

Defining shark ecological specialisation: concepts, context, and examples

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Abstract Sharks are traditionally classified as generalists that use a diverse range of habitats and prey. While this is an accurate description of some species, sharks exhibit a range of resource use strategies that affect their influence on communities. These strategies also influence resilience in the face of environmental and anthropogenic effects. Identifying resource use patterns is critical to understanding sharks in aquatic environments. However, despite the rapid increase in studies focused on measuring the dietary and habitat selection patterns of sharks, discussion on how to define the ecological specialisation of sharks has been limited. This is an impediment to communication and research as definitions of specialisation and how to measure it vary based on context. This review presents a conceptual framework within which to define the specialisation of sharks that can be applied to different

environmental scales and goals. We present examples of species with varying degrees of specialisation at large and small scales within the proposed context. The effects of specialisation on population stability are also briefly discussed. Specialists are more sensitive to environmental fluctuations and thus more susceptible to population depletion following environmental changes. Therefore identifying specialised species is key to understanding species vulnerabilities and advancing ecological discussions.

Keywords Niche-breadth · Selection · Habitat use · Diet · Sharks

Introduction

Sharks are found in the majority of aquatic environments and as higher trophic level consumers they have direct and indirect influences on community structure and function (Stevens et al. 2000; Heithaus et al. 2008). Given the significant influence sharks have on marine and freshwater ecosystems, a growing body of literature has quantified shark relationships with their environment, specifically habitat use, distribution, and diet (e.g. Carlisle and Starr 2009a, b; Cabrera-Chávez-Costa et al. 2010; Cartamil et al. 2010; Clarke et al. 2011). These data are critical to the creation of successful management solutions for declining and

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endangered populations as well as ecosystems as a whole. Recognition of differing strategies leads to a better understanding of a species' strengths and vulnerabilities in their environment and aids conservation programs (Dulvy et al. 2008; Chin et al. 2010; Simpfendorfer et al. 2011).

Two broad resource use strategies exist among organisms. There are generalists that have large ecological niches and use a wide range of resources; and specialists that have relatively small ecological niches and use a comparatively narrow range of resources (Futuyma and Moreno 1988; Irschick et al. 2005). In the past sharks have been depicted as mobile generalists with wide, sometimes global, ranges that feed opportunistically rather than foraging for specific prey items (Wetherbee et al. 1990). While this is an accurate description for some species, research has revealed others specialise in habitat and prey selection. In reality, species exhibit strategies across the continuum between these two extremes (Compagno 1990). The use of generalist or specialist strategies has distinct implications for the populations that adopt them, with costs and benefits resulting from each (DeWitt 1998; Richmond et al. 2005; Colles et al. 2009). Therefore, knowledge of which species uses each strategy is essential to not only understanding ecological interactions but also to the development of appropriate management schemes. For these reasons, as shark research advances, a greater number of studies will aim to define shark resource use as selective, opportunistic, specialised or generalised. The application of ecological theory to analyse variability in resource use is also likely to increase.

Unfortunately, similar to other fields of ecological research, definitions for what is meant by “selection”, “specialist” or “generalist” are rarely stated in literature. Lack of definition has led to confusion in shark ecology over the appropriate application of these important concepts. As a consequence of this confusion, specialisation is either poorly articulated in publications or inferred using inappropriate methodologies. These incorrect classifications inhibit discussion and make it difficult to accurately compare one species to another. There are two primary reasons for the absence of definition in shark literature. First, there is inherent difficulty associated with applying ecological theory to an analytical framework (Chase and Leibold 2009). Second, it has only recently become possible to develop accurate theoretical guidelines for

defining and measuring shark resource due to advancements in animal tracking and dietary analysis. As a result, there has been limited scientific discussion on how best to define specialisation and classify sharks. However, as the aforementioned terms are used more often (ex. Taylor and Bennett 2008; Wilga et al. 2012), it is important to link applied science with the theoretical concepts of resource use. Lack of definition will lead to the continued misuse of concepts, the incorrect classification of species, hinder research progress, and impede successful management efforts.

Definitions of each concept and how best to measure them can vary based on context and the authors analytical intent (Berenbaum 1996; Poisot et al. 2012). Therefore, a well structured definition and conceptual framework for specialisation should be tailored for specific types of research. How specialisation should be defined is dependant not only on broader ecological theory, but also on the organism, the scale of the study (species to individual), and the type of specialisation being evaluated (e.g. behavioural, dietary, habitat) (Irschick et al. 2005; Devictor et al. 2010). Moreover, selection and specialisation have similar quantitative and qualitative characteristics. Therefore, it is important to define each term in context to prevent interchangeable and inconsistent use. In order to alleviate the current confusion in shark literature, highlight the importance of contextual definitions in shark ecology, and showcase the diversity of strategies among sharks, this review will: (1) discuss the theoretical differences between the related but distinct ideas of selection and specialisation; (2) propose an ecological definition and conceptual framework for resource specialisation widely applicable to shark species; (3) review a range of ecological adaptations of sharks within the proposed context in two important foci: diet and habitat; and (4) briefly discuss the potential implications of these strategies on species resilience.

Defining shark specialisation: terminology and the continuum concept

Multiple forms of specialisation exist among sharks, including morphological specialisations such as the long upper caudal lobe of the common thresher shark *Alopias vulpinus* (Bonnaterre 1788) (Aalbers et al. 2010); behavioural specialisations such as the

ectoparasitic feeding strategy of the cookie cutter shark *Isistius brasiliensis* (Quoy & Gaimard 1824) (Papastamatiou et al. 2010); and ecological specialisations such as the specialised cephalopod-based diet of the whiskery shark *Furgaleus macki* (Whitley 1943) (Simpfendorfer et al. 2001b). Therefore differentiation between unique forms of specialisation requires definitions designed to suit the goals and scale of the research (Futuyma and Moreno 1988; Irschick et al. 2005). This review is focused on defining shark ecological specialisation. Therefore, all terminology has been tailored to fit within that context.

Four terms are primarily used to describe shark resource use. Selection is defined as the use of resources out of proportion or in different proportions to their availability. Opportunism, selection's conceptual opposite, is defined as the use of resources in the same proportion as their availability (Johnson 1980; Buskirk and Millspaugh 2006). Selective animals bypass certain resources in favour of others; whereas opportunistic animals use whatever is available. It is typically quantified for one resource at a time. Measurements of several resources are compared to each other to determine relative levels of selection for any given resource (Manly et al. 2002). The term specialist describes species, populations, or individuals that have a narrow or restricted niche breadth. Generalists are species, populations, or individuals that have a large niche breadth (Vandermeer 1972; Devictor et al. 2010). Niche breadth is a collective measurement of all resources used relative to the resources available within the environment as a whole (Colwell and Futuyma 1971). Although selection and specialisation may seem quite similar (i.e. a highly selective species is likely to have small niche breadth), the terms are not interchangeable. The main difference being one is measured in reference to an animal's niche (specialisation and generalisation) and the other measures the proportion of an animal's resource use (selection and opportunism). Therefore analytical methods that can determine an animal's selectivity may not be equally capable of measuring a species' level of specialisation.

To build a definition for specialisation that is more specific and better suited to shark resource use, an ecologically appropriate conceptual framework must be developed. Although animals are often defined using the opposing categories of specialist or generalist, in nature, specialisation is more accurately

depicted as a continuum, where species are ranked along a specialisation gradient ranging from the largest to smallest possible niche. In this framework, sharks become less specialised with increasing niche breadth. Highly specialised species are those with very small niche breadths. A continuum context for defining shark specialisation is beneficial because while some sharks may be good examples of specialists or generalists, most sharks will not meet the strict requirements of either definition. Such species cannot be easily categorized. For example, a hypothetical species that selects for specific resources in a given environment, while avoiding others, cannot be defined as a generalist without exception because it has a somewhat restricted niche. However, if the same species has a large niche compared to other species in the environment, it is also not a specialist. Such strategies and resulting niche breadth values exist somewhere between a generalist and a specialist. Therefore, when studying shark resource use patterns and defining behaviours, it is more appropriate to measure and refer to a species' degree of specialisation, rather than categorizing a species as one extreme or the other. This concept is also quantitatively appropriate as most traditional measurements of specialisation have used a sliding scale or index to measure specialisation (e.g. Levins 1968; Feinsinger et al. 1981; Smith 1982). Modern methods also measure specialisation using some form of gradient or relative comparison (e.g. Julliard et al. 2006; Fridley et al. 2007; Peers et al. 2012).

Defining shark specialisation: the ecological niche of a shark

To finalize a definition and contextual framework for shark specialisation, scientists must also define the ecological niche of sharks. This is necessary to implement a test for specialisation because it is the main component of the definition. However, there are a number of different definitions and contradictory visions of the niche concept. It is also an unpopular term with some ecologists (Chase and Leibold 2009). As a result, there can be confusion as to what ecologists mean when they discuss a species' niche (Leibold 1995; Peterson et al. 2011). This review will not enter into a broader discussion of niche theory, as we are only interested in finding a functional definition

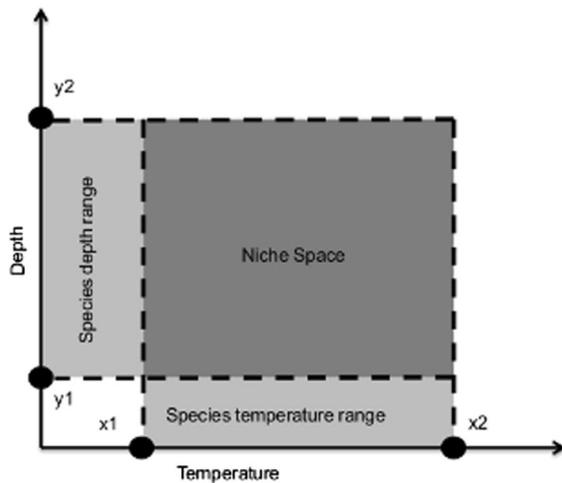


Fig. 1 A hypothetical example of Hutchinson's niche space with two commonly examined shark habitat use variables, depth (y) and temperature (x). x_1 and x_2 denote a species' temperature range, y_1 and y_2 denote a species' depth range. The dark grey space created by these overlapping ranges is the niche space of an organism, any point within which it can survive. Any point outside it is not considered a part of the species niche

for niche as it pertains to shark resource use. With that in mind, we will briefly review the most prevalent contributions to niche theory to develop an appropriate definition for shark specialisation.

Two major conceptual contributions to niche theory have dominated modern definitions. The first was put forward by Grinnell (1917) and advanced by Hutchinson (1957). According to these works a niche is defined as the range of resources a species uses in an environment or the conditions in which it can survive. In other words, a Grinnellian niche is defined by “what a species needs” or uses (Devictor et al. 2010). The second definition was developed by Elton (1927), who defined a species niche as the role of species in the environment or by “what the species is doing” (Devictor et al. 2010). This definition requires measurements of all the ways in which a species might directly and indirectly effect the environment (Leibold 1995; Devictor et al. 2010).

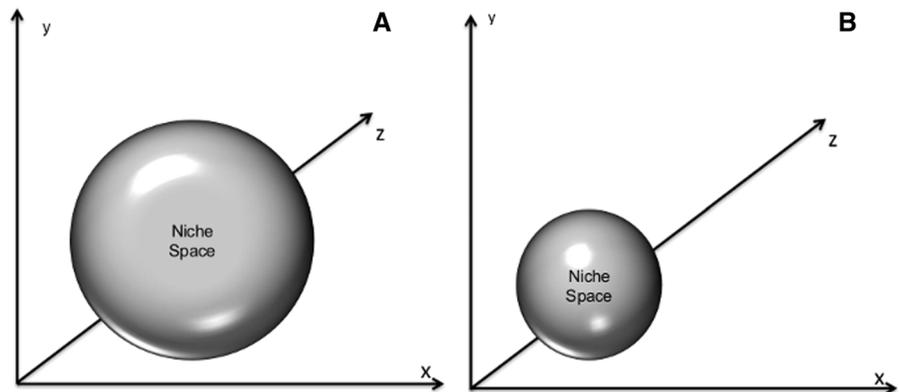
Hutchinson (1957) developed a physical schematic for his definition known as an n -dimensional hyper-volume. Hutchinson proposed that a niche could be plotted on a Cartesian coordinate system where the axes of the plot are environmental variables, such as temperature (x) or depth (y) (Fig. 1). The limiting values or range of values a species uses can be plotted

on each axis. The overlapping ranges of each variable result in a figure that represents the niche space for the species. Any point in this space represents an environmental state in which the species can survive. The space can be defined by any number of relevant environmental variables that affect the species (Hutchinson 1957; Chase and Leibold 2009), eventually creating a multi-dimensional hyper volume. A less specialised species niche space would be distributed among all or a large portion of the environment's resources and conditions (Vandermeer 1972; Fig. 2a). A highly specialised species niche space would be relatively concentrated over one or a few resources or conditions (Vandermeer 1972; Fig. 2b).

Modern applications of niche theory often incorporate both Hutchinson's and Elton's contributions, defining the ecological niche as the response that a species has to each point in Hutchinson's classical environmental space (measured as species survival rate, growth rate, or per capita rate of increase) and the effect that the species has on each point (measured as resource consumption, competition, etc.) (Leibold 1995; Shea and Chesson 2002; Chase and Leibold 2009). Information on species competition and predator–prey relationships is important when trying to define a shark's role in the environment or its relationship with other species. However, Hutchinson's definition is more appropriate when measuring resource specialisation because it only considers the resource requirements of species, which is precisely what resource use studies quantify. Moreover, although far from impossible, it can be difficult to measure the response of a species in the wild and relate that response to any given point and variable in the niche space. The advantage of using a “requirements only” approach is researchers do not need to measure response variables (Peterson et al. 2011). There are also numerous methods available to measure specialisation that incorporate Hutchinson's niche model. The best method for analysis will depend on the goals of the experiment. Regardless of the method chosen, at their core tests will compare the range of resources used by a species (the niche space) to the range of resources available in the environment, resulting in the relative niche breadth of the species (e.g. Smith 1982; Basille et al. 2008; Poisot et al. 2012). The inverse of the relative niche breadth can be used to measure the degree of specialisation.

Using Hutchinson's definition of niche space and the continuum concept described earlier, it is possible to develop a widely applicable definition for

Fig. 2 **a** Depiction of a hypothetical Hutchinson (1957) niche hyper-volume of a species with a large niche breadth, indicating a lesser degree of specialisation. **b** Depiction of a hypothetical Hutchinson (1957) niche hyper-volume of a species with a narrow niche breadth, indicating a greater degree of specialisation



measuring shark specialisation. We propose sharks, rather than being categorically defined, should be ranked along a continuum as more or less specialised relative to an index and other species. Ranks or positions along this continuum should be determined by measuring the resource niche breadth of a species as described by Hutchinson's hyper-volume. Therefore, a highly specialised species can be defined as those with a relatively narrow niche breadth compared to the range of resources or conditions available to the species within the environment. It is essential that the methods for measuring niche breadth use a scale or index. Methodologies should not rely solely on a binary system of classification or an arbitrarily value within an index above or below which a species is classified as a specialist. This violates the continuum concept that is the core of this definition. Note that the relevant environmental parameters will be based on the scale of the experiment and are best left to the researcher to define. However, definitions of the available environment will affect the interpretation of any measure of specialisation and its comparability to other studies. Therefore environment and scale should be carefully considered when utilizing ecological terminology, choosing appropriate methods, and making assessments.

This definition is well suited to sharks as specialisation is often measured at different temporal and physical scales. The environmental and temporal parameters of any study can be adjusted to suit a ranking system. The use of a continuum concept is also more ecologically realistic as many sharks are not

likely to meet the traditional definition of a specialist or generalists. A rank system avoids the use of definitive categorical language when it is not appropriate. Finally, a ranking system which defines species as more or less specialised also makes it easier to compare trends between groups, even those separated over large distances that may be exposed to different resources. A ranking system that compares niche breadth instead of selectivity for a single resource may better account for differences in environmental circumstances.

Unfortunately, limited information on the diet or habitat use of many sharks currently precludes the ability to fully assess species resource specialisation. Therefore, the ranking of some species as more or less specialised will be unavoidably speculative. However, having a clear understanding of what is meant by specialist gives researchers the ability to better classify species, study their role in the environment and communicate their findings.

Shark habitat specialisation

Habitat specialists, defined as species that use a narrow range of habitat types relative to the environment, inhabit a smaller niche space compared to their less specialised counterparts. As a result habitat restricted species will occupy one end of the specialist continuum and those that use a large number of habitats will occupy the other. More specific rankings of organisms are affected by the scale of the study and the habitat

parameters evaluated. Habitat use can be evaluated at large (e.g. Weng et al. 2005) or small scales (e.g. Morrissey and Gruber 1993) and selection can be measured across numerous variables, including depth (Knip et al. 2011), temperature (Campana and Joyce 2004), salinity (Heupel and Simpfendorfer 2008), and bottom type (Espinoza et al. 2011). Patterns in habitat use may also change over time (e.g. daily, seasonally) (Carlisle and Starr 2009a, b; Ortega et al. 2009). Therefore, when analysing habitat specialisation it is important to clarify the scale of the study in relation to the continuum definition. On a local scale, most sharks are thought to have relatively large habitat ranges; however, there are few measurements of niche breadth or broad studies of habitat use for many shark species. Moreover, scale and methodology differ widely between studies, making it difficult to rank species against one another. Therefore, this discussion will limit itself to better studied species and research testing selection or specialisation to highlight the importance of defining scale in resource use studies and the diversity among species.

On a global scale, species with low levels of habitat specialisation include the tiger shark, *Galeocerdo cuvier* (Péron & Lesueur, 1822) and the great white shark, *Carcharodon carcharias* (L. 1758). *Galeocerdo cuvier* has been found in temperate and tropical waters with reports of individuals being found as far north as Iceland and the United Kingdom (Compagno 1984; Randall 1992). They are also known to use coastal and offshore habitats e.g. (Randall 1992; Holland et al. 1999; Heithaus et al. 2007; Meyer et al. 2009). *Carcharodon carcharias* also have large, cosmopolitan geographic ranges and use both coastal and oceanic habitats (Compagno 2001; Bruce 2008; Jorgensen et al. 2010; Carlisle et al. 2012). *Carcharodon carcharias* are also known to undertake wide ranging migrations (Pardini et al. 2001; Boustany et al. 2002; Bonfil et al. 2005; Weng et al. 2007).

However, habitat use is more often evaluated at smaller scales (regionally and locally) and low specialisation rankings can be applied to species if the scale of evaluation is clear. For example, species may have low degrees of specialisation over a single environmental parameter. Juvenile lemon sharks, *Negaprion brevirostris* (Poey, 1868), acoustically tracked in nursery grounds in Bimini Island, Bahamas, showed no preference for specific water temperatures. Instead, individuals selected for the warmest possible

waters during the day and cooler waters in the evening (DiGirolamo et al. 2012). As a result, individuals used the range of available temperatures within its home range in a day (DiGirolamo et al. 2012). Based on the proposed definition and measured at a local scale, the use of a wide range of temperatures relative to the daily available range indicates this population has a low degree of temperature specialisation. However, DiGirolamo et al. (2012) did not directly test species niche breadth or selectivity. Also note that while juveniles have a low degree of specialisation, there was selection for temperatures depending on the time of day. This highlights the importance of separating the concepts of specialisation and selection.

Species that have moderate habitat niche breaths will have neither high nor low degrees of specialisation. Species with varying levels of resource selectivity, that may avoid some habitats while using others, will likely equate to a moderate niche breadth. Such species cannot be easily defined in categorical terms and demonstrate the usefulness of a continuum scheme for specialisation. For example, young bull sharks, *Carcharhinus leucas* (Müller & Henle, 1839), tracked in the Caloosahatchee River Estuary, Florida, showed strong avoidance for areas with salinities less than 7 while showing affinity for salinities between 12 and 20 (Heupel and Simpfendorfer 2008). Heupel and Simpfendorfer (2008) suggested juveniles may have been selecting for salinity ranges that reduced their osmoregulatory costs. The importance of salinity in predicting the distribution of young *C. leucas* was suggested by (Simpfendorfer et al. 2005), however, this study did not use selectivity indices to analyse behaviour. Although niche breadth was not measured, the avoidance of some salinity ranges and the selection of others would likely result in a moderate niche breadth and degree of specialisation for this population. This example also demonstrates the importance of clarifying definitions for selection and specialisation. *Carcharhinus leucas* may be selecting for specific salinities, but they are not highly ecologically specialised along this parameter. Scale and location will also affect how ranking is determined. For example, although *G. cuvier* utilizes a wide range of habitats globally, on a local scale they appear to select for specific microhabitats. Acoustically tracked *G. cuvier* in Shark Bay, Western Australia, selected for shallow banks covered in sea grass and avoided deeper sand habitats (Heithaus et al. 2006). Selectivity was

likely the result of increased prey availability within shallow areas (Heithaus et al. 2002, 2006). As a result the habitat niche breadth is likely smaller than that expected at a global level.

A lack of studies that measure the habitat niche breadth of sharks makes any speculative rankings presented here potentially controversial. However, some of the best examples of habitat specialisation among sharks are coral reef associated species, a notable exception being the blacktip reef shark, *Carcharhinus melanopterus* (Chin et al. 2012). Species with high degrees of specialisation likely include the whitetip reef shark *Triaenodon obesus* (Rüppell, 1837), the grey reef shark *Carcharhinus amblyrhynchos* (Bleeker, 1856), and the Caribbean reef shark, *Carcharhinus perezi* (Peoy, 1876). *Triaenodon obesus* is most often found within or very near reef habitat and their morphology indicates they are well adapted to forage in reef environments (Randall 1977; Last and Stevens 2009; Whitney et al. 2012). *Carcharhinus amblyrhynchos* are almost exclusively found on and near reef habitat (Compagno 1984; McKibben and Nelson 1986; Economakis and Lobel 1998; Heupel and Simpfendorfer, in press), although individuals may make long distance movements between habitat patches (Heupel et al. 2010). *Carcharhinus perezi* are also closely associated with reef habitat (Pikitch et al. 2005; Garla et al. 2006a, b; Chapman et al. 2007).

Unfortunately, determining where sharks should be placed along the specialist continuum is limited as little is known about the habitat preferences of most species. Data collection is hindered by the difficulties associated with habitat use evaluation, particularly in the marine environment. Traditional techniques used to evaluate animal movements and habitat preferences, such as tag and recapture and fishing surveys, only provide short-term (<10 years) data and do not monitor the lifetime of an individual. While these studies can offer valuable insight into animal distribution (Kohler and Turner 2001), population size (Dicken et al. 2008), and survival rates (Gruber et al. 2001), these techniques only provide snapshots of an individual's habitat use (Gruber et al. 1988; Holland et al. 1993; Holts and Bedford 1993). It may also be difficult to measure the availability of various habitat types and variables meaningful to the animals in the environment. Therefore, accumulating data for habitat use assessments can be a slow process and the degree of habitat specialisation of many species will remain

uncategorized in the near future. However, based on the previous examples it is clear there is significant variance in the habitat specialisation and selection patterns of sharks. These examples also demonstrate how defining scale and intent has a large influence on the use of ecological terminology and its interpretation. By utilizing a continuum concept of specialisation, parameters can be set according to the needs of the research and result in less arbitrary use of terms. Detailed analysis of shark habitat use incorporating sound definitions as well as new techniques may reveal that more species are highly selective or more specialised than currently known.

Shark dietary specialisation

Optimal foraging theory states that individuals in a population should attempt to forage at maximum efficiency to ensure a large net energy return for their efforts (Townsend and Winfield 1985; Stephens and Krebs 1986). However, evaluation of foraging theory and dietary specialisation are context dependant. Fluctuating factors such as competition may cause species that naturally adopt opportunistic feeding patterns to become highly selective (e.g. Papastamatiou et al. 2006). Diets may differ between species, populations of the same species, and between age classes and sexes within populations (Bethea et al. 2006; Edwards et al. 2011; Sommerville et al. 2011). Reasons for this include differences in body shape and size, ability to locate and capture prey, and ability to process and digest what has been caught (Lowe et al. 1996; Heupel and Bennett 1998; Dean et al. 2005; Bethea et al. 2006; Brischoux et al. 2011). Predator avoidance tactics may lead to a different diet than that predicted by optimal foraging theory (Gill 2003) and individuals may forage sub-optimally if doing so reduces their exposure to predation (Heithaus and Dill 2002). Finally, dietary analysis can be skewed by temporal shifts in prey availability where predators switch between prey items as they become more or less available (Lucifora et al. 2006). Therefore, evaluations over short time scales may be misleading in fluctuating environments. The method of evaluation may also affect definitions and interpretations of species dietary patterns. For example, traditional methods such as stomach content analysis may provide more detailed information on dietary patterns

(Ba et al. 2013), whereas stable isotope analysis, an increasingly popular method for shark diet and movement analysis, can provide long term, integrated data (Hussey et al. 2012). Therefore, when measuring niche breadth or diet selectivity it is necessary to consider environmental and morphological variables and what is available to the predator, both in terms of prey abundance and what it has the ability to capture (Backwell et al. 1998). Similar to habitat analysis it is important to clarify the temporal and spatial scale and intention of a study when calculating specialisation and selection.

At a global scale, species that are traditionally considered to have low degrees of dietary specialisation over a large scale include the spiny dogfish, *Squalus acanthias* L. 1758, which feeds on a diverse array of prey, including pelagic and benthic species, over its entire range (Jones and Geen 1977; Compagno 1984; Hanchet 1991; Tanasichuk et al. 1991; Link and Ford 2006; Brodeur et al. 2009). In Argentinean waters, *S. acanthias* feeds on teleosts, squid, ctenophores and molluscs (Alonso et al. 2002). In the southeastern Black Sea, *S. acanthias* preys on teleosts, crustaceans, sea anemones and nematodes (Avsar 2001). Larger species with a broad diet includes *G. cuvier*. In Hawaiian waters, large individuals (>200 cm) were found to have a varied diet including teleosts, elasmobranchs, crustaceans, birds, mammals, turtles, and cephalopods (Lowe et al. 1996). In Australian waters, *G. cuvier* also has a wide dietary niche. Individuals on the western Australian coast feed on teleosts, crustaceans, marine mammals and reptiles, elasmobranchs and cephalopods (Heithaus 2001; Simpfendorfer et al. 2001a), while on the north eastern coast *G. cuvier* feed on teleosts, marine reptiles, crustaceans, and to a lesser extent marine mammals and cephalopods (Simpfendorfer 1992). At a smaller regional scale, stomach content analysis of the small spotted cat shark, *Scyliorhinus canicula* (L. 1758), from the north eastern Atlantic coast found the species fed on a variety of prey, including crustaceans, teleosts, annelids, and molluscs (Ellis et al. 1996). *Scyliorhinus canicula*'s dietary niche breadth was calculated and equated to a low degree of dietary specialisation. In comparison to other species similarly surveyed in the same study, *S. canicula* had one of the smallest dietary niches.

Varying patterns in dietary selectivity can result in niche breadths that rank species in between the two

extremes of the specialisation continuum. For example, Baremore et al. (2008) examined the stomach content of Atlantic angel sharks, *Squatina dumeril* (Lesueur, 1818), captured in the northeastern Gulf of Mexico and compared it to the trawl fishery catch composition to calculate *S. dumeril* niche breadth index and dietary selectivity. Stomach content analysis revealed *S. dumeril* fed on a variety of prey, but relative to prey availability, *S. dumeril*'s diet equated to a moderate niche breadth [0.51 with Levin's standardized index (B_A)] (Baremore et al. 2008). These results indicated *S. dumeril* was neither highly specialised nor generalised. *S. squatina* demonstrated both opportunistic and selective behaviours by feeding on fish in high abundance (opportunistic) as well as fish and cephalopods (primarily squid) found in relatively low abundance (selective). This example also highlights the importance of using the continuum concept to measure specialisation rather than trying to categorically define species as either specialists or generalists. Varied patterns in behaviours and changing conditions may result in niche breadth values that cannot be easily designated as one or the other.

Dietary selectivity can also change as a result of fluctuations in prey abundance and availability over time and space. Changes in dietary patterns can affect niche breadth measurements and alter the predicted placement of a species on a specialisation continuum. For example, although juvenile *N. brevirostris* have broad dietary niches, and therefore would likely not have high degrees of specialisation, a controlled field-pen study found *N. brevirostris* may be a highly selective feeder. Caged *N. brevirostris* were fed varying ratios of two prominent prey in their diet, the grey snapper, *Lutjanus griseus* (L. 1758), and the yellow fin mojarra, *Gerres cinereus* (Walbaum, 1792). Results showed *G. cinereus* was selected for over *L. griseus* and that selectivity for *G. cinereus* increased as its relative abundance increased, highlighting the affect of changing prey abundance on diet and indicating *G. cinereus* is a highly preferred prey (Reeve et al. 2009). Both *N. brevirostris* dietary selectivity and preference for mojarra (Gerreidae) were supported by field based stomach content analysis (Newman et al. 2010). Populations within the bays of Bimini Island selected for prey based on type and size when environmental conditions were favourable and prey abundance was high (Newman et al. 2010). However, populations fed more

opportunistically in relatively poor conditions. Therefore, *N. brevirostris*' niche breadth will vary as feeding strategies change in response to environmental fluctuations. High levels of selectivity for specific types of prey in favourable conditions may result in a more specialised diet than when conditions are poor. In this case, the advantage of using the proposed definition is researchers can more easily make relative comparisons of behaviour in different conditions by comparing the relative degree of specialisation.

Competition can also have a powerful influence on dietary selection. Co-occurring shark species surveyed in the coastal waters of Hawaii showed limited dietary overlap, but when the diets of these species were surveyed in areas where they did not co-occur, high dietary overlap occurred (Papastamatiou et al. 2006). This suggests that to reduce competition for resources each species was selecting for a non-overlapping subset of resources in the environment. However, when competition was removed or reduced species adopted wider dietary niches. The spatial variation in selection would create variable rankings for the same species and confound a binary attempt to define the species or adjacent populations.

It is important to note that some populations that have large dietary niches may be composed of individual specialists, where each individual uses a subset of resources within the population's broader dietary niche (Bolnick et al. 2002). The combination of individual's non-overlapping, selective diets results in a wide dietary niche for the population. Surveys of populations that do not test for the presence of individual specialisation may incorrectly classify individuals as having large dietary niches (Bolnick et al. 2002, 2003). However, it is difficult to determine how common this strategy is among sharks as it has only recently been investigated among a few species. Matich et al. (2011) quantified the dietary patterns of *C. leucas* and *G. cuvier*, both of which have traditionally been defined as generalist predators, using several individual specialisation indices. The indices revealed that individual *G. cuvier* have wider ranging diets relative to *C. leucas* which had more specialised individual dietary profiles. This suggests the broad dietary range of *C. leucas* may be the result of individual specialisation, not each individual feeding on a large number of prey (Matich et al. 2011). More detailed analysis will hopefully determine if

individual specialisation is a widespread or significant strategy within the taxon.

To date there are few studies that have been able to identify species that exhibit high degrees of dietary specialisation and that can be labelled as such without debate. However, there are some examples where species can be classified as highly specialised. On a global scale, dietary specialists include basking sharks, *Cetorhinus maximus* (Gunnerus, 1765) and whale sharks, *Rhincodon typus* (Smith, 1828), both of which have a highly specialised feeding mechanism (Hallacher 1977; Colman 1997) evolved to capture prey of a specific size, namely zooplankton (Colman 1997; Sims and Quayle 1998; Stevens 2007). In the case of *R. typus*, prey include fish spawn and plankton (Martin 2007), crab larvae (Meekan et al. 2009), copepods (Clarke and Nelson 1997; Motta et al. 2010), and krill (Jarman and Wilson 2004). On smaller geographical scales, a potential dietary specialist includes *F. macki*, a species endemic to western Australia (Last and Stevens 2009). Although its diet was not compared to prey availability, stomach content analysis found the species feeds almost exclusively on octopus and other cephalopods. Its diet was significantly less varied than other shark species captured simultaneously in the same habitats (Simpfendorfer et al. 2001b). Also at a regional level, stomach content analysis of the starry smooth-hound, *Mustelus asterias* Cloquet, 1819, captured in trawl surveys on the north eastern Atlantic coast found the species feeds almost exclusively on brachyuran crabs. Niche breadth measurements revealed the species had a high degree of dietary specialisation in comparison to almost all other elasmobranchs examined in the study (Ellis et al. 1996).

The term specialist can also be applied at smaller physical or temporal scales; however context must be clearly articulated. For example, the stomach contents of the school shark, *Galeorhinus galeus* (L. 1758), surveyed in Anegata Bay, Argentina revealed the species had a broad dietary niche (Lucifora et al. 2006). However, Lucifora et al. (2006) found that during the austral summer *G. galeus*'s diet became highly specialised when individuals fed almost exclusively on the benthic teleost *Porichthys porosissimus*, the Atlantic midshipman (Cuvier 1829) (Lucifora et al. 2006). This seasonally small niche breadth is likely the result of opportunistic foraging on the seasonally vulnerable *P. porosissimus*, which mates in the spring and summer when males use sound and

bioluminescent displays to attract their mates. Lucifora et al. (2006) hypothesized these displays make *P. porosissimus* more vulnerable to predators and as a result are more easily targeted than at other times of the year. However, caution should be used when considering a species highly specialised over small scales to ensure there is no confusion over intent.

Implications of resource use strategies

Ecological theory states that the niche breadth differences between species are the product of an evolutionary trade-off between the ability of species to use multiple resources and their ability to use each one. Different strategies result in unique costs and benefits for species that have an effect on species ecology (Van Tienderen 1991; Kawecki 1994). Ecological specialisation of sharks will also affect their role in an ecosystem, such as the intensity and spread of direct and indirect effects of predation (Heupel et al. in press). Therefore, defining the resource use patterns of sharks can help to determine the implications of their depletion or removal. Understanding the trade-offs and the resultant vulnerabilities of ecological specialisation can create a clearer picture of environmental dynamics and the role of sharks.

The ability to use multiple resources, and therefore have a low degree of specialisation, is advantageous during times of environmental instability (Chapman and Mackay 1984; Heithaus et al. 2006; Meyer et al. 2010). Species with wide habitat and dietary niches can use resources unaffected by environmental fluctuations or use multiple resources at one time to compensate for the decline in any one resource (Richmond et al. 2005; Julliard et al. 2006; Verberk et al. 2010). Thus, species with wide resource niches can maintain a high level of fitness in unstable environments and will not be as greatly affected by exposure to environmental changes and anthropogenic interference as highly specialised species (Richmond et al. 2005; Julliard et al. 2006; Chin et al. 2010; Verberk et al. 2010). However, these plastic adaptations may incorporate anatomical, physiological, or behavioural mechanisms that require high levels of energy (DeWitt et al. 1998). If environments are stable, these high energetic costs may outweigh the benefits of being highly adaptive (Van Tienderen 1991; Wilson and Yoshimura 1994; DeWitt et al. 1998).

In contrast, high degrees of specialisation are associated with the reduction in or loss of physiological, morphological, or behavioural characteristics, which theoretically reduces energetic costs (Futuyma and Moreno 1988). By adapting to use only one or a few resources, species avoid the high costs of adaptive plasticity (Van Tienderen 1991). Resource detection performance is also greater when an animal is only searching for one item (Futuyma and Moreno 1988; Bernays and Wcislo 1994; Bernays and Funk 1999). Highly specialised species may also utilize resources and assimilate energy from preferred sources more efficiently than species with broad resource niches (Britt et al. 2006). Therefore, if fluctuations in the environment are limited and the preferred environmental state is abundant, then specialisation may be a more successful life strategy (Futuyma and Moreno 1988; Richmond et al. 2005). However, species with high degrees of specialisation incur costs when their preferred resource is not available. Such species cannot easily switch between resources and as a result, when environmental conditions are in a state of flux or resource availability declines, they may have difficulty adapting to the new environmental equilibrium (Dulvy et al. 2004; Munday 2004; Chin et al. 2010). Specialists are more likely to face an increased threat from environmental and anthropogenic changes than species with large ecological niches.

Conclusion

Sharks have been historically described as roaming generalists that feed on whatever resources become available. In reality, various strategies are present among shark species, including selective and opportunistic feeding behaviours as well as highly specialised patterns in resource use. As the field of shark ecology expands and advances, it is important to develop clear, inclusive, and theoretically sound definitions and methodologies to study resource use at small and large scales. Doing so will allow for efficient communication of ideas and more comparable research. Shark ecology, compared to other fields of ecological research, is in its early days, and detailed studies of resource selection and niche breadth have only recently become a prominent feature of the shark literature. This provides shark researchers with a unique opportunity. Shark ecologists can avoid some

hurdles associated with applied ecological studies by deciding now what the most appropriate theoretical basis is to ground analytical studies.

Although it is difficult to quantify the resource use patterns of many shark species due to limited data, this will change as research progresses, and having a structured paradigm within which to evaluate behaviours and consequences will be invaluable to furthering research and communication. Improved knowledge of where shark species lay on the specialisation continuum will result in more accurate predictions of the effects of human induced changes and the development of more effective environmental management. Future research aimed at examining resource use and selectivity of sharks should ensure that tests are based in well supported theoretical schemes and authors clarify their intent by defining terminology and ensuring they are only applied when appropriate.

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