ON CULTURAL INHERITANCE: EVOLUTION, BEHAVIOUR AND SOCIAL STRUCTURE OF EASTERN CARIBBEAN SPERM WHALES

by

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"She entered the story knowing she would emerge from it feeling she had been immersed in the lives of others, in plots that stretched back twenty years, her body full of sentences and moments, as if awaking from sleep with a heaviness caused by unremembered dreams."

-Michael Ondaatje, *The English Patient*

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ABSTRACT

Cultural inheritance is a “second inheritance system” which can affect ecology and evolution in unexpected ways. However, although its implications in humans are recognized and extensively studied, cultural inheritance has yet to be incorporated into mainstream biology. As such, the overreaching objective of my thesis is to highlight the role of culture in shaping the social structure, behaviour, and evolution of a non-primate species, the sperm whale (*Physeter macrocephalus*). I do so by expanding our knowledge on the implications of vocal clan membership (cultural groups which can be distinguished based on their repertoires of coda vocalizations) to the whales.

I first introduce the ramifications of cultural inheritance through the intraspecific group competition hypothesis, a new evolutionary framework which complement previous hypotheses for explaining large brain in species such as the sperm whale.

By greatly expanding the spatial scale of sperm whale research efforts in the Eastern Caribbean (from a single island, Dominica, where sperm whales have been documented since 2005, to encompass most of the Lesser Antilles), I show that sperm whales can partition habitat on a relatively fine scale with different vocal clans having distinct distributions along the Lesser Antilles chain and movements an order of magnitude smaller than those of the Eastern Tropical Pacific populations. I demonstrate that such segregation is most likely the result of site/island fidelity, further highlighting the role of cultural knowledge in shaping sometimes unexpected patterns of distribution. I update previous population estimates to account for such island residency. I conclude my thesis by suggesting the use of identity codas, coda types used consistently by one vocal clan, and rarely, if ever, by others, as symbolic markers of vocal clan identity. Suggesting that, more than a level of social structure, vocal clans are a vessel of cultural differences, giving cultural identity to the whales.

My findings highlight the overreaching role of cultural inheritance to Eastern Caribbean sperm whales, as well as the importance of incorporating this second inheritance system into biology and conservation, for sperm whales, and other cultural species.

LIST OF ABBREVIATIONS USED

Abyss	Distance to the nearest geomorphic feature abyss (variable)
AIC	Akaike Information Criterion
AUC	Area Under Curve
Canyon	Distance to the nearest geomorphic feature canyon (variable)
CCAC	Canadian Council on Animal Care
Channel	Distance to the center of the nearest channel (variable)
Chla	Chlorophyll-a concentration averaged over previous 3 months (variable)
critfact	by how much a call type's usage needs be higher in one clade than in another for it to be considered an identity call in IDcall
DNA	Deoxyribonucleic acid
DSLR	Digital single-lens reflex (camera)
DSWP	The Dominica Sperm Whale Project
EC	Eastern Caribbean
EC1	Eastern Caribbean 1 (vocal clan)
EC2	Eastern Caribbean 2 (vocal clan)
EC3	Eastern Caribbean 3 (vocal clan)
ECS	Eastern Caribbean survey
Ecurr	Eastward speed of near surface currents (variable)
ENSO	El Niño/South Oscillation
Env	Environment
EQ	Encephalization quotient
Escarp	Distance to the nearest geomorphic feature escarpment (variable)
ETP	Eastern Tropical Pacific
GEBCO	General Bathymetric Chart of the Oceans
GEE	Generalized Estimating Equations
GPS	Global Positioning System
GLM	General Linear Model

GVIF	Generalized Variance Inflation Factor
ICI	Inter-Click Interval
ID coda	Coda type used consistently by one vocal clan, and rarely, if ever, by others
IDN	Identification number
Inflow	Atlantic inflow (Sv) through the nearest channel (variable)
Island	Nearest island (categorical variable)
Lat	Latitude (variable)
Long	Longitude (variable)
minrep	Minimum number of repertoires to for an identity clade in IDcall
MED	Mediterranean
mtDNA	Mitochondrial DNA
Mvelv	Measure of near surface eddy energy along longitude (variable)
NA	Not applicable
Ncurr	Northward speed of near surface currents (variable)
NGS	National Geographic Society
NOAA	National Oceanic and Atmospheric Administration
Non-ID coda	Coda types that do not qualify as identity coda types (sometimes shared across vocal clans).
NSERC	National Sciences and Engineering Research Council of Canada
PC	Personal computer
Pres	Presence (in habitat models)
Q	Photograph quality rating (1-5)
QIC	Quasilikelihood under the Independence model Criterion
Reg	Regular (vocal clan)
RMS	Root-Mean-Squared displacement
ROC	Receiving Operating Characteristic
Shelf	Distance to the continental shelf (variable)
VIIRS	Visible Infrared Imaging Radiometer Suite

WAT	Watkins Marine Mammal Sound Database
Windward	Binary variable that reflects whether the location is leeward, west, (N) or windward,east (Y) of the Lesser Antilles island chain
Zvelv	Measure of near surface eddy energy along latitudes (variable)

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CHAPTER 1 –

Introduction

> “ Apprivoise-moi ! Que faut-il faire ? dit le petit prince. Il faut être très patient, répondit le renard. Tu t’assoiras d’abord un peu loin de moi, comme ça, dans l’herbe. Je te regarderai du coin de l’œil et tu ne diras rien. Le langage est source de malentendus.”
>
> – Antoine de Saint-Exupéry, *Le Petit Prince*

Culture, which can be defined as “behaviour or information shared within a community that is acquired from conspecifics through some form of social learning” (Whitehead & Rendell 2015), is increasingly recognized to have important repercussions on behaviour and evolution. This is extensively documented and accepted in on our own species (*Homo sapiens sapiens*) (Creanza & Feldman 2016; Creanza et al. 2017) but can remain somewhat controversial for other animals (Laland & Hoppit 2003; Laland & Janik 2006; Pagnotta 2014).

Homo sapiens sapiens’ cultural diversity is astounding –humans speak over 7,000 languages (www.etnologue.com), practice over 4,000 religions (Doniger 2006), produce a diverse array of music (Mehr et al. 2019), and have created tools and technologies to survive in every biome on Earth (Boyd & Richerson 2009). It is such diversity and reliance on social learning that allowed humans to become a successful, and ecologically dominant, species (Boyd et al. 2011). However, increasing evidence suggest that culture is not exclusively human, but rather widespread in the animal kingdom. For instance, there is evidence of culture and social learning in great apes (Whiten et al. 1999; Van Schaik et al. 2003; Robbins et al. 2016), monkeys (Perry 2011), cetaceans (Whitehead & Rendell 2015), birds (Aplin 2018), ungulates (Jesmer et al. 2018), rodents (Zohar & Terkel 1996), fish (Warner 1988), and insects (Alem et al. 2016). For some taxa, such as primates and cetaceans, researchers have extensive evidence of culture (reviewed in Whiten & van de Waal 2017; Whitehead & Rendell 2015) and its over-reaching influence on social structures (e.g., bottlenose dolphin – Ansmann et al. 2012, baboons – Sapolsky & Share 2004), distributions (e.g., sperm whale - Eguiguren et al. 2019), foraging (e.g., chimpanzee – Luncz et al. 2018; killer whales – Riesch et al. 2012), and communication (e.g., sperm whale – Rendell & Whitehead 2003b, bottlenose dolphin – Romeu et al.

2018). Cultural inheritance can further play an important role in non-human species' ecological success with chimpanzees and bottlenose dolphins socially learning intricate foraging strategies (e.g., nut cracking – Estienne et al. 2019, termite fishing – Boesch et al. 2020, sponging – Mann et al. 2012, shelling – Wild et al. 2020), orangutans learning their complex diet from their mothers (Schuppli et al. 2016), and killer whales developing different lifestyles and foraging strategies to adapt and thrive in all of the world's ocean (Riesch et al. 2012). As such, culture is pervasive in humans, and non-humans.

1.1 CULTURE AS AN EVOLUTIONARY FORCE

Cultural inheritance and genetic inheritance are similar in that they are heritable, variable and affect fitness (Mesoudi 2016) - both genes and cultures can be transmitted, drift, mutate and are selected by natural selection (Boyd & Richerson 1985; Mesoudi 2017). However, cultural inheritance also has its own properties which differ from that of genetic inheritance. Cultures are transmitted both within and across generations (Boyd and Richerson 1985) and can be actively shaped by individuals (Whiten 2017). Cultural transmission can occur faster than gene transmission (Creanza & Feldman 2016; Whitehead & Ford 2018), create atypical selection pressures (Feldman & Laland 1996), and introduces additional evolutionary mechanisms such as guided variation and biased transmission (Boyd and Richerson 1985). As such, culture can alter selection pressures in unexpected ways, spread change at a faster rate within a population, and increase (or decrease) plasticity (Whiten 2017; Creanza et al. 2017; Keith & Bull 2017). In extreme cases, it can also segregate populations into culturally, rather than morphologically or genetically, distinct groups through homophily (Centola et al. 2007), biased transmission (Boyd and Richerson 1985), conformity (Richerson and Boyd 2005, Henrich and Boyd 1998), cultural symbolic markers (Barth 1969), and/or ecological specialization (Beltman et al. 2004, Whitehead and Ford 2018). These cultural group memberships can then have overreaching impacts on behaviour and psychology (e.g., Cantarrero et al. 2013, Shulz et al. 2019).

As such, culture is a second inheritance system (Whiten 2005) which complements and interacts with genetic inheritance and the environment to shape evolution and behaviour. Cultural inheritance can play an important role in determining non-human species' behaviour and evolution and, therefore, should be incorporated into the framework of mainstream biology along with genetic and environmental variation. This might be especially important in long-lived social species for which we have prior evidence of social learning and culture, such as the sperm whale.

1.2 STUDY SYSTEM: THE SPERM WHALE

Sperm whales (*Physeter macrocephalus*) have been described as "ocean nomads" and "creatures of extreme". They inhabit all of the world's ocean where they thrive by feeding on mostly mesopelagic prey (Whitehead 2003). Such success is not only caused by their extremely large nose (which allows them to emit powerful echolocation clicks and forage at depths, Watwood et al. 2006) and brain (the largest in absolute size of any animal, Ridgway & Hanson 2014), but also their reliance on socially learned information, which they acquire via their complex multi-tier social structure (i.e., cultural inheritance).

While male sperm whales disperse to go live progressively more solitary lives at high latitudes at the onset of sexual maturity (Whitehead 2003; Kobayashi et al. 2020), females, calves and juveniles live in stable matrilineal groups at lower latitudes year-round. Most social interactions between sperm whales occur at the social unit level: one to two sperm whale families which are in constant acoustic contact with each other as they travel, forage and socialize (Gero et al. 2014). Social unit membership is stable over decades with very few reported cases of social unit splits and merges (Gero et al. 2015). Individuals within social units have preferred association with each other (Gero et al. 2015) and communally raise calves (Gero et al. 2009; Gero et al. 2013). However, interactions between individuals are not restricted to social unit members as social units will sometimes associate with other social units, forming *groups*, over hours to days to forage and socialize (Christal et al. 1998). Certain social units will preferentially associate with others (Gero et al. 2015), altogether creating a complex network of social interactions.

At the highest tier, sperm whale associations at the individual, social unit and group level are governed by their membership to cultural groups called *vocal clans.* – with whales' association restricted to members of their own vocal clan (Rendell & Whitehead 2003b; Gero et al. 2016b). Vocal clans can include hundreds to thousands of individuals which share an acoustic repertoire of *codas* (Rendell & Whitehead 2003b). Codas are 3-12 patterned clicks which sperm whales use in social settings (Watkins & Schevill 1977; Whitehead & Weilgart 1991). These patterns of clicks can be categorized into types based on their general length and tempo so that nine regularly spaced clicks would be termed 9 Regular (9R) and two regularly spaced slower clicks followed by three faster clicks would be termed 1+1+3 (Weilgart & Whitehead 1997). While some coda types are shared, others are specific to certain vocal clans and can be used to distinguish them – termed identity codas (Hersh et al. 2021). Social unit membership and individual identity clues have also been suggested to be conveyed within specific coda types (Gero et al. 2016a), although this does not interfere with our ability to clearly discern vocal clan membership. Vocal clans have been documented worldwide (Eastern Tropical Pacific - Rendell and Whitehead 2003, Eastern Caribbean - Gero et al. 2016b, Japan - Amano et al. 2014, Brazil - Amorim et al. 2020, and Mauritius - Huijser et al. 2019), with whales exclusively associating with members of their own vocal clan even if other vocal clans occur in sympatry. As individuals from different vocal clans are not genetically distinct (Rendell et al. 2012; Konrad et al. 2018b) and can overlap with each other (e.g., Gero et al. 2016b), vocal clans are a predominantly culturally mediated form of social structure. In the Eastern Tropical Pacific, this cultural membership has been shown to have over-reaching implications for sperm whales' social structure, habitat use, and fitness with sperm whales from different vocal clans showing different diving synchrony (Cantor and Whitehead 2015), movement patterns (Whitehead and Rendell 2004; Whitehead et al. 2008a), temporal stability of associations (Cantor and Whitehead 2015), reproductive and feeding success (Whitehead and Rendell 2004, Marcoux et al. 2007a), as well as distributions around the Galapagos islands (Eguiguren et al. 2019).

While the size of social units and groups, as well as their prevalence, can vary geographically (Whitehead et al. 2012), all female sperm whale societies are organized along these three broad categories: social unit < group < vocal clan.

1.3 RESEARCH CONTEXT: THE EASTERN CARIBBEAN

The Eastern Caribbean sperm whale population is one of the best-studied populations of sperm whales on Earth. Since 2005, The Dominica Sperm Whale Project

(DSWP) has been conducting dedicated and opportunistic surveys of sperm whales leeward of the island of Dominica in the Lesser Antilles, gathering photo identification, acoustic, behavioural, and GPS data on the species. Over these years, the DSWP documented the lives of over 19 social units of sperm whales, largely contributing to our understanding of sperm whales as a species (e.g., Gero et al. 2009; Gero et al. 2013; Gero et al. 2014) and how Eastern Caribbean sperm whales, specifically, differ from other populations (such as the Eastern Tropical Pacific; Whitehead et al. 2012).

Until recently, it was believed that sperm whales in the Eastern Caribbean were part of a single vocal clan (EC1) with codas varying geographically (Antunes 2009; Whitehead et al. 2012). However, the discovery of a second, rare, vocal clan in 2016 (EC2) comprised of two social units (Units P and K) (Gero et al. 2016b) warranted a change in perspective. Why hadn't the DSWP documented EC2 before? How different were EC1 whales from EC2 whales? How did the different vocal clans interact at a larger scale?

In order to answer those questions, and more, we conducted dedicated sperm whale surveys in the Lesser Antilles during the years 2019 (four two-week surveys: February to April) and 2020 (four two-week surveys: January to March). We expanded our survey area seven-fold to cover most of the Lesser Antilles (from St. Kitts & Nevis to Grenada) and surveyed for sperm whale presence along three pre-defined transect lines: Leeward inshore (5–7 nautical miles from coast), Leeward offshore (15 nautical miles from coast) and Windward offshore (5–7 nautical miles from coast). While very few data were available regarding sperm whale distribution in the Lesser Antilles beyond Dominica, transect lines were designed to overlap with sperm whale preferred habitat (i.e., steep topographic slopes - Pirotta et al. 2011) as well as cover previously un-surveyed zones (i.e., windward and offshore transects). We sailed day and night aboard a 40ft sailboat (*Balaena*) at speed of 3-5 knots. Sperm whale presence was monitored every 30 minutes by a trained listener using PAMGUARD software, sampling at 96kHz from a Fireface UC or UMC202HD USB audio interface recording continuously from a two-element hydrophone towed behind the vessel on a 100m long cable. When the characteristic echolocation clicks of sperm whales were heard, we deviated from survey transects and tracked sperm whales acoustically using the towed hydrophone with bearings estimated by the Click Detector module in PAMGUARD and/or a mechanical directional hydrophone. If the sea conditions allowed, we stayed with the same group of sperm whales for up to one day, or until we had multiple repeat photographs of individuals' flukes (for individual identification purposes, Arnbom 1987a) and at least 80 codas (for vocal clan identification purposes, Rendell & Whitehead 2003a). We spent more time with unknown groups of sperm whales (flukes which we were not able to match by eye with DSWP individual catalogue available on board) and left encounters with well-known DSWP social units after only a few hours. During daylight hours, we took photographs of sperm whale flukes using DSLR cameras with 300mm lenses and recorded sperm whale behaviour (i.e., activity, group size, association patterns). GPS fixes of the vessel tracks were obtained every five minutes through a GPS marine chart plotter (Standard Horizon in 2019 and Raymarine in 2020), and vocalizations were recorded continuously on the towed hydrophone (day and night). Males were encountered opportunistically as they interacted with females and overlapped with our survey routes.

Most of the results presented in this thesis are fully (Chapter 4 and 5) or partially (Chapter 3 and 6) derived from data collected during these 2019 and 2020 Eastern Caribbean surveys.

1.4 THESIS OBJECTIVES

The overreaching objective of this PhD thesis is to highlight the contribution of cultural inheritance on the evolution, behaviour and social structure of a non-human species: the sperm whale. This is achieved by:

- Introducing a new evolutionary pathway which emphasizes the role of culture, and cultural group selection, in achieving large brains and advanced cognition in certain odontocete and primate species (Chapter 2).
- Quantifying sperm whale cultural segregation in the absence of genetic and environmental barriers (Chapter 3-4) as well as the mechanisms maintaining it (Chapter 6).
- Describing how culture can lead to unexpected variation in behaviour across (Chapter 3) and within (Chapter 4) populations.

- Highlighting the importance of incorporating culture in conservation and management measures (Chapter 4, Chapter 5, Chapter 7).

I start with a broad approach in Chapter 2: "Intraspecific, intergroup competition as a driver of advanced cognition in primates and toothed whales". In this chapter, I introduce a new evolutionary hypothesis which complements the social brain (Dunbar 1998), ecological intelligence (Milton 1981), and cultural brain (van Schaik & Burkart 2011) hypotheses in explaining why certain primate and odontocete species converged in their large brains and advanced cognition. I suggest that it is a shift from interspecific to intraspecific, intergroup, competition that selected for exceptionally large brains and advanced cognition in species from the distant primate and odontocete lineages. I propose that competition between groups of the same species created an intraspecific evolutionary arms race towards social complexity and, therefore, led to large brains and advanced cognition (with a potential for cultural group selection) and illustrate this pathway in five species: chimpanzees (*Pan troglodytes)*, bottlenose dolphins (*Tursiops truncatus*), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*) and humans (*Homo sapiens sapiens*). This second chapter sets the scene for the remainder of my thesis by introducing the potential importance of cultural inheritance to sperm whale biology and evolution.

In my third chapter "Ocean nomads or island specialists? Culturally driven habitat partitioning contrasts in scale between geographically isolated sperm whale populations", I present the main findings from the 2019 and 2020 Eastern Caribbean surveys. I describe the vocal clan membership, distribution, and movement of 31 social units/groups of sperm whales (23 of which are social units/groups that had never been documented before) and document a potential third vocal clan in the Eastern Caribbean (EC3). By expanding the research area to cover most of the Lesser Antilles rather than only the island of Dominica, I find fine-scale differences in the distribution of sperm whale vocal clans in the Eastern Caribbean with island-specific residency of individuals and social units. This contrasts with data from the Eastern Tropical Pacific and suggests an order of magnitude difference in the movement and social structure of the two populations. I conclude by stating that rather than being ocean nomads, sperm whales can show high cultural ecological specialization and habitat partitioning on flexible spatial scales. This was published in the Royal Society Open Science (reference: Vachon et al. 2022).

My fourth chapter "Distinctive, fine-scale, distribution of Eastern Caribbean sperm whales' cultural groups relates to island fidelity rather than environmental variables" follows directly from my third chapter and investigates the mechanisms responsible for the stark differences in distribution between the two main Eastern Caribbean vocal clans (EC1 and EC2). I use habitat models and habitat suitability analyses to show that the differences in distribution between vocal clans in the Lesser Antilles most likely result from site/island fidelity rather than habitat specialization as environmental variables preferred by each vocal clan are not significantly different between "EC1 islands" and "EC2 islands" and that modelling habitat use separately for cultural groups results in much higher predictive accuracy.

My fifth chapter "Abundance estimate of Eastern Caribbean sperm whales using large scale regional surveys.", integrates knowledge from my two previous chapter to update the Eastern Caribbean sperm whale population estimate. As individual sperm whales do not range across the Lesser Antilles, but rather have much more restricted distribution along specific islands, previous Eastern Caribbean population estimates from Dominica cannot be extrapolated to the Eastern Caribbean. Using closed 2-sample Petersen and Schnabel models, I estimate a population of 414 adult sperm whales (51 social units/groups) in the Lesser Antilles, which more than doubles previous estimates. I highlight the importance of accounting for population structure in conservation and management.

My sixth chapter "Multidimensional distribution of sperm whale social vocalizations suggests identity codas are symbolic markers of cultural group membership" focuses on the boundaries between vocal clans and their meaning for sperm whale ecology and behaviour. More specifically, I investigate the use of identity codas as potential symbolic markers of vocal clan membership by sperm whales. I quantitively compare the structure of identity and non-identity codas across vocal clans from three isolated geographical areas (Eastern Caribbean, Eastern Tropical Pacific, Mediterranean) using two metrics: coda type overlap and volume in multidimensional space. I find that identity codas occupy significantly smaller volumes in multivariate space and overlap significantly less with other coda types, which supports the use of identity codas as symbolic markers and highlight the importance of these coda types as interpretable signals.

I conclude my thesis with a discussion chapter in which I present my findings within the broader framework of cultural inheritance. I highlight how results from my different chapters highlight the contribution of cultural inheritance to the ecology and evolution of a non-human, non-primate, species and stress the importance of incorporating the cultural inheritance framework into mainstream biology as well as conservation and management.

CHAPTER 2 –

Intraspecific, Intergroup Competition as a Driver of Advanced Cognition in Primates and Toothed Whales.

2.1 ABSTRACT

I propose that a shift from interspecific to intraspecific, intergroup, competition selected for exceptionally large brains and advanced cognition in species from two distant lineages: primates and toothed whales. Although primates and toothed whales evolved in extremely different environments, bottlenose dolphins (*Tursiops sp*.), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), chimpanzees (*Pan troglodytes*), and humans (*Homo sapiens*) converge in their complex, competitive, societies. I suggest that competition between groups of the same species created an intraspecific evolutionary arms race towards social complexity and, therefore, led to large brains and advanced cognition (with a potential for cultural group selection). The intraspecific group competition hypothesis supplements the social brain, cultural brain, and ecological intelligence hypotheses by providing a framework to explain why, although large social groups, environmental variability, social learning, and culture are widespread in the animal kingdom, only a few species display exceptionally large brains.

2.2 INTRODUCTION

The evolution of cognition has long fascinated humans. Questions such as "why are we so smart?" and "how did we became so successful" are common both in the scientific literature and general media and are investigated in a wide array of fields (anthropology (e.g.,Handley & Mathew 2020), psychology (e.g.,Henrich & Muthukrishna 2021), archeology (e.g., Shea 2003), neuroanatomy (e.g.,Liu & Konopka 2020), animal behavior (e.g.,Uomini et al. 2020)). As such, many hypotheses have been suggested to explain the presence of large brains and cognition in humans, and other animals, with an emphasis on social challenges (social brain hypothesis- Dunbar 1992; Barton 1996; Dunbar 1998; Dunbar & Shultz 2007; Dunbar 2009, Machiavellian intelligence hypothesis- Byrne & Whiten 1989; Byrne & Corp 2004, Vygotskian intelligence hypothesis - Moll & Tomasello 2007), ecological challenges (ecological intelligence hypothesis - Parker & Gibson 1977, Milton 1981, Milton 1988, diet - Clutton-Brock & Harvey 1980; MacLean et al. 2014; deCasien et al. 2017, cognitive buffer hypothesis –Sol 2009, Gonzalez-Lagos et al. 2010), life history traits (extended parenting hypothesis- Uomini et al. 2020), and culture (cultural intelligence/brain hypothesis - Reader & Laland

2002; Whiten & vanSchaik 2007; Herrmann et al. 2007; van Schaik & Burkart 2011; vanSchaik et al. 2012, cultural group selection – Soltis et al. 1995; Henrich 2004; Boyd & Richerson 2010; Richerson et al. 2016). The social brain hypothesis suggests that group living selects for large brains, the ecological intelligence hypothesis suggests that adapting to changing environments leads to large brains, and the cultural brain hypothesis suggests that larger brains evolved to better obtain and process information via social learning. Although all these hypotheses are supported by a large body of scientific literature, most were developed and tested with a focus on humans and their closest relatives, the great apes and primates (e.g., Clutton-Brock & Harvey 1980; Milton 1981; Dunbar 1998; Whiten & vanSchaik 2007). While this approach is not wrong (in fact, it makes evolutionary sense!), it only offers a single perspective into a complex problem and does not take full advantage of the diversity of life on Earth.

Cetaceans, whales and dolphins, diverged from the anthropoid line around 90 million years ago (Kumar & Hedges 1998; Bromham et al. 1999) and yet, although they evolved in a completely different world from our own, they show abundant evidence of social learning and culture (reviewed in Rendell & Whitehead 2001; Whitehead & Rendell 2015). Like primates, cetaceans, especially toothed whales (Odontocetes), have large brains in both absolute and relative size (Marino 1998; Marino et al. 2004), complex social networks (e.g., Connor & Krutzen 2015; Gero et al. 2016), slow life history traits (e.g., Mann et al. 2000; Connor et al. 2000), culture (e.g., Rendell & Whitehead 2003b; Mann et al. 2012; Riesch et al. 2012), and the ability to solve complex cognitive tasks (e.g., Reiss & Marino 2001; Herman 2012). As such, primates and cetaceans differentiate themselves from other mammals, with cetaceans offering a secondary, independent, evolutionary pathway to large brains and advanced cognition (I define “large brains” as brains that are unexpectedly large in absolute and/or relative size compared to other mammals and “advanced cognition” as the ability to solve complex cognitive tasks such a self-recognition, 3D body representation, and the use of complex acoustic signals, abilities which are not widespread in the animal kingdom).

There is considerable variability in brain size within the primate and cetacean taxa (Marino 2004; Connor & Mann 2006; Isler et al. 2008; Reader et al. 2011). Both include species for which we have evidence of exceptional brain size and cognition (i.e. humans, chimpanzees, delphinids and sperm whales) as well as some that do not (e.g., lemurs, porpoises). This suggests that the evolutionary pathway towards large brains and advanced cognition might be especially extreme, or altogether different, in these "outlier" large brain species, highlighting their importance in solving this evolutionary puzzle.

In this chapter, I use a comparative approach to uncover a converging evolutionary pathway to large brains and advance cognition in primates and Odontocetes. By comparing data on "outlier" species in both groups, I was able to identify common trends and potential mechanisms to explain the evolution of such extreme intelligence, twice. This new hypothesis, the *intraspecific group competition hypothesis*, complements previous theories and furthers our knowledge on the evolution of large brains, not only in humans, but also in species which evolved independently from primates.

2.3 THE HYPOTHESIS

2.3.1 Methods

I reviewed the literature using search engine Web of Science and keywords "social brain", "Machiavellian intelligence", "social intelligence", "cultural intelligence", "intraspecific competition", "cultural evolution", "(cooperation)AND(evolution)", "(competition)AND(evolution)", "(human)AND(culture)AND(evolution)", "(cetacean)AND(culture)", "(primate)AND(culture)", "(cognition)AND(evolution)", "(culture)AND(evolution)", "(cetacean)AND(competition)" and "(primate)AND(competition)". As this covered a wide array of topics, the initial Web of Science search returned 136,014 articles, 587 of which had relevant titles. Of these 587 articles, 304 were judged relevant based on their abstract and read. Relevant referenced articles within these 304 articles were supplemented to the literature review as I went along, adding 311 more articles. In total, 615 articles were read and included in this literature review, most of which are not referenced in this paper, but helped form the key ideas discussed in it (Figure 2.1).

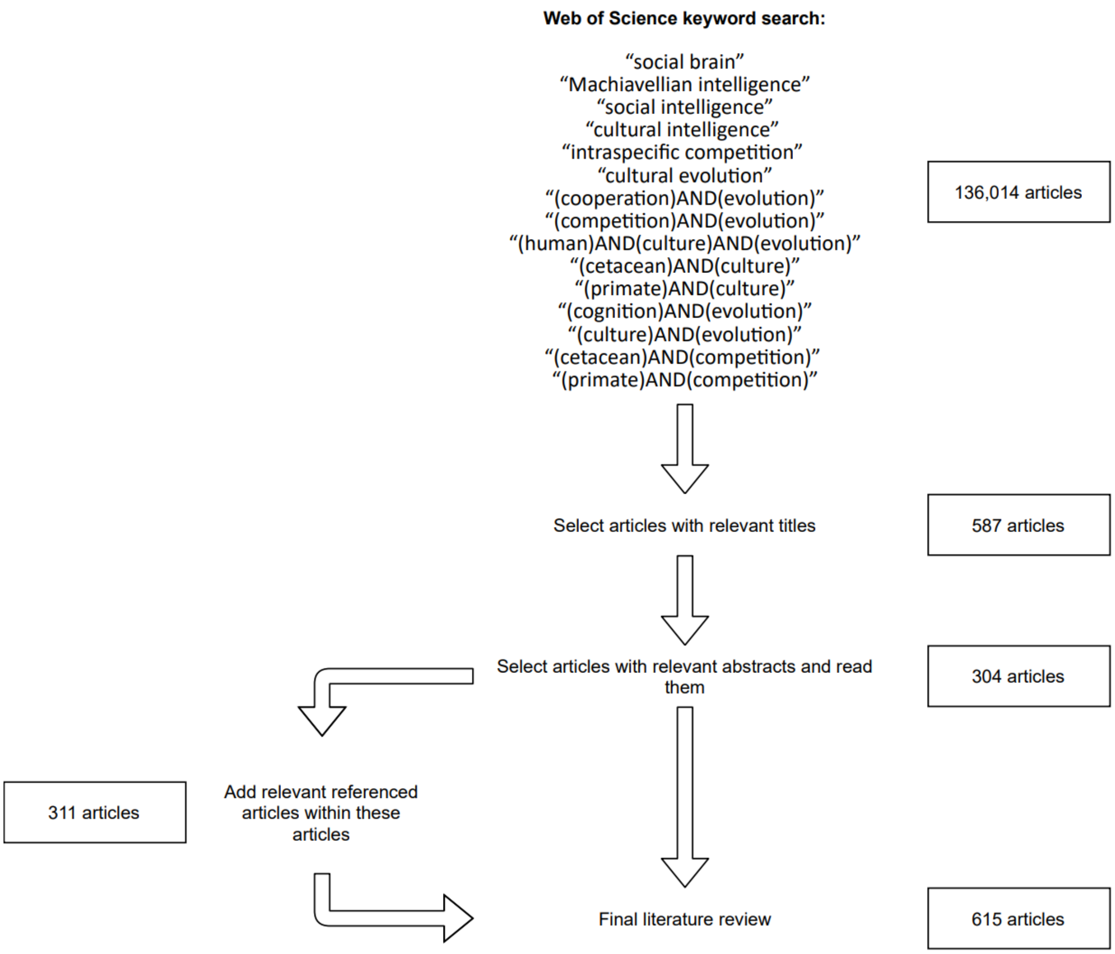

Figure 2.1. Literature review process.

2.3.2 Framework

The intraspecific group competition hypothesis suggests that it is a shift from interspecific competition to intraspecific, intergroup, competition that led to larger brains and advanced cognition in certain species. It posits that if fitness for individuals within a species depends more on intraspecific intergroup interactions rather than external factors (e.g., predation, disease, resources), natural selection would favor traits that increase cooperation within groups and competition across groups as more cooperative groups will have an evolutionary advantage over less cohesive groups (e.g., Turchin 2006; Choi & Bowles 2007; Bowles 2009; Puurtinen & Mappes 2009; Garcia & van den Bergh 2011). This would then result in an evolutionary arms race between groups of the same species for increased social cohesion and complexity, and therefore, larger brains. Below I expand on the framework of the intraspecific group competition hypothesis (illustrated in Figure 2.2).

Group living likely primarily evolved in response to predation. As primates moved from a nocturnal to a diurnal lifestyle and as cetaceans re-colonized the ocean (a three-dimensional environment without refuge) predation pressures most likely increased, and safety was found in numbers (Janson & Goldsmith 1995; Connor 2007; Shultz et al. 2011). Unlike sharks, big cats, and amphibians which invested in physiological means (i.e., large body size, claws, teeth, toxicity) to avoid predation or become predators themselves, primates and cetaceans principally avoided predation by grouping together, which brought benefits of increased vigilance, dilution, and communal defense. While these first primate and cetacean social groups were most likely simple, group living brought challenges (e.g., resource competition, free-rider problem) and opportunities (social learning). Not all group living species would take advantage of these opportunities (e.g., schooling fish) but for primates and cetaceans, these challenges and opportunities would work jointly to promote larger brains via pathways already explored by the social brain, ecological intelligence, and cultural brain hypotheses. Social learning allowed for the extraction of better, or more reliable, resources (Kaplan et al. 2000; Navarrete et al. 2016) which were used to fuel the expensive larger brains required to keep track of increasingly complex social group relationships and interactions (Dunbar 1998; Kudo & Dunbar 2001; Dunbar & Shultz 2007; Byrne & Bates 2007; Bickart et al. 2011). Slower life histories would then be promoted as longer lifespans allow for more opportunities to learn from others and benefit from learned skills (Boyd & Richerson 1985; Kaplan et al. 2000; vanSchaik & Burkart 2011) and makes this large energetic investment in a larger brain more worthwhile (Jerison 1973; Dunbar & Shultz 2007; Gonzalez-Lagos et al. 2010). Unlike cetaceans and primates, pinnipeds (although they are group-living and have slow life histories) have not followed this pathway, possibly because of a trade-off in the investment of larger body size for sexual selection and expensive brain tissue (expensive sexual tissue hypothesis (Pitnick et al. 2006; Fitzpatrick et al. 2012)), as well as reduced mother-pup relationships (Whitehead & Rendell 2015). As longer life histories, reliance on social learning and brain size co-evolved (Street et al. 2017), environmental variability (unstable climatic periods such the Pleistocene or via range expansions) exacerbates the benefits of social learning, reinforcing this pathway, as socially learned knowledge is more adaptive in variable environments (Boyd & Richerson 1985; Whitehead 2007; Grove 2017). Note, however, that ecological variation on its own is not enough to trigger this pathway toward exceptional brain size (e.g., bears face many ecological challenges but lack social complexity).

If life history parameters are slowed enough, group living shifts from being mostly kin-based to affiliation-based. Females produce less offspring and, therefore, individuals from similar age classes aren't close genetic relatives anymore. While this shift comes with many uncertainties, it is offset by the benefits of the group's reliance on social learning and non-kin (or more distant kin) group living is maintained (dosSantos & West 2018). We would expect a species with such reliance on social learning to become increasingly diverse as different individuals innovate and adapt differently to ecological and social challenges (vanSchaik & Pradhan 2003; Lefebvre et al. 2004, Sol et al. 2005). Such innovations can then spread socially within and across groups, resulting, not only in higher overall behavioral diversity at the species level, but also overall ecological success (via a larger toolkit to deal with ecological and social hardships). Species such as the sperm whale and the elephant, which are ecologically successful primarily due to their specialized noses but are also social, might have entered the framework via such ecological success, which then feedbacks into increased social complexity and increased reliance on social learning (Whitehead 2003).

I have now set the scene for what I believe to be the key factor promoting exceptionally large brains and advanced cognition. As this social learning-reliant species becomes more successful relative to competing species (due to its cultural toolkit), intraspecific competition increases. Individuals from the same species might now compete for mates, territory and/or food in ways that impact survivorship more than traditional ecological pressures such as predators, diseases, food availability, and/or abiotic environmental fluctuations. If this is the case, individual fitness shifts from being largely determined by interspecific interactions and environmental variation, to depending on intraspecific interactions. Such high levels of intraspecific competition would lead to higher diversity at the species level (as members of the same species co-exist via the use of different niches, perhaps culturally) (Slatkin 1980; Schluter 2000; Bolnick 2004;

Svanback & Bolnick 2007; Svanback et al. 2008; Hendry et al. 2009; Yoder et al. 2010; Jones & Post 2016), but also, and most importantly, select for increased cooperation within, and increased competition across, groups. This is expected if intraspecific competition is high and more cooperative, insular, groups have a fitness advantage over less cooperative groups. This phenomenon is well-documented in humans (Turchin 2006; Choi & Bowles 2007; Lehmann & Feldman2008; Bowles 2009; Puurtinen & Mappes 2009; Garcia & van den Bergh 2011) but also applies to other species (Langergraber et al. 2017; Samuni et al. 2020; Samuni et al. 2021). I hypothesize that this occurred in primates and cetaceans, but not in other mammalian species such as ungulates, which rely on social learning (e.g., Jesmer et al. 2018) but still have to cope with intense predation pressure, therefore preventing the shift from interspecific- to intraspecific-determined fitness. Such a shift is key as it creates a feedback loop in our evolutionary framework (Figure 2.2) via an intraspecific evolutionary arms-race for increased social complexity, which then selects for larger brains, longer life histories, and an increased reliance on social learning (Dunbar & Shultz 2007; Reader et al. 2011; Navarrete et al. 2016; Street et al. 2017). Under this framework, groups are increasingly successful, increasingly competitive, increasingly complex (socially), and, therefore, have increasingly large brains and cognitive capabilities as these traits feedback onto each other. As groups become more homogeneous within and heterogeneous across group boundaries (which would be expected with such high reliance on social leaning and such increased diversity due to competition), cultural group selection (Soltis et al. 1995; Henrich 2004; van der Bergh & Gowdy 2009; Boyd & Richerson 2010; Zefferman & Mathew 2015; Richerson et al. 2016) can ensue. Under this scenario, the unit of selection shifts from individuals to groups under the assumption that the fitness of individuals and/or cultures depends on the fitness of the group itself. For cultural group selection to be a meaningful evolutionary force, competition between cultural groups must be intense, variation in behavior greater across than within groups, and extinction rates high (Wilson 1975; Alexander 1989; Soltis et al. 1995; Henrich 2004; Richerson et al. 2016). Cultural group selection then accelerates the race to large brains and advanced cognition by further promoting social complexity (Figure 2.2).

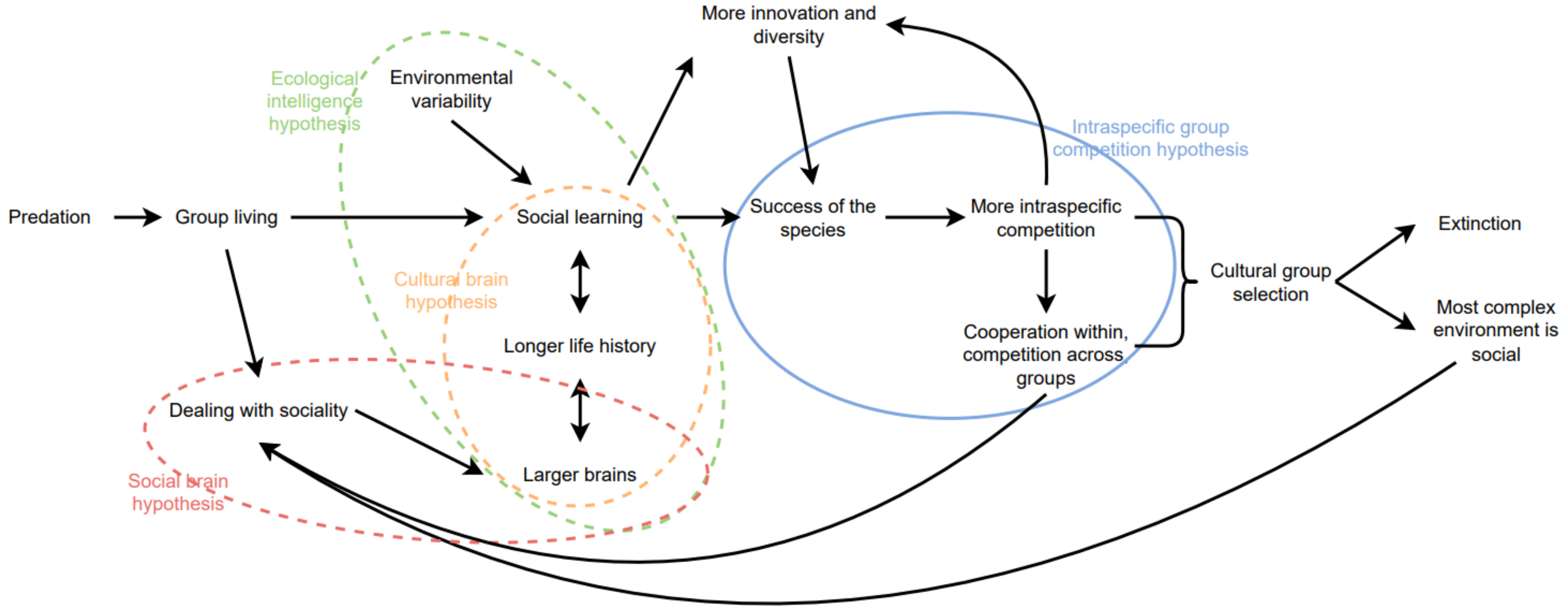

Figure 2.2. Intraspecific group competition hypothesis framework.

2.3.3 Predictions

The framework of the intraspecific group competition hypothesis makes predictions about species with large brains and advanced cognition. First, it suggests that such species would have a high reliance on social learning, with an emphasis on conformity and homophily, as these two social learning processes lead to higher group cohesion (Henrich 2004). Second, species with large brains and advanced cognition should be successful and diverse as success leads to increased intraspecific competition and diversity results from it. Third, the fitness of members of species with large brains and advanced cognition should depend on intraspecific, rather than interspecific, interactions as this triggers higher cooperation and competition and feedbacks into increased social complexity. Finally, if this framework is correct, we expect cultural group selection to operate as a result of group competition. While cultural group selection has mainly been considered in the context of human evolution (Soltis et al. 1995; Mathew & Boyd 2011; Zefferman & Mathew 2015; Henrich 2016; Handley & Mathew 2020), I make an argument here that it is likely to operate (although perhaps to a lesser extent, with less overlapping cultural groups and less individuals in cultural groups) in animal societies if they are structured around groups with more cultural differences across than within group boundaries, have ways to differentiate " us" from "them" (e.g. territorial boundaries or symbolic markers), show signs of cooperation within and competition across groups, and exhibit a resulting high extinction rate of groups/cultures.

While such an evolutionary pathway is not the norm for most animal species, I suggest that it has operated independently for certain outlier, large brain species of two distinct, distant, lineages: Odontocetes and primates. More specifically, bottlenose dolphins (*Tursiops sp*.), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). Below I expand on how these species fit the predictions of the intraspecific group competition hypothesis (Table 2.1).

2.4 ODONTOCETES

2.4.1 Bottlenose dolphins

2.4.1.1 Smart, diverse, and successful

Bottlenose dolphins' relative brain size is truly extraordinary, and second only to modern humans, with an EQ (Encephalization quotient) score (Jerison 1973) of around 4.5 (compared to 7 in humans, 2.5-7 in extinct hominids and 2.5-3 in chimpanzees) (Marino 1998). Beyond the sheer size of their brains, bottlenose dolphins also show signs of advanced cognition through their ability for self-recognition (Reiss & Marino 2001), long-term memory (Bruck 2013), socially transmitted tool use (Wild et al. 2019; Wild et al. 2020), body awareness (Herman 2012), complex communication (Janik 2013), and social intelligence (Connor 2007). Culture and social learning seem to permeate the lives of bottlenose dolphins (reviewed in Rendell & Whitehead 2001) and, as a species, the bottlenose dolphin shows extreme diversity, with different populations found in coastal and offshore areas of temperate and tropical waters around the world and different ecotypes, sometimes overlapping in range, displaying considerable morphological, behavioral, and genetic differences (Mead & Potter 1995; Natoli et al. 2004; Fruet et al. 2017). It is suggested that such diversity is the result of multiple resource specialization events in which bottlenose dolphins learned to adapt to new environmental conditions (Hoelzel 1998; Natoli et al. 2004; Tezanos-Pinto et al. 2009). In some extreme cases, this can lead to the emergence of new species (e.g., *Tursiops aduncus*) (LeDuc et al. 1999; Wang et al. 1999).

2.4.1.2 Intraspecific fitness

While bottlenose dolphins do have natural predators (sharks- Heithaus & Dill 2002; Sprogis et al. 2018), their fitness (survival, reproduction) seems to mostly depend on their ability to navigate their complex social world (Stanton & Mann 2012; Wiszniewski et al. 2012; Diaz-Aguirre et al. 2020). As such, it has been hypothesized that it is the fission fusion structure of bottlenose dolphin societies, in which relationships are constantly shifting and individuals need to keep track of third-party relationships, that lead to their larger brains (Smolker et al. 1992; Connor & Mann 2006; Connor 2007; Aureli et al. 2008). This is especially apparent in Shark Bay, Western Australia, where male Indo-Pacific bottlenose dolphins form overlapping nested alliances (on three different levels) to consort, herd, steal, and protect females (reviewed in Connor & Krutzen 2015). The intense intraspecific competition resulting from male alliance dynamics in Shark Bay fits the predictions of the intraspecific group competition hypothesis as males which are part of alliances, especially larger alliances, have a higher reproductive success (Krutzen et al. 2004; Wiszniewski et al. 2012) and females might prefer males who show higher synchrony in their behaviors (Connor et al. 2000; Connor et al. 2006). Therefore, cooperation offers a competitive advantage.

2.4.1.3 Cultural group selection?

While alliances can be highly fluid, they could be subject to group selection if members from different alliances employ different strategies, with varying success, to gain access to females. Males within second order alliances can recognize each other based on acoustic signals (King et al. 2021) with high cooperation within alliances and high competition across them (as evidenced by high intraspecific synchrony (Connor et al. 2006) and tooth-rake marks in adult male bottlenose dolphins of Shark Bay (Scott et al. 2005)). In this case, group selection would favor alliances with "better" more successful strategies in obtaining females over alliances with "bad" less successful strategies. Members from "bad" strategy alliances would then breakup to find better alliance partners (and therefore the cultural group "dies") or be unsuccessful in obtaining females, selecting for "better" alliance strategies at the group level. While there is evidence of variability in alliance strategies (Connor & Krutzen 2015), this has not been correlated with reproductive success, and therefore, we do not have clear evidence of group selection in Shark Bay male alliances as of now.

Cultural group selection could also occur between groups of bottlenose dolphins that differ in their foraging tactics. Sympatric differences in foraging tactics have been documented for bottlenose dolphins all around the world, with dolphins preferentially associating with individuals that share their foraging preference (Shark Bay spongers – Mann et al. 2012, Laguna Brazil artisanal fisherman cooperators – Daura-Jorge et al. 2012, Moreton Bay trawlers - Chilvers & Corkeron 2001). In this case, different foraging cultures compete for survival in the same environment. As discussed above, such diversity in foraging specializations is most likely a result of the bottlenose dolphins' high adaptability and propensity for social learning, as well as intraspecific competition (as predicted by the intraspecific group competition hypothesis). Different cultures can co-exist and thrive if resources are plentiful, competition is low, and/or strategies are complementary and yield similar fitness benefits (e.g. Strickland et al. 2021). Alternatively, dolphins with a "good" foraging strategy will have higher survival and reproductive success than dolphins with "bad" foraging strategies, leading the "good" cultural variants to spread and "bad" cultural variants to disappear from the population. Over evolutionary time, foraging strategies might fluctuate in their efficiency as resources are depleted and the environment fluctuates. This occurred in Moreton Bay when trawler dolphins were forced to revert to traditional foraging following the instigation of trawling regulations. Dolphins themselves did not necessarily die, instead, social networks merged (Ansmann et al. 2012) and the cultural variant of "foraging with trawlers" disappeared.

Altogether, this suggest that the intraspecific group competition hypothesis framework could be applied to bottlenose dolphins, a highly successful species that displays intraspecific competition in the form of male alliances and foraging culture diversity.

2.4.2 Matrilineal whales

2.4.2.1 Smart, diverse, and successful

While killer whales and sperm whales do not have large brains in relative size (due to their extreme body size (Marino 1998)), their brains are extraordinary in absolute size, with the sperm whale and killer whale having the largest brains of any animal on Earth (Ridgway & Hanson 2014). These species are also known for their complex, nested, social structure based around matrilineal family units. Social units of sperm whales and pods of killer whales are composed of one or few families (and/or extended family members) which always travel, socialize, and forage together (Gero et al. 2014; Ford 1991). Interactions between social units/pods are further governed by their membership to large-scale cultural groups called vocal clans in sperm whales and ecotypes in killer whales. Whales from different vocal clans/ecotypes have different acoustic signals and behaviors and do not associate with each other even if they occur in sympatry (Ford 1991; Barrett-Lennard et al. 1996; Rendell & Whitehead 2003b; Deecke et al. 2005, Riesch et al. 2012; Gero et al. 2016b). Such social structure promotes a reliance on social learning, with multiple examples of traditions and behaviors maintained and spread socially within clans, ecotypes or other social entities in both species (reviewed in Rendell & Whitehead 2001).

Sperm whales and killer whales are the most widely distributed vertebrate on Earth (after modern humans). They have learned to survive in all oceans, from the tropics to the poles, and show extreme diversity across geographical and cultural boundaries. For instance, sperm whales from different vocal clans have different movement patterns (Whitehead & Rendell 2004; Whitehead et al. 2008a; Vachon et al. 2022), social structure (Cantor & Whitehead 2015), preferred distributions (Eguiguren et al. 2019; Vachon et al. 2022), and diving synchrony (Cantor & Whitehead 2015) and killer whales from different ecotypes differ in their diet, social structure, morphology, and certain genes (reviewed in Riesch et al. 2012; deBruyn et al. 2013). In fact, killer whale ecotypes are so diverse that some have advocated for their recognition as separate species (Morin et al. 2010).

2.4.2.2 Intraspecific fitness

Due to their large size, sperm whales have very few predators. Harassment by blackfish (e.g., Palacios & Mate 1996) and attacks by killer whales have been reported, with no mortalities from blackfish encounters and mixed outcomes from killer whale attacks (e.g., Arnbom et al 1987b, Pitman et al. 2001). On the other hand, killer whales are the ocean's apex non-human predator. It is therefore likely that the fitness of both species is linked to intraspecific interactions rather than interspecific interactions.

2.4.2.3 Cultural group selection?

In many ways, sperm whale vocal clans and killer whale ecotype (via matrilines) are the perfect substrate for cultural group selection as they are insular, highly differentiated groups. Whales within cultural groups communally raise calves (Gero et al. 2009; Nattrass et al. 2019) and show high conformity in their behaviors and vocalizations (Ford 1991; Ford et al. 1998; Deecke et al. 2005; Rendell & Whitehead 2005; Konrad et al. 2018b), while whales across cultural groups show signs of xenophobia (Riesch et al. 2012) and avoidance (S.Gero pers. comm; Shields et al. 2018). It has been suggested that sperm whales use vocal clan-specific highly stereotypical codas called “identity codas” as symbolic markers to identify members of their own cultural group (Hersh et al. 2021) and killer whales might do the same using behavioral and acoustic cues (Deecke 2000; Riesch et al. 2012).

I suggest that competition between cultural groups of sperm whales and killer whales does not result in lethal violence or open conflict, but rather in intense scramble competition for resources. Different cultural groups come up with different strategies to exploit the environment (culturally driven ecological specialization), and, over time, cultural groups with “better” ideas survive while others go extinct (Whitehead & Ford 2018). In some cases, cultural groups with different, complementary, strategies will occupy different niches and co-exist (Whitehead & Ford 2018), leading to sympatric ecotypes/vocal clans, but this equilibrium can be altered by changing climatic conditions (Whitehead & Rendell 2004) and resource availability (Velez-Espino et al. 2014). This could relate to cultural hitchhiking (Whitehead 2005; Whitehead et al. 2017), and is supported by nuclear DNA and mitochondrial DNA genetic data (Foote et al. 2011; Morin et al. 2015; Foote et al. 2016; Morin et al. 2018), as well as a culturally driven ecological speciation model by Whitehead and Ford (2018), which suggest rapid diversification, multiple dispersal/founder events and high extirpation rate of cultural groups, all of which are consistent with my hypothesis.

Matrilineal whales therefore fit the framework of the intraspecific group competition hypothesis with the ecological success of sperm whales and killer whales leading to cultural group competition for resources, promoting culturally driven ecological specialization and, thereafter, cultural group selection.

2.5 PRIMATES

2.5.1 Chimpanzees

2.5.1.1 Smart, diverse, and successful

Our closest relatives, the chimpanzees, not only have larger brains than would be expected for their body size (Marino 1998), but also display mirror self-recognition (Gallup 1970), theory of mind (Call and Tomasello 2008), advanced social intelligence (reviewed in Hirata 2009), and a high reliance on social learning (reviewed in Whiten 2011). Chimpanzees are diverse in their cultures, which span a wide range of behaviors (e.g., tool use, food processing, social) (Whiten et al. 1999; van Leeuwen et al. 2012; Luncz & Boesch 2015) and allowed them to be successful through their range for thousands of years, as evidenced by nut cracking remains that have been dated back 4,300 years (Mercader et al. 2007).

Chimpanzees live in a fission-fusion society where groups of 1 to 20 individuals, from within larger communities of around 150 individuals, travel, sleep, and forage together (vanLawick-Goodall 1968; Watts et al. 2002). Male chimpanzees stay in their natal group while females emigrate to other communities at adolescence (Pusey 1979). Conformism has been extensively documented within chimpanzee communities (Hopper et al. 2007, Whiten et al. 2005, Whiten et al. 2007; Hopper et al. 2011), with female migrants adopting the traditions from their new communities even if it incurs a fitness cost (Watson et al. 2015; Luncz et al. 2018).

2.5.1.2 Intraspecific fitness

Chimpanzee fitness is affected by human activities, diseases, predation (leopards, lions), and conspecific interactions (reviewed in Anderson 2018). Although chimpanzees show cooperative and pro-social behaviors within groups from the same communities (Hamburg & McCown 1979; Boesch 2002; vanLeeuwen et al. 2021), interactions across communities are typically hostile (Wrangham 1999; Boesch & Boesch-Achermann 2000; Wrangham & Glowacki 2012; Furuichi 2020) and sometimes lethal (Wilson & Wrangham 2003; Watts et al. 2006; Wilson et al. 2014). Between 2004 and 2010, most of Gombe chimpanzees' mortalities were attributed to intraspecific interactions (Terio et al. 2011) and chimpanzee "wars" have resulted in the loss of entire communities (Goodall

1986; Wilson & Wrangham 2003). Inter-community conflicts (raids) can incur large fitness costs for losers: mortality, injury, stress, lower reproductive rate (Wilson & Wrangham 2003; Watts et al. 2006; Wilson et al. 2014; Lemoine et al. 2020) but yield benefits for victors: territory expansion, better access to females, increased resource acquisition (Wrangham 1999; Wilson & Wrangham 2003; Mitani et al. 2010). Successful communities will also have larger territories, which are correlated with shorter inter-birth intervals (Pusey 2001). Altogether, this suggests that intraspecific interactions have the potential to affect survival and reproduction at least as significantly as interspecific interactions.

2.5.1.3 Cultural group selection?

In chimpanzees, cultural group selection could operate at the community level: neighboring chimpanzee communities conform to different cultural variants (Luncz et al. 2012; Koops et al. 2015; Luncz & Boesch 2015; Pascual-Garrido 2019), members of chimpanzee out-groups are easily identified by their territorial range, and high individual fitness benefits and costs are associated with inter-community conflict outcomes. However, for cultural group selection to operate, evolution must also shift from being driven by individual-fitness to group-fitness (Read 2006), something that is only possible with high levels of within group cooperation. The hostile nature of intergroup interactions might promote cooperation within chimpanzee communities (as suggested by the intraspecific group competition hypothesis) with larger, more cohesive, raid parties being more successful and sustaining less severe injuries (Wilson et al. 2014; Pandit et al. 2016), and individual chimpanzees more likely to participate in raids if more individuals, or close associates and kin, are participating themselves (Samuni et al. 2021). However, intra-community competition in the form of contest and scramble competition over food (Wrangham 2000; Wittig & Boesch 2003), female spatial competition (Miller et al. 2014), male status competition (Gilby et al. 2013; Foerster et al. 2016), and sexual competition (Fawcett & Muhumuza 2000; Lowe et al. 2020) has also been documented for chimpanzees and could prevent cultural group selection if individual fitness benefits and costs of intra-community competition are higher than those resulting from inter-community interactions. Although intergroup competition has been documented to actively reduce intra-community aggression by males (Samuni et al. 2020), and although infanticides and intra-community lethal attacks are relatively rare (Nishida et al. 1995; Lowe et al. 2020), such intra-community competition would reduce the impact, or viability, of cultural group selection.

Altogether, chimpanzee behavior seems to support the framework and claims of the intraspecific group competition hypothesis, with inter-community competition promoting social complexity, although high levels of intra-community competition might limit the efficiency of cultural group selection.

2.5.2 Humans

2.5.2.1 Smart, diverse, and successful

Humans offer the most extreme case of the intraspecific group competition hypothesis. Humans have been described as hyper-cooperative (Burkart et al. 2014), hyper-cultural (Barkow 2001), and ultra-social (Tomasello 2014; Henrich & Muthukrishna 2021) and their propensity for social learning and culture (Henrich & McElreath 2003) has allowed them to colonize and thrive in all terrestrial biomes on Earth for 60,000 years (Henn et al. 2012).

2.5.2.2 Intraspecific fitness

Humans' fitness is almost solely dependent on intraspecific interactions (Alexander 1989, Alexander 1990), which are governed by complex social norms and often mediated by cultural group membership. To navigate such a complex social environment, humans make spontaneous in-group versus out-group classifications (Brewer 1979, Tajfel & Turner 1979) and show loyalty toward in-group members (Abrams et al. 1998; Van Vugt & Hart 2004, Zdaniuk & Levine 2001) and prejudice towards out-group members (Brewer & Brown 1998, Fiske 2002), even if groups are large and composed of mostly unknown individuals.

Warfare, an intense form of inter-group competition, has been a staple of human evolution (Keeley 1996; Bowles 2009; Leblanc & Register 2003) and is believed to have promoted cooperation (Turchin 2006; Choi & Bowles 2007; Puurtinen & Mappes 2009), shaped social behavior (Bowles 2006; Bowles 2009) and laid the foundation for modern nations and institutions (Richerson & Boyd 1999; Bowles 2012; Turchin et al. 2013). The extinction rate is high in the hominid lineage, with no remaining ancestral species or side branches in *Homo* (White 2003).

2.5.2.3 Cultural group selection

Therefore, humans display high levels of cultural diversity across groups, high intra-group cooperation, and high inter-group competition. As such, cultural group selection has been suggested as an important factor in human evolution (Soltis et al. 1995; Henrich 2004; Zefferman & Mathew 2015; Richerson et al. 2016), not only because of warfare but also other culturally transmitted behaviors such as differences in subsistence methods (Boyd & Richerson 2009). Therefore, the intraspecific group competition hypothesis framework is supported.

Table 2.1. Summary table of the intraspecific group competition hypothesis' predictions.

	Bottlenose dolphins	**Matrilineal whales**	**Chimpanzees**	**Humans**
Social learning	▪Social learning ▪Socially transmitted tool use	▪Overarching cultures ▪Conformism	▪Extensive evidence of conformism and social learning	▪ "Hyper cultural" ▪ "Ultra-social"
Successful and diverse	▪Distributed in temperate and tropical waters worldwide ▪Ecologically diverse	▪Worldwide distribution ▪Diverse cultures	▪Diverse cultures ▪Tradition maintained for over 4,300 years	▪Worldwide distribution ▪Ecological dominance
Survival depends on intraspecific interactions	▪Some predators ▪Complex social interactions that relate to reproductive success	▪No or few predators ▪Resource competition	▪Predation ▪Hostile and sometimes lethal inter-community interactions	▪No predators ▪Complex social norms
Cultural groups	▪Male alliances ▪Foraging cultural groups	▪Vocal clans ▪Ecotypes	▪Communities	▪Diverse (e.g., Institutions, ethnic groups, countries etc.)
Symbolic markers	▪Acoustic signals	▪Identity codas ▪Different acoustic repertoires ▪Behavioral cues	▪Ability to recognize individuals from other communities based on their territorial range	▪Spontaneous classification of new individuals as "in-group" or "out-group"
Cooperation within, competition across groups	▪Synchrony ▪Competition between male alliances ▪Social associations reflect foraging specialization	▪Social associations are exclusively within cultural groups ▪Communal care of calves ▪Avoidance across cultural groups (xenophobia) ▪Resource competition	▪Cooperative hunting and grooming within community ▪Hostile inter-community interactions (raids)	▪ "Hyper-cooperative" ▪Warfare
High extinction rate	▪Disappearance of foraging cultures ▪Unsuccessful males	▪Low mtDNA diversity (cultural hitchhiking) ▪Genetic evidence of bottlenecks/founder events	▪Inter-community wars	▪Extinction of *Homo* evolutionary side branches

*See general text for references

2.6 CONCLUSION

The intraspecific group competition hypothesis is intended as a complement to the social brain, ecological intelligence, and cultural brain hypotheses. It offers a theoretical framework that goes beyond social complexity, environmental variation, and the use of social learning to explain extraordinary brain size in species from two distant lineages (primates and Odontocetes). As such, it offers an explanation as to why, while many species have culture, rely on social learning, and have been subject to environmental variability, only a few developed exceptionally large brains. More specifically, I suggest that it is inter-group resource competition between male alliances and foraging cultures in bottlenose dolphins, vocal clans, and ecotypes (via matrilines) in matrilineal whales and communities in chimpanzees that created an intraspecific evolutionary arms race for exceptionally large brain and cognition in those species.

Although this study is limited in its scope (only considering a small set of species) and nature (qualitative comparison rather than quantitative statistical tests), I hope that it promotes further discussion and research in the field of cognitive evolution by applying evolutionary concepts such as cultural group selection to non-human species and considering the evolution of intelligence in multiple lineages. I think this framework could provide interesting insight regarding the behavior and evolution of other species (e.g., other delphinids, blackfish, other great apes, capuchins, baboons, elephants, bats).

I conclude with a cautionary remark. For the intraspecific group competition hypothesis to create a feedback loop toward extreme brain size and advanced cognition, intraspecific threats to fitness must exceed interspecific threats. This is suggested to be the case, evolutionarily, for bottlenose dolphins, killer whales, sperm whales and chimpanzees, but might have changed over the short evolutionary time since humans became ecologically dominant. Anthropogenic stressors such as overfishing, entanglement, whaling and vessel traffic are now major threats to bottlenose dolphin survival (Bejder et al. 2006; Bearzi et al. 2009; Tulloch et al. 2020) and caused steep decline in certain sperm whale and killer whale populations (Whitehead et al. 1997; Beck et al. 2014; Gero & Whitehead 2016, Clarke Murray et al. 2021). Chimpanzees are globally endangered, with certain sub-species (Western chimpanzees) classified as critically endangered and showing 80% population decline (Kuhl et al. 2017) due to human poaching, hunting, and habitat degradation (Hockings et al. 2015; Anderson 2018). Not only are these threats jeopardizing the fitness and survival of individuals from these species, but also their cultures, with anthropogenic stressors already linked to decreases in chimpanzee cultural diversity (Kuhl et al. 2019). In this case, the long life histories, cultural rigidity, and extreme intelligence that led to the success of bottlenose dolphins, killer whales, sperm whales, and chimpanzees might make them particularly vulnerable to threats from another large brained species (humans) and prevent them from achieving further brain expansion through the framework of the intraspecific group competition hypothesis.

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CHAPTER 3 –

Ocean Nomads or Island Specialists? Culturally Driven Habitat Partitioning Contrasts in Scale Between Geographically Isolated Sperm Whale Populations [1]

3.1 ABSTRACT

The sperm whale (*Physeter macrocephalus*) is a deep-diving cetacean with a global distribution and a multileveled, culturally segregated, social structure. While sperm whales have previously been described as “ocean nomads”, this might not be universal. We conducted surveys of sperm whales along the Lesser Antilles to document the acoustic repertoires, movements, and distributions of Eastern Caribbean sperm whale cultural groups (called vocal clans). In addition to documenting a potential third vocal clan in the Eastern Caribbean, we found strong evidence of fine-scale habitat partitioning between vocal clans with scales of horizontal movements an order of magnitude smaller than from comparable studies on Eastern Tropical Pacific sperm whales. These results suggest that sperm whales can display cultural ecological specialization and habitat partitioning on flexible spatial scales according to local conditions and broadens our perception of the ecological flexibility of the species. This study highlights the importance of incorporating multiple temporal and spatial scales to understand the impact of culture on ecological adaptability, as well as the dangers of extrapolating results across geographical areas and cultural groups.

3.2 INTRODUCTION

Levin (1992) highlighted that scale is a fundamental problem in ecology and that, to truly understand a system, we need to incorporate information from multiple scales. This is particularly relevant to the study of animal population structure as populations can be structured on multiple scales according to their genetics (Howard et al. 2002), life history (Baker et al. 2018), environment/distribution (Edelaar et al. 2012) and/or culture (Richerson & Boyd 2005; Centola et al. 2007; Whitehead & Ford 2018). It is important to understand population structure, and the scale at which it occurs, from an ecological and conservation standpoint as individuals within a subdivided population might have different behaviours, habitat use, and/or resource use, and, therefore, different exposure to human threats and conservation needs. Furthermore, the scale-dependent structural diversity of a species may reflect diversity in inherited information (cultural, genetic) that

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can be an important element of overall biodiversity. However, the large spatial and temporal scales over which many cetacean species live their lives create significant challenges to understanding their populations and ecology (Kaschner et al. 2012). This is especially the case in species like the sperm whale (*Physeter macrocephalus*), which can travel thousands of kilometres (Whitehead et al. 2008a; Mizroch et al. 2013) and has a complex, multi-level social structure (Whitehead 2003).

Sperm whales are a deep-diving marine predator with a worldwide distribution (Whitehead 2003; Jaquet 1996). Female sperm whales generally inhabit tropical pelagic waters while males disperse to high latitudes at the onset of maturity (Whitehead 2003). Females have a multi-level social structure centred around social units of one or two matrilines (Konrad et al. 2018a; Sarano et al. 2021). These social units usually contain 6-12 individuals and are stable over time (Whitehead et al. 2012; Gero et al. 2014; Cantor & whitehead 2015). Multiple social units will sometimes join each other for periods of hours to days, forming groups, which forage or socialise together (Christal et al. 1998; Gero et al. 2015). Interactions between social units are strongly influenced by their membership of cultural groups, called vocal clans, which we distinguish based on their distinctive repertoires of coda vocalizations (Rendell & Whitehead 2003a; Gero et al. 2016b).

Codas are stereotyped patterns of clicks (Watkins & Schevill 1977) used by sperm whales in social contexts (Whitehead & Weilgart 1991). Codas vary in their length (usually between 3 and 12 clicks), rhythmic pattern, and tempo, and can be classified into types based on their inter-click intervals (ICIs) (Weilgart & Whitehead 1997). The coda type repertoire of a social unit is made up of all the coda types that the unit produces, while the coda usage repertoire refers to the relative contributions of those types to the overall vocal output (following methods of Hersh et al. 2021). These repertoires are stable over time (Rendell & Whitehead 2003b; Rendell & Whitehead 2005; Gero et al. 2016a) and can be used to identify vocal clans, thought to represent a higher order social structure, by differentiating between social units that share coda usage repertoires and those that do not (Rendell & Whitehead 2003a). Vocal clans have been documented worldwide: in the Eastern Tropical Pacific (Rendell & Whitehead 2003b), off the island of Dominica in the Caribbean (Gero et al. 2016b), off Japan (Amano et al. 2014), off Brazil (Amorim et al. 2020), and off Mauritius (Huijser et al. 2020). Whales from different vocal clans have distinct coda type and usage repertoires and generally do not associate with each other, even when they occur in sympatry. Variation in these dialects is not consistent with genetic variation (Rendell et al. 2012; Konrad et al. 2018b), indicating that coda repertoires are socially learned. Vocal clans are therefore suggested to be a culturally mediated form of population structure (Rendell et al. 2012; Cantor et al. 2015).

In the Eastern Caribbean, research has been conducted since 2005 in the waters leeward of the island of Dominica by the Dominica Sperm Whale Project (DSWP). During this time, the DSWP documented the social structure and behaviour of 19 known social units (Gero et al. 2014; Gero et al. 2013) and identified two vocal clans: EC1 and EC2 (Gero et al. 2016b). However, one vocal clan (EC1) made up 97% of the documented 937 photo-identified sperm whale encounters between 2005 and 2019, with the second vocal clan (EC2) encountered so rarely it was only recently recognized as a distinct clan (i.e. 2016), although records show it has been present in the region for at least as long as EC1 (Gero et al. 2016b).

Around the Galápagos Islands, the presence of a rare vocal clan was a precursor to a large-scale population shift (the replacement of sympatric vocal clans Regular and Plus-One by sympatric vocal clans Short and Four-Plus) (Cantor et al. 2016), but there are no suggestions of such changes in the Eastern Caribbean as the same EC1 social units are still regularly encountered by the DSWP (Gero et al. 2007). The presence of a second, rare vocal clan off Dominica thus raised general questions about regional Eastern Caribbean sperm whale clan structure—how prevalent is the EC2 clan?—and globally—over which scales dothe processes generating vocal clans operate?

Here, we address these questions by expanding the spatial scale of the Eastern Caribbean research effort in two ways: first, by extending research beyond Dominica to encompass most of the Lesser Antilles; and second, by comparing the spatial scales of movement and population structure of sperm whales in the Eastern Caribbean to those in the Eastern Tropical Pacific.

3.3 METHODS

3.3.1 Field methods

The waters around the Lesser Antilles were surveyed from a 12-m auxiliary sailboat between the island of St. Kitts & Nevis and Grenada following three predefined transect lines: Leeward inshore (5–7 nautical miles from coast), Leeward offshore (15 nautical miles from coast) and Windward inshore (5–7 nautical miles from coast) (Figure S3.1). A total of eight approximately two-week long surveys were conducted from St. Lucia between the months of February and April in 2019 and January and March in 2020.

During the surveys, which were carried out whenever possible under sail, we used a two-element hydrophone array (two high frequency Magrec HPO3 elements with high pass filter set at 2kHz) towed behind the vessel on a 100-m cable to record sound continuously via a Fireface UC or UMC202HD USB audio interface connected to a PC computer running the PAMGuard software (Gillespie et al. 2009), sampling at 96kHz (this allows for the detection of most whale and dolphin species and clear sperm whale recordings). We listened to the hydrophone through PAMGuard every 30 minutes to determine whether there were sperm whales or other cetaceans in the area. When echolocation clicks of sperm whales were heard, groups of sperm whales were followed acoustically (using the towed hydrophone with bearings estimated by the Click Detector module in PAMGuard and/or a mechanical directional hydrophone) and visually (during daylight hours) for periods of hours up to one day. Most, but not all, acoustic detections of sperm whales led to visual detection. Photographs of flukes were taken using DSLR cameras with 300mm lenses for individual identification purposes (Arnbom 1987a), GPS fixes were obtained every five minutes through a GPS marine chart plotter (Standard Horizon in 2019 and Raymarine in 2020), and vocalizations were recorded continuously using the towed hydrophone. The boat travelled continuously (day and night) at an average speed of 4 knots. Whales were approached slowly from behind, no closer than 150m (unless whales voluntarily approached the vessel), to limit disturbance. We spent more time with groups of females compared to single mature males, and with individuals for which we did not have prior photo-identification data (based on comparison with an offline DSWP photo-identification catalogue available on board: 240 individuals from 34 social units/groups identified between 2005 and 2018). If the sea conditions allowed, we stayed with unknown groups until we heard at least 80 codas, to ensure that we would be able to extract and analyse at least 25 codas (Rendell & Whitehead 2003b) and had multiple repeat photographs of individuals' flukes.

Codas extracted from acoustic recordings from the 2019 and 2020 surveys were pooled with those from the DSWP (2005-2018) and the Watkins Marine Mammal Sound Database (Sayigh et al. 2017), which were recorded between 1981 and 1995 off Dominica, Canouan, Bequia, and St. Lucia. Together, they comprise a sample of Eastern Caribbean sperm whale codas covering a significant temporal (1981-2020) and spatial (St. Kitts & Nevis to Grenada, approximately 600km) scale.

3.3.2 Delineating groups and social units

A quality rating (Q) from 1 to 5 was given to each sperm whale fluke photograph (Arnbom 1987a; Dufault & Whitehead 1998) and only photographs with $Q \geq 3$ were included in this analysis. All flukes (even those that were initially assigned in the field) were matched against known Caribbean individuals using the software Flukebook (Blount et al. submitted) (https://www.flukebook.org/). Newly identified individuals were considered part of the same group (i.e., a short-term joining of at least two social units, lasting a few hours to a few days) if they were identified on the same day and had coordinated general behaviour and movement (Gero et al. 2014). As such, newly encountered sperm whales are assumed to be part of a group until we can confirm that the membership of all individuals is stable, at which point they are considered part of the same social unit. The criteria used to distinguish social units from groups has varied over time (Gero et al. 2014; Christal & Whitehead 1998) but we use the most restrictive definition here: members of a group which have been documented associating (i.e., observed within two hours of each other) in at least two different years are then defined as a social unit (Gero et al. 2014).This definition is the same as that used by the DSWP (Gero et al. 2014) and is more stringent than that used in the Eastern Tropical Pacific, which considers groups social units if they are re-identified over a timescale of at least 30 days (Christal & Whitehead 1998). In this paper we describe both social units and groups as not all newly encountered groups of sperm whales met the further requirements of stable membership in the definition of a social unit.

3.3.3 Vocal clan membership

Recordings were analyzed by trained auditors and codas were manually marked using CodaSorter (K. Beedholm, Aarhus University), a custom written LabView (National Instruments, TX, USA) program implemented in MATLAB. Only repertoires of 25 or more codas and only codas with 3–11 clicks were included in the analysis, following previous methods (Rendell & Whitehead 2003b). Three- to eleven-click codas constituted the bulk (98.9%) of marked codas and only considering them accounts for the potential of inconsistent marking of very short (<3 clicks) or very long (≥12 clicks) codas. All codas recorded on the same day were pooled together to form a repertoire that was assigned to the group of sperm whales identified on that day. Codas from days with multiple encountered social units were considered single repertoires and assigned to the combination of social units (Rendell & Whitehead 2003b).

To delineate vocal clans across social units and groups, we compared coda repertoires using the identity call method, IDcall (Hersh et al. 2021) to identify characteristic coda types, termed “identity codas” (i.e.,coda types that are used consistently by one set of repertoires and rarely by others). Codas were first separated according to their number of clicks and then classified into types according to their absolute ICIs using parsimonious mixtures of multivariate contaminated normal distributions (R package “ContaminatedMixt”) (Punzo et al. 2018). Vocal clans were then delineated based on differences in the presence and usage of identity coda types in repertoires (Hersh et al. 2021). We tested various combinations of the parameters of the IDcall method to show that our identification of vocal clans was robust to parameter variation (Table S3.1).

3.3.4 Movement analyses

We used the track of our research vessel as we followed groups of female sperm whales during the 2019 and 2020 surveys to measure fine scale Eastern Caribbean sperm whale movements. Tracks were broken into one-hour, three-hour and six-hour segments to compare movement across vocal clans. Displacement was measured as the shortest distance between two GPS fixes (5 minutes resolution). To account for any bias caused by the research vessel moving purposefully away from a group of whales while still in acoustic contact, only the portion of the vessel track which occurred between the time of the first and last sightings of sperm whale clusters (animals at the surface within 30m of each other and displaying coordinated behaviour) (Whitehead 2003) on any day were included in this analysis. For longer timescales (days, months, years), we used the likelihood method from Whitehead (2001) to describe patterns of movement. Photo-identification data collected during the 2019 and 2020 surveys were used to estimate root-mean-squared (RMS) displacement (an estimate of the shortest distance covered by an individual across a specific time lag based on its locations) across multiple time lags. The likelihood method corrects for an uneven distribution of effort and is appropriate for this analysis given the spatial variability in our survey effort. Only time lags greater than one day were included in this analysis since sperm whales were actively tracked for up to one day and, therefore, photoidentifications within a day are autocorrelated (Whitehead 2001). Error bars for RMS displacements were obtained using individual jackknifing, whereby individual sperm whales were removed from the analysis in turn and RMS displacement was recalculated (Efron & Gong 1983). We only included adult female and immature sperm whales in this analysis because calves were not reliably identified in the field and mature males have very low re-sighting rates in the Caribbean (Gero et al. 2014; Gero et al. 2015; Gero et al. 2016b) and display very different movement patterns (Dufault et al. 1999). This analysis was carried out using the continuous movement module of the SOCPROG software (Whitehead 2009).

3.3.5 Comparison with Eastern Tropical Pacific sperm whales

Finally, we compared our findings with data from previous studies describing the social structure (i.e., mean social unit size, mean typical group size) (Cantor & Whitehead 2015; Coakes & Whitehead 2004), movements (i.e., hourly to yearly displacement, range) (Whitehead 2001; Whitehead & Rendell 2004; Whitehead et al. 2008a), and distribution (i.e., vocal clans' range and potential overlap) (Rendell & Whitehead 2003b; Eguiguren et al. 2019) of Eastern Tropical Pacific sperm whales. These data were collected in the Eastern Tropical Pacific between 1985 and 2014 using very similar protocols (i.e., dedicated, vessel-based acoustic and visual sperm whale surveys), and analysed using similar methods (e.g., group and social unit definition, vocal clan assignation, RMS displacement), making our comparisons valid.

3.4 RESULTS

Over the 2019 and 2020 surveys, we obtained sperm whale photo-identifications on 56 days (24 in 2019; 32 in 2020), during which we obtained 778 hours of sperm whale recordings (339 in 2019; 439 in 2020) and 13,394 photographs (5,197 in 2019; 8,197 in 2020). From 4,267 photographs with a quality score of Q ≥3, we photo-identified 214 adult sperm whales, 145 of which were not in existing Eastern Caribbean catalogues (DSWP and other Flukebook contributors). These newly identified whales were from 23 groups (averaging 6 photo-identified adult individuals each), of which four qualified as social units using our definition. Our photo-identification results suggest that we encountered individuals that rarely, if ever, use the waters off Dominica, since expanding our research effort considerably increased the total number of identified individuals (from 536 whales identified over 15 years by the DSWP to 681, Figure S3.2).

3.4.1 Acoustic data

From the 2019 and 2020 survey recordings we marked 5,558 codas from 31 groups (23 newly discovered, and 8 which had previously been documented by the DSWP). These data were pooled with 13 years of acoustic data recorded primarily off Dominica from the DSWP (11,375 codas from 19 well-known social units), and data from the Watkins database (2,106 codas from 21 days between 1981 and 1995) giving a combined dataset of 19,039 codas. Of these, 163 codas were excluded from the analysis because they contained more than 11 clicks and 813 codas were excluded because they were from usage repertoires with fewer than 25 codas. The final dataset thus had 18,063 codas comprising 151 different usage repertoires that we used to identify vocal clans (Table S3.2).

The 42 groups (22 of which qualify as social units) of sperm whales included in this analysis (31 groups from the 2019 and 2020 surveys and 11 groups from DSWP data that were not encountered during the surveys) were divided into three different acoustic clades according to their use of ten identified identity coda types (Figure 3.1, Figure

S3.3). Our analysis recovered the previously documented EC1 and EC2 vocal clans, with EC1 repertoires dominated by the 1+1+3 coda type (54% of the recorded EC1 codas) and EC2 repertoires containing predominantly 5R and 2+1+1+1 codas (combining to 61% of the recorded EC2 codas). However, while EC2 was previously rarely encountered off Dominica (2.5% of all DSWP encounters between 2005 and 2019, Table S3.3) and therefore assumed to be uncommon in the Eastern Caribbean (Gero et al. 2016b), our results suggest that, on a regional scale, they are as numerous as EC1 groups—10 groups of EC1 whales and 11 groups of EC2 whales were identified during the 2019 and 2020 surveys and, cumulatively (including DSWP data), 18 distinct groups of EC1 whales and 14 distinct groups of EC2 whales have been identified in the Eastern Caribbean (most of which qualify as social units).

Furthermore, we found evidence for a potential third vocal clan (EC3) represented by a single social unit (Unit 12; comprised of 10 adults and 2 calves) with a coda usage repertoire dominated by long, regular identity codas, with 9R, 10R, and 11R types making up 57% of the recorded EC3 repertoire.

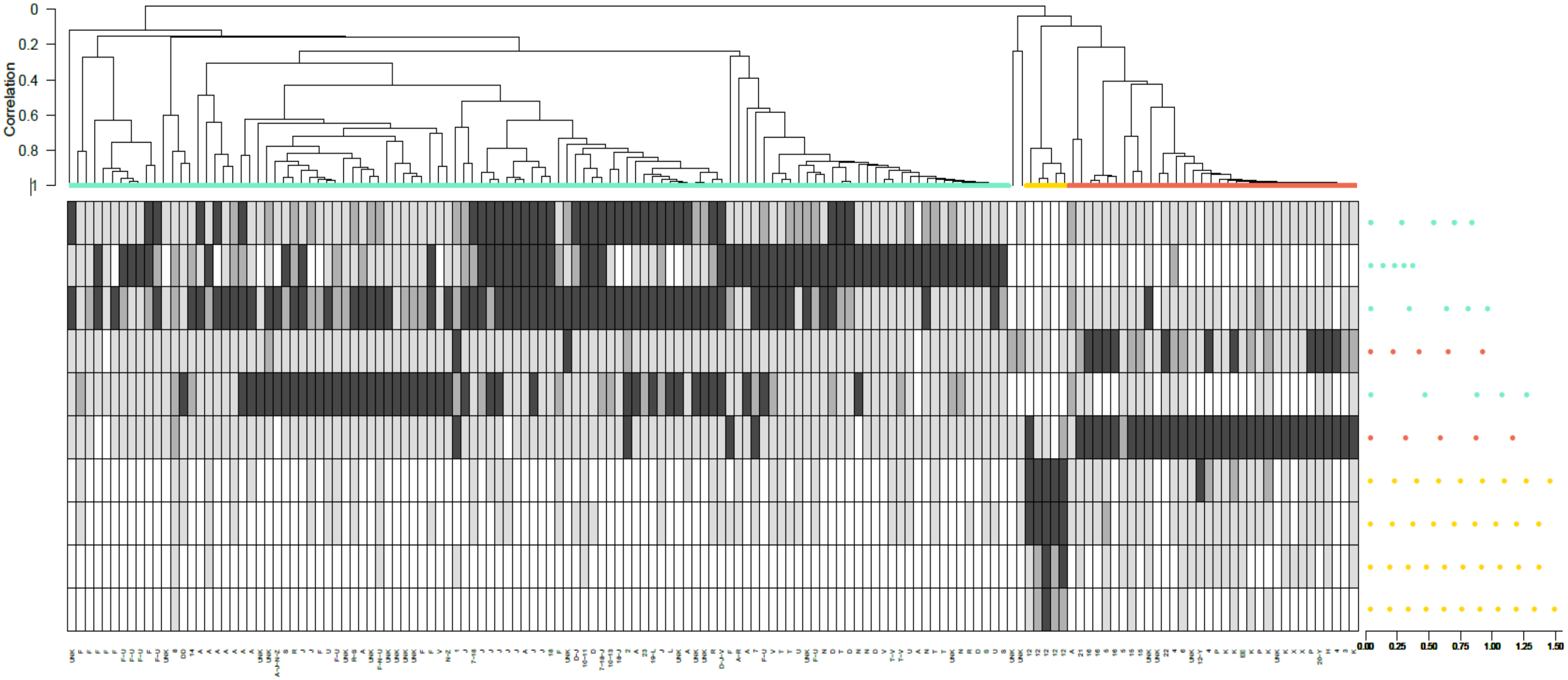

Figure 3.1. Average linkage hierarchical clustering dendrogram (top) depicting acoustic similarity among the three Eastern Caribbean sperm whale vocal clans: EC1 (blue), EC2 (red), and EC3 (yellow). Each branch corresponds to the coda repertoire of a certain group/social unit of sperm whales on a certain day (corresponding groups/social units labeled underneath). Each row of the heat map (bottom) shows probabilistic usage by repertoire of each identity coda type. Heat map shading corresponds to the percentage of the repertoire made up of each identity coda type with white 0%, light gray 0–5%, gray 5–10% and dark gray 10% or higher. Identity coda types are depicted to the right of the heat map by dots representing each click in the coda and are coloured according to clan with duration in seconds underneath. See Figure S3.3 for a version of this diagram showing all coda types.

3.4.2 Distribution and movements

Over our 2019 and 2020 surveys, we had a total of 50 encounters with sperm whales that lasted from 4.5 hours to 28 hours (mean 14 hours). 24 of these encounters were with EC1, 22 with EC2, 5 with EC3 and 1 with both EC2 and EC3. We had more encounters than groups (50 encounters with 31 groups) as some groups were encountered on multiple days. In total, we had acoustic track data that spanned 771 hours, making up the 9,249 GPS fixes that were used to map the kernel density of Eastern Caribbean vocal clans throughout the Lesser Antilles.

In the study area, very consistent winds (the 'trade winds'), divide the marine habitat around the Lesser Antilles into windward (east) and leeward (west) zones. All our sperm whale encounters were to leeward of the islands, with higher encounter rates around the central islands of Martinique, Dominica and St. Lucia. There was a clear divide in the distribution of the vocal clans, with little overlap between EC1 whales (encountered around St. Kitts & Nevis, Antigua, Guadeloupe, Dominica, and St. Vincent & the Grenadines) and EC2 whales (encountered around Martinique and St. Lucia). The EC3 unit's distribution overlapped with EC2, being mostly sighted off Martinique but also encountered off St. Lucia (Figure 3.2).

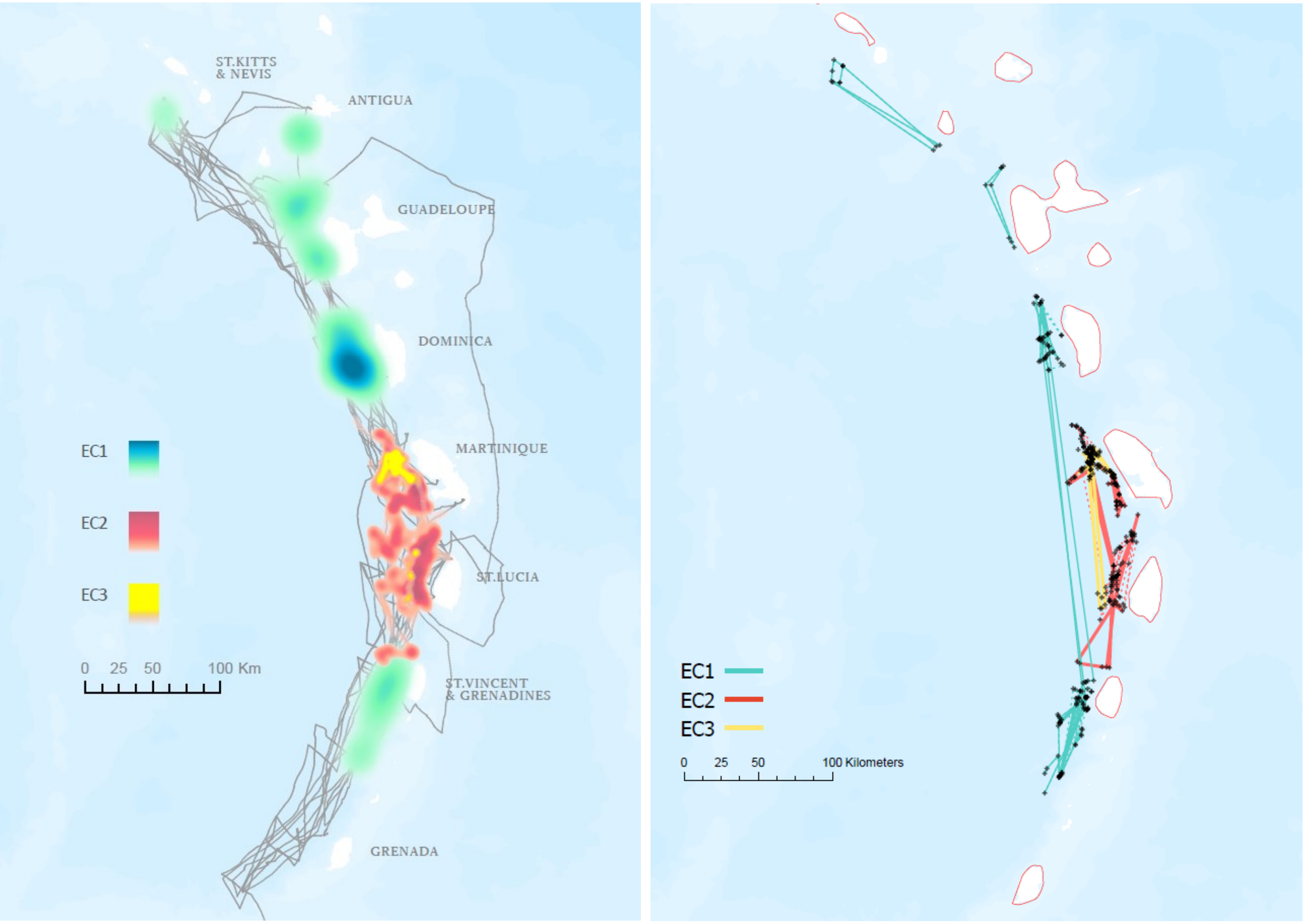

Figure 3.2. Left: Kernel density distribution of Eastern Caribbean vocal clans with track of the research vessel (light gray). We calculated the density of acoustic encounters with groups/social units from each clan at a 0.001° resolution (approximately 100m) using the kernel density spatial tool in ArcGIS. Right: Movement of photo-identified sperm whales between 2019 and 2020. Each dot corresponds to an individual identification. Full lines represent movement across years while dotted lines represent movement within years.

Eastern Caribbean sperm whales' mean and maximum displacement over 1 hour, 3 hours and 6 hours was similar across vocal clans, with about 3-4km displacement per hour (Figure S3.4). Estimates of movement over longer timescales from photo-identification data suggest that RMS displacement increased over time lags of up to one year, with daily displacements in the range of 10 to 20km (Figure 3.4). EC1 whales had slightly higher displacement then EC2 whales using the likelihood methods from Whitehead (Whitehead 2001) (Figure S3.5) and tended to be re-sighted more consistently around the same island, although a few made larger movements along the Lesser Antilles (Figure 3.2). For instance, 74% (17/23) of the EC1 individuals re-sighted across survey years were re-sighted off the same island, while this number decreases to 41.7% (5/12) for EC2. These data suggest that, overall, sperm whales in the Eastern Caribbean have a high degree of residency over our two-year survey timescale, with most displacements ranging across only one or two islands between years. This is consistent with the high re-sighting rate of EC1 social units in Dominica by the DSWP (Gero et al. 2007), the increase in the number of known individuals resulting from expanding our research area to include additional islands, and the fact that only one of the 26 known DSWP EC1 social units (Unit J) was encountered outside Dominica and Guadeloupe waters during our surveys.

3.4.3 Comparison with Eastern Tropical Pacific

Across all time scales, Eastern Caribbean sperm whales had lower displacement than Eastern Tropical Pacific sperm whales. This became more apparent as the time lag increased, from 1 hour (mean 36.1% lower), to 3 hours (mean 42.7% lower) to 6 hours (mean 45.9% lower) (Figure 3.3) and as we included daily and yearly displacement through photo-identification. Over timescales of up to a year, the residency of Eastern Caribbean sperm whales contrasts starkly with the movement of Eastern Tropical Pacific sperm whales. The difference in RMS displacement between the two geographical regions increases dramatically over time scales of a few hours to years to reach a factor of 10 difference over timescales of one year (100 km versus 1,000km mean displacement; Figure 3.4).

A similar trend can be observed at the vocal clan level, with the EC1 and EC2 vocal clans having lower mean and maximum 1-hour, 3-hour and 6-hour displacements (Figure S3.4) and lower RMS displacement across all time lags (Figure S3.5) compared to Eastern Tropical Pacific vocal clans.

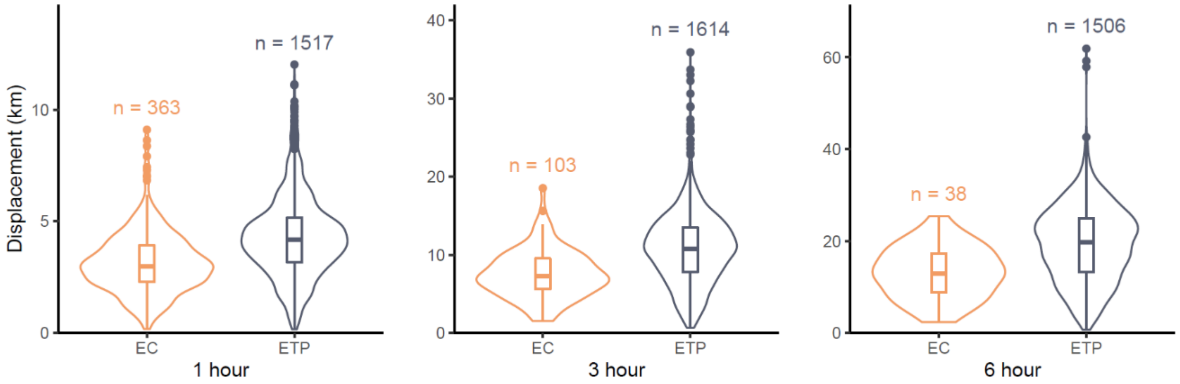

Figure 3.3. Violin plots displaying the one-hour, three-hour, and six-hour displacement of sperm whales from the Eastern Caribbean (EC) and Eastern Tropical Pacific (ETP). Sample size is displayed above each violin plot.

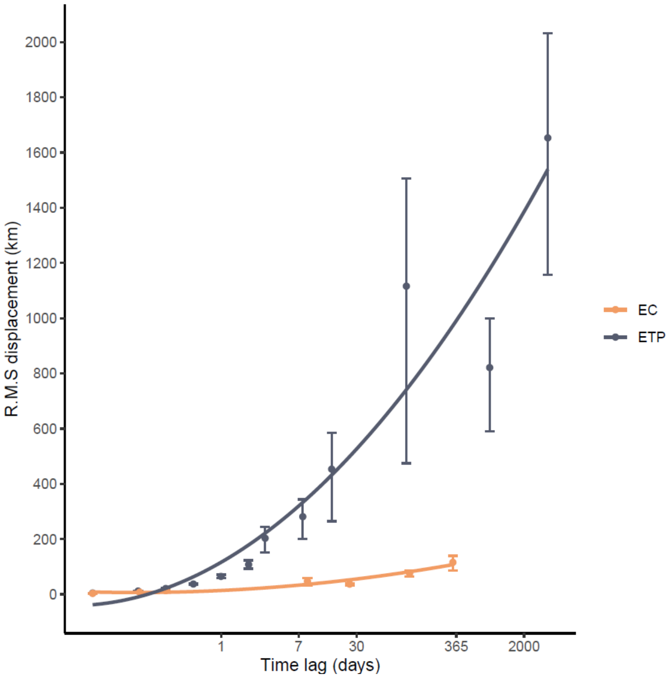

Figure 3.4. Root-mean squared displacement of Eastern Caribbean sperm whales (orange) and Eastern Tropical Pacific sperm whales (dark gray) over increasing time-lags. Error bars display jackknife standard error. Root-mean squared displacement was calculated using the likelihood method (Whitehead 2001) for time lags beyond one day for Eastern Caribbean (EC) data and two days for Eastern Tropical Pacific (ETP) data.

3.5 DISCUSSION

3.5.1 EC3: A new vocal clan?

We are cautious in our description of EC3 as a new vocal clan, given that it is comprised of a single social unit (Unit 12). This social unit was encountered on six different days over two years, one day of which was with Unit Y, an EC2 social unit. This is particularly unusual as encounters with two vocal clans (EC1 and EC2) on the same day have only been reported 4 times over 15 years by the DSWP (0.004% of photo-identification encounters). However, while Unit 12 (EC3) and Unit Y (EC2) individuals were photographed within 16 minutes of each other on February 17th 2020, only one whale from Unit 12 (IDN 6432) was observed in cluster (measure of association: when whales are within 30m of each other and moving in a coordinated fashion, Gero et al. 2014) with individuals from Unit Y (IDN 6223 and IDN 6221). Throughout that day, even if both groups were in the same area, individuals chose to disproportionally associate (in clusters) with individuals from their own vocal clan: out of the 18 clusters observed, only one contained individuals from both vocal clans. Therefore, it is possible that EC2 and EC3 ranges overlap, but that whales choose to disproportionally associate with individuals from their own vocal clan. Alternatively, EC3 could be actively branching off from EC2 or be an EC2 social unit with a highly stereotypical social unit coda repertoire (Gero et al. 2016a). As more evidence accumulates, so will our certainty of the existence of EC3 as a distinct sperm whale vocal clan. However, the fact that the coda repertoire and membership of the EC3 social unit were stable across years, and the former distinctive from both the EC1 and EC2 repertoires (with long, fast, regular identity codas and almost no overlap with identity codas of EC1 and EC2; Figure 3.1), suggests that a third vocal clan could be using the study area.

3.5.2 Ocean nomads?

Sperm whales have been described as “ocean nomads”, with male and female movements on the order of a thousand kilometres recorded in the Eastern Tropical Pacific (Jaquet et al. 2003; Whitehead et al. 2008a), North Pacific (Mizroch & Rice 2013) and Mediterranean (Rendell & Frantzis 2016). Our results show, however, that sperm whales in the Eastern Caribbean organize their societies on a much smaller geographic scale.

Eastern Caribbean vocal clans have distinctive distributions around the Lesser Antilles over spatial scales of up to a few hundreds of kilometres and temporal scales of at least two years (Figure 3.2). Social units tend to stay around the same one or two islands with high re-sighting rates within-islands and rare between-islands movements of up to 270km (Figure 3.2). Dominica, which we assumed was a good representation of the Eastern Caribbean sperm whale population, therefore only represents a biased subset. This is surprising as the spatial scales of individual movements, social unit movements, and the spatial distribution of clans are on the order of thousands of kilometres in the Eastern Tropical Pacific (Rendell & Whitehead 2003b; Whitehead & Rendell 2004; Whitehead et al. 2008a), and the Lesser Antilles span around 600 kilometres.

We also confirmed previous work that showed that Eastern Caribbean social units and group sizes are relatively small compared to the Eastern Tropical Pacific, with a mean social unit size of 6.8 individuals for EC1 (Gero et al. 2014), 8.1 individuals for EC2 (this study), and group sizes in the range of 7–9 individuals, compared with mean social unit sizes of 10–14 individuals and mean group sizes of about 30 individuals for the Eastern Tropical Pacific (Whitehead et al. 2012; Gero et al. 2014) (Table 3.1). This adds to accumulating evidence of the variable social structure of sperm whales on a global scale, with differences not only between the Pacific and Atlantic (Whitehead et al. 2012), but also the Mediterranean (Rendell & Frantzis 2016) and Mauritius (Indian Ocean) (Sarano et al 2021).

The vocal clan distribution and movement results from our 2019 and 2020 surveys are remarkable, with no overlap between EC1 and EC2 vocal clan distributions and very few long-range movements between years (Figure 3.2). These results are concurred by 15 years of DSWP data, which documented high residency of predominantly EC1 social units of Dominica (Gero et al. 2007) and never identified the 145 individual sperm whales that occupy neighbouring islands. However, over longer timescales, the lack of physical barriers in the ocean means such sharp delineations are unlikely to be impermeable. For instance, EC2 groups have been encountered, although rarely, outside of the waters of St. Lucia and Martinique by the DSWP in the past (Table S3.3, 2.6% of total DSWP encounters). Similarly, female movements on the order of hundreds of kilometres, while extremely rare, have been documented (e.g., Dominica to St. Lucia – Gero et al. 2007, Dominica to St. Vincent – this study; Bahamas to Azores, Gulf of Mexico to Bahama – Mullin et al. 2022). This highlights a caveat in this study: results presented here identify regional scale spatial patterns over a relatively small timescale.

Nonetheless our results suggest that there is an approximate order of magnitude difference in the scales of movements and range spans of Eastern Caribbean and Eastern Tropical Pacific sperm whales, with much larger groups of whales covering much greater areas in the Eastern Tropical Pacific compared to the Eastern Caribbean (Table 3.1).

Table 3.1. Summary of principal differences in scale between sperm whale vocal clans of the Eastern Caribbean (EC1, EC2) and Eastern Tropical Pacific (Regular, Plus-One). Presented as mean ±SD when appropriate.

	Eastern Caribbean	Eastern Tropical Pacific
Number of vocal clans	2-3	5 [a]
Number of individuals in vocal clans	Hundreds	On the order of 10,000 [a]
Mean social unit size	EC1: 6.8 ± 2.8 (3-12) [b] EC2: 8.1 ± 2.5 (6-13)	Regular: 13.6 ± 7.0 [c] Plus-One: 10.7 ± 4.2 [c]
Mean typical group size	7-9 [b]	30.4 [d]
3 hrs displacement	EC1: 8.0 ± 0.9km EC2: 7.0 ± 0.8km	Regular: 10.2 ± 2.4km [e] Plus-One: 10.7 ± 0.2km [e]
6 hrs displacement	EC1: 13.7 ± 2.6km EC2: 12.3 ± 2.4km	Regular: 16.8 ±4.6km [e] Plus-One: 19.4 ± 0.6km [e]
Daily root-mean-squared displacement	10 - 20km	50km [e f]
Maximum displacement of female	300 - 400km	5,000km [e]
Range	Few hundreds of kilometres	1,000-2,000km [e f]

[a]Rendell & Whitehead 2003b; [b]Gero et al. 2014; [c]Cantor & Whitehead 2015; [d]Coakes & Whitehead 2004; [e]Whitehead et al. 2008a; [f] Whitehead 2001

Eastern Caribbean sperm whales display a level of fidelity in their habitat choice and a degree of fine-scale habitat partitioning between cultural groups previously undocumented for females of this species, changing our perspective on how stereotypical sperm whale ecology and movement is worldwide. Such differences in scale between the Eastern Tropical Pacific and the Eastern Caribbean could be driven by cultural differences in movement patterns between vocal clans (e.g., Whitehead & Rendell 2004) and/or some type of response to differences in the distribution and ecology of sperm whales' main prey (squids) between the two areas. Sperm whale in the Eastern Tropical Pacific have been documented to prey on Humboldt squids (*Dosidicus gigas*) (Ruiz-Cooley et al. 2004; Díaz-Gamboa et al. 2018) – a highly mobile, migratory, species (Liu et al. 2016) which might be more broadly distributed than squid species in the Eastern Caribbean. While studies of sperm whale diet are lacking in the Eastern Caribbean, both neritic and pelagic squid species have been identified in the area (e.g., *Ommastrephes bartramii* and *Thysanoteuthis rhombus* (Judkins et al. 2010; Kiszka et al. 2021)) and a reliance on potentially patchier (Judkins et al. 2010) neritic species could explain variation in the scale of sperm whale movement across the two geographical areas.

However, the observations that Eastern Caribbean vocal clans were substantially restricted, during our two-year survey period, to specific islands (or pairs of neighbouring islands) in the Lesser Antilles, and that these preferences are maintained in sympatry without evidence of nuclear genetic differentiation (Konrad et al. 2018b) suggests that differences in habitat use between EC1 and EC2 are mostly culturally driven. The exact mechanism responsible for such a divide remains unknown, and is an important focus for future research, but we consider several potential explanations for this spatio-temporal pattern of behavioural variation below.

Territoriality: Vocal clans occupy different territories which they defend from each other.

While territoriality is a widespread phenomenon in terrestrial mammals and can result in observable differences in distributions (Bates 1970; Owen-Smith 1977), this explanation seems unlikely for sperm whales, as the three-dimensional structure and seasonal, patchy resources of marine environments make them almost impossible to defend (Miller 2018). Furthermore, there has been no record of aggression between female sperm whales, which would be expected if vocal clans defended their territories from each other. Evidence of overlap between EC1 and EC2 ranges, such as sightings of EC2 units in Dominica and Guadeloupe by the DSWP (Table S3.3), also refutes this hypothesis.

Prey type specialization: Vocal clans have learned to use, and specialised on, prey which are distributed differently around the islands.

Prey type specialization has been reported in several marine mammal species including killer whales (Orcinus orca) (Riesch et al. 2012), sea otters (Enhydra lutris) (Estes et al. 2003), and bottlenose dolphins (Tursiops spp.) (Sargeant & Mann 2009). In the case of sperm whales, social learning abilities might have resulted in improved plasticity (Baldwin 1896; Whitehead 2010), or the spread of innovation (Wilson 1985) when encountering new prey types. Over time, this could lead to vocal clans exploiting different niches (Whitehead & Ford 2018) with conformism reinforcing the divide in prey-type use (Richerson & Boyd 2005). This hypothesis makes ecological sense since other sperm whale traits, such as coda production, are thought to be maintained culturally over generational timescales (Rendell et al. 2011). Ecological specialization would theoretically decrease competition between vocal clans, and sperm whales have been shown to adapt to other ecological opportunities, such as the spread of fishery interactions (Schakner et al. 2014). However, prey-type specialization would only result in the distribution differences documented in this study if the prey on which the vocal clans are specialized are distributed differently across the different islands (for example, if Martinique and St. Lucia have different prey types than Dominica, Guadeloupe and St. Vincent), which is possible, but unlikely, given the ocean's general homogeneity over short spatial and temporal scales (Steele 1985) and lack of evidence for island-specific species diversity in the Lesser Antilles (Miloslavich et al. 2010).

Geographic or habitat specialization: Vocal clans have accumulated knowledge on specific habitat types or areas and have learned to use them efficiently.

Similar to resource specialization, geographic or habitat specialization could occur if, instead of improving their use of a specific prey, different clans preferentially selected particular areas (i.e., geographic specialization), or the features characteristic of particular areas, such as bathymetry or current flow (i.e., habitat specialization). For geographic or habitat specialization to be ecologically beneficial, it would require the presence of predictable resources that are tied to the geography of an area or to particular habitats. This might be the case in the Lesser Antilles, which are characterised by predictable winds (Fassig 1933), a fairly consistent inflow from the Atlantic to the Caribbean Sea through the channels between islands (Johns et al. 2002), and a bathymetry that can vary dramatically from one island to the next. The more predictable resources and more heterogeneous bathymetry of the Eastern Caribbean compared to the Eastern Tropical Pacific may have led to the higher residency of sperm whales in particular areas. Such fine-scale habitat choice is, perhaps, more akin to the predictable use of certain higher latitude canyons by male sperm whales (Rødland et al. 2015; Jaquet et al. 2000; Kobayashi & Amano 2020). We suggest that geographic and/or habitat specialization, transmitted through social learning within units and clans (i.e., culture), is the most parsimonious explanation for the fine-scale ecology of Eastern Caribbean sperm whales. Geographic and/or habitat specialization is most likely learned socially within social units within vocal clans, with certain social units showing high residency to certain islands and vocal clans having distinctive distributions in the Lesser Antilles as a whole. This is similar to African elephants (*Loxodonta 50fricana*), which also display socially learned patterns of site and resource use (Fishlock et al. 2016). Geographic or habitat specialization could account for differences in the scale of movements between Eastern Caribbean sperm whales and Eastern Tropical Pacific sperm whales, but also the general isolation of East and West Mediterranean sperm whales (Rendell & Frantzis 2016) and their fine-scale, bathymetry-related distribution (Pirotta et al. 2011). This demonstrates more ecological diversity in the sperm whale species as a whole than was previously assumed.

Our suggestion of cultural geographic or habitat specialization implies that Eastern Caribbean sperm whales utilize much smaller areas of habitat than sperm whales in the Pacific. This has three important implications for conservation. First, since current population estimates of the Eastern Caribbean sperm whale population are based primarily on sightings off Dominica, they might not accurately reflect the regional situation. The threats identified for the Dominica sperm whales, and resulting in EC1 population decline (Gero & Whitehead 2016), most likely apply to sperm whales with residency around different islands but need to be more thoroughly examined and assessed. Second, it raises the potential importance of protecting sperm whale vocal clans independently off the different islands in order to maintain cultural diversity and population resilience (Brakes et al. 2019). Finally, it highlights the dangers of extrapolating data across geographical areas and cultural groups.

While this study is limited in its temporal and spatial scale, it does show that sperm whales, often characterized as having a relatively uniform ecology (Watwood et al. 2006) compared to other cetacean species (Whitehead & Rendell 2005), may yet show considerable variability in how they use their environment, being adaptively successful both as ocean nomads and as local specialists. As more temporal and spatial scales of data are incorporated into the study of sperm whales, we may find more diverse ecological strategies and more ways in which culture shapes their lives.

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CHAPTER 4 –

Distinctive, Fine-scale Distribution of Eastern Caribbean Sperm Whale Cultural Groups Relates to Island Fidelity Rather than Environmental Variables

4.1 ABSTRACT

Environmental variables are often the primary drivers of species' distributions as they define their niche. However, individuals, or groups of individuals, may sometimes adopt a limited range within this larger suitable habitat as a result of social and cultural processes. This is the case for Eastern Caribbean sperm whales. While environmental variables are reasonably successful in describing the general distribution of sperm whales in the region, individuals from different cultural groups have distinct distributions around the Lesser Antilles islands. Using data collected over two years of dedicated surveys in the Eastern Caribbean, we conducted habitat modelling and habitat suitability analyses to investigate the mechanisms responsible for such fine-scale distribution patterns. Vocal clan-specific models were dramatically more successful at predicting distribution than general species models, showing how a failure to incorporate social factors can impede accurate predictions. Habitat variation between islands did not explain vocal clan distributions, suggesting that cultural group segregation in the Eastern Caribbean sperm whale is driven by traditions of site/island fidelity (most likely maintained through conformism and homophily) rather than habitat type specialization. Our results provide evidence for the key role of cultural knowledge in shaping habitat use of sperm whales within suitable environmental conditions and highlight the importance of cultural factors in shaping sperm whale ecology. We recommend that social and cultural information be incorporated into conservation and management as culture can segregate populations on fine spatial scales in the absence of environmental variability.

4.2 INTRODUCTION

It is not uncommon for species to only occupy a limited range within available suitable habitat. While environmental variables are often the primary driver of species distribution (as a failure to meet certain conditions will reduce fitness), social factors might also limit individuals' range within a wider suitable habitat. This is true for territorial species (e.g., wolves, *Canis lupus* -O'Neil et al. 2020, chimpanzees, *Pan troglodytes verus* - Herbinger et al. 2001), species that show site fidelity (e.g., fur seals, *Arctocephalus gazella* -Hoffman et al. 2006, reef fishes, *Thalassoma bifasciatum* – Warner 1988), as well as prey type specialists (e.g. killer whales, *Orcinus orca* -Filatova et al. 2019) and habitat specialists (e.g. bottlenose dolphins, *Tursiops truncatus* – Kopps et al. 2014, elephants, *Loxodonta africana* -Fishlock et al. 2016). In cases of prey or habitat specialization, individuals learn to use, and can specialize on, prey or habitat features that are distributed differently from the prey or habitat features used by other members of the same species, therefore resulting in an heterogenous distribution. Territoriality, site fidelity, prey type specialization and habitat specialization are often group-level processes that can relate to kinship and/or social learning/culture. For instance, individuals might learn prey or habitat preferences via social learning within cultural groups as is the case in killer whale ecotypes (reviewed in Riesch et al. 2012; deBruyn et al. 2013) or via vertical transmission from parents as is the case with bottlenose dolphin "spongers" (Krützen et al. 2005).

However, although their effect on distribution can be quite dramatic, social factors such as the ones described above are rarely included in analyses relating to animal conservation. For instance, habitat models, which are a widespread tool in conservation as they allow for the identification of critical habitats for species' recovery and survival (Cañadas et al. 2005; Redfern et al. 2006; Pérez-Jorge et al. 2015) and can offer invaluable information regarding a population's health (Matthiopoulos et al. 2019), consider environmental variables in detail but rarely include cultural and social information (exceptions see Filatova et al. 2019; Eguiguren et al. 2019).

As more and more evidence suggest that culture is widespread in the animal kingdom (e.g., Whiten 2017; Whitehead et al. 2019), there is increasing interest in the role of cultural transmission in determining species distribution (Whitehead 2010; Brakes et al. 2021). This might be particularly important for species for which many group-level behaviours are culturally transmitted, such as the sperm whale (*Physeter macrocephalus*).

Sperm whales are deep-diving cetaceans that live in all of the world's oceans (Whitehead 2003). They have a hierarchical social structure in which females and calves live at lower latitudes year-round in stable matrilineally-based social units of about 10 members (Christal et al. 1998). Interactions between individuals and social units are then restricted to members of the same vocal clan, a higher order social structure defined by vocal dialect that can occur in sympatry (Rendell & Whitehead 2003b; Gero et al. 2016b). Vocal clans can include hundreds to tens of thousands of whales (Rendell and Whitehead 2003), are identified by distinctive usage of stereotyped patterns of clicks called codas (Rendell and Whitehead 2003; Gero et al. 2016b) and have been documented worldwide (e.g., Eastern Tropical Pacific -Rendell and Whitehead 2003, Eastern Caribbean - Gero et al. 2016b; Vachon et al. 2022, Japan -Amano et al. 2014, Brazil - Amorim et al. 2020 and Mauritius - Huijser et al. 2019). Beyond acoustic differences, sperm whales from different vocal clans also display different social behaviour (Cantor and Whitehead 2015), movement patterns (Whitehead and Rendell 2004; Whitehead et al. 2008a, Vachon et al.2022) and distributions (Eguiguren et al. 2019, Vachon et al. 2022). Because of their sympatry, and because genetic variation is insufficient to explain behavioural variation (Rendell et al 2012), it is believed that vocal clans are cultural entities, with distinctive behaviours being socially learned largely within social units (Cantor et al.2015). The existence of these culturally driven vocal clans has important implications for the behaviour, ecology and distribution of sperm whales, in a similar way to the ecotypes of killer whales (Riesch et al. 2012). Therefore, considering conservation metrics such as habitat use without accounting for culture might lead to misinterpretation as culture can alter behavior, distribution and subdivide populations in unexpected ways (Richerson & Boyd 2005; Whiten 2017; Creanza et al. 2017).

The population of sperm whales in the Eastern Caribbean has been extensively studied but, until recently, at a relatively small spatial scale (i.e. largely around a single island). Since 2005, The Dominica Sperm Whale Project (DSWP) has studied over 19 sperm whale social units around Dominica (Gero et al. 2014), gaining important insight on sperm whale social structure and behaviour (Gero et al. 2013; Gero et al. 2014; Gero et al. 2016b). In 2019 and 2020, we extended this research area and conducted surveys to include a wider range along the Lesser Antillean chain (from St. Kitts & Nevis to Grenada). From this, we gained insight into the way vocal clans influenced the spatial organization of the Eastern Caribbean sperm whale population (Vachon et al. 2022). Eastern Caribbean vocal clans (EC1 and EC2) appear to have very distinctive small-scale distributions around the Lesser Antilles, with EC1 found predominantly around Dominica, Guadeloupe and St. Vincent & the Grenadines and EC2 found around the two central islands, St. Lucia and Martinique. This is not unheard of as sperm whale vocal clans in the Eastern Tropical Pacific have also been shown to have somewhat different distributions over a somewhat similar scale, 100's of km (Eguiguren et al. 2019). However, the causes of such segregation have not been investigated until now.

I propose two competing hypotheses could explain vocal clan island segregation in the Eastern Caribbean. The first is habitat specialization, where islands vary in the amount of each vocal clan's preferred habitat type. In this case, foraging strategies specialized to specific habitat types could be driving the distribution of Eastern Caribbean sperm whale vocal clans. As sperm whales spend about 75% of their time foraging (Whitehead & Weilgart 1991), differences in foraging strategies relating to environmental variation could lead to large differences in overall distribution. The second hypothesis is vocal clan-specific traditions of island preferences that are arbitrary with respect to the habitat each island offers. This is akin to a classic study of mating site choice in blue head wrasse (*Thalassoma bifasciatum*) by Warner (1988) which first showed that preferred coral heads were in physical terms no different from unused ones, a pattern robust to translocation with persistent preferences socially maintained by traditions. In the case of Caribbean sperm whales, the different Lesser Antilles islands might be analogous to the different wrasse mating sites, with individuals from different vocal clans preferentially staying in the vicinity of certain islands for reasons of tradition (site/island fidelity) rather than specific physical features. While translocation experiments are not possible for sperm whales, we can ask whether clan specific habitat preferences map onto variation in the amount of preferred habitat across islands to understand whether these preferences are likely to be traditional or not.

Therefore, in this chapter, we attempted to differentiate between habitat specialization and site/island fidelity by modelling sperm whale habitat use in the Eastern Caribbean, assessing the relative importance of island geography and habitat distribution in predicting sperm whale presence by identifying important environmental variables for EC1 and EC2 independently, and testing whether the distribution of these variables varies significantly across the EC1 and EC2 "islands". If Eastern Caribbean sperm whales are habitat specialists, we expect specific environmental variables to be closely linked with EC1 and EC2 distributions and there to be stark variation in at least some of these variables between EC1 and EC2 "islands". On the other hand, if Eastern Caribbean sperm whale distribution is the result of island/site fidelity, we expect island vicinity to be a better predictor of EC1/EC2 sperm whale presence and environmental variables to not be significant factors in our models. Such an approach not only aims for a deeper understanding of a group-living and cultural species' distribution and behaviour, but also yields a novel approach to integrate into conservation policy.

4.3 METHODS

4.3.1 Field Methods

Data were collected between the months of February and April 2019 and January and March 2020 in the Eastern Caribbean. We surveyed sperm whale presence between the islands of St. Kitts & Nevis and Grenada along three transect lines (Leeward Inshore: 5-7 nautical miles from coast, Leeward Offshore: 15 nautical miles from coast and Windward: 5-7 nautical miles from coast) (Figure 4.1) from a 12m auxiliary sailboat using a two-element hydrophone array (two high frequency Magrec HPO3 elements with low cut filter set at 2kHz) towed behind the vessel on a 100-m cable. Once encountered acoustically, female sperm whales were followed, using the towed hydrophone with the direction sensing software *Click Detector* on PAMGUARD, for hours to days. Codas to identify vocal clans were recorded via a Fireface UC or UMC202HD USB audio interface connected to a PC computer running software PAMGuard (Gillespie et al. 2009), sampling at 96kHz and recording continuously during surveys. The GPS location of our research vessel was recorded on a GPS marine chart plotter (Standard Horizon in 2019 and Raymarine in 2020) every five minutes. Given that we could identify social units in real time using photo identification (see Gero et al 2014), we intentionally spent more time with groups of whales for which we had little or no prior data and, if conditions allowed, stayed with unknown groups until we had repeats of multiple individual's flukes and had obtained at least 80 codas (this allowed for high confidence in identifying the vocal clan that the group belonged to) (Vachon et al. 2022).

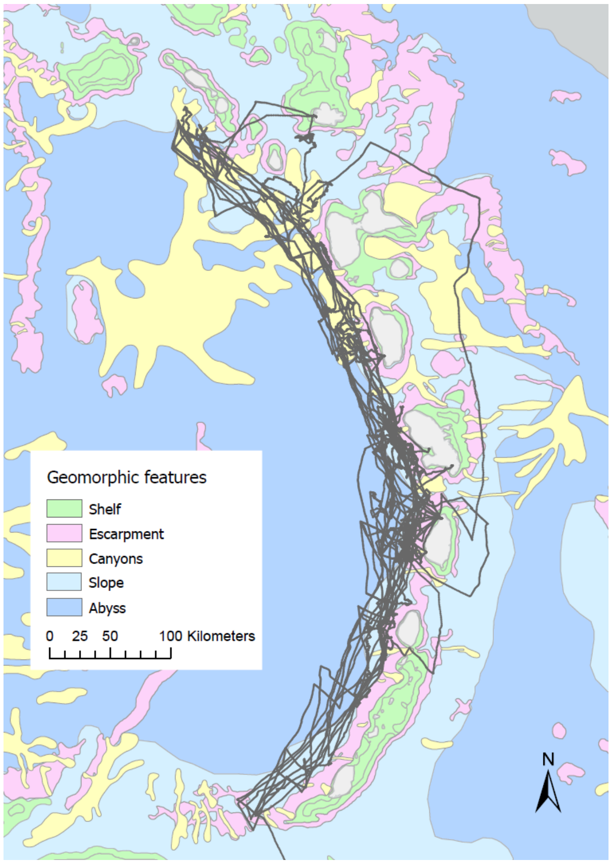


Figure 4.1. Map displaying the geomorphic features used to model sperm whale distribution in the Eastern Caribbean. Vessel tracks displayed in dark gray.

4.3.2 Assigning GPS coordinates to vocal clans

All individuals identified on the same day were considered part of the same group if they had coordinated behaviour and movement (Gero et al. 2014). Their codas were used to identify the group's vocal clan membership following methods by Hersh et al. (2021) (see Vachon et al. 2022). The GPS position of our research vessel was assigned to a vocal clan for the length of the encounter: from the time we first heard the characteristic echolocation clicks of sperm whales until we could not hear them or chose to leave the whales due to weather or logistical constraints (Whitehead 2003). We did not include encounters with Unit 12 (potential EC3 vocal clan) (Vachon et al. 2022) in this analysis as we have relatively little data regarding their distribution compared with EC1 and EC2. We considered GPS location for which we had EC3 presence as presence of sperm whales but did not include them as either EC1 or EC2 presence.

4.3.3 Habitat model variables

We included 7 topographical variables (water depth- *Depth*, slope -*Slope*, distance to nearest submarine canyon - *Canyon*, distance to the escarpment - *Escarp*, distance to the abyss - *Abyss*, distance to shelf -*Shelf*, and distance to the center of the nearest channel between islands - *Channel*), 6 oceanographic variables (eastward current speed - *Ecurr*, northward current speed - *Ncurr*, zonal velocity variance -*Zvelv*, meridional velocity variance -*Mvelv*, inflow through the nearest channel -*Inflow*, and chlorophyll-a concentration -*Chla*) and 4 general variables (latitude -*Lat*, longitude -*Long*, nearest island -*Island*, and whether the position is leeward or windward of the lesser Antilles island chain -*Windward*) - for a total of 17 potential variables (Table 4.1), in our habitat models. These predictor variables were chosen as they were useful in describing sperm whale habitat in the Mediterranean and South Pacific and/or are thought to relate to the aggregation of sperm whale's prey, mesopelagic squid (Pirotta et al. 2011; Eguiguren et al. 2019; Claro et al. 2020).

Bathymetric data were obtained from the 2020 General Bathymetric Chart of the Oceans (https://www.gebco.net/data_and_products/gridded_bathymetry_data/) and extracted using ArcGIS. Slope was calculated from the GEBCO bathymetric layer using ArcGIS *Slope* tool. We used distance to geomorphic features canyon, escarpment, abyss and shelf as predictor variables as in the habitat models of Claro et al. (2020). Geomorphic features' definitions and locations were obtained from Harris et al. (2014) via Blue Habitat (www.bluehabitats.org) (Figure 4.1). Oceanographic variables -eastward current speed, northward current speed, zonal velocity variance and meridional velocity variance- were obtained from the NOAA drifter-derived climatology of global near-surface currents database (Laurindo et al. 2017). Chlorophyll-a concentration was extracted from the NOAA visible infrared imaging radiometer suite (VIIRS) satellite data and averaged over the last 3 months prior to each datapoint to account for the lag between primary production and sperm whale prey availability (Jaquet 1996). Measures of inflow through the nearest channel were obtained from Johns et al. (2002). The four general predictors latitude, longitude, nearest island and windward/leeward were included to account for unexplained, or unaccounted, variation in our data. Nearest island is a categorical variable that corresponds to the nearest island (St. Kitts & Nevis, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent & the Grenadines or Grenada) to a GPS point (in geodesic distance) and was extracted using the *Near* tool in ArcGIS. Windward/leeward is a binary variable that describes whether a GPS point is leeward, west, (N) or windward, east (Y) of the Lesser Antilles island chain.

The variables depth and slope were recorded at 0.004° spatial resolution, variables eastward current speed, northward current speed, zonal velocity variance and meridional velocity variance were recorded at 0.25° resolution and Chlorophyll-a concentration were recorded at 0.036° resolution. As these resolutions are lower than that of our GPS coordinates, we used ArcGIS tools *Near* and *Spatial join* to extract the closest value for each variable to each GPS coordinate. We believe that the resolution at which those variables are available will not negatively affect our modelling approach as they have little small-scale variability (e.g., primary productivity).

Table 4.1. Description of predictor variables used in habitat models. Spatial resolution is in degrees of latitude.

Name	Referred in model as	Description	Spatial resolution	Source
Latitude	*Lat*	Latitude	NA	Chart plotter
Longitude	*Long*	Longitude	NA	Chart plotter
Depth	*Depth*	Bathymetry of the ocean	0.004°	GEBCO 2020
Slope	*Slope*	Steepness of the ocean floor calculated from depth in ArcGIS	0.004°	NA
Distance to nearest canyon	*Canyon*	Distance to the nearest geomorphic feature canyon	NA	Harris et al. 2014
Distance to escarpment	*Escarp*	Distance to the nearest geomorphic feature escarpment	NA	Harris et al. 2014
Distance to abyss	*Abyss*	Distance to the nearest geomorphic feature abyss	NA	Harris et al. 2014
Distance to shelf	*Shelf*	Distance to the continental shelf	NA	Harris et al. 2014
Eastward current speed	*Ecurr*	Eastward speed of near surface currents	0.25°	Laurindo et al. 2017

Northward current speed	*Ncurr*	Northward speed of near surface currents	0.25°	Laurindo et al. 2017
Zonal velocity variance	*Zvelv*	Measure of near surface eddy energy along Latitudes	0.25°	Laurindo et al. 2017
Meridional velocity variance	*Mvelv*	Measure of near surface eddy energy along Longitude	0.25°	Laurindo et al. 2017
Inflow from nearest channel	*Inflow*	Atlantic inflow (Sv) through the nearest channel	NA	Johns et al. 2002
Distance to center of nearest channel	*Channel*	Distance to the center of the nearest channel.	NA	NA
Chlorophyll-a concentration	*Chla*	Chlorophyll-a concentration averaged over the previous three months	0.036°	NOAA VIIRS
Windward	*Windward*	Binary predictor that reflects whether the location is leeward, west, (N) or windward, east (Y) of the Lesser Antilles island chain	NA	NA
Island	*Island*	Nearest island (categorical predictor)	NA	NA

4.3.4 Habitat modelling

We used GPS fixes from the research vessel's chart plotter taken at 5 minutes intervals as our habitat model units of analysis. Each data point corresponds to specific coordinates at a certain time, along with whether sperm whales were acoustically encountered at that point and time, as well as the clan to which encountered whales belonged to. We fitted four different habitat model types (*Presence/Absence*, *EC1*, *EC2*, *Vocal clan*) to our data using two independent sets of variables (*Environment*, *Island*) (Figure 4.2, defined below). Here we describe each model type and the rationale for testing them across the two variable sets.

- <u>Presence/ Absence:</u> This model described the general distribution of sperm whales in the Lesser Antilles, regardless of vocal clan membership. The response variable was 0 for acoustic absence of sperm whale and 1 for acoustic presence of sperm whales. This allowed us to identify key variables for sperm whale habitat in the Lesser Antilles and assess whether modeling sperm whale distribution independently for each vocal clan resulted in a significant improvement in predictive accuracy.

- EC1/EC2: These models described the distribution of sperm whales that were assigned to the EC1 and EC2 vocal clans respectively. For the *EC1* model, the response was 0 for the acoustic absence of sperm whales or the presence of EC2 and/or EC3 whales, and 1 for the acoustic presence of EC1 whales. Conversely, for the *EC2* model, the response was 1 for the acoustic presence of EC2 whales and 0 otherwise. These models allowed us to compare the performance of vocal-clan specific habitat models to that of general habitat models (i.e. *Presence/Absence*) as well as identify important environmental variables for predicting the presence of EC1 and EC2 whales respectively. These environmental variables were then used in our habitat suitability analysis (see below).

- Vocal clan: This model was fitted to identify the variables that best distinguish between the presence of EC1 and EC2. The response was 0 for EC1 acoustic presence and 1 for EC2 acoustic presence. Here, a high predictive accuracy would suggest that individuals from different vocal clans prefer contrasting variables and, therefore, suggest an important contribution of social factors (i.e., vocal clan membership) to sperm whale distribution. The dataset used for the *Vocal clan* model was smaller than that for the *Presence/Absence*, *EC1* and *EC2* models since we only used sperm whale presence datapoints.

We tested these four habitat model types independently on two sets of variables: either a full set of environmental variables (*Environment* set), or nearest island variables (*Island* set), and compared their predictive performance. The *Island* set includes variables *Island* and *Windward* while the *Environment* set includes all remaining 15 environmental predictors (see “Habitat model variables” section above) and *Windward*. We expect models using the *Environment* variable set to perform much better than the ones using the *Island* variable set if sperm whales are habitat specialist and the opposite if patterns of distribution are driven by site/island fidelity. To avoid confusion, model names on their own (*Presence/Absence*, *EC1*, *EC2*, *Vocal clan*) will refer to the models performed using the *Environment* variable set and models followed by "Island" will refer to the models performed using the *Island* variable set (e.g., *Presence/Absence Island*).

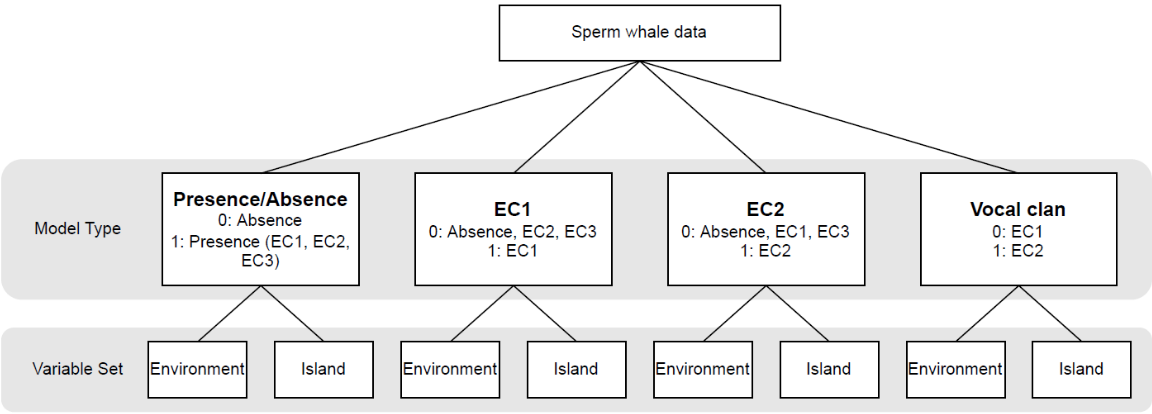


Figure 4.2. Summary of habitat modelling approach.

4.3.4.1 Modelling approach

Habitat models were fitted using Generalized Estimating Equations (GEEs; Liang & Zeger 1986), in which variables were used as predictors of sperm whale presence (*Presence/Absence*, *EC1* and *EC2* models) or vocal clan membership (*Vocal clan* model), following Pirotta et al. (2011) and using package *geepack* in R (Højsgaard et al. 2005). This approach has been used in other cetacean distribution studies (e.g. Eguiguren et al. 2019; Tepsich et al. 2014; Pirotta et al. 2014) and is appropriate when data are recorded continuously along survey transects. We chose GEEs over other methods since they explicitly account for autocorrelation (Liang & Zeger 1986). Data points were clumped into blocks that corresponded to sperm whale encounters and search periods. Under this framework, residuals are allowed to be correlated within blocks, but we assume independence between blocks. We used encounters as our blocking variable as it was successfully used in similar studies (Pirotta et al. 2011; Eguiguren et al. 2019) and we found this to be an appropriate grouping variable as the autocorrelation among data points eventually converged at 0 within each encounter (Figure S4.1). We modelled the relationship between variables and sperm whale presence as linear terms only, as including non-linear relationships as in previous studies (Pirotta et al. 2011; Eguiguren et al. 2019) only slightly increased overall fit and predictive accuracy, at the cost of interpretability.

We structured our modelling approach into five steps (Figure 4.3, described below), which were repeated independently for the *Presence/Absence*, *EC1*, *EC2* and *Vocal clan* models.

1) Preparing variables

We looked at the variables' distributions and logged ones which were highly skewed. All variables were then standardized by subtracting the mean and dividing by standard deviation to facilitate model convergence.

2) Removing collinearity

First, we calculated correlation coefficients between all pairs of predictor variables. Variables which had correlation coefficients above 0.4 were considered to be correlated and not included in the same model. From this we built all possible combinations of uncorrelated predictors into potential models which were then tested for multicollinearity by measuring the Generalized Variance Inflation Factor (GVIF) (*car* package in R). Models which had a predictor with a GVIF value above 3 were discarded and all other potential models with GVIF values below 3 were used as the first step in backward stepwise selection.

3) Model selection

We used QIC (Pan 2001), an extension of the Akaike Information Criterion (AIC) that applies to GEE models, to compare models using manual backward stepwise selection (package *MuMIn* in R, Barton 2013). We started from all the potential combinations of uncorrelated predictors (step 2) and compared their QIC (ΔQIC) as we removed a single variable in turn. The model with the lowest QIC is then used as the starting model for the next step, repeating this procedure until the removal of any variable in the model leads to an increase in QIC. The higher the absolute value of ΔQIC between models, the larger the gap in their predictive performance. As such, we chose models with fewer variables if their ΔQIC was 10 or less from the original model to encourage variable removal. The variables within the final model are then ordered according to how much their removal increases QIC (from highest to lowest).

4) Model validation

The best models from step 3 were then further evaluated using leave-one-out cross validation where encounters were iteratively removed from the data. We compared the percentage of datapoints that were correctly assigned (predictive accuracy, Hastie et al. 2009) between the step 3 models to that of the same model minus one variable. If the predictive accuracy of models with fewer variables was higher than that of the original model, we removed that variable and started this process again until predictive accuracy was highest for the model from which we did not remove variables. This was done as stepwise selection using QIC can sometimes retain spurious variables (Pirotta et al. 2011).

Model performance was then assessed in terms of how well models fit the data (Goodness-of-fit) by measuring the proportion of data points correctly assigned as presences or absences (or EC1/EC2 in the vocal clan models) using confusion matrices (Fielding & Bell 1997). To transform model predictions from a range of probabilities to a binary (presence or absence), we used the point of maximum distance between the Receiving Operating Characteristic (ROC) curve and the 45-degree diagonal as the cut-off probability, using the R package *ROCR* (Sing et al. 2005). Additionally, we measured model Goodness of Fit by calculating the Area Under the ROC curve (AUC), which also reflects overall model performance (Fielding & Bell 1997).

We finally compared the performance between models with *Environment* variables and *Island* variables for each model type (*Presence/Absence*, *EC1*, *EC2*, *Vocal clan*) to determine whether differences in distribution are driven primarily by habitat specialization or site/island fidelity.

5) Prediction maps

To display the results of our habitat models, we built prediction maps from the best post-cross validation *Presence/Absence*, *EC1*, *EC2* and *Vocal clan* models. Maps were built by importing our model predictions from R into ArcGIS Pro.

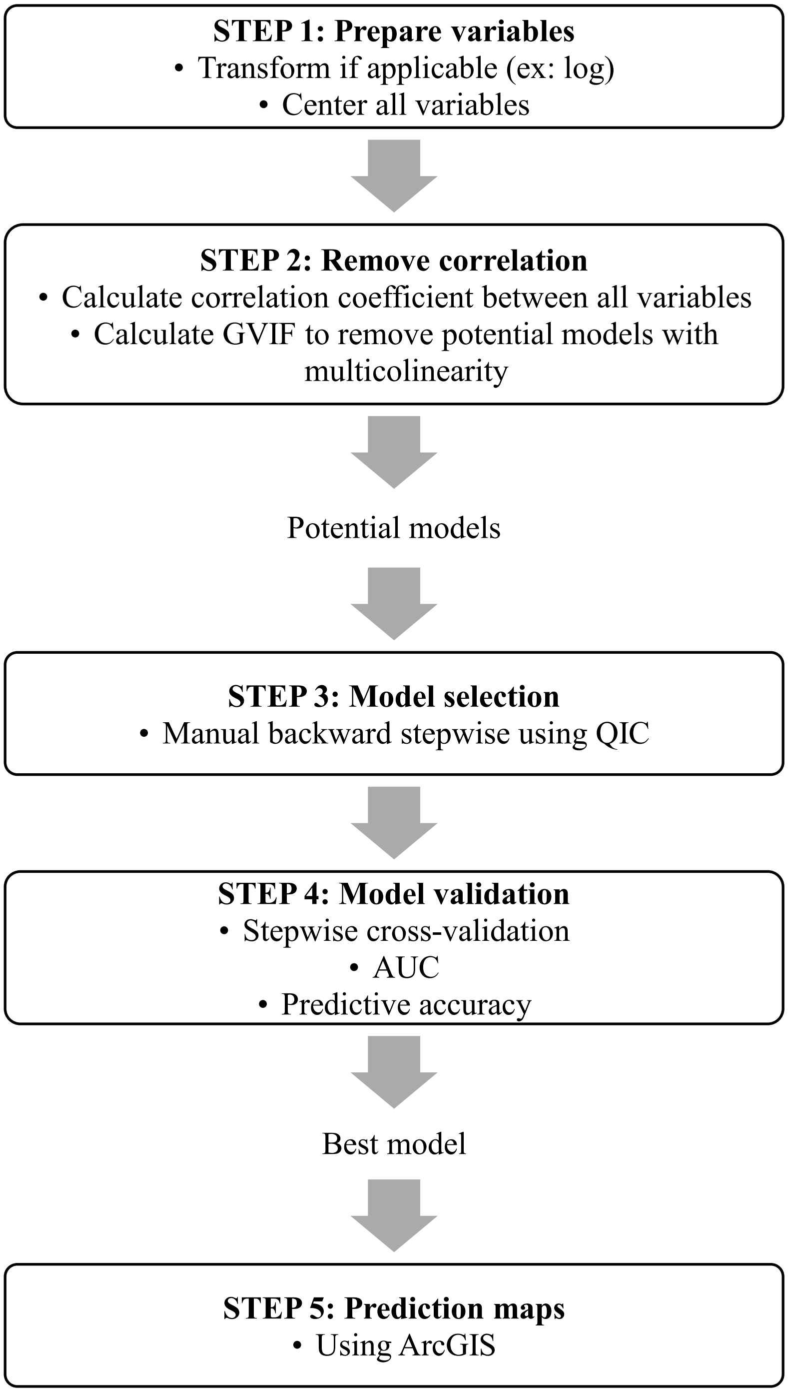


Figure 4.3. Summary diagram of habitat modelling steps. These were repeated independently for the *Presence/Absence*, *EC1*, *EC2* and *Vocal clan* model using the *Environment* variable set.

4.3.5 Habitat suitability analysis

To further establish whether vocal clans have distinct distributions as a result of habitat specialization or site/island traditions, we conducted a habitat suitability analysis for each Lesser Antilles island. This was done by creating a 0.1 degree grid of GPS points that extended 30 nautical miles offshore (representative of our effort, Figure 4.1) leeward of each island and assigning these points, and their corresponding environmental variable values, to the closest island. From this we obtained a range of values for each environmental variable for each island which we could then compare between "EC1" and "EC2" islands. Only environmental variables that were part of the final *EC1* and/or *EC2* models were included in these analyses as they were the one that were suggested to impact vocal clan distribution. We compared the environmental conditions between islands using t-tests to test whether each environmental variable significantly differed between islands predominantly used by EC1 and islands predominantly used by EC2.

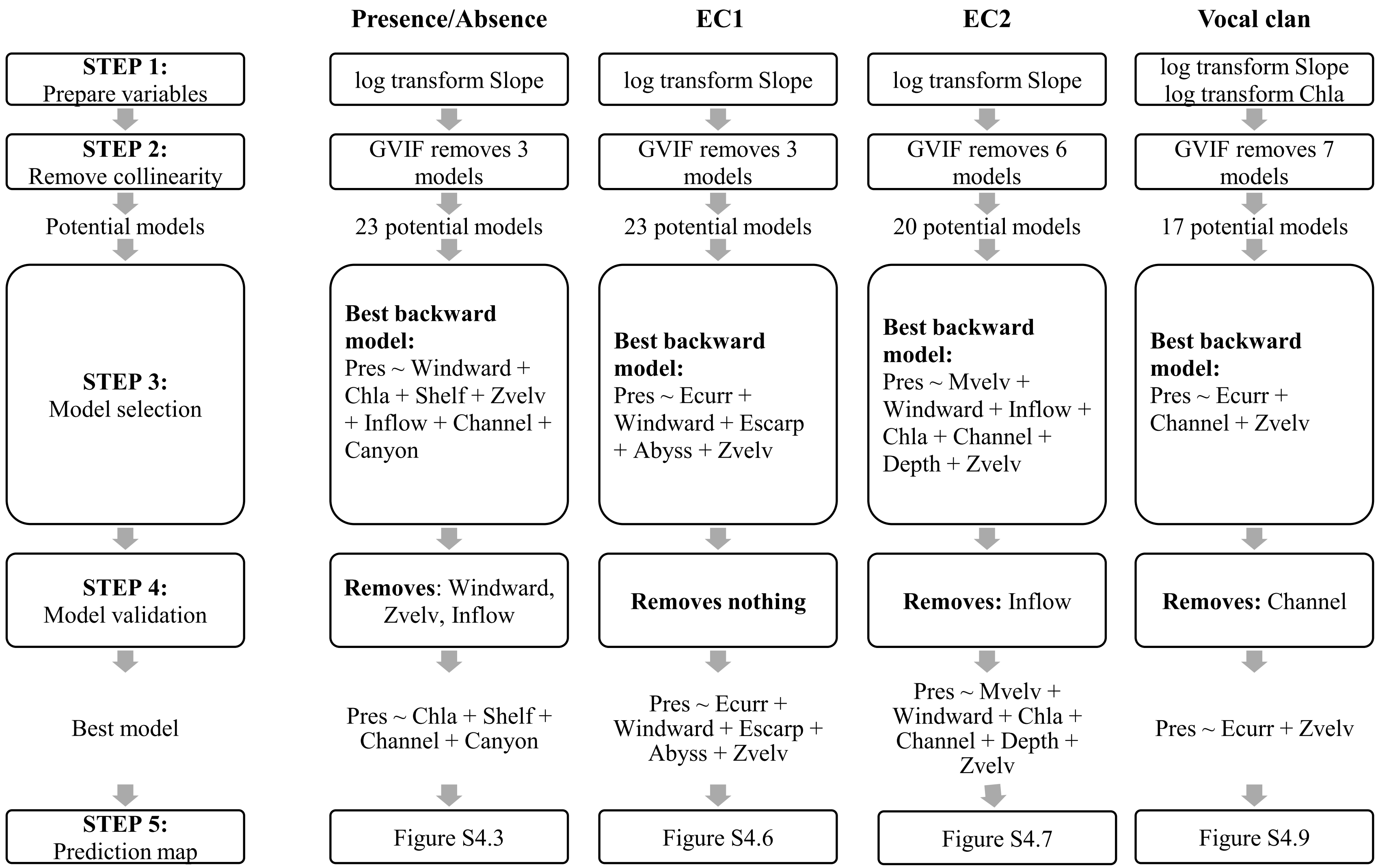
We expected environmental variables to be correlated to preferred islands if the environmental variables themselves are driving vocal clan distribution (e.g., EC1 whales prefer canyons and Dominica, Guadeloupe and St. Vincent have more canyons than St. Lucia and Martinique) and uncorrelated if vocal clans are distributed around different island due to site fidelity traditions (e.g., all islands have similar amounts of canyons but EC1 whale are only seen in Dominica, Guadeloupe and St. Vincent).

4.4 RESULTS

Over our two field seasons (February to April 2019 and January to March 2020) we spent 107 days at sea (Figure 4.1). Sperm whales were located throughout the leeward transects, with higher concentrations found around Martinique, St. Lucia and Dominica, but were not heard to windward (eastward) of the islands. We had a total of 50 sperm whale encounters, 24 encounters with EC1 groups, 22 encounters with EC2 groups, 5 encounters with an EC3 group and 1 encounter with both EC2 and EC3 (Vachon et al. 2022), from which we recorded 778 hours of sperm whale vocalizations. Altogether, we obtained 26,776 coordinate datapoints (9,249 presence datapoints – 4,154 EC1, 4,165 EC2, and 17,527 absence datapoints).

4.4.1 Habitat modeling

Refer to Figure 4.4 for a full breakdown of the *Presence/Absence*, *EC1*, *EC2* and *Vocal clan* habitat models at every selection step. Best pre-cross-validation and post-cross validation habitat models, as well as corresponding results using the *Island* variable set, can be found in Table 4.2 and Table S4.1 with associated QIC, AUC, goodness of fit and predictive accuracy. Below, we expand on general results from each model type.



	Presence/Absence	EC1	EC2	Vocal clan
STEP 1: Prepare variables	log transform Slope	log transform Slope	log transform Slope	log transform Slope log transform Chla
STEP 2: Remove collinearity	GVIF removes 3 models	GVIF removes 3 models	GVIF removes 6 models	GVIF removes 7 models
Potential models	23 potential models	23 potential models	20 potential models	17 potential models
STEP 3: Model selection	**Best backward model:** Pres ~ Windward + Chla + Shelf + Zvelv + Inflow + Channel + Canyon	**Best backward model:** Pres ~ Ecurr + Windward + Escarp + Abyss + Zvelv	**Best backward model:** Pres ~ Mvelv + Windward + Inflow + Chla + Channel + Depth + Zvelv	**Best backward model:** Pres ~ Ecurr + Channel + Zvelv
STEP 4: Model validation	**Removes**: Windward, Zvelv, Inflow	**Removes nothing**	**Removes:** Inflow	**Removes:** Channel
Best model	Pres ~ Chla + Shelf + Channel + Canyon	Pres ~ Ecurr + Windward + Escarp + Abyss + Zvelv	Pres ~ Mvelv + Windward + Chla + Channel + Depth + Zvelv	Pres ~ Ecurr + Zvelv
STEP 5: Prediction map	Figure S4.3	Figure S4.6	Figure S4.7	Figure S4.9

Figure 4.4. Summary of habitat modelling results for each habitat model at each step (*Environment* variable set).

4.4.1.1 Presence/Absence model

This model had 50.62% predictive accuracy and 69.8% goodness of fit in determining sperm whale presence, regardless of vocal clan, using environmental variables. Sperm whales were more often encountered in areas with low chlorophyll-a concentration, close to the continental shelf, relatively close to between-island channels and further away from canyons (Figure S4.2). The negative correlation between sperm whale presence and chlorophyll-a concentration could be caused by the relatively low chlorophyll-a concentrations across the Lesser Antilles chain, spatial lag between windward productivity and leeward biomass or the temporal lag between primary productivity and cephalopod biomass (Jaquet 1996; Pirotta et al. 2011), although we tried to account for this by considering chlorophyll-a concentration over the last 3 months as in Eguiguren et al. (2019). The final *Presence/Absence Island* model (Pres ~ *Windward* + *Island*) performed better than the *Presence/Absence* model (Pres ~ *Chla* + *Shelf* + *Channel* + *Canyon*) with ΔQIC of 2,281.4. The *Presence/Absence Island* model had 59.61%% predictive accuracy and 65.8% goodness of fit in determining sperm whale presence and suggests that more sperm whales occupy the waters off the central islands of Dominica and Martinique (Figure S4.3), for reasons not fully explained by the environmental variables that we considered.

4.4.1.2 EC1 and EC2 models

Modelling sperm whale distribution independently for EC1 and EC2 increased model predictive accuracy, goodness of fit and lowered QIC for both the models using *Environment* and *Island* variables (Table 4.2).

EC1 whales prefer areas of low eastward current speed, low zonal velocity variance, within the escarpment designation, away from the abyss, leeward of the Lesser Antilles chain (Figure S4.4). In contrast, EC2 whales prefer areas with high meridional velocity variance, low chlorophyll-a concentration, deeper in the ocean, low zonal velocity variance, closer to channels leeward of the Lesser Antilles chain (Figure S4.5). Unsurprisingly, variable *Windward* was important for both the *EC1* and the *EC2* model since sperm whales were not heard windward of the island chain. This result should be viewed cautiously since the leeward side of the island chain was much more extensively surveyed than the windward side (Figure 4.1). Zonal velocity variance (*Zvelv*) was also important for both models with EC1 sperm whales encountered in areas of high zonal velocity variance and EC2 sperm whales encountered in areas with low zonal velocity variance (Figure S4.4; S4.5).

The best *EC1* model (Pres ~ *Ecurr* + *Windward* + *Escarp* + *Abyss* + *Zvelv*) and the best *EC2* model (Pres ~ *Mvelv* + *Windward* + *Chla* + *Channel* + *Depth* + *Zvelv*) performed worse than the *EC1 Island* (Pres ~ *Windward* + *Island*) and *EC2 Island* (Pres ~ *Windward* + *Island*) models with respective ΔQIC of 3115.5 and 501.4. According to our prediction maps, we expect EC1 sperm whales to aggregate near Dominica, Guadeloupe, St. Vincent & the Grenadines and St.Kitts & Nevis and EC2 sperm whales to aggregate near St.Lucia and Martinique (Figure S4.6; S4.7). Such predictions not only reflect, as expected, the field observations that were used to construct this model (Vachon et al. 2022), but also results from the long-term research off Dominica by the DSWP, with EC2 groups seldom encountered off Dominica (only 2.5% of photo identification encounters; Gero et al. 2016b; Vachon et al. 2022).

4.4.1.3 Vocal clan model

This model had great accuracy in distinguishing between EC1 and EC2 vocal clan distribution using both the *Environment* and *Island* variable sets (92% and 96.5% goodness of fit, and 49.7% and 76.8% predictive accuracy respectively). EC1 whales were more often encountered in areas of low eastward current speed and high zonal velocity variance while EC2 whales were more often encountered in areas of high eastward current speed and low zonal velocity variance (Figure S4.8).

The *Vocal clan Island* model (Pres ~ *Windward* + *Island*) performed better than the *Vocal clan* model (Pres ~ *Ecurr* + *Zvelv*) with ΔQIC of 5033.8, and EC1 whales predominantly near the islands of Dominica, Guadeloupe and St. Vincent & the Grenadines and EC2 predominantly near St. Lucia and Martinique (Figure S4.9).

Table 4.2. Best variable combinations for each model type with associated QIC, ΔQIC, AUC, goodness of fit and predictive accuracy (post stepwise cross validation).

Model type	Variable set		QIC	ΔQIC	AUC	Goodness of fit	Predictive accuracy (±SE)
Presence/ Absence	Env	Chla + Shelf + Channel + Canyon	32966.3	2281.4	0.71	69.8%	50.62% ±0.02
	Island	Windward + Island	30684.9	-	0.69	65.8%	59.61% ±0.04
EC1	Env	Ecurr + Windward + Escarp + Abyss + Zvelv	19006.3	3115.5	0.79	77.1%	56.65% ±0.03
	Island	Windward + Island	15890.8	-	0.86	72.9%	72.05% ±0.04
EC2	Env	Mvelv + Windward + Chla + Channel + Depth + Zvelv	16522.2	501.4	0.86	75.35%	57.73% ±0.02
	Island	Windward + Island	16020.8	-	0.83	73.2%	62.27% ±0.04
Vocal clan	Env	Ecurr + Zvelv	6152.1	5033.8	0.92	92.0%	49.7% ± 0.05
	Island	Island	1118.3	-	0.99	96.5%	76.8% ± 0.14

4.4.2 Habitat suitability

The lower QIC and higher predictive accuracy of the *EC1 Island*, *EC2 Island* and *Vocal clan Island* models (Table 4.2) suggest that vocal clan distribution might be better explained by site/island fidelity than the use of specific habitat variables. Our habitat suitability results also corroborated this conclusion as the environmental variables that were considered significant predictors of EC1 and EC2 presence in the *EC1* and *EC2* models (*Escarp*, *Abyss*, *Mvelv*, *Ecurr*, *Zvelv*, *Depth*, *Chla*) did not significantly differ between EC1 and EC2 islands, apart from *Abyss* and *Depth* (t= -4.01, p-value = 0.007 and t= 3.68, p-value=0.010 respectively; Figure 4.5). Altogether this suggests that sperm whales from different vocal clans do not use different islands because they have a unique, or significantly different, selection of physical habitat properties.

Similar results were obtained if we only used surveyed grid points rather than the extrapolated 30 nautical mile offshore 0.1 degree grid to carry out this analysis (Figure S4.10).

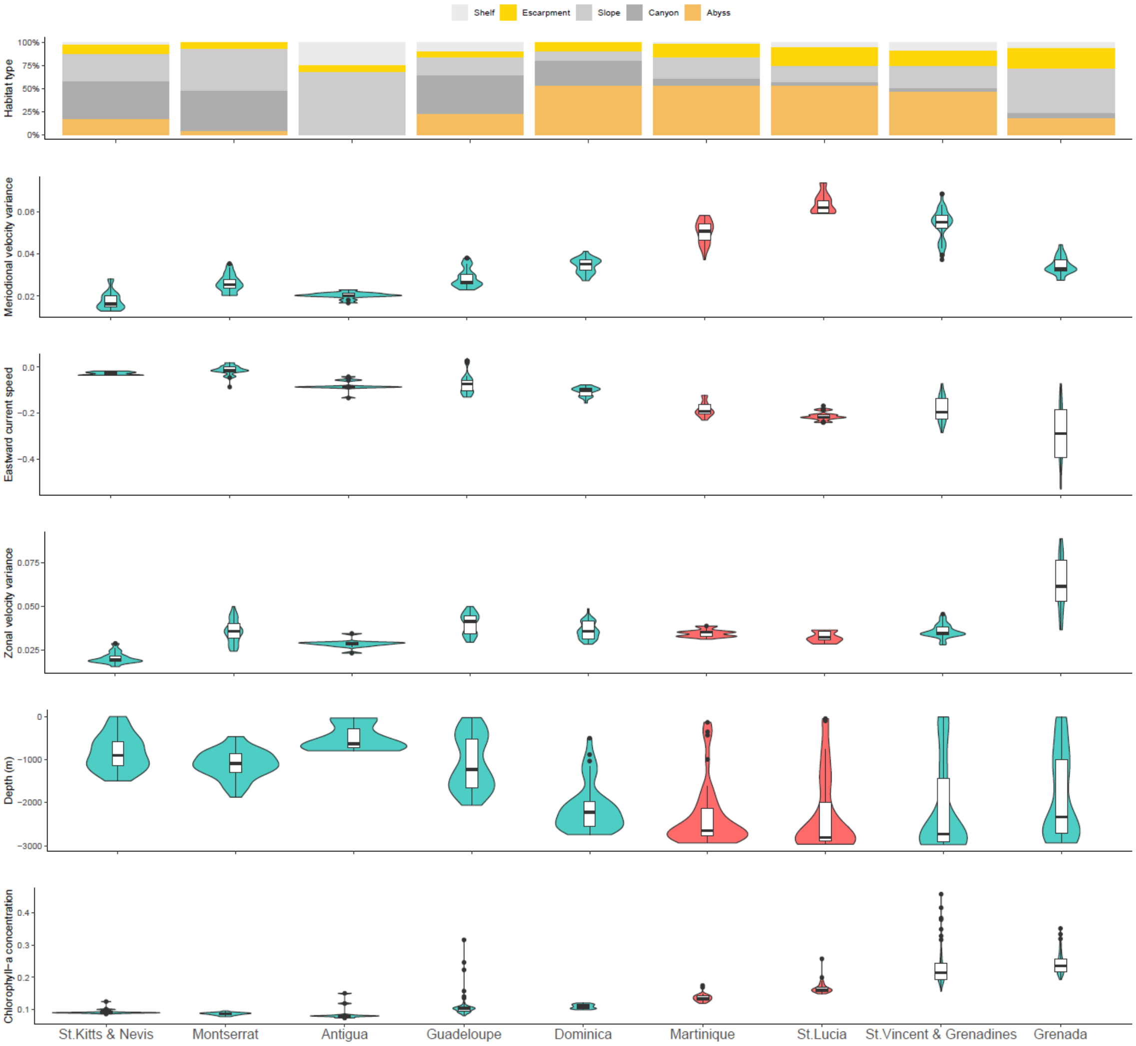


Figure 4.5. Habitat suitability of EC1 (aquamarine) and EC2 (red) islands according to significant environmental variable range within a 0.1 degree grid extending 30 nautical miles leeward of each island. No significant differences in variable values between EC1 and EC2 islands apart from *Abyss* and *Depth*.

4.5 DISCUSSION

In this study, we attempted to test the competing hypotheses of habitat specialization and traditional site/island fidelity in explaining the stark differentiation in EC1 and EC2 vocal clan distributions in the Eastern Caribbean. Our results suggest that site/island fidelity, rather than environmental variation, is the main driver of sperm whale distribution in the Lesser Antilles, with different processes operating at the species and vocal clan levels.

At the species level, sperm whales use areas that are close to the continental shelf and channels (*Presence/Absence* model). Such correlations between sperm whale distribution and topography have been documented for sperm whales elsewhere (Mediterranean- Pirotta et al. 2011; Claro et al. 2020; Sargasso - Wong & Whitehead 2014, New Zealand- Sagnol et al. 2014; Alaska- Rice et al. 2021) and most probably reflect food availability as vertical water movement associated with sloped areas likely promotes primary and secondary productivity (Tynan et al. 2005). However, such coarse models fail to capture the variability created by differences in unit movement, clan membership, and foraging success at finer spatial scales (as reported by Jaquet & Whitehead 1996 in the South Pacific) and seemed to be impacted, even at this scale, by the whales' bias towards certain islands with the *Presence/Absence Island* model performing better than the *Presence/Absence* model (Table 4.2).

The dramatic increase in the performance of vocal clan-specific models over a general species presence model is one of the most striking results of our study. The preference of the EC2 vocal clan for St. Lucia and Martinique and the EC1 vocal clan for Dominica, Guadeloupe, and St. Vincent & the Grenadines does not relate to environmental variables, as they do not significantly or substantially differ across islands (Figure 4.5), but rather seem to be caused by site/island fidelity with the *EC1 Island*, *EC2 Island* and *Vocal clan Island* models performing much better than their counterparts (Table 4.2). In this case, culture, via conformism and homophily to island preference traditions, would act as a barrier to population mixture (e.g., Henrich & Boyd 1998; Richerson & Boyd 2005; Centola et al. 2007; Riesch et al. 2012). Individual sperm whales stay in the vicinity of specific islands because those are the islands where they were raised, where they learned to forage, where their close associates and family members can be encountered and where they can avoid interactions with members of other vocal clans. Conformism and homophily have already been reported in Eastern Caribbean sperm whales with highly stereotypical vocal repertoires (conformity, Konrad et al. 2018b) and individuals exclusively associating with members of their own vocal clan (homophily, Gero et al. 2016b). It is also not surprising that individual sperm whales could learn island preferences from other members of their social units as other behaviours are culturally maintained within vocal clans (e.g., social vocalizations (Rendell & Whitehead 2003b; Gero et al. 2016b; Vachon et al. 2022), dive synchrony – (Cantor and Whitehead 2015), movement patterns (Whitehead and Rendell 2004; Whitehead et al. 2008a, Vachon et al. 2022), social structures (Cantor and Whitehead 2015)) and since cultural transmission has been suggested as the most likely mechanism for the emergence of vocal clans themselves (Cantor et al. 2015).

4.5.1 Limitations

This study is limited in its temporal scope. While EC1 and EC2 distribution patterns were stable over the two years of this study, and while they appear to have been stable since 2005 (Gero et al. 2014; Gero et al. 2016b; Vachon et al. 2022), shifts could still occur over longer timescales, as it did in the Galapagos (Cantor et al. 2016). However, while the location of Eastern Caribbean vocal clans might change in the future, the mechanisms responsible for their spatial segregation are likely to remain the same. This study might also be limited by the environmental variables that were included in habitat models. However, this is unlikely as we cover a wide array of environmental variable types (geomorphic features, oceanographic processes, biological processes), and include variables that were previously considered important sperm whale habitat (e.g., Pirotta et al. 2011; Eguiguren et al. 2019; Claro et al. 2020) and environmental variables are rarely totally uncorrelated.

4.5.2 Implications for conservation

The performance of our habitat models was greatly improved by the inclusion of culture (i.e., modelling vocal clans separately). We suggest that the low predictive accuracy of our *Presence/Absence* model is caused by confounding variables across vocal clans, something that could also explain why other sperm whale habitat models sometimes fail to reach high predictive accuracy when compared to other cetacean species (e.g. Tepsich et al. 2014; Claro et al. 2020).

Our results highlight how cultural factors can lead to important, management-relevant, variations in the way population segments use any given habitat. Even at relatively small geographic scales for a large, highly mobile, pelagic animal.

In this case, traditions of site/island fidelity (most likely fueled by conformism and homophily) appear to be a more important determinant of sperm whale distribution within suitable habitat than are environmental variables. Adding this cultural lens, not only allowed for a better understanding of population structure, but also habitat use – two crucial variables in conservation and management.

Like many other populations, Eastern Caribbean sperm whales are now facing unprecedented anthropogenic threats related to global warming, increased ocean noise and other human activities (e.g. Weilgart 2007; Whitehead et al. 2008b; Baulch & Perry 2014). Sperm whales studied off Dominica (predominantly made up of EC1 units) were declining at a 4.5%/yr rate between 2010 and 2015 (Gero & Whitehead 2016) and the same might be true for sperm whales inhabiting the other Lesser Antilles islands. Under these circumstances, it is critical to build proper habitat models which capture both important cultural and environmental variables. These habitat models can not only be used to help protect the population as a whole, but also identify areas of high importance for each cultural group. This aligns with recent conservation shift away from solely genetic diversity to the incorporation of cultural diversity as an important component of populations' health (Whitehead 2010; Brakes et al. 2021) and supports the recognition of sperm whale vocal clans as independent evolutionarily significant units (ESU) for conservation and management.

4.5.3 Implications for sperm whale ecology/psychology

This study aimed at incorporating both environmental and cultural variability into the commonly used ecological and conservation approach of habitat modelling. By independently modelling vocal clan distribution, we were able to gain a more detailed insight into sperm whale population structure, the mechanisms responsible for their distribution, and greatly increase habitat model accuracy. Our results suggests that sperm whale habitat use in the Eastern Caribbean is predominantly shaped by cultural information rather than environmental cues. This not only highlights the importance of older females, mothers, aunts and grandmothers as repositories of knowledge within social units and vocal clans (as is the case in elephants - McComb et al. 2001; McComb et al. 2011), but also implies that sperm whales are able to recognize and communicate fine-scale cultural boundaries in the absence of physical barriers or environmental gradients. Over long timescales, these boundaries are unlikely to be impermeable (as few EC2 encounters have been documented in Dominica; Gero et al. 2016b) and might change (e.g., Eastern Tropical Pacific vocal clan turnover – Cantor et al. 2016), but nonetheless remain culturally driven. As such, our findings have implications beyond the Eastern Caribbean, and beyond sperm whales, to our understanding of cultural species. It is crucial to assess the distribution, and behaviour, of complex creature in all their complexity (genetic, environmental, cultural and their intersections) in order to properly conserve and understand them.

4.6 ACKNOWLEDGMENTS

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CHAPTER 5 –

Abundance Estimate of Eastern Caribbean Sperm Whales Using Large Scale Regional Surveys

5.1 ABSTRACT

Dynamic and responsive wildlife management requires ongoing understanding of population size and trends. Therefore, it is important to maintain accurate population estimates as our understanding of individual movement and residency patterns evolve. Following the discovery that Eastern Caribbean sperm whale movement is much more limited than reported for other sperm whale populations (with cultural groups and individuals showing fine-scale island residency), we update previous population estimates to account for this culturally driven population structure. We used closed Peterson and Schnabel methods on mark-recapture photo identification data collected during dedicated sperm whale surveys in 2019 and 2020 in the Lesser Antilles (St. Kitts & Nevis to Grenada). Our population estimate (414 ±46 adults, 51 ±6 groups) more than doubles previous estimates from smaller scale studies and suggests that more sperm whales use the area than previously assumed. We highlight the importance of accounting for population structure (even in the absence of physical and genetic boundaries) for conservation and management and recommend that population estimates be calculated independently for different cultural groups. While longer term monitoring is required to assess population trends, we expect that threats identified and leading to population decline in Dominica and Guadeloupe most likely apply to neighboring islands.

5.2 INTRODUCTION

Many conservation management strategies rely on the knowledge of a species' habitat use and abundance. Consequently, population size is a central metric for species management (Yoccoz et al. 2001; Martin et al. 2007; Keith et al. 2015) and is an important determinant of conservation status (e.g., IUCN: Mace et al. 2008) in part due to its genetic implications (Hoffmann et al. 2017; Fenster et al. 2018). However, accurate population estimates can be hampered by an incomplete knowledge of species' movements, population structure, habitat use, and distribution (Boyce et al. 2016; Keiter et al. 2017; Ketz et al. 2018). Such challenges are particularly relevant to cetacean conservation as cetaceans are highly mobile (e.g., Whitehead et al. 2008a; Kennedy et al. 2014), often hard to monitor (Kaschner et al. 2012) and might have unexpected behaviour and distribution due to their reliance on social learning and culture (reviewed in Whitehead & Rendell 2015).

Although the sperm whale (*Physeter macrocephalus*) is one of the better studied cetacean species, population status assessment at the global and regional scales can be difficult to obtain due to the species' low genetic variation across ocean basins (Alexander et al. 2013; Morin et al. 2018), long range movements (Whitehead et al. 2008a; Mizroch & Rice 2013; Rendell & Frantzis 2016), and an incomplete understanding of their population structure—especially at the regional scale (Taylor et al. 2019). Sperm whale social structure is hierarchical. At the basal level, females and juvenile sperm whale live in stable matrilineal social units of 6 to 12 individuals (Whitehead et al. 2012). Social units will form temporary associations (on the scale of hours to days), called groups, with other social units to forage and socialize (Christal et al. 1998). Interactions between individuals, and between social units, are then structured at the highest level by their membership to different cultural groups called "vocal clans". Whales from different vocal clans have distinct acoustic repertoires and do not associate with each other, even if they occur in sympatry (e.g., Eastern Tropical Pacific: Rendell & Whitehead 2003b; Eastern Caribbean: Gero et al. 2016b, Vachon et al. 2022; Japan : Amano et al. 2014; Brazil : Amorim et al. 2020; Mauritius : Huijser et al. 2019). Vocal clans can contain hundreds to thousands of individuals (Rendell & Whitehead 2003b) and can also vary in their social structure (Cantor and Whitehead 2015), feeding success (Whitehead & Rendell 2004; Marcoux et al. 2007a), distribution (Eguiguren et al. 2019; Vachon et al. 2022) and movement patterns (Whitehead and Rendell 2004; Whitehead et al. 2008a, Vachon et al. 2022). This is important from a conservation perspective as such culturally driven population structure has the potential to skew population estimates if whales from different vocal clans occupy different areas, have different movement patterns or different preferred habitats. The recent discovery of fine-scale habitat use and habitat partitioning by Eastern Caribbean sperm whales vocal clans (Vachon et al. 2022) is such an example.

Since 2005, the Dominica Sperm Whale Project (DSWP) has carried out research off the island of Dominica, gathering photo identification, behavioural and acoustic data from 21 well-documented sperm whale social units, with 19 belonging to one vocal clan, called EC1, and 2 belonging to a second vocal clan, called EC2 (Gero et al. 2014, Gero et al. 2016b). From this, population estimates for the greater Eastern Caribbean were calculated under the assumption that identifications mainly from Dominica were an unbiased sample of the entire population (Gero et al. 2007, Whitehead & Gero 2015;

Gero & Whitehead 2016). This was assumed as sperm whales typically range over thousands of kilometers (Mizroch & Rice 2013; Whitehead 2001, Whitehead et al. 2008a), and the Lesser Antilles chain spans only 600 kms across.

However, recent work now challenges this assumption. Eastern Caribbean sperm whales show high island residency with yearly movement of less than 200 kilometres (Vachon et al. 2022). Eastern Caribbean sperm whales from different vocal clans also have distinct distributions around the Lesser Antilles chain (with EC1 sperm whales predominantly encountered off Dominica, St. Vincent & the Grenadines and Guadeloupe and EC2 sperm whales predominantly encountered off Martinique and St. Lucia) (Vachon et al. 2022). Therefore, the Eastern Caribbean sperm whale population is structured at a relatively small spatial scale in the absence of environmental barriers. This means that data from Dominica should not be extrapolated to the entire Eastern Caribbean population as it is a biased sample - disproportionately occupied by a single vocal clan (EC1) and with high residency of specific social units.

The objective of this paper is, therefore, to provide a more accurate population estimate for sperm whales living in the Eastern Caribbean by incorporating data from regional scale surveys across the Lesser Antilles. We also calculated estimates independently for each vocal clan, as they show different behaviours and distribution and therefore might be affected and react differently to threats.

5.3 METHODS

5.3.1 Data collection

We conducted eight two-week dedicated sperm whale surveys between the months of February and April 2019 (four surveys) and January and March 2020 (four surveys) in waters of the Lesser Antilles. During the surveys we sailed continuously between the islands of St. Kitts & Nevis and Grenada aboard a 12m auxiliary sailboat along three predefined transect lines (Leeward Inshore: 5-7 nautical miles from coast, Leeward Offshore: 15 nautical miles from coast and Windward Inshore: 5-7 nautical miles from shore) (Figure 5.1). Transects were designed to both overlap with known primary sperm whale habitat (Leeward inshore) and survey data-deficient areas (Leeward offshore and Windward). Underwater sounds were recorded continuously via a two-element hydrophone array (two high frequency Magrec HPO3 elements with low cut filter set at 2kHz) towed behind the vessel on a 100-m cable and connected to a Fireface UC or Tascam UMC202HD USB audio interface, itself connected to a PC computer running PAMGUARD software (Gillespie et al. 2009), sampling at 96kHz. The hydrophone was monitored every 30 minutes for the detection of the characteristic sperm whale echolocation clicks. When heard, whales were followed for hours to one day using angle-of-arrival information calculated in PAMGUARD's *Click Detector* module. Adult male sperm whales were encountered opportunistically with groups of females but were not purposefully followed (adult males can easily be differentiated as they are much larger in size, usually alone, and make acoustically distinct "clangs" (Whitehead 2003; Oliveira et al. 2013)). In addition to acoustic recordings, photo identification and behavioural data were collected during daylight hours.

5.3.2 Defining groups and vocal clans

Fluke photographs of sperm whales were given a quality rating (Q) of 1 to 5 based on the fluke's focus, resolution, angle and proportion within the frame (Arnbom 1987a, Dufault & Whitehead 1993). Only photographs with Q≥3 were used to match individuals using the online platform Flukebook (Blount et al. 2022 accessed at https://www.flukebook.org/). Whales that had never been documented before were given a new identification number and added to the catalogue. While 'group' has been defined above and in the literature as a temporary association of multiple long-term units, for our purposes here we defined "groups" as all individuals identified on a given day, with coordinated behaviour and movement, following methods by the DSWP (Gero et al. 2014). Due to the limited temporal scope of our data (2 years), we could not always know which animals were part of longer-term social units (i.e., individuals seen within two hours of each other, in at least 2 different years, Gero et al. 2014). However, in the Eastern Caribbean the great majority of groups contain just one social unit (Whitehead et al. 2012; Gero et al. 2014). In this paper, we present data on both social units and groups (as just defined), as some groups of sperm whales were only encountered within the same year and, therefore, did not meet the social unit criteria. Group/social unit's vocal clan membership was determined based on the acoustic repertoire recorded on the days they were encountered, using methods described by Hersh et al. (2021) (see Vachon et al. 2022). Therefore, each identified whale was assigned an individual number, a group/social unit identifier, and a vocal clan (when sufficient acoustic data were collected—see Vachon et al. 2022).

5.3.3 Population estimate

We define population as "all co-existing individuals of the same species living in the same area at the same time" (Van Dyke 2008). Its size (for adult sperm whales in the Eastern Caribbean), was then estimated from photo identification data using closed 2-sample Petersen models with Chapman modification (Seber 1982) and closed Schnabel models using maximum likelihood (Schnabel 1938). Using closed models assumes no immigration, emigration, births, or deaths in the population and no mark loss between sampling intervals, assumptions that are reasonable for sperm whales across two consecutive years of data. Existing work supports these assumptions in demonstrating that the effective adult mortality for sperm whales in the Eastern Caribbean is estimated to be 0.0505/year (Whitehead and Gero 2015), and resighting rates across years is high for this community based on long-term reidentification (Gero et al 2014). We did not include the existing DSWP multi-year photo-identification dataset from Dominica as this would have severely distorted the distribution of effort across the Eastern Caribbean. Since groups and vocal clans have been shown to have much smaller ranges than previously assumed (Vachon et al. 2022), including a disproportionate amount of data from a single island would skew results and would not give an accurate population estimate for the entire Lesser Antilles region. Only sightings that occurred during our 2019 and 2020 Eastern Caribbean regional surveys were included in the population estimate. Furthermore, we did not include dependent calves and mature males in our analyses as calves were not reliably identified in the field and mature males have very low residency in the Eastern Caribbean (Gero et al. 2014). We restricted our vocal clan specific population analyses to EC1 and EC2 as we have much less data on tentative vocal clan EC3, identified by Vachon et al. (2022) and comprised of a single social unit of 10 adult members (Unit #12). EC3 individuals were therefore included in the total population estimates, but not in separate vocal clan analyses.

Closed Petersen and Schnabel population estimate models were carried out at multiple levels (across and within years, at the individual and group/social unit level, by pooling, or separating, vocal clans), and using both years, and surveys within years, as sampling periods. We only used the Schnabel method when estimating population size across more than two sampling periods, as this is not supported by the Petersen method. All statistical analyses were carried out using MATLAB software SOCPROG 2.9 (Whitehead 2009). Below we expand on the nature of each of these analyses:

A. Number of individuals across years: This was done by including all adult individuals and calculating population size between years (2019 and 2020; two sampling periods) and between surveys (survey 1-8; eight sampling periods), giving an estimate of the total number of adult sperm whales that use the Lesser Antilles.
B. Number of EC1/EC2 individuals across years: This was done by further restricting our dataset to include only EC1 or EC2 adult sperm whales, and then calculating their population size between years (2019 and 2020; two sampling periods) and between surveys (survey 1-8; eight sampling periods). By calculating adult population size separately for EC1 and EC2 sperm whales, we were able to assess whether one clan was more numerous than the other.
C. Number of groups/social units across years: For this analysis, we replaced individual identifications by group or social unit encounters. We included both groups and social units in this analysis as many groups did not qualify as social units under our criteria (Gero et al. 2014), but Eastern Caribbean groups are often composed of a single social unit (Whitehead et al. 2012; Gero et al. 2014; Konrad et al. 2018a). In this case, we estimated the total number of social units in the Lesser Antilles between years (2019 and 2020; two sampling periods) and between surveys (survey 1-8; eight sampling periods).
D. Number of individuals within each year (2019 and 2020 separately): To do this, we included all adult individuals and calculated population size using surveys as sampling periods independently for 2019 (survey 1-4; four sampling periods) and 2020 (surveys 5-8, four sampling periods). This provided an estimate of the

number of adult sperm whales occupying the Lesser Antilles within one year. If this number differs significantly from the total population estimate using both years of data, it might suggest that social units enter or leave the study area across years.

E. Number of groups within each year (2019 and 2020 separately): Here, we replaced individual identifications by group/social unit encounters. However, this time, we estimated the number of groups/social units independently for 2019 and 2020 using surveys as sampling periods (survey 1-4 for 2019 and survey 5-8 for 2020). This provided an estimate of the number of sperm whale groups/social units that occupy the Lesser Antilles within one 4-month field season. Once again, disparity here between across year and within year results could suggest that sperm whale groups enter or leave the study area across years.

5.4 RESULTS

During our 2019 (February-April) and 2020 (January-March) surveys, we had a total of 53 sperm whale photo identification encounters. From 4,267 photoidentification pictures with Q≥3 (1,415 in 2019 and 2,852 in 2020), we identified 214 adult individuals and 15 males from 33 different groups, 23 of which were groups that had never been documented by the DSWP, of which four qualified as social units. Whales from all vocal clans were encountered (24 encounters with EC1 groups, 23 encounters with EC2 groups, 5 encounters with EC3 groups and 1 encounter with both EC2 and EC3) (Vachon et al. 2022) (Figure 5.1).

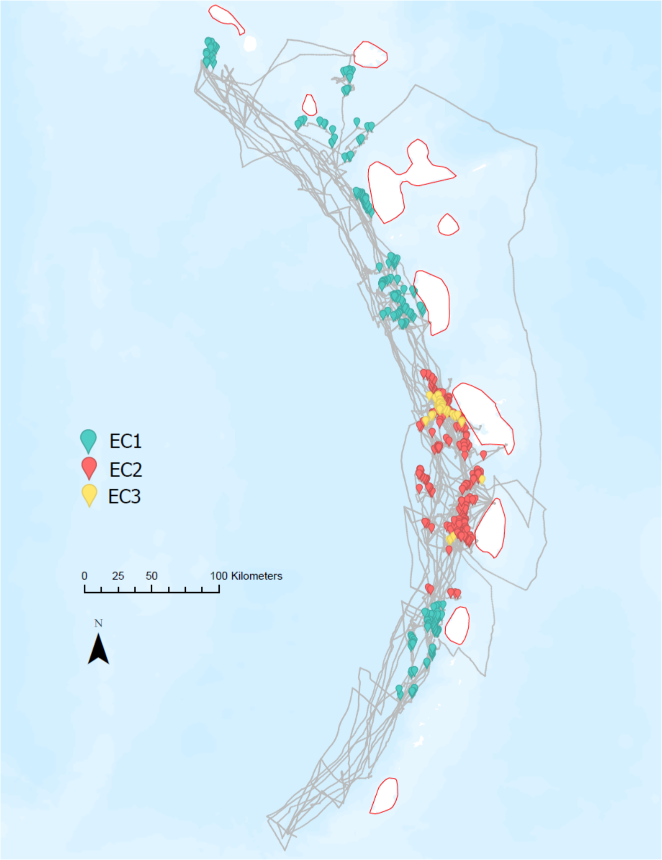

Figure 5.1. Photo-identified adult sperm whales from EC1 (aqua), EC2 (red), and EC3 (yellow). Each marker corresponds to the first sighting of an individual on a specific day. Tracks of the research vessel are shown in gray.

Our population estimate suggests a population of 414 (SE 46; 95%c.i. 338-490) adult (including non-calf juveniles) sperm whales and 51 (SE 6; 95% c.i. 41-62) sperm whale groups/social units in the Eastern Caribbean using Peterson methods and of 419 (SE 42; 95%c.i. 348 - 562) adult sperm whales and 52 (SE 6; 95% c.i. 43 - 68) sperm whale groups/social units using Schnabel methods (Table 5.1). These are consistent as the mean sperm whale group/unit size in the Eastern Caribbean is about 7-9 (Gero et al. 2014). These estimates are more than double previous adult population estimates of 156 (SE 18; 95% c.i. 126 – 195) and 11 (SE 2; 95% c.i. 5-14) groups in the Eastern Caribbean in 1998/1999, based predominantly on Dominica data (Whitehead & Gero 2015). There seem to be slightly more EC1 than EC2 sperm whales in the Lesser Antilles, with population estimates ranging, depending on the methods, from 205 - 219 for EC1 and 144 - 191 for EC2 (Table 5.1).

More sperm whales appear to have used the Lesser Antilles in the 2019 field season than in the 2020 field season, with a population estimate of 553 (SE 258; 95%c.i. 362-891) and number of groups/social units estimate of 47 (SE 14; 95% c.i. 34-86) in 2019 compared with a population estimate of 201 (SE 17; 95% c.i. 172-247) and number of groups/social units estimate of 29 (SE 2; 95% c.i. 26-35) in 2020 (Table 5.1). Furthermore, yearly population and group/social units estimates are lower than across year estimates (especially in 2020), suggesting that whales could be emigrating to non-surveyed areas across years and that the total abundance of sperm whales in the Lesser Antilles might be fluctuating from one year to the next. This result should be interpreted cautiously as standard errors are particularly high for the 2019 estimates and our dataset is limited in its temporal scale.

Table 5.1. Population, and group number estimate for Eastern Caribbean sperm whales using different methods across, and within years.

		Scale	Method	Population estimate	SE	95% c.i
Across years	A	Years, individual	Closed Peterson	413.6	46.1	337.7 - 489.5
			Closed Schnabel	419.03	42.3	348.4 - 562.1
		Surveys, Individual	Closed Schnabel	336.3	24.5	295.0 - 405.2
	B	Years, EC1 (individuals)	Closed Peterson	214.6	28.7	167.5 - 261.8
			Closed Schnabel	218.8	31.6	181.3 - 297.6
		Years, EC2 (individuals)	Closed Peterson	182.5	35.8	123.5 - 241.4
			Closed Schnabel	190.7	44.6	144.0 - 331.5
		Surveys, EC1 (individuals)	Closed Schnabel	205.1	22.8	167.4 - 262.5
		Surveys, EC2 (individuals)	Closed Schnabel	145.7	17.7	118.7 - 189.9

	C	Years, Groups/ social units	Closed Peterson	51.0	6.4	40.5 - 61.5
			Closed Schnabel	51.9	6.1	42.9 - 68.2
		Surveys, Groups	Closed Schnabel	43.5	3.2	38.6 - 51.0
Within years	D	Surveys 2019, individual	Closed Schnabel	553.2	257.9	361.9 - 890.6
		Surveys 2020, individual	Closed Schnabel	201.3	16.8	172.0 - 246.6
	E	Surveys 2019, Groups	Closed Schnabel	46.9	14.5	33.6 - 86.0
		Surveys 2020, Groups	Closed Schnabel	28.7	2.3	25.9 - 34.7

5.5 DISCUSSION

Increasing our survey scale to encompass the waters of most of the Lesser Antilles (from St. Kitts & Nevis to Grenada) has resulted in a larger population estimate (414 adults and 51 groups) than previous studies. This is most likely because the present surveys covered a more biologically appropriate scale than the previous studies, which used data that was heavily skewed by opportunistic sightings from the 1990s and more recent data predominantly collected off Dominica (145 adults by Gero et al. 2007 and 156 adults/12 social units by Whitehead & Gero 2015) and Guadeloupe (35-75 individuals per year, Rinaldi et al. 2021). The scale of the present study is more appropriate because of the unusually restricted movement patterns and high site fidelity of Eastern Caribbean sperm whales compared to other populations (Vachon et al. 2022). As most individual sperm whales do not move between the Lesser Antilles islands within and across years, island-specific data do not constitute an unbiased sample of the Eastern Caribbean population.

5.5.1 Mark-recapture methodology

In this paper, we used closed 2-sample Petersen and Schnabel methods as our dataset is temporally limited (eight surveys, two years) and other population estimate methods are designed to take advantage of datasets collected over longer temporal scales (e.g., those in MARK; CARE-2). The closed 2-sample Petersen and Schnabel methods differ from each other in that the Schnabel method can be applied over more than two mark-recapture events, which can prevent overestimates of population size (Seber 1982). However, both are limited by their inability to account for mortality, birth, immigration, emigration or heterogeneity in identification rate, with the latter leading to potentially large biases. While we can assume that mortality and birth rates are stable across two years (adult mortality is estimated at 0.0505/year in the Eastern Caribbean- Whitehead and Gero 2015, and calves were not included in the analysis), emigration or immigration is possible. In fact, our lower within-year population and group/social units number estimates and the fact that only 17.76% of individuals, and 39.4% of groups, sighted in 2019 were re-sighted in 2020, seem to suggest immigration/emigration out of our surveyed area is likely. Heterogeneity in identification is also likely as the probability to recapture an individual (or group/social units) is most likely influenced by behaviour, group size, habitat use and/or movement patterns (Whitehead & Wimmer 2005; see Vachon et al. 2022). Any heterogeneity in capture rates would bias our population estimates downwards (Hammond 1986). As more regional scale data becomes available over longer timescales, the current population estimate can be updated with more complex models that account for mortality, birth, immigration, emigration and/or heterogeneity of identifications, following Gero et al. (2007), Whitehead & Gero (2015) and Gero & Whitehead (2016), but over larger spatial scales.

5.5.2 Limitations

The population estimates presented here is a preliminary assessment of sperm whale abundance in the Eastern Caribbean region using the best available data. However, our study, is temporally (only two years) and spatially (St. Kitts & Nevis to Grenada) limited. Sperm whale densities were lower at the geographic ends of the survey route (St. Kitts & Nevis in the North, Grenada in the South) than off the central islands (Vachon et al. 2022) which may result from shallower water in those areas being typically less frequented by sperm whales. In addition, movements to the east into the Atlantic or west into the Caribbean Sea away from the islands are currently unknown and potentially more likely due to the bathymetry traditionally associated with sperm whale presence.

Estimated population sizes (Table 5.1) within and across years showed discrepancies that suggest movement of sperm whales into and out of the study area over timescales of one year. We advise caution when interpreting those results as they come from a limited data set but recommend that future studies further expand the spatial scale of the research effort. While no photo-identified females have been reidentified between the Eastern Caribbean and the photoidentification catalogues from the Gulf of Mexico, Azores and/or Sargasso Sea (Gero et al. 2007; Gero pers. comm), many areas remain poorly surveyed (especially further offshore).

5.5.3 Implications for conservation

While we have shown that there are more sperm whales in the Eastern Caribbean than previously thought, we lack information on trends at this scale. Critical yearly decline rates of 4.5% and 6.2% have been reported for Dominica and Guadeloupe respectively based on mortality of well-known individuals (Gero & Whitehead 2016; Rinaldi et al. 2021) and the threats identified for these whales (i.e. tourism, vessel strikes, entanglement, noise, pollution) are most likely also affecting whales off neighbouring islands. For instance, tourism is a major economic sector across the Lesser Antilles islands (Piraszewska 2006) and the effects of underwater noise and climate change (Jury & Bernard 2020) are most likely to be felt throughout the Eastern Caribbean. However, more localized threats such as whaling (Finneran 2016), entanglement (Gero & Whitehead 2016) and the presence of fast vessels (such as the high speed ferries connecting Guadeloupe, Dominica, Martinique and St. Lucia) might vary from one island to the next. Long term monitoring of the sperm whales inhabiting islands beyond Dominica and Guadeloupe is therefore necessary to project this population estimate into the future and obtain population trends of growth.

Our current results suggests that EC1 sperm whales are slightly more abundant than EC2 sperm whales. However, nothing is known about EC2 population trajectories (as EC2 whales are rarely encountered in Dominica and Guadeloupe, where most of the DSWP effort is concentrated and EC1 are prevalent). As our understanding of vocal clans across the Eastern Caribbean grows, and as the importance and impact of culture in conservation is increasingly recognized (Whitehead 2010; Brakes et al. 2019; Brakes et al. 2021), we also recommend the inclusion of vocal clan-specific abundance and trends (with vocal clans as distinct management units). Individuals from different cultural groups might be subject to different levels of stress and respond differently to threats or changes. This was reported for Eastern Tropical Pacific sperm whales, with Plus-One and Regular vocal clans having different feeding success during ENSO (El Niño/South Oscillation) and non-ENSO years (Whitehead & Rendell 2004) as well as differential reproductive success (Marcoux et al. 2007b) and might be especially important in the Eastern Caribbean where vocal clans are geographically segregated and appear to have smaller ranges (Vachon et al. 2022). Island specific threats, and island specific conservation management measures have the potential to affect vocal clans differentially. In this case, maintaining cultural diversity might be as important as maintaining genetic diversity for overall population health.

As our understanding of the Eastern Caribbean sperm whale population structure increases, and as we incorporate data from greater temporal and spatial scales, we will be able to better monitor, manage and conserve the Eastern Caribbean sperm whale population.

5.6 ACKNOWLEDGEMENTS

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CHAPTER 6 –

Multidimensional Distribution of Sperm Whale Social Vocalizations Suggests Identity Codas are Symbolic Markers of Cultural Group Membership

6.1 ABSRACT

Humans use symbolic markers (such as language, clothing, music and religious symbols) to delineate members of their own cultural group. Such markers have important evolutionary and social implications as they mark boundaries between individuals and can affect not only direct social interactions but also social structure and cultural/genetic inheritance. However, the possibility of symbolic markers in non-human species has received less attention. In this paper, we investigate whether sperm whales (Physeter macrocephalus) could use acoustic signals, called identity codas, as symbolic markers of cultural group membership. Identity codas differ from other sperm whale social vocalizations (i.e., non-identity codas) as they are predominantly made by members of one cultural group but seldom by others. Here, we compare the multidimensional distribution of identity coda types and non-identity coda types using two metrics (volume and pairwise overlap in multidimensional space) and data from three geographically isolated sperm whale populations (the Eastern Tropical Pacific, the Mediterranean, and the Eastern Caribbean). We find that identity codas are more stereotyped and overlap significantly less with other coda types in multidimensional space than non-identity codas. This aligns with the emerging view of identity codas as symbolic markers of sperm whale vocal clans and suggests the use of symbolic markers in non-human animals.

6.2 INTRODUCTION

Symbolic markers can be defined as arbitrary signals that delineate and maintain cultural/ethnic group boundaries (Barth 1969; Boyd & Richerson 1987; McElreath et al. 2003; Cohen 2012). They can vary in form (visual, acoustic, behavioural) but, regardless, have important implications for cultural evolution and social structure, as a cultural group's persistence depends on the maintenance of its boundaries (Barth 1969). Symbolic markers directly impact social interactions as they promote relationships between cultural in-group members and limit interactions with cultural out-group members. For instance, humans tend to favour in-group members which they identify via symbolic markers (Tajfel et al. 1971; Bernhard et al. 2006), are more likely to cooperate and trust in-group individuals (Van Vugt & Hart 2004; Zdaniuk & Levine 2001) and tend to have prejudice towards out-group members (Brewer & Brown 1998; Fiske 2002). By shaping such interactions, symbolic markers have an important influence on cultural and genetic inheritance as social learning, and mating, might be restricted to in-group members, even if other individuals occur in sympatry. These phenomena are known as biased transmission and assortative mating, respectively. As such, human language (Creanza & Feldman 2016), grammar (Matsumae et al. 2019), religion (Relethford & Crawford 1998; Zalloua et al. 2008), and music (Brown et al. 2014) can be more strongly correlated to genetic relatedness than geography. The study of symbolic markers can therefore not only yield important evolutionary information about cultural groups (e.g., human languages can inform about human expansion, Bouckart et al. 2012), cultural group formation (with the emergence of symbolic marker promoting ingroup favoritism - Efferson et al. 2008), but also current social structure and relationships (Barth 1969).

While symbolic markers have mostly been investigated in the context of human evolution (e.g., Boyd & Richerson 1987; McElreath et al. 2003; Efferson et al. 2008; Cohen 2012; Smaldino 2022), their existence might not be restricted to *Homo sapiens*. However, their consideration beyond humans can pose epistemological challenges as we are not able to assess them through verbal reports of internal association and meaning in other species. In this case, approaches that rely on assessing symbolic markers through their use, structure, and causation (e.g., Boyd & Richerson 1987; Efferson et al. 2008; Perry 2009), rather than their internal state of meaning, are particularly important. Especially as more and more evidence suggests that culture is widespread in the animal kingdom (reviewed in Allen et al. 2019; Whiten 2021), and symbolic markers have been suggested to play a potentially important role in navigating social interactions for non-human species which display large-scale cooperation, complex social structures, group-specific behaviours and big home ranges (Perry 2009).

One such species is the sperm whale (*Physeter macrocephalus*), which lives in a hierarchically organised matrilineal society. At the basal tier, females, calves, and juveniles are members of *social units*, which are stable assemblages of one to two sperm whale matrilines that always travel and forage together (Whitehead et al. 2012; Gero et al. 2014). Social units will often associate with other social units, forming *groups*, for periods of a few hours to a few days, during which whales from those units will forage and socialize together (Christal et al. 1998). At the highest tier, *vocal clans* represent the social segregation between sets of social units -with whales from different vocal clans not associating with each other even if they occur in sympatry-(Eastern Tropical Pacific - Rendell & Whitehead 2003b, Eastern Caribbean- Gero et al. 2016b and Vachon et al.2022, Brazil -Amorim et al. 2020, Mauritius -Huijser et al. 2020). Since individuals from different vocal clans are not genetically distinct (Rendell et al. 2012; Konrad et al. 2018b), and can display different behaviours (e.g., different movement patterns - Whitehead and Rendell 2004; Whitehead et al. 2008a, diving synchrony - Cantor & Whitehead 2015, distributions -Eguiguren et al. 2019; Vachon et al. 2022, and social organization -Cantor and Whitehead 2015), vocal clans are believed to be a culturally mediated tier of sperm whale social structure.

Vocal clans can be distinguished based on their members' characteristic acoustic repertoire of codas (Rendell & Whitehead 2003b): stereotyped patterns of 3–12 clicks produced by sperm whales in social contexts (Watkins & Schevill 1977; Whitehead & Weilgart 1991). Codas are classified into *types* based on their *interclick intervals* (ICIs the time between consecutive clicks – the ICI vector of a coda gives quantitative, multivariate measurement of rhythm and tempo), such that codas with, for example, five regularly spaced clicks belong to the 5 Regular (5R) coda type, while codas with four regularly spaced clicks followed by a longer pause and a final click belong to the 4+1 coda type (Weilgart & Whitehead 1997). Originally, vocal clans were discriminated based on the hierarchical clustering of highly similar coda repertoires of units within vocal clans compared to between vocal clans (Rendell & Whitehead 2003b; Gero et al. 2016b; Amorim et al. 2020; Huijser et al. 2020); more recently, new methods have allowed for researchers to define unique vocal clan-level identity codas (*vocal clan identity codas*) to delineate clans in larger datasets (Hersh et al. 2021; Hersh et al. in review; Vachon et al. 2022). Each vocal clan produces a characteristic repertoire of coda types, with some coda types that are shared across vocal clans—*non-identity (non-ID) coda types*—and some types that are almost exclusive to a single vocal clan—*identity (ID) coda types* (Hersh et al. 2021). Refer to Table S6.1 for a glossary of terms.

As clans may span thousands of kilometers (Whitehead 2001; Whitehead et al 2008; Hersh et al submitted) and may include thousands of individuals (Rendell and Whitehead, 2003); it is likely that sperm whales interact (at least in the minimal sense of hearing one another) with unknown individuals reasonably often and, therefore, have a clear need to assess the cultural group membership of new individuals. However, although the use of symbolic marker could explain how social units from socially segregated but sympatric vocal clans might recognize and classify their conspecifics and maintain observed social boundaries (Rendell & Whitehead 2003b; Cantor & Whitehead 2013; Gero et al. 2016a; Hersh et al. in review), the functional use of ID codas as symbolic markers of clan identity/membership by the whales themselves remains uncertain.

The objective of this paper is, therefore, to quantify the structure of ID and non-ID coda types in multidimensional space in order to assess their potential use as symbolic markers by sperm whales. If ID codas do function as identity signal in the context of ethnic marking, we expect them to be highly stereotypical, redundant, and discrete from non-ID coda types (Axelrod et al. 2004; Cohen 2012 ; Wiley 2013; Wiley 2017). This is the case for human accents and allows for the easy identification of an individual's cultural group membership, the honest cooperation of in-group members and prevents free riders (Cohen 2012). Failure to meet those criteria would lead to mis-associations over time and an erosion of cultural group boundaries (Barth 1969). Conversely, if ID codas are not symbolic markers but instead signals to known in-group members, perhaps like bond-testing social rituals in capuchin monkeys (Perry 2009), we expect them to be similar in structure to non-ID coda types. In this case, identities are not actively broadcasted to potential out-group members and misinterpretation of the signal has less severe social repercussions (i.e. erosion of cultural groups). Therefore, if ID codas act as symbolic markers of vocal clan membership, we expect them to be more redundant, stereotyped and discrete than non ID coda types in their structure.

Here, we compare the pairwise overlap (to quantify how discrete coda types are from each other), and volume in the multidimensional space (as a measure of stereotypy) defined by coda ICI vectors of non-ID and ID coda types from sperm whale vocal clans occurring in three geographically isolated areas: the Eastern Tropical Pacific (ETP), the Mediterranean (MED) and the Eastern Caribbean (EC). These populations are some of the best studied populations of sperm whales in the world, each with an extensive coda dataset (Table S6.2). By comparing coda types across isolated geographical regions, we are able to assess the evolutionary forces contributing to coda structure in multidimensional space and how these forces might differ in sympatry and across geographical scales. More specifically we test the hypotheses that: ID coda types should occupy less multidimensional space than non ID coda types (stereotypy) and be more discrete from each other (hypothesis A) and other coda types (hypothesis B) than non ID coda types (discreteness). We also further investigate the structure of ID coda types specifically and look at whether different ID codas from a same vocal clan overlap more with each other than they do with ID coda types form different vocal clans (hypothesis C) and whether ID coda types from sympatric vocal clans are less similar to each other than they are to geographically isolated vocal clans (hypothesis D). This is the case in human music, where variation is often greater within, rather than across, populations/societies as a result of more frequent interactions (Rzeszutek et al. 2012; Mehr et al. 2019; Daikoku et al. 2020).

We believe this work is significant as it will allow for a greater understanding of vocal clan social interactions and evolution (not unlike how the study of language can inform our understanding of human evolution; Bouckaert et al. 2012; Creanza et al. 2015; Baker et al. 2017).

6.3 METHODS

6.3.1 Dataset

We pooled sperm whale coda data from three geographically isolated regions: the ETP, MED, and EC (Table S6.2). Data from the ETP were collected between 1978 and 2014 via acoustic (1978) and dedicated sperm whale surveys (1985-2014) around the Galápagos islands (Weilgart & Whitehead 1997; Rendell & Whitehead 2003b; Cantor et al. 2016). MED data were collected off the Balearic Islands between 2004 and 2018 by the Balearic Sperm Whale Project (Pirotta et al. 2011; Rendell et al. 2014). EC data were collected leeward of the island of Dominica by The Dominica Sperm Whale project (DSWP) since 2005 (Gero et al. 2014; Gero et al. 2016b) and supplemented by the Watkins Marine Mammal Sound Database (1981-1995) (Sayigh et al. 2016), as well as dedicated sperm whale surveys that covered most of the Lesser Antilles (from St.Kitts & Nevis to Grenada) in 2019 and 2020 (Vachon et al. 2022). Codas were marked manually by trained auditors using the Rainbow Click software (Gillespie 1997) or Coda Sorter (custom LabView software implemented in MATLAB by K. Beedholm, Aarhus University). While these data have been collected over different spatio-temporal scales and using slightly different methods and equipment, they are comparable since the codas' ICIs (the primary variable of focus in this study) are robust to variation in recording system and protocols, and coda types have been distinguished using varying analytical and classification methods over the years and are generally temporally stable (Rendell & Whitehead 2005; Gero et al. 2016a; Hersh 2021, Chapter 5).

6.3.2 Vocal clan membership

All codas recorded on a given day were considered a *repertoire*. Only codas of 3-11 clicks and only repertoires with at least 25 such codas were included in the analysis, following previous methods (Rendell & Whitehead 2003b). Vocal clan membership was then determined for each repertoire using IDcall (Hersh et al. 2021, Whitehead & Hersh 2022). This routine uses parsimonious mixtures of multivariate contaminated normal distributions (R package "ContaminatedMixt") (Punzo et al. 2016) to classify codas of the same click length into types and then delineates repertoires into vocal clans based on their usage of ID coda types (codas that are extensively used by one set of repertoires and seldom by others).

Vocal clans have already been documented in the ETP (Regular, Plus-One, Short, Four-Plus, Slow Increasing, Rapid Increasing, and Palindrome; Rendell & Whitehead 2003b; Cantor et al. 2016; Hersh et al. in review), MED (Rendell & Frantzis 2016), and EC (EC1, EC2, and EC3; Gero et al. 2016b, Vachon et al. 2022). However, these analyses were performed independently from each other, meaning that the coda types detected in one region were not related or compared to the coda types detected in another region. Thus, previous analyses did not allow for the direct comparison of coda types across regions. Here, we used the IDcall method on a single dataset including codas from all three regions, not only to confirm vocal clan membership, but, more importantly, to delineate ID coda types (as well as non-ID coda types) for each vocal clan in each geographical region. This is necessary as we aimed to compare ID and non ID coda types within and across regions.

6.3.3 Coda type metrics in multivariate space

Each coda's ICI vector specifies its position in multidimensional space. The number of ICIs in a coda determines the dimensions of that space, such that 5-click codas can be located in a 4-dimensonal space , 6-click codas in a 5-dimensional space, and so forth. The collection of codas belonging to a given type therefore occupies a certain volume within the relevant multidimensional space. These volumes of ID and non-ID coda types in multivariate space can then be compared across vocal clans and geographical regions. Here, we did so using two metrics: coda type volume and coda type overlap.

Coda type volume was calculated for each coda type following the dynamic range box method from Junker et al. (2016) and implemented using the "dynRB" R package (Schreyer et al. 2021) by drawing an n-dimension hypervolume representing the distribution of codas of n+1 click length assigned to the same type in multidimensional space. The dynamic range box method has advantages over other hypervolume methods as it is a nonparametric approach that accounts for the underlying distribution of the data (Junker et al. 2016). Using this method, hypervolumes are not forced to include all data points, an approach that can lead to the overestimation of hypervolumes' volume in the presence of outliers and is greatly affected by varying sample sizes (e.g., Hutchinson 1957). This is especially important in our case as our sample sizes vary widely from one coda type to the next (with some codas recorded much more often than others), and certain coda types have been shown to vary at the individual and social unit levels, and therefore might show more variation (Gero et al. 2016a). Volume values range from 0 to 1, with increasingly larger volume values as one moves closer to 1 (Junker et al. 2016). We chose the mean method of volume (and overlap) aggregation as results from this method are not biased by the number of dimensions and can be compared across them (Junker et al. 2016, Schreyer et al. 2021). This is important as we aimed to compare coda type volume across click lengths.

6.3.4 Coda structure analysis

6.3.4.1 Volume

We performed general linear models (GLM) to test the null hypothesis that there is no association between coda category (ID or non-ID) and coda type volume.

Coda type volume ~ coda category + number of clicks + sample size

We included sample size and number of clicks in the model as they could act as confounding factors (i.e., coda types with larger sample size and longer click lengths might have larger volumes). GLM assumptions were tested prior to the analysis (Figure S6.1). As ID codas are predominantly made by a single vocal clan by definition (Hersh et al. 2021), but non-ID codas are often made across vocal clans, we repeated this volume analysis by restricting non-ID coda types to a single vocal clan (the one for which we had the largest sample size of that particular coda type) to correct for potential between-vocal clan variation in delivery of codas of a particular type.

6.3.4.2 Overlap

Coda type overlap was then quantified as the overlap of the hypervolumes of coda type A and coda type B in multidimensional space. Overlap values range from 0 to 1, with 0 being no overlap and 1 being complete overlap. This value is asymmetric as it is calculated as the proportion of coda type A hypervolume that overlaps with coda type B hypervolume. We took the mean of these two values (proportion of A overlapping B, and B overlapping A) to compare between coda types. We conducted Mantel tests (Legendre & Legendre 2012) on pairwise matrices of coda type overlaps to test a range of hypotheses regarding ID versus non-ID coda structure. Mantel tests were performed independently for each click length (as coda types of different click lengths have different dimensions their overlap cannot be measured) using R package “vegan” (Oksanen et al. 2020). Since the vegan package conducts Mantel tests on symmetric dissimilarity matrices exclusively, we measured dissimilarity as one minus the overlap value for the pair. The non-exclusive hypotheses we tested are visually depicted in Figure 6.1 and detailed below:

- *Hypothesis A:* Pairs of non-ID coda types are more similar to each other (i.e., overlap more with each other) than are pairs of ID coda types from different vocal clans. We expect this if an ID coda type from a specific vocal clan needs to be reliably distinguished (i.e., more discrete) from ID coda types from a different vocal clan, regardless of whether they are sympatric. This would be the case if ID codas are symbolic markers of vocal clan membership.

- *Hypothesis B:* ID coda types are more discrete from each other and from non-ID coda types (i.e., overlap less with each other) than are non-ID coda types to non-ID coda types. This would imply that ID coda types need to be reliably distinguished from other ID, and non-ID, coda types, regardless of vocal clan and/or level of sympatry and would be the case if ID codas are symbolic markers of vocal clan membership.

- *Hypothesis C:* ID coda types from the same vocal clan are less discrete from each other (i.e., overlap more with each other) than they are to ID coda types from different vocal clans. We expect this if forces acting on ID coda types are stronger across than within vocal clans (i.e., it is more important for the whales to differentiate ID codas from different vocal clans from their own than it is to differentiate their own ID codas from each other).

- *Hypothesis D:* ID coda types from different vocal clans are more discrete from each other (i.e., overlap less with each other) if vocal clans are sympatric, rather than geographically isolated. This would be the case if there is active pressure to distinguish ID coda types made by whales from different, but sympatric clans (i.e., if selection is shaping coda type structure to be more discrete between vocal clans that regularly interact with each other).

These hypotheses were tested by assigning binary variables to coda type pair categories (see Table 6.1). For each hypothesis, coda type pairs from categories that were not covered by these statements were labelled as missing values and excluded from the analysis. This binary category matrix was then compared to the coda type overlap matrices to test the null hypothesis that coda type overlap is not related to coda type categories.

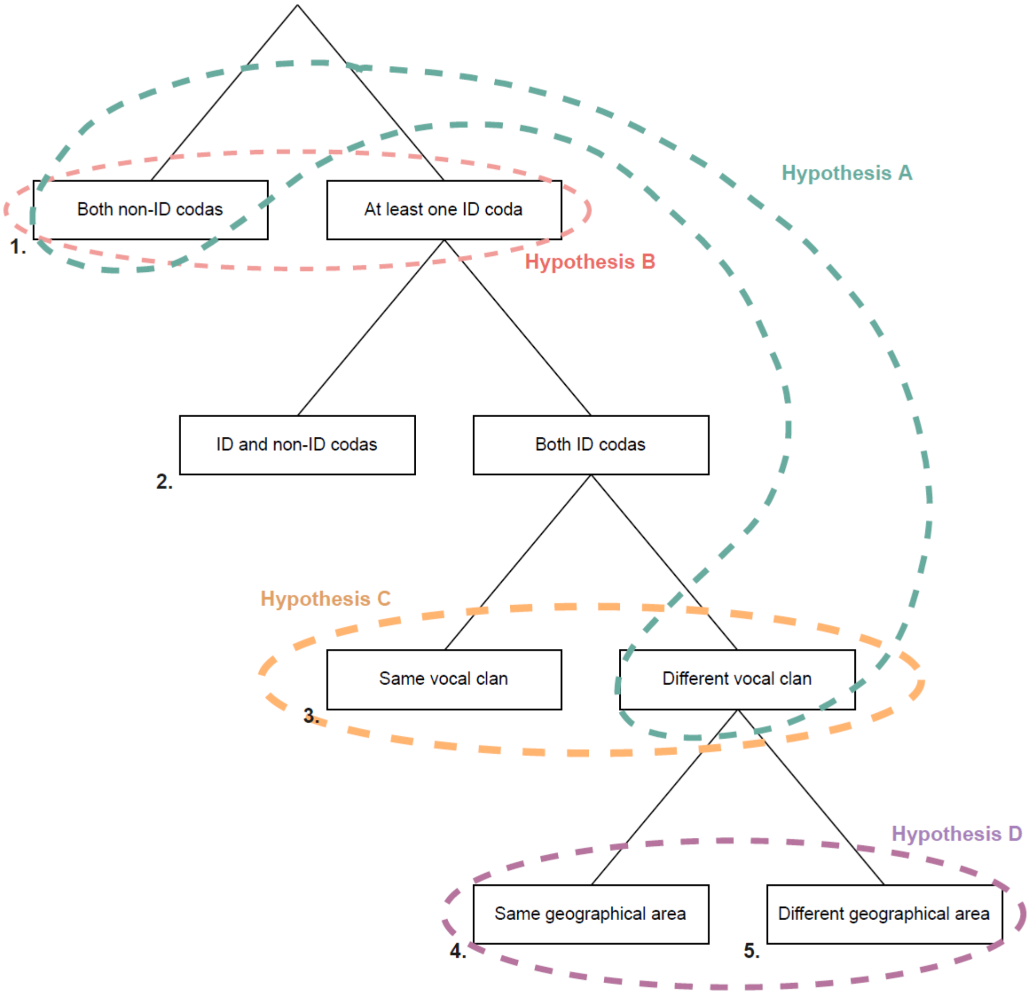

Figure 6.1. Hypothesis framework in comparing the structure (i.e., multidimensional overlap) between different coda types. The different coda type pair categories are numbered from one to five.

6.3.4.3 Visualization

As a visual depiction of our results, we plotted coda type overlap between pairs of coda types from each of five possible categories: 1) both non-ID coda types; 2) non-ID coda type and ID coda type; 3) ID coda type from the same vocal clan; 4) ID coda type from different vocal clans within the same geographical areas (i.e., sympatric clans); and

5) ID coda type from different vocal clans from different geographical areas (i.e., geographically isolated clans) (Figure 6.1). We also used principal components analysis (PCA) to visually depict (in two dimensions) differences in coda type overlap, and volume for each click length.

6.4 RESULTS

6.4.1 Dataset and vocal clan membership

Our final combined dataset contained 29,614 codas, spanning 42 years and three geographical regions. Altogether we had 274 repertoires: 108 from the ETP, 150 from the EC, and 16 from the MED (Table S6.2). We identified 119 distinct coda types: 19 ID, 29 non-ID, and 71 deemed as too rare and removed from subsequent analysis (mostly coda types with ≥ 9 clicks; Table S6.3).

Previously documented vocal clans were re-identified in our analysis (using IDcall parameters *critfact*=9, *minrep* = 5) with Regular, Plus-One, Short, Four-Plus, Slow Increasing, and Palindrome vocal clans in the ETP (Rendell & Whitehead 2003b; Cantor et al. 2016; Hersh et al. in review); the EC1, EC2, and EC3 vocal clans in the EC (Gero et al. 2016b; Vachon et al.2022); and a single vocal clan in the MED (Rendell & Frantzis 2016) (Figure 6.2, Figure S6.2). This was expected as the data used for this analysis were also used independently in each geographical region to uncover these same vocal clans, but their re-emergence in our larger, pooled coda dataset attests to their robustness.

We had pairs of coda types from all five potential pair categories (Figure 6.1) but not all click lengths include coda type pairs of each category (3 clicks: 3/5 categories, 4 clicks: 4/5 categories, 5 clicks: 5/5 categories, 6 clicks: 4/5 categories, 7 clicks: 3/5 categories, 8 clicks: 1/5 categories, 9 clicks: 1/5 categories). All 10 click and 11 click coda types were classified as too rare by IDcall and removed from the analysis. To prevent such small sample sizes from influencing our results, and in order to include coda type pairs from all potential categories, we limited our coda type overlap analyses to 5-click codas. 5-click codas appear to be the most prevalent coda types worldwide (making up 50.38% of our dataset) and trends seen in these codas were reproduced in those comparisons available across other coda length (see Figure S6.5, Figure S6.8).

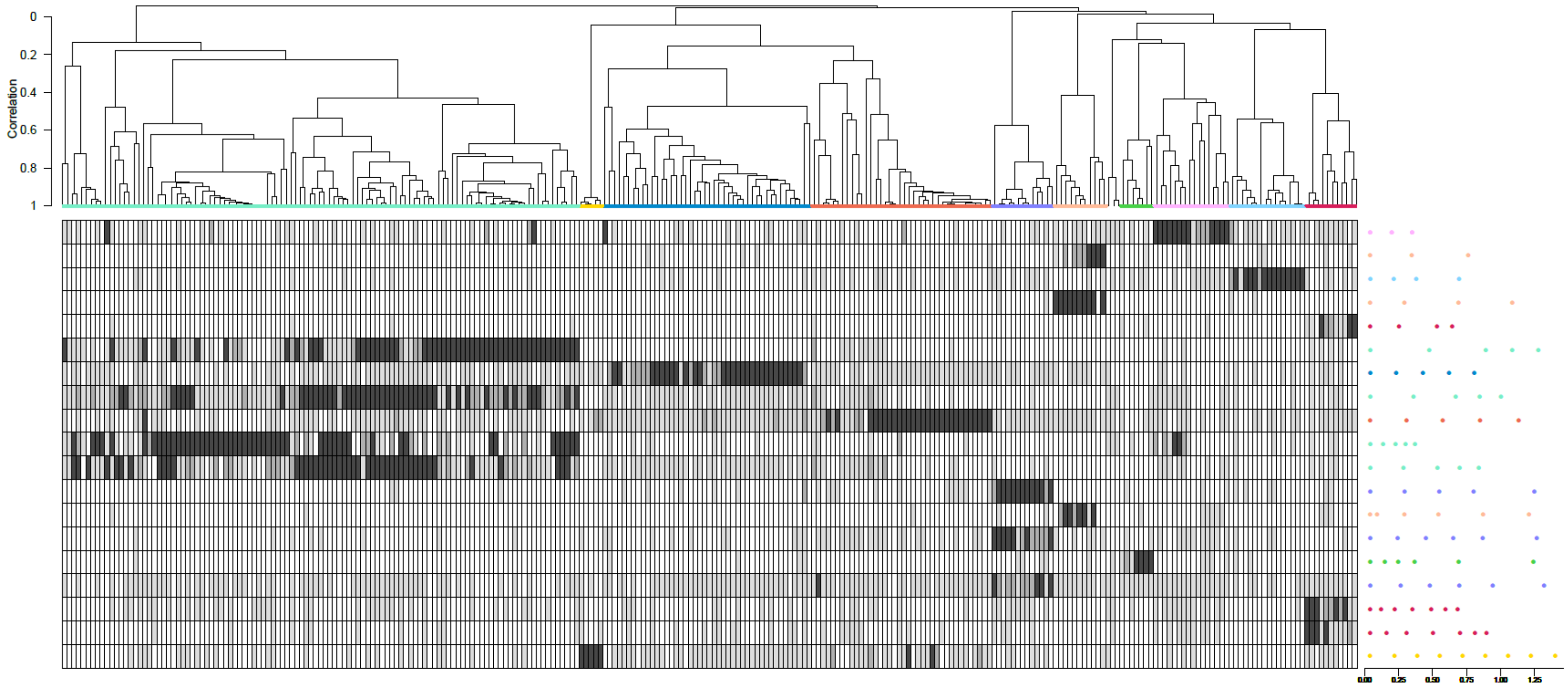

Figure 6.2. Average linkage hierarchical clustering dendrogram (top) depicting acoustic similarity among different vocal clans, left to right: EC1 (aqua), EC3 (yellow), Regular (blue), EC2 (orange), Plus-One (purple), Slow Increasing (peach), Four-Plus (green), Short (pink), Med (light blue), Palindrome (magenta). Each branch corresponds to the coda repertoire of a certain group of sperm whales on a certain day. Each row of the heat map (bottom) shows probabilistic usage by repertoire of an identity coda type. Heat map shading corresponds to the percentage of the repertoire made up of each identity coda type with white 0%, light gray 0–5%, gray 5–10%, and dark gray 10% or higher. The rhythmic and temporal patterns of identity coda types are depicted to the right of the heat map by dots representing each click in the coda and are colored according to clan with duration in seconds underneath. See Figure S6.2 for a version of this diagram showing all coda types. Analysis using IDcall (Hersh et al. 2021), with parameters critfact = 9, minrep = 5.

6.4.2 Volume

Hypervolume was significantly smaller for ID coda types than non-ID coda types (GLM*: Coda type volume ~ coda category* + *number of clicks* + *sample size*, with coda category t=-3.279, p-value= 0.002). This was not much influenced by click length or sample size, as these terms were not significant in the GLM (t=1.736, p-value=0.090 and t=1.88, p-value=0.066 respectively) and sample size effect on volume stabilized around 100 codas (Figure S6.3). Across all click lengths, mean hypervolume was lower for ID coda types than non-ID coda types with ID coda types 45% smaller in volume than non-ID coda types for 3 click coda types, 50% smaller for 4 click coda types, 58% smaller for 5 click coda types, 27% smaller for 6 click coda types, 20% smaller for 7 click coda types and overall, 40% smaller across all click lengths (Figure 6.3, Figure 6.4). Similar results are obtained if we restrict the non-ID coda type dataset to a single vocal clan per non-ID coda type (t= -3.124, p-value= 0.003, Figure S6.4, Figure S6.5).

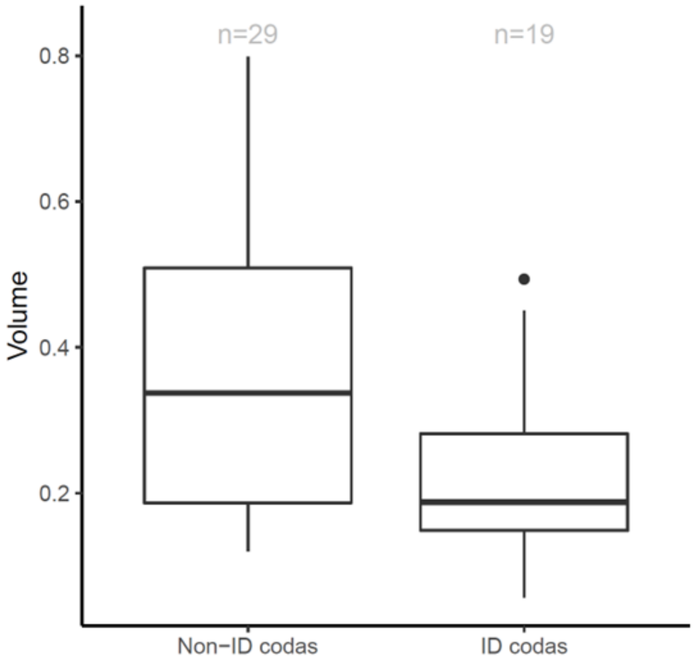

Figure 6.3. Coda type hypervolume for non-ID and ID coda types (all click lengths).

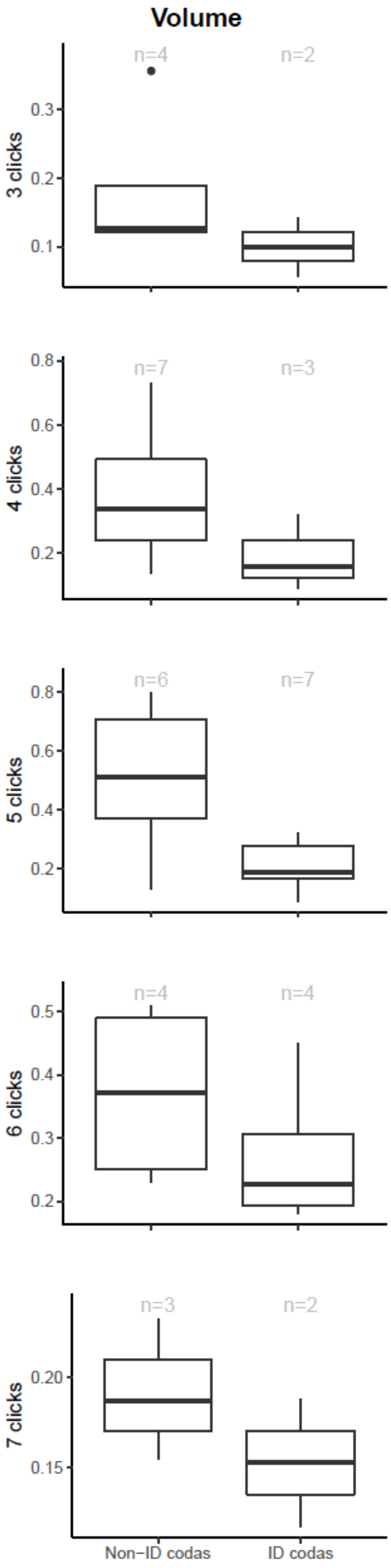

Figure 6.4. Coda type hypervolume for non-ID and ID codas. Results shown independently for each click length.

6.4.3 Overlap

Mantel tests were statistically significant in differentiating hypervolume overlap between non-ID coda type pairs and pairs including either both ID (hypothesis A, Mantel r= 0.606, p-value= 0.029) or a single ID coda type (hypothesis B, Mantel r=0.364, p-value=0.021), with less overlap in pairs of coda types that include ID coda types (Table 6.1). On the other hand, coda type hypervolume overlap was not significantly different between ID coda types from the same rather than different vocal clan (hypothesis C, Mantel r=-0.120, p-value=0.600) or between sympatric versus geographically isolated vocal clans (hypothesis D, Mantel r=0.198, p-value=0.238). Across all click lengths, mean overlap is lowest for ID coda types from different vocal clans (Figure 6.5, Figure 6.6, Figure S6.6).

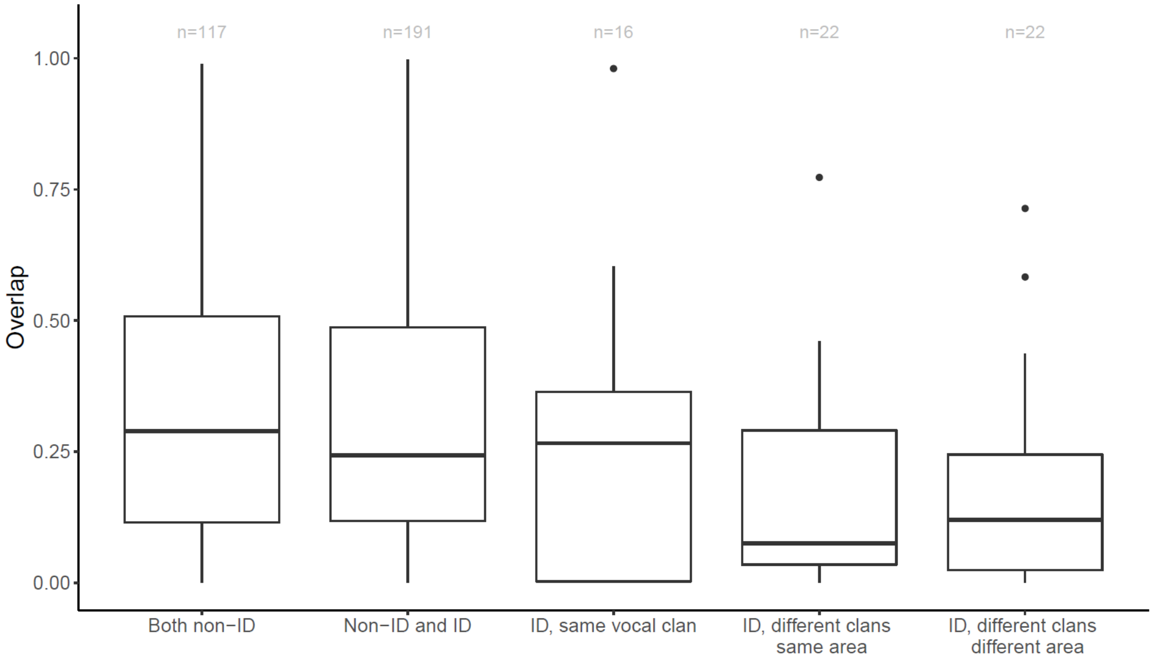

Figure 6.5. Overlap between pairs of coda types' hypervolumes based on the pair's categorization (all click lengths). A version of this figure standardized by click length is available in the Supplementary materials (Figure S6.4).

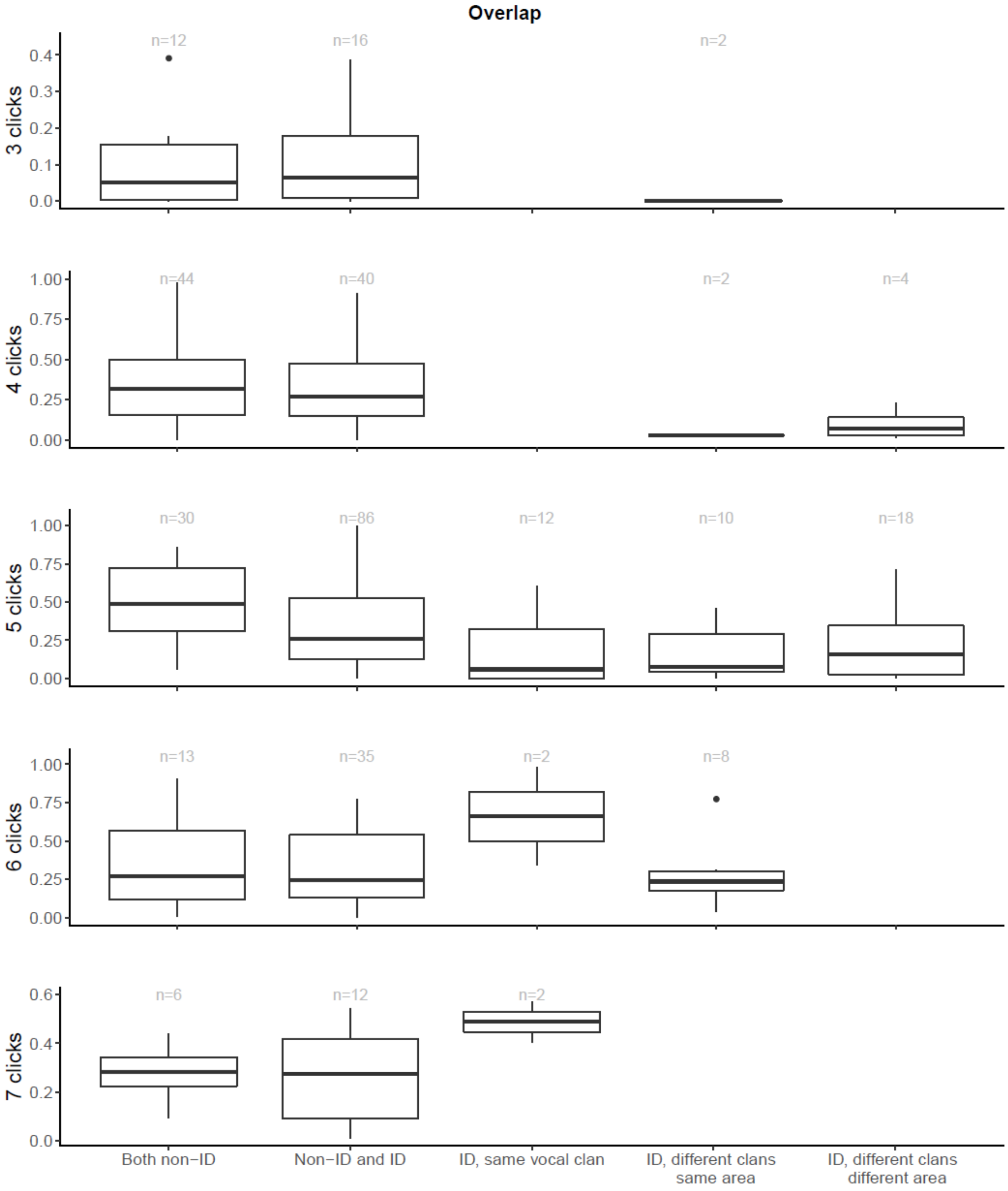

Figure 6.6. Overlap between pairs of coda types' hypervolumes based on the pair's categorization. Results shown independently for each click length.

Table 6.1. Mantel test results for coda type overlap (5-click codas). Mantel r is a measure of the correlation between the two matrices (1-overlap matrix and binary categorical matrix), with a positive r indicating that overlap is lower for the category with binary outcome 1. Significant results (p<0.05) are marked with *.

Hypothesis		Mantel *r*	Significance
A	0: Non-ID coda to non-ID coda 1: ID codas from different vocal clans	0.606	0.029 *
B	0: Non-ID coda to non-ID coda 1: Pair includes at least one ID coda	0.364	0.021 *
C	0: ID codas from the same vocal clan 1: ID codas from different vocal clans	-0.120	0.600
D	0: ID codas from different vocal clans occurring in different geographical regions 1: ID codas from different sympatric vocal clans	0.198	0.238

6.4.4 Principal components analysis

Results from our PCA analysis confirmed results from our Mantel tests and GLMs, and visually depict the smaller volume and lower overlap of ID coda types compared to non-ID coda types across all click lengths (Figure 6.7).

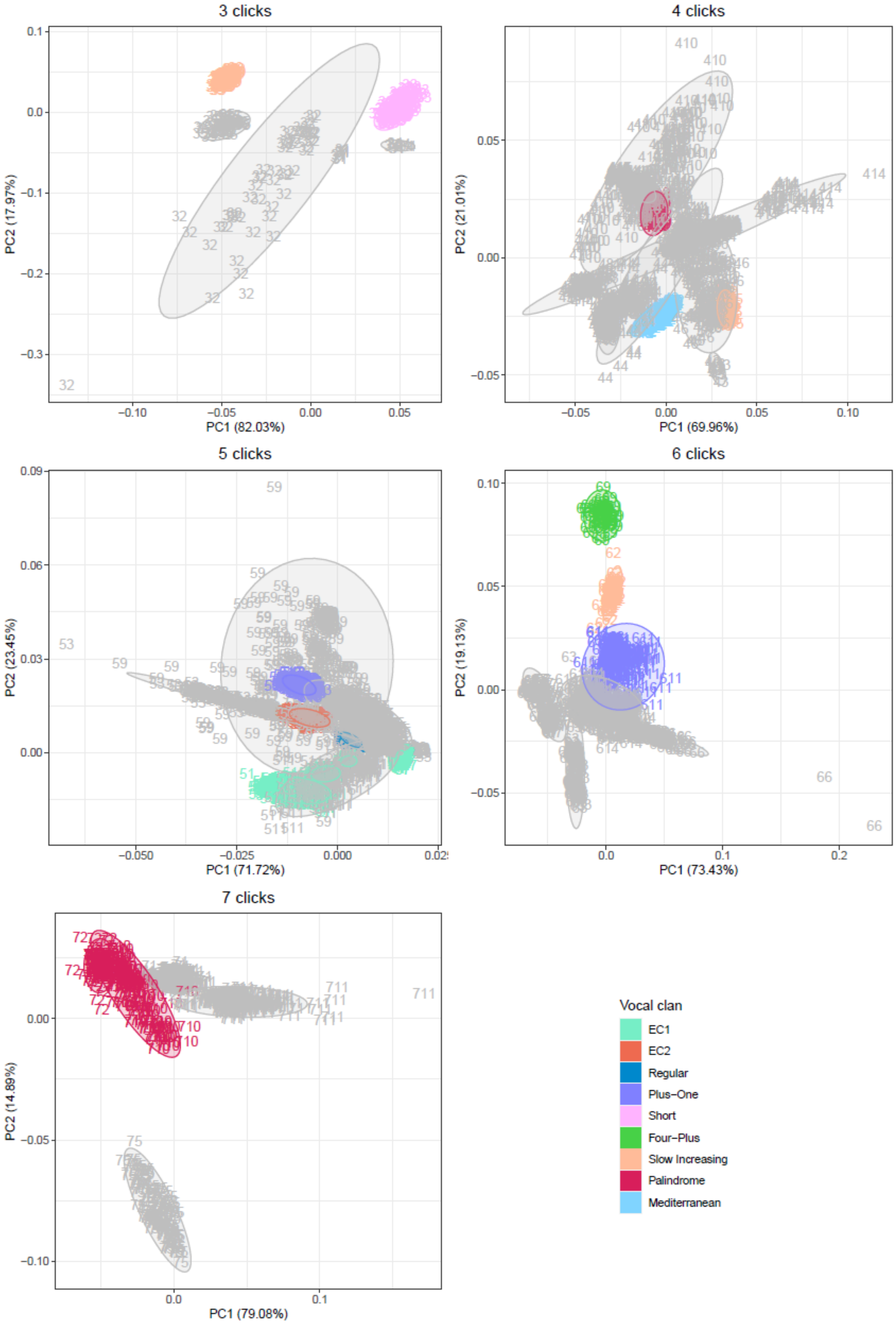

Figure 6.7. Principal component analysis (PCA) of coda types (with probability ellipses) for each click length. Numbers refer to the different coda types with ID coda types colored by vocal clan and non-ID coda types in gray.

6.5 DISCUSSION

Our results highlight the potential of ID coda types as symbolic markers of vocal clan membership. ID coda types have significantly smaller volumes in multidimensional space than non-ID coda types (Figure 6.3, Figure 6.4) which indicates that each individual instance of an ID coda is closer to that coda type's centroid, while individual instances of non-ID codas can be much further from their coda type centroid. ID coda types also overlap significantly less with other coda types (regardless of their categorization as ID or non-ID types, hypotheses A and B) than do non-ID coda types (Figure 6.5, Figure 6.6, Table 6.1), which means that ID coda types are less likely to be confounded with other coda types than are non-ID coda types. Altogether this suggests that ID coda types have evolved to be easily identifiable from one another, and other coda types. Our results are consistent with sperm whales using ID coda types, which are more stereotyped and discrete than non-ID coda types, to recognize other individuals as cultural in-group members or out-group members and then to associate with, or avoid them, accordingly.

Sympatric vocal clans have slightly less overlapping ID coda types than geographically isolated vocal clans (i.e. lower median - hypothesis D, Figure 6.5-6). However, the lack of statistical significance in this trend suggests that there are no strong, active, pressures for increased discreteness between ID coda types made by vocal clans that interact with each other on a more regular basis. As it is unlikely that sperm whale vocal clans from the ETP, EC and MED still interact with each other today (there have been no sightings of sperm whales from the EC, MED and ETP outside of their geographical regions despite long-term research effort in each area and as differences in mtDNA between oceans suggest very low rates of migration by females, Alexander et al. 2016), we have to assume that ID coda type discreteness is maintained in isolation. In this case, ID coda types might be artifacts of a time during which vocal clans that are now geographically isolated occurred in sympatry. As vocal clans are thought to have first originated via the biased social learning of codas (Cantor et al. 2015), and as vocalizations that are more important for group cohesion are expected to be more stable over time (Riesch et al. 2006; Rekdahl et al. 2013), differences in ID coda types from this sympatric period (consistent with the hypothesis of several Pacific to Atlantic colonization events by sperm whales; Morin et al. 2018) might have been maintained in geographic isolation. Although the rate of change of ID codas over decadal timespans was not significantly different from that of non-ID codas (Hersh 2021, Chapter 5), small enough rates of change could have maintained ID coda type discreteness in geographic isolation over much larger timespans. Alternatively, ID coda types could have changed in ways that maintain inter-vocal clan differences, similar to patterns of change in certain sympatric killer whale call types (Deecke et al. 2000), although this might be unlikely to occur across isolated regions.

ID coda types might be more or less arbitrary signals (in their tempo, i.e. 5R versus 1+1+4 versus 4+1) - just like many human symbolic markers (Barth 1969; Axelrod et al. 2004; Efferson et al. 2008; Ihara 2011) - as long as they are discrete enough from other ID coda types to not be confounded. In this case, discreteness is a threshold, and once this threshold is met there are no need for additional differences in structure, even in sympatry. Altogether, the maintenance of vocal clan's ID coda discreteness might be akin to how humans are still able to readily recognize and label ethnic groups from accent/languages (Rakić et al. 2011; Cohen 2012) even if accents and languages actively evolve via cultural drift and social/ecological drivers over time (Lupyan & Dale 2016; Harrington et al. 2019). As long as a certain level of discreteness is maintained between signals, so are the cultural group boundaries.

6.5.1 Are identity codas symbolic markers?

While we are a very long way from understanding what ID codas mean to the sperm whales themselves, and while we would require detailed playback experiments to definitively understand the functional and contextual use of these coda types in social recognition (with whales showing drastically different responses to non ID coda types and ID coda types from their own, and different, vocal clans), the evidence presented here is consistent with the patterns of variation expected if ID coda types were functioning as symbolic markers of vocal clan membership (Rendell & Whitehead 2003b; Cantor & Whitehead 2013; Gero et al. 2016a; Hersh et al. in review). ID coda types are some of the most prevalent coda types (often making up around 50% of sperm whale acoustic repertoires) (Hersh et al. 2021; Vachon et al. 2022), almost exclusively made by members of a same vocal clan (Hersh et al. 2021; Vachon et al. 2022; Hersh et al. in review), more stable across geographical scales than non-ID codas (Hersh et al. in review), and, as this work shows, overlap significantly less with other coda types and are significantly more accurately produced. Therefore, ID codas are redundant, unique, stereotyped and discrete, as would be expected of a symbolic marker (Axelrod et al. 2004; Cohen 2012; Wiley 2013; Wiley 2017). ID codas further meet Efferson's (2008) predictions for symbolic markers in that they predict behaviours (with different vocal clans displaying different movement patterns -Whitehead and Rendell 2004; Whitehead et al. 2008a, diving synchrony - Cantor & Whitehead 2015, distributions -Eguiguren et al. 2019; Vachon et al. 2022, and social organization -Cantor and Whitehead 2015), can change over time (Hersh 2021, Chapter 5) and have the potential to facilitate cooperation between social units of a same vocal clans (with social units only forming groups with other social units from a same vocal clan to forage and socialize - Gero et al. 2016b). If ID codas had unique, vocal clan-specific, uses and/or meanings to the whales, rather than being markers of vocal clan membership, we wouldn't expect their structure to be as drastically different from that of non ID coda types (as we expect non ID coda types to be means of social communication, Whitehead & Weilgart 1991) or pressures to reduce overlap with other vocal clans' ID coda types. The evidence presented here therefore complements the study of Hersh et al. (in review) which shows that between-clan repertoire similarity in terms of ID coda usage decreases as clan spatial overlap increases (whereas between-clan repertoire similarity in terms of non-ID coda usage does not vary with spatial overlap) and advances ID codas types from identity cues (e.g., Rendell & Whitehead 2003b; Gero et al. 2016b; Amorim et al. 2020; Huijser et al. 2020) to potential identity signals.

One hypothesis for the origin of vocal clans is biased transmission (Cantor et al. 2015) in response to intraspecific competition (Vachon 2022, Chapter 2), and this account would predict symbolic markers to have evolved alongside vocal clans to maintain segregation (Efferson et al. 2008). This would be especially important in early stages of vocal clan emergence, but also if vocal clans are vessels of cultural group selection as suggested by Vachon (2022, Chapter 2), and consistent with low mitochondrial DNA diversity (Whitehead 2005; Whitehead et al. 2017). Based on current knowledge, as well as what we know currently know of ID codas usage (Rendell & Whitehead 2003b; Gero et al. 2016b; Hersh et al. 2021; Vachon et al. 2022; Hersh et al. in review), and ID codas structure (presented here), we suggest that ID codas might have filled this role in sperm whales.

6.5.2 Caveats and ways forward

This study is limited in its scope, sample size, and by our statistical inability to compare codas across click lengths. Including more vocal clans in this analysis, as well as more regions with sympatric vocal clans, would allow for further understanding of the interactions between coda type overlap in multidimensional space and geographical overlap of vocal clans. Larger sample sizes would also allow for a more powerful comparison across a larger set of click lengths. While our coda dataset is large (29,614 individual codas), condensing it into click-length specific coda types led to small sample sizes, especially when comparing exclusively ID coda types (i.e., hypotheses C and D). Including more vocal clans would solve this issue as it would likely introduce more coda types into the analysis. An ability to compare coda type structure across click lengths would also yield further insight into these questions as sperm whales need to distinguish coda types regardless of their click lengths. ID codas within a vocal clan also often seem to follow "themes" (e.g., additional click at the end, "palindrome" shape, short length, regularly spaced clicks) which we cannot incorporate in this analysis due to their often different click lengths (Rendell & Whitehead 2003b; Hersh et al. 2021). Advances in machine learning and computational methods might be avenues to solve this issue (see Andreas et al 2022).

We had initially planned to include coda type pair centroid distance (the Mahalanobis distance between the centroids of two coda types' ICI's in multidimensional space (Mahalanobis 1936)) as an additional metric to compare coda type structure. Distances were extracted using package "distances" in R – version 4.1.2 (Savje 2019) for 5-click coda types and did appear to vary across coda type pair categories (Figure S6.7, Figure S6.8), but a lack of statistical power prevented us from meaningfully testing the significance of such differences. We recommend that future work with larger coda type sample sizes include Mahalanobis pairwise distance to further compare the multidimensional distributions of ID and non-ID coda types.

6.6 CONCLUSION

Our results are consistent with the hypothesis that ID coda types function as symbolic markers of vocal clan identity and have an important role in mediating/facilitating social interactions within the sperm whales' complex social structure. Not only are ID codas disproportionately made by members of a same vocal clan, but their structure in multidimensional space is also significantly different from that of other coda types: with smaller overall variation around coda type centroids (stereotypy) and less overlap with other coda types (discreteness). While it will be challenging to know exactly what ID codas mean to the whales themselves, our results offer significant support that symbolic markers might be used in non-human animals to facilitate complex, culturally mediated interactions such as social unit to social unit cooperation. Therefore, vocal clans are not only a level of social structure (Rendell & Whitehead 2003b; Gero et al. 2016b) and the primary vessel through which cultural differences exists (e.g., Whitehead & Rendell 2004; Cantor & Whitehead 2015; Eguiguren et al. 2019; Vachon et al. 2022, Chapter 4), but also, based on the structure and use of ID coda types, recognizable cultural identity for the whales themselves. As such, vocal clans meet all of Barth's (1969) criteria for ethnic groups.

6.7 ACKNOWLEDGEMENTS

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CHAPTER 7 –

Discussion

> "You can't see what you don't understand. But what you think you already understand, you'll fail to notice"
> – Richard Powers, *The Overstory*

Cultural inheritance is a second inheritance system (Whiten 2005) which complements genetic inheritance and interacts with the environment to shape species evolution, behaviour, and social structure (Richerson & Boyd 2005; Mesoudi 2017; Whiten 2019). However, although culture and social learning have been shown to be widespread in the animal kingdom (Whiten 2017; Allen 2019) and are often assumed as lead determinants for humans' behaviour and evolution (e.g., Henrich & McElreath 2003; Richerson & Boyd 2005; Henrich 2016), they have yet to be incorporated into mainstream biology. Especially as one moves further from *Homo sapiens sapiens* to the great apes, primates and other, more distant taxa (Boesch 2003; Laland & Janik 2006). For example, the "method of exclusion" is often used for non-human species, where behaviours are either categorized as resulting from geographical variation, genetics, or culture (Laland & Hoppit 2003), with little or no consideration for the interconnectedness between them (e.g, Whiten et al. 1999; Krützen et al. 2005). This approach is increasingly criticized (Schuppli & van Schaik 2019) as it sets different standard for human and non-human species' and fails to capture the intricacies and interconnectedness of social structure, culture, genes, evolution, behaviour, and the environment.

My thesis positions itself within the broader framework of cultural inheritance and makes a case for its importance and ramifications by demonstrating the over-reaching implications of culture on the social structure, behaviour, evolution, and conservation of a non-human, non-primate, species: the sperm whale (*Physeter macrocephalus*).

7.1 CULTURAL INHERITANCE IN THE SPERM WHALE (FINDINGS FROM THESIS)

The sperm whale has long been recognized as a cultural species (Rendell and Whitehead 2001). The discovery of vocal clans in the Eastern Tropical Pacific (Rendell & Whitehead 2003b), as well as their distinctive movement patterns (Whitehead & Rendell

2004, Whitehead et al. 2008a), reproductive and feeding success (Whitehead & Rendell 2004, Marcoux et al. 2007a), diving synchrony (Cantor & Whitehead 2015), social organization (Cantor & Whitehead 2015), and distribution (Eguiguren et al. 2019) regardless of genetic variation (Rendell et al. 2012; Konrad et al. 2018b), have highlighted the contribution of culture to Eastern tropical Pacific sperm whale ecology. However, the relatively new discovery of a second vocal clan in Dominica (EC2; Gero et al. 2016b) prevented a direct comparison with the Eastern Caribbean until recently. In fact, it was long assumed that vocal clans were a unique feature of the Pacific sperm whale population (Whitehead et al. 2012; Gero et al. 2016a). Now that vocal clans have been reported worldwide (Eastern Tropical Pacific -Rendell and Whitehead 2003, Dominica - Gero et al. 2016b; Chapter 3, Japan - Amano et al. 2014, Brazil - Amorim et al. 2020, and Mauritius - Huijser et al. 2019), and are accepted as the norm rather than the exception, it is important to further assess the contribution of cultural inheritance on a population of sperm whale which shows stark differences with that of the Eastern Tropical Pacific (Whitehead et al. 2012), but for which we still have long term data (e.g., Gero et al. 2009; Gero et al. 2013; Gero et al. 2014), the Eastern Caribbean population.

My thesis therefore extends and contrasts findings from the Eastern Tropical Pacific to the Eastern Caribbean and shows that while cultural inheritance might have different repercussion on these two geographically isolated sperm whale populations, it is an important determinant of their ecology and evolution. Below, I expand on my findings regarding the over-reaching impact of cultural inheritance on Eastern Caribbean sperm whales' social structure, behaviour, evolution and conservation.

7.1.1 Social structure

Extending our research area to cover most of the Lesser Antilles (from St. Kitts & Nevis to Grenada) rather than only the island of Dominica, allowed for a much clearer picture of Eastern Caribbean sperm whale social structure. While it was previously assumed that social units encountered in Dominica ranged throughout the Lesser Antilles, as sperm whale movement in the Eastern Tropical Pacific and Mediterranean is in the order of thousands of kilometers (Whitehead & Rendell 2004; Whitehead et al. 2008a; Rendell & Frantzis 2016) and the Lesser Antilles are less than 700km across, I show that

EC1 and EC2 individuals tend to stay within the vicinity of the same one or two islands with different social units predominantly encountered around different islands (Chapter 3). This realization came as, during our 2019 and 2020 surveys, I documented the presence of 145 new individuals and 23 new groups/social unit which had never been documented in over 15 years of research in Dominica. In fact, of the 26 EC1 DSWP social units (Gero et al. 2014; Chapter 3), only one (Unit J) was encountered beyond Dominica and Guadeloupe (Chapter 3). Therefore, much more sperm whales use the Lesser Antilles than we previously assumed, with an estimated adult population of 414 sperm whales (51 groups/social units) in the Lesser Antilles, more than double previous estimates based on Dominica-centric data (Gero et al. 2007; Whitehead & Gero 2015) (Chapter 5).

At the vocal clan level, I show that the EC2 vocal clan, which is "rare" in Dominica (only 3% of DSWP encounters; Gero et al. 2016b; Chapter 3) is almost as prevalent as the EC1 vocal clan in the Lesser Antilles (population estimates range of 205.1 - 218.8 for EC1 and 145.7 - 190.7 for EC2) (Chapter 5). I document, for the very first time, a third vocal clan, EC3, which was encountered in St. Lucia and Martinique and makes long regular codas (identity codas: 9R, 10R, 11R). This vocal clan was encountered six times over two survey years and while their acoustic repertoire is unique enough the be significantly different from that of other Eastern Caribbean vocal clans (Chapter 3) and that of vocal clans in the Eastern Tropical Pacific and Mediterranean (Chapter 6), we are cautious in its classification as a vocal clan as it is comprised of a single social unit (Unit 12: 10 adults and 2 calves) and has been seen, in the same area, on the same day, as an EC2 social, Unit Y. This is extremely rare between EC1 and EC2 (0.004% of DSWP photo-identification encounters and none of the survey photo-identification encounters) and social interactions are often, if not always, restricted to members of a same vocal clan (Gero et al. 2016b). In my 6th chapter, I propose that identity codas (coda type used consistently by one vocal clan, and rarely, if ever, by others; Hersh et al. 2021) are most likely used by sperm whales to maintain this social segregation. I proposed that identity codas, as they are more discrete from other codas (identity and non-identity) and produced with higher stereotypy, could be used by sperm whales as symbolic markers of vocal clan identity and, therefore, are important cues of sperm whale social structure.

Finally, spending time and getting to know sperm whales beyond Dominica during our 2019 and 2020 surveys soon made it apparent that the social structure, and movement of sperm whales in the Eastern Caribbean, is drastically different from that of sperm whales in the Eastern Tropical Pacific. While it was previously acknowledged that the two populations had intrinsic differences (Whitehead et al. 2012), I shed further light on their variations and suggest an order of magnitude difference in the social structure and movement of Eastern Tropical Pacific and Eastern Caribbean vocal clans (Chapter 3). This suggest that sperm whales can be successful both as ocean nomads or island-specialists and that results from different geographical areas should not be extrapolated. In this case, I hypothesize that sperm whales from different geographical areas culturally learned to take advantage of different environmental conditions, prey type availability and/or that vocal clans show cultural differences in movement patterns (e.g., Whitehead & Rendell 2004), which resulted in different social structure and distribution patterns.

Altogether, cultural inheritance shaped Eastern Caribbean sperm whales' social structure by segregating their population into somewhat sympatric, but socially isolated, cultural groups (EC1, EC2, EC3) which can vary in their social structure, numbers, and movement when compared to each other and other geographically isolated populations.

7.1.2 Behaviour

The social structure of sperm whale societies lends itself well to processes of social learning with mothers, aunts, and grandmothers as repositories of knowledge for stable social units and vocal clans (Rendell et al. 2019). Akin to other matrilineal species such as elephants (*Loxodonta africana*) (McComb et al. 2001; McComb et al. 2011) and killer whales (*Orcinus orca*) (Nattrass et al. 2019). However, as social interactions are predominantly restricted to vocal clan members (Cantor & Whitehead 2013; Cantor et al. 2015; Gero et al. 2016b), social learning opportunities and social knowledge is also restrained by these cultural boundaries. As such, vocal clan-specific behaviours can emerge and be maintained at the vocal clan level by processes of homophily and conformism (Henrich & Boyd 1998; Centola et al. 2007; Riesch et al. 2012; Cantor et al. 2015)

I show that this is the case in the Eastern Caribbean, where vocal clan EC1 and EC2 have drastically different, fine-scale, distributions around the Lesser Antilles islands with EC1 whales predominantly in the waters leeward of Dominica, Guadeloupe and St. Vincent & the Grenadines and EC2 whales predominantly in the waters leeward of Martinique and St. Lucia (Chapter 3). I show that these differences in distribution are most likely the result of site/island fidelity rather than habitat specialization (where sperm whale would learn to use different environmental parameters) as environmental variables do not vary significantly between EC1 and EC2 islands and habitat models that use site-specific characteristics have much higher predictive accuracy than ones using environmental parameters (Chapter 4). I relate these findings to Warner's (1988) study on blue head wrasse coral heads and highlight how, in this case, cultural group membership can drastically alter behaviour in the absence of genetic or environmental variation.

Altogether, I show that cultural inheritance shaped Eastern Caribbean sperm whales' behaviour by restricting the range of individuals, within cultural groups, to specific islands in the absence of significant environmental variation.

7.1.3 Evolution

I start my thesis by introducing the *intraspecific group competition hypothesis*, a new framework that highlights the importance of intraspecific competition and cultural group selection as drivers of advanced cognition and large brain size in certain primates and cetacean species (Chapter 2). While this chapter takes a broader approach to the question of sperm whales' (and four other cultural species') evolution, it directly relates and apply to my findings on the social structure and behaviour of Eastern Caribbean sperm whales.

I believe that findings from my thesis support Eastern Caribbean vocal clans as potential units of cultural group selection. EC1 and EC2 are socially and geographically (on a fine scale) segregated (Gero et al. 2016b; Chapter 3) in the absence of physical barriers, they can be easily identified with identity codas as potential symbolic markers (Chapter 6), and are most likely facing varying threats as a result of their different distributions and behaviours (Chapter 5). As such, culture is not only responsible for Eastern Caribbean sperm whale success, but also actively shaping their evolution. While very little is known about the radiation of vocal clans (i.e., Cantor et al. 2015) as these processes most likely act over long timescales, I believe that further insight on the cultural barriers between cultural groups (i.e., identity codas; Chapter 6) as well as further observation of vocal clan interactions (e.g., EC2 and EC3; Chapter 3) will allow for a greater understanding of the culturally mediated evolution of the sperm whale as a species.

Altogether, cultural inheritance shaped sperm whales' evolution as a foundation for intraspecific competition and cultural group selection between vocal clans, and a means (i.e social learning) for sperm whales to adapt and be successful under different environmental conditions,

7.1.4 Conservation

The importance of acknowledging culture in conservation and management is increasingly recognized (Whitehead 2010; Brakes et al. 2019; Brakes et al. 2021), with a recent push to incorporate culturally significant units (Whitehead et al. 2004; Ryan 2006), rather than only genetically or geographically distinct populations and sub-populations, into mainstream animal conservation. Results from my thesis further highlight the necessity of such a shift. I demonstrate that considering vocal clans as independent, culturally significant, units not only improve habitat models' predictive accuracy (with more informative EC1 and EC2 models than presence/absence models; Chapter 4), but is also informative in population estimate analyses (Chapter 5).

Eastern Caribbean sperm whales organize their societies at much smaller scale than Eastern Tropical Pacific sperm whales (Chapter 3) and have distributions which cannot be attributed to environmental variable gradients, but instead, are driven by cultural processes operating at the vocal clan level (Chapter 4). Consequently, not only can't results be extrapolated across geographical regions (e.g., Eastern Tropical Pacific and Eastern Caribbean), but also across vocal clans (e.g., EC1 and EC2). In fact, the combination of Eastern Caribbean sperm whales' small ranges (Chapter 3) and site/island fidelity (chapter 4) might make them particularly vulnerable to anthropogenic threats, as they might not be willing, or lack the knowledge, to find refuge outside of their culturally learned distribution. This is the case in bighorn sheep (*Ovis canadensis*) and moose (*Alces alces*) for which migratory routes are culturally learned and translocation result in a loss of such knowledge (Jesmer et al. 2018). Vocal clan behaviours might also be more rigid to change if it is rooted in conformism. For instance, Southern Resident killer whales, which have a similar social structure to that of sperm whales, are currently listed as *Endangered* (COSEWIC 2008) due to their reliance on chinook salmon (*Oncorhynchus tshawytscha*) (Vélez-Espino et al. 2015), regardless of the availability of other prey types in the area. Conversely, local conservation actions (e.g., better waste management, whale watching regulations, shipping lane restrictions) have the potential to have important positive repercussions on local social units and sperm whales' predisposition for social learning might allow them extra plasticity in the face of change (Laland et al. 2015).

While some threats are likely to impact sperm whales regardless of their vocal clan (e.g, climate change, fisheries collapse, underwater noise), other, more localized threats (such as entanglement, shipping routes, tourism, whaling, pollution) plausibly vary from one island to the next. As such, EC1 and EC2 whales most likely experience different anthropogenic stressors as they are distributed around different islands. Vocal clans might also respond differently to threats, as was documented in the Eastern Tropical Pacific where the Plus-One and Regular vocal clans experienced different and variable feeding success in response to El Niño/Southern Oscillation (ENSO) (Whitehead & Rendell 2004).

Finally, it is also important to note that culture and conservation are interconnected beyond the influence of culture on a species behaviour, as a specie's conservation status, or the level of anthropogenic stressors it faces, might also impact its culture. This is something I discuss in my second chapter as it was documented in chimpanzees (*Pan troglodytes*), with communities that face higher human impacts displaying less behavioural diversity (Kühl et al. 2019).

Altogether, cultural inheritance affects Eastern Caribbean sperm whales' conservation and management as their population is subdivided into culturally distinct, socially segregated, vocal clans which might be subject to different threats and respond differently to change. As such, the work from my thesis highlights the importance of recognizing sperm whale vocal clans as evolutionarily significant units.

7.2 BEYOND THE SPERM WHALE

My thesis therefore extends findings from the Eastern Tropical Pacific (e.g., Rendell & Whitehead 2003b; Whitehead & Rendell 2004; Whitehead et al. 2008a; Eguiguren et al. 2019) and knowledge from Dominica (e.g., Gero et al. 2007; Gero et al. 2014; Gero et al. 2016b) to further show the ramifications of cultural inheritance on sperm whale ecology. I introduce a new evolutionary framework (the intraspecific group competition hypothesis) which highlights the contribution of culture, and cultural group selection, in achieving large brains and cognition (Chapter 2), I describe and quantify sperm whale segregation in the absence of environmental or genetic barriers (chapter 3,4,6), I show how culture can create atypical behaviours across (Chapter 3) and within (Chapter4) populations and bring attention to the importance of incorporating culture in mainstream biology as well as conservation and management (Chapter 5). Altogether, I show how cultural inheritance greatly contributes to the social structure, behaviour and evolution of a non-human species: the sperm whale.

However, while most of my chapters focus on the sperm whale (and even more specifically, Eastern Caribbean sperm whales), I believe that the general conclusions from my thesis can be extrapolated to other species for which we have evidence of social learning and culture. While cultural inheritance might influence the social structure, behaviour, evolution, and conservation and management of other species in vastly different ways, I make the case that it should be incorporated into mainstream biology as it has the potential to significantly alter selection with, or without, genetic and/or environmental variation. Other cetacean species (i.e. killer whales – *Orcinus orca*, bottlenose dolphins-*Tursiops truncatus*, humpback whales - *Megaptera novaeangliae*, belugas - *Delphinapterus leucas*; reviewed in Whitehead & Rendell 2015) as well as primates (i.e. chimpanzees – *Pan troglodytes*; Whiten et al. 1999, orangutans – *Pongo pygmaeus*; van Schaik et al. 2003, capuchin monkeys –*Cebus sp.*; Perry 2011, baboons – *Papio Anubis*; Sapolsky & Share 2004) are obvious candidates for such an approach; but so are birds (songbirds, corvids; reviewed in Aplin 2019), ungulates (Jesmer et al. 2018), elephants (Fishlock et al. 2016) etc. As we shift away from an anthropocentric view of the world and open our eyes (and our minds) to the ways in which other species use social learning and culture to succeed, and the ways in which social learning and culture in turn impacts their ecology and evolution, our appreciation of cultural inheritance as an evolutionary force will increase, and so will our ability to understand and protect the natural world.

I hope that my work inspires others to look beyond — beyond what is expected, assumed, or known about non-human species and inspires you to understand the secrets, beauty, complexity, and intelligence of others whether on land, in the sky, or at sea. I hope that my work inspires change from a human-centric perception of nature to a more inclusive world — as it has changed me.

BIBLIOGRAPHY

Abrams D, Ando K, Hinkle S. 1998. Psychological attachment to the group: cross-cultural differences in organizational identification and subjective norms as predictors of workers' turnover intentions. Pers Soc Psychol Bull. 24(10):1027–1039. doi:10.1177/01461672982410001.

Alem S, Perry CJ, Zhu X, Loukola OJ, Ingraham T, Søvik E, Chittka L. 2016. Associative mechanisms allow for social learning and cultural transmission of string pulling in an insect. PLOS Biol. 14(10). doi: 10.1371/journal.pbio.1002564.

Alexander RD. 1989. Evolution of the human psyche. In: Stringer C, Mellars P, editors. The human revolution. University of Edinburgh Press. p. 455–513.

Alexander RD. 1990. How did humans evolve?: reflections on the uniquely unique species. Arbor A, editor. Museum of Zoology, University of Michigan.

Alexander A, Steel D, Slikas B, Hoekzema K, Carraher C, Parks M, Cronn R, Baker CS. 2013. Low diversity in the mitogenome of sperm whales revealed by next-generation sequencing. GBE. 5(1):113–129. doi:10.1093/gbe/evs126.

Alexander A, Steel D, Hoekzema K, Mesnick SL, Engelhaupt D, Kerr I, Payne R, Baker CS. 2016. What influences the worldwide genetic structure of sperm whales (*Physeter macrocephalus*)? Mol Ecol. 25(12):2754–2772. doi:10.1111/mec.13638.

Allen JA. 2019. Community through culture: from insects to whales. Bioessays. 41(11):1900060. doi:10.1002/bies.201900060.

Amano M, Kourogi A, Aoki K, Yoshioka M, Mori K. 2014. Differences in sperm whale codas between two waters off Japan: possible geographic separation of vocal clans. J Mammal. 95(1):169–175. doi:10.1644/13-MAMM-A-172.

Amorim TOS, Rendell L, Di Tullio J, Secchi ER, Castro FR, Andriolo A. 2020. Coda repertoire and vocal clans of sperm whales in the western Atlantic Ocean. Deep Sea Res Part I Oceanogr Res Pap. 160:103254. doi:10.1016/j.dsr.2020.103254.

Anderson JR. 2018. Chimpanzees and death. Philos Trans R Soc Lond B Biol Sci. 373(1754):20170257. doi:10.1098/rstb.2017.0257.

Andreas J, Beguš G, Bronstein MM, Diamant R, Delaney D, Gero S, Goldwasser S, Gruber DF, de Haas S, Malkin P, et al. 2022. Towards understanding the communication in sperm whales. iScience.:104393. doi:10.1016/j.isci.2022.104393.

Ansmann IC, Parra GJ, Chilvers BL, Lanyon JM. 2012. Dolphins restructure social system after reduction of commercial fisheries. Anim Behav. 84(3):575–581. doi:10.1016/j.anbehav.2012.06.009.

Antunes R. 2009. Variation in sperm whale (*Physeter macrocephalus*) coda vocalizations and social structure in the North Atlantic Ocean [Thesis]. University of St Andrews.

Aoki K, Amano M, Yoshioka M, Mori K, Tokuda D, Miyazaki N. 2007. Diel diving behavior of sperm whales off Japan. Mar Ecol Prog Ser. 349:277–287. doi:10.3354/meps07068.

Aplin LM. 2019. Culture and cultural evolution in birds: a review of the evidence. Anim Behav. 147:179–187. doi:10.1016/j.anbehav.2018.05.001.

Arnbom T. 1987a. Individual identification of sperm whales. Annual Report. International Whaling Commission.

Arnbom T, Papastavrou V, Weilgart LS, Whitehead H. 1987b. Sperm whales react to an attack by killer whales. J Mammal. 68(2):450–453. doi:10.2307/1381497.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor R, Fiore AD, Dunbar RIM, Henzi SP, et al. 2008. Fission-fusion dynamics: new research frameworks. Curr Anthropol. 49(4):627–654. doi:10.1086/586708.

Axelrod R, Hammond RA, Grafen A. 2004. Altruism via kin-selection strategies that rely on arbitrary tags with which they coevolve. Evolution. 58(8):1833–1838.

Baker JL, Rotimi CN, Shriner D. 2017. Human ancestry correlates with language and reveals that race is not an objective genomic classifier. Sci Rep. 7:1–10. doi: 10.1038/s41598-017-01837-7.

Baker I, O'Brien J, McHugh K, Ingram SN, Berrow S. 2018. Bottlenose dolphin (*Tursiops truncatus*) social structure in the Shannon Estuary, Ireland, is distinguished by age- and area-related associations. Mar Mamm Sci. 34(2):458–487. doi: 10.1111/mms.12462.

Baldwin JM. 1896. A new factor in evolution. Am Nat. 30(354):441–451.

Barkow JH. 2001. Culture and hyperculture: Why can’t a cetacean be more like a (hu)man? Behav Brain Sci. 24(2):324–325. doi:10.1017/S0140525X01223966.

Barrett-Lennard LG, Ford JKB, Heise KA. 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. Anim Behav. 51(3):553–565. doi:10.1006/anbe.1996.0059.

Barth F. 1969. Ethnic groups and boundaries. Waveland Press.

Bartoń K. 2013. MuMIn: ,ulti-model inference. R package version 1.42.1. https://CRAN.R-project.org/package= Mu MIn.

Bates BC. 1970. Territorial behavior in primates: a review of recent field studies. Primates. 11(3):271–284. doi:10.1007/BF01793893.

Baulch S, Perry C. 2014. Evaluating the impacts of marine debris on cetaceans. Mar Pollut Bull. 80(1):210–221. doi:10.1016/j.marpolbul.2013.12.050.

Bearzi G, Fortuna CM, Reeves RR. 2009. Ecology and conservation of common bottlenose dolphins *Tursiops truncatus* in the Mediterranean Sea. Mamm Rev. 39(2):92–123. doi:10.1111/j.1365-2907.2008.00133.x.

Beck S, Foote AD, Kötter S, Harries O, Mandleberg L, Stevick PT, Whooley P, Durban JW. 2014. Using opportunistic photo-identifications to detect a population decline of killer whales (*Orcinus orca*) in British and Irish waters. J Mar Biol Assoc U K. 94(6):1327–1333. doi:10.1017/S0025315413001124.

Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor R, Heithaus M, Watson-Capps J, Flaherty C, Krützen M. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conserv Biol. 20(6):1791–1798.

Beltman JB, Haccou P, Cate CT. 2004. Learning and colonization of new niches: a first step toward speciation. Evolution. 58(1):35–46.

Bernhard H, Fischbacher U, Fehr E. 2006. Parochial altruism in humans. Nature. 442(7105):912–5. doi:10.1038/nature04981.

Bickart KC, Wright CI, Dautoff RJ, Dickerson BC, Barrett LF. 2011. Amygdala volume and social network size in humans. Nat Neurosci. 14(2):163–164. doi:10.1038/nn.2724.

Blount D, Gero S, Van Oast J, Parham J, Kingen C, Scheiner B, Stere T, Fisher M, Minton G, Khan C, Dulau V, Thompson J, Moskvyak O, Berger-Wolf T, Stewart CV, Holmberg J, Levenson JJ. 2022. Flukebook: an open source AI platform for cetacean photo identification. Mamm Biol.

Boesch C, Boesch-Achermann H. 2000. The chimpanzees of the Taï forest: behavioural ecology and evolution. Oxford University Press.

Boesch C. 2002. Cooperative hunting roles among Taï chimpanzees. Hum Nat. 13(1):27–46. doi:10.1007/s12110-002-1013-6.

Boesch C. 2003. Is culture a golden barrier between human and chimpanzee? Evol Anthropol. 12(2):82–91. doi:10.1002/evan.10106.

Boesch C, Kalan AK, Mundry R, Arandjelovic M, Pika S, Dieguez P, Ayimisin EA, Barciela A, Coupland C, Egbe VE, et al. 2020. Chimpanzee ethnography reveals unexpected cultural diversity. Nat Hum Behav. 4(9):910–916. doi:10.1038/s41562-020-0890-1.

Bolnick DI. 2004. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. Evolution. 58(3):608–618.

Bouckaert R, Lemey P, Dunn M, Greenhill SJ, Alekseyenko AV, Drummond AJ, Gray RD, Suchard MA, Atkinson QD. 2012. Mapping the origins and expansion of the Indo-European language family. Science. 337(6097):957–960.

Bowles S. 2006. Group competition, reproductive leveling, and the evolution of human altruism. Science. 314(5805):1569–1572.

Bowles S. 2009. Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? Science. 324(5932):1293–1298.

Bowles S. 2012. Warriors, levelers, and the role of conflict in human social evolution. Science. 336(6083):876–879.

Boyce MS, Johnson CJ, Merrill EH, Nielsen SE, Solberg EJ, van Moorter B. 2016. Can habitat selection predict abundance? J Anim Ecol. 85(1):11–20. doi:10.1111/1365-2656.12359.

Boyd R, Richerson PJ. 1985. Culture and the evolutionary process. University of Chicago Press.

Boyd R, Richerson PJ. 1987. The evolution of ethnic markers. Cult Anthropol. 2(1):65–79. doi:10.1525/can.1987.2.1.02a00070.

Boyd R, Richerson PJ. 2009. Culture and the evolution of human cooperation. Philos Trans R Soc Biol Sci. 364(1533):3281–3288.

Boyd R, Richerson PJ. 2010. Transmission coupling mechanisms: cultural group selection. Philos Trans R Soc Biol Sci. 365(1559):3787–3795.

Boyd R, Richerson PJ, Henrich J. 2011. The cultural niche: why social learning is essential for human adaptation. PNAS. 108:10918–10925.

Brakes P, Dall SRX, Aplin LM, Bearhop S, Carroll EL, Ciucci P, Fishlock V, Ford JKB, Garland EC, Keith SA, et al. 2019. Animal cultures matter for conservation. Science. 363(6431):1032–1034. doi:10.1126/science.aaw3557.

Brakes P, Carroll EL, Dall SRX, Keith SA, McGregor PK, Mesnick SL, Noad MJ, Rendell L, Robbins MM, Rutz C, et al. 2021. A deepening understanding of animal culture suggests lessons for conservation. Proc Royal Soc B. 288(1949):20202718. doi:10.1098/rspb.2020.2718.

Brewer MB. 1979. In-group bias in the minimal intergroup situation: A cognitive-motivational analysis. Psychol Bull. 86(2):307–324. doi:10.1037/0033-2909.86.2.307.

Brewer MB, Brown RJ. 1998. Intergroup relations. In: The handbook of social psychology. NY: McGraw-Hill. p. 554–594.

Bromham L, Phillips MJ, Penny D. 1999. Growing up with dinosaurs: molecular dates and the mammalian radiation. Trends Ecol Evol. 14(3):113–118. doi:10.1016/S0169-5347(98)01507-9.

Brown S, Savage PE, Ko AM-S, Stoneking M, Ko Y-C, Loo J-H, Trejaut JA. 2014. Correlations in the population structure of music, genes and language. Proc Biol Sci. 281(1774):20132072. doi:10.1098/rspb.2013.2072.

Bruck JN. 2013. Decades-long social memory in bottlenose dolphins. Proc Biol Sci. 280(1768):1–6.

Burkart JM, Allon O, Amici F, Fichtel C, Finkenwirth C, Heschl A, Huber J, Isler K, Kosonen ZK, Martins E, et al. 2014. The evolutionary origin of human hyper-cooperation. Nat Commun. 5:4747. doi: 10.1038/ncomms5747.

Byrne RW, Whiten A. 1989. Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans. Oxford University Press.

Byrne RW, Corp N. 2004. Neocortex size predicts deception rate in primates. Proc Biol Sci. 271(1549):1693–1699.

Byrne RW, Bates LA. 2007. Sociality, evolution and cognition. Curr Biol. 17(16):R714–R723. doi:10.1016/j.cub.2007.05.069.

Call J, Tomasello M. 2008. Does the chimpanzee have a theory of mind? 30 years later. Trends in Cogn Sci. 12(5):187–192. doi:10.1016/j.tics.2008.02.010.

Cañadas A, Sagarminaga R, De Stephanis R, Urquiola E, Hammond PS. 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conserv: Mar Freshw Ecosyst. 15(5):495–521. doi:10.1002/aqc.689.

Cantarero L, Espeitx E, Gil Lacruz M, Martín P. 2013. Human food preferences and cultural identity: the case of Aragón (Spain). Int J Psychol. 48(5):881–890. doi:10.1080/00207594.2012.692792.

Cantor M, Whitehead H. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philos Trans R Soc Lond B Biol Sci. 368(1618):20120340. doi:10.1098/rstb.2012.0340.

Cantor M, Whitehead H. 2015. How does social behavior differ among sperm whale clans? Mar Mam Sci. 31(4):1275–1290. doi:10.1111/mms.12218.

Cantor M, Shoemaker LG, Cabral RB, Flores CO, Varga M, Whitehead H. 2015. Multilevel animal societies can emerge from cultural transmission. Nat Commun. 6:8091. doi: 10.1038/ncomms9091.

Cantor M, Whitehead H, Gero S, Rendell L. 2016. Cultural turnover among Galápagos sperm whales. R Soc Open Sci. 3(10):160615. doi:10.1098/rsos.160615.

Centola D, González-Avella JC, Eguíluz VM, San Miguel M. 2007. Homophily, cultural drift, and the co-evolution of cultural groups. J Conflict Resolut. 51(6):905–929.

Chilvers BL, Corkeron PJ. 2001. Trawling and bottlenose dolphins' social structure. Proc Biol Sci. 268(1479):1901–1905.

Choi J-K, Bowles S. 2007. The coevolution of parochial altruism and war. Science. 318(5850):636–640.

Christal J, Whitehead H, Lettevall E. 1998. Sperm whale social units: variation and change. Can J Zool. 76(8):1431–1440.

Clarke Murray CC, Hannah LC, Doniol-Valcroze T, Wright BM, Stredulinsky EH, Nelson JC, Locke A, Lacy RC. 2021. A cumulative effects model for population trajectories of resident killer whales in the Northeast Pacific. Biol Conserv. 257:109124. doi:10.1016/j.biocon.2021.109124.

Claro B, Pérez-Jorge S, Frey S. 2020. Seafloor geomorphic features as an alternative approach into modelling the distribution of cetaceans. Ecol Inform. 58:101092. doi:10.1016/j.ecoinf.2020.101092.

Clutton-Brock TH, Harvey PH. 1980. Primates, brains and ecology. J Zool. 190(3):309–323. doi:10.1111/j.1469-7998.1980.tb01430.x.

Coakes AK, Whitehead H. 2004. Social structure and mating system of sperm whales off northern Chile. Can J Zool. 82(8):1360–1369. doi:10.1139/z04-115.

Cohen E. 2012. The evolution of tag-based cooperation in humans: the case for accent. Curr Anthropol. 53(5):588–616. doi:10.1086/667654.

Connor R, Wells R, Mann J, Read A. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann J, Connor RC, Tyack P, Whitehead H, editors. Cetacean societies: field studies of whales and dolphins. University of Chicago Press.

Connor R, Mann J. 2006. Social cognition in the wild: Machiavellian dolphins? In: Hurley S, Nudds M, editors. Rational animals? Oxford University Press. p. 329–368.

Connor RC, Smolker R, Bejder L. 2006. Synchrony, social behaviour and alliance affiliation in Indian ocean bottlenose dolphins, *Tursiops aduncus*. Anim Behav. 72(6):1371–1378. doi:10.1016/j.anbehav.2006.03.014.

Connor RC. 2007. Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. Philos Trans R Soc Biol Sci. 362(1480):587–602.

Connor RC, Krützen M. 2015. Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. Anim Behav. 103:223–235. doi:10.1016/j.anbehav.2015.02.019.

COSWEIC. 2008. COSEWIC assessment and update status report on the killer whale, *Orcinus orca*: Southern resident population, Northern resident population, West Coast transient population, Offshore population, Northwest Atlantic/Eastern Arctic population in Canada. Ottawa: Committee on the Status of Endangered Wildlife in Canada.

Creanza N, Ruhlen M, Pemberton TJ, Rosenberg NA, Feldman MW, Ramachandran S. 2015. A comparison of worldwide phonemic and genetic variation in human populations. PNAS. 112(5):1265–1272.

Creanza N, Feldman MW. 2016. Worldwide genetic and cultural change in human evolution. Curr Opin Genet Dev. 41:85–92. doi:10.1016/j.gde.2016.08.006.

Creanza N, Kolodny O, Feldman MW. 2017. Cultural evolutionary theory: how culture evolves and why it matters. PNAS. 114(30):7782–7789. doi:10.1073/pnas.1620732114.

Daikoku H, Wood AL, Savage PE. 2020. Musical diversity in India a preliminary computational study using cantometrics. Keio SFC Journal. 20(2):34–61.

Daura-Jorge FG, Cantor M, Ingram SN, Lusseau D, Simões-Lopes PC. 2012. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biol Lett. 8(5):702–705. doi:10.1098/rsbl.2012.0174.

de Bruyn PJN de, Tosh CA, Terauds A. 2013. Killer whale ecotypes: is there a global model? Biol Rev. 88(1):62–80. doi:10.1111/j.1469-185X.2012.00239.x.

de Casien AR, Williams SA, Higham JP. 2017. Primate brain size is predicted by diet but not sociality. Nat Ecol Evol. 1(5). doi: 10.1038/s41559-017-0112.

Deecke VB, Ford JKB, Spong P. 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. Anim Behav. 60(5):629–638. doi:10.1006/anbe.2000.1454.

Deecke VB, Ford JKB, Slater PJB. 2005. The vocal behaviour of mammal-eating killer whales: communicating with costly calls. Anim Behav. 69(2):395–405. doi:10.1016/j.anbehav.2004.04.014.

Diaz-Aguirre F, Parra GJ, Cecilia P, Luciana M. 2020. Kinship and reproductive condition correlate with affiliation patterns in female southern Australian bottlenose dolphins. Sci Rep. 10(1).

Díaz-Gamboa RE, Gendron D, Busquets-Vass G. 2018. Isotopic niche width differentiation between common bottlenose dolphin ecotypes and sperm whales in the Gulf of California. Mar Mamm Sci. 34(2):440–457. doi:10.1111/mms.12465.

Doniger W. 2006. Britannica Encyclopedia of World Religions. Encyclopaedia Britannica, Incorporated.

dos Santos M, West SA. 2018. The coevolution of cooperation and cognition in humans. Proc Royal Soc B. 285(1879):20180723. doi:10.1098/rspb.2018.0723.

Dufault S, Whitehead H. 1998. Regional and group-level differences in fluke markings and notches of sperm whales. J Mammal. 79(2):514–520. doi:10.2307/1382982.

Dufault S, Whitehead H, Dillon M. 1999. An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide. J Cetacean Res Manage. 1(1):1–10.

Dunbar RIM. 1992. Neocortex size as a constraint on group size in primates. J Hum Evol. 22(6):469–493. doi:10.1016/0047-2484(92)90081-J.

Dunbar RIM. 1998. The social brain hypothesis. Evol Anthropol. 6(5):178–190. doi:10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8.

Dunbar RIM, Shultz S. 2007. Evolution in the social brain. Science. 317(5843):1344–1347.

Dunbar RIM. 2009. The social brain hypothesis and its implications for social evolution. Ann Hum Biol. 36(5):562–572. doi:10.1080/03014460902960289.

Edelaar P, Alonso D, Lagerveld S, Senar JC, Björklund M. 2012. Population differentiation and restricted gene flow in Spanish crossbills: not isolation-by-distance but isolation-by-ecology. J Evol Biol. 25(3):417–430. doi: 10.1111/j.1420-9101.2011.02443.x.

Efferson C, Lalive R, Fehr E. 2008. The coevolution of cultural groups and ingroup favoritism. Science. doi:10.1126/science.1155805.

Efron B, Gong G. 1983. A leisurely look at the bootstrap, the jackknife, and cross-validation. Am Stat. 37(1):36–48. doi:10.2307/2685844.

Eguiguren A, Pirotta E, Cantor M, Rendell L, Whitehead H. 2019. Habitat use of culturally distinct Galápagos sperm whale *Physeter macrocephalus* clans. Mar Ecol Prog Ser. 609:257–270. doi:10.3354/meps12822.

Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. J Anim Ecol. 72(1):144–155. doi:10.1046/j.1365-2656.2003.00690.x.

Estienne V, Cohen H, Wittig RM, Boesch C. 2019. Maternal influence on the development of nut-cracking skills in the chimpanzees of the Taï forest, Côte d'Ivoire (*Pan troglodytes verus*). Am J Primatol. 81(7):e23022. doi:10.1002/ajp.23022.

Fassig OL. 1933. The trade-winds of the eastern Caribbean. Eos Trans AGU. 14(1):69–78. doi: 10.1029/TR014i001p00069.

Fawcett K, Muhumuza G. 2000. Death of a wild chimpanzee community member: possible outcome of intense sexual competition. Am J Primatol. 51(4):243–247. doi:10.1002/1098-2345(200008).

Feldman MW, Laland KN. 1996. Gene-culture coevolutionary theory. Trends Ecol Evol. 11(11):453–457. doi:10.1016/0169-5347(96)10052-5.

Fenster CB, Ballou JD, Dudash MR, Eldridge MDB, Frankham R, Lacy RC, Ralls K, Sunnucks P. 2018. Conservation and genetics. Yale J Biol Med. 91(4):491–501.

Fielding AH, Bell JF. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ Conserv. 24(1):38–49. doi:10.1017/S0376892997000088.

Filatova OA, Shpak OV, Ivkovich TV, Volkova EV, Fedutin ID, Ovsyanikova EN, Burdin AM, Hoyt E. 2019. Large-scale habitat segregation of fish-eating and mammal-eating killer whales (*Orcinus orca*) in the western North Pacific. Polar Biol. 42(5):931–941. doi:10.1007/s00300-019-02484-6.

Finneran N. 2016. Slaves to sailors: the archaeology of traditional Caribbean shore whaling c.1850–2000. A case study from Barbados and Bequia (St Vincent Grenadines). Int J Naut Archaeol. 45(2):388–405. doi:10.1111/1095-9270.12184.

Fishlock V, Caldwell C, Lee PC. 2016. Elephant resource-use traditions. Anim Cogn. 19(2):429–433. doi:10.1007/s10071-015-0921-x.

Fiske ST. 2002. What we know now about bias and intergroup conflict, the problem of the century. APS. 11(4):123–128.

Fitzpatrick JL, Almbro M, Gonzalez-Voyer A, Hamada S, Pennington C, Scanlan J, Kolm N. 2012. Sexual selection uncouples the evolution of brain and body size in pinnipeds. J Evol Biol. 25(7):1321–1330. doi:10.1111/j.1420-9101.2012.02520.x.

Foerster S, Franz M, Murray CM, Gilby IC, Feldblum JT, Walker KK, Pusey AE. 2016. Chimpanzee females queue but males compete for social status. Sci Rep. 6:35404.

Foote AD, Morin PA, Durban JW, Willerslev E, Orlando L, Gilbert MTP. 2011. Out of the Pacific and back again: insights into the matrilineal history of Pacific killer whale ecotypes. PLOS One. 6(9):e24980.

Foote AD, Vijay N, Ávila-arcos MC, Baird RW, Durban JW, Fumagalli M, Gibbs RA, Hanson MB, Korneliussen TS, Martin MD, et al. 2016. Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. Nat Commun. 7:11693.

Ford JKB. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can J Zool. 69(6):1454–1483. doi:10.1139/z91-206.

Ford JKB, Ellis GM, Barrett-Lennard LG, Morton AB, al et. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can J Zool. 76(8):1456–1471.

Fruet PF, Secchi ER, Tullio JCD, Simões-Lopes PC, Daura-Jorge F, Costa APB, Vermeulen E, Flores PAC, Genoves RC, Laporta P, et al. 2017. Genetic divergence between two phenotypically distinct bottlenose dolphin ecotypes suggests separate evolutionary trajectories. Ecol Evol. 7(21):9131–9143. doi:10.1002/ece3.3335.

Furuichi T. 2020. Variation in intergroup relationships among species and among and within local populations of african apes. Int J Primatol. 41(2):203–223. doi:10.1007/s10764-020-00134-x.

Gallup GG. 1970. Chimpanzees: Self-Recognition. Science. 167(3914):86–87.

García J, van den Bergh JCJM. 2011. Evolution of parochial altruism by multilevel selection. Evol Hum Behav. 32(4):277–287. doi:10.1016/j.evolhumbehav.2010.07.007.

Gero S, Gordon J, Carlson C, Evans P, Whitehead H. 2007. Population estimate and inter-island movement of sperm whales, *Physeter macrocephalus*, in the Eastern Caribbean. J Cetacean Res Manag. 9:143–150.

Gero S, Engelhaupt D, Rendell L, Whitehead H. 2009. Who cares? Between-group variation in alloparental caregiving in sperm whales. Behav Ecol. 20(4):838–843. doi:10.1093/beheco/arp068.

Gero S, Gordon J, Whitehead H. 2013. Calves as social hubs: dynamics of the social network within sperm whale units. Proc Biol Sci. 280(1763):1–9.

Gero S, Milligan M, Rinaldi C, Francis P, Gordon J, Carlson C, Steffen A, Tyack P, Evans P, Whitehead H. 2014. Behavior and social structure of the sperm whales of Dominica, West Indies. Mar Mam Sci. 30(3):905–922. doi:10.1111/mms.12086.

Gero S, Gordon J, Whitehead H. 2015. Individualized social preferences and long-term social fidelity between social units of sperm whales. Anim Behav. 102:15–23. doi:10.1016/j.anbehav.2015.01.008.

Gero S, Whitehead H. 2016. Critical decline of the Eastern Caribbean sperm whale population. PLOS One. 11(10):e0162019. doi:10.1371/journal.pone.0162019.

Gero S, Whitehead H, Rendell L. 2016a. Individual, unit and vocal clan level identity cues in sperm whale codas. R Soc Open Sci. 3(1):150372. doi:10.1098/rsos.150372.

Gero S, Bøttcher A, Whitehead H, Madsen PT. 2016b. Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. R Soc Open Sci. 3(6):160061.

Gilby IC, Brent LJ, N, Wroblewski EE, Rudicell RS, Hahn BH, Goodall J, Pusey AE. 2013. Fitness benefits of coalitionary aggression in male chimpanzees. Behav Ecol Sociobiol. 67(3):373–381.

Gillespie D, Mellinger D, Gordon J, McLaren D, Redmond P, McHugh R, Trinder P, Deng X, Thode A. 2009. PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. J Acoust Soc Am. 125. doi:10.1121/1.4808713.

González-Lagos C, Sol D, Reader SM. 2010. Large-brained mammals live longer. J Evol Biol. 23(5):1064–1074. doi:10.1111/j.1420-9101.2010.01976.x.

Goodall J. 1986. The chimpanzees of Gombe: patterns of behavior. Cambridge, Mass: Belknap Press.

Grove M. 2017. Environmental complexity, life history, and encephalisation in human evolution. Biol Philos. 32(3):395–420.

Hamburg DA, McCown ER. 1979. The great apes. Menlo Park, Calif.: Benjamin/Cummings Pub. Co.

Hammond P. 1986. Estimating the size of naturally marked whale populations using capture–recapture techniques. Rep Int Whaling Comm Spec Issue. 8:253–282.

Handley C, Mathew S. 2020. Human large-scale cooperation as a product of competition between cultural groups. Nat Commun. 11(1):702.

Harrington J, Gubian M, Stevens M, Schiel F. 2019. Phonetic change in an Antarctic winter. J Acoust Soc. 146(5):3327–3332. doi:10.1121/1.5130709.

Harris PT, Macmillan-Lawler M, Rupp J, Baker EK. 2014. Geomorphology of the oceans. Mar Geol. 352:4–24. doi:10.1016/j.margeo.2014.01.011.

Hastie T, Tibshirani R, Friedman J. 2009. The elements of statistical learning. Hastie T, Tibshirani R, Friedman J, editors. New York, NY: Springer.

Heithaus MR, Dill LM. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology. 83(2):480–491. doi:10.2307/2680029.

Hendry AP, Huber SK, De León LF, Herrel A, Podos J. 2009. Disruptive selection in a bimodal population of Darwin's finches. Proc Biol Sci. 276(1657):753–759.

Henn BM, Cavalli-Sforza LL, Feldman MW. 2012. The great human expansion. PNAS. 109(44):17758–17764. doi:10.1073/pnas.1212380109.

Henrich J, Boyd R. 1998. The evolution of conformist transmission and the emergence of between-group differences. Evol Hum Behav. 19(4):215–241. doi:10.1016/S1090-5138(98)00018-X.

Henrich J, McElreath R. 2003. The evolution of cultural evolution. Evol Anthropol. 12(3):123–135. doi: 10.1002/evan.10110.

Henrich J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. J Econ Behav Organ. 53(1):3–35. doi:10.1016/S0167-2681(03)00094-5.

Henrich J. 2016. The secret of our success: how culture is driving human evolution, domesticating our species, and making us smarter. Princeton University Press.

Henrich J, Muthukrishna M. 2021. The origins and psychology of human cooperation. Annu Rev Psychol. 72(1):207–240. doi:10.1146/annurev-psych-081920-042106.

Herbinger I, Boesch C, Rothe H. 2001. Territory Characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. Int J Primatol. 22(2):143–167. doi:10.1023/A:1005663212997.

Herman LM. 2012. Body and self in dolphins. Conscious Cogn. 21(1):526–545. doi:10.1016/j.concog.2011.10.005.

Herrmann E, Call J, Hernández-Lloreda MV, Hare B, Tomasello M. 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. Science. 317(5843):1360–1366.

Hersh TA. 2021. Dialects over space and time: cultural identity and evolution in sperm whale codas [dissertation]. Dalhousie University. Chapter 5, Stability and evolution in sperm whale cultural dialects; p.88-111.

Hersh TA, Gero S, Rendell L, Cantor M, Weilgart L, Amano M, Dawson SM, Slooten E, Johnson CM, Kerr I, Payne R, Rogan A, Antunes R, Andrews O, Ferguson EL, Hom-Weaver CA, Norris TF, Barkley YM, Merkens KP, Oleson EM, Doniol-Valcroze T, Pilkington JF, Gordon J, Fernandes M, Guerra M, Hickmott L, Whitehead H. (in review). Symbolic marking in non-human cultures: evidence from sperm whale clans.

Hersh TA, Gero S, Rendell L, Whitehead H. 2021. Using identity calls to detect structure in acoustic datasets. Methods Ecol Evol. 12(9):1668–1678. doi:10.1111/2041-210X.13644.

Hirata S. 2009. Chimpanzee social intelligence: selfishness, altruism, and the mother-infant bond. Primates. 50(1):3–11.

Hockings KJ, McLennan MR, Carvalho S, Ancrenaz M, Bobe R, Byrne RW, Dunbar RIM, Matsuzawa T, McGrew WC, Williamson EA, et al. 2015. Apes in the Anthropocene: flexibility and survival. Trends Ecol Evol. 30(4):215–222. doi:10.1016/j.tree.2015.02.002.

Hoelzel A. 1998. Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. J Hered. 89(5):451–458. doi:10.1093/jhered/89.5.451.

Hoffman JI, Trathan PN, Amos W. 2006. Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals *Arctocephalus gazella*. Mol Ecol. 15(12):3841–3847. doi:10.1111/j.1365-294X.2006.03053.x.

Hoffmann AA, Sgrò CM, Kristensen TN. 2017. Revisiting adaptive potential, population size, and conservation. Trends Ecol Evol. 32(7):506–517. doi:10.1016/j.tree.2017.03.012.

Højsgaard S, Halekoh U, Yan J. 2005. The R Package geepack for generalized estimating equations. J Stat Softw. 15(1):1–11. doi:10.18637/jss.v015.i02.

Hopper LM, Spiteri A, Lambeth SP, Schapiro SJ, Horner V, Whiten A. 2007. Experimental studies of traditions and underlying transmission processes in chimpanzees. Anim Behav. 73(6):1021–1032. doi:10.1016/j.anbehav.2006.07.016.

Hopper LM, Schapiro SJ, Lambeth SP, Brosnan SF. 2011. Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. Anim Behav. 81(6):1195–1202. doi:10.1016/j.anbehav.2011.03.002.

Howard DJ, Marshall JL, Hampton DD, Britch SC, Draney ML, Jiming Chu, Cantrell RG. 2002. The genetics of reproductive isolation: a retrospective and prospective look with comments on ground crickets. Am Nat. 159(3):S8. doi:10.1086/338369.

Huijser LAE, Estrade V, Webster I, Mouysset L, Cadinouche A, Dulau-Drouot V. 2020. Vocal repertoires and insights into social structure of sperm whales (*Physeter macrocephalus*) in Mauritius, southwestern Indian Ocean. Mar Mam Sci. 36(2):638–657. doi:10.1111/mms.12673.

Hutchinson GE. 1957. Concluding remarks. Cold Spring Harb Symp Quant Biol. 22:415–427. doi:10.1101/SQB.1957.022.01.039.

Ihara Y. 2011. Evolution of culture-dependent discriminate sociality: a gene-culture coevolutionary model. Philos Trans R Soc Lond B Biol Sci. 366(1566):889–900.

Isler K, Christopher Kirk E, Miller JMA, Albrecht GA, Gelvin BR, Martin RD. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. J Hum Evol. 55(6):967–978. doi:10.1016/j.jhevol.2008.08.004.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6(3):326–336. doi:10.1093/beheco/6.3.326.

Jaquet N. 1996. How spatial and temporal scales influence understanding of sperm whale distribution: a review. Mammal Rev. 26(1):51–65. doi:10.1111/j.13652907.1996.tb00146.x.

Jaquet N, Whitehead H. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Mar Ecol Prog Ser. 135:1–9. doi:10.3354/meps135001.

Jaquet N, Dawson S, Slooten E. 2000. Seasonal distribution and diving behaviour of male sperm whales off Kaikoura: foraging implications. Can J Zool. 78(3):407–419. doi: 10.1139/cjz-78-3-407.

Jaquet N, Gendron D, Coakes A. 2003. Sperm whales in the gulf of California: residency, movements, behavior, and the possible influence of variation in food supply. Mar Mamm Sci. 19(3):545–562. doi:10.1111/j.1748-7692.2003.tb01320.x.

Jerison HJ. 1973. Evolution of the brain and intelligence. New York: Academic Press.

Jesmer BR, Merkle JA, Goheen JR, Aikens EO, Beck JL, Courtemanch AB, Hurley MA, McWhirter DE, Miyasaki HM, Monteith KL, et al. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science. 361(6406). doi:10.1126/science.aat0985.

Johns WE, Townsend TL, Fratantoni DM, Wilson WD. 2002. On the Atlantic inflow to the Caribbean Sea. Deep Sea Res Part I Oceanogr Res Pap. 49(2):211–243. doi:10.1016/S0967-0637(01)00041-3.

Jones AW, Post DM. 2016. Does intraspecific competition promote variation? A test via synthesis. Ecol Evol. 6(6):1646–1655.

Judkins HL, Vecchione M, Roper CFE, Torres J. 2010. Cephalopod species richness in the wider Caribbean region. ICES Mar Sci. 67(7):1392–1400. doi:10.1093/icesjms/fsq092.

Junker RR, Kuppler J, Bathke AC, Schreyer ML, Trutschnig W. 2016. Dynamic range boxes – a robust nonparametric approach to quantify size and overlap of n-dimensional hypervolumes. Methods Ecol Evol. 7(12):1503–1513. doi:10.1111/2041-210X.12611.

Jury MR, Bernard D. 2020. Climate trends in the East Antilles Islands. Int J Climatol. 40(1):36–51. doi:10.1002/joc.6191.

Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol. 9(4):156–185. doi:10.1002/1520-6505.

Kaschner K, Quick NJ, Jewell R, Williams R, Harris CM. 2012. Global coverage of cetacean line-transect surveys: status quo, data gaps and future challenges. PLOS One. 7(9):e44075. doi: 10.1371/journal.pone.0044075.

Keeley LH. 1996. War before civilization. Oxford University Press.

Keiter DA, Davis AJ, Rhodes OE, Cunningham FL, Kilgo JC, Pepin KM, Beasley JC. 2017. Effects of scale of movement, detection probability, and true population density on common methods of estimating population density. Sci Rep. 7:1–12. doi: 10.1038/s41598-017-09746-5.

Keith D, Akçakaya HR, Butchart SHM, Collen B, Dulvy NK, Holmes EE, Hutchings JA, Keinath D, Schwartz MK, Shelton AO, et al. 2015. Temporal correlations in population trends: conservation implications from time-series analysis of diverse animal taxa. Biol Conserv. 192:247–257. doi:10.1016/j.biocon.2015.09.021.

Keith SA, Bull JW. 2017. Animal culture impacts species’ capacity to realise climate-driven range shifts. Ecography. 40(2):296–304. doi:10.1111/ecog.02481.

Kennedy AS, Zerbini AN, Vásquez OV, Gandilhon N, Clapham PJ, Adam O. 2014. Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean. Can J Zool. 92(1):9–18. doi:10.1139/cjz-2013-0161.

Ketz AC, Johnson TL, Monello RJ, Mack JA, George JL, Kraft BR, Wild MA, Hooten MB, Hobbs NT. 2018. Estimating abundance of an open population with an N-mixture model using auxiliary data on animal movements. Ecol Appl. 28(3):816–825.

King SL, Connor RC, Krützen M, Allen SJ. 2021. Cooperation-based concept formation in male bottlenose dolphins. Nat Commun. 12(1):2373. doi:10.1038/s41467-021-22668-1.

Kiszka JJ, Caputo M, Méndez-Fernandez P, Fielding R. 2021. Feeding ecology of elusive Caribbean killer whales inferred from Bayesian stable isotope mixing models and whalers’ ecological knowledge. Front Mar Sci. 8. Doi:10.3389/fmars.2021.648421.

Kobayashi H, Amano M. 2020. Residency and abundance of sperm whales (*Physeter macrocephalus*) in Nemuro Strait, Hokkaido, Japan. Mar Mam Sci. 36(2):612–622. doi: 10.1111/mms.12662.

Kobayashi H, Whitehead H, Amano M. 2020. Long-term associations among male sperm whales (*Physeter macrocephalus*). PLOS One. 15(12):e0244204. doi:10.1371/journal.pone.0244204.

Konrad CM, Gero S, Frasier T, Whitehead H. 2018a. Kinship influences sperm whale social organization within, but generally not among, social units. R Soc Open Sci. 5(8):180914. doi:10.1098/rsos.180914.

Konrad CM, Frasier TR, Rendell L, Whitehead H, Gero S. 2018b. Kinship and association do not explain vocal repertoire variation among individual sperm whales or social units. Anim Behav. 145:131–140. doi:10.1016/j.anbehav.2018.09.011.

Kopps AM, Ackermann CY, Sherwin WB, Allen SJ, Bejder L, Krützen M. 2014. Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. Proc Biol Sci. 281(1782):1–8.

Koops K, Schöning C, Isaji M, Hashimoto C. 2015. Cultural differences in ant-dipping tool length between neighbouring chimpanzee communities at Kalinzu, Uganda. Sci Rep. 5:12456.

Krützen M, Barré LM, Connor RC, Mann J, Sherwin WB. 2004. 'O father: where art thou?'— Paternity assessment in an open fission–fusion society of wild bottlenose dolphins (*Tursiops sp.*) in Shark Bay, Western Australia. Mol Ecol. 13(7):1975–1990. doi:10.1111/j.1365-294X.2004.02192.x.

Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB. 2005. Cultural transmission of tool use in bottlenose dolphins. PNAS. 102(25):8939–8943. doi:10.1073/pnas.0500232102.

Kudo H, Dunbar RIM. 2001. Neocortex size and social network size in primates. Anim Behav. 62(4):711–722. doi:10.1006/anbe.2001.1808.

Kühl HS, Sop T, Williamson EA, Mundry R, Brugière D, Campbell G, Cohen H, Danquah E, Ginn L, Herbinger I, et al. 2017. The critically endangered western chimpanzee declines by 80%. Am J Primatol. 79(9):e22681. doi:10.1002/ajp.22681.

Kühl HS, Boesch C, Kulik L, Haas F, Arandjelovic M, Dieguez P, Bocksberger G, McElreath MB, Agbor A, Angedakin S, et al. 2019. Human impact erodes chimpanzee behavioral diversity. Science. 363(6434):1453–1455. doi:10.1126/science.aau4532.

Kumar S, Hedges SB. 1998. A molecular timescale for vertebrate evolution. Nature. 392(6679):917–920. doi:10.1038/31927.

Laland KN, Hoppitt W. 2003. Do animals have culture? Evol Anthropol. 12(3):150–159. doi:10.1002/evan.10111.

Laland KN, Janik VM. 2006. The animal cultures debate. TrendsEcol Evol. 21(10):542–547. doi:10.1016/j.tree.2006.06.005.

Laland KN, Uller T, Feldman MW, Sterelny K, Müller GB, Moczek A, Jablonka E, Odling-Smee J. 2015. The extended evolutionary synthesis: its structure, assumptions and predictions. Proc Royal Soc B. 282(1813):20151019. doi:10.1098/rspb.2015.1019.

Langergraber KE, Watts DP, Vigilant L, Mitani JC. 2017. Group augmentation, collective action, and territorial boundary patrols by male chimpanzees. PNAS. 114(28):7337–7342.

Laurindo LC, Mariano AJ, Lumpkin R. 2017. An improved near-surface velocity climatology for the global ocean from drifter observations. Deep Sea Res Part I Oceanogr Res Pap. 124:73–92. doi:10.1016/j.dsr.2017.04.009.

LeBlanc SA, Register KE. 2003. Constant battles: why we fight. New York: St. Martin's Griffin.

Leduc RG, Perrin WF, Dizon AE. 1999. Phylogenetic relationships among the Delphinid cetaceans based on full cytochrome B sequences. Mar Mamm Sci. 15(3):619–648. doi:10.1111/j.1748-7692.1999.tb00833.x.

Lefebvre L, Reader SM, Sol D. 2004. Brains, innovations and evolution in birds and primates. Brain Behav Evol. 63(4):233–246.

Legendre P, Legendre L. 2012. Numerical Ecology. Elsevier.

Lehmann L, Feldman MW. 2008. War and the evolution of belligerence and bravery. Proc Royal Soc B. 275(1653):2877–2885. doi:10.1098/rspb.2008.0842.

Lemoine S, Preis A, Samuni L, Boesch C, Crockford C, Wittig RM. 2020. Between-group competition impacts reproductive success in wild chimpanzees. Curr Biol. 30(2):312-318.e3. doi:10.1016/j.cub.2019.11.039.

Levin SA. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology. 73(6):1943–1967.

Liang K-Y, Zeger SL. 1986. Longitudinal data analysis using generalized linear models. Biometrika. 73(1):13–22. doi:10.2307/2336267.

Liu BL, Cao J, Truesdell SB, Chen Y, Chen XJ, Tian SQ. 2016. Reconstructing cephalopod migration with statolith elemental signatures: a case study using *Dosidicus gigas*. Fish Sci. 82(3):425–433. doi:10.1007/s12562-016-0978-8.

Liu Y, Konopka G. 2020. An integrative understanding of comparative cognition: lessons from human brain evolution. Integr Comp Biol. 60(4):991–1006. doi:10.1093/icb/icaa109.

Lowe AE, Hobaiter C, Klaus Z, Newton-Fisher NE. 2020. Intra-community infanticide in wild, eastern chimpanzees: a 24-year review. Primates. 61(1):69–82.

Luncz LV, Mundry R, Boesch C. 2012. Evidence for cultural differences between neighboring chimpanzee communities. Curr Biol. 22(10):922–926. doi:10.1016/j.cub.2012.03.031.

Luncz LV, Boesch C. 2015. The extent of cultural variation between adjacent chimpanzee (*Pan troglodytes verus*) communities; a microecological approach. Am J Phys. 156(1):67–75. doi:10.1002/ajpa.22628.

Luncz LV, Sirianni G, Mundry R, Boesch C. 2018. Costly culture: differences in nut-cracking efficiency between wild chimpanzee groups. Anim Behav. 137:63–73. doi:10.1016/j.anbehav.2017.12.017.

Lupyan G, Dale R. 2016. Why are there different languages? The role of adaptation in linguistic diversity. Trends Cogn Sci. 20(9):649–660. doi:10.1016/j.tics.2016.07.005.

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland E j., Stuart SN. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv Biol. 22(6):1424–1442. doi:10.1111/j.1523-1739.2008.01044.x.

MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, Aureli F, Baker JM, Bania AE, Barnard AM, et al. 2014. The evolution of self-control. PNAS. 111(20):E2140–E2148. doi:10.1073/pnas.1323533111.

Mahalanobis PC. 1936. On the generalized distance in statistics. Proc Natl Acad Sci India. 2:49–55.

Mann J, Connor RC, Barre LM, Heithaus MR. 2000. Female reproductive success in bottlenose dolphins (*Tursiops sp.*): life history, habitat, provisioning, and group-size effects. Behav Ecol. 11(2):210–219. doi:10.1093/beheco/11.2.210.

Mann J, Stanton M, Patterson E, Bienenstock E, Singh L. 2012. Social networks reveal cultural behaviour in tool-using using dolphins. Nat Commun. 3:980. doi:10.1038/ncomms1983.

Marcoux M, Whitehead H, Rendell L. 2007a. Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. Mar Ecol Prog Ser. 333:309–314. doi:10.3354/meps333309.

Marcoux M, Rendell L, Whitehead H. 2007b. Indications of fitness differences among vocal clans of sperm whales. Behav Ecol Sociobiol. 61(7):1093–1098. doi:10.1007/s00265-006-0342-6.

Marino L. 1998. A comparison of encephalization between Odontocete cetaceans and anthropoid primates. Brain Behav Evol. 51(4):230–238. doi:10.1159/000006540.

Marino L, McShea DW, Uhen MD. 2004. Origin and evolution of large brains in toothed whales. Anat. 281A(2):1247–1255. doi:10.1002/ar.a.20128.

Martin J, Kitchens WM, Hines JE. 2007. Importance of well-designed monitoring programs for the conservation of endangered species: case study of the snail kite. Conserv Biol. 21(2):472–481.

Mathew S, Boyd R. 2011. Punishment sustains large-scale cooperation in prestate warfare. PNAS. 108(28):11375–11380.

Matsumae H, Savage PE, Ranacher P, Blasi DE, Currie TE, Sato T, Tajima A, Brown S, Stoneking M, Shimizu KK, et al. 2019. Exploring deep-time relationships between cultural and genetic evolution in Northeast Asia. bioRxiv.:513929. doi:10.1101/513929.

Matthiopoulos J, Field C, MacLeod R. 2019. Predicting population change from models based on habitat availability and utilization. Proc Royal Soc B. 286(1901):20182911. doi:10.1098/rspb.2018.2911.

McComb K, Moss C, Durant SM, Baker L, Sayialel S. 2001. Matriarchs as repositories of social knowledge in african elephants. Science. 292(5516):491–494.

McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J, Moss C. 2011. Leadership in elephants: the adaptive value of age. Proc Biol Sci. 278(1722):3270–3276.

McElreath R, Boyd R, Richerson PeterJ. 2003. Shared norms and the evolution of ethnic markers. Curr Anthropol. 44(1):122–130. doi:10.1086/345689.

Mead JG, Potter CW. 1995. Recognizing two populations off the bottlenose dolphin (*Tursiops truncatus*) of the Atlantic coast of North America - morphologic and ecologic considerations. Mar Biol Res. 31-44.

Mehr SA, Singh M, Knox D, Ketter DM, Pickens-Jones D, Atwood S, Lucas C, Jacoby N, Egner AA, Hopkins EJ, et al. 2019. Universality and diversity in human song. Science. doi:10.1126/science.aax0868.

Mercader J, Barton H, Gillespie J, Harris J, Kuhn S, Tyler R, Boesch C. 2007. 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. PNAS. 104(9):3043–3048. doi:10.1073/pnas.0607909104.

Mesoudi A. 2016. Cultural evolution: integrating psychology, evolution and culture. Curr Opin Psychol. 7:17–22. doi:10.1016/j.copsyc.2015.07.001.

Mesoudi A. 2017. Pursuing Darwin’s curious parallel: prospects for a science of cultural evolution. Proc Natl Acad Sci USA. 114(30):7853–7860. doi:10.1073/pnas.1620741114.

Miller JA, Pusey AE, Gilby IC, Schroepfer-Walker K, Catherine Markham A, Murray CM. 2014. Competing for space: female chimpanzees are more aggressive inside than outside their core areas. Anim Behav. 87:147–152. doi:10.1016/j.anbehav.2013.10.023.

Miller EH. 2018. Territorial behavior. In: Würsig B, Thewissen J, Kovacs K, editors. Encyclopedia of marine mammals. Third edition. London: Academic Press. p. 983–990.

Miloslavich P, Diaz JM, Klein E, Alvarado JJ, Diaz C, Gobin J, Escobar-Briones E, Cruz-Motta JJ, Weil E, Cortes J, et al. 2010. Marine biodiversity in the Caribbean: regional estimates and distribution patterns. PLOS One. 5(8). doi:10.1371/journal.pone.0011916.

Milton K. 1981. Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. Am Anthropol. 83(3):534–548. doi:10.1525/aa.1981.83.3.02a00020.

Milton K. 1988. Foraging behaviour and the evolution of primate intelligence. In: Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans. New York, NY, US: Clarendon Press/Oxford University Press. p. 285–305.

Mitani JC, Watts DP, Amsler SJ. 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Curr Biol. 20(12):R507–R508. doi:10.1016/j.cub.2010.04.021.

Mizroch SA, Rice DW. 2013. Ocean nomads: distribution and movements of sperm whales in the North Pacific shown by whaling data and discovery marks. Mar Mam Sci. 29(2):E136–E165. doi:10.1111/j.1748-7692.2012.00601.x.

Moll H, Tomasello M. 2007. Cooperation and human cognition: The Vygotskian intelligence hypothesis. Philos Trans R Soc Biol Sci. 362(1480):639–648.

Morin PA, Archer FI, Foote AD, Vilstrup J, Allen EE, Wade P, Durban J, Parsons K, Pitman R, Li L, et al. 2010. Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. Genome Res. 20(7):908–916. doi:10.1101/gr.102954.109.

Morin PA, Parsons KM, Archer FI, Ávila-Arcos MC, Barrett-Lennard LG, Rosa LD, Duchêne S, Durban JW, Ellis GM, Ferguson SH, et al. 2015. Geographic and temporal dynamics of a global radiation and diversification in the killer whale. Mol Ecol. 24(15):3964–3979. doi:10.1111/mec.13284.

Morin PA, Foote AD, Baker CS, Hancock-Hanser BL, Kaschner K, Mate BR, Mesnick SL, Pease VL, Rosel PE, Alexander A. 2018. Demography or selection on linked cultural traits or genes? Investigating the driver of low mtDNA diversity in the sperm whale using complementary mitochondrial and nuclear genome analyses. Mol Ecol. 27(11):2604–2619. doi:10.1111/mec.14698.

Mullin KD, Steiner L, Dunn C, Claridge D, González García L, Gordon J, Lewis T. 2022. Long-range longitudinal movements of sperm whales (*Physeter macrocephalus*) in the North Atlantic ocean revealed by photo-identification. Aquat Mamm. 48(1):3–8. doi:10.1578/AM.48.1.2022.3.

Natoli A, Peddemors VM, Hoelzel AR. 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. J Evol Biol. 17(2):363–375. doi:10.1046/j.1420-9101.2003.00672.x.

Nattrass S, Croft DP, Ellis S, Cant MA, Weiss MN, Wright BM, Stredulinsky E, Doniol-Valcroze T, Ford JKB, Balcomb KC, et al. 2019. Postreproductive killer whale grandmothers improve the survival of their grandoffspring. PNAS. 116(52):26669–26673. doi:10.1073/pnas.1903844116.

Navarrete AF, Reader SM, Street SE, Whalen A, Laland KN. 2016. The coevolution of innovation and technical intelligence in primates. Philos Trans R Soc Lond B Biol Sci. 371(1690):20150186. doi:10.1098/rstb.2015.0186.

Nishida T, Hosaka K, Nakamura M, Hamai M. 1995. A within-group gang attack on a young adult male chimpanzee: ostracism of an ill-mannered member? Primates. 36(2):207–211. doi:10.1007/BF02381346.

O'Neil ST, Vucetich JA, Beyer DE, Hoy SR, Bump JK. 2020. Territoriality drives preemptive habitat selection in recovering wolves: implications for carnivore conservation. J Anim Ecol. 89(6):1433–1447. doi:10.1111/1365-2656.13199.

Oksanen J, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, et al. 2020. vegan: community ecology package. R package version 25-7.

Oliveira C, Wahlberg M, Johnson M, Miller PJO, Madsen PT. 2013. The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? J Acoust Soc Am. 133(5):3135–3144. doi:10.1121/1.4795798.

Owen-Smith N. 1977. On territoriality in ungulates and an evolutionary model. Q Rev Biol. 52(1):1–38.

Pagnotta M. 2014. On the controversy over non-human culture: the reasons for disagreement and possible directions toward consensus. Behav Processes. 109:95–100. doi:10.1016/j.beproc.2014.04.008.

Palacios DM, Mate BR. 1996. Attack by false killer whales (Pseudorca crassidens) on sperm whales (*Physeter macrocephalus*) in the Galápagos Islands. Mar Mam Sci. 12(4):582–587. doi:10.1111/j.1748-7692.1996.tb00070.x.

Pan W. 2001. Akaike's information criterion in generalized estimating equations. Biometrics. 57(1):120–125. doi:10.1111/j.0006-341x.2001.00120.x.

Pandit SA, Pradhan GR, Balashov H, Van Schaik CP. 2016. The conditions favoring between-community raiding in chimpanzees, bonobos, and human foragers. Hum Nat. 27(2):141–159. doi: 10.1007/s12110-015-9252-5.

Parker ST, Gibson KR. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in *cebus* monkeys and great apes. J Hum Evol. 6(7):623–641. doi:10.1016/S0047-2484(77)80135-8.

Pascual-Garrido A. 2019. Cultural variation between neighbouring communities of chimpanzees at Gombe, Tanzania. Sci Rep. 9(1):8260. doi:10.1038/s41598-019-44703-4.

Pérez-Jorge S, Pereira T, Corne C, Wijtten Z, Omar M, Katello J, Kinyua M, Oro D, Louzao M. 2015. Can static habitat protection encompass critical areas for highly mobile marine top predators? Insights from coastal East Africa. Steinke D, editor. PLOS One. 10(7):e0133265. doi:10.1371/journal.pone.0133265.

Perry S. 2009. Are nonhuman primates likely to exhibit cultural capacities like those of humans? In: Laland KN, Galef BG, editors. The Question of Animal Culture. Harvard University Press. p. 247–268.

Perry S. 2011. Social traditions and social learning in capuchin monkeys (*Cebus*). Philos Trans R Soc Biol Sci. 366(1567):988–996.

Piraszewska K. 2006. Economic significance of tourism in the Lesser Antilles. Misc Geogr. 12(1):269–275. doi:10.2478/mgrsd-2006-0031.

Pirotta E, Matthiopoulos J, MacKenzie M, Scott-Hayward L, Rendell L. 2011. Modelling sperm whale habitat preference: a novel approach combining transect and follow data. Mar Ecol Prog Ser. 436:257–272. doi:10.3354/meps09236.

Pirotta E, Thompson PM, Miller PI, Brookes KL, Cheney B, Barton TR, Graham IM, Lusseau D. 2014. Scale-dependent foraging ecology of a marine top predator modelled using passive acoustic data. Funct Ecol. 28(1):206–217. doi:10.1111/1365-2435.12146.

Pitman RL, Ballance LT, Mesnick SI, Chivers SJ. 2001. Killer whale predation on sperm whales: observations and implications. Mar Mam Sci. 17(3):494–507. doi:10.1111/j.1748-7692.2001.tb01000.x.

Pitnick S, Jones KE, Wilkinson GS. 2006. Mating system and brain size in bats. Proc Biol Sci. 273(1587):719–724.

Punzo A, Mazza A, McNicholas PD. 2018. ContaminatedMixt: an R Package for fitting parsimonious mixtures of multivariate contaminated normal distributions. J Stat Softw. 85:1–25. doi:10.18637/jss.v085.i10.

Pusey AE. 1979. Inter-community transfer of chimpanzees in Gombe National Park. In: Hamburg D, McCown ER, editors. The Great Apes. Benjamin Cummings Publishing Company.

Pusey AE. 2001. Of genes and apes: chimpanzee social organization and reproduction. Harvard University Press.

Puurtinen M, Mappes T. 2009. Between-group competition and human cooperation. Proc Biol Sci. 276(1655):355–360.

Rakić T, Steffens MC, Mummendey A. 2011. Blinded by the accent! The minor role of looks in ethnic categorization. J Pers Soc Psychol. 100(1):16–29. doi:10.1037/a0021522.

Read DW. 2006. Change in the form of evolution: transition from primate to hominid forms of social organization. J Math Sociol. 29(2):91–114. doi:10.1080/00222500590920842.

Reader SM, Laland KN. 2002. Social intelligence, innovation, and enhanced brain size in primates. PNAS. 99(7):4436–4441.

Reader SM, Hager Y, Laland KN. 2011. The evolution of primate general and cultural intelligence. Philos Trans R Soc Biol Sci. 366(1567):1017–1027.

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT, et al. 2006. Techniques for cetacean–habitat modeling. Mar Ecol Prog Ser. 310:271–295. doi:10.3354/meps310271.

Reiss D, Marino L. 2001. Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. PNAS. 98(10):5937–5942.

Rekdahl ML, Dunlop RA, Noad MJ, Goldizen AW. 2013. Temporal stability and change in the social call repertoire of migrating humpback whales. J Acoust Soc. 133(3):1785–1795. doi:10.1121/1.4789941.

Relethford JH, Crawford MH. 1998. Influence of religion and birthplace on the genetic structure of Northern Ireland. Ann Hum Biol. 25(2):117–125. doi:10.1080/03014469800005492.

Rendell L, Whitehead H. 2001. Culture in whales and dolphins. Behav Brain Sci. 24(2):309–24; discussion 324-82.

Rendell LE, Whitehead H. 2003a. Comparing repertoires of sperm whale codas: a multiple methods approach. Bioacoustics. 14(1):61–81. doi:10.1080/09524622.2003.9753513.

Rendell LE, Whitehead H. 2003b. Vocal clans in sperm whales (*Physeter macrocephalus*). Proc R Soc Lond B. 270(1512):225–231. doi:10.1098/rspb.2002.2239.

Rendell L, Whitehead H. 2005. Spatial and temporal variation in sperm whale coda vocalizations: stable usage and local dialects. Anim Behav. 70(1):191–198. doi:10.1016/j.anbehav.2005.03.001.

Rendell L, Mesnick SL, Dalebout ML, Burtenshaw J, Whitehead H. 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? Behav Genet. 42(2):332–343. doi:10.1007/s10519-011-9513-y.

Rendell L, Simião S, Brotons JM, Airoldi S, Fasano D, Gannier A. 2014. Abundance and movements of sperm whales in the western Mediterranean basin. Aquat Conserv. 24(S1):31–40. doi:10.1002/aqc.2426.

Rendell L, Frantzis A. 2016. Chapter two - Mediterranean sperm whales, *Physeter macrocephalus*: the precarious state of a lost tribe. Adv Mar Biol. 75:37–74. doi:10.1016/bs.amb.2016.08.001.

Rendell L, Cantor M, Gero S, Whitehead H, Mann J. 2019. Causes and consequences of female centrality in cetacean societies. Philos Trans R Soc Biol Sci. 374(1780):20180066. doi:10.1098/rstb.2018.0066.

Rice A, Širović A, Trickey JS, Debich AJ, Gottlieb RS, Wiggins SM, Hildebrand JA, Baumann-Pickering S. 2021. Cetacean occurrence in the Gulf of Alaska from long-term passive acoustic monitoring. Mar Biol. 168(5):72. doi:10.1007/s00227-021-03884-1.

Richerson PJ, Boyd R. 1999. Complex societies. Hum Nat. 10(3):253–289. doi:10.1007/s12110-999-1004-y.

Richerson P, Boyd R. 2005. Not by genes alone: how culture transformed human evolution. University of Chicago Press.

Richerson P, Baldini R, Bell AV, Demps K, Frost K, Hillis V, Mathew S, Newton EK, Naar N, Newson L, et al. 2016. Cultural group selection plays an essential role in explaining human cooperation: a sketch of the evidence. Behav Brain Sci. 39:e30.

Ridgway SH, Hanson AC. 2014. Sperm whales and killer whales with the largest brains of all toothed whales show extreme differences in cerebellum. Brain Behav Evol. 83(4):266–74.

Riesch R, Barrett-Lennard LG, Ellis GM, Ford JKB, Deecke VB. 2012. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? Biol J Linn Soc. 106(1):1–17. doi:10.1111/j.1095-8312.2012.01872.x.

Rinaldi C, Rinaldi R, Laine J, Barbraud C. 2021. Population dynamics of sperm whales (*Physeter macrocephalus*) in Guadeloupe, French Caribbean: a mark-recapture study from 2001 to 2013. Mar Mamm Sci. 37(4):1391–1405. doi:10.1111/mms.12837.

Robbins MM, Ando C, Fawcett KA, Grueter CC, Hedwig D, Iwata Y, Lodwick JL, Masi S, Salmi R, Stoinski TS, et al. 2016. Behavioral variation in gorillas: evidence of potential cultural traits. PLOS One. 11(9):e0160483. doi: 10.1371/journal.pone.0160483.

Rødland ES, Bjørge A. 2015. Residency and abundance of sperm whales (*Physeter macrocephalus*) in the Bleik Canyon, Norway. Mar Biol Res. 11:1–9. doi:10.1080/17451000.2015.1031800.

Romeu B, Cantor M, Bezamat C, Simões-Lopes PC, Daura-Jorge FG. 2017. Bottlenose dolphins that forage with artisanal fishermen whistle differently. Ethology. 123(12):906–915. doi:10.1111/eth.12665.

Ruiz-Cooley RI, Gendron D, Aguíñiga S, Mesnick S, Carriquiry JD. 2004. Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. Mar Ecol Prog. 277:275–283. doi:10.3354/meps277275.

Ryan SJ. 2006. The role of culture in conservation planning for small or endangered populations. Conserv Biol. 20(4):1321–1324.

Rzeszutek T, Savage PE, Brown S. 2012. The structure of cross-cultural musical diversity. Proc Biol Sci. 279(1733):1606–1612. doi:10.1098/rspb.2011.1750.

Sagnol O, Richter C, Field L, Reitsma F. 2014. Spatio-temporal distribution of sperm whales (*Physeter macrocephalus*) off Kaikoura, New Zealand, in relation to bathymetric features. N Z J Zool. 41(4):234–247. doi:10.1080/03014223.2014.936474.

Samuni L, Mielke A, Preis A, Crockford C, Wittig RM. 2020. Intergroup competition enhances chimpanzee (*Pan troglodytes verus*) in-group cohesion. Int J Primatol. 41(2):342–362. doi:10.1007/s10764-019-00112-y.

Samuni L, Crockford C, Wittig RM. 2021. Group-level cooperation in chimpanzees is shaped by strong social ties. Nat Commun. 12(1):539.

Sapolsky RM, Share LJ. 2004. A pacific culture among wild baboons: its emergence and transmission. PLOS Biology. 2(4):e106. doi:10.1371/journal.pbio.0020106.

Sarano F, Girardet J, Sarano V, Vitry H, Preud'homme A, Heuzey R, Garcia-Cegarra AM, Madon B, Delfour F, Glotin H, et al. 2021. Kin relationships in cultural species of the marine realm: case study of a matrilineal social group of sperm whales off Mauritius island, Indian Ocean. R Soc Open Sci. 8(2):201794. doi:10.1098/rsos.201794.

Sargeant BL, Mann J. 2009. From social learning to culture: intrapopulation variation in bottlenose dolphins. In: Galef B, Laland KN, editors. The Question of Animal Culture. Harvard University Press. p. 152–173.

Savje F. 2019. distances: tools for distance metrics. R package version 018. doi:https://CRAN.R-project.org/package=distances.

Sayigh L, Daher MA, Allen J, Gordon H, Joyce K, Stuhlmann C, Tyack P. 2016. The Watkins marine mammal sound database: an online, freely accessible resource. Proc Mtgs Acoust. 27(1):040013. doi:10.1121/2.0000358.

Schakner ZA, Lunsford C, Straley J, Eguchi T, Mesnick SL. 2014. Using models of social transmission to examine the spread of longline depredation behavior among sperm whales in the Gulf of Alaska. PLOS One. 9(10):e109079. doi:10.1371/journal.pone.0109079.

Schluter D. 2000. The ecology of adaptive radiation. Oxford Series in Ecology and Evolution.

Schnabel ZE. 1938. The estimation of total fish population of a lake. The American Mathematical Monthly. 45(6):348–352. doi:10.2307/2304025.

Schreyer M, Trutschnig W, Junker RR, Kuppler, J, Bathke A, Parkinson JH, Kutil R. 2021. dynRB: dynamic range boxes. R package version 016. doi:https://CRAN.R-project.org/package=dynRB.

Schulz JF, Bahrami-Rad D, Beauchamp JP, Henrich J. 2019. The Church, intensive kinship, and global psychological variation. Science. 366(6466):eaau5141. doi:10.1126/science.aau5141.

Schuppli C, Meulman EJM, Forss SIF, Aprilinayati F, van Noordwijk MA, vanSchaik CP. 2016. Observational social learning and socially induced practice of routine skills in immature wild orang-utans. Anim Behav. 119:87–98.doi:10.1016/j.anbehav.2016.06.014.

Schuppli C, vanSchaik CP. 2019. Animal cultures: how we've only seen the tip of the iceberg. Evol Hum Sci. 1. doi: 10.1017/ehs.2019.1.

Scott EM, Mann J, Watson-Capps JJ, Sargeant BL, Connor RC. 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. Behaviour. 142(1):21–44.

Seber GA. 1982. The Estimation of Animal Abundance and Related Parameters. 2nd ed. édition. Caldwell, N.J: Blackburn Pr.

Shea JJ. 2003. Neandertals, competition, and the origin of modern human behavior in the Levant. Evol Anthropol. 12(4):173–187. doi:10.1002/evan.10101.

Shields MW, Hysong-Shimazu S, Shields JC, Woodruff J. 2018 Dec 4. Increased presence of mammal-eating killer whales in the Salish Sea with implications for predator-prey dynamics. PeerJ. 6(4):e6062. doi: 10.7717/peerj.6062.

Shultz S, Opie C, Atkinson QD. 2011. Stepwise evolution of stable sociality in primates. Nature. 479(7372):219–222.

Sing T, Sander O, Beerenwinkel N, Lengauer T. 2005. ROCR: visualizing classifier performance in R. Bioinformatics. 21(20):3940–3941. doi:10.1093/bioinformatics/bti623.

Slatkin M. 1980. Ecological character displacement. Ecology. 61(1):163–177. doi:10.2307/1937166.

Smaldino PE. 2022. Models of identity signaling. Curr Dir Psychol Sci.:09637214221075609. doi:10.1177/09637214221075609.

Smolker RA, Richards AF, Connor RC, Pepper JW. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour. 123(1/2):38–69.

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L, Orians GH. 2005. Big brains, enhanced cognition, and response of birds to novel environments. PNAS. 102(15):5460–5465.

Sol D. 2009. Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biol Lett. 5(1):130–133. doi:10.1098/rsbl.2008.0621.

Soltis J, Boyd R, Richerson PJ. 1995. Can group-functional behaviors evolve by cultural group selection?: an empirical test. Curr Anthropol. 36(3):473–494.

Sprogis KR, King C, Bejder L, Loneragan NR. 2018. Frequency and temporal trends of shark predation attempts on bottlenose dolphins (*Tursiops aduncus*) in temperate Australian waters. J Exp Mar Bio Ecol. 508:35–43. doi:10.1016/j.jembe.2018.08.008.

Stanton MA, Mann J. 2012. Early social networks predict survival in wild bottlenose dolphins. PLOS One. 7(10):e47508.

Steele JH. 1985. A comparison of terrestrial and marine ecological systems. Nature. 313(6001):355–358. doi:10.1038/313355a0.

Street SE, Navarrete AF, Reader SM, Laland KN. 2017. Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. PNAS. 114(30):7908–7914.

Strickland K, Mann J, Foroughirad V, Levengood AL, Frère CH. 2021. Maternal effects and fitness consequences of individual variation in bottlenose dolphins' ecological niche. J Anim Ecol. doi:10.1111/1365-2656.13513.

Svanbäck R, Bolnick DI. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proc Biol Sci. 274(1611):839–844.

Svanbäck R, Eklöv P, Fransson R, Holmgren K. 2008. Intraspecific competition drives multiple species resource polymorphism in fish communities. Oikos. 117(1):114–124.

Tajfel H, Billig MG, Bundy RP, Flament C. 1971. Social categorization and intergroup behaviour. Eur J Soc Psychol. 1(2):149–178. doi:10.1002/ejsp.2420010202.

Tajfel H, Turner J. 1979. An integrative theory of intergroup conflict. In: Intergroup relations: Essential readings. Psychology Press. (Key readings in social psychology). p. 94–109.

Taylor BL, Baird R, Barlow J, Dawson SM, Ford J, Mead JG, Notarbartolo di Sciara G, Wade P, Pitman RL. 2019. *Physeter macrocephalus* (amended version of 2008 assessment). The IUCN Red List of Threatened Species 2019: e.T41755A160983555.

Tepsich P, Rosso M, Halpin PN, Moulins A. 2014. Habitat preferences of two deep-diving cetacean species in the northern Ligurian Sea. Mar Ecol Prog Ser. 508:247–260. doi:10.3354/meps10851.

Terio KA, Kinsel MJ, Raphael J, Mlengeya T, Lipende I, Kirchhoff CA, Gilagiza B, Wilson ML, Kamenya S, Estes JD, et al. 2011. Pathologic lesions in chimpanzees (*Pan trogylodytes schweinfurthii*) from Gombe National Park, Tanzania, 2004-2010. J Zoo Wildl Med. 42(4):597–607.

Tezanos-Pinto G, Baker CS, Russell K, Martien K, Baird RW, Hutt A, Stone G, Mignucci-Giannoni AA, Caballero S, Endo T, et al. 2009. A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. J Hered. 100(1):11–24. doi:10.1093/jhered/esn039.

Tomasello M. 2014. The ultra-social animal. Eur J Soc Psychol. 44(3):187–194. doi:10.1002/ejsp.2015.

Tulloch V, Pirotta V, Grech A, Crocetti S, Double M, How J, Kemper C, Meager J, Peddemors V, Waples K, et al. 2020. Long-term trends and a risk analysis of cetacean entanglements and bycatch in fisheries gear in Australian waters. Biodivers Conserv. 29(1):251–282. doi:10.1007/s10531-019-01881-x.

Turchin P. 2006. War and peace and war: the life cycles of imperial nations. PI Press.

Turchin P, Currie TE, Turner EAL, Gavrilets S. 2013. War, space, and the evolution of Old World complex societies. PNAS. 110(41):16384–16389.

Tynan CT, Ainley DG, Barth JA, Cowles TJ, Pierce SD, Spear LB. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. Deep Sea Res Part II Top Stud Oceanogr. 52(1):145–167. doi:10.1016/j.dsr2.2004.09.024.

Uomini N, Fairlie J, Gray RD, Griesser M. 2020. Extended parenting and the evolution of cognition. Philos Trans R Soc Biol Sci. 375(1803):20190495. doi:10.1098/rstb.2019.0495.

Vachon F. 2022. On cultural inheritance: evolution, behaviour and social structure of Eastern Caribbean sperm whales. [dissertation]. Dalhousie University. Chapter 2, Intraspecific, intergroup competition as a driver of advanced cognition in primates and toothed whales.

Vachon F. 2022. On cultural inheritance: evolution, behaviour and social structure of Eastern Caribbean sperm whales. [dissertation]. Dalhousie University. Chapter 4, Distinctive, fine-scale distribution of Eastern Caribbean sperm whale cultural groups relates to island fidelity rather than environmental variables.

Vachon F, Hersh TA, Rendell L, Gero S, Whitehead H. Ocean nomads or island specialists? Culturally driven habitat partitioning contrasts in scale between geographically isolated sperm whale populations. R Soc Open Sci. 9(5):211737. doi:10.1098/rsos.211737.

van den Bergh JCJM, Gowdy JM. 2009. A group selection perspective on economic behavior, institutions and organizations. J Econ Behav Organ. 72(1):1–20. doi:10.1016/j.jebo.2009.04.017.

van Dyke F. 2008. The conservation of populations: concept, theory, and analysis. In: Conservation biology: foundations, concepts, applications. London: Springer. p. 213–242.

van Lawick-Goodall J. 1968. The behaviour of free-living chimpanzees in the Gombe stream reserve. Anim Behav Monogr. 1:161-IN12. doi:10.1016/S0066-1856(68)80003-2.

van Leeuwen EJC, Cronin KA, Haun DBM, Mundry R, Bodamer MD. 2012. Neighbouring chimpanzee communities show different preferences in social grooming behaviour. Proc Royal Soc B. 279(1746):4362–4367. doi:10.1098/rspb.2012.1543.

van Leeuwen EJC van, DeTroy SE, Kaufhold SP, Dubois C, Schütte S, Call J, Haun DBM. 2021. Chimpanzees behave prosocially in a group-specific manner. Sci Adv. 7(9):eabc7982. doi:10.1126/sciadv.abc7982.

van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill M. 2003. Orangutan cultures and the evolution of material culture. Science. 299(5603):102–105.

van Schaik CP, Pradhan GR. 2003. A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. J Hum Evol. 44(6):645–664. doi:10.1016/S0047-2484(03)00041-1.

van Schaik CP, Burkart JM. 2011. Social learning and evolution: the cultural intelligence hypothesis. Philos Trans R Soc Biol Sci. 366(1567):1008–1016.

van Schaik CP, Isler K, Burkart JM. 2012. Explaining brain size variation: from social to cultural brain. TiCS. 16(5):277–284. doi:10.1016/j.tics.2012.04.004.

van Vugt M, Hart CM. 2004. Social identity as social glue: the origins of group loyalty. J Pers Soc Psychol. 86(4):585–598. doi:10.1037/0022-3514.86.4.585.

Vélez-Espino LA, Ford JKB, Araujo HA, Ellis G, Parken CK, Sharma R. 2015. Relative importance of chinook salmon abundance on resident killer whale population growth and viability. Aquat Conserv. 25(6):756–780. doi:10.1002/aqc.2494.

Wang JY, Chou L-S, White BN. 1999. Mitochondrial DNA analysis of sympatric morphotypes of bottlenose dolphins (genus: *Tursiops*) in Chinese waters. Mol Ecol. 8(10):1603–1612. doi:10.1046/j.1365-294x.1999.00741.x.

Warner RR. 1988. Traditionality of mating-site preferences in a coral reef fish. Nature. 335(6192):719–721. doi:10.1038/335719a0.

Watkins WA, Schevill WE. 1977. Sperm whale codas. J Acoust Soc Am. 62(6):1485. doi:10.1121/1.381678.

Watson SK, Townsend SW, Schel AM, Wilke C, Wallace EK, Cheng L, West V, Slocombe KE. 2015. Vocal learning in the functionally referential food grunts of chimpanzees. Curr Biol. 25(4):495–499. doi:10.1016/j.cub.2014.12.032.

Watts DP, Mitani JC, Sherrow HM. 2002. New cases of inter-community infanticide by male chimpanzees at Ngogo, Kibale National Park, Uganda. Primates. 43(4):263–270.

Watts DP, Muller M, Amsler SJ, Mbabazi G, Mitani JC. 2006. Lethal intergroup aggression by chimpanzees in Kibale National Park, Uganda. Am J Primatol. 68(2):161–180. doi:10.1002/ajp.20214.

Watwood SL, Miller PJO, Johnson M, Madsen PT, Tyack PL. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*).J Anim Ecol. 75(3):814–825.

Weilgart L, Whitehead H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behav Ecol Sociobiol. 40:277–285.

Weilgart LS. 2007. The impacts of anthropogenic ocean noise on cetaceans and implications for management. Can J Zool. 85(11):1091–1116. doi:10.1139/Z07-101.

White T. 2003. Paleoanthropology. Early hominids--diversity or distortion? Science. 299(5615):1994–1997.

Whitehead H, Weilgart L. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour. 118(3/4):275–296.

Whitehead H, Christal J, Dufault S. 1997. Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. Conserv Biol. 11(6):1387–1396.

Whitehead H. 2001. Analysis of animal movement using opportunistic individual identifications: application to sperm whales. Ecology. 82:1417–1432.

Whitehead H. 2003. Sperm whales: social evolution in the ocean. University of Chicago Press.

Whitehead H, Rendell L. 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. J Anim Ecol. 73(1):190–196.

Whitehead H, Rendell L, Osborne RW, Würsig B. 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biol Conserv. 120(3):427–437. doi:10.1016/j.biocon.2004.03.017.

Whitehead H. 2005. Genetic diversity in the matrilineal whales: models of cultural hitchhiking and group-specific non-heritable demographic variation. Mar Mam Sci. 21(1):58–79. doi:10.1111/j.1748-7692.2005.tb01208.x.

Whitehead H, Wimmer T. 2005. Heterogeneity and the mark-recapture assessment of the Scotian Shelf population of northern bottlenose whales (*Hyperoodon ampullatus*). Can J Fish Aquat Sci. 62(11):2573–2585. doi:10.1139/f05-178.

Whitehead H. 2007. Learning, climate and the evolution of cultural capacity. J Theor Biol. 245(2):341–350. doi:10.1016/j.jtbi.2006.10.001.

Whitehead H, Coakes A, Jaquet N, Lusseau S. 2008a. Movements of sperm whales in the tropical Pacific. Mar Ecol Prog Ser. 361:291–300. doi:10.3354/meps07412.

Whitehead Hal, McGill B, Worm B. 2008b. Diversity of deep-water cetaceans in relation to temperature: implications for ocean warming. Ecol Lett. 11(11):1198–1207.

Whitehead H. 2009. SOCPROG programs: analysing animal social structures. Behav Ecol Sociobiol. 63(5):765–778. doi:10.1007/s00265-008-0697-y.

Whitehead H. 2010. Conserving and managing animals that learn socially and share cultures. Learn Behav. 38(3):329–336. doi:10.3758/LB.38.3.329.

Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D, Rendell L. 2012. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? Int J Primatol. 33(5):1142–1164. doi:10.1007/s10764-012-9598-z.

Whitehead H, Gero S. 2015. Conflicting rates of increase in the sperm whale population of the Eastern Caribbean: positive observed rates do not reflect a healthy population. Endanger Species Res. 27(3):207–218. doi:10.3354/esr00657.

Whitehead H, Rendell L. 2015. The cultural lives of whales and dolphins. University of Chicago Press.

Whitehead H, Vachon F, Frasier TR. 2017. Cultural hitchhiking in the matrilineal whales. Behav Genet. 47(3):324–334. doi:10.1007/s10519-017-9840-8.

Whitehead H, Ford JKB. 2018. Consequences of culturally-driven ecological specialization: killer whales and beyond. J Theor Biol. 456:279–294. doi:10.1016/j.jtbi.2018.08.015.

Whitehead H, Laland KN, Rendell L, Thorogood R, Whiten A. 2019. The reach of gene–culture coevolution in animals. Nat Commun. 10(1).

Whitehead H, Hersh TA. 2022. Posterior probabilities of membership of repertoires in acoustic clades. PLOS One. 17(4):e0267501. doi:10.1371/journal.pone.0267501.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CE, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. Nature. 399(6737):682–685.

Whiten A. 2005. The second inheritance system of chimpanzees and humans. Nature. 437(7055):52–55.

Whiten A, Horner V, de Waal FBM. 2005. Conformity to cultural norms of tool use in chimpanzees. Nature. 437(7059):737–740.

Whiten A, van Schaik CP. 2007. The evolution of animal "cultures" and social intelligence. Philos Trans R Soc Biol Sci. 362(1480):603–620.

Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ, de Waal FBM. 2007. Transmission of multiple traditions within and between chimpanzee groups. Curr Biol. 17(12):1038–1043. doi:10.1016/j.cub.2007.05.031.

Whiten A. 2011. The scope of culture in chimpanzees, humans and ancestral apes. Philos Trans R Soc Biol Sci. 366(1567):997–1007.

Whiten A. 2017. A second inheritance system: the extension of biology through culture. Interface Focus. 7(5):20160142. doi:10.1098/rsfs.2016.0142.

Whiten A, van de Waal E. 2017. Social learning, culture and the 'socio-cultural brain' of human and non-human primates. Neurosci Biobehav Rev. 82:58–75. doi:10.1016/j.neubiorev.2016.12.018.

Whiten A. 2019. Cultural evolution in animals. Annu Rev Ecol Evol Syst. 50(1):27–48. doi:10.1146/annurev-ecolsys-110218-025040.

Whiten A. 2021. The burgeoning reach of animal culture. Science. 372(6537):eabe6514. doi:10.1126/science.abe6514.

Wild S, Allen SJ, Krützen M, King SL, Gerber L, Hoppitt WJE. 2019. Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. Biol Lett. 15(7):20190227. doi:10.1098/rsbl.2019.0227.

Wild S, Hoppitt WJE, Allen SJ, Krützen M. 2020. Integrating genetic, environmental, and social networks to reveal transmission pathways of a dolphin foraging innovation. Curr Biol. 30(15):3024-3030.e4. doi:10.1016/j.cub.2020.05.069.

Wiley RH. 2013. Signal detection, noise, and the evolution of communication. In: Brumm H, editor. Animal Communication and Noise. Berlin, Heidelberg: Springer. (Animal Signals and Communication). p. 7–30.

Wiley RH. 2017. How noise determines the evolution of communication. Anim Behav. 124:307–313. doi:10.1016/j.anbehav.2016.07.014.

Wilson DS. 1975. A theory of group selection. PNAS. 72(1):143–146.

Wilson AC. 1985. The molecular basis of evolution. Sci Am. 253(4):164–175.

Wilson ML, Wrangham RW. 2003. Intergroup relations in chimpanzees. Annu Rev Anthropol. 32:363–392.

Wilson ML, Boesch C, Fruth B, Furuichi T, Gilby IC, Hashimoto C, Hobaiter CL, Hohmann G, Itoh N, Koops K, et al. 2014. Lethal aggression in *Pan* is better explained by adaptive strategies than human impacts. Nature. 513(7518):414–417.

Wiszniewski J, Corrigan S, Beheregaray LB, Möller LM. 2012. Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). J Anim Ecol. 81(2):423–431.

Wittig RM, Boesch C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. Int J Primatol. 24(4):847–867. doi:10.1023/A:1024632923180.

Wong SNP, Whitehead H. 2014. Seasonal occurrence of sperm whales (*Physeter macrocephalus*) around Kelvin Seamount in the Sargasso Sea in relation to oceanographic processes. Deep Sea Res Part I Oceanogr Res Pap. 91:10–16. doi:10.1016/j.dsr.2014.05.001.

Wrangham RW. 1999. Evolution of coalitionary killing. Am J Phys Anthropol. 110(S29):1–30.

Wrangham RW, Glowacki L. 2012. Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: evaluating the chimpanzee model. Hum Nat. 23(1):5–29.

Wrangham RW. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Primate males. Cambridge University Press. p. 278–313.

Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time. Trends Ecol Evol. 16(8):446–453. doi:10.1016/S0169-5347(01)02205-4.

Yoder JB, Clancey E, Roches SD, Eastman JM, Gentry L, Godsoe W, Hagey TJ, Jochimsen D, Oswald BP, Robertson J, et al. 2010. Ecological opportunity and the origin of adaptive radiations. J Evol Biol. 23(8):1581–1596. doi:10.1111/j.1420-9101.2010.02029.x.

Zalloua PA, Xue Y, Khalife J, Makhoul N, Debiane L, Platt DE, Royyuru AK, Herrera RJ, Hernanz DFS, Blue-Smith J, et al. 2008. Y-chromosomal diversity in Lebanon is structured by recent historical events. Am J Hum Genet. 82(4):873–882. doi:10.1016/j.ajhg.2008.01.020.

Zdaniuk B, Levine JM. 2001. Group loyalty: impact of members' identification and contributions. J Exp Soc Psychol. 37(6):502–509. doi:10.1006/jesp.2000.1474.

Zefferman MR, Mathew S. 2015. An evolutionary theory of large-scale human warfare: group-structured cultural selection. Evol Anthropol. 24(2):50–61. doi:10.1002/evan.21439.

Zohar O, Terkel J. 1996. Social and environmental factors modulate the learning of pine-cone stripping techniques by black rats, *Rattus rattus*. Anim Behav. 51(3):611–618. doi:10.1006/anbe.1996.0065.

APPENDIX A: Chapter 3 Supplement

A3.1 - Table S3.1. Identity coda proportion results (overall and clan specific) using different parameters. The baseline parameters were used for analysis. crtifact corresponds to the factor by which the mean usage of a coda type must be higher in a given clade than in all other clades to be considered an identity coda and minrep the minimum number of repertoires required to form a clan. Similarity is the percentage of repertoires that share the same vocal clan assignation as in the baseline tree.

	crtifact	*minrep*	Number of identity coda types	Number of vocal clans produced	Overall identity coda proportion	EC1 identity coda proportion	EC2 identity coda proportion	EC3 identity coda proportion	Similarity
Baseline	8	5	10	3	55.8%	54.2%	60.7%	57.4%	
	5	5	11	5	32.6%				67.2%
	10	5	10	3	61.3%	62.4%	60.7%	41%	100%
	15	5	9	2	48.9%	47.4%	53%		97.8%
	20	5	7	2	47.5%	47.4%	47.9%		97.8%
	8	2	17	4	24.6%	14.9%	49%	57.4%	100%
	8	3	6	3	24.1%	14.9%	49%	57.4%	100%
	8	4	9	3	48%	43.7%	60.7%	57.4%	100%
	8	8	10	2	61.2%	62.4%	57.9%		97.8%
	8	10	11	2	62.1%	62.4%	61.3%		97.8%

A3.2 - Table S3.2. Total number of codas from each group/social unit from each year that were included in this analysis. Codas that were recorded on days with multiple social units/groups were assigned to both social units/groups in this table (apart from units F and U which are recorded separately since the units merged). The code in parentheses refers to whether the codas were recorded during the Eastern Caribbean surveys (ECS), by the Dominica Sperm Whale Project (DSWP), or from the Watkins Marine Mammal Sound Dataset (WAT).

Social Unit/ Group ID	Year	Number of codas
Unit A	2008 (DSWP)	40
	2009 (DSWP)	30
	2010 (DSWP)	202
	2014 (DSWP)	162
	2015 (DSWP)	1212
	2016 (DSWP)	45
	2018 (DSWP)	225
	2019 (ECS + DSWP)	389
Group D	2008 (DSWP)	155
	2010 (DSWP)	263
Unit F	2005 (DSWP)	324
	2008 (DSWP)	28
	2010 (DSWP)	648
Unit FU	2009 (DSWP)	32
	2010 (DSWP)	146
	2015 (DSWP)	853
	2019 (DSWP)	212
Unit H	2018 (DSWP)	329
Unit J	2007 (DSWP)	40
	2008 (DSWP)	221
	2009 (DSWP)	112
	2010 (DSWP)	221
	2014 (DSWP)	51
	2015 (DSWP)	217
	2016 (DSWP)	246
	2019 (ECS + DSWP)	114
	2020 (ECS)	466
Unit K	2012 (DSWP)	426
	2019 (ECS)	88
	2020 (ECS)	143
Unit L	2019 (DSWP)	67
	2020 (ECS)	300
Unit N	2009 (DSWP)	52
	2010 (DSWP)	201
	2015 (DSWP)	245
	2019 (ECS)	185

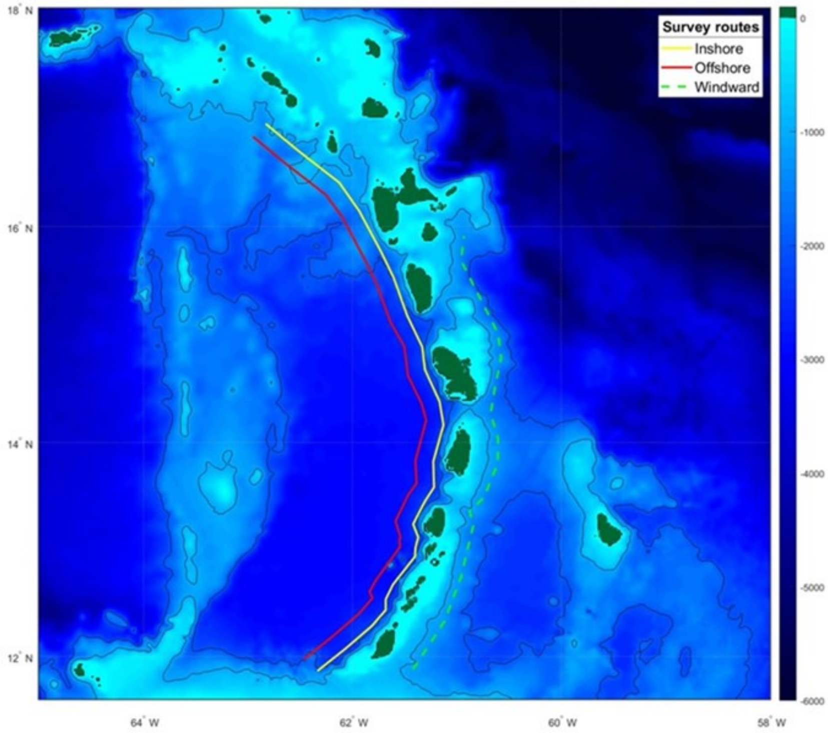
	2020 (ECS)	73
Unit P	2008 (DSWP)	272
	2011 (DSWP)	116
Unit R	2008 (DSWP)	307
	2018 (DSWP)	136
Group S	2014 (DSWP)	189
	2015 (DSWP)	276
	2018 (DSWP)	39
Unit T	2010 (DSWP)	710
Unit U	2009 (DSWP)	29
	2010 (DSWP)	91
	2015 (DSWP)	411
Unit V	2010 (DSWP)	756
Unit X	2018 (DSWP)	161
	2019 (ECS)	212
Unit Y	2020 (ECS)	345
Unit Z	2019 (ECS)	70
	2020 (ECS)	40
Group DD	2018 (DSWP)	175
Group EE	2016 (DSWP)	239
Group 1	2019 (ECS)	205
Group 2	2019 (ECS)	163
Group 3	2019 (ECS)	44
Unit 4	2019 (ECS)	334
	2020 (ECS)	35
Unit 5	2019 (ECS)	172
Group 6	2019 (ECS)	180
Unit 7	2019 (ECS)	116
	2020 (ECS)	348
Group 8	2019 (ECS)	194
Group 10	2019 (ECS)	125
	2020 (ECS)	217
Group 11	2019 (ECS)	125
Unit 12	2019 (ECS)	52
	2020 (ECS)	577
Group 13	2020 (ECS)	217
Group 14	2020 (ECS)	198
Group 15	2020 (ECS)	231
Group 16	2020 (ECS)	410
Group 18	2020 (ECS)	512
Group 19	2020 (ECS)	300
Group 20	2020 (ECS)	314
Group 21	2020 (ECS)	198
Group 22	2020 (ECS)	84
Group 23	2020 (ECS)	59

Unknown	1981 (WAT)	390
	1983 (WAT)	36
	1984 (WAT)	230
	1987 (WAT)	44
	1990 (WAT)	703
	1992 (WAT)	102
	1993 (WAT)	359
	1994 (WAT)	74
	1995 (WAT)	102
	2009 (DSWP)	25
	2012 (DSWP)	123
	2015 (DSWP)	42
	2018 (DSWP)	191
	2019 (DSWP)	118

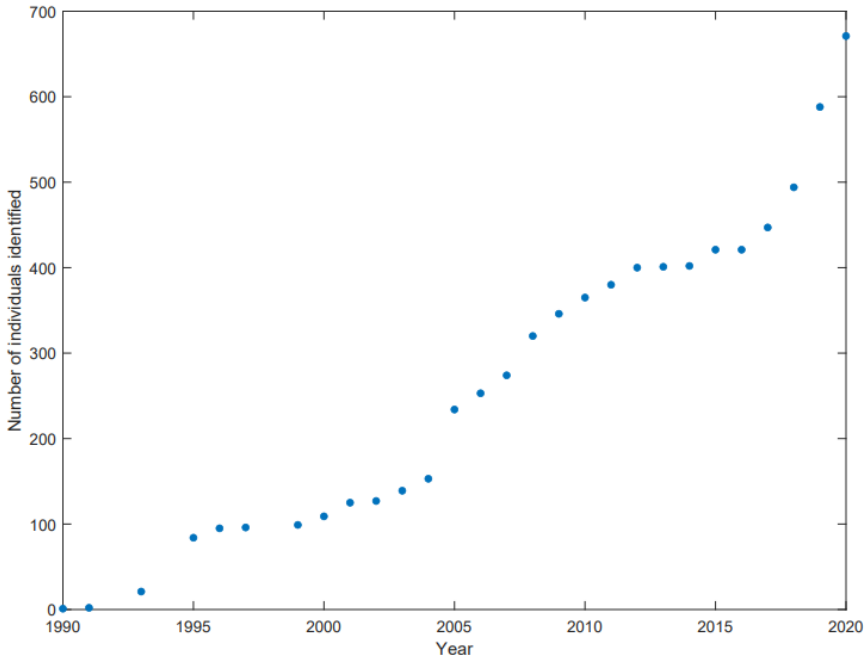
A3.3 - Table S3.3. All EC2 encounters from the DSWP database (from a total of 937 photo identifications encounters between 1990 and 2019).

Location	Unit	Dates
Dominica	P	Feb 1 1995
		Mar 25 1995
		Feb 6 2007
		March 3 2008
		March 5-6 2008
		April 24-25 2008
		March 5-6 2009
		March 5 2011
		May 23 2012
		May 26 2012
	H	February 26 2008
		March 1-2 2008
		May 11 2018
	K	March 11 2008
		June 2-3 2012
		May 1 2014
	X	April 20 2017
		March 30 2018
		April 14 2018
	Y	April 5 2017
		April 14 2017
		May 2 2018
Guadeloupe	P	Mar 7 2000
		Mar 22 2005

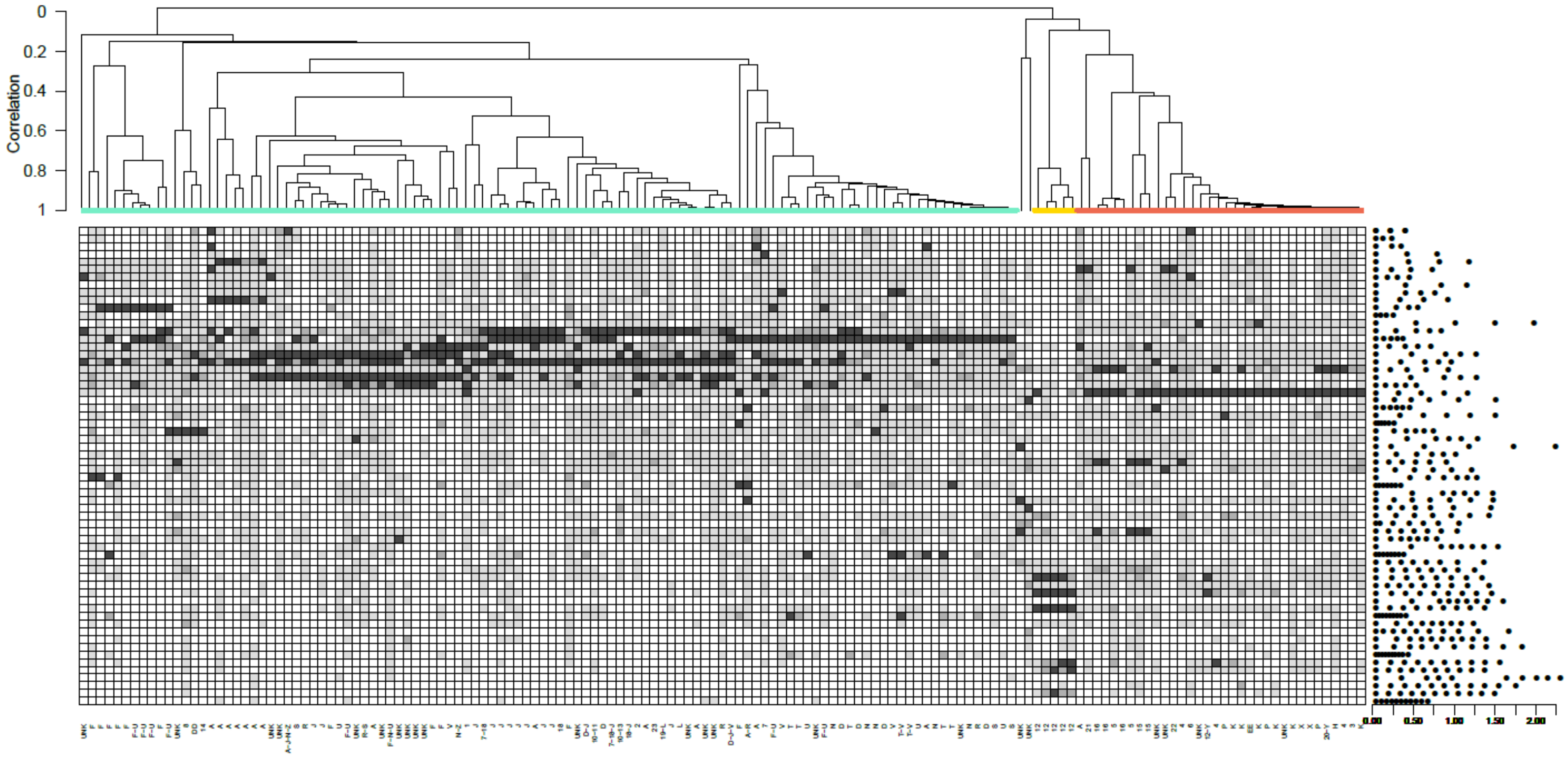
A3.4 - Figure S3.1. Planned survey routes for the 2019 and 2020 Eastern Caribbean field seasons.



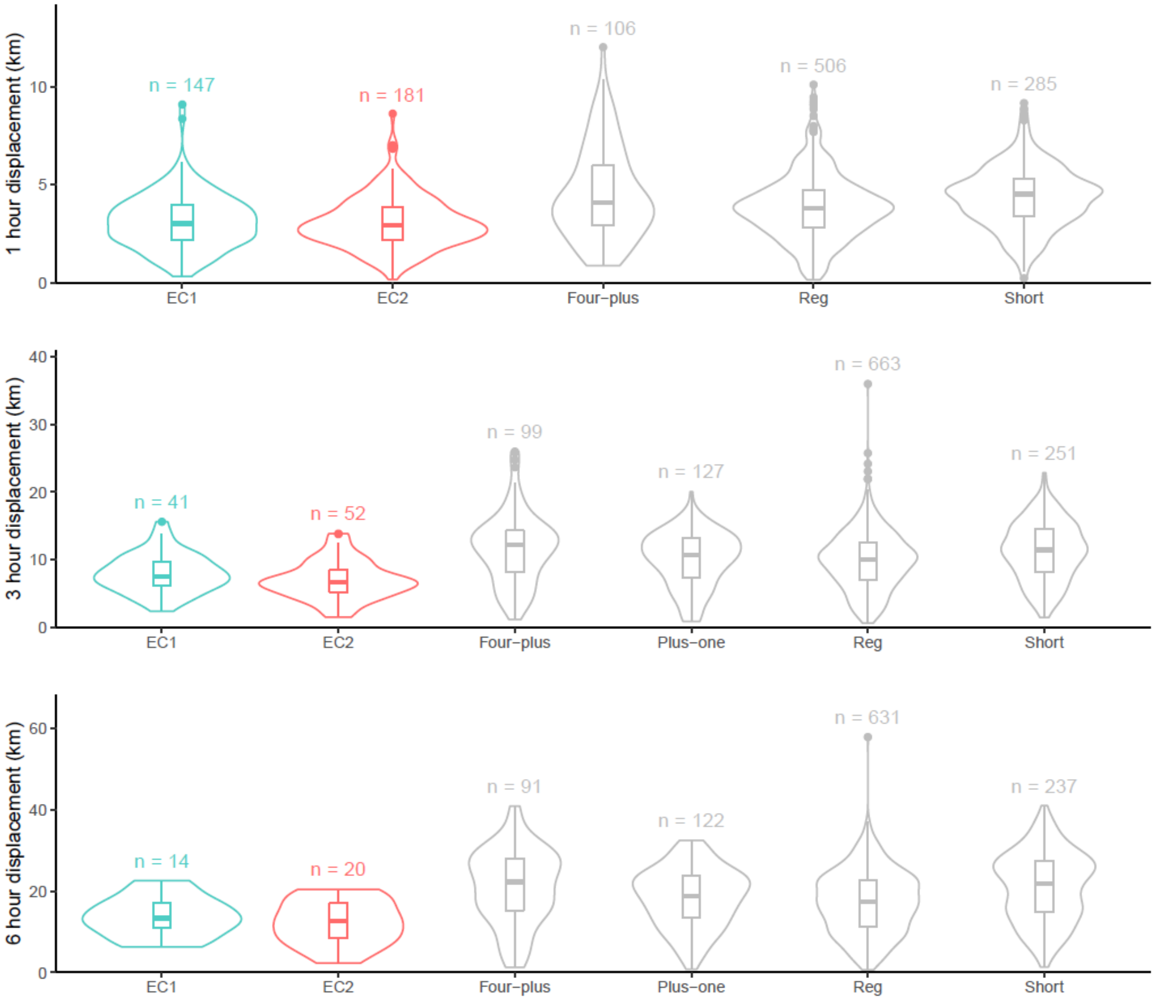
A3.5 - Figure S3.2. Discovery curve of Eastern Caribbean sperm whale individual identifications showing dramatic increase with Eastern Caribbean surveys in 2019 and 2020.



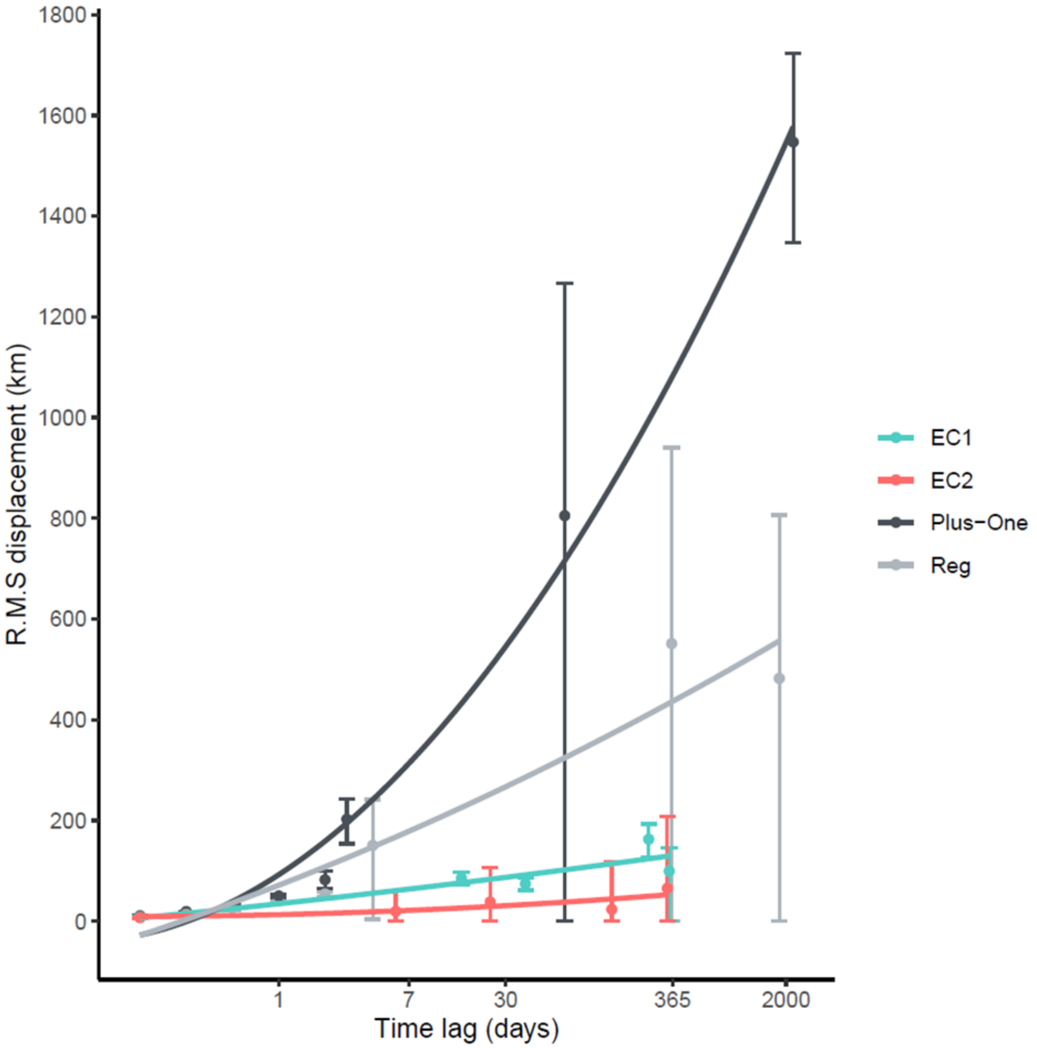
A3.6 - Figure S3.3. Average linkage hierarchical clustering dendrogram (top) depicting acoustic similarity among the three Eastern Caribbean sperm whale vocal clans: EC1 (blue), EC2 (red), and EC3 (yellow). Each branch corresponds to the coda repertoire of a certain group of sperm whales on a certain day (social unit letters and/or group ID numbers are displayed underneath each branch). Each row of the heat map (bottom) shows usage (calculated based on probabilistic assignment of codas to types) by repertoire of a coda type. Heat map shading corresponds to the percentage of the repertoire made up of each coda type with white 0%, light gray 0–5%, gray 5–10% and dark gray 10% or higher. Coda types are depicted to the right of the heat map by dots representing each click in the coda, and their length (in seconds) is displayed underneath. A version of this diagram showing only the identity codas is given in Figure 3.1 (main text).



A3.7 - Figure S3.4. Violin plots displaying the one-hour, three-hour and six-hour displacement of sperm whale vocal clans (Eastern Caribbean: EC1, EC2; Eastern Tropical Pacific: Four-Plus, Plus-One, Reg, Short). Sample size is displayed above each violin plot.



A3.8 - Figure S3.5. Root-mean-squared displacement for Eastern Caribbean vocal clans and Eastern Tropical Pacific vocal clans over increasing time-lags. Error bars display jackknife standard error. Root-mean-squared displacement was calculated using the likelihood method from Whitehead (2001) for time lags beyond 1 day for Eastern Caribbean (EC1 and EC2) data and 2 days for Eastern Tropical Pacific (Plus-One, Reg) data.



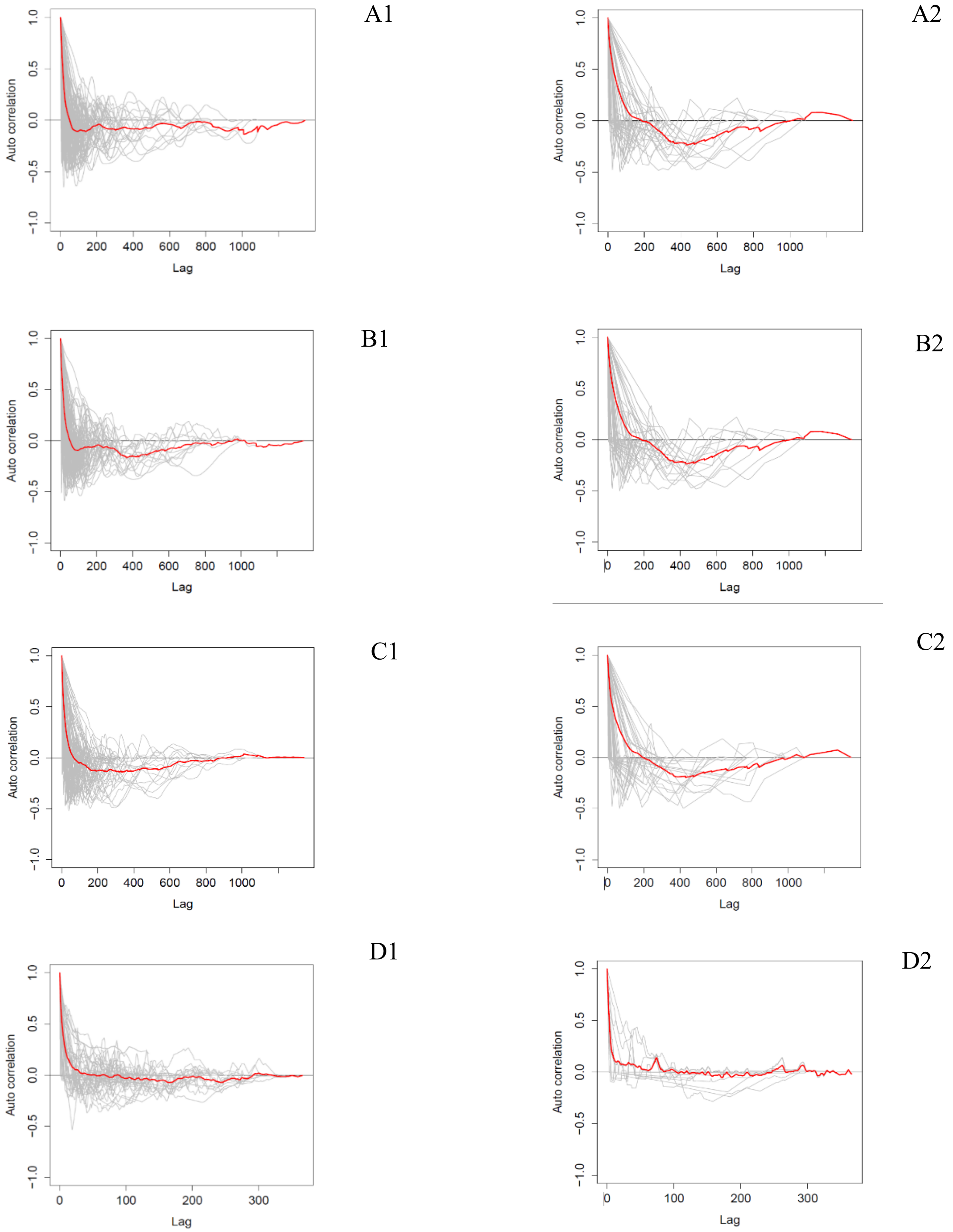
APPENDIX B: Chapter 4 Supplement

B4.1 - Table S4.1. Best variable combinations for each model type with associated QIC, AUC, goodness of fit and predictive accuracy (pre-cross validation).

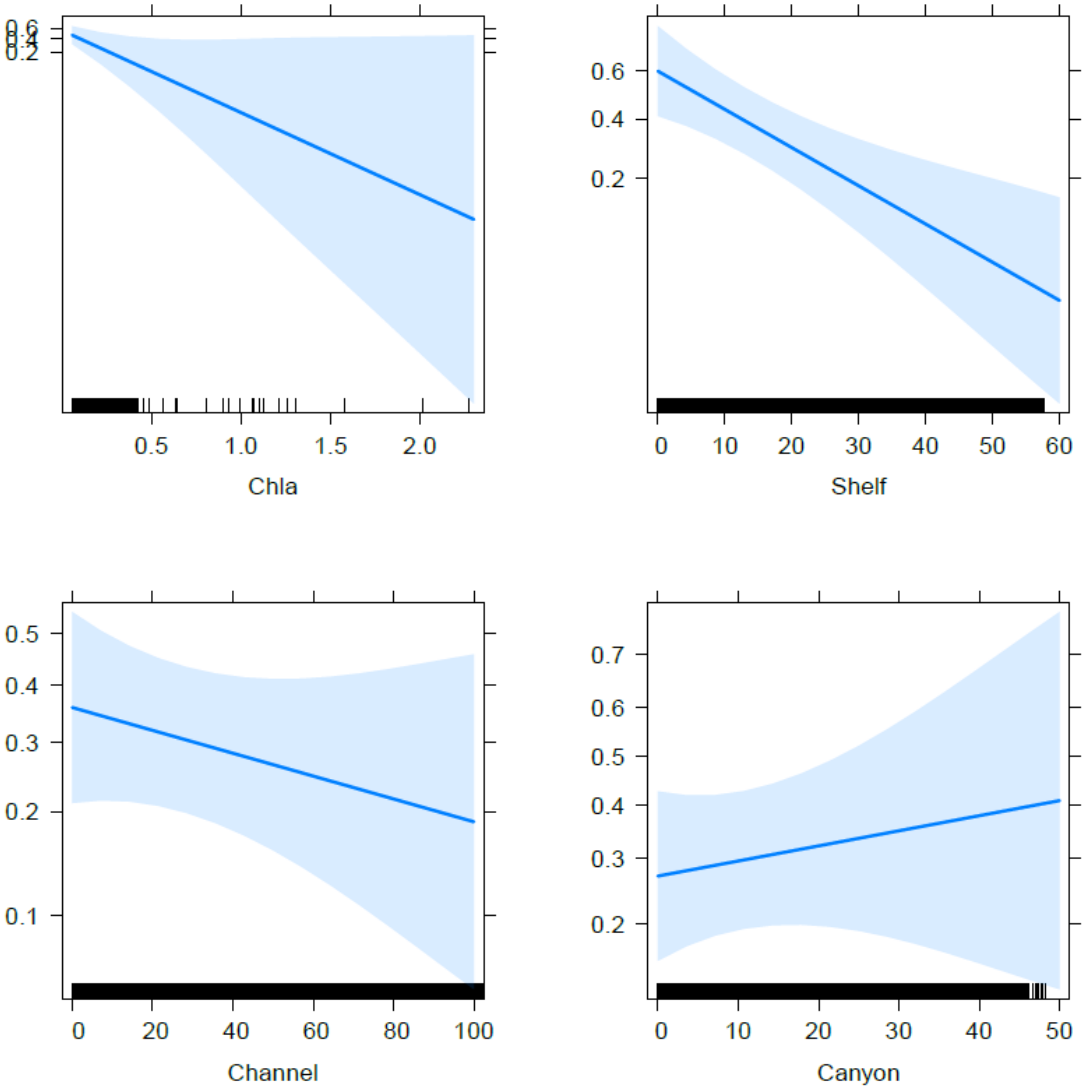
Model type	Variable type		QIC	AUC	Goodness of fit	Predictive accuracy (±SE)
Presence/ absence	Env	Windward* + Chla + Shelf + Zvelv* + Inflow* + Channel + Canyon	28541.9	0.765	68.98%	32.73% ±0.03
	Island	Windward + Island	30684.9	0.690	65.82%	59.61% ±0.04
EC1	Env	Ecurr + Windward + Escarp + Abyss + Zvelv	19006.3	0.786	77.14%	56.65% ±0.03
	Island	Windward + Island	15890.8	0.860	72.88%	72.05% ±0.04
EC2	Env	Mvelv + Windward + Inflow* + Chla + Channel + Depth + Zvelv	15710.9	0.879	74.55%	37.63% ± 0.03
	Island	Windward + Island	16020.8	0.833	73.19%	62.27% ±0.04
Vocal clan	Env	Ecurr + Channel* + Zvelv	5220.05	0.950	93.41%	46.26% ±0.03
	Island	Island	1118.3	0.99	96.5%	76.8% ± 0.14

* Variables removed by stepwise cross-validation

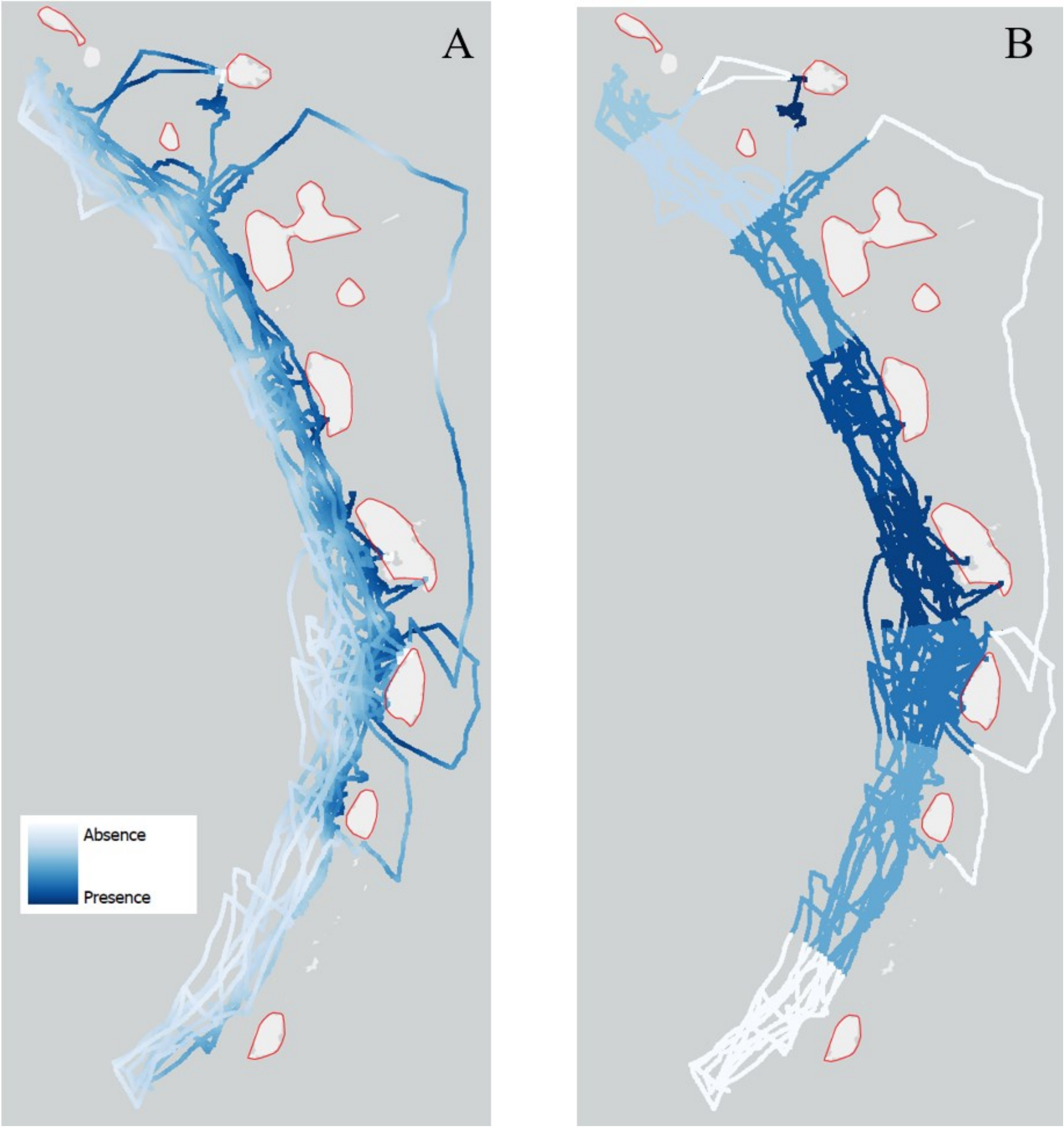
B4.2 – Figure S4.1. Auto correlation function (ACF) plots of residuals for the final models of the Presence/Absence (A), EC1 (B), EC2 (C) and Vocal clan (D) habitat models using the Environment (1) variable set and Island (2) variable set. Plots rapidly converge to zero, which suggests that encounter is an appropriate blocking variable.



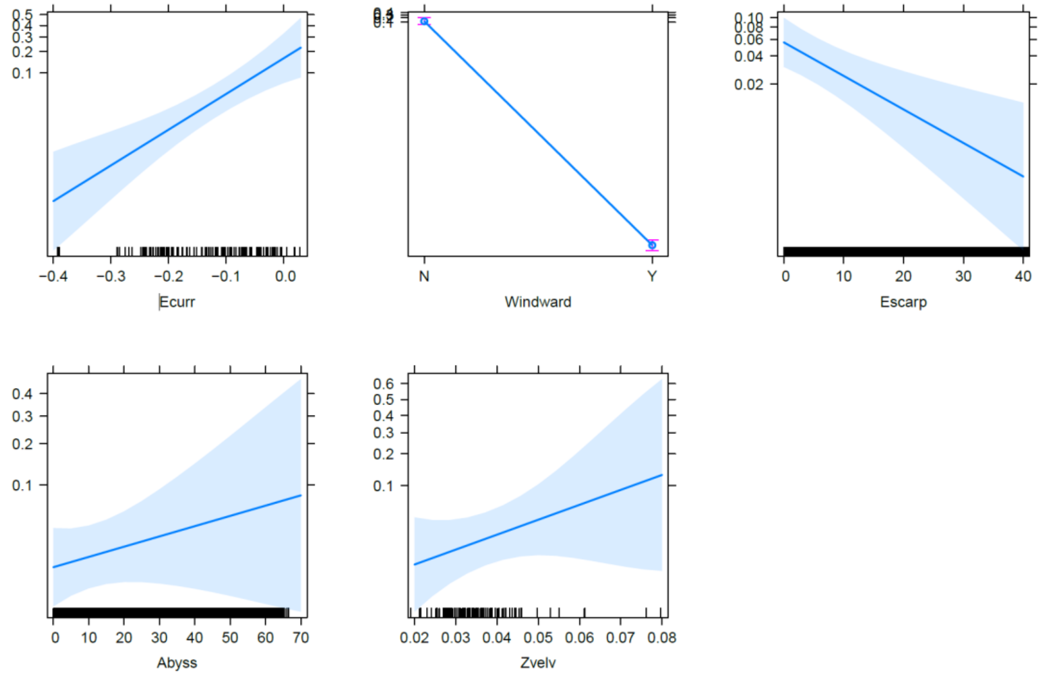
B4.3 - Figure S4.2. Effect plots of variables from the best Presence/Absence model (Pres ~ Chla + Shelf + Channel + Canyon).



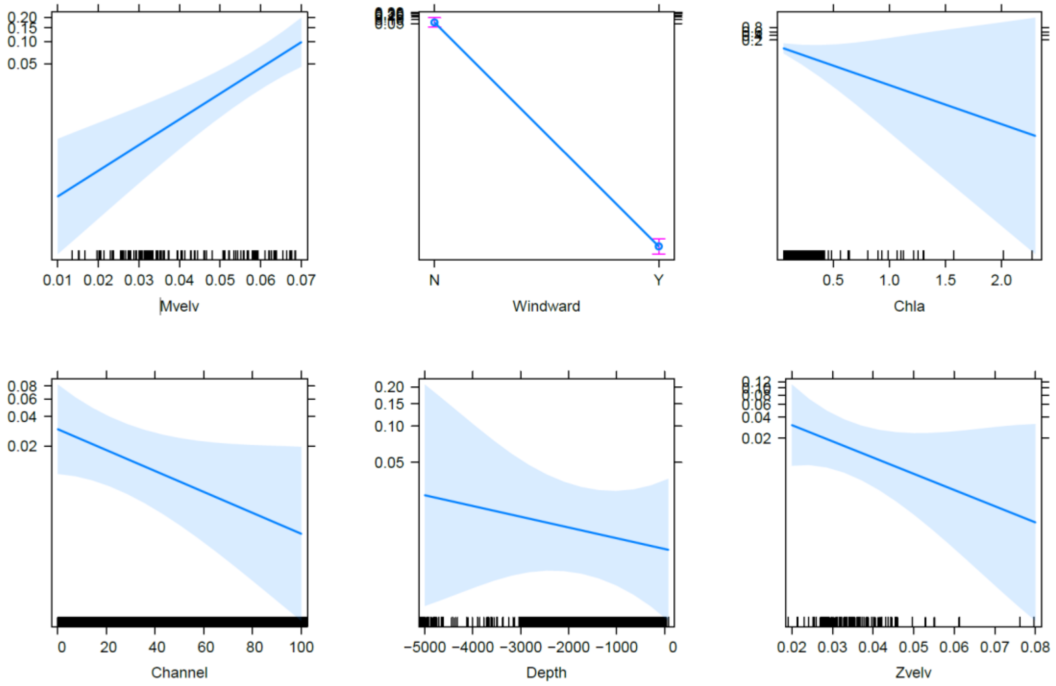
B4.4 – Figure S4.3. Prediction map of Eastern Caribbean sperm whale presence in the Lesser Antilles (Presence/Absence model). A) Environment variable set (Pres ~ Chla + Shelf + Channel + Canyon) B) Island variable set (Pres ~ Windward + Island).



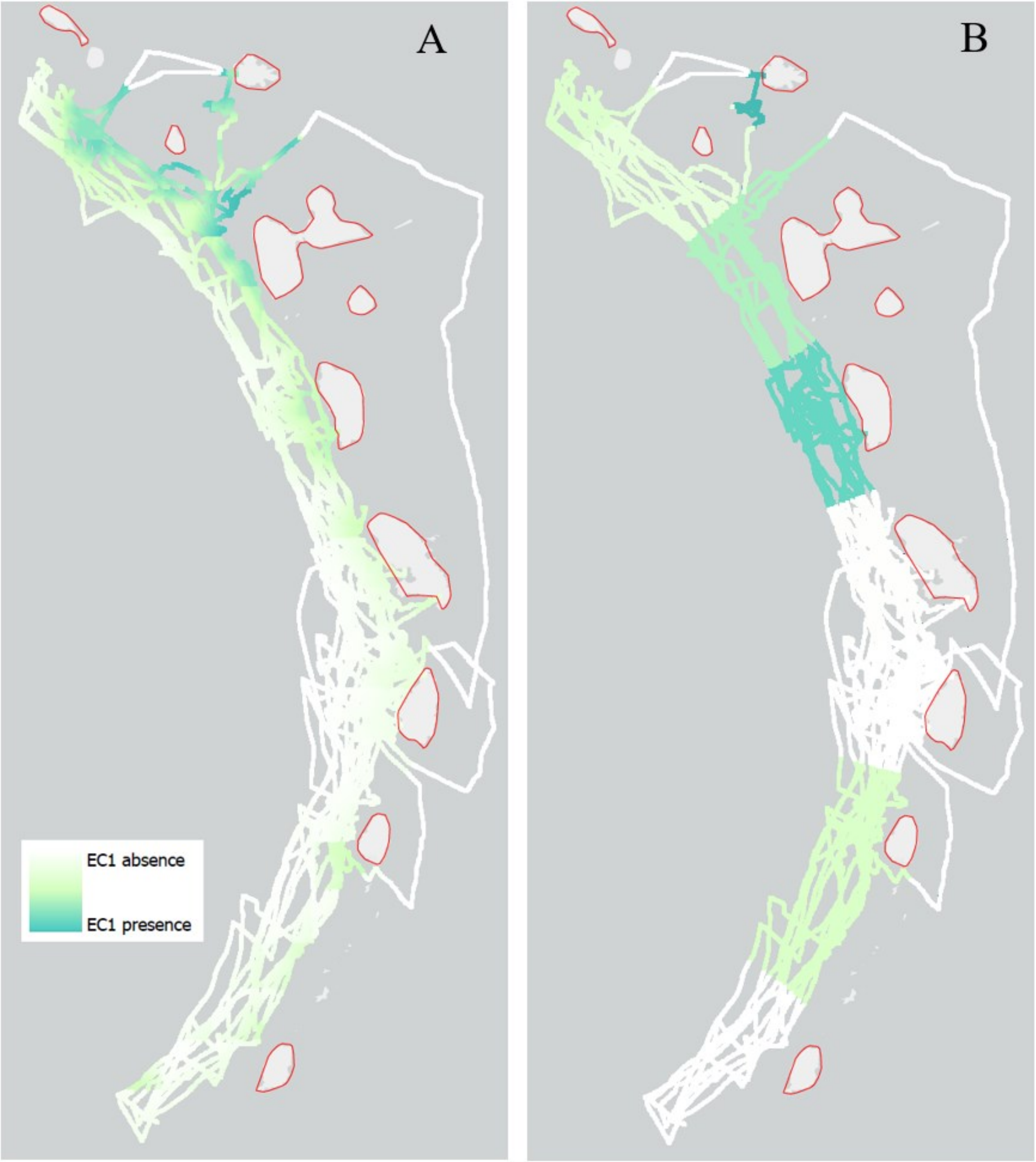
B4.5 - Figure S4.4. Effect plots of variables from the best EC1 model (Pres ~ Ecurr + Windward + Escarp + Abyss + Zvelv).



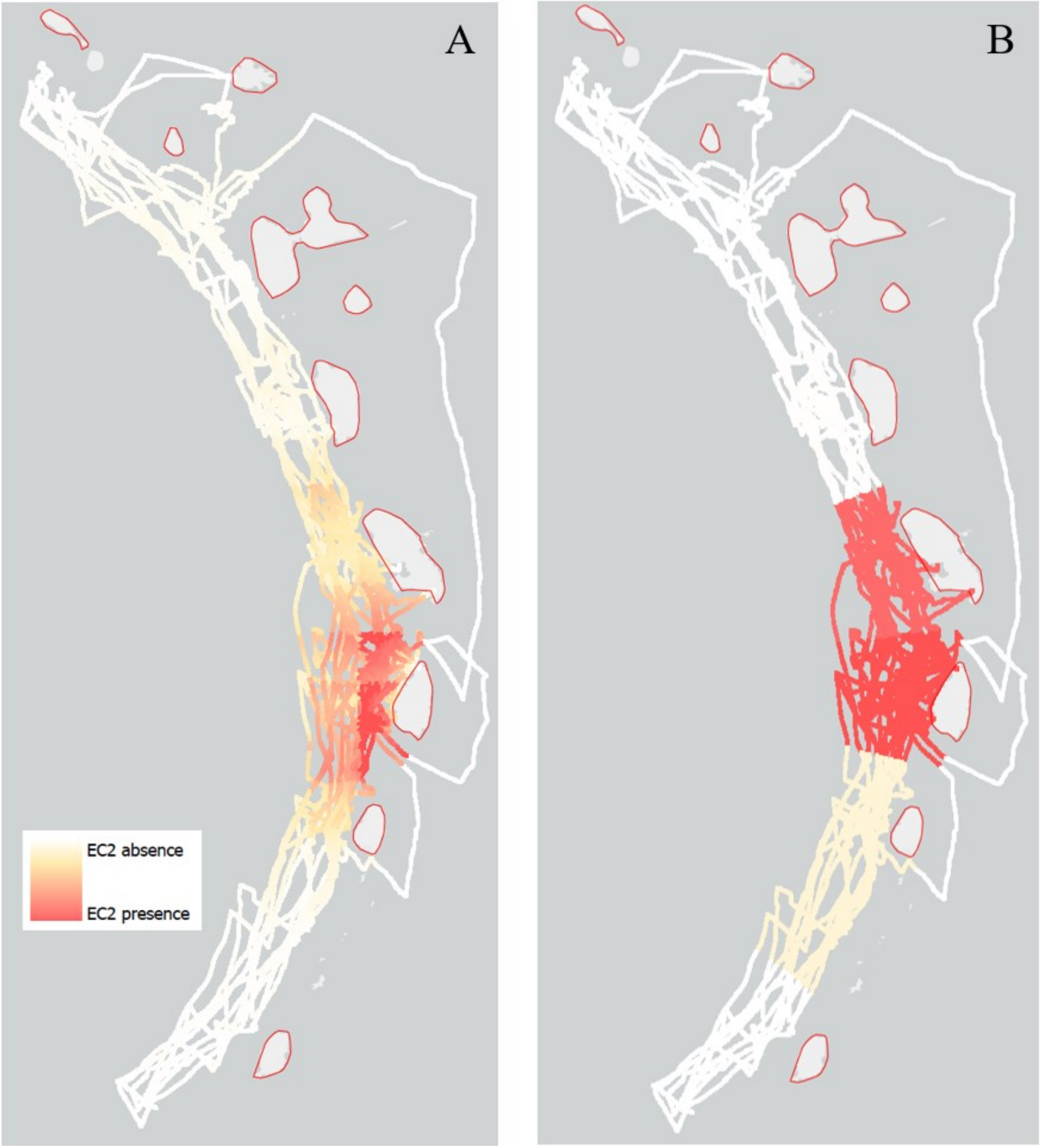
B4.6 - Figure S4.5. Effect plots of variables in the best *EC2* model (Pres ~ *Mvelv* + *Windward* + *Chla* + *Channel* + *Depth* + *Zvelv*).



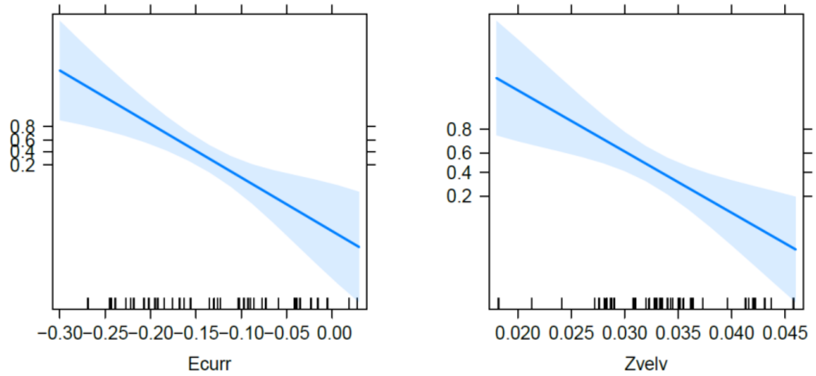
B4.7 - Figure S4.6. Prediction maps of EC1 sperm whale presence in the Lesser Antilles using the A) Environment variable set (Pres ~ Ecurr + Windward + Escarp + Abyss + Zvelv) B) Island variable set (Pres ~ Windward + Island).



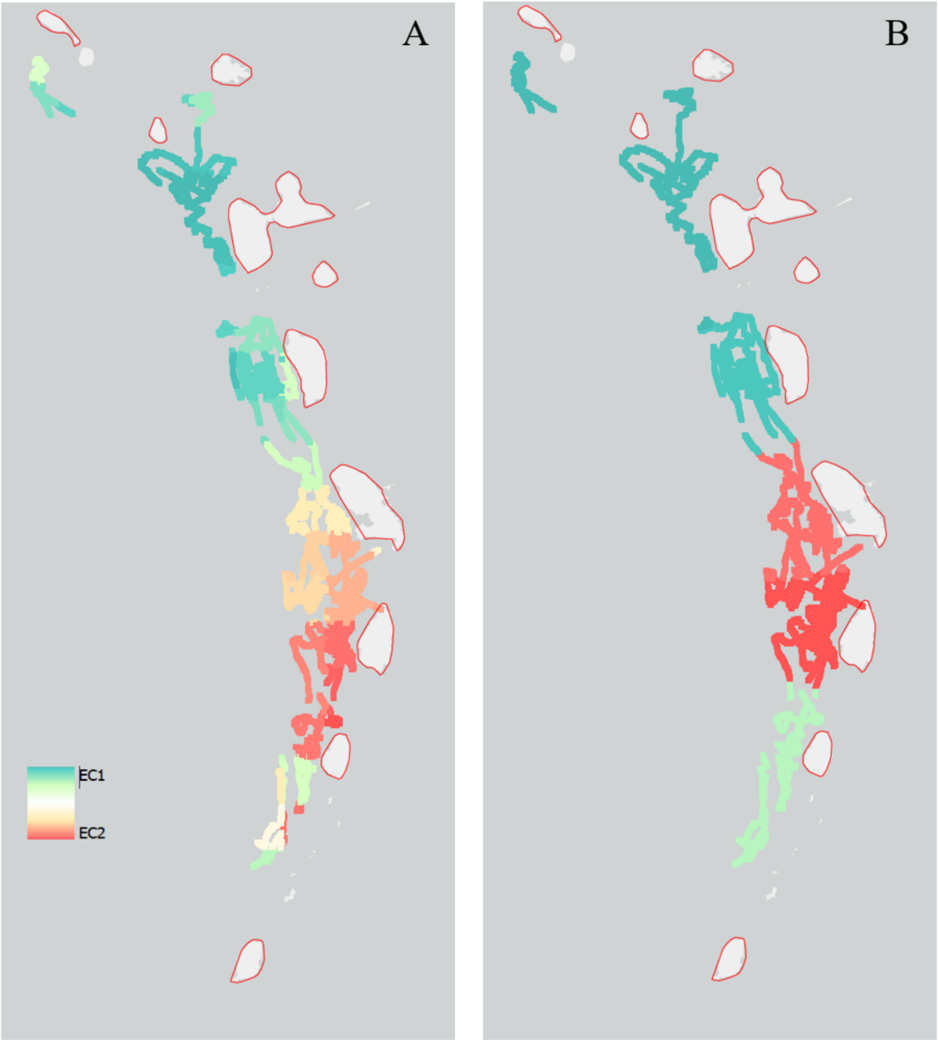
B4.8 - Figure S4.7. Prediction maps of EC2 sperm whale presence in the Lesser Antilles using the A) *Environment* variable set Pres ~ *Mvelv* + *Windward* + *Chla* + *Channel* + *Depth* + *Zvelv*) B) *Island* variable set (Pres ~ *Windward* + *Island*).



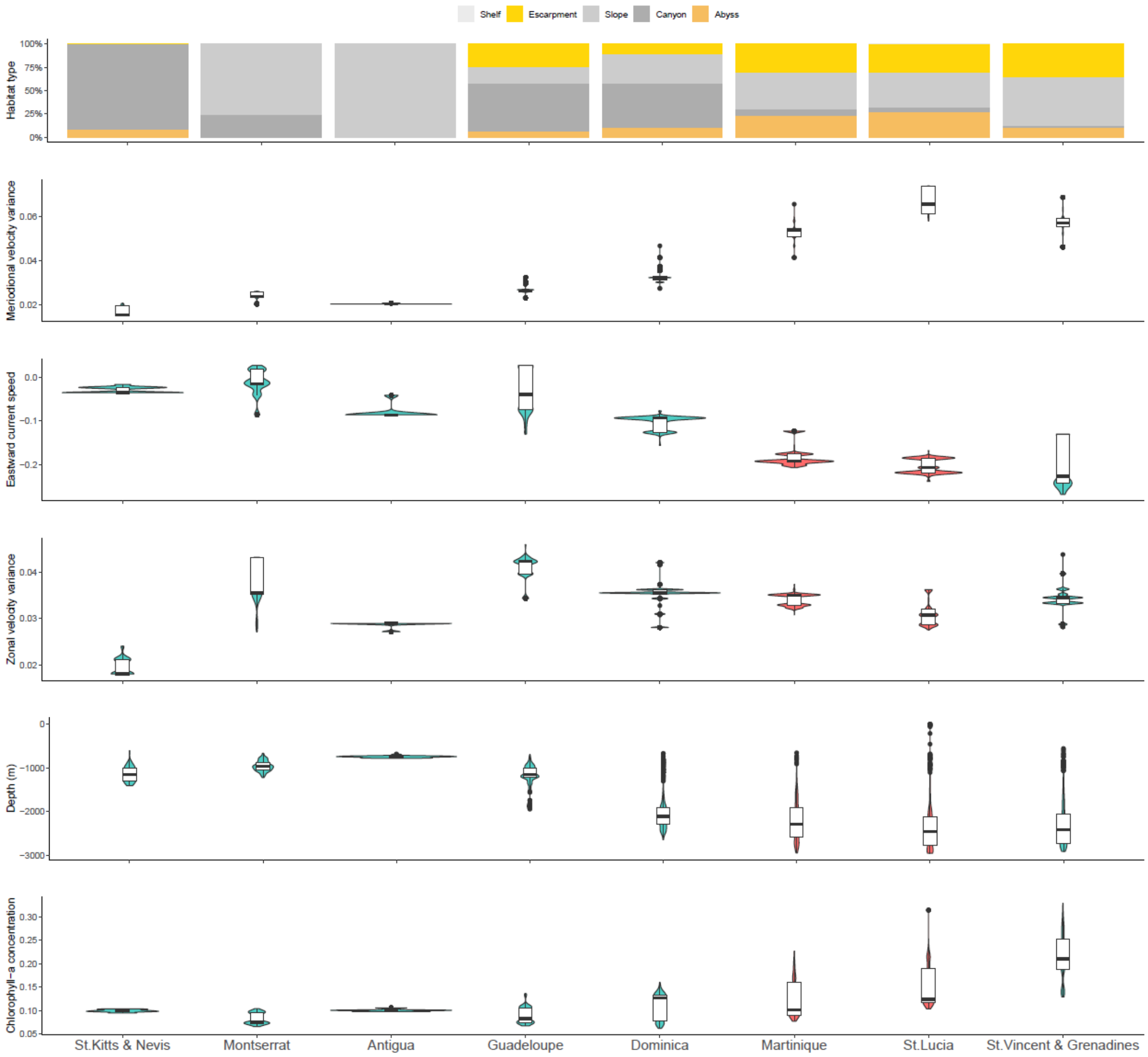
B4.9 - Figure S4.8. Effect plots of variables from the best *Vocal clan* model (Pres ~ *Ecurr* + *Zvelv*).



B4.10 -Figure S4.9. Prediction map of EC1 versus EC2 distribution in the Lesser Antilles (Vocal clan model). A) Environment variable set (Pres ~ Ecurr + Zvelv) B) Island variable set (Pres ~ Island).



B4.11 - Figure S4.10. Habitat suitability of EC1 (aquamarine) and EC2 (red) islands according to significant environmental variable range within sperm whale presence data points. No significant differences in variable values between EC1 and EC2 islands.



APPENDIX C: Chapter 6 Supplement

C6.1 – Table S6.1. Glossary of terms.

	Definition	Reference
Symbolic marker	Symbols that delineate and maintain cultural/ethnic group boundaries (e.g., language, clothing, music, religious symbol)	Barth 1969
Social unit (sperm whale)	Stable, core unit of sperm whale societies. 1-2 families of female, juvenile and calf sperm whales that always travel, forage and socialize together.	Christal et al. 1998
Group (sperm whale)	1-2 social units that associate over a few hours to days to forage and socialize.	Christal et al. 1998
Vocal clan (sperm whale)	Cultural tier of sperm whale societies. Sperm whales from different vocal clans have different acoustic repertoires and do not associate with each other, even if they occur in sympatry.	Rendell & Whitehead 2003b
Coda	3-12 patterned clicks that are used by sperm whales to socialize.	Watkins & Schevill 1977
Coda type	Categorization of codas based on their overall pattern of clicks.	Weilgart & Whitehead 1997
Interclick intervals (ICIs)	Quantitative measure of a coda's tempo that corresponds to the time between consecutive clicks.	Weilgart & Whitehead 1997
Identity coda types (ID coda)	Coda type used consistently by one vocal clan, and rarely, if ever, by others.	Hersh et al. 2021
Non-identity coda types (non-ID coda)	Coda types that do not qualify as identity coda types (sometimes shared across vocal clans).	Hersh et al. 2021
Repertoire	All codas recorded on a same day and, therefore, assumed to be a sample of a social unit/group dialect	Rendell & Whitehead 2003b

C6.2 - Table S6.2. Provenance of sperm whale codas included in this analysis.

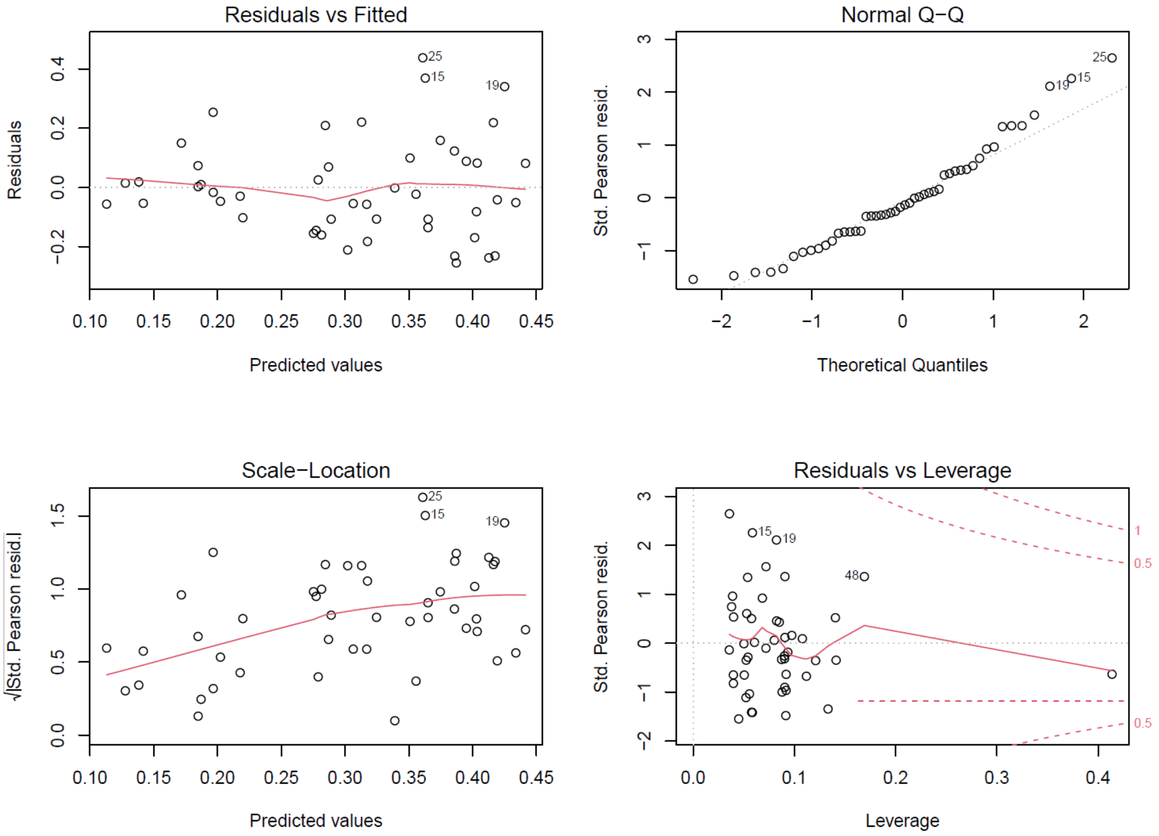
Geographical area	Organisation	Specific location	Years	Platform	Number of codas	Number of repertoires
Eastern Tropical Pacific	Watkins Marine Mammal Sound Database	Galapagos	1978	Marine mammal acoustic surveys	53	1
	Dalhousie University	Galapagos	1985, 1987, 1989, 1991, 1995, 1999, 2013-2014	Dedicated sperm whale surveys	10,262	107
Mediterranean	Balearic Sperm Whale Project	Balearic Islands	2004-2008, 2013, 2014, 2017, 2018	Dedicated research cruises	1,702	16
Eastern Caribbean	Watkins Marine Mammal Sound Database	Dominica, Canouan, Bequia, St. Lucia	1981-1995	Marine mammal acoustic surveys	1,683	15
	The Dominica Sperm Whale Project (DSWP)	Dominica	2005-2018	Dedicated sperm whale surveys, opportunistic data collection on whale watching vessels	10,480	91
	Dalhousie University	St.Kitts & Nevis, Antigua, Montserrat, Guadeloupe, Dominica, Martinique, St.Lucia, St.Vincent & Grenadines	2019-2020	Dedicated sperm whale surveys	5,434	44

C6.3 - Table S6.3. Coda types table with associated coda type category (ID or non-ID), vocal clan, geographical region (Eastern Tropical Pacific - ETP, Eastern Caribbean -EC, and Mediterranean -MED), sample size, repertoire size and volume. Excludes rare codas.

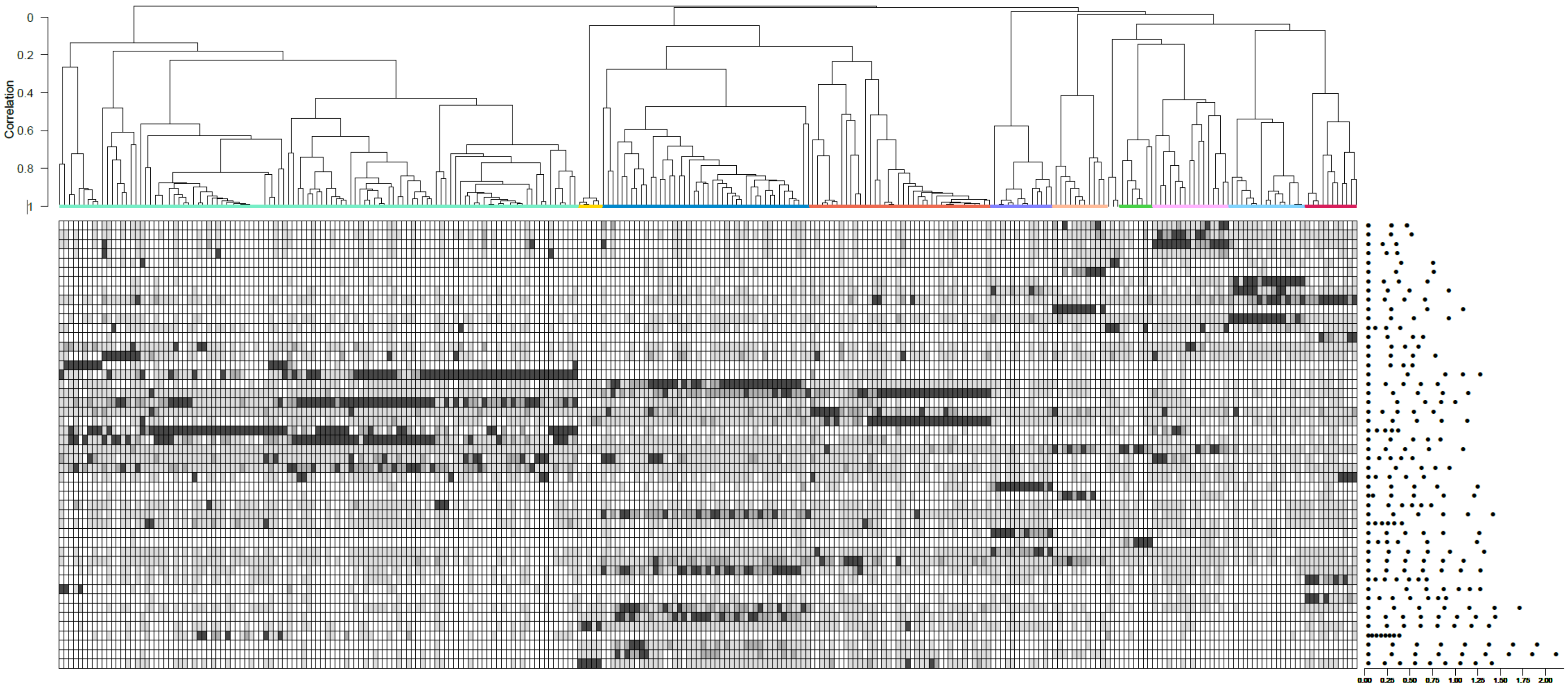
Click length	Coda type	Identity coda?	Vocal clan	Geographical region	Sample size	Volume
3	31		-		150	0.121
	32		-		214	0.356
	33	Yes	Short	ETP	321	0.142
	34		-		100	0.132
	35		-		76	0.120
	39	Yes	Slow Increasing	ETP	149	0.057
4	42	Yes	Mediterranean	MED	527	0.321
	43		-		346	0.218
	44		-		654	0.450
	45	Yes	Slow Increasing	ETP	177	0.088
	46		-		514	0.337
	48		-		256	0.260
	49	Yes	Palindrome	ETP	136	0.157
	410		-		209	0.533
	414		-		794	0.732
	415		-		263	0.135
5	51	Yes	EC1	EC	2929	0.321
	52	Yes	Regular	ETP	577	0.156
	53		-		1214	0.766
	54	Yes	EC1	EC	1475	0.304
	55		-		962	0.486
	56	Yes	EC2	EC	1797	0.252
	57	Yes	EC1	EC	1746	0.091
	58	Yes	EC1	EC	1594	0.182
	59		-		462	0.798
	510		-		770	0.133
	511		-		623	0.534
	512		-		400	0.333
	513	Yes	Plus-One	ETP	372	0.188
6	62	Yes	Slow Increasing	ETP	90	0.197
	63		-		201	0.229
	66		-		444	0.509
	67		-		202	0.258
	68	Yes	Plus-One	ETP	202	0.180
	69	Yes	Four-Plus	ETP	62	0.258
	611	Yes	Plus-One	ETP	201	0.450
	614		-		553	0.483
7	71		-		508	0.187
	72	Yes	Palindrome	ETP	165	0.118
	75		-		138	0.155
	710	Yes	Palindrome	ETP	140	0.188

	711		-		321	0.232
8	81		-		390	0.383
	82		-		184	0.635
	84		-		142	0.175
	810		-		220	0.378
9	99		-		170	0.523
	912	Yes	EC3	EC	305	0.494

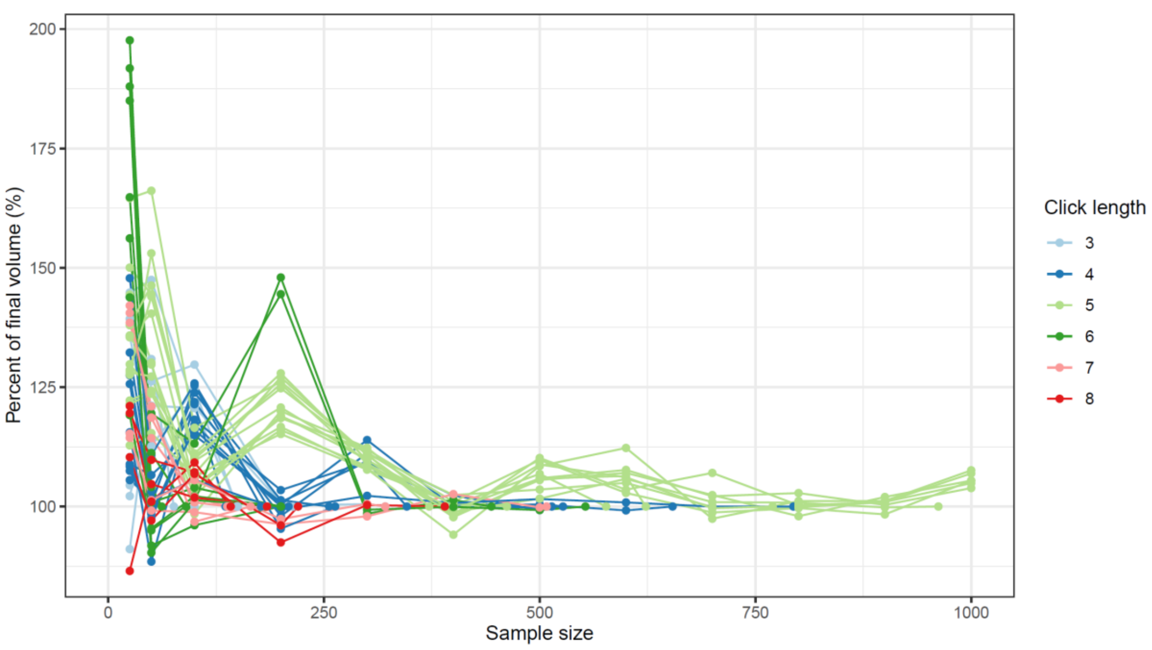
C6.4 – Figure S6.1. General linear model (GLM) assumptions for the coda type volume model.



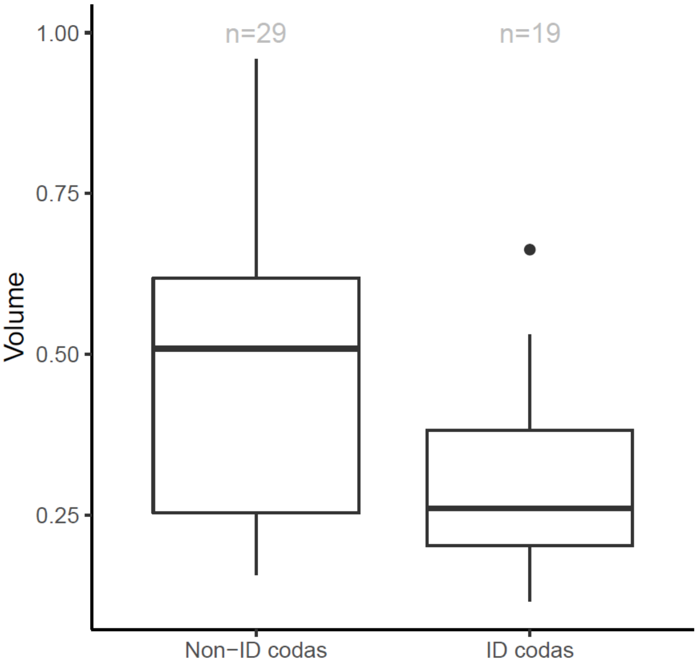
C6.5 - Figure S6.2. Average linkage hierarchical clustering dendrogram (top) depicting acoustic similarity among different vocal clans, left to right: EC1 (aqua), EC3 (yellow), Regular (blue), EC2 (orange), Plus-One (purple), Slow Increasing (peach), Four-Plus (green), Short (pink), Med (light blue), Palindrome (magenta). Each branch corresponds to the coda repertoire of a certain group of sperm whales on a certain day. Each row of the heat map (bottom) shows probabilistic usage by repertoire of an identity coda type. Heat map shading corresponds to the percentage of the repertoire made up of each identity coda type with white 0%, light gray 0–5%, gray 5–10%, and dark gray 10% or higher. Coda types are depicted to the right of the heat map by dots representing each click in the coda with duration in seconds underneath. We used parameters critfact =9, minrep = 5.



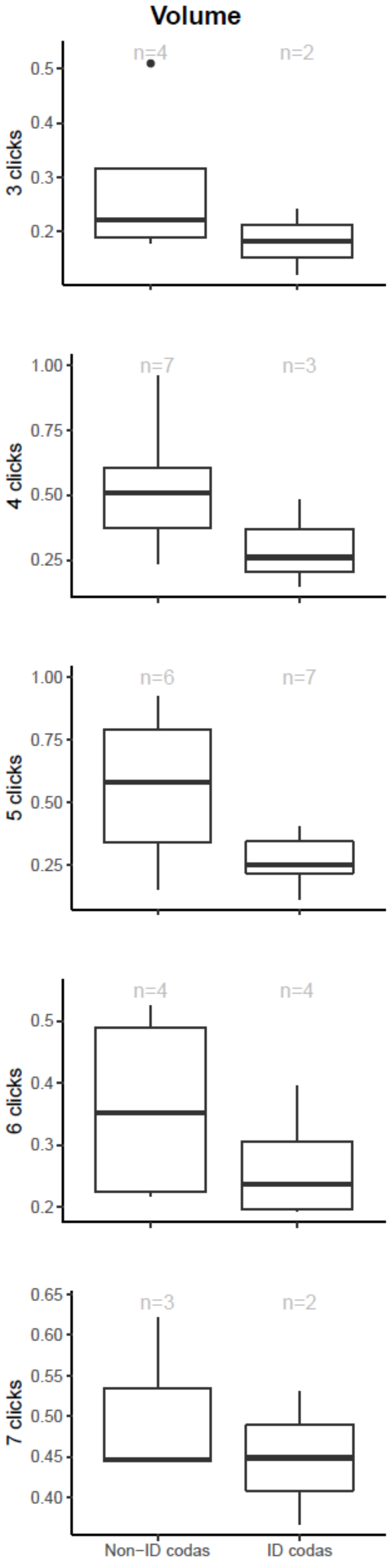
C6.6 - Figure S6.3. Depiction of the effect of sample size on coda type hypervolume volume value.



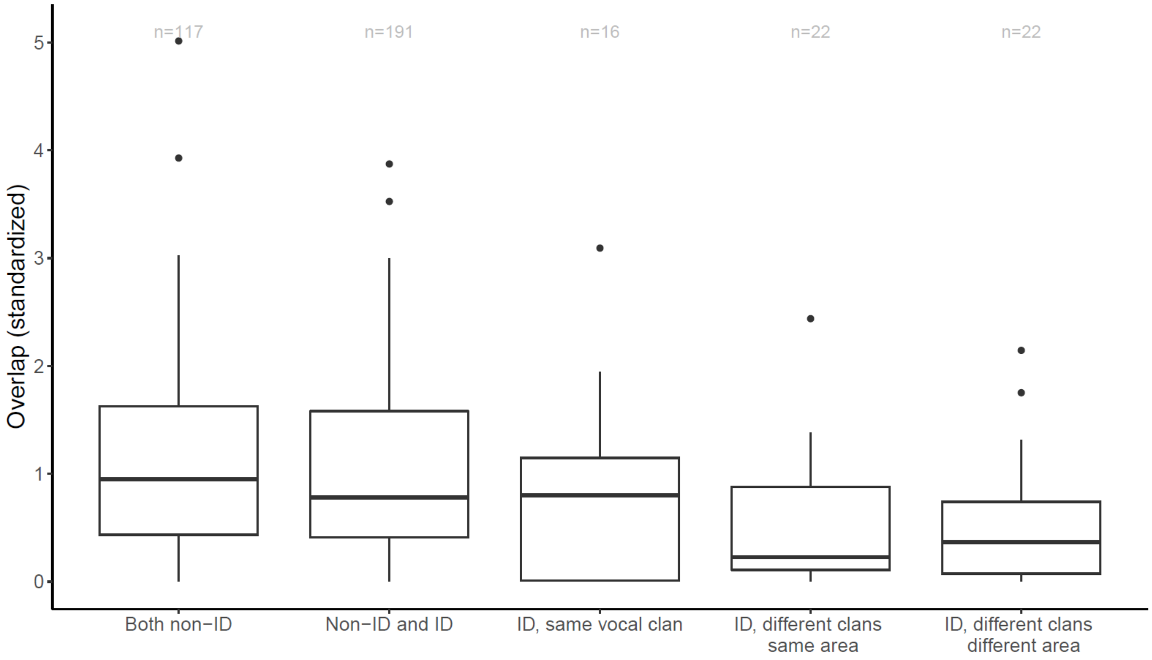
C6.7 – Figure S6.4. Coda type hypervolume volume for non-identity and identity coda types (all click lengths). Non-identity coda type's dataset is restricted to a single vocal clan per coda type.



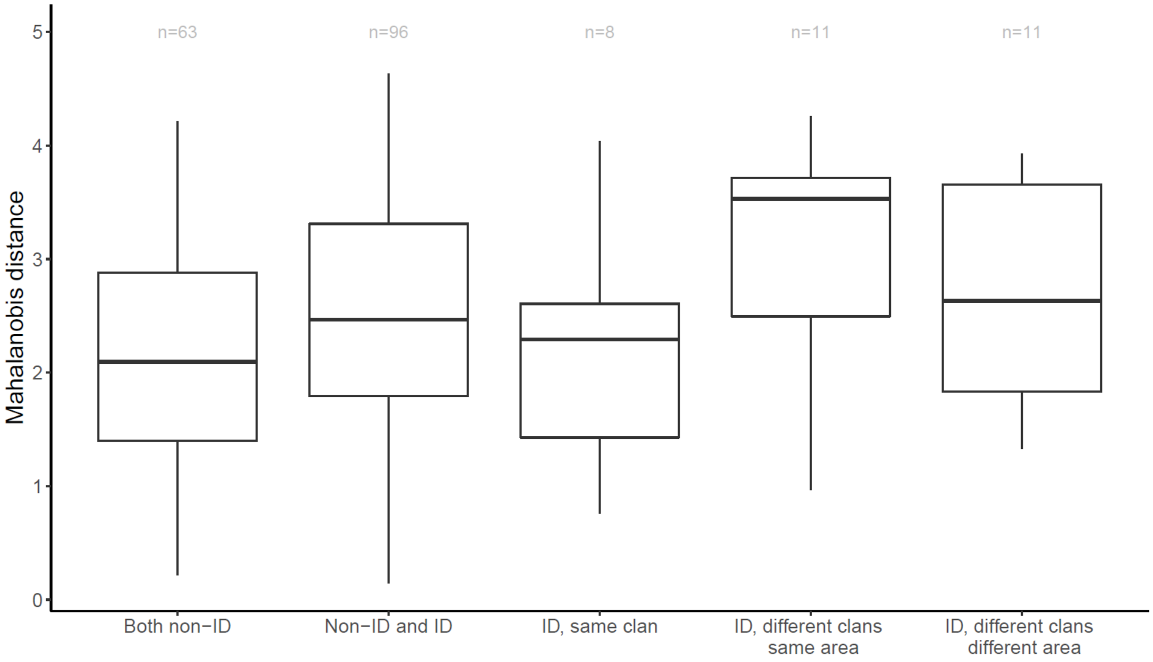
C6.8 - Figure S6.5. Coda type hypervolume volume for non-identity and identity codas, restricting non-identity coda type's dataset to a single vocal clan per coda type. Results shown independently for each click length.



C6.9 - Figure S6.6. Standardized overlap between pairs of coda types' hypervolumes based on the pair's categorization (all click lengths).



C6.10 – Figure S6.7. Distribution of Mahalanobis distances between pairs of coda type centroids based on the pair's categorization (all click lengths).



C6.11 - Figure S6.8. Mahalanobis distance between pairs of coda type centroids based on the pair's categorization. Results shown independently for each click length.