

A length-based approach to predator–prey relationships in marine predators¹

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Abstract: Body size is a critical feature of the ecology of most organisms and has been used to describe and understand predator–prey interactions in both terrestrial and aquatic environments. Most previous studies have used prey mass to examine the relationships between predator size and prey size; however, using prey lengths may provide a different perspective, particularly for gape-limited fishes. Using a large database of predator and prey lengths for marine aquatic predators, I found the expected positive wedge-shaped relationship between predator length and prey length and a negative converging relationship between relative prey length (prey–predator length ratio = a measure of trophic niche breadth) and predator length. Distinct patterns in the size scaling of this measure of trophic niche breadth were identified using quantile regression: converging relationships were common among adults but absent among larvae. This difference suggests contrasting ontogenetic foraging opportunities between adults and larvae: a lack of large relative prey sizes for the largest adult predators, and a greater ability of larvae to include larger prey items in their diet as they grow.

Résumé : La taille du corps est un aspect essentiel de l'écologie de la plupart des organismes et a été utilisée pour décrire et comprendre les interactions entre prédateurs et proies dans des milieux tant terrestres qu'aquatiques. Si la plupart des études antérieures se sont servies du poids des proies pour examiner les relations entre la taille des prédateurs et celle des proies, l'utilisation de la longueur des proies pourrait offrir une autre perspective, particulièrement pour les poissons dont l'alimentation est limitée par l'ouverture maximum de la bouche. En utilisant une imposante base de données sur la longueur de prédateurs et de proies pour des prédateurs aquatiques marins, j'ai décelé la relation positive en forme de biseau attendue entre la longueur des prédateurs et celles des proies et une relation convergente négative entre la longueur relative des proies (le rapport de longueurs proie:prédateur, une mesure de l'amplitude de la niche trophique) et la longueur des prédateurs. Différents motifs d'échelles de taille de cette mesure de l'amplitude de la niche trophique ont été décelés à l'aide de la régression quantile, les relations convergentes étant répandues chez les adultes, mais absentes chez les larves. Cette différence pourrait indiquer des différences ontogéniques des possibilités d'approvisionnement entre les adultes et les larves, soit le manque de proies de grande taille relative pour les plus grands prédateurs adultes et une plus grande capacité des larves, en grandissant, d'intégrer des proies plus grandes à leur alimentation. [Traduit par la Rédaction]

Introduction

Body size is a critical feature of the ecology of most organisms (Peters 1983) and has been used to describe and understand predator–prey interactions in both terrestrial and aquatic environments (Vézina 1985; Scharf et al. 2000; Juanes et al. 2002; Barnes et al. 2010). Peters (1983) predicted that the predator–prey size relationship would be positive but weak and that it was likely that “no general rule should apply” (Peters 1983, p. 109). However, many subsequent analyses have shown strong positive relationships between prey size and predator size across ecosystems (Riede et al. 2011; Tucker and Rogers 2014). Most of these general analyses have been performed using prey and predator masses, likely because metabolic and energy requirements are generally based on mass (Woodward et al. 2005; Sibly et al. 2012). However, using prey length and (or) width as metrics, instead of mass, may provide a different perspective, and these metrics are commonly used in behavioural experiments (see, for example, Scharf et al. 2003, 2009). Prey body length and depth are important constraints in fish predator–prey relationships as most fishes are gape limited and ingest their prey whole and maximum prey sizes are often correlated with changes in gape size (Scharf et al. 1997, 2000). Prey

body depth may be more relevant in defining gape-limited predator–prey relationships but are rarely available (see Scharf et al. 2000), and prey body lengths are usually taken as a proxy of depth. Also, prey mass estimated from stomach contents is usually reflective of the digested mass of the prey at the time of collection, whereas prey length analyses use whole prey or reconstruct original prey lengths from prey hard parts from known species-specific relationships (e.g., Scharf et al. 1998c; Staudinger et al. 2009). Also, in many analyses, prey mass is calculated from prey length, thus increasing potential error, particularly when species-specific length–mass conversions are not available. Further, even when such conversions exist, length–mass relationships in fishes are labile and can change seasonally, annually, and with ontogeny (Froese 2006).

Recent studies have also shown that when examining the edges of the predator size – prey size scatter, minimum prey sizes increase at a slower rate than maximum prey sizes in the “classic” wedge pattern as first described by Wilson (1975) and Peters (1983). Quantile regression (Scharf et al. 1998a; Cade and Noon 2003) has proved a valuable tool in quantifying the edges of such scatters for a variety of species (Scharf et al. 2000; Juanes et al. 2002; Juanes 2003; Pinnegar et al. 2003; Bethea et al. 2004; Menard et al. 2006;

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Rudershausen et al. 2010; Staudinger and Juanes 2010a; Teffer et al. 2015). In contrast to these previous results, Costa (2009), when analyzing the data compiled in Barnes et al. (2008), showed a “reverse” wedge wherein minimum prey sizes increased much faster than maximum prey sizes and attributed this result to the “optimal foraging hypothesis”.

Although prey size is generally found to increase with predator size for most fishes including sharks (Scharf et al. 2000; Bethea et al. 2004; Baker and Sheaves 2005; Daly et al. 2009; Rudershausen et al. 2010; Young et al. 2010), it is unclear what the general relationship between predator niche breadth and predator size should be. Ontogenetic patterns in trophic niche breadth (the range in relative prey size) are due to a combination of variation in predator and prey morphology and foraging behaviour, habitat associations, and diet overlap, as well as relative abundances (Scharf et al. 2000; Juanes 2003; Staudinger and Juanes 2010a; Teffer et al. 2015). Increases in trophic niche breadth with ontogeny indicate expanding prey resources, whereas decreases suggest constraints in relative prey size availability with predator growth (Scharf et al. 2000; Juanes 2003). In larval fishes, trophic niche breadth has been reported to increase (Pepin and Penney 1997) or be independent of predator length (Pearre 1986; Munk 1997; Sabatés and Saiz 2000), whereas in larger fishes, the trend is generally negative (Scharf et al. 2000; Barnes et al. 2010). Part of the reason for the discrepancy is the lack of agreement of a standard definition of trophic niche breadth but may also indicate fundamental ontogenetic differences in trophic niche breadth reflecting differences in foraging tactics between larvae and adults. Larvae are changing their foraging abilities quickly, enhanced by rapid development of prey detection and capture abilities likely leading to sharp changes in prey sizes consumed (Houde 1997; Fuiman and Higgs 1997). Also, few studies include the range of predator sizes (i.e., number of species) sufficient for detecting length-based shifts in niche breadth. Here I re-analyze a large database of predator and prey sizes for marine fishes (and one cephalopod) (Barnes et al. 2008) taking a length-based perspective and comparing results with those of previous studies based on mass using the same database (Costa 2009; Barnes et al. 2010). I re-examine evidence for the classical wedge patterns across species and focus my analyses on the scaling of trophic niche breadth estimated using quantiles of relative prey sizes (as in Scharf et al. 2000; Staudinger and Juanes 2010a) to ask whether there is a general pattern across all predator lengths and if larval and adult fishes show similar patterns.

Materials and methods

I used predator and prey lengths compiled in Barnes et al. (2008). The dataset contains almost 35 000 individual prey eaten at 27 marine locations (for more details, see Barnes et al. (2008)). The previous analyses of this dataset by Barnes et al. (2010) used only 29 582 records from 21 locations, 92 predator species, and 183 prey types and focused on food web differences among locations. The ~5000 missing records are those in which only low-quality length–mass conversions were available. Here I am able to use the entire dataset (expanding the analyzed data by 18%). I also separated the dataset into fish larvae–postlarvae (termed “larvae”) and juveniles–adults (termed “adults”). Fish defined as larvae or postlarvae by the original researchers comprised 27 predator species with average lengths of <5 cm and 5242 individual prey. Those defined as adults included 29 603 prey items and 62 predator species, but three of these species were represented by two separate datasets for a total of 65 predator datasets. Of these, only 15 larvae (4807 total data points) and 36 adults (29 217 total data points) had enough observations (>50 data points each) to calculate species-specific trophic niche breadths (for lists of species used, see Tables 3 and 4).

When using a large dataset such as this one, there are always statistical concerns about non-independence between sample points, especially for diet data where multiple prey are taken from an individual stomach and multiple predators are sampled concurrently (for a recent review, see Chipps and Garvey 2007). When analyzing multiple species, there is also the issue of phylogenetic independence. Fortunately, Costa (2009) in his analysis of this dataset dealt with both types of potential non-independence. First, his results were similar when using predators as independent data points or incorporating phylogenetically independent contrasts, implying that either method produces robust results. Also, because the results of using all of the individual data points vs. the species-specific analyses provided similar results (in both Costa’s and my analyses), this also suggests that phylogenetic non-independence is not a large issue here. Second, when assessing non-independence due to “location” and “predator” as random factors in a mixed-effect model, he found significant random effects but no interaction effects. However, the predator–prey relationship was still statistically significant and the slope was not statistically different from the one obtained using OLS regression, again suggesting minor effects of non-independence. Unfortunately, I am unaware of a way to assess multiple random effects in a quantile regression. However, given Costa’s (2009) results, it seems reasonable to assume that these effects would also be relatively unimportant when using quantile regression.

I used least squares linear regression to analyze the overall relationship between predator and prey lengths and quantile regression (Scharf et al. 1998a) to assess the upper and lower bounds of the relationship (i.e., how maximum and minimum prey lengths scale with predator length). Because of the large sample sizes (all $n \gg 1000$), lower and upper bounds were represented by the 0.01 and 0.99 quantiles (see Scharf et al. 1998a). In contrast to Costa’s (2009) analysis of the same dataset, I decided to analyze the raw data and not log-transform them. Although log-transforming the data is not incorrect, it leads to a different interpretation of the results. The primary advantage of using quantile regression is to detect changes in the distribution of y across the range of x . There is no specification of how variance should be related to the mean. The heterogeneity in the variance of y is accounted for in the model. Quantile regression is meant to be used with heterogeneous distributions. Quantile slopes were compared using a modified t test. To assess overall scaling of prey–predator ratios, I regressed relative prey length vs. predator length. Relative prey length ratio (PPR) is defined as prey length/predator length, as in most studies using a length-based approach (e.g., Scharf et al. 1998b, 2000; Menard et al. 2006; Young et al. 2010; Staudinger and Juanes 2010a). This definition is the inverse (predator mass/prey mass) of the one used by most studies analyzing masses, and it is unclear whether any differences emerge when using lengths instead of masses. I then compared the slopes of the upper (90th) and lower (10th) bounds of the relative prey length relationship with predator length using quantile regression to assess whether they were statistically similar (i.e., parallel) and, if dissimilar, whether they were converging or diverging. Parallel slopes indicate a constant range in relative prey lengths with predator ontogeny; converging slopes suggest a decreasing range and diverging slopes suggest an increasing range. The 10th and 90th quantiles were chosen to estimate the lower and upper bounds for all these species because they adequately described the shapes of relative body length distributions while remaining conservative even when sample size restrictions (Scharf et al. 1998a) were not strictly adhered to (Staudinger and Juanes 2010a).

I next assessed the relationship between average trophic niche breadth and predator length for individual species with enough data separated into larvae and adults. First, for each species used, I determined whether the relationship between relative prey length and predator length was parallel, converging, or diverging as above. To assess whether patterns in convergence or divergence

were different in larvae vs. adults, I ran a 2 × 3 contingency analysis with a χ^2 test. I then calculated the trophic niche breadth as the difference between the predicted minimum and maximum for each predator length in each predator dataset using eq. 1 from Staudinger and Juanes (2010a):

$$(1) \quad TNB = \frac{\sum_{i=1}^{i=n} [(m_{90})(PL_i) + (b_{90})] - [(m_{10})(PL_i) + (b_{10})]}{n}$$

where TNB is trophic niche breadth, i is an observation of predator length (PL), n is the total number of observed species-specific predator-prey length combinations, m is the slope, and b is the y intercept calculated from the 90th and 10th quantiles of relative prey length – predator length ratios regressed against each predator length. Using regression quantiles to estimate trophic niche breadths eliminates the need to subjectively partition predator size data into separate size classes to estimate means and standard deviations within each size class, as is done in previous ratio-based trophic-niche breadth studies (Pearre 1986; Munk 1997; Pepin and Penney 1997). I then regressed the mean species-specific trophic niche breadth against mean predator length to assess whether an overall relationship exists. I used median regression (because of a skewed distribution) for larvae and nonlinear regression for adults. All statistical analyses were performed in STATA (ver. 13.1; StataCorp 2013).

Results

As expected, I found a positive relationship between prey and predator length (Tables 1, 2). The scatter was wedge-shaped with minimum prey sizes (slope = 0.0088) increasing much slower than maximum prey sizes (slope = 0.2439) ($P < 0.0001$). Both lower and upper bound quantile slopes differed from the median slope (0.0685), suggesting that they were driven by a different set of ecological factors (Table 1). The least squares regression slope (0.0654, not shown) was very similar to the median slope. I found a negative relationship between relative prey length (prey length/predator length) and predator length (Table 2). Quantile regressions showed that the trophic niche breadth was converging, i.e., the difference in relative prey sizes was significantly larger at small predator sizes than at larger ones (Table 2). I obtained similar results when using data for adults (Tables 1, 2; Figs. 1a, 1b) but contrasting results for larvae (Tables 1, 2; Figs. 1c, 1d). Larval absolute prey sizes showed similar median slopes but larger upper bound slopes and smaller lower bound slopes (both $P < 0.001$) than adults (Table 1; Fig. 1c). However, larval relative prey sizes scaled positively with predator size and showed a diverging pattern between minimum and maximum quantile slopes (Table 2; Fig. 1d).

Of the 15 larvae datasets with enough data to compute trophic niche breadths, 11 species had parallel lower and upper bound slopes, four were diverging, and none was converging (Table 3; Supplemental Fig. S1²). When regressed against mean predator length, mean trophic niche breadth across larval species showed a positive relationship (Fig. 2a). In contrast, of the 36 adults with enough data, 16 of them had parallel lower and upper bound slopes, 6 were diverging, and 14 were converging (Table 4; Supplemental Fig. S2²). The general trend was for the smallest predators to show no significant changes in trophic niche breadth with predator length (i.e., parallel), whereas the largest predators tended to show converging patterns. The distribution of convergence and divergence was different between larvae and adults ($\chi^2 = 8.042, P = 0.0179$), with the largest discrepancy occurring with converging slopes. The relationship between mean trophic niche

Table 1. Median and lower (1%) and upper (99%) bound slopes and samples sizes (n) of prey length–predator length relationships using quantile regression of entire dataset (All predators), only larvae, and only adults.

	Median slope	Lower bound slope	Upper bound slope	n
All predators	0.0685	0.0088	0.2439	34845
Larvae	0.0515	0.0038	0.5116	5242
Adults	0.0437	0.0073	0.1992	29603

Note: All slopes were significant (all $P < 0.001$).

Table 2. Median and lower (10%) and upper (90%) bound slopes of relative prey length (prey length/predator length) vs. predator length relationships using quantile regression of entire dataset (all predators), only larvae, and only adults.

	Median slope	Lower bound slope	Upper bound slope	P	Change in TNB
All predators	-0.0002*	0	-0.0013*	<0.0001	con
Larvae	0.0025*	0	0.0515*	<0.0001	div
Adults	-0.0007*	-0.0002*	-0.0015*	<0.0001	con

Note: Asterisk (*) following slope value indicates significance ($P < 0.05$). P is significance of the difference between lower and upper bound slopes (TNB, trophic niche breadth) calculated using eq. 1. Change in TNB represents whether the lower and upper bound slopes are converging (con) or diverging (div). Samples sizes are as in Table 1.

breadth and mean predator length across adult datasets was negative (Fig. 2b).

Discussion

I found a positive relationship between predator and prey size using individual lengths as has been found in a variety of studies of predators across many ecosystems (Riede et al. 2011; Tucker and Rogers 2014) and a previous study using the same database (Costa 2009). However, in contrast to Costa’s (2009) results, maximum prey sizes increased much faster than minimum prey sizes in the “classic” wedge pattern, which has been found in many other analyses of fish diets (Juanes et al. 2002; Juanes 2003; Pinnegar et al. 2003; Menard et al. 2006; Young et al. 2010; Teffer et al. 2015). Such a wedge pattern suggests that predators keep including small prey lengths in their diets even when growing to large sizes, likely because these small prey are more abundant and easier to capture than the larger ones. Costa (2009) concluded the opposite: that minimum prey sizes increased much faster than maximum prey sizes (a “reverse” wedge) and that his results matched predictions of “the optimal foraging hypothesis” wherein small prey are avoided because they are harder to catch behaviourally and energetically. However, many studies have shown that small prey tend to be energetically and behaviourally easier to ingest (Juanes and Conover 1995; Scharf et al. 2009; Staudinger and Juanes 2010b) and that observed selection of small prey by piscivorous fishes is due to passive selection rather than active preference (Juanes 1994; Juanes et al. 2002). Thus, optimal foraging can still explain the results, but only if prey encounter rates and predator attack success rates are included in the predictions. These results are different to those of Costa (2009) because he used quantile regression on log-transformed data. To date, quantile regression (QR) of predator prey data has been used directly on untransformed data (see Scharf et al. 2000; Menard et al. 2006; Staudinger and Juanes 2010a) as it is a semiparametric technique with no distributional

²Supplemental figures are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0159>.

Fig. 1. (A) Relationship between predator length (cm) and prey length (cm) for adults. (B) Relationship between predator length (cm) and relative prey length (prey length/predator length) for adults. (C) Relationship between predator length (cm) and prey length (cm) for larvae. (D) Relationship between predator length (cm) and relative prey length (prey length/predator length) for larvae. Regression statistics for absolute relationships (A, C) are shown in Table 1. Regression statistics for relative relationships (B, D) are shown in Table 2. Quantile regression lines: median regressions and upper and lower bounds are indicated by solid, dashed, and dotted lines, respectively. Specific quantiles used to define lower and upper bounds are found in Tables 1 and 2. Data for entire dataset are not shown as the patterns and statistics are very similar to those for adults (Tables 1, 2).

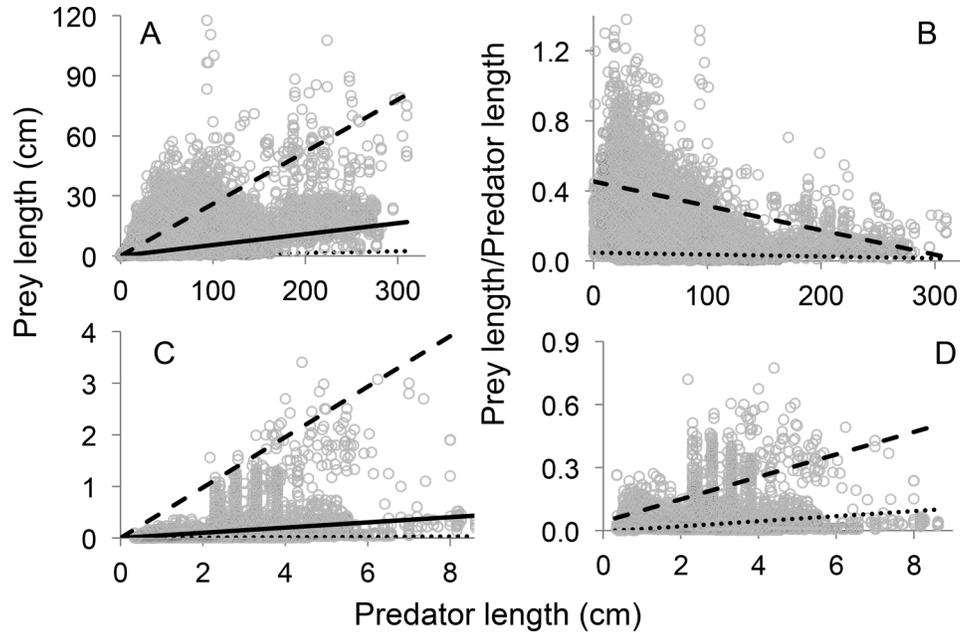


Table 3. Lower (10%) and upper (90%) bound slopes and sample sizes (n) of relative prey length (prey length/predator length) vs. predator length relationship using quantile regression of individual larval species ordered by mean predator length (cm).

Species no.	Predator species	Lower bound slope	Upper bound slope	Mean TNB	Mean predator length	n	P	Change in TNB
1	<i>Lampanyctus crocodilus</i>	0.0513	0.1081	0.0775	0.6046	89	0.727	par
2	<i>Ceratoscopelus maderensis</i>	0	0.0909*	0.0608	0.6884	64	0.099	par
3	<i>Benthoosema glaciale</i>	0	0.0952*	0.0927	0.7637	75	0.035	div
4	<i>Hygophum benoiti</i>	0	0	0.0900	0.7952	85	1	par
5	<i>Diaphus garmani</i>	0	-0.0541	0.0894	0.8767	218	0.205	par
6	<i>Notolepis rissoi</i>	0	0	0.0400	0.9937	70	1	par
7	<i>Myctophum asperum</i>	0	0.0137	0.1311	1.0821	229	0.781	par
8	<i>Myctophum punctatum</i>	0.0172	0	0.0471	1.1191	56	0.824	par
9	<i>Theragra chalcogramma</i>	0	-0.0130	0.0476	1.5173	117	0.85	par
10	<i>Nototheniops larseni</i>	-0.0022*	0.0069*	0.0289	2.0522	1268	<0.001	div
11	<i>Dicentrarchus labrax</i>	-0.0159*	0.0100	0.2300	2.9532	1315	0.069	par
12	<i>Ammodytes hexapterus</i>	0	0.0027	0.0400	3.1686	136	1	par
13	<i>Anarhichas lupus</i>	0	0.2917*	0.2855	3.3874	124	0.0001	div
14	<i>Pleuragramma antarcticum</i>	0	0.0047*	0.0301	3.9857	856	0.001	div
15	<i>Chionodraco rastrospinosus</i>	-0.0580	-0.0218	0.2820*	4.4716	105	0.301	par

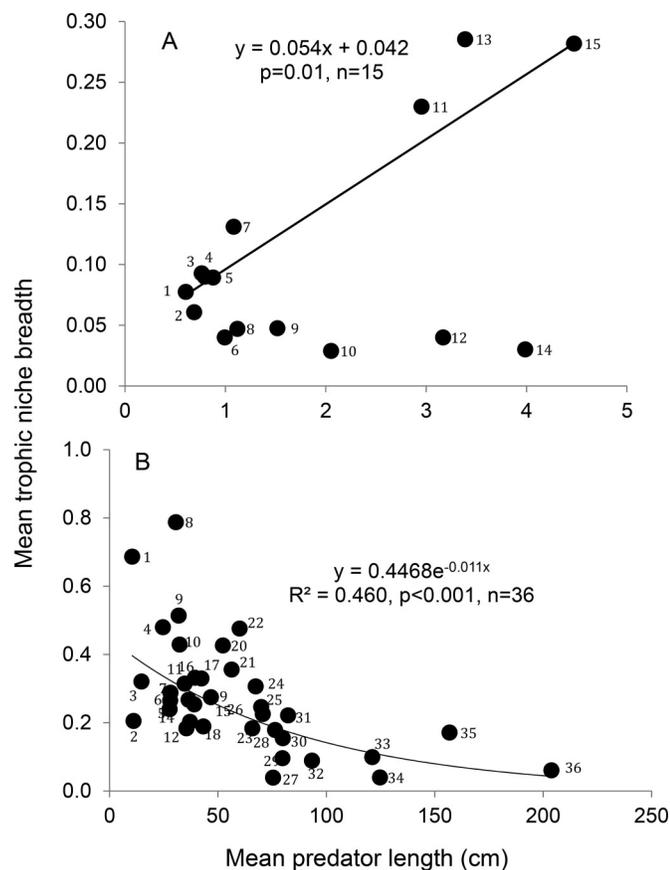
Note: Asterisk (*) following slope value indicates significance ($P < 0.05$). Mean trophic niche breadth (TNB) is the difference between lower and upper bound slopes calculated using eq. 1. P is significance of TNB. Change in TNB represents whether the lower and upper bound slopes are converging (con), diverging (div), or parallel (par, $P > 0.05$).

assumptions, and heterogeneity in the variance is accounted for in the model (Cade and Noon (2003). QR is intended to be used with heterogeneous distributions, and its primary advantage is to detect changes in the response variable at multiple points in the distribution when such changes are different (Davino et al. 2014). Thus, although log-transforming the data is not incorrect when using QR, log transformation distorts the distribution of the original data, making the interpretation of the results for the original data more difficult (Koenker 2005; Hao and Naiman 2007). In a recent textbook on QR, Davino et al. (2014), using a dataset with similar distributional properties to the one used here, show that when the data are log-transformed, the minimum slopes tend to increase and

the maximum slopes tend to be flattened compared with the quantile slopes on the raw data (see their fig. 4.4), exactly the result found by Costa (2009). Importantly, the differences between Costa's results and those presented here do not seem due to the use of mass vs. length, other than more data were available by using lengths.

Absolute predator-prey length patterns were similar even when larvae and adults were separated. In both cases, prey length increased with predator length as expected, and minimum prey lengths increased at a smaller rate than maximum prey lengths (Table 1). However, larvae had smaller lower bound slopes and larger upper bound slopes than adults, suggesting that larvae

Fig. 2. Relationship between mean trophic niche breadth and mean predator length (cm) for individual larvae (A) and adults (B). Regression lines ((A) median regression, (B) nonlinear regression) and statistics are indicated. Numbers by each point refer to species numbers in Tables 3 and 4, respectively.



both increased maximum prey sizes at faster rates and lower prey sizes at slower rates with ontogeny.

I found an overall negative relationship between relative prey size and predator size for adults, and the differences in the slopes suggested a converging relationship (Fig. 1b). Convergence indicates smaller trophic niche breadths as predator size increases. This negative pattern is further highlighted when looking at individual adults where the converging pattern is common (Table 4). Such a pattern across species was also found by Scharf et al. (2000) who examined 18 species from the Northeast Atlantic. Scharf et al.'s (2000) dataset is included in the Barnes et al. (2008) compilation and thus this study expands on it by including more species from different locations and increasing the range of predator sizes. The common converging pattern among adults (Table 4) shows that maximum relative prey sizes decline faster than minimum ones, suggesting that it is the largest relative prey sizes that tend to be absent in the diets of the largest predators, likely because those sizes are relatively scarce in the environment. Scharf et al. (2000) also found that average trophic niche breadths of individual predators showed a nonsignificant ($P = 0.081$) negative trend with average predator length. Here, by extending the range of the predator length data, there is now a strong and significant negative relationship between average trophic niche breadth and average predator length (Fig. 2b). The negative scaling of average trophic niche breadth suggests that although larger predators consume a broader range of absolute prey sizes (the asymmetric pattern first suggested by Wilson (1975)) compared with smaller predators, larger predators are constrained in the range of relative

prey sizes that they consume. Although Wilson (1975) predicted that the asymmetry in absolute prey sizes should confer a “competitive advantage” to larger predators, my results suggest that in relative terms, larger predators have smaller size-based niche breadths and may be at a disadvantage especially as prey size distributions and availability change. Further, the similar patterns in the scaling of trophic niche breadth within and between species suggests that similar forces drive both ontogenetic change within species and the overall pattern across species. In a study of cannibalistic gadid predators, Juanes (2003) showed that cannibalism led to increases in average trophic niche breadths because cannibals had access to and consumed larger relative prey sizes than non-cannibals. Future work should extend these analyses to larger (average lengths > 1 m) predators which are only represented by a few species in the Barnes et al. (2008) dataset. Such an expanded dataset should include data on large pelagic fishes (especially sharks) as well as cetaceans to assess whether the patterns observed here extend to the largest marine predators.

Patterns in the size scaling of larval relative prey length and average trophic niche differed from those observed for adults: when the slopes of upper and lower quantiles differed, the pattern was always divergent, suggesting an expanding prey length range with increases in larval predator size. Similar observations were made by Pepin and Penney (1997). A pattern of prey range expansion was suggested by Houde's (1997) conceptual re-analysis of the Munk (1997) and Pearre (1986) results as a way to increase prey encounter rates in growing larvae. The contrast between larval and adult individuals suggests an important ontogenetic shift in predatory behaviour that occurs at the critical larval to postlarval to juvenile transition phase in many fishes (see Houde 1987; Kaufman et al. 1992; Campana 1996; Juanes 2007). As an example, larval fish predators tend to select larger prey sizes when given a choice (Munk 1997; Sabatés and Saiz 2000), whereas juvenile and adult fishes consistently select small prey sizes (Juanes 1994), which could lead to the contrasting patterns that I found in this study. Unfortunately, even this large dataset is sparse for predators between about 5 and 15 cm. More data should be compiled to assess scaling patterns during this stage.

Comparisons with other size-based analyses are difficult as most focus on predator-prey mass ratios (PPMR) (Nakazawa et al. 2011), whereas this study and others focused on aquatic predators examine prey-predator length ratios. The contrasting definitions are likely due to the different perspectives. Researchers using mass take a community or trophic web perspective (e.g., Brose et al. 2006; Yvon-Durocher et al. 2011), whereas those using length-based approaches are primarily interested in a population perspective (e.g., Rudershausen et al. 2010; Staudinger and Juanes 2010a) and often include behavioural approaches where the important metric is what proportion of predator length is represented by each prey length. Various studies have shown that prey-predator length ratios are important drivers of foraging behaviour in piscivorous fishes (Juanes and Conover 1994, 1995; Scharf et al. 1998b, 2003, 2009; Staudinger and Juanes 2010b).

The approach used here is most like the individual-link PPMR as defined by Nakazawa et al. (2011) and used on the Barnes et al. (2008) dataset by Barnes et al. (2010). Barnes et al. (2010) found that PPMR increases with predator size, which agrees with our result as PPMR is essentially the inverse of PPR. Similarly, Reum and Hunsicker (2012), using a smaller dataset including marine fish and invertebrates, showed that PPMR scaled positively with predator mass but was domed-shaped for invertebrates. They also found strong seasonal variations in PPMR, higher in summer than fall or winter, likely due to changes in prey availability.

The definition of trophic niche breadth also varies substantially among researchers. For example, Costa (2009), in a previous analysis of the Barnes et al. (2010) dataset, found no relationship between diet niche breadth and predator mass using data on 55 predators excluding species defined as larvae. Costa (2009)

Table 4. Lower (10%) and upper (90%) bound slopes and sample sizes (*n*) of relative prey length (prey length/predator length) vs. predator length relationship using quantile regression of individual adult species ordered by mean predator length (cm).

Species no.	Predator species	Lower bound slope	Upper bound slope	Mean TNB	Mean predator length	<i>n</i>	<i>P</i>	Change in TNB
1	<i>Zeus faber</i>	0.0034	0.0008	0.6867	10.38	284	0.6143	par
2	<i>Pomatomus saltatrix</i>	-0.0073*	0.0068*	0.2055	11.01	297	<0.0001	div
3	<i>Loligo pealeii</i>	-0.0039	0.0120*	0.3208	14.65	113	0.0317	div
4	<i>Urophycis regia</i>	-0.0007	-0.0012	0.4802	24.53	286	0.9529	par
5	<i>Paralichthys oblongus</i>	0.0001	0.0056*	0.2401	27.67	450	0.002	div
6	<i>Scopthalmus aquosus</i>	0.0047	0.0054	0.2652	27.90	307	0.8494	par
7	<i>Myoxocephalus octodecimpinosus</i>	-0.0012*	-0.0068	0.2883	28.06	299	0.2072	par
8	<i>Hemitripterus americanus</i>	-0.0017*	0.0013	0.7877	30.52	403	0.1632	par
9	<i>Lophius budegassa</i>	0.0014	-0.0043*	0.5141	31.84	55	0.034	con
10	<i>Merluccius bilinearis</i>	0.0025*	0.0025*	0.4293	32.27	1391	0.9574	par
11	<i>Urophycis chuss</i>	-0.0006*	0.0067*	0.3148	34.56	552	<0.0001	div
12	<i>Cynoscion regalis</i>	-0.0012*	-0.0042*	0.1839	35.38	523	<0.0001	con
13	<i>Paralichthys dentatus</i>	0.0014*	0.0001	0.2677	36.38	373	0.2118	par
14	<i>Merlangius merlangus</i>	-0.0021*	-0.0038*	0.2029	37.04	294	0.2183	par
15	<i>Lepidorhombus whiffiagonis</i>	0.0035*	0.0000	0.2538	39.01	679	<0.0001	con
16	<i>Zeus faber</i>	0.0050*	-0.0028	0.3319	39.32	62	0.003	con
17	<i>Merluccius merluccius</i>	-0.0006*	-0.0046*	0.3299	42.31	280	<0.0001	con
18	<i>Raja erinacea</i>	0.0002	-0.0002	0.1894	43.22	838	0.91	par
19	<i>Pomatomus saltatrix</i>	-0.0019*	-0.0013*	0.2750	46.69	991	0.353	par
20	<i>Urophycis temuis</i>	0.0011*	-0.0023*	0.4266	52.24	791	0.0008	con
21	<i>Lophius piscatorius</i>	-0.0013*	-0.0060*	0.3561	56.26	54	0.0002	con
22	<i>Lophius americanus</i>	-0.0027*	-0.0077*	0.4763	59.95	409	<0.0001	con
23	<i>Rhizoprionodon terraenovae</i>	-0.0006	-0.0022*	0.1837	65.81	161	0.0041	con
24	<i>Gadus morhua</i>	0.0004*	-0.0007*	0.3066	67.36	2346	0.0002	con
25	<i>Pollachius virens</i>	-0.0011*	-0.0009	0.2464	69.87	271	0.7602	par
26	<i>Gadus morhua</i>	-0.0003	-0.0022*	0.2257	70.61	132	<0.0001	con
27	<i>Thunnus alalunga</i>	0.0013*	0.0032*	0.0394	75.38	3581	0.1306	par
28	<i>Raja ocellata</i>	0.0008*	-0.0019*	0.1790	76.29	1290	<0.0001	con
29	<i>Carcharhinus limbatus</i>	-0.0016	-0.0018*	0.0965	79.69	87	0.795	par
30	<i>Pollachius virens</i>	0.0000	-0.0016*	0.1550	79.86	305	0.0147	con
31	<i>Squalus acanthius</i>	0.0001	-0.0006*	0.2219	82.31	3253	0.0003	con
32	<i>Mustelus canis</i>	0.0000	-0.0002	0.0891	93.31	1313	0.4713	par
33	<i>Thunnus obesus</i>	-0.0003*	0.0001	0.0995	121.08	1898	0.0012	div
34	<i>Thunnus albacares</i>	0.0000	0.0000	0.0400	124.66	2113	1	par
35	<i>Xiphias gladius</i>	-0.0002*	0.0012*	0.1713	156.76	827	<0.0001	div
36	<i>Thunnus thynnus</i>	-0.0002*	0.0000	0.0609	203.76	1909	0.1094	par

Note: Asterisk (*) following slope value indicates significance ($P < 0.05$). Mean trophic niche breadth (TNB) is the difference between lower and upper bound slopes calculated using eq. 1. *P* is significance of TNB. Change in TNB represents whether the lower and upper bound slopes are converging (con), diverging (div), or parallel (par, $P > 0.05$).

defined diet breadth using the inverse of Simpson's diversity index based on the proportion of mass in defined prey categories, or species. In contrast, Sabatés and Saiz (2000) and Pepin and Penney (1997), both analyzing fish larvae, defined trophic niche breadth as the range of ingested prey sizes (estimated as the standard deviation of log-transformed prey sizes) and found no change and increases, respectively, with predator body size. The contrasting results suggest that aquatic predators may exhibit little differences in the types of prey that they consume as they grow but may be constrained by available prey sizes ontogenetically, i.e., strong prey size selectivity but weak prey type selectivity. Size selectivity has been shown to exhibit a consistent pattern in piscivorous fishes (Juanes 1994), but to my knowledge, there has not been a similar study comparing prey type selectivity across species, or a comparison of the relative importance of prey size vs. prey type selectivity in determining diets.

The contrasting patterns in the relationship between prey lengths, trophic niche breadths, and predator length suggests important differences in the development of foraging skills between larvae and adults. Although individual larvae and adults both developed wedge-shaped (or asymmetric) relationships between maximum and minimum prey lengths, when combined across species, larvae had a more asymmetric wedge, with both smaller lower bound and larger upper bound slopes (Fig. 1; Table 1), perhaps leading to the differences in scaling of relative prey sizes and

trophic niche breadths (Table 2). In the transition from larvae to postlarvae, larvae rapidly develop their foraging skills due to sharp changes in prey detection and capture abilities (Fuiman and Higgs 1997) combined with high encounter rates (Scharf et al. 2000). These changes are necessitated as growing larvae exhibit very high feeding rates (Kamler 1992) and must consume >55% of their body mass per day ($\text{bm}\cdot\text{day}^{-1}$) to maintain observed growth rates but can consume >100% $\text{bm}\cdot\text{day}^{-1}$ when food abundance is high (Houde 1997). It is likely that these rapid behavioural and morphological changes allow sharp increases in prey sizes consumed while still including the smallest prey in the diet, leading to expanded absolute prey sizes, increased relative prey size asymmetry, and larger trophic niche breadths. Importantly, such a foraging strategy would not be apparent if only mean absolute prey-predator length relationships were analyzed, highlighting the importance of analyzing the edges of data scatters to examine how upper and lower bounds scale with ontogeny and the consequences for trophic niche breadths.

These results have implications for the effects of fishing on food webs. Small and large species (and individuals) respond differently to harvesting (Andersen and Beyer 2015), which combined with the implications of fishing for reduced trophic niche breadth (Juanes 2003) and altered community size structure (Jennings et al. 2002), suggests that scaling of both metabolism and predator-prey relationships should be included when assessing the impacts of

fishing across species and the development of fisheries reference points. Also, because global warming tends to increase the proportion of small-sized species and young age classes and reduce size at age (Daufresne et al. 2009), it is likely that the availability of large prey sizes will continue to decline leading to further decreases in trophic niche breadth. As the largest predators have the narrowest breadths, they are likely to be the ones that are most affected. Reductions in prey–predator ratios are characteristic of less stable environments (Jennings and Warr 2003), and because larger bodied species tend to decline or go extinct more rapidly than smaller species (McKinney 1997; Cardillo 2003), the pattern will be re-inforced over the long term.

In conclusion, analysis of this large dataset suggests that, in contrast to what Peters (1983) thought, general rules do apply to prey size – predator size relationships, especially in aquatic predators. There appear to be few differences between using length as was done here and mass as was done in previous analyses of this dataset. However, the use of prey and predator lengths, rather than masses, allows for less conversion error, better approximation of ingested prey sizes, and greater data availability. The quantile regression approach to calculating trophic niche breadths provides a robust measure of minimum and maximum scaling relationships. Patterns based on absolute prey sizes vs. relative prey sizes offer different perspectives on the predator–prey relationship. Absolute prey size ranges increase with predator size for both larvae and adults, reflecting morphological and behavioural changes in prey capture dynamics (Scharf et al. 2000). In contrast, scaling of relative prey sizes differed between larvae and adults, suggesting different foraging strategies (Houde 1997). Finally, it is important to use both individual-based data as well as data aggregated into species. Although previous studies have shown that a comparison of approaches can lead to over- or under-estimation of relationship parameters (Gilljam et al. 2011), each approach provides a different perspective on the role of body size in communities.

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