Hydrogeomorphology and river impoundment affect food-chain length of diverse Neotropical food webs

David J. Hoeinghaus, Kirk O. Winemiller and Angelo A. Agostinho

D. J. Hoeinghaus (djhoeing@ksu.edu) and K. O. Winemiller, Section of Ecology, Evolutionary Biology and Systematics, Dept of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX 77843-2258, USA. Present address for DJH: Div. of Biology, Kansas State Univ., 104 Ackert Hall, Manhattan, KS 66506, USA. – A. A. Agostinho, Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura, Univ. Estadual de Maringá, Maringá, BR–87020-900 Paraná, Brasil.

Food-chain length is a central characteristic of ecological communities that affects community structure and ecosystem function. What determines the length of food chains is not well resolved for most ecosystems. Herein, we examine environmental correlates of food-chain length based on the productivity hypothesis, compare food-chain lengths among aquatic ecosystem types and identify bi-directional effects of river impoundment on food-chain length in the Paraná River Basin of South America. Both temperature regime, a surrogate of productivity, and ecosystem type significantly affected food-chain length in independent analyses. However, when analyzed together, only ecosystem type explained significant variation in food-chain length. Food chains were longest in reservoirs, and shortest in high-gradient rivers. The proximate mechanism driving this pattern appears to be body-size ratios of primary consumers to apex predators, which differ among trophic pathways. Food chains based on phytoplankton production may have an additional size-structured link not present in food chains based on other basal sources such as detritus and algae. Hydrogeomorphology is the ultimate mechanism influencing food-chain length because it affects the relative importance of basal carbon sources supporting higher trophic levels, which through differences in the number of trophic links along the different size-structured pathways, appears to drive the observed patterns in food-chain length. We discuss a hypothesis of food-chain length that integrates energy flow and size-structure, facilitates inclusion of temporal dynamics and which is readily testable in both 'closed' and 'open' ecosystems.

Food-chain length is the number of trophic transfers from the base to the top of a food web (Post 2002a). This aspect of vertical web structure strongly affects community structure (Paine 1980, Pace et al. 1999) and ecosystem function (Schindler et al. 1997, Duffy et al. 2005). For this reason, food-chain length is considered a central characteristic of ecological communities, and identifying the factors that determine food-chain length is a fundamental issue of ecology (Pimm 2002). Theoretical, experimental and comparative studies have suggested a suite of potential determinants of food-chain length, however, the study of what limits or otherwise determines the length of food chains has seen relatively limited progress (reviewed by Post 2002a).

The most frequently tested and cited food-chain hypotheses are based on energetic arguments. Because energetic efficiencies of trophic interactions are typically low (on average 10%), these hypotheses argue that the number of trophic levels in a given food chain should be limited by energy availability. The 'productivity hypothesis', attributed to Elton (1927) and later work by Hutchinson (1959), therefore predicts longer food chains occur in more productive habitats. Schoener (1989)

proposed a modification of this hypothesis, called the 'productive-space hypothesis', that predicts food-chain length increases as a function of total ecosystem productivity (the product of ecosystem size and a measure of per-unit-size productivity). Studies testing these energetic hypotheses in a variety of ecosystems have yielded mixed results (Briand and Cohen 1987, Jenkins et al. 1992, Spencer and Warren 1996, Kaunzinger and Morin 1998, Post et al. 2000). Two recent studies in temperate lakes (Vander Zanden et al. 1999a, Post et al. 2000) found no effect of productivity or productive space in determining food-chain length, but instead observed a direct correlation between food-chain length and ecosystem size.

Other potential determinants of food-chain length have received less attention. The history of community assembly (Kitching 2001), dynamic constraints or disturbance (Pimm and Lawton 1977, Pimm 2002), human-induced changes to communities (Pauly et al. 1998), and size-structure of predator–prey interactions (Hairston and Hairston 1993, Jennings and Warr 2003) also may affect food-chain length, but these factors are difficult to measure, oftentimes interact or are correlated with one another. Some evidence suggests that food-chain length may differ among

ecosystem types (Briand and Cohen 1987, Schoener 1989, Shurin et al. 2006), and a recent global-scale analysis of aquatic food webs found significant differences in food-chain length among stream, lake and marine ecosystems (Vander Zanden and Fetzer 2007). As for the ecosystem-size hypothesis, the functional aspects of these ecosystem differences are unclear, and a general theory of food-chain length remains elusive.

Most advances have been made in simple experimental assemblages (Jenkins et al. 1992, Kaunzinger and Morin 1998) or natural systems characterized by relatively discrete boundaries and low species richness, such as temperate lakes (Vander Zanden et al. 1999a, Post et al. 2000). Species-rich tropical webs and ecosystems with poorly defined boundaries, such as streams and rivers, have received comparatively little attention in this regard (but see Townsend et al. 1998, Thompson and Townsend 2005). A recent review of the determinants of food-chain length, Post (2002) suggested broadening the search for a single determinant to identify when and where a suite of potentially interacting factors affect the length of food chains. Diverse food webs in ecosystems with diffuse boundaries need to play a role in this search.

In this study we analyze carbon and nitrogen stable isotope ratios of basal sources and aquatic consumers to estimate food-chain lengths of ten species-rich aquatic food webs of a large river basin in South America. We examine relationships between food-chain length and surrogates of primary production, compare food-chain lengths among different aquatic ecosystem types, and identify effects of a common anthropogenic impact (river impoundment) on aquatic food-chain length. We further identify the potential ultimate and proximate mechanisms driving differences in food-chain length among the aquatic food webs examined here, and propose a readily testable mechanistic hypothesis of food-chain length.

Methods

Regional description

We examined correlates of aquatic food-chain length for 10 species-rich food webs dispersed across more than 500 km of the Upper Paraná River Basin, Brazil (Fig. 1, Table 1). The Paraná River is the fourth largest river in the world in drainage area (2.8×10^6 km^2) and the tenth largest in annual discharge (5.0×10^8 m^3 year^{-1}). The Upper Paraná Basin (upper third of the basin, approximately 891 000 km^2) is one of the most extensively dammed river basins in the world (Fig. 1), with over 140 major reservoirs (dam height ≥ 10 m) on the eastern side, among which 20% are larger than 10 000 ha (Gomes and Miranda 2001, Agostinho et al. 2007a). The last free-flowing stretch of the Upper Paraná River is approximately 230 km, located between Porto Primavera Reservoir and Itaipu Reservoir.
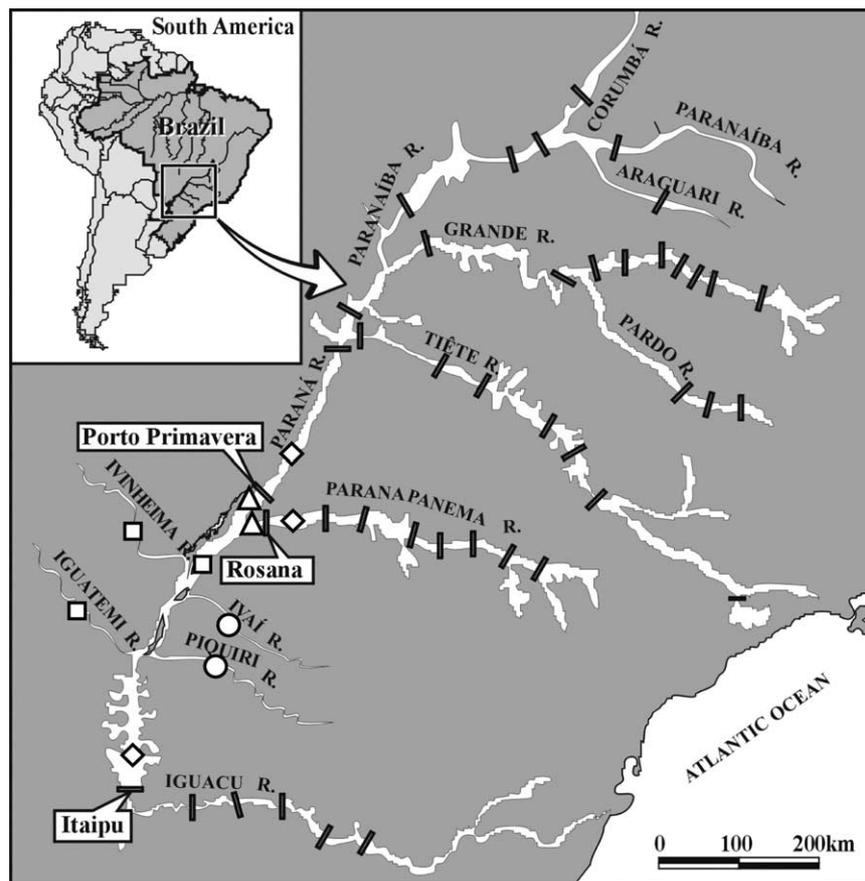
Figure 1. Study locations (white symbols) and large dams (black bars) of the Upper Paraná River basin, Brazil. □ = low-gradient rivers; ○ = high-gradient rivers; ◇ = reservoirs; △ = river stretches below reservoirs.

Table 1. Food-chain length and landscape-scale classifications for each food web from the Upper Paraná basin, Brazil.

Food web	Food-chain length	Temperature regime	Climate zone	Ecosystem type	Watershed type
Iguatemi	4.12	Warm	Tropical central	Low-gradient river	Savanna
Ivinheima	4.19	Warm	Tropical central	Low-gradient river	Savanna
Paraná	4.09	Warm	Tropical central	Low-gradient river	Savanna
Piquiri	4.00	Warm	Temperate	High-gradient river	Forest
Ivaí	4.02	Warm	Tropical central	High-gradient river	Forest
Itaipu	4.25	Warm	Temperate	Reservoir	Forest
Rosana	4.34	Hot	Tropical central	Reservoir	Forest
Porto Primavera	4.35	Hot	Tropical central	Reservoir	Savanna
Paranapanema below Rosana	4.09	Hot	Tropical central	Below reservoir	Forest
Paraná below Porto Primavera	4.30	Hot	Tropical central	Below reservoir	Savanna

This stretch has a wide floodplain (≤20 km) on the west margin and experiences a relatively predictable seasonal flood pulse influenced by several important tributaries that flow into the Paraná in this stretch. Eastern margin tributaries (e.g. Ivaí and Piquiri Rivers) have higher elevation gradients and restricted floodplains. Seasonal rainfall results in inundation of the floodplain and the lower courses of lowland rivers of the western margin (e.g. Ivinheima and Iguatemi Rivers) from December through April.

More than 600 fish species have been recorded in the Paraná Basin (Bonetto 1986), with about 170 species known to occur between Itaipu Reservoir and the mouth of the Paranapanema River (Agostinho et al. 2007b). Large-scale reproductive migrations of several fish species (e.g. *Prochilodus lineatus, Pseudoplatystoma corruscans, Salminus brasiliensis*) coincide with rising water levels and wet season flooding (Agostinho et al. 2004). The basin's fish fauna exhibits diverse trophic ecologies (Hahn et al. 2004), and fishes occupy a range of trophic levels in the aquatic food web, from grazers of algae, detritus and emergent grasses to omnivores, invertivores and piscivores (either consuming whole fish, or chunks of flesh or fins as in the case of piranhas). Detailed descriptions of the Upper Paraná River Basin and its flora and fauna, particularly the remaining floodplain stretch, can be found in Thomaz et al. (2004).

Field and laboratory methodology

Stable isotopes of carbon and nitrogen were used to estimate food-chain length and identify patterns of material flow through dominant trophic pathways for each food web (Hoeinghaus et al. 2007a). The aquatic food webs analyzed in this study were delimited by fishes as consumers plus their aquatic and riparian prey and production sources consumed throughout the web leading to those consumers. Parasites and non-aquatic organisms that feed on fish, such as birds and humans, were not included.

Samples for isotopic analysis were collected between September and early December 2003 (late dry season), prior to seasonally rising water levels and fish migrations. At each location, representative riparian and aquatic carbon sources (C_3 plants and C_4 grasses, fine particulate organic material, coarse detritus, periphyton, and phytoplankton), primary consumers (snails, bivalves, zooplankton, and herbivorous and detritivorous fishes) and secondary consumers (omnivorous and carnivorous fishes) were collected at multiple points along a 2–5 km sample reach to characterize trophic pathways from source to top consumer. Detailed methodology is described in Hoeinghaus et al. (2007a). Briefly, fishes were collected using multiple gears (seines, cast nets, gill nets and baited lines) to obtain a representative sample of the community at each site. Due to the high species richness, exhaustive sampling of each food web was not feasible. Therefore, special effort was given to obtain primary consumers (e.g. *Prochilodus lineatus, Pterygoplichthys anisitsi, Schizodon* spp.) and species potentially occurring at the top of the food web (e.g. piscivorous species such as *Pseudoplatystoma corruscans, Salminus brasiliensis, Plagioscion squamosissimus* and *Cichla* spp.) so that the vertical structure of the web could be estimated with confidence. For all species, 3–5 replicates were taken within each sample reach when possible.

Upon return to the lab, samples were prepared according to standard protocols (Hoeinghaus et al. 2007a). Prepared samples were sent to the Analytical Chemistry Laboratory of the Institute of Ecology, Univ. of Georgia, for analysis of carbon and nitrogen isotope ratios. Results are expressed in delta notation (parts per thousand deviation from a standard material): $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$; where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The standard material for carbon is Pee Dee Belemnite (PDB) limestone, and the nitrogen standard is atmospheric nitrogen. Standard deviations of $\delta^{13}C$ and $\delta^{15}N$ analyses were 0.18‰ and 0.19‰ respectively for plant replicates, and 0.04‰ and 0.10‰ respectively for animal replicates.

Estimates of food-chain length

Stable isotope ratios were used to calculate continuous estimates of species trophic positions which integrate energy assimilated and material flow along all pathways leading to the consumer. Food-chain length was estimated as the maximum species trophic position observed for each web (Post et al. 2000, Post 2002b). Trophic positions (TP) were calculated for all predatory species in each food web using the following equation:

$$TP = \lambda + (\delta^{15}N_{predator} - \delta^{15}N_{baseline})/F$$

where λ is the trophic level of consumers estimating the food web base (in this case $\lambda = 2$ because primary consumers were used, see below), $\delta^{15}N_{predator}$ is the nitrogen isotopic signature of the predator being evaluated, $\delta^{15}N_{baseline}$ is the average nitrogen isotope signature of the consumers used to estimate the base of the food web, and F is the per trophic level fractionation of nitrogen. We used a

δ^{15}N fractionation of +2.54‰ following the meta-analysis of Vanderklift and Ponsard (2003), which appears to be a more reliable estimate than the commonly used value of +3.4‰ (Post 2002b) based on qualitative comparison of nitrogen isotope signatures of dominant feeding relationships in our study system. An appropriate N baseline was calculated independently for each food web using δ^{15}N signatures of fish species known from prior studies to be primary consumers of benthic, pelagic and littoral/terrestrial production sources (e.g. *Prochilodus lineatus*, *Pterygoplichthys anisitsi*, *Metynnis maculatus*, *Schizodon* spp.). Other studies have used δ^{15}N signatures of bivalves and snails to estimate the pelagic and littoral base of the food web, respectively (Post et al. 2000). These approaches are fundamentally similar, as both use long-lived consumers to integrate temporal variability in source isotopic signatures. Fishes were chosen to estimate the N baseline because they are larger, more mobile consumers than either snails or bivalves, and therefore provide greater temporal and spatial integration of source variability. Tissue turnover rates of these species are also more comparable to those of top-consumers because of their similar body size. In species-rich tropical systems, numerous sources potentially support secondary consumers, and fishes likely provide a more robust estimate of the baseline nitrogen signature (Layman et al. 2005).

Statistical analyses

Each food web was classified according to landscape-scale environmental characteristics to test predictions derived from previously proposed environmental correlates of food-chain length. Effects of ecosystem type on food-chain length were tested by classifying each food web according to aquatic ecosystem type: low-gradient rivers (<0.10 m km^{-1}), high-gradient rivers (1.30–2.20 m km^{-1}), reservoirs, and river stretches below reservoirs (Fig. 1). Because inland aquatic environments may be strongly influenced by watershed characteristics (Allan 2004), each food web was also classified according to dominant watershed ecosystem type (either savanna or seasonal semi-deciduous forest). Primary productivity data are not available for all of the food webs studied here; therefore we cannot directly test the productivity hypothesis. Previous studies have used correlated factors (e.g. latitude and air temperature) to indirectly assess predictions based on the productivity hypothesis when primary productivity data are not available (Vander Zanden and Fetzer 2007). We used temperature regime and climate zone as surrogate factors which are typically correlated with primary productivity at the landscape scale. Temperature regimes were either hot (>18°C during all months) or warm (between 15 and 18°C in at least one month). Climate zone designations are based on temperature regimes combined with annual patterns of monthly rainfall, and were either tropical central or temperate. Watershed ecosystem type, climate zone, and temperature regime were determined using scale maps produced by the Brazilian Inst. of Geography and Statistics (Inst. Brasileiro de Geografia e Estatística, <www.ibge.gov.br>). The resulting food web classification scheme is presented in Table 1.

Food-chain length was compared among classes within each category independently using analysis of variance (ANOVA). Categories with significant effects in independent tests were included in a multiple regression analysis to determine the relative variance in food-chain length explained by each category. In the multiple regression analysis, food-chain length was the dependent variable, and independent variables were coded as dummy variables. Multicollinearity of independent variables was tested using variance inflation factors. Independent variables significant at p = 0.05 were included by stepwise selection. Significant variables were only retained if they increased the adjusted R^2 by 0.1 or more, otherwise the reduced model was selected. All analyses were performed using SPSS ver. 12.

Results

Food-chain lengths ranged from 4.00 to 4.35 (Table 1), and were within ranges reported elsewhere in the literature (typically between 3 and 5 trophic levels, Pimm 2002). In independent comparisons, temperature regime significantly affected food-chain length ($F_{1,8} = 5.27$, $p = 0.051$) in the manner predicted by the productivity hypothesis: longer food-chains were observed in locations with high year-round temperatures (Fig. 2). Food-chain length also differed among aquatic ecosystem types in independent analyses ($F_{3,6} = 7.02$, $p = 0.022$, Fig. 2). Post-hoc comparisons among ecosystem types found reservoir food-chains to be significantly longer than those of high-gradient rivers ($p = 0.017$), and marginally significantly longer than those of low-gradient rivers ($p = 0.092$). Within-habitat variation in food-chain length was greater for river stretches below reservoirs than the other ecosystem types (Table 1, Fig. 2). No differences were observed among food-chain length due to climate zone or watershed type (Fig. 2), although we may have lacked sufficient power for the climate zone comparison since all but two webs were classified as having 'tropical central' climates.

In the multiple regression analysis, the habitats 'reservoir' (β_1) and 'high-gradient river' (β_2) together explained 74.8% of the variation in food-chain length ($y = 0.155\beta_1 - 0.148\beta_2 + 4.16$; $F_{2,7} = 10.40$, $p = 0.008$). Inclusion of 'high-gradient river' in the model increased the adjusted R^2 from 0.48 to 0.68. In the reduced model, 'reservoir' alone accounted for 54.2% of the variation. The ecosystem category 'reservoir' was positively associated with food-chain length, whereas 'high-gradient river' was negatively associated. After inclusion of the ecosystem types in the model, temperature regime did not explain any additional variation. Two of the three reservoir food webs were classified as having 'hot' temperature regimes, and all low- and high-gradient rivers had 'warm' temperature regimes, which limits our ability to examine effects of temperature regimes within ecosystem types. Alongside the multiple regression results, this also suggests that the difference among 'warm' and 'hot' temperature regimes was due to the correlation with ecosystem type.
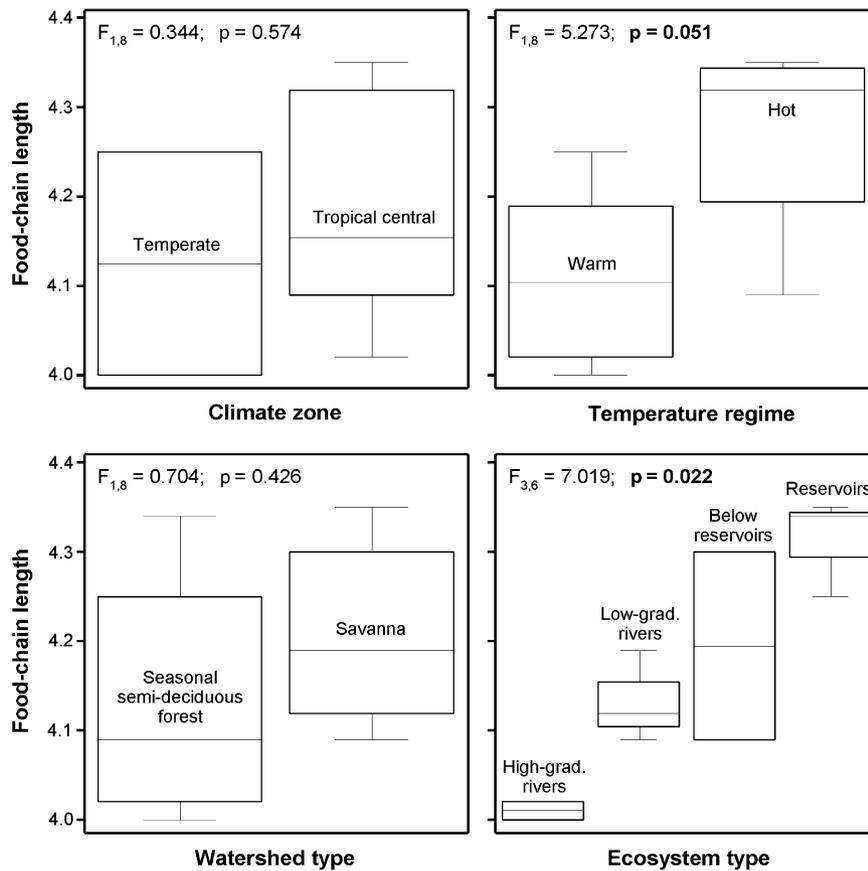
Figure 2. Box plots depicting independent comparisons of food-chain lengths among different categories of environmental characteristics. Mean (solid line within box), quartiles (box) and range (whiskers) are presented for each category.

Discussion

Perhaps the greatest roadblock in our understanding of the factors that determine the length of food chains is the inherent difficulty of compiling accurate and comparable food webs, and the consequent reliance on an oversimplified view of food webs as static networks (de Ruiter et al. 2005, Winemiller and Layman 2005). Studies of more highly-resolved webs suggest that patterns emerging from early comparisons of food web structure are biased by differences in methodologies or scales (Winemiller 1990, Goldwasser and Roughgarden 1997). Analyses of naturally occurring stable isotopes over the last couple decades has greatly affected the way ecologists study energy flow and trophic structure (Post 2002b). Continuous measures of realized trophic position estimated using stable isotopes allow detection of subtle differences in food-chain length that typify natural ecosystems (Vander Zanden et al. 1999a, Post et al. 2000, Vander Zanden and Fetzer 2007).

The differences among food-chain lengths observed in the present study (maximum difference of 0.35 trophic levels) are comparable with earlier studies in aquatic ecosystems in which fish occupied upper trophic levels and food-chain length was measured as maximum realized trophic position based on stable isotope data. For example, Vander Zanden and Fetzer (2007) observed an average difference of 0.5 trophic levels between stream and lake food chains in their global-scale analysis. Similarly, across

the 72 marine sites surveyed by Jennings and Warr (2003), maximum trophic position differed by at most 0.5 trophic levels among sites. A larger difference in food-chain lengths was observed by Post et al. (2000) after ecosystem size increased enough to include a different piscivore (lake trout) that was not present in the smallest lakes studied. Post et al. (2000) also attributed longer food chains to lower trophic omnivory in larger lakes, because predators generally increased in trophic position as lake size increased. Like aquatic food webs of other Neotropical systems, the ones studied here are characterized by greater trophic diversity, including a greater frequency of omnivory, than those of most temperate aquatic ecosystems (Winemiller 1990). Smaller differences in food-chain lengths across our food webs may therefore be expected.

It is important to note that similar piscivore assemblages occurred in all of our study locations, and that when a unique piscivore species was present it typically occurred as a replacement rather than an addition to the food web (i.e. lentic- vs lotic-adapted species). Longer food chains correspond to a greater number of trophic transfers within the web, not by adding new species to the top. We can therefore attribute the observed variation in food-chain lengths to the addition or deletion of trophic steps along the diverse and highly connected trophic pathways leading from the array of basal sources to the apex predators. This may occur via two proximate structural mechanisms: 1) the addition or removal of intermediate predators, or 2) a

change in the relative importance of omnivory (Post and Takimoto 2007). The insertion and omnivory mechanisms may either independently or simultaneously affect food-chain length along a single trophic pathway or via cumulative effects across numerous interconnected pathways (as is likely the case for these species-rich food webs).

Productivity and productive-space hypotheses

Energy availability probably does not limit food-chain length of the food webs studied here. Temperature regime, which significantly affected food-chain length when analyzed independently, did not contribute to the explained variation in food-chain length after taking into account 'reservoir' and 'high-gradient river' ecosystem types in the multiple regression. Although temperature and climate regimes may correlate only loosely with productivity, and actual productivity data are not available for all locations, the chain of reservoirs along the Paranapanema River and mainstem Paraná River (Fig. 1) are known to sequentially reduce aquatic primary productivity by retaining large amounts of phosphorous through sedimentation (Agostinho et al. 2007b). Un-impounded low-gradient and high-gradient rivers are assumed to have comparatively higher productivities because they drain similar landscapes but lack reservoirs. Contrary to expectations of the productivity hypothesis, food-chain lengths were longer in the least productive habitats (reservoirs). Our results are consistent with the observation that although available energy must ultimately constrain the maximum number of possible trophic levels due to low energetic efficiencies, most food chains are shorter than the maximum possible length and therefore are not determined by energy availability (Post 2002a).

Although the productive-space hypothesis (Schoener 1989) is perhaps the most widely investigated potential determinant of food-chain length (Post 2002a), we purposefully did not attempt to test it in the present study. To test the productive-space hypothesis, one must first define the bounds of the ecosystem. Some ecosystems, such as lakes and islands, are relatively well-bounded (i.e. community and resource processes occur at the same scale and are strongly associated with physical boundaries), and may be suitable for such investigations. Boundaries of other more 'open' ecosystems, such as rivers and even reservoirs with un-impounded tributaries, cannot be delimited appropriately to test the productive-space hypothesis because no strong association exists among community, resource and physical boundaries (Post et al. 2007). Solutions have been proposed to address this lack of correspondence with physical boundaries for communities (Cousins 1990) and resources (Power and Rainey 2000), however, these approaches typically cannot be integrated because of differences in the scale at which the two processes occur (Post et al. 2007). Furthermore, even seemingly closed systems such as lakes or islands, often receive considerable energetic subsidies from adjacent or even distant ecosystems (Pace et al. 2004, Polis et al. 2004).

Anthropogenic impacts and disturbance

Anthropogenic impacts may affect food-chain length both directly due to over-harvest or species introductions, and indirectly, through changes in disturbance regimes and other environmental drivers of food-web dynamics (e.g. productivity, habitat connectivity, hydrology). Contrary to 'fishing down' marine food webs (Pauly et al. 1998), over-exploitation of large primary consumers important in many tropical river fisheries may increase food-chain length as piscivores shift their diets from large detritivores to smaller omnivores and invertivores positioned higher in the food web (Layman et al. 2005). Artisanal fisheries in the Upper Paraná Basin do not concentrate on a single trophic group, but rather target many species representing all trophic groups in the food web. Furthermore, changes in the abundance and biomass of fishes in the Upper Paraná basin appear more strongly driven by recruitment dynamics tied to the hydrologic regime and impoundment effects (Agostinho et al. 2004). We therefore do not attribute the observed patterns in food-chain length to either 'fishing down' or 'fishing up' the food webs.

Several fish species have been introduced to the Upper Paraná Basin, but their positions in food webs differ among habitats. For example, the curvina *Plagioscion squamosissimus* (introduced from the Amazon Basin to reservoirs of southern Brazil) is found throughout the basin, except the high-gradient rivers, and is the top-consumer in both the Porto Primavera and Rosana Reservoir food webs. However, longer food chains of reservoirs are probably not attributable to the addition of the curvina, as this species is also found in low-gradient rivers and below reservoirs where it occupies lower trophic positions. Similar patterns can be observed for other introduced species, such as tucunaré *Cichla* spp. and piranha *Serrasalmus* spp. Native faunas of the food webs examined here are part of the same regional species pool, and the comparatively few introduced species that are established have had ample opportunities to disperse throughout the basin (Agostinho et al. 2005). Therefore, community differences among food webs are expected to be predominantly determined by environmental factors that drive community assembly rather than divergent evolutionary or colonization/introduction histories.

Hydrologic regimes are key drivers of lotic ecosystem dynamics, and anthropogenic alterations of hydrologic regimes have strong and complex ecological impacts (Bunn and Arthington 2002). Hydrogeomorphology has been shown to affect the functional organization of aquatic communities (Hoeinghaus et al. 2007b), and appears to drive patterns in food-chain length across the large-river food webs studied here. River impoundment, a common anthropogenic impact to lotic ecosystems worldwide (Nilsson et al. 2005), resulted in longer food chains in the upstream reservoir environment, and greater variation in food-chain length in river segments immediately below impoundments than observed for either natural low-gradient or high-gradient rivers. The anthropogenic and natural differences in hydrogeomorphology that affected food-chain lengths are also what distinguish the ecosystem types examined in this study, therefore, we will continue this discussion in our section on effects of ecosystem type on food-chain length.

Disturbance of natural flow regimes has been shown to affect food web structure and ecosystem processes in other lotic ecosystems (Power et al. 1996, Wootton et al. 1996, Townsend et al. 1998). Effects of disturbance on food-web structure are best analyzed by comparing the same food web before and after disturbance, such as effects of hurricanes on island food webs (Spiller and Schoener 2007). Comparisons among similar types of food webs may also be valid when disturbance is quantified and other potentially confounding factors can be controlled for either experimentally (Warren and Spencer 1996) or statistically (Townsend et al. 1998). Our study framework, which included a single survey of food webs across very different ecosystem types but limited replication within ecosystem types, restricts our ability to test the disturbance hypothesis. Although our high-gradient rivers might be considered to experience more natural disturbance from flow variation than the other ecosystem types, these rivers should not be confused with small headwater streams that undergo frequent catastrophic periods of desiccation and flash flooding. These large rivers with fast flowing water never desiccate and are not prone to stochastic flash floods, but instead have seasonal patterns of discharge and are characterized by a diverse community adapted for such conditions. Likewise for reservoirs, impoundment may also be considered a disturbance from natural flow conditions, however, these reservoirs are now (10–26 years following impoundment) comprised primarily of lentic-adapted species able to maintain stable populations in the reservoir environment. Different levels or degrees of disturbance could not be assigned to the food webs studied here.

Effects of ecosystem size and ecosystem type

Previous studies have found significant positive correlations between food-chain length and ecosystem size (Vander Zanden et al. 1999a, Post et al. 2000). Ultimately, the ecosystem-size hypothesis suffers from the same limitation as the productive-space hypothesis: its application is determined by the ability to objectively quantify ecosystem size. Although the method of Cousins (1990) may be used to estimate ecosystem size from the community standpoint, the productive-space hypothesis should be tested alongside the ecosystem-size hypothesis (sensu Post et al. 2000, Post 2007) which requires concordance between community and resource boundaries to be able to define ecosystem size as discussed above. Vander Zanden and Fetzer (2007) tried to avoid this issue for streams by classifying them as either 'large' or 'small' based on annual average discharge (greater or less than 20 m^3 s^{-1}), and found no significant difference in food-chain length between the two. Thompson and Townsend (2005), working in small streams, found a significant positive correlation between food-chain length and 'ecosystem size', which they quantified as the length of stream sampled (30 m) times the average width of the reach. This measure of ecosystem size likely does not correspond with community and resource process boundaries, and therefore does not actually test the ecosystem size hypothesis. Due to the inability to consistently estimate size across ecosystem types, we cannot make qualitative comparisons of 'large' vs 'small' with our dataset. For example, our food

webs would be ranked differently according to 'ecosystem size' measures based on watershed area, annual average discharge, width, or depth. As for the productive-space hypothesis, we did not attempt to test the ecosystem-size hypothesis with our dataset due to the underlying limitation on quantifying ecosystem size in 'open' systems.

Similar to previous studies (Briand and Cohen 1987, Schoener 1989, Vander Zanden and Fetzer 2007), we found food-chain lengths to differ significantly among ecosystem types, with the multiple regression model explaining almost 75% of the variation. Food-chain lengths of low-gradient rivers and rivers below reservoirs are intermediate (although it is interesting that food-chain lengths of river stretches below reservoirs had higher variation), and increases in river elevation gradient correspond to decreases in food-chain length, whereas river impoundment is associated with longer food chains. Food-chain length appears to correlate with landscape-scale hydrogeomorphic characteristics, especially with regard to water residence time, across our study locations. Similarly, Vander Zanden and Fetzer (2007) observed longer food chains in lakes and marine ecosystems and shorter food chains in lotic ecosystems. We discuss potential mechanisms for this pattern below.

Proximate and ultimate mechanisms determining food-chain length

A limitation of many studies investigating correlates of food-chain length is that mechanistic explanations are difficult to derive from observed patterns of association. For example, both Vander Zanden et al. (1999a) and Post et al. (2000) found ecosystem size to correlate with food-chain length in north-temperate lakes. But what functional
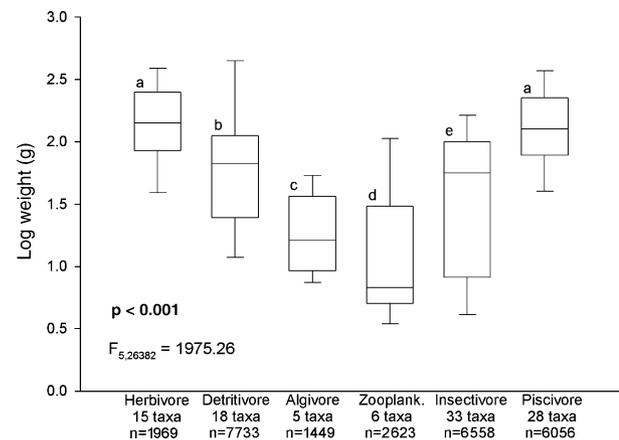
Figure 3. Body size (biomass) among trophic groups of fishes from the Upper Paraná basin, Brazil. Primary consumer trophic groups are herbivores (graze higher plants and consume fruits and seeds), detritivores, and algivores. Secondary and higher consumer trophic groups are zooplanktivores, insectivores and piscivores. Letters above boxes indicate significant differences in mean body size. Fishes were collected over a six year period in a variety of habitats (Agostinho et al. unpubl.). Data are for 91 taxa comprising body-size measurements of 22 423 individuals. Fishes were classified into trophic groups following Hahn et al. (2004). Measurements for omnivores were included in multiple groups according to their diet.
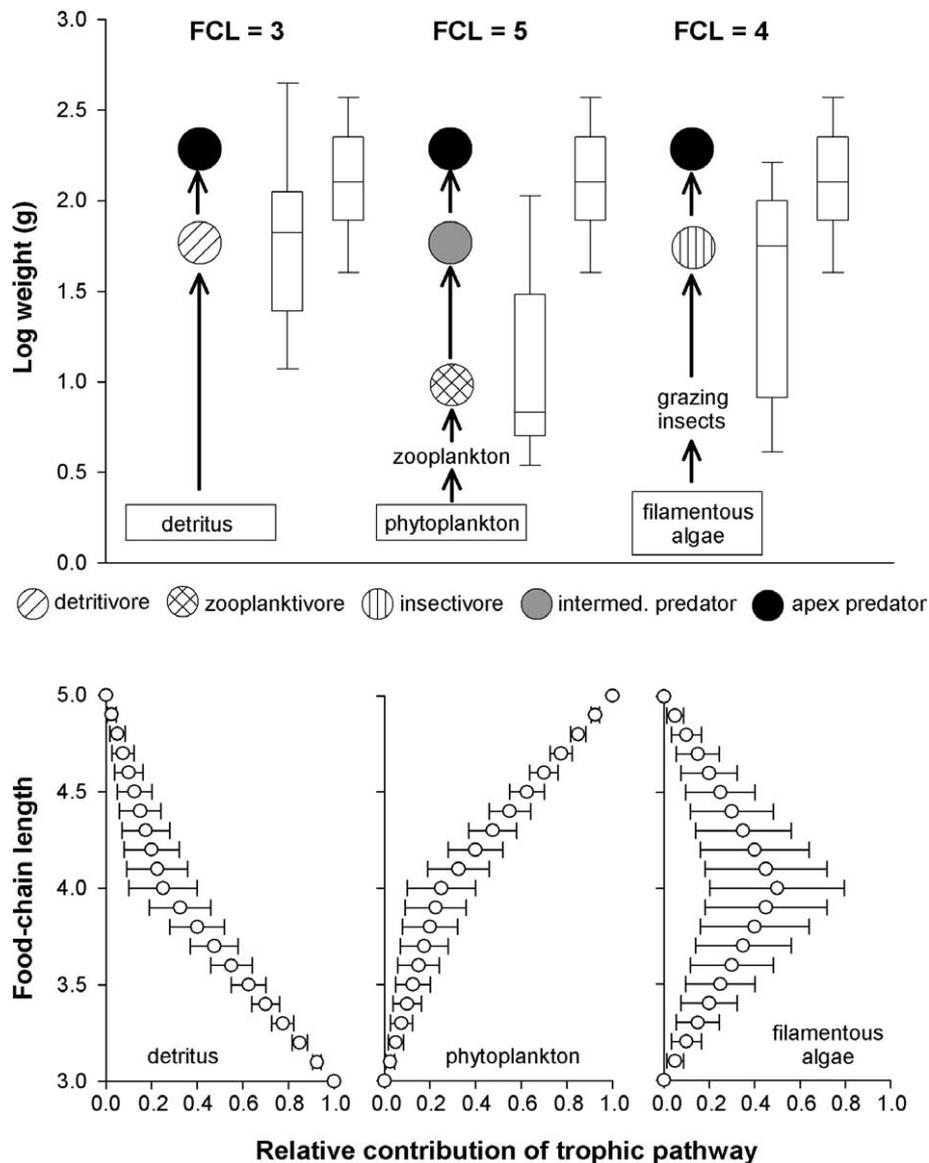
Figure 4. Conceptual diagram of differences in food-chain length (FCL) resulting from differences in body sizes of primary consumers of three trophic pathways, optimal foraging by secondary consumers, and the relative importance of those pathways to the diet of the apex predator. Top panel: circles represent fish trophic groups with adjacent box plots depicting the measured body size for each trophic group in the Upper Paraná River Basin (Fig. 3). Intermediate predators and apex predators are represented as body-size extremes of the same 'piscivore' trophic group. Basal sources and invertebrates are included (though not measured) to illustrate the number of trophic steps from the base of the food web to apex predator along different pathways. Bottom panel: when an apex predator feeds across multiple trophic pathways that have different lengths (from top panel), the relative importance of each pathway to its diet determines its trophic position and food-chain length.

aspect of ecosystem size is important? As noted above, a combination of increased functional diversity (addition of species not present in smaller lakes) and reduced trophic omnivory were suggested as the potential mechanisms increasing food-chain lengths in larger lakes. For the food webs we examined, a similar question can be asked: what are the mechanisms behind the apparent relationship between hydrogeomorphic characteristics and food-chain length? Based on past research of the ecology of these communities, including investigations of the relative importance of different basal energy sources supporting upper trophic levels of these food webs (Hoeinghaus et al. 2007a), we hypothesize that the observed pattern in food-chain length

is primarily attributable to differences in size-structured trophic interactions among carbon-source trophic pathways (e.g. detritus vs phytoplankton based). As Cousins (1987) points out, differences in the body size of primary consumers may result in longer food chains leading to the same apex predator due to optimal foraging. If primary consumer body sizes, and as a result the number of trophic transfers from basal resources to apex predator, differ among trophic pathways, differences in the relative importance of the pathways among food webs will affect maximum food-chain length.

Most food webs are size-structured with trophic position positively correlated with body size (Cohen et al. 1993,

Brose et al. 2006). Most fishes ingest their prey whole, so predator-prey sizes in aquatic food webs are necessarily correlated. Tropical fishes faunas exhibit great ecomorphological diversity (Winemiller 1991), including a wide range in body size of primary consumers. Fishes that are primary consumers range in body size from some of the smallest to largest species in tropical rivers, and are readily preyed upon by predators, allowing them to feed on optimally-sized prey while at the same time feeding low in the food web (Layman et al. 2005). In the Upper Paraná River Basin, fish trophic groups differ greatly in body size, with certain piscivores, herbivores and detritivores generally the largest species in the food web, whereas zooplanktivores tend to be the smallest fishes (Fig. 3). These differences in body size may affect food-chain length across trophic pathways. For example, a detritus-based food-chain could be as short as three trophic levels if the apex predator feeds directly on large-bodied detritivores. In contrast, zooplankton are the dominant primary consumers of phytoplankton, and are most efficiently consumed by small-sized zooplanktivorous fish species capable of capturing them from the water column. These small zooplanktivores are in turn likely consumed by the smallest piscivore species which may in turn be prey of the apex predator. Figure 4 illustrates how the pelagic phytoplankton-based pathway may include one or more additional size-based trophic steps not present in other pathways in which large fishes or macroinvertebrates are primary consumers. Figure 4 is obviously a simplification, as there are dozens if not hundreds of food chains reaching the apex predators in the species-rich food webs we studied. When an apex predator feeds across multiple food chains of different lengths, the relative importance of those trophic pathways to the predator's diet will affect its realized trophic position, and as a result, food-chain length (lower panel of Fig. 4).

To directly test our hypothesis we would need known feeding relationships for all species along with body-size data (e.g. derived from stomach contents analyses) for each of the food webs studied here (e.g. as in Cohen et al. 2003), which unfortunately are not presently available. Instead, we plotted food-chain length against 99th percentile estimates of the phytoplankton contribution to each food web (data from Hoeinghaus et al. 2007a) to indirectly evaluate our hypothesis. Although these estimates do not explicitly test our hypothesis, resultant trends would be highly informative. Food-chain length and 99th percentile estimates of phytoplankton contribution were positively correlated (Fig. 5), and the linear regression was marginally significant ($R^2 = 0.358$, $p = 0.068$). Regression was significant when high-gradient river food webs were excluded ($R^2 = 0.529$, $p = 0.041$); isotope mixing models for high-gradient river food webs likely overestimated the phytoplankton contribution due to its intermediate carbon isotope signature in relation to other potential source groups important in these food webs (i.e. filamentous algae, riparian and aquatic vegetation; Hoeinghaus et al. 2007a). The trend suggests that the added size-based trophic step along the phytoplankton-based pelagic pathway is potentially responsible for the differences in food-chain length observed for these aquatic ecosystems. The proximate mechanism determining between system variation in food-chain length appears to be the relative body size of
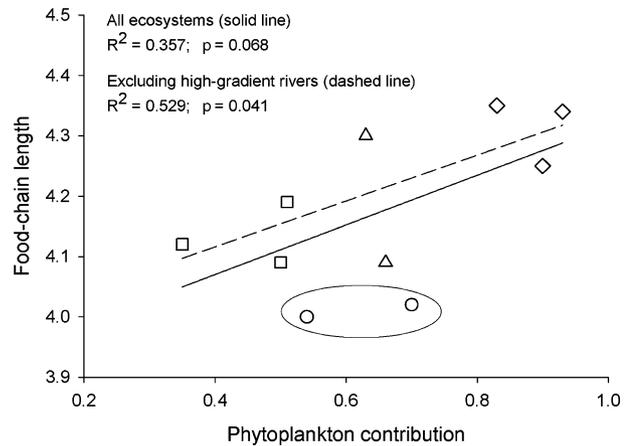
Figure 5. Relationship between food-chain length and 99th percentile estimates of phytoplankton contribution to each food web (from Hoeinghaus et al. 2007a). A second regression is plotted excluding high-gradient rivers because phytoplankton contributions are likely overestimates for these food webs (see text). □ = low-gradient rivers; ○ = high-gradient rivers; ◇ = reservoirs; △ = river stretches below reservoirs.

primary consumers to the apex predator (i.e. smaller primary consumer – apex predator body size ratios result in longer food chains as predators consume prey within an optimal size range). Hydrogeomorphology, through its effects on the relative importance of different trophic pathways in these food webs (e.g. detritus vs phytoplankton pathways), is the ultimate mechanism determining food-chain length for these ecosystems.

These proposed mechanisms may also apply to the Vander Zanden et al. (1999a) and Post et al. (2000) studies in temperate lakes, and the global analysis by Vander Zanden and Fetzer (2007). Increasing ecosystem size for lakes increases the relative proportion of pelagic vs littoral zones. Contribution of zoobenthos to the diet of lake trout (top consumers in both studies) in northern lakes decreases markedly with lake area, approaching zero for lakes >100 km^2 (Vadeboncoeur et al. 2002). A concomitant increase in the relative importance of the pelagic trophic pathway was observed. Likewise, food chains in lakes and marine ecosystems may be longer than in streams (Vander Zanden and Fetzer 2007) due to increased reliance on plankton in the former. Within marine ecosystems, comparatively large colony-forming phytoplankton are common in upwelling areas that, due to the size of colonies (several millimeters to several centimeters in diameter), are consumed by larger body-size fishes, which results in shorter food chains than those found in coastal and off-shore regions where the dominant forms of plankton are progressively smaller (Ryther 1969). Similarly in marine food webs, Jennings and Warr (2003) observed longer food-chains where smaller predator-prey body-size ratios were observed.

We propose that natural and human-induced conditions that affect the relative importance of size-structured trophic pathways on which apex predators feed may ultimately determine food-chain lengths within and across ecosystems. This hypothesis is potentially more readily testable than the ecosystem-size or productive-space hypotheses, because body sizes can be measured and the relative contributions

of different trophic pathways to predator diets can be determined, whereas an objective manner of estimating ecosystem size across both 'open' and 'closed' systems is lacking (Post et al. 2007). For example, food-chain length of a lake or island food web, even though it has relatively constant size (e.g. surface area), could be expected to vary seasonally with changes in relative abundances of constituent species, or as a result of species introductions (Vander Zanden et al. 1999b). The trophic interactions would still remain size-structured and fit our hypothesis, but the change in food-chain length would not support the productive space or ecosystem size hypotheses because the size of the ecosystem is constant but the food webs are dynamic.

This hypothesis facilitates inclusion of other previously proposed determinants of food-chain length, such as disturbance, overharvest and species introductions, primarily because it is dynamic and does not require ecosystem boundaries to be defined and secondarily because body size determines many other traits that may affect food web structure (Woodward et al. 2005). For example, life-history traits are strongly correlated with body size (Peters 1983), therefore disturbances that affect the persistence or recruitment dynamics of constituent species due to variation in life-history traits will likely also affect the size-structure of trophic interactions. As discussed above, effects of overharvest or introductions on food-chain length will likely depend on the body size and trophic position of the species being harvested or introduced and their relation to other species in the food web. These size-structured affects on food-chain length can be readily linked with our hypothesis if disturbance or species introductions/harvest affect the relative importance of trophic pathways in the food web or the size-structure of those pathways.

Conclusions

The proximate mechanism determining food-chain length in the ten species-rich aquatic food webs studied here appears to be relative primary consumer–apex predator body-size ratios, which lead to differences in food-chain length due to optimal foraging. Hydrogeomorphology (including the anthropogenic impact of river impoundment) was inferred to be the ultimate mechanism driving patterns of food-chain length through its effects on the relative importance of different size-structured trophic pathways leading to apex predators. Natural and human-induced conditions that affect the relative importance of size-structured trophic pathways on which apex predators feed may ultimately determine food-chain lengths within and across ecosystems. Elton (1927) clearly recognized the important role of body size in structuring animal communities and food webs. However, in the following decades, research shifted towards a Lindeman-inspired focus on biomass and energy flow (Lindeman 1942), and the important structuring role of body size was neglected. Yet as Warren (2005) points out "body size still matters in food webs" and has seen a renaissance in current food web research. Recent theoretical advances (Emmerson et al. 2005, Beckerman et al. 2006) and quantitative approaches (Cohen et al. 2003) have embraced the importance of body

size in trophic interactions, and provide new insights into food web structure and function.

The hypothesis we discuss here integrates the body size and energy-flow approaches advocated by Elton (1927) and Lindeman (1942). The energetic importance of different trophic pathways to the diet of the apex predator will determine its realized trophic position, and therefore maximum food-chain length, when the number of size-structured trophic interactions differs among pathways. Functional relationships between community composition, body sizes of constituent species, key environmental drivers such as seasonality and hydrology, energy flow and food-chain length deserve more attention. For example, Rooney et al. (2006) found that the coupling of weak and strong energy channels in complex food webs by upper trophic level consumers leads to local stability. Determinants of food-length may be linked to local food web stability if the relative importance of size-structured trophic pathways affects both food-chain length as described here and local stability as proposed by Rooney et al. (2006). Identifying patterns in size structure and energy flow across environmental and human-induced gradients will facilitate mechanistic understanding of what factors determine food-chain length and how anthropogenic impacts affect food-web structure and stability.

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