RIVER RESEARCH AND APPLICATIONS

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# RIVER IMPOUNDMENT AND SUNFISH GROWTH

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## ABSTRACT

Impoundment of rivers by dams is widespread and one of the most devastating anthropogenic impacts to freshwater environments. Linking theoretical and applied research on river impoundment requires an improved capacity for predicting how varying degrees of impoundment affects a range of species. Here, growth of 14 North American sunfish species resilient to river impoundment was compared in rivers versus impoundments. Growth response to river impoundment varied widely, but consistently among taxa: five species (shadow bass, rock bass, flier, redbreast sunfish and green sunfish) showed significantly higher growth in riverine ecosystems, four species (largemouth bass, smallmouth bass, spotted bass and longear sunfish) showed significantly higher growth in impounded ecosystems, and five species (bluegill, black crappie, white crappie, redear sunfish and warmouth) displayed no difference in growth between rivers and impoundments. Furthermore, significant linear models were developed for predicting growth of two species (largemouth bass, $R^2 = 0.75$ and warmouth, $R^2 = 0.44$) based on a physiographically specific index of reservoir retention time. For another species (white crappie), growth could not be predicted by the retention time index in Central Lowlands rivers ($R^2 = 0.001$), but was strongly predicted by this factor in southeastern Coastal Plain rivers ($R^2 = 0.76$) showing how impacts of impoundment, and prediction of its consequences, can vary across river landscape types. Further analysis of fish growth in response to river impoundment, regulation and fragmentation could greatly enhance conservation biology, restoration ecology and basic land use decisions in riverine landscapes.

Supporting information may be found in the online version of this paper.

KEY WORDS: Centrarchidae; climate; dams; fisheries management; natural flow regime; production; restoration; reservoir retention time

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## INTRODUCTION

The impoundment of rivers is increasingly recognized as a core driver of global freshwater biodiversity loss and attrition of aquatic ecosystem function at diverse scales (Dynesius and Nilsson, 1994; Pringle, 2001; Thorp *et al.*, 2006; Freeman *et al.*, 2007; Taylor *et al.*, 2008). Roughly 77% of rivers in the Northern Hemisphere suffer from severe impoundment by dams (Dynesius and Nilsson, 1994), and in the conterminous USA, a meager 42 high quality, unregulated rivers currently remain (Benke, 1990).

Studies of the ecological consequences of river impoundment have been overwhelmingly dominated by analyses of community structure (Bain *et al.*, 1988; Layzer *et al.*, 1993; Gehrke *et al.*, 1995; Poff and Allan, 1995). The two most common approaches have been comparisons of diversity and community structure of rivers before and after river impoundment (Quinn and Kwak, 2003; Taylor *et al.*, 2008), or comparisons of communities and diversity in a regulated river to one that is unregulated (Bain *et al.*, 1988; Winter *et al.*, 2008). These studies are invaluable for detecting long-term changes in riverine communities and declines in biodiversity. However, a shortcoming to these approaches is that they overlook dynamic, process-based impacts of impoundment on resilient taxa (i.e. species that can tolerate impoundment, but not collapse). For example, the presence (or even abundance) of a species in an ecosystem does not necessarily reflect optimal ecological conditions (Layman *et al.*, 2007; Rypel and Bayne, 2009). In impoundments, many lotic specialists are often relegated to suboptimal physical, physiochemical and ecological conditions from which they cannot emigrate (Beamesderfer *et al.*, 1995; Paukert and Fisher, 2001). However, variable degrees of resilience to impoundment allow these species to persist for variable periods of time in impounded rivers (Rypel *et al.*, 2006; Valentine-Rose *et al.*, 2007; Rypel and Layman, 2008; Rypel and Bayne, 2009). In such cases, other metrics are needed to better evaluate the consequences of river impoundment (Rypel and Bayne, 2009).

Fish growth rates have shown a strong potential for predicting response of resilient fish populations to impoundment (Rypel *et al.*, 2006; Schramm and Eggleton, 2006; Rypel and Bayne, 2009; Weyl *et al.*, 2009). Reproductive fitness is mediated through body size, e.g. due to the size required for maturity, size required to escape predation risks

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and the geometric relationship between size and fecundity (Mousseau and Roff, 1987; Semlitsch *et al*., 1988; Dunlop *et al*., 2005; Quince *et al*., 2008). And whereas growth rates regulate body size, fecundity and survival ability (Garvey *et al*., 1998; Arendt and Wilson, 2000), growth is perhaps the best temporally integrative proxy for organism fitness (Booth and Keast, 1986; Richner, 1989; Campana and Thorrold, 2001; Kirk, 2006; Rennie *et al*., 2008). Furthermore, fish growth rates vary across ecosystems with fundamentally different structural and functional properties (Belk, 1995; Purchase *et al*., 2005; Dunlop and Shuter, 2006), and river impoundment by dams significantly alters riverine ecosystem structure and function (Ward and Stanford, 1983; Freeman *et al*., 2007; Poff *et al*., 2007). Yet despite this, few studies have examined fish growth within the context of river impoundment.

To date, growth of 10 fish species has been compared between lentic and lotic ecosystems. Six species have shown significantly faster growth in lotic ecosystems (Rypel *et al*., 2006; Penczak, 2007; Valentine-Rose *et al*., 2007; Rypel and Layman, 2008; Weyl *et al*., 2009) while two species have shown no difference in growth between system types (Paukert and Fisher, 2001; Penczak, 2007). Vondracek *et al*. (1982) showed that temperature uncorrected growth of a sucker species was higher in a warmwater reservoir compared to surrounding coldwater mountain streams. Only one species (northern pike (*Esox lucius*) in Europe) has shown a significant increase in growth in lentic relative to lotic environments that appears unrelated to temperature effects (Paukert and Fisher, 2001; Rypel *et al*., 2006; Penczak, 2007; Valentine-Rose *et al*., 2007; Rypel and Layman, 2008; Weyl *et al*., 2009). Additionally, for two species whose growth was significantly inhibited by impoundment, the extent of growth depression was strongly and positively correlated with indices of hydrologic retention (Rypel *et al*., 2006; Rypel and Layman, 2008). Furthermore, while annual growth of some riverine fishes appears to respond to annual flow variations (Gutreuter *et al*., 1999), growth of other species apparently does not (Rutherford *et al*., 1995; Gutreuter *et al*., 1999). More examples within this context are needed to better appreciate how impoundment of rivers by dams affects a full spectrum of taxa. For example, little is known on what species might actually benefit from impoundment and why.

The sunfish family, Centrarchidae, is an ideal group of organisms from which this conceptual framework can be extended. This is one of the most diverse, and economically relevant groups of freshwater organisms in North America (Roe *et al*., 2002; Chen *et al*., 2003). Several of these species form the nucleus for many freshwater recreational fisheries and remain vital in some areas as an abundant fish food resource (Jackson, 2003; A. L. Rypel, unpublished data). Black basses in particular wield unprecedented economic sway. Chen *et al*. (2003) estimated that a single largemouth bass fishery in Texas generated ~27.5 million US Dollars during 1995 alone.

Although basic life-history has been extensively studied for various freshwater fishes in the past, many have focused on observations from impoundments (Maceina *et al*., 1991; Guy and Willis, 1995) as opposed to rivers (but see Sammons and Maceina, 2008). As a result, an assumption has long circulated in both management and ecology groups that sunfishes are better adapted for lentic environments than rivers. In this study, I evaluated this assumption by examining whether growth of 14 resilient sunfish species differed between lotic ecosystems and rivers, and explored whether hydrologic retention of impoundments could be useful for predicting sunfish growth. In doing so, a predictive context was generated on how river impoundment differentially affects the growth of diverse sunfish species.

## METHODS

Size (total length)-at-age data for 14 sunfish species were obtained from peer-reviewed and grey literature, solicited from fisheries biologists and developed from field collected data. Only rivers and impoundments were analysed in this study. No natural lakes, e.g. glacial bowl lakes, were examined in this study due to the uncertainty of how these systems differ ecologically from impoundments. For this reason, the convention was not followed of referring to these comparisons as being ‘lentic versus lotic’, and instead I refer to these comparisons as being between rivers (or lotic ecosystems) versus impoundments. Data were limited to back-calculated length-at-age data and Von Bertalanffy growth models from which mean lengths-at-ages could be extracted. For largemouth bass, the analysis focused only on southeastern USA populations in Alabama, Mississippi and Georgia so as to limit effects due to known geographical variation in genetic strains (e.g. northern vs. southern vs. Florida LMB). Any growth data from recently impounded ecosystems were not used as growth always surges temporarily following impoundment (e.g. Penczak, 1995); however any available pre-impoundment growth data were used and treated as being riverine. Aerial images from the software program Google Earth (Mountain View, CA, USA) were used to assist in evaluation of whether a given site was riverine or impounded. This included inspection of channel morphology, and searching for any dams, milldams or large road crossings in the 40 km of reach down-river that might impound water. If it was unclear from the original research papers and the aerial images whether hydrologic habitat from a study was impounded or lotic or hybrid, the data were excluded. A complete list of ecosystems for which data were collected and used can be found in the Supporting information section.

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For every site, latitude–longitude data were collected using Google Earth. Latitude–longitude data were then uploaded into the climate interpolation software program New LocClim 1.1 (FAO/SDRN, Rome, Italy). New LocClim provides local estimates of elevation, and mean annual indices of temperature, minimum temperature, maximum temperature, precipitation, water vapour pressure, potential evapotranspiration, wind speed and sunshine fraction based on interpolations of weather station data around the geographical points of interest. Thus estimates of latitude, longitude, elevation, mean annual temperature, minimum temperature, maximum temperature, precipitation, water vapour pressure, potential evapotranspiration, wind speed and sunshine fraction were available for all sites. Because many of these factors are collinear with one another, a principle components analysis was used to reduce these variables into two significant principle component factors (defined as those with eigenvalues $>1$) that describe the major climatic and geographic variations in these data. Observations for PC Factors 1 and 2 were then used as covariates in subsequent analyses of growth between rivers and impoundments.

There are limitations and assumptions to all meta-analyses (Egger *et al.*, 1997). Here, the main assumption was that any growth differences between rivers and impoundments were attributable to inherent structural and functional differences between these system types. Even though myriad other factors (e.g. densities, physiochemistry and pollution) affect growth (Kramer, 1987; Mittelbach, 1988; Power and McKinley, 1997), these effects can be compensated for by using sufficiently strong sample sizes to average out these effects (Egger *et al.*, 1997), and by including variables with consistent, linear effects as covariates in statistical models (e.g. geographical and climate data – Power and McKinley 1997). Furthermore, many variables affecting growth (physiochemistry, densities, etc.) often change alongside the impoundment of rivers (Ward and Stanford, 1983). Thus while including factors such as density or productivity would be desirable, it is often unreasonable because the data does not exist, and because many of these factors might be more important at the intra-system type level (i.e. between impoundments) rather than at the between system type level (i.e. between rivers and impoundments). Meta-analyses of this sort remain one of the few means by which scientists can gather empirical information on growth differences among ecosystems (Schindler *et al.*, 2000; Paukert and Fisher, 2001; Blenckner and Hillebrand, 2002; Rypel *et al.*, 2006; Sakaris *et al.*, 2006; Penczak, 2007; Valentine-Rose *et al.*, 2007; Rypel and Layman, 2008).

For each population from an ecosystem, a set of mean lengths-at-ages were available. All mean lengths-at-ages for the entire dataset of a species were then used as observations in Analysis of Covariance (ANCOVA) models (Noltie, 1988; Rypel *et al.*, 2006; Sakaris *et al.*, 2006), with each mean length-at-age for a population being used as an observation. In each species' model, length was the independent variable, and $\log_{10}$(age), and PC Factors 1 and 2 were covariates. If any significant effect due to covariates was found, the effect was removed via ANCOVA prior to testing for the primary treatment effect of impoundment. Finally, the mean of means for was used to develop a generalized Von Bertalanffy growth function for impounded and riverine ecosystems. These functions are provided as a simple visual example of how growth does or does not differ in these two ecosystem types. The Von Bertalanffy Growth Function is calculated as, $L_t = L_\infty[1 - e^{-k(t-t_0)}]$, where $L_t$ is the length at time $t$, $L_\infty$ is the theoretical maximum length, $k$ is a growth coefficient (the rate at which length approaches $L_\infty$), $t$ is the fish age in years and $t_0$ is the theoretical time at age zero.

To assess how sunfish growth varied across impoundments of differing hydrology and dam types, impoundment retention times (i.e. 'reservoir retention times', or the 'water renewal rate' or 'residence time') were collected for as many of the studied impoundments and species as were available. Whereas this information was missing or unavailable for most of the systems and species used in the above evaluation of growth between rivers and impoundments, this analysis was performed on three of the species that had broad coverage within certain physiographic regions, with available retention time data (largemouth bass, warmouth and white crappie). Retention times vary based on a number of factors such as impoundment depth, volume, outflow rate and lake purpose, e.g. hydroelectric, navigation, recreation (Thornton *et al.*, 1990; Wetzel, 2000). 'Run-of-the river' mainstem impoundments usually have retention times of $<7$ days, but large-scale impoundments often have retention times $>100$ days (Thornton *et al.*, 1990). Retention times are strongly influenced by physiography; therefore this portion of the analysis focused only on rivers and impoundments within the same physiographic province. Physiographic provinces follow the convention used by Benke and Cushing (2005), and are based on Hunt (1974) and the United States Geological Survey Tapestry Web Site (http://tapestry.usgs.gov). Recorded impoundment retention times (days per year) were converted to a physiographic per cent retention value by dividing each retention time value by the maximum retention time value known from that physiographic province. For example, for white crappie from the southeastern Coastal Plains, the maximum retention time for an impoundment was 164 days, thus all other retention times were divided by this value to approximate a physiographic per cent retention value. Free flowing rivers were assumed to have a retention time of zero days. Linear regressions were used to evaluate whether physiographic per cent retention values could assist in predicting sunfish growth, assayed as the slope of the length-$\log_{10}$(age) regression for a given site

(Rypel *et al.*, 2006; Rypel and Layman, 2008). All statistics were considered significant at $\alpha < 0.05$.

## RESULTS

Growth was documented between riverine and impounded ecosystems for 14 sunfishes using Von Bertalanffy growth functions (Table II, Figure 1). In total, 3966 mean lengths at ages were available across all the species. The amount of length-age data available varied tremendously among species and hydrologic environments (Table II, Supporting information). In general, growth data for rivers were more difficult to obtain, whereas growth information from impoundments were more common. Growth data for black basses and crappies were relatively easy to find, whereas growth data on smaller sunfishes, sunfishes with restricted geographic ranges, or unmanaged sunfishes were uncommon. Sample sizes for species like shadow bass, flier and redbreast sunfish exemplify this differential (Table II). Furthermore, population size for some for these species may be negatively affected by impoundment itself, further reducing the ability to study these species relative to more impoundment-resilient species.

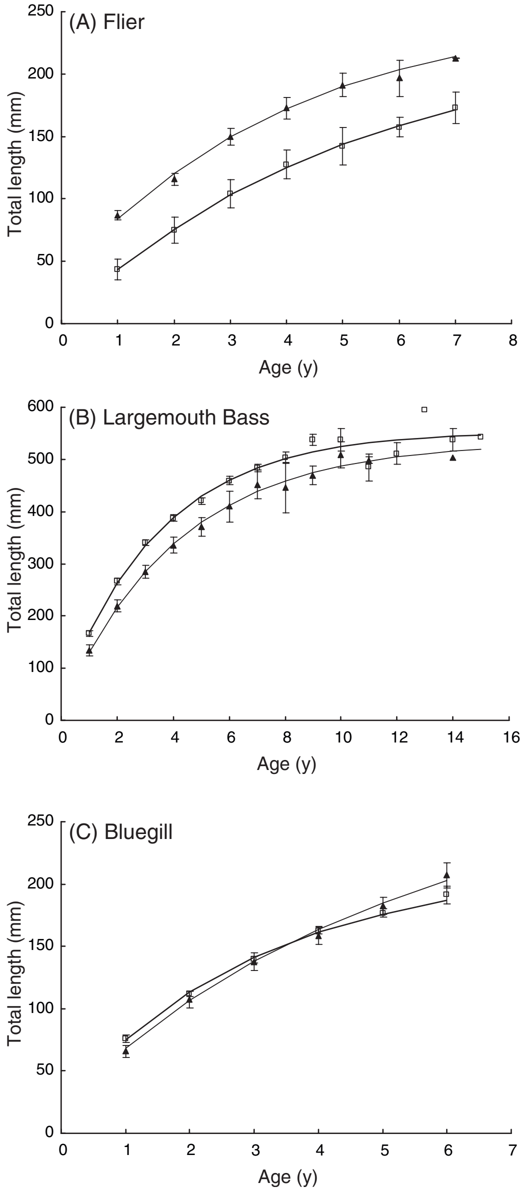

Figure 1. Three examples of growth trajectories for sunfishes from impounded (open squares, dashed curve) and riverine ecosystems (closed triangles, solid curve). Growth can be (A) depressed by impoundment, (B) enhanced by impoundment or (C) not affected by impoundment. Each symbol represents the mean of mean lengths for an age class in impounded or riverine ecosystems ±1 SE (also of the mean of means), and curves are Von Bertalanffy growth functions (parameters in Table II)

PCA of climatic and geographical variables produced two factors which described 80% of variations in these variables across sites (Table I). Factor one was driven largely by temperature and latitude. Maximum, minimum and mean temperature, vapour pressure and latitude together combined to describe 74% of variability in Factor 1. Factor 2 was driven primarily by longitude, sunshine fraction, precipitation, evapotranspiration and wind. Together, these five factors explained 95% of variability in Factor 2. Factor scores for each mean length at age for each site were subsequently used as covariates in ANCOVA models evaluating growth differences between rivers and impoundments. Growth effects due to Factors 1 and 2 were removed via ANCOVA allowing for detection of the primary effect of interest – impoundment.

All ANCOVA models were significant and yielded $R^2$ values that ranged from 0.72 to 0.94. $\text{Log}_{10}$(age) was

Table I. Factor loadings and per cent contribution of variables (adjacent in parentheses) extracted from PCA of geographical and climatological variables at each site

| Geographic/climatological variable | Factor 1 | Factor 2 |
|---|---|---|
| Latitude | −0.97 (14.9) | −0.04 (0.06) |
| Longitude | 0.12 (0.2) | 0.78 (25.5) |
| Elevation | −0.52 (4.3) | −0.26 (2.9) |
| Potential evapotranspiration | 0.75 (8.8) | −0.59 (14.6) |
| Annual precipitation | 0.57 (5.1) | 0.65 (17.5) |
| Sunshine fraction | 0.50 (4.0) | −0.72 (21.4) |
| Mean temperature | 0.98 (15.4) | −0.09 (0.4) |
| Maximum temperature | 0.97 (15.0) | −0.12 (0.6) |
| Minimum temperature | 0.97 (14.8) | −0.06 (0.2) |
| Water vapour pressure | 0.94 (14.0) | 0.15 (1.0) |
| Wind speed | −0.47 (3.5) | −0.62 (2.9) |

Eigenvalues were 6.3 and 2.4 for Factors 1 and 2, respectively. Other PCA factors were not used because Eigenvalues were <1.0. Factors 1 and 2 were subsequently used as covariates in ANCOVA evaluations of fish growth between rivers and impoundments.

Table II. Generalized Von Bertalanffy growth functions for 14 sunfish species from impounded and riverine ecosystems

| Species | Common name | Riverine ecosystems | | | | Impoundments | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | No. populations | $L_\infty$ | $k$ | $t_0$ | No. populations | $L_\infty$ | $k$ | $t_0$ |
| *Ambloplites ariommus* | Shadow bass | 10 | 261.4 | 0.25 | −0.39 | 5 | 724.2 | 0.05 | −1.72 |
| *Ambloplites rupestris* | Rock bass | 31 | 269.4 | 0.23 | −0.17 | 11 | 308.1 | 0.13 | −0.11 |
| *Centrarchus macropterus* | Flier | 10 | 252.7 | 0.25 | −0.63 | 11 | 230.6 | 0.19 | −0.08 |
| *Lepomis auritus* | Redbreast sunfish | 29 | 223.7 | 0.40 | 0.30 | 12 | 147.3 | 0.49 | 0.00 |
| *Lepomis cyanellus* | Green sunfish | 21 | 199.6 | 0.41 | 0.31 | 11 | 277.8 | 0.18 | −0.22 |
| *Lepomis gulosus* | Warmouth | 14 | 223.0 | 0.34 | 0.11 | 34 | 206.9 | 0.45 | 0.13 |
| *Lepomis macrochirus* | Bluegill | 26 | 280.6 | 0.20 | −0.38 | 70 | 213.7 | 0.36 | −0.19 |
| *Lepomis megalotis* | Longear sunfish | 29 | 244.5 | 0.14 | −0.34 | 13 | 215.7 | 0.32 | −0.36 |
| *Lepomis microlophus* | Redear sunfish | 10 | 329.7 | 0.24 | −0.29 | 16 | 251.6 | 0.41 | 0.04 |
| *Micropterus dolomieu* | Smallmouth bass | 70 | 543.1 | 0.18 | −0.18 | 19 | 491.1 | 0.42 | 0.42 |
| *Micropterus punctulatus* | Spotted bass | 29 | 794.4 | 0.11 | −0.37 | 56 | 505.6 | 0.32 | 0.12 |
| *Micropterus salmoides* | Largemouth bass | 15 | 532.9 | 0.24 | −0.16 | 17 | 554.5 | 0.28 | −0.28 |
| *Pomoxis annularis* | White crappie | 26 | 454.8 | 0.21 | 0.06 | 56 | 376.7 | 0.31 | −0.03 |
| *Pomoxis nigromaculatus* | Black crappie | 13 | 287.7 | 0.51 | 0.40 | 77 | 329.9 | 0.38 | 0.27 |

significantly, positively correlated with fish length for every species (Table III). For 11 of 14 species, Factor 1 significantly, and positively correlated with growth, and in all cases, this was a positive correlation (i.e. growth was faster in more southern latitudes and decreased moving northwards); the three species that were unaffected by Factor 1 were species with relatively small geographic ranges or had datasets composed of more localized populations where climate varied less. For 7 of 14 species, growth also correlated with Factor 2, however, the results were not as straightforward. Four species, all three black basses and bluegill, showed a significant positive correlation with Factor 2 (amounting to positive correlations with longitude and precipitation, and negative correlations with potential evaporation, sunshine fraction and wind), but three species (green sunfish, warmouth and black crappie) showed a significant negative correlation with this same factor (i.e. negative correlations with longitude, and precipitation, and positive correlations with potential evaporation, sunshine fraction and wind). Effects due to these covariates were removed prior to determination of the primary treatment effect of river impoundment. After accounting for significant effects of covariates, five species (shadow bass, rock bass, flier, redbreast sunfish and green sunfish) had significantly

Table III. Results of ANCOVA for the effects of impoundment on growth of 14 sunfishes

| Species | Common name | Model | | Main effect | | Covariates | | |
|---|---|---|---|---|---|---|---|---|
| | | $p$ | $R^2$ | Impoundment | $t$-Score | PCA factor 1 | PCA factor 2 | Log age |
| *Ambloplites ariommus* | Shadow bass | **<0.0001** | 0.94 | **<0.0001** | **6.26** | **<0.0001 (+)** | 0.11 | **<0.0001** |
| *Ambloplites rupestris* | Rock bass | **<0.0001** | 0.85 | **<0.0001** | **6.77** | 0.54 | 0.40 | **<0.0001** |
| *Centrarchus macropterus* | Flier | **<0.0001** | 0.79 | **<0.0001** | **7.02** | **0.05 (+)** | 0.24 | **<0.0001** |
| *Lepomis auritus* | Redbreast sunfish | **<0.0001** | 0.80 | **<0.0001** | **5.39** | 0.46 | 0.68 | **<0.0001** |
| *Lepomis cyanellus* | Green sunfish | **<0.0001** | 0.87 | **0.05** | **1.94** | **0.004 (+)** | **<0.0001** (−) | **<0.0001** |
| *Lepomis gulosus* | Warmouth | **<0.0001** | 0.82 | 0.24 | 1.17 | **0.002 (+)** | **<0.0001** (−) | **<0.0001** |
| *Lepomis macrochirus* | Bluegill | **<0.0001** | 0.77 | 0.77 | 0.30 | **<0.0001 (+)** | **0.02 (+)** | **<0.0001** |
| *Lepomis megalotis* | Longear sunfish | **<0.0001** | 0.72 | **0.0001** | **−3.94** | **<0.0001 (+)** | 0.97 | **<0.0001** |
| *Lepomis microlophus* | Redear sunfish | **<0.0001** | 0.85 | 0.12 | 1.56 | **<0.0001 (+)** | 0.32 | **<0.0001** |
| *Micropterus dolomieu* | Smallmouth bass | **<0.0001** | 0.87 | **<0.0001** | **−6.59** | 0.08 | **0.008 (+)** | **<0.0001** |
| *Micropterus salmoides* | Largemouth bass | **<0.0001** | 0.91 | **<0.0001** | **−8.37** | **0.05 (+)** | **0.005 (+)** | **<0.0001** |
| *Micropterus punctulatus* | Spotted bass | **<0.0001** | 0.86 | **0.0001** | **−3.57** | **<0.0001 (+)** | **0.02 (+)** | **<0.0001** |
| *Pomoxis annularis* | White crappie | **<0.0001** | 0.81 | 0.43 | −0.79 | **<0.0001 (+)** | 0.13 | **<0.0001** |
| *Pomoxis nigromaculatus* | Black crappie | **<0.0001** | 0.77 | 0.94 | −0.08 | **<0.0001 (+)** | **0.05** (−) | **<0.0001** |

Positive $t$-test statistics indicate higher growth in riverine systems whereas negative scores indicate higher growth in impoundments. Significant direction correlations of growth to Factors 1 and 2 are listed in parentheses. All numbers indicate $p$-values unless otherwise notated and significant differences and correlations are indicated in bold.

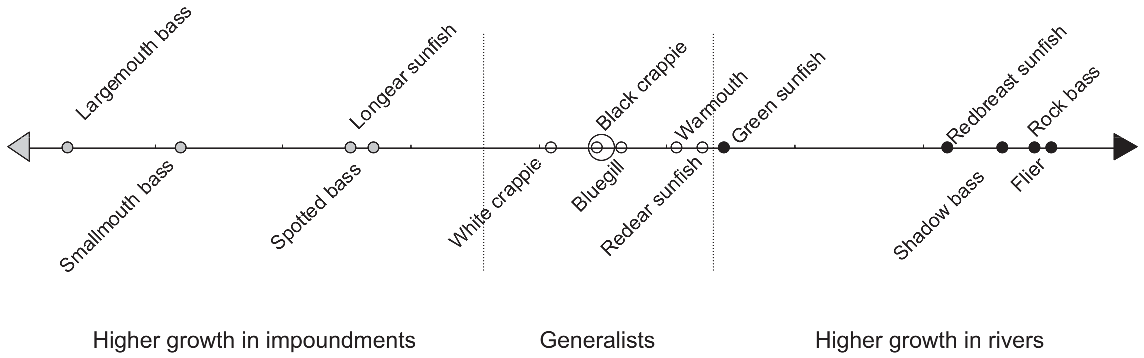

Figure 2. Conceptual model of sunfish growth differences across the impoundment gradient. Species positions along the gradient are based on ANCOVA *t*-test statistics for species growth differences between impounded and riverine ecosystems (i.e. from Table III). Vertical dashed bars represent approximate position for significant differences and the large open circle represents a value of zero (i.e. absolutely no difference in growth between impounded and riverine ecosystems)

higher growth in riverine ecosystems, four species (longear sunfish, spotted bass smallmouth bass and largemouth bass) had significantly higher growth in impounded ecosystems and five species (bluegill, redear, warmouth, white crappie and black crappie) showed no difference in growth between impounded and riverine ecosystems (Table III).

Species varied in the degree to which growth differences were expressed due to impoundment (Table III, Figure 2). Shadow bass showed the largest decline in growth rate due to impoundment, but largemouth bass showed the largest increase in growth due to impoundment. The degree to which growth changed due to impoundment can be quantified using the *t*-test statistics from ANCOVAs (Table III). A high, positive *t*-test statistic showed that growth was significantly higher in lotic systems, but a highly negative *t*-test statistic showed that growth was significantly higher in impoundments. Species with *t*-test statistics approaching zero had neither higher nor lower growth in impoundments or riverine ecosystems. To visualize the differences among species in growth response to impoundment, *t*-test statistics were plotted along a single ‘axis of impoundment’ in Figure 2.

The extent to which physiographic per cent retention could predict growth of sunfishes was evaluated for three species from four physiographic provinces for which hydrologic retention time data were available. For warmouth in Central Lowlands rivers, growth rate was highest in riverine ecosystems and declined predictably ($R^2 = 0.63$) with increases in hydrologic retention (Figure 3). For largemouth bass in Coastal Plain rivers, the opposite was true. Largemouth bass growth was lowest in rivers and increased predictably ($R^2 = 0.75$) with increasing hydrologic retention (i.e. lentic habitat, Figure 3). White crappie in the Central Lowland rivers (i.e. Southern Plains rivers) showed no predictability in growth with varying degrees of hydrologic retention ($R^2 = 0.001$, Figure 3). However, in Coastal Plain rivers, white crappie growth was highest in rivers and declined predictably with increasing hydrologic retention ($R^2 = 0.76$, Figure 3).

## DISCUSSION

Humans have long undervalued the significance of rivers for providing ecosystem services such as fish production (Decamps *et al*., 1988; Welcomme, 1995; Kingsford, 2000; Naiman and Turner, 2000; Tockner and Stanford, 2002; Pringle, 2003b; Dudgeon *et al*., 2005). As a consequence, fundamental land use decisions regarding impoundment of freshwater ecosystems have usually proceeded in the absence of information on how lotic ecosystems differ from impoundments, simply because this information rarely exists. The prevalence of farm ponds, dikes, dams and road crossings that lack sufficient flow conveyance and impound diverse freshwaters typifies how pervasive this problem has become. It is imperative that a more predictive understanding of effects of impoundment be generated and incorporated into theoretical and applied aspects of conservation biology, and basic land use decision making (Ward and Stanford, 1983; Pringle, 2003a). Most studies seeking to predict effects of impoundment have relied on community-based metrics (Bain *et al*., 1988; Freeman *et al*., 2005; Zeug *et al*., 2005; Taylor *et al*., 2008). However, community-level data tends to ignore impacts on species resilient to impoundment (Rypel and Layman, 2008; Rypel and Bayne, 2009). Thus, it is often assumed that if a species is present or abundant in an impounded ecosystem, that such a species is not affected by impoundment.

In this study, predictive models were generated showing potential consequences of river impoundment on a critical population characteristic (growth) of impoundment-resilient sunfishes. Four species grew significantly faster in

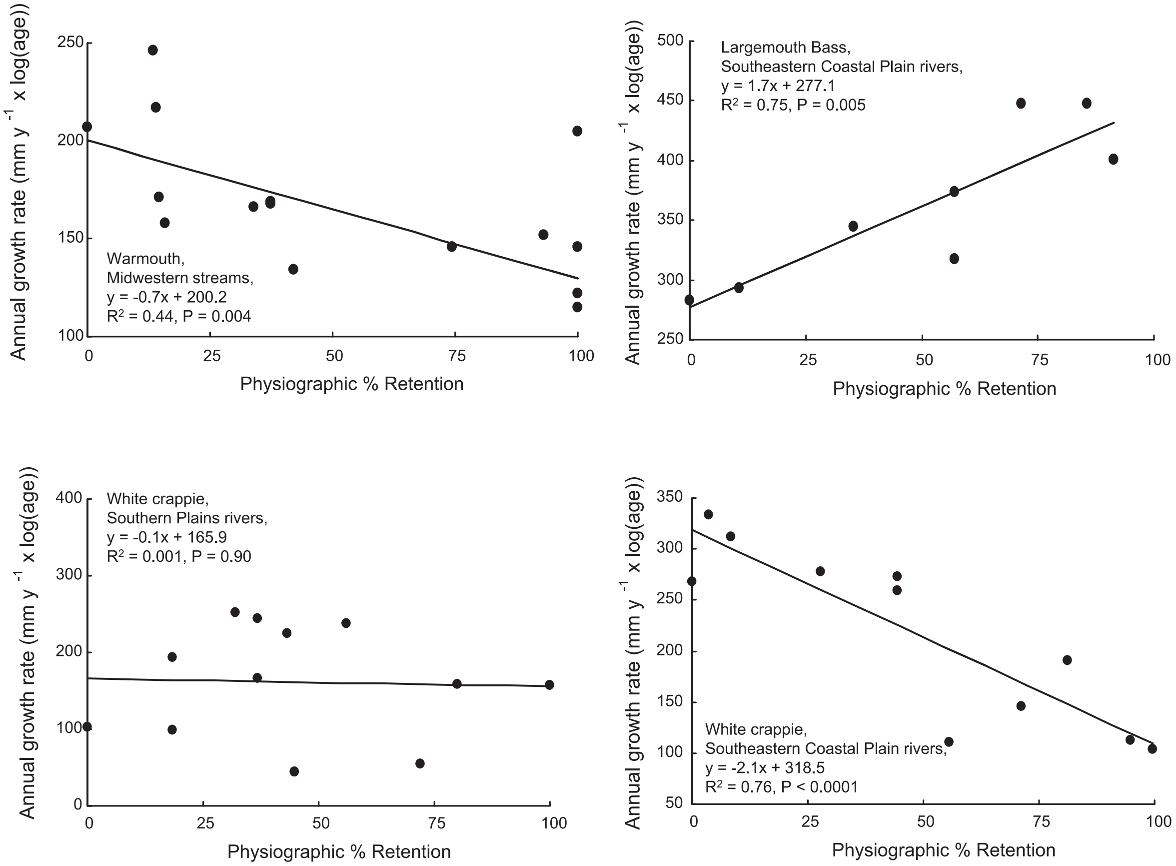

Figure 3. Site-specific growth rates for three fish species (from different physiographic zones) expressed as linear functions of physiographic per cent retention time values

impounded ecosystems, five species grew significantly faster in riverine ecosystems and five species showed no difference in growth between hydrologic habitat types. These data deepen our understanding of impacts of river impoundment on fishes.

Until now, it has been presumed that fish growth responds in one of two basic directions to river impoundment/alteration: growth either increases or decreases (e.g. Rypel *et al*., 2006; Schramm and Eggleton, 2006; Rypel and Layman, 2008). However, it can be seen from these data that such a perspective ignores a large number of species that are cosmopolitan (i.e. species whose growth does not differ between rivers and impoundments, and that can therefore occupy a wide variety of ecosystem types). This is a subtle, but key departure from the notion that species are adapted exclusively for either lentic or lotic environments alone. This perspective is supported through previous research. In similar studies, growth has been shown to be consistently higher for certain species in lotic ecosystems (Rypel *et al*., 2006; Penczak, 2007; Rypel and Layman, 2008), but for other select species there was no change in growth rate (Paukert and Fisher, 2001; Penczak, 2007). In this study, I expanded this perspective by introducing four species (largemouth, smallmouth and spotted bass, and longear sunfish) whose growth was significantly enhanced by river impoundment. Thus growth (and possibly also, species persistence) in flow-altered environments appears to lie along a continuum where growth can be reduced, not affected or enhanced through impoundment.

I attempted to visualize this continuum by plotting *t*-test statistics for each species from ANCOVA models (Figure 2). Using this conceptual diagram, important patterns regarding effects of river impoundment begin to emerge that require future investigation. For example, closely related species (e.g. *Micropterus* spp., *Pomoxis* spp. and *Ambloplites* spp.) apparently respond in highly similar ways to impoundment suggesting common explanations and adaptations (e.g. life history, diet and ecology) underlying these patterns (Lytle and Poff, 2004). For example, black basses may have higher growth in impoundments because an energetically rich food item that these species are well adapted to capitalize upon becomes more abundant in these environments, e.g. shads. Conversely, *Ambloplites* spp. may have higher growth in riverine environments because these species specialize on

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prey items common to unregulated streams (e.g. aquatic insects on snags, crayfishes and bivalve mussels) or on terrestrial items in constituent floodplains (Wheeler and Allen, 2003), and not on prey common to impoundments. Additionally, factors such as physiology (Smoot and Findlay, 2000), body size, home range size, relative motility (Bayne *et al*., 2002), age-at-maturity, juvenile survivorship, fecundity, etc. (Winemiller and Rose, 1992), may all influence these patterns to an unknown degree. Further research is needed to ascertain which specific life-history attributes drive susceptibility of different species to river impoundment.

Physiographic-specific indices of hydrologic retention can predict growth rates for certain sunfishes in certain areas. There was a strong positive relationship between hydrologic retention and growth for largemouth bass (a lentic specialist), and a strong negative relationship between hydrologic retention and growth for warmouth (a riverine specialist). However, hydrologic retention did not predict growth of a cosmopolitan species like white crappie in one region, but could in another. Once again, further research is required to identify key factors that drive these patterns, i.e. factors that track these trend lines similarly across the impoundment gradient and place other factors (e.g. nutrients, density-dependence) in more appropriate contexts. However, these results show that impacts of impoundment on fish growth (and likely also production) are often predictable.

Additionally, it is important to recognize that effects of impoundment can become more or less prominent in different regions with landscape types. In the southeastern Coastal Plain, hydrologic retention was a strong, negative predictor of white crappie growth ($R^2 = 0.76$). Yet in the Central Lowlands, white crappie growth showed no relationship with this factor ($R^2 = 0.001$). Such a change in response could be explained by the differences in landscapes and hydrologic function of rivers in these two very different areas. Free-flowing rivers in the southeastern Coastal Plain are dynamic, subtropical, low-lying rivers that experience massive annual floodplain inundations during the wet season (Ward *et al*., 2005; Rypel *et al*., 2008). These floods provide fishes access to the floodplain and to feed and reproduce (Slipke *et al*., 2005; Ward *et al*., 2005). Excising access to these critical zones through impoundment and stabilization of flow constitutes a major alteration to these ecosystems and to the availability of food for its constituent organisms (Slipke *et al*., 2005). In contrast, rivers in the Central Lowlands region of Oklahoma (where these white crappie growth data were all derived from) are some of the more extreme riverine environments (in terms of high temperatures and hydrologic variation) on the continent (Matthews *et al*., 2005). Rivers in this area are characterized mainly as low gradient prairie streams with wide, shallow, braided sand-bed channels and sparsely forested floodplains (Matthews *et al*., 2005). Flooding provides fish limited access to the floodplain, however these floodplains are considerably less productive relative to coastal plain rivers (Benke, 1998; Matthews *et al*., 2005). For example, these ecosystems contain far fewer trees and submerged woody habitat, i.e. less snags and more brush (Benke *et al*., 1985; Benke and Wallace, 1990; Matthews *et al*., 2005), and the floodplains are inundated for shorter periods of time. It is therefore understandable that the same species does not respond to impoundment in the same ways in these disparate environments.

Riverine ecosystems require more attention from both a fisheries management and conservation perspective. In collecting the data for this study, it was immediately apparent that little is known concerning fish population characteristics in rivers relative to lakes and impoundments. Even for popular gamefishes (e.g. black basses and crappies) very little information was available, historically or contemporarily, on population characteristics in rivers. Yet rivers clearly produce large, fast growing, trophy-sized sunfishes. And while angling pressure may be light on certain rivers, in many others (e.g. those with a significant subsistence fisheries) angling pressures can be substantial (Welcomme, 1976; Welcomme, 1979; Burger, 1998; Jackson, 2003; A. L. Rypel unpublished data). Managers should be encouraged to inventory these fish populations and their population characteristics to better understand the scope and integrity of these resources. This will provide data that can assist in current, but especially, future conservation and management of these species and ecosystems.

The impoundment of freshwater ecosystems should be approached with caution and with knowledge on how impoundment might alter ecosystem function and services. This study provided examples of how differing levels of impoundment can affect an entire suite of economically valuable fishes. The results highlight that species respond to impoundment in different, but consistent ways. For example, it would be unreasonable, based on these data, to expect that shadow bass or flier would be capable of sustaining robust populations in rivers with extensive impoundments. And while the growth of a relatively small number of species might be benefitted by impoundment, this is clearly at the expense of lotic specialist fitness. This also ignores a large number of non-resilient species that are quickly extirpated due to impoundment.

The assumption that lentic waters in impoundments are favourable environments for sunfishes was only true for 4 of 14 species – 3 of which were the black basses. Therefore, the notion that sunfishes excel in impounded ecosystems relative to rivers should be discarded. It is possible the only reason this assumption has been perpetuated for as long as it has is because black basses (species for which pervasive

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and valuable recreational fisheries exist) are the main group of sunfishes for which impoundment favours. However, another possibility (and area of research opportunity) is that impoundment affects abundance in addition to growth rate. This leads to an important question that needs to be addressed: Can impoundment increase or decrease secondary production in spite of hampered or enhanced growth? In other words, could production of a species like bluegill be higher in impoundments because of increased densities, even though growth does not vary between system types. Such questions represent an essential bridge between the community studies that have dominated the river ecology literature in the past, and recent studies emphasizing the need to incorporate dynamic processes such as growth into ecological evaluations of rivers and their biological communities. Thus future studies must expand to considerations of ecosystem functions (e.g. secondary production, decomposition, nutrient cycling) that incorporate multiple correlative factors such as density and growth to see how these more fully integrative metrics change with river impoundment and flow regulation.

Nonetheless, this study also suggests that growth itself is an underutilized metric for examining the response of fish populations to various restoration initiatives (e.g. Gore and Shields, 1995; Sparks, 1995; Kanehl *et al*., 1997; Poff *et al*., 1997; Sparks *et al*., 1998; Galat and Lipkin, 2000). Parallel research tracks have been followed in restoration ecology and river ecology, and both fields have relied heavily on community-based approaches. Furthermore, growth and other population-level data (e.g. mortality, condition factor and stock assessment) are the backbone of fisheries science, and would be of great value to most fisheries biologists, especially considering the great need for increased data on fisheries dynamics in rivers. Acquisition of such data on rivers and in the context of river restoration may be a 'win–win' situation for both river ecologists and fisheries managers. Forging professional relationships between both these groups might facilitate more rapid acquisition of data on river fishes, improve funding opportunities and enhance interdisciplinary river science as a whole.

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