelagic cephalopods of highly patchy and variable distributions (Clarke *et al.* 1988; Clarke 1996; Smith and Whitehead 2000; Jaquet and Gendron 2002; Markaida 2006). Over hours and days, sperm whales change direction and cover less distance where feeding success is high, and travel longer, straighter distances if it is low (Whitehead 1996). Over years and decades, sperm whales likely move away from areas were resources are depleted towards areas of expected higher prey density (Whitehead 1996; Whitehead *et al.* 1997).

But, because sperm whales feed on meso- and bathypelagic squid at least 300m below the surface (Kawakami 1980; Papastavrou *et al.* 1989; Drouot *et al.* 2004; Gilly *et al.* 2006; Davis *et al.* 2007), direct measurements of sperm whale prey are rare (Jaquet and Gendron 2002; Davis *et al.* 2007, but see Benoit-Bird *et al.* 2017). Instead, the habitat of sperm whales has been described through environmental proxies that are associated with prey-aggregating features such as upwelling, fronts, and mesoscale eddies and can be observed from the surface (Jaquet and Whitehead 1996; Praca *et al.* 2009; Pirotta *et al.* 2011; Milligan 2013; Wong and Whitehead 2014). The degree to which sperm whales associate with these proxies is largely scale-dependent; over spatial scales of more than 600 km, abundance of sperm whales was associated to highly productive waters along shelf breaks (Jaquet and Whitehead 1996) while over 5- 100 km, associations between sperm whale presence and environmental variables are less clear (Cañadas *et al.* 2002; Praca and Gannier 2007; Pirotta *et al.* 2011; Milligan 2013).

Sperm whales have been highly successful inhabitants of the unpredictable oceanic environment, but for the past three centuries, interactions with humans have threatened their survival. Sperm whales were heavily hunted until the late 1980's. This resulted in a population depletion from an estimated 1,000,000 individuals globally pre-whaling to 360,000 currently, although uncertainty in the estimation of these numbers is high (Whitehead 2002). While the moratorium on whaling ended the commercial hunt for sperm whales in 1986 (Whitehead 2002), they are still considered vulnerable due to very slow life history processes and little evidence of recovery (Whitehead *et al.* 1997; Taylor *et al.* 2008). Furthermore, some populations experience ongoing decline as a result of entanglements with fishing gear, vessel collisions, chemical and acoustic pollution, and incautious whale watching (Notarbartolo di Sciara 2014; Gero and Whitehead 2016).

Off the Galápagos Islands, sperm whales were hunted intensively during the early 19th century (Starbuck 1878; Hope and Whitehead 1991) and, although the Islands were not the site of modern whaling, they seem to have experienced low recruitment rates probably as a result of the preferential removal of males by modern whaling in the waters off Perú (Whitehead *et al.* 1997). More recently, while within the Galápagos region, no sperm whale mortality has been reported, off the coasts of Ecuador (ca. 1000 km away) and Chile (ca 2900 km away) sperm whale deaths have been associated with gillnet, purse-seiner, and long-line entanglements (Félix *et al.* 1997; Hucke-Gaete *et al.* 2004; Félix *et al.* 2007; Galleti-Vernazzany and Cabrera 2007), which suggests that, if they do occur, interactions between sperm whales and fishing gear may be risky for sperm whales. The Galápagos marine region is currently protected by the Galápagos Marine Reserve, which extends 74 km off the archipelago. Most of the GMR's pelagic waters allow artisanal fisheries and tourism, except areas designated as no-take zones in 2016, which cover all the GMR north of 0.40º N (MAE 2016). Within the GMR, only artisanal fisheries are allowed, with gillnets and industrial fisheries being prohibited (Comisión Técnica Pesquera de la Junta de Manejo Participativo 2009; LOREG 2015).

In this sense, the GMR could be a refuge for sperm whales within the Eastern Tropical Pacific. However, the degree to which sperm whale habitat is protected by the GMR has not been studied. Additionally, industrial fisheries shoulder against the GMR and on occasions violate its limits (Camhi 1995; Carr *et al.* 2013; Schiller *et al.* 2015; Alava and Paladines 2017). The deep waters of the GMR are particularly hard to monitor, but recently, local authorities along with international conservation organizations have promoted the use of Automatic Identification Systems (AIS) to remotely track fishing vessels within the GMR (Sea Shepherd Conservation Society 2011). This remote surveillance system could significantly improve management and enforcement (see Zainuddin *et al.* 2006; McCauley *et al.* 2016: Cutlip, 2017). To date, however, implementation has been slow and is not mandatory for artisanal fishing vessels.

Here, we investigated the distribution of sperm whales in the Galápagos region in recent surveys (1985-2014) as well as during 19th century whaling period (1830-1850). For recent surveys, we modelled sperm whale habitat with respect to geographic, topographic, and oceanographic variables. To determine whether the traits that delineated sperm whale habitat were variable over time, we analyzed sperm whale habitat at annual, decadal, and tri-decadal scales. We compared this recent distribution to that recorded over 150 years ago in whaler's logbooks (data from Hope and Whitehead 1991) to determine if present areas of high sperm whale occurrence were similar to those found historically. Using these data, we studied the degree to which sperm whales are protected by the GMR. Finally, we compared the recent distribution of predicted sperm whale presences to that of AIS-derived fishing effort has been recorded.

2.3 Methods

2.3.1 Modelling modern habitat

2.3.1.i Field Methods

We studied whales off the Galapagos Archipelago (93ºW 88ºW; 2ºN 3ºS) in years between January and June of 1985 through 2014 (1985, 1987, 1989, 1991, 1995, 2013 and 2014) from a dedicated sailboat (10-12m) (Table 2.1). We searched for whales visually during daylight hours with a search range between 0.2 - 2.0 km, and acoustically day and night using a directional hydrophone that was monitored every 15-60 min and could detect sperm whale clicks up to about 7 km away (Whitehead 2003). We refer to the periods during which whales were within visual/acoustic contact as *encounters*, and to the periods during which no whales were found as *search periods*. Encounters initiated when whales were first detected and ended when visual/acoustic contact was disrupted for > 6 hr. During encounters and search periods, the geographic position of the boat, and thus of the whales, was estimated by extrapolation from SATNAV fixes at least every 3 hr before 1993, and every 1-5 min through GPS afterwards (Whitehead and Rendell 2004). Encounters with lone males, or small groups of males, were omitted from analysis since we typically followed them only for less than a few hours.

Table 2. 1 Summary of time spent searching for and following female and juvenile sperm whales, and the number of encounters between 1985-2014 off the Galápagos Islands. Encounters are defined as sets of consecutive geographic positions within < 6 hr of each other when following sperm whales. Surveyed months are indicated by "x."

Year	**Days in study area**	**Total encounters**	**Months Surveyed** **January**	**February**	**March**	**April**	**May**	**June**
1985	37	12		x	x	x		
1987	76	21	x	x	x	x	x	x
1989	34	14				x	x	
1991	23	4			x	x		
1995	40	10				x	x	x
2013	49	4		x	x	x		
2014	83	10	x	x	x	x	x	
Total	342	75						

2.3.1.ii Modelling approach

All modelling procedures were carried out in the R environment (R Development Core Team 2017). To model the habitat use of sperm whales off the Galapagos archipelago, we used logistic Generalized Additive Models (GAMs) in which oceanographic and topographic variables were used as predictors of sperm whale presence, based on Pirotta et al.'s (2011) approach. GAMs allow for the inclusion of non-linear relationships between the response variable and covariates (Hastie and Tibshirani 1986; Wood 2006), which results in more accurate representation of ecological processes (Bio *et al.* 1998; Wintle *et al.* 2005). Additionally, because our data were collected continuously, they were spatially and temporally autocorrelated. We dealt with this violation of independence using Generalized Estimating Equations to fit the GAMs (GEE-GAMs) (Pirotta *et al.* 2011). We fit separate models with data collected in the 1980's, 1990's, and 2010's to explore temporal variation in habitat use patterns, as well as a full habitat model including all study years to gain an overall image of sperm whale habitat.

We used single encounters and search periods as the blocking variables. All locations within each encounter or search period were included within a block. Autocorrelation function (ACF) plots of individual encounters for final models converged at zero, indicating that encounter was an appropriate blocking variable (MRSea package) (Scott-

Hayward *et al.* 2013) (Appendix I). Presence points collected during encounters were coded as “1” and absence points collected during searching periods as “0”.

Because geographic positions were collected at irregular intervals with SATNAV, we linearly interpolated latitude and longitude so that positions were available approximately every hour. This was an effort to avoid bias that results when the intervals at which data are collected depend on unknown factors that may affect the response (i.e., presence or absence of whales) (Bůžková *et al.* 2010). We chose a linear interpolation method due to its simplicity and because the error that arises from linear interpolation (Tremblay *et al.* 2006) is expected to be smaller than the ca. 0.5-3.0 km spread of a sperm whale group (Whitehead 2003), and much smaller than the scale at which we analyzed environmental variables (>10 km). For data from 2013 and 2014, which were collected more often, we subsampled geographic positions so that they were also available approximately every hour, for consistency with previous years.

We restricted our analysis to regions that were consistently surveyed throughout study years (Milligan 2013). For this, we calculated the total number of geographic positions recorded by decade during and between encounters in 0.10º x 0.10º cells and selected only geographic positions that fell where the count exceeded the 70th percentile for that decade. We also included only the geographic positions that occurred >1,000 m deep as shallow waters were not consistently monitored acoustically.

2.3.1.iii Variables

We included topographic and oceanographic habitat characteristics that have been associated with the concentration of cephalopod prey of sperm whales (Jaquet 1996; Praca *et al.* 2009). The topographical variables included in this study were depth, obtained from the General Bathymetric Chart of the Oceans, available at 0.008º, (http://www.gebco.net/data_and_products/gridded_bathymetry_data/), and slope, calculated using Spatial Analysis tools in ArcGIS. Oceanographic variables included satellite-derived relative mean sea surface temperature (relSST), and standard deviation of SST (sdSST) (Griffin 1999; Praca *et al.* 2009; Pirotta *et al.* 2011). Sea surface temperature data for the 1980’s and 1990’s geographic positions was obtained from the Pathfinder Version 5.0 & 5.1 dataset at 4km resolution, collected by the Advanced Very

High Resolution Radiometer (AVHRR) and processed by the NOAA National Oceanographic Data Center, and from Aqua-MODIS satellite images at 4 km resolution, distributed by the NOAA CoastWatch Program and NASA's Goddard Space Flight Center, for geographic positions from the 2010's. Satellite data were extracted using the rerddapXtracto R Package (Mendelssohn 2016). We used relSST instead of actual SST to correct for annual variations in temperature, and calculated it as the difference in SST in a given geographic position and the mean SST of the whole Galapagos region for the corresponding month (Pirotta *et al.* 2011). We excluded geographic positions that occurred over 5 km away from shore since the quality of Pathfinder data <5 km away from coastlines is low (NOAA 2009). Additionally, we included geographical variables (latitude and longitude) to account for spatial variation unexplained by environmental and topographical variables.

The relationship between sperm whale presence and environmental variables is strongly dependent on the spatiotemporal scales at which both sperm whale occurrence and environmental variables are measured (Jaquet 1996; Wong and Whitehead 2014). To find appropriate spatial scales at which environmental variables should be included we generated models in which variables were included at fine (0.10°), medium (0.30°), or coarse (0.50°) spatial resolutions. The coarse spatial resolution was chosen to reflect the average distance travelled by sperm whales within a day (ca. 50 km) (Whitehead *et al.* 2008); the fine spatial resolution reflected the approximate distance over which sperm whales could be detected (ca. 10 km), and the intermediate scale was chosen as a mid-way between the other two spatial scales. We also explored models where temporally-fluctuating variables were included either as weekly or monthly averages to reflect the duration of mesoscale features (such us upwelling, fronts, and eddies), which we assumed would influence sperm whale distribution (Mannocci *et al.* 2017).

To identify and avoid collinearity, we calculated correlation coefficients for all explanatory variables at each spatial and temporal resolution. We fit alternative initial models in which only uncorrelated ($|r| < 0.4$) variables were included. All explanatory variables were standardised by subtracting the mean and dividing by the standard deviation.

2.3.1.iv Model selection

Model selection was carried out using the quasi-likelihood criterion (QIC), which is an adaptation of Akaike's information criterion (AIC) for GEEs (Pan 2001), available through the MuMIn library (Barton 2016) (Fig. 2.2) . Initially, we fit candidate models at alternative spatial (0.10°, 0.30°, or 0.50°) and temporal (weekly or monthly) resolutions.

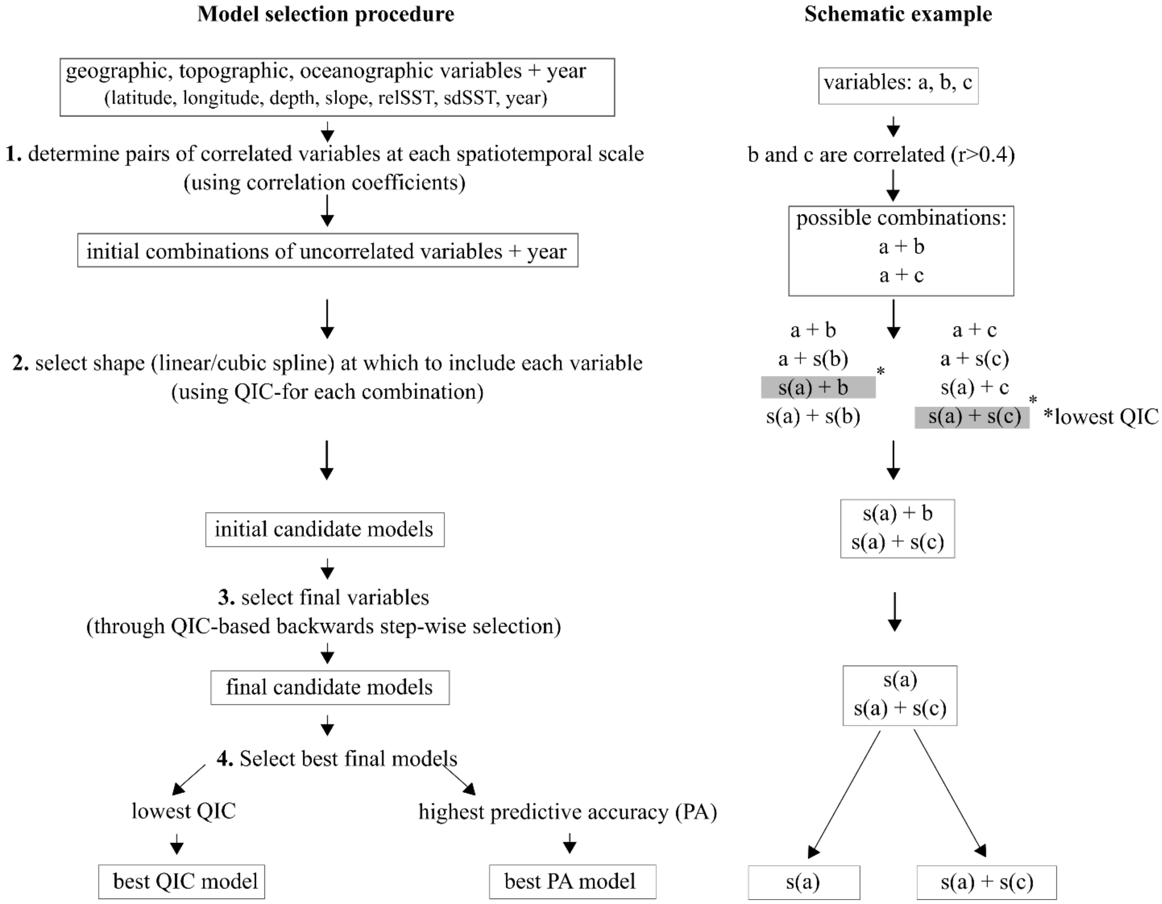


Figure 2. 1 Selection procedure steps (1-4) for sperm whale habitat models off the Galápagos Islands. A schematic example is shown where, a, b and c represent environmental variables. In step 2, variables included in models as cubic splines are bounded by "s()" and variables included as linear terms are unbounded.

Initial "*dynamic"* candidate models included uncorrelated geographic, topographic, and oceanographic variables, year as a categorical factor, and interactions between topographic and oceanographic variables and year:

Presence ~ geographic variables + topographic variables + oceanographic variables + year + topographic variables:year + oceanographic variables:year

We alternatively included non-categorical variables as linear terms or cubic splines and selected the best combination of independent variables for each spatiotemporal resolution (Fig 2.1). Next, we used a backwards selection method in which variables were removed from the best initial candidate models if they improved QIC (Fig. 2.1). From the resulting models, we selected the one with the lowest QIC (best QIC) and the one with the highest predictive accuracy (see *Validation* section for measurement of predictive accuracy) (Fig. 2.1). This resulted in 48 initial candidate models for the 1980's, 44 for the 1990's, and 68 for the 2010's (Appendix II Tables S.21-S2.3).

Through preliminary analysis, we found that QIC tended to favor complex models (i.e., those that included interactions) that in some cases had poorer predictive accuracy (see *Validation* section) than simpler models. For this reason, we repeated the model selection process above (Fig. 2.1) starting with "*static"* candidate models that did not include interactions with year:

Presence ~ geographic variables + topographic variables + oceanographic variables + year

From resulting *dynamic* and *static* candidate models, we selected one with the lowest QIC (best QIC) and the one with the highest predictive ability for each decade (Fig. 2.1). For the full habitat model, we only carried out selection (Fig. 2.1) on *static* candidate models only, which resulted in a total of 34 initial models (Appendix II Table S2.4).

2.3.1.v Validation—model fit and predictive accuracy

To validate final models for each study period, we analyzed how well the final models fit the data (i.e., goodness of fit), and how accurately they predicted sperm whale presence when encounters and searching periods were iteratively removed from the data. To measure goodness of fit (GOF), we calculated the percentage of data points which were correctly identified as presences and absences (Fielding and Bell 1997). We measured predictive accuracy of models through leave-one-out cross-validation (LOO) during which we calculated the percentage of correctly assigned geographic positions from each encounter or searching period after removing the encounter or searching period from the dataset (Hastie *et al.* 2009). We transformed predicted probability values for GOF and predictive accuracy measurements into a binary assignment using a cut-off that maximized distance between the Receiver Operating Characteristic (ROC) curve (which plots true positive ratio against false positive ratio for any possible cut-off value), and a 1:1 line using the ROCR library in R (Fielding and Bell 1997; Sing *et al.* 2005).

We compared GOF and predictive accuracy of final models for each study period to those of a *null model,* which included only latitude longitude, and year. The null models were intended to capture variation in relative habitat use patterns that could not be accounted for by any of the oceanographic or topographic variables available, while investigating the degree to which oceanographic and topographic variables retained in the model improved predictive ability.

Additionally, to study the effect of spatial and temporal scale on performance, we compared GOF and predictive accuracy for the final model to those of equivalent models in which the same variables were included at alternative spatiotemporal scales.

2.3.1.vi Prediction maps

We produced decadal and full maps of predicted sperm whale distribution of modern data as in Pirotta et al. (2011) using a 0.12° grid. We mapped only cells within 20 km of areas over which whales were searched for or followed, and excluded sample points in waters shallower than 1000 m. We calculated predicted probabilities for each sample point using both the final models with highest predictive accuracy and lowest QIC and converted the grid of sample points to a raster image with the R raster package (Hijmans *et al.* 2016).

2.3.2 Comparing modern habitat to historic distribution

Sperm whale sightings between 1830-1850 were obtained from microfilm copies of the logbooks of whaling vessels that transited the Galápagos region (93ºW - 88ºW; 2ºN - 3ºS) (from Hope and Whitehead 1991). These logbooks represent 68% of those available for the region and record activity for 7% of the vessels that transited the Galápagos whaling grounds (Hope and Whitehead 1991). Geographic locations of sightings were obtained from logbooks either directly from latitude and longitude annotations, from directional distances to landmarks around the archipelago, or interpolated in the case that positions were available the day before and after reported sightings (Hope and Whitehead 1991). We generated a map of point kernel density for the entire period (1830-1850) to visualize past sperm whale habitat as well as decadal densities in ArcGIS and exported the resulting raster to R. To make full and decadal densities comparable, we scaled resulting kerned densities from 0-1 by dividing original kernel density by the corresponding maximum value. We compared decadal distributions within this period by calculating the absolute difference between decadal scaled densities.

2.3.3 Identifying sperm whale habitat overlap with fishing activity

Fishing effort (hours/0.12° cell * year) in 2013 and 2014 was obtained through Global Fishing Watch, which compiles global automatic identification signals (AIS) from vessels and determines fishing activity and type of fishing activity through analyses of their movement patterns (De Souza *et al.* 2016; McCauley *et al.* 2016; data provided by Kristina Boerder; Biology Department, Dalhousie University). Using AIS to represent fishing effort, especially near marine protected areas, is imperfect in that AIS can be turned off during illegal activities and the mandatory implementation of AIS in fishing vessels only is recent and incomplete (De Souza *et al.* 2016; McCauley *et al.* 2016). Nevertheless, it can be a useful tool to identify areas where fishing effort concentrates and how it fluctuates over time. We investigated the degree to which AIS data captured fishing activity off the GMR by mapping the observed fishing vessels and gear (i.e., fishing lines or flags) recorded in our logbooks (1985-2014 field work). While this is also an incomplete representation of fishing activity as fishing vessels were not annotated systematically, it allows the identification of gaps in AIS data.

To identify regions in 2013 and 2014 where sperm whales were most likely to overlap with fishing activity, we calculated an overlap score. For each year, we multiplied predicted distributions by the amount of fishing hours in each year and divided this value by the maximum number of hours recorded for each year (see Leigh *et al.* 2013). Additionally, we calculated the proportion of time that was spent with whales that occurred outside of the GMR for each decade in historic records and our modern data.

2.4 Results

Between 1985 and 2014, we spent 342 days searching for and following female and juvenile sperm whales off the Galápagos Islands (Table 2.1, Fig. 2.2). During this time, there were 75 encounters that lasted between 1 hr and 9 d (average 1 d and 15 hr).

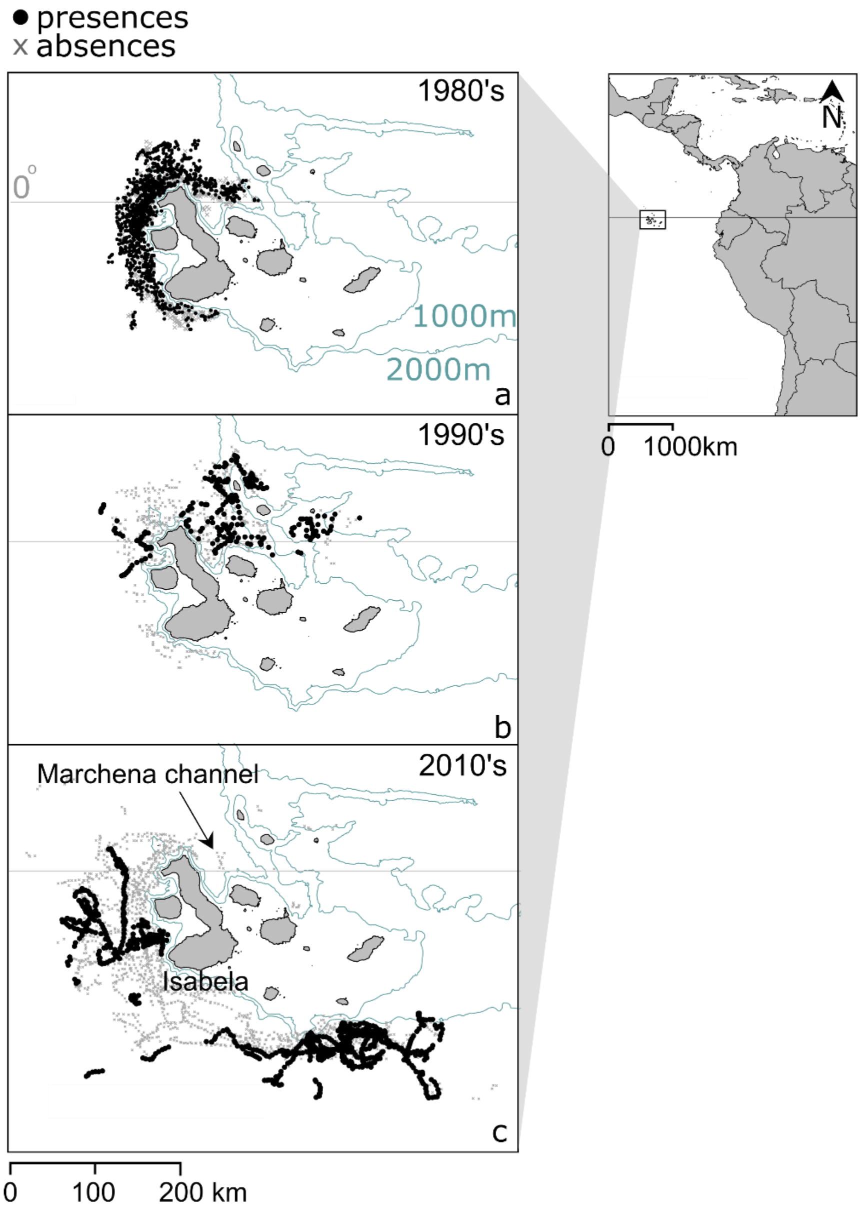


Figure 2. 2 Presence and absence positions of sperm whales off the Galapagos Islands in (a) 1980's, (b) 1990's, and (c) 2010's. An insert of South America is shown for reference.

2.4.1 Modern habitat modelling

For all decades, interactions between oceanographic and topographic variables with year were retained in almost all final models (Table 2.2). Decadal models fitted data more closely and predicted sperm whale presence more accurately than the full static habitat models (Table 2.2). Model selection favored models in which relationships with geographic, topographic, and oceanographic variables were non-linear (Table 2.2). All final decadal models, except that preferred based on QIC for the 1980's, had better performance than null models (Table 2.2). On the other hand, the final models for the entire study period performed worse than the corresponding null model (Table 2.2).

Table 2. 2 Final models selected for each decade through QIC and predictive ability (PA). Null models are included for comparison, and ΔQIC is calculated with respect to the null model. Models included as cubic splines are indicated as “b()”, and interactions between terms are indicated by an asterisk (*).

Decade	**Selection method**	**Selected models**	**Spatial scale**	**ΔQIC**[a]	**GOF**	**PA**[b]
1980’s	QIC	b(longitude) + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year	0.5	-398.52	0.80	0.52 ± 0.04
	PA	latitude + longitude + b(monthly relSST) + b(monthly sdSST)	0.5	-95.19	0.73	0.64 ± 0.05
	null	b(latitude) + longitude + year	NA	0	0.68	0.58 ± 0.05
1990’s	QIC	latitude + b(longitude) + b(slope)*year + b(weekly relSST)*year	0.5	-111.88	0.80	0.56 ± 0.06
	PA	b(latitude) + b(depth)*year + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year	0.3	-78.23	0.76	0.65 ± 0.08
	null	latitude + b(longitude) + year	NA	0	0.73	0.47 ± 0.07
2010’s	QIC	b(slope)*year + b(monthly relSST)*year + b(weekly sdSST)*year	0.3	-1059.57	0.77	0.70 ± 0.05
	PA	b(latitude) + b(depth)*year + b(monthly relSST)*year	0.5	-960.14	0.84	0.71 ± 0.06
	null	b(latitude) + longitude + year	-	0	0.59	0.59 ± 0.06
1980’s-2010’s	QIC	b(longitude) + slope + b(weekly relSST) + b(weekly sdSST) + year	0.5	-102.96	0.78	0.54 ± 0.03
	PA	b(latitude) + b(weekly relSST) + monthly sdSST +year	0.1	91.12	0.75	0.55 ± 0.03
	null	longitude + b(latitude) + year	NA	0	0.73	0.58 ± 0.04

a. ΔQIC measures the difference between a model’s QIC and the null model
b. Predictive ability measured through leave-one-out cross-validation ± standard error

Models fitted with topographic and oceanographic variables at intermediate/coarse spatial scales were preferred based on QIC over fine-scale alternatives (Table 2.2). However, varying the spatial scale of final models did not considerably affect predictive accuracy (Fig. 2.3). Conversely, although modifying the temporal scale of final models affected predictive ability, no single temporal scale of dynamic variables was consistently preferred over decades (Fig. 2.3). The predictive ability of full static models was very similar among alternative spatiotemporal resolutions (Appendix III).

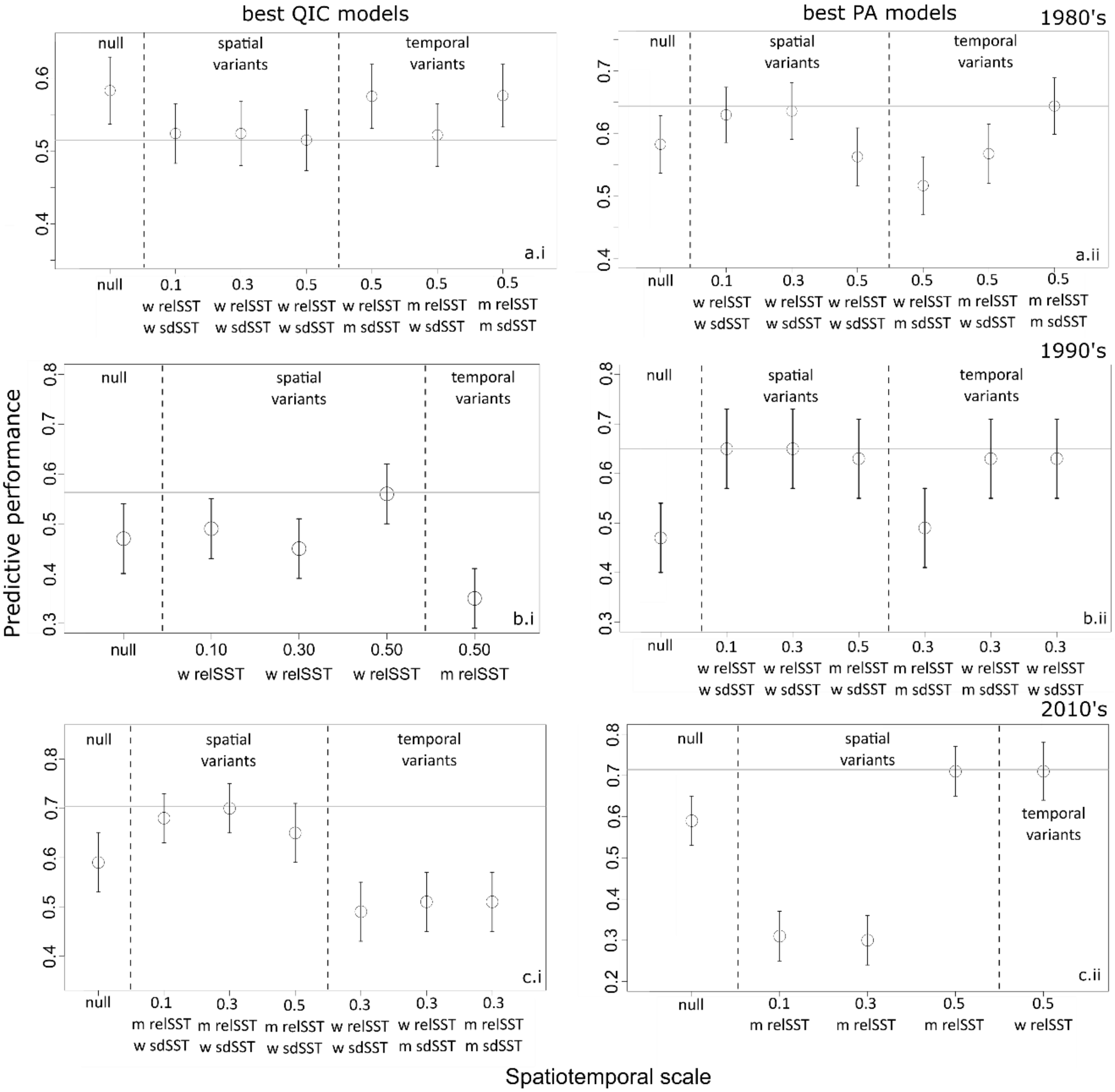
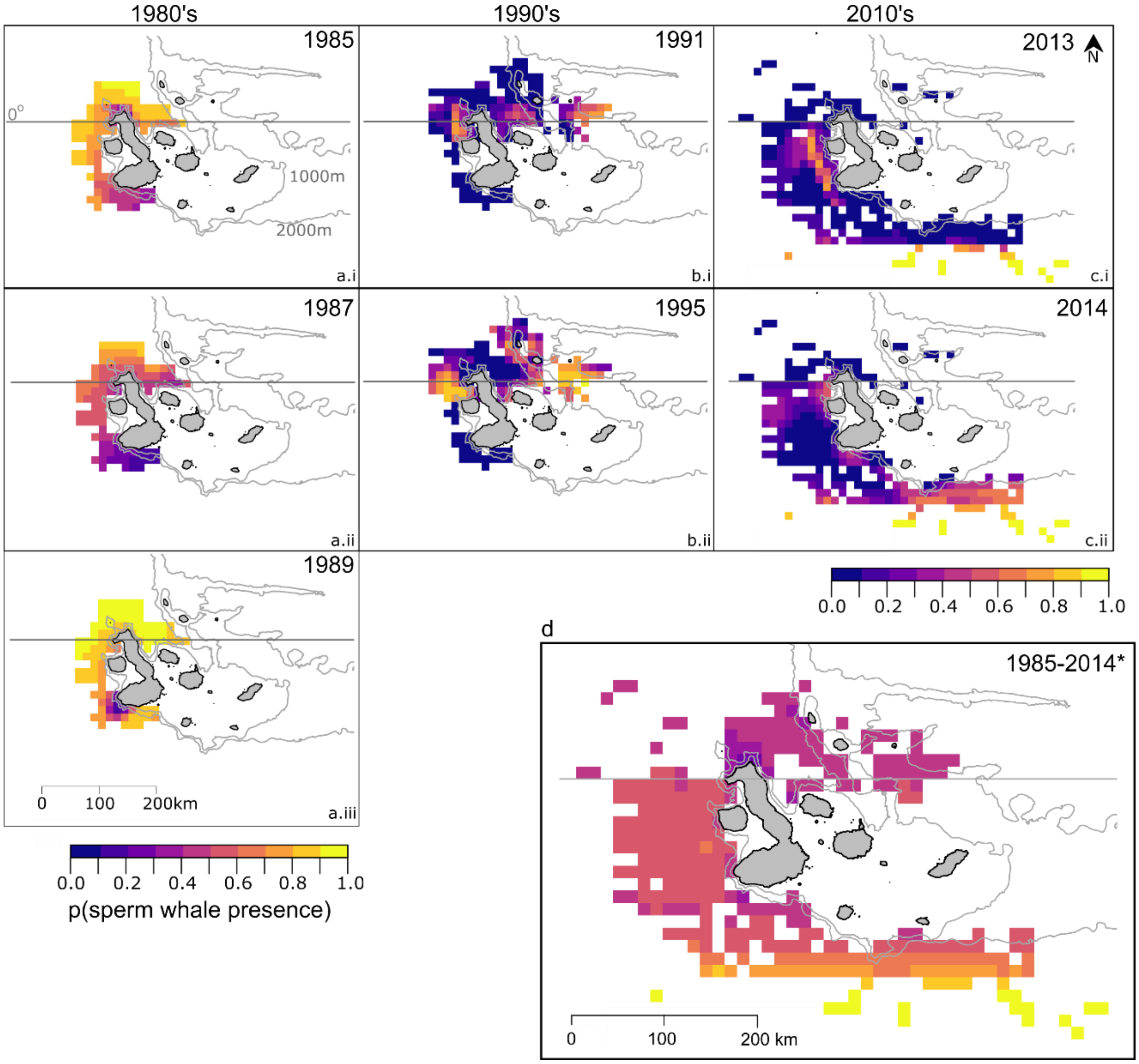


Figure 2. 3 Predictive performance (measured through leave-one-out cross-validation) of final models predicting presence of sperm whales off the Galápagos Islands in the 1980's,

1990’s, and 2010’s selected through QIC (a.i, b.i, c.i) and PA (a.ii, b.ii, c.ii). Null models (including only latitude and longitude) as well as variants fitted with topographic and oceanographic variables at alternative spatial (0.1º, 0.3º, 0.4º) and temporal (averaged over weeks (w) or months (m)) resolutions are shown.

Throughout the three decades, waters west of the steep slopes of Isabela (~92°W) had higher probability of sperm whale presence (Fig. 2.4). In the 1980’s and 1990’s, high probabilities also occurred in the Marchena Channel, which divides northern islands, (Pinta, Marchena, and Genovesa) from the rest (Fig. 2.4) with the highest likelihood of finding whales in this region in the 1990’s (Fig. 2.4-b). In the 2010’s, areas south of the 1000 m depth contour also had high probability of sperm whale presence (Fig. 2.4-c).



*Model includes data collected in 1985, 1987, 1989, 1991, 1995, 2013 and 2014.

Figure 2. 4 Maps of annual probabilities of sperm whale presence as a function of geographic, topographic, and oceanographic variables for (a) 1980's—(i) 1985, (ii), 1987, and (iii) 1989, (b) 1990's—(i) 1991 and (ii) 1995, (c) 2010's—(i) 2013 and (ii) 2014, and (d) 1985-2010's from models preferred based on predictive accuracy. Depth contours at 1000 and 2000 m are shown. Probability maps generated through models preferred based on QIC, which were very similar, are shown in Appendix IV.

The overall probability of finding whales was higher in the 1980's than in following decades (Figs. 2.5a-v, 2.5b-v, 2.6a-v, 2.6b-vi, 2.7a-v, and 2.7b-iv). But, while whales were widely distributed within the study area in 1985 and 1989 (Fig. 2.4-a), in 1987, an El Niño year, regions where probability of sperm whale presence was highest were restricted to the west of Isabela and the Marchena channel (Fig. 2.4a-ii). In the 1990's and 2010’s, areas with higher probability of sperm whale presence were also restricted when compared to 1985 and 1989 (Fig. 2.4).

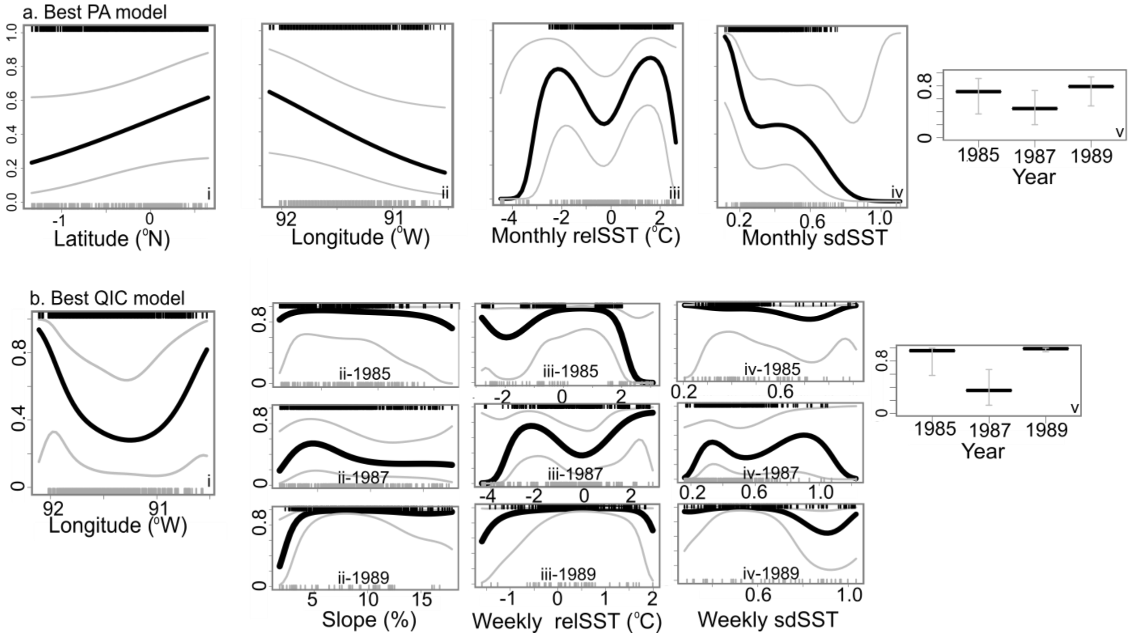


Figure 2. 5 Modelled effect of geographic, topographic, and oceanographic variables on sperm whale presences for the 1980’s study period. In (a) the model with best predictive accuracy (PA), sperm whale presence is modelled as a function of (i) latitude, (ii) longitude, (iii) monthly relative sea surface temperature (relSST), (iv) monthly standard deviation of sea surface temperature (sdSST0, and (v) year, at 0.5º spatial resolution. For the model preferred based on QIC, sperm whale presence is modelled as a function of (i) longitude, (ii) slope and its interaction with year, (iii) weekly relSST and its interaction with year, (iv) weekly sdSST and its interaction with year, and year at 0.5º spatial resolution. Rug plots of observed data from positions during which whales were found in black, and when they were being searched for in grey.

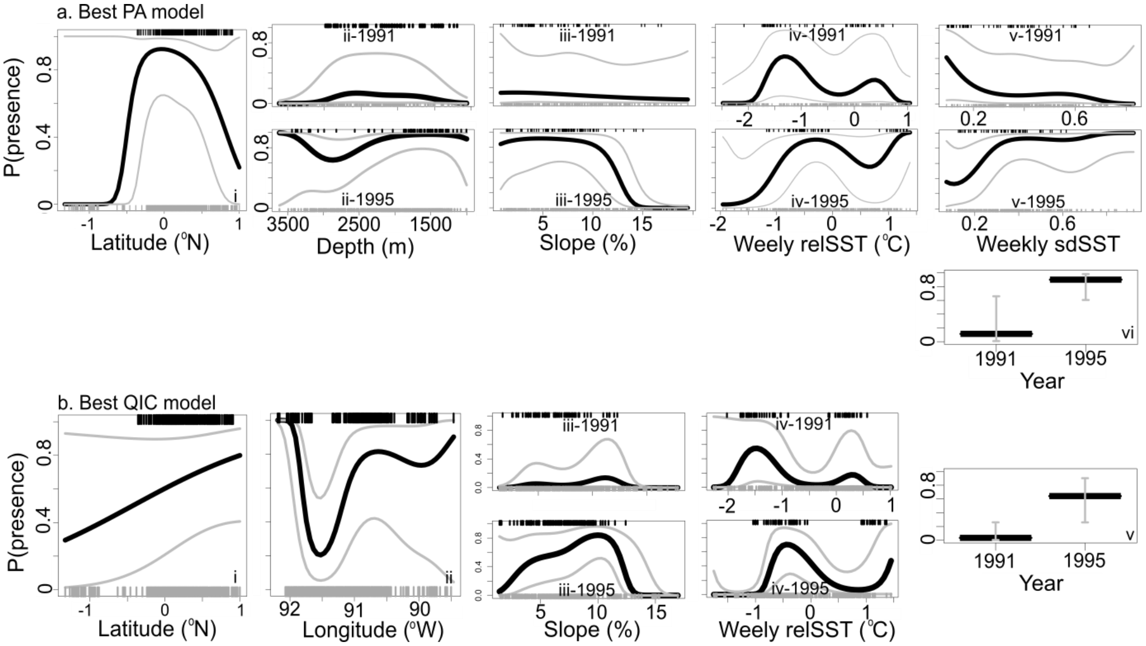


Figure 2. 6 Modelled effect of geographic, topographic, and oceanographic variables on sperm whale presences for the 1990's study period. In (a) the model with best predictive accuracy (PA), sperm whale presence is modelled as a function of (i) latitude, (ii) depth and its interaction with year, (iii) slope and its interaction with year, (iv) weekly relative sea surface temperature (relSST) and its interaction with year, (v) weekly standard deviation of sea surface temperature (sdSST), and (v) year at 0.5º spatial resolution. For the model preferred based on QIC, sperm whale presence is modelled as a function of (i) latitude, (ii) longitude, (iii) slope and its interaction with year, (iv) weekly relSST) and its interaction with year, and (v) year at 0.3º spatial resolution. Rug plots of observed data from positions during which whales were found in black, and when they were being searched for in grey.

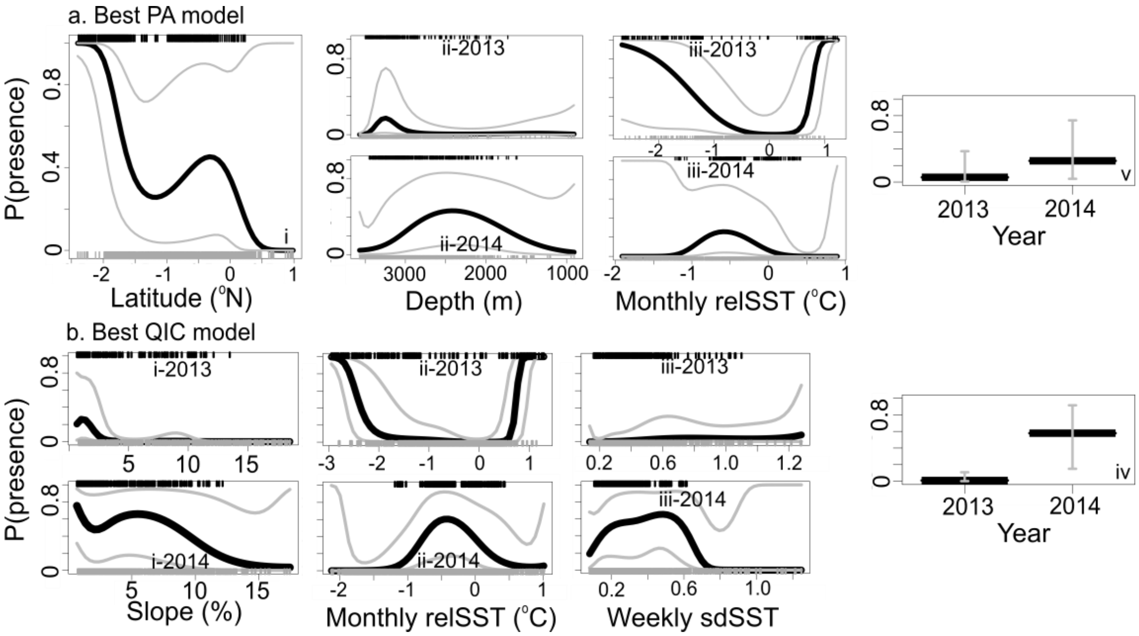
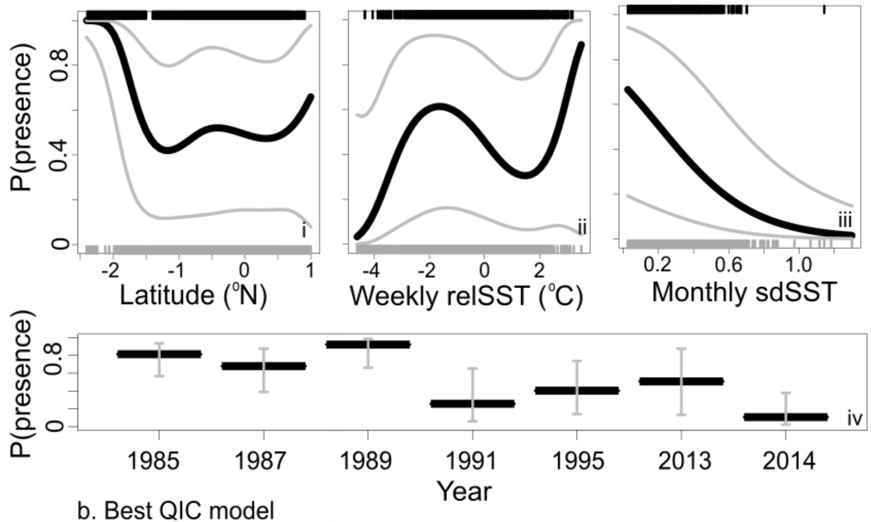


Figure 2. 7 Modelled effect of geographic, topographic, and oceanographic variables on sperm whale presences for the 2010's study period. In (a) the model with best predictive accuracy (PA), sperm whale presence is modelled as a function of (i) latitude, (ii) depth and its interaction with year, (iii) monthly relative sea surface temperature (relSST) and its interaction with year, and (iv) year at 0.3º spatial resolution. For the model preferred based on QIC, sperm whale presence is modelled as a function of (i) slope and its interaction with year, (ii) monthly relSST and its interaction with year, (iii) weekly sdSST and its interaction with year, and (iv) year at 0.5º spatial resolution. Rug plots of observed data from positions during which whales were found in black, and when they were being searched for in grey.

Through decadal models, the distribution of sperm whales in relation to topographic and oceanographic variables was mostly consistent, but specific ranges over which whales were found varied across time. Overall, whale encounters were associated with deep (3000-1500 m) (Figs. 2.6a-ii & 2.7a-ii) and flat (~5% slope) waters (Figs. 2.5b-ii, 2.6a-iii, 2.6b-iii, & 2.7b-i). The association between sperm whale presence and relSST was bimodal in most cases (Fig. 2.5a-iii, 2.5b-iii, 2.6a-iv, 2.6b-iv, 2.7a-iii, & 2.7b-ii), which in part reflects monthly differences in the relSST in which whales were searched for as well as found (Appendix V). Specifically, relatively cooler waters were surveyed during January-February, and relatively warmer waters were surveyed during May and June. Although we removed the effect of monthly variability in SST due to seasonal changes, this did not remove the fact that surveys in given months were associated with particular relSST ranges. In most years, whales were more likely to be found in areas of lower sdSST values, but this was not case in all years (Figs. 2.5a-iv, 2.5b-iv, 2.6a-v, 2.7b-iii). Overall, trends identified at yearly and decadal scales were characterized by wide confidence intervals in regions where data were sparse for particular values, so that interpretations of patterns identified within those ranges should be taken with caution (Figs. 2.5, 2.6, & 2.7).

When modelling the entire study period, we found the overall topographic and oceanographic characteristics of sperm whale habitat generally mirrored decadal patterns (Figs. 2.8 & 2.9b). However, while the full model captured the prevalence of sperm whales in northwestern and northeastern waters off the archipelago, it appears to overestimate the likelihood of sperm whale presence towards the southern and eastern limits of the study area, which were mostly characteristic of the 2010's study period (Fig. 2.4d). Furthermore, excluding interactions between environmental variables and year resulted in low predictive accuracy and GOF compared to dynamic decadal models (Table 2.2).

a. Best PA model



b. Best QIC model

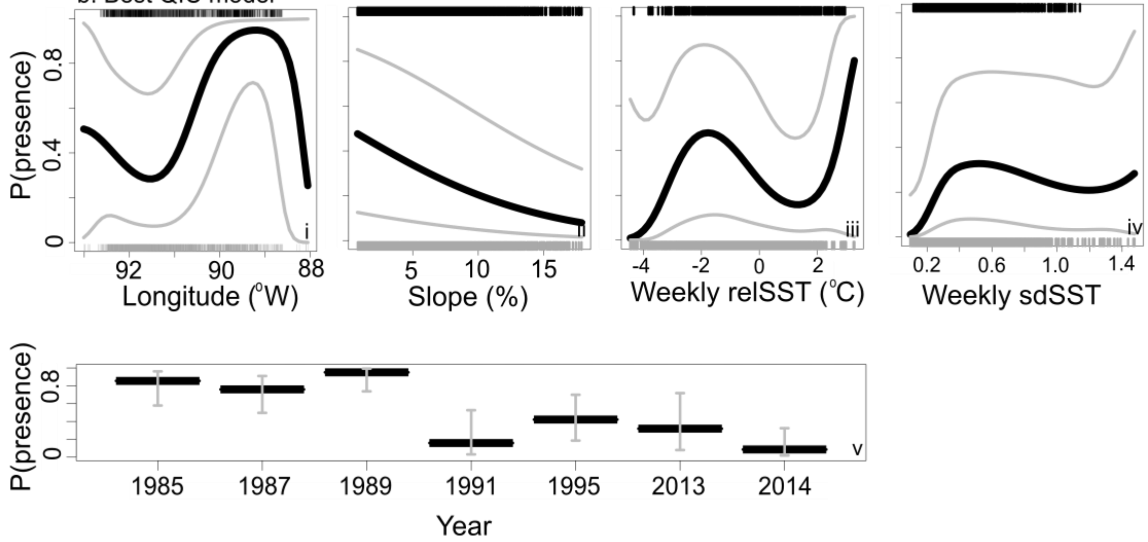
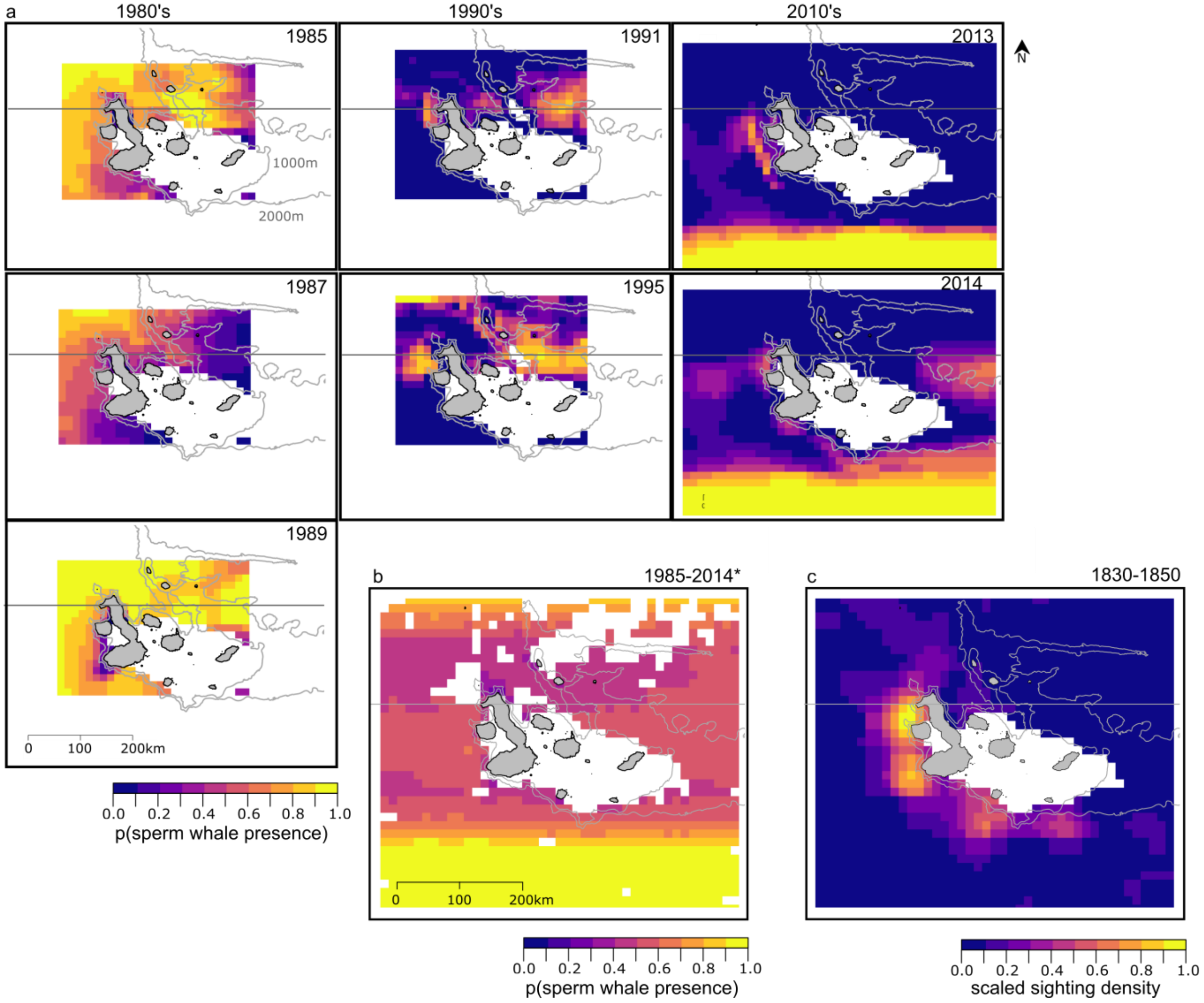


Figure 2. 8 Modelled effect of geographic, topographic, and oceanographic variables on sperm whale presences for the 1985-2010's study period. In (a) the model with best predictive accuracy (PA), sperm whale presence is modelled as a function of (i) latitude, (ii) weekly relative sea surface temperature (relSST), (iii) monthly standard deviation of sea surface temperature (sdSST), and (iv) year at 0.1° spatial resolution. For the model preferred based on QIC, sperm whale presence is modelled as a function of (i) longitude, (ii) slope, (iii) weekly relSST, (iv) weekly sdSST, and (v) year at 0.5° spatial resolution. Rug plots of observed data from positions during which whales were found in black, and when whales were being searched for in grey.

2.4.2 Comparing modern habitat to historic distribution

The modern modelled distribution of whales within surveyed areas resembles historic areas of high sighting density (Fig. 2.9). However, the predicted distribution of whales outside of each decade's study area was very different from the historic distribution in those regions (Fig. 2.9a & b). In 1985 and 1989, whales were predicted over most of the surrounding waters off the archipelago (Fig. 2.9a). Similarly, models for the 2010's predicted a high prevalence of whales south of 2ºS (Fig. 2.9a).



*Model includes data collected in 1985, 1987, 1989, 1991, 1995, 2013 and 2014.

Figure 2. 9 Maps of (a) annual probabilities of sperm whale presence as a function of geographic, topographic, and oceanographic variables for the1980's—1985, 1987, and 1989, 1990's—1991 and 1995, 2010's— 2013 and 2014, (b) the entire study period (1985-2014) from models preferred based on predictive accuracy, and (c) kernel density of sperm whale sightings recorded in by whaling vessels' logbooks off the Galápagos Islands between the 1830's-1850's. Historic data from Hope & Whitehead (1991). Predicted annual probabilities are extrapolated outside of the study region. The equator, 1000 m, and 2000 m contours are shown.

In the 1830-1850 records, relative densities surrounding the south, west, and northwest of the islands did vary among decades (Fig. 2.10), but there was little to no variation in distant regions, over which low sighting densities occurred throughout (Fig. 2.10c). Some of these differences between historic and modern distributions may reflect real displacements in modern sperm whale habitat. However, they may also arise from sampling bias towards regions where sperm whales were expected to occur. This is expected since *both* whales were searched for *and* where they were found were regions where sighting densities were high during whaling days. This indicates that we did not sufficiently sample areas outside of the sperm whale's habitat.

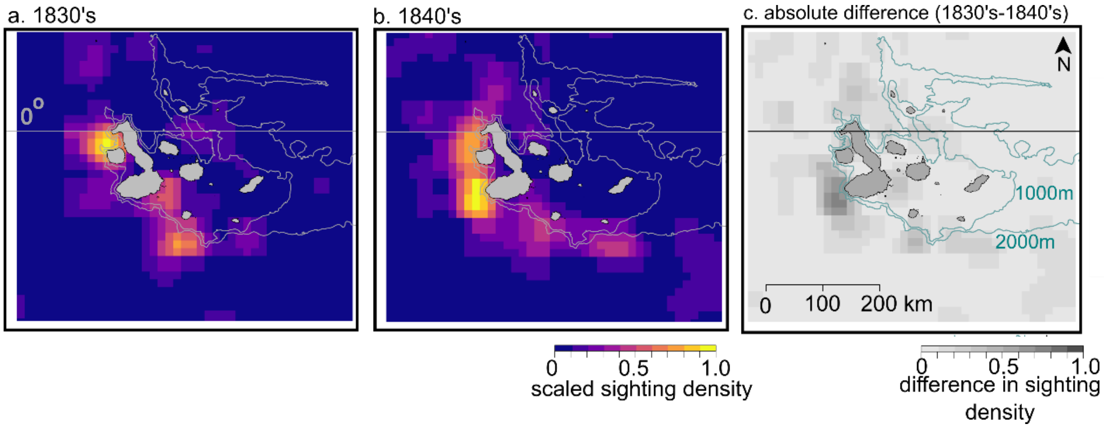


Figure 2. 10 Scaled kernel density maps of sperm whale sightings recorded in whaling vessels' logbooks off the Galápagos Islands in (a) the 1830's, (b) the 1840's, and (c) absolute differences between the two decades. Historic data was compiled by Hope & Whitehead (1991). The equator and 1000 and 2000 m contours are shown for reference.

2.4.3 Overlap of sperm whale habitat and fishing activity

All fishing hours recorded through AIS in 2013 and 2014 were assigned to purse-seine vessels. In 2013, fishing effort concentrated inside the GMR (Fig. 11a), but AIS data failed to capture most fishing activity observed during field work. Coverage was more complete in 2014, during which fishing was exclusively identified outside of the GMR (Fig. 11b). In 2013, high overlap scores occurred in a small area within the GMR west of Isabela (Fig. 12a). However, we believe that this image mostly represents gaps in data rather than an accurate account of potential areas of overlap among sperm whales and fishing activity. In 2014, overlap scores were highest outside the southwestern border of the GMR (Fig. 12b) and outside regions where the highest probabilities of sperm whale occurrence were predicted (Fig. 9a).

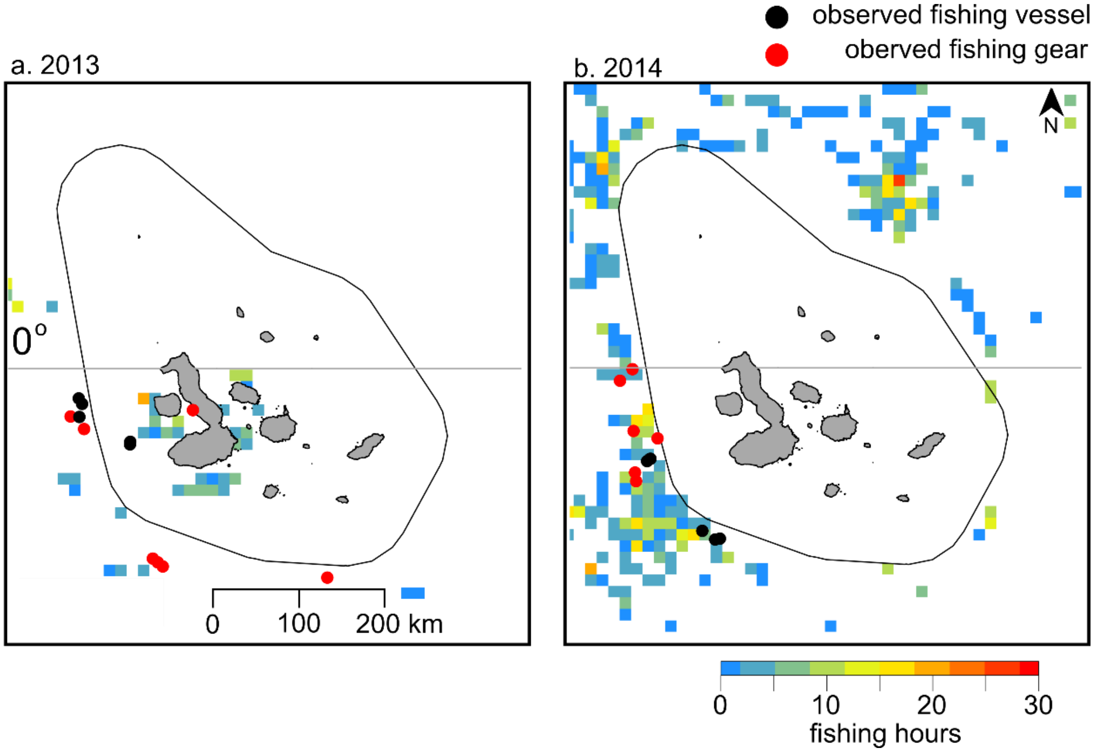


Figure 2. 11 Fishing effort (hours/0.12° cell * year) in (a) 2013 and (b) 2014 measured by automatic information system (AIS). Fishing vessels and fishing gear observed during 2013 and 2014 surveys are shown. The Galápagos Marine Reserve boundary and equator are shown for reference.

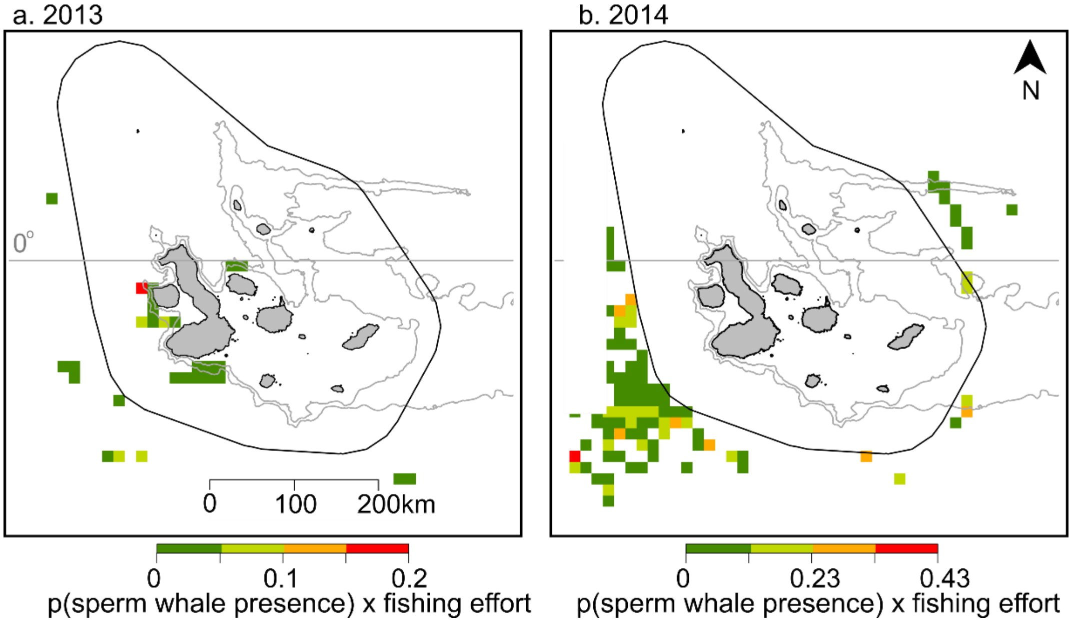


Figure 2. 12 Sperm whale habitat and fishing activity overlap scores (p(whale presence)*fishing hours/maximum(fishing hours)) in (a) 2013 and (b) 2014 off the Galápagos Islands. The Galápagos Marine Reserve boundary, equator, 1000 and 2000 m depth contours are shown for reference.

Historically, although sperm whale sighting densities were highest within the GMR (Fig. 2.9c), sightings frequently occurred outside its boundaries; 41.2% of recorded sightings in the 1830's and 58.1% in the 1840's occurred outside the GMR. In modern surveys, whales were followed outside of the GMPA boundaries 2.5% of the time in the 1980s, 0.6% of the time in the 1990's, and 30.1% of the time in the 2010's. However, these values likely under-estimate habitat use outside of the GMR as most of the modern survey effort occurred within GMR boundaries.

2.5 Discussion

We show that, while the geographical distribution of sperm whales off the Galápagos Islands is quite consistent over long temporal (>100 years) scales, over finer scales (years to decades), sperm whales occupied different regions with different environmental conditions. Both during the 19th century whaling days and modern surveys (1985-2014), whales were found in the western flanks off the Galápagos Archipelago's continental shelf. However, the topography and oceanography over which sperm whales concentrated at the annual and decadal scales shifted. Similarly, where whales were prevalent during one decade, they could be sparse in others. Large scale constancy and fine scale variation in sperm whale habitat have important implications for conservation; although historic and modern sperm whale habitat mostly occurred within the GMR boundaries, in some years whales were prevalent outside, which poses challenges for management.

2.5.1 Sperm whale habitat over centuries, decades, and years

Over centuries and across the Galápagos Archipelago, sperm whales were consistently found in deep waters off the western flanks of the continental shelf, as previously described by Hope and Whitehead (1991) and Whitehead and Hope (1991). This distribution corresponds with highly productive waters influenced by topographically induced upwelling of the Equatorial Undercurrent (Houvenaghel 1978; Palacios 2003; Palacios *et al.* 2006). Sperm whale affinity for areas of high productivity and proximity to steep slopes of oceanic islands at large spatiotemporal scales has been recognized across the Pacific Ocean (Gaskin 1973; Jaquet 1996; Jaquet *et al.* 1996; Rendell *et al.* 2004). The overall association with topographic variables that we identified were similar to those found off Dominica (Milligan 2013) and the Mediterranean (Pirotta *et al.* 2011), although generally deeper waters were used off the Galápagos than in the Mediterranean. Similarly, whales were found in deeper waters in our study than they are usually in the Gulf of California (Jaquet and Gendron 2002; Irvine *et al.* 2017). Differences in depth ranges occupied across ocean basins likely result from different habitat use patterns of squid (Jaquet and Gendron 2002), as well as the availability of waters of different depths (Jaquet and Gendron 2002; Irvine *et al.* 2017). On the other hand, while we expected whales would more likely be found in colder waters associated with upwelling events, we found they were likely to occur in relatively colder *as well as at times* warmer waters. We attribute some of this variation to seasonal changes in the relative SST over which whales were surveyed and found. Additionally, there is a lack of consensus in the association between sperm whale occurrence and SST across studies of sperm whale habitat; Mediterranean whales have been found in colder waters (Pirotta *et al.* 2011) while over the Pacific Ocean and the Gulf of California no straightforward relationships with SST could be identified (Jaquet and Gendron 2002; Jaquet and Whitehead 1996).

Although modern sperm whale habitat was consistent with that of the 19th century, over a finer spatiotemporal scale the location and the environmental conditions over which sperm whales were found varied across decades and years. While in the 1980's, sperm whales were found throughout the study area over a wide range of topographic conditions, their distribution shifted north to the shallow and steep waters of the Marchena Channel in the 1990's, and in the 2010's shifted south of the islands where bottom topography is deeper and flatter. Likewise, the probability of encountering whales also varied across decades so that encounters were more likely to occur in the 1980's than the 1990's and 2010's, which is consistent with previously described sighting rates (Cantor *et al.* 2017). The differences in where, and the topographic and oceanographic conditions in which, sperm whales were found at fine spatiotemporal scales could reflect differences in the distribution of squid patches. Additionally, this variation in habitat use may reflect clan-specific habitat selection behaviours and be driven by the cultural turnover of sperm whale clans that took place between 1985 and 2014 (Cantor *et al.* 2016).

The annual distribution of sperm whales could reflect that of patches of their cephalopod prey (Jaquet and 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 (Taipe *et al.* 2001; Nevárez-Martínez *et al.* 2002; Waluda *et al.* 2006; Waluda *et al.* 2006). We found indications that sperm whales respond to El Niño-induced changes in prey abundance in that for two (1987 and 1991) out of three El Niño years we surveyed (1987, 1991, and 2014), the probability of finding whales was lower than other years within the corresponding decade. However, we did not find consistent patterns in habitat shifts across El Niño years; while in some El Niño years the range of oceanographic and topographic conditions occupied widened, in others it was restricted with respect other years within the same decade. Off the Gulf of California, the distribution and aggregative behaviour of sperm whales was also found to change significantly in relation to dramatic shifts in catch rates of *D. gigas* following a strong El Niño event in 1998 (Jaquet and Gendron 2002). In that case, the distribution of sperm whales during the 1998 El Niño was more widespread than the following cooler year (Jaquet and Gendron 2002).

Variability in the apparent response to decreased prey availability and in topographic, oceanographic conditions where whales were found could result from 1) the ability of sperm whales to endure long periods of time without access to food (Whitehead 2003), 2) culturally driven differences in behavioural responses to environmental challenges, and 3) in the case of our study, a lack of data on the actual location of sperm whale prey. Over short periods (<~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 cost of remaining within a region with relatively low prey density. Even within regions, sperm whales are not most abundant where squid aggregations are densest (Jaquet and Gendron 2002). For instance, off the Galápagos, 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, whales may occupy unsuitable habitat over weeks or even months, which corroborates that presence as a sole an indicator of habitat preferences and quality is inappropriate (Johnson 1980; Morrison *et al.* 2006).

Additionally, different regional, topographic, and oceanographic habitat use patterns found across decades may be a reflection of the cultural shift the region underwent between 2013 and 2014 (Cantor *et al.* 2016). While whales in the 1980's and early 1990's were predominantly of the *Plus-one* and *Regular* clans, in the 2010's they belonged to the *Four-plus* and *Short* clans (Cantor *et al.* 2016). When clans occur sympatrically, members of different clans tend to occupy distinct areas off the archipelago (Eguiguren et al., *in prep.*). 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 and Rendell 2004), which could lead to clan-specific habitat selection behaviours for topographic and oceanographic conditions. Hence, a shift in the cultural composition of the region across decades could explain some of the variation in where and under what environmental conditions sperm whales were found across decades.

Finally, some of the variability and uncertainty in topographic and oceanographic conditions over which whales occurred could be caused by these being indicators, not actual measurements, of the distribution of sperm whale prey. While topography, SST, and SST-derived indicators of oceanic fronts are commonly used to model sperm whale habitat (Jaquet 1996; Jaquet and Whitehead 1996; Praca *et al.* 2009; Pirotta *et al.* 2011; Wong and Whitehead 2014), these do not indicate the actual distribution of bathypelagic squid off the Galápagos Islands. Additionally, the use of surface indicators to infer pelagic productivity directly below may be inadequate in cases where surface processes are spatially and temporally displaced with respect to the deep water environment (Jaquet 1996). However, incorporating prey data to model the habitat of top oceanic predators does not necessarily increase model performance (Torres *et al.* 2008). Other environmental characteristics could improve certainty and consistency in modelling sperm whale distributions. For instance, Palacios *et al*. hypothesized that sperm whales may be drawn to areas where the oxygen minimum zone (OMR)—within which bathypelagic squid tend to concentrate—is closer to the surface (2013). Thus, measuring OMR depth could contribute in more precisely modelling sperm whale habitat over fine and meso-scales (Palacios *et al.* 2013).

2.5.2 Effect of scale

While final decadal habitat models that were chosen based on QIC and predictive accuracy were of intermediate or coarse spatial resolutions, we found no consistent relationship between spatial scale and predictive accuracy. Similarly, we found no relationship between predictive accuracy and the temporal scale (weekly or monthly) at which oceanographic variables were included. This was initially unexpected given previous findings that the strength of relationships between environmental variables and sperm whale presence was dependent on spatial resolution (Jaquet and Whitehead 1996). However, it is possible that scale dependency can only be detected if both the species response and explanatory variables are analyzed over varying scales (Cotté *et al.* 2011; Graf *et al.* 2005). Our habitat models spanned spatial scales from ca. 10-50 km. While these reflect hourly and daily sperm whale displacement distances (Whitehead *et al.* 2008), they represent only mesoscale oceanographic processes (Mannocci *et al.* 2017; Torres 2017). Thus scale dependency is likely only detectable when a broader range of scales (fine: 100 m – 5 km, and large: 500 km – 1000 km), is considered (Jaquet and Whitehead 1996; Mannocci *et al.* 2017; Torres 2017).

2.5.3 Implications for conservation

Our analysis of sperm whale distribution provides insights into the strengths and weaknesses of the GMR as a tool to protect the habitat of a highly mobile nomad. While regions where sperm whales were most commonly sighted 200 years ago and in modern times occurred within GMR boundaries, historically and recently they also occupied waters outside the GMR. Most recently, we spent as much as a third of our time following whales outside the protected area. Therefore, descriptions of suitable habitat for sperm whales over short periods of time (i.e. a few decades) may not capture their overall use of space. The temporal variability in marine mammal distribution has been recognized as a challenge for place-based conservation efforts with fixed boundaries (Reeves 2000; di Sciara *et al.* 2016). Our results provide an example of the value of using long term studies to identify critical habitat (Gerber *et al.* 2003; Hooker and Gerber 2004), as well as the potential importance of a dynamic and adaptive approach to the management of highly-mobile long-lived marine mammals (Hyrenbach *et al.* 2000; Hobday and Hartman 2006; Wedding *et al.* 2016).

Specifically, the overlap between fishing effort and sperm whale habitat that we found southwest of the GMR boundary in 2014 could be the basis for a precautionary buffer zone against fishing activities surrounding the marine reserve. Although we underline that our representation of fishing activity is currently incomplete, if the use of AIS continues to be promoted by national governments and international agencies, valuable information could be generated towards identifying areas of overlap between vulnerable species and commercial fisheries throughout the region.

2.6 Conclusions

We show that, while over centuries sperm whale habitat around the Galápagos Archipelago is consistent, within decades and within the region, it is highly variable and hard to predict. We suggest that the variable and complex nature of sperm whale distribution should be taken into account to evaluate existing protected areas and inform conservation efforts. However, the Galápagos Archipelago represents only a fraction of the home range of Eastern Tropical Pacific sperm whales (Whitehead *et al.* 2008a; Cantor *et al.* 2016), and little is known about how this nomadic species moves across the basin. The use of long-term basin-wide passive acoustic monitoring (PAM) would help clarify conditions that drive large scale movements within the Pacific, as well as provide valuable information for basin-wide conservation efforts.

CHAPTER 3 – Habitat use of culturally distinct Galápagos sperm whale (*Physeter macrocephalus*) clans[1,2,3]

3.1 Abstract

Ecological niches are traditionally defined at the species level, but individual niches can vary considerably within species. Research on intra-specific niche variation has been focused 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 theorized to generate culturally distinct clans which at times occur sympatrically. Clans have distinct dialects, social norms, 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 vocalizations and association, and collected environmental variables as proxies of sperm whale prey. We used logistic Generalized Additive Models, fitted with Generalized Estimating Equations to account for spatiotemporal autocorrelation, to predict clan identity as a function of environmental variables. To account for the effect of scale, we fitted models at alternative spatiotemporal resolutions. Spatiotemporal scale did not affect predictive ability or overall differences in habitat use patterns between the clans. 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 selecting areas where members of their clans occur. By identifying differences among clans' space use, we

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[2] *Author's contributions: A Eguiguren analyzed data and wrote the initial version of the manuscript, E Pirotta assisted in conceptual design and statistical analysis, M Cantor and L Rendell collected data and analyzed acoustic data, and H Whitehead initiated the conceptual design, supervised the project, and collected data, and all authors participated in writing and editing.*

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have uncovered another level of sperm whale life that is likely influenced by their cultural nature.

3.2 Introduction

Traditionally, ecological niches and habitats have been defined at the species level (Hutchinson 1957; Leibold 1995). However, mounting evidence for individuals of the same population having niches that overlap only slightly attests that conspecifics are not always ecologically equivalent (Bolnick *et al.* 2003). To date, most of the theoretical work on individual niche variation has focused on intrinsic sources of variation, such as morphological, physiological, and ontogenic traits (Roughgarden 1972; Van Valen 1965; Svanbäck and Persson 2004). Less attention has been given to the contribution of drivers of individual niche variation operating at shorter time scales, such as social transmission (Galef 1976; Laland *et al.* 2000; Slagsvold and Wiebe 2007; Sargeant and Mann 2009).

When behavioural traits are socially learned and shared among groups of individuals, there is culture (Boyd and Richerson 1996; Laland and 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. Examples in the wild abound (Laland and Galef 2009; Whitehead and Rendell 2014). Notable cases include apes and monkeys using different tools to exploit nuts and termites (McGrew *et al.* 1979; Boesch *et al.* 1994; Whiten *et al.* 1999; van Schaik *et al.* 2003; Ottoni and Izar 2008), birds copying feeding areas and prey sizes of their parents (Slagsvold and Wiebe 2011), female mountain sheep retaining the home ranges of their social groups (Geist 1971), dolphins using the foraging tactics of their mothers or peers (Mann and Patterson 2013; Whitehead and Rendell 2014), 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 individuals of the same population (Jaeggi *et al.* 2010; Slagsvold and 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 (Laland and Galef 2009; Koops *et al.* 2013). One way to overcome this issue is excluding all sources of non-cultural behavioural variation (Whiten *et al.* 1999), but this has proved to be problematic (Laland and 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 but feed exclusively on very different prey (Ford *et al.* 1998). Off Shark Bay, Australia, a subset of a bottlenose dolphin population use marine sponges as tools to forage on the seafloor for prey that are hard to access otherwise (Mann *et al.* 2012), 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 (Krützen *et al.* 2005; Mann *et al.* 2012; Riesch *et al.* 2012).

Ranging over much wider spatial scales, is the case of sympatric cultural divergence among female sperm whales (*Physeter macrocephalus*) into clans. While males lead mostly solitary lives in higher 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 and 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 and Whitehead 2003). Members of different clans can encounter one another easily, in theory, but they not only maintain distinct vocal dialects over time (Rendell and Whitehead 2005), but also differ in movement patterns, reproductive and foraging success, and isotope signatures (Whitehead and Rendell 2004; Marcoux 2005; Marcoux *et al.* 2007; Cantor and Whitehead 2015). These divergences suggest that sperm whales belonging to culturally distinct but sympatric clans may have distinct habitat selection behaviour or resource use patterns, but this has not yet been studied.

Understanding the sperm whale habitat is hampered by logistical constraints. Their trophic niche, for instance, remains relatively unknown because they live offshore and feed at great depths (Papastavrou *et al.* 1989), making direct observations of predation very rare until recently. Over the last decade, the use of bio-logging and acoustic tags and passive acoustic monitoring (PAM) have provided insights on sperm whales' foraging behaviours (Amano and Yoshioka 2003; Thode *et al.* 2004; Aoki *et al.* 2007; Aoki *et al.*2012). However, the specific composition of sperm whale diet remains uncertain; different sources of indirect evidence (such as stomach content or defecation analyses) yield contrasting results regarding the species composition of sperm whale cephalopod prey (see Clarke et al. 1988; Smith and Whitehead 2000; Clarke and Paliza 2001).

Alternatively, the relationship between sperm whales and their habitat can be characterized by the environmental variables—such as bottom topographic features and oceanographic conditions associated to upwelling and frontal activity (Jaquet and Whitehead 1996)— that influence the distribution of their cephalopod prey (Jaquet and Whitehead 1996; Pirotta *et al.* 2011; Wong and Whitehead 2014). Although relationships between sperm whale presence and oceanographic variables tend to become stronger over larger spatial scales (Jaquet 1996; Wong and Whitehead 2014), scale-dependent relationships between organisms and their habitats can be incorporated by a multi-scale modelling approach (Levin 1992; Graf *et al.* 2005; Pirotta *et al.* 2014).

Here, we employed a multi-scale approach to evaluate whether sympatric sperm whale clans differ in habitat use. We analyzed potential differences in spatial, oceanographic, and topographic characteristics of the waters occupied by clans off the Galápagos Islands over a range of spatial and temporal scales. Specifically, we compared the habitat use of two vocal clans that were particularly common in the area in the 1980's (Rendell and Whitehead 2003), and of two other clans that have recently replaced them in the 2010's (Rendell and Whitehead 2003; Cantor *et al.* 2016). 3.3 Methods

3.3.1 Field Methods

We studied whales off the Galápagos Archipelago (93º-88ºW; 3ºN-3ºS) aboard dedicated research sailboats (10-12 m) between January and June, in years from 1985 to 2014 (1985, 1987, 1989, 2013 and 2014) (Table 3.1). 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 conditions. Upon encountering 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 hr) visual and/or acoustic contact with the same group of females as *encounters*.

Table 3. 1 Summary of time spent following female and juvenile sperm whales during the 1980's and 2010's surveys off the Galápagos Islands. Encounters were defined as consecutive geographic positions that were assigned to the same clan and occurred within < 6 hr of each other.

				Encounters with identified clans			
Year	Surveyed period	Days spent following whales	Encounters with females and immatures[a]	*Regular*	*Plus-One*	*Short*	*Four-Plus*
1985[c]	Jan 18 – Apr 22	29	12	10	1	1	0
1987	Jan 2 – Jun 30	51	21	12	7	1	0
1989	Apr 4 – May 22	32	16	10	3	0	1
2013 (Southern)[b]	Apr 9 – Apr 12	4	9	0	0	3	2
2013[c] (Western)[b]	Jan 3 – Feb 21	10	2	0	0	0	2
2014 (Southern)[b]	Jan 23 – May 22	24	11	0	0	2	3
2014[c] (Western)[b]	Jan. 13 – Feb 10	2	1	0	0	0	1
	Total	167	80	36	11	7	7

a. Encounter number includes encounters for which clan identity was not assigned

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

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

Groups of females and immatures (identified based on body size and behaviour as in Whitehead 2003) were followed for as long as possible, during which the vessel's geographic location (and thus the whales') was recorded. Between 1985 through 1993, positions were estimated by interpolation from SATNAV fixes at least every 3 hr; after 1993, positions were recorded every 1-5 min using GPS (Whitehead and Rendell 2004).

3.3.2 Clan identification

We assigned clan identity to groups of female and immature sperm whales based on the similarity of their communication sounds, called codas (Rendell and 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 and Whitehead 2003). At least 4 vocal clans were commonly sighted around Galápagos: *Regular* (typically produce 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 that begin with a set of 4 regular clicks; Rendell and Whitehead 2003, Cantor *et al.* 2016).

We assigned clan memberships to all groups of whales that were photo-identified together and had their acoustic repertoire sufficiently sampled (see Rendell and Whitehead 2003, Cantor et al. 2016). Geographic positions within a day were assigned to a corresponding clan because: 1) typically only one group of 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 and Rendell 2004). However, in 4 multiple-day encounters, more than one 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 (06:00-18:00h GMT-6), during which photo-identifications were available (Whitehead and Rendell 2004).

3.3.3 Environmental variables

We used topographic and oceanographic variables associated with increased bathypelagic cephalopod prey biomass (Jaquet and Whitehead 1996; Jaquet and Gendron 2002; Pirotta *et al.* 2011; Wong and Whitehead 2014). As topographical variables, we used depth, obtained from the General Bathymetric Chart of the Oceans at 0.008 º resolution (http://www.gebco.net/data_and_products/gridded_bathymetry_data/),slope incline (%), calculated using 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) at 4km resolution and processed by the NOAA National Oceanographic Data Center for 1980's data points, and Aqua-MODIS satellite images at 4km resolution distributed by the NOAA CoastWatch Program and NASA's Goddard Space Flight Center for 2010's data points ((Griffin 1999; Praca *et al.* 2009; Pirotta *et al.* 2011; Table 3.2). We used relSST instead of actual SST to account for annual variations in temperature, and calculated it as the difference between SST at a geographic position and the mean SST over the entire Galápagos region (defined as 93º-88ºW; 2ºN-2ºS for the 1980's period and 93º-88ºW; 1.5ºN-2ºS for the 2010's period) for the corresponding month (Pirotta *et al.* 2011).

Table 3. 2 Oceanographic and topographical variables and corresponding spatial and temporal resolutions used to model niche differences among sperm whale clans off the Galápagos Islands in 1980's and 2010's study periods.

Covariates	**Temporal resolutions**
Depth (m)	-
Slope (% rise)	-
Relative sea surface temperature (relSST) (ºC)	weekly, monthly
Standard deviation of sea surface temperature (sdSST)	weekly, monthly
Chlorophyll-a concentration (Chla) (mg m^{-3})[a]	weekly, monthly
Eddy kinetic energy (EKE) (cm^2 s^{-2})[a]	weekly, monthly
Sea surface height anomaly (SSHA) (cm)[a]	weekly, monthly

We also considered the following oceanographic variables for 2013 and 2014 positions which were not available for earlier study years: surface chlorophyll-a concentration (Chla) as a measure of primary productivity available through the NOAA CoastWatch

Program Aqua-MODIS satellite images; eddy kinetic energy (EKE) as a measure of mesoscale turbulent activity, and sea surface height anomaly (SSHA) as an indicator of upwelling/downwelling (available through AVISO services and downloaded using ArcGIS Marine Geospatial Ecology Tools; Roberts *et al.* 2010). The latter has been found to be associated with the distribution of top predators (Nel *et al.* 2001; Tew Kai *et al.* 2009; Wong and Whitehead 2014). Since the cephalopods that sperm whales prey upon are themselves predatory, there is an expected temporal lag of about 3-4 months between primary productivity peaks and increases in cephalopod biomass (Jaquet 1996; Pirotta *et al.* 2011). Thus, we considered the Chla concentration averaged over the three months prior to the encounter date. Finally, we used latitude and longitude to account for spatial variation unexplained by oceanographic and topographical variables.

We extracted values of depth, slope, EKE and SSHA data for geographic positions using the raster package in R environment (R Core Team 2016). We obtained SST and Chla values for each geographic position using the rerddapXtracto R package (Mendelssohn 2016). To find appropriate temporal and spatial scales at which differences in clan niches could be identified we generated models that included variables extracted at fine (0.10°), medium (0.30°), or coarse (0.50°) spatial resolutions. Oceanographic variables were included either as weekly or monthly averages to reflect the duration of mesoscale oceanic features (upwelling, fronts, and eddies) which we assumed to influence sperm whale distribution (Mannocci *et al.* 2017) (Table 3.2).

3.3.4 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). We used a working independence model within GEEs, which is preferred when the true nature of the correlation is unknown (Liang and Zeger 1986; McDonald 1993; Pan 2001). The independence GEE model results in inflated—

and more realistic—estimates of uncertainty compared with a GAM lacking correction for autocorrelation, but does not affect parameter estimation.

We analyzed data collected in the 1980's and in the 2010's separately, because different clans were sighted during each of these periods (Table 1; see also Cantor et al. 2016): *Plus-One* and *Regular* in the 1980's; *Short* and *Four-Plus* in the 2010's. We binarized records in each pairwise comparison (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 represents one group of whales. All locations within each encounter were included within a block. Autocorrelation function (ACF) plots of individual encounters for final models (see below) converged to zero, indicating that encounter was an appropriate blocking variable (Scott-Hayward et al. 2013;Appendix VI). We only entered latitude and longitude as cubic splines, while other variables were treated as linear terms, because we expected that differences in habitat use patterns for oceanographic and topographic variables would be monotonic. However, this assumption means that our results were not able to capture differences in habitat use if these are actually not monotonic.

We subsampled/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 (see Appendix VII for further details).

To identify and avoid collinearity, we calculated correlation coefficients for all pairs of explanatory variables at each spatial and temporal resolution (Appendix VIII). When variables were collinear ($|r| > 0.4$), we fit alternative initial models that included only uncorrelated variables.

3.3.5 Model selection

To select the most parsimonious spatiotemporal scale, combination of uncorrelated variables, and the best shape (either linear or cubic splined) at which latitude and longitude should be included, we used the quasi-likelihood under the assumption of independence criterion (QIC)— an adaptation of Akaike's information criterion (AIC) for GEEs (Pan 2001; Cui and Qian 2007) available in the MuMIn R package (Barton 2016).

First, we fitted alternative initial models of uncorrelated variables at each spatiotemporal resolution, in which latitude and longitude were entered as either linear terms or cubic splines, and used QIC to select the best shape at which these should be entered (Fig. 3.1). Next, we used backwards stepwise selection to determine which variables should be retained at each spatiotemporal scale (Fig. 3.1). We finally chose the model with the spatiotemporal resolution that resulted in the lowest QIC (Fig. 3.1).

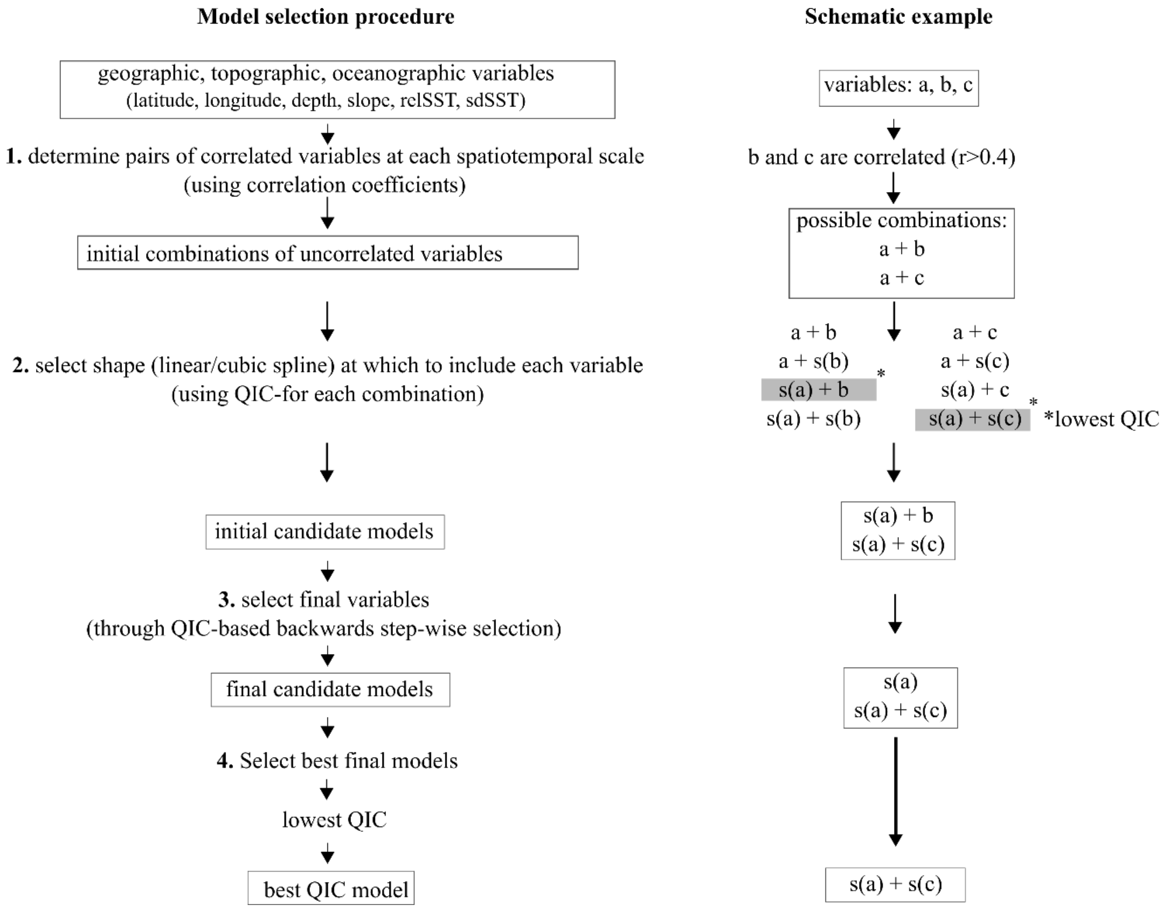

Figure 3. 1 Selection procedure steps (1-4) for modeling differences in habitat use of sperm whale clans off the Galápagos Islands. A schematic example is shown where a, b and c represent environmental variables. In step 2, variables included in models as cubic splines are bounded by “s()” and variables included as linear terms are unbounded.

We also fit null models which included only latitude and longitude, aiming to capture variation in the differences in clan habitat use that could not be accounted for by any of the oceanographic or topographic variables available, while investigating 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.

3.3.6 Prediction maps

To examine the 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 (Appendix IX). We also generated a map 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.

3.3.7 Validation

To validate the final models, we analyzed the following three aspects of predictive performance. First, we used goodness of fit (GOF), i.e. how well the final models fit the data. To measure GOF, we generated confusion matrices assessing model accuracy in predicting the data used to fit models (Fielding and Bell 1997). Second, we used leave-one-out cross validation (LOO), which quantifies how accurately a model predicted clan identity for an encounter when that encounter was iteratively removed from the data used to fit the model. We calculated the percentage of geographic positions in each encounter for which clan identity was correctly assigned (Hastie *et al.* 2009). Finally, we used external cross-validation, i.e. 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 1980's models and for whales found in the western region during 2013 and 2014 for the 2010's models.

We compared these three aspects of performance of the final models for each study period to those of corresponding null models. To account for the effect of spatial and temporal scale on the performance of the final model, we compared its three performance indicators to those of equivalent models in which the same variables were included at alternative spatiotemporal scales. We only compared performance measurements across models of different spatiotemporal scales when altering spatial scale did not result in collinearity.

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 and Bell 1997; Sing *et al.* 2005).

3.4 Results

3.4.1 1980's clans

We analyzed 596 geographic positions collected between 1987 and 1989. Most encounters occurred in the west and northwest of the archipelago (Fig. 3.2a), and lasted between an hour and 6 days, averaging 1.6 days (SD = 1.4 days). We fit 8 alternative initial models at the fine spatial resolution, and 6 at intermediate and coarse resolutions (Appendix X Tables S10.1-S10.3). Our final model included latitude and longitude as cubic splines and slope, weekly relSST, and weekly sdSST as linear terms at a fine spatial resolution (GOF = 89.77%) (Appendix X Tables S10.4-S10.6). These variables were also included in preferred models at intermediate and coarse spatial resolutions (except for weekly sdSST, which was correlated with slope).

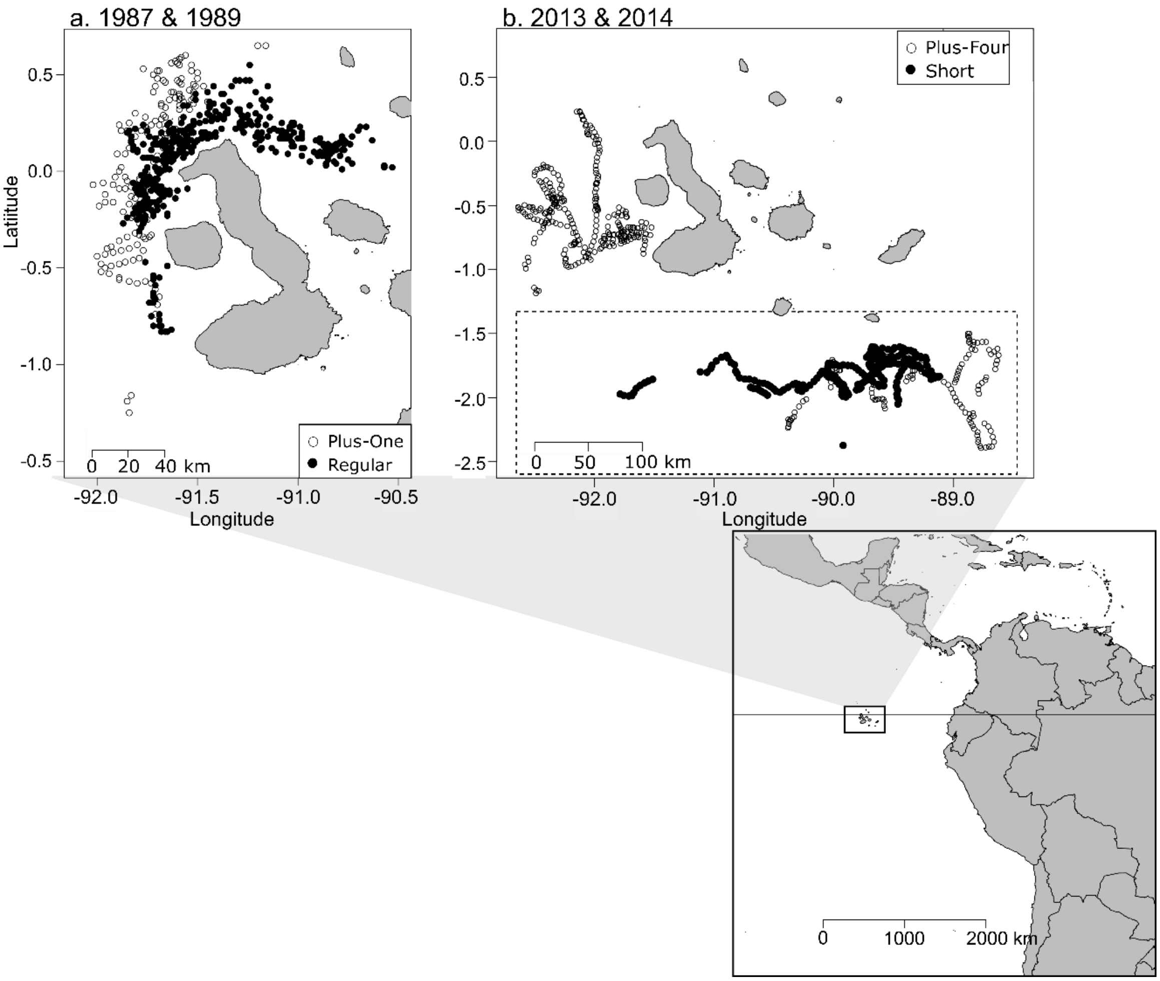

Figure 3. 2 Geographic positions in (a) 1987 and 1989 of Plus-One and Regular clan sperm whales, and (b) in 2013 and 2013 of Plus-Four and Short clan sperm whales off the Galápagos Islands. The southern region that was included in the 2010's period is delineated by the dashed rectangle. Insert shows position of islands in relation to South and Central America.

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. 3.3a-i). The predominantly northern distribution of *Plus-One* whales identified by the final model 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 found (Fig. 3.4a-i). *Plus-One* whales were also found to predominantly in more western waters, but uncertainty in predicting clan identity increased east of the archipelago (91° W; Fig. 3.3a-ii). The western distribution of *Plus-*

One whales identified by the model is consistent with the observed distribution of *Plus-One* whales throughout study years, which was restricted to areas west of 91.5º W, and with the distribution of *Regular* clan whales, which occurred throughout the longitudinal range of sperm whale distribution (Fig. 3.4a-ii). High uncertainty in predicting clan identity in the east likely resulted from the small number of encounters that occurred in that area (Fig. 3.4a-ii). Although our final model included slope, weekly relSST, and weekly sdSST, the modelled relationship among these variables and clan identity (Figs. 3.3a-iii-v)did not reflect the observed slope, relSST, and sdSST at which the clans were found (Figs. 3.4a-iii-v).

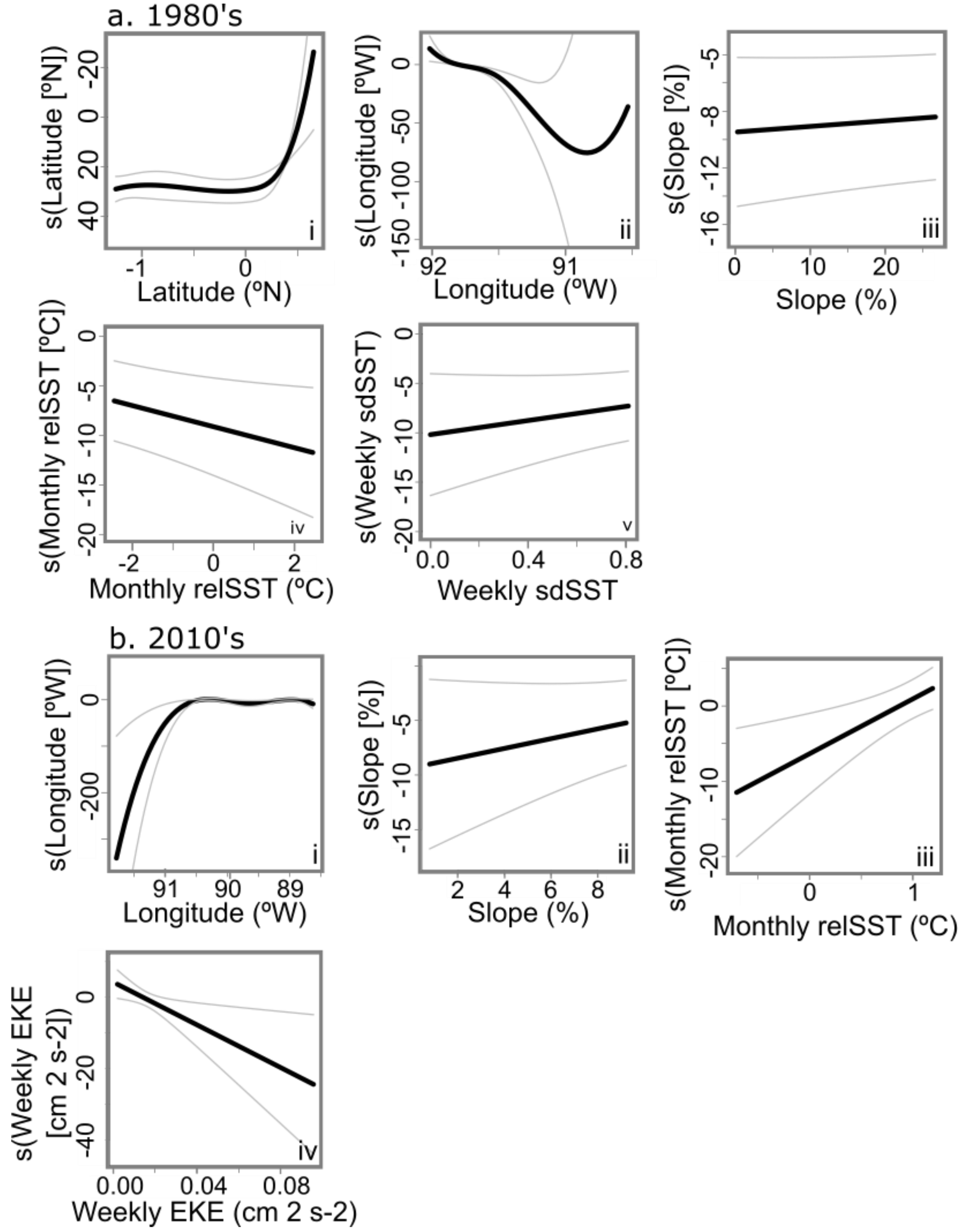

Figure 3. 3 Partial plots of loge(odds) of female and juvenile sperm whales found off the Galápagos Islands belonging to (a) the Plus-One clan in the 1980's study period and (b) the Plus-Four clan in the 2010's study period. (a) In the 1980's, clan identity = Plus-One is modelled as function of (a-i) latitude, (a-ii) longitude, (a-iii) slope incline, (a-iv) monthly relative sea surface temperature (relSST), and (a-v) weekly standard deviation of SST (sdSST) at fine spatial resolution (0.10º). (b) In the 2010's, clan identity = Plus-Four is modelled as a function of (b-i) longitude, (b-ii) slope incline, (b-iii) monthly relSST, and (b-iv) weekly eddy kinetic energy (EKE) at coarse spatial resolution (0.50º). Grey lines represent 95% confidence intervals.

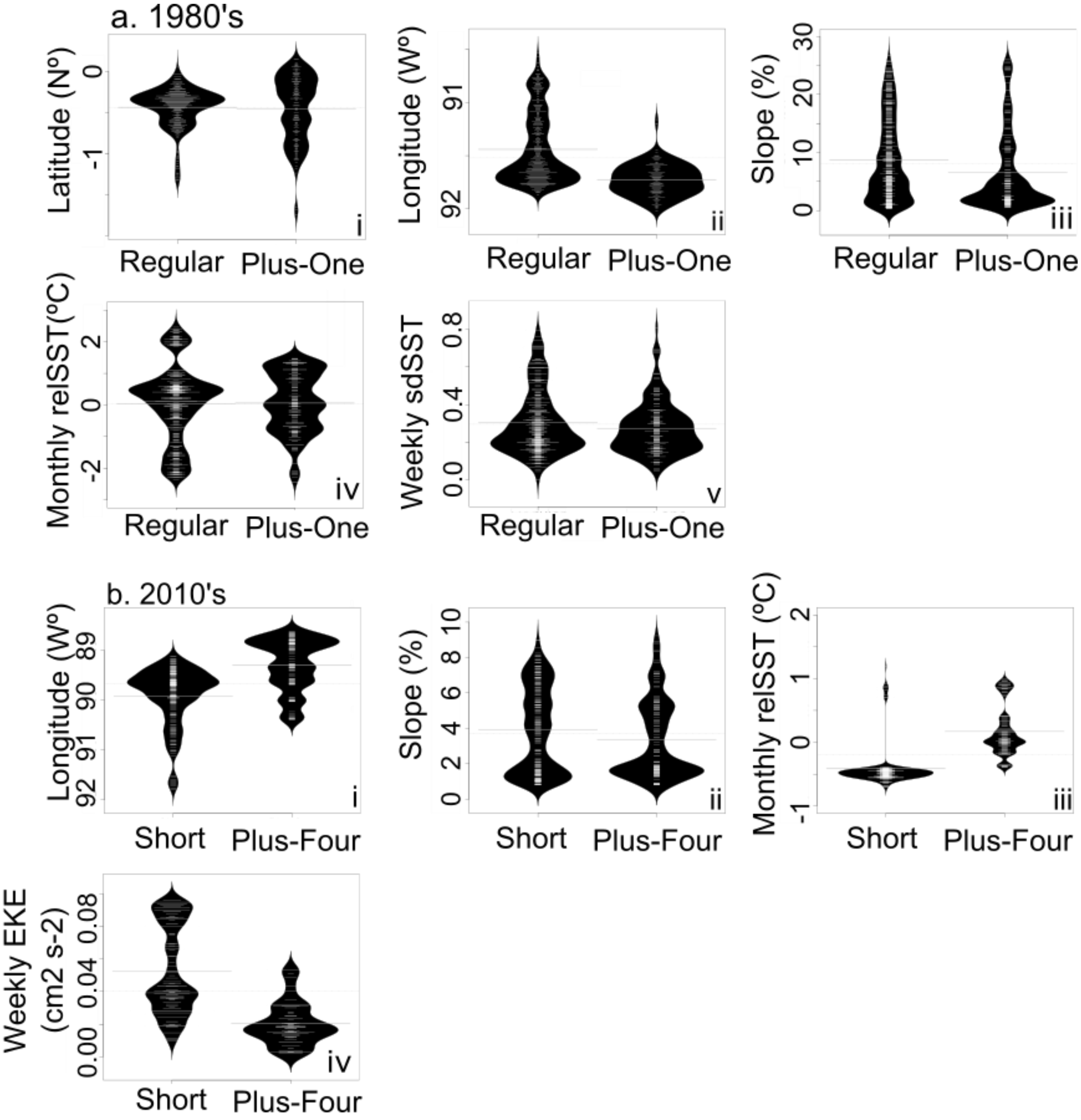

Figure 3. 4 Bean-plots of observed geographic and oceanographic variables by clan; (a) shows the 1980's distribution of variables at a fine spatial resolution (0.10°) in which Plus-One and Regular clan whales were found off the Galápagos Islands: (a-i) latitude, (a-ii) longitude, (a-iii) slope incline, (a-iv) monthly relative sea surface temperature (relSST), and (a-v) weekly standard deviation of sea surface temperature (sdSST); (b) shows the 2010's distribution of variables at a coarse spatial resolution (0.50º) in which Plus-Four and Short clan sperm whales were found: (b-i) longitude, (b-ii) slope incline (%), (b-iii) monthly relSST, and (b-iv) weekly eddy kinetic energy (EKE).

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 (Figs. 3.5a-i & ii). These two models predicted identical clan distributions in areas close or far to 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. 3.5a-iii).

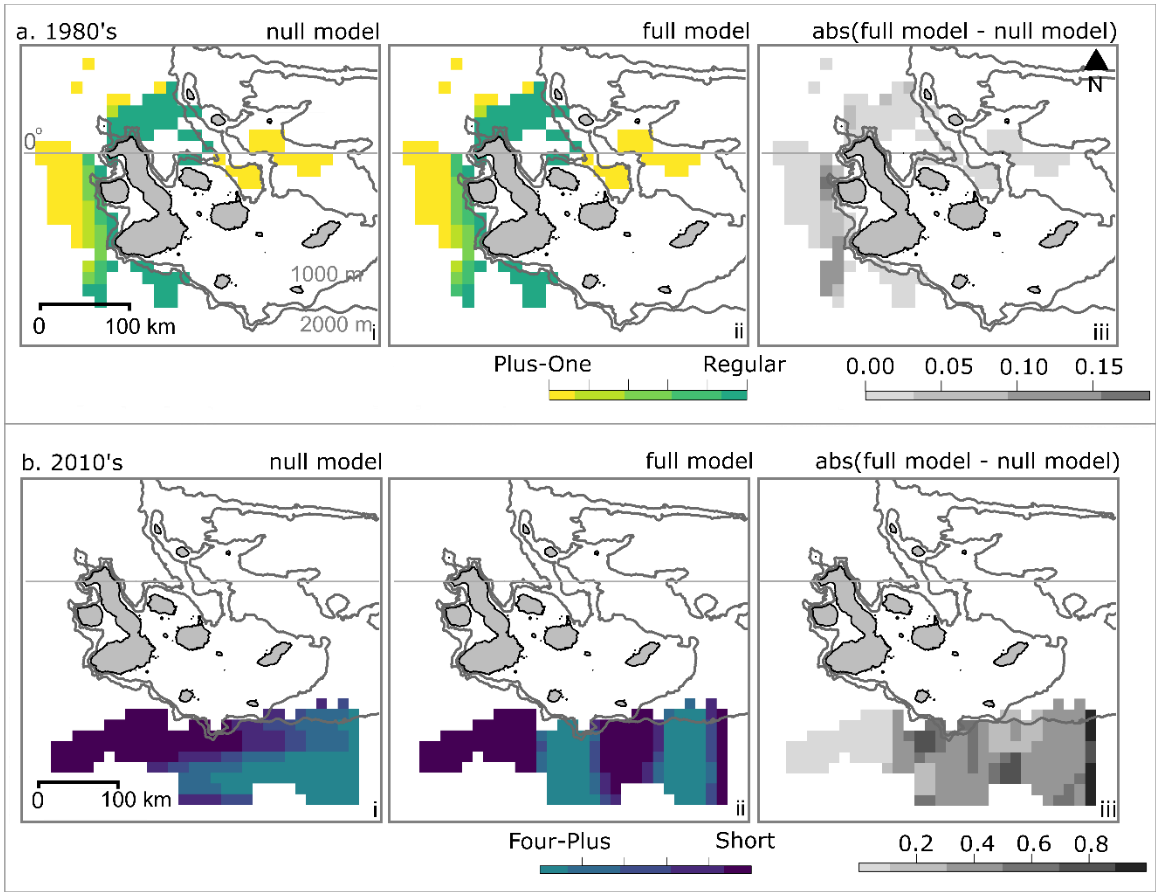

Figure 3. 5 Predicted distribution of sperm whales of different clans off the Galápagos Islands. (a) Sperm whales of the *Plus-One* and *Regular* clans in 1987 and1989 as a function of (a-i) a full model, (a-ii) a null model (latitude and longitude only), and (a-iii) absolute difference between the full and null models. (b) sperm whales of the *Short* and *Plus-Four* clans in 2013 and 2014 as a function of (b-i) a full model, (b-ii) a null model (latitude and longitude only), and (b-iii) the absolute difference between the full and null models. 1000 and 2000 m depth contours are shown.

The inclusion of oceanographic and topographic variables in the final model did not significantly improve the goodness of fit or the average predictive accuracy through LOO cross-validation in comparison to the null model (Fig. 3.6a). Moreover, the inclusion of these variables did not improve the null model's ability to predict the clan identity of whales found in 1985 (Fig. 3.6a).

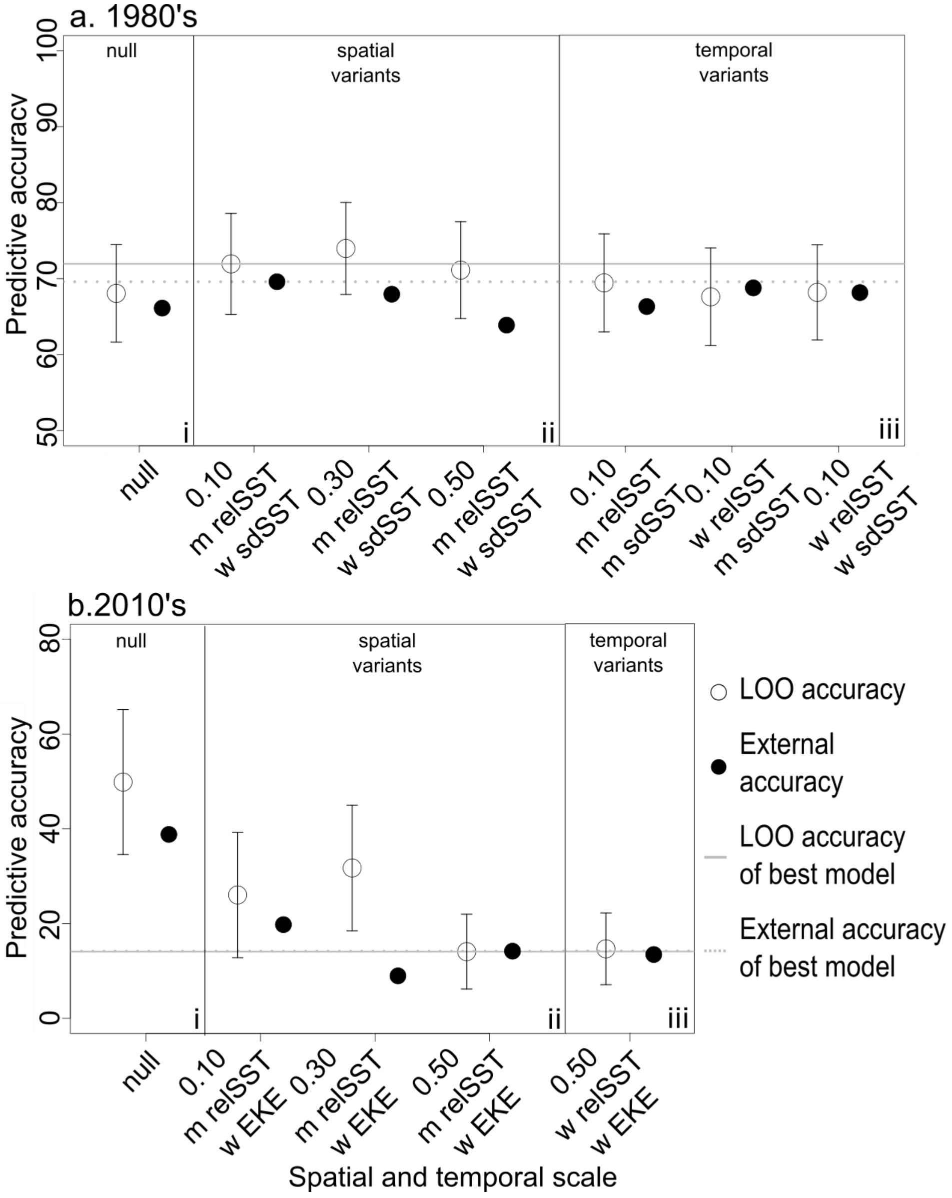

Figure 3. 6 Predictive accuracy (%) of models of clan identity of sperm whales off the Galápagos Islands in (a) 1987 and 1989, and (b) 2013 and 2014 in which only latitude and longitude are included (null; a-i, b-i), at alternative spatial (a-ii, b-ii) and temporal (a-iii, b-iii) (w = weekly, m = monthly) resolutions. Predictive accuracy was measured through leave-one-out (LOO) and external cross-validation. Standard errors are shown for LOO accuracy.

The predictive performance of models varied slightly over different spatial and temporal resolutions (Fig. 3.6a). The most parsimonious model based on QIC (0.10° spatial resolution, relSST at monthly resolution and sdSST at weekly resolution) had higher predictive accuracy for external data than other spatial resolutions, but lower LOO accuracy than an intermediate (0.30°) spatial resolution model (Fig. 3.6a-i). Compared to alternative combinations of temporal resolutions of relSST and sdSST, the final model had higher performance based on LOO and external evaluations (Fig. 3.6a-ii). However, parameter estimates had similar magnitude and direction for all variables across spatial scales, except that including sdSST at a monthly resolution resulted in an opposite effect (Appendix X Table S10.7).

3.4.2 2010's clans

Between 2013 and 2014, we analyzed 370 geographic positions to the south of the Galápagos Islands (Fig. 3.2b). Encounters lasted between 1 hour and 8 days, and averaged 1.3 d (SD = 2.3 d). We fitted 32 candidate models at fine spatial resolution, 27 at intermediate spatial resolution, and 25 at coarse spatial resolution (Appendix X Tables S10.8-S10.10). The best final model included longitude as a cubic spline and slope, monthly relSST, and weekly EKE as linear terms at coarse spatial resolution (Appendix X Table S10.13) (GOF = 97.30%). The same variables were preferred at fine and intermediate spatial scales (Appendix X Tables S10.11-10.12).

The variation in clan distribution during this period was explained by geographic, oceanographic and topographic variables. We found that *Four-Plus* whales were more likely to occur east of 90.5°W, but uncertainty in predicting clan identity was high further west, where there was only one encounter (with *Short* clan whales; Fig. 3.3b-i). This predicted geographic distribution reproduced the observed distribution of clans during the 2010's study period (Fig. 3.3b-i). *Four-Plus* whales' presence was also more likely to occur in areas of higher slope incline (Fig. 3.3b-ii), higher monthly relSST (Fig. 3.3b-iii), and lower weekly EKE (Fig. 3.3b-iv). However, the modelled relationship between slope and the presence of *Four-Plus* clan whales did not reflect the actual overlapping slopes occupied by both clans during the study period (Fig. 3.4b-ii). On the other hand, the modelled relationship between monthly relSST and weekly EKE and clan identity was consistent with the oceanographic conditions measured during encounters with *Four-Plus* and *Short* clans in the 2010's study period (Figs. 3.4b-iii, iv). However, we note that relSST 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. 3.5b-i, ii). 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 were both clans overlapped (Fig. 3.5b-iii)

However, while modelled differences in the oceanographic conditions over which *Four-Plus* and *Short* occurred were consistent with observed differences in distribution among clans, models that included oceanographic and topographic performed worse in terms of LOO than the null model (Fig. 3.6b). The same was true regarding performance measured through external cross-validation (Fig. 3.6b). Further, the performance measured through LOO and external cross-validation of both null and full model was poor overall (<50%; Fig. 3.6b).

We found the relative effect sizes and directions of parameter estimates of oceanographic and topographic variables on clan identity did not vary across spatial and temporal resolutions (Appendix X Table S10.14). Likewise, whether relSST was included at monthly or weekly temporal resolutions had a negligible effect on all measures of model performance (Fig. 3.6b-ii). However, predictive performance measured through LOO and accuracy in predicting external data varied across spatial resolutions. Measured through LOO, models at coarse-scale spatial resolution had the lowest predictive ability. Measured through external cross-validation, models at the coarse spatial resolution performed better than the intermediate scale but worse than the fine scale (Fig. 3.6b-i).

3.5 Discussion

We found that culturally distinct sperm whale clans living in sympatry at the regional scale use habitats that are largely delineated by meso-scale spatial partitioning and, to a lesser degree, by the oceanographic characteristics of their habitat. In the 1980’s, whales from the *Regular* and *Plus-One* clan used different geographical locations, while in the 2010’s, *Plus-Four* and *Short* clan whales used waters with different oceanographic features. Contrary to our expectations, we found little effect of spatial scale on differentiating clan habitat use. In the following sections, we discuss how the social lives of this species may influence their space use patterns through social transmission of behaviours that can influence habitat use patterns and foraging.

3.5.1 Spatial partitioning

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

Over days up to a few weeks, single areas are predominantly occupied by groups of whales of a single clan (Whitehead and Rendell 2004). Social units within clans may group to forage together. Individuals may benefit from eavesdropping on group members' echolocation clicks and locate prey more easily, or perhaps share information on prey location (Whitehead 1989; Whitehead *et al.* 1991). At daily-weekly scales, units would therefore benefit from remaining in an area where other clan members are found and avoiding areas dominated by units of other clans. Active avoidance of members of different cultural entities, which is evident among *transient* and *resident* orcas (Bigg 1979; Baird and Dill 1995), may explain how whales maintain social isolation in sympatry.

We found that the spatial partitioning among sperm whale clans over few days and weeks to be consistent throughout the months over at least two years. This was most remarkable in the 1980's during which the overall distribution of the clans was maintained despite variation in environmental conditions and fitness between 1987 and 1989 (Whitehead and Rendell 2004). Over the annual temporal scale, site fidelity may be maintained if units use the presence of other clan members as a cue for habitat selection.

However, over even greater temporal scales and spatial scales, clan-specific habitat use patterns become diluted. Our study focused on a window of up to four years around the Galápagos. This represents a snapshot of a female sperm whale's lifespan—60 to 70 years (Rice 1989)—and a portion of the home range of such nomadic animals—at least 2000 km across the Eastern Pacific (Whitehead *et al.* 2008; Mizroch and 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 1980's, to the *Regular* clan in the 1990's, and to the *Short* and *Plus-Four* clans in the 2010's (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). Additionally, patterns of habitat use for the same clans in other areas were less discrete (Whitehead and Rendell 2004). Off the coast of Chile in the year 2000, *Regular, Short,* and *Plus-One* clans ranges overlapped more than off the Galápagos (Whitehead and 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 and Rendell 2004). Although our methods were not designed to identify habitat preferences, our findings suggest that, if they exist, annual-scale site preferences within clans may be modified by new environmental information over extended temporal and spatial scales.

3.5.2 Oceanographic variation

Whether oceanographic conditions drive variation in clan space use remains uncertain. During the 1980's, oceanographic variables did not contribute to discriminating the space use of *Plus-One* and *Regular* clans. However, three 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 fecal samples off the Galápagos Islands (Smith and Whitehead 2000). Second, *Regular* clan whales in this period had a higher carbon-13 isotope signature compared to *Plus-One* clan whales (Marcoux *et al.* 2007). Higher C-13 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.* 2007). And third, *Regular* and *Plus-One* clan whales had significantly different movement patterns and foraging success rates during this period (Whitehead and Rendell 2004). Thus, conditions between the areas in which the clans were found may have existed but were not 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 behaviour among the clans (Whitehead and Rendell 2004).

In the 2010's, *Plus-Four* clan whales were found in warmer and less turbulent waters 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 were found in association with different environmental conditions. Alternatively, these differences might also be a by-product of the spatial partitioning described above. While top predators have been found to track turbulent oceanic features (Tew Kai *et al.* 2009), the range of EKE values off the archipelago during the 2010's was lower and less variable than that reported in other regions, and four orders of magnitude lower than that associated with mesoscale eddies (Waugh *et al.* 2006; Teo *et al.* 2007; Brown and Fiechter 2012; Wong and Whitehead 2014). Furthermore, the turbulent oceanic features that have been associated with top predators usually occur over scales of 10s of metres, which is a much finer resolution than was available from AVISO-derived EKE (Tew Kai *et al.* 2009 D.M. Palacios, personal communication, 2017). It is also the case that these patterns were described based on a limited number of unevenly represented encounters and that, although GOF was high, models that captured these patterns performed poorly through cross-validation. Thus, our sample may not be sufficient to accurately represent the habitat of the *Short* and *Plus-One* 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. Although the oceanographic and topographic variables we used are valid proxies for the distribution of sperm whale prey (Jaquet and Whitehead 1996; Pirotta *et al.* 2011; Wong and Whitehead 2014), they do not equate to their presence. Furthermore, our measurements of oceanographic variables describe surface conditions; it is uncertain to what degree indicators of upwelling or frontal activity at the sea surface represent these in deeper waters as these features are displaced or dissipated at greater depths (Jaquet 1996). Additionally, we aimed to identify differences in the niches traits among the clans but did not evaluate the possibility of niche width varying among the clans, which has been found among orca 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.

3.5.3 Spatiotemporal scales

Including oceanographic and topographic variables at different spatiotemporal scales affected model ranking but did not substantially alter model performance, which suggests that the breadth of spatial scales we used did adequately capture the breadth of spatial scales that sperm whales experience. Moreover, different spatial resolutions were more appropriate for the data from the 1980's and 2010's study periods. This contrasts with previous findings that correlations between sperm whale occurrence and environmental variables increase over larger spatial scales, ca 150-120 km (Jaquet and Whitehead 1996), although our study covered smaller spatial scales, 10-50 km. Our range of spatial scales was constrained by the study area off the Galapagos. However, our results highlight that the effect of spatial scale may only be detectable when the tested scales are comparable to the size of the home range of a species, which in the case of Pacific female and juvenile sperm whales spans ca. 2200 km (Carrol *et al.* 1999; Graf *et al.* 2005; Whitehead *et al.* 2008).

3.6 Conclusions

Our study adds another layer of complexity to the cultural lives of sperm whales. We show that clans differ in fine-scale space use, in addition to vocal repertoire (Rendell and Whitehead 2003; Whitehead and Rendell 2004; Marcoux *et al.* 2007; Cantor and Whitehead 2015). Taken together, these findings suggest the niche of sperm whale clans is constructed on the basis of social and environmental information, both of which interact over different spatial and temporal scales (Boyd and Richerson 1988; Whitehead 2007; van der Post and 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 (Laland *et al.* 2000; Whitehead 2007).

Our findings highlight the importance of considering cultural identity when studying the habitat of female and immature sperm whales, and in using these studies to inform conservation efforts. Specifically, the monitoring actions urged by the Expert Working group on Culture and Social Complexity during the 12th meeting of the conference of the parties of the Convention on Migratory Species (Manila, 2017) emphasized the potential significance of culturally-driven population structure in conservation (see also Whitehead *et al.* 2004). Our understanding of clan-specific habitat-use would also greatly benefit from analysis of data from other regions of the eastern Tropical Pacific. Furthermore, coupling descriptions of clan niches with diving data originating from tag technologies (Watwood *et al.* 2006) could clarify whether clans have consistently different foraging strategies or if these behaviours are a response to environmental conditions.

3.7 Ethics statement

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

3.8 Acknowledgements

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CHAPTER 4 – Conclusion

In this thesis, I investigated the habitat use of sperm whales around the Galápagos Islands, taking into consideration their cultural way of life. I explored the characteristics of their habitat within the region over a 30-year period and studied how these characteristics shifted across years, decades, and centuries. I used my findings to evaluate the degree to which sperm whale habitat is protected by the Galápagos Marine Reserve (GMR). Finally, I analyzed the effect of cultural identity on sperm whale habitat use.

4.1 The habitat of Galápagos sperm whales

Over fine spatiotemporal scales (<150 km, < 1 yr), associations between sperm whale presence and environmental variables have been found to be less robust compared to those identified over larger scales (Jaquet and Whitehead 1996; Jaquet and Gendron 2002; Milligan 2013). Difficulties in identifying environmental variables associated with the habitat use of sperm whales over small spatial scales can be attributed to a truly uniform distribution over small scales, but also to the lack of information on the distribution of sperm whale prey at the appropriate resolution (Jaquet 1996; Palacios *et a.* 2013), and to responses to prey density changes other than shifting distribution—for example, modifying their aggregative behaviour (Jaquet and Gendron 2002). I showed that, within the Galápagos region, whales were distributed over areas of distinct topography and oceanography, but that these traits were somewhat variable across years and decades. Additionally, I found that over fine spatial and temporal scales (<50km, <10 yrs), sperm whale distribution may be influenced by socially acquired information. Specifically, sperm whales seem to use in areas where other clan members are found and remain in these regions across years, despite significant environmental variation (Whitehead and Rendell 2004). Therefore, I added temporal variability and social information to the probable causes of inconsistency in describing sperm whale habitat use over fine spatial scales.

On the other hand, when I compared the region-wide (ca 100km) distribution of sperm whales two centuries apart, I found that whales occurred consistently in areas of known high productivity and close to the archipelago's abrupt western slopes. This is consistent with scale-dependent habitat selection theory (Morris 1987; Wiens *et al.* 1987), and provides further evidence that, over regional spatial scales (ca >100km), sperm whales habitat is associated with prey enhancing features (Jaquet *et al.* 1996).

4.2 Implications for conservation

For the past 40 years, threats to the survival of sperm whales have shifted from intensive whaling to the increased risk of entanglement with fishing gear, vessel collisions, chemical and acoustic pollution, and irresponsible tourism (Notarbartolo di Sciara 2014; Gero and Whitehead 2016). Off the western coast of South America, entanglements with fishing gear, and antagonistic interactions with fisheries have been reported (Félix *et al.* 1997; Hucke-Gaete *et al.* 2004; Felix *et al.* 2007; Galleti Vernazzany and Cabrera 2007). Place-based approaches to marine mammal conservation are often used to mitigate these threats within a species' habitat (Hooker and Gerber 2004; Bailey and Thompson 2009), but are often impaired by the high mobility of some species and the dynamic nature of their habitat (Hyrenbach *et al.* 2000; Milligan 2013; di Sciara *et al.* 2016).

I found that most of the regions that sperm whales primarily occupy off the Galápagos archipelago are contained within the GMR. Thus, the existing restrictions of the reserve could ameliorate threats experienced by whales visiting the archipelago. However, I show that in some years, sperm whale occurrence was high outside the GMR boundaries, where it overlapped with fishing effort. This, coupled with the nomadic nature of sperm whales throughout the eastern tropical Pacific, corroborates that place-based conservation of this species is likely insufficient on its own (Milligan 2013). We also found further evidence of illegal effort within the GMR as well as a peak in effort along its boundary (Carr *et al.* 2013; Schiller *et al.* 2015). This is a common issue faced by pelagic protected areas where enforcement is logistically prohibitive (Game *et al.* 2009). This problem could be in part addressed by the use of mandatory AIS monitoring systems (McCauley *et al.* 2016; De Souza *et al.* 2016), but I show that coverage is not yet sufficient.

4.3 Culture and habitat

Culturally held and socially transmitted information can influence how species interact with their environment and utilize resources (McGrew *et al.* 1979; Ford *et al.* 1998; Estes *et al.* 2003; Mann *et al.* 2012). This ability to learn from others and to accumulate socially transmitted information is likely part of the reason why sperm whales are highly successful in the vast and highly dynamic marine ecosystem (Whitehead and Rendell 2015). In addition, the social transmission of information among preferentially associating sperm whales also likely originated culturally distinct clans that have different dialects, social behaviours, movement patterns, feeding success, and fine scale spatial distribution, even though they occur sympatrically (Whitehead and Rendell 2004; Marcoux *et al.* 2007; Cantor and Whitehead 2013; Cantor and Whitehead 2015). It is plausible, then, that clans have different habitat preferences, which may result in different habitat use patterns. However, we found that the oceanic and topographic characteristics over which sympatric clans off the Galápagos were found did not explain their distribution. Rather, we found that sperm whales mostly occupied waters where other clan members were found. This may suggest that sperm whales rely not only environmental cues for habitat selection, but also respond to the distribution conspecifics with shared cultural identity. Our results provide further evidence that culture is a noteworthy component of a species habitat selection process, one which it would benefit to incorporate it in conservation efforts (Whitehead and Rendell 2015) as well as in habitat models. Recently, the Expert Working Group on Social and Cultural complexity during the 12th meeting of the conference of the parties of the Convention on Migratory Species (Manila, 2017) emphasised the need to actively protect cultural traits along with other aspects of biodiversity (see Whitehead *et al.* 2004; Cantor and Whitehead 2015). Our findings suggest that efforts to preserve cultural variants would benefit from acknowledging their differential use of space.

4.3 Future directions

Because sperm whales exploit resources deep in the water column, our description of their habitat is constrained to indirect measurements. To understand what brings sperm whales to where they are, we need information on the deep environment in which they forage (such as that which can be obtained from suction cup technologies (Watwood *et al.* 2006)). Additionally, we analyzed a narrow window within their wide home range and life span and only in areas that have been historically recognized as sperm whale habitat. Studying movements of sperm whales across the Eastern Pacific over long term studies will help us understand; what drives sperm whales to move between regions? How does culture influence these movements? And what threats do they face along the way?

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APPENDIX I – ACF plots of habitat models

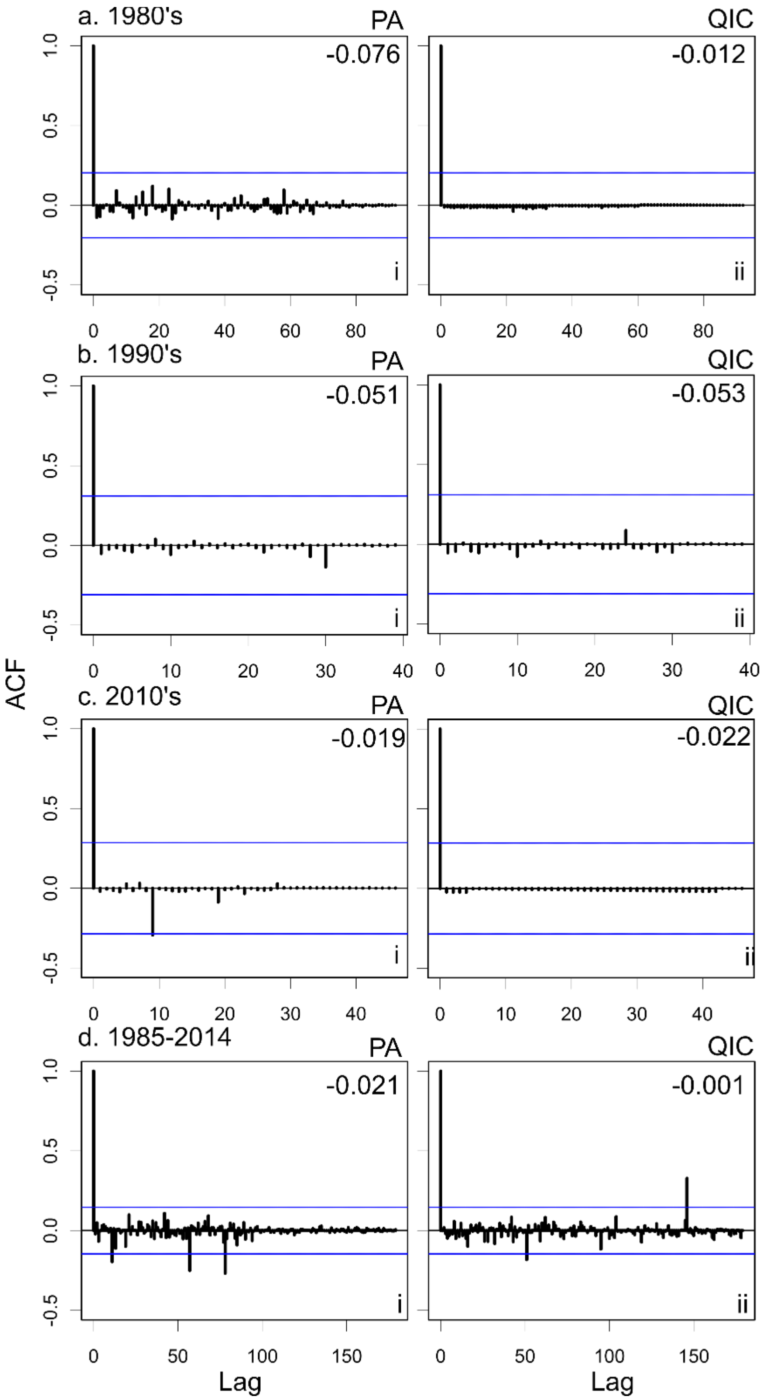


Figure A1. ACF plot of residuals of first geographic positions in each encounter/searching period for models preferred based on predictive accuracy (i) and QIC (ii) for predicting sperm whale presence off the Galápagos Islands in (a) the 1980's, (b) 1990's, (c) 2010's, and (d) 1985-2014. Lag-1 autocorrelation values are shown. Lags represent number of encounters.

APPENDIX II – Candidate initial models for predicting sperm whale presence off the Galápagos Islands

Table S2.1.a. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 1980's study period at fine spatial resolution (0.10°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model type	Formula
dynamic	latitude + b(longitude) + b(slope)*year + b (monthly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + longitude + b(slope)*year + b(weekly relSST)*year + b(monthly sdSST)*year + year
dynamic	latitude + b(longitude + b(slope)*year + b(monthly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(latitude) + longitude + slope*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	latitude + b(longitude) + b(depth)*year + b(monthly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + longitude + b(depth)*year + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	latitude + b(longitude) + b(depth)*year + b(monthly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(latitude) + longitude + b(depth)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
static	b(latitude) + longitude + slope + weekly relSST + bs(weekly sdSST) + year
static	b(latitude) + longitude + slope + weekly relSST + monthly sdSST + year
static	latitude + b(longitude) + b(slope) + b(monthly relSST) + b(monthly
static	latitude + b(longitude) + b(slope) + b(monthly relSST) + b(weekly sdSST)
static	b(latitude) + longitude + depth + weekly relSST + b(weekly sdSST) + year
static	b(latitude) + longitude + depth + weekly relSST + monthly sdSST + year
static	latitude + b(longitude) + b(depth) + b(monthly relSST) + b(monthly sdSST)
static	latitude + b(longitude) + b(depth) + b(monthly relSST) + b(weekly sdSST)

Table S2.1.b. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 1980's study period at fine spatial resolution (0.30°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	Formula
dynamic	latitude + longitude + b(monthly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + longitude + b(weekly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + longitude + b(slope)*year + b(monthly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(latitude) + longitude + b(slope)*year + b(weekly relSST)*year + weekly sdSST*year + year
dynamic	b(latitude) + depth*year + b(monthly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + depth*year + b(weekly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + b(depth)*year + b(monthly relSST)*year + weekly sdSST*year + year
dynamic	b(latitude) + depth*year + b(weekly relSST)*year + weekly sdSST*year + year
static	latitude + longitude + b(monthly relSST) + b(monthly sdSST) + year
static	latitude + longitude + weekly relSST + monthly sdSST + year
static	latitude + b(longitude) + slope + b(monthly relSST) + b(weekly sdSST) + year
static	b(latitude) + longitude + slope + weekly relSST + weekly sdSST + year
static	b(latitude) + depth + b(monthly relSST) + b(monthly sdSST) + year
static	b(latitude) + depth + weekly relSST + monthly sdSST + year
static	b(latitude) + depth + b(monthly relSST) + weekly sdSST + year
static	b(latitude) + depth + weekly relSST + weekly sdSST + year

Table S2.1.c. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 1980's study period at fine spatial resolution (0.50°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	**Formula**
dynamic	latitude + longitude + b(monthly relSST)*year + b(monthly sdSST)*year +
dynamic	b(latitude) + longitude + b(weekly relSST)*year + b(monthly sdSST)*year
dynamic	b(latitude) + longitude + b(slope)*year + b(monthly relSST)*year +
dynamic	b(latitude) + b(longitude) + b(slope)*year + b(weekly relSST)*year +
dynamic	latitude + b(depth)*year + b(monthly relSST)*year + b(monthly
dynamic	b(latitude) + depth*year + b(weekly relSST)*year + b(monthly
dynamic	b(latitude) + depth*year + b(monthly relSST)*year + b(weekly
dynamic	b(latitude) + depth*year + b(weekly relSST)*year + b(weekly sdSST)*year
static	latitude + longitude + b(monthly relSST) + b(monthly relSST) + year
static	b(latitude) + longitude + b(weekly relSST) + b(monthly sdSST) + year
static	latitude + b(longitude) + slope + b(monthly relSST) + b(weekly sdSST) +
static	latitude + longitude + slope + weekly relSST + b(weekly sdSST) + year
static	b(latitude) + depth + b(monthly relSST) + b(monthly sdSST) + year
static	b(latitude) + depth + b(weekly relSST) + b(monthly sdSST) + year
static	b(latitude) + depth + b(monthly relSST) + b(weekly sdSST) + year
static	latitude + depth + weekly relSST + b(weekly sdSST) + year

Table S2.2.a. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 1990's study period at fine spatial resolution (0.10°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	Formula
dynamic	latitude + b(longitude) + slope*year + monthly relSST*year + b(weekly sdSST)*year + year
dynamic	latitude + b(longitude) + slope*year + weekly relSST*year + b(weekly sdSST)*year + year
dynamic	latitude + b(longitude) + monthly relSST*year + monthly sdSST*year + year
dynamic	latitude + depth*year + monthly relSST*year + b(weekly sdSST)*year + year
dynamic	latitude + b(longitude) + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	latitude + depth*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	latitude + depth*year + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	latitude + depth*year + monthly relSST*year + monthly sdSST*year + year
static	latitude + b(longitude) + slope + b(monthly relSST) + weekly sdSST + year
static	latitude + b(longitude) + slope + weekly relSST + weekly sdSST + year
static	latitude + b(longitude) + b(monthly relSST) + monthly sdSST + year
static	latitude + b(longitude) + weekly relSST + b(monthly sdSST) + year
static	latitude + depth + b(monthly relSST) + monthly sdSST + year
static	latitude + depth + weekly relSST + monthly sdSST + year
static	latitude + depth + b(monthly relSST) + weekly sdSST + year
static	latitude + depth + weekly relSST + weekly sdSST + year

Table S2.2.b. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 1990's study period at fine spatial resolution (0.30°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	**Formula**
dynamic	latitude + b(longitude) + slope*year + monthly relSST*year + year
dynamic	latitude + b(longitude) + b(slope)*year + b(weekly relSST)*year + year
dynamic	latitude + depth*year + monthly relSST*year + monthly sdSST*year + year
dynamic	b(latitude) + b(depth)*year + b(weekly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + b(depth)*year + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	latitude + depth*year + slope*year + monthly relSST*year + year
static	latitude + depth + b(slope) + weekly relSST + weekly sdSST + year
static	latitude + b(longitude) + slope + b(monthly relSST) + year
static	latitude + b(longitude) + slope + weekly relSST + year
static	latitude + depth + b(slope) + monthly relSST + year
static	latitude + depth + monthly relSST + monthly sdSST + year
static	latitude + depth + weekly relSST + monthly sdSST + year

Table S2.2.c. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 1990's study period at fine spatial resolution (0.50°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	Formula
dynamic	latitude + b(longitude) + slope*year + monthly relSST*year + year
dynamic	latitude + b(longitude) + b(slope)*year + b(weekly relSST)*year + year
dynamic	latitude + depth*year + slope*year + monthly relSST*year + year
dynamic	latitude + depth*year + b(slope)*year + b(weekly relSST)*year + year
dynamic	latitude + b(slope)*year + monthly relSST*year + b(weekly sdSST)*year + year
dynamic	b(latitude) + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	latitude + depth*year + monthly relSST*year + b(monthly sdSST)*year + year
dynamic	latitude + depth*year + b(weekly relSST)*year + b(monthly sdSST)*year + year
static	latitude + b(longitude) + b(slope) + monthly relSST + year
static	latitude + b(longitude) + b(slope) + weekly relSST + year
static	latitude + depth + slope + monthly relSST + year
static	latitude + depth + slope + weekly relSST + year
static	latitude + b(slope) + monthly relSST + weekly sdSST + year
static	latitude + b(slope) + weekly relSST + weekly sdSST + year
static	latitude + depth + monthly relSST + monthly sdSST + year
static	latitude + depth + weekly relSST + monthly sdSST + year

Table S2.3.a. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 2010's study period at fine spatial resolution (0.10°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	Formula
dynamic	b(longitude) + b(depth)*year + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	b(longitude) + b(depth)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(depth)*year + b(monthly relSST)*year + b(monthly sdSST)*year + year
dynamic	b(latitude) + b(depth)*year + b(monthly relSST)*year + weekly sdSST*year + year
dynamic	b(latitude) + depth*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(longitude) + slope*year + b(weekly relSST)*year + b(monthly sdSST)*year + year
dynamic	longitude + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(slope)*year + b(monthly relSST)*year + monthly sdSST*year + year
dynamic	b(latitude) + b(slope)*year + b(monthly relSST)*year + weekly sdSST*year + year
dynamic	b(latitude) + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
static	longitude + b(depth) + b(weekly relSST) + monthly sdSST + year
static	longitude + b(depth) + b(weekly relSST) + b(weekly sdSST) + year
static	b(depth) + b(monthly relSST) + b(monthly sdSST) + year
static	b(latitude) + b(depth) + b(monthly relSST) + b(weekly sdSST) + year
static	b(latitude) + b(depth) + b(weekly relSST) + b(weekly sdSST) + year
static	longitude + b(slope) + b(weekly relSST) + monthly sdSST + year
static	longitude + b(slope) + b(weekly relSST) + b(weekly sdSST) + year
static	slope + b(monthly relSST) + b(monthly sdSST) + year
static	b(latitude) + slope + b(monthly relSST) + b(weekly sdSST) + year
static	b(latitude) + b(slope) + b(weekly relSST) + b(weekly sdSST) + year

Table S2.3.b. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 2010's study period at fine spatial resolution (0.30°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	Formula
dynamic	longitude + b(depth)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	depth*year + b(monthly relSST)*year + monthly sdSST*year + year
dynamic	b(depth)*year + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	b(depth)*year + b(monthly relSST)*year + weekly sdSST*year + year
dynamic	b(latitude) + b(depth)*year + b(monthly relSST)*year + year
dynamic	b(latitude) + b(depth)*year + b(weekly relSST)*year + year
dynamic	longitude + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(slope)*year + b(monthly relSST)*year + monthly sdSST*year + year
dynamic	b(slope)*year + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	b(slope)*year + b(monthly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(latitude) + b(slope)*year + b(monthly relSST)*year + year
dynamic	b(latitude) + b(slope)*year + b(weekly relSST)*year + year
static	longitude + b(depth) + b(weekly relSST) + b(weekly sdSST) + year
static	b(depth) + b(monthly relSST) + b(monthly sdSST) + year
static	b(depth) + b(weekly relSST) + b(monthly sdSST) + year
static	b(depth) + b(monthly relSST) + weekly sdSST + year
static	b(latitude) + b(depth) + b(monthly relSST) + year
static	b(latitude) + depth + b(weekly relSST) + year
static	longitude + slope + b(weekly relSST) + b(weekly sdSST) + year
static	slope + b(monthly relSST) + b(monthly sdSST) + year
static	b(slope) + b(weekly relSST) + b(monthly sdSST) + year
static	b(slope) + b(monthly relSST) + b(weekly sdSST) + year
static	b(latitude) + slope + b(monthly relSST) + year
static	b(latitude) + slope + b(weekly relSST) + year

Table S2.3.c. Candidate initial models for predicting sperm whale presence off the Galápagos Islands in the 2010's study period at fine spatial resolution (0.50°). Variables included as cubic splines are indicated as "b()", and interactions between terms are indicated by an asterisk (*). Dynamic models include interactions with years, while static models do not.

Model	Formula
dynamic	b(longitude) + depth*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(depth)*year + b(monthly relSST)*year + monthly sdSST*year + year
dynamic	b(depth)*year + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	b(depth)*year + b(monthly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(latitude)*year + b(depth)*year + b(monthly relSST)*year + year
dynamic	b(latitude) + b(depth)*year + b(weekly relSST)*year + year
dynamic	b(longitude) + b(slope)*year + b(weekly relSST)*year + b(weekly sdSST)*year + year
dynamic	slope*year + b(monthly relSST)*year + monthly sdSST*year + year
dynamic	b(slope)*year + b(weekly relSST)*year + monthly sdSST*year + year
dynamic	b(slope)*year + b(monthly relSST)*year + b(weekly sdSST)*year + year
dynamic	b(latitude)*year + b(slope)*year + b(monthly relSST)*year + year
dynamic	b(latitude)*year + b(slope)*year + b(weekly relSST)*year + year
satitc	longitude + b(depth) + b(weekly relSST) + b(weekly sdSST) + year
satitc	b(depth) + b(monthly relSST) + monthly sdSST + year
satitc	b(depth) + weekly relSST + b(monthly sdSST) + year
satitc	b(depth) + b(monthly relSST) + weekly sdSST + year
satitc	b(latitude) + depth + monthly relSST + year
satitc	b(latitude) + b(depth) + b(weekly relSST) + year
satitc	longitude + slope + b(weekly relSST) + b(weekly sdSST) + year
satitc	slope + b(monthly relSST) + monthly sdSST + year
satitc	b(slope) + b(weekly relSST) + b(monthly sdSST) + year
satitc	b(slope) + b(monthly relSST) + weekly sdSST + year
satitc	b(latitude) + slope + monthly relSST + year
satitc	b(latitude) + slope + b(weekly relSST) + year

Table S2.4.a. Candidate initial models for predicting sperm whale presence off the Galápagos Islands for the 1985-2014 study period at fine spatial resolution (0.10°). Variables included as cubic splines are indicated as "b()".

Model	Formula
static	b(longitude) + b(depth) + b(monthly relSST) + b(monthly sdSST + year
static	b(longitude) + b(depth) + b(weekly relSST) + b(monthly sdSST) + year
static	b(longitude) + b(depth) + b(monthly relSST) + b(weekly sdSST) + year
static	b(longitude) + b(depth) + b(weekly relSST) + b(weekly sdSST) + year
static	b(longitude) + slope + b(monthly relSST) + b(monthly sdSST) + year
static	b(longitude) + slope + b(weekly relSST) + b(monthly sdSST) + year
static	b(longitude) + slope + b(monthly relSST) + b(weekly sdSST) + year
static	b(longitude) + slope + b(weekly relSST) + b(weekly sdSST) + year
static	b(latitude) + b(slope) + monthly relSST + monthly sdSST + year
static	b(latitude) + b(slope) + b(weekly relSST) + monthly sdSST + year
static	b(latitude) + b(slope) + b(monthly relSST) + b(weekly sdSST) + year
static	b(latitude) + b(slope) + b(weekly relSST) + b(weekly sdSST) + year

Table S2.4.b. Candidate initial models for predicting sperm whale presence off the Galápagos Islands for the 1985-2014 study period at fine spatial resolution (0.30°). Variables included as cubic splines are indicated as "b()".

Model	Formula
static	longitude + b(depth) + b(monthly relSST) + monthly sdSST + year
static	longitude + b(depth) + b(weekly relSST) + b(monthly sdSST) + year
static	b(longitude) + b(depth) + b(monthly relSST) + b(weekly sdSST) + year
static	b(longitude) + b(depth) + b(weekly relSST) + b(weekly sdSST) + year
static	b(longitude) + slope + b(monthly relSST) + monthly sdSST + year
static	b(longitude) + slope + b(weekly relSST) + b(monthly sdSST) + year
static	b(longitude) + slope + b(monthly relSST) + b(weekly sdSST) + year
static	b(longitude) + slope + b(weekly relSST) + b(weekly sdSST) + year
static	b(latitude) + slope + b(monthly relSST) + monthly sdSST + year
static	b(latitude) + b(slope) + b(weekly relSST) + monthly sdSST + year
static	b(latitude) + b(slope) + b(monthly relSST) + b(weekly sdSST) + year
static	b(latitude) + b(slope) + b(weekly relSST) + b(weekly sdSST) + year

Table S2.4.c. Candidate initial models for predicting sperm whale presence off the Galápagos Islands for the 1985-2014 study period at fine spatial resolution (0.50°). Variables included as cubic splines are indicated as "b()".

Model	**Formula**
static	b(longitude) + depth + b(monthly relSST) + b(weekly sdSST) + year
static	b(longitude) + b(depth) + b(weekly relSST) + b(weekly sdSST) + year
static	b(longitude) + slope + b(monthly relSST) + b(weekly sdSST) + year
static	b(longitude) + slope + b(weekly relSST) + b(weekly sdSST) + year
static	b(depth) + monthly relSST + b(monthly sdSST) + year
static	b(depth) + b(weekly relSST) + b(monthly sdSST) + year
static	slope + monthly relSST + b(monthly sdSST) + year
static	slope + b(weekly relSST) + b(monthly sdSST) + year
static	b(latitude) + b(monthly relSST) + b(weekly sdSST) + year
static	b(latitude) + b(weekly relSST) + b(weekly sdSST) + year

APPENDIX III– Average predictive accuracy of final full habitat models fit with topographic and oceanographic variables at alternative spatiotemporal scales

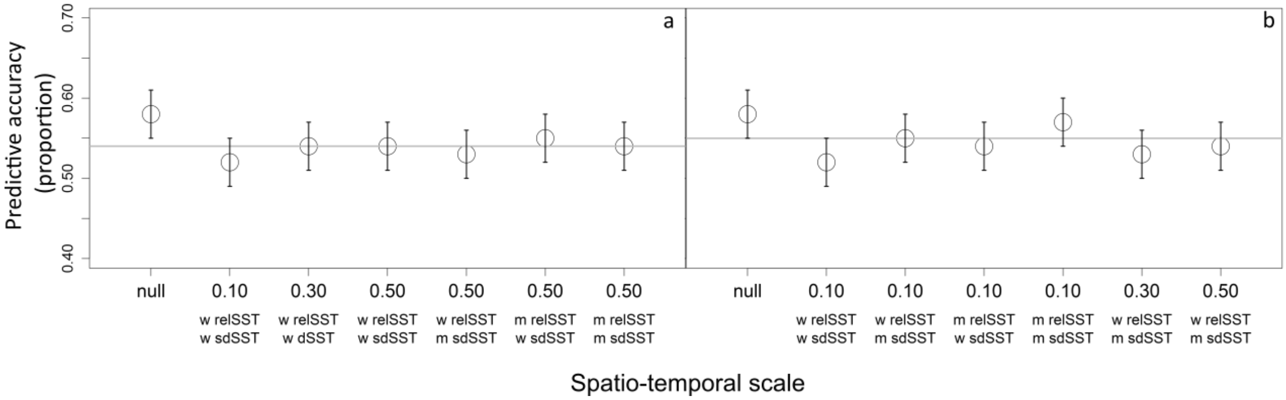
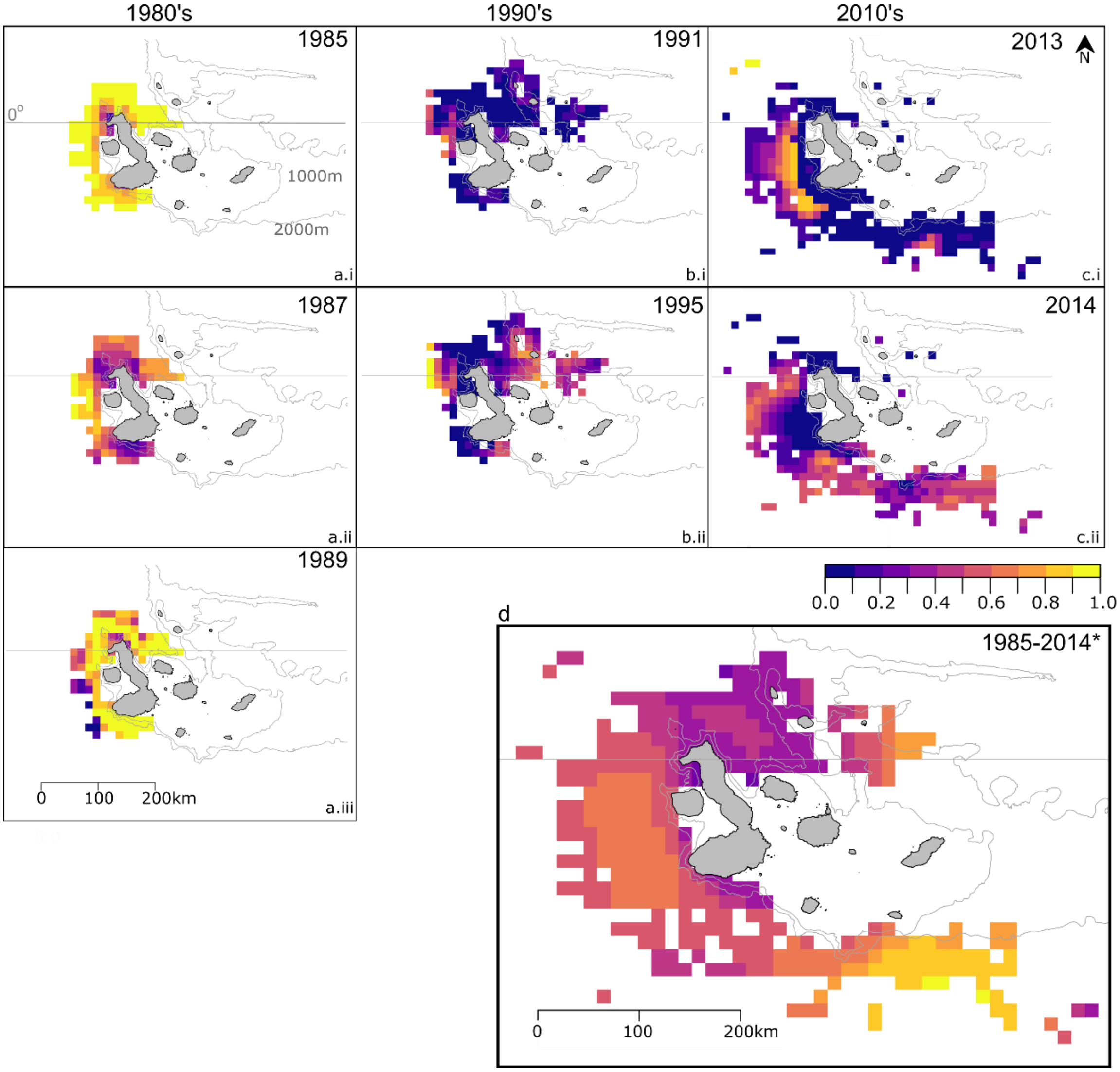


Figure S3.1. Average predictive accuracy ± SD (standard error) of final models for predicting sperm whale presence of Galápagos sperm whales between 1985-2010 at alternate spatiotemporal scales. Topographic and oceanographic variables were included at alternative spatial scales (0.10º, 0.30º, and 0.50º) and oceanographic variables (relative sea surface temperature (relSST) and standard deviation of sea surface temperature (sdSST) were included at the weekly (w) or monthly (m) temporal scales. (a) shows alternative resolutions with respect to the final model preferred based on QIC and (b) shows alternative resolution which respect to the final model preferred based on predictive accuracy. Grey horizontal lines represent predictive accuracy of the models preferred based on QIC (a) and predictive accuracy (b).

APPENDIX IV– Predictive probability of sperm whale presence (models preferred based on QIC)



*Model includes data collected in 1985, 1987, 1989, 1991, 1995, 2013 and 2014.

Figure S4.1. Predicted probability of sperm whale presence as a function of geographic, topographic, and oceanographic variables for (a) 1980’s—(i) 1985, (ii), 1987, and (iii) 1989, (b) 1990’s—(i) 1991 and (ii) 1995, (c) 2010’s—(i) 2013 and (ii) 2014, and (d) the entire study period (1985-2010’s) through models preferred based on QIC. Depth contours of 1000 and 2000 m are shown.

APPENDIX V– Monthly variation in relative sea surface temperature where whales were found and searched for

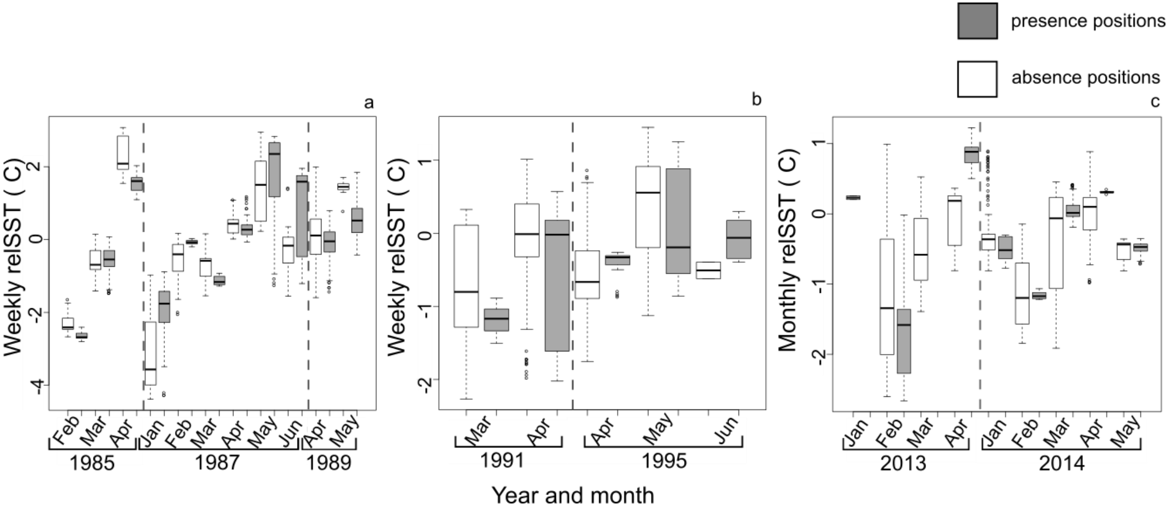


Figure S5.1. Boxplots showing monthly variation in relative sea surface temperature (relSST) for geographic positions collected during encounters and searching periods off the Galápagos Islands in (a) the 1980’s, (b) the 1990’s, and (c) the 2010’s surveys. In the 1980’s and 1990’s, relSST values were extracted at a weekly resolution and in the 2010’s they were extracted at a monthly resolution.

APPENDIX VI– ACF plots of models for predicting clan identity in the 1980’s and 2010’s

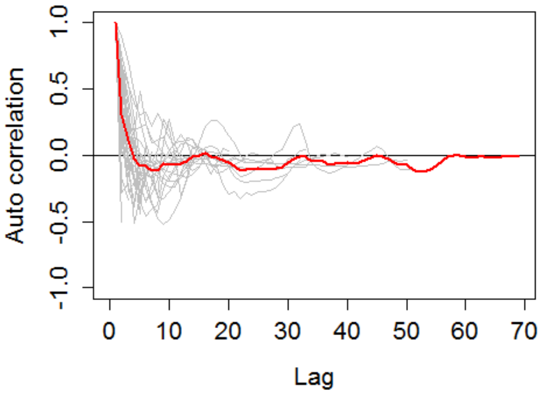


Figure S6.1. ACF plot of best model residuals for predicting clan identity of sperm whales off the Galápagos Islands in the 1980’s study period for individual encounters. Data points were collected approximately every hour, so a lag represents ~1hr. Grey lines show autocorrelation within encounters and the red line represents the mean autocorrelation between encounters.

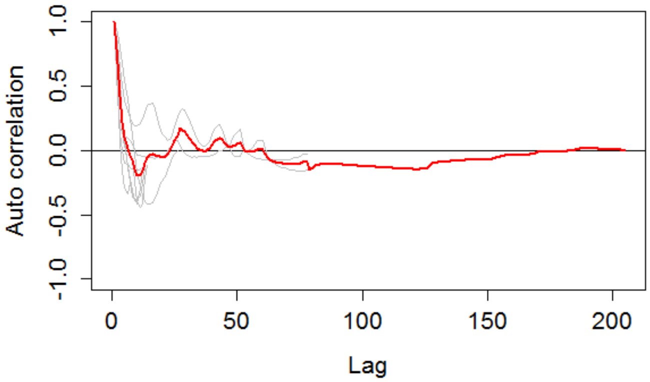


Figure S6.2. ACF plot of best model residuals for predicting clan identity of sperm whales off the Galápagos Islands in the 2010’s study period for individual encounters. Data points were collected approximately every hour, so a lag represents ~1hr. Grey lines show autocorrelation within encounters and the red line represents the mean autocorrelation between encounters.

APPENDIX VII.a– Interpolation and data filtering methods

Since the geographic positions were collected at irregular intervals in the 1980's period using SATNAV, we linearly interpolated latitude and longitude so that positions were available approximately every hour. This aimed to minimize biases that result when the intervals at which data are collected depend on unknown factors that may affect the response (i.e., clan identity) (Bůžková *et al*. 2010). We chose a linear interpolation method for simplicity and because the resulting error that arises from linear interpolation (Tremblay *et al.* 2006) is expected to be smaller than the *ca.* 0.5-3.0 kilometre spread of a sperm whale group (Whitehead 2003), and much smaller than the scale at which we analyzed environmental variables (> 10 km). The 2010's study period data were collected more often and regularly. To make them consistent with previous years, we subsampled geographic positions so that they were also available approximately every hour.

We restricted our analysis to regions that were consistently surveyed throughout study years (see Milligan 2013). To do this, we calculated the total number of geographic positions recorded each decade during and between encounters in 0.10º by 0.10º cells and selected only geographic positions in cells where the count exceeded the 70th percentile for that decade. We also included only the geographic positions that occurred over waters >1,000m deep because shallow waters were not consistently monitored acoustically, as well as points that occurred over five kilometres away from shore because the quality of Pathfinder data around coastlines is low (NDOC/SOG 2009). For the 2010's study period, we only included geographic positions south of the archipelago (Fig. 3.1b), because we were interested in evaluating if clans had differential preferences when in sympatry. Thus, including locations to the west of the archipelago (where only the *Plus-Four* clan was found) would confound the analysis.

APPENDIX VII.b– References for Appendix VII.a

Bůžková, P., Brown, E.R., John-Stewart, G.C. (2010). Longitudinal data analysis for generalized linear models under participant-driven informative follow-up: an application in maternal health epidemiology. American Journal of Epidemiology 171:189–197.

Milligan, M. (2013). Fine-scale distribution, habitat use, and movements of sperm whales. MSc dissertation, Dalhousie University, Halifax, NS.

NODC/SOG. (2009). 4 km Pathfinder version 5 user guide. Satellite Oceanography Group, National Oceanographic Data Center (NDOC), NOAA Satellite and Information Service (NEDSIS). Available at: www.nodc.noaa.gov/sog/pathfinder4km/userguide.html (accessed 6 Jun 2017).

Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, C.E., McDonald, B.I., Weise, M.J., Bost, C.-A., Weimerskirch, H., Crocker, D. E., Goebel, M. E. and Costa, D. (2006). Interpolation of animal tracking data in a fluid environment. Journal of Experimental Biology 209:128–140.

Whitehead, H. (2003). Sperm Whales, Social Evolution in the Ocean. The University of Chicago Press, London.

APPENDIX VIII– Correlation matrices for variables used to predict clan identity

Table S8.1. Correlation matrix for variables used to model differences in the niche of sperm whale clans off the Galápagos Islands extracted at fine spatial resolution (0.10°) for the 1980's study period. Black blocks represent combinations of the same variables extracted at different temporal resolutions which where not intended to be included in the same model. Coefficients > the 0.4 threshold are bolded.

	latitude	depth	slope	month relSST	month sdSST	weekly relSST	weekly sdSST
longitude	0.39	0.11	-0.16	0.10	-0.22	-0.16	-0.06
latitude		0.18	0.02	0.23	-0.12	0.09	0.09
depth			**0.81**	0.01	0.32	-0.07	0.20
slope				-0.02	0.31	-0.04	0.25
month relSST					-0.11	0.78	0.09
month sdSST						-0.14	0.21
weekly relSST							0.14

Table S8.2. Correlation matrix for variables used to model differences in the niche of sperm whale clans off the Galápagos Islands extracted at intermediate spatial resolution (0.30°) for the 1980's study period. Black blocks represent combinations of the same variables extracted at different temporal resolutions which where not intended to go together in a single model. Coefficients > the 0.4 threshold are bolded.

	latitude	depth	slope	month relSST	month sdSST	weekly relSST	weekly sdSST
longitude	0.39	0.21	-0.14	0.10	-0.38	-0.18	-0.14
latitude		0.24	0.06	0.22	-0.07	0.08	0.10
depth			**0.84**	0.02	0.32	-0.09	0.33
slope				-0.03	**0.51**	-0.07	**0.42**
month relSST					-0.17	0.80	0.08
month sdSST						-0.25	0.46
weekly relSST							0.07

Table S8.3. Correlation matrix for variables used to model differences in the niche of sperm whale clans off the Galápagos Islands extracted at coarse spatial resolution (0.50°) for the 1980’s study period. Black blocks represent combinations of the same variables extracted at different temporal resolutions which where not intended to go together in a single model. Coefficients > the 0.4 threshold are bolded.

	latitude	depth	slope	month relSST	month sdSST	weekly relSST	weekly sdSST
longitude	0.39	0.42	-0.09	0.09	-0.48	-0.19	-0.30
latitude		0.30	0.07	0.19	-0.03	0.06	0.15
depth			**0.76**	0.09	0.16	-0.08	0.24
slope				-0.02	**0.52**	-0.07	**0.43**
month relSST					-0.07	0.80	0.13
month sdSST						-0.18	0.65
weekly relSST							0.07

Table S8.4. Correlation matrix for variables used to model differences in the niche of sperm whale clans off the Galápagos Islands extracted at fine spatial resolution (0.10°) for the 2010s's study period. Black blocks represent combinations of the same variables extracted at different temporal resolutions which where not intended to go together in a single model. Coefficients > the 0.4 threshold are bolded.

	latitude	depth	slope	month relSST	month sdSST	week relSST	week sdSST	Chla	month EKE	month SSHA	week EKE	week SSHA
longitude	0.05	**0.41**	0.02	0.25	-0.17	0.23	-0.10	0.10	**-0.45**	**-0.60**	-0.34	**-0.50**
latitude		**0.59**	**0.45**	-0.33	-0.17	-0.35	0.00	0.05	0.05	0.13	-0.04	0.19
depth			**0.68**	0.01	-0.03	-0.17	-0.14	0.12	-0.24	-0.27	-0.22	-0.16
slope				-0.03	0.09	-0.01	-0.12	-0.02	0.13	0.05	0.10	0.11
month relSST					**0.70**	0.85	-0.32	**0.75**	**-0.44**	**-0.80**	-0.24	**-0.71**
month sdSST						0.61	-0.17	**0.67**	-0.02	-0.37	0.09	-0.35
week relSST							-0.22	**0.67**	-0.16	**-0.56**	-0.06	**-0.48**
week sdSST								-0.24	0.23	0.29	-0.01	0.35
Chla									-0.30	**-0.54**	-0.29	**-0.41**
month EKE										**0.79**	**0.72**	**0.69**
month SSHA											**0.49**	0.89
week EKE												0.19

Table S8.5. Correlation matrix for variables used to model differences in the niche of sperm whale clans off the Galápagos Islands extracted at intermediate spatial resolution (0.30°) for the 2010s's study period. Black blocks represent combinations of the same variables extracted at different temporal resolutions which where not intended to go together in a single model. Coefficients > the 0.4 threshold are bolded.

	latitude	depth	slope	month relSST	month sdSST	week relSST	week sdSST	Chla	month EKE	month SSHA	week EKE	week SSHA
longitude	0.05	0.38	0.07	0.28	-0.16	0.23	0.00	0.07	**-0.45**	**-0.60**	-0.34	**-0.50**
latitude		**0.65**	**0.56**	-0.32	-0.17	-0.40	0.18	0.02	0.05	0.13	-0.04	0.19
depth			**0.79**	0.01	-0.03	-0.18	-0.02	0.11	-0.16	-0.21	-0.17	-0.09
slope				-0.06	0.03	-0.08	0.05	-0.02	0.16	0.06	0.09	0.16
month relSST					**0.79**	0.86	**-0.42**	0.79	**-0.46**	**-0.83**	-0.25	**-0.74**
month sdSST						0.73	-0.25	**0.86**	-0.06	**-0.43**	0.06	-0.38
week relSST							-0.20	**0.69**	-0.15	**-0.56**	-0.03	**-0.49**
week sdSST								-0.15	0.32	0.42	-0.08	**0.55**
Chla									-0.30	-0.56	-0.25	**-0.44**
month EKE										**0.79**	0.72	**0.69**
month SSHA											0.49	0.89
week EKE												0.19

Table S8.6. Correlation matrix for variables used to model differences in the niche of sperm whale clans off the Galápagos Islands extracted at coarse spatial resolution (0.50°) for the 2010s's study period. Black blocks represent combinations of the same variables extracted at different temporal resolutions which where not intended to go together in a single model. Coefficients > the 0.4 threshold are bolded.

	latitude	depth	slope	month relSST	month sdSST	week relSST	week sdSST	Chla	month EKE	month SSHA	week EKE	week SSHA
longitude	0.05	0.37	0.12	0.30	-0.12	0.23	0.28	0.07	**-0.48**	**-0.60**	-0.35	**-0.49**
latitude		**0.73**	**0.66**	-0.32	-0.16	-0.41	0.25	0.00	0.05	0.13	-0.03	0.19
depth			**0.86**	-0.05	-0.09	-0.20	0.27	0.05	-0.08	-0.14	-0.15	0.00
slope				-0.13	-0.11	-0.14	0.26	-0.06	0.20	0.09	0.14	0.17
month relSST					**0.82**	0.87	-0.36	**0.82**	**-0.48**	**-0.84**	-0.27	**-0.75**
month sdSST						**0.77**	-0.24	**0.93**	-0.12	**-0.49**	-0.03	-0.42
week relSST							-0.13	**0.73**	-0.16	**-0.57**	-0.04	**-0.51**
week sdSST								-0.18	0.27	0.30	-0.06	**0.45**
Chla									-0.27	**-0.58**	-0.19	**-0.48**
month EKE										**0.80**	0.73	**0.71**
month SSHA											**0.53**	0.89
week EKE												0.22

APPENDIX IX.a– Prediction maps—methods for limiting mapped regions and rasterizing probability grid

To produce maps of expected annual clan distribution within areas where whales were found as a function of final models, we generated a regular grid of sample points separated by 0.10º latitude and 0.10º longitude for which we extracted topographic and oceanographic variables at the appropriate spatial and temporal scales in the R environment, using the packages rerddapXtracto, sp and raster (Pebesma and Bivand 2005; Bivand *et al.* 2016, Hijmans 2016; Mendelsson 2016). For oceanographic variables, which fluctuate over time, we extracted data at the appropriate temporal scale for all months surveyed during study years. We calculated averages of these variables for each point in the grid in each study period and used these as input to calculate the probability of whales belonging to a given clan using final models.

To map predictions only in the regions where whales were found, we generated a raster map of the geographic positions recorded during encounters with identified *Plus-One* and *Regular* clan whales in 0.10º by 0.10º cells between 1985 and 1989, and with the *Short and Plus-One* clans between 2013 and 2014. We included only sample points within 20 km of a cell where whales were found. We also excluded sample points in waters shallower than 1000 m. We standardized variables of remaining sample points with respect to the mean and standard deviation of the data used to fit the final models. We calculated predicted probabilities for each sample point using the final models and converted the grid of sample points to a raster image. The Galápagos coastline shapefile is available through StatSilk (www.statsilk.com/maps/ download-free-shapefile-maps).

APPENDIX IX.b– References for Appendix IX.a

Bivand, R., Keitt, T., and Rowlingson, B. (2016). rdgal: bindings for the geospatial data abstraction library. R package version 1.2-5. Available at: https://cran.r-project.org/web/packages/rgdal/index.html.

Hijmans, R. (2016). raster: geographic data analysis and modeling. R Package version 2.5-8. Available at: https://cran.r-project.org/package=raster%0A.

Mendelssohn, R. (2016). rerddapXtracto: extracts environmental data from ERD'S ERDDAP web service. R package version 0.1.0. Available at: github.com/rmendels/rerddapXtracto

Pebesma, E. and Bivand, R. (2005). Classes and methods for spatial data in R. R News 5:9-13.

APPENDIX X– Summary tables of initial candidate models and final models

Table S10.1. Candidate initial models for predicting clan identity of sperm whales found off the Galápagos Islands in the 1980's study period at fine spatial resolution (0.10°).

Model	Formula
A	Latitude + longitude + slope + weekly relSST + weekly sdSST
B	Latitude + longitude + slope + weekly relSST + monthly sdSST
C	Latitude + longitude + slope + monthly relSST + weekly sdSST
D	Latitude + longitude + slope + monthly relSST + monthly sdSST
E	Latitude + longitude + depth + weekly relSST + monthly sdSST
F	Latitude + longitude + depth + monthly relSST + monthly sdSST
G	Latitude + longitude + depth + monthly relSST + weekly sdSST
H	Latitude + longitude + depth + monthly relSST + monthly sdSST

Table S10.2. Candidate initial models for predicting clan identity of sperm whales found off the Galápagos Islands in the 1980's study period at intermediate spatial resolution (0.30°).

Model	Formula
A	Latitude + longitude + slope + weekly relSST
B	Latitude + longitude + slope + monthly relSST
C	Latitude + longitude + depth + weekly relSST + monthly sdSST
D	Latitude + longitude + depth + monthly relSST + monthly sdSST
E	Latitude + longitude + depth + monthly relSST + weekly sdSST
F	Latitude + longitude + depth + monthly relSST + monthly sdSST

Table S10.3. Candidate initial models for predicting clan identity of sperm whales found off the Galápagos Islands in the 1980's study period at coarse spatial resolution (0.50°).

Model	Formula
A	Latitude + longitude + slope + weekly relSST
B	Latitude + longitude + slope + monthly relSST
C	Latitude + longitude + depth + weekly relSST + monthly sdSST
D	Latitude + longitude + depth + monthly relSST + monthly sdSST
E	Latitude + longitude + depth + monthly relSST + weekly sdSST
F	Latitude + longitude + depth + monthly relSST + monthly sdSST

Table S10.4. QIC and ΔQIC of final models of sperm whale clan identity for the Galápagos selected through back-wards stepwise selection in the 1980's study period at fine spatial resolution (0.10°). "s()" indicates variables that were selected as cubic splines rather than linear terms.

Model	Formula	QIC	ΔQIC
A	s(latitude) + s(longitude) + slope + weekly sdSST	451.07	102.26
B	s(latitude) + s(longitude) + slope	468.03	119.22
C	**s(latitude) + s(longitude) + slope + monthly relSST + weekly sdSST**	**348.81**	**0.00**
D	s(latitude) + s(longitude) + slope + monthly relSST	397.21	48.40
E	s(latitude) + s(longitude) + weekly sdSST	465.03	116.22
F	s(latitude) + s(longitude)	478.24	129.43
G	s(latitude) + s(longitude) + monthly relSST + weekly sdSST	352.51	3.70
H	s(latitude) + s(longitude) + monthly relSST	404.08	55.27

Table S10.5. QIC and ΔQIC of final models of sperm whale clan identity for the Galápagos selected through back-wards stepwise selection in the 1980's study period at intermediate spatial resolution (0.30°). s()" indicates variables that were selected as cubic splines rather than linear terms.

Model	Formula	QIC	ΔQIC
A	s(latitude) + s(longitude) + slope	441.88	69.23
C	**s(latitude) + s(longitude) + slope + monthly relSST**	**372.65**	**0.00**
E	latitude + s(longitude) + depth	468.78	96.13
F	latitude + s(longitude) + depth	468.78	96.13
G	s(latitude) + s(longitude) + monthly relSST + weekly sdSST	393.53	20.88
H	s(latitude) + s(longitude) + monthly relSST	396.56	23.91

Table S10.6. QIC and ΔQIC of final models of sperm whale clan identity for the Galápagos selected through back-wards stepwise selection in the 1980's study period at fine coarse resolution (0.50°). s()" indicates variables that were selected as cubic splines rather than linear terms.

Model	Formula	QIC	ΔQIC
A	s(latitude) + slope	449.31	81.09
C	**s(latitude) + s(longitude) + slope + monthly relSST**	**368.22**	**0.00**
E	latitude + s(longitude) + depth	403.59	35.37
F	latitude + s(longitude) + depth	403.59	35.37
G	latitude + s(longitude) + depth + monthly relSST	385.01	16.79
H	latitude + s(longitude) + depth + monthly relSST	385.01	16.79

Table S10.7. Parameter estimates (multiplicative increase in odds ratio) of models of sperm whale clan identity for whales found in the 1980's study period off the Galápagos Islands. The best model, equivalent models at alternate spatiotemporal scales, and a null model (with just latitude and longitude) are shown. Terms included as cubic splines are broken down. Parameter estimates that differ in direction from the final best model are bolded

	Models						
Variables	null	Final best (0.10° monthly relSST weekly sdSST)	0.30° monthly relSST weekly sdSST	0.50° monthly relSST weekly sdSST	0.10° monthly relSST monthly sdSST	0.10° weekly relSST monthly sdSST	0.10° weekly relSST weekly sdSST
intercept	1.67E+06	1.06E+06	2.45E+06	4.91E+07	5.51E+05	3.61E+06	7.42E+06
latitude(1)	2.45E+01	1.40E+02	5.04E+01	5.63E+01	5.25E+01	2.26E+01	5.97E+01
latitude(2)	1.69E-02	7.39E-04	3.10E-04	1.05E-04	4.65E-03	1.16E-02	1.58E-03
latitude(3)	7.77E+00	1.94E+02	5.41E+01	3.77E+01	1.06E+02	1.26E+01	1.95E+01
latitude(4)	3.25E+16	1.16E+24	3.12E+24	7.12E+26	4.33E+21	5.85E+17	5.26E+19
longitude(1)	7.58E-10	3.57E-09	5.87E-08	2.15E-09	3.99E-09	6.79E-10	7.74E-10
longitude(2)	2.55E+02	4.17E+01	**5.93E-04**	**1.26E-03**	3.41E+01	1.14E+01	6.82E+00
longitude(3)	3.93E-50	9.80E-63	1.64E-48	4.65E-57	2.93E-56	9.51E-51	6.20E-56
longitude(4)	4.15E-09	2.40E-22	3.13E-128	1.22E-112	1.04E-25	2.09E-10	6.27E-10
slope	NA	1.32E+00	2.64E+00	3.90E+00	1.39E+00	1.45E+00	1.39E+00
relSST	NA	2.98E-01	3.40E-01	3.23E-01	3.43E-01	6.77E-01	6.31E-01
sdSST	NA	1.79E+00	1.30E+00	1.07E+00	**8.61E-01**	**7.87E-01**	1.75E+00

Table S10.8. Candidate initial models for predicting clan identity of sperm whales found off the Galápagos Islands in the 2010's study period at fine spatial resolution (0.10°).

Model	Formula
A	bs(longitude) + latitude + monthly relSST + weekly sdSST + monthly EKE
B	bs(longitude) + latitude + weekly relSST + weekly sdSST + monthly EKE
C	bs(longitude) + latitude + monthly sdSST + weekly EKE
D	bs(longitude) + latitude + weekly sdSST + chla + weekly EKE
E	bs(longitude) + slope + monthly relSST + weekly sdSST + weekly EKE
F	bs(longitude) + slope + weekly relSST + weekly sdSST + weekly EKE
G	bs(longitude) + slope + monthly sdSST + weekly EKE
H	bs(longitude) + slope + weekly sdSST + chla + weekly EKE
I	bs(latitude) + weekly relSST + weekly sdSST + monthly EKE
J	bs(latitude) + monthly relSST + monthly EKE
K	bs(latitude) + monthly sdSST + weekly EKE + weekly SSHA
L	latitude + monthly sdSST + monthly SSHA
M	bs(latitude) + weekly sdSST + chla + monthly EKE
N	bs(latitude) + weekly sdSST + weekly EKE + weekly SSHA
O	bs(latitude) + weekly sdSST + monthly SSHA
P	depth + monthly relSST + weekly sdSST + weekly EKE
Q	depth + weekly relSST + weekly sdSST + monthly EKE
R	depth + weekly relSST + weekly sdSST + weekly EKE
S	depth + monthly sdSST + monthly EKE
T	depth + monthly sdSST + weekly EKE + weekly SSHA
U	depth + monthly sdSST + weekly SSHA
V	depth + weekly sdSST + chla + monthly EKE
W	depth + weekly sdSST + chla + weekly EKE
X	depth + weekly sdSST + weekly EKE + weekly SSHA
Y	depth + weekly sdSST + monthly SSHA
Z	slope + weekly relSST + weekly sdSST + monthly EKE
AA	slope + monthly relSST + monthly EKE
AB	slope + monthly sdSST + weekly EKE + weekly SSHA
AC	slope + monthly sdSST + monthly SSHA
AD	slope + weekly sdSST + chla + monthly EKE
AE	slope + weekly sdSST + weekly EKE + weekly SSHA
AF	slope + weekly sdSST + monthly SSHA

Table S10.9. Candidate initial models for predicting clan identity of sperm whales found off the Galápagos Islands in the 2010's study period at intermediate spatial resolution (0.30°).

Models	Formula
A	bs(longitude) + latitude + monthly relSST + weekly EKE
B	bs(longitude) + latitude + weekly relSST + weekly sdSST + weekly EKE
C	bs(longitude) + latitude + monthly sdSST + weekly EKE
D	bs(longitude) + latitude + weekly sdSST + chla + weekly EKE
E	bs(longitude) + depth + monthly relSST + weekly EKE
F	bs(longitude) + depth + weekly relSST + weekly sdSST + weekly EKE
G	bs(longitude) + depth + monthly sdSST + weekly EKE
H	bs(longitude) + depth + weekly sdSST + chla + weekly EKE
I	bs(longitude) + slope + monthly relSST + weekly EKE
J	bs(longitude) + slope + weekly relSST + weekly sdSST + weekly EKE
K	bs(longitude) + slope + monthly sdSST + weekly EKE
L	bs(longitude) + slope + weekly sdSST + chla + weekly EKE
M	bs(latitude) + weekly relSST + weekly sdSST + monthly EKE
N	bs(latitude) + monthly sdSST + monthly EKE
O	bs(latitude) + monthly sdSST + weekly EKE + weekly SSHA
P	bs(latitude) + weekly sdSST + chla + monthly EKE
Q	bs(latitude) + monthly SSHA
R	depth + weekly relSST + weekly sdSST + monthly EKE
S	depth + monthly sdSST + monthly EKE
T	depth + monthly sdSST + weekly EKE
U	depth + weekly sdSST + chla + monthly EKE
V	depth + monthly SSHA
W	slope + weekly relSST + weekly sdSST + monthly EKE
X	slope + monthly sdSST + monthly EKE
Y	slope + monthly sdSST + weekly EKE + weekly SSHA
Z	slope + weekly sdSST + chla + monthly EKE
AA	slope + monthly SSHA

Table S10.10. Candidate initial models for predicting clan identity of sperm whales found off the Galápagos Islands in the 2010's study period at coarse spatial resolution (0.50°).

Model	Formula
A	bs(longitude) + latitude + monthly relSST + weekly sdSST + weekly EKE
B	bs(longitude) + latitude + weekly sdSST + chla + weekly EKE
C	bs(longitude) + latitude + monthly sdSST + weekly EKE
D	bs(longitude) + depth + monthly relSST + weekly sdSST + weekly EKE
E	bs(longitude) + depth + weekly relSST + weekly sdSST + weekly EKE
F	bs(longitude) + depth + weekly sdSST + chla + weekly EKE
G	bs(longitude) + depth + monthly sdSST + weekly EKE
H	bs(longitude) + slope + monthly relSST + weekly sdSST + weekly EKE
I	bs(longitude) + slope + weekly relSST + weekly sdSST + weekly EKE
J	bs(longitude) + slope + weekly sdSST + chla + weekly EKE
K	bs(longitude) + slope + monthly sdSST + weekly EKE
L	bs(latitude) + weekly sdSST + chla + monthly EKE
M	bs(latitude) + monthly sdSST + monthly EKE
N	latitude + weekly EKE + weekly SSHA
O	bs(latitude) + weekly sdSST + monthly SSHA
P	depth + weekly relSST + weekly sdSST + monthly EKE
Q	depth + weekly sdSST + chla + monthly EKE
R	depth + monthly sdSST + monthly EKE
S	depth + weekly EKE + weekly SSHA
T	depth + weekly sdSST + monthly SSHA
U	slope + weekly relSST + weekly sdSST + monthly EKE
V	slope + weekly sdSST + chla + monthly EKE
W	slope + monthly sdSST + monthly EKE
X	slope + weekly EKE + weekly SSHA
Y	slope + weekly sdSST + monthly SSHA

Table S10.11. QIC and ΔQIC of final models of sperm whale clan identity for the Galápagos selected through back-wards stepwise selection in the 2010's study period at fine spatial resolution (0.10°).

Model	Formulas	QIC	ΔQIC
A	bs(longitude) + latitude + weekly sdSST + monthly EKE	117.52	8.68
B	bs(longitude) + latitude + weekly sdSST + monthly EKE	117.52	8.68
C	bs(longitude) + latitude + weekly EKE	190.81	81.97
D	bs(longitude) + latitude + weekly EKE	190.81	81.97
E	**bs(longitude) + slope + monthly relSST + weekly EKE**	**108.84**	**0.00**
F	bs(longitude) + slope + weekly relSST + weekly EKE	147.21	38.37
G	bs(longitude) + monthly sdSST + weekly EKE	212.64	103.80
H	bs(longitude) + chla + weekly EKE	219.56	110.72
I	bs(latitude) + weekly relSST + weekly sdSST + monthly EKE	273.33	164.49
J	bs(latitude) + monthly relSST + monthly EKE	243.72	134.88
K	bs(latitude) + weekly EKE + weekly SSHA	167.73	58.89
L	latitude + monthly sdSST + monthly SSHA	241.02	132.18
M	bs(latitude) + weekly sdSST + monthly EKE	283.04	174.20
N	bs(latitude) + weekly sdSST + weekly EKE + weekly SSHA	149.06	40.22
O	bs(latitude) + weekly sdSST + monthly SSHA	184.11	75.27
P	depth + monthly relSST + weekly sdSST + weekly EKE	216.65	107.81
Q	depth + weekly relSST + monthly EKE	287.85	179.01
R	weekly relSST + weekly EKE	445.50	336.66
S	depth + monthly sdSST + monthly EKE	300.94	192.10
T	weekly EKE + weekly SSHA	298.77	189.93
U	depth + weekly SSHA	311.76	202.92
V	depth + chla + monthly EKE	320.04	211.20
W	weekly EKE	504.01	395.17
X	depth + weekly sdSST + weekly EKE + weekly SSHA	236.63	127.79
Y	weekly sdSST + monthly SSHA	225.19	116.35
Z	slope + weekly relSST + monthly EKE	294.23	185.39
AA	slope + monthly relSST + monthly EKE	307.75	198.91
AB	slope + weekly EKE + weekly SSHA	283.55	174.71
AC	monthly SSHA	275.00	166.16
AD	slope + chla + monthly EKE	324.71	215.87
AE	slope + weekly sdSST + weekly EKE + weekly SSHA	222.16	113.32
AF	weekly sdSST + monthly SSHA	225.19	116.35

Table S10.12. QIC and ΔQIC of final models of sperm whale clan identity for the Galápagos selected through back-wards stepwise selection in the 2010's study period at intermediate spatial resolution (0.30°).

Models	**Formula**	**QIC**	**ΔQIC**
A	bs(longitude) + monthly relSST + weekly EKE	119.95	24.89
B	bs(longitude) + weekly relSST + weekly EKE	153.3	58.24
C	bs(longitude) + monthly sdSST + weekly EKE	185.92	90.86
D	bs(longitude) + latitude + weekly EKE	191.01	95.95
E	bs(longitude) + depth + monthly relSST + weekly EKE	99.54	4.48
F	bs(longitude) + depth + weekly relSST + weekly EKE	140.98	45.92
G	bs(longitude) + depth + monthly sdSST + weekly EKE	177.74	82.68
H	bs(longitude) + chla + weekly EKE	191.49	96.43
I	**bs(longitude) + slope + monthly relSST + weekly EKE**	**95.06**	**0**
J	bs(longitude) + slope + weekly relSST + weekly EKE	140.13	45.07
K	bs(longitude) + slope + monthly sdSST + weekly EKE	176.04	80.98
L	bs(longitude) + slope + chla + weekly EKE	188.04	92.98
M	bs(latitude) + weekly relSST + weekly sdSST + monthly EKE	245.38	150.32
N	bs(latitude) + monthly sdSST + monthly EKE	283.26	188.2
O	bs(latitude) + monthly sdSST + weekly EKE	143.62	48.56
P	bs(latitude) + weekly sdSST + monthly EKE	282.83	187.77
Q	bs(latitude) + monthly SSHA	226.73	131.67
R	depth + weekly relSST + monthly EKE	284.21	189.15
S	depth + monthly sdSST + monthly EKE	308.02	212.96
T	depth + weekly SSHA	299.05	203.99
U	depth + chla + monthly EKE	314.27	219.21
V	monthly SSHA	275.1	180.04
W	slope + weekly relSST + monthly EKE	287.86	192.8
X	slope + monthly sdSST + monthly EKE	312.24	217.18
Y	slope + weekly EKE + weekly SSHA	284.07	189.01
Z	slope + chla + monthly EKE	316.67	221.61
AA	monthly SSHA	275.1	180.04

Table S10.13. QIC and ΔQIC of final models of sperm whale clan identity for the Galápagos selected through back-wards stepwise selection in the 2010's study period at coarse spatial resolution (0.50°).

Model	Formula	QIC	ΔQIC
A	bs(longitude) + latitude + monthly relSST + weekly sdSST + weekly EKE	80.83	0.97
B	bs(longitude) + chla + weekly EKE	127.40	47.54
C	bs(longitude) + monthly sdSST + weekly EKE	123.42	43.56
D	bs(longitude) + depth + monthly relSST + weekly EKE	81.08	1.22
E	bs(longitude) + depth + weekly relSST + weekly EKE**0.00**	92.97	13.11
F	bs(longitude) + chla + weekly EKE	127.40	47.54
G	bs(longitude) + monthly sdSST + weekly EKE	123.42	43.56
H	**bs(longitude) + slope + monthly relSST + weekly EKE**	**79.86**	**0.00**
I	bs(longitude) + slope + weekly relSST + weekly EKE	88.82	8.96
J	bs(longitude) + slope + chla + weekly EKE	123.08	43.22
K	bs(longitude) + slope + monthly sdSST + weekly EKE	114.21	34.35
L	bs(latitude) + weekly sdSST + monthly EKE	249.76	169.90
M	bs(latitude) + monthly sdSST + monthly EKE	272.57	192.71
N	latitude + weekly EKE + weekly SSHA	208.95	129.09
O	bs(latitude) + weekly sdSST + monthly SSHA	184.51	104.65
P	depth + weekly relSST + monthly EKE	276.82	196.96
Q	depth + chla + monthly EKE	306.40	226.54
R	depth + monthly sdSST + monthly EKE	307.40	227.54
S	weekly EKE + weekly SSHA	289.57	209.71
T	weekly sdSST + monthly SSHA	221.37	141.51
U	slope + weekly relSST + monthly EKE	280.63	200.77
V	slope + chla + monthly EKE	307.95	228.09
W	slope + monthly sdSST + monthly EKE	310.26	230.40
X	weekly EKE + weekly SSHA	289.57	209.71
Y	weekly sdSST + monthly SSHA	221.37	141.51

Table S10.14. Parameter estimates (multiplicative increase in odds ratio) of models of sperm whale clan identity in the 2010's study period off the Galápagos Islands. The best model, equivalent models at alternate spatiotemporal scales, and a null model are shown. Terms included as cubic splines are broken down.

Variables	**0.10° monthly relSST, weekly EKE**	**0.30° monthly relSST, weekly EKE**	**0.50° monthly relSST, weekly EKE**	**0.50° weekly relSST, weekly EKE**	**null**
intercept	1.74E-136	4.72E-140	3.58E-149	1.54E-177	9.86E-29
longitude (1)	1.62E+166	6.04E+173	3.33E+184	1.53E+220	8.20E+31
longitude (2)	7.90E+117	1.66E+118	8.59E+126	7.70E+151	1.33E+25
longitude (3)	3.32E+139	1.37E+144	2.58E+153	7.89E+181	4.70E+28
longitude (4)	4.22E+132	4.59E+135	5.16E+144	1.44E+173	9.45E+31
latitude	-	-	-	-	4.39E-01
slope	3.39E+00	5.22E+00	2.88E+00	3.92E+00	-
relSST	1.66E+01	3.48E+01	2.69E+01	4.74E+01	-
EKE	6.67E-04	3.64E-04	2.36E-04	5.61E-05	-