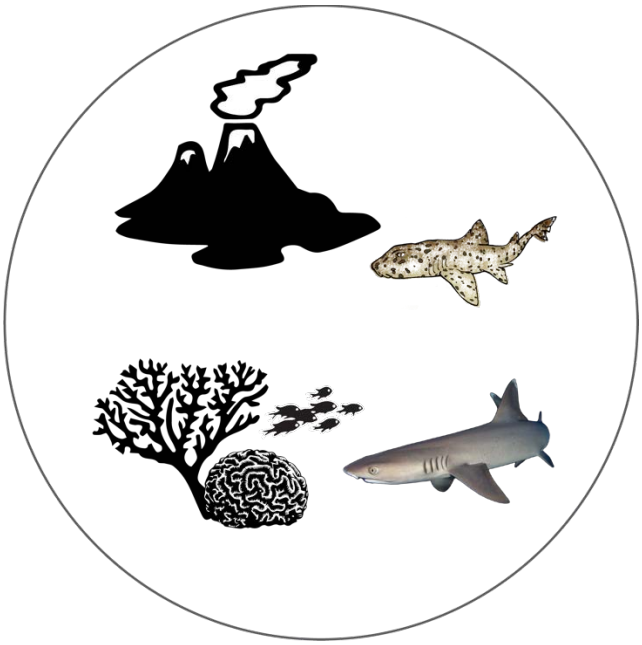
Population structure and connectivity of demersal sharks in isolation



by

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Abstract

Barriers to dispersal shape the geographic distribution of biodiversity on earth. In the ocean, the interaction of physical barriers and dispersal has primarily been examined for organisms with juvenile larvae that disperse with the aid of ocean currents. This has led to the general view that there are fewer barriers to dispersal in the ocean than on land, and that marine organisms maintain high genetic connectivity and large population sizes. Elasmobranchs (sharks, rays and skates), however, produce a small number of offspring, lack a planktonic larval stage, and depend on self-propelled dispersal to maintain genetic connectivity. These fundamental differences in life history strategies are likely to generate distinct geographic patterns of genetic variation in relation to marine barriers.

The aim of this thesis was therefore to examine how marine barriers and elasmobranch dispersal ecology shape genetic connectivity. First, I provided a global synthesis of barriers to dispersal that affect elasmobranchs. I synthesized the environmental drivers and spatio-temporal scales of different barrier types and examined the effect of species-specific life history traits on genetic connectivity. Ocean depth was found to constitute a strong barrier for species that live in shallow water and are associated with the sea floor. However, some shallow-water species have managed to colonize isolated volcanic islands and highly fragmented coral reefs. Such scenarios provide exceptional opportunities to study evolutionary processes and their consequences for genetic and biogeographic patterns in marine populations.

I designed two case studies using shallow-water reef sharks and fragmented tropical seascapes as model systems to test *a priori* hypotheses about the effect of physical barriers. In the first case study, I used the Galapagos bullhead shark (*Heterodontus quoyi*) and single nucleotide polymorphisms (SNPs) to assess genetic and biogeographic patterns in the Galapagos archipelago. Sequential island formation gradually established different levels of ocean depths between individual islands that pose barriers to dispersal in *H. quoyi*. Using isolation by resistance analysis, I showed that ocean bathymetry and historical sea level fluctuations influence genetic connectivity in this species. This study was the first to expose that oscillating sea levels alter genetic connectivity in marine organisms by changing the seascape of oceanic archipelagos. This resulted in four geographically isolated genetic clusters that exhibit low genetic diversity and effective population sizes that scale with island size.

Whitetip reef sharks (*Triaenodon obesus*), used in the second case study, are closely associated with shallow-water coral reefs. I combined the mitochondrial DNA control region and nuclear genomic markers (SNPs) with extensive sampling of whitetip reef sharks across Indo-Pacific coral reefs to assess barriers to dispersal and seascape connectivity. Large distances of open ocean and the recurring

closure of the Torres Strait were the primary barriers to historical and contemporary connectivity at large geographic scales. Fine-scale genetic structure was found among reefs in the Coral Sea with nuclear genomic but not mitochondrial markers. Spatial genetic patterns implied that shark site-fidelity causes isolation at small geographic scales, while occasional oceanic dispersal may create connectivity pathways between distant reefs and across deep ocean. These results indicated that dispersal may be context-dependent and balanced by the trade-offs for individual fitness and population persistence in sharks that are associated with fragmented and dynamic coral reef systems.

Overall, my results revealed that barriers generate genetic and biogeographic signatures in elasmobranchs that may resemble patterns found in terrestrial animals and in other cases those of marine organisms that use ocean currents for dispersal. This research provides a marine perspective on the evolutionary processes that shape natural populations and highlights the importance of considering species with different life histories and dispersal modes to study barriers to dispersal.

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Chapter 1 - General Introduction

Barriers to dispersal shape the geographic and temporal distribution of individuals and their genetic variation. The distribution of individuals is often patchy because the conditions that provide suitable habitats for survival are fragmented (Kimura & Weiss, 1964; Slatkin, 1987). Dispersal sustains the exchange of individuals and genetic information among disjunct habitats (Clobert et al., 2012; Fahrig & Merriam, 1994; Slatkin, 1987). But the dispersal of individuals is commonly restricted by the presence of physical barriers, which limit the distribution of species and the genetic connectivity among populations (Avise, 2000; Kimura & Weiss, 1964; Manel et al., 2003). The study of barriers to dispersal is therefore central to understand the evolutionary processes that create genetic and biogeographic patterns in natural populations (Avise, 2000; Moritz, 2002).

Dispersal generates demographic and genetic connectivity among spatially discrete units of the same species (Fahrig & Merriam, 1994; Levin et al., 1984; Lowe & Allendorf, 2010). Demographic connectivity measures the relative contribution of dispersing, compared to resident individuals, to local population growth and therefore requires knowledge on local demographic rates (i.e., immigration and emigration, births and deaths) and is dependent on local population sizes (Lowe & Allendorf, 2010; Ovenden, 2013; Waples & Gaggiotti, 2006). Given their survival and successful reproduction, dispersing individuals contribute their DNA to the gene pool of the local population at their destination (Bradbury et al., 2008; Ovenden, 2013). In this case, dispersal becomes *effective* and translates into genetic connectivity (Lowe & Allendorf, 2010; Selkoe et al., 2016). Genetic connectivity, is therefore related to the number of dispersing individuals that reproduce successfully at their destination and modify the allele frequencies of future generations. Measures of genetic connectivity rely on population genetic models and are subject to differences in mutation rates of molecular markers (Epps & Keyghobadi, 2015; Storfer et al., 2018). Therefore, the two measures, demographic and genetic connectivity, cannot be simply interpreted in terms of each other (Lowe & Allendorf, 2010; Waples & Gaggiotti, 2006). This thesis is concerned with barriers to *effective* dispersal that impact genetic connectivity, which can be measured in terms of the geographic distribution of allele frequencies.

Barriers to dispersal can lead to the accumulation of genetic differences across space, generating intra-specific genetic divergence that may ultimately results in speciation, and therefore delineate species' range limits (Avise, 2004, 2000; Kirkpatrick & Barton, 1997). Physical barriers are comprised of landscape features or discontinuities in the abiotic environment that are established through a combination of geologic and climatic processes (Avise, 2000; Slatkin, 1987). However, individual

behaviour and ecological interactions can also limit dispersal in the absence of, or in combination with physical barriers (Pearce, 2007; Pyron & Burbrink, 2010).

Physical barriers are established and modified by geological processes and variations in global climate (Briggs & Bowen, 2013; Cowman & Bellwood, 2013; Emerson & Hewitt, 2005; Hewitt, 2004). They generate genetic divergence through vicariance, the division of previously connected populations, or trans-barrier dispersal (Pyron & Burbrink, 2010). For instance, the movement of tectonic plates, a slow geologic process, drove the speciation of terrestrial organisms through the physical separation of continents and the uplift of mountain ranges (McIntyre et al., 2017; O'Connell et al., 2017; Upchurch, 2008). But vicariance also occurs over shorter time scales. For example, abrupt geologic processes such as volcanic eruptions can separate populations by breaking up suitable habitat (Beheregaray et al., 2003; Macías-Hernández et al., 2013). The geographical separation of populations can also be established through the colonization of new habitat across established barriers. For example, dispersal across the Andes mountains drove the divergence among genetic lineages of terrestrial organisms (Turchetto-Zolet et al., 2013).

Some physical barriers such as rivers have clearly defined geographical breaks (Soltis et al., 2006). Rivers in the Amazon basin, for example, constitute barriers to dispersal that drove genetic divergence in terrestrial taxa (Ayres & Clutton-Brock, 1992; Turchetto-Zolet et al., 2013). Other barriers are formed by gradients in environmental conditions that create diffuse transitions, often over larger distances.

Hard barriers, such as land bridges, impede connectivity between disjunct populations entirely (Cowman & Bellwood, 2013; Knowlton et al., 1993; Pyron & Burbrink, 2010). In contrast, soft barriers are permeable and reduce genetic connectivity at varying levels for different species, according to their dispersal capacity (Cowman & Bellwood, 2013; Pyron & Burbrink, 2010). The permeability of barriers can change over time (Hewitt, 2004). For example, variations in global climate cause shifts in the elevation of terrestrial vegetation expanding and contracting dispersal corridors across mountain ranges (Hazzi et al., 2018). In its extreme form, climatic variations lead to transitions from soft to hard barriers. During colder climates, receding sea levels expose the shallow sea floor of the Torres Strait, separating the Indian from the Pacific Ocean, but the seaway reopens when global temperatures rise again (Voris, 2000).

Since geologic processes and climatic variations determine the beginning, duration, and permeability of barriers, they leave traces in the genetic structure of natural populations that can be detected using molecular tools (Dudgeon et al., 2012; Emerson & Hewitt, 2005). Different types of molecular markers can be used to examine the effect of physical barriers on genetic connectivity at varying spatial resolution and at historical and contemporary time scales (Thomson et al., 2010; Wang, 2010). Further,

genomic sequencing techniques have significantly improved the statistical power to detect barriers to dispersal at finer temporal and spatial scales (Avise, 2010; Luikart et al., 2003; Morin et al., 2009, 2004). However, these methods have primarily been applied to study the effect of barriers to dispersal on spatial genetic patterns in terrestrial populations but to a lesser extent in marine organisms (Gagnaire et al., 2015; Kelley et al., 2016).

In the ocean, genetic divergence and species' distributions are also regulated by physical barriers that are subject to geological processes and climatic variations (Cowman & Bellwood, 2013; Ovenden, 2013). But the life history strategies and mechanisms used for dispersal in the ocean are distinct because organisms have adapted to living and moving in an aquatic medium (Capdevila et al., 2020). Marine barriers may therefore generate genetic and biogeographic patterns that contrast or resemble those of terrestrial systems.

In the past it was assumed that marine systems generally have fewer physical barriers than terrestrial systems, because many marine organisms can exploit the movement of the water masses during a juvenile larvae phase (Cowen & Sponaugle, 2009; Hellberg, 2009; Palumbi, 2003). However, the field has seen a shift towards recognizing the complexity and diversity of marine dispersal (Levin, 2006). Active movements in marine larvae that utilize ocean currents as dispersal agents can have significant influence on dispersal trajectories and distances (Leis, 2006; Levin, 2006). Other marine organisms switch between different dispersal modes (e.g., self-propelled swimming versus passively drifting) at different life stages or during dispersal events (Hays, 2017). Some marine organisms disperse as juveniles and have sessile or highly site-attached adults (Liggins et al., 2013). Others, have both dispersive juvenile larvae and dispersive adults (Roff, 1988). Marine mammals, marine reptiles, cartilaginous fish (Chondrichthyes), and some teleost fish (e.g., viviparous or brooding species) lack juvenile larvae (Kelly & Palumbi, 2010). The capacity to overcome potential physical barriers and maintain genetic connectivity in the ocean is therefore subject to species-specific life history traits, behaviour, and the mechanisms used for dispersal (Baguette et al., 2013; Massol & Débarre, 2015; Selkoe et al., 2016).

Despite the great diversity in life histories and dispersal strategies in the ocean, there is a bias in marine research towards organisms with dispersive juvenile larvae (Bradbury et al., 2008). Genetic connectivity in relation to dispersal barriers has been studied to a much lesser extent in species that lack juvenile larvae, but has the potential to improve our understanding of the evolutionary processes that shape genetic and biogeographic patterns in the ocean (Bowen & Karl, 2007; Dudgeon et al., 2012).

Elasmobranchs (sharks rays and skates) form a taxonomic group comprising over 1150 species that live in diverse marine and freshwater habitats from tropical to polar regions (Ebert et al., 2013; Last et al., 2016; Lucifora et al., 2015). They lack a planktonic larval stage and mostly disperse as adults while juveniles are more site attached (Grubbs 2010; Ebert et al. 2013). Compared to the majority of teleost fishes and marine invertebrates, elasmobranchs generally have longer life spans, mature at a later age, and produce fewer offspring (Ebert et al., 2013). Individual species range in body size from merely 20 cm to 20 m and occur at the surface down to the deep sea (Ebert et al., 2013; Last et al., 2016). Elasmobranchs inhabit fresh and brackish water, continental shelves, and the open ocean (Last et al., 2016; Musick et al., 2000). Pelagic species swim suspended in the water column while demersal species live on or closely associated to the sea floor. The diverse life histories of elasmobranchs are likely to result in species-specific genetic and biogeographic patterns that may contrast or resemble those of larval dispersers and terrestrial organisms. However, the combined effect of species-specific life history and marine barriers on population connectivity in elasmobranchs is not well understood.

Shallow-water marine habitats cover a smaller area than the open ocean and are fragmented by deeper water. Individual fragments may serve as spatial units to study barriers to dispersal in marine organisms that are strongly associated to shallow-water habitat (Edmunds et al., 2018; Hawkes, 2009). Elasmobranchs that live in shallow-water and are closely associated to the sea floor are thought to have lower dispersal capacity compared to pelagic species (Iosilevskii & Papastamatiou, 2016) and often show lower genetic connectivity between fragmented shallow-water habitats (Chevolot et al., 2006b; Gubili et al., 2014; Plank et al., 2010; Ramírez-Amaro et al., 2018). However, few studies have been designed to explicitly test the effect of ocean depth as a barrier. Demersal elasmobranchs that inhabit fragmented shallow-water habitats may therefore offer a suitable system to study the effect of barriers to dispersal on genetic and biogeographic patterns.

Thesis aims

The overarching aim of this research was to examine how barriers to dispersal shape genetic connectivity and biogeographic patterns in elasmobranchs.

In Chapter 2, I synthesized the underlying mechanisms and the spatio-temporal extent of barriers to dispersal in the ocean. I examined how species-specific dispersal ecology regulates connectivity across barriers in elasmobranchs. In this chapter I also reviewed methodological sources that can bias the detection of barriers and provided concise recommendations for studies that aim to test hypotheses about the effect of marine barriers.

Based on the findings of Chapter 2, I designed two case studies to examine barriers to dispersal. Two shallow-water reef sharks that are strongly associated to the sea floor and inhabit fragmented tropical seascapes presented suitable model systems.

In Chapter 3, I used the Galapagos bullhead shark (*Heterodontus quoyi*) and the Galapagos archipelago as a model system to study evolutionary processes and their consequences on genetic connectivity and island biogeography. I showed how island formation and sea level fluctuations establish and modify depth barriers, resulting in distinct genetic and biogeographic patterns.

Whitetip reef sharks (*Triaenodon obesus*) and Indo-Pacific coral reefs were used as a model system in Chapter 4 to assess genetic connectivity in fragmented coral reef seascapes. Sharks were sampled across various magnitudes of fragmentation, including contiguous reefs along continental shelves, semi-isolated offshore reefs, and reefs on isolated oceanic islands and seamounts. I found contrasting genetic patterns with local isolation and large-scale connectivity pathways that were likely created by the sharks' high site fidelity and context-dependent oceanic dispersal.

This research revealed general trends in the effects of barriers on genetic connectivity in elasmobranchs, but also identified species-specific and context-dependent differences. Chapter 3 was the first to show that genetic and biogeographic signatures in coastal marine species may resemble those found terrestrial island biota. Chapter 4 constitutes the most comprehensive sampling of a reef shark in the Coral Sea region to date. This chapter illustrated that ecological and evolutionary trade-offs balance high site-fidelity and rare oceanic dispersal events in reef-associated sharks. The results of this thesis contribute to our understanding of how barriers in the ocean affect marine connectivity and biogeography and showcase possible avenues for future research.

The diagram in Figure 1 on the following page provides a visual overview of the thesis chapters.

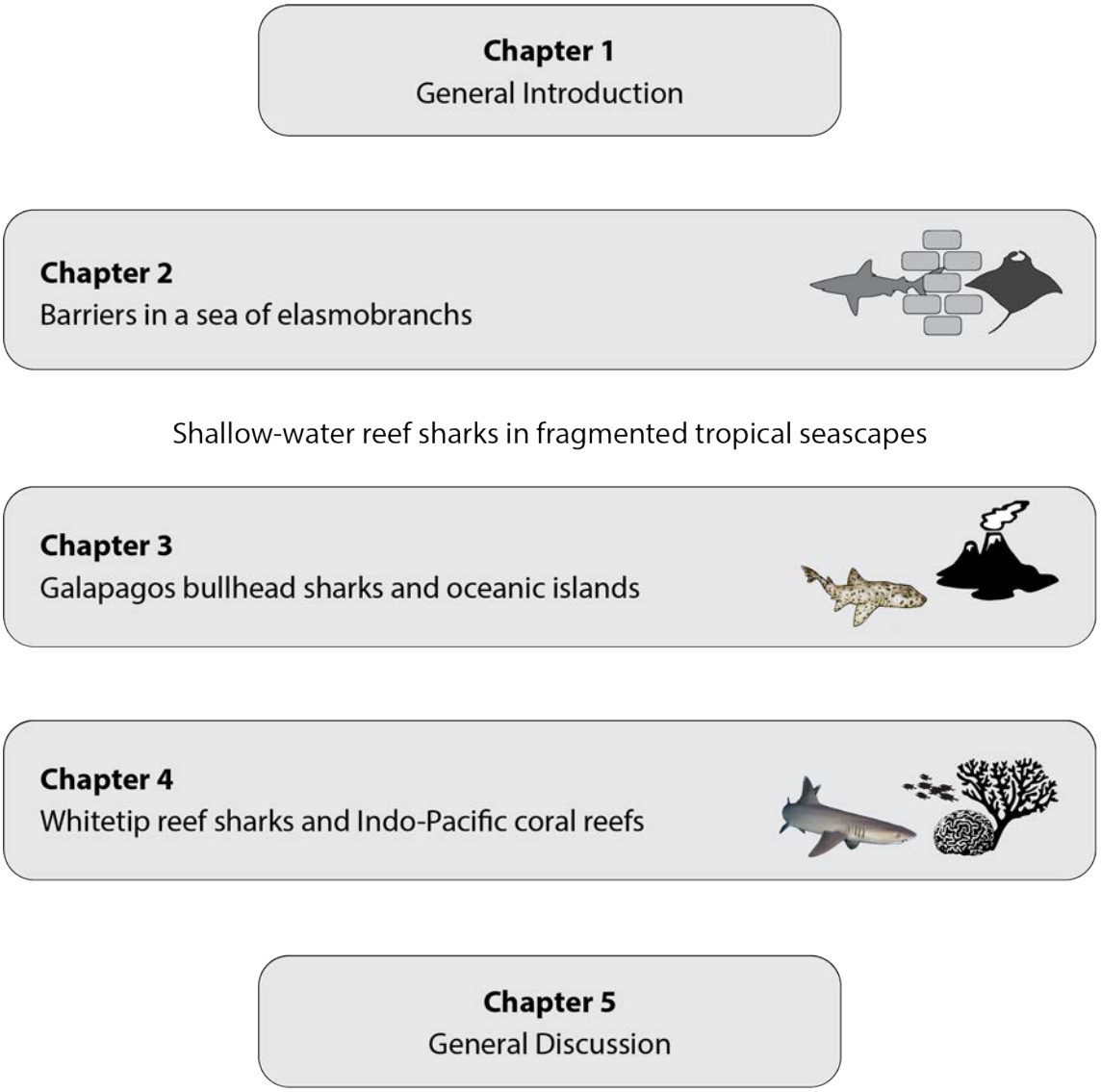
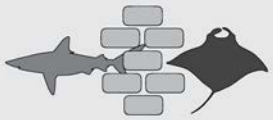


Figure 1. Thesis chapter overview. This overview will be repeated in the title page of each chapter to guide the reader through the thesis structure.

Chapter 2 – Barriers in a sea of elasmobranchs: From *fishing* for populations to testing hypotheses in population genetics

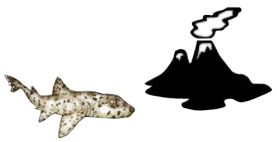
Chapter 1
General Introduction

Chapter 2
Barriers in a sea of elasmobranchs



Shallow-water reef sharks in fragmented tropical seascapes

Chapter 3
Galapagos bullhead sharks and oceanic islands



Chapter 4
Whitetip reef sharks and Indo-Pacific coral reefs

Chapter 5
General Discussion

This chapter has been accepted with minor revisions for publication in *Global Ecology and Biogeography*. The submitted manuscript has been modified to fit the style of the thesis and avoid redundancies.

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Contributions: M. Hirschfeld designed the study, collected, curated, analysed, and interpreted the data, and wrote the manuscript. A. Barnett, C. Dudgeon., M. Sheaves participated in study conception, interpreted the data, and contributed to the structure and content of the manuscript.

Introduction

The dispersal of animals across the landscape is one of the major evolutionary forces responsible for biodiversity and its distribution on earth. Animal dispersal is the geographical displacement of individuals that has the potential to generate gene flow (Ronce, 2007). Evolution has generated a remarkable number of dispersal mechanisms. Some species of spiders, for example, produce threads that lift them into the air where they passively drift with the wind and electric fields (Morley & Robert, 2018; Weyman, 1993). Marine mammals, in contrast, actively propel their large bodies on migrations between polar feeding areas and tropical birthing areas (Dawbin, 1966). Dispersal and subsequent reproduction sustain the exchange of genetic information among habitats that provide suitable conditions for a species' survival (Slatkin, 1987). Unrestricted dispersal and gene flow theoretically results in panmixia; the lack of genetic population structure throughout a species' geographical range (Kimura & Weiss, 1964; Slatkin, 1987). But the dispersal of individuals is commonly restricted by the presence of geographic features or unfavourable environmental conditions that create physical barriers between patches of suitable habitat, generating genetic divergence among populations (Avise, 2000; Guillot et al., 2009; Hellberg et al., 2002). For instance, in the ocean, large distances across deep ocean or strong gradients in temperature and salinity, pose barriers to dispersal (Riginos & Liggins, 2013; Rocha et al., 2007). Animal behaviour, such as the preference for a specific habitat for reproduction, can also reduce genetic connectivity in the absence of, or in combination with, physical barriers (Avise et al., 1992; Pearce, 2007; Shields, 1983).

The permeability of physical barriers defines how effective they are in limiting dispersal and gene flow. Permeability of marine barriers is dependent on the hydrologic and geographic factors that form barriers and can vary over time due to a combination of geologic and climatic processes (Cowman & Bellwood, 2013; Ovenden, 2013). Hard barriers are formed by landmasses that prevent gene flow altogether. The most prominent example is the rise of the Isthmus of Panama, which has driven the divergence of many marine taxa between the Atlantic and Pacific Oceans (Knowlton et al., 1993; O'Dea et al., 2016). In contrast, soft barriers are permeable. They are formed by geographic features or environmental discontinuities that can restrict genetic connectivity between regions that are physically connected by water masses (Bowen et al., 2016; Teske et al., 2011). Hard barriers can reopen with rising sea levels during interglacial cycles and the permeability of soft barriers, for example the strong temperature gradients around the Benguela upwelling system, fluctuate with the earth's climate (Henriques et al., 2014; Krammer et al., 2006; Marlow et al., 2000). Understanding the temporal variability of marine barriers is therefore central to the interpretation of the spatial genetic structure in marine populations.

Life history and physiology determine an organism's potential to disperse between suitable habitats and its capacity to overcome physical barriers. Many marine organisms, including teleost fishes and marine invertebrates, have juvenile larvae the use ocean currents as dispersal agents (Cowen & Sponaugle, 2009; Hellberg, 2009). But marine animals that lack dispersive larvae, such as elasmobranchs (Ebert et al., 2013; Grubbs, 2010), are likely to produce distinct geographic patterns of genetic variation.

Several reviews have focused on the effect of marine barriers on genetic population structure in marine invertebrates and teleost fish at global (Bowen et al., 2016; Rocha et al., 2007) or regional scales (Avise, 1992; Burton, 1998; Colgan, 2016; Patarnello et al., 2007; Teske et al., 2011). These processes have been examined in some marine animals that depend on self-propelled dispersal, including sharks and rays, cetaceans, and to a lesser extent in teleosts that lack larval dispersal (Bernardi, 2000; Fontaine et al., 2007; Ovenden, 2013; Puckridge et al., 2013). Dudgeon et al. (2012) highlighted the importance of several recognized marine barriers in shaping the genetic structure of elasmobranchs. Here we take a closer look at this taxonomic group to gain a deeper understanding of the physical and ecological drivers that determine the effect of barriers on population connectivity in marine animals that depend on active dispersal. First, we present a global geographic overview of barriers that affect elasmobranchs and synthesize how physical factors, spatial and temporal scales determine barrier permeability. We assess the effect of elasmobranch dispersal potential on genetic connectivity in relation to different types of barriers, and debate the influence of environmental tolerance and behaviour on connectivity in elasmobranchs and other marine animals with active dispersal. Finally, we consider the limitations of our results by showcasing methodological sources that affect the measurement of genetic connectivity across marine barriers, and highlight potential solutions for future research.

Methods

Peer-reviewed publications that reported intra-specific genetic or genomic differentiation in one or more elasmobranch species were obtained via the online search engines Google Scholar and Web of Science by entering combinations of the key words, 'shark', 'ray', 'genetic*', 'genomic*', 'phylogeograph*', 'population structure', 'connectivity' (until 16 January 2020) and were screened to discover additional publications. Obligate fresh-water species were excluded. Additional information was compiled on the taxonomy and biology (*maximum depth of occurrence*, *maximum body size*, and *habitat*) for each elasmobranch species from secondary literature and fishbase.org (Ebert et al., 2013; Froese & Pauly., 2018; Last et al., 2016; Weigmann, 2016). Elasmobranch habitat was described as one

of three broad categories: 1. Benthopelagic habitat on the continental shelves and upper slopes, 2. neritic habitat of the water column above the continental shelves and upper slopes, 3. oceanic habitat including the pelagic and deep sea. Finally, we extracted information on the type and number of genetic markers used to study elasmobranch population genetic structure from the primary literature.

Genetic comparisons across barriers were then extracted from the publications. A genetic comparison was recorded as a single data point if sampling design was adequate to formally test for intra-specific genetic differentiation across a single barrier. Sampling was considered adequate if there was at least one sampling location with a minimum of five samples on either side of a barrier and there were no other barriers that could simultaneously act on the genetic differentiation between the same locations. Genetic differentiation between the locations must have been statistically assessed using pairwise fixation or differentiation indices between individual locations or analysis of molecular variance (AMOVA) between groups of sampling locations (Excoffier et al., 1992; Meirmans & Hedrick, 2011; Weir & Cockerham, 1984). Pairs of locations that lack any physical barriers between them and are separated by the same or smaller geographic distances than locations on either side of a barrier of interest can be used as controls because genetic differences are likely caused by geographic distance alone, not a barrier. Therefore, data points of significant genetic differences across barriers were not included if authors also reported significant differences between control locations. Data points were also excluded if behaviour, specifically reproductive philopatry, was identified as the main driver of genetic differentiation between locations on either side of a physical barrier in question. They were excluded to avoid bias in our synthesis because it is not possible to distinguish between the effect of a physical barrier or behaviour on genetic differentiation if not explicitly tested for separately. We then synthesized information on the barriers extracted from the literature to characterize different barrier types based on similarity of the geographic and hydrologic factors that form each barrier, their geographic scale, time scale and temporal variability. Detailed information on each barrier and source references are reported in Appendix A Table 7.

To quantify the relative contribution of barrier type and dispersal potential on genetic differentiation we applied generalised linear models (GLMs) on a subset of three barrier types that had a minimum of 30 observations and a minimum of five observations in each habitat category. We used *barrier type* and three proxies for dispersal potential, *maximum depth of occurrence*, *maximum body size* and *habitat* as independent factors. Directly comparing measures of genetic differentiation between studies is complicated by the range of genetic indexes that are applied to different types and numbers of molecular markers. Genetic differentiation, the dependent variable, was therefore recorded as a binomial response, either being significant or not significant. Whenever a study used more than one type of genetic marker to measure genetic differentiation based on the same set of samples, we only

included results based on nuclear not mitochondrial markers to address non-independence. The model included interactions between *barrier type* and *maximum depth of occurrence* as well as *barrier type* and *habitat*. Multi-collinearity among all predictors included in the models was assessed by calculating the generalized variance inflation factors (GVIFs) to account for predictors with several levels (Fox & Monette, 1992; Zuur et al., 2010). GLMs with decreasing complexity were fitted by removing the term with the least effect at each step. Models were first fitted with a binomial error distribution and then with a quasi-binomial error distribution to assess over- or under dispersion of the data (Pekar & Brabec, 2016). We assessed the presence of influential observations using Cook's distance and applied a lack-of-fit test to detect significant correlations between the residuals and the fitted values and the predictors (Cook, 1977; Zhang, 2016; Zuur & Ieno, 2016). Finally, we calculated the Pseudo McFadden R^2 and Akaike's information criterion corrected for small sample sizes (AICc) to identify the model that best explained the amount of variance in the data while accounting for model complexity (McFadden, 1974; Menard, 2000).

Results

Intraspecific genetic differentiation was reported for 102 elasmobranch species across 173 publications (Figure 2). The number of publications was highly skewed towards sharks (superorders Galeomorphii and Squalomorphii) with 137 studies covering 70 species, compared to skates and rays (superorder Batoidea) with 37 publications covering 32 species. Only one study included population structure of both shark and ray species (Ferrari et al., 2018). A total of 21 shark families belonging to six orders were covered by the literature with most studies focusing on the family Carcharhinidae. Three orders of batoids containing eight families were studied with the number of publications biased towards the families Rajidae and Pristidae.

Barriers in a sea of elasmobranchs

A total of 65 studies (37.6%) were not included in our barrier synthesis (Appendix A Table 8) either because there were no physical barriers present in the geographic area sampled (n=32, 18.5%) or because they did not meet our sampling design criteria (n=33, 19.1%). We excluded 44 genetic comparisons (24 studies) across potential barriers due to inadequate spatial sampling and 21 comparisons (12 studies) with small sample sizes. Six comparisons (5 studies) were excluded because significant genetic differences were also shown for control locations that lack physical barriers, and for 16 comparisons (12 studies) no statistical results for pairwise comparisons or AMOVAs were reported. Finally, 18 observations (14 studies) were excluded because philopatric behaviour was reported to likely generate the observed genetic differences.

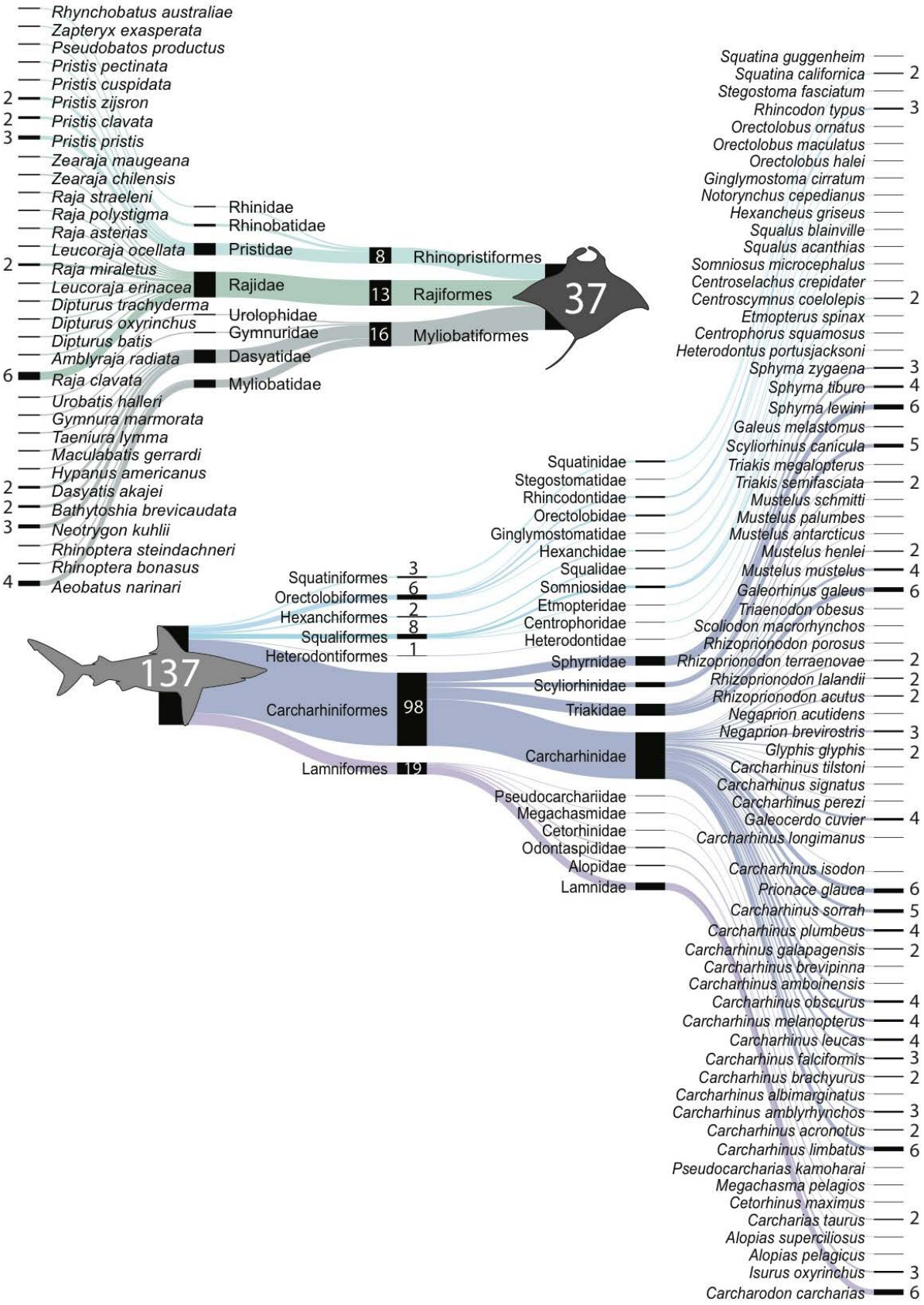


Figure 2. Taxonomic overview of elasmobranch species in the population genetics or phylogeography literature. The number of studies in taxonomic units are presented above the nodes for each order and next to the species name if there was more than one study on a single species.

Across all publications, I extracted a total of 226 data points on genetic comparisons for 45 unique physical barriers in the world's oceans (Figure 3). For the purpose of this synthesis, I grouped individual barriers that are formed by similar geographic or hydrologic factors and operate on comparable spatial scales into nine types of barriers (Figure 4 and Appendix A Table 7). Spatial scales ranged from barriers affecting connectivity at global to intermediate and local scales. Barriers were concentrated in five regional areas: the north-eastern Pacific, western Atlantic, north-eastern Atlantic and Mediterranean, southern Africa and the western Indo-Pacific and New Zealand. Four barrier types are formed by geographic factors. At large scale, the physical separation of major ocean basins was formed through the collision of continents moving on tectonic plates (O'Dea et al., 2016; Seton et al., 2012). Mid ocean barriers separate marine shelf habitats over vast distances of deep ocean. Straits are shallow and narrow stretches that separate larger water bodies on either side, and ocean depth below the edge of continental shelves creates barriers at intermediate down to small spatial scales of less than 100km (Patarnello et al., 2007). Another four barrier types are formed by hydrologic factors. Warm surface water at the equator creates a large-scale thermal barrier that divides cold and temperate habitats of the northern and southern hemisphere (Bowen et al., 2016). The strong temperature gradients at current fronts form small-scale thermal barriers (Henriques et al., 2014; Stephens et al., 2016). We use the term haline barriers for barriers caused by drastic gradients in salinity, for example through freshwater outflows of major river deltas (Rocha, 2003). Haline barriers and ocean currents (Santos et al., 2006) form barriers to dispersal and gene flow at intermediate and small spatial scales. As a unique case, the Florida Peninsula constitutes a barrier that is formed by a combination of hydrologic and geographic factors. The large land mass of the Peninsula forms a barrier between the Gulf of Mexico and the Atlantic by extending from temperate into subtropical waters and is reinforced by a narrow continental shelf on the Atlantic coast and strong currents pushing through the Florida Straits into the Atlantic (Avise, 1992; Gold & Richardson, 1998). Geologic processes and global climate act in concert to determine the onset, duration and permeability of marine barriers over geologic time scales. The Pleistocene epoch, in particular, marks the beginning and end or a period of dramatic fluctuations in barrier permeability (Figure 4) coupled to modern glacial cycles that amplified global climate oscillations (Hansen et al., 2013).

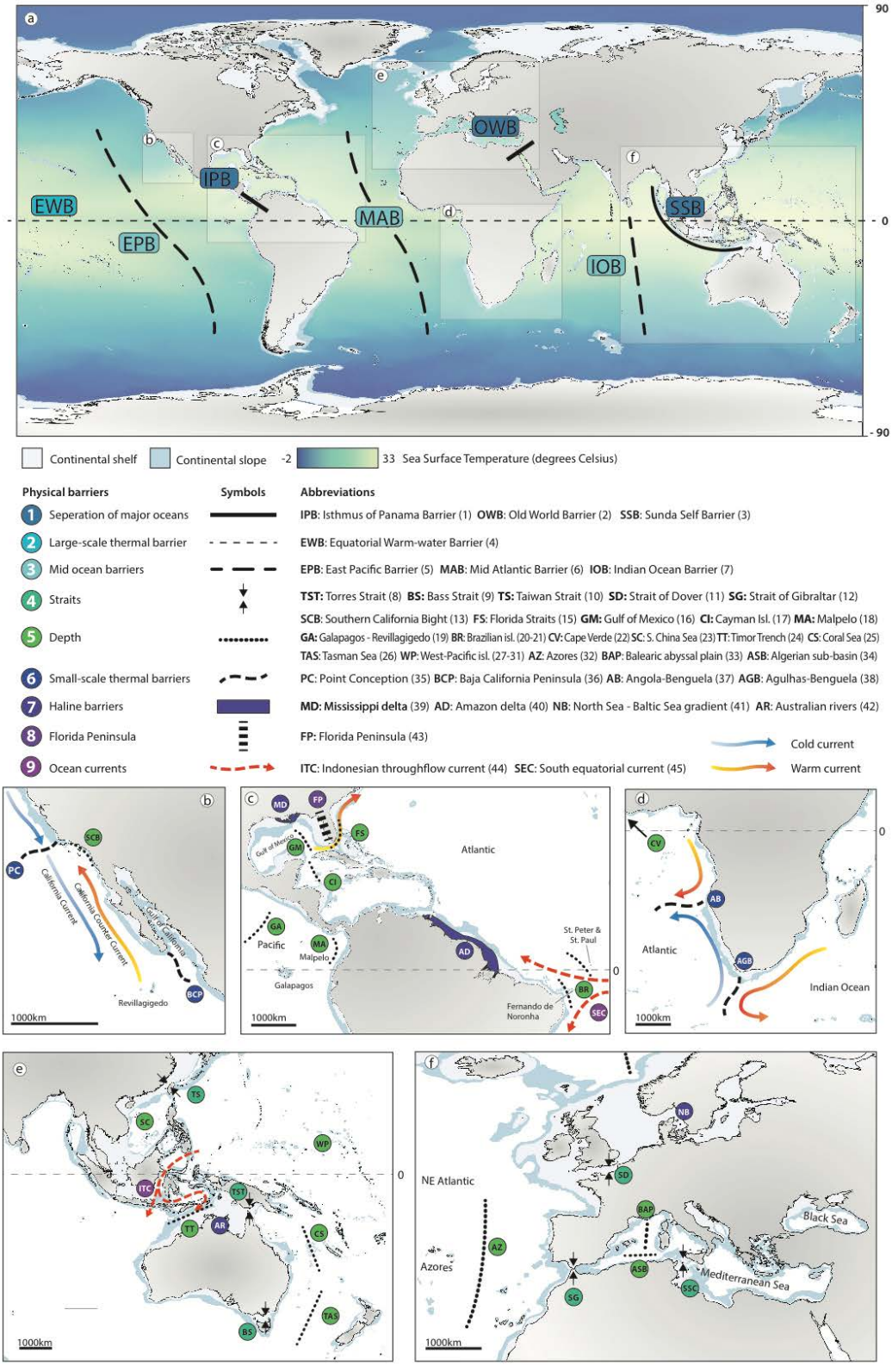


Figure 3. Barriers to elasmobranch dispersal and genetic connectivity in the global ocean. (a) Map of the world with barriers that act on a global scale. Regional areas: (b) north-eastern Pacific, (c) western Atlantic, (d) southern Africa, (e) western Indo-Pacific and New Zealand, (f) north-eastern Atlantic and Mediterranean. Abbreviations correspond to the barriers described in Appendix A Table 5) and numbers in parenthesis indicate the cumulative count of individual barriers.

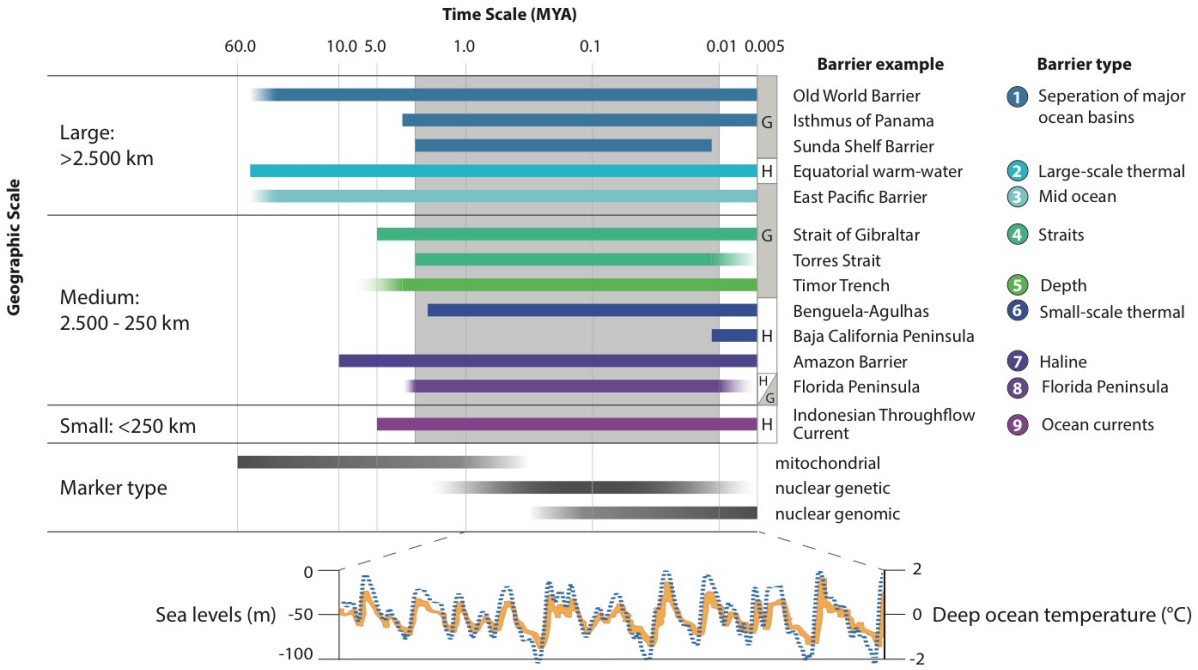


Figure 4. Geographic and temporal scales, and temporal variability of selected examples of each barrier type. Coloured bars correspond to barrier types numbered from 1-9 that are formed by geographic (G, grey vertical bars) or hydrologic factors (H, white vertical bars). The time in million years ago (MYA) is depicted on a logarithmic scale and the grey shaded area represents the Pleistocene epoch (2.58 to 0.0117 MYA). Graduated horizontal black bars at the bottom depict the time window at which different molecular markers are commonly used to detect genetic differentiation, adapted from (Dudgeon et al., 2012). The bottom inset depicts fluctuations in global average sea levels and deep ocean temperature over the last one million years on a normal scale, adapted from (Hansen et al., 2013). Details and references are reported in Appendix A Table 7.

Drivers of elasmobranch population connectivity

Our analysis suggests that genetic structure across physical barriers in elasmobranchs is a function of species-specific dispersal potential and its interaction with the type of barrier (Table 1 and Figure 5). Validation of the full model including several barrier types indicated no violations of model assumptions, outliers or multicollinearity (all GVIF below 1.5) of the predictors. All proxies for elasmobranch dispersal potential used as predictors (*maximum depth of occurrence*, *maximum body size* and *habitat*) explained whether a given species was likely to show significant genetic differentiation across physical barriers, but the relative contribution of each predictor and the direction of its effect differed between the three types of barriers examined (Figure 5). The full model best explained genetic differentiation across three barrier types. Compared to all other models, it captured the largest amount of the variance in the data, indicated by an R^2 value of 0.3 and the lowest AICc value (McFadden, 1978). The probability of significant genetic differentiation consistently decreased with larger *maximum body size* independently of the *barrier type*. In contrast, species that

had a larger *maximum depth of occurrence* were less likely to show genetic differences across depth and mid ocean barriers but the effect was reversed for straits. Benthopelagic species, elasmobranchs that are associated with the seafloor above the continental shelves and slopes, were more likely to demonstrate genetic differentiation across depth and mid ocean barriers compared to species that occupy neritic and oceanic habitats. Across narrow and shallow straits, however, oceanic species were more likely to exhibit genetic differentiation compared to neritic and benthopelagic species.

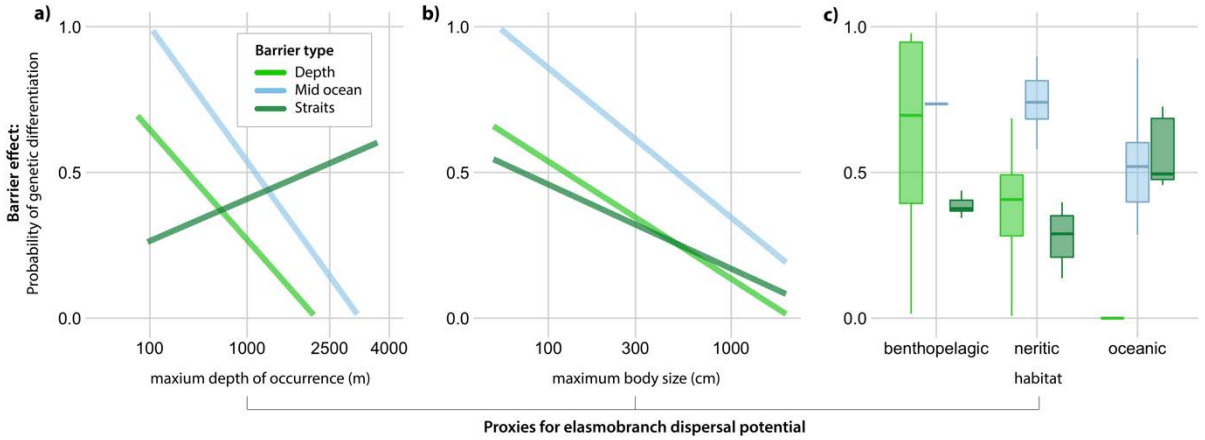


Figure 5. Probability of genetic differentiation across depth barriers (light green), mid ocean barriers (blue), and straits (dark green), in relation to proxies for elasmobranch dispersal potential maximum depth of occurrence a), maximum body size b) and habitat c). Regression lines (panels a and b) represent the mean of the fitted values of the full model (Table 1) and boxplots (panel c) represent the mean and interquartile range of the fitted values, coloured by barrier type.

Table 1. Summary of generalized linear models assessing the contribution of three proxies for elasmobranch dispersal potential and barrier type on the probability of genetic differentiation. K indicates the number of parameters in the model and LL is the log likelihood score. AICc is the Akaike information criterion corrected for small sample sizes, ΔAICc is the change in AICc compared to the model with the lowest value, and R2 is the variance explained by each model estimated using McFadden's Pseudo-R2.

Model structure	K	LL	AICc	ΔAICc	AICc Weight	R^2
1) ~ barrier type x habitat + barrier type x maximum depth of occurrence + maximum body size	13	-66.03	161.05	0.00	0.9	0.296
2) ~ barrier type x habitat + maximum depth of occurrence + maximum body size	11	-70.76	165.65	4.60	0.09	0.245
3) ~ barrier type + habitat + maximum depth of occurrence + maximum body size	7	-77.89	170.65	9.59	0.01	0.169
4) ~ habitat + maximum depth of occurrence + maximum body size	5	-83.59	177.65	16.60	0.00	0.108
5) ~ maximum depth of occurrence + maximum body size	3	-85.96	178.11	17.05	0.00	0.083
6) ~ maximum depth of occurrence	2	-88.86	181.81	20.76	0.00	0.052

Discussion

Our global synthesis identified nine main types of physical barriers that influence population connectivity in elasmobranchs. Their impact on genetic connectivity depends on the species-specific dispersal ecology and the spatio-temporal characteristics that define each barrier type. The most common barriers affecting this group are related to ocean bathymetry at large through to remarkably small spatial scales.

From global to local scales

Some oceanic elasmobranchs undertake large migrations across and between major ocean basins (Queiroz et al., 2019). But great dispersal potential does not inevitably result in global connectivity and a world without barriers. The Old World Barrier, Isthmus of Panama Barrier, and Sunda Shelf Barrier pose the most potent barriers and define the planet's subdivision into major ocean basins. Tropical sharks that are capable of large-scale migrations show genetic structure between major ocean basins because cold water limits their dispersal around the northern and southern extremes of continental landmasses (Clarke et al., 2015; Daly-Engel et al., 2012; Vignaud et al., 2014a). However, pelagic oceanic sharks and migratory teleost fish that occupy a broader range of temperatures are able to maintain genetic connectivity between the Atlantic and south-west Indian Ocean, likely because the tip of South-Africa is located in lower latitudes (Díaz-Jaimes et al., 2010; Da Silva Ferrette et al., 2015; Theisen et al., 2008; Veríssimo et al., 2017). In tropical marine organisms with limited dispersal this ocean subdivision has led to the evolution of new species (Bowen et al., 2016; Cowman & Bellwood, 2013), including sharks and rays (Sales et al., 2019; Schultz et al., 2008), and prevented the colonization of the Atlantic Ocean by species with active dispersal that have an Indo-West Pacific centre of origin (Lillywhite et al., 2018; Whitney et al., 2012b). The establishment of these land bridges has been dated providing approximate time stamps to calibrate molecular clocks and estimate divergence times of genetic lineages (Dudgeon et al., 2012; O'Dea et al., 2016; Seton et al., 2012). But the permeability of marine barriers can fluctuate over geological time scales due to oscillations in the earth's climate. For example, the cyclical exposure of the Sunda Shelf during low sea levels caused the recurring isolation and reconnection of the Indian and Pacific oceans, and has fuelled the speciation of tropical marine taxa including coastal ray species (Carpenter et al., 2011; Puckridge et al., 2013). Compared to tropical species, connectivity between oceans is preserved in some temperate and cold-water elasmobranchs, but limited between hemispheres by warm-water masses along the equator (Chabot, 2015; Veríssimo et al., 2010). Some large sharks may largely avoid the warm surface water on trans-equatorial migrations by swimming through deeper water for extended periods (Gore et al., 2008; Skomal et al., 2009). Global connectivity may only be possible in species with large-scale horizontal dispersal if they

also tolerate a broad range of environmental conditions and/or are capable of extensive vertical movement.

Marine barriers limit genetic connectivity at sub-global scales in most elasmobranchs and ocean depth is the most common barrier generating genetic structure at intermediate down to surprisingly small geographical scales. The depths of Mediterranean sub-basins (Fig. 2f) form barriers at distances of less than 500 kms in benthopelagic sharks and skates with intermediate depth distribution (*maximum depth of occurrence* of 800m and 630m, respectively) that maintain connectivity along continuous shelf habitat (Frodella et al., 2016; Gubili et al., 2014; Kousteni et al., 2015). In shallow-water benthopelagic species that depend on active dispersal, depth can create genetic structure at extremely small spatial scales. The steep bathymetry of the Southern California Bight (Fig. 2b) generates genetic differences between shallow-water habitat separated by 100km in Pacific angel sharks (*Squatina californica*) and only 42 km in round stingrays, *Urobatis halleri* (Gaida, 1997; Plank et al., 2010). Water depth separating shallow-water habitat of the bight was also found to be a strong barrier to dispersal in the black surfperch (*Embiotoca jacksoni*), a shallow-water teleost fish that lacks a planktonic larval stage (Bernardi, 2000). In contrast, depth does not constitute a barrier in organisms with pelagic larval dispersal because they primarily depend on ocean currents and larval duration to connect shallow-water habitat (Chust et al., 2016; Galarza et al., 2009; Pelc et al., 2009). In turn, strong ocean currents may restrict connectivity in species with active dispersal. The Indonesian through-flow current was related to genetic differences in benthopelagic zebra sharks (*Stegostoma fasciatum*) and blue-spotted maskrays (*Neotrygon kuhlii*) at a small geographic scale (Borsa et al., 2012; Dudgeon et al., 2009; Puckridge et al., 2013). Some pelagic species are unaffected by the Indonesian through-flow current (Giles et al., 2014) but the South Equatorial Current was suggested to generate genetic differences in coastal and even oceanic pelagic sharks at large geographic scale (Carmo et al., 2019; Domingues et al., 2018a, 2018c).

Dispersal ecology

The dispersal ecology of elasmobranchs, and any marine animal that can control or direct its movements to some extent, can be condensed into three main factors: dispersal potential, environmental tolerance and dispersal behaviour (Hawkes, 2009). The relative contribution of each factor to dispersal and population connectivity is, however, highly dependent on the species-specific life history, the modes of dispersal used, the environmental context, and individual phenotype (Bowler & Benton, 2005; Cote et al., 2017; Levin, 2006).

The potential to disperse in three-dimensional space is limited by an organism's tolerance to conditions of the aquatic environment and therefore determines their capacity to overcome potential physical barriers. An allometric relationship between dispersal potential and body size has been described for a range of taxa (Jenkins et al., 2007; Stevens et al., 2014). In elasmobranchs, larger species are more likely to maintain genetic connectivity across barriers related to ocean bathymetry. However, body size may not always be a good predictor for genetic connectivity in elasmobranchs. For example, *habitat* and *maximum depth of occurrence* provide a better explanation for trans-Atlantic connectivity in smaller (<150cm) oceanic and the deep-sea sharks (Da Silva Ferrette et al., 2015; Veríssimo et al., 2011; Weigmann, 2016). Further, spiny dogfish (*Squalus acanthias*) are relatively small sharks (max. 160 cm) but are capable of transoceanic movements (Mcfarlane & King, 1979). Neither their body size nor preference for shelf and slope habitat would indicate they maintain population connectivity across and between major ocean basins (Veríssimo et al., 2010). Unsurprisingly, elasmobranchs with a larger depth distribution and that inhabit oceanic habitats are less likely to show genetic differentiation across depth and mid ocean barriers compared to species that are associated to the sea floor of continental shelves. But this trend may be reversed for shallow straits. The Strait of Gibraltar connects the Mediterranean to the eastern Atlantic by a mere 14km wide stretch. While permeable to most species, the shallow connection drives genetic differentiation in deep-sea oceanic and benthopelagic sharks that have a large depth distribution (Catarino et al., 2015; Gubili et al., 2016; Ramírez-Amaro et al., 2018). Further, pelagic oceanic species that make large vertical movements, for example blue sharks (*Prionace glauca*), may also lack gene flow because they avoid movement across shallow straits (Leone et al., 2017; Queiroz et al., 2012; Vandeperre et al., 2014). Our models show that all three proxies for dispersal potential were important to explain genetic differences across barriers. However, the examples discussed illustrate that there are other biological drivers likely affecting genetic connectivity that were not captured by the models, due to the lack of knowledge on the biology of many elasmobranchs.

Physiological tolerance to environmental conditions determines the capacity of elasmobranchs to disperse across potential barriers. For instance, dispersal across barriers that are formed by hydrologic factors, can be explained in terms of a species' thermal tolerance and its potential to circumnavigate unfavourable conditions. Strong temperature gradients at the tip of the Baja California Peninsula (Fig. 2b) impede dispersal between the Gulf of California and the Pacific coast in some benthic shark and ray species (Castillo-Páez et al., 2014; Sandoval-Castillo et al., 2004; Smith et al., 2009). However, round stingrays (*Urobatis halleri*) maintain genetic connectivity despite their limited short-term dispersal, likely because they tolerate warm surface waters (Plank et al., 2010; Vaudo & Lowe, 2006). Some neritic species that prefer cooler temperatures may lack dispersal across this barrier if restricted to the

upper water column, while others circumnavigate the warmer surface waters by swimming at depth (Félix-López et al., 2019; Sandoval-Castillo & Rocha-Olivares, 2011). Similarly, physiological tolerance to strong gradients in salinity is critical to maintain connectivity across haline barriers. For example, the Mississippi River plume, has been suggested to restrict dispersal in coastal sharks (Portnoy et al., 2014, 2016). In contrast, other shark species maintain connectivity across the vast freshwater plume of the Amazon and Orinoco rivers, likely by descending below the margins of the continental shelves (Bernard et al., 2016; Domingues et al., 2018c). Similarly, salt water between river drainages can pose barriers to dispersal in sharks and batoids that are associated with fresh and brackish water (Feutry et al., 2014, 2015; Phillips et al., 2016). Environmental tolerance can be a limiting factor for the connectivity across marine barriers even in elasmobranchs with high dispersal potential.

Behaviour can regulate genetic connectivity in the absence of, or in combination with physical barriers (Hawkes, 2009). In marine animals with active dispersal, including elasmobranchs, marine mammals, marine reptiles, and teleost fish, dispersal linked to reproductive behaviour can restrict genetic connectivity even in species high dispersal potential and broad environmental tolerance. Reproductive philopatry is the residency or the return migration to a specific geographic area for reproduction (Pearce, 2007; Shields, 1983). This behaviour is common in elasmobranchs (Chapman et al., 2015; Flowers et al., 2016) and has mostly been associated with females repeatedly returning to the same areas for parturition and the use of nurseries by juveniles (Heupel et al., 2018; Martins et al., 2018). This results in congruent genetic patterns between elasmobranchs and other marine animals with active dispersal and similar dispersal ecology. For example, white sharks (*Carcharodon carcharias*) and some marine mammals, including humpback (*Megaptera novaeangliae*) and sperm whales (*Physeter macrocephalus*) have exceptional dispersal potential and environmental tolerance but their distinct reproductive behaviour limits gene flow in the absence of obvious physical barriers to dispersal (Bonfil et al., 2005; Engelhaupt et al., 2009; Jorgensen et al., 2010; Rosenbaum et al., 2009; Weng et al., 2007). Tiger sharks (*Galeocerdo cuvier*) and green sea turtles (*Chelonia mydas*) are capable of oceanic migrations, but cold water in high latitudes limits connectivity between major ocean basins and philopatric behaviour likely drives genetic structure within the Atlantic Ocean (Bernard et al., 2016; Jensen et al., 2019; Lea et al., 2015). Bull sharks (*Carcharhinus leucas*) and Atlantic Salmon (*Salmo salar*) have large dispersal potential and are euryhaline, tolerating a wide range of salinities, but genetic differences were found among reproductive areas in estuarine and freshwater habitat at small spatial scales (Garant et al., 2000; Tillett et al., 2012b). Reproductive behaviour can have a strong influence on genetic patterns in marine animals with active dispersal, but exposing its relative impact on connectivity compared to dispersal potential and environmental tolerance, particularly in relation to physical barriers, remains a major challenge for researchers.

From fishing for populations to testing hypotheses

Two main factors limit the inferences that can be made about the effect of elasmobranch dispersal ecology and physical barriers on genetic connectivity. First, studies commonly lack appropriate study designs based on *a priori* hypotheses to test for the effect of physical and behavioural barriers. Researchers often rely on the opportunistic collection of samples, for example through fisheries or museum collections, then attempt to "fish" for genetically distinct populations and use physical features and animal behaviour afterwards to interpret genetic patterns. Consequently, studies may lack compelling evidence to elucidate evolutionary processes, over or underestimate genetic population structure, and are biased towards economically interesting or charismatic species. Secondly, the ability to detect genetic structure varies vastly among studies due to the diverse range of molecular and analytical methods used. Although the differences in sampling design, molecular markers and analytical methods used in the elasmobranch literature introduce biases that limit the predictive power of our models, they are valuable to reveal general trends and highlight exceptions to the rule. Here we outline methodological sources that can affect measures of genetic differentiation across physical barriers in the literature to illustrate the limitations of our models and showcase important considerations for researchers assessing barriers to gene flow in natural populations (*Table 2*).

Table 2. Methodological sources of potential bias in measuring genetic differences across physical barriers and potential solutions.

Source	Effect/bias	Solution
Sampling design		
Spatial: Geographic distance	Genetic differences may due to genetic isolation by geographic distance and/or presence of other physical barriers.	• Space sampling locations closely around barrier of interest Sample control locations at similar geographic distance in the absence of barriers
Spatio-temporal: Philopatry	Genetic differences result from philopatric behaviour not physical barriers, or both.	• Test physical barriers and behaviour separately • Sample control locations in the absence of physical barriers or behaviour and in the absence of both
Spatio-temporal: Kinship bias	Observed genetic structure is an artefact of closely related individuals sampled at the same location.	• Sample at multiple time points to reduce the number of related individuals in the sample • Include locations with unrelated individuals to examine the effects of kinship bias • Examine effect of related individuals and exclude from analyses only if justified (Waples & Anderson, 2017)
Sample size	Low or highly variable sample sizes bias genetic variation captured and estimates of genetic differences between locations.	• Use sufficient sample sizes and balanced sampling (equal number of samples per location, sex and size/age)
Molecular and analytical methods		
Type of molecular marker	Molecular evolutionary rate and marker polymorphism affect the time scale and resolution at which genetic structure is detected.	• Select genetic markers based on a priori hypotheses about physical barrier of interest and their spatio-temporal scale • Conduct trials to identify the most suitable markers
Number of molecular markers	Larger numbers of markers generally increase the resolution at which population structure is detected, but can also increase the number of markers that may result from genotyping errors or do not conform with population genetics assumptions.	• Identify and exclude markers that are physically linked or deviate from Hardy-Weinberg equilibrium or result from genotyping errors (Bonin et al., 2004; O'Leary et al., 2018; Waples & Allendorf, 2015)
Markers under selection (adaptive genetic variation)	Genetic differences may be generated by selection rather than barriers to dispersal.	• Account for selection when testing the effect of barriers: Identify molecular markers putatively under selection and examine their effect in relation to physical barriers and behaviour
Statistical analyses	Measuring genetic structure and its statistical significance is influenced by: (i) the spatial and temporal sampling design, (ii) number of samples, (iii) type and number of markers, (iv) the statistical analyses used.	• Construct strong priori hypotheses and apply appropriate sampling design • Carefully select molecular markers and analytical methods • Confirm results are biologically meaningful using multiple analytical methods

Spatial and temporal sampling affects the ability to capture accurate levels of genetic differentiation in relation to physical barriers. For example, if sampling locations are too far spaced, genetic differences may arise due to genetic isolation by geographic distance and obscure the impact of the barrier of interest (Guillot et al., 2009). To discern the effect of a barrier from unknown variables, additional sampling locations can be used as controls if they are located at a similar geographic distance and have no barriers to dispersal between them. For philopatric species, sampling adults at locations that are used for mating and/or parturition or sampling juveniles from nursery habitats can capture genetic signals caused by reproductive behaviour rather than limited dispersal capacity. For instance, genetic differences in juvenile blacktip sharks (*Carcharhinus limbatus*) sampled from coastal nurseries in the Atlantic and Gulf of Mexico could be entirely caused by philopatric behaviour or in combination with the Florida Peninsula barrier (Keeney et al., 2005). The effects of physical barriers and behaviour may be distinguished by testing them separately or by using control locations (see Table 2). However, none of the reviewed studies presented a sampling design that would allow to effectively test for philopatry while accounting for physical barriers or vice versa. Although other behaviours such as the preference for feeding areas could generate genetic structure if they are linked to reproduction, this has not been tested. Large numbers of related individuals can also inflate genetic population structure. For example, sampling at a single time point at a geographic location where individuals of a particular life stage aggregate increases the probability of capturing related individuals which elevates the genetic difference to other locations even if individuals of other life stages mix and reproduce (Devloo-Delva et al., 2019).

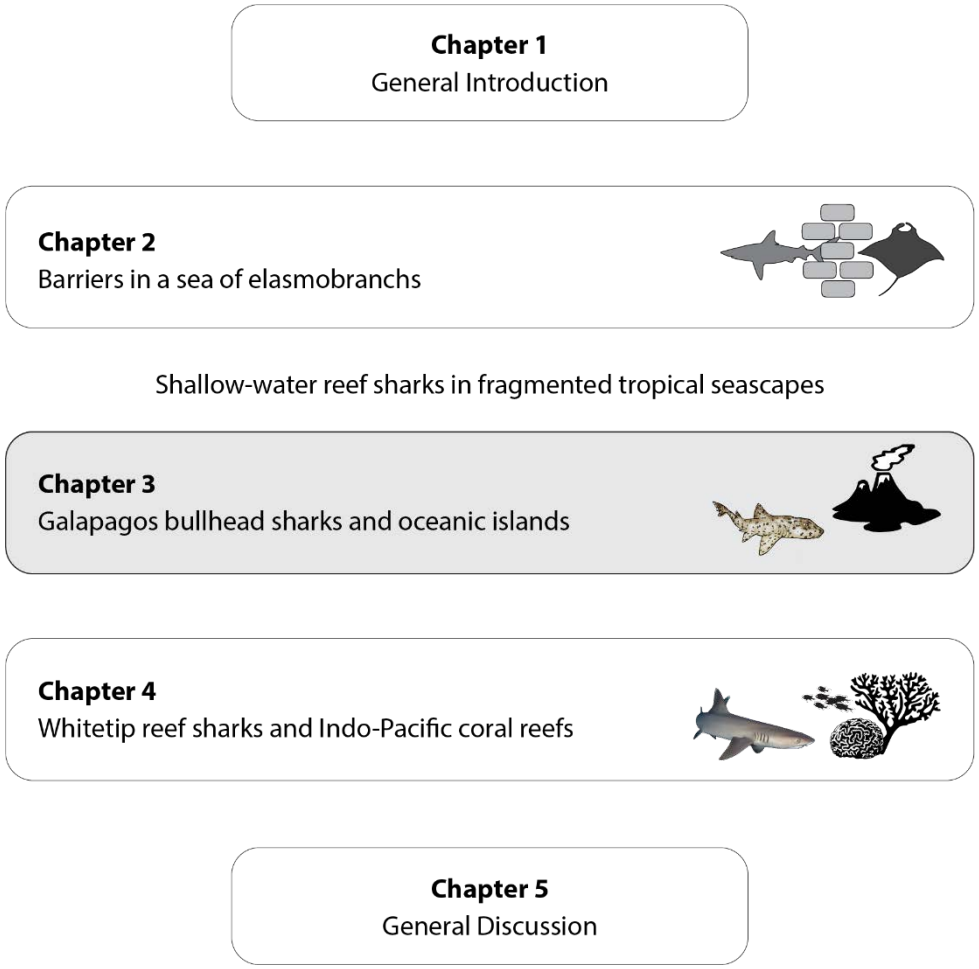
Detecting genetic differences also depends on the molecular and analytical methods used. The type and number of molecular markers has substantial impact on the spatial and temporal resolution at which genetic structure is measured due to differences in polymorphism (variability in the DNA sequences of the same molecular marker) caused by distinct molecular evolutionary rates (Liu et al., 2005; Rosenberg et al., 2003; Wang, 2010). Because mitochondrial DNA markers evolve at slower rates than nuclear markers, they may capture historical events or processes at large spatial scales but may not reflect recent or ongoing processes (Anderson et al., 2010; Wang, 2010). Highly polymorphic microsatellites and large numbers of genomic markers are suitable to examine more recent processes at smaller geographic scales (Riginos & Liggins, 2013; Wang, 2010) but may override older signatures (Anderson et al., 2010). Genomic markers that are randomly sampled across the genome, for example single nucleotide polymorphisms (SNPs), are difficult to compare between species and even between studies on the same species when a different set of markers is generated for every sample collection. Strong population structure was detected in Galapagos sharks (*Carcharhinus galapagensis*) using SNPs generated for samples from the Galapagos archipelago (Pazmiño et al., 2017a) but the signal vanished

when incorporating the data into a larger sample collection spanning the Pacific Ocean (Pazmiño et al., 2018a). Including locations at larger geographic distance outside the main area of interest may therefore provide a reference to assess the magnitude of genetic differentiation, in particular when working with samples from a small fraction of a species' geographic distribution. However, strong genetic differentiation at large geographic scales can mask structure at finer geographic scales. Processes at larger and smaller geographic and temporal scales can be examined using a combination of nuclear and mitochondrial markers and by generating global and local data sets (Vähä et al., 2007; Wang, 2010). Further, markers that are under selection by the environment should be accounted for because they can create genetic structure even if dispersal is relatively high and therefore conceal the effect of neutral processes, such as the lack of dispersal across barriers (Riginos & Liggins, 2013; Storfer et al., 2018). Finally, the analytical tools used to infer genetic population structure and statistical significance are susceptible to the number and type of molecular markers and the sampling design used (Pearse & Crandall, 2004; Sham & Purcell, 2014). However, statistical significance is not always biologically meaningful. We recommend that researchers first establish clear *a priori* hypotheses about potential barriers to dispersal in the target population, identify suitable molecular methods and sampling designs, and then apply multiple analytical approaches to obtain results that are meaningful in an evolutionary and management context.

Conclusions

Our synthesis provides new insight into how the physical characteristics of different marine barriers and animal dispersal ecology act together to rearrange genetic variation across the seascape. Methodological challenges in the field have undermined the ability to account for the complexity of dispersal and limit our understanding of genetic connectivity in the ocean. Over- or underestimating population connectivity poses a major impediment to the advancement of the field and to fisheries and conservation management (Domingues et al., 2018b; Funk et al., 2012; Ouborg et al., 2010). The genomic revolution and new collaborative tools (e.g., the online sample sharing platforms Otlet, https://otlet.io/) may provide opportunities to overcome some of the issues discussed but do not lessen the importance of adequate sampling design and hypothesis testing (Helyar et al., 2011; Luikart et al., 2003; Morin et al., 2009). The considerations for study designs discussed here are applicable across different taxa and may encourage future research to embrace the complexity of marine dispersal ecology when assessing the effect of physical barriers on genetic connectivity.

Chapter 3 – What Darwin couldn't see: Island formation and historical sea levels shape genetic isolation by depth and island biogeography in a coastal marine species



This chapter has been submitted for publication in *Molecular Ecology*. The submitted manuscript has been modified to fit the style of the thesis and avoid redundancies.

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Contributions: M. Hirschfeld designed the study, collected, curated, analysed, and interpreted the data, and wrote the manuscript. A. Barnett, C. Dudgeon, M. Sheaves participated in study conception, interpreted the data, and contributed to the structure and content of the manuscript, and C. Dudgeon contributed to the data analysis.

Introduction

Oceanic archipelagos are ideal model systems to study evolutionary processes and their consequences on genetic variation in the light of island formation (Emerson, 2002; Parent et al., 2008; Warren et al., 2015). Individual islands of archipelagos constitute independent experimental units to examine how barriers to dispersal influence the arrangement of spatial genetic variation in natural populations (Emerson, 2002; Parent et al., 2008). Two principal mechanisms of genetic divergence can be observed in oceanic archipelagos. The first is rapid adaptation, which leads to genetic divergence through selection and the exploitation of diverse ecological niches after colonization of new island environments, often in the absence of obvious physical barriers (Schluter 2000; Schluter & Conte 2009; Langerhans & Riesch 2013). In the second instance, divergence is generated through genetic drift among populations that are separated by physical barriers to dispersal (Avise, 2000; Slatkin, 1987). Barriers can be established through vicariance events dividing previously connected populations or through the colonization of new habitat by dispersing across existing barriers (Cowie & Holland, 2006; Sanmartín, 2003). Vicariance events often occur over longer time scales, for example through tectonic plate movement separation of landmasses (Vences et al., 2009; Yoder & Nowak, 2006), thus gradually reducing gene flow (McIntyre et al., 2017). Colonization events across established barriers occur at distinct time points and result in genetic drift because founding populations pass through genetic bottle necks (Emerson, 2002; Illera et al., 2007). The geographic isolation through barriers results in distinct genetic signatures that are exacerbated in island populations (Frankham, 1998). The low standing genetic variation of few founding individuals and limited dispersal between small fragmented patches of habitat that provide limited resources result in low genetic diversity and small population sizes (Brüniche-Olsen et al., 2019; Frankham, 1996, 1997).

In volcanic archipelagos individual islands are formed sequentially through recurring volcanic activity as tectonic plates move across hotspots. The progression rule describes the sequential colonization and subsequent genetic divergence from older towards younger volcanic islands in terrestrial organisms (Fleischer et al., 1998; Shaw & Gillespie, 2016). However, a progressive divergence may be absent in island species that have high levels of inter-island dispersal, arrived recently or through multiple colonization events, or underwent strong divergent selection (Juan et al., 2000; Parent et al., 2008; Shaw & Gillespie, 2016). Strong sea level fluctuations of the late Quaternary period altered island configuration at faster rates and shorter geological time scales than plate movement, but the impact of this process on divergence and island biogeography remains largely unclear (Fernández-Palacios et al., 2016; Weigelt et al., 2016). Island biogeography of marine organisms differs from their terrestrial counterparts because higher dispersal in the marine environment increases inter-island connectivity and rates of immigration to oceanic archipelagos (Pinheiro et al., 2017). As a result, the ecological

niches of marine island ecosystems are occupied faster and thus provide fewer opportunities for adaptive radiation and in-situ divergence compared to terrestrial ecosystems (Pinheiro et al., 2017).

In the ocean, just as on land, dispersal regulates population connectivity and is therefore a fundamental driver of biogeographic and genetic patterns in oceanic islands (Cowie & Holland, 2006). But what constitutes a physical barrier to dispersal in the ocean is largely dependent on the mode of dispersal (Hachich et al., 2015). A diverse array of marine barriers, including mid ocean barriers (Lessios & Robertson, 2006; Rocha et al., 2007), current fronts (Burton, 1998; Teske et al., 2011), and strong salinity or temperature gradients (Johannesson & André, 2006; Wright et al., 2015), have been shown to restrict gene flow in marine organisms with planktonic larvae (Bohonak, 1999; Chust et al., 2016). In contrast, marine taxa that lack planktonic larvae, including mammals, reptiles and elasmobranchs (sharks, skates and rays), depend on the active dispersal of individuals to maintain genetic connectivity. Many pelagic sharks undertake large-scale transoceanic and inter-oceanic migrations (Block et al., 2011; Queiroz et al., 2019) and oceanic and deep-sea species can maintain genetic connectivity between continental coasts and oceanic islands (Domingues et al., 2018c; Gubili et al., 2016), and across major ocean basins (Catarino et al., 2015; Veríssimo et al., 2017). Ocean depth between shallow coastal habitat, however, is a strong barrier to dispersal in some shallow-water benthic sharks and rays, generating genetic differences between individual islands at extremely small spatial scales (Gaida, 1997; Plank et al., 2010). Shallow-water marine organisms that lack dispersive larvae are therefore likely to produce unique genetic and biogeographic patterns in oceanic archipelagos compared to terrestrial organisms and marine species with planktonic dispersal, but have rarely been studied (Cowie & Holland, 2006; Dawson, 2016; Vieira et al., 2019; Weigelt et al., 2016).

The Galapagos archipelago and the Galapagos bullhead shark (*Heterodontus quoyi*) provide a unique model system for the study of evolutionary processes in oceanic islands. The volcanic islands are separated from the Pacific South American coast by approximately 1000 kms of up to 2000 m deep ocean (Figure 6a). The eastward movement of the NASCA plate across the Galapagos hotspot resulted in the sequential formation of volcanic islands and the complex bathymetry of the Galapagos plateau (Brewington et al., 2014; Snell et al., 1996). The convergence of three major ocean currents creates contrasting oceanographic conditions and diverse marine biogeography on a small spatial scale (Edgar et al., 2004; Houvenaghel, 1978). In the Galapagos, terrestrial organisms with limited inter-island dispersal generally follow a progressive genetic divergence that reflects the sequential formation of clusters of islands with similar age (Parent et al., 2008). Recent paleogeographic reconstructions of the Galapagos account for the periodical fusion and fission of landmasses through historical sea-level fluctuations, which has left its footprint on the biogeography of terrestrial organisms (Ali & Aitchison, 2014; Karnauskas et al., 2017). Here we use a shallow-water shark to test if paleogeographic dynamics

also influence genetic divergence in coastal marine organisms with limited dispersal. The Galapagos bullhead shark, *Heterodontus quoyi* (Figure 6b), has a small geographic range comprising the southcentral and western Galapagos archipelago and the continental shelf of northern Perú and possibly southern Ecuador (Acuña-Marrero et al., 2018; Bearez, 1996; Compagno, 1984). The small bodied shark (<100 cm) has a strictly benthic lifestyle, spending the majority of time on or close to the ocean floor, and is thought to inhabit rocky reefs at less than 40 m depth (Ebert et al., 2013; Weigmann, 2016). Here we test the hypothesis that ocean depth is a barrier to dispersal and gene flow in Galapagos bullhead sharks and assess the role of island formation and historical sea level changes in shaping genomic signatures of geographic isolation.

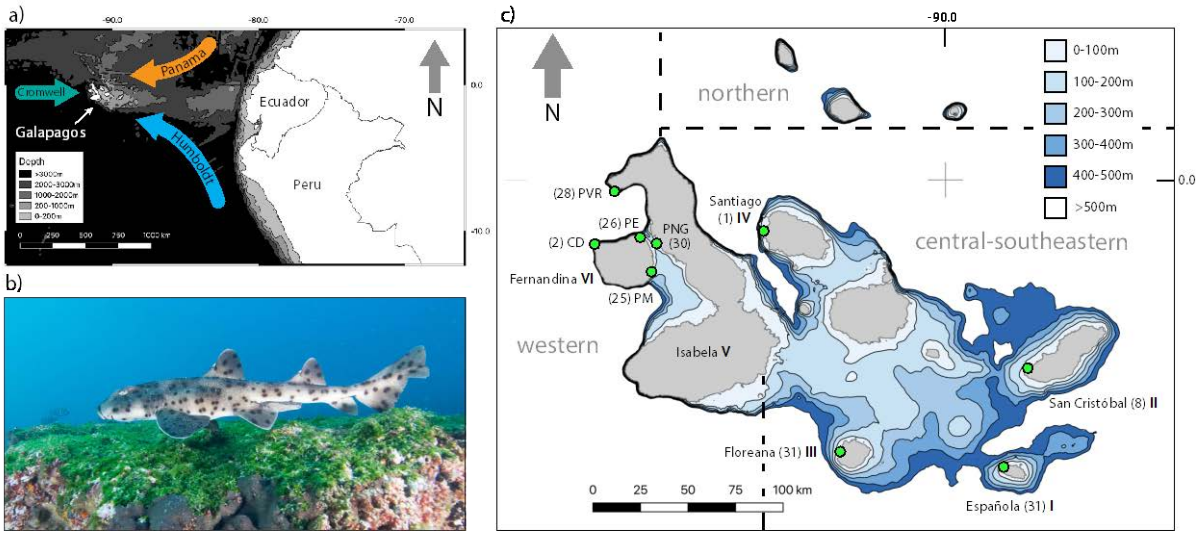


Figure 6. a) Location of the Galapagos Islands in the Eastern Tropical Pacific and in relation to ocean bathymetry and the Panama Current, the Humboldt Current, and the Cromwell Current; b) Adult male Galapagos bullhead shark (*Heterodontus quoyi*); c) Sampling design: Sampling locations (green circles) with island name or name of location (where more than one location was sampled on the same island), and number of samples in brackets. Sequential island emergence is given in bold roman letters next to island names: Española (I), San Cristóbal (II), Floreana (III), Santiago (IV), Isabela (V), and Fernandina (VI). Dashed lines and grey letters indicate the separation between the Western, Central-Southeastern and northern bioregions. Abbreviations for sampling location names: PVR (Punta Vicente Roca) and PNG (Parque Nacional Galapagos), PE (Punta Espinoza), PM (Punta Mangle), and CD (Cabo Douglas).

Materials and methods

Study area and sampling design

To examine the effect of ocean bathymetry on spatial genetic structure, Galapagos bullhead sharks were sampled from six islands in the Galapagos archipelago that are separated by varying levels of depth (Figure 6c). We assessed the role of island formation and historical sea level fluctuations on genetic patterns by sampling islands that emerged at different geological times, in an approximate East to West sequence (Geist et al., 2014; Karnauskas et al., 2017). We also sampled multiple locations on the same island (on Fernandina and Isabela Island) that are connected by continuous shallow-water habitat to evaluate potential genetic isolation by distance (IBD) due to limited dispersal capacity in the absence of depth barriers. Sampling locations on Española and Floreana Islands, located within five kilometres of each other, were combined (Appendix B Figure 15). The Galapagos also present contrasting oceanographic conditions and diverse subtidal communities on a small spatial scale that are created by the convergence of several major ocean currents (Edgar et al., 2004; Houvenaghel, 1978). Our sampling locations were located in the western bioregion, which is influenced by the upwelling of the nutrient-rich Cromwell Current, and in the central-southeastern bioregion, which is governed by the cold Humboldt current (Edgar et al., 2004; Palacios, 2004). Galapagos bullhead sharks are thought to be absent from the northern and far-northern bioregions that are separated from the main Galapagos platform by water over 1000 m deep and are characterized by warmer water of the Panama Current. This sampling design allowed us to explore the effect of contrasting marine environments on spatial genetic variation in genomic regions that are putatively under selection by the environment. Sharks were captured and released by hand during SCUBA to collect tissue samples from fin clips. Underwater sampling was designed to minimize handling time and stress responses in the sharks (approval for animal ethics, field work, access to and export of biological samples are detailed in the *Research and Ethics Approval* section). A total of 33 locations on seven islands were visited between 2015 and 2018 (Appendix B Figure 15) to search for the presence of *H. quoyi*. Nine locations on six islands that revealed higher abundances of sharks were visited repeatedly to increase the number of samples per location and achieve a balanced sampling design.

SNP genotyping and quality control

DNA extraction, sequencing and SNP genotyping was conducted by Diversity Array Technologies (DArT, Canberra, Australia; see Appendix B Table 11). The samples were processed using the proprietary DArT Pty Ltd analytical pipelines, which includes technical replicates from a subset of samples to assess genotyping reproducibility (Georges et al., 2018; Kilian et al., 2012; Sansaloni et al., 2011). The

following quality control steps were applied in addition to the DArT pipeline to avert potential downstream effects of SNP selection on the inference of population structure in non-model organisms (Linck & Battey, 2019; O'Leary et al., 2018; Waples & Allendorf, 2015). We randomized tissue samples from all sampling locations across sequencing plates and replicated tissue samples from two individuals within and across sequencing plates to independently assure genotyping consistency and generate baseline values to quickly assess relatedness and potential sample contamination during data filtering (Meirmans, 2015; O'Leary et al., 2018). To assure high quality of our SNP data set for reliably and adequately assessing population structure in relation to our hypotheses we filtered the raw data set using the R package *radiator* (Gosselin, 2019). First, SNPs below 98% reproducibility and markers that were not present in all sampling locations were removed. We excluded markers with a low minor allele count (MAC<4) to reduce genotyping error while retaining a higher probability of discovering outlier loci putatively under selection compared to applying a commonly used 5 % minor allele frequency (MAF) threshold (Ahrens et al., 2018). Further, SNPs with a coverage (read depth) below 10 and above 50, and a call rate of less than 95% were removed. We reduced the likelihood of physical linkage by keeping only one SNP per sequence. Departures from Hardy-Weinberg-Equilibrium (HWE) were tested using the *HardyWeinberg* R package (Graffelman, 2015, 2019; Graffelman & Morales-Camarena, 2008). Markers were removed that were out of HWE in at least three sampling locations based on a mid p-value threshold of 0.05. Moreover, we identified and removed putatively sex-linked SNP markers with the *sexy_markers* function in the *radiator* R package (Gosselin, 2019).

SNPs putatively under selection

Markers that are putatively under selection (outlier SNPs) were identified using two approaches that are well suited for spatially structured populations. We first applied the individual based method of the *PCadapt* R package (Luu et al., 2017). A minor allele frequency threshold of 5% was used to derive p-values. Outliers were selected that fell below a 5% percent false discovery rate (FDR) based on q-values, which are transformed from p-values, using the R package *qvalue* (Storey et al., 2019). We further used OutFLANK, which constructs a null distribution of loci that generate population structure through neutral processes and then iteratively trims loci that are putatively under selection, resulting in fewer false positives compared to F_{ST} based methods (Whitlock & Lotterhos, 2015). We ran OutFLANK using the *gl.outflank* wrapper function in the R package *DartR* (Gruber & Georges, 2019). To avoid bias we excluded samples from locations with small sample size (Cabo Douglas and Santiago) prior to the analysis. We trimmed the upper and lower 5% of loci and excluded loci with less than 10% expected heterozygosity to generate the null distribution and applied a 5% FDR threshold (Whitlock & Lotterhos, 2015). Loci that were identified as putative outliers with both methods were then removed

to create a neutral SNP data set to assess genetic patterns generated through neutral processes. Two outlier SNP data sets were used to explore the role of selection. One set contained outlier SNPs identified by both outlier methods, which is less likely to contain false positives, but may be too conservative to retain sufficient markers to detect genetic structure caused by divergent selection. To assure results were not biased by the conservative outlier detection approach, we created another, less conservative data set, which contained outlier SNPs detected by PCadapt only.

Population structure

Population structure was assessed using Bayesian clustering and pairwise fixation and differentiation indices. First, neutral SNPs were analyzed to infer proportions of genetic admixture for all individuals from *K* hypothetical ancestral populations using the R package *tess3r* (Caye et al., 2016). This method uses spatially explicit Bayesian models and is free from assumptions about MAF, HWE and linkage disequilibrium. Individual admixture proportions were estimated for *K* ancestral populations between one and eight, with ten replicate runs for each value of *K*, 10000 iterations, a tolerance value of 10^{-6} and a spatial parameter of alpha equals 0.01. As the spatial parameter approximates zero the algorithm produces results approximating those of the program STRUCTURE (Caye et al., 2016). The most likely number for *K* ancestral populations was estimated based on the lowest value of the cross-entropy criterion (Alexander & Lange, 2011; Frichot et al., 2014), generated using the cross-validation method and masking 10% of the data in training data sets (Caye et al., 2016; Liu et al., 2013). Because unequal sample sizes in our data set may bias admixture results, we also ran the analysis, with the same parameters, on a subsample of 56 individuals. For locations with more than 8 samples a subset of individuals was randomly chosen and all samples were kept for all locations with less than 8 samples. The data set contained ten individuals from Española, Floreana, and Punta Vicente Roca (PVR), five from Punta Espinoza (PE), Punta Mangle (PM) and Parque Nacional Galapagos (PNG), eight from San Cristóbal, two from Cabo Douglas (CD) and one from Santiago Island (SAN). To examine potential differences in genetic divergence through neutral and selective processes, we also applied the *tess3r* Bayesian clustering methods to the filtered data set containing all sharks and a more balanced subsample of 56 sharks (subsampled as described for neutral SNPs) for each outlier SNP data sets. We calculated pairwise fixation, F_{ST} (Weir & Cockerham, 1984), and pairwise differentiation, D_{ST} (Jost, 2008), indices between all locations with at least eight samples for the neutral SNPs using the R package *strataG* (Archer et al., 2017). Significance of pairwise comparisons and their corresponding p-values were calculated based on 1000 bootstraps and corrected for false positives using the FDR correction (Benjamini & Hochberg, 1995) implemented in the *p.adjust* R base function (R Core Team, 2019). We tested for directional gene flow among sampling locations with at least eight samples using

relative migration rates (based on *Nei's* G_{ST} and 1000 bootstraps) calculated for neutral SNPs with the *divMigrate* function of the *diveRsity* R package (Keenan et al., 2013; Sundqvist et al., 2016). Finally, we examined the relationship between spatial genetic patterns and progressive island formation using the most recent information on the approximate age of emergence (Geist et al., 2014) and paleogeographic reconstructions of the Galapagos (Ali & Aitchison, 2014; Karnauskas et al., 2017).

Isolation by depth

To test for the effect of contemporary bathymetry and historical sea level fluctuations on genetic connectivity we adapted isolation by resistance (IBR) analysis (McRae, 2006) using depth profiles of the Galapagos to represent landscape resistance to animal dispersal. Two isolation by resistance models were built, one based on contemporary bathymetry and another based on paleogeographic bathymetry that accounts for historical sea level fluctuations. We compared the resistance models to a null model based on isolation by distance analyses that only uses geographic distance and does not account for potential depth barriers (Guillot et al., 2009; Slatkin, 1993; Wright, 1943). Geographic distance was measured as straightest over-water distance between sampling locations using simple least cost analysis in the R package *marmap* (Pante & Simon-Bouhet, 2013). Next, we used a high resolution (15 arc-seconds) digital elevation model (DEM) of the Galapagos archipelago obtained from GEBCO (General Bathymetric Chart of the Oceans) to create the contemporary and paleogeographic isolation by resistance models (GEBCO Bathymetric Compilation Group, 2019). The DEM was reclassified using the *raster* R package (Hijmans, 2019) to generate resistance surfaces that represent positive values of increasing resistance between 1 to 100 (see Appendix B Table 10). For the contemporary IBR model, shallow coastal water less than 40 m deep, commonly occupied by bullhead sharks, were assigned the lowest resistance of 1. Areas between 40 to 900 m deep, corresponding to the extent of the Galapagos platform, were assigned increasingly higher resistances between 50-90 to represent barriers to dispersal. The highest resistance, 100, was assigned to land areas. Paleogeographic models of the Galapagos archipelago spanning the last 700 thousand years estimated extreme sea level low stands were repeatedly between 145 and 210 m deeper during glacial maxima (Ali & Aitchison, 2014). To test if low sea levels during glacial periods may have facilitated historical dispersal, the paleogeographic IBR analysis included low resistance for areas that were between 0-40 m deep when sea levels receded. Areas were assigned resistance values between 2 and 6, according to the number of times they were less than 40 m deep in the past. For example, areas that are currently 145-185 m deep were six times less than 40 m deep in the past and received a low resistance value of 2. Areas between 185-194 m deep were five times, and areas between 229-250 m only one time less than 40 m deep, and were assigned resistance values of 3 and 6, respectively (see Appendix B Table

10). Resistance distances (Shah & McRae, 2008) were calculated for the contemporary and paleogeographic resistance surfaces using the *commuteDistance* function in the R package *gdistance* and divided by a constant of 10.000 (van Etten, 2017). The linear relationship between linearized genetic distances (FST/(1 FST) and straightest over-water distances and between linearized genetic distances and contemporary and paleogeographic resistance distances was plotted and quantified using Pearson's correlation coefficient (r^2) and Mantel tests with 1000 permutations with the R package *DartR* (Gruber & Georges, 2019). The performance of each model was compared using a causal modeling approach (Cushman et al., 2006; McRae & Beier, 2007).

Signatures of isolation

To assess signatures of isolation we calculated several genetic diversity indices for each sampling location with a sample size larger than five for the neutral SNP data set using the *diveRsity* R package (Keenan et al., 2013). Indices included allelic richness (A_R), observed heterozygosity (H_O), expected heterozygosity (H_E), and inbreeding coefficients (F_{IS}). We estimated local contemporary genetic effective population size (N_e) for each genetically distinct unit identified by clustering analyses using the bias-corrected linkage disequilibrium (LD) method implemented in NeEstimator v.2.01 (Do et al., 2014; Waples & Do, 2008). The method assumes closed populations, no mutation or selection and can provide robust estimates of local N_e if migration rates between demes are low (Waples & Do, 2008, 2010). The likelihood that SNP loci are physically linked, potentially biasing N_e estimates based on LD, is low in our data set because we only kept one SNP locus per sequence and because of the large genome size in heterodont sharks (Akey et al., 2001; Waples et al., 2016; Waples, 2006). Sharks in each cluster also covered a large range of size classes spanning several generations, which reduces downward bias in single sample N_e estimates based on LD in organisms with overlapping generations (Waples et al., 2014). We determined the best minor allele frequency threshold (*Pcrit*) for each individual genetic cluster using the formula 1/(2S) < *Pcrit* <= 1/S (S=number of samples) as suggested by (Waples & Do, 2010). Because no life history parameters are known for *H. quoyi* no correction based on life span and maturity could be applied. Finally, we corrected N_e estimates for the number of haploid chromosomes found in the congeneric *H. japonicus* and *H. francisci (n=51)* using the formula $N_{ecor} = N_e/(0.098+0.219 \times lnChr)$, where *Chr* is the number of chromosomes (Stingo & Rocco, 2001; Waples et al., 2016).

Results

Sampling and genotyping

At total of 182 sharks were sampled from nine locations on six islands. Between 25 and 30 individuals were collected at each of four locations in the western bioregion (Fernandina and Isabela Islands) and on each of two islands in the central-southeastern bioregion (Española and Floreana Islands). Despite exploring eight locations on 20 dives between 2015-2018 only eight individuals were sampled on San Cristóbal Island. Only a single individual was captured after diving at six locations around Santiago Island, which was not revisited after. The DArT pipeline generated 33606 SNPs and after quality filtering we retained a total of 9223 neutral SNPs and 180 individuals (Appendix B Table 11). Briefly, none of the samples had large amounts of missing data and none showed signs of cross contamination or sample degradation based on excessively low or high heterozygosity. Two sharks, one on Fernandina and another on Isabela Island, were recaptured at the same location after a period of approximately one year. The individuals were identified as duplicate samples during the filtering process and their identity was also confirmed by comparing the shark's unique spot pattern on photographs taken in the field. For each pair of resampled sharks, we kept the sample with less missing data (higher call rate). We removed five putatively female-linked SNPs that had higher heterozygosity in females. These SNPs were present in around 50% of males compared to females indicating male heterogamety in Galapagos Bullhead sharks. Eleven loci putatively under selection were recovered by both outlier methods (75 SNPs in PCadapt, 14 SNPs in OutFLANK). We used two data sets with 9223 neutral SNPs in downstream analyses. One with 180 sharks (all individuals) and another with a subset of 56 sharks (balanced subset). We further explored signatures of adaptation using two data sets with 11 overlapping outlier SNPs and 180 (all individuals) and 56 (balanced subset) sharks, and another two with 75 outliers detected with the PCadapt method and 180 (all individuals) and 56 (balanced subset) sharks.

Population structure

Pairwise comparisons using neutral SNPs showed increasing genetic divergence with greater depth among sampling locations and older island emergence time (Figure 7 and Appendix B Table 12). Española Island, the oldest and most isolated island, consistently exhibited the highest genetic differentiation from all other locations. San Cristóbal and Floreana Islands showed the second highest differentiation. San Cristóbal Island revealed similar levels of differentiation (F_{ST}: 0.0133-0.0169) with the western locations compared to Floreana Island (F_{ST}: 0.0139-0.0161) based on F_{ST} values, but higher differentiation using D_{ST} (0.00038-0.00047 vs. 0.0003-0.00034). All pairwise comparisons within the western region were low for F_{ST} (0.0003-0.0028) and D_{ST} (0.000094-0.00014). With the exception of Punta Vicente Roca (PVR), the northernmost location on Isabela Island, all pairwise comparisons in the western region were not significant before and after false discovery rate (FDR) correction. We found no significant directional gene flow among any pair of sampling locations based on relative migration rates of the *divMigrate* method.

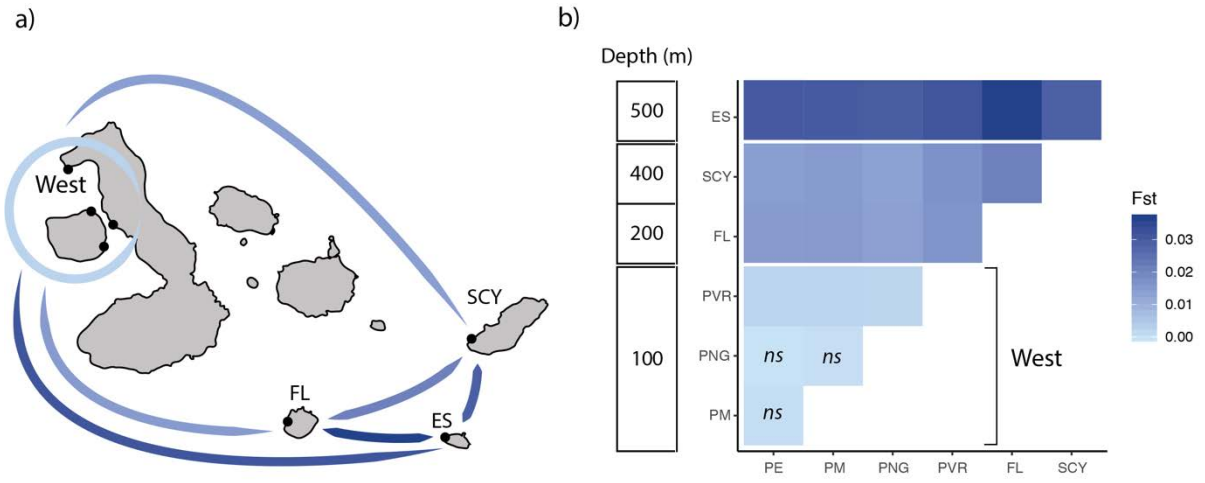


Figure 7 Pairwise comparisons between sampling locations based on genetic fixation index (F_{ST}) and 9223 neutral SNPs. a) Visualization of the level of genetic differentiation between locations. Comparisons between the western locations and all other inter-island comparisons are indicated by blue lines with colour intensity increasing with F_{ST} values. Low levels of genetic differentiation among the western locations are indicated by a light blue circle. b) Levels of F_{ST} and ocean depth between locations (ES = Española, SCY = San Cristóbal, FL = Floreana, PVR = Punta Vicente Roca, PNG = Parque National Galapagos, PM = Punta Mangle, PE = Punta Espinoza). The vertical bar shows the minimum ocean depth between pairs of locations.

Admixture analyses of 9223 neutral SNPs for all 180 sharks identified the most likely number of ancestral populations (*K*) as three (Appendix B Figure 16a). Sharks from Española and Floreana Islands formed two distinct ancestral populations, and individuals from all locations in the western archipelago (Isabela and Fernandina Islands) together with Santiago Island formed a third ancestral population. Individuals from San Cristóbal showed approximately one third genetic admixture from each of the three ancestral populations. Using the more balanced subset of 56 sharks, however, the admixture analyses distinguished Española, San Cristobal, Floreana Islands, and the western archipelago with Santiago Island each as distinct ancestral populations (Figure 8a and Appendix B Figure 17). The ancestral populations corresponded to individual islands that sequentially separated from a central island cluster over the last two million years (Figure 8b,c). Española Island was differentiated first, at *K* = 2 ancestral populations. Although Floreana Island is differentiated next, at *K* = 3, San Cristóbal Island carries larger amount of admixture from the most ancestral population, Española. Individuals from San Cristóbal Island had similar levels of admixture from Floreana Island, the western archipelago and Española Island at *K* = 3, using the full and balanced data sets, and were assigned a distinct ancestral population at *K* = 4 using the more balanced data set (Figure 8a). Admixture analyses based on 11 (overlapping Outflank and PCadapt outliers) and 75 outlier SNPs (PCadapt only) for all 180 sharks and for subsets of 56 sharks showed weaker genetic structure compared to neutral SNPs. Outlier SNPs only differentiated individuals from Española Island, primarily reflected genetic variation among individual sharks, and showed no pattern in relation to biogeographic regions (data not shown).

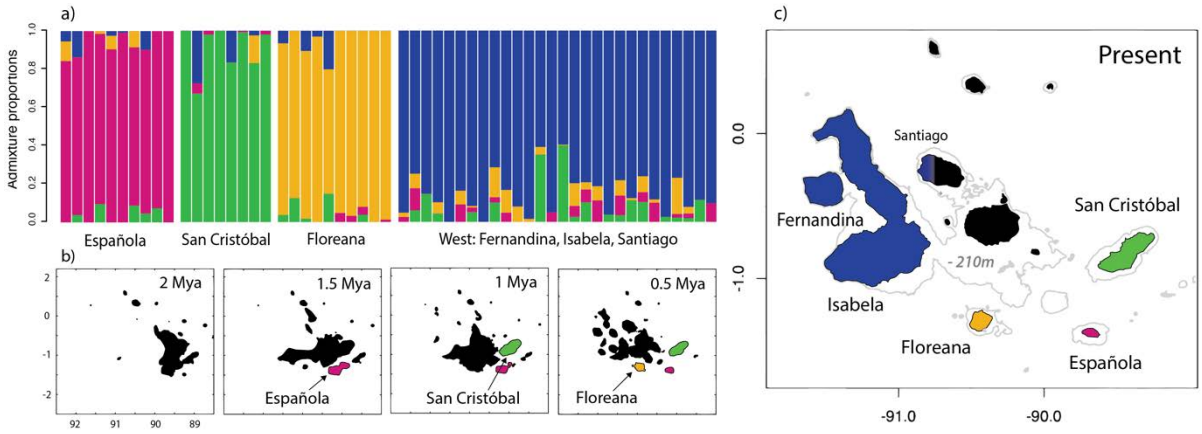


Figure 8. a) Individual admixture proportions for 56 individuals, 9223 neutral SNPs and K = 4 ancestral populations ordered from left to right following sequential island separation. b) Paleogeographic formation of the Galapagos archipelago with sequential separation of Española Island (purple) at 2-1.5 million years ago (Mya), San Crsitóbal Island (green) at 1.5-1 Mya, and Floreana Island (yellow) at 1-0.5 Mya, and the emergence of individual islands that formed Isabela and Fernandina Islands since 0.5 Mya, adapted from (Karnauskas et al., 2017). c) Present day Galapagos with 210m isobath indicating the land area that was exposed at the lowest sea level during the last 700 thousand years.

Isolation by depth

Model comparison showed that although all three models presented a significant relationship with genetic distance, the model fit improved when considering contemporary bathymetry, and accounting for historical sea level fluctuations provided the best model fit *(Figure 9*). Isolation by distance (IBD) based on shortest over-water distances between sampling locations resulted in significant correlation with genetic distance (mantel rest: r^2= 0.57, p=0.01). However, the scatter plot (*Figure 9b*) revealed a large gap between western and southeastern locations, indicating the presence of barriers between those locations and pairwise genetic distances among southeastern locations (Española, Floreana and San Cristóbal Islands) were high despite their geographical proximity. Contemporary IBR, which accounted for ocean depth between sampling locations, resulted in a higher correlation with genetic distance (Mantel test: r^2: 0.721, p=0.003; *Figure 9c*). The scatter plot with heatmap visualization displays that the model partially accounts for depth barriers, providing a better fit for the data (*Figure 9*d). Finally, the paleogeographic IBR model revealed the strongest correlation with genetic distances (Mantel test: r^2: 0.88, p=0.003) by taking into account ocean depth and historical sea level oscillations (*Figure 9e,f*).

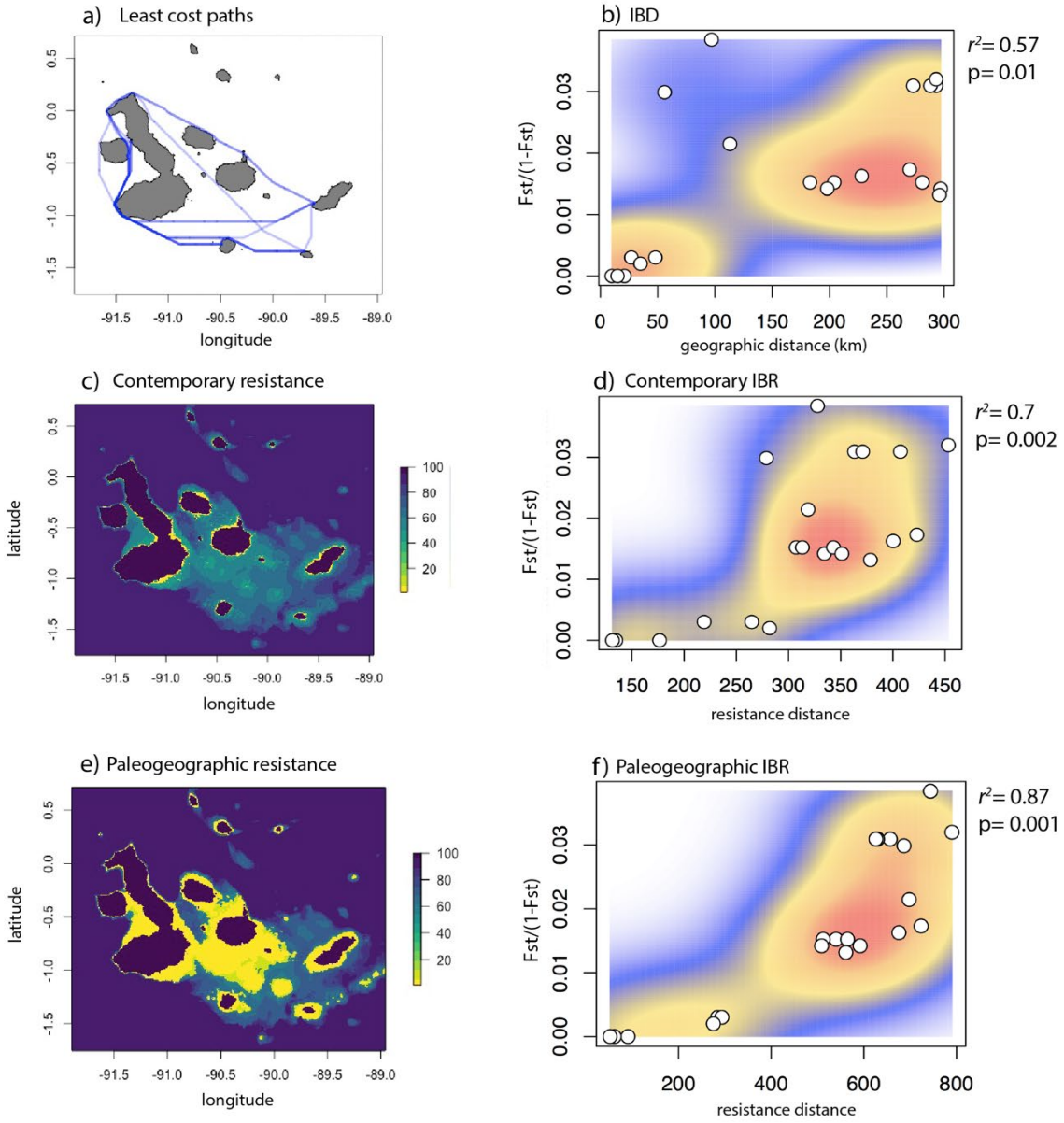


Figure 9. Comparison between IBD (isolation by distance), contemporary IBR (isolation by resistance), and paleogeographic IBR (isolation by resistance) models. a) Least-cost paths for shortest over-water distance between pairs of locations. b) scatter plot with heatmap visualization of the correlation between geographic distance and genetic distance (IBD model). c) resistance surface based on contemporary bathymetry of the Galapagos archipelago. d) correlation between contemporary resistance distance and genetic distance (contemporary IBR model). e) resistance surface based on paleogeographic bathymetry of the Galapagos archipelago. f) correlation between paleogeographic resistance distance and genetic distance (paleogeographic IBR model). Darker colours in resistance surfaces represent higher resistance for the hypothetical movement of sharks among locations. Bright yellow shading in resistance surfaces corresponds to coastal areas that were exposed or had less than 40 m depth during glacial maxima.

Genomic signatures of isolation

Genomic diversity was similarly low for all sampling locations. Allelic richness (A_R) ranged from 1.31 to 1.39 and observed heterozygosity (H_O) from 0.091 to 0.098 (*Table 3*). Similar levels of expected and observed heterozygosity and inbreeding coefficients (F_{IS}) close to zero indicate the absence of recent bottlenecks.

Table 3. Genetic diversity of Galapagos bullhead sharks (*Heterodontus quoyi*) based on 9223 neutral SNPs. Sampling locations: Española (ES), San Cristobal (SCY), Floreana (FL), Punta Espinoza (PE), Punta Mangle (PM), Parque Nacional Galapagos (PNG), Punta Vicente Roca (PVR). n=sample size, A_R = allelic richness, H_O =observed heterozygosity, H_E =expected heterozygosity, F_{IS} = inbreeding coefficient.

Location	n	A_R	H_O	H_E	F_{IS}
ES	30	1.37	0.098	0.098	0.004
SCY	8	1.31	0.089	0.089	-0.007
FL	29	1.36	0.091	0.093	0.013
PE	25	1.39	0.097	0.097	0
PM	24	1.38	0.096	0.095	-0.002
PNG	30	1.39	0.096	0.096	0
PVR	26	1.39	0.098	0.098	0.003

Genetic effective population size (N_e) was corrected for a 4% downward bias ($N_{ecor} = N_e/0.959$) to account for the number of chromosomes based on the congeneric *H. japonicus* and *H. francisci*. This resulted in the lowest N_{ecor} for Española, the most isolated and smallest island, followed by Floreana islands, which is geographically less isolated and about three times the size (*Table 4*). The largest effective population size was estimated for combined locations on Isabela and Fernandina islands (West) that formed a single population based on clustering analyses.

Table 4. Genetic effective population sizes (N_e) with confidence intervals (CI) and corrected effective population sizes (N_{ecor}) for the three main genetic clusters. Pcrit indicates the optimal minor allele frequency threshold based on sample size used to estimate Ne.

Location (sample size)	***Ne*** **(CI)**	Ne_{cor}
Española (30) *Pcrit*=0.03	**342.9** (334.4 - 351.9)	**358**
Floreana (30) *Pcrit*=0.03	**1641** (1464.1-1866.2)	**1711**
West (107) *Pcrit*=0.005	**7415.3** (6853.5-8077.1)	**7732**

Discussion

The Galapagos archipelago and the Galapagos bullhead shark were used as a model system to provide novel insight into the evolutionary processes that shape genetic structure and biogeographic patterns of shallow-water marine organisms in oceanic islands. Sequential island formation gradually established contemporary depth barriers between islands that varied in strength due to historical sea level fluctuations. This resulted in four distinct genetic clusters that exhibit low genetic diversity and effective population sizes that decrease from larger to smaller islands and with stronger isolation through historical and contemporary seascape configuration.

Isolation by depth

The application of isolation by resistance (IBR) analysis to a marine model system showcases the impact of contemporary and historical ocean bathymetry on genetic connectivity in coastal marine species with limited dispersal. Galapagos bullhead sharks showed contemporary genetic connectivity along short distances (20 kms) of continuous coastlines and across less than 10kms of 100m deep water, but larger ocean depths between islands pose effective barriers at distances of only 50kms. Similarly, other benthic sharks (*Squatina californica*) and rays (*Urobatis halleri*) with low dispersal capacity and shallow depth distributions can maintain connectivity along continuous coastlines but show genetic differences across deep water at less than 50kms distance (Ebert et al., 2013; Gaida, 1997; Last et al., 2016; Plank et al., 2010; Standora & Nelson, 1977; Vaudo & Lowe, 2006). Benthic Port Jackson sharks (*Heterodontus portusjacksoni*) migrate up to 1000kms along the Australian coast and manage to cross the Bass Strait to Tasmania, likely because the strait is relatively shallow (on average 60m) and has several islands that can be used as stepping stones (Bass et al., 2016). Our study supports previous findings that ocean depth may limit dispersal in shallow-water elasmobranchs at short geographic distances, while oceanic and deep-sea species have been found to maintain connectivity across depth barriers (Domingues et al., 2018c; Gubili et al., 2016). Ocean depth plays a minor role in shaping connectivity of coastal marine organisms with juvenile larvae that use ocean currents to sustain dispersal between shallow-water habitat across various levels of bathymetry (Galarza et al., 2009). In contrast, for species that lack juvenile larvae, such as coastal sharks and rays, bathymetry can play a similar role in marine connectivity than topography does in some terrestrial systems. For instance, terrestrial sky islands are high-altitude habitats that are separated by lower elevation. Genetic isolation among sky islands is common in a range of taxa, including insects (Masta, 2000; Smith & Farrell, 2005) reptiles (Holycross & Douglas, 2007) and amphibians (Osborne et al., 2019) and can be attributed to a limited tolerance to environmental conditions in lower elevations and low dispersal

capacity (Polato et al., 2018). In sky islands, climatic fluctuations have altered connectivity through elevational shifts in environmental conditions, similar to the effect of sea level oscillations in oceanic islands (Mastretta-Yanes et al., 2015; Rijsdijk et al., 2014). In oceanic islands, shallow-water marine species with limited dispersal are likely to produce genetic patterns that are more similar to some terrestrial organisms compared to marine organisms with juvenile larvae that disperse with ocean currents.

Flickering connectivity in oceanic archipelagos

The periodical fusion and fission of landmasses through historical sea-level fluctuations may have played a major role in shaping coastal marine populations in oceanic islands. In the Galapagos, low sea levels during the Pleistocene (2,588,000 to 11,700 years ago) repeatedly connected landmasses of the central and western archipelago and exposed seamounts between the central and southeastern islands (Geist et al., 2014; Parent et al., 2008). The paleogeographic IBR analysis showed that historical sea level fluctuations likely created dispersal corridors between the western and central islands and sea mounts provided stepping stones for the dispersal of Galapagos bullhead sharks between the central and southeastern islands. Similar admixture proportions among individual sharks within each genetic cluster imply that dispersal occurred before the establishment of a currently impermeable barrier and sufficient time has passed to homogenize genetic material received from other regions. In comparison, recent dispersal would result in distinctive admixture patterns. For example, recent dispersal events between islands resulted in two genetic clusters on the same island in Galapagos giant tortoises and marine iguanas, and hybridization among subspecies in the latter (Macleod et al., 2015; Poulakakis et al., 2012; Steinfartz et al., 2009). Dispersal and connectivity are subject to climatic variations in both marine and terrestrial systems. In terrestrial systems, climatic fluctuations caused the repeated fusion and fission of high-altitude environments that shift to lower elevations during glacial cycles (Hazzi et al., 2018). This mechanism generated recurring population connectivity in mountain salamanders in the sky islands of New Mexico (Osborne et al., 2019) and rodents in East African mountain ranges (Bryja et al., 2014). It also created the flickering connectivity system of the Andean alpine biome called *Páramo* and is largely responsible for its extraordinary diversity (Flantua et al., 2019). Historical fluctuations in global climate also altered island configuration with the rise and fall of sea levels and left its imprint on genetic divergence and biogeography of Galapagos' terrestrial fauna (Ali & Aitchison, 2014). This process may also drive patterns in marine organisms that inhabit oceanic islands around the globe, but there was no clear empirical evidence prior to this study (Vieira et al., 2019; Weigelt et al., 2016). The case of Galapagos bullhead sharks exemplifies that flickering

connectivity systems of oceanic archipelagos not only shape the evolution of terrestrial species but also coastal marine organisms with limited dispersal.

Island formation and genetic drift

Genetic population structure in Galapagos bullhead sharks likely reflects the gradual separation of individual islands and sequential vicariance events rather than progressive dispersal and colonization of newly formed islands. Paleogeographic reconstructions of the Galapagos archipelago that account for historical climate propose the sequential separation of individual islands from a central island cluster (Karnauskas et al., 2017). Galapagos bullhead sharks may have colonized the central island cluster prior to the separation of the oldest island, Española, between 2-1.5 million years ago. Subsequently, individual islands separated sequentially, gradually forming bathymetric barriers that slowly reduced migration rates and increased genetic drift, resulting in four distinct genetic clusters. Historical reconnections during lower sea levels, and potentially the lower sample size for San Cristóbal Island, marginally altered the general pattern. Bayesian admixture analyses first differentiated Española, then Floreana, and then San Cristóbal Island from the western archipelago. However, in contrast to Floreana Island and the western archipelago San Cristobal Island consistently showed greater admixture with the oldest Island, Española. But it also showed genetic admixture with Floreana Island and the western archipelago. Admixture results and a stronger differentiation based on genetic differentiation index (D_{ST}) between San Cristóbal, compared to Floreana Island, and the western archipelago, indicate that San Cristóbal Island may have separated second in sequence but partially reconnected during lower sea levels. To reinforce the sequential vicariance viewpoint we consider four alternative scenarios that have shaped genetic divergence in Galapagos fauna: (1) High levels of inter-island dispersal, (2) recent arrival, (3) multiple colonization events, and (4) strong divergent selection (Juan et al., 2000; Parent et al., 2008).

In the first scenario, high dispersal rates found in mobile marine species, for example Galapagos Penguins (Akst et al., 2002) and Galapagos sea lions (Wolf et al., 2008), lead to high genetic connectivity between islands that are separated by deep ocean. In contrast, species with limited capacity to swim over open ocean, may show a sequential divergence from older to younger islands (Parent et al., 2008; Poulakakis et al., 2020). This general pattern can be interrupted by occasional inter-island migrations, which was apparent in Galapagos marine iguanas but not Galapagos bullhead sharks (Macleod et al., 2015; Steinfartz et al., 2009).

Recent colonization and subsequent expansion throughout the archipelago, the second alternative, resulted in inter-island differentiation over the last 125.000 years in Galapagos hawks, a bird with

limited over-water dispersal (Bollmer et al., 2005). Although this scenario could generate the isolation by depth pattern in Galapagos bullhead sharks, it would also result in strong population bottlenecks and directional gene flow towards islands that are colonized after the arrival of a small founder population (Chaves et al., 2012; Clegg et al., 2002).

The third alternative are multiple colonization events from continental ranges to oceanic islands, which commonly result in the genetic divergence among paraphyletic groups that do reflect a sequential island formation pattern (Emerson, 2002; Schluter, 2009; Schluter & Conte, 2009). Paraphyletic groups have been found in Galapagos lava lizards and leaf-toed geckos (Benavides et al., 2009; Torres-Carvajal et al., 2014). However, samples from the continental coast of South America will be required to rule out multiple colonization events in Galapagos bullhead sharks in the future (Emerson, 2002).

Genetic diversification through natural selection and adaptation to the environment, the fourth alternative, is common in terrestrial, but less common in marine organisms that colonize oceanic archipelagos (Hedrick, 2019; Pinheiro et al., 2017). Outlier SNPs may represent genetic variants that are putatively selected for by the environment (Allendorf et al., 2010; Nielsen et al., 2009) and showed stronger spatial genetic structure compared to neutral SNPs at the scale of ocean basins in pelagic teleosts and sharks (Anderson et al., 2019; Pazmiño et al., 2018a; Pecoraro et al., 2018). At the scale of the Galapagos, low genetic structure found with outlier SNPs in *H. quoyi* may be explained by a lack of available niches due to overall high dispersal rates in marine organisms and a low selective pressure between the two Galapagos cold-water bioregions sampled (Pinheiro et al., 2017). However, Galapagos bullhead sharks may also be short of potentially adaptive standing genetic variation, characteristic of populations with small effective population size and low genetic diversity (Kelley et al., 2016), and the discovery of genomic regions putatively under selection in non-model organisms is limited by the sequencing and statistical methods applied here (Ahrens et al., 2018; Lowry et al., 2017; Tiffin & Ross-Ibarra, 2014).

In conclusion, the lack of recent bottlenecks and directional gene flow, and the absence of paraphyletic groups and selective divergence underpin that single colonization of a central island cluster and gradual genetic drift among sequentially separating islands is the most likely scenario for genetic divergence in Galapagos bullhead sharks.

Genomic signatures of isolation

Genomic signatures of isolation in Galapagos bullhead sharks are consistent with the gradual formation of barriers to dispersal and resemble those typical of terrestrial island biogeography. In oceanic islands, species with low dispersal commonly have lower genetic diversity and smaller population sizes compared to mainland populations owing to the reduced genetic variation of few founding individuals and because limited resources in small and fragmented habitats sustain smaller populations (Frankham, 1996, 1997). Galapagos bullhead sharks show lower diversity, based on similar sequencing techniques and numbers of markers, compared to shark species with higher dispersal or that were sampled along continental ranges (Appendix B *Table 13*). However, comparing levels of genomic diversity based on SNP markers among studies remains a challenge (Cariou et al., 2016). Future island-mainland comparisons in our study species may confirm lower genomic diversity in marine island populations. In some cases, relatively high genetic diversity in island populations is also possible. For example, large numbers of founding individuals in island-colonizing song birds, or high dispersal rates and a large population size that offset the founder effect in Christmas Island red crabs (*Gecarcoidea natalis*), led to relatively high genetic diversity (Aleixandre et al., 2013; Weeks et al., 2014). Galapagos bullhead sharks have low dispersal capacity and small populations sizes. Therefore, low genomic diversity may be traced back to a founder effect caused by few colonizing individuals, a common feature in terrestrial island populations (Frankham, 1997). Another parallel between Galapagos bullhead sharks and terrestrial species are small effective populations sizes (N_e) that scale with habitat availability in oceanic archipelagos (Brüniche-Olsen et al., 2019; Frankham, 1997). In some sharks, N_e approximates the census size (N_c) because of their low fecundity, consistent reproductive success, long life spans and late age at maturity (Dudgeon & Ovenden, 2015; Portnoy et al., 2009; Waples et al., 2013), a life history also characteristic of Heterodont sharks (Powter & Gladstone, 2008). This contrasts with many marine species because they have high dispersal rates, large-scale genetic connectivity, high fecundity, and large population sizes (Palumbi, 1994). Large populations of marine species have genetic effective population sizes (N_e) that are orders of magnitude smaller than the true number of adults in the population (N_c) owing to the high fecundity and variability in reproductive success (Palstra & Ruzzante, 2008; Waples et al., 2016). The life history of Galapagos bullhead sharks and lack of dispersal and genetic connectivity therefore suggest that N_e estimates for individual islands approximate true population sizes. Low genetic diversity and small population sizes that scale to the amount of available resources are common in terrestrial island biogeography but, to our knowledge, unprecedented in marine organisms (Dawson, 2016).

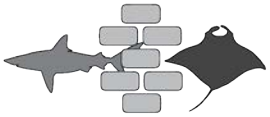
Conclusion

This study shows that in oceanic archipelagos shallow-water marine organisms without dispersive larvae produce unique genetic and biogeographic signatures when compared to terrestrial organisms and marine taxa with larval dispersal. The resulting geographically isolated marine populations with small effective population sizes and low genetic diversity are at high risk of extinction because they have reduced adaptive potential and lack replenishment from adjacent locations (Frankham et al., 2014; Ryman et al., 2019). This highlights the importance of preserving coastal marine habitat to bolster the resilience of marine island populations (Vieira et al., 2019). Future research on marine species with similar characteristics to our study species may broaden our understanding of island evolution and biogeography and enhance efforts to preserve the biodiversity of oceanic archipelagos.

Chapter 4 – Seascape connectivity of whitetip reef sharks (*Triaenodon obesus*) in Indo-Pacific coral reefs

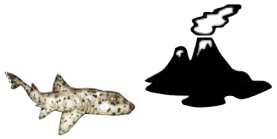
Chapter 1
General Introduction

Chapter 2
Barriers in a sea of elasmobranchs



Shallow-water reef sharks in fragmented tropical seascapes

Chapter 3
Galapagos bullhead sharks and oceanic islands



Chapter 4
Whitetip reef sharks and Indo-Pacific coral reefs

Chapter 5
General Discussion

This chapter has been prepared to be submitted to *Heredity*. The manuscript has been modified to fit the style of the thesis and avoid redundancies.

Contributions: M. Hirschfeld designed the study, collected, curated, analysed, and interpreted the data, and wrote the manuscript. A. Barnett, C. Dudgeon, and M. Sheaves, participated in study conception, interpreted the data, and contributed to the structure and content of the manuscript. H. Harrison, S. Payet, and W. Robbins contributed to the study conception, data collection and interpreted the data, and C. Dudgeon contributed to the data analysis.

Introduction

Connectivity is central to the persistence of natural populations and the resilience of fragmented marine systems to disturbance (Frankham, 2010; Gunderson, 2000). Dispersal generates demographic and genetic connectivity among disjunct habitats through the exchange of individuals and genetic information (Hellberg, 2009; Lowe & Allendorf, 2010). In the ocean, dispersal strategies are more diverse and the geographic scale of dispersal often more restricted than previously thought (Cowen et al., 2006; Levin, 2006; Winston, 2012). Marine population and seascape genetics and genomics can identify emerging spatial patterns of connectivity, delineate genetic subunits, and evaluate their resilience to disturbance (Allendorf et al., 2010; Von Der Heyden et al., 2014; Selkoe et al., 2016).

In coral reefs, patches of shallow-water habitat are fragmented at various spatial scales. Contiguous barrier reefs can stretch over thousands of kilometres along continental shelves, individual coral reefs within oceanic atolls and archipelagos present a higher level of fragmentation, and reefs on remote oceanic islands and seamounts are geographically isolated. The spatial arrangement of coral reefs shifts with global climate over long time scales, and extreme climatic (e.g., El Niño) and stochastic events (e.g., storms) cause variability in coral habitat quality and distribution at shorter time scales (Edmunds et al., 2018; Webster et al., 2018). The natural fragmentation and dynamic nature of coral reefs facilitate the study of spatial and temporal patterns of dispersal and gene flow in marine populations (Edmunds et al., 2018).

Coral reefs only cover less than one percent of the world's oceans but are hotspots for biodiversity (Van Oppen & Gates, 2006). At the same time, they are threatened from overfishing, habitat destruction, pollution and global warming (Bellwood et al., 2004; De'Ath et al., 2012; Hughes et al., 2017; Pandolfi et al., 2003). Understanding coral reef connectivity is therefore key to gauge the resilience of coral reefs to disturbance and their potential for recovery, and can be used as an effective tool to assure long-term persistence of reef communities (Hock et al., 2017; Krueck et al., 2017; Van Oppen & Gates, 2006). However, knowledge on connectivity in coral reefs is generally scarce and has primarily been evaluated for coral reef organisms with bipartite life histories, i.e., animals with site-attached or sessile adult life stages that produce large numbers of dispersive juvenile larvae (Cowen & Sponaugle, 2009; Riginos et al., 2019). Organisms that lack juvenile larvae, such as sharks, have received less attention but could provide a distinct perspective on the ecological and evolutionary drivers of dispersal and connectivity in coral reefs.

Reef sharks live in close proximity to shallow-water coral reefs and are often highly site-attached to individual reefs or reef clusters at the scale of tens of kilometres (Barnett et al., 2012; Dwyer et al., 2020; Espinoza et al., 2015a). While larger distances across open ocean may pose barriers to dispersal

in reef sharks, spatial patterns of genetic connectivity vary among species and depend on the molecular methods used (Boissin et al., 2019; Momigliano et al., 2017; Vignaud et al., 2013). Recent advances in molecular and statistical methods have increased the spatial and temporal resolution at which seascape connectivity can be measured (Kelley et al., 2016; Riginos et al., 2016; Selkoe et al., 2016). The use of multiple molecular marker types can further provide insight into evolutionary processes that shape reef shark dispersal and genetic connectivity at various spatio-temporal scales (Dudgeon et al., 2012; Green et al., 2018). Studying connectivity in reef-associated sharks using a mixed-marker approach may therefore enhance our understanding of coral reef connectivity and improve the spatial management of these fragmented systems.

In this study we use a combination of molecular markers to assess patterns of dispersal and connectivity in a highly resident reef shark. Whitetip reef sharks (*Triaenodon obesus*) are medium-sized (max. 200cm) benthopelagic sharks that are strongly associated with reef structure, where they are commonly found resting on the sea floor, in caves and in crevices, for long periods (Espinoza et al., 2014; Randall, 1977; Whitney et al., 2008). They exhibit high levels of residency and long-term site fidelity at individual reefs (Barnett et al., 2012; Whitney et al., 2012a) and primarily inhabit shallow water from just below the surface to 100 m deep (Asher et al., 2017; Randall, 1977), with the deepest occurrence recorded at 301 m in the oceanic Cocos Islands, Costa Rica (Cortés et al., 2012). Whitetip reef sharks are among the five most abundant coral reef-associated shark species, of which they are the most site-attached (Dwyer et al., 2020). The strong association to the substrate of shallow-water reefs would suggest that this species has a low dispersal capacity and that larger distances of deep ocean between shallow reef habitat may pose barriers to dispersal and genetic connectivity. Paradoxically, whitetip reef sharks have a vast geographic distribution, encompassing tropical and subtropical reefs across the Pacific and Indian Ocean, and have colonized some of the most remote oceanic locations, including the Hawaiian Archipelago, the Galapagos and Cocos Islands (Compagno, 1984; Ebert et al., 2013). Whitney et al. (2012) found genetic differences within contiguous coastal reef systems, but genetic connectivity across large oceanic distances in the Pacific Ocean, based on a single mitochondrial DNA marker, and proposed that *T. obesus* is a site-attached reef shark with oceanic dispersal. Here we combine mitochondrial DNA with thousands of genomic markers to assess genetic population structure and connectivity of whitetip reef sharks across the Indo-Pacific seascape. We use extensive sampling of reefs in the Coral Sea to test the oceanic dispersal hypothesis and explore potential ecological and evolutionary drivers of dispersal over various spatial and temporal scales.

Methods

Sampling and study design

Whitetip reef sharks were sampled from Indo-Pacific coral reefs across different geographic scales. At the large geographic scale, we sampled sharks from reefs on either side of the Torres Strait barrier and from oceanic islands that are separated from continental shelf habitat by large distances of open ocean and deep waters (*Figure 10a*). At a regional scale, we extensively sampled sharks from reefs in the Coral Sea that represent various levels of fragmentation (*Figure 10b*). The Great Barrier Reef (GBR) is formed by contiguous coral reefs spanning more than 3000 kms. Only the Capricorn Group, the southern extent of the GBR, is separated from the main GBR by the up to 200 m deep Capricorn Channel. Coral reefs on the Queensland and Marion Plateaus are more fragmented, with tens to hundreds of kilometres and often over 500 m deep water between them. The Queensland Plateau is separated from the GBR by the 1000-2000 m deep Coral Sea Trough. Osprey, Kenn and Wreck Reefs are small, highly isolated reefs at the tip of oceanic seamounts that are surrounded by 2000-4000 m deep water. Shark tissue samples (muscle biopsies and fin clips) were collected during SCUBA diving between 2017 and 2019 and additional samples were sourced from various research groups in Australia (Table 5).

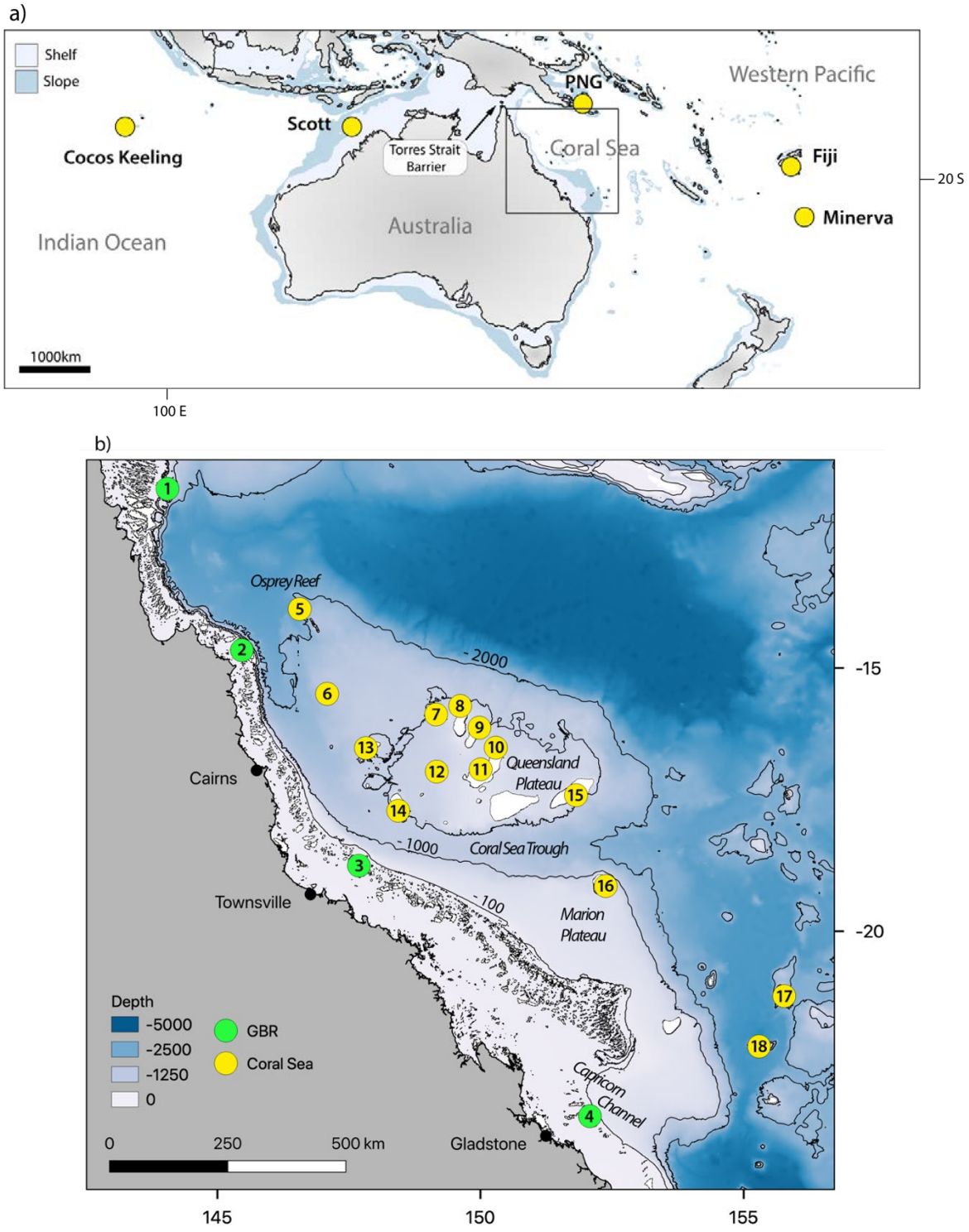


Figure 10. Whitetip reef shark sampling locations. a) Coral reefs sampled (yellow dots) across the Indo-Pacific. PNG = Papua New Guinea. The black box indicates the area of extensive sampling in the Coral Sea. b) Sampling locations in the Australian Great Barrier Reef (GBR; green dots) and offshore Coral Sea (yellow dots). Bathymetry, key geographic features, and the names of key sampling locations referred to in the text are indicated. (1) Raine Island, (2) Northern GBR, (3) Central GBR, (4) Capricorn Group, (5) Osprey, (6) Bougainville, (7) Moore, (8) Bianca, (9) Willis, (10) Magdelaine, (11) Chilcott, (12) Herald, (13) Holmes, (14) Flinders, (15) Lihou, (16) Marion, (17) Kenn, (18) Wreck.

DNA extraction, sequencing, genotyping and data filtering

Genomic DNA was extracted from fin clips and muscle tissues using a modified salting out protocol detailed in Appendix C (Sunnucks & Hales, 1996).

Mitochondrial DNA control region (mtDNA CR)

We amplified 819 bp of the mtDNA CR using the light strand primer Pro-L and the heavy strand primer 282-H following Whitney et al. (2012) with slight modification to the PCR cycling conditions. Sequencing of clean PCR products was performed by the Australian Equine Genetics Research Centre (AEGRC) at the University of Queensland, Australia, using BigDye™ terminators with the Pro-L primer and the internal light strand primer Rf45 (Whitney et al., 2012b). We complimented our mtDNA CR data set (n=90) with 68 sequences generated by (Whitney et al., 2012b) that overlapped with our study locations. All 158 sequences were assessed and aligned using Geneious Prime® 2019.2.3 (https://www.geneious.com). Detailed PCR protocols can be found in Appendix C.

Single nucleotide polymorphisms (SNPs)

Sequencing and genotyping of SNPs from extracted DNA was conducted by Diversity Array Technologies (DArT, Canberra, Australia) and processed using the proprietary DArT Pty Ltd analytical pipelines (Georges et al., 2018; Kilian et al., 2012; Sansaloni et al., 2011). The resulting SNPs data set was filtered using the R package *radiator* to assure high quality of the samples, reduce genotyping error and account for potential biases in downstream analyses (Gosselin, 2019; Linck & Battey, 2019; O'Leary et al., 2018; Waples & Allendorf, 2015). Loci putatively under selection (outlier loci) were identified using spatially explicit methods implemented in PCadapt (Luu et al., 2017) and OutFLANK (Whitlock & Lotterhos, 2015) and were excluded from the data set to assess neutral processes shaping genetic population structure. A summary of the data filtering protocol and outlier detection analyses are reported in Appendix C Table 14).

Genetic diversity, population structure and seascape connectivity

mtDNA CR

We calculated population-wide haplotype diversity (*h*) and nucleotide diversity (π) using DnaSP v.5.10.1 (Librado & Rozas, 2009). To assess mtDNA population structure we visualized haplotype distributions among sampling sites by constructing a median-joining network in popart v.1.7 (Leigh & Bryant, 2015). We used *Arlequin* version 3.5 to calculate pairwise genetic differentiation (Φ_{ST}) for populations with more than five samples, assessed significance based on 10000 bootstraps and corrected p-values for multiple comparisons using the false-discovery rate correction (Benjamini & Hochberg, 1995) implemented in the *p.adjust* R base function (Excoffier & Lischer, 2010; R Core Team, 2019).

SNPs

Genomic diversity of whitetip reef sharks was assessed by calculating allelic richness (A_R), observed (H_O) and expected heterozygosity (H_E), as well as inbreeding coefficients (F_{IS}) for each sampling location with a sample size larger than five using the *diveRsity* R package (Keenan et al., 2013). The pairwise fixation index F_{ST} (Weir & Cockerham, 1984) was estimated for all locations with more than 5 samples using the R package *strataG* (Archer et al., 2017) and their significance and corresponding p-values were calculated based on 10000 bootstraps. P-values were corrected for multiple comparisons using the *p.adjust* R base function and false-discovery rate correction (Benjamini & Hochberg, 1995; R Core Team, 2019).

The spatial design in this study is of a hierarchical nature, with five geographically distant (>2000 kms) sampling locations at the level of the Indo-Pacific and 18 locations at the regional level of the Coral Sea that are separated by smaller geographic distances (<1000 kms). We therefore, applied a hierarchical assessment of genetic population structure to be able to detect lower-level structure that can be masked by higher level differentiation (Rosenberg et al., 2002; Vähä et al., 2007). To assess the number of genetic clusters and their spatial distribution we inferred proportions of genetic admixture using the R package *tess3r* (Caye et al., 2016). To account for the hierarchical structure of our sampling design we first estimated admixture proportions for the entire data set and then for a subset of samples that were assigned to a single genetic cluster, which contained all GBR and Coral Sea locations, but not the Capricorn Group. For both levels, we estimated admixture proportions for *K* ancestral populations between one and eight, with ten replicate runs for each value of *K*, 1000 iterations, a tolerance value of 10^{-6} and a spatial parameter of alpha equals 0.01. As the spatial parameter approximates zero the algorithm produces results comparable to the programs STRUCTURE or Admixture (Caye et al., 2016). The most likely number for *K* ancestral populations was then chosen based on the lowest value of the cross-entropy criterion (Alexander & Lange, 2011; Frichot et al., 2014), which was generated using the cross-validation method and masking 10% of the data in training data sets (Caye et al., 2016; Liu et al., 2013). Finally, we generated geographic maps by interpolating admixture proportions using the *tess3r maps* function to visualize genetic gradients across the Australian GBR and Coral Sea seascape.

The influence of seascape features on population genomic patterns was assessed using isolation by distance (IBD) and isolation by resistance (IBR) analyses and by superimposing genetic gradients with major ocean currents in the Coral Sea (McRae, 2006; Slatkin, 1993). First, we measured the shortest over-water distance between reef locations using least cost paths analysis in the R package *marmap* (Pante & Simon-Bouhet, 2013) to assess the effect of geographic distance on genetic differentiation (Wright, 1943). Secondly, we used bathymetry data from the Coral Sea and IBR analysis to test if increasing ocean depth acts as barrier to gene flow in whitetip reef sharks (McRae, 2006). The

bathymetry raster (ETOPO1 1 Arc-Minute Global Relief Model) was reclassified using the *raster* R package to generate a resistance surface representing positive values of increasing resistance between 1 to 100 (Amante & Eakins, 2009; Hijmans, 2019). To reflect the preference of *T. obesus* for reef habitat less than 100 m deep and account for extreme observations at larger depth, we assigned the lowest resistance (1) to depths between 1 and 100 m, a resistance of 2 for depths between 101-200m, and a resistance of 3 for depths between 201-300 m (Asher et al., 2017; Cortés et al., 2012; Randall, 1977). Since this species has not been reported below 301m we incremented resistance values by 3 for each step of 100m (e.g., 301-400m depth equals a resistance value of 6) to the lowest water depth between sampling locations (2801-2900m depths equals a resistance value of 90) and assigned the highest resistance value of 100 to land surfaces. Pairwise resistance distances between sampling locations were then calculated from the resistance surface using the *commuteDistance* function in the R package *gdistance* (van Etten, 2017; Shah & McRae, 2008). We tested for isolation by distance by assessing association between genetic distances (F_{ST}) and shortest over-water distances (least cost paths) and for isolation by resistance by assessing the association between F_{ST} values and resistance distances using Pearson's correlation coefficient (r^2) and Mantel tests based on 1000 permutations implemented in the *DartR* package (Gruber & Georges, 2019). Finally, we visually assessed the potential relationship between genetic patterns and ocean circulation by overlaying major ocean currents in the Coral Sea with genetic gradient maps (Schiller et al., 2015).

Results

Genetic diversity

Tissue samples from 183 individual whitetip reef sharks from 23 coral reef locations were analysed (Table 5). Mitochondrial DNA sequencing of 90 samples discovered six unique control region haplotypes of 819bp (base pairs) lengths and seven variable sites. Five haplotypes had been previously described by Whitney et al. (2012), except a single haplotype (Hap 3) that was unique to North Minerva Island. Analysis of 158 mtDNA CR sequences from 19 coral reef locations resulted in a population wide haplotype diversity (*h*) of 0.639 and nucleotide diversity (π) of 0.00284.

Initial genotyping generated 33466 SNPs for 209 individuals and we retained a total of 8559 neutral SNPs and 183 individuals after quality filtering and removing putative outlier loci (Appendix C Table 14). No samples were missing large amounts of data. Three samples had excessively low heterozygosity, indicating sample degradation, and one sample had excessively high heterozygosity, potentially due to cross contamination. All four samples were removed during data filtering. The inclusion of duplicate samples allowed us to detect a pair of samples that were collected from the same individual shark and at the same location on Heron Island in the Capricorn Group, after a period of seven years. We only kept one sample with lower amount of missing data for each pair of duplicate samples, resulting in the removal of 22 samples. A total of 36 putative outlier loci that were identified by both outlier methods were excluded from the data set to assess neutral genetic population structure in downstream analyses.

Genomic diversity was similar for all reef locations but Cocos Keeling Islands (Table 5). Observed heterozygosity (H_O) ranged from 0.13 - 0.151 and allelic richness (A_R) ranged from 1.348 to 1.289 but were lower, 0.122 and 1.25, respectively, for Cocos Keeling. The inbreeding co-efficient (F_{IS}) was close to zero for all sampling locations.

Table 5. Sample sizes (n) for mtDNA and SNPs data sets and genomic diversity. n= number of samples, nH number of mtDNA haplotypes present at location. A_R = allelic richness, H_O = observed heterozygosity, H_E = expected heterozygosity, F_{IS} = inbreeding coefficient. NGBR= northern GBR, CGBR=central GBR, PNG=Papua New Guinea.

		mtDNA		**SNPs**				
Region	**Location**	**n**	***nH***	**n**	A_R	H_O	H_E	F_{IS}
Indian Ocean	Cocos Keeling	22	4	5	1.25	0.122	0.118	-0.051
Great Barrier Reef	Scott			13	1.325	0.141	0.146	**0.02**
	Raine Island			1				
	NGBR	20	4	15	1.348	0.149	0.15	-0.004
	CGBR	19	3	20	1.345	0.143	0.151	**0.034**
Offshore Coral Sea	Capricorn Group	20	2	26	1.323	0.138	0.142	0.014
	Osprey	18	2	22	1.341	0.143	0.151	**0.038**
	Bougainville	6	2	6	1.288	0.131	0.131	-0.017
	Moore	9	2	16	1.341	0.147	0.15	0.011
	Bianca	1	1	1				
	Willis	1	1	1				
	Magdelaine	10	2	12	1.335	0.145	0.146	-0.006
	Chilcott	1	1	2				
	Herald			1				
	Holmes	4	1	4	1.296	0.146	0.133	-0.11
	Flinders	3	2	3	1.289	0.149	0.13	-0.16
	Lihou	7	1	8	1.324	0.145	0.142	-0.03
	Marion	1	1	6	1.297	0.134	0.134	-0.023
	Kenn	2	1	4	1.29	0.142	0.13	-0.1
	Wreck	5	2	5	1.293	0.138	0.131	-0.066
Western Pacific	PNG			3	1.293	0.153	0.131	-0.178
	Fiji	7	2	7	1.328	0.15	0.146	-0.037
	Minerva	2	1	2				
		158	6	**183**				

Large scale population structure

mtDNA CR

The vast majority of samples corresponded to one of two control region haplotypes, Hap1 (n=67) and Hap2 (n=64), of which at least one was present at any sampling location (Figure 11). Cocos Keeling in the Indian Ocean revealed two unique haplotypes (Hap5 and Hap6) and a third haplotype (Hap4) that was only shared with the northern GBR (NGBR). Pairwise genetic comparisons (Φ_{ST}) also reflected the isolation of the Indian Ocean and to some extent the Capricorn Group from all other coral reefs, which showed no significant genetic differences among each other (*Table 6*).

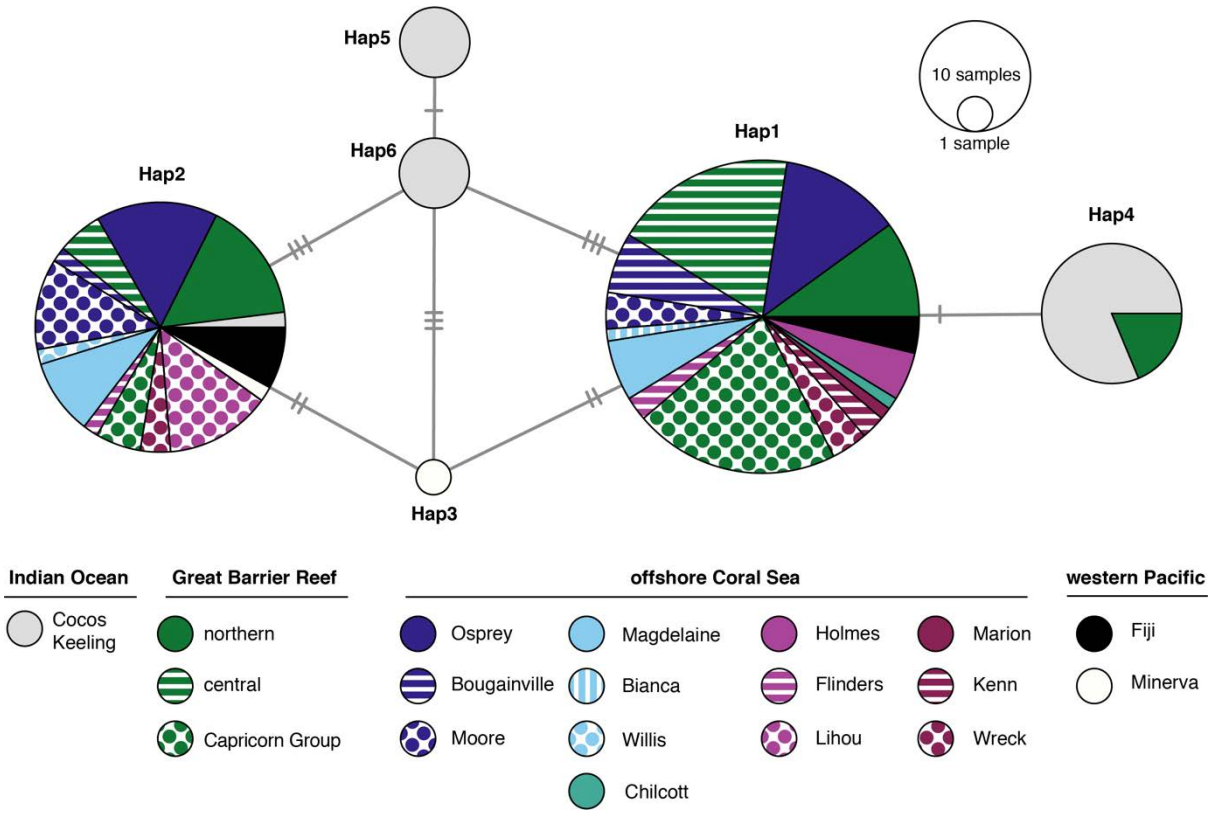


Figure 11. Median-joining network based on 819bp mitochondrial DNA control region sequences and 158 individuals. The size of the circles is proportional to the number of samples with the same haplotype (Hap1-6) and the different colour-pattern combinations represent sampling locations. The number of mutations between haplotypes is represented by the number of strokes on the connecting branches.

SNPs

Admixture analyses at the highest level suggested three as the most likely number of ancestral populations and distinguished whitetip reef sharks from the Indian Ocean and the Capricorn Group from all other locations (*Figure 12* and Appendix C *Figure 18*). Sharks from the main section of the GBR and offshore Coral sea locations were primarily composed of the third ancestral group with varying admixture proportions suggesting regional substructure. Fiji, Minerva and PNG were also assigned to the third ancestral group but also showed some admixture with the Indian Ocean. All pairwise comparisons (F_{ST}) based on neutral SNPs were significant after correcting for multiple comparisons (*Table 6*). The strongest genetic differentiation was found between locations on either side of the Torres Strait, between Cocos Keeling (F_{ST} =0.24-0.2) or Scott Reef (F_{ST} = 0.13-0.09) and all Pacific Ocean locations. Further, Cocos Keeling also showed high genetic differentiation with Scott reef (F_{ST} =0.17) on the Western Australian continental shelf. In the Pacific, the Capricorn Group (F_{ST} =0.4-0.9) and Fiji (F_{ST} =0.5-0.9) showed the strongest differentiation with the rest of coral reefs in the western Pacific, followed by more subtle differentiation of Osprey (F_{ST} =0.3-0.5), Bougainville (F_{ST} =0.5-0.7) and Moore (F_{ST} =0.3-0.5) with other Coral Sea reefs.

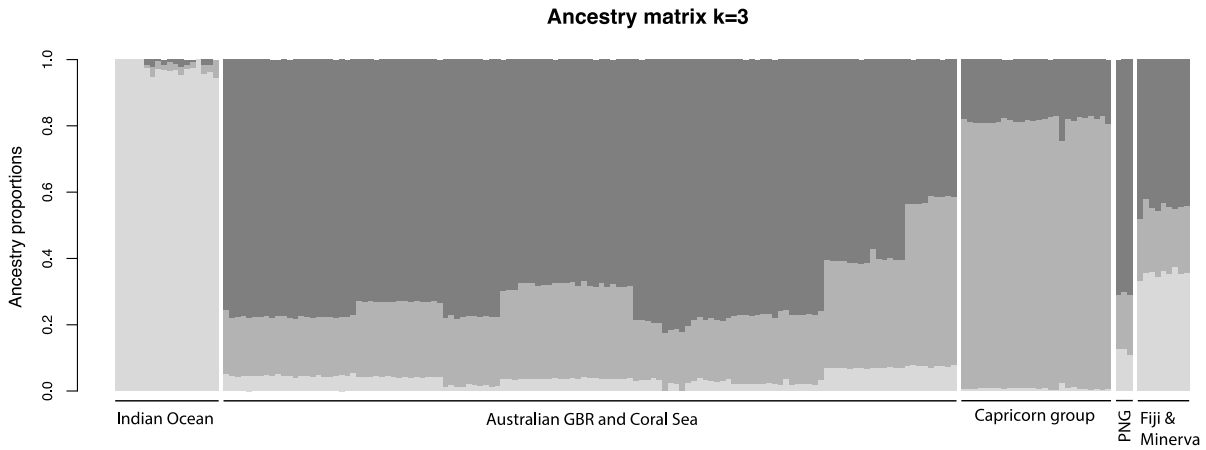


Figure 12. Individual admixture proportions for 183 sharks (vertical bars) based on 8559 neutral SNPs for K = 3 ancestral populations.

Table 6. Pairwise genetic differences for sampling locations with more than 5 samples. Φ_{ST} based on 819bp of the mtDNA control region (top matrix), and F_{ST} based on 8559 neutral SNPs (bottom matrix). Bold letters indicate significant values after false discovery rate correction at p = 0.05 (mtDNA) and p = 0.01 (SNPs).

	Cocos	Scott	NGBR	CGBR	Osprey	Bougainville	Moore	Magdelaine	Lihou	Marion	Wreck	Capricorn	Fiji
Cocos		**0.17**	-	**0.51**	**0.24**	**0.45**	**0.34**	0.24	**0.59**		**0.16**	**0.24**	0.27
Scott	**0.19**		-	-	-	-	-	-	-	-	-	-	-
NGBR	**0.20**	**0.09**		**0.28**	-0.04	0.20	0.05	-0.05	0.42	-	-0.13	0.10	-0.04
CGBR	**0.20**	**0.09**	**0.01**		0.24	-0.12	0.00	0.18	0.01	-	0.28	**0.61**	0.08
Osprey	**0.20**	**0.10**	**0.02**	**0.03**		0.17	0.01	-0.08	0.41	-	-0.14	0.15	-0.07
Bougainville	**0.24**	**0.13**	**0.05**	**0.05**	**0.05**		-0.08	0.09	0.03	-	0.19	**0.61**	-0.01
Moore	**0.21**	**0.11**	**0.04**	**0.04**	**0.05**	**0.05**		-0.06	0.21	-	-0.02	0.42	-0.12
Magdelaine	**0.21**	**0.10**	**0.03**	**0.02**	**0.04**	**0.05**	**0.03**		0.39	-	-0.15	0.21	-0.13
Lihou	**0.21**	**0.10**	**0.02**	**0.02**	**0.03**	**0.05**	**0.04**	**0.02**		-	0.57	**0.78**	0.33
Marion	**0.22**	**0.11**	**0.03**	**0.03**	**0.05**	**0.07**	**0.05**	**0.04**	**0.03**		-	-	-
Wreck	**0.22**	**0.10**	**0.04**	**0.03**	**0.05**	**0.07**	**0.05**	**0.04**	**0.04**	**0.05**		0.06	-0.14
Capricorn	**0.23**	**0.12**	**0.05**	**0.04**	**0.06**	**0.08**	**0.07**	**0.06**	**0.05**	**0.06**	**0.06**		0.30
Fiji	**0.20**	**0.09**	**0.06**	**0.05**	**0.06**	**0.09**	**0.07**	**0.06**	**0.06**	**0.07**	**0.07**	**0.09**	

Regional scale population structure

Admixture analyses of the regional data set (main GBR and offshore Coral Sea reefs) revealed a slight increase in the cross-entropy criterion between one and two, with a plateau at three, suggesting that the most likely number of ancestral populations lies between *K* = 1 to 3 (Appendix C *Figure 19*). Admixture proportions for three ancestral populations clearly distinguish Osprey and Moore reef from the rest of the reef locations, which showed a subtle genetic gradient among them (Figure 13a). Spatial interpolation of genetic admixture proportions visualized the strongest genetic breaks between Osprey Reef and all other locations and between Moore Reef and adjacent reefs of the Queensland plateau at less than 100 km distance (Figure 13b). The analysis further suggested connectivity between isolated oceanic reefs in the southern Coral Sea (Kenn and Wreck) with the Queensland Plateau and the Central and Northern GBR over a distance of 1300 kms and across deep offshore water and the deep Coral Sea Trough.

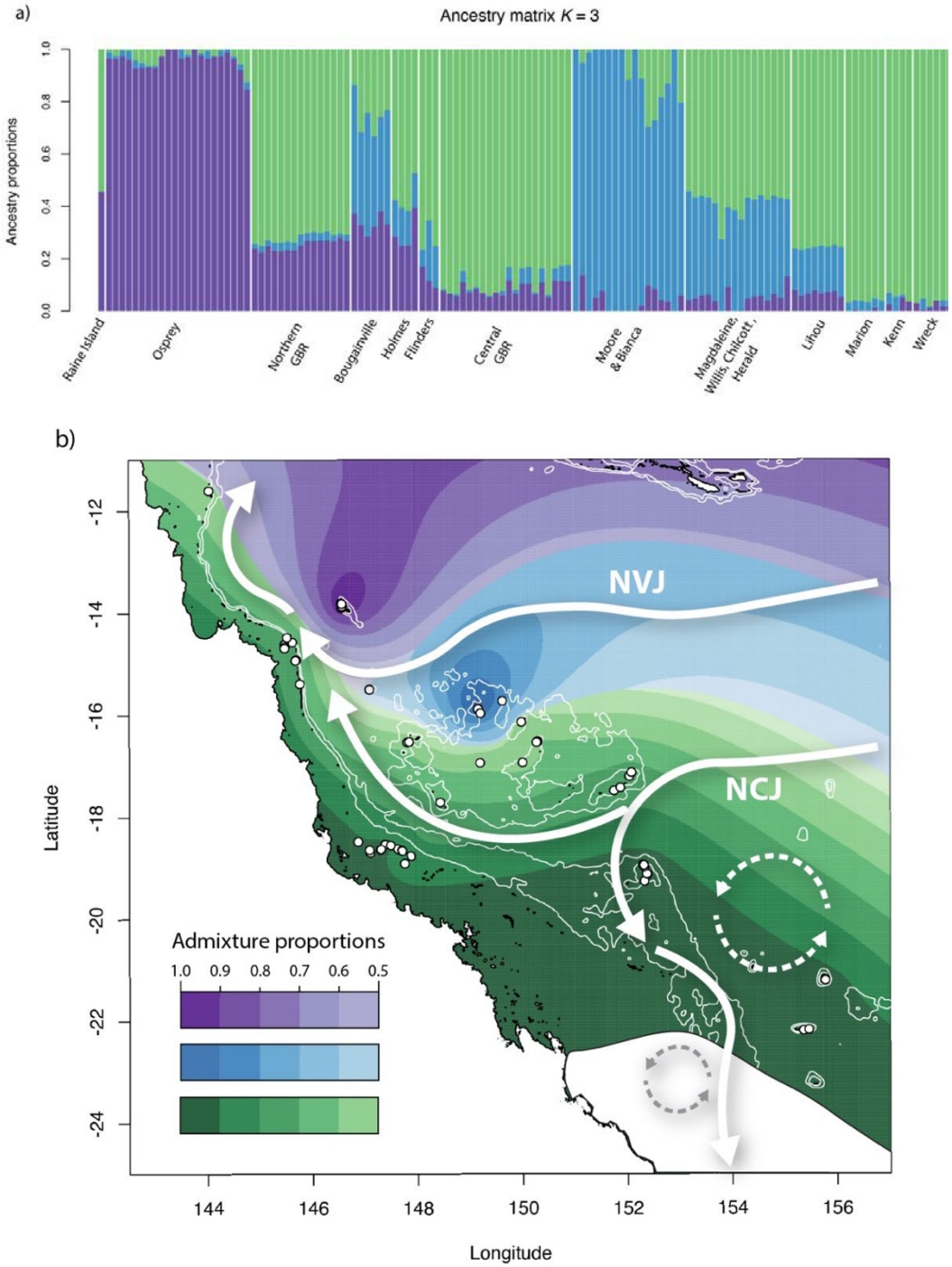


Figure 13. Regional scale population structure. a) Individual admixture proportions for 127 sharks (vertical bars) for *K* = 3 ancestral populations and b) geographic distribution of admixture proportions in the Coral Sea. Areas are coloured according to the ancestral population that contributes the highest admixture proportion to sharks sampled from that area. Gradients of the same colour indicate the admixture proportion in intervals of 0.1. White dots represent sampling locations used for the spatial interpolation and white lines represent 200 m and 1000 m depth contours to visualize the continental shelf, the Queensland and Marion Plateaus, and the isolation of oceanic reefs. Broad white lines with arrow heads indicate the main ocean currents and their flow direction in the Coral Sea, adapted from (Schiller et al., 2015). NVJ=North Vanuatu Jet, NCJ= New Caledonia Jet.

Seascape connectivity

Isolation by distance analysis revealed that levels of genetic differentiation in whitetip reef sharks were not significantly correlated with geographic distance among coral reefs (mantel test: r^2= 0.3164, p= 0.085). Further, isolation by resistance analysis showed that ocean depth, as potential barrier to dispersal, was also not significantly correlated with genetic differences between coral reefs (mantel test: r^2= 0.3332, p= 0.176). Visualization of major ocean currents in the Coral Sea revealed a loose alignment of water circulation patterns with genetic gradients (Figure 13b).

Discussion

Complementary molecular markers revealed contrasting patterns of local isolation and large-scale connectivity in whitetip reef sharks across Indo-Pacific coral reefs. The most comprehensive sampling of sharks from reefs in the Coral Sea to date and genomic markers affirm oceanic dispersal despite high site-fidelity in whitetip reef sharks. Oceanic dispersal may result in genetic pathways that align with ocean currents in reef-associated sharks that have limited capacity to account for the displacement caused by water flow (i.e., drift). The ecological and evolutionary costs and benefits of dispersal vary with the characteristics of individual coral reefs and may therefore result in reef-specific genetic connectivity and population resilience.

Large-scale population structure

The Torres Strait forms the primary barrier to historical and contemporary dispersal between Indian and Pacific Ocean whitetip reef shark populations. The barrier is formed by a shallow strait between Australia and Papua New Guinea which intermittently exposed a land bridge when sea levels dropped repeatedly during the Pleistocene epoch (Mirams et al., 2011; Voris, 2000). The Torres Strait has generated intra-specific genetic divergence in many reef fish (Gaither et al., 2010, 2011; Van Herwerden et al., 2009; Liggins et al., 2016), with some exceptions (Bay et al., 2004; Horne et al., 2008), and in marine species that lack planktonic larvae, including sea snakes (Lukoschek et al., 2007), dugongs (Blair et al., 2014) and sea turtles (Dethmers et al., 2006). The historical closure of the strait also caused genetic divergence in the mitochondrial DNA of some sharks but connectivity measured in nuclear markers indicated a contemporary permeability of the barrier (Daly-Engel et al., 2012; Duncan et al., 2006; Green et al., 2018). The Torres Strait may however form an effective barrier to historical and contemporary gene flow in reef-associated sharks. Grey reef sharks (*Carcharhinus amblyrhynchos*), and whitetip reef sharks (this study) show genetic divergence at mitochondrial and nuclear markers across the strait, likely due to high levels of site-attachment and strong association

with shallow-water coral reefs (Espinoza et al., 2015a; Momigliano et al., 2017; Whitney et al., 2012b). The presence of an Indian Ocean haplotype in whitetip reef sharks from the northern Great Barrier Reef (GBR) may further reflect historical dispersal events when the Torres Strait was flooded, after an initial colonization of the Pacific Ocean (Whitney et al., 2012b).

Large distances of open ocean also form barriers to contemporary gene flow in reef-associated sharks. The resulting genetic isolation may cause reduced genetic diversity in oceanic islands compared to continental shelves (Frankham, 1997). In whitetip reef sharks, strong differentiation at nuclear genomic markers resulted in lower genetic diversity at Cocos Keeling Islands compared with Scott Reef on the Australian continental shelf. Lower genetic diversity in oceanic compared to shelf populations has been found in other coastal sharks and rays (Ashe et al., 2015; Chevolot et al., 2006b; Hull et al., 2019; Momigliano et al., 2017), but pelagic oceanic and deep-sea sharks maintain sufficient gene flow to override signatures of genetic isolation and show comparable genetic diversity (Catarino et al., 2015; Cunha et al., 2012; Gubili et al., 2016; Veríssimo et al., 2017). The less pronounced genetic differentiation in whitetip reefs sharks between the Pacific Islands (Fiji and Minerva), PNG and the Coral Sea, compared to Cocos Keeling, is likely a result of dispersal along stepping-stones island chains and resulted in similar levels of genetic diversity in this species and grey reef sharks (Duncan et al., 2006; Momigliano et al., 2017; Schultz et al., 2008).

Regional scale population structure

Comprehensive sampling of whitetip reef sharks in the Coral Sea revealed contrasting genetic patterns of local isolation and large-scale connectivity. Genetic patterns also differed between molecular markers. The lack of mtDNA CR differences among *T. obesus* from most Coral Sea reefs may reflect a recent colonization of the Coral Sea and the slow evolutionary rate of the mitochondrial control region in sharks (Martin et al., 1992; Whitney et al., 2012b). However, small sample sizes for most of the individual reefs may have also influenced the genetic differentiation (Meirmans, 2015).

The historical (mtDNA) and contemporary genetic differentiation (SNPs), of sharks from the Capricorn Group likely reflect its consistent separation from the main section of the GBR. The deeper waters (100-200 m) of the Capricorn Channel lack any subaerial structures that could serve as stepping stones for dispersal and large paleo-rivers that flowed into the channel when sea levels were lower may have acted as additional barriers in the past (Ryan et al., 2007; Yokoyama et al., 2006). A genetic break across the Capricorn Channel has also been suggested in two coral species (Lukoschek et al., 2016). However, one of the species also showed directional gene flow between the main GBR southward across the channel (Riginos et al., 2019). Few studies are available that measure genetic connectivity of marine

species along the entire stretch of the GBR and future research may clarify if the Capricorn Channel functions as a barrier for other marine species (Van Oppen et al., 2011).

Ocean depths between shallow-water reefs together with high site-fidelity may have limited contemporary connectivity in whitetip reef sharks. Genomic markers have greater resolving power to detect population structure when sample sizes are small and detected genetic differences among all Coral Sea locations (Allendorf et al., 2010; Coates et al., 2009). Subtle differences were found between many reefs that are not separated by larger distances of deeper water, including reefs in the contiguous GBR and the semi-fragmented reefs of the Queensland plateau. This indicates that whitetip reef sharks generally remain and reproduce within the same reefs or reef clusters, because few individuals per generation that migrate between reefs and reproduce successfully would be sufficient to homogenize these differences (Waples, 1998; Waples & Gaggiotti, 2006). In contrast, whitetip reef sharks at Osprey Reef, the top of an oceanic seamount in the Coral Sea, were genetically isolated from all other reefs. This exemplifies that limited capacity to traverse deep ocean combined with high levels of site-fidelity may amplify genetic differentiation in some isolated reefs.

Varying levels of genetic connectivity in other Indo-Pacific reef sharks likely also result from differences in species-specific dispersal capacity and site-fidelity. For example, silvertip sharks (*Carcharhinus albimarginatus)* are resident at coral reefs, but also occur in deeper water down to 800 m and move offshore with occasional large-scale oceanic movements (Bond et al., 2015; Curnick et al., 2020; Espinoza et al., 2015b). Accordingly, silvertip sharks show contemporary connectivity across large distances of deep ocean in the Coral Sea (Green et al., 2018). Grey reef sharks (*Carcharhinus amblyrhynchos*) show strong residency to individual reefs in some cases but also move between adjacent reefs in the GBR and between the GBR and Coral Sea reefs (Espinoza et al., 2015a; Heupel et al., 2010). As a result, this species shows strong genetic differentiation across large distances of open ocean, but not at short distances between individual reefs (Boissin et al., 2019; Momigliano et al., 2017, 2015). In contrast, black-tip reef sharks (*Carcharhinus melanopterus*) have the highest fidelity to specific reefs which can create genetic differences between individual islands at small-scales of less than 100 km (Mourier & Planes, 2013; Vignaud et al., 2013, 2014b). Long-term site-fidelity in whitetip reef sharks, as suggested by previous tagging and tracking studies, was further corroborated in this study by the genetic recapture of an individual shark at the same reef location after seven years (Barnett et al., 2012; Whitney et al., 2012a). High site-fidelity is likely an important driver of genetic differentiation in *T. obesus* that can be exacerbated by depth barriers in some cases. At the same time, connectivity found across large distances of deep water in some Coral Sea reefs underpins that whitetip reef sharks are also capable of oceanic dispersal.

Oceanic dispersal

Mitochondrial and nuclear genomic DNA provide evidence of oceanic dispersal in whitetip reef sharks. Oceanic dispersal events drove the historical colonization of Pacific islands and archipelagos and form contemporary connectivity pathways among fragmented Coral Sea reefs. Most of the Pacific islands are of volcanic origin and have never been connected to continental landmasses. Colonization by whitetip reef sharks likely occurred from an Indo-West Pacific centre of origin and is therefore a consequence of oceanic dispersal at various spatial scales (Cowie & Holland, 2006; Whitney et al., 2012b). Oceanic dispersal may have occurred at shorter distances along island chains in the western Pacific, but whitetip reef sharks must have crossed vast oceanic expanses to reach the eastern pacific archipelagos, including the Galapagos and Cocos Islands. Recently, a large-scale oceanic dispersal event was observed in this species. A single female whitetip reef sharks was recorded in the Easter Islands, one of the most isolated oceanic locations on the planet (Morales et al., 2019). However, it is unknown where this individual came from and how it traveled across open ocean (Morales et al., 2019).

Our spatial analysis of genetic gradients confirms oceanic dispersal in whitetip reef sharks at the extent of the Coral Sea and conveys a possible link between genetic patterns and ocean currents. The lack of correlation between genetic differences and geographic distances or ocean bathymetry indicates that an underlying process promotes gene flow irrespectively of distance and depth (McRae, 2006; Wang & Bradburd, 2014). The impact of ocean currents on dispersal trajectories and gene flow depends on an animals' capacity to detect and either exploit or compensate for drift (Chapman et al., 2011b). In whitetip reef sharks oceanic dispersal trajectories may be influenced by currents because morphological adaptations of reef-associated sharks limit their capacity to compensate for drift (Iosilevskii & Papastamatiou, 2016). To be reflected in measures of genetic connectivity, dispersal trajectories have to occur along similar routes and over evolutionary time scales (Lowe & Allendorf, 2010). Although genetic connectivity has been related to currents in some marine organisms with juvenile larvae, their short generation times and high variability in reproductive success, and the variability of current patterns, often result in chaotic patterns (Hedgecock & Pudovkin, 2011; Selkoe et al., 2010). Several long-lived marine animals without juvenile larvae, including sea turtles (Cardona & Hays, 2018) and sea snakes (Brischoux et al., 2016), also showed genetic patterns that were influenced by ocean currents. These examples suggest that oceanic dispersal may produce traceable pathways shaped by ocean currents in marine animals with long generation times and consistent reproductive success that either exploit currents or have limited capacity to compensate for drift.

Ecological and evolutionary drivers of dispersal

Although dispersal across large distances of open ocean stands in contrast with the high site-fidelity of reef-associated sharks, it may have evolved because it has advantages for individual organisms and populations. Oceanic dispersal in whitetip reef sharks is likely a rare and context-dependent event due to the ecological and evolutionary trade-offs for population persistence. Whitney et al. (2012b) suggested dispersal events could be motivated by ecological factors such as density-dependence. Higher population density may trigger dispersal because the avoidance of conspecific competition through emigration can improve individual fitness (Bowler & Benton, 2005; Clobert et al., 2012). However, oceanic dispersal comes with a drawback, because the high energetic costs of dispersal and the risk of settling in an unfavourable habitat lower survival rates (McPeek & Holt, 1992). From an evolutionary perspective, heterosis, the increased fitness of offspring that have parents from genetically distant populations, can offset the negative effects of inbreeding and hence promote dispersal in spatially structured metapopulations (Bowler & Benton, 2005; Ronce, 2007). But long distance dispersal and outbreeding, the reproduction among individuals from genetically distinct populations that are adapted to contrasting environments, can also result in lower fitness of offspring (Brown, 1991; Lynch, 1991; Oakley et al., 2015). These ecological and evolutionary drivers may favour dispersal in small and isolated compared to larger and contiguous patches of habitat, due to limited resources, lower carrying capacity, and higher genetic relatedness (Bowler & Benton, 2005). The high dispersal propensity could explain the lack of genetic breaks over thousands of kilometres between some of the smallest and most isolated reefs in the southern Coral Sea and reefs in the GBR and the Queensland Plateau. However, dispersal trade-offs may shift with environmental contexts. For example, whitetip reef sharks lack contemporary connectivity between the isolated seamount Osprey Reef and all other Coral Sea reefs, but there is also a strong genetic break between Moore Reef and adjacent locations on the Queensland Plateau. Individual reefs have unique and dynamic environmental contexts that lead to temporal variations in local population densities. Reef environments are influenced by tropical cyclones, extreme climatic events (i.e., El Niño and La Niña), and oscillating sea levels that modify coral reef habitat quality and resource availability and thus alter density-dependent dispersal rates (Edmunds et al., 2018; Olivieri et al., 1995). In whitetip reef sharks, differences in environmental variability, habitat size, and the magnitude of habitat fragmentation may create reef-specific dispersal rates and genetic connectivity (Cote et al., 2017; Dieckmann et al., 1999).

Implications for whitetip reef shark populations

Genetic signatures resulting from a combination of geographic isolation and oceanic dispersal determine the resilience of Indo-Pacific whitetip reef shark populations. The most geographically

isolated location, Cocos Keeling, had lower genetic diversity compared to all other coral reefs, which is characteristic of small, highly isolated populations that experience strong genetic drift (Frankham, 1997). Consequently, the local population may have a low resilience to disturbances because it has a reduced adaptive potential and lacks replenishment from other reefs (Frankham et al., 2014; Ryman et al., 2019). In the Coral Sea, three genetic clusters that correspond to the Capricorn Group, Osprey Reef, and Moore Reef (including Bianca and Bougainville Reefs), may be considered demographically and genetically independent (Lowe & Allendorf, 2010). Although gene flow may be sufficient to maintain genetic diversity over evolutionary time scales, it cannot bolster local populations against stochastic events or fisheries exploitation that act on shorter time scales (Ovenden, 2013; Ovenden et al., 2015; Reiss et al., 2009). In contrast, the genetic cluster covering large parts of the offshore Coral Sea and main GBR may be a case of crinkled connectivity (Ovenden, 2013). Subtle genetic differences suggest that less than few individuals per generation disperse among sampled reefs, which results in genetic inter-dependence at evolutionary time scales but is insufficient to completely homogenize the genetic structure (Lowe & Allendorf, 2010; Ovenden, 2013; Wright, 1949). However, an important consideration for management is that low levels of genetic differences do not imply demographic connectivity (Lowe & Allendorf, 2010; Ovenden, 2013; Waples & Gaggiotti, 2006). Although SNPs have a high power to detect subtle genetic differences and thus may have a stronger correlation with demographic connectivity, more empirical data is needed to quantify this relationship (Waples & Gaggiotti, 2006). Finally, to estimate connectivity and potential for replenishment between contiguous reefs of the entire GBR, additional data from currently unsampled locations is required (Meirmans, 2015).

Conclusions

This study used a mixed-marker approach and extensive sampling of a reef-associated shark to assess historical and contemporary connectivity pathways across the Indo-Pacific coral reef seascape. High site fidelity and rare oceanic dispersal events generate contrasting genetic patterns of local isolation and large-scale connectivity in whitetip reef sharks. Connectivity in reef-associated sharks is likely balanced by the costs and benefits of density-dependent dispersal for individual fitness and population persistence that vary with reef-specific dynamics (Johnson & Gaines, 2016; Ronce, 2007). Location specific connectivity implies that locally adapted management may be more appropriate than large-scale umbrella strategies for some reef-associated sharks. In local populations with crinkled connectivity, it would be beneficial to compliment genetic data with methods that measure demographic connectivity (Dudgeon et al., 2012; Ovenden, 2013). Future research that integrates measures of connectivity at different evolutionary and ecological time scales and reef-associated species with contrasting life histories may improve our understanding of connectivity in fragmented coral reefs and maximize the implementation of protected area networks.

Chapter 5 - General Discussion

Synthesis of main results

The research presented in the previous chapters illustrated that the same key components determine the impact of barriers to dispersal on the geographic distribution of individuals and genetic variation in the sea and on land (Bowen, 2016). Discontinuities in the environment form barriers that vary in space and time due to geologic activity and climatic fluctuations on earth (Avise, 2000; Dudgeon et al., 2012; Rocha et al., 2007). The ability of organisms for trans-barrier dispersal is defined by species-specific life history traits and the mode of dispersal (Baguette et al., 2013; Bowler & Benton, 2005; Clobert et al., 2012). The propensity of individuals to disperse is balanced by the costs and benefits for individual survival and population persistence (Parvinen et al., 2020; Ronce, 2007). Marine and terrestrial populations are influenced by the same evolutionary forces, dispersal, genetic drift, selection, and mutation (Avise, 2004). The sum of these factors therefore regulates genetic links in natural populations. However, marine and terrestrial organisms have evolved life history strategies and dispersal mechanisms in fundamentally different environments and are therefore expected to have distinct genetic and biogeographic patterns (Bowen, 2016; Bowen et al., 2016).

Overall, this research showed that different types of marine barriers may generate general trends in genetic connectivity in relation to elasmobranch life history traits (Chapter 2). However, the two shallow-water reef sharks and fragmented seascapes also illustrated that species-specific dispersal capacity and geologic, geographic, and climatic contexts affect connectivity. This resulted in differences and commonalities in genetic and biogeographic patterns between elasmobranch species and between elasmobranchs and marine organisms with larval dispersal as well as terrestrial species.

Basic elasmobranch life history traits (*body size*, *depth occurrence*, and *habitat*) may be useful indicators for trans-barrier dispersal (Chapter 2). However, the two case studies (Chapter 3 and 4) revealed strong differences among two species with broadly comparable life histories. Limited dispersal across depth barriers found in Galapagos bullhead sharks (*Heterodontus quoyi*), Chapter 3, reconfirmed the results from Chapter 2 and empirical studies, which proposed that ocean depth can create genetic differences at small geographic scales in small-bodied elasmobranchs that live in shallow water and are associated to the sea floor (Chevolot et al., 2006b; Gubili et al., 2014; Plank et al., 2010; Ramírez-Amaro et al., 2018). While ocean depth also restricted dispersal in whitetip reef sharks (*Triaenodon obesus*) in some locations (Chapter 4), the genetic connectivity found across large distances of open ocean contrast the general assumption that reef-associated sharks have limited dispersal capacity. The contrasting patterns of local isolation and large-scale connectivity in *T. obesus*

and the differences between the two study species illustrate the context dependence of dispersal in elasmobranchs.

Animal dispersal is context-dependent because the propensity to disperse is controlled by internal (phenotype and genotype) and external (environmental conditions and variability) factors (Bowler & Benton, 2005; Cote et al., 2017; Levin, 2006). In addition, dispersal propensity is heritable. If higher dispersal rates results in higher individual or population level fitness, the genes encoding for traits that facilitate such behaviour are more likely to be passed on to future generations (Ronce, 2007). The lack of inter-island connectivity in Galapagos bullhead sharks therefore indicates that the risks of dispersal for individual survival outweigh the potential evolutionary benefits (Bonte et al., 2012). The exacerbated risks of dispersal in highly isolated locations, due to the low probability of finding suitable habitat, has resulted in a reduction of dispersal ability in many other taxa that colonized oceanic islands (Waters et al., 2020). Oceanic dispersal in whitetip reef sharks likely implies high costs to individual fitness. But intermediate levels of genetic connectivity over larger distances and between isolated coral reefs, in some cases, show that under specific circumstances the benefits for population persistence may overcome high risks of dispersal (Bowler & Benton, 2005; McPeek & Holt, 1992). This may have caused the evolution of rare long-distance dispersal behaviour in this species, making whitetip reef sharks a species with high site-fidelity that is also an exceptional colonizer (Gillespie et al., 2012; Ronce, 2007).

Marine versus terrestrial systems

Barriers to dispersal may create both contrasting and analogous patterns of genetic divergence in marine and terrestrial systems (Bowen et al., 2016). One similarity is the allometry of dispersal in marine and terrestrial species that depend on self-propelled dispersal, as opposed to those transported by dispersal agents (Jenkins et al., 2007; Stevens et al., 2014). This research further revealed that in elasmobranchs body size is also positively correlated with the capacity to overcome potential physical barriers (Chapter 2).

The case of Galapagos Bullhead sharks (Chapter 3) was the first study to show that marine species with limited dispersal that colonized in oceanic islands may produce genetic and biogeographic patterns comparable to terrestrial species. Progressive island formation found in *H. quoyi* (Chapter 3), has been shown for terrestrial species in the Hawaiian and Galapagos archipelagos (Fleischer et al., 1998; Shaw & Gillespie, 2016), but contrasts the general assumption that higher dispersal in marine organisms limits *in situ* divergence in oceanic islands (Bowen, 2016; Pinheiro et al., 2017).

Prior to this research, the effect of historical sea level fluctuations on genetic connectivity had been shown in terrestrial but not marine island populations (Ali & Aitchison, 2014; Vieira et al., 2019). Recently, isolation by resistance analyses were used to study the impact of historical in sea level fluctuations on genetic divergence in island-colonizing ant communities (Darwell et al., 2020). Here I presented the first application of isolation by resistance analysis to quantify the effect of sea level fluctuations on inter-island connectivity in a marine organism.

Galapagos bullhead sharks also showed that genetic effective population size (N_E) scaled with islands area. Such patterns have been found in terrestrial organisms. For example, N_E scaled with breeding pond size in salamanders (Wang et al., 2011). However, this research constitutes the first account of this relationship for marine species with limited inter-island dispersal (Dawson, 2016).

In terrestrial species that depend on self-propelled dispersal, genetic connectivity often correlates with geographic distances and topography, or habitat continuity that provides dispersal corridors (Manel & Holderegger, 2013; McRae & Beier, 2007). In contrast, genetic connectivity in whitetip reef sharks was unrelated to geographic distances or ocean bathymetry. Such patterns are common in marine organisms with extended juvenile larval stages, which supports the idea that morphological adaptations and the high density of the aquatic medium generate higher dispersal in the ocean than on land (White et al., 2010). However, terrestrial species also exploit dispersal agents, such as wind, for long distance dispersal. For example, some birds may utilize wind currents to support large distance dispersal (Senner et al., 2018) and ballooning spiders, carried by winds, have colonized isolated oceanic locations (Lee et al., 2015). These examples and results from whitetip reef sharks highlight the complexity of animal dispersal and that both marine and terrestrial organisms may have evolved mechanisms to exploit dispersal agents due to the ecological and evolutionary benefits of long-distance dispersal (Gillespie et al., 2012).

Designing studies to test the effect of barriers to dispersal

The recommendations for designing studies based on *a priori* hypotheses, illustrated in Chapter 2, were applied to test the effect of barriers to dispersal on genetic connectivity in two shallow-water reef sharks (Chapters 3 and 4). In each study I adopted a different sampling approach according to expectations about the sharks' dispersal capacity and the geographic setting.

Oceanic archipelagos have a long history of being used for in situ experiments to study evolutionary processes in terrestrial species (Warren et al., 2015). In this research, I took advantage of the reduced complexity of the Galapagos archipelago to implement a discrete sampling approach, which allowed to examine genetic divergence and island biogeography in a shallow-water marine organism. I sampled

at least 20 Galapagos bullhead sharks from individual islands that represented discrete experimental units (Emerson, 2002; Parent et al., 2008). This sampling design allowed me to generate robust estimates of genetic differentiation, genetic diversity, genetic effective population size (N_E) for each *a priori* defined experimental unit (Dudgeon & Ovenden, 2015; Meirmans & Hedrick, 2011). Individual genetic units found in Galapagos bullhead sharks corresponded to the local populations of individual islands, or island clusters with a recently shared geologic history. These well-defined genetic units, in addition to the life history characteristics of sharks, provided robust estimates of N_E because they approximate idealized populations (Waples & Do, 2008, 2010). In contrast, delineating units and estimating effective population size is particularly challenging in marine organisms with bipartite life-history strategies because they commonly have large open populations, high fecundity and variable reproductive success (Hare et al., 2011; Palstra & Ruzzante, 2008; Waples et al., 2016).

There were also several limitations to this approach. For example, sampling sharks from individual islands was logistically challenging due to the general lack of knowledge on the biology of Galapagos bullhead sharks (Acuña-Marrero et al., 2018). This resulted in a lack of samples from the central islands (see *Figure 6* in Chapter 3). Since the central islands were more recently connected to the western archipelago compared to the islands sampled in Chapter 3, sampling this region could have further improved the examination of sequential island formation (Geist et al., 2014; Karnauskas et al., 2017). Moreover, fewer sharks were sampled from San Cristóbal island (see *Figure 6* in Chapter 3), despite substantial efforts. This may have introduced some bias in the genetic differentiation of this island despite the high statistical power of the genomic markers used (Morin et al., 2009). However, the consistent patterns found across different genetic analyses suggest that they reflect a true biological signal. Further, samples from the continental range of *H. quoyi* could be used as geographical outgroup to put inter-island comparisons into context (see section on future directions). One of the outcomes of this thesis is the establishment of a network of collaborators that have already provided samples of *H. quoyi* from the coast of Perú, South America, for future comparisons.

A different sampling approach was used to study whitetip reef sharks in fragmented coral reefs. Coral reefs have higher spatial and temporal complexity compared to oceanic islands. Coral reef habitat is scattered over larger geographic areas, fragmented at different magnitudes from tens to thousands of kilometres, and many reefs have a younger and unvalidated geologic history (Davies, 2011). In Chapter 4, I therefore used extensive and relatively continuous sampling of sharks from reef habitats that represented different magnitudes of fragmentation. In combination with high resolution genomic markers, this sampling provided a suitable approach to locate genetic breaks and delineate connectivity pathways across large areas and complex seascapes (Manel et al., 2003; Riginos & Liggins, 2013).

A downside of this approach was that each reef was represented by fewer samples. Low sample sizes can bias estimates of genetic diversity and inter-reef comparisons, and precluded the calculation of directional gene flow and effective population sizes, N_E (Marandel et al., 2019; Meirmans, 2014, 2015). Estimating N_E is particularly challenging in populations with crinkled connectivity that have intermediate levels of gene flow, such as found in whitetip reef sharks (Ryman et al., 2019). Intermediate levels of gene flow bias the N_E estimates of individual local populations and the respective metapopulation (Ryman et al., 2019; Wang & Whitlock, 2003; Waples & Do, 2010). Low sample sizes also introduce bias in N_E estimates, because they are a poor representation of local genetic drift, age structure and sex ratios (Hare et al., 2011; Waples et al., 2014).

The influence of global climate on barrier permeability and range dynamics

Variations in global climate alter the permeability of barriers to dispersal in land- and seascapes (Hewitt, 2004; Ludt & Rocha, 2015). Climate-driven changes in sea levels have also left distinct genetic signatures in the reef-associated sharks studied in this thesis. Lower sea levels during glacial cycles have reduced historical connectivity in whitetip reef sharks across the Torres Strait (Chapter 4). The cyclical closure of straits temporarily discontinues gene flow, which has created phylogeographic and biogeographic breaks in marine organisms with diverse life histories and dispersal modes, and has catalysed the evolution of marine biodiversity (Bowen et al., 2016; Cowman, 2014; Cowman & Bellwood, 2013; Liggins et al., 2016). In combination with geologic processes changes in sea levels form isthmuses, narrow stretches of land that connect two larger landmasses separated by water bodies (Coates et al., 2004). Isthmuses pose barriers for marine taxa but have the opposite effect in terrestrial biota. For example, the formation of the isthmus of Panamá lead to the Great American Biotic Interchange by joining the continental landmasses of North and South America, which allowed for the dispersal of previously isolated terrestrial biota (Marshall et al., 1982; O'Dea et al., 2016).

Climatic oscillations create shifts in the vertical stratification of marine and terrestrial environments and therefore influence genetic connectivity both on land and in the sea. In oceanic archipelagos, sea level fluctuations alter island configurations, which has been shown to impact the genetic divergence and biogeography of terrestrial organisms (Ali & Aitchison, 2014; Norder et al., 2019). Recently, receding sea levels have also been suggested to increase connectivity in marine organisms that live in coastal habitat of oceanic islands, but without explicit genetic evidence prior to this research (Rijsdijk et al., 2014; Vieira et al., 2019).

Parallels have been drawn between connectivity of terrestrial populations in high altitude sky islands and oceanic archipelagos (Flantua et al., 2020). The research presented here further suggests that

climatic fluctuations cause corresponding patterns of connectivity in coastal marine species with limited dispersal and in terrestrial biota of oceanic archipelagos and sky islands. However, there is a great difference in the magnitude of vertical shift in marine compared to terrestrial habitats. Global sea levels fluctuate on average over 100 m (Hansen et al., 2013), while high altitude ecosystems fluctuate in elevation over thousands of meters (Hazzi et al., 2018). In montane ecosystems of continental mountain ranges, and in mountains on oceanic islands, shifts to lower elevations often increase habitat area and genetic connectivity (Flantua et al., 2020; Hewitt, 2000; Salces-Castellano et al., 2020). In contrast to oceanic islands, glaciation in continental mountain ranges can also reduce alpine habitat, reduce connectivity, and drive isolation and extinction in terrestrial species (Schönswetter et al., 2005; Svenning et al., 2015). Due to difference in magnitude of vertical shift and overall higher dispersal in the aquatic medium, changes in connectivity in relation to climatic fluctuations may be less common or more subtle in the ocean. However, results from Galapagos bullhead sharks illustrate that marine species with narrow depth ranges and limited capacity to cross deeper water are likely to reveal parallels between oceanic archipelagos and terrestrial sky islands.

Variations in global climate also influence range dynamics in marine and terrestrial organisms (Kokko & López-Sepulcre, 2006; Pinsky et al., 2020). One of the most described processes is the poleward shift of terrestrial species' distributions due to increasing global temperatures (Parmesan & Yohe, 2003; Root et al., 2003). Poleward range shifts have also been described in marine species (Booth et al., 2011; Sorte et al., 2010). Inversely, climate-driven range contractions also occur in marine and terrestrial organisms, but have been described to a lesser extent (Hampe & Petit, 2005; Pinsky et al., 2020).

Range dynamics are influenced by the capacity of species to disperse across potential barriers and their ability to colonize new habitat (Jønsson et al., 2016). For instance, increasing temperatures may cause range contractions in species with limited dispersal ability that are confined to geographically isolated locations, as is the case for Galapagos bullhead sharks (Pinsky et al., 2020; Smale & Wernberg, 2013). Global warming can cause habitat reductions in high altitude systems that result in range contractions in terrestrial species with limited dispersal (Hampe & Petit, 2005). In contrast, tropical species with higher dispersal capacity or propensity, including whitetip reef sharks, may experience range expansions under increasing temperatures (Kubisch et al., 2014). For example, dispersal around the tip of South Africa during warmer climates has been identified as the primary route of colonization between Atlantic and Indian Ocean tropical marine fauna (Bowen et al., 2016). Further, dispersal propensity may be higher in isolated or highly fragmented populations, which are common at the edge of a species' range (Holt, 2003; Kubisch et al., 2014). High dispersal propensity at range edges in whitetip reef sharks and increasing ocean temperatures could be responsible for the arrival of this

species in the Easter Islands, the Kermadec Islands, and the Atlantic coast of Brazil (Bornatowski et al., 2018; Duffy et al., 2017; Morales et al., 2019).

Future directions

The global synthesis presented in this study (Chapter 2) indicated that research on population genetics and phylogeography in elasmobranchs was biased towards specific taxonomic groups and geographic areas. More than double the number of shark species were studied, representing two thirds of the publications examined, compared to batoids. However, batoids (rays and skates) are more speciose (over 600 species) than sharks (over 500 species) and make up a slightly larger number of the global chondrichthyan fisheries catch (Dulvy et al., 2014; Ebert et al., 2013; Last et al., 2016). Moreover, species that are of particular interest to the media and the general public due to human-wildlife conflicts, conservation concerns, and their value for tourism, including white sharks (*Carcharodon Carcharias*) and scalloped hammerheads (*Sphyrna lewini*), have received considerably more attention (Albert et al., 2018; Friedrich et al., 2014; McClenachan et al., 2012). A higher number of publications was also found for species such as blue sharks (*Prionace glauca*), spiny dogfish (*Squalus acanthias*), school sharks (*Galeorhinus galeus*), and thorny skates (*Raja clavata*) because they are of economic importance to fisheries (Barker & Schluessel, 2005; Fowler et al., 2005; Musick et al., 2000; Simpfendorfer & Dulvy, 2017). Further, research on barriers in elasmobranch populations has, to some extent, concentrated on geographic areas that are of particular interest due to their geological and oceanographic complexity (Chapter 2). However, areas that have received less attention (i.e., the north-western Pacific, the northern Indian Ocean, the coastal waters of tropical Africa, and the coasts of South America) often correspond to the Exclusive Economic Zones of developing countries, some of which harbour higher elasmobranch diversity (i.e., South America and India), but have less resources available for research (Halpern et al., 2006; Lucifora et al., 2011; Waldron et al., 2017).

The two case studies produced as part of this thesis address some of the taxonomic and geographic gaps and may set precedents for future research that use marine organisms without dispersive larvae to study the impact of geologic and climatic processes on marine connectivity and biogeography (Bernardi, 2000; Vieira et al., 2019). For example, island-mainland comparisons in shallow-water organisms with limited dispersal, including *H. quoyi* and *T. obesus*, could provide new insight into the genomic signatures of geographic isolation in oceanic locations caused by colonization and island formation (Cowie & Holland, 2006; Patiño et al., 2017). To test hypotheses about the timing of arrival and multiple versus single colonization events, phylogeographic and phylogenetic analyses could be

applied to samples of *H. quoyi* from the Galapagos Islands and the continental coast of South America, and closely related species (Emerson, 2002; Juan et al., 2000).

Lower genetic diversity has been found in oceanic locations compared to the continental ranges of some elasmobranchs. For example, lower genetic diversity in oceanic compared to continental populations were found in the common smooth-hound (*Mustelus mustelus*) in Cape Verde (Hull et al., 2019), grey reef sharks (*Carcharhinus amblyrhynchos*) and whitetip reef sharks (*T. obesus*; Chapter 4) in Cocos Keeling Islands (Momigliano et al., 2017), lemon sharks (*Negaprion brevirostris*) in Atol das Rocas (Ashe et al., 2015), and the thornback ray (*Raja clavata*) in the Azores (Chevolot et al., 2006b). Lower genetic diversity was also found in two teleost reef fish with small populations that are endemic to Clipperton Atoll, Eastern Pacific, when compared to reef fish with broader geographic ranges and larger population sizes (Crane et al., 2018). Future island-comparisons of population sizes and genetic diversity in species with limited dispersal may reveal similarities with terrestrial populations that challenge our current understanding of marine island biogeography (Dawson, 2016; Pinheiro et al., 2017).

There are several elasmobranchs that could be used in future island-mainland comparisons to study evolution and island biogeography because they have life histories and geographic distributions similar to Galapagos bullhead sharks (*Figure 14*). The Pacific guitarfish *(Pseudobatos planiceps*), the Velez ray (*Raja velezi*) and the Peruvian torpedo *(Torpedo peruana*), are shallow-water demersal species that are found in the Galapagos and the continental coast of South America (Hearn et al., 2014; Last et al., 2016). Demersal species that could be studied in other oceanic archipelagos, include the California horn shark (*Heterodontus francisci*) in the Channel Islands and the angel shark (*Squatina squatina*) in the Canary Islands (Ebert et al., 2013; Lawson et al., 2020).

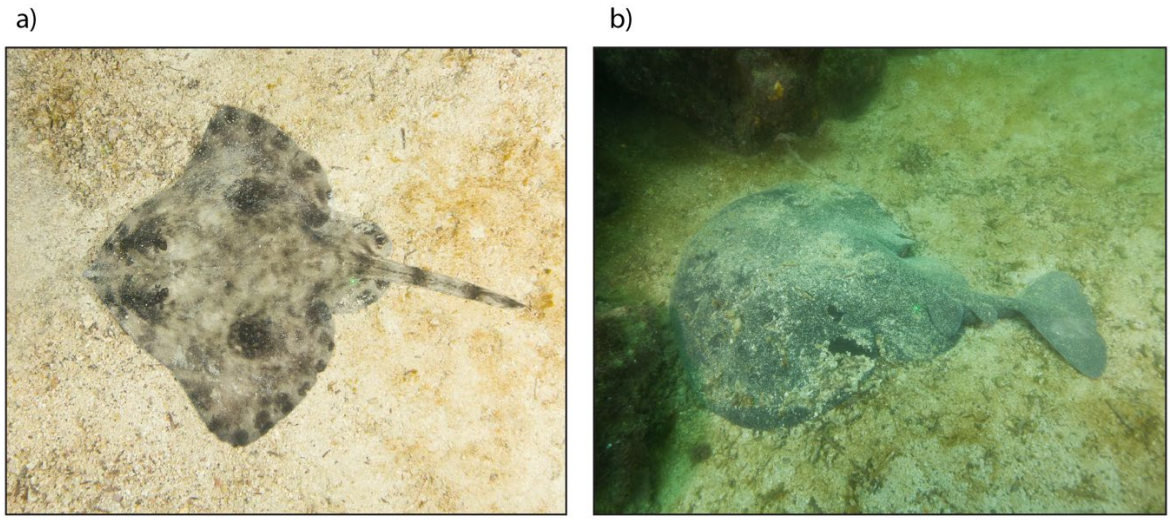


Figure 14. Demersal elasmobranchs, a) Velez ray (*Raja velezi*) and b) Peruvian torpedo (*Torpedo peruana*), that inhabit coastal waters of the Galapagos archipelago and the continental coasts of South America. Photographs by Maximilian Hirschfeld.

Reef-associated species with vast geographic ranges, such as whitetip reef sharks, are suitable candidates to examine the eco-evolutionary drivers and genetic consequences of rare long-distance dispersal in the ocean (Gillespie et al., 2012). Rare long-distance dispersal may have evolved in reef-associated species to outweigh the negative effects of genetic isolation. Large-scale sampling across different magnitudes of habitat fragmentation and the use of genomic markers in other reef-associated sharks and species that lack dispersive larvae, may reveal dispersal pathways and their relation to ocean currents (Gillespie et al., 2012; Riginos et al., 2016). Traditional (external and photographic tagging) and genetic mark-recapture methods could be employed to trace dispersal events (Selkoe et al., 2016). For example, large networks of acoustic monitoring systems could be combined with genetic sampling of reef sharks across the Coral Sea to link site-fidelity and dispersal behaviour to genetic patterns (Brodie et al., 2018; Ovenden, 2013). However, long-distance dispersal events are often rare. Population and seascape genetics approaches therefore have an advantage because they capture genetic signatures that results from dispersal events that occurred over longer (evolutionary) times scales. Moreover, genetic sampling of sharks that appear to have only recently arrived at isolated locations could provide insight into their origin and identify possible dispersal routes.

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Appendix A

Table 7. *Description of nine main barrier types with spatio-temporal information and source references used to construct* Figure 4 *in Chapter 2.*

Category	Barrier type and description	Spatial scale (kms)	Factors that form the barrier	Barriers in category (abbreviations used in Figure 3)	Temporal scale	Temporal variability	References
1	Separation of major oceans basins: Geologic processes form land bridges	10000s-1000s	Geographic	Old World Barrier (OWB)	55-35 Mya – present	Stable (But: Artificial opening of the Suez Channel)	(Ricou, 1987; Seton et al., 2012)
				Isthmus of Panama Barrier (IPB)	3.5 Mya – present	Stable	(Coates et al., 2004; O'Dea et al., 2016)
				Sunda Shelf Barrier (SSB)	2.58 (Pleistocene) - 0.012 Mya	Fluctuates with sea level	(Voris, 2000)
2	Large scale thermal barrier separating hemispheres	10000s-1000s	Hydrologic (thermal)	Equatorial warm water barrier (EWB)	NA	Fluctuates with global climate	(Bowen et al., 2016)
3	Mid ocean barriers: Large distances across major ocean basins	10000s-1000s	Geographic	East Pacific Barrier (EPB) Mid Atlantic Barrier (MAB) Indian Ocean Barrier (IOB)	Gradual formation of major ocean basins: ca. 55-3.5 Mya – present	Stable	(Dudgeon et al., 2012; Rocha et al., 2007)
4	Straits	1000s-100s	Geographic	Strait of Gibraltar (SG) Strait of Sicily (SS)	SG: Closed 5.6 Mya and reopened 5.3 Mya SS: NA	Fluctuates with sea level	(Patarnello et al., 2007).
				Torres Strait (TS)	2.58 (Pleistocene) - 0.012 Mya	Fluctuates with sea level	(Mirams et al., 2011)
				Taiwan strait (TWS)	2.58 (Pleistocene) - 0.012 Mya	Fluctuates with sea level	(Voris, 2000)
5	Depth: Ocean depth below the edge of the continental shelf at	1000s-100s	Geographic	Depth of oceanic sub-basins: e.g. Mediterranean sub-basins, Tasman Sea, Coral Sea Depth between the continental shelf and oceanic islands: e.g.	Varies individually. E.g. Time of formation of volcanic oceanic islands	Stable (may fluctuate with sea level in some cases)	See Table S1 for individual references TT:(Saqab et al., 2017)

	intermediate to small scales			Channel Islands, Brazilian off-shore islands. Ocean trenches: e.g. Timor Trench (TT)	TT: Since 6-3 Mya (Saqab et al., 2017)		
6	Small scale thermal barriers	1000s-100s	Hydrologic (thermal)	Agulhas-Benguela current front (AGB) and Angola-Benguela current front (AB)	Since 2 Mya	Fluctuates with global climate (ocean temperatures and circulation)	(Henriques et al., 2014; Hutchings et al., 2009; Krammer et al., 2006; Marlow et al., 2000)
				Baja California Peninsula (BCP)	Seaway between Pacific coast and Gulf of California closed about 3 Mya and warm temperatures established around the tip of the peninsula from 0.0117 Mya	May fluctuate with global climate (ocean temperatures and circulation)	(Holt et al., 2000; Jacobs et al., 2004; Stepien et al., 2001)
				Point Conception (PC)	NA	Fluctuates with global climate (ocean temperatures and circulation)	(Burton 1998; Sivasundar & Palumbi 2010; Stephens *et al.* 2016)
7	Haline barriers	1000s-100s	Hydrologic – (haline)	North Sea – Baltic Sea salinity gradient	Since 8500 Kya	Fluctuates with global climate (Precipitation)	(Johannesson & André, 2006)
				Freshwater plume of river deltas: Amazon Barrier (AD) Mississippi delta (MD)	Since formation of the amazon river ca. 10.4 Mya	Fluctuates with global climate (Precipitation)	Amazon: (Rocha, 2003) Mississippi: (Portnoy et al., 2014, 2016)
				Saltwater: Marine environment between river systems (in brackish and freshwater species)	Geologic history of individual rivers/river systems	Fluctuates with global climate (Precipitation)	(Feutry et al., 2014, 2015;

							Phillips et al., 2016)
8	Currents	1000s-100s	Hydrologic (current)	Indonesian throughflow current (ITC)	Since 5 Mya	Fluctuates with global climate (ocean circulation)	(Cane & Molnar, 2001)
				South Equatorial current (SEC)	NA	Fluctuates with global climate (ocean circulation)	(Santos et al., 2006)
9	Florida Peninsula: Separation of the Gulf of Mexico and Western Atlantic	1000-100s	Hydrologic (currents) and Geographic (geomorphology of the peninsula)	Florida Peninsula (FB)	Debated	Fluctuates with global climate (ocean temperatures, circulation and sea level)	(Avise, 1992; Gold & Richardson, 1998)

Table 8. Summary of elasmobranch population genetic studies excluded from the synthesis and reasons for their exclusion. *Abbreviations for mitochondrial DNA markers:* mtDNA: Mitochondrial DNA markers, CR: control region, cytb: cytochrome b, COI: cytochrome C oxidase subunit I, ND2/ND4/ND5: NADH dehydrogenase 2/4/5, rDNA: ribosomal DNA, rRNA: ribosomal RNA, tRNA: transfer RNA, RFLP: Restriction fragment length polymorphism. *Abbreviations for nuclear markers:* msat: microsatellites (with number of markers in parenthesis), ITS2: nuclear ribosomal internal transcribed spacer 2, ISSRs: inter simple sequence repeats, RAG1: Recombination activating gene 1, AFLP: Amplified fragment length polymorphism, SNPs: Single nucleotide polymorphisms.

Reference	Species	Max. body size	Max. depth of occurrence	Habitat	Barrier type	Barriers present and reasons for exclusion (abbreviations used in Figure 3)	Marker type
Sharks							
(Almojil et al., 2018)	*Carcharhinus limbatus*	286	100	neritic	NA	No barrier present	msat (11)
	Carcharhinus sorrah	166	140	neritic	NA	No barrier present	msat (15)
Barbieri 2014	*Scyliorhinus canicula*	100	800	benthopelagic	Strait	Sample size and spatial sampling: The Strait of Sicily (SSC) could not be assessed as barrier because of low sample sizes (i.e. Ionian Sea: n=4) and samples were obtained from waters within the strait.	mtDNA (COI)
(Bernard et al., 2018)	*Carcharodon carcharias*	595	1200	oceanic	Oceanic distance	Reproductive philopatry and the East Pacific Barrier (EPB) may act simultaneously on genetic differentiation.	msat (30)
(Blower et al., 2012)	*Carcharodon carcharias*	595	1200	oceanic	Strait	Reproductive philopatry was identified by the authors as the main driver of genetic differentiation between regions on either side of the Bass Strait (BS).	mtDNA (CR), msat (6)
(Corrigan et al., 2015)	*Orectolobus halei*	256	195	benthopelagic	NA	No barrier present	mtDNA (CR, ATPase 6 and ATPase 8), AFLP
	Orectolobus maculatus	320	248	benthopelagic	NA	No barrier present	mtDNA (CR, ATPase 6 and ATPase 8), AFLP

	Orectolobus ornatus	110	100	benthopelagic	NA	No barrier present	mtDNA (CR, ATPase 6 and ATPase 8), AFLP
(Day et al., 2019)	*Heterodontus portusjacksoni*	165	275	benthopelagic	NA	No barrier present	mtDNA (CR), msat (10)
(Dimens et al., 2019)	*Carcharhinus acronotus*	164	100	neritic	Florida Peninsula	Reproductive philopatry was identified by the authors as the main driver of genetic differentiation between regions on either side of the Florida Peninsula (FP).	SNPs
(Feutry et al., 2014)	*Glyphis glyphis*	260	10	benthopelagic	Haline	Reproductive philopatry was identified by the authors as driver of genetic differentiation between river drainages in Northern Australia (AR).	mitogenome
(Feutry et al., 2017)	*Glyphis glyphis*	260	10	benthopelagic	Haline	Reproductive philopatry was identified by the authors as driver of genetic differentiation between river drainages in Northern Australia (AR).	mitogenome, SNPs
(Galván-Tirado et al., 2013)	*Carcharhinus falciformis*	350	500	oceanic	Oceanic distance	Spatial sampling: Samples not taken from either side of the East Pacific Barrier (EPB) but spread across the Eastern Pacific.	mtDNA (CR)
(Garcia et al., 2014)	*Squatina guggenheim*	129	360	benthopelagic	NA	No barrier present	mtDNA (cytb), internal transcribed spacer 2
(Gardner & Ward, 1998)	*Mustelus antarcticus*	185	350	benthopelagic	Strait	Study design would allow to test for the effect of the Bass Strait (BS) as barrier, but no statistical comparisons were reported.	mtDNA (restriction enzymes), allozyme
(Gonzalez et al., 2019)	*Sphyrna tiburo*	150	90	neritic	NA	No barrier present	mtDNA (COI)
(Gubili et al., 2011)	*Carcharodon carcharias*	595	1200	oceanic	NA	No barrier present/studied	mtDNA (CR)
(Gubili et al., 2015)	*Carcharodon carcharias*	595	1200	oceanic	NA	No barrier present/studied	mtDNA (CR)
(Heist et al., 1996a)	*Isurus oxyrinchus*	445	750	oceanic	Oceanic distance	(Schrey & Heist, 2003) use the same samples and microsatellite markers and were used instead to assess the effect of the East Pacific Barrier (EPB).	mtDNA (RFLP)

(Heist et al., 1996b)	*Rhizoprionodon terraenovae*	113	280	benthopelagic	Florida Peninsula	No pairwise statistical comparison was reported across the Florida Peninsula (FP).	mtDNA (RFLP)
(Hoelzel et al., 2006)	*Cetorhinus maximus*	1097	1264	oceanic	Oceanic distance	Spatial sampling: Low sample sizes are pooled across larger geographic areas across the Mid Atlantic Barrier (MAB).	mtDNA (CR)
(Jorgensen et al., 2010)	*Carcharodon carcharias*	595	1200	oceanic	Oceanic distance	Reproductive philopatry was identified by the authors as the main driver of genetic differentiation between regions on either side of the East Pacific Barrier (EPB).	mtDNA (CR)
(Keeney et al., 2003)	*Carcharhinus limbatus*	268	100	neritic	Florida Peninsula	Reproductive philopatry was identified by the authors as driver of genetic differentiation between neonate and juvenile sharks sampled in nursery areas on either side of the Florida Peninsula (FP).	mtDNA (CR)
(Keeney et al., 2005)	*Carcharhinus limbatus*	268	100	neritic	Florida Peninsula, Haline	Reproductive philopatry was identified by the authors as driver of genetic differentiation between neonate and juvenile sharks sampled in nursery areas on either side of the Florida Peninsula (FP) and the Mississippi Delta (MD).	mtDNA (CR), msat (8)
(Klein et al., 2019)	*Carcharias taurus*	384	232	neritic	NA	No barrier present/studied	mtDNA (ND4, ND5), msat (12)
(Kuguru et al., 2019)	*Sphyrna zygaena*	500	200	neritic	NA	No barrier present/studied	mtDNA (ND2), msat (7)
(Larson et al., 2015)	*Notorynchus cepedianus*	296	570	benthopelagic	NA	No barrier present/studied	msat (7)
(Lavery & Shaklee, 1989)	*Carcharhinus tilstoni*	200	150	neritic	NA	No barrier present/studied	Enzyme loci (47)
	Carcharhinus sorrah	166	140	neritic	NA	No barrier present/studied	Enzyme loci (47)
(Lewallen et al., 2007)	*Triakis semifasciata*	214	156	benthopelagic	Small-scale thermal barrier	No pairwise statistical comparison was reported across Point Conception (PC).	mtDNA (CR), ISSRs
(Li et al., 2017)	*Prionace glauca*	384	1116	oceanic	NA	No barrier present/studied	mtDNA (cytb)

(Liu et al., 2018)	*Megachasma pelagios*	709	600	oceanic	Oceanic distance	Sample size: Only a single location (Taiwan) has more than 5 samples precluding the assessment of the East Pacific Barrier (EPB) and the Isthmus of Panama (IPB).	mtDNA (cox1), msat (1)
(Maisano Delser et al., 2016)	*Carcharhinus melanopterus*	180	100	neritic	NA	No barrier studied (not main objective)	Autosomal target genes
(Manuzzi et al., 2019)	*Scyliorhinus canicula*	384	800	benthopelagic	NA	No barrier present/studied	SNPs
(Mendonça et al., 2009)	*Rhizoprionodon lalandii*	102	70	benthopelagic	NA	No barrier present/studied	mtDNA (CR)
(Mendonça et al., 2013)	*Rhizoprionodon lalandii*	102	70	benthopelagic	Haline, Current	Spatial sampling: Sampling locations are too far spaced to assess the Amazon Barrier (AB) and South Equatorial Current (SEC). Both potential barriers are present between sampling locations.	mtDNA (CR)
(Mourier & Planes, 2013)	*Carcharhinus melanopterus*	180	100	neritic	NA	No barrier present/studied	msat (17)
(Nance et al., 2011)	*Sphyrna lewini*	430	1043	oceanic	NA	No barrier present/studied	mtDNA (CR), msat (15)
(O'Leary et al., 2015)	*Carcharodon carcharias*	595	1200	oceanic	Large-scale thermal barrier	Spatial sampling: Two barriers, the Equatorial warm water barrier (EWB) and the Mid Atlantic Barrier (MAB) are present between sampling locations in the Northwest Atlantic and South Africa.	mtDNA (CR), msat (14)
(Oñate-González et al., 2015)	*Carcharodon carcharias*	595	1200	oceanic	Small-scale thermal barrier	Reproductive philopatry may act simultaneously on genetic differentiation between locations on either side of the Baja California Peninsula (BCP) and Point Conception (PC).	mtDNA (CR)
(Ovenden et al., 2011)	*Rhizoprionodon acutus*	178	200	benthopelagic	Depth, Strait, Current	Spatial Sampling: Three potential barriers, Timor Trench (TT), Torres Strait (TST), and Indonesian throughflow current (ITC) are present	mtDNA (ND4), msat (6)

	Sphyrna lewini	430	1043	oceanic	Depth, Strait, Current	between sampling locations in Northern Australia and Indonesia. Spatial Sampling: Three potential barriers, Timor Trench (TT), Torres Strait (TST), and Indonesian throughflow current (ITC) are present between sampling locations in Northern Australia and Indonesia.	mtDNA (ND4), msat (8)
(Pardini et al., 2001)	*Carcharodon carcharias*	595	1200	oceanic	Oceanic distance	Reproductive philopatry was identified by the authors as the main driver of genetic differentiation between regions (South Africa vs. New Zealand and Australia) on either side of the Indian Ocean Barrier IOB.	mtDNA (CR), msat (5)
(Pazmiño et al., 2017b)	*Carcharhinus galapagensis*	370	286	neritic	NA	No barrier present/studied	mtDNA (CR), SNPs
(Pereyra et al., 2010)	*Mustelus schmitti*	95	195	benthopelagic	NA	No barrier present/studied	mtDNA (cytb)
(Portnoy et al., 2015)	*Sphyrna tiburo*	150	90	neritic	Florida Peninsula	Reproductive philopatry was identified by the authors as driver of genetic differentiation between coastal locations on either side of the Florida Peninsula (FP).	mtDNA (CR), SNPs
(Portnoy et al., 2016)	*Carcharhinus isodon*	200	20	benthopelagic	Florida Peninsula	Reproductive philopatry was identified by the authors as possible driver of genetic differentiation between coastal locations on either side of the Florida Peninsula (FP) and the Mississippi Delta (MD).	mtDNA (CR), msat (16)
(Sodré et al., 2012)	*Carcharhinus limbatus*	286	100	neritic	Florida Peninsula, Haline	This study used the data from (Keeney et al., 2003) and (Keeney et al., 2005) which were also excluded (see above).	mtDNA (CR)
(Spaet et al., 2015)	*Carcharhinus limbatus*	286	100	neritic	NA	No barrier present	mtDNA (CR), msat (12)
	Carcharhinus sorrah	166	140	neritic	NA	No barrier present	mtDNA (CR), msat (9)

	Rhizoprionodon acutus	178	200	benthopelagic	NA	No barrier present	mtDNA (CR), msat (9)
	Sphyrna lewini	430	1043	oceanic	NA	No barrier present	mtDNA (CR), msat (12)
(Suárez-Moo et al., 2013)	*Rhizoprionodon terraenovae*	113	280	benthopelagic	NA	No barrier present	AFLP
(Taguchi et al., 2015)	*Prionace glauca*	384	1116	oceanic	Oceanic distance, Large-scale thermal barrier	Samples from locations on both sides of the East Pacific Barrier (EPB) and the Equatorial warm water barrier (EWB) were pooled and no pairwise comparisons reported.	mtDNA (cytb)
(Tillett et al., 2012b)	*Carcharhinus leucas*	366	164	neritic	NA	No barrier present	mtDNA (CR, ND4), msat (3)
(Vella & Vella, 2017)	*Hexancheus griseus*	550	2490	oceanic	Strait	Spatial sampling: The Strait of Sicily (SSC) could not be assessed as barrier because samples were also obtained from waters within the strait.	mtDNA (CR, cytb, 16S rRNA, 12S rRNA, 3 tRNA genes)
					Oceanic distance, Large-scale thermal barrier, Strait	Sample sizes were too low (n < 5) to test genetic differences across the East Pacific Barrier (EPB), the Equatorial warm water barrier (EWB), the Strait of Gibraltar (SG), and the Strait of Dardanelles.	
(Walter et al., 2017)	*Somniosus microcephalus*	730	2647	oceanic	NA	No barrier present	NA
Batoids							
(Chapman et al., 2011a)	*Pristis pectinata*	553	122	benthopelagic	NA	No barrier present	msat (8)
(Chevolot et al., 2008)	*Raja clavata*	139	1020	benthopelagic	NA	No barrier present	msat (5)
(Griffiths et al., 2010)	*Dipturus batis*	143	600	benthopelagic	NA	No barrier present	mtDNA (CR), msat (6)
(Griffiths et al., 2011)	*Dipturus oxyrinchus*	150	1230	benthopelagic	Strait	Spatial sampling: Sampling locations on either side of the Strait of Gibraltar are too far spaced. Other potential barriers are present.	(CR, ATPase6, ATPase8)

(Le Port & Lavery, 2012)	*Bathytoshia brevicaudata*	430	480	benthopelagic	Oceanic distance, Depth	(Roycroft et al., 2019) use the same samples and microsatellite markers and were used instead to assess the effect of Indian Ocean Barrier IOB and depth between Australia and New Zealand, and Tasman Sea (TAS).	mtDNA (CR)
(Li et al., 2013)	*Dasyatis akajei*	138	50	benthopelagic	Depth	The effect of the ocean depths of the Ryukyu Trench and Okinawa Trough as potential barriers could not be determined because significant genetic differences were also shown for control locations that lack physical barriers.	AFLP
(Li et al., 2015)	*Dasyatis akajei*	138	50	benthopelagic	Depth	The effect of the ocean depths of the Ryukyu Trench and Okinawa Trough as potential barriers could not be determined because significant genetic differences were also shown for control locations that lack physical barriers.	mtDNA (CR)
(O'Connell et al., 2019)	*Leucoraja ocellata*	113	723	benthopelagic	NA	No barrier present/studied	SNPs
	Leucoraja erinacea	62	914	benthopelagic	NA	No barrier present/studied	SNPs
(Phillips et al., 2011)	*Pristis clavata*	318	20	benthopelagic	NA	No barrier present/studied	mtDNA (CR)
	Pristis pristis	700	60	benthopelagic	NA	No barrier present/studied	mtDNA (CR)
	Pristis zijsron	730	100	benthopelagic	NA	No barrier present/studied	mtDNA (CR)
(Phillips et al., 2016)	*Pristis clavata*	318	20	benthopelagic	NA	No barrier present/studied	msat (8)
	Pristis pristis	700	60	benthopelagic	NA	No barrier present/studied	msat (7)
	Pristis zijsron	730	100	benthopelagic	NA	No barrier present/studied	msat (8)
(Puckridge et al., 2013)	*Neotrygon kuhlii*	70	170	benthopelagic	Depth, Strait, Current	No pairwise statistical comparison was reported across Timor Trench (TT), Torres Strait (TST), and Indonesian throughflow current (ITC).	mtDNA (COI, 16S), RAG1
(Richards et al., 2009)	*Aeobatus narinari*	330	80	neritic	NA	No barrier studied, focus on phylogeny	mtDNA (cytb, COI), ITS2

(Schluessel et al., 2010)	*Aeobatus narinari*	330	80	neritic	Small-scale thermal barrier, Land bridge	Spatial sampling: Sampling locations on the Western Atlantic and East-coast of South Africa too far spaced to test for the effect of the Agulhas-Benguela Front (AGB). The effect of the Sunda Shelf Barrier (SSB) could not be tested because samples were pooled from locations across this barrier.	mtDNA (cytb, ND4)
					Mid ocean barrier, Land bridge	Sample sizes were too low (n < 5) to test genetic differences across the East Pacific Barrier (EPB), Indian Ocean Barrier IOB, Isthmus of Panama (IPB).	
(Valsecchi et al., 2005)	*Raja asterias*	70	343	benthopelagic	Strait	Sample size to low at sampling locations on either side of the barrier to test the effect of the Strait of Sicily (SSC)	mtDNA (CR)
	Raja clavata	139	1020	benthopelagic	Strait	Sample size to low at sampling locations on either side of the barrier to test the effect of the Strait of Sicily (SSC)	mtDNA (CR)
	Raja miraletus	71	462	benthopelagic	Strait	Sample size to low at sampling locations on either side of the barrier to test the effect of the Strait of Sicily (SSC)	mtDNA (CR)
(Vargas-Caro et al., 2017)	*Dipturus trachyderma*	264	480	benthopelagic	NA	No barrier present/studied	mtDNA (CR), msat (10)
	Zearaja chilensis	168	600	benthopelagic	NA	No barrier present/studied	mtDNA (CR), msat (10)
(Weltz et al., 2018)	*Zearaja maugeana*	84	10	benthopelagic	NA	No barrier present/studied	mtDNA (CR, ND2, ND4, cytb), msat (10)

Table 9. Summary of physical barriers examined in elasmobranch population genetic studies. *Abbreviations for mitochondrial DNA markers:* mtDNA: Mitochondrial DNA markers, CR: control region, cytb: cytochrome b, COI: cytochrome C oxidase subunit I, ND2 and ND4: NADH dehydrogenase 2/4, rDNA: ribosomal DNA, tRNA: transfer RNA. *Abbreviations for nuclear markers:* msat: microsatellites (with number of markers in parenthesis), ITS2: nuclear ribosomal internal transcribed spacer 2, EPICs: Exon-primed, intron crossing DNA markers, LDH: lactate dehydrogenase, AFLP: Amplified fragment length polymorphism, SNPs: Single nucleotide polymorphisms.

Reference	**Species**	**Max. body size**	**Max. depth of occurrence**	**Habitat**	**Barrier type**	**Barrier description (abbreviations used in Figure 3)**	**Marker type** (significant genetic differentiation across barrier marked in bold)
Sharks							
(Ahonen et al., 2009)	*Carcharias taurus*	325	232	neritic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	**mtDNA** (CR), **msat** (6)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR), **msat** (6)
(Andreotti et al., 2016)	*Carcharodon carcharias*	595	1200	oceanic	Current front	Agulhas-Benguela Front (AGB)	mtDNA (CR), msat (14)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	mtDNA (CR)
(Ashe et al., 2015)	*Negaprion brevirostris*	368	120	benthopelagic	Florida Peninsula	Florida Peninsula (FP)	**mtDNA** (CR, ND2), msat (9)
					Depth	Florida Straits (FS)	**mtDNA** (CR, ND2), msat (9)
(Bailleul et al., 2018)	*Prionace glauca*	384	1116	oceanic	Depth	Depth between North-East Atlantic coast and Azores (AZ)	mtDNA (cytb), msat (9)
					Strait	Strait of Gibraltar (SG)	mtDNA (cytb), msat (9)
					Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	mtDNA (cytb), msat (9)
(Barker et al., 2015)	*Triakis semifasciata*	214	156	benthopelagic	Current front	Point Conception (PC)	**msat** (5)
					Depth	Southern California Bight (SCB)	**msat** (5)
(Benavides et al., 2011a)	*Carcharhinus brachyurus*	325	360	neritic	Current front	Agulhas-Benguela Front (AGB)	mtDNA (CR)
					Mid ocean barrier	East Pacific Barrier (EPB)	**mtDNA** (CR)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR)
					Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	mtDNA (CR)

(Benavides et al., 2011b)	*Carcharhinus obscurus*	420	500	neritic	Florida Peninsula	Florida Peninsula (FP)	mtDNA (CR)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR)
(Bernard et al., 2016)	*Galeocerdo cuvier*	550	1112	neritic	Florida Peninsula	Florida Peninsula (FP)	mtDNA (CR, COI), msat (10)
					Depth	Florida Straits (FS)	**mtDNA** (CR, COI), msat (10)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	msat (10)
(Bernard et al., 2017)	*Carcharhinus perezi*	295	378	neritic	Depth	Depth between Cayman Islands and Belize (CI)	**mtDNA** (CR, ND4), msat (7), **LDH**
(Bester-van der Merwe et al., 2017)	*Galeorhinus galeus*	195	1100	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	mtDNA (ND2), msat (19)
					Mid ocean barrier	East Pacific Barrier (EPB)	**msat** (19)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (ND2), msat (19)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	**mtDNA** (ND2), **msat** (19)
					Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	mtDNA (ND2), msat (19)
(Bitalo et al., 2015)	*Galeorhinus galeus*	195	1100	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	msat (12)
	Mustelus mustelus	175	800	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	**msat** (12)
(Boissin et al., 2019)	*Carcharhinus amblyrhynchos*	265	275	neritic	Depth	Coral Sea (CS): Depth between coast and island (East Australia vs. Chesterfield)	**msat** (13)
					Depth	West Pacific islands (WP): Depth between coast and island (Palmyra vs. Tuamotu)	**msat** (13)
					Depth	West Pacific islands (WP): Depth between coast and island (Society vs. Phoenix Is.)	**msat** (13)
					Depth	Coral Sea (CS): Depth between islands (Chesterfield vs. New Caledonia)	msat (13)
					Depth	West Pacific islands (WP): Depth between islands (Palmyra vs. Phoenix)	**msat** (13)

					Depth	West Pacific islands(WP): Depth between islands (Society Is. vs. Tuamotu)	msat (13)
(Bolaño-Martínez et al., 2019)	*Sphyrna zygaena*	500	200	neritic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	**mtDNA** (CR)
(Camargo et al., 2016)	*Carcharhinus longimanus*	395	1082	oceanic	Current front	Agulhas-Benguela Front (AGB)	mtDNA (CR)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	**mtDNA** (CR)
(Cardeñosa et al., 2014)	*Alopias pelagicus*	428	300	oceanic	Mid ocean barrier	East Pacific Barrier (EPB)	**mtDNA** (COI), **msat** (7)
(Carmo et al., 2019)	*Galeocerdo cuvier*	550	1112	neritic	Land bridge	Isthmus of Panama (IPB)	**mtDNA** (CR)
					Depth	Depth: South American continent and Brazilian offshore islands (BR)	mtDNA (CR)
					Current	South Equatorial Current (SEC)	**mtDNA** (CR)
(Castillo-Olguín et al., 2012)	*Sphyrna lewini*	430	1043	oceanic	Land bridge	Isthmus of Panama (IPB)	**mtDNA** (CR), msat (5)
(Castro et al., 2007)	*Rhincodon typus*	1700	1928	oceanic	Current front	Agulhas-Benguela Front (AGB)	**mtDNA** (CR)
					Mid ocean barrier	East Pacific Barrier (EPB)	mtDNA (CR)
					Land bridge	Isthmus of Panama (IPB)	**mtDNA** (CR)
(Catarino et al., 2015)	*Centroscymnus coelolepis*	130	3675	oceanic	Mid ocean barrier	Indian Ocean Barrier (IOB)	mtDNA (CR)
					Depth	Depth between North-East Atlantic coast and Azores (AZ)	mtDNA (CR), msat (11)
					Strait	Strait of Gibraltar (SG)	**mtDNA** (CR), **msat** (11)
(Chabot & Allen, 2009)	*Galeorhinus galeus*	195	1100	benthopelagic	Mid ocean barrier	East Pacific Barrier (EPB)	**mtDNA** (CR)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	**mtDNA** (CR)
(Chabot, 2015)	*Galeorhinus galeus*	195	1100	benthopelagic	Mid ocean barrier	East Pacific Barrier (EPB)	**msat** (11)
					Large-scale thermal barrier	Equatorial warm water barrier (EWB)	**msat** (11)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**msat** (11)
(Chabot et al., 2015)	*Mustelus henlei*	100	281	benthopelagic	Current front	Baja California Peninsula (BCP)	mtDNA (CR), msat (6)

					Depth	Southern California Bight (SCB)	mtDNA (CR), msat (6)
					Current front	Point Conception (PC)	**mtDNA** (CR), **msat** (6)
(Chen et al., 2017)	*Scoliodon macrorhynchos*	71	NA	benthopelagic	Land bridge	Taiwan Strait (TS)	mtDNA (CR)
(Clarke et al., 2015)	*Carcharhinus falciformis*	350	500	oceanic	Mid ocean barrier	East Pacific Barrier (EPB)	mtDNA (CR)
					Land bridge	Isthmus of Panama (IPB)	**mtDNA** (CR)
					Land bridge	Sunda Shelf Barrier (SSB)	**mtDNA** (CR)
(Corrigan et al., 2018)	*Isurus oxyrinchus*	445	750	oceanic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	**mtDNA** (CR, flanking tRNAs), msat (10)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR, flanking tRNAs), **msat** (10)
					Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	mtDNA (CR, flanking tRNAs), msat (10)
(Cunha et al., 2012)	*Centroselachus crepidater*	105	2080	oceanic	Depth	Depth between North-East Atlantic coast and Azores (AZ)	mtDNA (CR), msat (7)
(Da Silva Ferrette et al., 2015)	*Pseudocarcharias kamoharai*	122	590	oceanic	Current front	Agulhas-Benguela Front (AGB)	mtDNA (CR)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	mtDNA (CR)
(Daly-Engel et al., 2012)	*Sphyrna lewini*	430	1043	oceanic	Current front	Agulhas-Benguela Front (AGB)	**msat** (13)
					Mid ocean barrier	East Pacific Barrier (EPB)	**msat** (13)
					Florida Peninsula	Florida Peninsula (FP)	**msat** (13)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	msat (13)
					Land bridge	Isthmus of Panama (IPB)	**msat** (13)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	**msat** (13)
					Land bridge	Sunda Shelf Barrier (SSB)	msat (13)
					Strait	Torres Strait (TST)	msat (13)
(Deng et al., 2019)	*Carcharhinus leucas*	366	164	neritic	Depth	South China Sea: Depth between two islands	mtDNA (CR)
(Devloo-Delva et al., 2019)	*Galeorhinus galeus*	195	1100	benthopelagic	Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	SNPs
(Domingues et al., 2018c)	*Carcharhinus falciformis*	350	500	oceanic	Depth	Depth between Brazilian coast and oceanic archipelago St. Peter and St. Paul (BR)	mtDNA (CR)

					Florida Peninsula	Florida Peninsula (FP)	mtDNA (CR)
					Current	South Equatorial Current (SEC)	**mtDNA (CR)**
(Domingues et al., 2018a)	*Carcharhinus signatus*	280	600	oceanic	Haline	Amazon Barrier (AB)	mtDNA (CR)
					Florida Peninsula	Florida Peninsula (FP)	mtDNA (CR), msat (9)
					Current	South Equatorial Current (SEC)	**mtDNA** (CR), msat (9)
(Dudgeon et al., 2009)	*Stegostoma fasciatum*	250	90	benthopelagic	Strait	Torres Strait (TST)	mtDNA (ND4), msat (13)
(Duncan et al., 2006)	*Sphyrna lewini*	430	1043	oceanic	Mid ocean barrier	East Pacific Barrier (EPB)	**mtDNA** (CR)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	**mtDNA** (CR)
					Strait	Torres Strait (TST)	**mtDNA** (CR)
(Escatel-Luna et al., 2015)	*Sphyrna tiburo*	150	90	neritic	Depth	Depth of the Gulf of Mexico between Florida shelf and Yucatan (GM)	**mtDNA** (CR)
					Florida Peninsula	Florida Peninsula (FP)	**mtDNA** (CR)
(Feldheim et al., 2001)	*Negaprion brevirostris*	368	120	benthopelagic	Depth	Florida Straits (FS)	**msat** (4)
(Félix-López et al., 2019)	*Sphyrna zygaena*	500	200	neritic	Current front	Baja California Peninsula (BCP)	mtDNA (CR)
(Ferrari et al., 2018)	*Galeus melastomus*	90	2000	benthopelagic	Strait	Strait of Sicily (SSC)	mtDNA (CR, COI, ND2)
	Scyliorhinus canicula	100	800	benthopelagic	Strait	Strait of Sicily (SSC)	mtDNA (CR, COI, ND2)
(Fields et al., 2016)	*Sphyrna tiburo*	150	90	neritic	Depth	Florida Straits (FS)	**mtDNA** (CR)
(Gaida, 1997)	*Squatina californica*	175	205	benthopelagic	Depth	Southern California Bight (SCB): Depth between islands of the Channel Islands	**allozyme**
(Geraghty et al., 2013)	*Carcharhinus brevipinna*	304	200	neritic	Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (ND4)
					Strait	Torres Strait (TST)	mtDNA (ND4)
(Geraghty et al., 2014)	*Carcharhinus obscurus*	420	500	neritic	Depth	Timor Trench (TT)	mtDNA (ND4)
					Strait	Torres Strait (TT)	mtDNA (ND4)

(Giles et al., 2014)	*Carcharhinus sorrah*	166	140	neritic	Depth	Coral Sea: Depth between Eastern Australia and New Caledonia (CS)	**mtDNA** (CR)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR)
					Current	Indonesian throughflow current (ITC)	mtDNA (CR)
					Land bridge	Sunda Shelf Barrier	mtDNA (CR)
					Depth	Timor Trench (TT)	**mtDNA** (CR)
					Strait	Torres Strait (TST)	mtDNA (CR)
(Gledhill et al., 2015)	*Carcharhinus limbatus*	286	100	neritic	Depth	Florida Straits (FS)	**mtDNA** (CR)
(Green et al., 2019)	*Carcharhinus albimarginatus*	300	800	neritic	Depth	Coral Sea (CS): Depth between Eastern Australia and Papua New Guinea	**mtDNA** (CR), msat (12), SNPs
(Gubili et al., 2014)	*Scyliorhinus canicula*	100	800	benthopelagic	Depth	Depth: Balearic abyssal plain (BAP)	mtDNA (CR), **msat** (12)
					Strait	Strait of Gibraltar (SG)	mtDNA (CR), **msat** (12)
					Strait	Strait of Sicily (SSC)	**mtDNA** (CR), **msat** (12)
(Gubili et al., 2016)	*Etmopterus spinax*	55	2490	oceanic	Depth	Depth between North-East Atlantic coast and Azores (AZ)	mtDNA (CR), ITS2
					Strait	Strait of Gibraltar (SG)	mtDNA (CR), ITS2
					Strait	Strait of Sicily (SSC)	mtDNA (CR), ITS2
(Heist et al., 1995)	*Carcharhinus plumbeus*	243	500	neritic	Florida Peninsula	Florida Peninsula (FP)	mtDNA (RFLP), allozymes
(Heist & Gold, 1999)	*Carcharhinus plumbeus*	243	500	neritic	Florida Peninsula	Florida Peninsula (FP)	msat (3)
(Hernández et al., 2015)	*Galeorhinus galeus*	195	1100	benthopelagic	Mid ocean barrier	East Pacific Barrier (EPB)	**mtDNA** (CR) **msat** (8)
					Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	mtDNA (CR) msat (8)
(Holmes et al., 2017)	*Galeocerdo cuvier*	550	1112	neritic	Depth	Coral Sea (CS): Depth between Coral Sea reefs and New Caledonia	msat (9)
					Strait	Torres Strait (TST)	msat (9)
(Hull et al., 2019)	*Mustelus mustelus*	175	800	benthopelagic	Depth	Depth: African coast (Giunea-Bissau) and Cape Verde (CV)	**mtDNA** (CR), **msat** (9)

					Strait	Strait of Gibraltar (SG)	**mtDNA** (CR), **msat** (9)
(Junge et al., 2019)	*Carcharhinus brachyurus*	325	360	neritic	Strait	Bass Strait (BS)	SNPs
					Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	SNPs
	Carcharhinus obscurus	420	500	neritic	Strait	Bass Strait (BS)	SNPs
					Depth	Timor Trench (TT)	SNPs
(Karl et al., 2011)	*Carcharhinus leucas*	366	164	neritic	Florida Peninsula	Florida Peninsula (FP)	mtDNA (CR), msat (5)
(Karl et al., 2012)	*Ginglymostoma cirratum*	308	130	benthopelagic	Depth	Florida Straits (FS)	mtDNA (CR), msat (8)
					Depth	Depth: South American continent and Brazilian offshore islands (BR)	**mtDNA** (CR), **msat** (8)
(Keeney & Heist, 2006)	*Carcharhinus limbatus*	286	100	neritic	Mid ocean barrier	East Pacific Barrier (EPB)	mtDNA (CR)
(King et al., 2015) King 2015	*Prionace glauca*	384	1116	oceanic	Mid ocean barrier	East Pacific Barrier (EPB)	msat (14)
(Kousteni et al., 2015)	*Scyliorhinus canicula*	384	800	benthopelagic	Depth	Depth: Algerian Sub-basin (ASB)	mtDNA (COI), **msat** (12)
					Strait	Strait of Gibraltar (SG)	mtDNA (COI)
					Strait	Strait of Sicily (SSC)	**mtDNA** (COI), **msat** (12)
(Kousteni et al., 2016)	*Squalus blainville*	92	1500	benthopelagic	Depth	Depth: Balearic abyssal plain (BAP)	mtDNA (COI)
(Leone et al., 2017)	*Prionace glauca*	384	1116	oceanic	Strait	Strait of Gibraltar (SG)	**mtDNA** (CR, cytb)
(Maduna et al., 2016)	*Mustelus mustelus*	175	800	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	mtDNA (ND4), **msat** (8)
					Current front	Angola-Benguela Front (AB)	mtDNA (ND4), **msat** (8)
(Maduna et al., 2017)	*Galeorhinus galeus*	195	1100	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	msat (11)
	Mustelus mustelus	175	800	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	**msat** (11)
	Mustelus palumbes	113	443	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	**msat** (11)
	Triakis megalopterus	207	50	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	msat (11)
(Mendonça et al., 2011)	*Rhizoprionodon porosus*	110	500	neritic	Current	South Equatorial Current (SEC)	mtDNA (CR)
(Momigliano et al., 2015)	*Carcharhinus amblyrhynchos*	265	275	neritic	Depth	Coral Sea (CS): Depth of the Coral Sea Through	mtDNA (ND4), msat (16)

(Momigliano et al., 2017)	*Carcharhinus amblyrhynchos*	265	275	neritic	Depth	Coral Sea (CS): Depth of the Coral Sea Through	SNPs, mtDNA (ND4)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**SNPs**, **mtDNA** (ND4)
					Depth	Timor Trench (TT)	SNPs, mtDNA (ND4)
					Strait	Torres Strait (TST)	**SNPs**, **mtDNA** (ND4)
(Morales et al., 2018)	*Alopias superciliosus*	484	723	oceanic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	mtDNA (CR)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	mtDNA (CR)
(Ovenden et al., 2009)	*Carcharhinus sorrah*	166	140	neritic	Strait	Torres Strait (TST)	mtDNA (CR), msat (5)
(Pazmiño et al., 2018a)	*Carcharhinus galapagensis*	370	286	neritic	Mid ocean barrier	East Pacific Barrier (EPB)	**SNPs**, mtDNA (CR)
					Depth	Depth between Mexican offshore Island (Revillagigedo) and Galapagos islands (GA)	SNPs, **mtDNA** (CR)
					Depth	Tasman Sea: Depth between Australian offshore islands and New Zealand (TAS)	SNPs, mtDNA (CR)
(Pirog et al., 2019)	*Galeocerdo cuvier*	550	1112	neritic	Depth	Coral Sea (CS): Depth between Eastern Australia and New Caledonia	msat (27)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR, COI, cytb), msat (27)
					Strait	Torres Strait (TST)	msat (27)
(Portnoy et al., 2010)	*Carcharhinus plumbeus*	243	500	neritic	Florida Peninsula	Florida Peninsula (FP)	mtDNA (CR), msat (8)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	**mtDNA** (CR), msat (8)
(Portnoy et al., 2014)	*Carcharhinus acronotus*	164	100	neritic	Depth	Depth of the Gulf of Mexico between Florida shelf and Yucatan (GM)	**mtDNA** (CR), **msat** (23)
					Florida Peninsula	Florida Peninsula (FP)	**mtDNA** (CR), **msat** (23)
					Depth	Florida Straits (FS)	**mtDNA** (CR), **msat** (23)
					Haline	Mississippi Delta (MD)	mtDNA (CR), msat (23)
(Quintanilla et al., 2015)	*Sphyrna lewini*	430	1043	oceanic	Depth	Depth between Colombian coast and Malpeo Island (MA)	mtDNA (CR), msat (15)

(Ramírez-Amaro et al., 2018)	*Galeus melastomus*	90	2000	benthopelagic	Depth	Western Mediterranean: Depth of the Alboran and Balearic basins (BAP)	mtDNA (CR, cytb, ND2)
	Scyliorhinus canicula	384	800	benthopelagic	Depth	Western Mediterranean: Depth of the Alboran and Balearic basins (BAP)	**mtDNA** (CR, cytb, ND2), **msat** (12)
(Ramírez-Amaro et al., 2017)	*Squatina californica*	175	205	benthopelagic	Current front	Baja California Peninsula (BCP)	mtDNA
(Sandoval Laurrabaquio-A et al., 2019)	*Carcharhinus leucas*	366	164	neritic	Florida Peninsula	Florida Peninsula (FP)	mtDNA (CR), msat (8)
(Sandoval-Castillo & Beheregaray, 2015)	*Mustelus henlei*	100	281	benthopelagic	Current front	Baja California Peninsula (BCP)	mtDNA (CR), msat (12)
(Schmidt et al., 2009)	*Rhincodon typus*	1700	1928	oceanic	Land bridge	Isthmus of Panama (IPB)	**msat** (8)
(Schrey & Heist, 2003)	*Isurus oxyrinchus*	445	750	oceanic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	msat (4)
(Schultz et al., 2008)	*Negaprion brevirostris*	368	120	benthopelagic	Land bridge	Isthmus of Panama (IPB)	**mtDNA** (CR)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	**mtDNA** (CR), **msat** (9)
(Tillett et al., 2012a)	*Carcharhinus amboinensis*	280	100	neritic	Strait	Torres Strait (TST)	**mtDNA** (CR, ND4)
(Veríssimo et al., 2010)	*Squalus acanthias*	160	1978	benthopelagic	Mid ocean barrier	East Pacific Barrier (EPB)	mtDNA (ND2), msat (8)
					Large-scale thermal barrier	Equatorial warm water barrier (EWB)	**mtDNA** (ND2), **msat** (8)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	mtDNA (ND2), msat (8)
(Veríssimo et al., 2011)	*Centroscymnus coelolepis*	130	3675	oceanic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	mtDNA (CR), msat (8)
					Depth	Depth between North-East Atlantic coast and Azores (AZ)	mtDNA (ND2), msat (8)
(Veríssimo et al., 2012)	*Centrophorus squamosus*	166	3366	oceanic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	mtDNA (ND2), msat (6)
					Depth	Depth between North-East Atlantic coast and Azores (AZ)	mtDNA (ND2), msat (8)

(Veríssimo et al., 2017)	*Prionace glauca*	384	1116	oceanic	Large-scale thermal barrier	Equatorial warm water barrier (EWB)	mtDNA (CR), msat (12)
					Mid ocean barrier	Mid Atlantic Barrier (MAB)	mtDNA (CR), msat (12)
					Depth	Depth between North-East Atlantic coast and Azores (AZ)	mtDNA (CR), msat (12)
(Vignaud et al., 2013)	*Carcharhinus melanopterus*	180	100	neritic	Depth	West Pacific islands (WP): Depth between islands (Tetiaroa and Rangiroa)	**msat** (11)
(Vignaud et al., 2014b)	*Carcharhinus melanopterus*	180	100	neritic	Depth	Coral Sea (CS): Depth between Eastern Australia and New Caledonia	**msat** (14)
					Strait	Torres Strait (TST)	**msat** (14)
(Vignaud et al., 2014a)	*Rhincodon typus*	1700	1928	oceanic	Mid ocean barrier	East Pacific Barrier (EPB)	mtDNA (CR)
					Mid ocean barrier	Indian Ocean Barrier (IOB)	mtDNA (CR), msat (14)
					Land bridge	Isthmus of Panama (IPB)	**mtDNA** (CR), **msat** (14)
					Land bridge	Sunda Shelf Barrier (SSB)	mtDNA (CR)
(Whitney et al., 2012b)	*Triaenodon obesus*	213	330	benthopelagic	Depth	Coral Sea (CS): Depth of the Coral Sea Through	mtDNA (CR)
					Mid ocean barrier	East Pacific Barrier (EPB)	**mtDNA** (CR)
					Land bridge	Sunda Shelf Barrier (SSB)	**mtDNA** (CR)
Batoids							
(Arlyza et al., 2013)	*Neotrygon kuhlii*	70	170	benthopelagic	Land bridge	Sunda Shelf Barrier (SSB)	**mtDNA** (COI)
(Borsa et al., 2012)	*Neotrygon kuhlii*	70	170	benthopelagic	Current	Indonesian throughflow current (ITC)	**EPICs** (7)
(Carney et al., 2017)	*Rhinoptera bonasus*	107	60	benthopelagic	Florida Peninsula	Florida Peninsula (FP)	**mtDNA** (COI, cytb)
(Castillo-Páez et al., 2014)	*Zapteryx exasperata*	97	200	benthopelagic	Current front	Baja California Peninsula (BCP)	**mtDNA** (CR, ND2)
(Chevolot et al., 2006a)	*Raja clavata*	139	1020	benthopelagic	Strait	Strait of Dover (SD)	msat (5)
(Chevolot et al., 2006b)	*Raja clavata*	139	1020	benthopelagic	Depth	Depth between North-East Atlantic coast and Azores (AZ)	**mtDNA** (cytb), **msat** (5)
					Strait	Strait of Gibraltar (SG)	**mtDNA** (cytb), **msat** (5)

(Chevolot et al., 2007)	*Amblyraja radiata*	111	1400	benthopelagic	Mid ocean barrier	Mid Atlantic Barrier (MAB)	mtDNA (cytb)
					Haline	Salinity and temperature gradient between the North Sea and the Baltic Sea (NB)	mtDNA (cytb)
(Ferrari et al., 2018)	*Raja clavata*	139	1020	benthopelagic	Strait	Strait of Sicily (SSC)	mtDNA (CR, COI, ND2)
	Raja miraletus	71	462	benthopelagic	Strait	Strait of Sicily (SSC)	mtDNA (CR, COI, ND2)
(Feutry et al., 2015)	*Pristis pristis*	700	60	benthopelagic	Haline	Salt water between river drainages in Northern Australia (AR)	**mitogenome**
(Frodella et al., 2016)	*Raja polystigma*	71	633	benthopelagic	Depth	Depth: Algerian Sub-basin (ASB)	**msat** (7)
					Strait	Strait of Sicily (SSC)	mtDNA (CR, COI, 16S), msat (7)
(Giles et al., 2016)	*Rhynchobatus australiae*	300	60	benthopelagic	Land bridge	Sunda Shelf Barrier (SBB)	**mtDNA** (CR)
					Depth	Timor Trench (TT)	**mtDNA** (CR)
(Green et al., 2018)	*Pristis cuspidata*	350	128	benthopelagic	Strait	Torres Strait (TST)	**mtDNA** (CR, ND4), msat (5)
(Newby et al., 2014)	*Aeobatus narinari*	330	80	neritic	Florida Peninsula	Florida Peninsula (FP)	msat (8)
(Pasolini et al., 2011)	*Raja clavata*	139	1020	benthopelagic	Strait	Strait of Gibraltar (SG)	mtDNA (CR), **AFLP**
					Strait	Strait of Sicily (SSC)	mtDNA (CR), AFLP
	Raja straeleni	91	690	benthopelagic	Current front	Agulhas-Benguela Front (AGB)	**mtDNA** (CR)
(Plank et al., 2010)	*Urobatis halleri*	58	91	benthopelagic	Current front	Baja California Peninsula (BCP)	msat (7)
					Depth	Southern California Bight (SCB): Depth between California Coast and Santa Catalina Island	**msat** (7)
(Richards et al., 2019)	*Hypanus americanus*	200	53	benthopelagic	Depth	Depth between Cayman Islands and Belize (CI)	**mtDNA** (CR)
					Florida Peninsula	Florida Peninsula (FP)	**mtDNA** (CR)
					Depth	Florida Straits (FS)	**mtDNA** (CR)
(Roycroft et al., 2019)	*Bathytoshia brevicaudata*	430	476	benthopelagic	Mid ocean barrier	Indian Ocean Barrier (IOB)	**msat** (11)

					Depth	Tasman Sea: Depth between Australia and New Zealand (TAS)	**msat** (11)
(Sandoval-Castillo et al., 2004)	*Pseudobatos productus*	170	92	benthopelagic	Current front	Baja California Peninsula (BCP)	**mtDNA** (cytb, 12S rDNA)
(Sandoval-Castillo & Rocha-Olivares, 2011)	*Rhinoptera steindachneri*	107	77	neritic	Current front	Baja California Peninsula (BCP)	**mtDNA** (ND2)
(Sellas et al., 2015)	*Aeobatus narinari*	330	80	neritic	Depth	Depth of the Gulf of Mexico between Florida and Yucatan (GM)	**mtDNA** (cytb), msat (10)
(Smith et al., 2009)	*Gymnura marmorata*	125	95	benthopelagic	Current front	Baja California Peninsula (BCP)	**mtDNA** (cytb)

Appendix B

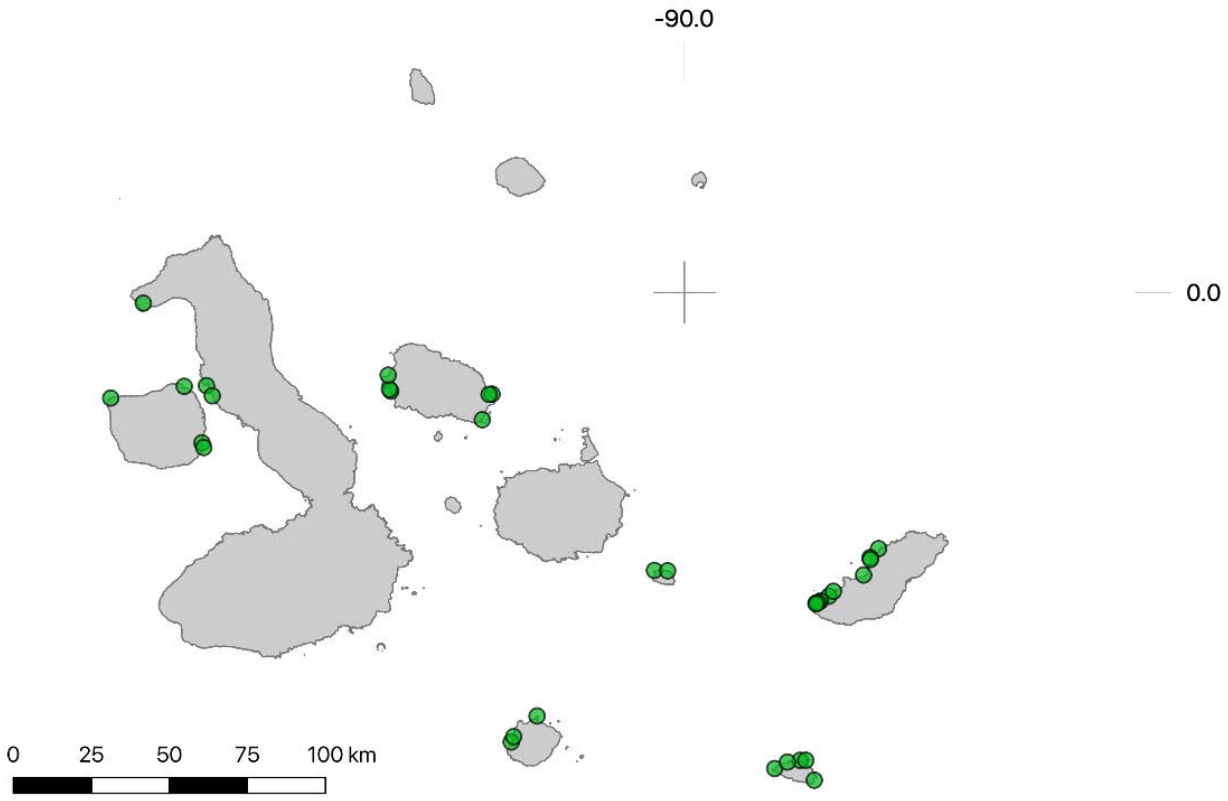


Figure 15. All 33 dive locations surveyed for Galapagos bullhead sharks between 2015 and 2018.

Table 10. Details of resistance surfaces used in isolation by resistance (IBR) analyses.

a) Resistance values used to generate the resistance surface for the contemporary IBR model based on GEBCO bathymetry data (GEBCO Bathymetric Compilation Group, 2019).

GEBCO bathymetry depth (m)	**Resistance**
0-40	1
40-100	50
100-200	55
200-300	60
300-400	65
400-500	70
500-600	75
600-700	80
700-800	85
800-900	90
<0	100

b) Resistance values used to generate the resistance surface for the paleogeographic IBR model using historical sea levels over the last 700 thousand years ago (kyr) based on (Ali & Aitchison, 2014).

GEBCO bathymetry (m)	**Time (kyr)**	**Historical sea level**	**Number of times less than 40 m deep**	**Resistance**
0-40	-	-	-	1
40-185	20	145	6	2
185-194	138	154	5	3
194-200	342	160	4	4
200-229	432	189	2	5
229-250	630	210	1	6
250-300	-	-	-	60
300-400	-	-	-	65
400-500	-	-	-	70
500-600	-	-	-	75
600-700	-	-	-	80
700-800	-	-	-	85
>800	-	-	-	90
<0	-	-	-	100

Table 11. SNP filtering steps for Galapagos bullhead sharks (SNP sequencing and genotyping by Diversity Arrays Technologies is described below), corresponding thresholds and resulting number of SNPs and individuals kept in the data set. Tow data sets, outlier SNPs detected by both outlier methods and neutral SNPs excluding the outliers were retained for analyses.

Filter	Values/thresholds	SNPs (samples) retained
Raw data		33606 (188)
DArT reproducibility	98%	31196 (188)
Common markers		29522 (188)
Minor allele count	4	12423 (188)
Coverage	Min 10 max 50	10396 (188)
Genotyping (call rate)	0.05	9742 (188)
SNPs thinning (short linkage)	keep one SNP with lowest MAC	9280 (188)
Heterozygosity	None removed	9280 (188)
Detect duplicate genomes	Duplicate samples (n=6) Recaptures (n=2)	9280 (180)
Hardy-Weinberg equilibrium	In 3 populations/0.05 mid p-value	9239 (180)
Sex-linked markers	5	9234 (180)
Total number of SNPs and individuals retained		
Outlier data set		**11** (180)
Neutral data set		**9223** (180)

SNP sequencing and genotyping

Genomic DNA was extracted from 15-20 mg of tissue samples (preserved in 96% ethanol and stored at -20˚C until processing) and then sequenced for single nucleotide polymorphism (SNP) genotyping by Diversity Arrays Technologies (DArT Pty Ltd, Canberra, Australia). The DArTseq™ protocol (DArT Pty Ltd), a next generation sequencing and complexity reduction method using a combination of PstI and SphI restriction enzymes (Kilian et al., 2012), is similar to ddRAD (double-digest restriction-associated DNA) sequencing (Peterson et al., 2012), but works with lower quantities of DNA and has lower allelic dropout rates (Sansaloni et al., 2011). SNP genotyping was done using the standard procedure of the proprietary DArT Pty Ltd analytical pipeline (Georges et al., 2018; Grewe et al., 2015). Briefly, the analytical pipeline generated short fixed-length sequence fragments (69bp for this study) that are aggregated into clusters using the DArT Pty Ltd proprietary clustering algorithm (Georges et al., 2018). The fixed fragment length sequences were then analysed using the proprietary DArT software (DArTsoft14), which identifies candidate SNP markers within each cluster by assessing the call rate, average and variance of sequencing depth, and the average counts for each SNP allele (Georges et al., 2018). Further, one third of samples were used as technical replicates and were processed twice from DNA to assess SNP genotyping consistency, called reproducibility (Kilian et al., 2012).

Table 12. Pairwise genetic comparisons in Galapagos bullhead sharks. Pairwise genetic fixation index (F_{ST}) index below, and corresponding p-values, above diagonal (top table). Pairwise genetic differentiation index (D_{ST}) below, and corresponding p-values, above diagonal (bottom table). Bold numbers indicate significant values after Benjamin-Hochberg false discovery correction. ES = Española, FL = Floreana, PE = Punta Espinoza, PM = Punta Mangle, PNG = Parque National Galapagos, PVR = Punta Vicente Roca, SCY = San Cristóbal.

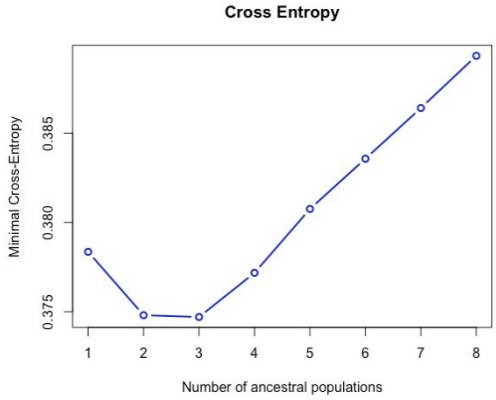
F_{ST}

	ES	**FL**	**PE**	**PM**	**PNG**	**PVR**	**SCY**
ES		0.001	0.001	0.001	0.001	0.001	0.001
FL	**0.0368**		0.001	0.001	0.001	0.001	0.001
PE	**0.0304**	**0.0149**		0.27	0.84	0.001	0.001
PM	**0.0303**	**0.0150**	0.0004		0.29	0.001	0.001
PNG	**0.0297**	**0.0139**	-0.0004	0.0003		0.001	0.001
PVR	**0.0315**	**0.0161**	**0.0027**	**0.0028**	**0.0023**		0.001
SCY	**0.0289**	**0.0207**	**0.0140**	**0.0149**	**0.0133**	**0.0169**	

D_{ST}

	ES	**FL**	**PE**	**PM**	**PNG**	**PVR**	**SCY**
ES		0.001	0.001	0.001	0.001	0.001	0.001
FL	***0.00079***		0.001	0.001	0.001	0.001	0.001
PE	***0.00061***	***0.00032***		0.78	0.27	0.001	0.001
PM	***0.00062***	***0.00032***	0.00009		0.24	0.001	0.001
PNG	***0.00064***	***0.00030***	0.0001	0.0001		0.001	0.001
PVR	***0.00063***	***0.00034***	***0.00014***	***0.00014***	***0.00012***		0.001
SCY	***0.00064***	***0.00057***	***0.00042***	***0.0004***	***0.00038***	***0.00047***	

a)



b)

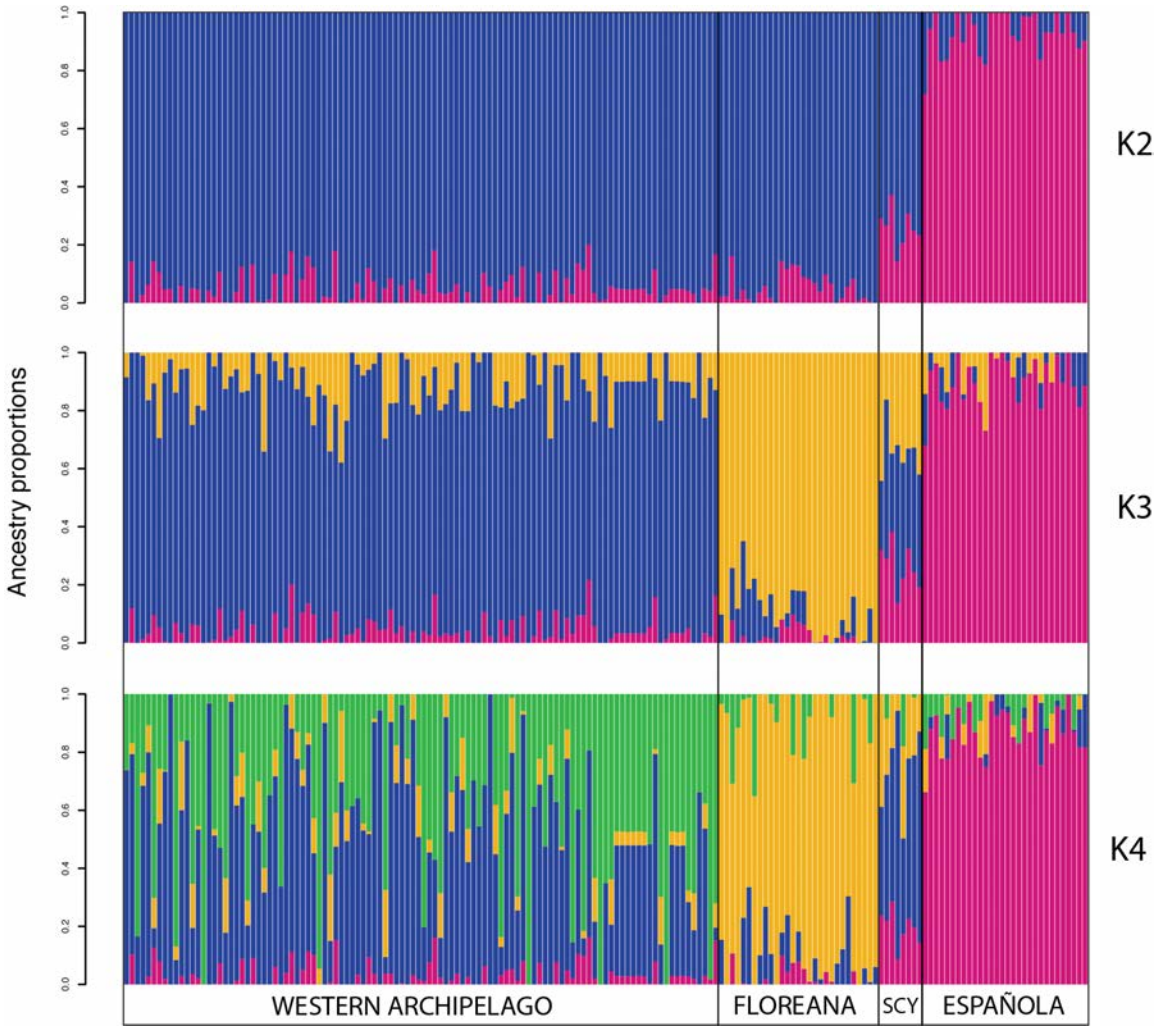
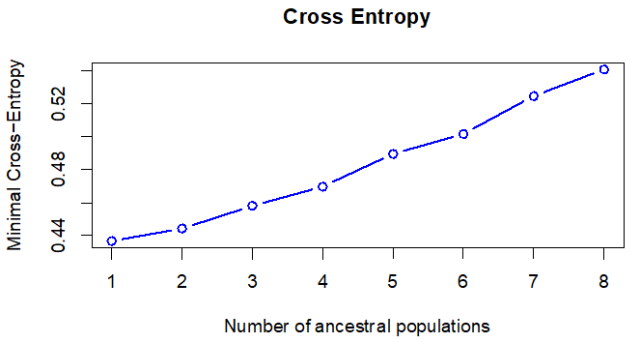


Figure 16. Admixture analysis for Galapagos bullhead sharks. a) The most likely number of K ancestral populations indicated by the lowest cross-entropy criterion generated for 180 sharks and 9223 neutral SNPs using the R package tess3R. b) Admixture proportions of K 2-4 ancestral populations for 180 sharks (shown as individual bars) and 9223 neutral SNPs.

a)



b)

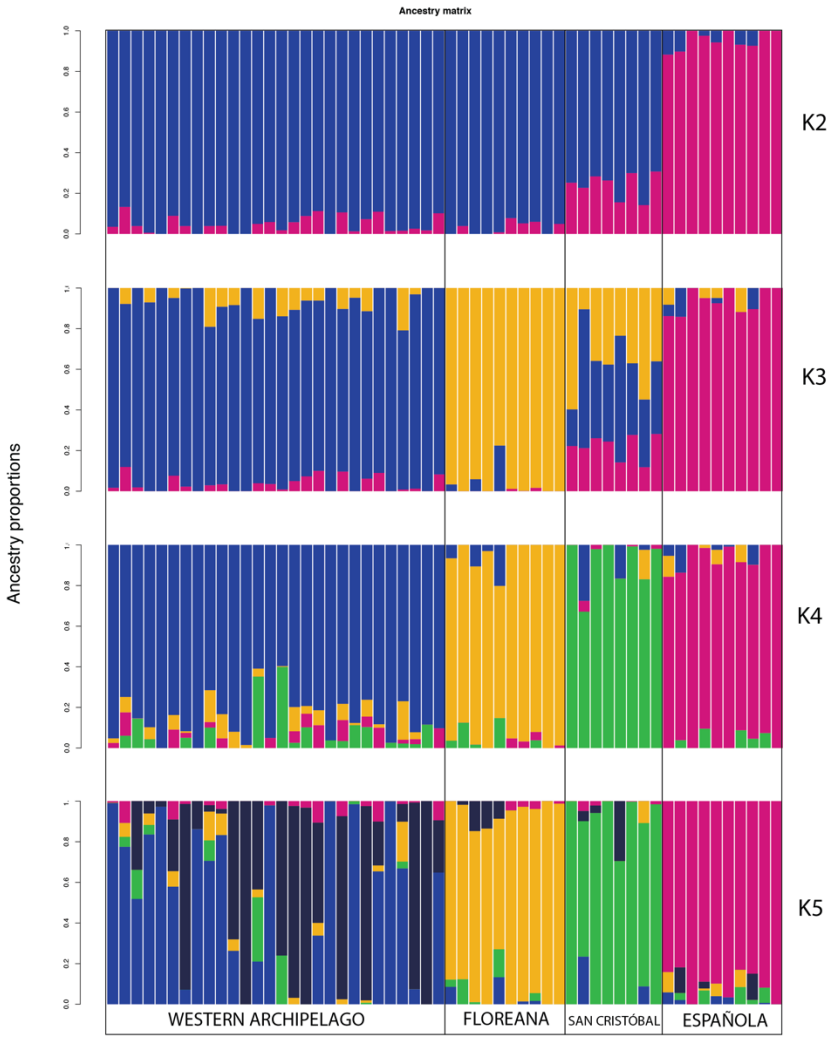


Figure 17. Admixture analysis for a subset of Galapagos bullhead sharks. a) The most likely number of K ancestral populations indicated by the lowest cross-entropy criterion generated for the subset of 56 sharks and 9223 neutral SNPs. b) Admixture proportions of K 2-5 ancestral populations the subset of 56 sharks (shown as individual bars) and 9223 neutral SNPs.

Table 13. Genomic diversity of shark species studied using similar genotyping approaches.

Species	Genotyping approach	SNPs/individuals	Ho (Range)	Reference
Galeorhinus galeus	DArTseq*	6587/76	0.264- 0.265	(Devloo-Delva et al., 2019)
Glyphis glyphis	DArTseq	1330/356	0.2597-0.2623	(Feutry et al., 2017)
Carcharhinus albimarginatus	ddRAD (Peterson et al., 2012)	6461/ 92	0.126 - 0.13	(Green et al., 2018)
Carcharhinus brachyurus	DArTseq	3766/106	0.208 - 0.261	(Junge et al., 2019)
Carcharhinus obscurus	DArTseq	8886/207	0.159 - 0.200	(Junge et al., 2019)
Carcharhinus amblyrhynchos	DArTseq	4798/170	0.288 - 0.312 (0.139 in Chagos Archipelago)	(Momigliano et al., 2017)
Carcharhinus galapagensis	DArTseq	8103/85	0.188 - 0.193	(Pazmiño et al., 2017a)
Carcharhinus galapagensis	DArTseq	7784/206	0.202- 0.237	(Pazmiño et al., 2018b)
Scyliorhinus canicula	2b-RAD (Wang et al., 2012)	2674/71	0.53 - 0.73	(Manuzzi et al., 2019)
Heterodontus quoyi	DArTseq	9223/180	0.089-0.098	This study

* DartSeq methods and references can be found in the main manuscript.

Appendix C

DNA extraction and sequencing

Salting out protocol

Genomic DNA was extracted from fin clips and muscle tissues using a modified salting out protocol (Sunnucks & Hales, 1996). Approximately 30 mg of tissue was cut into small pieces, added to 2ml tubes with 600µl lysis buffer (5-mM tris-HCl pH 8.0, 20mM EDTA pH 8.0, 2% SDS) and 5 µl of 20mg/ml Proteinase K and digested overnight at 55˚ C on a heat block. Proteins were then precipitated by adding 200µl NaCl (5M), shaking for 20 seconds and centrifuging at the tubes at 14000rpm for 2 min. DNA was then pelleted by decanting the supernatant into new tubes, adding 1ml cold Isopropyl (100%), inverting the tubes 50x and then centrifuging them at 14000rpm for 5 min. After pouring off the supernatant isopropyl, the DNA pellets were washed in 75% ethanol for 15 min twice. The pellets were then air-dried overnight and resuspended in 30-70µl deionized water. The quality of extracted DNA was assessed using electrophoresis in a 1% agarose gel in 1× TBE buffer and DNA concentration was quantified using Invitrogen Qubit 4 Fluorometer (Thermo Fisher Scientific).

Mitochondrial DNA control region sequencing

We amplified 819 bp of the mitochondrial control region using the light strand primer Pro-L and the heavy strand primer 282-H following Whitney et al. (2012). PCR was performed on a 20µL master mix containing 10µL MyTag™ Mix (Bioline, Meridian Bioscience) 2µL of each primer, 2µL template DNA and 4 µL purified water (Milli-Q®, Merck). Cycling conditions differed slightly from Whitney et al. (2012) and included an initial 5 min denaturation at 95°C, followed by 30 cycles of 30 s denaturation at 95°C, 30 s annealing at 51 °C, and an extension of 1 min at 72 °C, and ended with a final 10 min extension at 72°C. Subsequently 7 µL aliquots of PCR product were purified with 3 µL of ExoSAP-IT™ PCR Product Cleanup Reagent (Thermo Fisher Scientific Inc.) at 37 degrees for 15 min and reagent was inactivated 80 °C degrees for 15 min. Sequencing of clean PCR products was performed by the Australian Equine Genetics Research Centre (AEGRC) at the University of Queensland, Australia, using BigDye™ terminators with the Pro-L primer and a the internal light strand primer Rf45 (Whitney et al., 2012b). Sequences were assessed and aligned using Geneious Prime® 2019.2.3 (https://www.geneious.com).

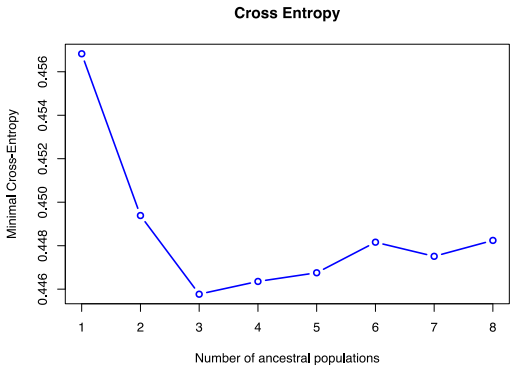
Table 14. SNP filtering steps for whitetip reef sharks (SNP sequencing and genotyping by Diversity Arrays Technologies is described below), corresponding thresholds, and resulting number of SNPs and individuals kept in the data set.

Filter	Values/thresholds	SNPs (samples) retained
Raw data		33466 (209)
DArT reproducibility	98%	24700 (209)
Common markers		23399 (209)
Minor allele count	4	14235 (209)
Coverage	Min 10 max 50	11244 (209)
Genotyping (call rate)	0.05	9216 (209)
Maximum number of SNPs per locus	2	9138 (209)
SNPs thinning (short linkage)	keep one SNP with lowest MAC	8649 (209)
Heterozygosity	0.1> x < 0.2	9280 (205)
Detect duplicate genomes	Duplicate samples (n=21) Recaptures (n=1)	9280 (183)
Hardy-Weinberg equilibrium	In 3 populations/0.05 mid p-value	8595 (183)
Sex-linked markers		8595 (183)
Outliers	36 overlapping SNPs (PCadapt: 193, OutFlank: 38)	8559 (183)
Total number of neutral SNPs and individuals retained		**8559** (183)

SNP sequencing and genotyping

Extraction, and sequencing of DNA and the genotyping of SNPs was done using the same steps as described in Chapter 2 (Appendix B description below Table 11).

a)



b)

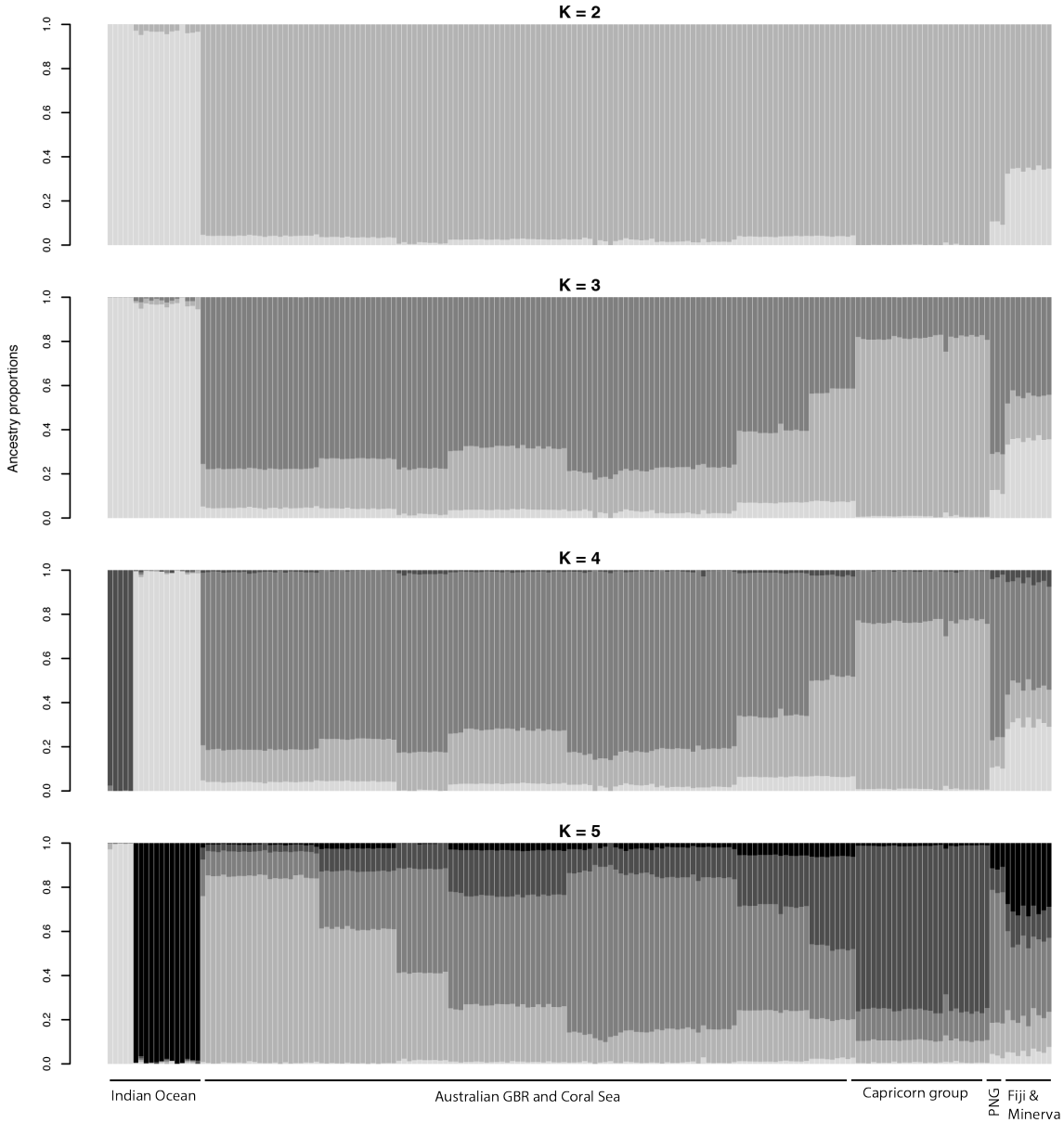
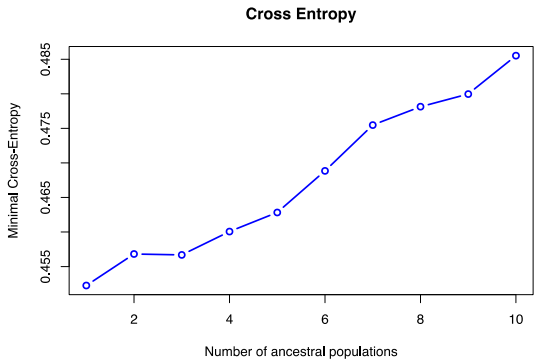


Figure 18. Admixture analyses of the Indo-Pacific data set for whitetip reef sharks. Admixture proportions of neutral SNPs including all sampling location in the Indo-Pacific: a) Cross entropy values for K=1-8 ancestral populations; The most likely number of K corresponds to the smallest cross-entropy value. b) Bar plot of individual admixture proportions (each bar represents one individual) for K=2–5 ancestral populations.

a)



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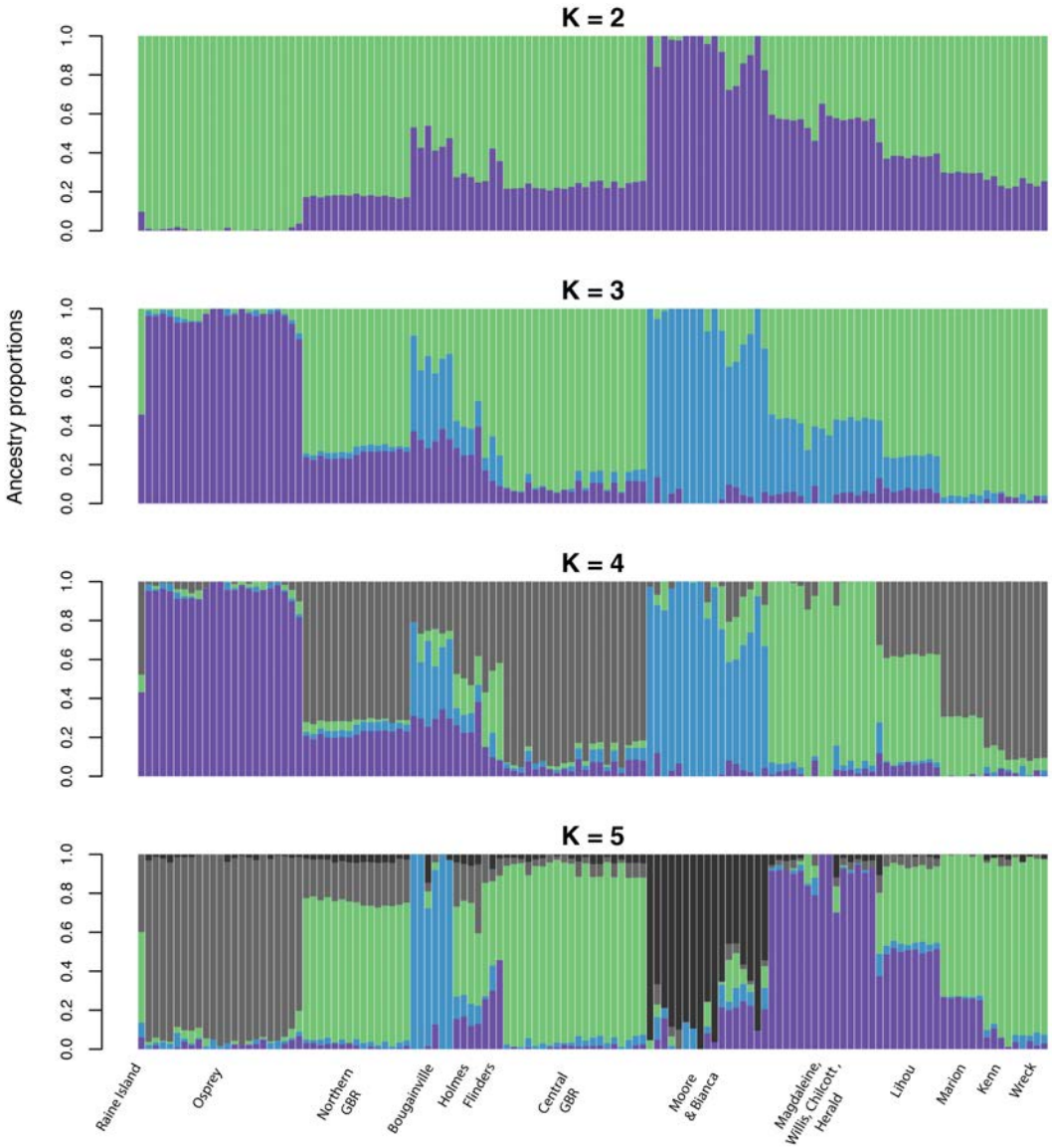

Figure 19. Admixture analysis of the regional data set for whitetip reef sharks. Admixture proportions of neutral SNPs including sampling locations in the Coral Sea (Capricorn Group excluded). a) Cross entropy values for K=1-8 ancestral populations; The most likely number of K corresponds to the smallest cross-entropy value. b) Bar plot of individual admixture proportions (each bar represents one individual) for K=2–5 ancestral populations.