



Food web structure and body size: trophic position and resource acquisition

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Body size is recognized as an important determinant of trophic structure as it affects individual energetic demands, population density, and the interaction between potential prey and predators. However, its relationship with trophic position remains unclear. It has been hypothesized that a positive relationship between body size and trophic position would be associated to some particular trophic structures, which would allow larger organisms to satisfy their energetic demand and sustain viable population sizes at higher trophic positions, where fewer resources are available. To test this hypothesis, we analyzed the diet of 619 killifishes from four species (*Austrolebias cheradophilus*, *A. luteoflammulatus*, *A. viarius* and *Cynopoecilus melanotaenia*), collected in temporary ponds occurring in the grasslands of Rocha, Uruguay. Trophic position, diet richness, number of energy sources, and evenness were estimated for 20 size classes, formed by consecutive groups of 31 individuals. Gape limitation and preference for the larger available prey were evaluated as explanations for observed patterns with an individual based model (IBM). In agreement with the hypothesis, killifishes presented a strong positive relationship between trophic position and body size ($R^2 = 0.86$), associated with a trophic structure that could allow larger organisms to have access to more energy from the environment. This was reflected in a positive relationship between body size and 1) prey richness, 2) number of basal energy sources (i.e. plants, detritus, phytoplankton and terrestrial prey), and 3) evenness in prey use. IBM results showed that changes in trophic structure with body size are well explained by gape limitation, but not by size preferences. Our results suggest that the fulfilment of the greater energetic demands of larger organism will depend on community diversity, which typically increases with ecosystem size, indicating a novel connection between area, diversity, body size, and food chain length.

Human activities impact natural ecosystems by changing their diversity, area and productivity. However, the connections between these changes and community organization or species persistence are not always evident (Gotelli and Ellison 2006). Top predators usually have a key role in community structure and dynamics (Gotelli and Ellison 2006), and are widely used by humans as resources (Sibert et al. 2006). Large predators are also particularly sensitive to human activities, showing higher extinction rates (Olden et al. 2007), which highlights the theoretical and applied relevance of understanding the determinants of their persistence (Marquet and Taper 1998, Valkenburgh et al. 2004). Food webs represent the predator–prey mediated routes through which energy and matter flow across species in ecosystems; their structure and dynamics determine the potential for large predators to satisfy their energetic demands and persist (Cohen et al. 2003, McCann 2007).

Body size is one of the most important traits differentiating individuals that compose a community (Woodward et al. 2005, Raffaelli 2007). Body size was early recognized as a potential determinant of species interactions

and food web structure at different ecological levels (Warren 2005, Petchey et al. 2008). The more evident connection between body size and food web structure is the hierarchy in trophic interactions, and the expected increase in a predator trophic position with its size (Woodward et al. 2005). However, the positive relationship between energy demands and body size, and the negative relationship between available energy and trophic position in food webs (Brown and Gillooly 2003, Cohen et al. 2003, Jennings and Mackinson 2003, Long et al. 2006, Maxwell and Jennings 2006), counteract and constrain this tendency. Recently, Arim et al. (2007a) hypothesized that a humped association between trophic position and body size is expected, unless food web structure allows for enough energy to become available for predators at high trophic positions. Those changes in trophic structure, that could potentially increase the amount of resources available to large size predators, are those that: 1) increase the number of energy paths from an energy source (e.g. an increase in the number of prey feeding on plants or detritus, Krumins et al. 2006, Long et al. 2006, Layman et al. 2007, Miki

et al. 2008), 2) promote a diet that balances the flow of energy from alternative basal energy sources (e.g. plants and detritus, Rooney et al. 2006), and/or 3) allow for higher-trophic-position predators to consume prey from other communities, as a consequence of predator (McCann et al. 2005) or prey dispersal. It should be noted that these three mechanisms are directly or indirectly related with the diversity of prey in the ecosystem exploited by predators.

As predator body size increases, the greater energetic demands and the relaxation in gape limitation could account for the increase in prey richness. Relaxation in gape limitation involves the morphological changes with body size that both allow the consumption of larger prey and/or increase the searching ability and handling efficiency (Mittelbach 1981, Hairston and Hairston 1993, Brose et al. 2006a). Furthermore, this gape limitation is what determines the size hierarchy in trophic interactions (Brose et al. 2006a). However, together with the relaxation in gape limitation, a preference for larger-bodied prey with greater energetic return could also take place (Werner and Hall 1974, Mittelbach 1981, Schmitt and Holbrook 1984, Sherwood et al. 2002a). Finally, the requirement to satisfy greater energetic demands could be translated to an increase in the number of prey consumed by large predators. The consumption of more prey items implies a larger sample of individuals from the prey community, which is expected in more diverse communities (Gotelli and Graves 1996). Thus, gape limitation, preference for larger prey, and consumption rate, represent the main body-size dependent attributes of individual predators, which could lead to a systematic increase in diet richness, and consequently, to variations in the range of resources used by larger predators within communities. In addition, the movement of large predators on larger spatial scales, thus feeding within different communities, could result in an increase in the range of resources consumed.

In this paper, we report a strong association between trophic position and body size, and the existence of systematic changes in diet related to body size, which could be critical to satisfy the energetic demands of larger organisms at higher trophic positions. Further, we present a simple individual based model which supports the role of relaxation in gape limitation with body size, but not prey size preference, as the putative mechanism determining the observed patterns.

Material and methods

Study site and sampling

We analyzed the diet, through gut content analysis, of a total of 619 killifishes from four species (*Austrolebias cheradophilus*, *A. luteoflammulatus*, *A. viarius* and *Cynopoeilus melanotaenia*), collected in temporary ponds occurring in the grasslands of Rocha, Uruguay. Killifishes were obtained from temporary ponds located in a wetland area surrounding Castillos Lagoon, Uruguay. Fishes were sampled with a hand net, euthanized with an overdose of 2-phenoxyethanol, and fixed with 4% formaldehyde. Prey items in the gut contents were identified under a stereomicroscope, to the finest possible taxonomic resolution

(Supplementary material Table S1). Killifishes were sorted by size, and grouped into 20 size classes formed by consecutive groups of 31 individuals, with 30 individuals in the largest-bodied group. Trophic position, diet richness, number of energy sources, and evenness, were estimated for each size class. Prey were categorized as primary consumers (herbivorous and detritivorous) or non-primary; and, in addition, each prey was also associated with an energy source, i.e. plants, phytoplankton, detritus, and terrestrial prey (Supplementary material Table A1). Trophic position was estimated as the proportion of non-primary-consumers prey in fish diet (Arim et al. 2007b). For example, a killifish with a diet composed of only primary-consumer prey has the lowest possible trophic position, while a diet composed entirely of non-primary consumer prey will represent the topmost trophic position that our index can yield. The index is positively associated with the food chain length, and thus yields a direct index of predator trophic position (Arim et al. 2007b). Prey richness and number of energy sources were standardized by rarefaction, in order to remove the effect of unequal number of individual prey observed within each size class (Gotelli and Graves 1996). Hurlbert's evenness was estimated as the difference between the expected richness (by rarefaction) in a sample of two and one individuals (Olszewski 2004). Considering that the deconstruction of ecological patterns at different levels of organization could bring insights on how patterns emerge (Marquet et al. 2004, Arim and Jaksic 2005, Arim et al. 2007b), we also evaluated the congruence of all the patterns reported for the predator ensemble, with those observed when species are analyzed separately.

Individual based model

To evaluate the plausibility, and the relative importance, of gape limitation and prey size preference in explaining the empirical patterns reported herein, we implemented an individual based model, mimicking the interaction between individual predators and prey in a pond ecosystem. The IBM consists of a predator feeding on four trophic groups – herbivorous (H), detritivorous (D), aquatic consumers (A) and terrestrial consumers (T). Each group has a diversity S_i , with species abundances determined by a broken stick process, and body sizes randomly obtained from a lognormal distribution with mean values conforming to the empirically observed ranking in size $H < D < A < T$. Predators are characterized by a body size value (M). At each iteration, prey and predators are randomly located. Prey are consumed if they fall within a predator's home range (R), which scales with body size as $R \propto M^{0.75}$ (Kramer and Chapman 1999), according to a type II functional response with asymptote $C \propto M^{1.0}$ (Sherwood et al. 2002b). When the predator does not satisfy its energetic demands (D), which scale with body size as $D \propto M^{0.75}$ (Clarke and Johnston 1999), it is removed from the system. The identities of the consumed prey were retained, and trophic position, prey richness and evenness were calculated from the median of 30 simulations for each predator mass (a detailed description of the IBM is available in Supplementary material Appendix 1).

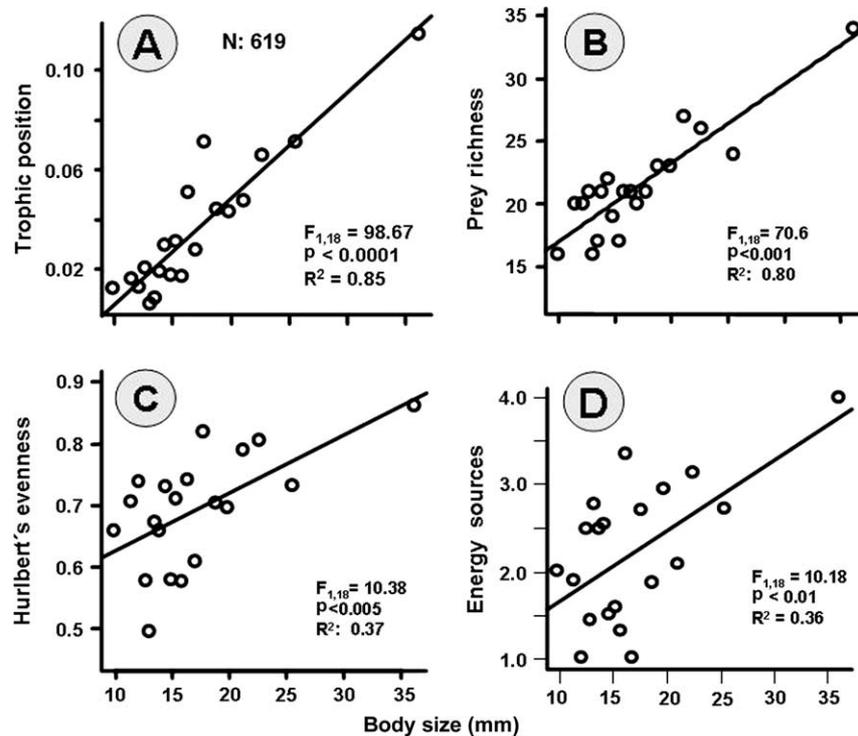


Figure 1. Association between trophic interactions and body size. (A) association between trophic position – proportion of non-primary consumers prey – and body size. (B) and (C) association between prey richness, evenness and body size. (D) association between number of energy sources (phytoplankton, detritus, plants and terrestrial) standardized by rarefaction ($n = 200$) and body size.

Results

Killifish trophic position strikingly increased with body size (Fig. 1A). In addition, the richness and evenness of prey species systematically increased with body size (Fig. 1B–C). Both observed prey richness, and richness standardized by rarefaction to the same number of individual prey ($n = 200$) in all body size categories, were significantly associated with body size ($F_{1,18} = 70.6$ and $F_{1,18} = 13.9$, respectively; $p < 0.001$ for both regressions). The number of energy sources (i.e. plants, phytoplankton, detritus, and terrestrial prey) also showed a positive association with predator body size (Fig. 1D). The exclusion of the last size class, with larger values in all the metrics, did not affect the observed associations or their significance. The four empirical patterns herein reported are congruent with the increase in the amount of energy that larger organisms must obtain from the food web, and this is usually associated with access to novel resources (Fig. 2). All four killifish species showed the same pattern observed in the complete ensemble, although the strength of the association was reduced (Supplementary material Fig. A1, A2).

The individual based model results show that the changes in trophic structure with body size are explained well by gape limitation, but not by prey size preference or by an increase in consumption rate. In all the combinations of gape limitation and prey size preference, the consumption rate increased with body size. The model including gape limitation replicated the observed patterns of an increase in trophic position, prey richness, evenness and number of energy sources with body size (Fig. 3). However,

the models that only considered prey size preference did not reproduce the observed patterns (Fig. 3).

Discussion

Our results point to a strong pattern of variation in killifish trophic interactions related to body size. The potential for relaxation in gape limitation with body size, as a main determinant of trophic interaction, has been proposed several times elsewhere (Hairston and Hairston 1993, Williams and Martinez 2000, Sherwood et al. 2002a, Woodward et al. 2005, Brose et al. 2006b, Raffaelli 2007). Congruently, the IBM results suggest that the gradual relaxation in gape limitation at larger predator sizes allows the diversification of energy sources and of the prey consumed within each source. In some systems, diet diversification may be needed at larger body sizes, in order to satisfy energetic demands, particularly at higher trophic positions where less energy is available (Arim et al. 2007a).

Several empirical studies have reported a positive effect of prey diversity in predator growth and biomass (Duffy et al. 2007), a pattern that is explained by the balanced diet hypothesis: a complete range of nutritional resources is achieved at high prey diversity, which translates into higher consumer biomass (Duffy et al. 2007). This interpretation emphasizes a quality effect of the prey, ignoring the importance of a resource quantity effect, determined by prey diversity (Long et al. 2006). Furthermore, in those cases where predators and prey have similar body composition, a balanced diet could be of minor relevance (Sturner and Elser 2002). The increase in prey diversity could also

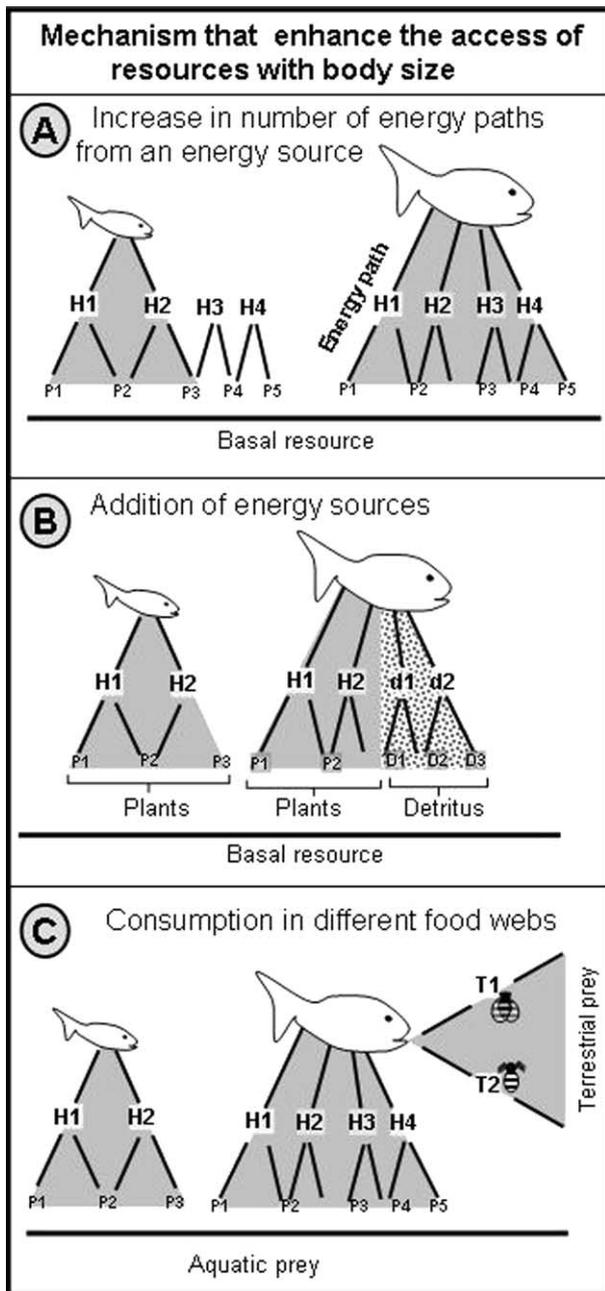


Figure 2. Conceptual explanation of the mechanisms that could allow a large predator to satisfy its energetic demand at higher trophic positions. (A) species richness is associated with standing biomass and resource flow, as a consequence, great prey richness implies a potential access to more resources. (B) the number of energy sources increases with body size, each source implies the incorporation of new resources increasing the total amount. (C) the incorporation of prey from other communities further increases the amount of resources.

have a large effect on energy acquisition, because of the integration of energy paths from basal resources (Fig. 2A). Studies about the effects of diversity on standing stock have shown that each species translates into biomass a fraction of their resources. Thus, a predator feeding only on one prey has indirect access to the fraction of basal resource

translated into its prey biomass, while remaining basal resources are therefore not available (Adams et al. 2003, Long et al. 2006, Miki et al. 2008), unless other prey types are consumed. In this way, each prey represents an alternative, and potentially compensatory, energy path, from basal resources to predators (Fig. 2A). Consequently, empirical patterns reported here and elsewhere (Sherwood et al. 2002b, Krumins et al. 2006, Long et al. 2006, Duffy et al. 2007, Layman et al. 2007, Miki et al. 2008) indicate that prey biodiversity not only affects resource quality, but could have a large effect on predator persistence by increasing the total amount of resources available.

The expansion of killifish diet with body size implies an integration of energy channels from alternative resources, and the consumption of prey from external sources (Fig. 1). Through these changes in predator diet with body size, large predators are able to have direct or indirect access to most basal resources in the system (Fig. 2B–C). As is represented in Fig. 2, our results suggest that the way in which large predators exploit resources within a food web could allow them to obtain more resources than those expected from the passive loss of energy through food chains (Brown and Gillooly 2003, Jennings and Mackinson 2003). Moreover, the exploitation of different energy channels, the increase in prey diversity and the consumption of prey from different food webs, could have large stabilizing effects (McCann et al. 2005, Rooney et al. 2006, Otto et al. 2007). These processes, together with the increase in total resources with diversity could be key to ensure the persistence of large top predators (Long et al. 2006, Rooney et al. 2006, Arim et al. 2007a).

As has been proposed elsewhere (Jennings et al. 2002, Woodward et al. 2005, Raffaelli 2007), the description of trophic relationships based on assigning latin binomials to nodes in a food web could be misleading, particularly in size-structured aquatic ecosystems. In fact, it has been shown that when intra-node differences in body size are considered, a strong pattern of trophic structure and energy flow related to body size emerges. The strength of the patterns herein presented suggests that, much of the unexplained variation in food web patterns, could be explained considering individuals of very different sizes as a single node in food webs (Supplementary material Fig. A1, A2). Intraspecific variation in killifishes body sizes in our system was notably larger than interspecific differences; a pattern shared by most species in other communities (Woodward et al. 2005). The existence of a strong pattern of food web structure related to body size becomes evident when information from a large number of individual predators is analyzed within size classes, here and elsewhere (Jennings et al. 2002). These studies suggest that, at least in (lentic) aquatic systems, food web patterns are particularly evident when analyzed using size class subdivisions. This suggests that the response in predator trophic position could be a property of the ensemble, and not necessary of its individual components.

The relationship between available resources, trophic position and body size is of paramount importance for understanding trophic structure. In fact, our explanation for the relationship between trophic position and body size implies that system size (e.g. pond area), through its effect on species diversity (MacArthur and Wilson 1967) and

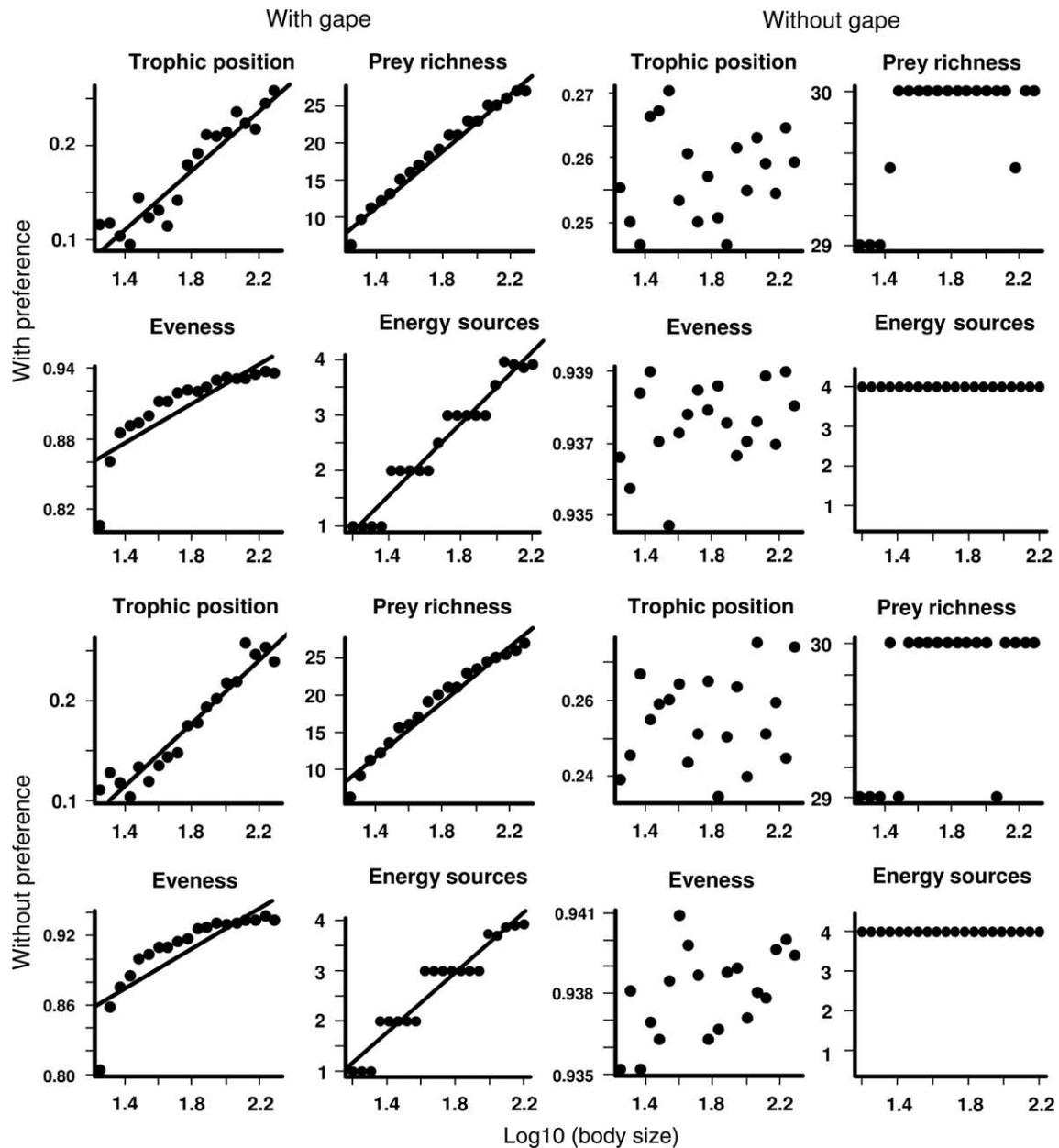


Figure 3. IBM evaluation of gape limitation and size preference as determinants of changes in trophic structure with body size. Gape limitation is identified as a necessary condition to reproduce the observed patterns, while size preference neither reproduces the patterns nor interacts with the effect produced by gape limitation.

maximum body size (Marquet and Taper 1998), should affect food chain length, as has been observed elsewhere (Briand and Cohen 1987, Spencer and Warren 1996, Post et al. 2000, Post 2002). In order to integrate different energy channels and satisfy energy demands at higher trophic positions, a large set of available prey should be present in the system (Long et al. 2006, Miki et al. 2008). In fact, it has been shown that a reduction in prey biodiversity could constrain the addition of new prey at larger-bodied sizes, resulting in a reduction in energy acquisition (Sherwood et al. 2002b). Similarly, fragmented ecosystems show a reduced number of prey species, hence a low number of energy paths from basal resources with a

consequent decrease in food chain length (Layman et al. 2007). Our results indicate a new mechanism potentially connecting ecosystem area, diversity and food chain length. Larger areas have longer food chains, because top predators potentially exploit a larger prey diversity, thus increasing their energy availability and persistence (Fig. 2).

Ours, and previous analyses (McCann et al. 2005, Rooney et al. 2006, 2008), suggest that the energy available to predators is not a property of the system, but rather emerges as a consequence of the interaction between system opportunities, which are mainly determined by prey diversity and predator use of these opportunities, the number of energy sources and the energy paths that are

integrated in their diet (as determined by gape constrains). Human activities impact natural ecosystems by changes in their diversity, area (through fragmentation and habitat degradation) and productivity (through fertilization and organic contaminants) (Arim and Jaksic 2005, Rooney et al. 2006, Layman et al. 2007). Not surprisingly, top predators are particularly sensitive to these impacts, massively declining in many systems around the world (Diamond 2001). Their persistence requires the preservation of the structure of the food web topology that supports them (McCann 2007), and in particular, body size diversity with its variation within and among species.

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Supplementary material available online as Appendix O17768 at www.oikos.ekol.lu.se/appendix. Appendix 1. Supplementary protocol: detailed description of the individual based model. Figure A1. Association between trophic position and body size within fish species. Figure A2. Association between prey richness and body size within fish species. Table A1. Size classes diet composition.