

Spatial and Temporal Trade-Offs by Bluegills in Floodplain River Ecosystems

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ABSTRACT

Ecological trade-offs by organisms to minimize mortality and maximize growth is a foundational theme in ecology. Yet, these trade-offs are rarely examined within spatially complex, temporally variable ecosystems, such as floodplain rivers. Here, we evaluate ecological trade-offs across space and time for the bluegill (*Lepomis macrochirus*) in two unregulated river ecosystems in southeastern USA. Life-history differences among spatially segregated main channel and floodplain lake populations were used to assess effects of habitat type on bluegill fitness. Growth, condition, and gonadal somatic index were all significantly enhanced in floodplain lakes relative to the main channel. Furthermore, stomach fullness was significantly higher, and predator densities significantly lower in floodplain lakes thereby providing an ecological explanation for the life-history plasticity observed across the riverscape. However, historical observations

suggested that although floodplain lakes are highly productive for bluegills, they are also prone to complete desiccation by drought approximately every 5 years, revealing the ultimate value of channel habitat, which does not dry, as desiccation refugia. Bluegills are faced with a balancing act associated with variation in foraging opportunities, and risks to predation and desiccation, that change in both the temporal and the spatial dimensions of floodplain rivers. The differential responses to these opportunities and risks help to explain why both habitats remain actively populated by bluegills, as well as many other organisms, in these and many other natural rivers.

Key words: cost-benefit; fitness; flood pulse; food availability; habitat selection; morphology; predation; resource use.

INTRODUCTION

Cost-benefit trade-offs by organisms is a core theme in ecology and evolution (Pianka 1974; Lima 1985;

Wellborn and others 1996). The most common trade-offs observed by organisms involve attempts to maximize fitness by optimizing growth against predation risk (Vanni 1987; Werner and Hall 1988; Lima 1998). Body size may be the foremost factor regulating trade-offs for many organisms because fecundity, foraging efficacy, and predation risk are intimately linked with body size, and these factors vary across ecosystems and habitat types (Blanchenhorn 2000; Layman and others 2005; Rypel and others 2007). An extensive literature on this topic

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has focused overwhelmingly on habitat shifts within relatively closed, environmentally stable ecosystems (Dickman 1992; Sih and others 1992; Werner and McPeck 1994). The classic example of predation-growth trade-offs is in fact that of the bluegill (*Lepomis macrochirus*) shifting between littoral and pelagic habitats of temporally stable pond systems (Werner and Hall 1988). Yet, ecological trade-offs in complex, temporally variable environments have not been evaluated in great detail.

Historically, ecological trade-offs have been studied in relatively stable environments at time scales shorter than the lifespan of species (Godvik and others 2009). It is assumed that such patterns remain relatively static over time due to the temporal stability of the environment. Yet examples are myriad on how habitats in ecosystems can dramatically vary over time due to disturbance and climate variability (Rood and others 2007), and that ecosystems themselves differ in temporal variability. Long-range, episodic events are likely to alter predation-growth trade-offs, an effect that may cascade to other functional metrics such as recruitment, competition, and production (Schlosser 1990; Benke and others 2000).

Floodplain rivers exhibit a distinct spatial patch structure in which the degree of connectedness among patches changes dramatically through time (Wiens 2002). Riverine organisms purportedly shift among these patches to maximize fitness, and this apparent pattern forms the basis for one of the most widely cited river ecology paradigms (that is, Junk and others 1989). Yet surprisingly few empirical examples actually exist of fish exploiting fluctuating river patches to maximize predator avoidance or growth (but see Langerhans and others 2003). Furthermore, timing is likely critical to the relative success or failure of spatial trade-offs in rivers. The flood pulse is the main dispersal agent in rivers (Junk and others 1989; Sousa and Freitas 2008), however, the frequency, magnitude, duration, rate of change, and timing of flows varies considerably through time (Poff and others 1997; Benke and others 2000; Sabo and Post 2008). At first glance, this level of complexity seems to render floodplain rivers challenging if not impossible to understand ecologically. However, elucidating some basic spatial and temporal trade-offs occurring at an ecosystem-scale could reveal simple yet pervasive processes governing the distribution of organisms in rivers. In this article, we assessed trade-offs between growth and mortality for bluegills in two southeastern USA floodplain rivers occurring across spatial and temporal dimensions. Spatially, we examined the extent to which life-history traits

varied between main channel and floodplain lake environments. However, we also show how annual variations in water levels interact with, and at times, override otherwise spatially exclusive ecological drivers.

METHODS

Field sampling took place in the unregulated Sipsey River in western Alabama (near Elrod, Alabama, USA) and was then replicated in an unregulated, upstream reach of the Pearl River in eastern Mississippi (near Philadelphia, Mississippi, USA) during summer and fall of 2005. Both rivers are located in the Coastal Plain physiographic province and flow through bottomland hardwood forest, cypress, and tupelo-gum swamps. Mean annual discharge for the 2005 water year in the Sipsey and Pearl Rivers at the sampling sites was 30.0 and 25.0 m s⁻¹, respectively. Species diversity is high in both the Sipsey and Pearl Rivers (Ward and others 2005), however, in both rivers, the bluegill is the most abundant fish species (Rypel 2008; Kennedy 2009). In these rivers, high winter discharge, along with a lack of evapotranspiration inundates the riparian floodplain landscape (Ward and others 2005). This period of hydrologic connectivity is a critical ecological period for reconnecting organisms in spatially segregated floodplain lakes and beaver ponds with those in the main river channel. In early summer, receding streamflows isolate floodplain lakes which typically remain isolated for the remainder of the growing season.

Bluegills were sampled by boat (main channel) and barge (floodplain lake) electrofishing in both rivers during the mid-summer period of disconnectedness. In each river, bluegills were sampled on three separate dates in June and July 2005 in the main channel and in two nearby floodplain lakes (one small lake and one large lake) (Table 1). All sampled fishes were retained for further analysis. In the lab, the total length (TL, mm) of each bluegill was measured and its wet weight recorded (g). Otolith sagittae were removed from each fish and stored for later age determination. To obtain morphological data, each fish was photographed alongside a small ruler on a flat, lateral grid below a mounted 5.1 mega pixel digital camera (Casio EX-Z57).

Differences in morphology were evaluated using geometric morphometrics. We used TpsDig software (State University of New York, Stony Brook, New York) to digitize 13 landmarks on each bluegill image (Figure 1). We then used TpsRegr software (State University of New York, Stony Brook, New

Table 1. Physical and Chemical Characteristics of Study Sites on Both Rivers

Measurements	Sipsey River			Pearl River		
	Main channel	Floodplain lake 1	Floodplain lake 2	Main channel	Floodplain lake 1	Floodplain lake 2
Latitude	33°14'00.19"N	33°13'51.71"N	33°13'33.47"N	32°50'37.62"N	32°50'29.66"N	32°50'29.72"N
Longitude	87°46'37.35"W	87°46'39.62"W	87°46'42.87"W	89°5'36.48"W	89°5'22.58"W	89°5'42.49"W
¹ Area (m ²)	N/A	4735	9025	N/A	4613	3723
² Distance to main channel (m)	0	100	275	0	412	73
³ Max. depth (m)	N/A	1.2	2.7	N/A	1.7	1.7
⁴ Dissolved oxygen (mg l ⁻¹)	8.0-8.3	1.3-3.0	0.6-2.9	2.8-7.3	2.1-2.9	2.3-2.9
⁴ Temperature (°C)	23.3-23.7	24.2-26.2	24.1-27.3	26.0-28.4	28.6-29.3	28.1-29.6
⁴ Nitrate (µg l ⁻¹)	165.6-167.5	0.0-0.9	0.0-0.0	141.6-142.8	0.0-0.2	0.0-3.5
⁴ Nitrite (µg l ⁻¹)	1.9-2.0	1.3-2.0	0.1-1.8	5.9-6.2	2.2-2.4	4.3-7.6
⁴ Ammonium (µg l ⁻¹)	15.6-23.4	12.4-17.6	4.4-6.1	100.6-100.1	31.6-35.2	8.5-14.5
⁴ Soluble reactive phosphorus (µg l ⁻¹)	0.0-0.0	0.0-0.0	0.6-1.2	5.8-7.1	0.0-0.6	7.0-10.6
⁴ Dissolved organic carbon (mgC l ⁻¹)	7.2-8.4	11.7-13.0	12.4-13.9	2.2-3.0	6.8-9.0	8.4-9.3

¹Estimated as an average from aerial imagery taken on 9/2004, 9/2006, 9/2010.

²Estimated as the shortest distance to the main channel from each lake's geographic centroid.

³Estimated at the deepest known portion of each lake on 9/21/2005.

⁴Value range from replicate water samples (n = 2) at each site on 9/21/2005.

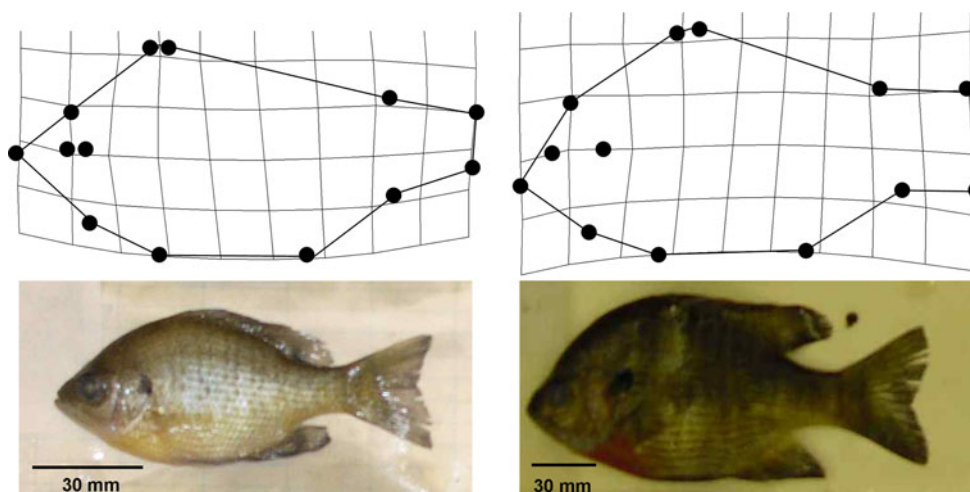


Figure 1. Thin plate spline deformations depicting typical body morphologies of bluegills from main river channel (*left*, $N = 159$ fish) and floodplain lake (*right*, $N = 349$ fish) habitats of the Sipsey and Pearl Rivers. *Black circles* (13 per fish) indicate the position of standardized landmarks. Floodplain lake bluegills had globiform bodies, large eyes, thick tails, and benthic-oriented jaws. Comparatively, main channel bluegills had fusiform bodies, small eyes, thin tails and upturned, pelagic-oriented jaws.

York) to rotate, translate, and scale landmarks using least-squares imposition and describe variations in landmark positions between floodplain lake and main channel habitat using thin plate spline transformation. This was then used to calculate partial warp deformations in TpsRegr which describes morphological variation associated with each habitat type. To statistically test the strength of morphological differences, and estimate percentage correct classification to habitat based on morphology, a discriminant function analysis (DFA) was performed.

Fish ages were determined by examining otolith sagittae under a dissecting microscope. Ages were determined blindly twice, and any disagreements in ages between reads one and two were settled using another independent reader. Gonads of each individual were dissected out, blotted dry, and wet weights recorded for calculation of gonadal somatic index (GSI)—an index of fecundity. The stomach of each fish was also removed, blotted dry, and stomach content wet weight used as an estimate of biomass of consumed prey. In total, 505 bluegills were examined across both the Sipsey and Pearl Rivers for morphological, length-at-age, GSI, and biomass of consumed prey differences among habitat types. Catch per unit effort (CPUE) of all known bluegill predators was averaged across replicate sampling dates for each lake and main channel as an index of predator density. We defined bluegill predators as any species in which we have previously observed a bluegill in a stomach of in these systems, or has been

found in the literature to commonly consume bluegills as prey [predator species were primarily bowfin (*Amia calva*), spotted gar (*Lepisosteus oculatus*), longnose gar (*Lepisosteus osseus*), largemouth bass (*Micropterus salmoides*), spotted bass (*Micropterus punctatus*), and flathead catfish (*Pylodictis olivaris*)].

We used analysis of covariance (ANCOVA) using a relaxed P value ($P < 0.20 = \text{significant}$) to test whether growth differed significantly among the four floodplain lakes, or between the main channels of the Sipsey River and the Pearl River. No significant differences were found among floodplain lakes or between main channels ($P = 0.86$), therefore data were grouped by habitat (floodplain lake vs. main channel) for all further analyses. Bluegill growth was modeled using the Von Bertalanffy growth function (VBGF):

$$L_t = L_\infty(1 - e^{-K(t-t_0)})$$

where L_t is length (mm) at time t (age in years), L_∞ is length (mm) at time ∞ (the predicted mean maximum length for the population), K is a growth constant that describes the rate at which L_∞ is attained (mm y^{-1}), t is age (years) and t_0 is the time at which length = 0 (Ricker 1975).

Likelihood ratio tests were used to test the significance of growth between main channel and floodplain lake habitat types (Kimura 1980). A bootstrapping method (Rypel 2007) was applied to generate confidence limits for each VBGF. Significant differences in condition factor (relative weight), GSI, and predator densities between habitats were

examined using *t* tests. Significant differences between habitats in biomass of consumed prey were tested with ANCOVA where log biomass of consumed prey was the dependent variable, TL was the independent variable and habitat type was a categorical variable.

RESULTS

We found major differences in body morphology between main channel and floodplain lake populations of wild-caught bluegills (Figure 1). Floodplain lake bluegills were morphologically larger in almost every aspect after controlling for sex and age (for example, larger eyes, more globiform body, “fatter tails”), and presented with more benthic-oriented mouths as opposed to main channel bluegills that typically had upturned, pelagic-oriented mouths. This polymorphism occurred in both the Sipse and Pearl River populations. Discriminant analysis correctly classified 95% of fish to habitat of capture (main channel vs. floodplain lake) using morphological measurements with the age and sex of fish known.

Growth rates were significantly faster in floodplain lakes compared to the main channel (Figure 2A, likelihood ratio test of coincident curves, $P < 0.0001$). Bluegills in floodplain lakes reached significantly larger maximum sizes (likelihood ratio test of L_{∞} , $P < 0.0001$), and had significantly higher bootstrapped growth rate constants (Figure 2, likelihood ratio test of K , $P < 0.0001$). Both GSI (Figure 2B, *t* test, $t = 2.62$, $P = 0.009$) and condition factor (*t* test, $t = 6.84$, $P < 0.0001$, mean main channel = 86.4, mean floodplain lake = 95.8) were significantly higher in floodplain lake habitat compared to the main channel habitat. Mean biomass of ingested prey was significantly higher in floodplain lake habitat than in main channel habitat (Figure 3A, ANCOVA, $F = 523.8$, $P < 0.0001$). Bluegill predator CPUE was significantly higher in main channel habitat than in floodplain lake habitat (Figure 3B, *t* test, $t = 2.85$, $P = 0.01$).

DISCUSSION

Food and predation are the two ecological factors classically thought to influence animal fitness (Harrold and Reed 1985; Werner and Hall 1988; Komdeur and others 1997; Saper and others 2002). In the floodplain rivers of this study, this paradigm was initially supported. Floodplain lake habitats carried both predation and food/growth advantages for bluegills, apparently leading to faster growth rates, a more globiform morphology, and higher

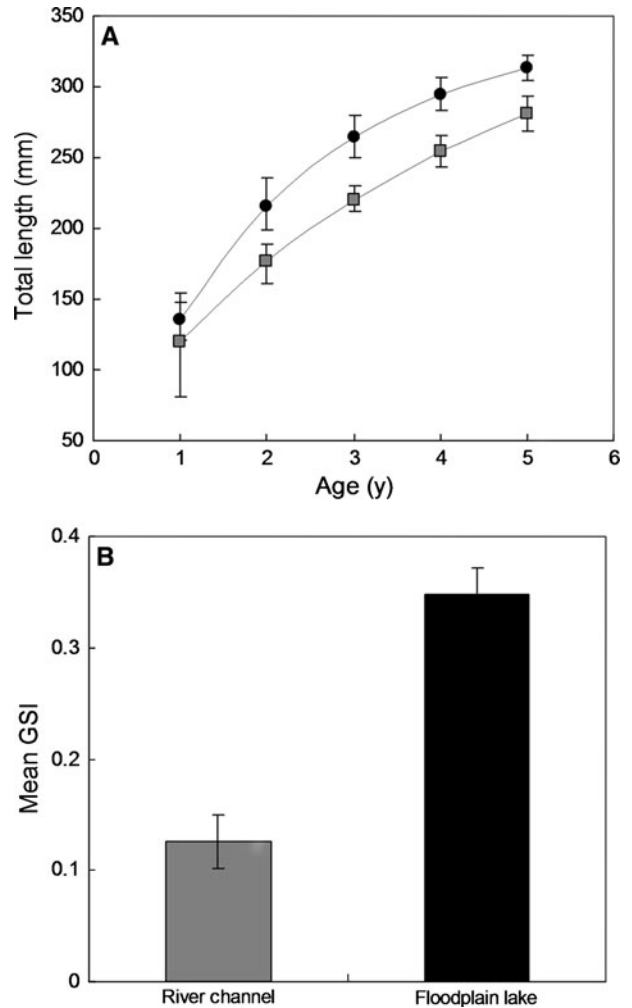


Figure 2. **A** Mean lengths-at-age and growth curves for bluegills from the main channel (gray squares, $N = 159$ fish) and floodplain lakes (black circles, $N = 349$ fish) of both rivers. Ninety-five percent confidence intervals were derived using a bootstrapping technique. **B** Mean GSI values of bluegills from main channel and floodplain lake habitats. Error bars ± 1 SE.

indices of reproductive fitness. Conversely, main channel bluegills had a fusiform morphology characterized by lower growth rates, body sizes, and reproductive indices. This rangy main channel ecomorph could develop because of a need for faster burst swimming speeds as a defense mechanism against increased predation risk (Taylor and McPhail 1985; Langerhans and others 2004), and/or hydrodynamics, as the fusiform body reduces hydrologic drag allowing fish to maintain position better in current (Riddell and Leggett 1981). Thus, at first glance, predation and food differences appear to be the primary mechanisms giving rise to the divergent morphologies and life-history strategies of bluegills in these rivers.

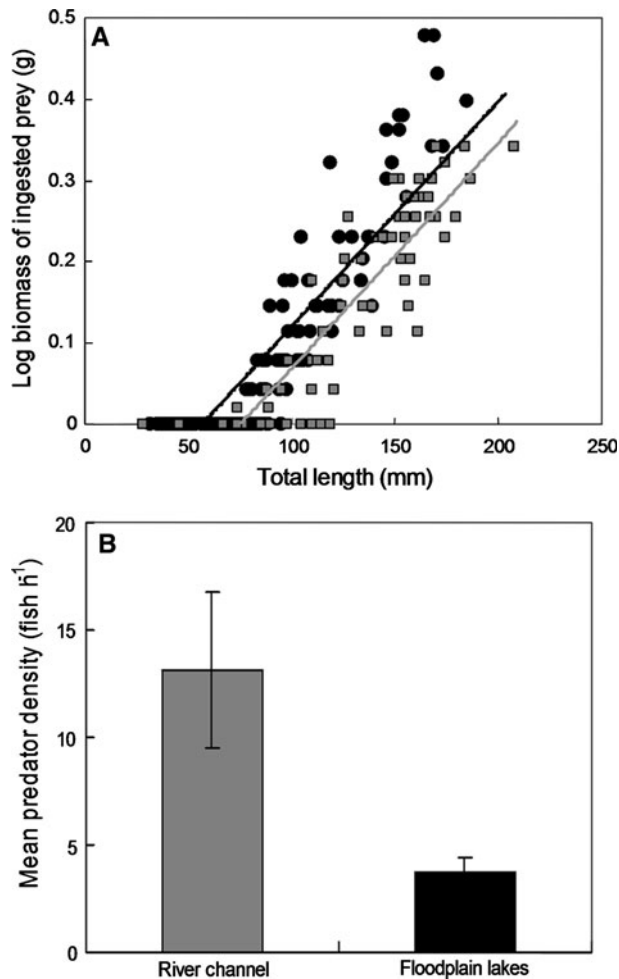


Figure 3. **A** Comparison of biomass of ingested prey from bluegill stomachs relative to body size in river channel (gray squares, gray line, $N = 159$ fish) and floodplain lakes (black circles, black line, $N = 349$ fish). Each symbol represents data from a single fish and the line is a linear regression best-fit line. **B** Average predator densities in river channel and floodplain lake habitats. Electrofishing CPUE was averaged across sampling dates and habitats. Error bars ± 1 SE.

However, if main channel habitats were truly sub-optimal in every way, then these life-history data would leave unexplained why bluegills would ever choose to reside in, or maintain the phenotypic plasticity necessary to inhabit the main channel. In other words, food and predation data alone do not explain the overall distribution of bluegills in these ecosystems. To understand this paradox, the temporal dimension must be incorporated (Wiens 2002). During summer 2006 (the year after sampling), severe drought across southeastern USA in late summer desiccated all floodplain lakes examined in this study, and to the best of our knowledge, all floodplain lakes in both

river channels, killing all floodplain lake fish populations (Figure 4). During the following wet season (winter 2006–2007), lakes were replenished with water and presumably re-colonized by fishes. However, persistent and increasingly severe drought during the summer of 2007 again desiccated all floodplain lakes and killed all floodplain lake fish in both rivers. Interviews with wildlife personnel and local fishermen indicated that complete desiccation of these floodplain lakes also occurred in 2000, 1992, 1988, and 1986. By combining these ground-truthed floodplain lake drying events with historical stream-flow data, we can conservatively estimate that floodplain lakes in these rivers suffer complete desiccation, on average, every 5 years (Figure 4). However, smaller, less permanent floodplain lakes may dry annually or even biannually, and the approximately 5-year time frame itself is highly variable. This leads to two salient points from this study:

- (1) Morphological and life-history diversification by bluegills in floodplain rivers occurs rapidly. For example, if the temporal dimension had not been considered, our study might have suggested that the two body morphs were based in genetic differentiation. However, because bluegill populations in floodplain lakes suffer local extinction approximately every 5 years, adoption of a particular morph depends either on habitat choice by individuals (that is, a decision was made based on unknown cues to migrate) or the stochasticity of point of origin (that is, which habitat individuals recruited from, or washed into, and the degree to which these processes are random).
- (2) Main channel bluegills are likely the sole source population for bluegills in floodplain lakes. Main channel individuals are essentially consigned to an environment characterized by growth stunting and higher predation risks in an apparent “bet-hedge” on floodplain lake drying by themselves or their parent fish. For example, if floodplain lakes suffer complete desiccation, on average, every 5 years (Figure 4), then the annual chance of death in large floodplain lakes due to drying alone is about 20%. However, if fish remain in floodplain lake habitat for an entire life-cycle (5 years), probability of drought-induced mortality rises to 67%. Thus, over the course of a life, survival odds from drought actually favor main channel individuals over floodplain individuals in spite of low food and growth in the channel. However, this survival benefit in the main channel is offset by an enhanced risk of mortality due to

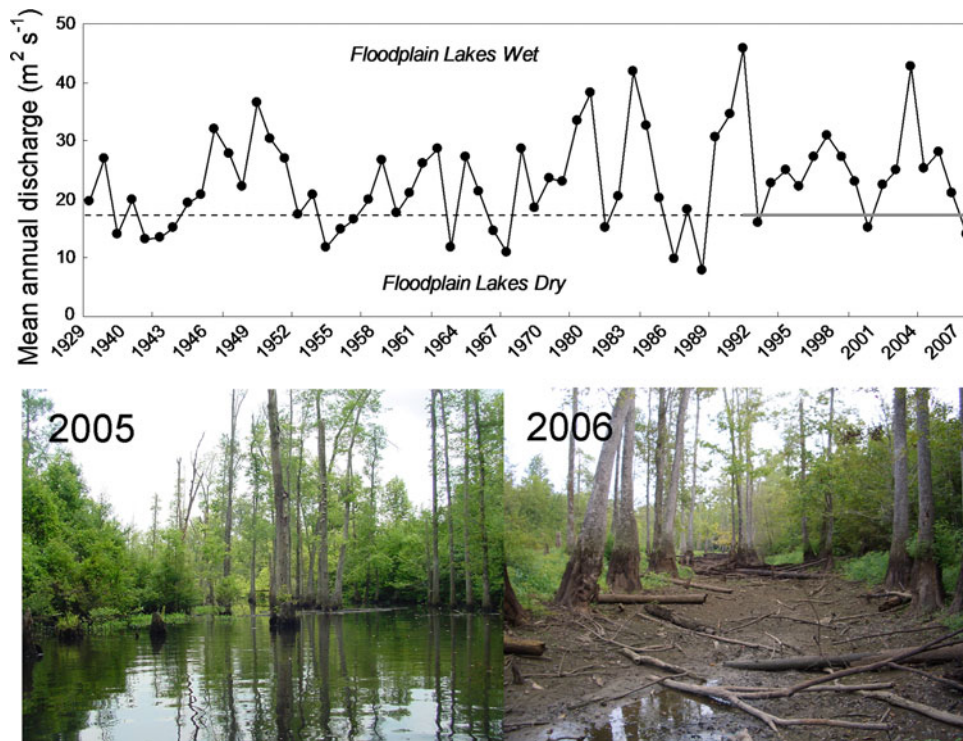


Figure 4. Mean annual discharge in the Sipsey River near Elrod, Alabama. Solid gray line indicates drought years where we, local fisherman, wildlife professionals, and/or landowners observed all floodplain lakes across the landscape had dried.

Dashed line projects drying estimates back through the historical streamflow data. Note that flow data were not collected every year (for example, the 1970s). Bottom panels show the same lake in the Sipsey River floodplain in 2005 (normal water year) and 2006 (drought year).

predation. Therefore, both environments carry fitness advantages—but advantages that are dimensionally dependent.

It remains unclear to what extent individuals are successful at or attempt to obtain maximum fitness advantage by selectively utilizing both habitats over time. For example, if individuals migrate from floodplain lakes to the main channel or vice versa on an annual or super-annual basis, they could reap growth advantages from floodplain lakes during wet years, and exploit the main channel habitat as desiccation refugia during dry years. The extent to which such migrations or “gaming of the ecosystem” occurs is unknown, but an assumption of a zero error rate for classification by DFA provides an approximation that 5% of the fish captured were the incorrect ecomorph for the habitat and hence had recently migrated. Further research is needed on the behavioral ecology and movement of bluegills in these systems to better examine this possibility.

Elucidating ecological trade-offs across multiple ecosystem dimensions helps establish the links between ecological systems and different fitness payouts. These links are vital for understanding the distribution of organisms across landscapes and how best to conserve and properly manage them. In this study, the combination of food, predation, and a temporal risk factor helped to explain the natural distributions of a common fish species in floodplain

ivers. Such multi-dimensional trade-offs likely typify the range of risks and rewards common to other large, highly heterogeneous ecosystems (for example, Godvik and others 2009; Grol and others 2011). Ecosystem-level approaches that incorporate multi-dimensional trade-offs could be used on a broader basis to examine the dependency of species, particularly those that are imperiled, on the unique physical and temporal architecture of ecosystems. For example, amphibians in ephemeral ponds (Wellborn and others 1996), fish in streams (Schlosser 1991; Fausch and others 2002), cavity nesting birds in dead and dying trees (Martin and Eadie 1999), chickadees (Lima 1985), and large grazing mammals (Walters 2001) all appear to exhibit metapopulation dynamics that could also vary both spatially and temporally. In floodplain rivers, although only the bluegill was examined in this study, a large number of other motile riverine organisms purportedly share this same metapopulation dynamic and are therefore also faced with similar trade-offs (for example, Sabo and Kelso 1991; Meschiatti and others 2000; Slipke and others 2005).

Perhaps the simplest message from this study is that habitats which appear unproductive over the short term can be critical in the long-term. Thus, habitat “values” based solely on snapshots of productivity might in fact be highly deceiving. Floodplain lake and main channel fish populations that segregate at base flows and phenotypically respond

to different food resources and predation risk are not truly segregated over time but are in fact highly interconnected and dependent on one another. Connectivity, albeit variable at several temporal scales, may underlie the high and stable levels of productivity often observed in floodplain river environments (Costanza and others 1997). Thus, a “portfolio effect” exists in these systems, that is, variance dampening due to diversification (Schindler and others 2010), yet in this case, one based in habitat quality variance across space and time. Conservation efforts must therefore consider the entire portfolios of ecosystems (Schlosser 1990; Lima and Zollner 1996) and resist the urge to evaluate habitats based only on brief snapshots of productivity. For floodplain rivers, we should value and conserve both floodplain and main channel habitats to optimize the fitness payouts for a wide range of organisms and conserve the evolved life-history plasticity that allows them to exploit spatially and temporally complex riverscapes.

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