

Hunting high or low: body size drives trophic position among and within marine predators

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ABSTRACT: A positive relationship between body size and trophic position amplitude is expected based on mobility and gape size. Using a dataset of marine consumers' diet, we illuminated mechanisms driving the relationship between consumers' body mass (a proxy for body size) and trophic position parameters within and among populations. We found that across a body size gradient, maximum trophic position increased, while minimum trophic position did not vary, resulting in a positive relationship between species body size and trophic position amplitude. However, using single individuals as data points, we found a positive correlation between trophic position and body mass. The correlation was stronger for larger species, indicating that as mean species body size increased, there was an increasing tendency for smaller individuals to forage on lower levels and larger individuals to forage mainly on higher levels. Therefore, the wider variation in trophic positions we observed for larger species is possibly related to an ontogenetic diet shift in size-structured populations. Our results corroborate the idea that on an individual level larger consumers do not show a positive relationship between body size and diet niche breadth, and support the notion that ontogenetic niche differences can drive the amplitude of trophic position among marine predator species.

KEY WORDS: Trophic chain · Ontogenetic diet shifts · Niche breadth · Consumer–resource interactions · Food web topology

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INTRODUCTION

Body size is a fundamental trait that affects ecological dynamics from individuals to ecosystems (Cohen et al. 1993, Arim et al. 2007, Jennings & Cogan 2015). This trait also shapes energetic demands (Elliott & Hurley 2000, West & Brown 2005) and plays an important role in structuring ecological interactions within and among species (Peters & Wassenberg 1983), which influences food web dynamics and ecosystem functioning (Emmerson & Raffaelli 2004, Basset & Angelis 2007, Séguin et al. 2014). In general, body size constrains the size of prey that predators can consume (Cohen et al. 1993, Woodward et al. 2005, Arim et al. 2007), as well as the ability of organism to forage throughout various food webs (Edmunds et al. 2016).

The constraint of gape limitation and the opportunities arising from enhanced foraging capabilities due to increased body size give rise to body size hierarchy in many aquatic food webs (Williams & Martinez 2000, Petchey et al. 2008), characterized by a positive relationship between a predator's trophic position (TP) and body size (Hairston & Hairston 1993, Jennings et al. 2001, Layman et al. 2005, Arim et al. 2007, Romanuk et al. 2011). Therefore, we predicted a positive correlation between predator body size and maximum TP at the species level, whereas minimum TP was expected to remain constant or increase only slightly with increased body size; thus, TP amplitude should be positively correlated to species' body mass (Fig. 1A).

Although most studies use mean body size as a predictor for species TP (Schoener 1971, Williams &

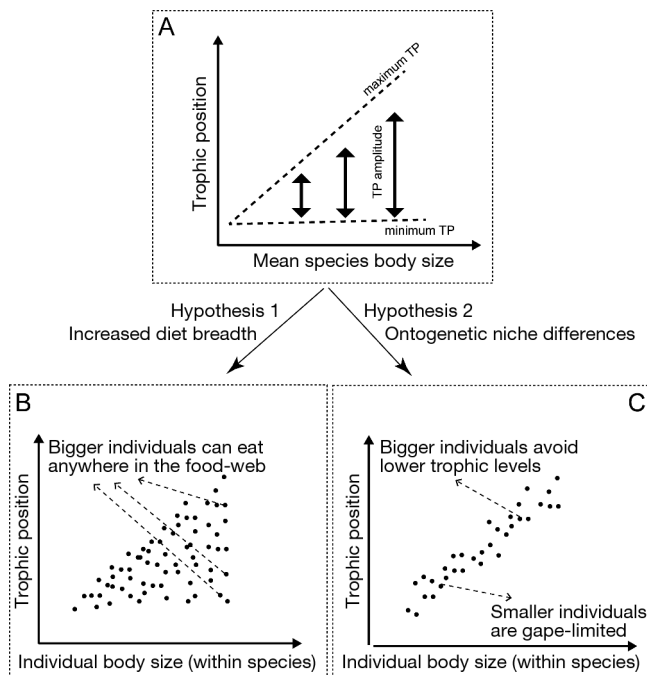


Fig. 1. (A) Predicted relationship between trophic position (TP) and body size of marine predator species, whereby larger consumer species present wider trophic niche breadth, and 2 hypotheses to explain this relationship: (B) gape size limits small individuals to foraging only on lower trophic levels, while large individuals forage on both higher and lower trophic levels; (C) both minimum and maximum TP increase with similar slopes, so that greater diet niche breadth is only observed at the population level

Martinez 2000, Ou et al. 2017), ecologists have only recently considered the implications of individual traits within size-distributed populations on TP patterns (Ramos-Jiliberto et al. 2011, Rudolf & Lafferty 2011). Previous studies have shown that individuals from the same species have different prey preferences (e.g. ontogenetic diet shifts), with minimum and maximum prey size increasing along with predator size (Thompson 1975, Cohen et al. 1993, Scharf et al. 2000, Costa 2009). These studies highlight that large predators might avoid smaller prey because the energetic costs may exceed energetic gains, constraining the shape of the relationship between body size and diet niche breadth (Costa 2009). Therefore, 2 distinct mechanisms may lead to the same proposed pattern of TP–body size relationship shown in Fig. 1A: (1) the lack of gape size limitation for large predators, which allows them to feed anywhere in the food web (Fig. 1B); or (2) ontogenetic diet shifts, leading to increased dietary niche breadth at the population level only (Fig. 1C).

In this study, we explored the relationships between consumer body size and minimum, mean, maximum,

and standard deviation of TP across and within species of marine fishes and squids. We tested the hypothesis that maximum TP increases, while minimum TP remains constant, along a gradient of mean species body size, which leads to an increase in TP amplitude within each population. We also investigated whether such a relationship emerges because larger individuals forage throughout the whole food web (i.e. large dietary niche breadth) or because of restrictions related to individual size distribution within populations (i.e. ontogenetic niche specialization).

METHODS

Sampling

The original dataset consists of data published by Jennings & Cogan (2015) and Jennings & van der Molen (2015) containing TP measurements and body sizes for 5535 individuals of 62 fish and squid species. Trophic positions of individual consumers were estimated using the variation in stable nitrogen isotope ($\delta^{15}\text{N}$) concentrations in tissues where these concentrations are related to trophic position and environmental variables. For marine environments, which vary in depth, temperature, salinity, and the main source of nitrogen in the food web (e.g. pelagic vs. benthic environments), consumer TP calculated by $\delta^{15}\text{N}$ must be evaluated in relation to a baseline $\delta^{15}\text{N}$, since such variables affect $\delta^{15}\text{N}$ at the base of the food web and how it transfers through food chains (Layman et al. 2012). Trophic fractionation, or the increase in $\delta^{15}\text{N}$ between consumer and resource ($\Delta^{15}\text{N}$), has been described by 2 models: one model that considers a fixed increase of 3.4‰ per TP and a scaling model that accounts for the decrease of $\Delta^{15}\text{N}$ for higher TP (Hussey et al. 2014).

For this dataset, the relationship between $\delta^{15}\text{N}$ and TP is based on the diet of a basal consumer, the suspension-feeding queen scallop *Aequipecten opercularis*, the calculation of TP for each individual was based on tissue $\delta^{15}\text{N}$ variation and uncertainty about basal TP related to environmental variables. A 3-stage calculation was used to determine TP. First, a statistical relationship between the $\delta^{15}\text{N}$ of queen scallops, temperature, and salinity was established. The highest predictive power was achieved with models considering annual mean bottom temperature, annual mean bottom salinity, and minimum salinity with an interaction between bottom temperature and salinity. Second, the statistical relationship between the $\delta^{15}\text{N}$ of queen scallops, temperature,

and salinity previously established was used in conjunction with modeled temperature and modeled salinity data and TP estimates for queen scallops. TP of queen scallops was calculated from the main source of nitrogen in the water column where scallops were sampled to predict a $\delta^{15}\text{N}$ baseline and create a model of mean TP fluctuation in response to environmental variables. TP baselines were set as 2.4 in depths <40 m (where phytoplankton is the main food source), 3 in depths >100 m (where phytoplankton is absent) and increased linearly with depth between 40 and 100 m depth. Third, $\delta^{15}\text{N}$ measurements of sampled fish and squids were used to predict individual TP using the queen scallop model as a basis for the relationship between the increase in $\delta^{15}\text{N}$ and TP. The increments in $\delta^{15}\text{N}$ were used to build fixed and scaled trophic fractionation models. Information about confidence intervals of 5, 25, 50, 75, and 95% of estimated TP for all individuals is available in Jennings & van der Molen (2015). We used the median TP value to determine TP for every individual. TP estimations from isotopic $\delta^{15}\text{N}$ can be considered integrative measurements of an organism's diet in the short- to mid-term before sampling (Post 2002). Values of $\delta^{15}\text{N}$ in an organism's body may vary reflecting the organism's main diet over timescales, from months to years, depending on the speed of growth and body size of the organism (Peters & Wassenberg 1983, Hesslein et al. 1993, Post 2002). In general, small short-living organisms present faster turnover rates than large long-living organisms. Therefore, $\delta^{15}\text{N}$ can be considered a good proxy of proportional importance of food items consumed by an organism throughout its lifetime (Post 2002, Perkins et al. 2014).

Body mass was used as a measurement of body size. To guarantee a good representation of size distributions and TP variation within species, especially in the analysis using individuals as data points, we only used species with more than 20 individuals in our analyses. This procedure reduced the final data set to 5378 individuals belonging to 48 species, representing a reduction of 20% of the species pool, eliminating under-sampled species.

Statistical analyses

To account for biases caused by species relatedness in TP, we used standardized phylogenetic independent contrasts (PIC) of consumer body size and minimum, mean, maximum, and standard deviations of TP. Here, we used population standard deviation

of TP as a proxy for trophic niche amplitude, instead of differences between maximum and minimum TP, to avoid giving too much weight on outliers. Phylogenetic hypotheses address the influence that species relatedness has on their responses to variables, reducing biases caused by species relatedness and improving statistical power in trait analysis (Felsenstein 1985, Garland et al. 1992). PIC was calculated using the PIC function in the R package 'ape' (Paradis et al. 2004) for independent phylogenetic contrasts. We built a composite phylogenetic hypothesis for the 48 species used in the analyses (see Fig. S1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m597p039_supp.pdf) based on different phylogenies and the Tree of Life Web Project (available at <http://tolweb.org/tree/>). Since branch length was not available, all branches were set to a value of 1, a procedure that reduces Type I error rates (Purvis et al. 1994). This proxy method provides a simple but reasonable estimate of evolutionary relationships among species of diverse assemblages and is widely used in trophic chain studies (Costa 2009, Ou et al. 2017). We present results of slopes and r^2 of both non-phylogenetic and phylogenetic analysis. Some authors support this approach (Price et al. 1997, Blackburn & Gaston 1998), despite the strong arguments for the explicit consideration of phylogeny in comparative analyses. This issue has been the subject of considerable debate in ecological literature on both conceptual and practical grounds (Ricklefs & Starck 1996), especially since controlling for phylogenetic relatedness can affect the sign of predictor estimates (Elgar & Harvey 1987, Blackburn 1991, Harvey & Pagel 1991, Nee et al. 1991, Kelly & Purvis 1993, Kelly & Beerling 1995). Significance levels of non-phylogenetic analysis are omitted because they are biased (Costa 2009).

Prior to analysis, we \log_{10} -transformed all variables to meet linearity assumptions. To assess the overall trend between body mass and TP at the individual level, we performed a linear regression using each individual's TP as the dependent variable and body mass as the predictor variable. To investigate the relationships between body size and TP parameters at the species level we regressed mean, minimum, maximum, and amplitude of species TP against mean species body mass.

To uncover the relationship between body size and TP for different sized individuals within the same species we performed a Pearson's correlation analysis between individual body mass and TP for each species (Fig. S2 in the Supplement). To evaluate the consistency of the body size–TP relationship across

species with different sizes, we regressed the Pearson's correlation coefficients against species mean body mass. All analyses were performed in the R software version 3.2.1 (R Development Core Team 2016).

RESULTS

We observed a positive relationship between body size and TP using individuals as data points, regardless of the species (Fig. 2A; adjusted $R^2 = 0.14$, slope = 0.028, $p < 0.005$). Within species, we observed a positive relationship between individual body mass and trophic position (Fig. S2). The PIC values of Pearson's correlations between TP and body mass increased significantly as mean species body mass increased (Fig. 2B; adjusted $R^2 = 0.19$, slope = 0.107, $p = 0.001$). Across species, we observed significant positive relationships for mean, maximum, and amplitude of TP with species' mean body mass (Fig. 3 A,C,D). However, we did not observe a significant relationship between species' minimum TP and body mass (Fig. 3B). When controlling for the phylogeny, we observed that signs of slopes were preserved despite differences in their magnitudes. Thus, controlling for phylogeny did not affect the sign of the observed trend. The slopes and r^2 of linear models using both the raw data and PIC values and p-values of linear models using PIC values are presented in Table 1.

DISCUSSION

Our results showed that smaller individuals of both small and large species presented low TP. Therefore, they primarily foraged lower in the food web, highlighting that gape limitation may play a strong role in determining maximum TP. Moreover, large individuals mostly occupied higher TP, suggesting that they primarily forage on high TP organisms. Additionally, body size was positively correlated with mean and variance of TP at the species level but had no relationship with the lowest TP recorded for each species, leading to an increased amplitude of TP within species as mean species body size increased. Overall, larger individuals rarely occupied low TP and this pattern became more evident as species increased in size, as the correlation between an individual's TP and body size increased with increased mean species body mass. Thus, increased amplitude of TP was related to species body size but not individual body size. Therefore, the amplitude of TP within species

was consistent with ontogenetic niche shifts in size-structured populations.

We found that species with piscivorous habits as adults showed the most pronounced correlations between body size and TP, regardless of preferred habitat and hunting behaviour, among bottom-dwelling (e.g. *Amblyraja radiata*) as well as pelagic species (e.g. cod *Gadus morhua*). Small-bodied species (body mass: mean \pm SD 48 ± 34 g, range 22–90 g) showed weak negative correlations between body size and TP

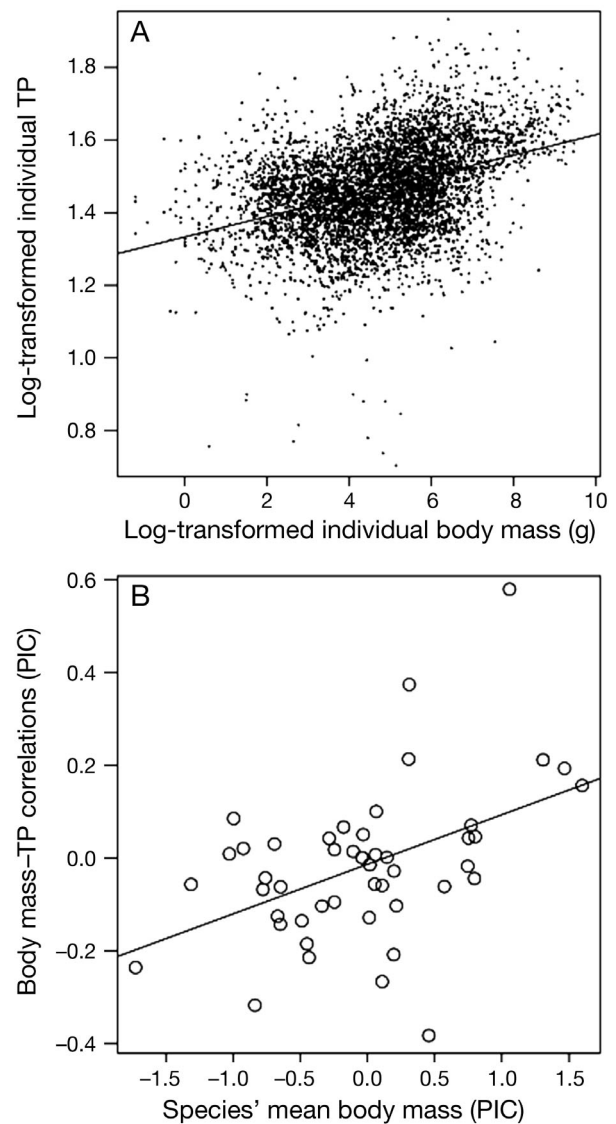


Fig. 2. Individual-level and species-level analyses of the relationship between trophic position (TP) and body size of marine predators, showing linear regressions (A) between log-transformed body mass and log-transformed TP for all individuals in the data set, and (B) between predator body size and Pearson's correlations between TP and species mean body mass, using phylogenetic independent contrasts (PIC) of predator body size and TP parameters

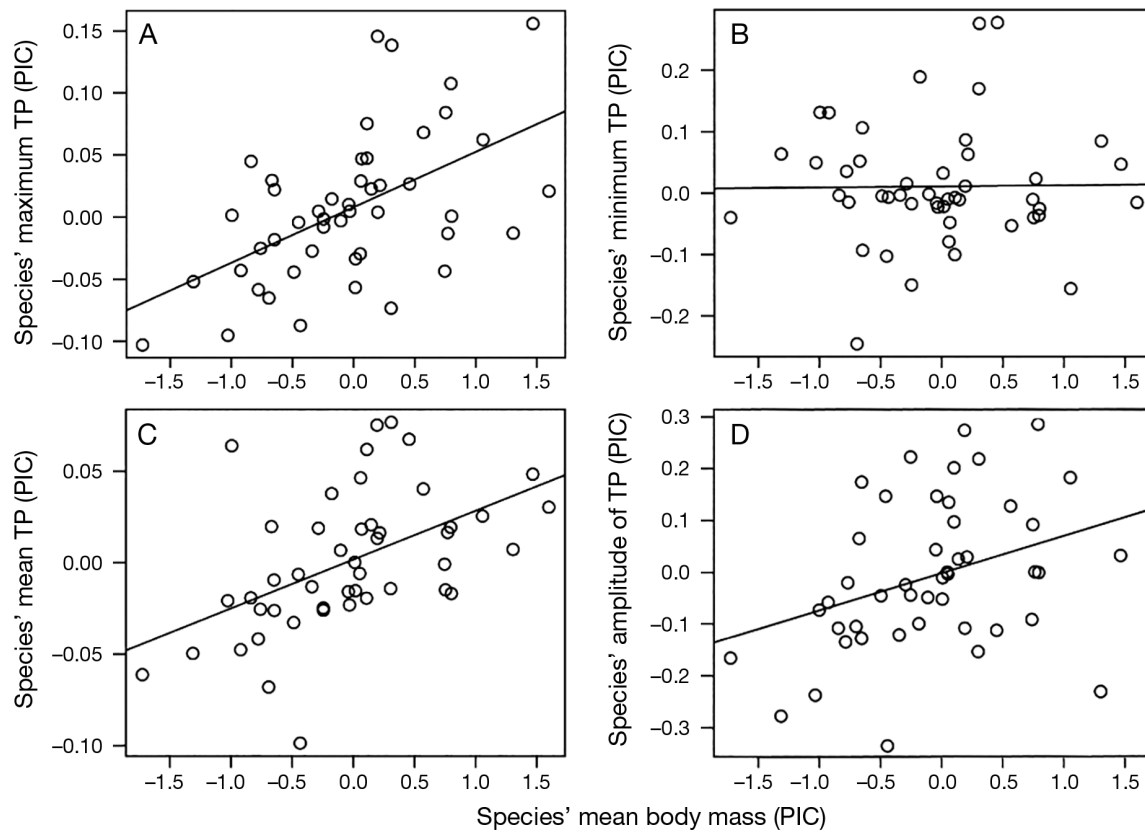


Fig. 3. Species-level analyses of the relationship between trophic position (TP) and body size of marine predators, showing linear regressions between phylogenetic independent contrasts (PIC) of species' mean body mass and PIC of (A) species' maximum TP, (B) species' minimum TP, (C) species' mean TP and (D) amplitude of species TP (measured as 1 standard deviation)

and were most often zooplanktivorous or invertebrate-feeding species. For these species, gape limitation may not play a role, as organisms forage throughout their lives on small prey that can be swallowed by adults and juveniles. Flatfishes (Pleuronectiformes) and the lesser weever *Echiichthys vipera* had weak positive correlations between body size and TP, a pattern generated by large individuals presenting either low or high TP. This result may be related to the life

history of these fish, who forage on large prey when adults and reach high TP. They also have benthic behaviours, defending foraging grounds where they may be limited to the most abundant prey in their areas. Studies of these species' feeding ecology show that adults have piscivorous habits; however, throughout their lifespan, their diet also includes a large proportion of macrobenthic invertebrate prey (mainly Polychaeta and thin-shelled Mollusca) if these are available in their environment, which would have the effect of lowering the TP of some adult individuals (Amara et al. 2001, Andersen et al. 2005, Guedes & Araujo 2008).

Table 1. Species-level linear models of the influence of mean body mass of marine predators on their trophic position (TP), showing results for amplitude of TP (measured as 1 standard deviation), mean, maximum and minimum TP, and the correlation between TP and body mass. Results are shown for the raw data and for phylogenetic independent contrasts (PIC) of predator body size and TP parameters

Variable	Raw data		PIC		
	Slope	r^2	Slope	r^2	p
Amplitude of TP	3.4×10^{-2}	0.15	0.073	0.11	0.01
Mean TP	2.1×10^{-2}	0.15	0.026	0.23	0.0003
Maximum TP	0.037	0.25	0.044	0.27	<0.001
Minimum TP	-1.0×10^{-2}	0.0057	0.001	0.02	0.932
Correlation mass/TP	9.0×10^{-2}	0.23	0.107	0.19	0.001

Overall, the positive relationship between body size and TP is a general pattern observed in several food webs across different systems (Elton 1927, Scharf et al. 2000, Romanuk et al. 2011). However, energetic and maneuverability constraints may cause a hump-shaped pattern where trophic positions increase with size until a threshold

when very large animals (e.g. baleen whales) start to feed on lower trophic levels (Webb et al. 1996, Arim et al. 2007). If the organisms within the TP–size relationship are mostly carnivores, an increasing linear relationship is expected (Arim et al. 2007, Romanuk et al. 2011). Body masses of individuals used in this study ranged from 2 to 15 750 g, and all samples came from marine environments. Therefore, our observations may only concern the ascending portion of the body size–TP relationship of marine food webs (Romanuk et al. 2011). In addition, ecosystem size of marine environments may play an important role in structuring longer food webs, whereby larger individuals may find enough resources to meet their energetic demands in upper trophic levels (Post et al. 2000).

Individuals from certain size classes may be restricted from exploring different trophic levels due to constraints that hinder smaller individuals from feeding higher in the food web. A key constraint is gape limitation, since most consumers are limited by what they can swallow, except for a few specialized taxa that take chunks of large prey (e.g. the *Serrasalminae* family in freshwater environments and *Squatiniiformes* in saltwater environments) (Werner & Gilliam 1984, Romanuk et al. 2011). For large individuals, the constraints that limit feeding throughout the food web could be related to optimal foraging behaviour: taking account of the time spent in searching and handling prey, many more net calories are gained from capturing a single large prey than from capturing several smaller prey (Harper & Blake 1988, Akin & Winemiller 2008, Costa 2009). Limited maneuverability and capacity to recognize very small prey may also be important in increasing the handling time and reducing the profitability of capturing small prey (Breck & Gitter 1983, Persson 1987, Heglund & Taylor 1988, Webb et al. 1996, Dudley 2002). In addition, the patchy distribution of large prey (Kerr 1974) may be perceived differently by predators of different sizes, as larger individuals are less affected by water viscosity. Large individuals are able to accomplish faster and more sustained movements in the water, have enhanced visual acuity, and have more body reserves that provide endurance against starvation (Ware 1978, Webb 1978, Mittelbach 1981, Hubbs & Blaxter 1986, Müller et al. 2000, Cohen et al. 2003). Therefore, for larger individuals, scattered rates of encounter with large prey are compensated by their different perception of the habitat and wider use of areas (Mittelbach 1981, Scharf et al. 2000, Truemper & Lauer 2005). Finally, as the basal metabolic rate of animals changes with body mass, larger animals have higher requirements for food

resources and must select resources that satisfy the minimum energy requirements for sustaining their activities (Schoener 1971, Crowder & Cooper 1982, Robinson et al. 1983, Krebs & Davies 1987, Clarke & Johnston 1999, Gillooly et al. 2001, De Roos et al. 2003).

Our results indirectly corroborate the notion that a positive relationship between consumer body size and diet niche breadth does not exist, and that the broader dietary niche breadth observed for larger species results from ontogenetic niche shifts (Olson 1996, Costa 2009). Overall, the absence of low $\delta^{15}\text{N}$ signature as body size increased suggests that marine consumers avoided preying on small organisms, and highlights the generality of this macroecological pattern for both marine and terrestrial ecosystems (Costa 2009). It is important to mention that when other niche axes are examined, such as microhabitat and home range, a positive relationship between body size and niche breadth can be observed for invertebrates (Pyron 1999).

The results of this study highlight that understanding of the structure of food webs may be enhanced by recognizing ontogenetic niche shifts. As larger species need food resources from specific trophic levels at specific stages of their life histories (Scharf et al. 2000, Costa 2009), depletion of resources anywhere in the food web may affect at least one part of the population (Persson 1985, Petchey et al. 1999). Furthermore, our results support recent models which suggest that TP and body size are positively correlated (Cohen et al. 1993, Jennings et al. 2001, Costa 2009), and that this relationship is not contingent on evolutionary history. We also support the notion that morphological constraints associated with gape limitation determine species maximum TP, while energetic constraints may prevent large individuals from foraging on low TP. Hence, ontogenetic niche shifts in size-structured populations may represent the major ecological drivers of TP amplitude.

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