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Hydrologic habitat preferences of select southeastern USA fishes resilient to river ecosystem fragmentation

Andrew L. Rypel[1]* and David R. Bayne[2]

[1] *Biology Department, The University of Mississippi, USDA Forest Service Stream Hydrology Lab, 1000 Front Street, Oxford, MS 38655, USA*
[2] *Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, AL 36849, USA*

ABSTRACT

Large-scale habitat preferences of riverine taxa are not always revealed by examining community data. Here, we show how lipid and growth can be used to evaluate hydrologic habitat preferences of fishes resilient to river fragmentation (i.e. species that can tolerate river fragmentation by dams, but not collapse). Lipid content was examined for seven fishes in a major southeastern USA reservoir and its largest lotic tributary over the 5 years. Controlling for effects of sex, size and year of collection, largemouth bass, spotted bass and black crappie had significantly higher lipid in lentic habitat. Conversely, channel catfish and freshwater drum had significantly higher lipid in lotic habitat. There were no significant differences in lipid of bluegill and blacktail shiner between hydrologic habitat types. Fish growth produced concordant results as largemouth bass and spotted bass had significantly faster growth in lentic habitat, whereas channel catfish and freshwater drum had significantly faster growth in lotic habitat. We were also able to document a synchronous spike in lipids of these species in both habitat types during a major drought. We surmise that the spike was driven by enhanced primary production, predator-prey concentration and possibly also reduced reproduction during intense drought. Two conclusions are drawn from this study as a whole. First, long-term lipid and growth observations hold promise for evaluating ecological effects of droughts over long time spans. Second, population characteristics are excellent indicators of habitat preferences and could be used more broadly to elucidate how organisms react to river ecosystem fragmentation and restoration initiatives.

KEY WORDS climate change; dams; flow; food web; predation; production; species requirements; water reallocation

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INTRODUCTION

Hydrology is the fundamental driver of the structure and function of riverine ecosystems (Poff *et al*., 1997; Galat and Lipkin, 2000; Pringle, 2001; Rypel *et al*., 2009). However, rivers worldwide have been extensively fragmented by dams such that the majority of rivers in the northern hemisphere are now severely fragmented (Dynesius and Nilsson, 1994), and only 42 high-quality, free-flowing rivers remain in the conterminous USA (Benke, 1990). One of the foremost consequences of river ecosystem fragmentation of this scope has been an overall thinning of aquatic biodiversity (Richter *et al*., 1997; Naiman *et al*., 2002; Xenopoulos and Lodge, 2006). An overwhelmed percentage of the most severely endangered species across the world are aquatic, many are riverine (Ricciardi and Rasmussen, 1999; Hughes *et al*., 2005) and declines of taxa have been traced to the proliferation of dams (Bain *et al*., 1988; Freeman *et al*., 2005; Matthews and Marsh-Mathews, 2007; Taylor *et al*., 2008).

Understanding hydrologic habitat preferences of riverine taxa is essential to conservation and management of these species (Orians and Wittenberger, 1991; Pringle *et al*., 2000; Pringle, 2001). The common mode for delineating riverine habitat preferences has been by analysing community data in relation to habitat characteristics (Jowett and Richardson, 1995; Layzer and Madison, 1995; Lamouroux *et al*., 1999; Newcomb *et al*., 2007; Knight *et al*., 2008). However, community data alone can be misleading when delineating habitat requirements for resilient riverine species.

When hydrologic connectivity between river segments has been compromised, resilient organisms are often relegated to sub-optimal environments from which they cannot emigrate (Pringle *et al*., 2000; Pringle, 2003; Taylor *et al*., 2008). Baldcypress trees (*Taxodium distichum*) exemplify this problem. This species cannot recruit in the stable hydrologic conditions of southern USA reservoirs (Keeland and Young, 1997). Thus, stands of old baldcypress trees in reservoirs do not reflect a preference or requirement for reservoir habitat as might be inferred from presence–absence data alone. Instead, these stands resulted from natural flow conditions prior to reservoir creation that promoted recruitment (Keeland and Young, 1997). While this extreme example is of a tree, similar patterns hold for mobile poikilotherms. In southern USA Rivers, freshwater drum (*Aplodinotus grunniens*) is a common component of both river and reservoir fish communities (Swingle, 1954), but in reservoir environments experience stunted growth rates and reduced condition factors (Rypel *et al*., 2006). Likewise in Bahamian

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* Correspondence to: Andrew L. Rypel, Biology Department, The University of Mississippi, USDA Forest Service Stream Hydrology Lab, 1000 Front Street, Oxford, MS 38655, USA. E-mail: andrewrypel@yahoo.com

tidal creeks fragmented by road crossings, gray snapper (*Lutjanus griseus*) can be highly abundant despite a lack of recruitment, mass parasitism by trematodes, stunted growth rates and extremely low levels of secondary production (Valentine-Rose *et al*., 2007; Rypel and Layman, 2008). Thus, resilient organisms are often present in fragmented ecosystems, but this is not necessarily indicative of optimal habitat.

For resilient taxa, energy storage and growth might be more integrative proxies of habitat quality than community data alone. Lipid levels vary widely across organisms with different life histories, but are generally a good composite measure of an individual's recent ecological success (Adams *et al*., 1985; Adams, 1998). Energy reserves are essential for carrying out fundamental physiological and ecological processes such as over-wintering, migration, sexual reproduction and growth (Reznick and Braun, 1987; Phleger *et al*., 1995; Adams, 1998; Arrington *et al*., 2006). All these activities engender reproductive output (i.e. fitness), and because they are tightly constrained by energy reserves, lipids are core to maintaining long-term population viability (Shuter and Post, 1990; Adams, 1998).

In this study, we examined population characteristics (lipid and growth) of fishes resilient to river fragmentation in a large southeastern USA impoundment and its largest unregulated lotic tributary. Furthermore, because our study took place over 5 years, we were also able to document the effect a major drought had on lipids of these fishes.

METHODS

Field sampling was conducted in Lake Logan Martin and Choccolocco Creek, AL, USA (Figure 1). Both of these systems lie entirely within the Valley and Ridge physiographic province. Lake Logan Martin is a large (6179 ha), shallow (mean depth 5·5 m) impoundment of the Coosa River. Choccolocco Creek is the lake's largest tributary (fourth order stream) and flows into the lake at mid-reservoir. While there has been some channelisation to the smaller tributaries of Choccolocco Creek in and around the vicinity of Anniston AL, there are no dams, and the hydrology is free-flowing up to its confluence with the reservoir.

Fishes were collected from five locations in Lake Logan Martin and two locations in Choccolocco Creek during autumn (October–November, the time of the highest lipid storage) in 1996 and 1999–2002 (Figure 1). In total, 11 fish species were examined for lipid content: freshwater drum (*Aplodinotus grunniens*), blacktail shiner (*Cyprinella venusta stigmatura*), gizzard shad (*Dorosoma cepedianum*), threadfin shad (*Dorosoma petenense*), channel catfish (*Ictalurus punctatus*), bluegill (*Lepomis macrochirus*), spotted bass (*Micropterus punctulatus*), largemouth bass (*Micropterus salmoides*), striped bass (*Morone saxatilis*), hybrid striped bass (*Morone saxatilis X. M. chrysops*) and black crappie (*Pomoxis nigromaculatus*). However, only seven of these species (largemouth bass, spotted bass, black crappie, channel catfish, freshwater drum, bluegill and blacktail shiner) were collected in sufficient quantities to permit comparisons of lipid between lentic and lotic habitats. Data for all other species were only used for the time series drought analysis. While time before and after spawning can influence fillet lipid content, especially for highly migratory fishes (Jonsson *et al*., 1997; Mesa and Magie, 2006; Lloret *et al*., 2007), the spawning season of these study species does not occur during autumn, therefore we assume this effect to be negligible. We refer to individuals collected from Choccolocco Creek as

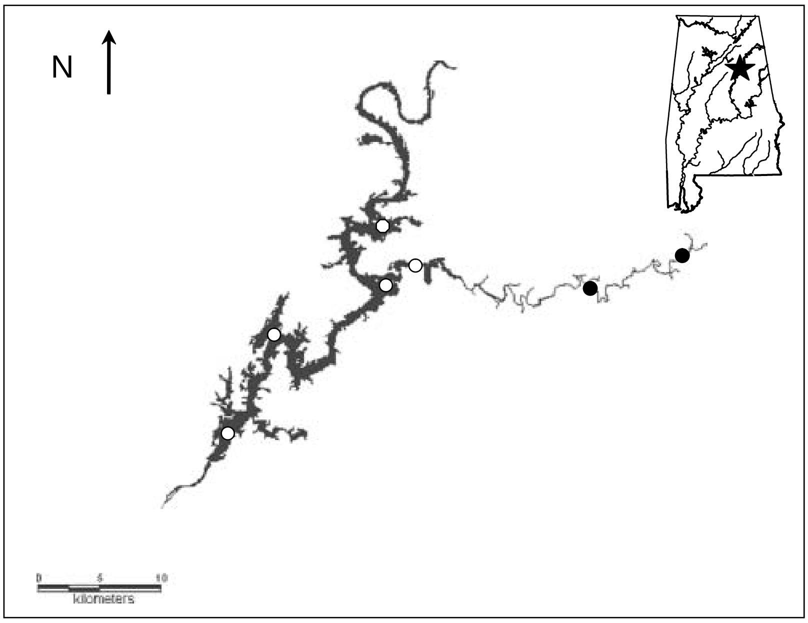

Figure 1. Map of seven sampling sites in Lake Logan Martin and Choccolocco Creek near Anniston, AL, USA (1996–2002). Black circles represent sites grouped as 'lotic habitat' and white circles represent collection sites grouped as 'lentic habitat'.

being from 'lotic habitat' and individuals collected from Lake Logan Martin as being from 'lentic habitat'. Fish movement between lotic and lentic sites is unlikely or minimal due to the distance between both habitat types (34–61 km), and the presence of several large shoals below the lotic sampling sites that block major fish movements.

Individuals were collected using Smith Root® boat electrofishers and gill nets (3·81–5·08 cm mesh sizes), and each fish qualified within a predetermined size range. Captured fish were wrapped in aluminium foil, placed in airtight plastic bags and positioned on ice for transport back to an Auburn University laboratory. Each fish was identified with a unique number, and its total length (TL), weight and sex were recorded. In 2001 and 2002, otolith sagittae were extracted from four species (largemouth bass, spotted bass, channel catfish and freshwater drum) for age determinations using standard methodology (Maceina, 1988; DeVries and Frie, 1996). These four species were chosen for growth comparisons because their abundance in both lentic and lotic habitats made the generation of robust growth equations possible for both habitats. For example, only five black crappies were captured in lotic habitat and four of these individuals were age-3 precluding the development of any meaningful growth model for this species. The age determination process involved examining whole and cross-sectioned otoliths under a dissecting microscope using reflected light. Ages were determined independently for each otolith by two experienced readers, and disagreements between age determinations (∼5%) were settled using concert reads.

Fillet samples were extracted from each fish and shipped overnight to Savannah Laboratories, Savannah, GA, USA for percent lipid analysis using standard methods (Bligh and Dyer, 1959). Interannual variations in lipid were examined by calculating the annual mean lipid value for each species and habitat type and plotting it through time. Annual drought data (Palmer's Drought Severity Index, PDSI) for the Lake Logan Martin—Choccolocco Creek hydrological unit were obtained from the National Oceanic and Atmospheric Administration (NOAA), National Climatic Data Center. Pearson's product-moment correlations ($\alpha < 0{\cdot}05 =$ significant) were calculated by relating annual lipid variations in fishes from each habitat type to annual PDSI. As supporting evidence, we also present secchi disc data averages for Lake Logan Martin, taken by Alabama Water Watch at mid-reservoir for the growing season (April–September) during the lipid sample years (http://www.aces.edu/dept/fisheries/aww/aww/index.php).

We used two-way analysis of covariance (ANCOVA, $\alpha < 0{\cdot}05$) to test for significant differences in lipid content between lotic and lentic habitats and between males and females of each species. Percent lipid data for each species were not normally distributed and were arcsine square root transformed prior to further statistical analysis to meet assumptions of normality. Year of collection and TL were used as covariates in models. Because no individuals were collected from Choccolocco Creek during the years 1996 and 1999, and because of the large effect the year 2000 had on lipids (and thus how unequal sample sizes during this year could affect results), we eliminated data collected from these years in Lake Logan Martin from this statistical analysis, and used only years 2001 and 2002 data (our most robust collection years) to test for effects of habitat type on lipids.

For the four species from which ages were determined from otoliths, fish growth was modelled using length-at-age data. Because our fish were collected using a predetermined size range that excluded very small and large fish, growth was modelled using TL–$\log_{10}$(age) regressions rather than traditional Von Bertalanffy growth functions (Sakaris *et al*., 2006; Rypel and Layman, 2008). Significant differences in growth between habitats were examined using ANCOVA (Rypel *et al*., 2006; Sakaris *et al*., 2006; Rypel and Layman, 2008) where length was a dependant variable, habitat type (lentic or lotic) was the independent variable and $\log_{10}$(age) was a covariate.

RESULTS

A grand total of 2765 individual fish of all species were collected and analysed for lipid content. Interannual lipid content of fishes varied through time (Figure 2(A), (B)). Lipid content was synchronous among fishes from both lentic and lotic habitats and was driven by a large amount of lipid accumulation for all species in both habitats during the year 2000 (Figure 2(A), (B)). Interannual lipid variations were significantly correlated to interannual variations in drought. All but two species (striped bass, whose lipids were not sampled in 2000, and gizzard shad) showed significant correlations with PDSI in lentic habitat and all species showed significant correlations with PDSI in lotic habitat (Table I). Secchi disc measurements through time appeared to match the trend in lipid through time (Figure 2(C)).

Lipid content and growth of fishes varied by hydrologic habitat. Largemouth bass, spotted bass and black crappie had significantly higher lipid content in lentic habitat compared with lotic habitat (Table II, Figure 3). Channel catfish and freshwater drum had significantly higher lipid content in lotic habitat. There were no significant differences in lipid storage of bluegill and blacktail shiner between hydrologic habitats. Growth mirrored the trends in lipid (Figure 4). Largemouth bass, spotted bass and black crappie had significantly faster growth in lentic habitat (Figure 4, ANCOVAs, largemouth bass $T = 4{\cdot}2$, $P < 0{\cdot}0001$, spotted bass $T = 12{\cdot}1$, $P < 0{\cdot}0001$), whereas channel catfish and freshwater drum had significantly faster growth in lotic habitat (Figure 4, ANCOVAs, channel catfish $T = 19{\cdot}1$, $P < 0{\cdot}0001$, freshwater drum $T = 6{\cdot}6$, $P < 0{\cdot}0001$). Growth equations and size ranges for each species by habitat can be found in Table III.

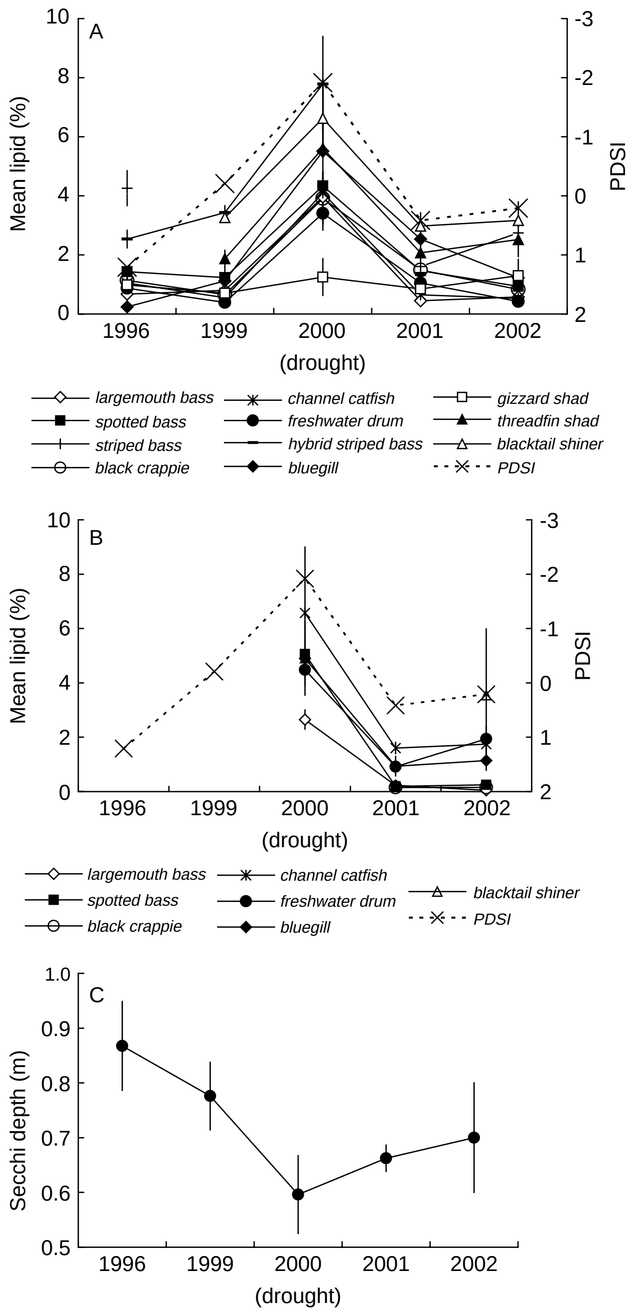

Figure 2. Lipid chronologies for (A) 11 fish species captured from lentic habitat in Lake Logan Martin, AL, USA (1996, 1999–2002) and for (B) seven fish species captured from lotic habitat in Choccolocco Creek, AL (2000–2002). Error bars represent the mean ± 1 SE. The PDSI is plotted on the secondary *y*-axis. More negative values indicate progressively more severe drought conditions. (C) Secchi disc measurements taken in Lake Logan Martin at mid-reservoir over the course of the lipid study. Values are annual averages of monthly measurements taking during the growing season (April–September) ± 1 SE.

DISCUSSION

Effects of a drought on lipid levels

We observed a major spike in the lipid levels of all fishes during the drought year of 2000. On average, lipid levels rose by at least an order of magnitude for species relative to other years. This trend was consistent for nearly every species and in both hydrologic habitat types. We suggest three possible reasons for this pattern.

Table I. Pearson correlations (R) of lipid time series measurements for fishes in both habitat types to the PDSI.

Lentic habitat	Correlation to PDSI
Largemouth bass	**−0·90**
Spotted bass	**−0·85**
Striped bass*	0·80
Hybrid striped bass	**−0·95**
Black crappie	**−0·81**
Bluegill	**−0·90**
Channel catfish	**−0·83**
Freshwater drum	**−0·81**
Gizzard shad	−0·37
Threadfin shad	**−0·94**
Blacktail shiner	**−0·98**
Lotic habitat	
Largemouth bass	**−0·99**
Spotted bass	**−1·00**
Bluegill	**−1·00**
Blacktail shiner	**−0·98**
Black crappie	**−0·84**
Channel catfish	**−1·00**
Freshwater drum	**−0·98**

Significant correlations are in bold.
* denotes a species for which no fish were not collected in year 2000.

1. Bottom up effects. The widespread amplification of lipids during the drought could be at least partially explained by a stimulation of the nitrogen and/or phosphorus cycles (Vitousek *et al.*, 1997; Carpenter *et al.*, 1998; Correll, 1998). This hypothesis was supported by a time series of secchi disc data taken over the length of our lipid estimates from Lake Logan Martin that shows a major drop in the secchi disc readings during the growing season of year 2000 (Figure 2(C)), presumably because of increased phytoplankton densities. Other studies have also shown that annual growth of freshwater mussels (i.e. primary consumers) across numerous southeastern rivers was also significantly stimulated by droughts, including the drought year of 2000 (Rypel *et al.*, 2008; Rypel *et al.*, 2009).
2. Top-down effects (i.e. predator and prey concentration). As the bathymetry of a lake or river retreats and the littoral zone collapses due to water-level loss (e.g. during drought), the shallow water 'refugia zone' (Rypel *et al.*, 2007) for mobile prey is lost and the water's edge becomes juxtaposed against deeper, predator-enriched water (i.e. the river channel). At higher predator densities, the probability of prey encountering and being attacked by a predator increases (Sih, 1984) allowing predators to forage more effectively.
3. Reproductive failure during drought years. Both fishes and aquatic salamanders are known to produce small year classes during drought years (Semlitsch, 1983; Matthews and Marsh-Matthews, 2003). Fishes may divest energy reserves from eggs and gametes back to somatic lipids (Encina and Granado-Lorencio, 1997)

Table II. Results from two-way ANCOVA for the effects of hydrologic habitat and sex on lipid accumulation of seven fishes.

Common name	Species	*n* lotic	*n* lentic	Main effects		Covariates	
				Hydrologic habitat	Sex	Year of collection	TL
Spotted bass	*Micropterus punctatus*	52	229	**<0·0001 Lentic**	0·106	**<0·0001**	**<0·0001**
Freshwater drum	*Aplodinotus grunniens*	33	153	**<0·0001 Lotic**	0·784	**0·014**	**0·001**
Black crappie	*Pomoxis nigromaculatus*	5	158	**<0·0001 Lentic**	0·090	**0·001**	**0·001**
Largemouth bass	*Micropterus salmoides*	19	261	**<0·0001 Lentic**	0·896	0·836	0·576
Channel catfish	*Ictalurus punctulatus*	111	274	**0·020 Lotic**	**0·001**	**0·001**	**<0·0001**
Blacktail shiner	*Cyprinella venusta*	5	14	0·584 N/D	n/a	0·244	0·797
Bluegill	*Lepomis macrochirus*	6	44	0·791 N/D	n/a	0·778	**<0·0001**

All values are *P*-values unless referred to as otherwise. Significant effects are noted in bold. Habitats for which lipids were significantly higher are indicated in the hydrologic habitat column next to the *P*-values. N/D refers to no difference.

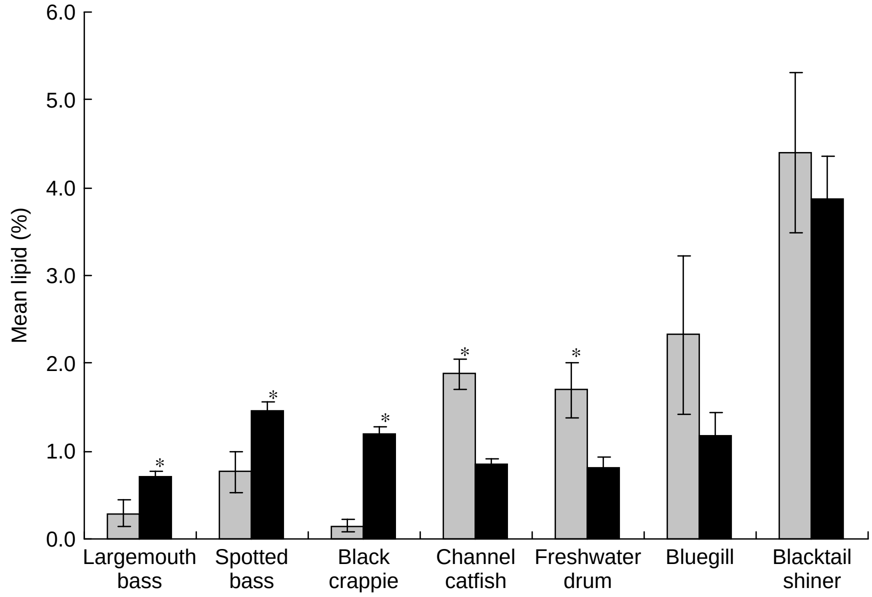

Figure 3. Comparisons of lipid content between lotic (black bars) and lentic (gray bars) habitats for seven fishes. Error bars represent the mean ± 1 SE. Significant differences for Tukey's pair wise comparisons are indicated by an*. Full details of these statistics can be found in Table II.

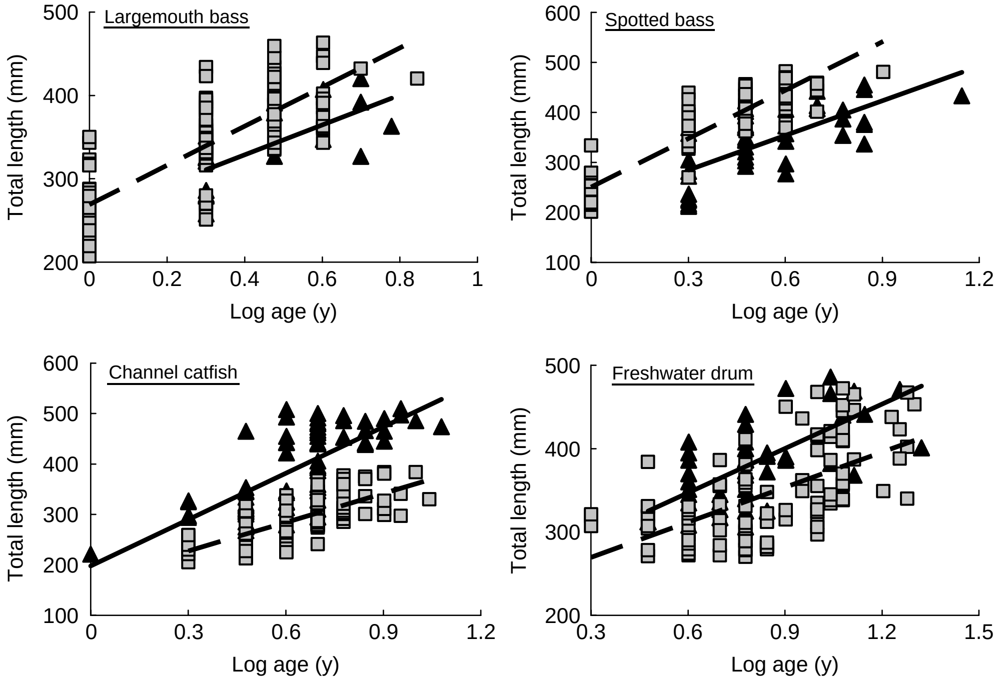

Figure 4. Length-at-$\log_{10}$(age) regressions for four fish species between lotic (black triangles, solid line) and lentic (grey square, dashed line) habitats. Full regression statistics are provided in Table III.

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Table III. Length-$\log_{10}$(age) regressions of four fishes between hydrologic habitat types.

Species	Size range (TL, mm)	Lotic growth equation	n	r^2	Lentic growth equation	n	r^2
Freshwater drum	270–472	$TL = 177{\cdot}5(\log_{10}age)+240{\cdot}3$	77	0·42	$TL = 140{\cdot}3(\log_{10}age)+227{\cdot}0$	104	0·40
Channel catfish	205–510	$TL = 305{\cdot}8(\log_{10}age)+198{\cdot}2$	71	0·54	$TL = 190{\cdot}4(\log_{10}age)+169{\cdot}7$	199	0·54
Spotted bass	201–482	$TL = 230{\cdot}9(\log_{10}age)+215{\cdot}4$	47	0·50	$TL = 322{\cdot}9(\log_{10}age)+250{\cdot}4$	148	0·86
Largemouth bass	207–463	$TL = 179{\cdot}5(\log_{10}age)+257{\cdot}0$	47	0·55	$TL = 235{\cdot}0(\log_{10}age)+269{\cdot}1$	148	0·70

in response to drought stressors (Schreck *et al*., 2001) to expend more generously the following year when environmental conditions might be more favourable. Matthews and Marsh-Matthews (2003) reported explosions in reproduction of minnow and darter species in spring of 2001 following the drought of 2000 in Briar Creek, OK, USA.

Drought observation: conclusions

This ecological pattern deserves future research consideration. For example, if a drought continued over consecutive years (i.e. multi-year droughts), would this pattern persist? And for how long? According to the National Climatic Data Center (http://www.ncdc.noaa.gov), the consecutive droughts of 2006 and 2007 in the southeastern USA brought about the most severe surface water shortages and water-level reductions in the region since record-keeping began in 1895. Recent legal battles between states over water rights (i.e. 'water wars') have enveloped regional politics and even further exasperated flow and water-level conditions (Carter *et al*., 2008; Rokach, 2008). Time series estimates of lipid (this study) and growth (Black *et al*., 2008; Rypel *et al*., 2009) may hold value for studying environmental effects of drought and water extraction on aquatic ecosystems. And while they may not be as 'complete' as certain ecosystem-level metrics (e.g. nutrient cycling, primary and secondary production, decomposition. etc.), they might be inexpensive and rapid surrogates for examining food web effects arising from climate and anthropogenic change.

Differences in lipid and growth between hydrologic habitats

We found significant differences in lipid and growth of fishes between fundamentally different hydrologic habitat types. Freshwater drum and channel catfish had significantly higher lipid content in lotic habitats, whereas largemouth bass, spotted bass and black crappie had significantly higher lipid content in lentic habitat, and bluegill and blacktail shiners showed no difference in lipid content between hydrologic habitat types. Growth data matched observed patterns in lipids for all four species for which age and growth data were available. Freshwater drum and channel catfish grew significantly faster in lotic habitat, but largemouth and spotted bass grew significantly faster in lentic habitats. For bluegill, sample size in lotic habitat was low; however, results from an independent study of bluegill growth between rivers and reservoirs (Rypel, unpublished data) confirmed the same lack of difference between habitat types.

We suspect differences in lipid and growth between hydrologic habitats is driven to a large degree by changes in the abundance of preferred prey types. For example, shads (*Dorosoma* spp.) are the primary prey for black basses in southeastern reservoirs (Hubert, 1977; Miranda and Muncy, 1989; Scott and Angermeier, 1998; Pope *et al*., 2001), but in southeastern rivers, black basses normally consume diverse types of prey, e.g. crayfishes, aquatic insects, small sunfishes, minnows and darters (Davies, 1981; Schramm and Maceina, 1986; Wheeler and Allen, 2003). Thus, growth rates are higher for largemouth bass where abundance of an energetically rich prey item (shad) is higher. This same reasoning likely applies to freshwater drum, but in the opposite way. Freshwater mussels are a primary prey for drum, and mussels are considerably more abundant and diverse in rivers as opposed to reservoirs (Daiber, 1952; Wahl *et al*., 1988; Bogan, 1993; Dreves *et al*., 1996; Rypel *et al*., 2006). Thus growth and lipids of drum tends to be higher in rivers where this prey is more abundant.

Other factors may also drive differences in lipid and growth among habitats. For example, differing levels of abundance, competition and mortality could lead to changes in fish growth and energy reserve dynamics (Adams *et al*., 1985; Heggenes *et al*., 1999; Armstrong *et al*., 2003; Morley *et al*., 2007). Furthermore, morphological differences could contribute to variations in lipid and growth among hydrologic habitats (Pettersson and Hedenström, 2000). In a set of swimming trials, the more globiform largemouth bass used less thrust energy than rainbow trout (*Oncorhynchus mykiss*) to maintain position in slower currents, but used more thrust energy than rainbow trout to maintain position in faster currents (Jayne and Lauder, 1995).

This study supports previous research on the hydrologic habitat preferences of these species. Rypel *et al*. (2006) found a concordant pattern for freshwater drum across southeastern USA ecosystems where growth was always higher in rivers than in reservoirs. Rypel (unpublished data) found growth of multiple black bass species across their ranges was higher in lentic ecosystems, whereas bluegills showed no difference in growth between lotic and lentic ecosystems across their natural range. For some of these taxa (e.g. bluegill, channel catfish), these emerging patterns in habitat preference do not necessarily conform to pre-conceived notions. For example, bluegills are not normally considered a riverine species by fisheries managers even though multiple recent studies have found robust bluegill populations in rivers (Jackson, 2003; Katano *et al*., 2005; Zeug *et al*., 2005; Sammons and Maceina, 2008). Thus, lipid and growth data are useful for examining and challenging pre-conceived notions of habitat suitability.

Species vary substantially in their responses to ecosystem fragmentation. A certain percentage of species (e.g. those with a narrow, strictly riverine ecological niche) are often extirpated outright from fragmented habitats. For example, many darters, minnows, madtoms, diadromous shads and sturgeons are rapidly extirpated from highly fragmented rivers in the southeastern USA (Freeman *et al*., 2005; Taylor *et al*., 2008). For these species, abundance and presence–absence surveys likely do reflect habitat preference as lipid and growth comparisons between habitats simply cannot be made. Black basses and black crappie apparently benefit from river regulation perhaps explaining the widespread sport fisheries that exist for these species in regulated rivers (e.g. Chen *et al*., 2003). Some species showed no consistent trend suggesting that either habitat might be suitable for these cosmopolitan species. However, other species apparently subsist within reservoirs where environmental conditions are sub-optimal (e.g. freshwater drum, channel catfish). This leads to the question: why do resilient persist in reservoirs at all? We propose four general ways that such an ecological pattern could emerge.

1. Individuals could have immigrated to sub-optimal habitats by emigrating from optimal habitats.
2. All individuals in a population may be long-lived adults that pre-date creation of the lentic habitat.
3. The population may originate from eggs or juveniles wash and settle into impounded areas from riverine source populations upriver.
4. Individuals could reproduce at normal or reduced levels (i.e. year class strength is either not affected or may be declining over time).

Hydrologic habitat analysis: conclusions

We suggest that population characteristics have been long underutilized in the sciences of dam removal (Bednarek, 2001; Hart *et al*., 2002; Poff and Hart, 2002; Sethi *et al*., 2004), river restoration (Galat and Lipkin, 2000; Irwin and Freeman, 2002; Souchon *et al*., 2008; Taylor *et al*., 2008), and river ecology in general. Dam removal projects that analyse only community data may be missing opportunities to elucidate more of the positive ecological effects that river restorations generate, and the reality of some important socioeconomic trade-offs that might exist. For example, it is possible, and supported by previous research (Schramm and Eggleton, 2006), that riverine catfish production would be significantly benefited by restoration initiatives in regulated rivers. Whereas channel catfish are a commercially (Mestl, 1999) and now recreationally relevant species (Wilde and Ditton, 1999), this could be a massive production gain that has not been previously addressed or quantified in river restoration studies. Conversely, production of black basses may decrease due to restoration. Numerous other resilient riverine fishes not examined in this study are also likely impacted in terms of lipid and growth through river fragmentation (e.g. suckers). What are the ecological and socioeconomic realities of such trade-offs? Lipid and growth data are relatively easy and inexpensive data to generate and we contend that more intense applications of these metrics could greatly enhance the field of river ecology as a whole.

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