Optimal response to habitat linkage of local fish diversity and mean trophic level

Jun Xu,*1 Huan Zhang,1,2 Yongjiu Cai,3 Jorge García Molinos,4,5 Min Zhang6
1Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology of China, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, P. R. China
2Institute of Biology/Aquatic Ecology, Ecology Building, Lund University, Lund, Sweden
3Key Laboratory of Watershed Geographic Sciences, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing, P. R. China
4Center for Environmental Biology and Ecosystem Studies, National Institute of Environmental Studies, Tsukuba, Ibaraki, Japan
5Arctic Research Center, Hokkaido University, Sapporo, Hokkaido, Japan
6College of Fisheries, Huazhong Agricultural University, Wuhan, P. R. China

Abstract

Spatially segregated ecosystems are frequently subsidized by cross-habitat linkages, but the extent to which the functional links between habitats influence local community attributes, such as consumer and food web structure is still poorly understood. Using the bidirectional linkage between benthic and pelagic habitats in floodplain lakes, we address this important question by looking for evidence of an optimal extent of habitat linkage supporting maximum taxonomic richness and mean trophic level. We then ask if there are significant changes in these local community attributes between historical and current communities, and if these reflect the history of species loss resulting from the intense human alteration of these lakes. We found a strong optimal response of maximum richness and mean trophic level along the pelagic-benthic gradient, both across and within individual lakes. This is consistent with the expectation of optimal resource availability along the habitat linkage gradient supporting more and taxonomically richer communities. Comparison between historical and current assemblages revealed a significant decrease in the optimal linkage for maximum richness in response to the history of species loss, but not for maximum mean trophic level, probably a response to the increased habitat homogenization and enhanced productivity caused by the recent history of nutrient-enrichment and habitat alteration. Our study provides strong evidence of high diversity and trophic level occurring at intermediate levels of coupling between pelagic and benthic resources, suggesting assemblage reliance on multiple production sources, and offers novel insight into the responses of this relationship to species loss due to human activities.

Spatially segregated ecosystems are frequently subsidized by cross-habitat linkages, persistent or recurrent processes and attributes connecting ecosystems across ecological levels (Polis et al. 1997; Schindler and Scheuerell 2002; Lamberti et al. 2010; Sawyer et al. 2011). They are ubiquitous in nature, and involve the movement of species, materials and energy flow across ecosystem boundaries with profound structural and functional implications for the subsidized systems (Polis et al. 1997; Schindler and Scheuerell 2002). Understanding the mechanisms governing, and implications derived from, these linkages has been an area of intense research over recent years (Rosenberger et al. 2008; Lamberti et al. 2010; Sawyer et al. 2011). Many knowledge gaps remain, especially in the context of environmental change and ecosystem conservation (Reinhardt et al. 2013; Tunney et al. 2014).

Food webs based on energy flow provide estimates of species’ realized resource use and trophic position, representing the resource and energy transferred through the food web among consumers (Post 2002). Accounting for energy pathways between linked habitats is crucial given that the trophic position of any species is based on all available energy sources (Eloranta et al. 2015; Ziegler et al. 2015). Although considerable progress has been made in understanding the effects of trophic interactions on ecological
processes and food web dynamics (Carpenter et al. 1987; Polis et al. 1997), our understanding of how habitat linkages influence trophic structures in natural systems is still limited (Olds et al. 2012). The implications of functionally linked habitats for some community attributes, such as consumer diversity and food web structure, are particularly poorly understood (Wardle et al. 2004; Gagic et al. 2011). Linkages between different habitats facilitate increasing energy availability by incorporating more basal resources (Brookes et al. 2005; Burdon and Harding 2008). Therefore, local species diversity and trophic position may have a unimodal relationship with benthic–pelagic coupling. This relationship is expected to arise if energy is maximized at intermediate levels of coupling and if these properties are restricted by the partitioning of energy among species (i.e., the energy limitation hypothesis; Post 2002; Reinhardt et al. 2013).

Lakes are good natural systems to study these questions because of the strong bidirectional linkage between benthic and pelagic habitats, for which key ecological processes are well understood (Vadeboncoeur et al. 2002; Vadeboncoeur et al. 2003). Pelagic habitats are relatively homogeneous and inhabited predominantly by planktonic organisms, while benthic habitats are heterogeneously associated with diverse resources from not only benthic algae, macrophytes, and allochthonous terrestrial inputs, but also suspended or deposited plankton from pelagic habitats (Dermott et al. 1977; Strayer and Likens 1986; Kajak 1988; Covich et al. 1999). Therefore, mobile omnivorous consumers, e.g., fishes, can benefit from energy available in coupled pelagic and benthic food webs (Threlkeld 1994). Although the energy pathways in benthic food webs are arguably more complicated than those of pelagic food webs, the linkage between the two habitats suggests that responses of community-level properties, such as taxonomic richness and trophic position, to resource availability should vary along the habitat linkage gradient. Because many species of fishes in flood plain lakes are omnivorous, with some species moving across pelagic and benthic/littoral regions and feeding on resources from both habitats (Xu et al. 2012; Zhang et al. 2013; Xu et al. 2014), we expected that the taxonomic diversity and trophic positions should change along the pelagic-benthic linkage gradient. This opens up the possibility of searching for the existence of optimal values along the linkage gradient supporting maximum taxonomic diversity and mean trophic level.

Lakes and their watersheds are typically areas of intense human activity, which often has resulted in the intense decline of the diversity of fish species (Rahel 2002; Jones and Brett 2014). Such changes also result in structural community alterations across trophic levels or along the benthic-pelagic linkage gradient (Petchey et al. 2004; Baiser and Lockwood 2011). In addition, the outcome of a species extinction is also influenced by the trophic position of the species in the food web (Pimm 1980), and on the resources it utilizes (Petchey et al. 2004; Eklöf and Ebenman 2006; Baiser and Lockwood 2011). Thus, the order in which species are lost is crucial in multi trophic-level systems, while such changes in trophic structure may alter the flow of energy through the food web, change food-web stability, or both (Petchey et al. 2004; Eklöf and Ebenman 2006; Baiser and Lockwood 2011). However, much less attention has been paid to the effects of species loss on the alterations of community and trophic structure along habitat linkage gradients. Fish assemblages in lakes have been impoverished over recent decades as a result of intense anthropogenic activities (Xu et al. 2012; Zhang et al. 2013; Xu et al. 2014), offering an ideal opportunity to study how patterns of change in taxonomic richness and mean trophic level across the benthic-littoral linkage gradient have changed over time as a result of local species extinctions under human impact.

To test these hypotheses, we measured the historical (1980–1995) and current (2008–2013) taxonomic richness of benthic and pelagic fish assemblages and trophic levels of constituent species along the benthic-pelagic linkage gradient for 22 flood plain lakes located within the middle and lower reaches of Yangzi River in southeast China (Fig. 1). These relatively large and shallow lakes (Supporting Information Table S1) are ideal for the purposes of this study because of their many rich and complex linkage pathways between benthic and pelagic habitats. By using a broad range of species and lake ecosystems, we tried to make generalizations about the importance of pelagic-benthic gradient supporting diverse species and function, which may have important implications for our understanding of ecosystem processes and dynamics.

Materials and methods

Fish assemblage data

Historical (1980–1995) fish assemblages from each of the 22 study lakes (Fig. 1; Supporting Information Table S1), were compiled based on presence/absence data from reported field surveys in the literature. To ensure good quality of the dataset, we excluded those studies with poor sampling efforts (i.e., survey time less than one year), and pooled the data where more than one survey was available for the same lake. Current fish assemblages are based on data from field surveys conducted between 2008 and 2013. fishes were caught by fish trap, gill net and trawl net according to the specific methods used in historical surveys for each lake. Each lake was sampled by randomly assigning 4–6 transects for every 20 km² of lake surface area. Fishes were collected by volunteer fishermen as part of routine commercial fishery, compliant with local fishery regulations. Each lake was sampled during the summer and autumn, and was visited at least twice during the studied period (i.e., a minimum of four surveys per lake). This procedure was assumed to
control for the intra-annual variation in fish distribution. To ensure consistency among historical and present-day surveys, abundance data from the surveys was converted into presence-absence data. Abundance data is also likely to be prone to bias introduced by variability in the catchability of fishes by the gear types. Further, some species may be efficient pelagic-benthic connectors and not equally available to the same gear. Finally, fluctuations in abundance of individual species may result from changes in fish distributions, differing from year to year due to changes in lake morphology or food availability. The taxonomy of both historical and current field records was checked using recent taxonomical monographs (Chen 1998; Chu et al. 1999; Yue 2000). Despite the difficulties in comparing historical and present-day surveys (i.e., the exact replication of historical surveys is impossible), we believe our efforts to keep consistency should allow comparison of the two data sets.

Trophic level, benthivory and richness

Trophic level and the reliance on benthic and pelagic resources, i.e., degree of benthivory, of each species were first estimated by gut content analysis following Zhang et al. (2013). Though Zhang et al. used both gut content analysis and stable isotope analysis, here we relied only on gut content analysis because stable isotope information for some fishes, present in historical assemblages but absent from current assemblages, was not available, whereas gut content information existed for all species from the literature. Comparison of our trophic level and benthivory estimates with those derived from the combined method (i.e., gut content plus stable isotopes) for the 46 fish species common to both studies showed nevertheless a strong statistically significant correlation for both metrics (trophic position, \( r^2 = 0.794, p < 0.001 \); benthivory, \( r^2 = 0.665, p < 0.001 \)), indicating that our approach gives valid estimates for the studied fish species and lakes.

Trophic level is a basic metric collected for ecological studies with a wide range of applications. It describes the position of a consumer between primary producers and predators throughout the food web and helps define its role in the energy transfer within an ecosystem. Following Winemiller (1990) and Vander Zanden et al. (1997), we first calculated the trophic level of each prey organism based on the percentage of weight contributed by each food item and the percentage of the total number of prey organisms to the percentage of weight (Supporting Information Table S2). We then calculated the trophic level (TL) for each fish species using

![Fig. 1. Locations of studied lakes. Description of the lakes is given in Supporting Information Table S1, with numbers in the figure corresponding to the IDs in the table.](image)

Xu et al. Optimal response to habitat linkage
Benthivory complements trophic level as a synthetic metric of a species’ resource utilization, which provides an indicator for benthic/littoral energy mobilization based on the estimated reliance on benthic resources. It reflects the position of a species along the pelagic and benthic linkage gradient ranging from 0 to 1. For example, a value of 0.75 in benthivory reflects a 25/75 percent energy utilization derived from pelagic and benthic resources (Vander Zanden and Vadeboncoeur 2002). Estimates on the dietary contribution of benthic energy sources towards each consumer (Supporting Information Table S2) were first conducted based on expert judgement and our knowledge on the ecology of these lakes. In this study, we interpret benthic resources as any resource that is consumed from the benthos, independently of this being autochthonous or allochthonous in origin. For example, in these lakes, most of which are eutrophic or even hypereutrophic (Supporting Information Table S2), deposited planktonic material represents a main benthic energy source though its pelagic in origin (Xu et al. 2014). Conversely, direct interception of the same material from the water column by, for example, filter-feeding organisms was considered a pelagic energy source. We then estimated benthivory for each fish species as the relative contribution of different prey items to their diets using the formula $B = \sum (W_i \times B_i)$, where $W_i$ and $B_i$ represent respectively the weight contribution and benthivory of the $i$th prey organism. We computed mean estimates of trophic level and benthivory for each species based on those calculated for multiple specimens collected from lakes in the region (Zhang et al. 2013).

We calculated the taxonomic richness and mean trophic level along the pelagic-benthic gradient using a moving window algorithm (Fig. 2, Booth et al. 2006). Taxonomic richness and trophic level were recursively estimated at 0.01 benthivory increment steps across the pelagic-benthic gradient

\[ TL = \sum (W_i \times TL_i) + 1, \]  
where $W_i$ and $TL_i$ denote respectively the weight contribution and trophic level of the $i$th food item [see Zhang et al. (2013)].
linkage gradient (0 ≤ benthivory ≤ 1), from the richness and trophic level values of all species observations falling within a given window centered at each step. We set the window width \( (b_w) \) as twice the standard deviation of the mean values of species benthivory from our species pool (i.e., \( b_w = 2 \times 0.14; \) see Supporting Information Table S3). Therefore, for any given point \( b_c \) along the benthivory gradient, its corresponding taxonomic richness and mean trophic level were calculated from the pseudo-assemblage comprising those species falling within the range \( b_c \pm (b_w/2) \). Note that some degree of window overlap existed involving the repetition of some species between neighboring windows. This procedure controls for the intra-annual variation in resource use along the pelagic and benthic linkage gradient, characteristic of local fish communities in these lakes (Xu et al. 2012; Xu et al. 2014), thus improving the signal to noise ratio. Taxonomic richness was therefore assessed as the number of species in each pseudo-assemblage, and its corresponding mean trophic level calculated by dividing the sum of trophic levels for each species by the taxonomic richness. High mean trophic level in a pseudo-assemblage thus reflects high food chain length per species unit, i.e., the height of the food web from the basal to the maximum trophic level (Post 2002).

**Statistical analysis**

To detect the optimal benthivory that supports maximum taxonomic richness and mean trophic level (response variables), we first used a locally weighted scatter smoother (Cleveland 1981), to fit a smooth curve (span = 0.75) on these variables using benthivory as the predictor variable. The optimal values of taxonomic richness and mean trophic level were then obtained by finding the benthivory value that maximized the fitted curve. The span controls the size of the window neighborhood. For a span < 1, the neighborhood includes a proportion of the points equal to the span and these have tricubic weighting. Sensitivity analysis on this parameter showed nevertheless high consistency of results to alternative span choices (Supporting Information Fig. S1).

To test if trophic level and benthivory affect probability of species presence, we used generalized linear mixed models (GLMMs (Bolker et al. 2009)), using presence/absence of each historical species in current lake assemblages as response variable, and species trophic level and benthivory as predictors. The model predicts the probability of species presence (bounded between 0 and 1) as a function of the predictor variables. We also introduced a site (lake) effect as a random predictor variable to avoid pseudoreplication by introducing correlation among species (Hurlbert 1984). The random effects may also account for any other unknown factors that influence the probability of occurrence of all species in a lake, such as differences in size and nutrient content amongst sites.

Finally, to analyze the links between species loss and mean species trophic level and benthivory, we used recursive partitioning to draw a decision tree by analysis of variance (Therneau and Atkinson 1997). This technique allowed us to group species extinction frequency (i.e., the number of times a historical species was absent from present lake assemblages) as a function of their benthivory and trophic level. The complexity parameter associated with the smallest cross-validated error was set as 0.05 to avoid overfitting.

All statistical analyses were conducted in R 3.1.0 (R Development Core Team 2014) using the built-in functions and those in the packages reshape2 (Wickham 2007), lme4 (Bates et al. 2011), sjPlot (Lüdecke 2015), rpart (Therneau et al. 2015) and ggplot2 (Wickham 2009).

**Results and discussion**

**Optimal responses along the benthic-pelagic gradient**

A total of 93 species were recorded from the 22 lakes over both study periods, spanning a wide range of benthivory and trophic positions (Fig. 2A; Supporting Information Table S3). Mean (+ standard deviation) benthivory and trophic positions were 0.648 ± 0.225 and 2.947 ± 0.488. Detection of the optimal response by mean trophic level and taxonomic richness along the pelagic-benthic gradient indicated that, across lakes (i.e., regional species pool data), a maximum richness of 31 species was attained at an optimal benthivory value of 0.68 (i.e., resource reliance of 68% and 32% from benthic and pelagic pathways; Fig. 2B), while the maximum mean trophic level was 3.24, corresponding to an optimal benthivory of 0.59 (Fig. 2C). The same analysis applied to individual historical and current lake assemblages showed similar clear patterns of optimal responses for both parameters along the habitat linkage gradient (Fig. 3).

The importance of energy or resource availability in explaining variation in local diversity and higher trophic species is a long-standing debate in ecological theory (Elton 1927; Hutchinson 1959; Rosenzweig 1971; Oksanen et al. 1981; Post 2002). Several hypothesis have been proposed as an explanation of the productivity-diversity paradigm. The competitive exclusion hypothesis (Grime 1973; Huston 1979; Tilman 1982) assumes a unimodal “hump-backed” relationship between diversity and productivity (or rate of energy supply), where diversity increases first with productivity up to a maximum for intermediate values, then declines in highly productive environments. Niche competition in heterogeneous environments is frequently invoked as an explanation of this pattern, by which the antagonistic selection among species facilitates high diversity among niches within a heterogeneous environment. At low productivities the number of species is limited by stress and lack of resources, while at high productivity increased competition (Grime 1973), a decreased heterogeneity of limiting resources (Huston 1979; Tilman 1982) or both reduce again the number of species that can coexist. The energy-richness hypothesis (Wright 1983) is based instead on a monotonically positive
relationship. Under the assumption that energy limits the number of coexisting individuals, increasing productivity is expected to sustain more species with enough individuals to form viable populations, hence less vulnerable to extinction by disturbance (Pimm et al. 1988; Lande 1993; Ricklefs 2012). This hypothesis is also used in food web theory to explain patterns between energy availability and food-web structure (Pimm 1982), where higher number of trophic levels are expected under increasing basal productivity because energetic inefficiencies associated with trophic transfers reduce the amount of energy available to support each subsequent trophic level (Post 2002).

Our results could be explained in principle by either or both of these hypotheses if resource heterogeneity (competitive exclusion hypothesis), resource availability (energy-richness hypothesis), or both were maximized at intermediate levels of coupling between both habitats across and within lakes. This situation could promote more diverse and potentially trophically complex assemblages, i.e., more consumer species exploiting different resources resulting in an increased energy transfer up the food web.

Because of mobility and omnivory, fishes effectively link these two ecological systems by participating in both benthic and pelagic habitats (Vander Zanden and Vadeboncoeur 2002). Benthic habitats are nevertheless highly heterogeneous and complex compared to pelagic habitats, and provide more diverse resources to consumer communities. They provide nursery habitats for juveniles of many fish species, and a highly heterogeneous habitat template including swamps, grasses beds, muddy or sandy sediments (Lodge et al. 1988; Schindler and Scheuerell 2002). This is reflected in our results by both taxonomic diversity and mean trophic level distributing non-normally (Shapiro-Wilk normality test, $p < 0.0001$ for diversity and $p < 0.05$ for trophic levels), with a strong negative skewness along the benthivory gradient (Fig. 2); indicative of higher productivity of benthic compared to pelagic habitats. This characteristic was consistent across periods and individual lakes (Fig. 3). These results suggest that benthic habitats in these shallow and well-mixed flood

---

**Fig. 3.** Optimal responses of (A, B) taxonomic richness and (C, D) mean trophic level along habitat linkage gradient (i.e., from pelagic to benthic resource coupling measured as benthivory) for pseudo-assemblages created from (A and C) historical and (B and D) current fish assemblages in our studied lakes. Pseudo-assemblages were created in the same way as for Fig. 2.
plain lakes provide a more rich and heterogeneous energy source that sustains more diverse and complex assemblages (France 1995; Hecky and Hesslein 1995), and are indicative of the importance of energy pathways from benthic habitats to the whole-lake food web complexity.

**Responses to species loss**

Between periods, the taxonomic richness of historical assemblages ranged from 26 to 76 while that of current assemblages was between 7 and 54 (Supporting Information Tables S4, S5), corresponding to a significant decrease in richness

---

**Fig. 4.** Comparison of historical and current assemblage metrics. Box plots for historical and current assemblage (A) overall taxonomic richness and mean trophic level (MTL; B) and maximum (D) taxonomic richness (MTR) and (F) mean trophic level (MMTL) at which corresponding (C, E) optimal benthivory values where registered for each lake. Significant differences between historical and present assemblages are indicated by the corresponding p-values within the panels. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]
(Fig. 4A), though mean trophic level remained stable (Fig. 4B). Interestingly, these patterns were also reflected in a statistically significant decrease of the maximum taxonomic richness and its corresponding optimal benthivory for current lake assemblages (Fig. 4C,D), while the maximum mean trophic level and optimal benthivory remained unchanged (Fig. 4E,F). These results suggest some degree of robustness or stability of mean trophic level against species loss in these lakes. A characteristic that was further supported by the results from the GLMMs, which revealed a strong negative relationship between probability of presence of a species in a lake and benthivory ($p < 0.0001$; Fig. 5A), but not with trophic position ($p = 0.06$; Fig. 5B). This relationship suggests that species with high benthic resource reliance were more sensitive to extinction than those with high trophic level (see Supporting Information Figs. S2, S3 for lake individual responses). The absence of a significant relationship between mean trophic level and species loss (which still bordered significance) was unexpected as higher extinction risk is frequently associated with the longer generation times, relative rarity of resting stages and small population sizes that characterizes high trophic level species (Pimm et al. 1988; Lande 1993; Eklöf and Ebenman 2006). Furthermore, because they depend on species occupying lower trophic levels, they are also at risk of extirpation through secondary extinction (Pimm et al. 1988; Lande 1993; Eklöf and Ebenman 2006).

Decision tree analysis (Fig. 6) further supported these results, showing that trophic level discriminated for low frequency of extinction in these lakes, corresponding to basal species (trophic level $<2.52$), while benthivory reliance (0.74) discriminated for high extinction frequency (twice as much species from the low frequency group). Intermediate species are usually multi-pathway omnivores (preying upon multiple trophic levels and resources), and are widespread and common, providing high trophic complementary and redundancy (Zhang et al. 1999; Zhang et al. 2013). Further, the removal of intermediate trophic level species may change patterns of energy flow by modifying omnivory, but may otherwise not change significantly the mean trophic level at the optimal benthivory (Xu et al. 2012; Xu et al. 2014). Since much of the productive benthic habitat is nearshore, in the littoral zone, benthic habitats are more exposed to the direct effect of anthropogenic impacts (Zhang et al. 1999; Cai et al. 2012). Human impacts are multiple in these lakes due to drastic land use change, acceleration of lake shore urbanization, disruption of their hydrological network, and nutrient enrichment (Zhang et al. 1999; Zhang et al. 2013). These human activities have strongly modified benthic littoral habitats in our study lakes (Xu et al. 2012; Xu et al. 2014), on which a majority of fish species depend (Fig. 2). Under the theories we have explored, the observed significant decrease in richness and relative insensitivity of mean trophic level could be explained by homogenization of benthic littoral habitats coupled with increased productivity associated with nutrient enrichment. Such a relationship may occur if competitive exclusion is intensified by a reduced number of niches, limiting the number of intermediate consumer species, while productivity is yet enhanced and allows existing trophic levels to persist. Nevertheless, structural changes in these food webs are not as much driven by the loss of top consumers (Pimm 1980; Post

**Fig. 5.** Probability of species presence as a function of species benthivory and trophic level. Relationship between the probability of species being present in any given lake and (A) its benthivory and (B) trophic level as predicted by the generalized linear mixed models fitted on each individual lake (thin colored lines) and the overall data set (thick black line with shaded 95% confidence intervals).
2002), but rather of intermediate-level benthivorous species. Such a mechanism has received comparatively much less attention in the literature and stresses the importance of using complementary food web metrics to capture the multiple complex effects of species extirpations on trophic structure.

Taken together, our results provide novel insight into the complex relationships governing energy-diversity-trophic dynamics in natural systems and demonstrate the importance of studying them in the context of existing linkages between different habitats, particularly for the management and conservation of ecosystems increasingly subject to alteration by human activities.

**References**


![Fig. 6. (A) Species loss frequency as a function of benthivory and mean trophic level, and (B) decision tree showing the resulting significant grouping of species. The size of points represent the species loss frequency in the local lake assemblages and the leaf values represent the mean number of species loss. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]]


**Acknowledgments**

For data compiling and sampling we wish to thank Yingying Chen and Yi Yang at the Huazhong aquaculture Univ., and Xiaohu Huang at Hubei Univ. We also thank local volunteer fishermen, who provided invaluable help in sampling. We thank two anonymous reviewers, whose insightful comments contributed to improve substantially the manuscript. This research was supported by the National Natural Science Foundation of China (Grant No. 31370437), and the Water Pollution Control and Management Project of China (Grant No. 2012ZX07101-001). There are no actual or potential competing financial interests. The funders had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Submitted 9 September 2015

Revised 25 November 2015; 1 March 2016

Accepted 24 March 2016

Associate editor: Stephanie Hampton