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Breadth of the Wild: Global Patterns in Elasmobranch Dietary Niche Breadth

By

Sarah Popov

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Breadth of the Wild: Global Patterns in Elasmobranch Dietary Niche Breadth

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August 31, 2020

DECLARATION OF CO-AUTHORSHIP

I. Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research which was undertaken under the supervision of Dr. Nigel Hussey in all cases. The unpublished manuscript presented in Chapter 2 was co-authored by S. Popov, A. Barkley, K. J. Lees, and N. E. Hussey. The author was responsible for providing the main ideas, data analysis and figure creation, interpretation, and writing the final manuscript. Co-authors contributed to the original literature search and data analysis. N. E. Hussey additionally provided guidance on theoretical knowledge input and conducted revisions of all written contributions.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

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ABSTRACT

A widely recognized pattern in ecology is the latitudinal diversity gradient: increasing biodiversity with decreasing latitude. The latitude niche-breadth hypothesis states that the stable climate of the tropics allows for increased specialization (smaller niche), promoting greater biodiversity in the available niche space. The highly dynamic climate of the poles drives the evolution of generalists (larger niche), limiting biodiversity. While the fundamental question of “what drives species richness?” on land remains debated, it is even less understood in the marine environment. Elasmobranchs (sharks, skates, and rays) are a data-rich, globally distributed group that occupy an array of functional roles, inhabiting coastal to open ocean habitats from the poles to the tropics. In this thesis, I use a global-scale stomach contents dataset to calculate standardized Levin’s niche breadth for 237 populations of 85 elasmobranch species in order to examine spatial patterns in niche breadth. I find that niche breadth varies widely across all functional, taxonomic, and regional groups, highlighting the diversity and potential resiliency of this clade. Niche breadth of elasmobranchs does not follow a latitudinal gradient. Instead, niche varies with depth, with niche breadth generally increasing with increasing depth. This depth gradient is strongest in bottom-dwelling elasmobranchs with smaller range sizes and weakest in wide-ranging pelagic elasmobranchs. This pattern suggests that for species with limited mobility, specialization may mediate coexistence in highly biodiverse areas with elevated competition. Why this pattern applies in a depth, but not latitudinal, gradient remains unclear.

DEDICATION

This thesis is dedicated to my parents, who left everything they knew to chase the evanescent American Dream. Спасибо, что подбодрили эту лягушку путешественницу, and for not being too upset when at the age of 17, I vehemently opposed pursuing a safe career at J.P. Morgan Chase. Without your encouragement and sacrifice I would not be here today. I am so proud to have the family name Popov on this document.

I also dedicate this work to all other graduate students struggling to see the relevance of their work, something I have been grappling with in the midst of a global pandemic, ecosystem and biodiversity collapse, and erosion of social fabric and racial reckoning. Your work is valuable, whether now or in 10, 100, 500 years.

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CHAPTER 1

General Introduction

Biodiversity has long been recognized as variable on the planet, with species richness peaking at the tropics and decreasing with increasing latitude. This latitudinal diversity gradient (**LDG**) was first described scientifically in 1808 by Alexander von Humboldt, who noted that plant biodiversity was far greater in tropical Venezuela than in temperate Europe (von Humboldt, 1808). Numerous other gradients have since been explored in the literature, including altitudinal and depth gradients in biodiversity (Macpherson, 2002; Rahbek, 1995; Rohde, 1992), yet no gradient is so widespread or well documented as the LDG (Brown, 2014; Rohde, 1992). Since von Humboldt's initial observations, latitudinal gradients in diversity have been documented in myriad taxa across geologic time, ranging from Permian brachiopods and Triassic ammonoids (Crame, 2001) to modern trees, ants, and marine fishes (Krebs, 1972; Macpherson & Duarte, 1994; Wright, 2002). For example, Krebs (1972) documents 22 species of snake in Canada, 126 in the US, and 293 in Mexico; 7 species of ant in Alaska, 63 in Utah, 101 in Cuba, and 222 in Brazil; and 10-15 species of tree in two hectares in Michigan versus 227 species of tree in two hectares in Malaysia. There are some exceptions to the rule, with cold-adapted taxa notably having the highest biodiversity at temperate latitudes. Penguins, pinnipeds, cetaceans, and their associated parasites, for example, have the highest diversity at higher latitudes (Lomolino et al., 2010; Tittensor et al., 2010). However, these exceptions are comparatively rare and can serve as "natural experiments" to understand which potentially differing processes are driving their biogeography (Brown, 2014).

While the LDG has been a well observed phenomenon for the past two centuries, the cause of the LDG has been a hotly debated topic in the literature. von Humboldt was the first European to formally suggest that temperature was the primary force shaping regional biodiversity, though others before him had noted it in their journals (Caldas, 1966; Forster, 1778; von Humboldt, 1808). The drivers behind the LDG have since proven to be of enduring interest in the field of ecology, with no agreed upon mechanism accounting for the pattern (Brown, 2014; Rohde, 1992). The topic has stimulated much research throughout the last century: Pianka (1966), Stevens (1989), Rohde (1992), Gaston (2000), Mittelbach et al. (2007), Brown (2014), and Kinlock et al. (2018), among many others, have all published influential work on the causes and consequences of the LDG. Indeed, understanding the mechanisms underlying spatial patterns of biodiversity, in particular the LDG, has been declared as one of the top questions of the early 21st century (Kennedy & Norman, 2005; Pennisi, 2005).

Over two dozen hypotheses have been proposed as mechanisms driving the LDG since von Humboldt's temperature theorem. Rohde (1992) summarized 28 potential hypotheses, which were broadly categorized into three groups: 12 "circular", 11 "insufficient", and 5 "time" hypotheses. Circular hypotheses are ecological in nature and rely upon increased biodiversity in the tropics as a pre-existing condition (*e.g.*, increased levels of predation, parasitism, and competition resulting in further increased diversification). As such, circular "explanations" are in fact phenomena that are a consequence of high species richness rather than an explanation thereof (Brown & Gibson, 1983; Rohde, 1992). Insufficient hypotheses are those that have little evidence to support them: for example, increased productivity has been postulated as an explanation for increased species richness; in reality, this is a correlation which does not always exist. For example, tropical coral reefs, some of the most biodiverse ecosystems on the planet, occur in relatively nutrient-poor waters (Begon et al., 1986; Rohde, 1992). Finally, time hypotheses hinge upon speciation rates and evolutionary time as the primary mechanism by which the tropics have higher biodiversity. While there is considerable fossil and phylogenetic evidence to support the hypothesis that extratropical species originate from the “cradle” or “museum” of the tropics (Bowen et al., 2013; Jablonski et al., 2006), there are likely certain underlying traits of equatorial ecosystems creating these “cradles” in the first place (Arita & Vázquez-Domínguez, 2008; Belmaker & Jetz, 2015). Additionally, recent work contradicts the commonly held assumption of increased speciation rates in the tropics, at least within the marine environment (Rabosky et al., 2018). Ultimately, agreement into what causes the LDG has yet to be reached, despite this being a long recognized and well-studied pattern.

1.1 Overview of study system: why the oceans?

The oceans are vast compared to continents, with a correspondingly vast knowledge gap on what drives the biodiversity gradient in the marine environment as opposed to on land (Bowen et al., 2013; Brown, 2014; Roy et al., 1998). The marine realm differs considerably from the terrestrial, with these differences potentially leading to contrasting drivers of the latitudinal diversity gradient on land versus sea (Brown, 2014; Valentine & Jablonski, 2015). The oceans are characterized by limited barriers and high species mobility, high larval dispersal driven by ocean currents, and significant movement of biomass into the depths in addition to across latitude (Garland et al., 2002; Sequeira et al., 2018). Rapid vertical variations in temperature are largely driven by water stratification, particularly in the tropics (Tomczak, 2019), while more gradual horizontal variations in temperature are generated by seasonality at higher latitudes (Clarke & Gaston, 2006). In contrast, dispersal is limited in terrestrial systems, with major geographic barriers such as mountain ranges and canyons; the majority of terrestrial movement is in two dimensions, and seasonality is far greater at higher latitudes in terrestrial systems. For example, species' thermal tolerance ranges (and in turn, exploitable habitat) differ markedly from the terrestrial to the marine, with marine thermal ranges limited at the poles and extreme at the equator (Sunday et al., 2011). The inverse occurs in the terrestrial environment (Stevens, 1989).

The difficulty of monitoring environmental conditions and organismal life histories in such a dynamic, three-dimensional environment has prevented the study of the mechanistic drivers behind the marine latitudinal diversity gradient until the more recent synthesis of large, global scale datasets, technological advances such as remote sensing and biotelemetry (Cooke et al., 2004; Hussey et al., 2015a; Payne et al., 2014), and the application of biochemical tracers (*e.g.* stable isotopes; Fry, 2006). As such, patterns and drivers associated with the LDG have yet to be rigorously tested in the marine environment.

1.2 The lens of niche

One particularly compelling means of studying the marine LDG is through the lens of niche (MacArthur, 1968). Exploring broad patterns of individual species' behavior, limitations to survival, and environmental and dietary preferences – in short, studying the ecological "space" that an organism occupies – can provide valuable insights into what drives the LDG, as it allows researchers to quantify latitudinal patterns of other ecosystem traits aside from biodiversity (Brown, 2014; Schemske, 2002).

The niche of a species is typically described on a scale from "specialist" to "generalist" (Krebs, 2014). The term "specialist" describes a species that has narrow environmental or dietary range and is thus "specialized" in certain environmental conditions or food items. In contrast, a "generalist" describes a species that can utilize a wide variety of environments or food items. Niche breadth is a term used to describe the degree to which a species is specialized or generalized: a narrow or small niche breadth indicates a specialist, while a wide or large niche breadth indicates a generalist.

The concept of "niche" was first formally discussed in the literature in 1917 by Joseph Grinnell, who sought to quantify the biogeographic variables that were associated with the presence of one species of bird over another. Grinnell argued that the environment both shaped the organism living within it while at the same time constraining where it could live: "The [California Thrasher] may be characterized as semi- terrestrial, but always dependent upon vegetational cover; and this cover must be of the chaparral type, ... and upon its ability to co-operate in making use of this cover. The Thrasher has strong feet and legs, and muscular thighs, an equipment which betokens powers of running.... These various circumstances, which emphasize dependence upon cover, and adaptation in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California Thrasher" (Grinnell, 1917). In the intervening years Grinnellian, or "spatial", niche has come to be more formally defined as the biogeographic parameters and environmental conditions where a species can persist indefinitely (Krebs, 2014; Leibold, 1995; Peterson et al., 2011).

Following Grinnell's publication, the field of niche theory was born. The second major contribution to the field was Charles Elton's theory of niche, in which he defined niche as the "role" or trophic position of an organism within its ecosystem (Elton, 1927). Elton's primary interest in niche was to quantify inter- and intra-specific competition for resources. This is typically done by examining stomach contents in order to determine which food resources a species consumes (Krebs, 2014). Dietary niche, therefore, is defined as the dietary composition required by an organism to persist indefinitely.

Finally, Evelyn Hutchinson in 1957 unified the two differing theories of niche into a single concept: that of the "*n*-dimensional hypervolume" (Hutchinson, 1957). The *n*-dimensional hypervolume describes, on *n*-number of axes, every possible biological and physical niche of an organism, from thermal tolerance ranges to dietary preferences. The hypervolume therefore encompasses all points where a population of an organism can exist in perpetuity. In his 1957 "Concluding Remarks", Hutchinson additionally discusses the concepts of "fundamental" versus "realized" niche (Hutchinson, 1957). The *n*-dimensional hypervolume is equivalent to the "fundamental" niche: the maximum theoretical space in which an organism can persist. In reality, inter- and intra-specific competition and limitations to dispersal constrain the size of the *n*-dimensional hypervolume. This constrained set of conditions where a species exists in reality is referred to as the "realized" niche.

1.3 The latitude-niche breadth hypothesis

In 1972, MacArthur unified the disparate concepts of niche theory and the LDG (MacArthur, 1972). The latitude-niche breadth hypothesis states that there is a relationship between the niche breadth of an organism and latitude, and predicts that the stable, uniform climate at the equator promotes increased specialization (narrower niche), allowing more species to occupy the total available niche space, while the highly dynamic climate at the poles drives the evolution of generalists (wider niche). This in turn results in increased species richness at the equator and limited richness at the poles. In short, the total available niche space remains constant at all latitudes.

The null hypothesis of the above is that niche breadth does not vary with latitude. Instead, there are two alternatives to account for the LDG: the theoretical total available niche space in the tropics is simply wider than at the poles, permitting the coexistence of a greater number of species, or the total available niche space at the poles simply has not yet been filled (Pielou, 1979; Rabosky et al., 2018; Rohde, 1992).

Because niche breadth is representative of a species' adaptations to its environment, it is expected that certain biotic traits will also correlate with niche breadth. For example, body size can be correlated with home range size (Brown et al., 1996), geographic range size (Pyron, 1999), trophic position (Akin & Winemiller, 2008; Cohen et al., 1993; Jennings et al., 2001), and prey item size (Barclay & Brigham, 1991). As such, one may expect body size to be correlated with spatial (Grinnellian) niche breadth (Rapoport's rule; Stevens, 1989) and dietary (Eltonian) niche breadth.

While the latitude-niche breadth hypothesis is frequently implicated in latitudinal diversity gradient research, empirical testing of it has been minimal, particularly in the marine environment (Vázquez & Stevens, 2004). Rohde (1978) found that host specificity of trematode parasites decreased with latitude, while Monogenean parasites overall showed no trend; however, caution must be taken when interpreting latitudinal trends in any internal parasite, as they are buffered from the environmental conditions of the region (Stevens, 1989). Two other studies identified increasing thermal niche breadth with latitude in the marine environment (Sunday et al., 2011, 2012), but a wide thermal niche breadth does not necessarily correlate with greater diet breadth. Teleost larvae consume a greater variety of prey at lower latitudes, but specialize in one particular prey group, suggesting greater resource specialization at lower latitudes (Llopiz, 2013). Only one study tested the latitude-niche breadth hypothesis in the marine environment using diet as a metric for resource use while accounting for the potentially confounding variables of body size, range size, and phylogenetic relatedness (Papacostas & Freestone, 2016). The study found that niche breadth increased with latitude in temperate brachyuran crabs, but that the relationship did not extend to tropical taxa. For tropical brachyuran crabs, the evolutionary age of the clade was the major determinant of dietary niche breadth, suggesting evolutionary history and competition play a stronger role in structuring tropical marine community dynamics.

1.4 Study taxon and thesis objectives

There has been one recently published study examining patterns of niche breadth and depth range in skates (Elasmobranchii: Batoidea), indicating that this is a historically understudied yet currently active body of research (Barbini et al., 2018). Barbini et al.

(2018) note that to their knowledge, “this is the first study on [niche breadth] focused on elasmobranch fishes.” To date, there have been no published studies testing patterns of niche breadth and latitude in elasmobranch fishes.

This thesis seeks to empirically test the latitude-niche breadth hypothesis in the marine environment using elasmobranchs (sharks, skates, and rays) as the study taxon and dietary breadth as the measure of niche. Compared to taxa examined in other marine latitude-niche breadth hypothesis studies (*e.g.* flatworms, teleost larvae, brachyuran crabs), elasmobranchs are notably larger, more mobile, and of a higher trophic level. Elasmobranchs are also data-rich, with hundreds of diet content datasets published to date, and comprise the largest, most diverse predatory clade in the oceans both today and in the last several hundred million years (Compagno, 1990). As such, dietary niche values for this single clade can capture a wealth of evolutionary history and information about marine food webs. Studying this group within the context of the latitude-niche breadth hypothesis therefore provides a novel opportunity to study variables shaping the biogeography of marine predators.

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CHAPTER 2

A Depth Gradient in Elasmobranch Dietary Niche Breadth

2.1 Introduction

The latitudinal diversity gradient is the dominant pattern in global-scale biogeography: species richness for nearly all taxa on earth increases with decreasing latitude (Brown, 2014; von Humboldt, 1808). This biodiversity gradient has been examined through the lens of niche theory, which can be used to describe facets of biodiversity beyond taxonomic richness (Costa et al., 2008; Lamanna et al., 2014; Pigot et al., 2016). Niche is broadly defined as the role an organism plays in its ecosystem (Elton, 1927), and niche breadth describes the range of environmental and dietary resources that an organism can exploit (Hutchinson, 1957; MacArthur, 1968). Species with narrow niche breadths are considered specialists, while a species with wide niche breadths are generalists (Krebs, 2014). Niche dynamics underpin a wide variety of ecological processes, providing insight into coexistence and competition (Bolnick et al., 2010), community resilience to disturbance (Devictor et al., 2008), and evolutionary dynamics (Roughgarden, 1972). As such, it has been hypothesized that there is a relationship between niche breadth and biodiversity, and, consequently, latitude (the latitude-niche breadth hypothesis; MacArthur, 1972; reviewed by Vázquez & Stevens, 2004).

The latitude-niche breadth hypothesis states that with increasing latitude there will be a corresponding increase in resource use and niche breadth. MacArthur (1972) postulated that the relatively uniform climate of the low-latitude tropics supports stable population dynamics, which promotes increased specialization and narrower niches over time

(Dobzhansky, 1950; Vázquez & Stevens, 2004). Greater specialization frees species from resource competition, allowing higher coexistence among species (Bolnick et al., 2010; Dyer et al., 2007). In contrast, MacArthur (1972) suggests the dynamic climate at the poles drives the evolution of generalists that are adapted to a wide range of environmental conditions. The latitude-niche breadth hypothesis therefore predicts that niche breadth will be wider, coexistence will be limited, and diversity will be lower at the poles as a result. Implicit in the latitude-niche breadth hypothesis is the assumption that environmental conditions become increasingly unstable as one moves poleward from the tropics (Vázquez & Stevens, 2004).

While there are indeed greater fluctuations in yearly mean air temperature with increasing latitude, there is mixed support for MacArthur's assumption that there is a latitudinal gradient in overall environmental variability or "harshness" in both terrestrial and marine systems (Rohde, 1992; Vázquez & Stevens, 2004). For example, marine systems exhibit a parabolic, as opposed to linear, relationship between temperature variability and latitude (Tomczak, 2019). If temperature variability is the strongest determinant of niche breadth, this pronounced parabolic relationship may produce different latitude-niche breadth dynamics between the terrestrial and marine environments (Cirtwill et al., 2015; Valentine & Jablonski, 2015).

Seasonal fluctuations in sea surface temperature peaks at temperate latitudes and are dampened near the equator and the poles (Dunstan et al., 2018; Jain et al., 1999; Tomczak, 2019), while the global deep sea remains a steady -1°C to 4°C for the entire year (Gage & Tyler, 1991). The yearly temperature range of water at the poles is remarkably stable, with a seasonal sea surface temperature amplitude of approximately 4°C across much of the Arctic (Shevenell et al., 2011) and 3.5°C in the Antarctic (-1.5 to 2°C; Chepurin & Carton, 2012). In sharp contrast, terrestrial polar systems can experience yearly fluctuations in temperature in excess of 80°C (*e.g.*, Verkhoyansk, Siberia, -67.8°C to 38°C; Menne et al., 2012a, 2012b). Polar and deepwater marine species ultimately have a strikingly small temperature range to adapt to than their terrestrial counterparts, and this may result in markedly different niche breadth patterns compared to what MacArthur's hypothesis predicts for polar terrestrial systems.

This pattern is uniquely inverted in the tropics. Temperature drops as large as 15°C over a 200 m depth gradient are driven by thermal stratification caused by the permanent tropical oceanic thermocline (Tomczak, 2019). At the same time, air temperatures in the tropics remain comparatively stable, even across a 200 m altitudinal gradient (~-5.5°C·km^{-1} of altitude; Córdova et al., 2016; Loomis et al., 2017; Peixoto & Oort, 1992). Consequently, tropical marine species may be adapted to greater temperature variability than polar marine species. We therefore expect niche breadth to be widest in species with large depth ranges in regions with a strong thermocline, as is the case in tropical brachyuran crabs (Papacostas & Freestone, 2016). In temperate environments, water column position plays a stronger role than seasonal variability in structuring bacterioplankton community composition across a depth gradient (Fortunato et al., 2012). If MacArthur's latitude-niche breadth hypothesis is primarily driven by adaptation to a gradient of thermal variability ("harshness"), thermocline dynamics would likely dominate over latitude in determining spatial patterns of niche in the marine environment.

A more recent alternative to the "harshness" hypothesis is that a latitudinal gradient in energy availability or productivity determines specialization (Brown, 2014;

Forister et al., 2015), such that highly productive tropical forests support a greater diversity of niches than productivity-poor boreal forests (Brown, 2014). In this scenario, niche breadth would also not follow a latitudinal gradient in the oceans. Spatial patterns of marine productivity differ substantially from the terrestrial and are often patchy and unevenly distributed, with peaks occurring in upwelling zones at the continental margins and at temperate latitudes instead of along a latitudinal gradient (Dunstan et al., 2018; Tomczak, 2019). Moreover, in contrast to land, the world's tropical seas are generally nutrient limited and characterized by low primary productivity, despite high biodiversity (Sigman & Hain, 2012).

Recent evidence also suggests that absolute latitude may not be as influential in shaping the niche breadth of a particular species' population as the proximity to its polar range limit. In a global scale study of lepidopteran niche breadth, Lancaster (2020) found that lepidopteran populations sampled closer to their poleward range limit had wider niche breadths relative to their counterparts located more centrally within their range. This suggests that colonization dynamics, rather than thermal stability or productivity of the region, plays a greater role in structuring niche (Lancaster, 2020).

2.1.1 Other variables affecting niche breadth.

Evolutionary history, body size, and range size are all known to influence niche breadth while concomitantly varying with latitude (Hillebrand, 2004a, 2004b).

Closely related species often occupy similar ecological roles and therefore have similar niche breadths (phylogenetic niche conservatism; Kerkhoff et al., 2014; Wiens &

Graham, 2005). Regions with a high proportion of newer, closely related clades might therefore have a greater number of species with similar, or conserved, niches, while regions with a high proportion of older and evolutionarily distinct lineages might have greater niche diversity (Wiens & Graham, 2005).

Body size can influence dietary specialism/generalism via two diverging mechanisms. Firstly, with increasing body and gape size, a predator can physically consume a larger variety of prey, thus potentially widening its niche (Shine & Sun, 2003; Simon & Toft, 1991; Sloggett, 2008). Alternatively, optimal foraging theory suggests that predators become more specialized as they grow larger, targeting only the most profitable prey in order to most efficiently meet caloric needs (Costa et al., 2008). Previous work on marine predators (primarily teleosts but including some elasmobranchs) has found there to be no relationship between body size and diet breadth, suggesting the latter mechanism dominates in marine food webs (Costa 2009).

Larger animals also tend to have larger home and geographic ranges (Brown et al., 1996; Pyron, 1999). A species with a wide geographic range has access to a greater number of resources and may therefore be more generalist (Brown, 1984). In a systematic review of niche breadth and geographic range size, Slatyer et al. (2013) found this to be true of both dietary and environmental niche breadth. Given this, we expect niche breadth to increase in tandem with both body and range size.

These three factors — evolutionary history, body size, and range size — concomitantly vary with latitude, which may potentially confound the latitude-niche breadth relationship. Speciation rates in marine teleost fishes have been shown to increase with latitude (Rabosky et al., 2018), and the evolutionary age of Chondrichthyan (sharks, skates, rays, and chimaeras) clades decreases with latitude (Stein et al., 2018), indicating younger clades inhabit polar regions. Large body sizes are more efficient to keep warm due to the ratio between surface area and volume, and Bergmann's rule predicts that body size will increase with increasing latitude as temperature decreases (Bergmann, 1848), but it is unclear whether this pattern is widely applicable to the marine environment (Berke et al., 2013; Fisher et al., 2010; Lindsey, 1966). Finally, Rapoport's rule predicts that range size will increase with latitude (Stevens, 1989), as species at higher latitudes are selected to survive broader climatic variability and thus can colonize a wider latitudinal range. A similar mechanism has been proposed for species with wide altitudinal (Stevens, 1992) and depth ranges (*e.g.* a "depth variant" of Rapoport's rule; Stevens, 1996).

2.1.2 Study objectives.

The elasmobranchs (sharks, skates, rays) are a widely distributed, evolutionarily old and diverse group with a disproportionately high number of threatened to critically endangered species (Dulvy et al., 2014; Stein et al., 2018). Large sharks in particular play a globally important role in stabilizing food webs across the oceans (Heupel et al., 2014), structuring the trophic linkages of marine ecosystems (Burkholder et al., 2013; Hussey et al., 2015b). How smaller sharks and batoids fit into the larger marine ecosystem, however, is less well studied (*e.g.*, as in the case of the cownose ray in the northwest Atlantic; see Myers et al., 2007 and Grubbs et al., 2016). Understanding dietary niche breadth dynamics across all elasmobranchs will provide insight into the trophic role this globally threatened group plays while also highlighting their adaptability potential in the face of climate change. On land, large carnivorous specialists are strongly negatively impacted by habitat loss and range contraction (Middleton et al., 2020). As regions of the oceans warm, numerous sharks and batoids will experience range contractions and shifts as a response (Cheung et al., 2009; Morley et al., 2018; Sunday et al., 2012), and quantifying elasmobranch specialism/generalism is an important first step in determining whether range contractions in the oceans will negatively affect marine predators to the same degree. Quantifying dietary niche on a latitudinal scale also acts as a proxy for resource overlap and competition, and can be used to explore global-scale patterns in species interaction strength in the marine environment (Schemske et al., 2009). Ultimately, understanding the macroecological processes that shape dietary niche breadth can serve to both enhance our understanding of the field of marine biogeography and inform biodiversity conservation.

Our overarching goal is to examine whether niche breadth varies with latitude and to test MacArthur's latitude-niche breadth hypothesis in the marine environment (MacArthur, 1972; Vázquez & Stevens, 2004). To date, only one study has explicitly examined niche breadth versus latitude in the marine environment while accounting for the confounding variables of phylogenetic relatedness, body size, and range size (Papacostas & Freestone, 2016). Here, we test this hypothesis using dietary niche as our metric for resource use and elasmobranchs as our study taxon. We additionally examine relationships between niche breadth and clade (niche conservatism hypothesis; Kerkhoff et al., 2014; Wiens & Graham, 2005); niche breadth and body size (Costa, 2009); and niche breadth and range size (Slatyer et al., 2013). We also test for potentially confounding relationships between these focal variables, *e.g.*, range size vs. latitude (Rapoport's rule, including testing the "depth variant" of Rapoport's rule; Stevens, 1989, 1996), body size vs. latitude (Bergmann's rule; Bergmann, 1848; Berke et al., 2013), and body size vs. range size (Brown et al., 1996; Pyron, 1999).

Assuming MacArthur's mechanism for determining niche breadth holds true, *i.e.*, that variation in seasonality is the primary driver of niche width, we do not predict niche breadth to follow a latitudinal gradient in the marine environment. Instead, we expect to see greater specialization in the poles and the deep ocean, where water is most thermally stable; if niche breadth is primarily driven by productivity, we expect to see greater specialization in upwelling regions and temperate latitudes.

2.2 Methods

2.2.1 Data collection.

Global elasmobranch stomach content studies were first compiled from a previous synthesis estimating standardized diet compositions of sharks (Cortés, 1999). These data were then updated and supplemented with a systematic literature search (Web of Science, conducted throughout 2016-2020) using the terms 'feeding' OR 'diet' OR 'stomach content*' in combination with 'elasmobranch*' OR 'shark*' OR 'ray*' OR 'skate*' to form a global-scale database of elasmobranch diet. This literature search yielded a total of 211 studies. Diet contents are typically reported in a standardized format: a sample population of *n* predators are captured at a given sampling location, stomachs are dissected from each sample population, and the number of empty vs. non-empty stomachs are typically reported. The stomach contents of each predator population are then identified to the finest taxonomic resolution and reported as standardized metrics such as percent frequency, percent number, and percent mass (Supplementary Table 1; Cortés, 1997; Hyslop, 1980). The dataset was filtered to only include percent frequency diet (number of stomachs containing a food item, divided by the total number of stomachs). Percent frequency is both the most commonly reported diet metric (reported in 79% of studies; Supplementary Table 2) and the only metric to represent dietary preference or choice (*e.g.*, whether many or few individuals of a particular predator population ate a diet item), and was thus chosen for niche calculations.

2.2.2 Data cleaning and standardization.

As stomach content data were extracted from a large number of studies spanning global regions and decades, data were first cleaned and standardized prior to any niche calculations. All analyses were run in the RStudio environment using **R** version 3.6 (R Core Team, 2020). All maps and figures were made using QGIS (QGIS Development Team, 2018) and the **R** package `ggplot` (version 3.3.2; Wickham, 2016). A full list of packages used can be found in Appendix 4.8.

2.2.2.1 Taxonomy.

All predator and prey species listed in publications were standardized according to the most recently accepted taxonomy. The World Register of Marine Species (WoRMS; https://www.marinespecies.org/; Horton et al., 2019) was used to standardize and update marine species taxonomy, while the Integrated Taxonomic Information System (ITIS; https://www.itis.gov/) was used to standardize all remaining species (*e.g.*, terrestrial mammals, birds, and plants).

2.2.2.2 Predator metadata.

Metadata for each predator population were extracted from published papers, including dates of sampling (start year and end year); number of total, non-empty, empty, and everted stomachs; sex; and predator size (total, fork, or precaudal lengths for sharks, disc width for rays). In most cases, stomach content papers report the minimum and maximum size of a sampled predator population, and from this information the median size and size range (maximum minus minimum size) were calculated. Mean size was taken in lieu of median size whenever reported. If sizes were specifically reported for predators with non-empty stomachs, those were recorded; otherwise, the sizes reported for the entire sampled population (including predators with empty stomachs) were used instead. In certain instances where length was not reported in the text, length information was inferred from figures in the text (*e.g.*, from body length frequency histograms).

2.2.2.3 Study location.

A single latitude and longitude coordinate was assigned to every predator population in the database (Fig. 2.1) using the following criteria: (i) If the paper reported a sampling coordinate, that was used. (ii) If the paper reported multiple latitude/longitude sampling coordinates, the geographic midpoint average was used. (iii) If the study reported a broader sampling region, an estimated central coordinate of that region was used. In cases where the coordinate fell over land, we ensured the coordinate was adjusted to fall upon the nearest water body. For example, if the study reported the coordinate of the port of landing, we assumed the sharks or rays were sampled from the adjacent waters. The majority of these study locations represent an average or estimated sampling region as opposed to a precise sampling coordinate, and thus there will be a radius of error in these sampling locations. However, as this is a global scale study, we do not expect this error to substantially impact the overall results.

2.2.2.4 Sampling ecosystem.

One of five categorical ecosystems was assigned to a predator population based on the study location: estuary, coastal, shelf, and offshore. Predator populations were assigned "estuary" if caught within a river mouth or estuarine bay; "coastal" if caught using beach safety nets or within 10 km of the shore; "shelf" if caught >10 km from shore but within waters over a continental shelf; and "offshore" if caught off-shelf. These ecosystems were used in tandem with water column position (see "Predator functional group" below) as a proxy for depth.

2.2.3 External data supplements.

Predator metadata gleaned from stomach content studies were supplemented with life history data from the following outside sources: Fishbase (http://www.fishbase.org/; Froese & Pauly, 2019), the Ocean Biogeographic Information System (OBIS; https://obis.org), and *Sharks of the World: A Fully Illustrated Guide* (Ebert et al., 2013). In all cases where Fishbase was used, the data were extracted using the **R** package `rfishbase` (Boettiger et al., 2012).

2.2.3.1 Predator functional group.

Predator species were assigned one of four functional groups using Fishbase, denoting their typical position within the water column: demersal, reef-associated (including non-tropical, non-coral reefs), benthopelagic, and pelagic. “Bathydemersal” species were re-assigned as “demersal”, while “pelagic-neritic” and “pelagic-oceanic” sharks were all grouped into the “pelagic” category. Within the “offshore” ecosystem (see “Sampling ecosystem” above), all species sampled in the upper water column using driftnets and longlines fell within the “pelagic” functional group, while all species sampled in deep water using bottom trawls and longlines fell within the “demersal” or “benthopelagic” functional groups.

2.2.3.2 Predator depth and latitudinal ranges.

Minimum and maximum latitude and depth ranges for each predator species were extracted from Fishbase and/or OBIS. Latitudinal and depth ranges were calculated as the difference between minimum and maximum latitude and depth, respectively. “Distance to polar edge” was calculated as polar edge minus sampling latitude, following similar methods as a study on global patterns of lepidopteran niche breadth (Lancaster, 2020). Polar edge was defined as the maximum absolute latitude of a species within whatever hemisphere it was sampled in. For example, if a species' latitudinal range limits are 39°N to 25°S, the polar edge for populations sampled in the northern hemisphere would be 39°, while the polar edge for populations sampled in the southern hemisphere would be 25°.

2.2.3.3 Predator clade.

All predators within the database were categorized into one of 10 clades using the phylogeny presented in Stein et al. (2018). Fully resolved 10 fossil trees were downloaded from http://sharktree.org in order to create phylogenetic groupings for predators which were visually grouped into clades A through J, with A being the oldest clade and J being the youngest (Appendix 4.2). In cases where more recently described predators were not included in the phylogeny, a clade was assigned based on other closely related species according to Linnaean taxonomy. Visual exploration and grouping of clades were done using FigTree (v.1.4.4; https://github.com/rambaut/figtree/).

2.2.4 Exclusion criteria.

The final standardized diet content dataset was then filtered to exclude studies that did not match our minimum criteria for niche calculations. Any review studies that amalgamated data previously reported in older diet content studies were removed to avoid duplication. Studies that did not report or did not meet a minimum sample size of 11 non-empty stomachs were excluded.

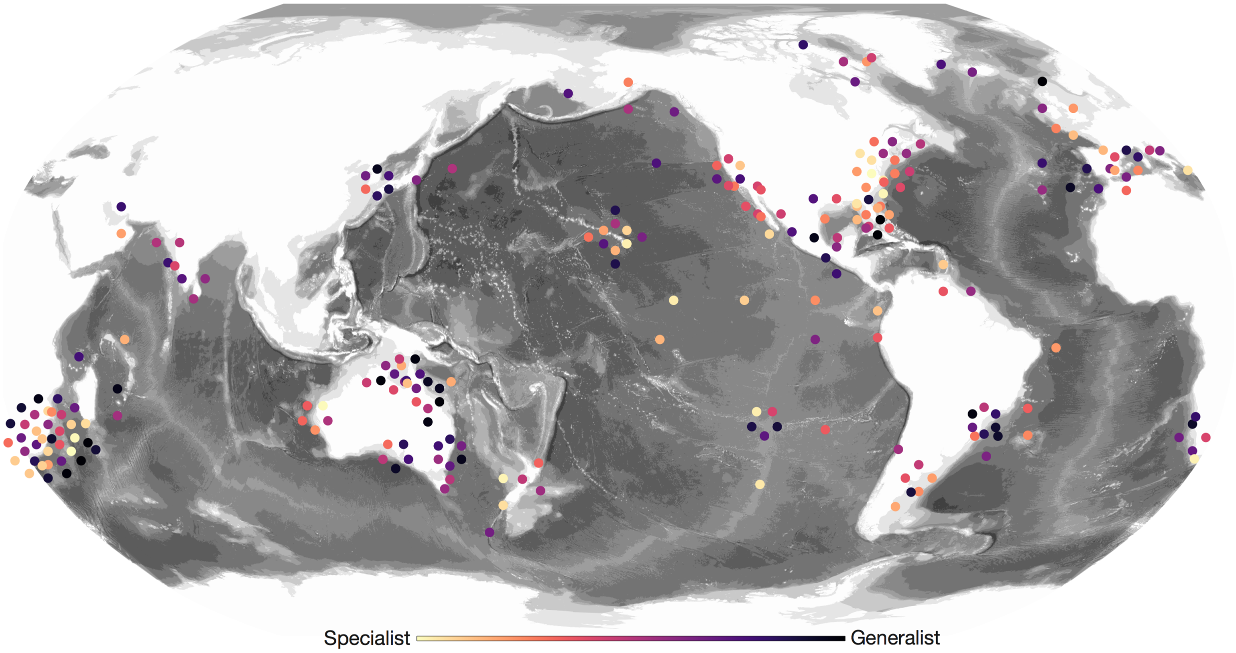


Figure 2.1 Map of stomach content sampling locations (*n* = 237; 118 in the northern hemisphere; 119 in the southern). Each point represents a single elasmobranch population where diet contents were reported from a minimum of 10 individuals; Levin's niche breadth for that particular population was then calculated. In cases where multiple size or sex classes were reported from a single location, niche breadth was averaged together to create one single estimate of niche per point. Levin's niche breadth was then standardized on a scale from 0 (specialist) to 1 (generalist). Locations are either reported as the latitude and longitude of capture or closest port of landing. Points are fanned out in regions with high sampling density to minimize overlap.

2.2.5 Niche calculations.

Levin's niche breadth was calculated for every predator population and then standardized on a scale from 0 (specialist) to 1 (generalist; Krebs, 2014). Course and uninformative taxonomic groups such as "Teleosts" or "Cephalopods" were removed prior to any niche calculations, as they can often make up a large proportion of the diet and skew niche to "specialize" in Teleosts (for example). Additionally, unidentified diet items such as "organic matter" or "vegetal remains", non-organic diet items such as "mud" or "pebbles", and anthropogenic pollutants such as “plastic” and “fishing nets” were excluded from niche calculations.

Niche breadth was calculated by study in order to gain an estimate of whether or not a species was generalist or specialist within the context of that study. Some studies report the diet contents of multiple different predator species. In these cases, niche was calculated for each species individually (instead of pooling diet contents of multiple predator species together) in order to prevent a bias towards specialism. Including diet items unique to one predator (*e.g.,* reef fishes for a reef shark) into the diet matrix of another predator within the same study (*e.g.*, a non-reef dwelling pelagic shark) would result in a skew towards specialism, as the pelagic shark would appear to “specialize” in non-reef fishes. As such, specialism would be artificially inflated in studies with multiple predators that report a large number of prey species. If a study reported diet contents for multiple sex, size, or age classes for one species, niche was first calculated for each sex, size and/or age class, then averaged together to obtain a single niche breadth estimate per species per study.

2.2.6 Modeling.

We first tested for linear relationships between (i) latitudinal range size and latitude (Rapoport’s rule), (ii) depth range size and latitude (“depth variant” of Rapoport’s rule), (iii) body size and latitude (Bergmann’s rule), (iv) body size and latitudinal range, and (v) body size and depth range.

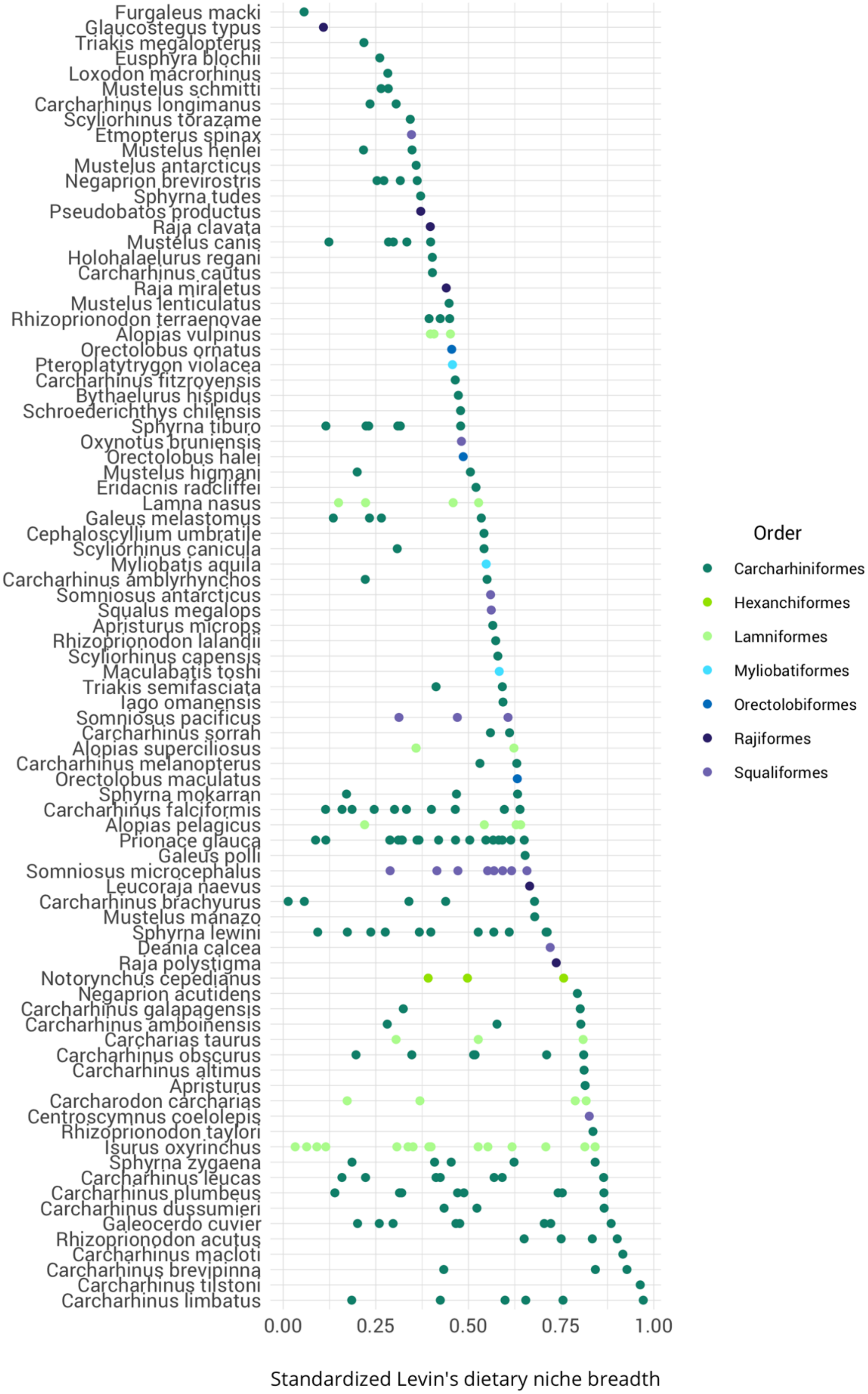
Four suites of linear models were then run in order to test the effects of (i) latitude and (ii) distance from polar edge on niche breadth per hemisphere. Hemispheres were analyzed separately because (i) the expected relationship between niche breadth and latitude is non-linear across both hemispheres and (ii) because the large difference in land and sea surface area causes marked contrasts in mean annual water temperature, circulation patterns, and availability of shoreline habitat between the two hemispheres, potentially influencing niche breadth in different ways (Tomczak, 2019).

The following variables were included in the full models (see above for derivation of these variables): number of non-empty stomachs sampled (to account for varying sample sizes across studies), ecosystem (*i.e.*, estuary, coastal, shelf, offshore), depth range, latitudinal range, body size, body size range (to control for size sampling bias in the dataset), functional group (*i.e.*, demersal, reef-associated, benthopelagic, pelagic), and clade (taxonomic groups A through J, with A being the oldest and J being the youngest). Prior to model selection, we first tested for correlations between continuous variables using the Spearman correlation coefficient and for multicollinearity in the dataset using variance inflation factors (VIF; Craney & Surles, 2002). With the exception of the body size and size range pair of variables, any highly correlated (Spearman > 0.5) or highly collinear (VIF > 3.0) variables were removed from the base model of each hemisphere prior to adding interaction terms and model selection. Because clade was highly correlated with all other non-geographic predictors, separate models were run for clade. Interaction terms were then one by one systematically added to each base model using the `add1` command in base **R** in order to determine which interaction terms, if any, were significant. Significant and biologically meaningful interaction terms were then added sequentially to create the full model. Additionally, three different random effects structures were incorporated into the full models: (i) random effect for study (to account for studies that report multiple different predator species in one study location); (ii) random effect for predator species, nested within genus and family (to account for phylogenetic relatedness and species that appear multiple times in the dataset); and (iii) random effects for both study and predator species, nested within genus and family. Mixed effects models with each random effect structure were compared to a fixed effects model with no random terms. We then conducted backward stepwise model selection for each full model using the Akaike information criterion (AIC; Akaike, 1974; Zuur et al., 2009). One outlier, blue sharks (*Prionace glauca*) sampled in New Zealand waters (*n* = 23,217 stomachs sampled in one study), was identified and removed.

2.3 Results

After excluding studies that did not fit our minimum criteria, 128 elasmobranch stomach content studies remained. These studies spanned 64 years, from 1952 to 2016, and had a wide geographic coverage. Every major ocean basin was represented with a latitudinal spread of 55°S to 79°N (Fig. 2.1). Data from a total of 43,193 stomachs from 237 predator populations (*n* = 118 in the northern hemisphere, *n* = 119 in the southern) were extracted, representing 85 unique elasmobranch predator species (Fig. 2.2; Supplementary Table 3). Within these stomachs, ~5,000 prey items from 1,730 unique prey species were identified.

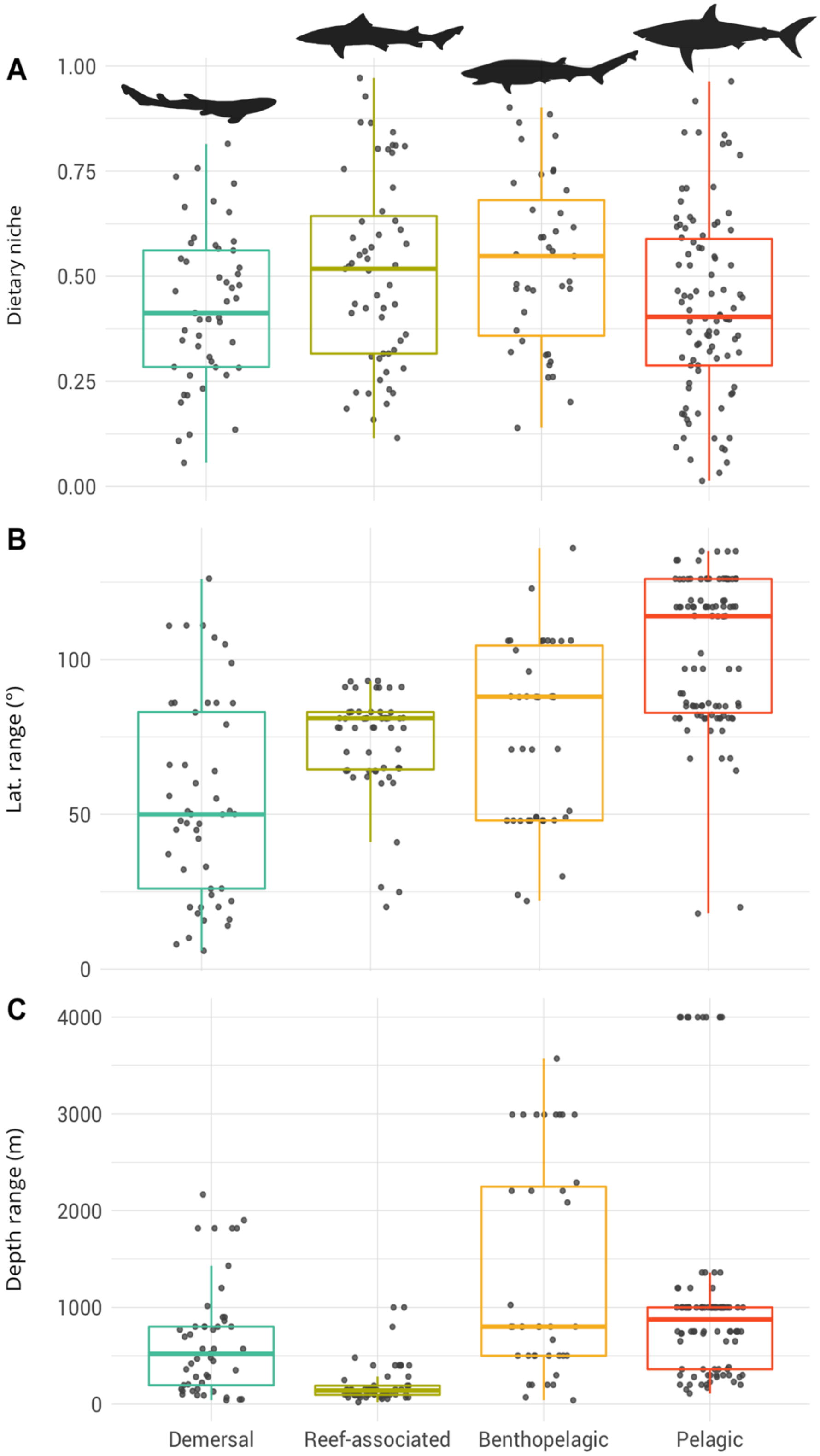
Figure 2.2 Dietary niche breadths of 85 elasmobranch species, ordered by maximum niche. Each point represents the niche of an individual population of a species. Figure includes data from both the southern and northern hemispheres.



2.3.1 Overall trends.

Sharks and batoids (skates, rays) exhibited a wide degree of dietary preferences and spanned the entire specialist-generalist spectrum. The mean niche value for both sharks and batoids was 0.47, indicating elasmobranchs as a whole cannot be broadly classified as either specialists or generalists. Among sharks, niche values ranged from a minimum of 0.01 (copper sharks *Carcharhinus brachyurus* off South Africa feeding almost entirely on pilchard; Fig. 2.2; see Appendix 4.3 for this and all following examples) to a maximum of 0.97 (blacktip sharks *Carcharhinus limbatus* off South Africa foraging on a variety of teleosts, elasmobranchs, cephalopods, and crustaceans). Among skates and rays, niche ranged from 0.1 (giant shovelnose rays *Glaucostegus typus* in Western Australia feeding largely on penaeid prawns) to 0.74 (speckled rays *Raja polystigma* in the deep waters of the western Mediterranean). Carcharhinid sharks in particular showed wide variation in niche breadth, ranging from the specialist whiskery shark (*Furgaleus macki*), which feeds almost exclusively on octopuses, to the generalist blacktip and Australian blacktip sharks (*C. limbatus* and *C. tilstoni*, respectively; Fig 2.2). There was a large spread in niche breadth even within elasmobranch functional groups (Fig. 2.3A) and across various ecosystems, with the notable exception of elasmobranchs sampled in estuarine systems, which tended to be more specialized (Fig. 2.4). No elasmobranch functional group, order, or clade appeared to exclusively occupy a specific region of the specialism-generalism spectrum (Figs. 2.3A, 2.5, 2.6), though demersal and reef-associated elasmobranchs did tend to have lower range sizes (Fig. 2.3B-C). Niche breadth did not increase or decrease with clade age (Fig. 2.6).

Figure 2.3 (**A**) Standardized Levin's dietary niche breadth, (**B**) latitudinal range in degrees, and (**C**) depth range in meters within each elasmobranch functional group. Bottom-dwelling elasmobranchs (demersal and reef-associated) overall have lower latitudinal and bathymetric ranges than benthopelagics and pelagics. Figure includes data from both the southern and northern hemispheres.



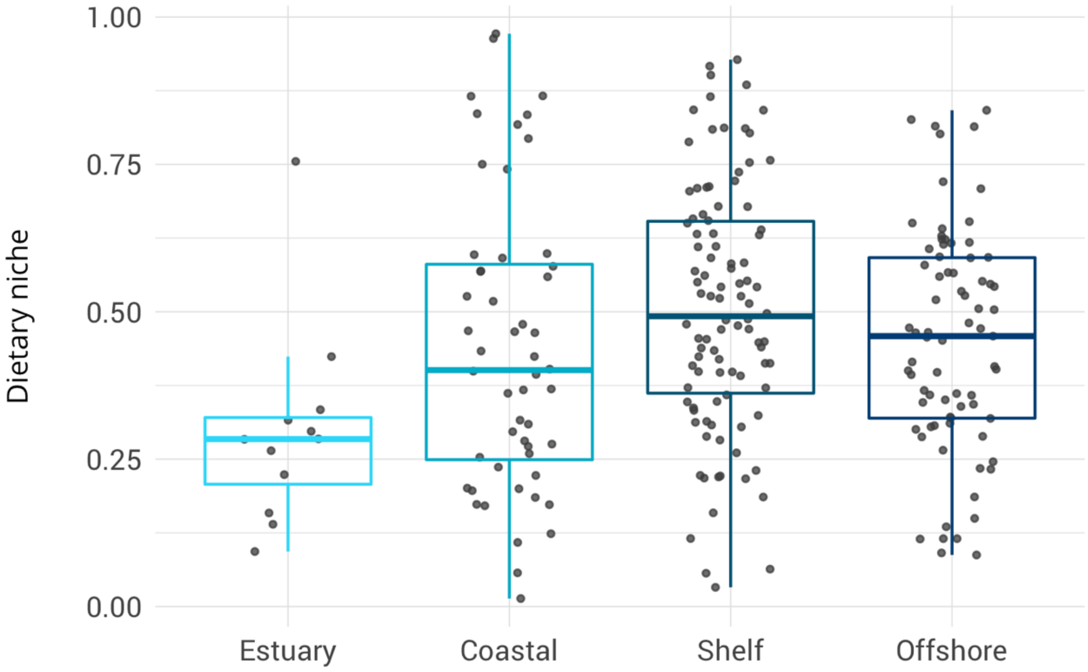


Figure 2.4 Standardized Levin's dietary niche breadth within each ecosystem. Figure includes data from both the southern and northern hemispheres.

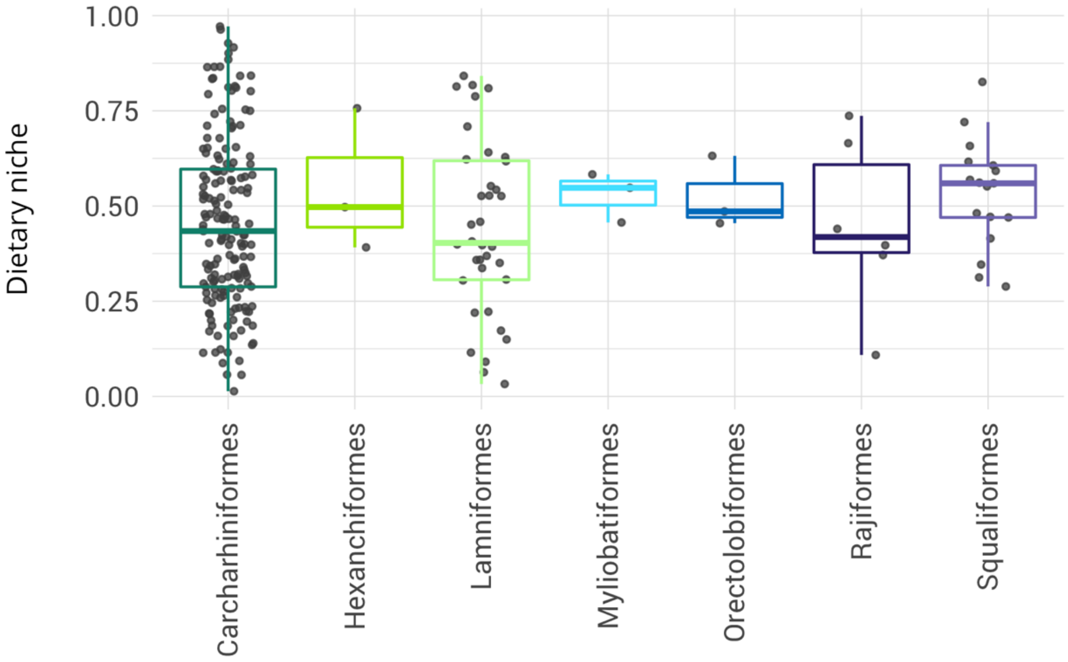


Figure 2.5 Standardized Levin's dietary niche breadth by elasmobranch order. Figure includes data from both the southern and northern hemispheres.

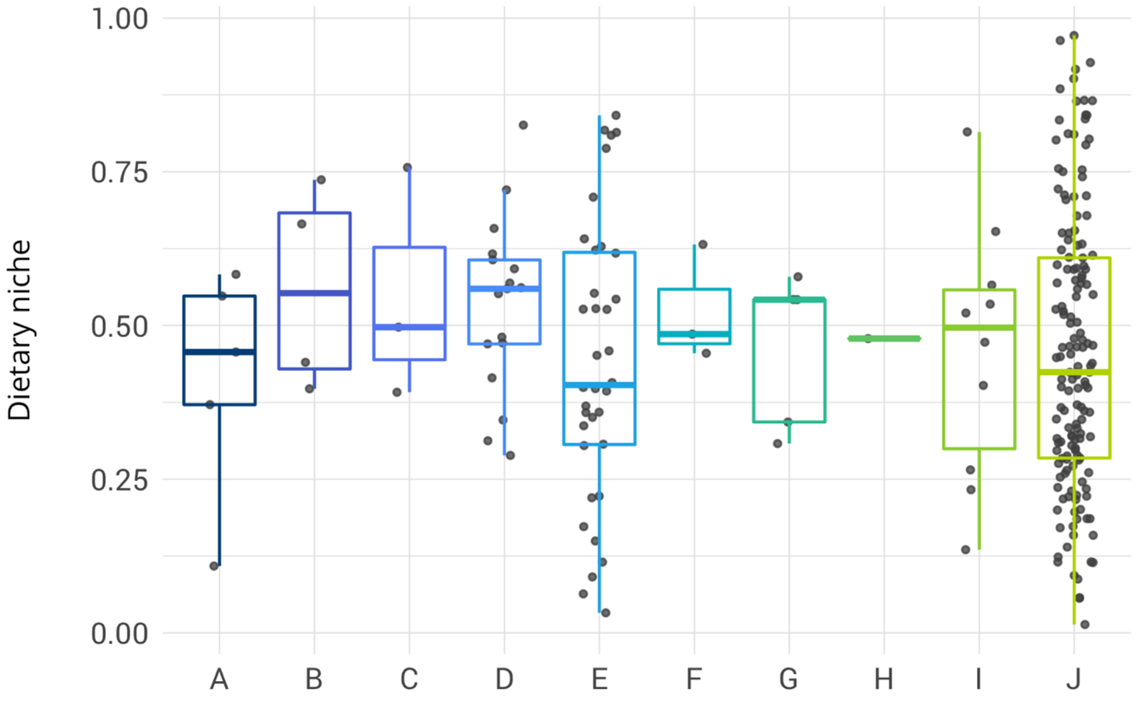


Figure 2.6 Standardized Levin's dietary niche breadth by elasmobranch clade. Clades are ordered by age, with A being the oldest and J being the youngest (see Appendix 4.2 for clade methodology). Figure includes data from both the southern and northern hemispheres.

Individual species additionally displayed varying degrees of intraspecific variation in niche breadth. Certain species tended to cluster around a specific niche breadth value, such as the common thresher (*Alopias vulpinus*; 0.36-0.45; *n* = 4), while other species showed higher variability in niche breadth, such as the porbeagle (*Lamna nasus*; 0.15-0.53; *n* = 4). The tiger shark (*Galeocerdo cuvier*), traditionally seen as a "fearless, voracious, and omnivorous" generalist (Gudger, 1949), had one of the larger niche breadth ranges in the dataset (0.20-0.89; *n* = 9). While these data indicate that tiger sharks do indeed consume a large variety of prey items (*n* = 318 unique prey items, including birds, turtles, fish, gastropods, seasnakes, crustaceans, other elasmobranchs, marine mammals, and plastics), there may be regional variation in which prey item a particular population of tiger sharks prefers. Tiger sharks caught in protective beach nets off the coast of South Africa, for example, appeared to specialize in marine mammals (Dicken et al., 2017), while tiger sharks caught in similar protective nets off the coast of Queensland, Australia, specialized in Hydrophiid seasnakes, with approximately 50% of all sharks sampled sharks having consumed them (Simpfendorfer, 1992). Similar patterns were found in shortfin mako sharks (*Isurus oxyrinchus*), bull sharks (*C. leucas*), and blacktip sharks (*C. limbatus*), among others, with niche breadth varying greatly across sampling regions (Fig. 2.2).

2.3.2 Patterns in latitude, body size, and range size.

Latitudinal range and depth range were both significantly positively correlated with body size, though which relationship was stronger differed by hemisphere. In the northern hemisphere, body size was more correlated with depth range ($p < 0.01$, $r^2 = 0.11$; Fig. 2.7B) than latitudinal range ($p = 0.02$, $r^2 = 0.05$; Fig. 2.7A), while in the southern hemisphere, body size was more strongly correlated with latitudinal range ($p < 0.01$, $r^2 = 0.33$; Fig. 2.7A) than depth range ($p = 0.01$, $r^2 = 0.05$; Fig. 2.7B). Body size increased with latitude as predicted by Bergmann's rule, with the effect being stronger in the northern hemisphere ($p < 0.01$, $r^2 = 0.25$; $p = 0.1$, $r^2 = 0.02$; for the northern and southern hemispheres, respectively; Fig. 2.8). The hypothesis that range size increases with latitude (Rapoport's rule and depth variant Rapoport's rule) is weakly supported in these data and was strongest for depth range in the northern hemisphere ($p = 0.03$, $r^2 = 0.04$; Fig. 2.9). Rapoport's rule (both latitudinal and depth variants) was strongest in Lamniform sharks (Fig. 2.9).

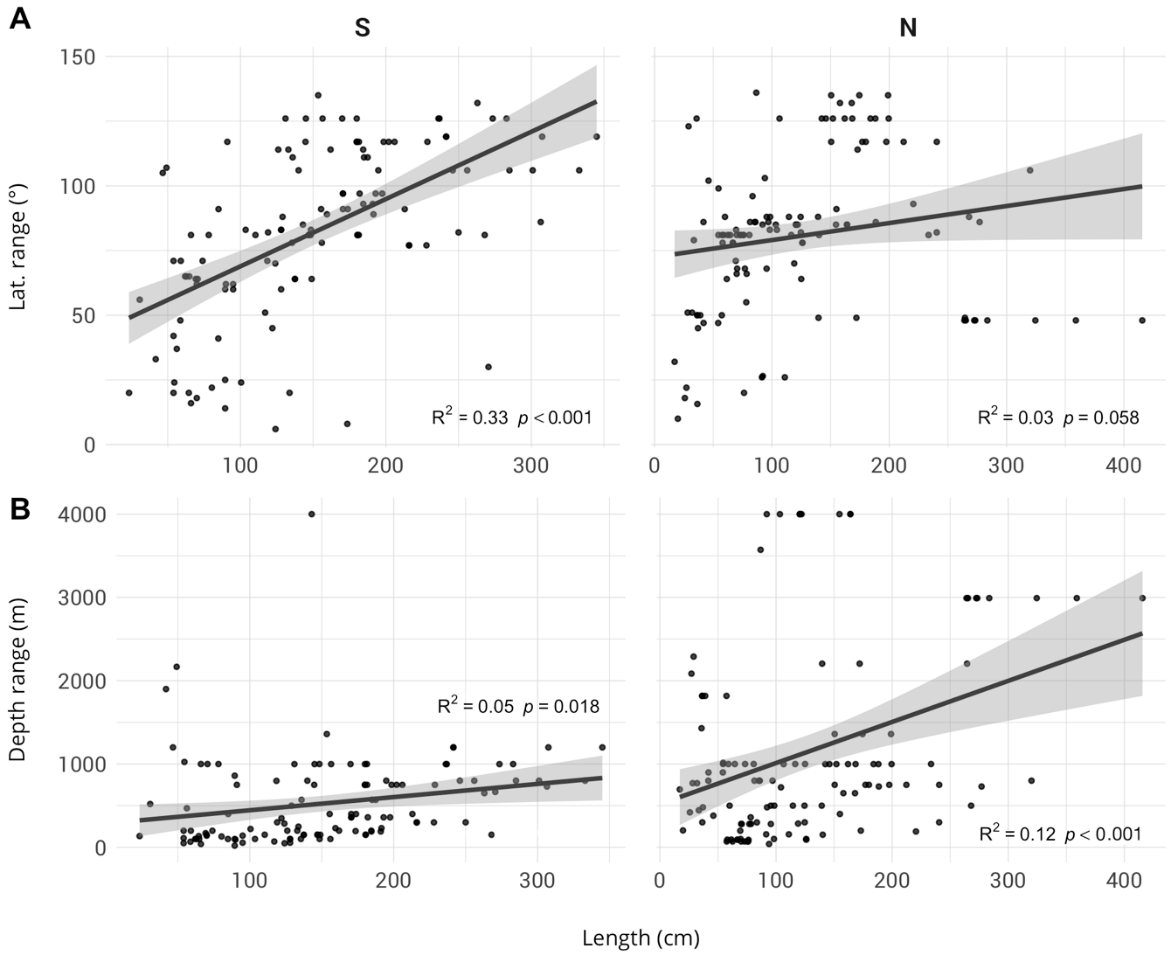


Figure 2.7 Body size versus (**A**) latitudinal range and (**B**) depth range in the southern (S) and northern (N) hemispheres.

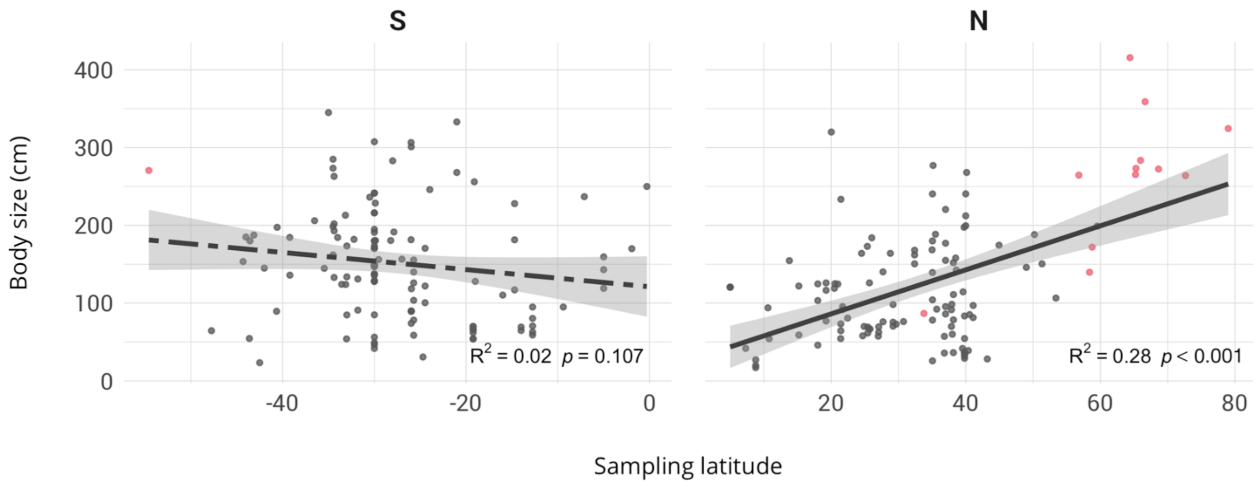


Figure 2.8 Latitude versus body size in the southern (S) and northern (N) hemispheres. Sleeper sharks (Somniosidae), which attain some of the largest body sizes among elasmobranchs and occur in high latitudes, are highlighted in pink. Bergmann's rule predicts that body size will increase with latitude.

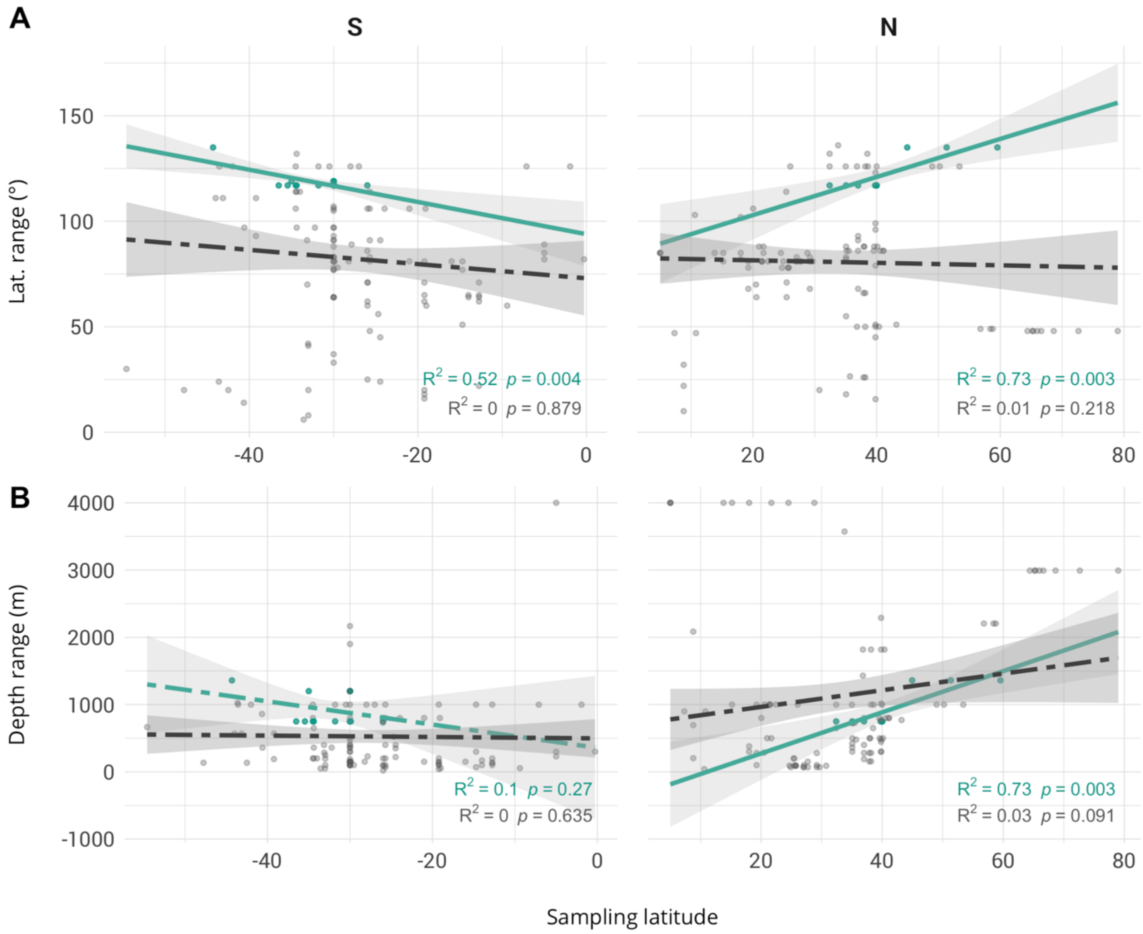


Figure 2.9 Rapoport's rule (**A**) and depth variant of Rapoport's rule (**B**) in the southern (S) and northern (N) hemispheres. Endothermic Lamniform sharks (highlighted in teal) show a stronger relationship between sampling latitude and range size. Rapoport's rule predicts that range size will increase with sampling latitude.

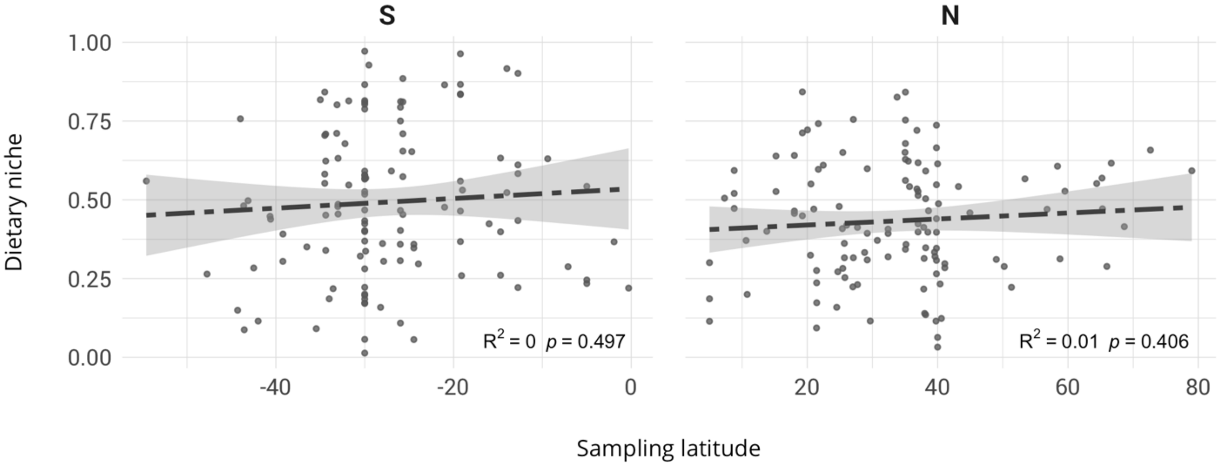


Figure 2.10 Standardized Levin's niche breadth versus sampling latitude in the southern (S) and northern (N) hemispheres.

2.3.3 Model results.

Our model results did not support the latitude-niche breadth hypothesis in either hemisphere (Tables 1, 2; Fig. 2.10). After controlling for other variables, species sampled closer to their polar range limit had wider niches, indicating that the "distance from polar edge" hypothesis had weak but significant support in both hemispheres (Tables 1, 2; Figs. 2.13, 2.14). Sample size had a significant negative correlation with niche breadth in all models. This significant relationship indicates caution should be taken when interpreting dietary niche results in the literature. By including sample size in our models, we "correct" for this effect, thus variation in niche breadth caused by other variables reflects true relationships. Overall trends were similar across both hemispheres in all other variables (Tables 1, 2), with body size, depth range, ecosystem, and functional group appearing in the best-fit models for both the northern and the southern hemispheres. Final best-fit models retained these terms even when smaller sample sizes (<100 non-empty stomachs) were excluded (Appendix 4.5). Clade was a poor predictor of niche breadth across all models (Appendix 4.6). In all cases, inclusion of any random effects structure led to minimal differences in fit compared to the base linear model with no random effects (Tables 1, 2).

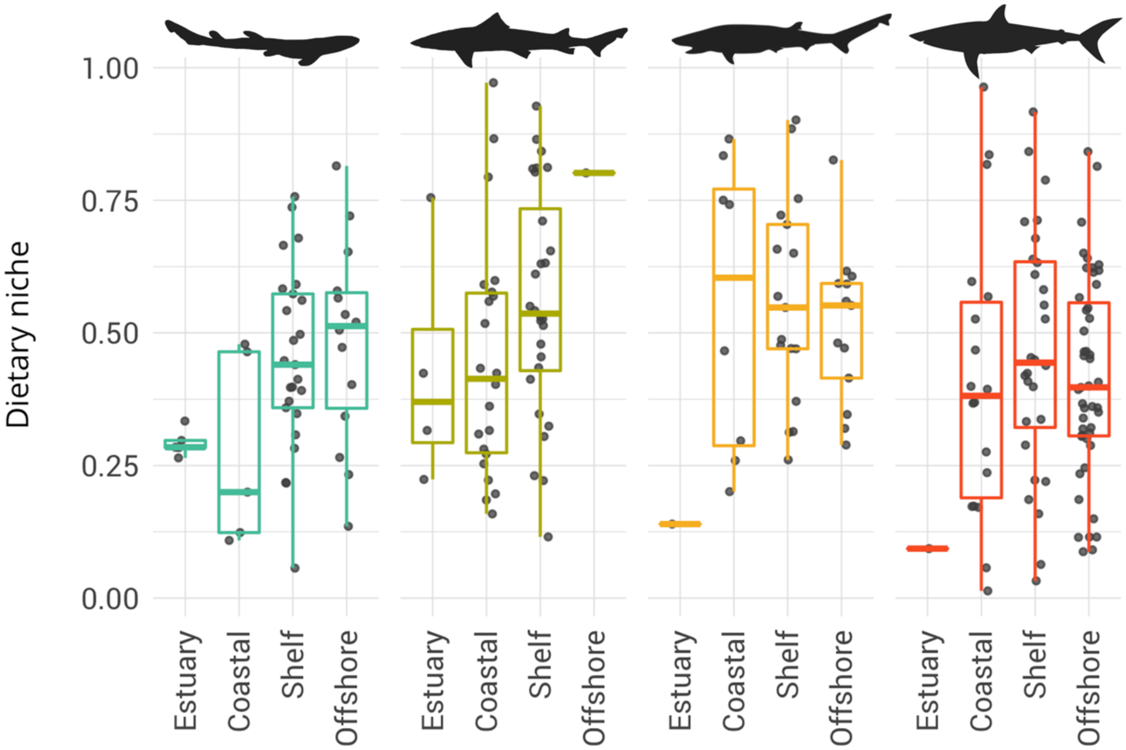


Figure 2.11 Ecosystem depth versus niche breadth within each functional group (colored groupings from left to right: demersal, reef-associated, benthopelagic, and pelagic). Distance from shore has a stronger positive relationship with niche breadth for bottom-dwelling (demersal and reef-associated) elasmobranchs than for benthopelagic and pelagic elasmobranchs. Figure includes data from both the southern and northern hemispheres.

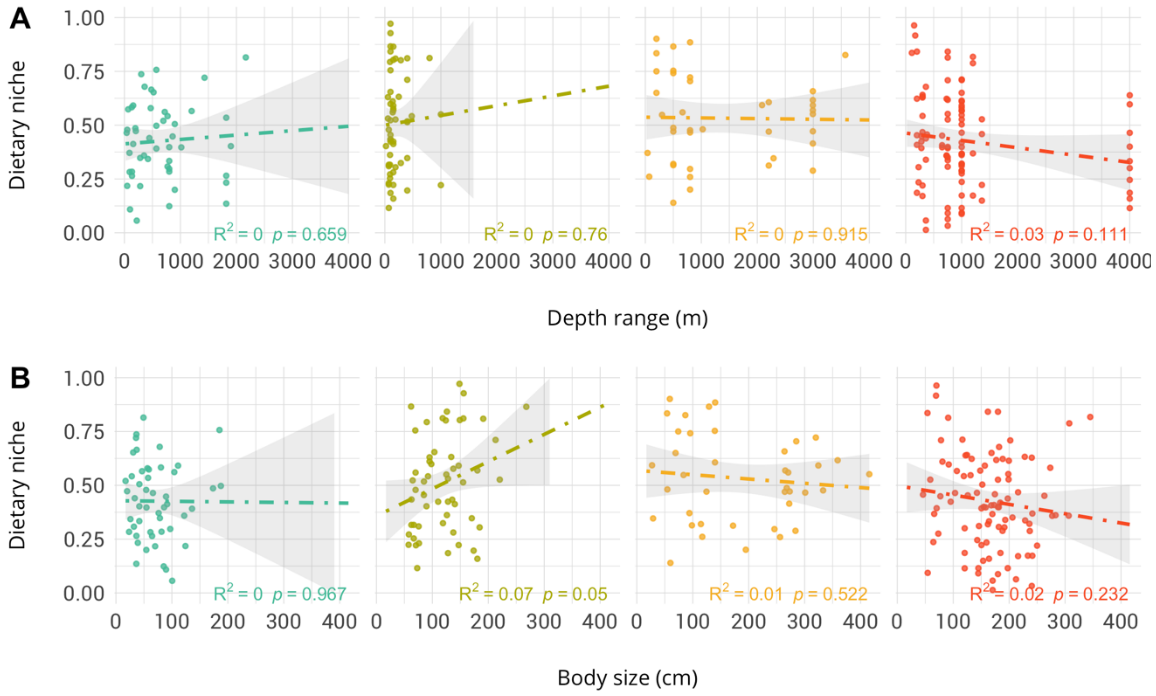


Figure 2.12 Depth range (**A**) and body size (**B**) versus niche breadth by functional group (colored panels from left to right: demersal, reef-associated, benthopelagic, and pelagic). Pelagic species grow more specialized with increasing bathymetric range (**A**) and body size (**B**). Note that while each model interaction term is significant, the effects alone are not. Figure includes data from both the southern and northern hemispheres.

Ecosystem was highly influential in both hemispheres, with niche breadth generally increasing for species sampled further from shore (Fig. 2.4); this effect was particularly strong within bottom-dwelling (demersal and reef-associated) functional groups (Fig. 2.11). Taken together, this interaction (ecosystem × functional group) highlights the importance of depth on niche breadth.

Depth range was also influential: niche breadth generally decreased for pelagic species with wider depth ranges, suggesting that pelagic species occupying a larger depth range were more specialized (Fig 2.12A; note that while the model interaction terms are significant, the effects alone are not). Finally, functional group, ecosystem, and depth range all significantly interacted with body size. In both the northern and southern hemispheres, pelagic species grew more specialized with increasing body size (Figs. 2.12B, 2.13, 2.14). The direction of the body size × ecosystem and body size × depth range relationships, however, differed by hemisphere (Figs. 2.13, 2.14).

Table 1. Four best-fit linear models applied to northern hemisphere dietary niche breadth. *N* = 118

Expression	**df (df resid)**	**AIC**	**ΔAIC**	**R^2**
ss + dpe + s + lr + dr + e + fg + e:fg + e:lr + e:dr + s:fg + s:dr + s:lr + s:e + dpe:lr + RE(Study)	36 (82)	-119.5	—	0.75
ss + lat + long + s + sr + lr + e + fg + e:lr + e:fg + s:fg + s:lr	29 (89)	-118.5	1.0	0.62
ss + lat + long + s + sr + lr + e + fg + e:lr + e:fg + s:lr + s:fg + RE(Study)	30 (88)	-116.3	3.2	0.61
ss + dpe + s + lr + dr + e + fg + e:fg + e:lr + e:dr + s:fg + s:dr + s:lr + s:e + dpe:lr	35 (83)	-116.5	3.0	0.64

ss, sample size; dpe, distance to polar edge; s, predator size; sr, predator size range; lr, latitudinal range; dr, depth range; e, ecosystem; fg, functional group; long, sampling longitude; lat, sampling latitude; RE(Study), study as random effect.

Table 2. Four best-fit linear models applied to southern hemisphere dietary niche breadth. *N* = 119

Expression	**df (df resid)**	**AIC**	**ΔAIC**	**R^2**
ss + dpe + s + sr + dr + e + fg + s:d + s:fg + s:dr + fg:dr	23 (96)	-67.0	—	0.60
ss + dpe + s + sr + dr + e + fg + s:e + s:fg + s:dr + fg:dr + RE(Study)	24 (95)	-64.9	2.1	0.60
ss + s + sr + dr + e + fg + s:d + s:fg + s:dr + fg:dr	22 (97)	-64.8	2.2	0.59
ss + long + s + sr + dr + e + fg + s:d + s:fg + s:dr + fg:dr + RE(Study)	24 (95)	-63.4	3.6	0.62

ss, sample size; lat, sampling latitude; long, sampling longitude; s, predator size; lr, latitudinal range; dr, depth range; e, ecosystem; fg, functional group; dpe, distance to polar edge.

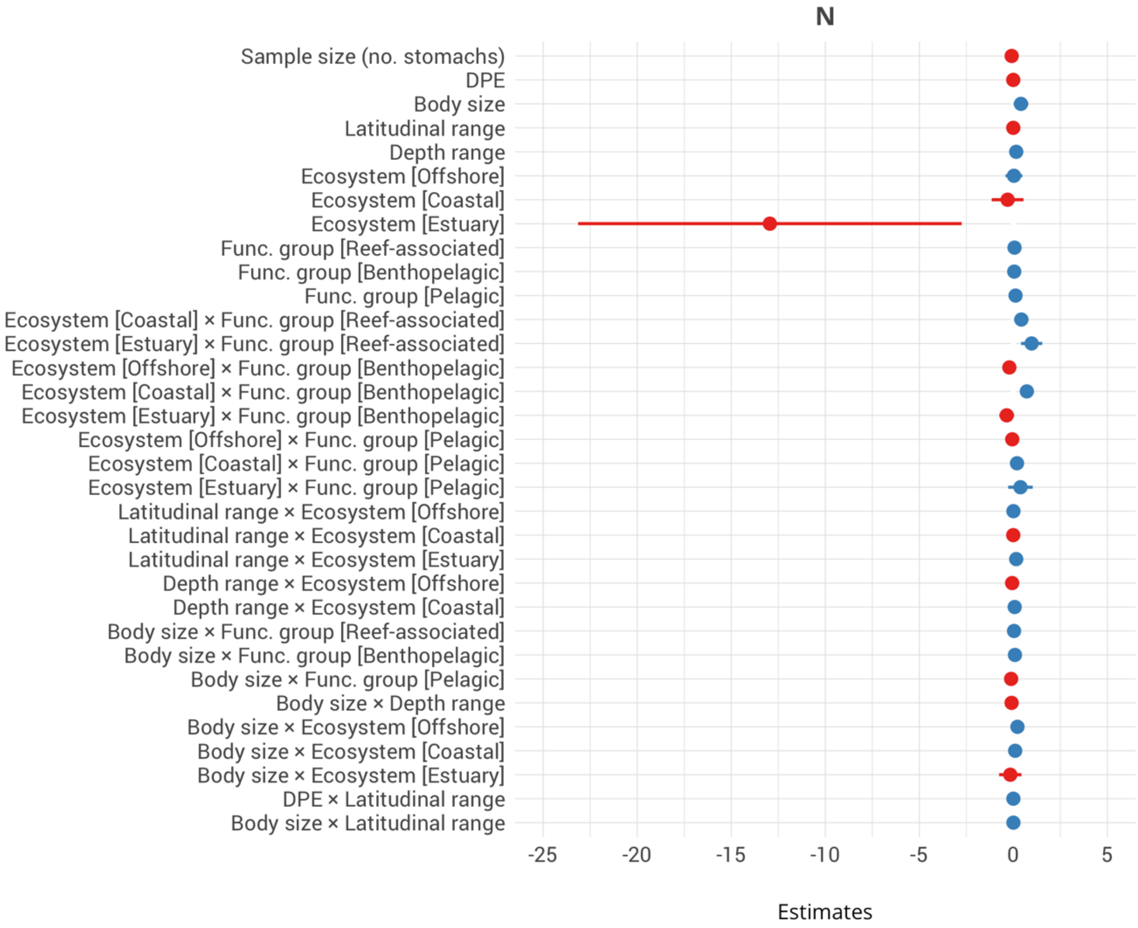


Figure 2.13 Forest plot of northern hemisphere best-fit model showing effect sizes of each model term on dietary niche breadth (DPE, distance to polar edge). Red dots indicate negative effects, while blue indicate positive. Sampling ecosystem (estuary, coastal, shelf, and offshore) has the greatest effect on niche breadth, with the effects of estuaries being particularly strong. (N = 118; R^2 = 0.75)

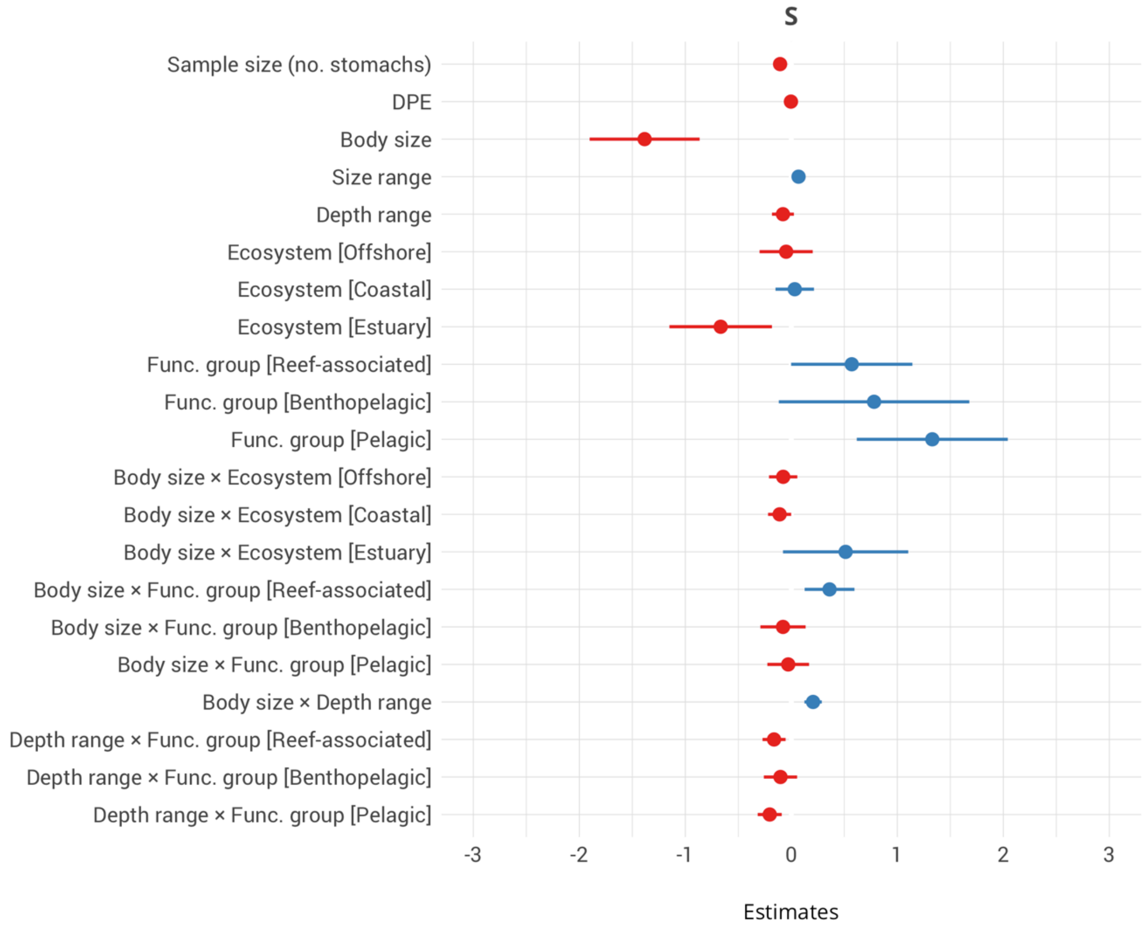


Figure 2.14 Forest plot of southern hemisphere best-fit model showing effect sizes of each model term on dietary niche breadth (DPE, distance to polar edge). Red dots indicate negative effects, while blue indicate positive. (*N* = 119; R^2 = 0.60)

2.4 Discussion

The elasmobranchs are a highly successful group of vertebrates. They have existed for roughly 450 million years, with major radiations in the Jurassic and Cretaceous producing over 1200 species of elasmobranchs today (Compagno, 1990; Stein et al., 2018). Throughout their evolutionary history, sharks, skates, and rays have repeatedly radiated, colonized, and exploited the marine environment, evolving a veritable “battery of sense organs … and diverse feeding mechanisms” to produce predators across the trophic spectrum and outcompeting bony fishes, marine mammals, and seabirds as the primary consumers of the oceans (Compagno, 1990). This immense diversity is reflected in their dietary niches, which span the entire specialist-generalist continuum across all taxonomic and functional groups of elasmobranchs (Figs. 2.3A, 2.5, 2.6). While our results highlight the great diversity of diet and life history preferences among the elasmobranchs, this diversity in niche is not explained by latitude. Overall, there is a depth, as opposed to latitudinal, gradient in elasmobranch niche breadth, whereby niche breadth generally increases with increasing depths. This depth gradient persists even after accounting for the effects of ontogenetic and/or size-based shifts in diet and is stronger in species with smaller geographic ranges and/or limited movement capabilities.

Our results suggest that niche in the marine environment may be shaped by more complex processes than those associated with latitude (Valentine & Jablonski, 2015). A major assumption of MacArthur's latitude-niche breadth hypothesis is that the environment grows thermally unstable with higher latitudes, which consequently drives the adoption of generalist survival strategies (Vázquez & Stevens, 2004). Thermal variability or instability does not follow a latitudinal gradient in the marine environment (Tomczak, 2019), and thus this major assumption of the hypothesis fails to hold true, potentially influencing our results (Valentine & Jablonski, 2015). Proximity of sampling location to the polar range limit ("distance to polar edge" hypothesis) was significant in both hemispheres, but the strength of the effect was minimal when compared to sampling ecosystem (Figs. 2.13, 2.14).

2.4.1 If not latitude, then what drives niche breadth?

Niche breadth in elasmobranchs is narrowest in estuarine, intermediate in coastal, and broadest in shelf and offshore ecosystems, respectively (Fig. 2.4). Sampling ecosystem appears to be particularly influential for bottom-dwelling elasmobranchs, with niche breadth rapidly increasing with distance from shore in demersal and reef-associated species (Fig. 2.11; "reef-associated" species include non-tropical reefs). Bottom-dwelling elasmobranchs tend to be less mobile (Compagno, 1990) and have lower depth and latitudinal ranges (Fig. 2.3), and these smaller range sizes (in comparison to pelagic species) may make it difficult to seek out specific prey items. In shallower, resource rich coastal systems, bottom-dwelling sharks may compensate for lower mobility by exploiting the greater variety of prey diversity and biomass available within a short distance. For example, common smooth-hounds off South Africa (*M. mustelus*; Sauer & Smale, 1991) and common shovelnose rays off Western Australia (*G. typus*; White et al., 2004) consumed ~15 different species, but appeared to take advantage of locally abundant Cape Hope squid (*Loligo reynaudii*) and penaeid shrimps, respectively, which drove narrower niche breadths.

In contrast, deep sea ecosystems are notably nutrient limited, and the broad niche breadths of deep-sea, bottom-dwelling elasmobranchs may reflect the paucity of available resources in these ecosystems. For example, deep sea birdbeak dogfish off Portugal (*Deania calcea*), ghost catsharks off South Africa (*Apristurus spp.*), and African sawtail sharks off Namibia (*Galeus polli*) all consumed a relatively low variety of prey ($n < 10$ species), but did not discriminate between any particular fish, cephalopod, or crustacean prey species (Ebert et al., 1996; Saldanha et al., 1995). Wider niche breadths may ultimately be a dietary adaptation in elasmobranchs with lower mobility to survive in such a prey-poor environment.

Pelagic species, with their wide-ranging life histories (Compagno, 1990) and generally larger range sizes (Fig. 2.3), do not appear to have a strong relationship between niche breadth and distance from shore (Fig. 2.11). In general, pelagic predators such as pelagic stingrays (*Pteroplatytrygon violacea*), thresher sharks (*A. vulpinus*), blue sharks (*Prionace glauca*), and silky sharks (*C. falciformis*) tended to prefer high biomass prey items such as schooling fish and swarming crustaceans. In cases where multiple different species of high biomass prey items were available, pelagic predators generally did not specialize in one over the other (for example, shortfin makos in the Sea of Korea indiscriminately consuming sardines, mullet, and mackerel; Huh et al., 2010), driving broader niche breadths within the pelagic functional group. The highly mobile life history of pelagic elasmobranchs, in combination with high biomass of preferred prey items, may reflect an opportunistic foraging strategy that is also employed by other pelagic predators (*e.g.*, Casale et al., 2008; Potier et al., 2007; Warwick-Evans et al., 2015). The influence of increasing depth and distance from shore on niche breadth, therefore, varies between bottom-dwelling and pelagic functional groups, likely as a consequence of differing life histories and foraging strategies.

Shallow, estuarine environments across both hemispheres hosted the most specialized elasmobranchs across all functional groups (Figs. 2.4, 2.11, 2.13, 2.14). Estuarine ecosystems have the highest regular nutrient input of any of the other three ecosystems (Sharples et al., 2017) and are often safe refugia for many juvenile elasmobranch species (Heupel et al., 2007; Schlaff et al., 2014), and the high degree of specialization in this ecosystem may reflect conditions favorable for primary production or ontogenetic associated dietary specialization. Many sharks sampled in estuarine waters were juveniles. This could be driving narrower niches, though adult elasmobranchs (*e.g.* adult bull *C. leucas*, bonnethead *Sphyrna tiburo*, dusky smooth-hound *Mustelus canis*, and narrownose smooth-hound *M. schmitti* sharks; Fig. 2.2) sampled in estuaries are also notably specialized, while similarly sized adult elasmobranchs in shelf or offshore ecosystems, such as the smalleye smooth-hound (*M. higmani*), starspotted smooth-hound (*M. manazo*), or bigeye houndshark (*Iago omanensis*), were more generalist. In larval teleost diets sampled across ecosystems and latitudes, larvae sampled within estuarine systems had consistently narrower diet breadths (Llopiz, 2013), suggesting that estuarine food webs promote dietary specialization regardless of consumer age class, though the author does note the limited sample size makes it difficult to draw firm conclusions. It remains unclear whether estuarine elasmobranch specialization is largely driven by age class, the ecosystem itself, or simply as an artifact of smaller sample size.

2.4.2 Effects of clade, range size, and body size.

In the tropics, niche breadth in brachyuran crabs is primarily driven by the age of the crab clade, with younger clades significantly more specialized than older clades (Papacostas & Freestone, 2016). Recent molecular work in Chondrichthyans shows that the tropics and subtropics harbor a greater proportion of older, more basal and evolutionarily distinct lineages than the poles (Stein et al., 2018). This is complemented by another recent study on marine teleost fishes showing that speciation rates are higher in the poles than the tropics

(Rabosky et al., 2018). As such, we expected a relationship between clade age, niche breadth, and latitude, but no such relationship was found. This is potentially due to the coarseness of the clade groupings in the dataset: Carcharhinids make up the entirety of clade A and constitute approximately 65% of the dataset, and as such any phylogenetic variation in niche breadth occurring within clade A would be masked. Future analyses incorporating explicit phylogenetic relationships, *e.g.* phylogenetic distance, could reveal relationships between clade, niche breadth, and geography that are not immediately apparent here.

In both terrestrial and marine systems, dietary and environmental niche breadth have generally been found to increase with geographic range size (Slatyer et al., 2013). This appears to be the case only for bottom-dwelling elasmobranchs; for pelagic elasmobranchs, niche breadth actually decreases with range size (Tables 1, 2; Fig. 2.12A). In species that tend to have lower mobility, such as bottom-dwelling sharks and batoids, a wider depth range may ultimately be of greater importance in finding a suitable amount and variety of prey. Similarly, highly localized estuarine elasmobranchs, constrained to their habitat either by specific environmental requirements (e.g., salinity or temperature; Ward-Paige et al., 2015) or small range sizes associated with the juvenile life stage (Bouyoucos et al., 2020), have a strong positive relationship between range size and niche breadth. A previous study on deep-sea skates, which also display a lower degree of mobility, found a positive correlation between niche breadth and depth range (Barbini et al., 2018). Pelagic elasmobranchs, with their contrastingly large range sizes, have narrower niche breadths across all ecosystems (Fig. 2.11), suggesting that their wide ranges may facilitate preferential prey capture, allowing them to specialize. This pattern of wide geographic ranges but narrow niches is similarly reflected in migratory whales (Prieto et al., 2017), marine turtles (Hawkes et al., 2007), and (in the terrestrial system) migratory birds that "track" their preferred niches throughout the year (Stevens, 1989; Zurell et al., 2018).

Increasing body size strengthens the range size-niche breadth relationship. Large bodied pelagics are on average more specialized than small pelagics (Figs. 2.12B, 2.13, 2.14). With reef-associated and estuarine elasmobranchs, increasing body size is associated with greater generalization (Figs 2.12B, 2.13, 2.14). It is important to note that the body size terms within each model represent actual, reported lengths from each study. As such, there are two potential, mutually non-exclusive reasons for this. First, large animals generally have larger geographic ranges (Brown et al., 1996; Pyron, 1999), and elasmobranchs are no exception to this rule (Fig. 2.7). Increasing body size, therefore, could be indicative of sampling wider ranging individuals within a particular species. Second, these results could reflect ontogenetic-associated dietary shifts occurring within the overall range size-niche breadth relationship. For example, large pelagics such as the white shark grow more specialized with age, reflecting a shift in preference from fish and cephalopod prey in juveniles to marine mammals in adults (Grainger et al., 2020; Hussey et al., 2012). Similarly, the pattern of increasing generalization with size seen specifically in estuaries could be driven by increasing dietary diversity as sharks mature, expand their localized home ranges, and explore more food options (*e.g.*, as in Galapagos sharks, Wetherbee et al., 1996; or sandbar sharks, McElroy et al., 2006).

2.4.3 Bergmann's rule and Rapoport's rule.

Overall, our results showed weak but positive support for Bergmann's rule (body size increasing with latitude; Fig. 2.8) in elasmobranchs, a result that is generally consistent with freshwater (Lindsey, 1966) and marine (Fisher et al., 2010) teleosts, but not marine bivalvles (Berke et al., 2013). Particularly striking in this trend are the deep-water and high latitude sleeper sharks (Squaliformes: Somniosidae) and the broadnose sevengill shark (Hexanchiformes: Hexanchidae), both of which are known to attain some of the largest sizes among the elasmobranchs (5.5 and 3 m, respectively; Froese & Pauly, 2019). In their analysis of over 12,000 teleost body size records, Fisher et al. (2010) found that the strength of the latitude-body size relationship was strongest in the North Atlantic, with latitude explaining 50% of variation in mean lengths of North Atlantic fishes. Similarly, the relationship between body size and latitude in elasmobranchs is stronger in the northern hemisphere than the southern, largely driven by the large bodied sleeper sharks (Fig. 2.8).

Rapoport's rule (range size increasing with latitude; Fig. 2.9) received weak but positive support in elasmobranchs, with the depth variant of Rapoport's rule receiving greater support than the latitude variant, a pattern reflected in marine teleost fishes (Fortes & Absalão, 2010). The strength of the depth, over latitudinal, variant of Rapoport's rule in both teleosts and elasmobranchs supports the notion that thermocline associated temperature stratification is of greater importance than latitude in setting range boundaries in the marine environment. Temperature is highly depth-dependent in the marine environment (Tomczak, 2019), and many species are geographically limited by acute thermal boundaries (Sunday et al., 2011, 2012). Latitudinal range increasing with sampling latitude is potentially weaker in the marine environment due to the parabolic relationship between temperature variability with latitude (see "Introduction" above), which would result in the widest latitudinal ranges in temperate species. In marine teleost fishes, latitudinal range increased with latitude in all regions except for the northern Pacific and Atlantic Oceans, the Arctic, and tropical Indian Ocean (*i.e.*, the pattern was stronger in temperate regions; Fortes & Absalão, 2010). In elasmobranchs, latitudinal range was generally wider in temperate regions than in tropical or polar regions (Fig. 2.15), which may be contributing to the poor linear fit between sampling latitude and latitudinal range (Fig. 2.9A). Notably, both variants of Rapoport's rule were much stronger for the so-called "warm blooded" sharks (family Lamniformes; Fig. 2.9), suggesting that there may be variation in how universal the rule is for ectotherms vs. endotherms.

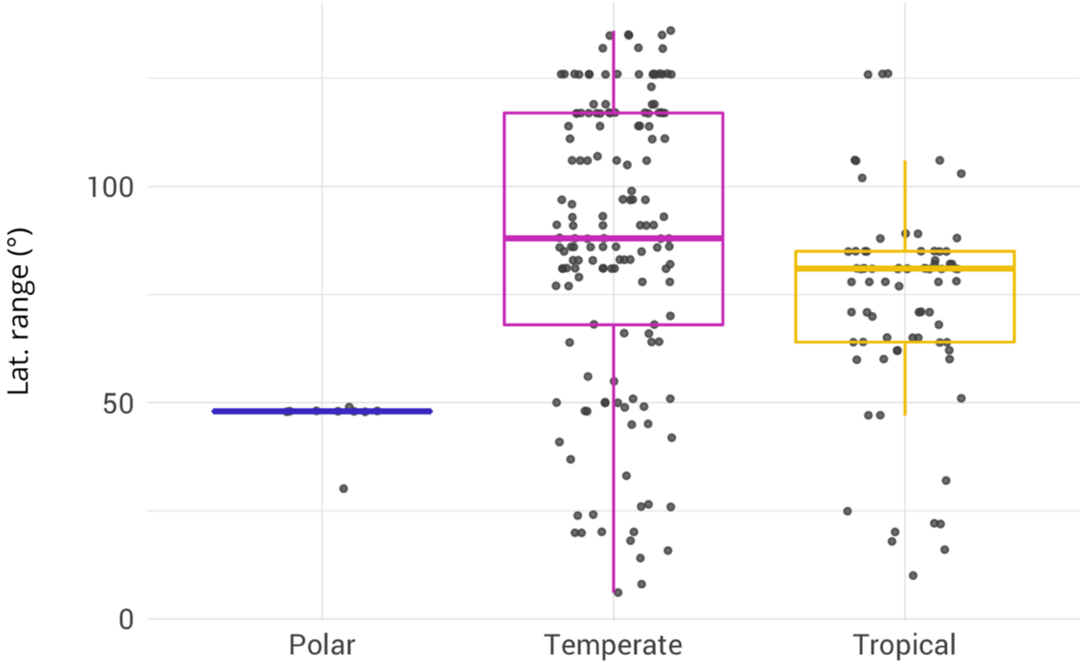


Figure 2.15 Latitudinal range is generally higher in elasmobranchs sampled in temperate regions than tropical or polar regions. Regions were categorized as "polar", "temperate", and "tropical" according to the Marine Ecoregions of the World (MEOW) classification scheme. Figure includes data from both the southern and northern hemispheres.

For both Bergmann's rule and Rapoport's rule (depth variant), the strength of the relationship was stronger in the northern hemisphere than the southern (Figs. 2.8, 2.9). The northern hemisphere has a greater ratio of landmass to water. As a result, seasonal temperatures are more variable in the northern hemisphere, because there is less water to buffer seasonal thermal variability (Ghalambor, 2006; Sunday et al., 2011). The northern hemisphere also receives a greater amount of freshwater input from these landmasses, resulting in a stronger thermohalocline (de Vernal & Hillaire-Marcel, 2000; Knutti et al., 2004; Warren, 1983). Stronger thermal boundaries in the northern hemisphere may therefore be causing these hemispheric differences in both Bergmann's rule and depth variant Rapoport's rule.

2.4.4 Conservation implications.

2.4.4.1 Estuaries.

Estuaries are globally threatened habitats that are being lost at elevated rates to coastal development (Kennish, 2002; Polidoro et al., 2010), with multiple estimates indicating that over 50% of coastal wetlands have been lost since 1900 (Davidson, 2014; Li et al., 2018). These habitats serve as important refugia and nursery areas for a variety of species (Beck et al., 2001; Nagelkerken et al., 2008) and harbored a greater proportion of elasmobranch specialists than any other ecosystem in this study (Fig. 2.4). Our results suggest that estuaries may serve as important provisioning sites for both juvenile and adult elasmobranchs, particularly for species that rely on crustaceans for sustenance (Whitfield, 2017). In Hawaii, alpheid shrimps constituted a major dietary component for critically endangered scalloped hammerhead (*Sphyrna lewini*) shark pups sampled in an estuary, with 76% of sampled individuals having consumed them (Clarke, 1971). Similarly, 67% of juvenile sandbar (*C. plumbeus*) sharks sampled in wetlands of the eastern United States had consumed blue crabs (*Callinectes sapidus*; Medved et al., 1985), indicating that estuaries may fulfill important dietary needs for early life stage elasmobranchs that typically spend their adult lives further from shore (Whitfield, 2017).

Specialization in estuaries was not only limited to young-of-the-year or juvenile elasmobranchs. Specialized adults included the endangered narrownose smoothhound (*M. schmitti*) in Patagonian waters, where roughly half of all individuals sampled had consumed either the Argentine stiletto shrimp (*Artemesia longinaris*) and/or a species of Patagonian crab (*Cyrtograpsus angulatus*; Chiaramonte & Pettovello, 2000; Molen & Caille, 2001); in the waters off Long Island, USA, dusky smoothhounds (*M. canis*) exhibited a preference for *Libinia spp.* spider crabs and Atlantic rock crabs (*Cancer irroratus*; Montemarano et al., 2016). Between half to three quarters of all bonnetheads (*S. tiburo*) sampled in the Gulf of Mexico had eaten blue crabs (*C. sapidus*) and seagrasses, indicating that for at least one species in this study, estuaries provided not only important crustacean food sources, but vegetation too (Cortes et al., 1996; Hueter & Manire, 1994).

Three out of the eight species sampled in estuaries are currently listed as either vulnerable, endangered, or critically endangered on the IUCN Red List (*C. plumbeus*, *M. schmitti*, and *S. lewini*, respectively; IUCN, 2020). Specialists in particular are more at risk to ecosystem perturbation and extinction than generalists (Boyles & Storm, 2007; Graham et al., 2011; Munday, 2004; Pratchett et al., 2006), and the combination of Red List status with specialist life histories suggests that estuarine elasmobranchs may be particularly vulnerable to habitat loss. This vulnerability additionally does not appear to be limited to one particular age class of elasmobranchs. Given this, further research on the interaction between dietary specialization and habitat loss in estuaries is warranted, as the number of studies synthesizing diet contents of estuarine elasmobranchs (*e.g.*, this study) and teleosts (Llopiz, 2013) is extremely limited.

2.4.4.2 Offshore.

In terrestrial systems, large apex predators with broad range sizes are consistently hyper-specialized carnivores (Van Valkenburgh, 2004) that experience increased extinction risk due to the combination of specific dietary requirements and reliance on large range sizes in order to hunt their prey (Middleton et al., 2020; Van Valkenburgh, 2004). It is unclear whether a similar dynamic can be generalized to the marine environment. Pinnipeds, for example, occupy the top trophic position in many marine ecosystems where elasmobranchs are not dominant (Ferguson et al., 2014), but are considered to be opportunistic, generalist carnivores overall, with the notable exception of the leopard seal (Jones & Goswami, 2010). In contrast, cetaceans with large body sizes are associated with increased dietary specialization in squid (sperm whales, family Physeteroidea) and marine mammals (orca, *Orcinus orca*; Slater et al., 2010). Large, top trophic level elasmobranchs (*e.g.*, adult white, porbeagle, or shortfin mako sharks) in this study follow a similar trend and grow more specialized with increasing body and range size (Appendix 4.3).

If wide-ranging and large-bodied marine carnivores follow similar dynamics as on land, contracting range sizes may have a particularly strong negative impact on large, specialist sharks. Such range contractions could come about as a result of climate change (García Molinos et al., 2016; Perry et al., 2005), either due to warm waters pushing polewards and reducing habitat for cold-water species (Fossheim et al., 2015) or due to deoxygenation reducing available habitat in warmer regions (Storch et al., 2014). This, in combination with intensive and growing offshore fishing effort, could effectively reduce foraging space for pelagic species even in seemingly untouched offshore ecosystems (Coulter et al., 2020; Queiroz et al., 2016). Over the last twenty years alone, global fishing fleets have encroached upon 24% of the mean monthly space use used by pelagic sharks, with that number increasing to 64% for internationally protected species (Queiroz et al., 2019), effectively contracting range size by 24-64% via fishing induced mortality. This is of particular concern for certain species that specialize in food items that humans also target. For example, porbeagles, listed as globally vulnerable by the IUCN, specialize in mackerels (*Scomber scombrus* and *Trachurus spp.*; Ellis & Shackley, 1995; Horn et al., 2013), which are commonly targeted by commercial fisheries (Froese & Pauly, 2019); the North Atlantic population of shortfin makos, listed as endangered, specialize in mackerels and bluefish (*Pomatomus saltatrix*; Stillwell & Kohler, 1982; Wood et al., 2009), which has historically been overfished in the region (Wood, 2013). Similar results have been found for blue whales, where foraging range has contracted due to a combination of reduced krill density and avoidance of vessel interactions, thus resulting in negative consequences for fitness (Guilpin et al., 2020). Given the impacts of range contraction on terrestrial specialist carnivores (Middleton et al., 2020), there is the potential that range size dynamics in combination with unprecedented levels of offshore fishing pressure (Coulter et al., 2020) could result in similarly negative impacts for dietary specialists in the marine environment.

2.4.5 Greater macroecological implications.

Depth is the greatest predictor of biodiversity in the marine environment: diversity steadily declines with depth in the world's oceans (Costello & Chaudhary, 2017; Gagné et al., 2020). Elasmobranch diversity and abundance is no exception (O' Hea et al., 2020; Priede et al., 2006). Elasmobranch niche breadth, similarly, follows a depth gradient, with a greater proportion of specialists inshore and generalists offshore (Fig. 2.4). Temperature is strongly depth-dependent in aquatic environments (Tomczak, 2019), with depth conferring far more thermal variability than altitude in terrestrial systems, and the relationship between depth, diversity, and niche breadth adds to the growing body of evidence that thermodynamics play a major role in shaping global patterns of diversity and community composition (Brown, 2014; Sunday et al., 2012).

While elasmobranch niche breadth does not vary with latitude, the depth gradient in niche breadth suggests that the "stability" component of MacArthur's latitude-niche breadth hypothesis may be supported in part. Marine biodiversity peaks not where the absolute value of primary productivity or temperature is highest throughout the year, but in regions where the yearly variability in both is minimal (Valentine & Jablonski, 2015); *e.g.*, in shallow tropical seas and mesopelagic (400-500 m) depths (Costello & Chaudhary, 2017). After excluding large pelagics that "track" their preferred niches (See "Effects of clade…" above), some of the most specialized elasmobranchs occur in regions where both temperature and nutrient inputs throughout the year are steady, such as in tropical estuaries (*e.g.*, juvenile pigeye sharks *Carcharhinus amboinensis* in the Gulf of Carpentaria, Australia) or the midwater Mediterranean (*e.g.*, blackmouth catsharks *Galeus melastomus* in the Ionian Sea). Temperate seas with seasonal changes to the thermocline and patchy distribution of nutrients, in contrast, host some of the more generalist elasmobranchs, such as in coastal upwelling regions (numerous carcharhinids off the coast of Natal, South Africa), while deep water polar seas fall somewhere in the middle (*e.g.*, Greenland sharks *Somniosus microcephalus* throughout the subarctic). It is possible that the interaction between thermal and productivity stability of the former ecosystems promotes specialization, though there are always exceptions to the rule (*e.g.,* generalist milk sharks *Rhizoprionodon acutus* in the Gulf of Carpentaria). Future research exploring depth-niche breadth gradients should explicitly account for ecosystem stability in order to determine whether specialization co-occurring with depth-based ecosystem stability is a rule that can be generalized across all oceans.

Similarly, the “distance to polar range edge” hypothesis may not be very influential for marine niche breadth as it does not account for any depth component. In terrestrial lepidoptera, populations of a given species colonizing the polar edges of their ranges have wider niches than populations located more centrally within their range (Lancaster, 2020). Given range limits are more often set by thermal boundaries than latitude in the marine environment (Fredston-Hermann et al., 2020; Sunday et al., 2011, 2012), a more appropriate measure of marine niche-range edge dynamics would incorporate proximity to thermal barrier. Such experiments are now possible with the deployment of telemetry technology in conjunction with traditional dietary analyses (Cooke et al., 2004; Hussey et al., 2015a). For example, tagged leatherback sea turtles diving into near-freezing waters at the very limits of their thermal capabilities (James et al., 2006) may be the generalist dietary “mavericks” of their species, expanding their foraging territories to compete with oceanic sunfish (Hays et al., 2009).

Narrower niches associated with stable regions of high biodiversity ultimately suggests a weakening of species’ resource overlap and competition and strengthening of interactions as species grow more specialized (Schemske et al., 2009). While there is mixed evidence to support a latitudinal gradient in species interaction strength in the oceans (Schemske et al., 2009, but see Roesti et al., 2020), this study supports the existence of a depth gradient in marine species interaction strength. Elasmobranchs in high diversity estuarine and coastal ecosystems have overall narrower niche breadths than in lower diversity shelf and offshore systems (Fig. 2.4). Notably, this depth gradient is strongest for reef-associated species (regardless of latitude; Fig. 2.11), which live in the most complex communities of the oceans, suggesting that deeper, less biodiverse waters free reef-associated species from resource competition. The strength of clade as a predictor for tropical crabs similarly highlights the importance of evolutionary interactions in shaping niche breadth in complex, biodiverse ecosystems (Papacostas & Freestone, 2016). Thus, interaction strength, as measured by niche breadth, likely plays a role in the maintenance of bathymetric gradients in marine biodiversity.

2.4.6 Conclusion.

The role that sharks play in their ecosystems as apex predators is clear (Burkholder et al., 2013; Heupel et al., 2014). Less clear, however, are the ecological roles of their many smaller and less well-known cousins. On an evolutionary timescale, elasmobranchs have been highly successful predators, surviving numerous mass extinction events and radiating afterwards to quickly fill any predatory niches (Compagno, 1990). Quantifying niche breadth, or interaction strength, of sharks, skates, and rays helps us to better understand how these charismatic predators contribute to the mechanisms that shape macroscale patterns of diversity in the world's oceans, both today and in an uncertain future characterized by the sixth mass extinction (Dulvy et al., 2014; Schemske et al., 2009). The great variation in elasmobranch niche breadth highlights the diversity we risk losing if urgent conservation action to protect elasmobranchs is not taken, but also highlights a bright spot: the wide range of niche breadth across taxonomic groups, functional groups, ecosystems, and regions is a testament to how truly adaptable sharks and batoids are on an evolutionary time scale.

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CHAPTER 3

General Discussion

The cause of the latitudinal gradient in biodiversity remains an enigma in the field of ecology that has persisted since first incorporated into the scientific literature over 200 years ago (Brown, 2014; Kennedy & Norman, 2005; Pennisi, 2005; von Humboldt, 1808). While notable progress has been made in terrestrial ecosystems (Brown, 1999), a general explanation for latitudinal gradients in biodiversity remains elusive, and must incorporate both terrestrial and marine systems in order to present a holistic theory for the entire earth. Patterns and processes of biodiversity are especially difficult to monitor in the oceans, which are enormous, complex, and highly dynamic. It is only with the recent development of global, large scale datasets that robust biogeographical studies incorporating marine gradients have become possible (*e.g.*, Gagné et al., 2020).

This thesis presents the most comprehensive estimates to date of diet and dietary niche across the elasmobranch clade, incorporating stomach content data from sharks, skates, and rays across coastal, deep-water, and offshore ecosystems around the globe. While the ecological role of larger, more charismatic sharks has been studied in detail (Burkholder et al., 2013; Heupel et al., 2014; Hussey et al., 2015b), their many smaller and flatter cousins remain understudied. This thesis fills a gap in the literature where previously a lack of comprehensive elasmobranch diet data hampered efforts to achieve a global scale understanding of marine ecosystem interactions. Diet information is valuable in its own right, but here, I make use of dietary niche specifically in order to shed light on the biogeography of the single largest predatory clade in the oceans. The results show that with increasing distance from shore, lower mobility, bottom-dwelling elasmobranchs widen their dietary niche breadths, while wide-ranging, pelagic elasmobranchs grow more specialized with increasing body size. Conversely, species close to shore are the most specialized of all the elasmobranchs. This pattern suggests that particularly for low range size, low mobility species in highly biodiverse areas, specialization may be an adaptation to higher levels of competition (Bolnick et al., 2010). These results highlight the utility of dietary niche as a metric to test global scale hypotheses of biogeography.

A particular difficulty the field of biogeography has faced has been evolving beyond descriptive phenomena to mechanistic explanations driving biogeographic patterns (Brown, 1999; Vermeij, 2005). Seemingly simple patterns such as the latitudinal diversity gradient are the products of complex, emergent processes, and untangling the various causal factors behind this pattern requires testable hypotheses (Brown, 1999). One way to move in this direction is by studying spatial patterns of ecological interactions, as they can shed light on which biodiversity processes are shaped by abiotic versus biotic factors (Mittelbach et al., 2007; Rohde, 1992). Biotic interactions are generally believed to be important in maintaining local species diversity by expanding available niche space in a given ecosystem as species coevolve together (*e.g.*, the “Red Queen” hypothesis; Brockhurst et al., 2014; MacArthur, 1969; Thompson, 1994; Vermeij, 2005). Some examples include the evolution of new host organisms that then stimulate the evolution of new, specialized parasites (*e.g.*, parasitoid wasps, which are then themselves hosts of hyperparasitoid wasps); plants evolving chemical and physical defenses to deter herbivory, with consumers coevolving more specialized means of overcoming these defenses (*e.g.*, monarch caterpillars *Danaus plexippus*, which are immune to milkweed *Asclepias spp.* toxins); and increasingly specialized mutualistic interactions, where one species can no longer exist without the other (*e.g.*, coral or lichen symbionts). Stronger biotic interactions appear to be more concentrated around the equator, and as such it has been proposed that there is a latitudinal gradient in species interaction strength (Schemske et al., 2009). Similarly, MacArthur's (1972) latitude-niche breadth hypothesis states that niche breadth decreases with decreasing latitude, mediating high coexistence at tropical latitudes. Schemske's (2009) hypothesis of increasing interaction strength with decreasing latitude is broadly similar: narrower niches (a proxy for increased interaction strength) are more prevalent in the tropics and support greater coexistence. Niche breadth is therefore a single elegant metric to measure interaction strength that can be used to formally test biotic hypotheses of biodiversity maintenance. Dietary, or Eltonian, niche is particularly appropriate in this context, as a narrower diet indicates greater interaction strength between consumer and prey.

Given the assumption that narrower dietary niches imply greater interaction strength, spatial patterns in elasmobranch niche breadth tentatively support certain aspects of both MacArthur's and Schemske's hypotheses; namely, that communities with high biodiversity indeed host greater niche specialization. Reef-associated elasmobranchs, which live in some of the most biodiverse and complex ecosystems on earth, show the strongest relationship between diet breadth and depth/distance from shore (Fig. 2.11), suggesting that any spatial gradients in species interaction strength are most readily observed in complex ecosystems. Reef complexity and biodiversity attenuate with depth, and reef elasmobranchs consequently grow more generalized. Pelagic ecosystems are uniformly less diverse than reef ecosystems, both in terms of species and habitat composition – there is no substrate to interact with, thus removing a major driver of complexity and competition (Friedman et al., 2020). Pelagic species are then potentially freed from any depth gradient in species interaction strength, and this is reflected in their lack of a niche-depth gradient (Fig. 2.11). Specialization in elasmobranchs therefore appears to be primarily driven by the intensity of competition, with the greatest competition in shallow benthic ecosystems. Even in cases where population level niche of coastal elasmobranchs appears to be generalist, for example, individual specialization is thought to be a mechanism by which species with similar diets and life histories can coexist in highly biodiverse ecosystems characterized by elevated levels of competition (*e.g.*, Matich et al., 2011; Vaudo & Heithaus, 2011).

If elasmobranch specialization is primarily driven by competition in biodiverse habitats (*i.e.*, the coastal benthos), it follows that species in the biodiverse tropics should be more specialized than temperate and polar species. This is not the case, as these results show no latitudinal niche gradient (Fig. 2.10). A potential explanation for this is that prey availability (*i.e.*, biomass) interacts with biodiversity to influence niche breadth: marine biomass does not decrease with latitude, but it does with depth (Jennings et al., 2008; Wei et al., 2010). This lends support to the hypothesis that deep-water, benthic elasmobranchs are generalists in regions with low prey availability. Assembling robust datasets of marine diversity and biomass at specific locations and depths is difficult but could be used to test the influence of prey biomass on elasmobranch niche breadth in future models.

The depth-niche breadth gradient ultimately suggests that, in elasmobranchs, large scale maintenance of biodiversity depends strongly on biotic variables (*e.g.*, mobility, range size, local scale diversity, and competition) as opposed to abiotic variables, as MacArthur originally hypothesized (*e.g.*, thermal stability in equatorial regions; MacArthur, 1972). This means that while there is support for MacArthur's hypothesis that niche breadth is narrower in more diverse communities, there is limited support for the abiotic mechanism by which MacArthur proposed niche breadth to vary. For example, despite remarkable thermal stability, elasmobranchs in the deep sea are not particularly specialized (Fig. 2.11). Including more precise climatic variables, such as yearly mean and range in temperature at each sampling location and depth, would shed light on how influential abiotic factors are compared to biotic interactions.

3.1 Only one piece of the marine environment

Two major caveats prevent the generalization of the depth-niche breadth gradient across all regions and predatory taxa in the oceans: first, tropical and polar areas are undersampled relative to temperate areas, and second, while elasmobranchs are the largest predatory clade in the oceans, other predatory clades including large teleosts, cetaceans, and pinnipeds are excluded from this thesis.

The biological sciences have been and continue to be a colonial endeavor, with scientific resources, and thus scientific data, concentrated in the majority white, colonial powers of Europe, the United States, and Australia. The marine sciences are no exception, with a tendency of conducting "parachute science," wherein comparatively wealthy scientists from the global north voyage to equatorial and polar regions to conduct fieldwork but fail to invest in meaningful scientific relationships at the local level (David-

Chavez & Gavin, 2018; de Vos, 2020).[1] Today, most resources on tropical diversity are relegated to museum collections from these parachute expeditions, while tropical scientists remain understaffed and underfunded (Rodriguez et al., 2007). This bias is reflected in the sampling coverage of this dataset, with the tropics and poles underrepresented compared to mid-latitude sites (Fig. 2.1). I acknowledge that the conclusions this thesis draws regarding latitude are predicated on this spatial bias. Researchers studying marine latitudinal gradients in the future should seek to expand their networks to include local scientists and knowledge holders in the tropics and poles wherever possible, both to strengthen ecological findings and bring a greater diversity of thought into the field.

In order to advance our global scale understanding of marine food webs, sampled predators should ideally include representative taxa from all major predatory clades in the oceans, *i.e.*, other elasmobranchs, piscivorous teleosts, cetaceans, and pinnipeds. Critically endangered elasmobranch taxa are excluded from this dataset due to low sample sizes (*e.g.*, sawfishes, order Rhinopristiformes, or angelsharks, order Squatiniformes), while less charismatic taxa are understudied overall (*e.g.*, skates, order Rajidae) and are underrepresented in this thesis. Similarly, even taxa already present within this study would benefit from greater sampling. While there are some exceptions, extreme values in niche breadth (both specialists and generalists) are more prevalent in species with greater sample sizes (Fig. 2.2). Mako sharks, for example, range from 0.03 to 0.84 in dietary niche breadth, (*n* = 15); blue sharks range from 0.08 to 0.65 (*n* = 18). For a more robust

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[1] The Prussian "Father of Biogeography" himself, Alexander von Humboldt, failed to ever acknowledge the contributions of the Colombian cartographer Francisco José de Caldas, the originator of altitudinal diversity gradient maps (Caldas, 1966).

understanding of niche plasticity at the species level, greater sampling or statistical approaches that assess the sensitivity of species-level niche to sample size (*e.g.* bootstrapping) is necessary.

Predatory marine mammals, in particular, would be a valuable addition to future predator biogeography research, as they are some of the few "natural experiments" that defy the latitudinal diversity gradient, with higher species richness at higher latitudes (Brown, 2014). This pattern is potentially as a result of outcompeting elasmobranchs (Ferguson et al., 2014). If marine mammals show a similar niche gradient with foraging depth, that could strengthen the hypothesis that drivers of marine dietary breadth are truly independent of latitudinal patterns of biodiversity.

3.2 Only one piece of niche

Hutchinson in 1957 formalized the many concepts of niche into the theoretical *n*-dimensional hypervolume, which accommodates all possible niche axes – dietary, environmental, thermal, and so on – into one hypothetical space (Blonder et al., 2014; Hutchinson, 1957). Dietary niche represents only one niche axis encompassed within the *n*-dimensional hypervolume, but the most rigorous tests of niche-based hypotheses should include multiple niche axes. Additionally, dietary niche calculated as-is has some limitations. Levin's niche is a metric that efficiently summarizes dietary diversity into a single number, but this number fails to reflect changes in prey preference if the overall diversity of diet remains the same. For example, specialization from one prey item to another due to ontogenetic or behavioral changes (*i.e.*, prey switching) would not be detectable with

Levin's niche. Alternative methods, such as stable isotope analysis, can be used in conjunction with Levin's dietary niche to better understand prey switching processes, and may be of particular relevance for studying specialist predators that compete for prey items targeted by human fisheries (*e.g.*, Polo-Silva et al., 2013). Future research building off of this thesis should incorporate telemetric and isotopic niche for a more holistic approach towards understanding elasmobranch niche breadth and the associated conservation implications.

Grinnellian, or spatial, niche is most commonly determined by inferring the preferred environmental conditions of a species based on mapped occurrence records, a process that has evolved into the field of environmental niche modelling today (Grinnell, 1917; Peterson et al., 2011). Telemetry technology represents a significant step forward in this regard by allowing the animal itself to tell the researcher its preferred home ranges, temperatures, salinities, dissolved oxygen levels, and so on, via biologger (Cooke et al., 2004; Hussey et al., 2015a; Payne et al., 2014). This so-called "telemetric niche" can be used to add a spatial axis to elasmobranch niche breadth. Elasmobranchs are well-suited to such studies, being large-bodied and long-lived, though available data is currently limited to larger, more charismatic species that are both capable of bearing a biologger for an extended period of time and are popular to study (Hammerschlag et al., 2011). The Global Shark Movement Project maintains the largest available elasmobranch telemetry dataset to date, largely composed of Carcharhiniform and Lamniform sharks (GSMP; https://www.globalsharkmovement.org/). Due to time constraints, generating a standardized dataset of thermal, salinity, and dissolved oxygen conditions derived from the multiple tag types contained within the GSMP dataset proved difficult (D. Sims & N.

Humphries, *pers. comm.*). Instead, I calculated home range size (50% and 95% kernel density estimates) for 38 populations of 16 species of sharks in order to compare home range size to dietary niche breadth. Preliminary results suggest that increasing dietary niche breadth is associated with decreasing home range size (Fig. 3.1A), a result that is consistent with the negative relationship between latitudinal/depth range and dietary niche breadth in large pelagics (Figs. 2.12A, 2.13, 2.14). Future research should further explore this relationship and aim to incorporate oceanographic measurements (*e.g.*, temperature, salinity, dissolved oxygen concentration) into analyses of telemetric and dietary niche breadth.

Isotopic niche is a considerably more flexible approach for measuring both a spatial and dietary niche component, as it is inexpensive and non-lethal, and a single tissue sample provides a wealth of information on an individual. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes provide insight into foraging location and trophic position, respectively, and in combination can be used to calculate a species' niche "footprint" (*i.e.*, what it ate and where it was; Bearhop et al., 2004; Newsome et al., 2007). The Chondrichthyan Stable Isotope Data Project (CSIDP; https://github.com/Shark-Isotopes/CSIDP) maintains an isotope database from elasmobranchs sampled across the world that can complement the diet data in this thesis. Previous work using the CSIDP database explored the trophic geography of sharks by using $\delta^{13}C$ to determine which food webs sharks derive their carbon from, finding that offshore species source their carbon from mid-latitude food webs, while shelf species generally source carbon more locally (Bird et al., 2018). This work can be extended by including $\delta^{15}N$ and calculating Bayesian standard ellipse areas (SEA_B) as a proxy for niche breadth (Jackson et al., 2011). For example, isotopic niche could be used to further test hypotheses related to dietary specialization in estuarine ecosystems (*e.g.*, Shiffman et al., 2019; Shipley et al., 2019a), or to compare ecological findings obtained via traditional diet content analysis versus isotopic analysis (*e.g.*, Shipley et al., 2019b). Direct comparisons between dietary and isotopic niche have been limited; in South African elasmobranchs, the two are not always correlated (Petta et al., 2020). This is an area ripe for further research: preliminary results tentatively show that when extended to a global scale, dietary niche breadth is in fact negatively correlated with isotopic niche breadth (Fig. 3.1B).

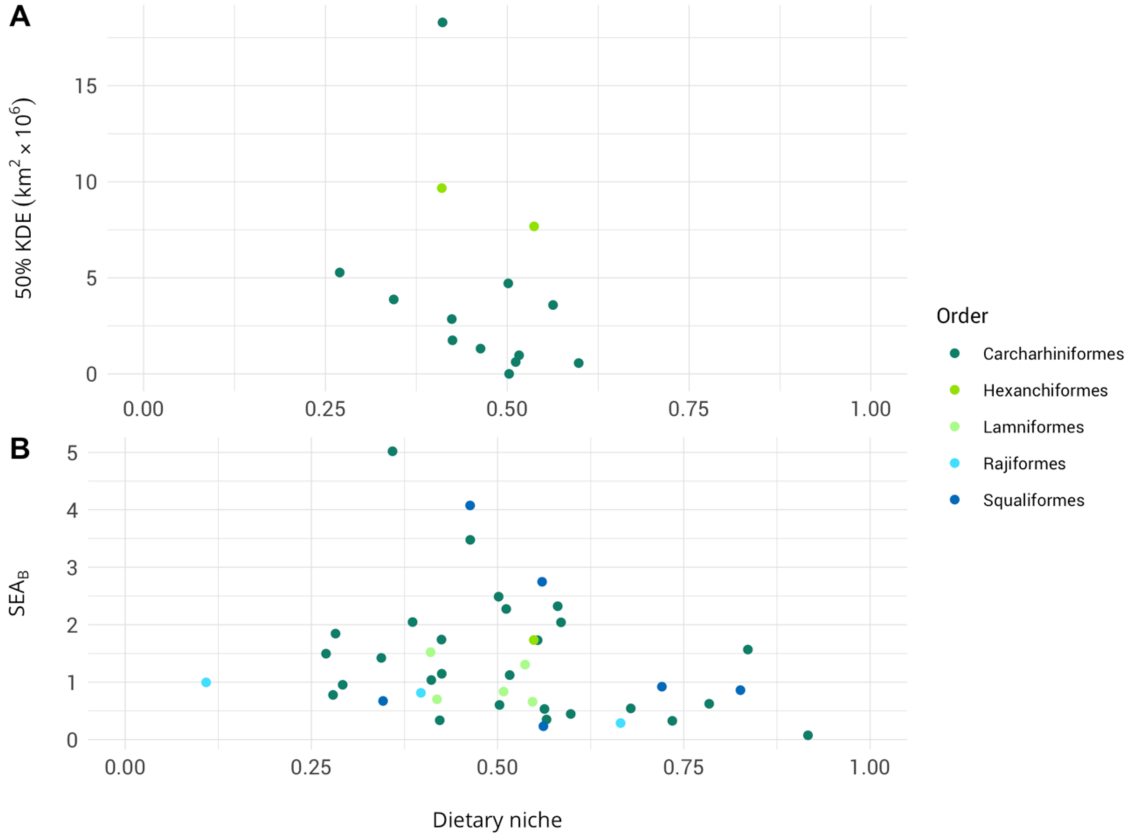

Figure 3.1 Elasmobranch standardized Levin's niche breadth ("Dietary niche") versus (**A**) telemetric niche, measured as 50% kernel density estimations (KDE) of space use (*i.e.*, home range size; $km^2 \cdot 10^6$) and (**B**) isotopic niche, measured as Bayesian standard ellipse area (SEA$_B$). Home range was calculated across the entire lifetime of the tag; SEA$_B$ was calculated in $\delta^{13}C$ and $\delta^{15}N$ isotopic space. Each point represents the mean of each niche measure (dietary niche, SEA$_B$, KDE) of a single elasmobranch species. A holistic version of niche in *n*-dimensional space ideally includes multiple metrics of niche; in this case, three axes are present. As diet breadth increases, telemetric and isotopic breadth appear to decrease. Telemetric niche (**A**) is currently limited to larger, more charismatic Carcharhiniform and Lamniform sharks, while isotopic niche (**B**) is more flexible in which species can be sampled. Figure includes data from both the southern and northern hemispheres. See Appendix 4.7 for SEA$_B$ and KDE methodology.

Modern technological advances represent exciting new opportunities in the avenue of niche research. Telemetry technology is evolving towards ever-smaller tag sizes and sophisticated, real-time data networks (Hays et al., 2016; Lennox et al., 2017), while new methods of isotope analysis are now being used to reconstruct everything from the everyday minutiae to the large scale movements of marine life (Chung et al., 2019; Trueman & St John Glew, 2019). Regarding dietary niche specifically, alternative measures of stomach contents such as camera recordings and DNA metabarcoding can be used as non-lethal methods to observe novel feeding mechanisms, confirm existing stomach content studies, and identify prey that would otherwise be difficult to identify or is quickly digested (Amundsen & Sánchez-Hernández, 2019; Papastamatiou et al., 2018; Sousa et al., 2019). Animal-borne cameras, for example, have been used to record leatherback turtles consuming a variety of jellyfish (Heaslip et al., 2012), penguins foraging under sea ice (Watanabe & Takahashi, 2013), and tiger sharks ambushing prey from above (Nakamura et al., 2011), while DNA metabarcoding has revealed the diets of European brown shrimp (Siegenthaler et al., 2019), invasive Caribbean lionfish (Harms-Tuohy et al., 2016), and dietary niches of gobies (Brandl et al., 2020). All of these tools combined provide a powerful new means of moving niche theory forward.

The mosaic of biodiversity across our planet is pieced together by a multitude of processes, abiotic and biotic alike, and more sophisticated approaches such as the above would help tease apart the intricate connections that structure our ecosystems. This is all the more urgent in an era defined by rapid global climate change, environmental degradation, and biodiversity loss. The diversity of flora and fauna that makes up our ecosystems is striking and worthy of further study: both to better understand this biodiversity today, and to predict what it will look like in an uncertain future.

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APPENDICES

4.1 Dietary indices within the database

There are six types of dietary indices commonly reported in the literature (Supplementary Table 1). In order of decreasing prevalence, the following metrics are present within the database: frequency of occurrence (%F), number or relative frequency of prey items (%N), mass of prey items (%M), percent Index of Relative Importance (%IRI), raw Index of Relative Importance (IRI), and percent volume of prey items (%V; Supplementary Table 2; for detailed discussion on each dietary index, see Cortés, 1997 and Hyslop, 1980).

Supplementary Table 2. Number of studies that report each index (*n* = 211 studies; note this number includes some studies that do not meet certain criteria and were ultimately excluded from analyses; see "Exclusion criteria" above). The majority of studies report multiple indices.

%F	%N	%M	%IRI	IRI	%V
167	113	95	59	30	18

4.1.1 References

Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(3), 726–738. https://doi.org/10.1139/f96-316

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Supplementary Table 1. Common reporting standards of stomach content data. Abbreviations used in the literature can vary widely, and the reader must use context to determine which method of reporting is employed within an individual study.

	Method name	Abbreviation	Description	Formula
Stomach occurrence reporting	Frequency of Occurrence, Occurrence	%F, %O, %FO	Number of stomachs containing food item, expressed as a percentage of all stomachs or all stomachs containing food.	$\frac{Stomachs\ with\ prey\ item\ i}{Total\ number\ of\ stomachs}$
Prey proportion reporting	Number of prey items, Frequency of prey items	%N, %F	Numerical proportion of one prey item out of the total count of all stomach contents.	$\frac{Count\ of\ prey\ item\ i}{Total\ count\ of\ prey\ all\ prey\ items}$
	Volume of prey items	%V	Volumetric proportion of one prey item out of the total volume of all stomach contents.	$\frac{Volume\ of\ prey\ item\ i}{Total\ volume\ of\ all\ prey\ items}$
	Mass of prey items, Weight of prey items, Biomass of prey items, Gravimetric proportion	%M, %W, %B, %G	Proportion of prey items, by mass, out of total mass of all stomach contents.	$\frac{Mass\ of\ prey\ item\ i}{Total\ mass\ of\ all\ prey\ items}$
Composite reporting	Index of Relative Importance	IRI	A composite index of all of the above, incorporating number, volume (or weight), and frequency of occurrence into one number.	$IRI = (\%N + \%V^{\dagger}) \times \ \%F$ $^{\dagger}{}_{or\ \%M}$
	Percent Index of Relative Importance	%IRI, %R	IRI expressed as a percentage to permit comparisons across studies.	$\%IRI_i = \frac{100\ IRI_i}{\sum IRI_i}$

4.2 Elasmobranch clades

Elasmobranchs were visually grouped into clades using phylogenies presented in Stein et al. (2018; downloaded from http://sharktree.org/ on May 12, 2020) and the FigTree application (Fig. 4.1; v. 1.4.4; https://github.com/rambaut/figtree/). Clades were ordered by evolutionary age using the mean branch length per group, with shorter branch lengths indicating younger age. For a list of elasmobranch species by clade, see Supplementary Table 3.

4.2.1 References

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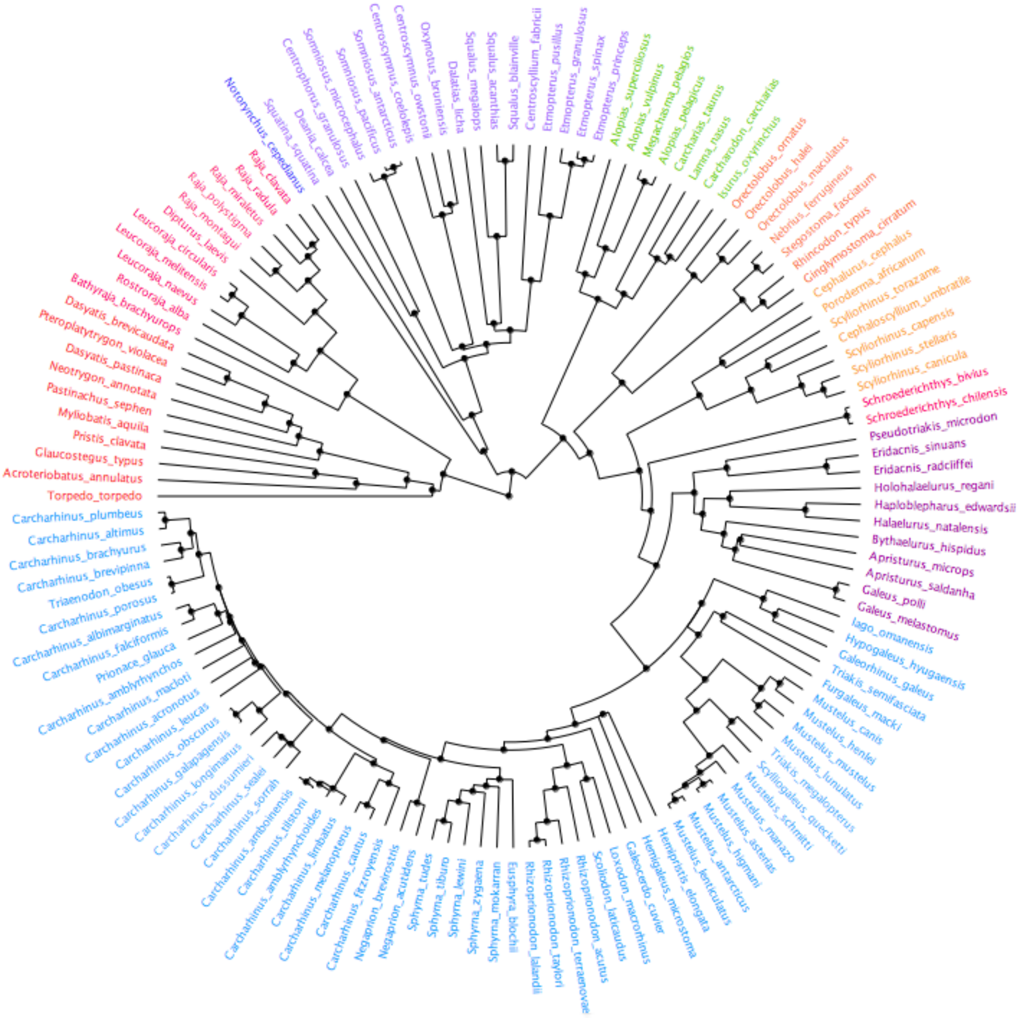

Figure 4.1 Elasmobranch clade groupings. Clades are grouped by age based on mean branch lengths within each group.

4.3 Niche results

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Alopias pelagicus	0.22	Polo-Silva et al. (2013)	85	1.6	3.4	-0.29	-81.28	41.71	82	300	pelagic	E
Alopias pelagicus	0.54	Moteki et al. (2001)	20	0.77	1.61	-5.00	-100.00	37.00	82	300	pelagic	E
Alopias pelagicus	0.63	Huh et al. (2010)	25	1.408	3.401	35.06	129.04	4.94	82	300	pelagic	E
Alopias pelagicus	0.64	Varghese et al. (2014)	56	1.0155	1.4785	18.02	70.82	21.98	82	300	pelagic	E
Alopias superciliosus	0.36	Stillwell & Casey (1976)	18	1.55	3.99	35.15	-75.43	10.85	86	730	pelagic	E
Alopias superciliosus	0.36	Gorni et al. (2013)	16	2.04	4.09	-26.00	-35.00	14.00	86	730	pelagic	E
Alopias superciliosus	0.62	Preti et al. (2008)	23	1.47	2.3	35.50	-121.94	10.50	86	730	pelagic	E
Alopias vulpinus	0.40	Preti & Smith (2001)	107	0.79	2.37	38.50	-123.82	35.50	132	650	pelagic	E
Alopias vulpinus	0.41	Preti et al. (2012)	157	1.08	2.28	32.40	-118.24	41.60	132	650	pelagic	E
Alopias vulpinus	0.45	Rogers & Huveneers (2009)	16	1.39	3.87	-34.39	134.82	23.61	132	650	pelagic	E
Apristurus microps	0.57	Ebert et al. (1996)	64	0.322	0.61	-30.00	16.00	8.00	105	1200	demersal	I

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Apristurus spp.	0.81	Ebert et al. (1996)	17	0.298	0.685	-30.00	16.00	10.00	107	2167	demersal	I
Bythaelurus hispidus	0.47	Nair & Appukkuttan (1973)	184	0.121	0.276	8.79	79.67	6.21	10	203	demersal	I
Carcharhinus altimus	0.81	Bass et al. (1973)	18	0.78	1.59	-25.96	33.62	5.04	71	798	reef	J
Carcharhinus amblyrhynchos	0.22	Brewer et al. (1991)	36	0.42	0.992	-12.75	141.50	22.25	64	1000	reef	J
Carcharhinus amblyrhynchos	0.55	Wetherbee et al. (1997)	61	0.5	2	20.56	-157.13	8.44	64	1000	reef	J
Carcharhinus amboinensis	0.28	Cliff & Dudley (1991b)	42	0.99	1.76	-30.00	31.25	8.00	64	150	reef	J
Carcharhinus amboinensis	0.58	Cliff & Dudley (1991b)	61	0.99	1.76	-30.00	31.25	8.00	64	150	reef	J
Carcharhinus amboinensis	0.80	Bass et al. (1973)	15	0.75	2.23	-30.00	31.25	8.00	64	150	reef	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Carcharhinus brachyurus	0.01	Cliff & Dudley (1992)	229	1.02	2.39	-30.00	31.25	22.00	97	360	pelagic	J
Carcharhinus brachyurus	0.06	Cliff & Dudley (1992)	184	1.02	2.39	-30.00	31.25	22.00	97	360	pelagic	J
Carcharhinus brachyurus	0.34	Rogers & Huveneers (2009)	33	0.85	3.01	-34.39	134.82	17.61	97	360	pelagic	J
Carcharhinus brachyurus	0.44	Lucifora et al. (2009b)	149	1	2.56	-40.60	-61.90	11.40	97	360	pelagic	J
Carcharhinus brachyurus	0.68	Bass et al. (1973)	33	0.72	2.92	-32.22	29.49	19.78	97	360	pelagic	J
Carcharhinus brevipinna	0.43	Allen & Cliff (2000)	379	0.51	2.2	-30.00	31.25	8.00	78	100	reef	J
Carcharhinus brevipinna	0.84	Avendaño-Alvarez et al. (2013)	14	0.76	1.76	19.25	-96.00	20.75	78	100	reef	J
Carcharhinus brevipinna	0.93	Bass et al. (1973)	106	0.46	2.66	-29.53	31.65	8.47	78	100	reef	J
Carcharhinus cautus	0.40	White et al. (2004)	118	0.59	1.2	-25.98	-113.78	4.02	25	20	reef	J
Carcharhinus dussumieri	0.43	Brewer et al. (1991)	85	0.425	0.83	-12.75	141.50	22.25	65	100	reef	J
Carcharhinus dussumieri	0.52	Salini et al. (1994)	128	0.475	0.821	-14.00	139.00	21.00	65	100	reef	J
Carcharhinus dussumieri	0.87	Simpfendorfer & Milward (1993)	18	0.46	0.78	-19.23	146.82	15.77	65	100	reef	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Carcharhinus falciformis	0.11	Duffy et al. (2015)	143	0.9	1.51	5.00	-141.00	37.00	85	4000	pelagic	J
Carcharhinus falciformis	0.16	Cabrera-Chávez-Costa et al. (2010)	123	1	2.28	24.52	-112.03	17.48	85	4000	pelagic	J
Carcharhinus falciformis	0.19	Duffy et al. (2015)	550	0.9	1.51	5.00	-120.50	37.00	85	4000	pelagic	J
Carcharhinus falciformis	0.25	Filmalter et al. (2017)	206	0.52	2.34	-5.00	60.00	38.00	85	4000	pelagic	J
Carcharhinus falciformis	0.30	Duffy et al. (2015)	124	0.9	1.51	5.00	-100.00	37.00	85	4000	pelagic	J
Carcharhinus falciformis	0.33	Cabrera-Chávez-Costa et al. (2010)	19	1	2.28	28.80	-114.40	13.20	85	4000	pelagic	J
Carcharhinus falciformis	0.40	Varghese et al. (2016)	66	1.091	2.0017	13.79	73.61	28.21	85	4000	pelagic	J
Carcharhinus falciformis	0.46	Varghese et al. (2014)	56	0.833	1.2334	18.02	70.82	23.98	85	4000	pelagic	J
Carcharhinus falciformis	0.60	Wass (1971)	27	0.47	1.37	21.70	-159.06	20.30	85	4000	pelagic	J
Carcharhinus falciformis	0.64	Flores-Martínez et al. (2016)	30	0.78	1.66	15.20	-93.21	26.80	85	4000	pelagic	J
Carcharhinus fitzroyensis	0.46	Simpfendorfer & Milward (1993)	12	0.46	0.86	-19.23	146.82	6.77	16	40	demersal	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Carcharhinus galapagensis	0.32	Wetherbee et al. (1996)	96	0	3	20.49	-156.87	15.51	70	285	reef	J
Carcharhinus galapagensis	0.80	Bass et al. (1973)	18	0.78	1.7	-33.12	43.88	0.88	70	285	reef	J
Carcharhinus leucas	0.16	Bass et al. (1973)	99	0.61	3	-28.22	32.44	10.78	81	151	reef	J
Carcharhinus leucas	0.22	Cliff & Dudley (1991a)	99	0.74	2.2	-30.00	31.25	9.00	81	151	reef	J
Carcharhinus leucas	0.41	Snelson et al. (1984)	50	1.402	1.402	27.70	-80.39	14.30	81	151	reef	J
Carcharhinus leucas	0.42	Thorburn (2006)	76	0.687	1.52	-16.00	129.34	23.00	81	151	reef	J
Carcharhinus leucas	0.57	Bass et al. (1973)	102	0.61	3	-29.88	31.09	9.12	81	151	reef	J
Carcharhinus leucas	0.59	Cliff & Dudley (1991a)	210	0.74	2.2	-30.00	31.25	9.00	81	151	reef	J
Carcharhinus leucas	0.86	Trystram et al. (2017)	16	2.29	3.07	-21.01	55.24	17.99	81	151	reef	J
Carcharhinus limbatus	0.18	Dudley & Cliff (1993)	213	0.66	1.9	-30.00	31.25	8.00	83	100	reef	J
Carcharhinus limbatus	0.42	Dudley & Cliff (1993)	443	0.66	1.9	-30.00	31.25	8.00	83	100	reef	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Carcharhinus limbatus	0.60	Plumlee & Wells (2016)	22	0.527	1.437	29.20	-94.90	15.80	83	100	reef	J
Carcharhinus limbatus	0.65	Bornatowski et al. (2014)	48	0.434	1.638	-25.71	-48.10	12.29	83	100	reef	J
Carcharhinus limbatus	0.76	Hueter & Manire (1994)	65	0.45	0.94	27.07	-82.51	17.93	83	100	reef	J
Carcharhinus limbatus	0.97	Bass et al. (1973)	55	0.6	2.37	-30.00	31.25	8.00	83	100	reef	J
Carcharhinus longimanus	0.23	Strasburg (1958)	38	0.8	2.39	-5.00	-145.00	38.00	89	230	pelagic	J
Carcharhinus longimanus	0.30	Bass et al. (1973)	23	1.13	2.7	-27.87	33.92	15.13	89	230	pelagic	J
Carcharhinus macloti	0.92	Salini et al. (1994)	33	0.56	0.825	-14.00	139.00	13.00	64	170	pelagic	J
Carcharhinus melanopterus	0.53	Frisch et al. (2016)	26	1.253	1.307	-19.00	148.00	6.00	60	55	reef	J
Carcharhinus melanopterus	0.63	Stevens (1984b)	21	0.45	1.45	-9.40	46.33	15.60	60	55	reef	J
Carcharhinus obscurus	0.20	Dudley et al. (2005)	725	0.57	2.84	-30.00	31.25	16.00	91	400	reef	J
Carcharhinus obscurus	0.35	Simpfendorfer et al. (2001b)	1322	0.59	2.82	-24.47	112.49	21.53	91	400	reef	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Carcharhinus obscurus	0.51	Gelsleichter et al. (1999)	59	0.85	2.25	37.00	-75.75	8.00	91	400	reef	J
Carcharhinus obscurus	0.52	van der Elst (1979)	216	0.65	1.049	-30.00	31.25	16.00	91	400	reef	J
Carcharhinus obscurus	0.71	Bass et al. (1973)	118	0.69	3.57	-33.15	28.25	12.85	91	400	reef	J
Carcharhinus obscurus	0.81	Bornatowski et al. (2014)	36	1.076	2.034	-25.71	-48.10	20.29	91	400	reef	J
Carcharhinus plumbeus	0.14	Medved et al. (1985)	340	0.4	0.8	38.01	-75.31	6.99	88	500	benthopelagic	J
Carcharhinus plumbeus	0.31	Medved & Marshall (1981)	64	0.6	1.37	37.93	-75.39	7.07	88	500	benthopelagic	J
Carcharhinus plumbeus	0.32	Stillwell (1993)	53	1.145	1.145	39.60	-72.96	5.40	88	500	benthopelagic	J
Carcharhinus plumbeus	0.47	McElroy et al. (2006)	263	0.59	1.9	21.00	-160.00	24.00	88	500	benthopelagic	J
Carcharhinus plumbeus	0.49	Stillwell (1993)	268	2.68	2.68	40.13	-74.01	4.87	88	500	benthopelagic	J
Carcharhinus plumbeus	0.74	Wass (1971)	244	0.45	1.46	21.70	-159.06	23.30	88	500	benthopelagic	J
Carcharhinus plumbeus	0.75	Huh et al. (2010)	25	0.813	1.974	35.06	129.04	9.94	88	500	benthopelagic	J
Carcharhinus plumbeus	0.87	Bass et al. (1973)	29	0.63	1.95	-30.00	31.25	13.00	88	500	benthopelagic	J

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Species	**Niche**	**Source**	S_n	**Min size (m)**	**Max size (m)**	**Lat.**	**Long.**	**DPE**	**LR°**	**DR (m)**	**Func. grp**	**C**
Carcharhinus sorrah	0.56	Simpfendorfer & Milward (1993)	18	0.54	0.86	-19.23	146.82	11.77	62	140	reef	J
Carcharhinus sorrah	0.61	Brewer et al. (1991)	12	0.75	1.15	-12.75	141.50	18.25	62	140	reef	J
Carcharhinus tilstoni	0.96	Simpfendorfer & Milward (1993)	30	0.54	0.86	-19.23	146.82	8.77	18	150	pelagic	J
Carcharias taurus	0.30	Lucifora et al. (2009a)	164	0.89	2.8	-39.22	-61.73	8.78	93	190	reef	E
Carcharias taurus	0.53	Gelsleichter et al. (1999)	42	1.61	2.8	37.00	-75.75	8.00	93	190	reef	E
Carcharias taurus	0.81	Bass et al. (1975)	22	1	2.82	-30.00	31.25	18.00	93	190	reef	E
Carcharodon carcharias	0.17	Cliff et al. (1989)	122	1.35	3.48	-30.00	31.25	28.00	119	1200	pelagic	E
Carcharodon carcharias	0.37	Cliff et al. (1989)	58	1.35	3.48	-30.00	31.25	28.00	119	1200	pelagic	E
Carcharodon carcharias	0.79	Bass et al. (1975)	20	1.7	4.45	-30.00	31.25	28.00	119	1200	pelagic	E
Carcharodon carcharias	0.82	Malcolm et al. (2001)	49	1.4	5.5	-35.00	135.00	23.00	119	1200	pelagic	E
Centroscymnus coelolepis	0.83	Clarke & Merrett (1972)	12	0.67	1.064	33.78	-18.93	41.22	136	3572	benthopelagic	D

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Cephaloscyllium umbratile	0.54	Taniuchi (1988)	278	0.7	1.145	35.69	140.92	4.31	26.5	480	reef	G
Deania calcea	0.72	Saldanha et al. (1995)	28	0.3583	0.3583	36.82	-8.18	33.18	126	1430	demersal	D
Eridacnis radcliffei	0.52	Nair & Appukkuttan (1973)	277	0.131	0.211	8.79	79.67	13.21	32	695	demersal	I
Etmopterus spinax	0.35	Valls et al. (2011)	25	0.11	0.47	39.82	2.48	35.18	123	2290	benthopelagic	D
Eusphyra blochii	0.26	Stevens & Lyle (1989)	287	0.65	1.69	-14.71	136.28	5.29	51	70	benthopelagic	J
Furgaleus macki	0.06	Simpfendorfer et al. (2001b)	372	0.72	1.29	-24.47	112.49	20.53	24	220	demersal	J
Galeocerdo cuvier	0.20	Dicken et al. (2017)	612	0.94	3.35	-30.00	31.25	14.00	106	800	benthopelagic	J
Galeocerdo cuvier	0.26	Simpfendorfer (1992)	558	0.84	4.28	-19.10	147.19	24.90	106	800	benthopelagic	J
Galeocerdo cuvier	0.30	Simpfendorfer et al. (2001a)	84	1.31	3.61	-23.95	113.47	20.05	106	800	benthopelagic	J
Galeocerdo cuvier	0.47	Heithaus (2001)	15	2.13	3.89	-25.98	113.73	18.02	106	800	benthopelagic	J
Galeocerdo cuvier	0.48	Trystram et al. (2017)	30	2.99	3.67	-21.01	55.24	22.99	106	800	benthopelagic	J

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Galeocerdo cuvier	0.70	Stevens (1984a)	29	1.88	3.82	-34.50	151.27	9.50	106	800	benthopelagic	J
Galeocerdo cuvier	0.72	Randall (1992)	12	2.2	4.2	20.03	-155.84	41.97	106	800	benthopelagic	J
Galeocerdo cuvier	0.88	Bornatowski et al. (2014)	22	0.7	2.1	-25.71	-48.10	18.29	106	800	benthopelagic	J
Galeus melastomus	0.14	Anastasopoulou et al. (2013)	727	0.181	0.546	38.16	20.20	25.84	50	1818	demersal	I
Galeus melastomus	0.23	Carrasson et al. (1992)	149	0.1	0.75	40.38	1.90	23.62	50	1818	demersal	I
Galeus melastomus	0.27	Valls et al. (2011)	257	0.1	0.63	39.82	2.48	24.18	50	1818	demersal	I
Galeus melastomus	0.53	Saldanha et al. (1995)	52	0.5733	0.5733	36.82	-8.18	27.18	50	1818	demersal	I
Galeus polli	0.65	Ebert et al. (1996)	84	0.155	0.46	-24.70	14.50	3.30	56	520	demersal	I
Glaucostegus typus	0.11	White et al. (2004)	268	0.59	1.2	-25.98	-113.78	6.02	60	100	demersal	A
Holohalaelurus regani	0.40	Ebert et al. (1996)	291	0.15	0.685	-30.00	16.00	7.00	33	1900	demersal	I
Iago omanensis	0.59	Nair & Appukkuttan (1973)	23	0.215	0.328	8.79	79.67	21.21	22	2085	benthopelagic	J
Isurus oxyrinchus	0.03	Wood et al. (2009)	120	1.46	3.35	40.00	-73.00	21.00	117	750	pelagic	E

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Isurus oxyrinchus	0.06	Wood et al. (2009)	221	0.86	3.385	40.00	-73.00	21.00	117	750	pelagic	E
Isurus oxyrinchus	0.09	Groeneveld et al. (2014)	169	1.12	1.775	-35.46	20.12	20.54	117	750	pelagic	E
Isurus oxyrinchus	0.12	Stillwell & Kohler (1982)	273	0.67	3.28	39.75	-73.27	21.25	117	750	pelagic	E
Isurus oxyrinchus	0.31	Gorni et al. (2013)	47	0.82	2.81	-26.00	-35.00	30.00	117	750	pelagic	E
Isurus oxyrinchus	0.34	Groeneveld et al. (2014)	185	2.021	2.551	-29.90	31.06	26.10	117	750	pelagic	E
Isurus oxyrinchus	0.35	Horn et al. (2013)	993	0.62	3.5	-36.52	178.44	19.48	117	750	pelagic	E
Isurus oxyrinchus	0.39	Preti et al. (2012)	238	0.53	2.48	32.40	-118.24	28.60	117	750	pelagic	E
Isurus oxyrinchus	0.40	Cliff et al. (1990)	41	0.84	2.76	-30.00	31.25	26.00	117	750	pelagic	E
Isurus oxyrinchus	0.53	Cliff et al. (1990)	47	0.84	2.76	-30.00	31.25	26.00	117	750	pelagic	E
Isurus oxyrinchus	0.55	Stevens (1984a)	63	1.27	2.7	-34.50	151.27	21.50	117	750	pelagic	E
Isurus oxyrinchus	0.62	Maia et al. (2006)	99	0.64	2.9	37.00	-9.00	24.00	117	750	pelagic	E
Isurus oxyrinchus	0.71	Rogers & Huveneers (2009)	13	1.02	3.02	-34.39	134.82	21.61	117	750	pelagic	E

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Isurus oxyrinchus	0.81	Vaske-Júnior & Rincón-Filho (1998)	19	0.48	1.34	-31.80	-45.70	24.20	117	750	pelagic	E
Isurus oxyrinchus	0.84	Huh et al. (2010)	37	0.872	2.728	35.06	129.04	25.94	117	750	pelagic	E
Lamna nasus	0.15	Horn et al. (2013)	1489	0.61	2.46	-44.31	166.05	14.69	135	1360	pelagic	E
Lamna nasus	0.22	Ellis & Shackley (1995)	24	1.14	1.87	51.33	-4.50	24.67	135	1360	pelagic	E
Lamna nasus	0.46	Joyce et al. (2002)	497	0.85	2.64	44.95	-59.41	31.05	135	1360	pelagic	E
Lamna nasus	0.53	Gauld (1989)	86	0.81	3.17	59.53	-1.82	16.47	135	1360	pelagic	E
Leucoraja naevus	0.67	Valls et al. (2011)	24	0.22	0.52	39.82	2.48	20.18	45	480	demersal	B
Loxodon macrorhinus	0.28	Jabado et al. (2015)	48	0.517	0.714	25.45	55.09	8.55	64	93	demersal	J
Maculabatis toshi	0.58	Brewer et al. (1991)	160	0.207	1.4	-12.75	141.50	17.25	22	130	demersal	A
Mustelus antarcticus	0.36	Simpfendorfer et al. (2001b)	923	0.81	1.63	-24.47	112.49	26.53	45	350	demersal	J
Mustelus canis	0.12	Montemarano et al. (2016)	25	0.842	0.864	40.58	-73.66	1.42	86	800	demersal	J

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Mustelus canis	0.28	Montemarano et al. (2016)	21	0.785	0.843	41.10	-72.29	0.90	86	800	demersal	J
Mustelus canis	0.30	Montemarano et al. (2016)	25	0.957	0.983	41.10	-72.21	0.90	86	800	demersal	J
Mustelus canis	0.33	Rountree & Able (1996)	85	0.417	0.417	39.52	-74.35	2.48	86	800	demersal	J
Mustelus canis	0.40	Gelsleichter et al. (1999)	64	0.46	1.26	37.00	-75.75	5.00	86	800	demersal	J
Mustelus henlei	0.22	Russo (1975)	21	0.53	0.87	37.87	-122.48	10.13	66	281	demersal	J
Mustelus henlei	0.35	Russo (1975)	47	0.63	0.94	38.17	-122.91	9.83	66	281	demersal	J
Mustelus higmani	0.20	Tagliafico et al. (2015)	1957	0.2	0.884	10.78	-64.06	0.22	47	899	demersal	J
Mustelus higmani	0.51	Springer & Lowe (1963)	54	0.201	0.635	7.31	-54.78	3.69	47	899	demersal	J
Mustelus lenticulatus	0.45	King & Clark (1984)	428	0.6	1.19	-40.66	172.86	7.34	14	860	demersal	J
Mustelus manazo	0.68	Huh et al. (2010)	96	0.551	1.012	35.06	129.04	9.94	55	360	demersal	J
Mustelus schmitti	0.26	Chiaramonte & Pettovello (2000)	67	0.252	0.913	-47.76	-65.92	0.24	20	135	demersal	J

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Mustelus schmitti	0.28	Molen & Caille (2001)	24	0.167	0.301	-42.50	-64.50	5.50	20	135	demersal	J
Myliobatis aquila	0.55	Valls et al. (2011)	22	0.51	1.16	39.82	2.48	20.18	96	299	benthopelagic	A
Negaprion acutidens	0.79	White et al. (2004)	20	0.6	1.2	-25.98	-113.78	6.02	62	92	reef	J
Negaprion brevirostris	0.25	Newman et al. (2009)	265	0.435	0.9	25.77	-79.26	19.23	78	92	reef	J
Negaprion brevirostris	0.27	Cortés & Gruber (1990)	64	0.496	0.664	24.69	-81.15	20.31	78	92	reef	J
Negaprion brevirostris	0.32	Newman et al. (2009)	131	0.435	0.9	25.70	-79.27	19.30	78	92	reef	J
Negaprion brevirostris	0.36	Cortés & Gruber (1990)	78	0.47	2.05	25.69	-79.30	19.31	78	92	reef	J
Notorynchus cepedianus	0.39	Lucifora et al. (2005)	45	0.532	2.2398	-39.21	-61.72	15.79	111	570	demersal	C
Notorynchus cepedianus	0.50	Barnett et al. (2010)	203	1.05	2.7	-43.14	147.67	11.86	111	570	demersal	C
Notorynchus cepedianus	0.76	Crespi-Abril et al. (2003)	20	1.26	2.44	-44.00	-63.00	11.00	111	570	demersal	C
Orectolobus halei	0.49	Huveneers et al. (2007)	41	1.735	1.735	-33.00	152.00	6.00	8	195	demersal	F
Orectolobus maculatus	0.63	Huveneers et al. (2007)	39	1.338	1.338	-33.00	152.00	7.00	20	248	reef	F

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Orectolobus ornatus	0.45	Huveneers et al. (2007)	64	0.848	0.848	-33.00	152.00	7.00	41	100	reef	F
Oxynotus bruniensis	0.48	Finucci et al. (2016)	23	0.335	0.756	-43.63	178.17	11.37	24	1025	benthopelagic	D
Prionace glauca	0.09	Horn et al. (2013)	8584	0.5	3.1	-43.56	166.26	11.44	126	999	pelagic	J
Prionace glauca	0.12	Yatsu (1995)	26	0.85	2.05	-42.00	-112.00	13.00	126	999	pelagic	J
Prionace glauca	0.29	Vaske Júnior et al. (2009)	116	2.369	2.369	-7.11	-30.11	47.89	126	999	pelagic	J
Prionace glauca	0.29	Stevens (1973)	60	1.462	2.301	50.21	-4.25	20.79	126	999	pelagic	J
Prionace glauca	0.31	Henderson et al. (2001)	126	0.64	2.28	49.00	-12.00	22.00	126	999	pelagic	J
Prionace glauca	0.32	Preti et al. (2012)	114	0.76	2.48	32.40	-118.24	38.60	126	999	pelagic	J
Prionace glauca	0.32	Vaske Júnior et al. (2009)	106	2.362	2.362	-30.50	-45.40	24.50	126	999	pelagic	J
Prionace glauca	0.36	Lopez et al. (2010)	172	0.75	4.91	-28.00	-95.00	27.00	126	999	pelagic	J
Prionace glauca	0.37	Rosas-Luis et al. (2016)	114	0.8	2.6	-1.93	-82.77	53.07	126	999	pelagic	J
Prionace glauca	0.42	Hernández-Aguilar et al. (2016)	210	0.99	2.69	26.04	-112.38	44.96	126	999	pelagic	J

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Prionace glauca	0.47	Fujinami et al. (2018)	221	0.609	2.24	38.60	151.30	32.40	126	999	pelagic	J
Prionace glauca	0.50	Clarke et al. (1996)	112	1.103	1.937	38.16	-27.06	32.84	126	999	pelagic	J
Prionace glauca	0.55	Vaske-Júnior & Rincón-Filho (1998)	40	1	1.62	-31.80	-45.70	23.20	126	999	pelagic	J
Prionace glauca	0.57	LeBrasseur (1964)	24	0.76	1.37	53.40	-137.70	17.60	126	999	pelagic	J
Prionace glauca	0.58	Stevens (1984a)	31	2.21	3.26	-34.50	151.27	20.50	126	999	pelagic	J
Prionace glauca	0.59	Yatsu (1995)	16	0.98	2.15	-27.00	-112.00	28.00	126	999	pelagic	J
Prionace glauca	0.61	Strasburg (1958)	64	0.8	3.19	40.00	-145.00	31.00	126	999	pelagic	J
Prionace glauca	0.65	Mendonça (2009)	137	0.79	2.58	35.00	-25.00	36.00	126	999	pelagic	J
Pseudobatos productus	0.37	Valenzuela-Quiñonez et al. (2018)	100	0.435	1.09	30.75	-113.67	7.25	20	90	demersal	A
Pteroplatytrygon violacea	0.46	Varghese et al. (2014)	43	0.4137	0.5063	18.02	70.82	33.98	102	380	pelagic	A
Raja clavata	0.40	Valls et al. (2011)	291	0.18	0.91	39.82	2.48	30.18	99	1015	demersal	B

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Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Raja miraletus	0.44	Valls et al. (2011)	31	0.24	0.43	39.82	2.48	4.18	79	445	demersal	B
Raja polystigma	0.74	Valls et al. (2011)	15	0.28	0.45	39.82	2.48	5.88	15.7	300	demersal	B
Rhizoprionodon acutus	0.65	Jabado et al. (2015)	38	0.509	0.875	25.45	55.09	15.55	71	199	benthopelagic	J
Rhizoprionodon acutus	0.75	White et al. (2004)	28	0.59	0.89	-25.98	-113.78	4.02	71	199	benthopelagic	J
Rhizoprionodon acutus	0.83	Simpfendorfer & Milward (1993)	50	0.34	0.74	-19.23	146.82	10.77	71	199	benthopelagic	J
Rhizoprionodon acutus	0.90	Brewer et al. (1991)	106	0.3	0.88	-12.75	141.50	17.25	71	199	benthopelagic	J
Rhizoprionodon lalandii	0.57	Bornatowski et al. (2014)	124	0.481	0.693	-25.71	-48.10	9.29	48	67	demersal	J
Rhizoprionodon taylori	0.84	Simpfendorfer & Milward (1993)	207	0.3	0.78	-19.23	146.82	8.77	20	110	pelagic	J
Rhizoprionodon terraenovae	0.39	Plumlee & Wells (2016)	51	0.513	0.895	29.20	-94.90	13.80	68	280	pelagic	J
Rhizoprionodon terraenovae	0.42	Gelsleichter et al. (1999)	129	0.81	1.1	37.00	-75.75	6.00	68	280	pelagic	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Rhizoprionodon terraenovae	0.45	Avendaño-Alvarez et al. (2013)	25	0.5	1.04	19.25	-96.00	23.75	68	280	pelagic	J
Schroederichthys chilensis	0.48	Fariña & Ojeda (1993)	201	0.42	0.66	-33.03	-71.71	17.97	42	50	demersal	H
Scyliorhinus canicula	0.31	Valls et al. (2011)	706	0.11	0.53	39.82	2.48	23.18	51	770	demersal	G
Scyliorhinus canicula	0.54	Šantić et al. (2012)	852	0.104	0.46	43.20	16.02	19.80	51	770	demersal	G
Scyliorhinus capensis	0.58	Ebert et al. (1996)	97	0.245	0.88	-30.00	16.00	7.00	37	469	demersal	G
Scyliorhinus torazame	0.34	Huh et al. (2010)	160	0.131	0.385	35.06	129.04	4.94	18	420	demersal	G
Somniosus antarcticus	0.56	Yano et al. (2007)	12	1.032	4.38	-54.59	158.73	0.41	30	665	benthopelagic	D
Somniosus microcephalus	0.29	Fisk et al. (2002)	14	2.779	2.893	65.97	-66.68	17.03	48	2992	benthopelagic	D
Somniosus microcephalus	0.41	Yano et al. (2007)	37	0.648	4.8	68.64	-56.29	14.36	48	2992	benthopelagic	D

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Somniosus microcephalus	0.47	McMeans et al. (2015)	51	2.418	3.048	65.29	-65.78	17.71	48	2992	benthopelagic	D
Somniosus microcephalus	0.55	McMeans et al. (2010)	18	3.904	4.408	64.40	-22.78	18.60	48	2992	benthopelagic	D
Somniosus microcephalus	0.57	McMeans et al. (2012)	18	2.324	2.982	65.22	-65.75	17.78	48	2992	benthopelagic	D
Somniosus microcephalus	0.59	Leclerc et al. (2012)	33	2.45	4.04	79.00	11.67	4.00	48	2992	benthopelagic	D
Somniosus microcephalus	0.62	Nielsen et al. (2014)	24	2.58	4.6	66.64	-31.59	16.36	48	2992	benthopelagic	D
Somniosus microcephalus	0.66	Beck & Mansfield (1969)	13	2.17	3.11	72.65	-79.67	10.35	48	2992	benthopelagic	D
Somniosus pacificus	0.31	Sigler et al. (2006)	165	1.06	2.4	58.78	-151.21	13.22	49	2205	benthopelagic	D

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Somniosus pacificus	0.47	Yang & Page (1999)	11	2.396	2.894	56.80	-155.30	15.20	49	2205	benthopelagic	D
Somniosus pacificus	0.61	Yano et al. (2007)	16	1.05	1.744	58.39	-174.66	13.61	49	2205	benthopelagic	D
Sphyrna lewini	0.09	Clarke (1971)	33	0.395	0.693	21.42	-157.77	24.58	81	1000	pelagic	J
Sphyrna lewini	0.17	Clarke (1971)	35	1.95	2.72	21.45	-157.79	24.55	81	1000	pelagic	J
Sphyrna lewini	0.24	Clarke (1971)	108	0.395	0.895	21.44	-157.79	24.56	81	1000	pelagic	J
Sphyrna lewini	0.28	Bush (2003)	625	0.422	1.045	21.43	-157.79	24.57	81	1000	pelagic	J
Sphyrna lewini	0.37	Simpfendorfer & Milward (1993)	81	0.46	0.86	-19.23	146.82	15.77	81	1000	pelagic	J
Sphyrna lewini	0.40	Stevens & Lyle (1989)	518	0.468	3.16	-14.71	136.28	20.29	81	1000	pelagic	J
Sphyrna lewini	0.53	Flores-Martínez et al. (2016)	96	0.43	0.75	15.20	-93.21	30.80	81	1000	pelagic	J
Sphyrna lewini	0.57	de Bruyn et al. (2005)	832	0.537	2.43	-30.00	31.25	5.00	81	1000	pelagic	J
Sphyrna lewini	0.61	Bergés-Tiznado et al. (2015)	20	0.53	1.085	22.45	-105.65	23.55	81	1000	pelagic	J
Sphyrna lewini	0.71	Avendaño-Alvarez et al. (2013)	12	0.66	1.67	19.25	-96.00	26.75	81	1000	pelagic	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Sphyrna lewini	0.71	Bornatowski et al. (2014)	123	0.291	1.273	-25.71	-48.10	9.29	81	1000	pelagic	J
Sphyrna mokarran	0.17	Cliff (1995)	42	1.06	3.26	-30.00	31.25	7.00	77	299	pelagic	J
Sphyrna mokarran	0.47	Cliff (1995)	77	1.06	3.26	-30.00	31.25	7.00	77	299	pelagic	J
Sphyrna mokarran	0.63	Stevens & Lyle (1989)	304	0.659	3.9	-14.71	136.28	22.29	77	299	pelagic	J
Sphyrna tiburo	0.12	Bethea et al. (2007)	502	0.506	0.916	29.67	-85.22	15.33	81	70	reef	J
Sphyrna tiburo	0.22	Cortes et al. (1996)	338	0.31	0.84	27.00	-82.50	18.00	81	70	reef	J
Sphyrna tiburo	0.23	Parsons (1987)	92	0.37	1.15	27.71	-82.58	17.29	81	70	reef	J
Sphyrna tiburo	0.31	Plumlee & Wells (2016)	18	0.49	1.02	29.20	-94.90	15.80	81	70	reef	J
Sphyrna tiburo	0.32	Hueter & Manire (1994)	314	0.34	0.91	27.07	-82.51	17.93	81	70	reef	J
Sphyrna tiburo	0.48	Parsons (1987)	36	0.35	1.05	24.90	-80.70	20.10	81	70	reef	J
Sphyrna tudes	0.37	Castro (1989)	116	0.67	1.21	10.61	-61.02	35.39	103	40	benthopelagic	J
Sphyrna zygaena	0.19	Smale (1991)	370	0.543	3.03	-34.00	27.00	21.00	114	200	pelagic	J

Supplementary Table 3. Standardized Levin's dietary niche for all elasmobranch species in the present thesis. S_n, number of non-empty stomachs sampled. DPE, distance to polar edge. LR, latitudinal range in degrees. DR, depth range in meters. C, clade.

Species	Niche	Source	S_n	Min size (m)	Max size (m)	Lat.	Long.	DPE	LR°	DR (m)	Func. grp	C
Sphyrna zygaena	0.41	Ochoa-Díaz (2013)	48	0.63	2.83	25.38	-111.78	33.62	114	200	pelagic	J
Sphyrna zygaena	0.45	Bornatowski et al. (2014)	77	0.671	1.85	-25.71	-48.10	29.29	114	200	pelagic	J
Sphyrna zygaena	0.62	Rogers & Huveneers (2009)	19	0.98	1.68	-34.39	134.82	20.61	114	200	pelagic	J
Sphyrna zygaena	0.84	Stevens (1984a)	42	0.81	2.43	-34.50	151.27	20.50	114	200	pelagic	J
Squalus megalops	0.56	Huh et al. (2010)	38	0.76	1.325	35.06	129.04	6.94	83	720	demersal	D
Triakis megalopterus	0.22	Smale & Goosen (1999)	92	0.576	2.075	-33.56	27.25	2.44	6	49	demersal	J
Triakis semifasciata	0.41	Russo (1975)	37	0.53	1.3	37.87	-122.48	7.13	26	156	demersal	J
Triakis semifasciata	0.59	Russo (1975)	67	0.72	1.5	38.17	-122.91	6.83	26	156	demersal	J

4.3.1 Stomach content references.

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4.4 Model covariate sample sizes and residuals

Supplementary Table 4. Sample sizes of categorical covariates in the northern and southern hemisphere models.

Covariate	Hemisphere	
	N	**S**
Ecosystem		
Estuary	8	4
Coastal	14	38
Shelf	51	47
Offshore	45	30
Functional group		
Demersal	29	20
Reef-associated	19	36
Benthopelagic	25	14
Pelagic	45	49

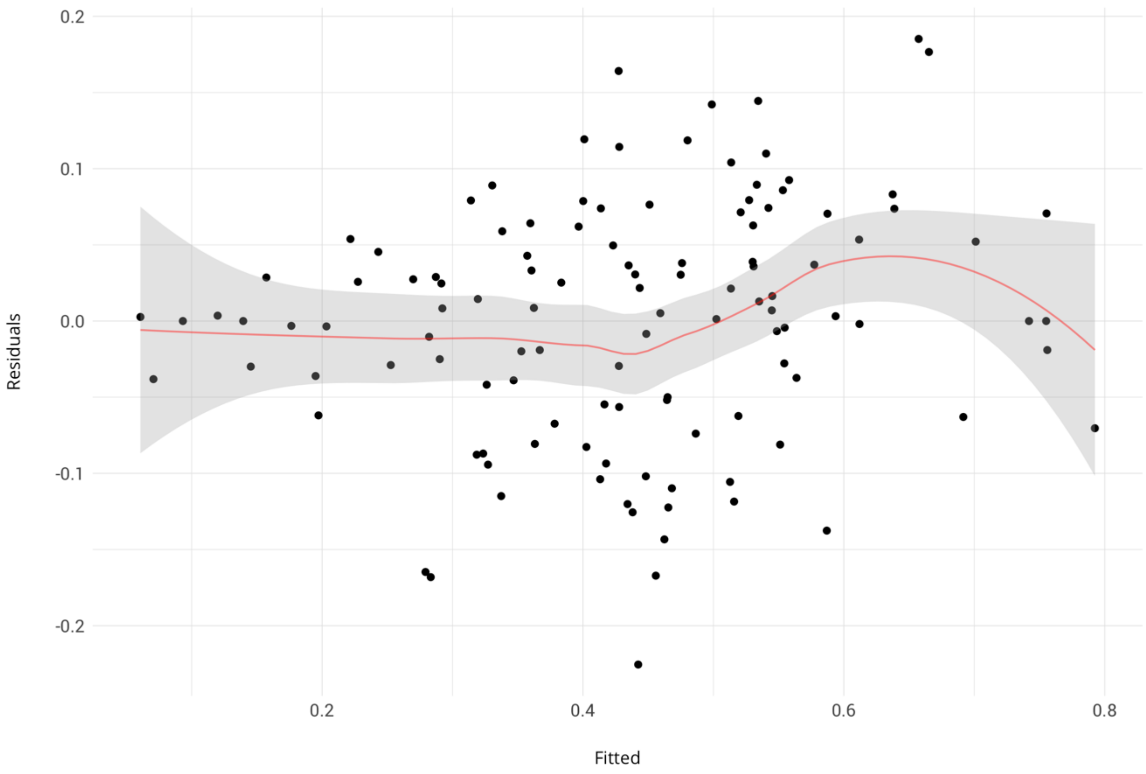

Figure 4.2 Pearson residuals versus fitted values (Standardized Levin's dietary niche) for the best-fit northern hemisphere linear mixed effects model applied to the full niche dataset.

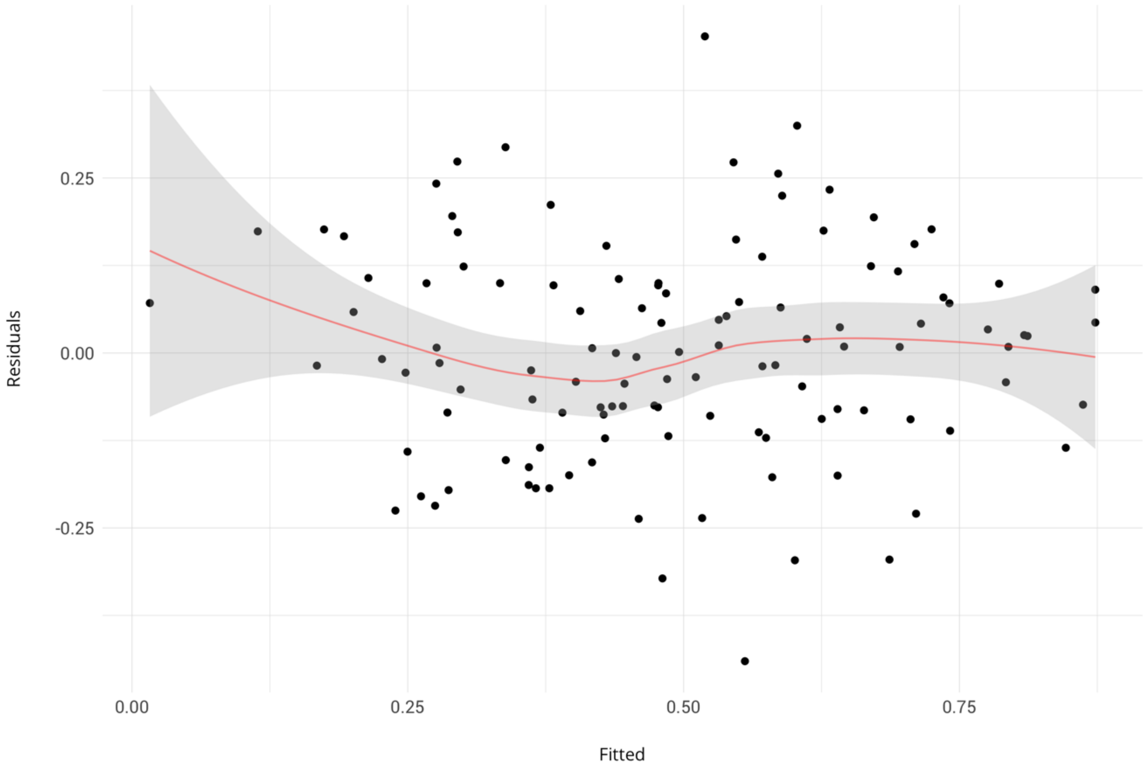

Figure 4.3 Pearson residuals versus fitted values (Standardized Levin’s dietary niche) for the best-fit southern hemisphere linear model applied to the full niche dataset.

4.5 Model results with smaller sample sizes excluded

In order to further test the effects of sample size (*e.g.*, number of stomachs sampled within each predator population) on niche breadth, a second set of models was run with a higher sample size cutoff. Any studies that reported fewer than 100 non-empty stomachs were excluded from the dataset and models re-run. In all models, ecosystem, body size, and their interaction were retained as variables explaining the greatest variance in niche breadth.

In the northern hemisphere, the effect of sample size completely disappeared (Supplemental Table 6). Estuarine and coastal species were more specialized than offshore species (Fig. 4.5). In the southern hemisphere, offshore species were more specialized than coastal species (Fig. 4.7), which may reflect the greater number of larger, more specialized pelagic sharks, such as white and shortfin mako sharks, in the southern hemisphere dataset.

Supplementary Table 5. Sample sizes of categorical covariates in the northern and southern hemisphere models with smaller stomach sample sizes excluded.

	Hemisphere	
Covariate	**N**	**S**
Ecosystem		
Estuary	3	-
Coastal	6	17
Shelf	14	19
Offshore	19	9
Functional group		
Demersal	10	9
Reef-associated	6	13
Benthopelagic	6	4
Pelagic	20	19

Supplementary Table 6. Three best-fit models applied to northern hemisphere niche breadth, with a minimum stomach sample size of 100 stomachs. *N* = 42

Expression	df (df resid)	AIC	ΔAIC	R^2
lat + long + s + sr + e + s:sr + s:e + lat:long + lat:sr + RE(Study)	16 (26)	-59.1	—	0.93
dpe + s + sr + dr + e + dpe:sr + dpe:dr + dpe:s + e:s + e:sr	18 (24)	-58.3	0.8	0.75
lat + long + s + sr + e + s:sr + s:e + lat:long + lat:sr	15 (27)	-57.9	1.2	0.71

lat, sampling latitude; long, sampling longitude; s, predator size; sr, predator size range; e, ecosystem; dpe, distance to polar edge; dr, depth range; RE(Study), study as random effect.

Supplementary Table 7. Four best-fit models applied to southern hemisphere niche breadth, with a minimum stomach sample size of 100 stomachs. *N* = 45

Expression	df (df resid)	AIC	ΔAIC	R^2
ss + long + s + sr + e + e:s + e:sr	12 (33)	-25.2	—	0.59
ss + s + sr + e + e:s + e:sr	11 (34)	-22.0	3.2	0.53
ss + s + sr + e + e:s + e:sr + RE(Study)	12 (33)	-19.8	5.4	0.54
ss + long + s + sr + e + e:s + RE(Study)	11 (34)	-17.8	7.4	0.58

ss, sample size; long, sampling longitude; s, predator size; sr, predator size range; e, ecosystem; RE(Study), study as random effect.

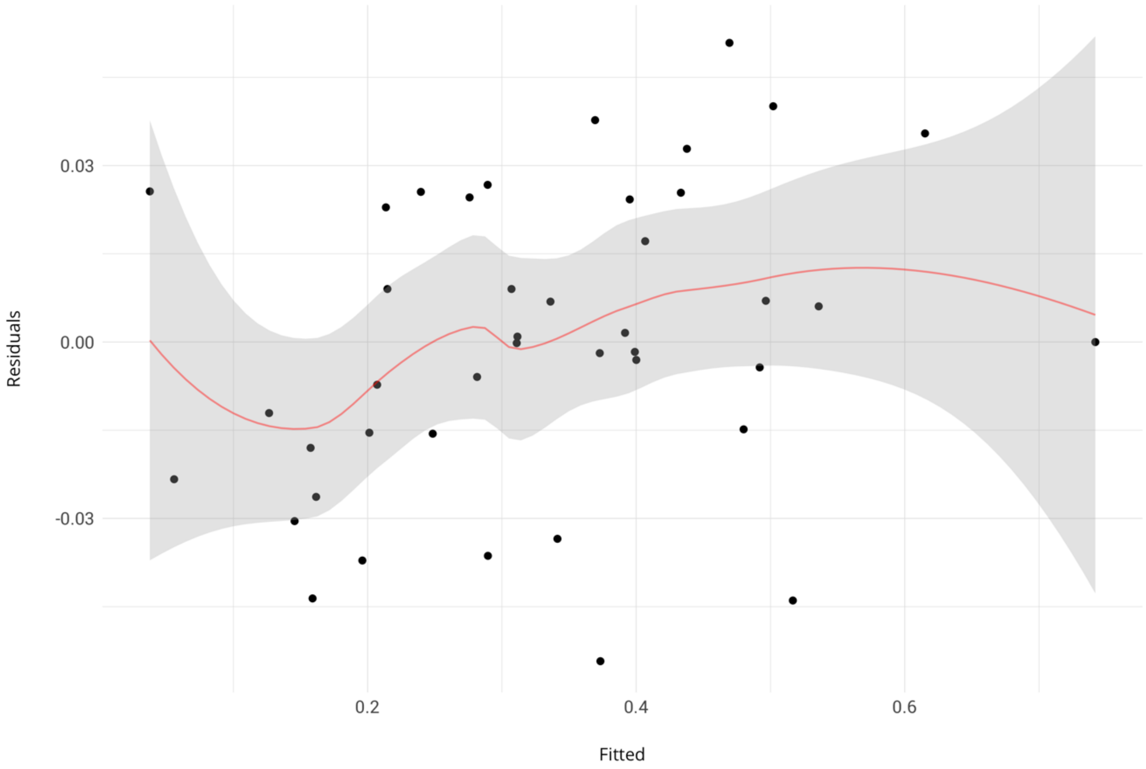

Figure 4.4 Pearson residuals versus fitted values (Standardized Levin's dietary niche) for the northern hemisphere linear mixed effects model applied to data with small sample sizes (*n* <100) excluded.

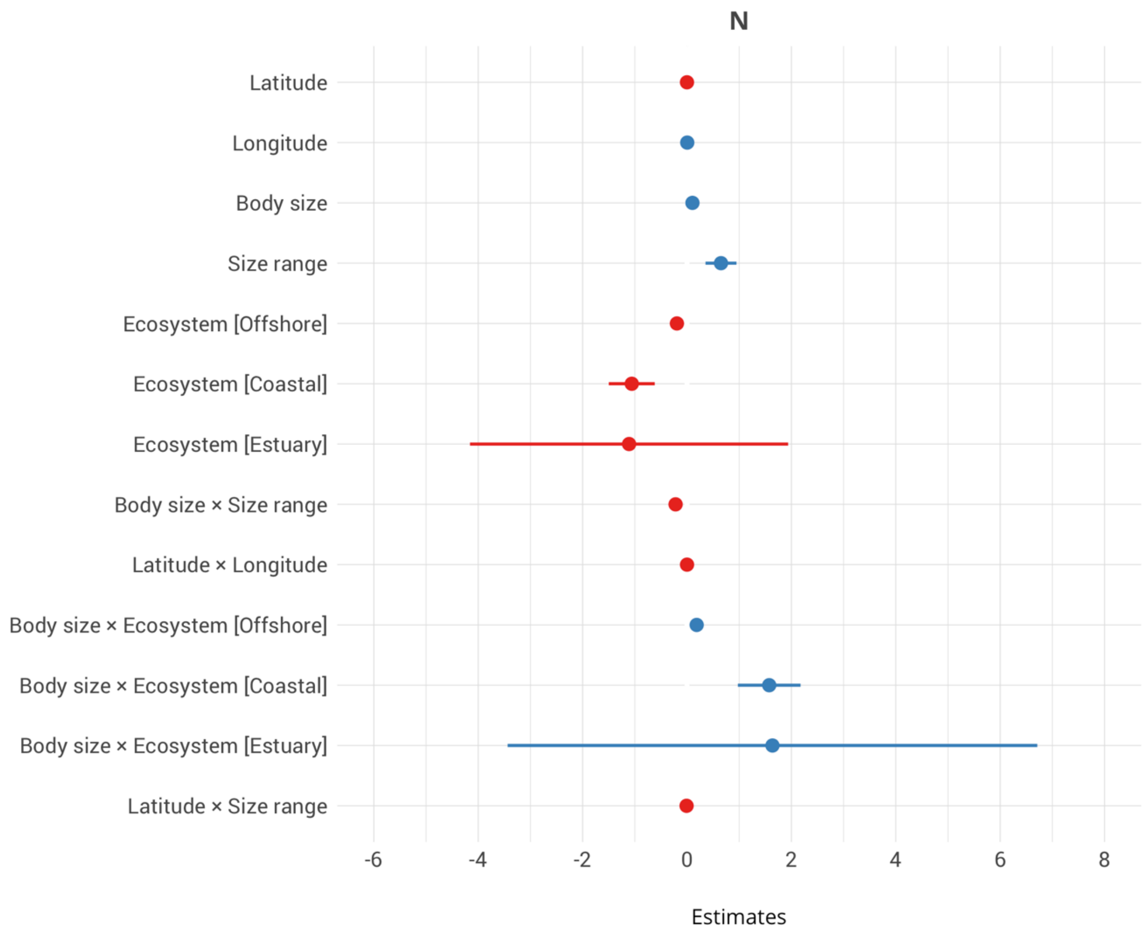

Figure 4.5 Forest plot of northern hemisphere best-fit model applied to dietary niche data with small sample sizes (*n* <100) excluded. Red dots indicate negative effects, while blue indicate positive. Ecosystem, body size, and their interaction remain significant and explain a large amount of variation in niche breadth. (N = 42; R^2 = 0.93)

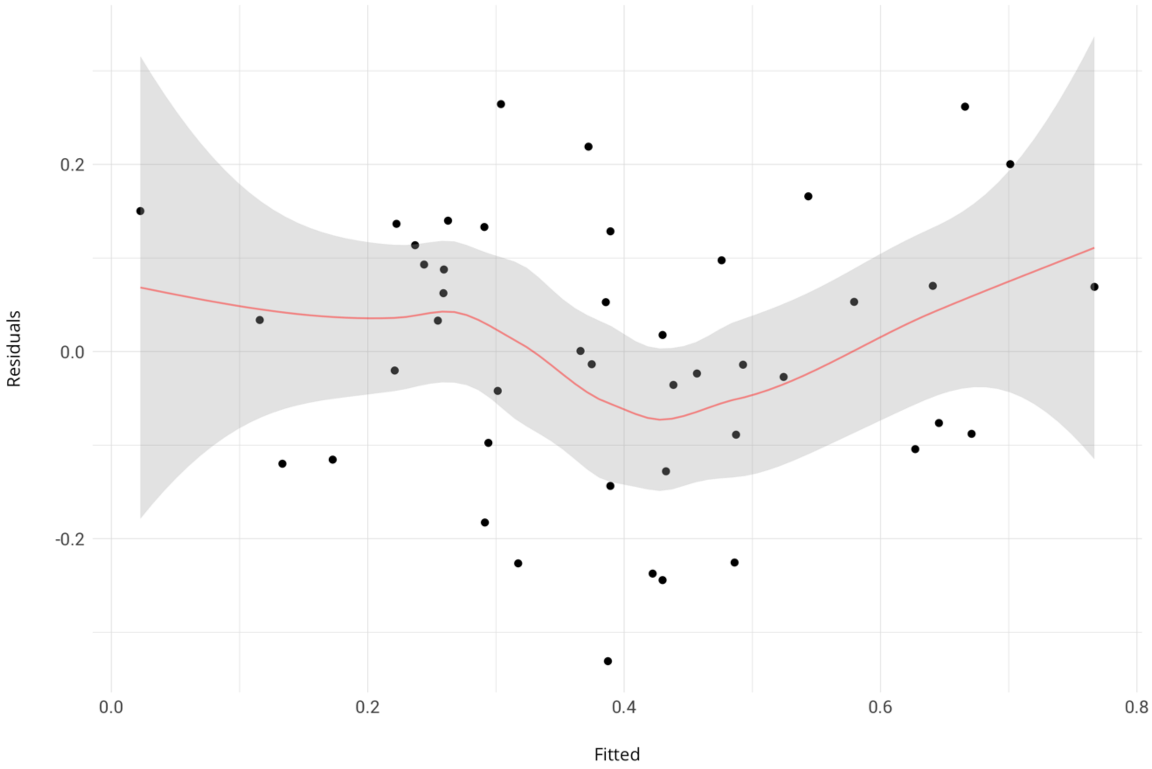

Figure 4.6 Pearson residuals versus fitted values (Standardized Levin's dietary niche) for the southern hemisphere linear model applied to data with small sample sizes (*n* <100) excluded.

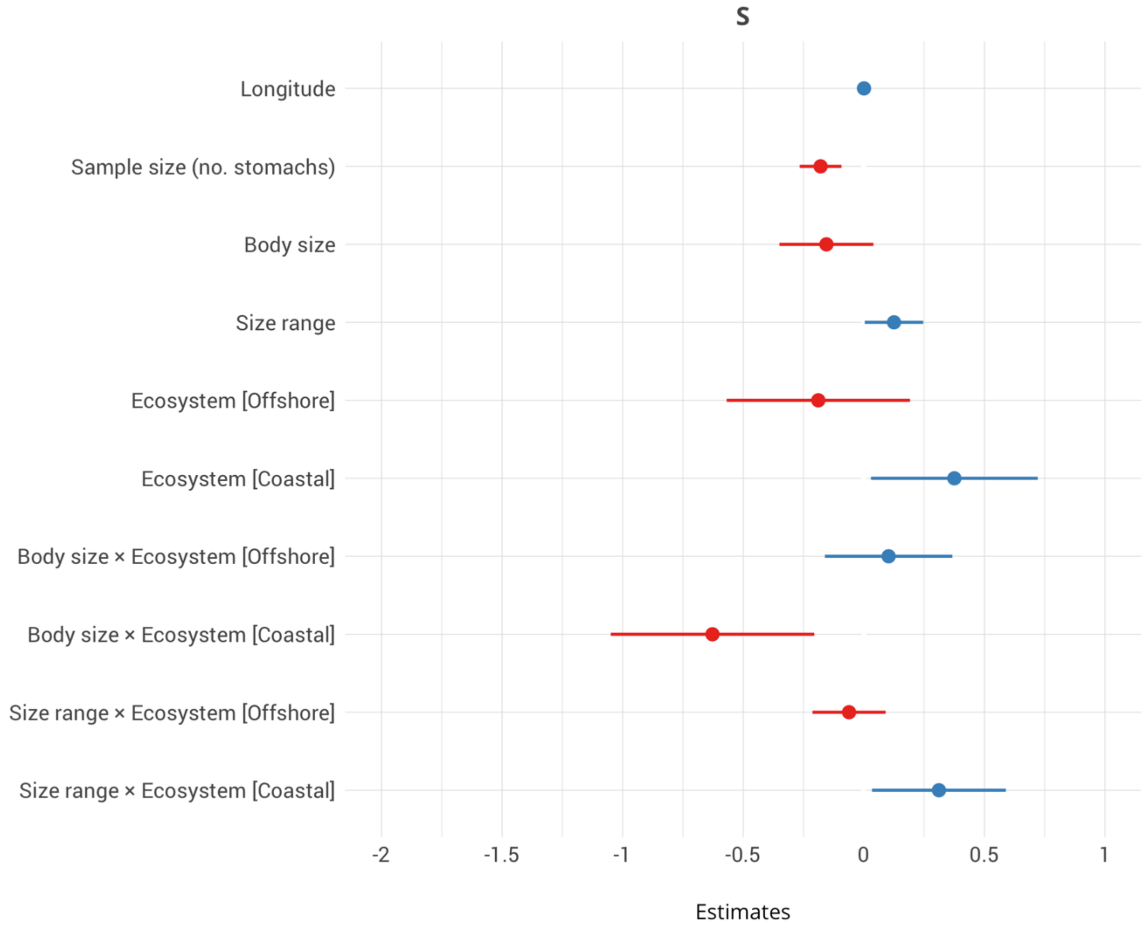

Figure 4.7 Forest plot of best fit southern hemisphere model applied to dietary niche data with small sample sizes (*n* <100) excluded. Red dots indicate negative effects, while blue indicate positive. Ecosystem, body size, and their interaction remain significant and explain a large amount of variation in niche breadth. (N = 45; R^2 = 0.59)

4.6 *Clade-only models*

As clade was highly colinear with other model parameters, a separate suite of models was run in order to test the effect of clade on niche breadth. Model selection then proceeded as described in the main text (see "Methods" above). In both the northern and southern hemispheres, clade was a poor predictor of niche breadth (Supplemental Table 8).

Supplementary Table 8. Best-fit northern and southern models applied to niche breadth without clade compared to best-fit northern and southern models with clade.

Hemisphere	**Expression**	**df (df resid)**	**AIC**	**ΔAIC**	**R^2**
Northern *n* = 118	ss + dpe + s + lr + dr + e + fg + e:fg + e:lr + e:dr + s:fg + s:dr + s:lr + s:e + dpe:lr + RE(Study)	36 (82)	-119.5	—	0.75
	ss + dr + c + e + e:c + e:dr	18 (100)	-84.3	35.2	0.39
Southern *n* = 119	ss + dpe + s + sr + dr + e + fg + s:d + s:fg + s:dr + fg:dr	23 (96)	-67.0	—	0.60
	ss + dpe + s + sr + lr + dr + c + e + e:c + e:lr + s:sr + lr:dr	25 (94)	-39.0	28.0	0.53

c, clade; ss, sample size; dpe, distance to polar edge; s, predator size; sr, predator size range; lr, latitudinal range; dr, depth range; e, ecosystem; fg, functional group; long, sampling longitude; lat, sampling latitude; RE(Study), study as random effect.

4.7 SEA$_B$ and KDE methodology

Dietary niche was averaged together by species in order to obtain a single mean dietary niche value per elasmobranch species. This mean value was then compared to mean isotopic or telemetric niche value (see below) in order to create Fig. 3.1.

4.7.1 Isotopic niche

Isotopic ratios derived from animal tissues can be used to estimate isotopic niche (Bearhop et al., 2004; Newsome et al., 2007). Isotopic niche was calculated as Bayesian standard ellipse areas (SEA$_B$) in carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic space with the **`R`** package `SIBER`, following methodology outlined in Jackson et al. (2011) and using data prepared by the Chondrichthyan Stable Isotope Project (CSIDP; https://github.com/Shark-Isotopes/CSIDP; see Bird et al., 2018 for detailed methodology on compilation of the CSIDP dataset). SEA$_B$ was calculated for each species in the CSIDP dataset by sampling region. In order to derive a single isotopic niche value per species, SEA$_B$ for each species across all regions was then averaged together.

4.7.2 Telemetric niche

Home range size can be used as a proxy for space use and is frequently used in studies comparing other metrics of niche breadth to home range size (Slatyer et al., 2013). Home ranges were calculated as 50% kernel density estimates (KDE) using telemetry data (Kie et al., 2010; Silva-Opps et al., 2011) of satellite tagged sharks prepared by the Global Shark Movement Project (GSMP; https://www.globalsharkmovement.org; for detailed methodology of telemetry data preparation, see Queiroz et al., 2019). GSMP data were first filtered to only include telemetry tracks 1) derived from SPOT tags, as they have higher spatial accuracy (Hammerschlag et al., 2011) and 2) with greater than 5 detections. Detections were then gridded at a 0.25° spatial resolution and reprojected into equal area projections by UTM zone in order to obtain eastings and northings, in meters, for each detection, prior to any spatial analysis involving area calculations. Home range, measured as 50% kernel density estimations in m^2, was then calculated for each species in each region using the **R** package `latticeDensity` (Barry & McIntyre, 2011), resulting in one KDE estimate for each species-region combination (*i.e.*, one KDE estimate per regional population). Detection data were not temporally partitioned and as such this estimate represents a 50% KDE across the entire lifetime of the tag. KDE estimations for each species within a region were then averaged together to derive a mean home range size per species.

4.7.3 References

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