Body size is negatively correlated with trophic position among cyprinids

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Body size has many ecological and evolutionary implications that extend across multiple levels of organization. Body size is often positively correlated with species traits such as metabolism, prey size and trophic position (TP) due to physiological and mechanical constraints. We used stable isotope analysis to quantify TP among minnows across multiple assemblages that differed in their species composition, diversity and food web structure. Body size significantly predicted TP across different lineages and assemblages, and indicated a significant negative relationship. The observed negative relationship between body size and TP is contrary to conventional knowledge, and is likely to have arisen owing to highly clade-specific patterns, such that clades consist of either large benthic species or small pelagic species. Cyprinids probably subvert the physiological and mechanical constraints that generally produce a positive relationship between body size and TP using anatomical modifications and by consuming small-bodied prey, respectively. The need for herbivorous cyprinids to digest cellulose-rich foods probably selected for larger bodies to accommodate longer intestinal tracts and thereby to facilitate digestion of nutrient-poor resources, such as algae. Therefore, body size and TP are likely to have coevolved in cyprinids in association with specialization along the benthic to pelagic resource axis.

1. Background

Body size is a fundamental characteristic of an organism, and it has myriad implications for behaviour, metabolism, population dynamics, community structure and evolution. Body size affects behavioural traits such as locomotion, habitat use and prey exploitation [1]. For example, consumer body size is positively...
correlated with prey size [2,3], which is probably due to either relaxed gape limitations or increased metabolic demands associated with larger body sizes [4]. Many metabolic factors are influenced by body size such as growth, reproduction and respiration [5,6]. Body size also affects population characteristics such as density and abundance [7,8] as well as community characteristics such as food web structure and food chain length [9].

In a broad survey of fish body size and trophic position (TP), Romanuk et al. [10] found that 26 of 57 orders of fishes exhibited a significant positive relationship, whereas none showed a negative correlation. A combination of physiological and mechanical constraints probably produces this relationship. For example, larger bodies have higher energy demands such that large-bodied organisms must consume nutrient-rich prey [4]. Additionally, with increasing body size, relaxed gape limitation allows for the consumption of large-bodied prey such as animals rather than plants. Here, we test the relationship between body size and TP among eastern North American cyprinids (Teleostei: Cyprinidae) across several stream assemblages. Cyprinids present conditions in which a novel, negative relationship may exist. For example, many benthic-oriented, omnivorous clades are larger bodied than pelagic-oriented, carnivorous clades, and top cyprinid predators are generally drift feeding insectivores rather than piscivores [11,12]. Cyprinids are ubiquitous in North American streams and often dominate stream communities in terms of abundance and species diversity [11,13]. Cyprinids have also frequently diversified along the benthic to pelagic axis [12,14] and thus exploit a variety of resources associated with the substrate, water column and water surface. Therefore, cyprinids provide a group that may exhibit variable TPs. In this study, we evaluate the relationship between body size and TP in five diverse cyprinid assemblages across four distinct river drainages.

2. Material and methods

We sampled five cyprinid assemblages (figure 1): the Watauga River and New River (Tennessee and Ohio river basins) in western North Carolina in March and July 2012, and Uphapee Creek and Hillabee Creek (Mobile River Basin) and Halawakee Creek (Apalachicola River Basin) in southeastern Alabama in November 2014 and February 2015, using a combination of seine and backpack Electro-fisher (Smith-Root, Inc.). The Watauga and New rivers are high gradient mountain streams with rocky substrate. Therefore, these cyprinid assemblages consist of species adapted to cold, well-oxygenated and high velocity conditions [15]. Hillabee and Halawakee creeks are low gradient piedmont streams with mostly rocky substrates. Uphapee Creek is a low gradient coastal plain stream and has mostly sand substrate. Therefore, the Alabama cyprinid assemblages consist of species adapted to warm, low velocity conditions, including many species (i.e. Notropis) that prefer sandy habitats [11]. Despite the close geographical proximity of the two North Carolina rivers and the three Alabama creeks that were sampled (figure 1), they have different assemblages associated with the four major river basins in which they drain, and thus represent a robust sampling of the major cyprinid lineages found in the eastern USA [12]. All species that we sampled (table 1), except Semotilus and Clinostomus, are part of a strongly supported clade united by the osteological character of a small opening at the base of the skull known as the open posterior myodome (OPM).

Only adult specimens (i.e. near maximum body size) were retained for analyses to reduce ontogenetic variation. If present, we also surveyed potentially important production sources: algae (scraped from rock surfaces), terrestrial leaves (representing common riparian species), C3 aquatic macrophytes, C4 grasses (from the stream bank) and biofilm (generally from the substrate; electronic supplementary material, table S1). Additionally, we sampled invertebrate taxa that are common prey items of benthic and pelagic cyprinids [14]: Ephemeroptera (Maccaffertium and Isosyncha), Diptera (Chironomidae), Trichoptera (Hydropsyche and Philopotamidae) and Plecoptera (Acronemura), among others (electronic supplementary material, table S1). Cyprinids, prey items and production sources were frozen after collection. In the laboratory, we dissected approximately 5–10 mg of caudal muscle tissue, which was lyophilized until dry (i.e. asymptotic weight), ground into a homogeneous powder and weighed (approx. 1 mg) into tin capsules. Whole invertebrates and subsamples of production sources were prepared in the same way. These materials were analysed for 15N and 13C at the University of Georgia stable isotope laboratory. Cyprinid isotope values were not corrected for lipid content because their C/N ratios (i.e. less than 3.5) suggest that their lipid content is sufficiently low to prevent biases [16]. Furthermore, cyprinid lipid content (estimated from C/N ratios) was similar among species suggesting uniform effects, if any, from lipids [14]. Fishes were measured from the tip of the snout to the end of the hypural plate (standard length, SL) and were identified using keys [11,15]. Additionally, we dissected the entire digestive tract.
Table 1. Data used to assess the relationship between body size and TP among cyprinids: guild designation, relative gut length (RGL), body size (SL; cm) and TP.

| Sample                  | n  | Site     | Guild    | RGL  | SL ± 1.7 | TP ± 1.7 | δ¹⁵N ± 1.7 | δ¹³C ± 1.7 |
|-------------------------|----|----------|----------|------|----------|----------|------------|------------|
| Rhinichthys cataractae | 8  | new      | benthic  | 0.92 | 5.8 ± 1.7| 2.30 ± 1.7| 10.8 ± 0.4| -21.8 ± 1.1 |
| Luxilus coccogenis      | 3  | new      | pelagic  | 0.60 | 7.2 ± 0.3| 1.78 ± 0.3| 9.5 ± 0.2  | -22.1 ± 0.2 |
| Semotilus atromaculatus | 5  | new      | benthic  | 0.94 | 7.9 ± 1.9| 1.83 ± 1.9| 9.1 ± 0.8  | -23.9 ± 0.1 |
| Notropis photogenis     | 4  | new      | pelagic  | 0.65 | 8.6 ± 0.7| 2.02 ± 0.7| 10.0 ± 0.4| -22.1 ± 0.1 |
| Clinostomus funduloides | 8  | new      | pelagic  | 0.64 | 6.1 ± 0.7| 2.06 ± 0.7| 10.1 ± 0.4| -22.6 ± 0.3 |
| Nocomis leptocephalus   | 8  | new      | benthic  | 1.65 | 13.0 ± 2.3| 1.76 ± 2.3| 9.4 ± 0.4  | -23.4 ± 1.3 |
| Nocomis platyrhynchos   | 8  | new      | benthic  | 1.47 | 11.9 ± 4.6| 2.21 ± 4.6| 10.5 ± 0.4| -22.9 ± 0.9 |
| Notropis rubellus       | 8  | new      | pelagic  | 0.94 | 5.6 ± 0.8| 2.01 ± 0.8| 10.0 ± 0.5| -22.5 ± 0.9 |
| Phracobius teretulus    | 8  | new      | benthic  | 0.85 | 7.1 ± 0.5| 2.37 ± 0.5| 10.9 ± 0.4| -18.3 ± 1.1 |
| Pimephales notatus      | 8  | new      | pelagic  | 1.59 | 7.1 ± 1.0| 2.11 ± 1.0| 10.3 ± 0.2| -23.3 ± 0.6 |
| Notropis scabriceps     | 8  | new      | pelagic  | 0.65 | 5.6 ± 0.4| 2.43 ± 0.4| 11.1 ± 0.2| -22.0 ± 0.4 |
| Esoxlossum laurae       | 8  | new      | benthic  | 0.92 | 8.3 ± 1.8| 2.36 ± 1.8| 10.9 ± 0.5| -22.5 ± 1.7 |
| Campostoma anomalum     | 8  | new      | benthic  | 3.27 | 10.6 ± 1.9| 2.11 ± 1.9| 10.3 ± 0.2| -18.7 ± 0.8 |
| Rhinichthys atratus     | 8  | new      | benthic  | 0.88 | 5.4 ± 0.9| 2.50 ± 0.9| 11.2 ± 0.2| -22.3 ± 0.7 |
| Cyprinella sploptera    | 5  | new      | pelagic  | 0.95 | 4.9 ± 0.3| 1.76 ± 0.3| 9.4 ± 0.1  | -22.1 ± 0.1 |
| Luxilus coccogenis      | 6  | Watauga  | pelagic  | 0.60 | 10.9 ± 0.3| 2.41 ± 0.3| 11.4 ± 0.1| -22.3 ± 0.3 |
| Notropis leuciodus      | 6  | Watauga  | pelagic  | 0.65 | 6.3 ± 0.1| 2.38 ± 0.1| 11.3 ± 0.5| -23.5 ± 0.4 |
| Rhinichthys atratus     | 6  | Watauga  | benthic  | 0.88 | 6.5 ± 0.2| 2.01 ± 0.2| 10.4 ± 0.6| -22.8 ± 0.2 |

(Continued.)
We calculated TP using consumer $^{15}$N signatures such that $\text{TP}_{\text{cyprinid}} = (^{15}\text{N}_{\text{cyprinid}} - ^{15}\text{N}_{\text{base}})/2.5 + 1$, where $^{15}\text{N}_{\text{cyprinid}}$ is the mean $^{15}$N ratio for a given cyprinid species, $^{15}\text{N}_{\text{base}}$ is the mean $^{15}$N ratio among potential invertebrate prey, and 2.5 is a generic fractionation factor derived from meta-analyses [18] that has been confirmed as appropriate for cyprinids by comparing the $^{15}$N ratios of cyprinids and their gut contents [19]. We compared TP among the five cyprinid assemblages (i.e. sampling sites) using the aov function, and calculated relative gut length (RGL) as the linear distance from the oesophagus to the anus divided by SL [177].

We tested if RGL could predict TP using the lm function; however, the observed RGL measurements were not normally distributed, so we used the log-transformed values. We also tested if RGL could predict TP using the lm (linear model) function in R based on both the observed and log-transformed values. We tested if RGL could predict TP using the lm function; however, the observed RGL measurements were

| sample                  | n   | site     | guild | RGL | SL    | TP    | $^{15}$N | $^{13}$C |
|-------------------------|-----|----------|-------|-----|------|-------|---------|---------|
| Campostoma anomalum     | 6   | Watauga  | benthic | 3.27 | 10.2 ± 0.4 | 2.04 | 10.4 ± 0.4 | −20.1 ± 0.4 |
| Clinostomus funduloides | 6   | Watauga  | pelagic | 0.64 | 7.2 ± 0.1 | 2.45 | 11.5 ± 0.4 | −21.5 ± 0.5 |
| Cyprinella galactura    | 6   | Watauga  | pelagic | 0.71 | 11.5 ± 0.3 | 2.18 | 10.8 ± 0.4 | −23.5 ± 0.7 |
| Nocomis micropogon      | 6   | Watauga  | benthic | 0.91 | 14.7 ± 0.4 | 1.95 | 10.2 ± 0.7 | −21.2 ± 0.5 |
| Semotilus atromaculatus | 4   | Watauga  | benthic | 0.94 | 10.6 ± 0.4 | 1.89 | 10.1 ± 0.3 | −23.0 ± 1.2 |
| Campostoma pauciradii   | 5   | Halawakee| benthic | 3.27 | 8.1 ± 0.2 | 2.67 | 8.1 ± 2.1 | −29.6 ± 0.9 |
| Ericymba amplanala      | 4   | Halawakee| pelagic | 0.79 | 5.0 ± 0.2 | 3.46 | 10.1 ± 1.0 | −30.6 ± 1.8 |
| Semotilus theoaruanus   | 5   | Halawakee| benthic | 1.12 | 8.0 ± 0.3 | 1.95 | 6.3 ± 0.3 | −27.8 ± 0.6 |
| Hybopsis winchelli      | 3   | Halawakee| benthic | 0.80 | 4.2 ± 0.1 | 3.04 | 9.0 ± 0.7 | −28.7 ± 0.6 |
| Cyprinella gibbi        | 5   | Hillabee | pelagic | 0.69 | 6.3 ± 0.2 | 2.08 | 9.6 ± 0.8 | −24.8 ± 0.7 |
| Campostoma oligolepis   | 5   | Hillabee | benthic | 3.03 | 9.7 ± 0.4 | 1.98 | 9.3 ± 0.2 | −20.9 ± 0.5 |
| Luxilus chryscephalus    | 1   | Hillabee | pelagic | 0.78 | 5.7 ± 0.0 | 1.78 | 8.9 ± 0.0 | −24.8 ± 0.0 |
| Macropodus aestivialis  | 2   | Hillabee | pelagic | 0.97 | 5.9 ± 0.2 | 2.18 | 9.9 ± 2.1 | −23.1 ± 1.9 |
| Notropis stibius        | 5   | Hillabee | pelagic | 0.66 | 6.8 ± 0.1 | 2.47 | 10.6 ± 0.3 | −23.0 ± 0.5 |
| Phenacobius catastomus  | 5   | Hillabee | benthic | 0.95 | 8.0 ± 0.2 | 2.24 | 10.0 ± 0.3 | −21.4 ± 0.3 |
| Pimephales vigilax      | 1   | Uphapee  | pelagic | 1.46 | 5.5 ± 0.0 | 2.66 | 11.1 ± 0.0 | −23.8 ± 0.0 |
| Cyprinella venusta      | 5   | Uphapee  | pelagic | 0.76 | 7.7 ± 0.4 | 1.67 | 14.4 ± 1.6 | −33.4 ± 0.5 |
| Ericymba amplanala      | 3   | Uphapee  | pelagic | 0.79 | 5.9 ± 0.3 | 3.21 | 18.3 ± 0.0 | −21.5 ± 0.5 |
| Lythrurus bellus        | 6   | Uphapee  | pelagic | 0.71 | 5.0 ± 0.2 | 1.84 | 14.8 ± 0.6 | −23.7 ± 0.5 |
| Luxilus chryscephalus    | 6   | Uphapee  | pelagic | 0.78 | 5.5 ± 0.3 | 2.87 | 17.4 ± 0.3 | −23.5 ± 0.7 |
| Macropodus aestivialis  | 6   | Uphapee  | benthic | 0.76 | 4.5 ± 0.1 | 2.96 | 17.6 ± 0.4 | −24.5 ± 0.6 |
| Notropis ammophilus      | 5   | Uphapee  | pelagic | 1.01 | 4.6 ± 0.3 | 2.60 | 16.7 ± 0.4 | −21.5 ± 0.1 |
| Notropis baileyi        | 5   | Uphapee  | pelagic | 0.97 | 5.0 ± 0.3 | 2.98 | 17.7 ± 0.3 | −23.4 ± 0.5 |
| Nocomis leptochephalus  | 3   | Uphapee  | benthic | 1.65 | 5.8 ± 0.5 | 1.87 | 14.9 ± 0.3 | −22.9 ± 0.8 |
| Notropis stibius        | 4   | Uphapee  | pelagic | 0.66 | 6.6 ± 0.3 | 2.19 | 15.7 ± 1.0 | −23.6 ± 0.8 |
| Notropis texanus         | 5   | Uphapee  | pelagic | 0.72 | 4.1 ± 0.2 | 2.89 | 17.4 ± 0.8 | −22.5 ± 0.9 |
| Notropis uranoscopus     | 5   | Uphapee  | pelagic | 0.64 | 5.0 ± 0.1 | 2.46 | 16.4 ± 0.1 | −23.6 ± 0.4 |
| Notropis volucellus      | 5   | Uphapee  | pelagic | 0.74 | 5.2 ± 0.2 | 2.53 | 16.6 ± 1.9 | −22.0 ± 0.8 |
| Pimephales vigilax      | 3   | Uphapee  | pelagic | 1.46 | 5.7 ± 0.2 | 2.98 | 17.7 ± 0.5 | −22.0 ± 0.4 |
| Macropodus aestivialis  | 5   | Uphapee  | benthic | 0.89 | 7.8 ± 0.3 | 2.22 | 15.8 ± 0.4 | −22.7 ± 0.6 |
| Campostoma anomalum     | 3   | Uphapee  | benthic | 3.03 | 6.5 ± 0.4 | 2.32 | 15.1 ± 0.7 | −26.1 ± 0.3 |
Figure 2. Stable isotope (mean ± s.d.) bi-plots representing the food web structure of five cyprinid assemblages: (a) New River, (b) Watauga River, (c) Hillabee Creek, (d) Uphapee Creek and (e) Halawakee Creek.

not linearly distributed, so we only used the log-transformed values for this analysis. To further examine the SL–TP relationship, and take advantage of the tendency for cyprinids to be either benthic or pelagic [12], we coded species as either ‘benthic’ or ‘pelagic’ and compared TP, SL and RGL between these two groups using t-tests in R. Designations followed Hollingsworth et al. [12], except for N. ammophilus and N. amplamala, which were coded as ‘pelagic’ because they were consistently sampled in association with pelagic species, usually as large mixed species schools or aggregations. Although we restricted sampling to adult specimens, to test the generality of the potential size difference between guilds, we compared the SL of benthic (n = 21) and pelagic (n = 62) species based on the maximum body sizes reported by Boschung & Mayden [11].

3. Results

Production sources were well differentiated in the five study streams (electronic supplementary material, table S1; figure 2). Invertebrates were associated with different production sources in each stream based on their $^{13}$C signatures. For example, they were associated with biofilm in the New and Watauga rivers, with algae in Hillabee Creek, and detritus in Halawakee Creek (figure 2). Cyprinids, however, had stable isotope ratios that were associated with those of invertebrates in all five streams based on $^{13}$C (figure 2). We sampled a total of 50 populations representing 15 genera and 38 species of cyprinid,
Figure 3. TP among the five cyprinid assemblages (a). Relationship between observed (b) and log transformed (c) body size and TP among cyprinids. Comparison (mean ± s.d.) of maximum SL based on published maximum body sizes (d), TP (e) and RGL (f) between benthic and pelagic cyprinids. Different letters above bars denote statistical significance (p < 0.05).

35 species of which are part of the OPM clade (approx. 14% of the OPM clade; table 1) [12]. Cyprinid assemblages (i.e. streams) had different TP ($F = 3.9$, $p = 0.0074$; figure 3a). Cyprinids in Halawakee Creek had significantly higher TP than cyprinids in the New River ($p = 0.019$; figure 3a). There were also non-significant trends when comparing cyprinid TP in Watauga River and Halawakee Creek ($p = 0.059$) and Uphapee Creek and New River ($p = 0.055$). Cyprinid body size significantly predicted TP using both the observed ($R^2 = -0.222$, $F_{1,49} = 13.97$, $p < 0.001$; figure 3b) and log-transformed ($R^2 = -0.254$, $F_{1,49} = 16.66$, $p = 0.00016$; figure 3c) values such that they had a negative relationship. The smallest cyprinids were approximately half a TP higher in the food chain than the largest cyprinids based on the best-fit line (figure 3b). This relationship was also present among benthic species ($R^2 = 0.457$, $F_{1,21} = 15.96$, $p < 0.001$), but not among pelagic species ($R^2 = 0.089$, $F_{1,27} = 2.55$, $p = 0.123$). Log-transformed RGL did not significantly predict log-transformed TP ($R^2 = 0.0098$, $F_{1,49} = 0.48$, $p = 0.49$). Benthic species had, on average, significantly larger observed body sizes than pelagic species ($T = 3.06$, $p < 0.005$).
4. Discussion

Contrary to the pattern seen across fishes of an increase in TP with body size, we demonstrate that TP is negatively correlated with body size in cyprinids among five diverse assemblages across four major river drainages. This may be due to strongly clade-specific patterns of body size and diet [12] such that the two traits are coevolved with respect to specialization along the benthic–pelagic axis. Several species-poor clades consisting of benthic species such as Noemis, Campostoma and Phenacobius, among others consume prey directly from, or just above, the substrate and frequently consume biofilm, detritus and algae either intentionally or inadvertently [12]. These materials are depleted in $^{15}$N relative to invertebrates and consequently higher rates of omnivory results in lower consumer TPs [21]. By contrast, several speciose clades consist of pelagic species such as Notropis, Cyprinella and Luxilus, among others that feed either from the water surface or from the water column via drift [12,14]. Therefore, these species tend to be less omnivorous because they are unlikely to inadvertently consume biofilm, detritus or algae while foraging. Higher degrees of carnivory result in higher TPs among these species [21]. Benthic and pelagic species also tend to be different sizes such that benthic species are larger (figure 3d).

Selection pressures that lead to distinct large-bodied benthic and small-bodied pelagic lineages of cyprinids have resulted in body size and TP being coupled during their evolutionary history. The negative relationship between body size and TP is in contrast to general predictions about body size in trophic networks. Body size often increases with TP, either because consumers must eat more nutrient-rich foods to satisfy increased metabolic demands [4] or eat larger prey due to relaxed gape constraints [10]. It is unclear how cyprinids subvert these physiological and mechanical constraints, but we propose that mechanical constraints (i.e. gape) may not be a particularly important limitation because many common invertebrate prey items such as dipterans, ephemeropterans and trichopterans are small [22], and therefore unlikely to impose significant gape limitation among cyprinids. Furthermore, teleost intestines do not produce cellulose to digest plant cell walls [23], and although microorganisms produce these in many teleost guts, such symbiotic production is minimal in cyprinids [24,25]. However, cyprinids use two anatomical modifications to facilitate digestion of plant matter. First, cyprinids have modified pharyngeal arches that assist with prey processing. Mechanical processing (i.e. grinding and tearing) by the pharyngeal arches ruptures plant cell walls prior to digestion [25,26]. Secondly, long digestive tracts increase passage time through the gut thereby increasing exposure to digestive enzymes [17]. In combination, pharyngeal processing and long digestive tracts provide a means for cyprinids to subvert the physiological constraints that generally result in a positive relationship between body size and TP. Indeed, several groups of benthic cyprinids (e.g. Noemis and Campostoma) are capable of assimilating nutrients from algae [17,27] and thus may not be particularly nutrient limited by their lower quality food resources. Although benthic cyprinids had longer RGL than pelagic cyprinids, there was not a relationship between RGL and TP. This may be because few cyprinids have intermediate RGL such that cyprinids generally have either poorly developed or well-developed ability to assimilate nutrients from plant material. Additionally, larger cyprinids may avoid metabolic demands by simply eating more, or by saving energy compared with pelagic species by avoiding prolonged swimming in open water [28].

The Cypriniformes as a whole exhibit a weak positive relationship between body size and TP [10]; however, our results suggest that scale (e.g. assemblage, order, global) is important when assessing the relationship between body size and TP. Although there are large-bodied piscivores such as pikeminnows (Ptychocheilus) in western North America, most cyprinid assemblages lack representatives from this top trophic level. For example, in eastern North America, where Nearctic cyprinid diversity is concentrated in the OPM clade (more than 250 species), the top predators are drift- or surface-feeding insectivores [11,12]. Therefore, the patterns observed in the four major river basins studied here are likely to be ubiquitous among cyprinids at the assemblage scale. Additionally, negative relationships between body size and TP may occur in many cyprinid assemblages worldwide, because the dominant large-bodied species of cyprinids in Africa and Asia are benthic grazers such as Labeo, Tor and Catlocarpio [29–32]. Our assemblage-based approach is more likely to elucidate local trends than global approaches that pool species into broad taxonomic groups [10], where ecological processes may drive unique relationships.
among traits. Additionally, global approaches are likely to mask ubiquitous local trends by placing emphasis on taxa that do not ecologically characterize the group, such as large, predatory taxa among cyprinids. Lastly, accessing patterns at various evolutionary and geographical scales may elucidate potential mechanisms that result in associations between body size and TP. For example, some lineages such as Nocomis are more diverse in higher latitude temperate streams (i.e. the North Carolina streams) than in lower latitude sub-tropical streams (i.e. the Alabama streams) [11,15], and thus evolutionary history and species distributions are likely to influence the relationship between body size and TP.

5. Conclusion

We demonstrate that, contrary to general expectations, there is a negative relationship between body size and TP among cyprinids at the assemblage scale. Our results suggest that scale is important when accessing relationships between body size and TP such that this relationship differs at global and assemblage scales. Highly clade-specific patterns in body size and diet among cyprinids [12,14] have resulted in a counterintuitive negative relationship between these variables. This relationship is probably due to coevolution such that body size and TP are functionally linked. For example, larger bodies are necessary to accommodate the long digestive tracts required by herbivorous and highly omnivorous cyprinids to efficiently breakdown the cellulose-rich foods they consume. Therefore, covariation in these traits probably reflects specialization along the benthic to pelagic axis, which is perhaps the fundamental axis of diversification among fishes [33–36].

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