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# The Nutritional Ecology of Marine Apex Predators

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## Keywords

carnivores, nutrition, human impacts, marine pollution, captivity,  
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## Abstract

Apex predators play pivotal roles in marine ecosystems, mediated principally through diet and nutrition. Yet, compared with terrestrial animals, the nutritional ecology of marine predators is poorly understood. One reason is that the field has adhered to an approach that evaluates diet principally in terms of energy gain. Studies in terrestrial systems, by contrast, increasingly adopt a multidimensional approach, the nutritional geometry framework, that distinguishes specific nutrients and calories. We provide evidence that a nutritional approach is likewise relevant to marine apex predators, then demonstrate how nutritional geometry can characterize the nutrient and energy content of marine prey. Next, we show how this framework can be used to reconceptualize ecological interactions via the ecological niche concept, and close with a consideration of its application to problems in marine predator research.

## INTRODUCTION

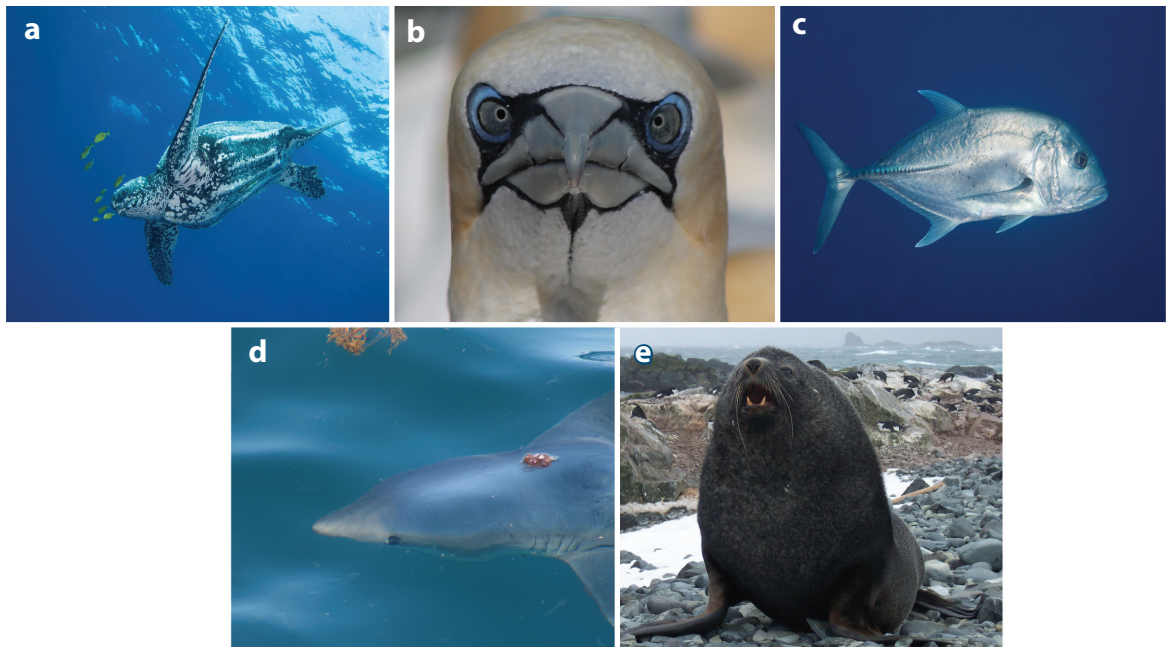
More than 100 years ago, Atwater (1902, p. 12) noted that “to understand what fuels a body we must take into account the chemical composition of the foods and the proportion of nutrients actually digested and oxidized in the body.” Considering that nutrients are fundamental to almost all aspects of an animal’s existence, we could assume that this approach would become the foundation of our knowledge of foraging. Yet dominant frameworks in foraging and community ecology, including optimal foraging theory and such fundamental ecological concepts as food webs and trophic pyramids, are conceptualized largely around single nutritional currencies, usually energy but occasionally nitrogen (protein), rather than the balance of nutrients (Lindeman 1942, Schoener 1971, Pyke 1984, Stephens & Krebs 1986). One framework, ecological stoichiometry, considers the balance of elements (usually carbon, nitrogen, and phosphorus) (Sterner & Elser 2002), but modeling elements is fundamentally different from modeling the balance of nutrients (Raubenheimer et al. 2009).

Recent work in nutritional ecology, including laboratory (Rowe et al. 2018), field (Machovsky-Capuska et al. 2016c, 2018), and theoretical (Kearney et al. 2010; Machovsky-Capuska et al. 2016d, 2019) studies, have demonstrated the potential of moving beyond single currencies such as energy to explicit consideration of nutrient mixtures in order to generate new insights into foraging and its role in structuring populations, communities, and ecosystems (Simpson et al. 2010, Wilder et al. 2013, Tait et al. 2014). The conceptual and methodological approach around which these studies have been structured, known as the nutritional geometry framework, models nutrition as a multidimensional process (Raubenheimer & Simpson 1993, Simpson & Raubenheimer 1993). The application of nutritional geometry to terrestrial animals has shown that protein, lipids, and carbohydrates each play specific roles in foraging over and above their energy contributions, and that this is true for herbivores, omnivores, and carnivores alike (Jensen et al. 2012, Nie et al. 2014, Machovsky-Capuska et al. 2015).

Predators have a fundamental influence on the structure and functioning of marine communities (Boyd et al. 2006). Marine apex predators, which include large predatory fish and sharks, mammals, seabirds, and turtles, often exploit marine habitats and resources at spatial and temporal scales similar to those used by humans (Young et al. 2015). This ecological overlap has stimulated research into their trophic role not only to protect their populations but also to prevent and manage potential conflicts with humans over the use of marine food sources (Maxwell et al. 2013).

Understanding the nutritional ecology of marine predators is thus critical for a range of ecological applications, including theoretical and applied ecology, conservation, and management. Yet the field remains poorly characterized, as evidenced, for example, by the small number of published systematic reviews of the foraging ecology of marine mammals (e.g., Croll et al. 1998, Würsig et al. 2018), turtles (Bjorndal 1997), seabirds (e.g., Croll et al. 1998, Schreiber & Burger 2001), and marine predatory fish (e.g., Ivlev 1961, Scharf et al. 2000).

Our aim here is to demonstrate how multidimensional nutrition offers an alternative framework for examining the nutritional ecology of marine apex vertebrate predators. We first review the existing literature to provide fresh insights into the nutritional drivers of marine vertebrate predators, identify priorities for future research, and present a framework for guiding this research. We then use nutritional geometry to examine the nutritional requirements of marine vertebrate predators and explore how their foraging and nutritional goals shape trophic interactions. We draw on theory from nutritional ecology to understand the nutritional bases for these questions. This comparative view, in turn, provides a broader biological, ecological, and evolutionary perspective on the role of nutrition and foraging choices in marine predators.



**Figure 1**

A selection of marine predators illustrating their diverse habitats and foraging strategies. (a) The critically endangered leatherback turtle (*Dermochelys coriacea*) is the largest of all living turtles and preys on jellyfish worldwide (Heaslip et al. 2012). (b) The Australasian gannet (*Morus serrator*) is a highly specialized visual predator that plunge dives from the air into the water to capture pelagic fish and squid (Machovsky-Capuska et al. 2016c). (c) The giant trevally (*Caranx ignobilis*) inhabits a wide range of warm habitats, including shallow bays, estuaries, and deep reefs, and consumes principally fish, cephalopods, and crustaceans (Scharf et al. 2000). (d) The blue shark (*Prionace glauca*) is the most wide-ranging shark species, having been recorded in all tropical and temperate seas. Blue sharks make daily vertical dives from the surface to depths of 250 m and have a heterogenous diet that spans cephalopods, crustaceans, fish, and birds (Carrier et al. 2012). (e) The Antarctic fur seal (*Arctocephalus gazella*) lives primarily in breeding colonies on islands close to the Antarctic Convergence. These seals can dive up to 180 m to prey on Antarctic krill, penguins, and a wide range of Antarctic fish species (Würsig et al. 2018). Panels a and c are from Scubazoo (<http://www.scubazoo.com>), panels b and e were taken by Gabriel E. Machovsky-Capuska, and panel d was taken by Sarah Dwyer.

## PREDATORS IN COMPLEX MARINE ECOSYSTEMS

Long-lived marine apex predators include more than 1,000 different species of mammals, elasmobranchs, turtles, seabirds, and large teleost fish (Schreiber & Burger 2001, Carrier et al. 2012, Rasmussen et al. 2011, van Denderen et al. 2018, Würsig et al. 2018). From polar to tropical areas, predators are present in all the oceans and peripheral seas of the world, albeit generally at much lower abundances than they reached historically (Heithaus et al. 2008) (**Figure 1**). To forage or reproduce, many species navigate thousands of kilometers each year, linking disparate ecosystems (Maxwell et al. 2013). While life in the ocean is predominant, some species have land life-cycle phases (e.g., pinnipeds, turtles, and seabirds) (Boyd et al. 2006).

Evidence on the trophodynamics of marine predators demonstrates their ability to capture and consume sparse and patchily distributed prey in coastal, benthic, and pelagic habitats, linking multiple trophic levels (Young et al. 2015). Although many species forage solitarily, the formation of single- and multispecies feeding associations demonstrates considerable behavioral plasticity to adjust to the challenges presented by schooling prey (reviewed in Würsig et al. 2018). Predators

are often exposed to multiple marine anthropogenic stressors because of their long-distance movements, and therefore can serve as indicators of ecosystem health (Maxwell et al. 2013).

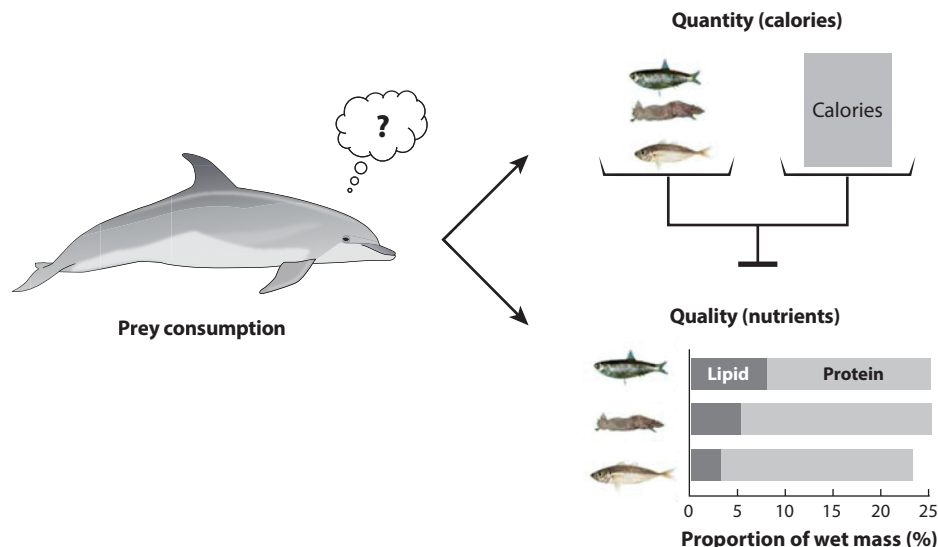
## WHAT DRIVES THE FORAGING CHOICES OF PREDATORS?

### The Importance of the Foraging Currency: Energy, Elements, or Nutrients

As in terrestrial ecology, modern marine ecology is dominated by energy-based and element-based models, but this was not always the case. Redfield (1934) noted a strong correlation between the elemental ratios of plankton biomass and the seawater in which they live, and since then the elemental composition of organisms has been considered a lens for understanding marine ecosystems. This approach was subsequently generalized into the field of ecological stoichiometry (Sternner & Elser 2002), which seeks to understand biological and ecological processes in terms of the abundances and balance of biologically important chemical elements. Despite their benefits for ecosystem studies, however, element-based approaches are severely limited for the study of functional traits, such as foraging and its consequences, because animal behavior and physiology have evolved to relate to nutrients and not elements per se (Raubenheimer et al. 2009). In some cases—for example, calcium and phosphorus—nutrients are themselves elements and are thus tightly linked to functional traits such as animal foraging (e.g., Nie et al. 2014). However, a major class of nutrients, the energetic macronutrients (proteins, fats, and carbohydrates), are poorly represented by elements, and answering questions regarding these nutrients requires an approach based on macromolecules (Raubenheimer et al. 2009). Given the fundamental importance of macronutrients in many aspects of animal biology (Simpson & Raubenheimer 2012), this is a substantial limitation of element-based approaches.

From the beginning of the nineteenth century, attention was drawn toward the study of the macromolecular (protein, lipids, and carbohydrates) as well as inorganic (ash and water) composition of marine organisms (e.g., plankton, molluscs, and fish) consumed by humans (reviewed in Vinogradov 1953). The history of the study of nutrients in marine organisms has been tied to questions and applications related to the resources that benefit humans (Vinogradov 1953). In 1867, Victor Hensen highlighted the importance of understanding nutrients as food sources for marine animals, pioneering the conceptual basis for marine ecology (Wessel 2010). Although nutrients have been important in marine studies, the need to quantify fish productivity (e.g., growth) led to the use of energy values (Ivlev 1939). Since then, the budgetary interpretation of the fate of food consumed by animals has referred exclusively to the amount of energy that each ingested prey item contributes toward the total amount of energy needed to support life (Tomlinson et al. 2014). This concept was then used to simplify the trophic structure of communities by using energy (e.g., calories or joules) as a common denominator in ecology (Lindeman 1942, Paine 1971). Under the premise that predators maximize their fitness by optimizing their rate of energy intake, several authors have developed energy-centered mathematical models to predict the foraging choices of animals (Stephens & Krebs 1986, Tomlinson et al. 2014; reviewed in Pyke 1984) (Figure 2).

Recent evidence suggests that the energy assumption might need rethinking. Many predators do not consume their prey as a whole (Sih 1980, Kohl et al. 2015), but instead selectively eat different body parts. White sharks (*Carcharodon carcharias*), blue sharks (*Prionace glauca*), and Greenland sharks (*Somniosus microcephalus*) seem to selectively feed on the high-lipid blubber layers of marine mammal carcasses (reviewed in Heithaus 2004). During summer, the Mediterranean bogue (*Boops boops*) mainly consumes the gonads of mauve stinger jellyfish (*Pelagia noctiluca*), which have higher lipid concentrations than the rest of the jellyfish's body (Milisenda et al. 2014). Thiebot et al. (2016) observed a similar selection pattern in Adélie penguins (*Pygoscelis adeliae*) preying on the gonads of jellyfish (*Periphylla periphylla*). Seals are also known for selecting different body parts (reviewed



**Figure 2**

Conceptual illustration of the foraging decisions of marine apex predators. A prey-consumption view based on an energy-centered concept translates into predators maximizing their fitness by optimizing their rate of energy intake (i.e., quantity of calories consumed). A nutritional view shows that prey are complex mixtures of many nutrients, and the incentive for foraging is to combine nutritionally complementary foods to achieve specific nutritional goals. The three prey species shown are, from top to bottom, the yellowtail kingfish (*Seriola lalandi*), arrow squid (*Nototodarus* sp.), and yellowtail jack mackerel (*Trachurus* sp.); the lipid and protein composition of the yellowtail kingfish is from Machovsky-Capuska et al. (2016b), and those of the arrow squid and yellowtail jack mackerel are from Machovsky-Capuska et al. (2016c).

in Roffe & Mate 1984). For example, harp seals (*Phoca groenlandica*), gray seals (*Halichoerus grypus*), and harbor seals (*Phoca vitulina*) are known for consuming only the viscera of their prey and discard the heads of captured fish (e.g., Roffe & Mate 1984, Benoît et al. 2011). Harbor seals, in particular, are not strictly marine and enter freshwater habitats to forage on seasonally abundant anadromous fishes, particularly sockeye salmon (*Oncorhynchus nerka*) (Hauser et al. 2008). Over the course of their in-stream life, salmon drastically deplete their energy stores and die having lost nearly 90% of their protein and lipid reserves (Gende et al. 2004). There is extensive evidence of orcas (*Orcinus orcas*) consuming only the livers of different shark species around the world (Pyle et al. 1999, Ford et al. 2011). In elasmobranchs, livers are the single largest visceral organ and are 90% composed of energy-rich lipids (Del Raye et al. 2013). Mammal-hunting orcas often strip porpoises of their blubber and discard the rest of the carcass (Ford et al. 2011). Polar bears (*Ursus maritimus*) feed predominantly on the blubber of ringed seals (*Phoca hispida*), often leaving large portions of the body uneaten even though this prey is available only at certain times of the year (Stirling & McEwan 1975). A recent study on Australasian gannets (*Morus serrator*) showed that environmental fluctuations (i.e., cold- and warm-water events) affect the protein-to-lipid (P:L) ratios of their prey, which in turn influences their foraging behavior and habitat used to achieve their nutritional intake (Machovsky-Capuska et al. 2018).

There is, therefore, substantial evidence that predators are more selective than previously thought. An important question is what drives this selectivity. The common pattern, in which selective feeding is targeted at high-lipid prey or components of prey, might be interpreted to support the contention that marine predators are primarily energy limited (reviewed in Österblom

et al. 2008). Also, the decrease in the availability of high-lipid prey species has been linked to fitness and breeding declines in different marine predator populations (Wanless et al. 2005, Kitaysky et al. 2006, Österblom et al. 2008). A common denominator of these studies is the use of energy density (i.e., the sum of calories from all macronutrients) or digestibility as a measure of nutritional quality (Fritz & Hinckley 2005, Kohl et al. 2015). However, several factors suggest that the situation is less straightforward than this, and selective feeding by marine predators might be driven by more complex foraging goals.

For many marine and terrestrial predators, both protein and lipids are important metabolic fuels (Geraci 1975, Mayntz et al. 2009, Jensen et al. 2014), and yet selectivity of the dietary ratio of protein to lipid seems to be widespread. Given that predators are often food deprived in the wild (Fretwell 1987), this raises the question of why, if they were energy limited, predators would specifically target particular body parts—for example, those that are lipid rich—and leave muscle, a rich source of protein energy, uneaten. This would make sense only if gut capacity were a constraint—for instance, the way the meal size and gut length of flying seabirds are weight limited (Jackson & Place 1990)—and sufficient lipids were available to fill this capacity, because lipids have twice the energy of protein per unit mass (Atwater 1902). It remains to be tested, however, whether this is always the case when predators leave significant quantities of prey muscle uneaten.

In some predators, the ability to convert lipids into metabolized energy is a likely factor underlying macronutrient-specific food preferences (Hilton et al. 2000, Fritz & Hinckley 2005). Given that fast-moving avian predators evolved digestive systems to process high-lipid prey quickly but inefficiently, this might explain why some seabird species are less likely to successfully breed on low-lipid prey (Grémillet et al. 2008). By contrast, pinnipeds are known for their restricted ability to metabolize prey with a very high lipid content (Fritz & Hinckley 2005). In Hawaiian monk seals (*Monachus schauinslandi*), diets high in protein and low in lipids provided more metabolizable energy (Goodman-Lowe et al. 1999), whereas in ringed seals (*Pusa hispida*) and Pacific harbor seals (*Phoca vitulina*), lipid digestibility declined with lipid intake, and excess lipids in the diet were excreted in the feces (Trumble et al. 2003).

Such factors suggest that selective feeding is a method of nutrient balancing. Precedents from the terrestrial literature strongly suggest that the nutrient-balancing hypothesis warrants serious attention, and the application of the nutritional geometry framework in studies of terrestrial animals strongly supports this idea (Raubenheimer & Simpson 1993, Simpson & Raubenheimer 1993). A substantial body of research in controlled laboratory settings has shown that, among terrestrial herbivores and omnivores, nutrient balancing and not the acquisition of energy per se is unequivocally the primary aim of foraging (Simpson & Raubenheimer 2012, Raubenheimer & Simpson 2018), and the same has been demonstrated for several species of vertebrate in the field (Coogan et al. 2014; Machovsky-Capuska et al. 2015, 2016c; Raubenheimer et al. 2015). Laboratory studies have shown that foraging by some terrestrial predators is also driven by nutrient balancing (Mayntz et al. 2009; Jensen et al. 2012, 2014). Although there are no equivalent studies of mammalian marine predators, studies of marine predatory fish suggest that they too forage selectively to balance their macronutrient intake (Ruohonen et al. 2007).

## The Dimensions of Diet Quality

The nutritional geometry framework was designed to formulate and test predictions related to the factors that drive feeding, foraging, and their consequences for individuals, populations, communities, and ecosystems (Simpson et al. 2010, Tait et al. 2014). A fundamental point of difference with energy-centered models is that nutritional geometry explicitly distinguishes between dietary energy and nutrients, including both nonenergetic nutrients (e.g., minerals and vitamins)



and the macronutritional substrates of energy, protein, lipids, and carbohydrates (Raubenheimer et al. 2012b). This enables the relative roles of energy versus specific nutrients to be disentangled, thus empirically establishing the nutritional drivers of foraging rather than assuming them.

A second distinguishing feature of the nutritional geometry framework is that it integrates the multidimensional approach to nutrition with animal homeostasis, introducing a powerful predictive set of traits that underpin much of foraging behavior (Kearney et al. 2010, Raubenheimer et al. 2012b). Among these traits, appetite systems are the component most immediately linked to foraging and are thus central to geometric modeling. Currently, there are two different but complementary and interrelated geometric constructs within which nutritional geometry models are implemented. In amounts-based nutritional geometry plots, the axes, each of which represents a nutrient in the model, are scaled in units of amounts—for example, the amounts of protein and fat eaten over a stipulated time expressed in either grams or calories (Raubenheimer & Simpson 1993, Simpson & Raubenheimer 2012). In proportions-based nutritional geometry plots, the axes are scaled as the proportional contribution of each nutrient in the model to a mixture (Raubenheimer 2011).

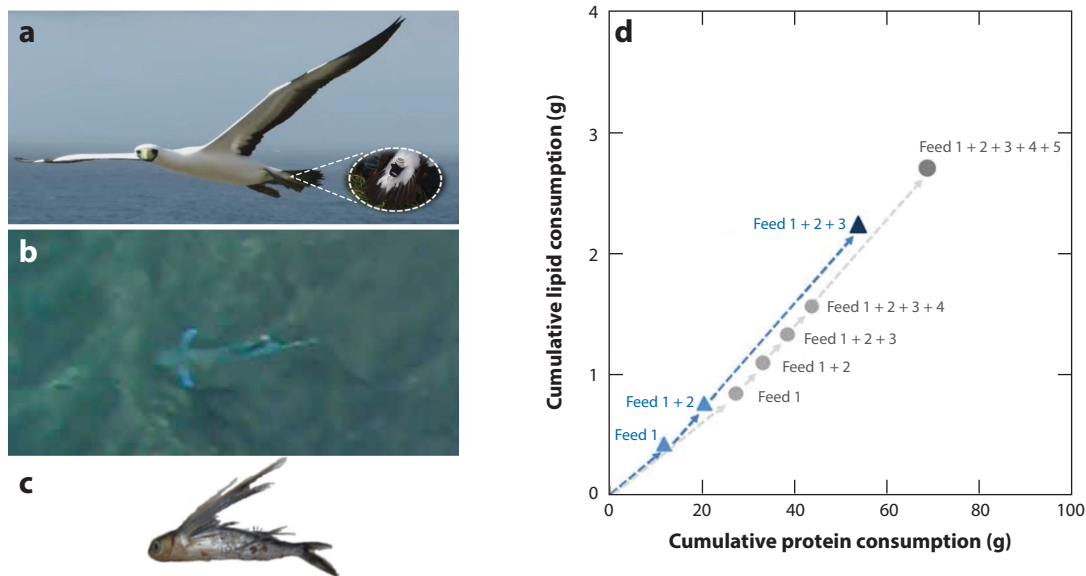
In general, data for amounts-based models are more demanding to collect than those for proportions-based models, usually requiring records of accumulated meal compositions over long periods. Such data can readily be collected in experiments on captive animals but are more difficult to collect in field contexts because they require prolonged observations of animal feeding in an undisturbed situation, combined with collection and nutritional analysis of each food type eaten. A field in which these data have been successfully gathered and applied is the study of primates, which can readily be habituated to the presence of human observers in the wild, enabling continuous feeding records to be collected across a full day (Rothman et al. 2008) or even an entire month (Johnson et al. 2013). The challenges of doing this for predators in the wild, especially marine predators, are formidable (Machovsky-Capuska et al. 2016a). Nonetheless, technological advances in the development of animal-borne devices are opening up new opportunities for the collection of these data (Machovsky-Capuska et al. 2016b) (**Figure 3**).

In contrast to amounts-based geometry, the proportions-based approach offers opportunities for constructing models using data that are routinely collected in marine field studies, including compositional analysis of different food categories, gut content analysis (Croll et al. 1998, Bunce 2001, Majdi et al. 2018), and analysis of predator body compositions (Stansby 1969, Donnelly et al. 1994, Spitz et al. 2010, Denuncio et al. 2017). An important advantage of proportions models is that they plot three nutritional dimensions in a single two-dimensional plot (**Figure 4**). This modeling approach is well suited to proximate composition analysis because it enables the examination of interrelationships among the three energetic macronutrients. Alternatively, models can be constructed that include two macronutrients and a third, non-macronutritional component, such as water, ash, or non-macronutrient fresh or dry mass. Such modeling provides a powerful way to show how energetic categorizations alone can confound proteins and lipids as parameters for prey quality (**Figure 4**).

In the following section, to better understand the importance of protein and lipids as parameters for quality, we extend this analysis to encompass the main prey groups of marine apex predators.

## THE NUTRITIONAL QUALITY OF PREY

A widespread assumption is that food captured by carnivores is of relatively uniform nutrient quality and is readily digested and assimilated (Stevens & Hume 2004). However, there is ample evidence in marine environments that the nutritional composition of foods is subject to inter- and intraspecific variation driven by geographic, seasonal, sex, ontogenetic, and other factors (Stansby



**Figure 3**

Coupling biologging with amounts-based nutritional geometry to establish the macronutrient intake per foraging trip in a central place forager, the masked booby feeding on flying fish. (a) Miniaturized animal-borne cameras deployed on the central feathers of two male chick-rearing masked boobies (*Sula dactylatra tasmani*). (b) Aerial image of a flying fish (family Exocoetidae) prey obtained from one of the six prey capture events recorded. (c) An example from the six undigested individual flying fish prey collected from the regurgitations of two individual boobies upon arrival at the colony. (d) An amounts-based nutritional geometry model based on two separate foraging trips (represented by *light blue* and *light gray*). To build the model, we first established the macronutrient composition of each individual flying fish captured. We then multiplied the nutritional composition of each prey by the mass of prey ingested at each plunge dive (represented by *light blue triangles* and *light gray circles*) and summed the macronutrient consumption of all plunge dives to obtain the macronutrient intake for each foraging trip (represented by the *dark blue triangle* and *dark gray circle*). The balance of nutrients of the prey consumed in each foraging trip is plotted cumulatively to represent the respective diets and how they are composed from separate ingestion events. Figure adapted from Machovsky-Capuska et al. (2016a,b) with permission.

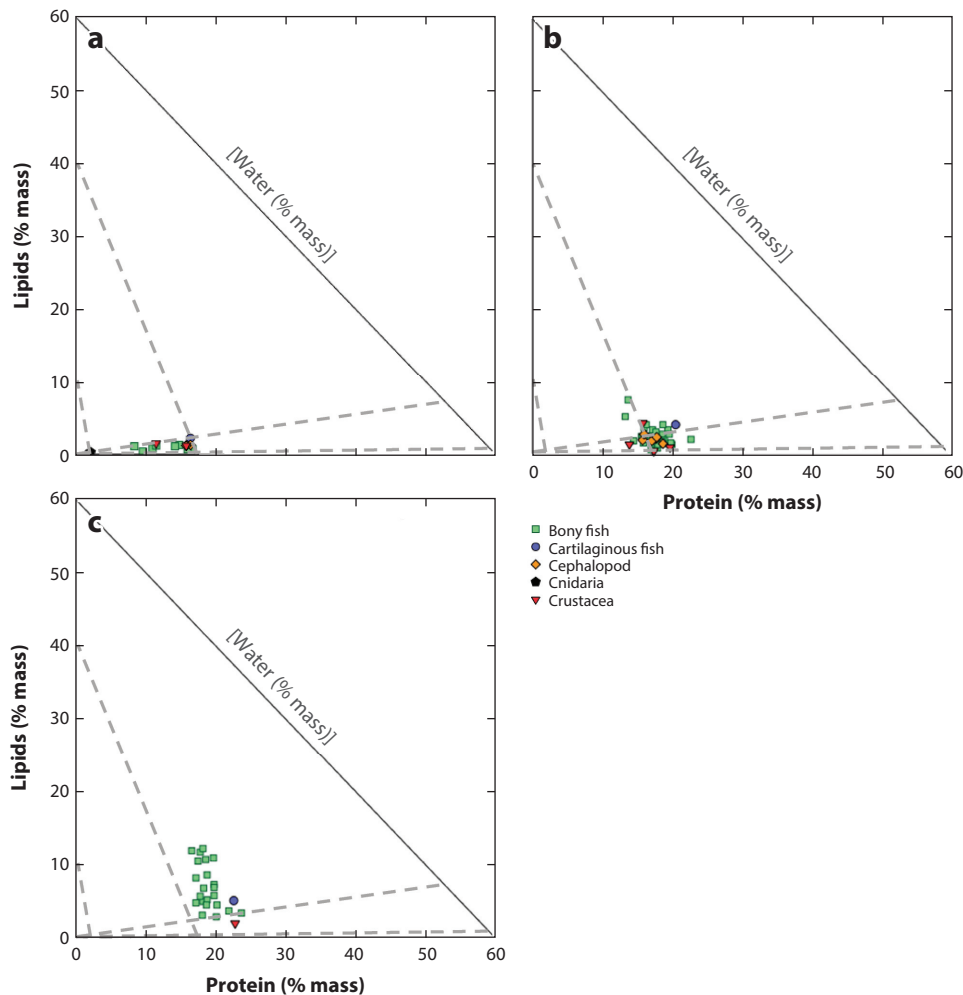
1969, Donnelly et al. 1994, Spitz et al. 2010, Lenky et al. 2012, Tait et al. 2014; reviewed in Vinogradov 1953).

Vinogradov (1953) suggested that data on the proximate composition of marine foods are scattered and often incomplete, yet the absence of a universal method for expressing nutrient values still limits the ability of researchers to compare their results (Dierenfeld 2005). The potential costs and complexity of proximate composition analysis (Majdi et al. 2018) and the lack of agreement on the accuracy of energetic conversion factors linked to macronutrients (Schaafsma et al. 2018) are the main hurdles hampering our understanding of the nutritional variability of foods in the wild. Technological developments in data sharing could provide a crucial pathway for integrating and updating nutritional information that could lead to strong interdisciplinary integration (Dierenfeld 2005).

We next summarize knowledge of the wet-mass nutritional composition of 63 families and 154 species from the main groups of marine prey: pelagic zooplankton (crustaceans, chaetognaths, polychaetes, and gelatinous organisms), cephalopods, and small and large teleost fish (Young et al. 2015). We have also added incidental prey (17 families and 30 species), comprising marine mammals, elasmobranchs, turtles, and seabirds (Pauly et al. 1998) (see **Supplemental Table 1**).

Our intention for doing this is twofold. First, the analysis illustrates the variability in the compositions of prey of marine apex predators. Such variability is itself a predictor of nutrient-specific





**Figure 4**

An example of how proportions-based nutritional geometry can be used to distinguish the dimensions of food quality. The plots show the wet-mass body composition of 78 forage species from the Bay of Biscay (data from Spitz et al. 2010). Given that carbohydrate content is a minimal nutritional component of most marine prey (Vinogradov 1953), each prey represents a proportional mixture of protein, lipids, and water. To geometrically define prey in a right-angled mixture triangle, the percentage of protein is plotted against the percentage of lipids. Considering that the three components in the mixture are made to sum to 100%, plotting the percentage of protein (first axis) and percentage of lipids (second axis) will automatically determine the percentage of water (Raubenheimer 2011). A particular value on the third axis is therefore represented by a negatively sloped line, such that any point along this line equates to the same proportion of water, with covarying proportions of protein and lipids. The percentage of water increases with decreasing distance from the origin. Prey subsets were classified by Spitz et al. (2010) on the basis of energy content as (a) low quality (less than 4 kJ/g), (b) medium quality (between 4 and 6 kJ/g), and (c) high quality (more than 6 kJ/g). However, the pattern of increasing energy density from panel a to panel c is based on both an increase in the overall concentration of macronutrients (movement away from the origin) and an increasing ratio of energy-dense lipids to protein (movement away from the x axis). In this example, the negative-sloped dashed lines represent energy isolines. Figure adapted from Raubenheimer (2011).

foraging (Simpson & Raubenheimer 2012). Second, we hope that the data can serve as a reference source for researchers interested in marine apex predators. For ease of reference, we have grouped prey into specific categories, each of which is represented by a separate panel in **Figure 5**.

## Pelagic Zooplankton

The nutritional composition data on crustaceans include copepods, euphausiids, ostracods, and decapods. Copepods (family Calanidae) are the most dominant group of crustaceans in the ocean in number and biomass (Vinogradov 1953) and showed the highest lipid concentration as a proportion of wet mass, reaching up to 9.0% (**Figure 5a**). Because of their ability to convert proteins and carbohydrates from algae into high-energy lipids (i.e., wax esters), copepods are the main animal energy and nutrient source within food webs (Grigor et al. 2017). They are also vital prey for a broad range of zooplankton, fish, seabirds, and marine mammals (Schaafsma et al. 2018).

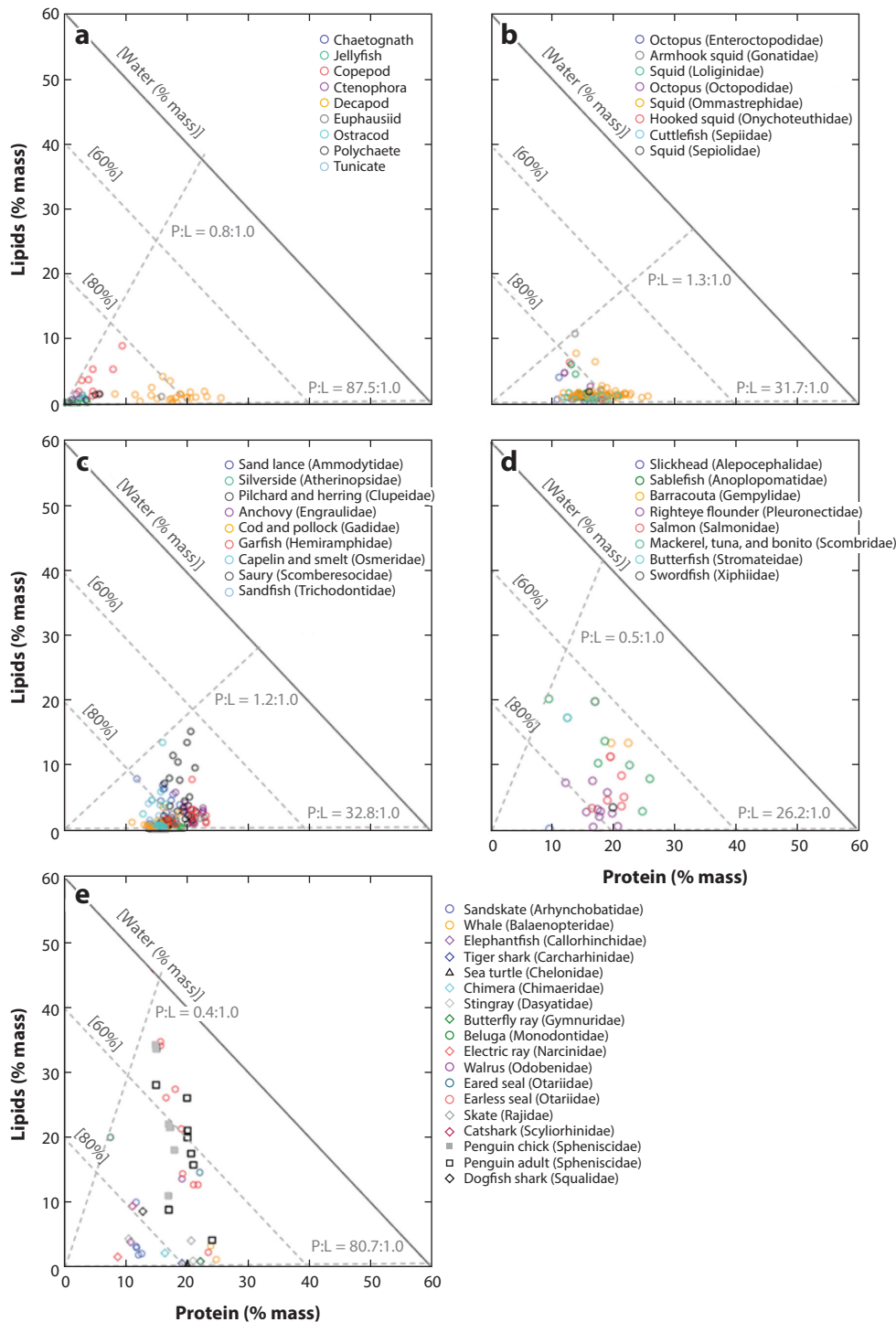
Decapods, in particular Portunidae (swimming crabs), represent a substantial source of protein (up to 25.5%; **Figure 5a**) for cephalopods, large teleost fishes, sharks, seagulls, seals, sea otters, and sea lions (reviewed in Boudreau & Worm 2012). In a similar nutritional range, euphausiids also represent a substantial protein source (15.8%) for small teleost fishes (forage fish, e.g., sardines, anchovies, herrings, and mackerels) (Young et al. 2015). High concentrations of water (>84.1%) and low proportions of protein (<6%) and lipids (<1.5%) were found in chaetognaths, ostracods, and polychaetes (**Figure 5a**).

Pelagic gelatinous organisms, which are loosely termed jellyfish, encompass cnidarians (e.g., scyphozoan true jellyfish and siphonophores), ctenophores (comb jellies), and chordates (salps) (reviewed in Thiebot et al. 2016). Although jellyfish are often depicted as trophic dead ends, extensive evidence suggests that a large variety of animals feed on this group (Arai 2005). Our nutritional analysis of 15 species of gelatinous organisms shows that the wet-mass average P:L is 4.8:1.0, with protein ranging from 0.1% to 3.7%, lipids ranging from 0.1% to 1.6%, and water ranging from 91.0% to 97.0% (**Figure 5a**).

It has been suggested that predators would need up to 30 times the amount of gelatinous tissue compared with crustaceans or fish to meet their energetic and nutritional demands (Doyle et al. 2007; reviewed in Hays et al. 2018). Leatherback turtles consume an average of 73% of their body mass each day in wet mass of jellyfish (Heaslip et al. 2012), and gelatinous organisms constitute up to 42% of the diet of penguins (Thiebot et al. 2017). Despite their low nutritional content, jellyfish often exhibit dense blooming patterns of hundreds of individuals, making them easy to capture (Arai 2005). Widespread consumption of this group may be facilitated by the ease of rapidly digesting them in comparison with fish and shrimp, providing comparable rates of nutrient and energy intake (reviewed in Hays et al. 2018).

## Cephalopods

Squid, cuttlefish, and octopuses are members of the Cephalopoda class, which plays a central role in most marine pelagic webs by linking micronekton with marine predators (Young et al. 2013). Cephalopods are important prey for marine mammals (Clarke 1996, Klages 1996), elasmobranchs (Janse et al. 2004), seabirds (Croxall & Prince 1996), and teleost fish (Smale 1996, Young et al. 2013). Data from 40 species of cephalopods from 8 families showed that this group has an average P:L of 13.4:1.0, with a wide range of percentages of protein (10.8–25.6%), lipids (0.3–10.9%), and water (71.3–86.1%) (**Figure 5b**). Studies of the diets of marine predators from the major oceans underline the fundamental importance as prey of the squid family Ommastrephidae (Young et al. 2013), which is characterized by high concentrations of protein (up to 25.6%) and lipids (up to 7.9%) (**Figure 5b**). Doubleday et al. (2016) suggested that the global reduction of fish stocks



**Figure 5**

Proportions-based nutritional geometry showing the nutritional variability of marine prey.

**Supplemental Table 1** summarizes knowledge of the wet-mass nutritional compositions of 80 families and 184 species from the following taxonomic groups: (a) crustaceans, chaetognaths, polychaetes, and gelatinous organisms; (b) cephalopods; (c) small teleost fish (forage fish); (d) large teleost fish; and (e) marine mammals, elasmobranchs, turtles, and seabirds.

Abbreviation: P:L, protein-to-lipid ratio.

**Supplemental Material** >

caused by fishing has released cephalopods from competition pressure, driving growth in their populations that benefits the marine predators that rely on them for food.

## Teleost Fish

Forage fish are primarily small and medium-sized pelagic fish that play a crucial role in most ecosystems, linking plankton with higher trophic levels (reviewed in Springer & Speckman 1997). The empirical data show that 34 species of teleost fish from 9 families exhibit a wide range of percentages of protein (11.1–23.2%), lipids (0.5–15.4%), and water (60.7–84.4%), with an average P:L of 13.5:1.0 (**Figure 5c**). The highest lipid concentrations were in the family Clupeidae (herrings), which is likely a result of their reproductive strategy and diet (Røjbek et al. 2013). Clupeids feed largely on copepods, which have a higher lipid content than ostracods and euphausiids (**Figure 5a**), and the clupeids that prey on them are therefore likely to have higher lipid intakes (**Figure 5c**).

The schooling behavior of pelagic fish makes them accessible prey in large numbers. They play an important role in the diets of large teleost fish (Springer & Speckman 1997) and represent up to 12% of the overall annual protein and lipid intake of marine mammal and seabird populations worldwide (Kaschner et al. 2006, Alder et al. 2008). The nutrient composition, abundance, and availability of schooling pelagic (forage) fish are known to be critical to the reproductive success (Wanless et al. 2005, Österblom et al. 2008), foraging behavior, and nutrient intake of marine apex predators (Machovsky-Capuska et al. 2018).

Stansby (1969) suggested that the wet-mass concentrations of nutrients in marine fish should span 13.0–26.0% protein and 0.2–25.0% lipids, along with 65.0–80.0% water. A representative analysis of 27 species from 8 families of teleost fish showed broad variation in composition, with protein ranging from 8.4% to 25.9%, lipids ranging from 0.4% to 20.4%, and water ranging from 63.5% to 87.5% (**Figure 5d**). Pelagic fish species are known for their high lipid content, which enables buoyancy adjustments for high speeds (Eder & Lewis 2005). In support of this pattern, we found high protein and lipid contents in Scombridae (mackerels, tunas, and bonitos), Gempylidae (barracoutas), Salmonidae (salmons), and Stromateidae (butterfishes), whereas Xiphiidae (swordfishes) presented extraordinarily low nutritional values. Demersal fish species have been referred to as lean, with low concentrations of protein and lipids (Eder & Lewis 2005); for example, members of Alepocephalidae (slickheads) were found to have protein and lipid contents of only 9.6% and 0.4%, respectively. However, members of the Pleuronectidae (righteye flounders) and Anoplopo-matidae (sablefishes) families were an exception, with protein and lipid concentrations that reach 17.0% and 20.7%, respectively.

## Marine Mammals, Elasmobranchs, Turtles, and Seabirds

Although marine mammals are accomplished and sophisticated hunters, they also serve as prey for a wide range of marine predators (reviewed in Würsig et al. 2018). The nutritional compositions of pup to adult ringed seals (*Phoca hispida*, Phocidae), walruses (*Odobenus rosmarus*), and Steller sea lions (*Eumetopias jubatus*) range from 13.6% to 23.5% protein, 2.3% to 34.7% lipids, and 46.4% to 78.6% water (**Figure 5e**). The lipid compositions of these species of pinnipeds are higher than those of any of the other prey species (**Figure 5a–d**). Pinnipeds (both pups or adults) are preyed on by leopard seals (*Hydrurga leptonyx*), great white sharks (*Carcharodon carcharias*), tiger sharks (*Galeocerdo cuvier*), white-tip sharks (*Triaenodon obesus*), killer whales (*Orcinus orca*), and polar bears (*Ursus maritimus*) (reviewed in Würsig et al. 2018). Killer whales, sharks, and to a lesser extent polar bears prey on whales, dolphins, and porpoises. Belugas (*Delphinapterus leucas*) and minke whales (*Balaenoptera* spp.) could provide a diet of up to 24.8% protein, 20.0% lipids, and 73.1% water (**Figure 5e**).

Killer whale predation on cartilaginous fish (e.g., sharks, skates, and rays) has been reported worldwide (reviewed in Visser 2005), and rays are their main prey in New Zealand. Eder & Lewis (2005) suggested that, by preying on rays and skates, killer whales ingest low lipid and energy content compared with foraging on teleost prey. Rays and skates within the *Dasyatidae*, *Gymnuridae*, *Arhynchobatidae*, and *Rajidae* families can provide protein (8.7–24.2%) and lipid (0.3–10.0%) concentrations that are within the low range of macronutrients found in cephalopods (**Figure 5b**), forage fish (**Figure 5c**), and large teleosts (**Figure 5d**). Sharks (*Carcharhinidae* and *Squalidae*) can provide a more substantial lipid source, with compositions of up to 8.6% lipids and 19.2% protein (**Figure 5e**). Green turtles (*Chelonia mydas*) can be a large source of protein (20.0%) for white and tiger sharks (Carrier et al. 2012) (**Figure 5e**).

Penguin chicks and adults (*Spheniscidae*) are preyed on by giant petrels (*Macronectes* spp.) and great skuas (*Catharacta skua*) on land (Schreiber & Burger 2001), whereas adults are consumed mostly in the water by sharks, killer whales, leopard seals, and sea lions (Carrier et al. 2012, Trites & Spitz 2018). Depending on molting stage, penguin chicks can be up to 18.0% protein and 34.0% lipids, whereas adults can be up to 24.1% protein and 28% lipids (**Figure 5e**).

## THE NUTRITIONAL NICHE OF MARINE APEX PREDATORS

Knowing what marine apex predators eat and their ecological niche is a cornerstone of marine ecology. Current estimates of amounts of prey consumed by marine predators in the wild are rough at best and require refinement (Trites & Spitz 2018). There is a general consensus that planktonic crustaceans, forage fish, and cephalopods are vital to the mixed diets of most marine predators (Pauly et al. 1998, Schreiber & Burger 2001, Rasmussen et al. 2011, Carrier et al. 2012, van Denderen et al. 2018). The diets of marine predators are usually estimated by indirect techniques (e.g., analyses of stomach contents, regurgitations, feces, isotopes, and fatty acids; reviewed in Young et al. 2015) that have their own relative strengths and weaknesses. Linking multiple approaches can overcome the limitations of specific methods and improve these estimates (Majdi et al. 2018).

Functional traits of organisms, in particular those related to foraging, could be fundamental to better understanding the factors driving foraging and food choice in food webs and ecological communities (Kearney et al. 2010). Particular emphasis should be given to traits that enable testing of predictions on wild animals in field studies (Houlahan et al. 2017). Recently, proportions-based nutritional geometry has provided the basis for the development of the multidimensional nutritional niche framework for integrating nutrition, physiology, and behavior with food-level approaches to the dietary niche (Machovsky-Capuska et al. 2016d).

Typically, dietary niches are characterized in relation to the foods an animal eats. For example, dietary generalists are usually defined as animals that eat a wide range of different food types. By contrast, the multidimensional niche concept distinguishes between food-based dimensions of the niche and nutrient-based dimensions.

This is an important distinction, because an animal might be classified differently with regard to the food- and nutrient-based dimensions of its niche. For example, an animal that eats a wide variety of foods (i.e., is a food generalist) might do so specifically because this enables it to maintain its nutrient intake within narrow boundaries (i.e., to be a nutrient specialist). Nie et al. (2019) recently showed that even such fundamental ecological categorizations as herbivore versus carnivore might be less straightforward when viewed through the lens of multidimensional niches. The diet of giant pandas consists almost exclusively of bamboo, and on this basis the species is considered an example of extreme herbivory. Yet geometric analysis has shown that the macronutrient proportions of their diet clusters among those of hypercarnivores in the nutrient space, with

more than 50% of their energy coming from protein—equivalent to the proportions consumed by wolves and wild cats. Giant pandas are thus herbivores at the level of foods eaten, and simultaneously macronutritional carnivores. This suggests that their transition from a carnivorous ancestry to extreme herbivory might not have been as abrupt as commonly believed, and might also explain their unusual mix of herbivorous and carnivorous traits (Nie et al. 2019).

This characterization of the ecological niche has the advantage that it can help to characterize the ecological requirement of animals and relate diet selection to nutrient requirements. This could prove important for understanding the nutritional needs of wild marine predators and how these needs drive ecological interactions that are ultimately shaped by environmental fluctuations (Machovsky-Capuska et al. 2018).

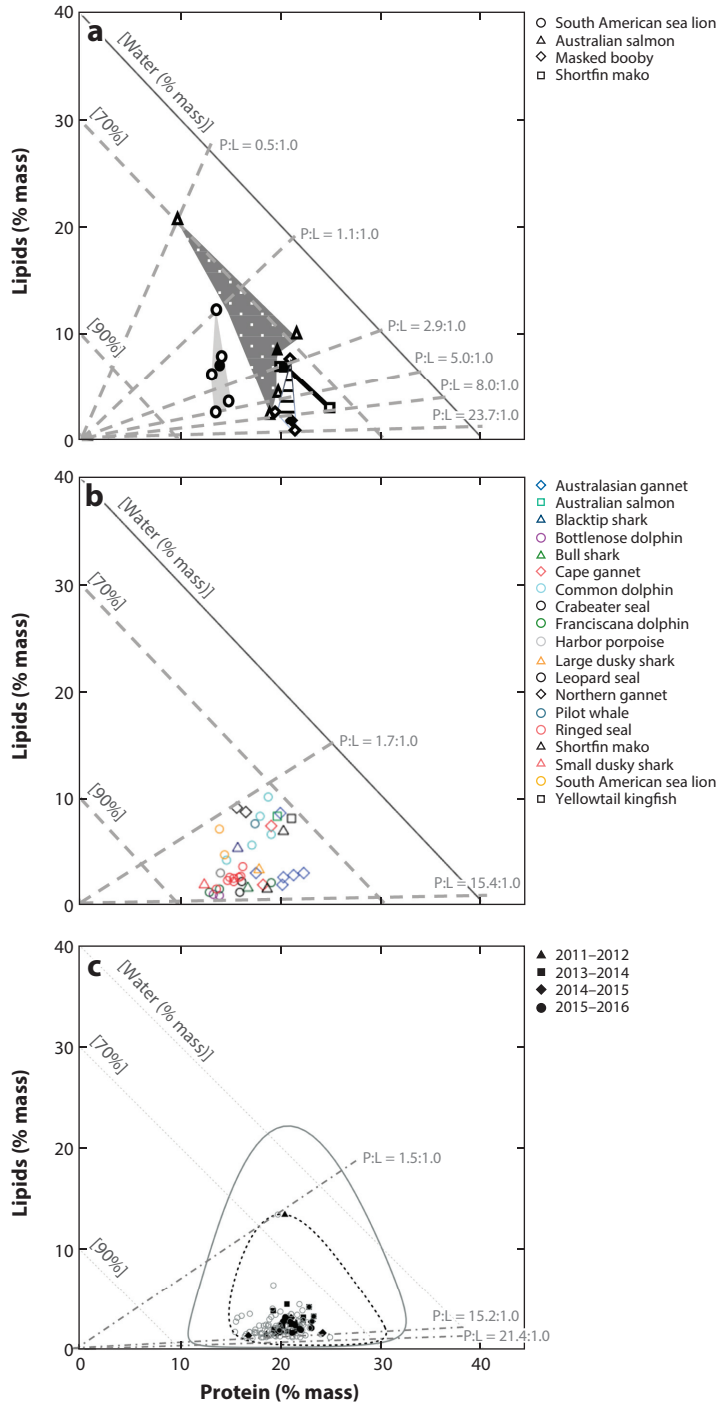
Few studies in marine environments have been able to synchronously collect proximate composition data on both prey availability and realized diet (Bunce 2001; Tait et al. 2014; Machovsky-Capuska et al. 2016b,c, 2018; Miller et al. 2017). Under these circumstances, the use of published data on the proximate compositions of prey, albeit with limitations, provides an opportunity to integrate spatiotemporal scales that could lead to novel insights into the ecology of marine species that are difficult to study (Tait et al. 2014).

To illustrate, we combined multidimensional niche modeling with fine-scale, detailed dietary studies of four different marine predator species and the proximate compositions of their prey from the available literature (**Figure 5, Supplemental Table 1**) to estimate the prey composition niche and the nutritional niche (**Figure 6a**). The prey composition niche represents the range of compositions of prey from which the population assembles its diet. The nutritional niche represents the range of compositions of the resulting diets across individuals in the population. To reduce uncertainties regarding the consistency and validation of the methods used, we prioritized prey values obtained within a similar spatiotemporal proximity to the study when possible (Tait et al. 2014).

For illustration (**Figure 6a**), we used data on the diet of the shortfin mako (*Isurus oxyrinchus*) from Wood et al. (2009) to estimate a minimum prey composition niche, which had P:L ratios ranging from 2.9:1.0 to 8.0:1.0. By mixing its intake mainly from bluefish (*Pomatomus saltatrix*, 92.6% total wet mass) and to a minor extent from yellowfin tuna (*Thunnus albacares*, 2.5% total wet mass), shortfin mako can consume a diet with 20.1% protein, 6.9% lipids, and a P:L ratio of 2.9:1.0, similar to the nutritional composition of bluefish. Based on data from Machovsky-Capuska et al. (2016b), masked boobies (*Sula dactylatra tasmani*) consume flying fish (*Cheilopogon* spp., 72.0% total wet mass), yellowtail kingfish (*Seriola lalandi*, 18.1% total wet mass), and mackerel scad (*Decapterus macarellus*, 9.9% total wet mass), creating a minimum prey composition niche with P:L ratios ranging from 2.9:1.0 to 23.7:1.0 and an estimated diet consisting of 20.9% protein and 1.8% lipids, with a P:L ratio of 11.6:1.0. Hughes et al. (2013) showed that Australian salmon (*Arripis trutta*) from northern New South Wales consume four prey species (77.8% total wet mass), constituting a minimum prey composition niche ranging from 0.5:1.0 to 7.9:1.0, and have a diet that consists of 19.5% protein and 8.3% lipids, with a P:L ratio of 2.4:1.0. Analysis of the stomach contents of South American sea lion (*Otaria flavescens*) females showed five main prey species (99.2% total wet mass) (Koen Alonso et al. 2000) that constituted a minimum prey composition niche with P:L ratios ranging from 1.1:1.0 to 5.0:1.0, leading to an estimated diet of 13.8% protein and 7.1% lipids, with a P:L ratio of 2.0:1.0. While the species described above are often regarded as generalist predators, often a relatively small number of species account for the majority of their diets (Bowen 2018) and nutritional intake.

In terrestrial environments, as trophic levels increase, selective feeding and growth lead to body compositions with higher P:L ratios (Raubenheimer et al. 2009, Wilder et al. 2013). Under these circumstances, marine apex predators may also become lipid restricted with increasing trophic





(Caption appears on following page)

Proportions-based geometric models illustrating the nutritional variability of the prey compositions and nutritional niches of marine predators. Each prey and diet represents a wet-mass proportional mixture of protein, lipid, and water (for an explanation of how the three variables are plotted in two dimensions, see **Figure 4**). (a) Comparison of different prey species (*open black circles*) that make up the prey composition niches (*areas and line*) and diets (*solid black circles*) of four marine apex predators. Niches were estimated by combining prey data available in the literature (**Supplemental Table 1**) with published fine-scale dietary analyses of South American sea lion females (Koen Alonso et al. 2000; *circles and light gray area*), Australian salmon (Hughes et al. 2013; *triangles and dark gray dotted area*), masked booby (Machovsky-Capuska et al. 2016b; *diamonds and striped area*), and shortfin mako (Wood et al. 2009; *squares and black line*). (b) Wet-mass nutritional compositions of diets from 9 families and 19 species of marine predators (**Supplemental Table 2**). (c) Nutritional compositions of prey (*open gray circles*) and diets (*solid black circles, squares, and diamonds*) of chick-rearing adult Australasian gannets at the Farewell Spit colony (Machovsky-Capuska et al. 2018). The breadth of the prey composition niche (all prey consumed by gannets) is measured as the standard ellipse area (SEAc = 9.19; *gray solid ellipse*), as is the realized nutritional niche breadth of gannets (all individual diets from the four breeding seasons studied: 2011–2012, *triangle*; 2013–2014, *square*; 2014–2015, *diamond*; 2015–2016, *circle*) (SEAc = 4.65; *black dotted ellipse*). Abbreviation: P:L, protein-to-lipid ratio. Figure adapted from Machovsky-Capuska et al. (2018).

level, providing an incentive to eat high-lipid body parts of prey (see the section titled What Drives the Foraging Choices of Predators?) from the same trophic level and/or to select whole prey from lower trophic levels. To further explore this pattern within marine environments, we extended our analysis to 19 species from 9 families (**Figure 6b**, **Supplemental Table 2**). The estimated nutritional compositions of the diets of different predator populations had P:L ratios ranging from 1.7:1.0 to 15.4:1.0, supporting previous suggestions regarding the incentive for marine predators to consume prey across multiple trophic levels (**Figure 5a–d**), with the particular nutritional advantage gained by preying on other conspecific and heterospecific predators (**Figure 5e**).

Although we acknowledge the challenges of collecting reliable data that combine the proportional mass of each prey ingested and the nutritional compositions of prey, studies with large sample sizes will certainly provide robust conclusions about prey composition and nutritional niches. **Figure 6c** illustrates an ideal scenario from data collected on adult chick-rearing Australasian gannets over four breeding seasons, showing the range of prey compositions eaten (i.e., the prey composition niche) and the range of individual diets composed through feeding on that prey (i.e., the realized nutritional niche). The examples suggest an incentive for these predators to combine individually imbalanced but nutritionally complementary foods to achieve dietary balance, further highlighting the likelihood that prey selection is guided by the balance of macronutrients rather than energy alone (Machovsky-Capuska et al. 2016c).

## NUTRITIONAL ECOLOGY AND REAL-WORLD PROBLEMS INVOLVING MARINE APEX PREDATORS

In this section we illustrate how the nutritional geometry framework can be applied to solving complex real-world problems (Machovsky-Capuska et al. 2016d, 2018, 2019; Raubenheimer & Simpson 2018; reviewed in Simpson & Raubenheimer 2012). We have chosen for illustration three examples relevant to marine apex predators.

### Marine Pollution

Marine pollution includes a variety of substances that alter the physical, chemical, and biological characteristics of the ocean and coastal areas, negatively affecting biodiversity and the health of ecosystems (Verity et al. 2002). These anthropogenic pollutants are present in the form of

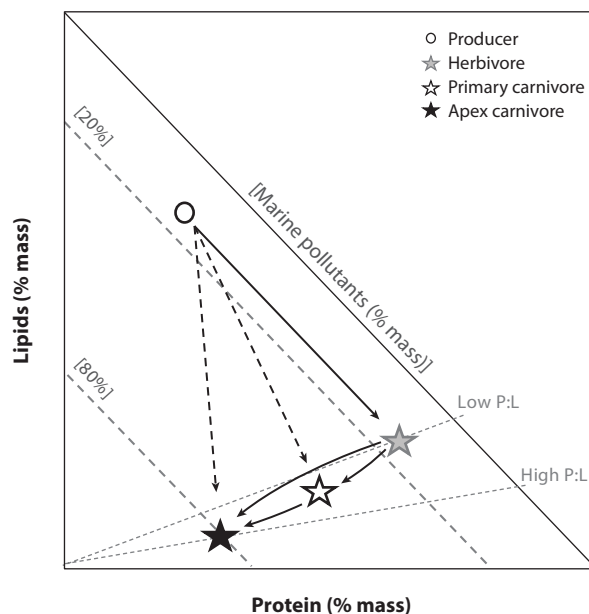
marine debris (e.g., glass, metals, paper, and plastics), persistent organic pollutants [POPs, e.g., organochlorinated compounds such as dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyls (PCBs)], and nonessential metals (e.g., mercury, cadmium, and lead) (reviewed in Gall & Thompson 2015). Plastics, POPs, and nonessential metals have been implicated in causing physiological reproductive effects that affect individuals, populations, and species (Underwood & Peterson 1988). Diet composition and trophic level influence the ingestion of plastics (Provencher et al. 2017) and the accumulation of POPs and metals in marine apex predators (Ramos & González-Solís 2012). Hence, understanding the underlying drivers and the magnitude of the impacts of pollutants on marine apex predators requires more comprehensive insight into their feeding ecology (Ramos & González-Solís 2012).

Underwood & Peterson (1988) recognized the need for a sensitive, robust, and quantitative framework to predict marine ecological impacts on organisms ranging from consumers to apex predators that are susceptible to marine pollution, but this need remains unmet (Machovsky-Capuska et al. 2019). There are extensive data on the chemical links between nutrients and pollutants (reviewed in Bignert et al. 1993). The lipid composition of organisms within pelagic food webs may influence the intake of POPs (Larsson et al. 2000) and methylmercury (Chen et al. 2008). Triglycerides, phospholipids, and sterols are present in different concentrations within phytoplankton (producers) and zooplankton, fish, birds, and mammals (consumers) (Moriarty 1991, Newman 2014). Marine apex predators, in particular, tend to live longer than their prey and have more time to bioaccumulate contaminants (Newman 2014). When predators consume prey, lipids are digested, and the contaminant concentrations are bioaccumulated, as seen in pelagic piscivorous fish (Larsson et al. 2000), marine mammals (Würsig et al. 2018), elasmobranchs (Del Raye et al. 2013), and seabirds (Phillips & Hamer 1999). Thus, a higher lipid content in apex predators than in their prey leads to increases in contaminant concentrations with trophic level, also known as biomagnification (Moriarty 1991; reviewed in Chen et al. 2008). The hitherto unexplored ecological links between nutrients and marine pollutants (e.g., POPs and trace metals) could yield powerful insights into the nutritional effects of pollutant concentrations in marine apex predators.

Machovsky-Capuska et al. (2019) presented an example of how nutritional geometry can be used to integrate diet and nutrition with pollution. The authors examined the potential influence of types of plastics (e.g., hard plastics and packaging) and habitat use (e.g., marine, coastal, or estuarine) on the nutritional niches of Franciscana dolphins (*Pontoporia blainvillei*) in Argentina. They also considered likely scenarios for nutrient and plastic interactions in the context of food webs. We propose the extension of geometric modeling to other forms of marine debris (e.g., glass and metals), POPs, and nonessential metals (e.g., mercury, cadmium, and lead) (Figure 7). Such an extension could provide fresh insights into the links between pollutant concentrations and nutritional niches in wild predators to elucidate the nature and consequences of their trophic interactions (Machovsky-Capuska et al. 2019) and help unravel the complex interplay of contaminant concentrations with trophodynamics (Borgmann & Whittle 1992). Specifically, it could elucidate the ways in which prey availability, prey selection, and feeding rates influence pollutant concentrations in predators.

## Captivity and Rehabilitation

Since the mid-1800s, marine predators have been brought into captivity for entertainment, education, conservation, research, and rehabilitation (Mazzaro et al. 2016). To be healthy and effective, captivity must meticulously recreate the marine environment, providing not only space and nutrition but also a carefully controlled chemical and physical environment (Choromanski 2004). Although nutrition is a basic foundation of animal husbandry and integral to longevity, disease prevention, growth, and reproduction, it has received insufficient focus in the captive



**Figure 7**

Hypothetical scenarios for macronutrients and marine pollutant interactions within trophic levels, illustrated via a right-angled mixture triangle. These relationships are based on the nutritional needs of organisms from different trophic levels and the ability of these organisms to bioaccumulate pollutants. These anthropogenic substances can be in the form of marine debris (e.g., glass, metals, paper, and plastics), persistent organic pollutants, and nonessential metals (e.g., mercury, cadmium, and lead). Direct trophic interactions are indicated by solid arrows, and indirect trophic interactions are indicated by dashed arrows. Abbreviation: P:L, protein-to-lipid ratio. Figure adapted from Machovsky-Capuska et al. (2019).

management community (Dierenfeld 1997). Unfortunately, energy-centered models have been widely used to quantify the amount of food consumed in captivity and rehabilitation of marine mammals (Worthy 2001), sharks and rays (Janse et al. 2004), and seabirds (Crissey et al. 2001). Dietary choices in wild marine predators are nutritionally complex (Machovsky-Capuska et al. 2016a), and while it is extremely challenging to duplicate their diets in captivity, our priority should be the specific blends of nutrients rather than energy per se (Dierenfeld 1997).

The literature provides abundant descriptive overviews of the diet compositions of marine mammals, elasmobranchs, seabirds, and predatory fish (reviewed in Janse et al. 2004 and Young et al. 2015). However, the lack of information on the macro- and micronutrient compositions of foods and the ecological variables that shape them (e.g., species, season, age, and sex) negatively influences our ability to translate this knowledge into feeding programs for captivity (Dierenfeld 1997, Mazzaro et al. 2016). Difficulties in establishing a relationship between the food requirements of captive and free-living marine predators has led to nutritional problems from poor feeding management, including inappropriate or unpalatable foods that cause malnutrition (Crissey et al. 2001). Carnivores that are over- or underweight are likely to be under physiological and behavioral stress (Janse et al. 2004). Underfed elasmobranchs, in particular, can become more aggressive and prey on smaller or less dominant conspecific and heterospecific animals (Charbeneau 2004). To solve nutritional deficiency issues in marine mammals, elasmobranchs, and seabirds, captive facilities are known to provide foods beyond their basic needs that often lead to obesity (Charbeneau 2004, Fidgett & Gardner 2014).

While progress has been made in understanding the nutrient requirements and metabolic adaptations of some wild species, a cross-disciplinary approach that links field-based and applied research is needed to provide direction for optimal diets for captive animal management (Dierenfeld 1997, 2005). Nutritional ecology provides a framework for comparative physiological, behavioral, and ecological approaches, with nutritional applied goals enabling a better understanding of animals' responses to their environment (Martinez del Rio & Cork 1997, Raubenheimer et al. 2009).

Captive carnivores need to adjust to a myriad of specific challenges related to their new environment, including environmental factors (e.g., temperature and exposure to sunlight), feeding behavior, and nutrition (Dierenfeld 2005). Injury and illness can become an additional obstacle to welfare and rehabilitation (Janse et al. 2004, Fidgett & Gardner 2014). Nutrition is intimately linked to immune defense and the health of individual organisms (Ponton et al. 2011). Trial and error is not a luxury that one can afford when developing feeding programs upon which the welfare, rehabilitation, or survival of a given species may depend, particularly for threatened or endangered species (Dierenfeld 2005).

As discussed above (see the section titled What Drives the Foraging Choices of Predators?), recent applications of nutritional geometry have shown that, in captivity, both invertebrate and vertebrate predators forage to optimize macronutrient balance rather than maximize energy. Vertebrate carnivores, including European sea bass (*Dicentrarchus labrax*) (Vivas et al. 2003); rainbow trout (*Oncorhynchus mykiss*) (Sánchez-Vázquez et al. 1999); and domesticated cats (*Felis catus*) (Hewson-Hughes et al. 2011), dogs (*Canis lupus familiaris*) (Hewson-Hughes et al. 2013), and minks (*Neovison vison*) (Mayntz et al. 2009, Jensen et al. 2014), have the ability to self-select proportions of macronutrients from complementary foods (Simpson & Raubenheimer 2012). Understanding the patterns of nutrient regulation that carnivores use in diet selection will help to unravel how they respond to diet imbalances (Jensen et al. 2012, Raubenheimer et al. 2012b). While we advocate the collection of field data on the nutrient composition of foods, self-selection experiments are also needed to provide fundamental information for the design of foods and diets to improve the health and welfare of animals in captivity.

There is much to be gained from field research to explore links among prey selection, nutrient regulation processes, abiotic factors (e.g., sea surface temperature and bathymetry), physiology, and behavior (Machovsky-Capuska et al. 2018). The integration of these variables has already begun with the coupling of the nutritional geometry framework with biologging science in a marine predator (Machovsky-Capuska et al. 2016b) (**Figure 3**). This approach enabled the estimation of important nutritional performance parameters, including the relationships between the gain of specific nutrients (e.g., proteins and lipids) and foraging effort (e.g., time spent foraging, distance traveled, or predation effort) (Machovsky-Capuska et al. 2016b). Such information can influence welfare, rehabilitation, translocation, and release practices.

## Aquaculture

Fisheries and aquaculture make crucial contributions to global food security, nutrition, and livelihoods (Food Agric. Organ. UN 2016). Forage fish (e.g., sardines, anchovies, herrings, and mackerels), which are key prey for marine apex predators, are also used directly for human food (Alder et al. 2008). Because human consumption of fish-derived protein has been increasing steadily (Tacon & Metian 2008), forage fish have been under fishing pressures that have led to frequent population collapses (Naylor et al. 2009). To meet demand for fish protein, aquaculture has focused on especially valuable carnivorous fish (Alder et al. 2008, Troell et al. 2014), which requires increasing amounts of fish meal and fish oil (Mullon et al. 2009). The demand is met, in part, by fishing large carnivorous finfish species that are suitable for human consumption, which can have

serious ecological consequences (Naylor et al. 2000, Pauly & Watson 2005). Considering that the fish meal and fish oil used to feed farmed carnivorous fish are limited resources, an increasing proportion of cereal and soya have been channeled to aquaculture as feed substitutes (Troell et al. 2014, Food Agric. Organ. UN 2016). As a downside, these plant ingredients are a key source for human food consumption and contain endogenous antinutritional factors that negatively influence fish health (Kaushik 1990). Hence, there is an urgent need for alternative naturally available and low-cost fish feeds that do not compete with human consumption (Tacon & Metian 2008, Food Agric. Organ. UN 2016).

An additional shortcoming is the lack of information on the dietary nutrient requirements of fish species, which influence their immune systems and welfare (Naylor et al. 2000). Under these circumstances, manufacturers often overformulate feeds and exceed nutritional requirements, leading to higher levels of uneaten feeds and feces that contribute to nutrient pollution (Naylor et al. 2009). Proteins and lipids are essential nutrients for carnivorous fish to thrive and grow well, whereas there is no specific requirement for carbohydrates, which can be obtained through the oxidation of certain amino acids and lipids (gluconeogenesis) (Raubenheimer et al. 2012a). Most carnivorous fish have a poor capacity to metabolize carbohydrates, and their overconsumption could lead to physiological disorders (Fu & Xie 2004); in addition, the excess carbohydrates in some feed formulations are a significant source of environmental pollution (Letelier-Gordo et al. 2017). However, manufacturers also tend to add inexpensive carbohydrates to fish feed as an energy source, which allows them to reduce the amount of dietary protein and consequently lower the feed cost (Craig et al. 2017). Nutritional ecology can help to elucidate the specific nutritional mixes that fish need, the behavioral mechanisms that they use to acquire these mixes, and the physiological systems that enable them to process and assimilate the food once eaten (Raubenheimer et al. 2012a). Such information can be used to establish a balance among nutritional requirements, processing, and economic and environmental constraints in feed formulations (Ruohonen et al. 2007).

The ability of fish to select nutritionally appropriate diets, based in part on previous experience, has been demonstrated by studies of macronutrient self-selection and regulation (Raubenheimer et al. 2012a). Nutritional self-selection experiments on fish require short periods of time to accurately estimate fish consumption and regulation linked to multiple factors that are valuable to aquaculture practices (e.g., growth, digestibility, welfare, and immune systems) (Raubenheimer et al. 2012a). Therefore, when designing feeds and feeding regimes in aquaculture, it is critical for economic, welfare, and environmental reasons to understand which nutrients are behaviorally regulated (Simpson & Raubenheimer 2001).

## CONCLUSIONS

Verity et al. (2002) suggested that reconsidering existing dogmas may prove useful in understanding complex marine environments, not by discarding the old paradigms, but by suggesting their clarification and welcoming fresh insights. Standardized and widely applicable sets of metrics and models grounded in well-established mechanisms are critical in the transferability of ecological models (Yates et al. 2018). Here, we have explored the potential of a multidimensional framework from nutritional ecology, nutritional geometry, to meet this challenge. Compared with its implementation in terrestrial systems (Machovsky-Capuska et al. 2015, Raubenheimer et al. 2015; reviewed in Simpson & Raubenheimer 2012), data for marine predators are scant, and consequently our emphasis has been on the fundamental issue of how nutritional geometry can reveal the variation in the nutritional composition of prey and its influences on marine predators, from individuals to populations and species.



One reason that multidimensional nutrition is relatively poorly developed for marine predators concerns the challenges of collecting dietary and other relevant data for these animals, especially in the wild. A promising way to overcome individual methodological shortfalls and improve our estimates of diets (Majdi et al. 2018) for geometric analysis is to combine biologging techniques (Machovsky-Capuska et al. 2016b, 2018), stable isotope signatures (Machovsky-Capuska et al. 2016c), and quantitative approaches such as Bayesian ellipses to estimate nutritional niche breadths (Machovsky-Capuska et al. 2018). A further priority is to integrate the understanding of foraging needs in individuals with their community-level consequences.

Numerous important research questions remain unanswered, and answering them will require first addressing some fundamental issues. Not least among these is the collection and standardization of reliable data for proximate composition analysis of prey that reflect spatiotemporal and species variation and can be linked to foraging behavior and environmental variables (e.g., sea surface temperature), as has been implemented recently in marine environments (Machovsky-Capuska et al. 2018). A second priority is increased multidisciplinary collaboration to enhance cross-field communication, improve the conservation and management of apex predator populations, and predict how they will respond to impacts on their marine environments (Denuncio et al. 2017).

### SUMMARY POINTS

1. Despite the importance of diet and nutrition for apex predators in marine systems, their nutritional ecology is poorly understood.
2. This situation could be improved if marine predator nutritional ecology were framed within a nutritionally explicit framework, as opposed to the energy-focused approach that currently dominates.
3. The nutritional geometry framework developed in studies of terrestrial animals can distinguish the roles of nutrients and energy.
4. Literature data on the nutritional compositions of marine prey and estimates of predator diet compositions show that nutritional geometry is equally applicable to the ecology of marine predators.
5. Examples of applications of nutritional geometry include new nutrient-focused approaches to the concept of the ecological niche, marine pollution, captive management and rehabilitation, and aquaculture.

### DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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