

Comparative analysis of feeding habits and dietary niche breadth in skates: the importance of body size, snout length, and depth

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Abstract Skates (Elasmobranchii, Rajiformes) are a morphologically conservative group of bentophagous chondrichthyan fishes with a high degree of endemism, that occur on marine soft bottoms. Subtle morphological aspects and bathymetric distribution are traits that vary among skate species that could have implications for their feeding ecology. We test how body size, snout length and bathymetric distribution influence the feeding habits and dietary niche breadth in skates using data on 71 species taken from the literature. We hypothesized that snout length has an effect on diet composition. We also hypothesized that dietary niche breadth increases with increasing depth range and decreases with increasing body size of skate species. Generalized additive models for location scale and shape were fitted with taxonomic level

(genera nested within family) included as a random effect term in each model. A model selection approach to test the level of support for alternative models was applied. We found that skate species that forage on large prey have the largest body size and skate species with the smallest body size prey on small and medium-sized invertebrates. The results indicated that body size has an effect on feeding habits of skates, whereas an effect of snout length was not supported. Bathymetric variables have an effect on the diet of skates. Our prediction that dietary niche breadth increases with increasing depth range and decreases with increasing body size of skate species was supported in part: in a first phase the relationship between dietary niche breadth and body size is positive, then in a second phase, including species larger than 1000 mm total length, the relationship become negative.

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Keywords Elasmobranch fishes · GAMLSS · Levins' standardized index · Macroecology · Rajiformes

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Introduction

Body size is a fundamental trait that varies over many orders of magnitude among species, and has major implications for life history and other aspects of an organism's ecology (Brown 1995; Costa et al. 2008). Many patterns in macroecology are related to body

size, such as geographic range size (Smith and Brown 2002; Goodwin et al. 2005), trophic level (Layman et al. 2005; Tucker and Rogers 2014) and niche breadth (Costa et al. 2008; Costa 2009). Intra-specifically, many aquatic predators incorporate, multiple prey in their diet as they grow, leading to a positive relationship between predator body size and niche breadth (e.g. Vögler et al. 2003; López-García et al. 2012; Kadri et al. 2014). However, according to optimal foraging theory, large-bodied individuals may have access to a wider range of prey, but they might restrict their diet to only large prey to maximize their energy intake. On the other hand, small-bodied individuals should be more selective to optimize energy intake because their diet is limited to small-bodied prey (Costa et al. 2008). Among species, contrasting patterns between predator body size and dietary niche breadth emerge, exhibiting positive (Brändle et al. 2002) and negative (Costa et al. 2008) relationships.

Feeding habits may be strongly influenced by processes involving traits associated with other niche dimensions (Fitzgerald et al. 2017). Thus, the extent of habitat breadth could influence the trophic ecology of a predator (Winemiller et al. 2015). Species with a broader habitat niche will have a greater amplitude in resource use because they encounter a wider variety of prey as compared with species with a narrower habitat niche (Brown 1984; Gaston et al. 1997). In this way, the combined effect of body size and habitat breadth may explain macroecological patterns with respect to diets and dietary niche breadth of predators.

In some cases, among related species, subtle morphological differences are more important in shaping ecological relationships than body size (Brandl et al. 1994). For example, prey manipulation may be correlated with morphological traits that cause differences in feeding habits among closely related species, such as bill size in birds (Díaz 1994), degree of jaw protrusion in butterflyfishes (Motta 1988) and skull shape in snakes (Klaczko et al. 2016). Ecomorphological studies have shown that even minor morphological differences may have profound impacts on ecology and evolution among closely-related species (Motta 1988).

Skates (Elasmobranchii, Rajiformes) are good models for macroecological studies because they are a monophyletic group, show a wide range of maximum body size, occur at different depths and have

subtle morphological variability among species. Skates are the most speciose group of chondrichthyan fishes with a high degree of endemism (Ebert and Compagno 2007). These species are a morphologically conservative group that occur on marine soft bottoms from the intertidal to depths of about 3000 m (Ebert and Compagno 2007). As benthophagous predators, skates consume a wide range of prey: amphipods, isopods, polychaetes, shrimps, crabs, cephalopods and fishes (Wetherbee and Cortés 2004). It has been hypothesized that large skate species are predatory on fishes, that smaller skate species consume mainly small benthic invertebrates, and that mid-sized skate species feed on both small and large crustaceans, and occasionally, on cephalopods and fishes (Orlov 1998; Wetherbee and Cortés 2004). In this way, body size is an important predictor of the feeding habits of skates. However, although morphological aspects and bathymetric distribution are inter-specific traits that vary even among closely related skate species, the potential effects of these traits on feeding ecology remain largely unexplored.

Elasmobranchs concentrate high densities of sensory organs in the oro-nasal region of their heads, that aid them in prey detection. Some species have an enlarged oro-nasal area, which increases their electroreceptive ability. For example, hammerhead sharks (Carcharhiniformes, Sphyrnidae) have a dorso-ventrally compressed and laterally expanded head, called cephalophoil, that enhances prey detection (Kajiura 2001). This unmistakable morphological trait of hammerhead sharks provides a greater electrosensory search area and increases the probability of detecting prey, as compared with similar sized shark species that lack a cephalophoil (Kajiura and Holland 2002). Also, the elongated rostrum of sawfishes enhances their electroreceptive search area in the bottom and into the water column enabling them to target free-swimming prey (Wueringer et al. 2012). Snout length (i.e. distance from tip of snout to the anterior margin of the orbit) varies greatly among skate species. This suggests that sensory capabilities for prey detection may also vary with snout length. In addition, differences in snout length of skates could translate into different capabilities to handle and capture prey. It has been shown that skates also use their snout to stun and handle prey (Wilga et al. 2012).

The present study is a macroecological examination to test how body size, snout length and bathymetric

distribution influence feeding habits and dietary niche breadth in skate species. We hypothesized that snout length has an effect on the diet composition of skates, because this morphological trait may influence the detection, capture and manipulation of prey. For example, a diet based on teleosts is a phenomenon widely observed in skates with an elongated snout, as in some species of the genera *Dipturus* (Forman and Dunn 2012; Mulas et al. 2015), *Dentiraja* (Kyne et al. 2008), *Zearaja* (Lucifora et al. 2000; Koen Alonso et al. 2001; Belleggia et al. 2016), *Sympterygia* (Barbini and Lucifora 2016), and *Beringraja* (Bizzarro et al. 2007; Robinson et al. 2007). Furthermore, we hypothesize that dietary niche breadth increases with increasing depth range, since a wide habitat (i.e. depth) range provides an opportunity to encounter a variety of prey. Finally, we also test two competing hypotheses regarding the relationship between niche breadth and body size. The first hypothesis is that, as observed in many aquatic predators, niche breadth increases with skate body size, since they are able to incorporate multiple prey as they grow. The second hypothesis, based on optimal foraging theory as stated above, is that niche breadth decreases with increasing body size of skate species.

Materials and methods

Data collection

We used data obtained from published literature on maximum body size and minimum and maximum depth distributions of species of skates (Appendix S1 in the Supplementary Material). We interpreted minimum and maximum values of depth as lower and upper bathymetric limits of the distribution. Depth range was calculated as the difference between maximum and minimum depth. Depth range was interpreted as a measurement of the extent of niche breadth of skates in the habitat dimension (Winemiller et al. 2015). We considered depth range a good indicator of habitat breadth, because it provides an indirect measurement of tolerance with respect to different abiotic factors. To confirm the taxonomic validity of skate species we used the work by Last et al. (2016).

We quantified snout length of each species with digital images. Fourteen images were obtained from

authors, and 58 images were obtained from biodiversity websites (Appendix S2 in the Supplementary Material). All photographs used were from the dorsal side and the taxonomic identification was checked. From each digital image, we took two measurements: snout length, as the distance from tip of snout to the anterior margin of the orbit in pixels; and total length, as the distance from tip of snout to posteriormost point of tail in pixels. The measurements followed the definitions of these morphometric variables for skates proposed by Last et al. (2008). Then, we calculated the proportion of snout length relative to total length, as the ratio between the number of pixels of snout length and the number of pixels of total length multiplied by 100. The measurements in the digital images were obtained using the ImageJ software (<http://imagej.nih.gov/ij/>).

Diet composition data were obtained from peer-reviewed articles and theses (Appendix S1 in the Supplementary Material). In order to compare diet among skate species, prey were grouped into eight general categories: teleost fishes, chondrichthyan fishes, cephalopods, hard molluscs such as gastropods and bivalves, small benthic crustaceans such as amphipods, isopods and cumaceans, euphausiids and mysids, decapods and stomatopods, and polychaetes. These categories were chosen because they reflected the ecological variability of the diet among skate species. As different dietary indices exist and more than one diet study was available for many species, we calculated an index of standardized diet composition to determine the proportion of each prey category in the diet of a species (Cortés 1999; Ebert and Bizzarro 2007). The equation is the following:

$$P_j = \frac{\sum_{i=1}^n P_{ij}N_i}{\sum_{j=1}^8 (\sum_{i=1}^n P_{ij}N_i)}$$

where P_j is the proportion of each prey category, P_{ij} is the proportion of prey category j in study i , N_i is the number of stomach samples containing food used to calculate P_{ij} in study i , n is the number of studies, j is the number of the prey categories, and $\sum P_j = 1$ (Cortés 1999). For each feeding study, the proportion of each prey category P_{ij} was determined using the quantitative method in the original study, following the ranking criteria proposed by Cortés (1999). Ebert and

Bizzarro (2007) presented a global standardized diet composition of skate species, but we updated this information with new published literature.

Statistical analyses

To determine how body size, snout length and depth influence diet among different skate species we adopted a multiple hypothesis modelling approach (Symonds and Moussalli 2011). To test these hypotheses, we fitted generalized additive models for location scale and shape (GAMLSS) (Stasinopoulos and Rigby 2007). GAMLSS are defined as semi-parametric regression type models, where a general distribution family can be adopted in the models, including highly skewed, kurtotic, continuous or discrete distributions, and the systematic part is extended to allow modeling the parameters of a given distribution by parametric and/or nonparametric functions of explanatory variables and/or random-effects terms (Stasinopoulos and Rigby 2007). In each model, the response variable was the proportion of each prey category P_j and the explanatory variables were maximum body size, minimum depth, maximum depth, depth range and proportion of snout length relative to total length. Models with combinations among explanatory variables were fitted. To avoid multicollinearity among explanatory variables, pairs of predictors that had a correlation coefficient > 0.5 were not included together in the same model. Models without any of the explanatory variables (i.e. null models) were also fitted to test whether none of the candidate set of models had an effect on P_j . The response variables took values in a known restricted range including the endpoints of the range (i.e. 0–1), therefore we fitted the models assuming a beta-inflated error distribution (Stasinopoulos et al. 2008). Because the P_j values were very small for chondrichthyans, cephalopods, hard molluscs and euphausiids and mysids, we fitted GAMLSS assuming a binomial distribution. Thus, in these prey categories the P_j values were changed to presence-absence response. The models were fitted with a cubic smoothing splines function for each explanatory variable (Stasinopoulos et al. 2008).

Studies that compare traits of species must include phylogenetic relationships because closely related species tend to resemble each other (Pyron 1999). The taxonomic level (genera nested within families) was included as a random effect term in each model in

order to correct for any phylogenetic non-independence among samples (species). The classification scheme of Last et al. (2016) was used.

We applied a model selection approach to test the level of support for alternative models. (Franklin et al. 2001). The Akaike information criterion (AIC) was calculated for each GAMLSS and the model with the lowest AIC value was chosen as the model with the highest support (Johnson and Omland 2004).

For each skate species, we calculated Levins' standardized index of niche breadth (Krebs 1989) using standardized diet composition. Levins' standardized index provides a continuous measure of niche breadth on a scale from 0 to 1. Species closer to 0 have a narrower diet and are more specialized than species with values closer to 1, which have a broader diet and are more generalist (Krebs 1989). Then, to test the two competing hypotheses that diet breadth increases or decreases with increasing body size and increases with depth range, we fitted GAMLSS, where the response variable was Levins' standardized index and the explanatory variables were maximum body size, depth range and proportion of snout length relative to total length. Combinations among explanatory variables were fitted. We fitted a null model to judge whether or not explanatory variables had an effect on niche breadth. The models assumed a beta-inflated error distribution (Stasinopoulos et al. 2008) and random effect terms (genera nested within families) were included in each model. The best model was selected by minimising AIC (Johnson and Omland 2004).

The adequacy of model assumptions and fit were examined using Filliben coefficient, Worm plots and residual analyses (Stasinopoulos et al. 2008). The analyses were performed using the GAMLSS package (Stasinopoulos and Rigby 2007) under the R statistical environment, version 3.1.0 (R Core Team 2018).

Results

Data from 71 skate species were obtained, that included three families and 19 genera. Maximum body size ranged from 346 to 2440 mm for *Psammobatis extenta* and *Beringraja binoculata*, respectively. The longest snout belonged to *Dipturus oxyrinchus* with 24.29% of the total length. The maximum depth was 2300 m for *Rajella bathyphila* and the widest

depth range was 1880 m for *Bathyrāja matsubarae*. On a presence-absence basis of prey categories among all considered skate species in this study, decapods and stomatopods had the highest occurrence with a 98.61%. Teleosts was the second major prey category among skate species, contributing with values of 93.05% of occurrence, followed by small crustaceans (80.55%), cephalopods (70.83%) and polychaetes (69.44%). Euphausiids and mysids, hard molluscs and chondrichthyans had occurrences of 50, 34.72 and 25%, respectively.

Standardized diet compositions of skate species are available in Appendix S3 in the Supplementary Material. Decapods and stomatopods was the main prey category (> 90%) in six species: *Neoraja stehmanni*, *Sympterygia lima*, *Dentiraja cerva*, *Leucoraja garmani*, *Okamejei kenoei* and *Amblyraja doellojuradoi*. The species that consumed a very high proportion of teleosts (> 90%) were *Atlantoraja castelnaui* and *Bathyrāja spinicauda*. Seven species, *Bathyrāja brachyurops*, *B. griseocauda*, *Leucoraja erinacea*, *L. ocellata*, *Psammobatis rudis*, *Rajella bathyphila* and *R. bigelowi*, had a diet represented with more than 50% of small crustaceans. Polychaetes were of great importance to the diet of *Bathyrāja macloviana* (84%), followed by *B. albomaculata* (58%), *Amblyraja radiata* (45%) and *Psammobatis lentiginosa* (41%). Euphausiids and mysids was the main prey consumed (37.6%) by *Cruriraja parcomaculata*. In three species of the genus *Bathyrāja* (*B. maculata*, *B. matsubarae* and *B. parmifera*), cephalopods were an important prey (> 20%).

For some prey categories the AIC value of the second best model was very close to the AIC value of the best model (Tables 1, 2). This means that the second model can be considered to be essentially as good as the best model (Richards 2005; Symonds and Moussalli 2011). In this way, for cephalopods and chondrichthyans the second best model is shown because this model includes the variables of the best model (Table 2). In the same way, for decapods and stomatopods AIC values of the best model (null) and the second best model (maximum body size) differ very little (Table 1). Therefore, the effect of maximum body size for the consumption of decapods and stomatopods is shown.

Skate maximum body size had a significant effect on the consumption of teleosts, chondrichthyans, decapods and stomatopods, small crustaceans and

hard molluscs. The consumption of teleost and chondrichthyan prey increased with increasing maximum body size of skate species (Fig. 1a, e, respectively). In contrast decapods and stomatopods decreased with increasing maximum body size (Fig. 1b). A humped relationship between small crustaceans and maximum body size was found with a maximum peak at a maximum body size of about 1000 mm (Fig. 1c). The occurrence of hard molluscs as prey of skates increased with maximum body size until about 1700 mm, and then at higher maximum body size this trend became negative (Fig. 1d).

Snout length affected the consumption of only a few invertebrate prey. The use of prey category polychaetes as prey by skates decreased with snout length (Fig. 2a). Also, the occurrence of euphausiids and mysids showed a decreasing trend with a minimum between 16 and 18% of snout length (Fig. 2b). Clear trends between cephalopods with snout length were not found (Fig. 2c).

Depth range affected the consumption of six prey groups, namely, teleosts, polychaetes, small crustaceans, euphausiids and mysids, cephalopods, and hard molluscs. Teleost consumption was negatively related with depth range (Fig. 3a), while, on the contrary, polychaetes were positively related with depth range (Fig. 3b). The relationship between consumption of small crustaceans and depth range was hump shaped, peaking at about 900 m of depth range (Fig. 3c). Use of euphausiid and mysid prey had a sinusoidal relationship with depth range, with a minimum and maximum of occurrence at about 500 and 1400 m, respectively (Fig. 3d). A clear relationship between consumption of cephalopods and depth range was not found (Fig. 3e). The occurrence of hard molluscs in the diet of skates smoothly increased with increasing depth range (Fig. 3f).

Minimum depth of occurrence was a predictor of the consumption of teleosts, polychaetes, euphausiids and mysids, hard molluscs, and cephalopods. Teleosts were increasingly preyed upon with increasing minimum depth until about 300 m, then their consumption by skates started to decline (Fig. 4a). Polychaete consumption had a weak negative trend with minimum depth until about 500 m, where the trend became positive (Fig. 4b). Euphausiids and mysids had a minimum occurrence in the diet of skate species at about 300 m of minimum depth (Fig. 4c). The occurrence of hard molluscs and cephalopods smoothly

Table 1 Performance of generalized additive models for location scale and shape (GAMLSS) fitted between the proportion of consumed prey (P_j) by skate species and the explanatory variables with cubic smoothing spline function

Explanatory variables	AIC			
	Teleosts	Polychaetes	Decapods and stomatopods	Small crustaceans
Maximum body size	– 1.64	– 86.36	20.42 (0.99)	– 55.12
Maximum body size + depth range	– 6.61	– 84.79	23.47	– 62.48 (0.99)
Maximum body size + minimum depth	– 5.21	– 80.57	23.84	– 51.29
Maximum body size + maximum depth	– 7.36	– 83.92	25.84	– 59.83
Maximum body size + depth range + Minimum depth	– 16.58 (0.99)	– 80.36	25.29	– 57.32
Snout length	– 2.97	– 88.08	25.20	– 44.31
Snout length + depth range	0.53	– 81.61	29.02	– 47.53
Snout length + minimum depth	– 6.91	– 81.96	29.06	– 38.60
Snout length + maximum depth	– 2.88	– 83.01	30.05	– 46.55
Snout length + depth range + minimum depth	– 12.34	– 99.01 (0.98)	23.26	– 48.48
Depth range	5.07	– 86.13	24.92	– 51.03
Minimum depth	1.70	– 85.18	24.21	– 42.97
Maximum depth	2.21	– 86.36	26.10	– 50.15
1*	3.42	– 91.52	20.34 (0.99)	– 48.20

All models included a random term (genera nested within family)

AIC Akaike information criterion

*Null model. The Filliben coefficients are given in parentheses (Filliben coefficient > 0.95 means high goodness of fit performance of the model). AIC in bold denote the smallest for each prey

decreased with increasing minimum depth (Fig. 4d, e, respectively).

Maximum depth of skate occurrence had an effect on only one prey group. The consumption of chondrichthyan prey by skates slightly decreased with increasing maximum depth (Fig. 5).

Our prediction that diet breadth decreased with increasing body size and increased with increasing depth range was supported only in part. The best model included the combined effects of maximum body size and depth range (Table 3). The relationship between Levins' standardized index and maximum body size had a quadratic shape with a maximum peak at about 1000 mm (Fig. 6). On the other hand, Levins' standardized index clearly increased with increasing depth range (Fig. 6).

The Filliben coefficients of all the best models were higher than 0.95 (Tables 1, 2, 3). The Worm plots and residual analyses also showed that the models had a good fit (Appendix S4 in the Supplementary Material).

Discussion

This study tested whether body size, snout length and bathymetric distribution influence the feeding habits and dietary niche breadth in skate species. The hypothesis that snout length has an important effect on the diet composition of skates was not supported. In contrast, body size has an important influence on the feeding habits of skates, as suggested earlier (Orlov 1998; Wetherbee and Cortés 2004). On the other hand, our prediction that dietary niche breadth increases with increasing depth range and decreases with increasing body size of skate species was supported in part.

Our results clearly show that feeding habits in skate species are strongly associated with body size. In general, we found that skate species that forage on large prey (i.e. teleost and chondrichthyan fishes) have the largest body size. On the contrary, skate species with the smallest body size prey on small and medium-sized invertebrates, mainly decapods, amphipods and

Table 2 Performance of generalized additive models for location scale and shape (GAMLSS) fitted between occurrence of prey (presence-absence response) by skate species and the explanatory variables with cubic smoothing spline function

Explanatory variables	AIC			
	Euphausiids and mysids	Cephalopods	Hard molluscs	Chondrichthyes
Maximum body size	99.20	93.92	94.54	75.77 (0.98)
Maximum body size + depth range	103.23	96.45	95.49	78.45
Maximum body size + minimum depth	98.34	89.08	90.38 (0.99)	78.89
Maximum body size + maximum depth	103.05	96.64	97.42	76.35 (0.99)
Maximum body size + depth range + minimum depth	100.30	92.01	90.24 (0.99)	81.71
Snout length	98.19	97.16	99.63	79.87
Snout length + depth range	92.47	98.57	99.92	86.46
Snout length + minimum depth	88.28	92.49	96.16	81.26
Snout length + maximum depth	93.56	98.67	102.13	85.10
Snout length + depth range + minimum depth	84.74 (0.99)	88.47 (0.99)	90.90	86.76
Depth range	98.40	94.94	94.01	88.26
Minimum depth	94.15	88.42 (0.99)	90.77	84.57
Maximum depth	98.19	95.05	96.31	86.85
1*	94.34	93.19	94.09	81.79

All models included a random term (genera nested within family)

AIC Akaike information criterion

*Null model. The Filliben coefficients are given in parentheses (Filliben coefficient > 0.95 means high goodness of fit performance of the model). AIC in bold denote the smallest for each prey

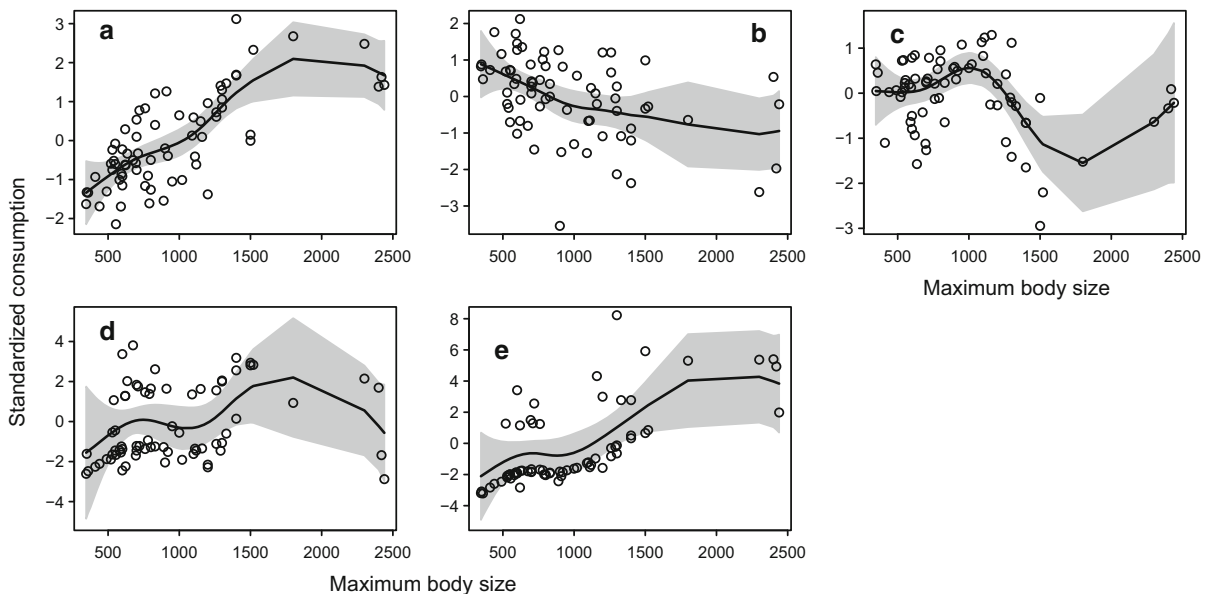


Fig. 1 GAMLSS cubic smoothing spline curves fitted to partial effects of maximum body size for the consumption of **a** teleosts, **b** decapods and stomatopods, **c** small crustaceans, **d** hard

molluscs and **e** chondrichthyans by skate species. The models had a beta inflated (**a**, **b**, and **c**) and binomial (**d** and **e**) error distribution. The shaded region represents standard errors

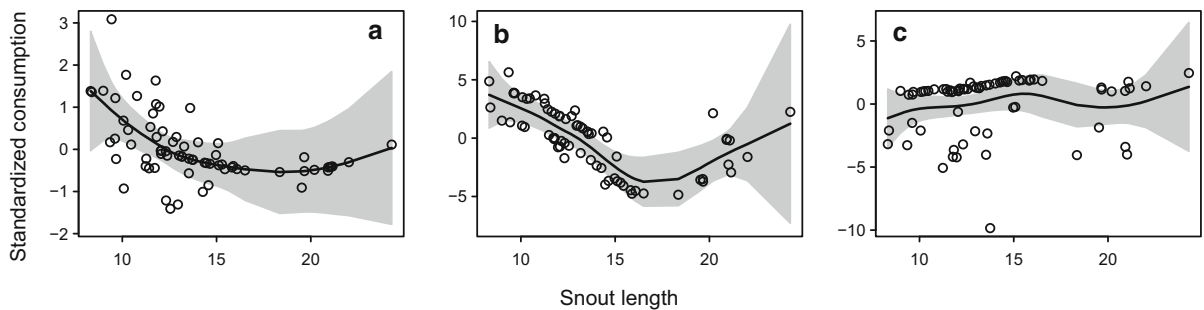


Fig. 2 GAMLSS cubic smoothing spline curves fitted to partial effects of snout length for the consumption of **a** polychaetes, **b** euphausiids and mysids and **c** cephalopods by skate species.

The models had a beta inflated (**a**) and binomial (**b** and **c**) error distribution. The shaded region represents standard errors

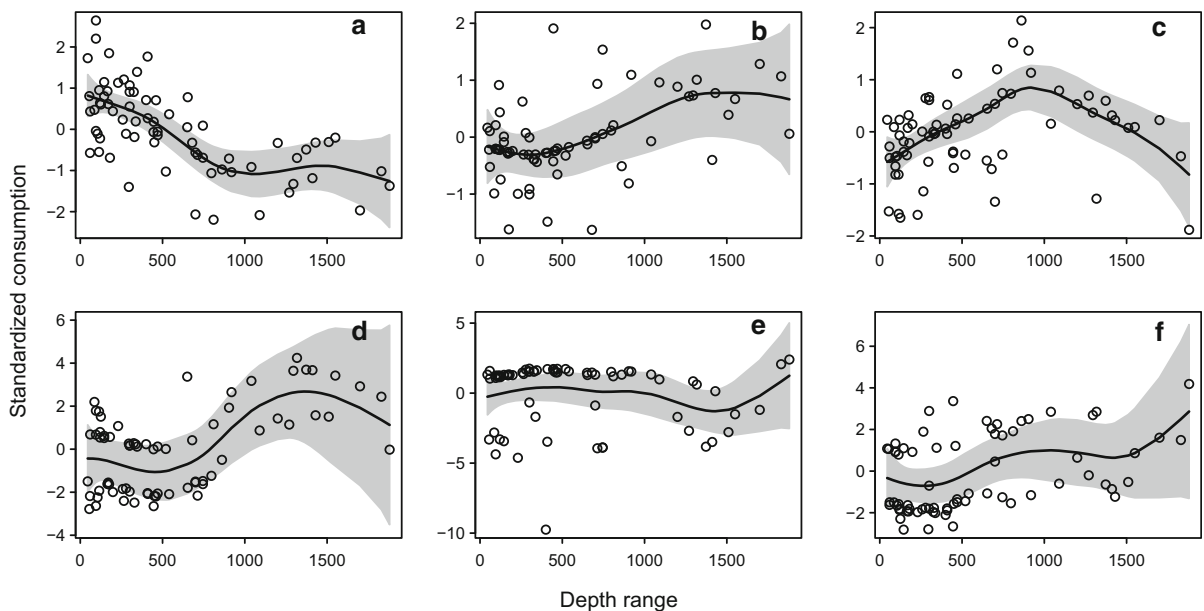


Fig. 3 GAMLSS cubic smoothing spline curves fitted to partial effects of depth range for the consumption of **a** teleosts, **b** polychaetes, **c** small crustaceans, **d** euphausiids and mysids,

e cephalopods and **f** hard molluscs by skate species. The models had a beta inflated (**a**, **b** and **c**) and binomial (**d**, **e** and **f**) error distribution. The shaded region represents standard errors

cumaceans. Contrary to our expectation, snout length has no effect on the feeding habits of skates. In models where snout length was selected, like those for polychaetes and euphausiids and mysids, a negative relationship with increasing snout length was found. These findings suggest that a large snout size in skates could not be a factor determining the improvement of the handling and capture of prey. Skates use their firm snout during suction feeding, but the pressures that they produce are weaker than that of stingrays (Myliobatiformes), which have a more flexible snout than skates (Wilga et al. 2012). Skates have also been

observed to use their firm snout to excavate for buried prey (Wilga et al. 2012). This indicates that an elongated snout in skates has multiple functions during feeding and that the effect of snout use on skate foraging ecology could not be measured in terms of diet composition, but in a different aspect of the prey acquisition process such as prey detection.

Prey capture behaviour and morphology are highly variable in elasmobranch fishes (Dean et al. 2005; Wilga et al. 2007). Prey-capture mechanisms that have allowed elasmobranchs to radiate in numerous niches comprise mainly three types: biting, suction-feeding

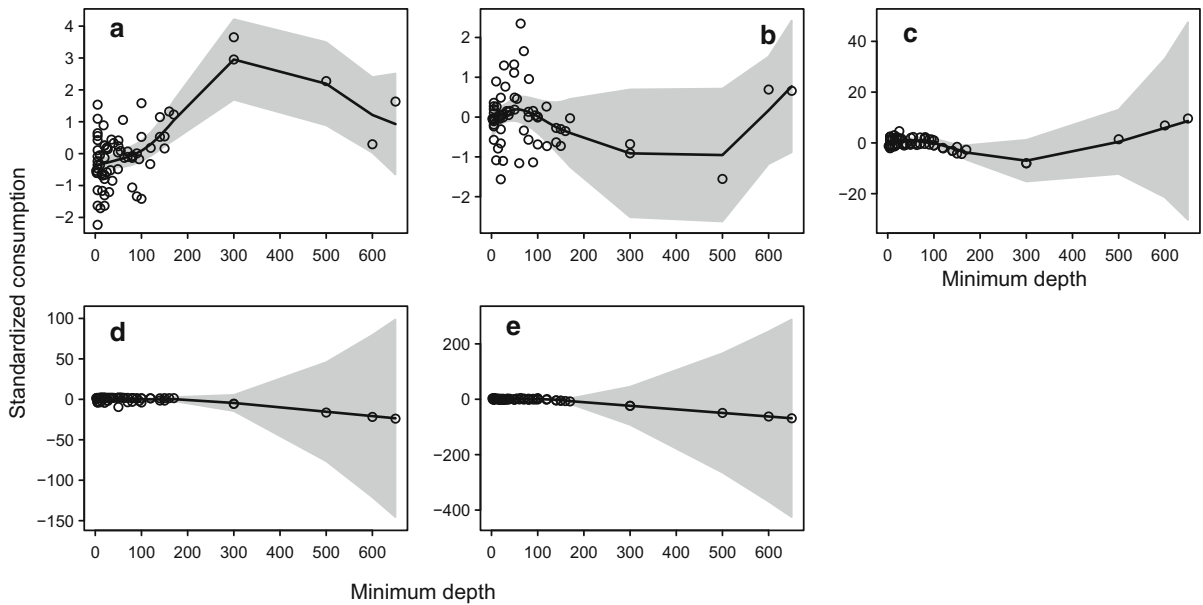


Fig. 4 GAMLSS cubic smoothing spline curves fitted to partial effects of depth range for the consumption of **a** teleosts, **b** polychaetes, **c** euphausiids and mysids, **d** cephalopods and

e hard molluscs by skate species. The models had a beta inflated (**a** and **b**) and binomial (**c**, **d** and **e**) error distribution. The shaded region represents standard errors

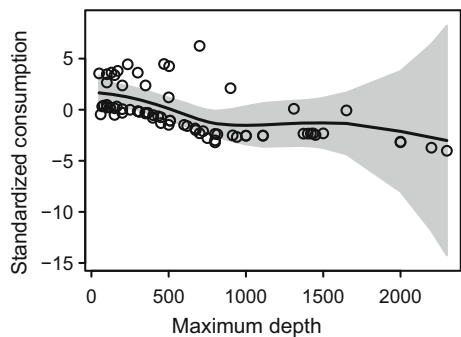


Fig. 5 GAMLSS cubic smoothing spline curves fitted to partial effects of maximum depth for the consumption of chondrichthyans by skate species. The model had a binomial error distribution. The shaded region represents standard errors

and filter-feeding (Motta 2004). In skates, prey capture performance combines both biting and suction. For example, in captivity, the little skate, *Leucoraja erinacea*, captures its prey by grasping them with the jaws, through biting combined with weak suction; then the little skate exerts a stronger suction to transport the prey inward (Wilga et al. 2007). Besides, skates are gape-limited because their teeth are not able to cut prey. Mouth size and morphology are important determinants of variation in prey types and sizes

Table 3 Performance of generalized additive models for location scale and shape (GAMLSS) fitted between Levins’ standardized index by skate species and the explanatory variables with cubic smoothing spline function

Explanatory variables	AIC
Maximum body size	– 49.91
Maximum body size + depth range	– 54.19 (0.99)
Snout length	– 43.80
Snout length + depth range	– 43.20
Depth range	– 43.15
1*	– 44.35

All models included a random term (genera nested within family)

AIC Akaike information criterion

*Null model. The Filliben coefficients are given in parentheses (Filliben coefficient > 0.95 means high goodness of fit performance of the model). AIC in bold denote the smallest

consumed by predatory fishes (Karpouzi and Stergiou 2003). In general, gape size of fishes increases linearly with body size, as for example in the winter skate, *Leucoraja ocellata* (Scharf et al. 2000). Therefore, the only way skates can to increase the consumption of large prey would be by increasing body size.

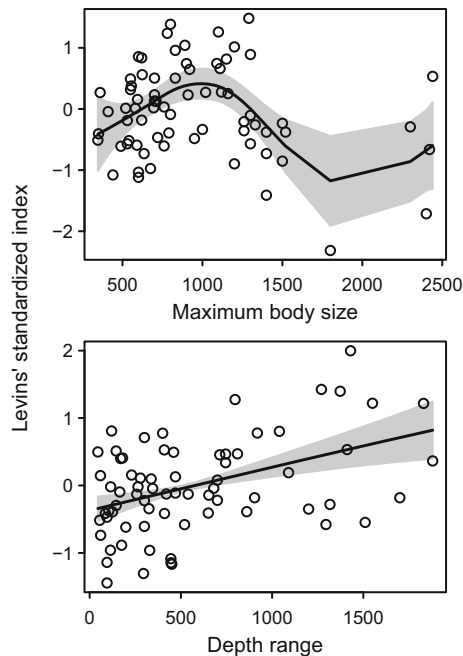


Fig. 6 GAMLSS cubic smoothing spline curves fitted to partial effects of maximum body size and depth range with Levins' standardized index of skate species. The models had a beta inflated error distribution. The shaded region represents standard errors

Bathymetric variables have an important effect on the feeding habits of skates. These patterns may be linked to biotic factors correlated with depth, such as prey abundance and distribution. The biomass and distribution of the benthic fauna varies with depth (Witman and Roy 2009), but there is no available information on macroecological patterns of prey distributions. It remains a question for future studies to determine a general macroecological relationship.

Species that are able to live under a wide variety of conditions and use a broad range of resources should also be able to obtain more resources (Brown 1984; Gaston et al. 1997). The link between ecological traits, such as habitat breadth and dietary breadth, has not been described previously for elasmobranch fishes. Our prediction that dietary niche breadth of skates increases with increasing depth range is clearly supported, indicating that the trophic niche dimension of skates is influenced by their habitat niche dimension. A possible explanation of this relationship is that skate species with a wide depth range occur in a wider variety of benthic environments, therefore they encounter a higher variety of prey compared with

skate species with narrow depth ranges. While our results apply to a morphologically conservative group of benthic species with a high degree of endemism, other species of elasmobranch fishes may show different relationships between these niche dimensions. Many large shark species are migratory, cosmopolitan and use a wide variety of marine environments, but tend to be specialized on a small set of prey (e.g. large white sharks, *Carcharodon carcharias*, feeding predominantly on marine mammals; Cliff et al. 1989).

General macroecological patterns between dietary niche breadth and body size of predators are contradictory and a general consensus has not emerged. For example, in lizards a negative association between both variables was found (Costa et al. 2008). A relationship between body size and diet breadth for passerine birds (Brandl et al. 1994) or marine predators (Costa 2009) was not found. Butterflies and moths (Wasserman and Mitter 1978) and land birds (Brändle et al. 2002) exhibit positive relationships. To our knowledge, this is the first study on this aspect focused on elasmobranch fishes. For skate species, the relationship found between body size and dietary niche breadth can be divided into two phases. In a first phase, up to a maximum body size of 1000 mm total length, the relationship between body size and dietary niche breadth is positive. We hypothesize that the increase in dietary niche breadth may be a result of an improved ability to capture a high diversity of prey with increasing body size. In a second phase, including species larger than 1000 mm total length, the relationship becomes negative. We propose that larger skate species avoid small and medium-sized prey (i.e. benthic invertebrates), because large skates have a competitive advantage to selectively catch large and mobile prey (i.e. fishes) offering a higher net energy gain. This translates in a narrowing of the dietary niche breadth. An interesting observation is that both the smallest and largest skate species have a narrow dietary niche breadth, but most likely the processes leading to this outcome are different.

Predicting the extinction risk of species is one of the most challenging and urgent assignments facing ecologists. Relative to bony fishes, elasmobranchs such as skates are highly vulnerable to an intense exploitation due to their large body size, late maturation, low fecundity (Dulvy and Reynolds 2002) and mainly to their late age at maturity (Hutchings et al.

2012). Another challenge to ecologists is to evaluate the relationship between ecological characteristics and extinction risk. Narrow niches lead to an increment in the dependence on some specific resources (Begon et al. 2006). Hence, interspecific differences in dietary niche breadth may be related to extinction risk because dietary specialists should be more sensitive than generalists to the loss of prey and/or the loss of prey habitat (Boyles and Storm 2007). Among chondrichthyans, species with narrower depth ranges are more likely to be threatened than species with wider depth ranges (Dulvy et al. 2014), suggesting that habitat specialists have a higher extinction risk. The effect of dietary niche breadth on extinction risk remains still to be tested.

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References

- Barbini SA, Lucifora LO (2016) Big fish (and a smallish skate) eat small fish: diet variation and trophic level of *Sympterygia acuta*, a medium-sized skate high in the food web. *Mar Ecol* 37:283–293
- Begon ME, Harper JL, Townsend CR (2006) *Ecology. From individuals to ecosystems*, 4th edn. Blackwell Science, Oxford
- Belleggia M, Andrada N, Paglieri S, Cortés F, Massa AM, Figueroa DE, Bremec C (2016) Trophic ecology of yellownose skate *Zearaja chilensis*, a top predator in the south-western Atlantic Ocean. *J Fish Biol* 88:1070–1087
- Bizzarro JJ, Robinson HJ, Rinewalt CS, Ebert DA (2007) Comparative feeding ecology of four sympatric skate species off central California, USA. *Environ Biol Fish* 80:197–220
- Boyles JG, Storm JJ (2007) The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. *PLoS ONE* 7:e672
- Brandl R, Kristín A, Leisler B (1994) Dietary niche breadth in a local community of passerine birds: an analysis using phylogenetic contrasts. *Oecologia* 98:109–116
- Brändle M, Prinzing A, Pfeifer R, Brandl R (2002) Dietary niche breadth for Central European birds: correlations with species-specific traits. *Evol Ecol Res* 4:643–657
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279
- Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago
- Cliff G, Dudley SFJ, Davis B (1989) Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). *S Afr J Mar Sci* 8:131–144
- Cortés E (1999) Standardized diet compositions and trophic levels of sharks. *ICES J Mar Sci* 56:707–717
- Costa GC (2009) Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* 90:2014–2019
- Costa GC, Vitt LJ, Pianka ER, Mesquita DO, Colli GR (2008) Optimal foraging constraints macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecol Biogeogr* 17:570–677
- Dean MN, Wilga CD, Summers AP (2005) Eating without hands or tongue: specialization, elaboration and the evolution of prey processing mechanisms in cartilaginous fishes. *Biol Lett* 1:357–361
- Díaz M (1994) Variability in seed size selection by granivorous passerines: effects of bird size, bird size variability, and ecological plasticity. *Oecologia* 99:1–6
- Dulvy NK, Reynolds JD (2002) Predicting extinction in skates. *Conserv Biol* 16:440–450
- Dulvy NK, Fowler SL, Musick JA et al (2014) Extinction risk and conservation of the world's sharks and rays. *ELife* 3:e00590
- Ebert DA, Bizzarro JJ (2007) Standardized diet compositions and trophic levels of skates (Chondrichthyes, Rajiformes, Rajoidei). *Environ Biol Fish* 80:221–237
- Ebert DA, Compagno LJV (2007) Biodiversity and systematics of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environ Biol Fish* 80:111–124
- Fitzgerald DB, Winemiller KO, Sabaj Perez MH, Sousa LM (2017) Using trophic structure to reveal patterns of trait-based community assembly across niche dimensions. *Funct Ecol* 31:1135–1144
- Forman JS, Dunn MR (2012) Diet and scavenging habits of the smooth skate *Dipturus innominatus*. *J Fish Biol* 80:1546–1562
- Franklin AB, Sheik TM, Anderson DR, Burnham KP (2001) Statistical model selection: an alternative to null hypothesis testing. In: Shenk TM, Franklin AM (eds) *Modeling in natural resources management: development, interpretation, and application*. Island Press, Washington, pp 75–90
- Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance range size relationships: an appraisal of mechanisms. *J Anim Ecol* 66:579–601
- Goodwin NB, Dulvy NK, Reynolds JD (2005) Macroecology of live-bearing in fishes: latitudinal and depth range comparisons with egg-laying relatives. *Oikos* 110:209–218
- Hutchings JA, Myers RA, García VB, Lucifora LO, Kuparinen A (2012) Life-history correlates of extinction risk and recovery potential. *Ecol Appl* 22:1061–1067
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Kadri H, Marouani S, Bradai NM, Bouaïn A (2014) Food habits of the brown ray *Raja miraletus* (Chondrichthyes: Rajidae) from the Gulf of Gabès (Tunisia). *Mar Biol Res* 10:426–434
- Kajiura SM (2001) Head morphology and electrosensory pore distribution of carcharhinid and sphyrnid sharks. *Environ Biol Fish* 61:125–133

- Kajiura SM, Holland KN (2002) Electroreception in juvenile scalloped hammerhead and sandbar shark. *J Exp Biol* 205:3609–3621
- Karpouzi VS, Stergiou KI (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *J Fish Biol* 62:1353–1365
- Klaczko J, Sherratt E, Setz EZF (2016) Are diet preferences associated to skulls shape diversification in Xenodontidae snakes? *PLoS ONE* 11:e0148375
- Koen Alonso M, Crespo EA, Gracia NA, Pedraza SN, Mariotti PA, Berón Vega B, Mora NJ (2001) Food habits of *Dipturus chilensis* (Pisces: Rajidae) off Patagonia, Argentina. *ICES J Mar Sci* 58:288–297
- Krebs CJ (1989) *Ecological methodology*. Harper Collins Publishers, New York
- Kyne PM, Courtney AJ, Bennett MB (2008) Aspects of reproduction and diet of the Australian endemic skate *Dipturus polyommata* (Ogilby) (Elasmobranchii: Rajidae), by-catch of a commercial prawn trawl fishery. *J Fish Biol* 72:61–77
- Last PR, White WT, Pogonoski JJ, Gledhill DC (2008) New Australian skates (Batoidea: Rajoidei)-background and methodology. In: Last PR, White WT, Pogonoski JJ, Gledhill DC (eds) *Descriptions of New Australian skates Batoidea: Rajoidei*. CSIRO, Hobart
- Last P, White W, de Carvalho M, Séret B, Stehmann M, Naylor G (2016) *Rays of the world*. CSIRO Publishing, Clayton
- Layman CA, Winemiller KO, Arrington DA, Jepsen DB (2005) Body size and trophic position in a diverse tropical food web. *Ecology* 86:2530–2535
- López-García J, Navia AF, Mejía-Falla PA, Rubio EA (2012) Feeding habits and trophic ecology of *Dasyatis longa* (Elasmobranchii: Myliobatiformes): sexual, temporal and ontogenetic shifts. *J Fish Biol* 80:1563–1579
- Lucifora LO, Valero JL, Bremec CS, Lasta ML (2000) Feeding habits and prey selection by the skate *Dipturus chilensis* (Elasmobranchii: Rajidae) from the south-western Atlantic. *J Mar Biol Assoc UK* 80:953–954
- Motta PJ (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environ Biol Fish* 22:39–67
- Motta PJ (2004) Prey capture behavior and feeding mechanics of elasmobranchs. In: Carrier JC, Musick JA, Heithaus MR (eds) *Biology of sharks and their relatives*. CRC Press, Boca Raton, pp 165–202
- Mulas A, Bellodi A, Cannas R, Cau A, Cuccu D, Marongiu MF, Porcu C, Follesa MC (2015) Diet and feeding behaviour of longnosed skate *Dipturus oxyrinchus*. *J Fish Biol* 86:121–138
- Orlov AM (1998) The diets and feeding habits of some deep-water benthic skates (*Rajidae*) in the Pacific waters off the Northern Kuril Islands and Southeastern Kamchatka. *Alaska Fish Res Bull* 5:1–17
- Pyron M (1999) Relationships between geographical range size, body size, local abundance, and habitat breadth in North American suckers and sunfishes. *J Biogeogr* 26:549–558
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86:2805–2814
- Robinson HJ, Cailliet GM, Ebert DA (2007) Food habits of the longnose skate, *Raja rhina* (Jordan and Gilbert, 1880), in central California waters. *Environ Biol Fish* 80:165–179
- Scharf FS, Juanes F, Rountree RA (2000) Predator size – prey size relationships of marine fish predators: interespecific variation and effects of ontogeny and body size trophic-niche breadth. *Mar Ecol Prog Ser* 208:229–248
- Smith KF, Brown JH (2002) Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. *Global Ecol Biogeogr* 11:313–322
- Stasinopoulos DM, Rigby RA (2007) Generalized additive models for location scale and shape (GAMLSS) in R. *J Stat Softw* 23:1–46
- Stasinopoulos DM, Rigby RA, Akantziliotou C (2008) Instructions on how to use the GAMLSS package in R. Second edition. Technical Report 01/08, STORM Research Centre, Metropolitan University, London
- Symonds ME, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* 65:13–21
- Tucker MA, Rogers TL (2014) Examining predator-prey body size, trophic level and body mass across marine and terrestrial mammals. *P Roy Soc B* 281:20142103
- Vögler R, Milessi AC, Quiñones RA (2003) Trophic ecology of *Squatina guggenheim* on the continental shelf off Uruguay and northern Argentina. *J Fish Biol* 62:1254–1267
- Wasserman SS, Mitter C (1978) The relationship of body size to breadth of diet in some Lepidoptera. *Ecol Entomol* 3:155–160
- Wetherbee BM, Cortés E (2004) Food consumption and feeding habits. In: Carrier JC, Musick JA, Heithaus MR (eds) *Biology of sharks and their relatives*. CRC Press, Boca Raton, pp 225–246
- Wilga CD, Motta PJ, Sanford CP (2007) Evolution and ecology of feeding in elasmobranchs. *Integr Comp Biol* 47:55–69
- Wilga CD, Maia A, Nauwelaerts S, Lauder GV (2012) Prey handling using whole-body fluid dynamics in batoids. *Zoology* 115:47–57
- Winemiller KO, Fitzgerald DB, Bower LM, Pianka ER (2015) Functional traits, convergence evolution, and periodic tables of niches. *Ecol Lett* 18:737–751
- Witmann JD, Roy K (2009) *Marine macroecology*. The University of Chicago Press, Chicago
- Wueringer EB, Squire Jnr L, Kajiura SM, Tibbets IR, Hart NS (2012) Electric field detection in sawfish and shovelnose rays. *Plos ONE* 7:e41605