RIVER RESEARCH AND APPLICATIONS

River Res. Applic. **28**: 1567–1586 (2012)

Published online 5 June 2011 in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/rra.1545

POPULATION DEMOGRAPHICS OF CATOSTOMIDS IN LARGE RIVER ECOSYSTEMS: EFFECTS OF DISCHARGE AND TEMPERATURE ON RECRUITMENT DYNAMICS AND GROWTH[§]

M. C. QUIST[a]* and J. R. SPIEGEL[b†]

[a] *U.S. Geological Survey—Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Resources, University of Idaho, P.O. Box 44114, Moscow, Idaho 83844, USA*

[b] *Department of Natural Resource Ecology and Management, Iowa State University, Ames, Iowa 50011, USA*

ABSTRACT

Catostomids are among the most widespread and ecologically important groups of fishes in North America, particularly in large river systems. Despite their importance, little information is available on their population demographics and even less is known about factors influencing their population dynamics. The objectives of this study were to describe annual mortality, recruitment variation, and growth of eight catostomid species, and to evaluate the effects of discharge and temperature on year-class strength and growth in Iowa rivers. Catostomids were sampled from 3-km reaches in four nonwadable rivers during June–August 2009. Northern hogsucker, *Hypentelium nigricans*, golden redhorse, *Moxostoma erythrurum*, and shorthead redhorse, *M. macrolepidotum*, typically lived 6–8 years, had very stable recruitment, and had high total annual mortality (i.e., 40–60%). Golden redhorse exhibited the fastest growth of all species. Growth of northern hogsucker and shorthead redhorse was intermediate to the other catostomids. Highfin carpsucker, *Carpiodes velifer*, quillback, *Carpiodes cyprinus*, and white sucker, *Catostomus commersonii*, had high growth rates, low mortality (i.e., 25–30%), and relatively stable recruitment. River carpsucker, *Carpiodes carpio*, and silver redhorse, *M. anisurum*, had higher maximum ages (up to age 11), slower growth, lower total annual mortality (20–25%), and higher recruitment variability than the other species. Neither discharge nor temperature was strongly related to recruitment of catostomids. In contrast, several interesting patterns were observed with regard to growth. Species (e.g., carpsuckers, *Carpiodes* spp.) that typically consume prey items most common in fine substrates (e.g., chironomids) had higher growth rates in reaches dominated by sand and silt substrate. Species (e.g., northern hogsucker) that consume prey associated with large substrates (e.g., plecopterans) had much faster growth in reaches with a high proportion of rocky substrates. Temperature was weakly related to growth of catostomids; however, discharge explained a substantial amount of the variation in growth of nearly all species. Results of this study provide important information on the autecology of catostomids that can be used for comparison among species and systems. These data also suggest that connection of rivers with their floodplain is an important feature for catostomids in temperate river systems. Published in 2011 by John Wiley & Sons, Ltd.

KEY WORDS: Catostomidae; flood pulse concept; temperate river ecology; age and growth; recruitment

Received 27 January 2011; Revised 30 March 2011; Accepted 22 April 2011

INTRODUCTION

Large rivers are considered among the world's most dynamic, diverse, and complex ecosystems and serve a number of human needs, including routes for transportation, and as sources of food, industrial and municipal water, power, and recreation (Dynesius and Nilsson, 1994; Spink *et al.*, 1998). Unfortunately, large rivers are also among our most severely degraded systems because of the negative effects of impoundment, channelization, discharge of pollutants from urban and industrial sources, and high nutrient and sediment loads (Jurajda, 1995; Puckridge *et al.*, 1998; Bunn *et al.*, 1999; Rosenberg *et al.*, 2000; Turner and Rabalais, 2003; Nilsson *et al.*, 2005; Rinne *et al.*, 2005). In turn, degradation of physical and chemical habitat has had a variety of negative effects on aquatic organisms where 35% of fish, 75% of unionid mussels, and 65% of crayfishes in North America are imperiled or have gone extinct, compared with only 11–14% of terrestrial vertebrates (i.e., birds, mammals, and reptiles; Master, 1990). Anthropogenic effects on aquatic ecosystems are particularly evident in the midwestern US where row-crop agriculture, pasture, and urban development dominate watershed land uses (Wehmeyer *et al.*, 2011). For example, more than 85% of the landscape in Iowa has been altered by either agriculture or urban development (Natural Resources Conservation Service, 2000). Like much of North America, these disturbances have

*Correspondence to: M. C. Quist, U.S. Geological Survey—Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Resources, University of Idaho, P.O. Box 44114, Moscow, Idaho 83844, USA.
E-mail: mcquist@uidaho.edu
[†]Current address: U.S. Fish and Wildlife Service, Green Bay Fish and Wildlife Conservation Office, 2661 Scott Tower Road, New Franken, Wisconsin 54229, USA.

had a significant effect on aquatic biota in stream and river systems. Of the 297 species classified by the Iowa Department of Natural Resources as species of greatest conservation need (SGCN), 135 (48.4%) are aquatic species with fishes representing the highest proportion of sensitive species (24.4% of all SGCN; Zohrer, 2006). In addition, approximately 44% of Iowa's native fishes are identified as SGCN, a proportion exceeded only by freshwater mussels (53% of all mussel species are SGCN). Although a few of these fish species are found in small streams and lakes, most are restricted to large river systems (e.g., western silvery minnow, *Hybognathus argyritis*). Catostomids are of particular interest in Iowa and elsewhere because of their widespread distribution and because an increasing number of species are considered vulnerable, threatened, or endangered (Cooke *et al.*, 2005).

Catostomids are among the most diverse groups of fishes in North America and although they are common in nearly all aquatic habitats, from small streams to wetlands, they are especially prevalent in large rivers (Minckley and Deacon, 1991; Jenkins and Burkhead, 1994; Cooke *et al.*, 2005). For instance, Bunt and Cooke (2001) found that catostomids (primarily redhorse, *Moxostoma* spp.) dominated the total biomass of the fish assemblage in middle reaches of the Grand River, Ontario, Canada. Neebling and Quist (2010) reported that catostomids were among the most widely distributed groups of fishes in nonwadable rivers across Iowa and comprised nearly 65% of the total fish biomass sampled. Probably because of their ubiquity and abundance, catostomids are also important components of commercial, recreational, and subsistence fisheries in river systems (Carlander, 1954; Harlan *et al.*, 1987; Scoppettone and Vinyard, 1991; Markle and Cooperman, 2002; Cooke *et al.*, 2005). Although catostomids maintain social, economic, and ecological importance, little research has focused on their population characteristics.

Understanding the demographics (e.g., age structure, longevity) and dynamics (e.g., somatic growth) of fish populations is central to management and conservation activities (Ricker, 1975; Allen and Hightower, 2010). Fish population dynamics are often compartmentalized to include recruitment, mortality, and growth (typically termed dynamic rate functions; Ricker, 1975). Recruitment is considered the governing yet most variable component of fish population dynamics (Gulland, 1982). Consequently, understanding factors related to year-class strength and recruitment variability continues to be an active area of research in fishery science (Brunel and Boucher, 2007; Zeug and Winemiller, 2008; Zhao *et al.*, 2009). Mortality is also an important component of fish population dynamics, and changes in mortality often reflect alterations in physical or chemical habitat conditions, biological interactions, or exploitation (e.g., Johnson, 2007; Swain *et al.*, 2007). Although recruitment and mortality play critical roles in regulating the number of fish in a population, growth is particularly important from an ecological perspective (DeVries and Frie, 1996). Nearly all events in a fish's life history are regulated by size; thus, growth of an individual has a direct influence on survival and reproduction (e.g., Quinn and Peterson, 1996). As such, describing growth rates and understanding factors influencing growth is critical not only for understanding population dynamics but also for better understanding how ecosystems function (e.g., nutrient and energy flow; McIntyre *et al.*, 2008).

A number of conceptual frameworks have been proposed for understanding the structure and function of lotic systems and for conceptualizing factors that might influence fish population dynamics. Of particular relevance is the flood pulse concept (FPC) that was developed to describe the function of large, floodplain rivers (Junk *et al.*, 1989). The FPC contends that the most important hydrologic feature of large rivers is the annual flood pulse that connects the river to its floodplain. As a result, the FPC argues that the majority of a river's productivity is derived from the floodplain rather than from simple downstream transport. During flood conditions, some organisms move onto the floodplain to secure new resources and spawn. When flood waters recede, nutrients, organic matter, and organisms (e.g., insects, juvenile fishes) are transported back to the main channel. Most research focused on the FPC has been conducted on tropical systems (Junk *et al.*, 1989), and although research on temperate floodplain systems has increased over the last 10–15 years (e.g., Rutherford *et al.*, 1995; Schramm and Eggleton, 2006; Shoup and Wahl, 2009), comparatively little is known about how floodplain dynamics influence fish populations in temperate river systems. This study was conducted to describe recruitment, mortality, and growth, and to evaluate factors related to recruitment and growth of catostomids in four large Iowa river systems. We were particularly interested in testing the hypothesis that warm temperature and high flows (i.e., flood) would have a positive effect on recruitment and growth of catostomids.

METHODS

Four 3-km long sampling reaches were identified on the Boone, North Raccoon, Shell Rock, and Wapsipinicon rivers in Iowa (Figure 1). Reaches were selected to encompass the diversity of habitat characteristics (Table I) and catostomid assemblages typical of large, nonwadable rivers in Iowa (Neebling and Quist, 2010). All four rivers are located in the Mississippi River basin, and all are fifth-order (i.e., Strahler stream order) systems at the location of sampling. The Boone and North Raccoon rivers originate in north-central Iowa and flow south where they meet the Des Moines River in central Iowa. The Des Moines River reaches the Mississippi River at the extreme southeastern corner of the state near

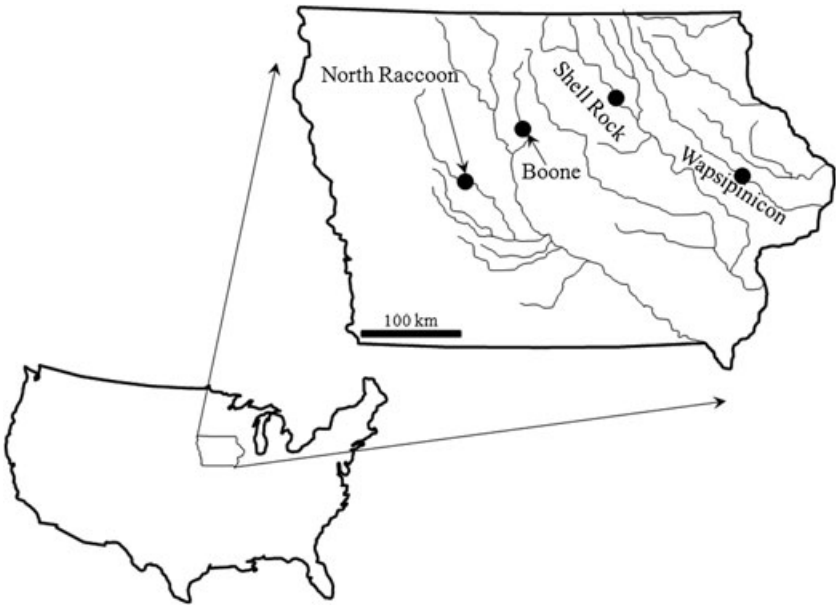

Figure 1. Location of sampling reaches from four nonwadable river systems in Iowa, 2009.

Keokuk, Iowa. The Shell Rock River originates in south-central Minnesota, flows south through northeastern Iowa, and reaches the Cedar River at Columbus Junction, Iowa. The Cedar River meets the Iowa River and flows east to the Mississippi River near Iowa City, Iowa. The Wapsipinicon River originates in south-central Minnesota and flows south and east to meet the Mississippi River near Clinton, Iowa. Although the landscape of Iowa has been highly altered by agriculture, other major anthropogenic disturbances to the river systems are minimal. Specifically, none of the study rivers are influenced by large dams, connections with the floodplain are common due to the lack of extensive channelization and levees (especially near the study reaches), and riparian forests are well developed in all four river systems (Neebling and Quist, 2010).

Fishes were sampled from each reach using pulsed-DC boat electrofishing (Smith-Root VVP-15B; Smith-Root, Inc., Vancouver, WA) during June–August 2009. Catostomids were identified, measured to the nearest millimeter (total length), and weighed to the nearest gram. The left marginal pectoral fin ray was removed by cutting just proximal to the point of where the fin ray joined the body wall (Koch *et al.*, 2008; Spiegel *et al.*, 2010). After drying, fin rays were mounted in epoxy following the methods provided in the study by Koch and Quist (2007). Fin rays were cut into 1.0-mm thick sections using a low-speed saw (Buehler Isomet; Buehler, Inc., Lake Bluff, IL). Sections were aged with a stereoscope connected to a computer. Measurements of annulus spacing and fin ray radii were obtained using image analysis software (Image ProPlus; Media Cybernetics, Inc., Bethesda, MD).

Table I. Mean annual discharge (1955–2009; m^3/s), wetted and bank-full channel width (m), depth (m), percentage of fine substrate (%; silt, sand), percentage of large rocky substrate (%; gravel, cobble, boulder), and volume of large woody debris (m^3/km) in four nonwadable rivers in Iowa, 2009

River	Discharge	Width		Depth	Substrate		Large woody debris
		Wetted	Bank-full		Fine	Rocky	
Boone	21.3 (2.3)	39.0 (8.6)	49.9 (9.8)	1.1 (0.4)	60.2 (16.0)	28.5 (14.9)	4.5 (2.5)
North Raccoon	35.2 (2.8)	43.0 (15.4)	72.8 (13.4	0.9 (0.6)	81.4 (18.1)	12.8 (7.4)	19.5 (11.3)
Shell Rock	44.4 (3.5)	65.1 (10.4)	76.8 (12.9)	1.2 (0.8)	30.4 (12.4)	65.4 (14.3)	7.6 (2.9)
Wapsipinicon	24.5 (1.9)	68.7 (18.2)	87.5 (23.8)	1.2 (0.5)	98.1 (11.1)	0.7 (0.4)	5.5 (2.6)

Number in parenthesis represents one standard error.

Published in 2011 by John Wiley & Sons, Ltd.

DOI: 10.1002/rra

All fin ray sections were independently aged by two readers. Readers assigned ages without knowledge of the fish's length or the age estimate of the other reader. When disagreements occurred between age estimates (<10% of fish), readers attempted to reach a consensus age. Fish were removed from further analysis if readers could not agree on an age. The accuracy of using fin rays for estimating age has not been evaluated for all of the species examined in this study. However, formation of annuli in pectoral fin rays has been validated for a number of species (e.g., lake sturgeon, *Acipenser fulvescens*; Bruch *et al.*, 2009), including shorthead redhorse (Harbicht, 1990).

Total annual mortality (A) was estimated using a weighted catch curve (Miranda and Bettoli, 2007). Only age-3 and older fish appeared to be consistently recruited to the sampling gear; thus, A was estimated for age-3 and older fish.

Evaluating recruitment is best accomplished using long-term data collected with standard methods. Because such data are often lacking for fish populations, particularly for little-studied species like those in the current study, techniques have been developed to index year-class strength and recruitment variability using age structure data from one-time samples. Maceina (1997) described a technique of using Studentized residuals from catch–curve regressions as an index of year-class strength (hereafter termed the residual technique). Positive residuals represent strong year-classes and negative residuals represent weak year-classes. Two methods have been proposed to index recruitment variability. The first method, termed the recruitment coefficient of determination (RCD; Isermann *et al.*, 2002) is the coefficient of determination (R^2) resulting from a catch curve. In populations with stable recruitment, age explains most of the variation in the number of fish at each age (i.e., via mortality) thereby resulting in high RCD values. Inconsistent recruitment results in less predictable trends in the number at age and therefore low RCD values. The other method, the recruitment variability index (RVI), was developed by Guy and Willis (1995). The RVI is estimated as

$$\mathrm{RVI} = [S_N/(N_\mathrm{M} + N_\mathrm{P})] - (N_\mathrm{M}/N_\mathrm{P})$$

where S_N is the sum of the cumulative relative frequencies across year-classes included in the sample, N_M is the number of year-classes missing from the sample (year-classes beyond the oldest year-class in the sample are excluded), and N_P is the number of year-classes present in the sample (N_P must be greater than N_M). Recruitment variability index values vary from −1 to 1, with values close to 1 representing stable recruitment. The RVI is more sensitive to missing year-classes than RCD (Isermann *et al.*, 2002; Quist, 2007). The RCD and RVI assume that total mortality is equal among year-classes, and the RCD further assumes that variation in the number of fish at each age not explained by age is solely a function of recruitment variation. The residual technique was used to identify strong and weak year-classes, and RCD and RVI were used to characterize recruitment variability for catostomid populations in each reach.

Mean back-calculated lengths at age were estimated using the Dahl-Lea method (DeVries and Frie, 1996)

$$L_i = L_c \times (S_i/S_c)$$

where L_i is the length at annulus i, L_c is the length at capture, S_i is the fin ray radius at annulus i, and S_c is the fin ray radius at capture. Growth was also summarized by fitting von Bertalanffy growth models to each species at each reach (von Bertalanffy, 1938):

$$L_t = L_\infty\left(1 - e^{-K(t-t)}0\right)$$

where L_t is the mean length at age of capture, L_∞ is the theoretical maximum length, K is the growth coefficient, and t_0 is the theoretical age when length equals 0 mm. Growth models were fit to L_t data using nonlinear regression techniques (Freund and Littell, 1991).

Much like recruitment variation, long-term data sets are often required to examine factors related to variation in growth among years. Fortunately, techniques have been developed to examine patterns in growth from short-term (e.g., one-time) samples. Hard structures (e.g., fin rays) contain data that span the life of the fish. Accessing this information has traditionally been problematic for a variety of reasons. A particular problem is that growth of fish is a function of both environmental conditions in a given year and the size of the individual; thus, the effect of a given year is confounded with the size or age of a fish. Weisberg (1993) proposed using a fixed-effects linear model to partition annual growth increments into a size or "age" effect and an environmental or "year" effect. The method has a few limitations, including the fact that the model ignores within-fish correlations in growth and correlations between fish in the same year. Also, comparisons among studies, locations, or periods are nearly impossible because of how the effects are estimated. More recently, Weisberg *et al.* (2010) refined the method to overcome these shortcomings. Instead of fixed-effects models, mixed-effects models are used to examine the effects of age and year on growth increments. As such, a repeated-measures mixed-effects model as described by Weisberg *et al.* (2010) was used to evaluate factors influencing growth of catostomids in Iowa rivers. Age was treated as a fixed effect, year was a random effect in the model, and repeated measures were taken from individual fish. An autoregressive covariance structure was used in all models (SAS, 2005; Weisberg *et al.*, 2010).

Although describing catostomid rate functions was an important objective of the study, the other objective was to understand factors related to the population dynamics of the

study species. We focused on temperature and discharge as possible factors influencing recruitment and growth of catostomids. Water temperature data were unavailable for the study reaches; therefore, air temperature data (°C) were obtained from National Oceanic and Atmospheric Administration weather stations. All weather stations were within 70 km of the sampling reaches. Mean air temperature during the growing season (defined as 1 April to 30 September) was estimated for each year and used as an independent variable in regression models (see below). Discharge (m^3/s) data from 1955 to 2009 were obtained from U.S. Geological Survey gaging stations. The nearest gaging station was selected for each reach; all stations were within 30 km of sampling reaches. Similar to air temperature, mean discharge during the growing season was estimated for each year. We were unable to quantify the extent and duration of flooding in the reaches; however, flows near the 75th percentiles (Figure 2) typically result in connections with the floodplain (Needham *et al.*, 2000; Mutel, 2010). An excellent example is when discharge exceeded the 75th percentile in 2008, and all of the study rivers experienced extensive flooding (Mutel, 2010). The number of days during the growing season with discharge greater than the 75th percentile in discharge (i.e., estimated using data from 1955 to 2009) was estimated for each reach and used as an index of flooding. The number of days with discharge exceeding the 75th percentile was used as an independent variable in regression models.

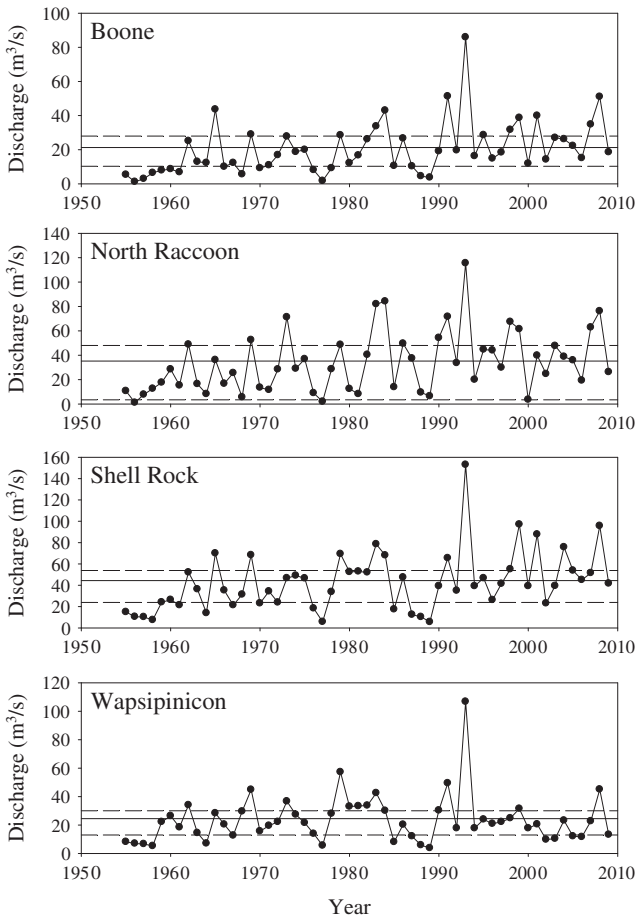

Figure 2. Mean annual discharge for four nonwadable river systems in Iowa. Solid line represents the average annual discharge, and dashed lines represent the 25th and 75th percentiles of annual discharge from 1955 to 2009.

An information-theoretic approach was used to choose among competing linear multiple-regression models developed to explain variation in recruitment and growth (Burnham and Anderson, 2002). The information-theoretic approach relies on an accumulation of evidence for *a priori* hypotheses and fosters the concept of statistical evidence and level of support for each model and its alternatives. We developed three models for each species and reach, including a model with just temperature, just discharge (i.e., days with discharge exceeding the 75th percentile), and both temperature and discharge (additive effects). Models were developed using year-class strength (i.e., catch–curve residuals) and growth increments as dependent variables. Akaike's information criterion corrected for small sample bias (AIC_c) was used to compare candidate models; the best model is the one with the lowest AIC_c (Burnham and Anderson, 2002). Akaike weights (w_i) were used to assess the relative plausibility of each candidate model as described by Burnham and Anderson (2002). Evidence ratios were calculated to provide strength of evidence for the model with the lowest AIC_c by dividing the maximum observed w_i (i.e., lowest AIC_c) by the model's w_i. Although the information-theoretic method selects the best model from a series of competing models, the competing models could all be poor models. Thus, the coefficient of determination (R^2) was calculated for each model to provide an indication of model fit.

RESULTS

A total of 1161 individual catostomids representing eight species and four genera was sampled from the sampling reaches. Although species composition varied among reaches, carpsuckers and redhorse (particularly golden redhorse, *Moxostoma erythrurum*, and shorthead redhorse, *M. macrolepidotum*) dominated the samples (92.4% of all individuals; Table II). All of the species were relatively abundant in all reaches. The only exceptions were that river carpsucker, *Carpiodes carpio*, was absent from the Wapsipinicon River; only one river carpsucker was sampled from the Shell Rock River; and white sucker, *Catostomus commersonii*, was only sampled in the Boone River. A few species tended to dominate the catostomid assemblage at each reach. For instance, river carpsucker and shorthead redhorse were the most

Table II. Mean back-calculated length at age (mm), von Bertalanffy growth equation, total annual mortality (A), recruitment coefficient of determination, and recruitment variability index for catostomids sampled from four nonwadable rivers in Iowa, 2009

River	n	Mean back-calculated length at age											von Bertalanffy	A	RCD	RVI
		1	2	3	4	5	6	7	8	9	10	11				
Highfin carpsucker																
Boone	40	70.4 (2.7)	152.2 (6.8)	226.4 (6.2)	282.3 (4.9)	320.9 (5.3)	347.5 (11.8)	401.7 (17.9)	393.8 (a)	423.0 (a)			$L_{age}=486(1-e^{(-0.235(age-0.349))})$	0.30	0.65	0.68
North Raccoon	6	73.7 (9.7)	142.5 (14.2)	202.1 (16.6)	220.8 (20.9)	280.0 (7.0)							$L_{age}=439(1-e^{(-0.196(age-0.030))})$	0.21	0.72	0.72
Shell Rock	9	72.8 (5.3)	141.7 (9.4)	215.8 (12.7)	280.1 (15.4)	309.6 (16.2)	334.9 (18.5)	352.4 (18.8)	377.5 (0.5)				$L_{age}=431(1-e^{(-0.269(age-0.369))})$	0.26	0.61	0.75
Wapsipinicon	75	74.1 (1.6)	160.5 (3.8)	241.2 (4.5)	291.0 (3.3)	312.8 (3.7)	359.4 (14.6)						$L_{age}=438(1-e^{(-0.294(age-0.379))})$	0.28	0.81	0.73
Overall	130	72.8 (1.4)	155.8 (3.2)	233.3 (3.5)	285.2 (3.1)	314.6 (3.5)	347.3 (8.2)	380.6 (15.5)	382.9 (5.5)	423.0 (a)			$L_{age}=465(1-e^{(-0.249(age-0.309))})$			
Quillback																
Boone	87	67.6 (1.1)	154.8 (3.2)	232.0 (4.1)	279.9 (4.1)	328.7 (4.1)	362.3 (3.8)	393.9 (4.4)	398.3 (6.3)				$L_{age}=473(1-e^{(-0.257(age-0.417))})$	0.25	0.59	0.69
North Raccoon	27	69.3 (2.2)	142.2 (4.9)	209.2 (5.7)	261.2 (7.7)	310.1 (6.3)	353.7 (6.2)	391.9 (8.5)	406.0 (a)				$L_{age}=574(1-e^{(-0.164(age-0.237))})$	0.36	0.79	0.78
Shell Rock	46	57.9 (1.4)	129.9 (3.6)	197.9 (5.1)	260.3 (6.3)	308.3 (5.2)	345.6 (4.7)	370.8 (4.3)	395.8 (6.2)	401.0 (a)	424.0 (a)		$L_{age}=486(1-e^{(-0.218(age-0.485))})$	0.32	0.74	0.75
Wapsipinicon	19	68.3 (6.1)	156.0 (13.7)	218.1 (5.5)	281.3 (5.6)	331.0 (6.9)	361.9 (4.9)	382.7 (2.7)	412.5 (11.5)				$L_{age}=501(1-e^{(-0.226(age-0.358))})$	0.28	0.65	0.73
Overall	179	65.4 (1.0)	146.3 (2.5)	218.4 (2.8)	271.4 (3.0)	319.9 (2.8)	354.8 (2.6)	384.0 (2.9)	399.9 (3.9)	401.0 (a)	424.0 (a)		$L_{age}=467(1-e^{(-0.251(age-0.438))})$			
River carpsucker																
Boone	25	66.8 (2.2)	141.1 (4.9)	215.9 (7.6)	287.0 (8.5)	328.2 (6.3)	360.9 (5.4)	384.4 (6.7)	407.7 (15.5)				$L_{age}=497(1-e^{(-0.231(age-0.435))})$	0.19	0.60	0.55
North Raccoon	118	73.9 (1.1)	142.3 (2.5)	205.2 (2.9)	261.1 (3.3)	308.7 (3.3)	352.6 (3.9)	398.4 (4.9)	426.1 (6.2)	445.8 (6.5)	454.0 (a)	507.0 (a)	$L_{age}=641(1-e^{(-0.136(age-0.127))})$	0.24	0.55	0.63
Shell Rock	1	74.3 (a)	171.9 (a)	226.7 (a)	271.6 (a)	302.9 (a)	334.2 (a)	355.6 (a)	383.0 (a)				$L_{age}=429(1-e^{(-0.268(age-0.228))})$	(a)	(a)	(a)
Overall	144	72.6 (1.0)	142.3 (2.2)	207.3 (2.7)	266.3 (3.2)	312.3 (2.9)	353.8 (3.4)	395.9 (4.4)	422.9 (5.7)	445.8 (6.5)	454.0 (a)	507.0 (a)	$L_{age}=627(1-e^{(-0.142(age-0.149))})$			
Northern hogsucker																
Boone	27	59.3 (2.7)	148.5 (7.2)	222.9 (6.8)	231.7 (13.8)	302.1 (24.1)	305.4 (a)	335.0 (a)					$L_{age}=380(1-e^{(-0.313(age-0.434))})$	0.51	0.79	0.66
North Raccoon	10	66.5 (5.5)	165.1 (12.6)	245.6 (13.9)									$L_{age}=606(1-e^{(-0.202(age-0.424))})$	(a)	(a)	(a)
Shell Rock	18	59.7 (4.9)	164.5 (16.1)	250.9 (20.6)	271.9 (9.5)	338.7 (20.1)	363.3 (2.3)	394.0 (a)					$L_{age}=462(1-e^{(-0.285(age-0.486))})$	0.44	0.95	0.80
Wapsipinicon	12	55.9 (2.8)	143.9 (12.3)	197.2 (22.5)	243.9 (29.1)	277.9 (28.8)	328.2 (19.9)	368.9 (19.8)	414.0 (26.7)				$L_{age}=725(1-e^{(-0.104(age-0.073))})$	0.28	0.56	0.74

Published in 2011 by John Wiley & Sons, Ltd.
River Res. Applic. **28**: 1567–1586 (2012)
DOI: 10.1002/rra

Overall	67	59.6 (1.8)	152.6 (5.5)	225.2 (7.6)	248.5 (13.3)	303.0 (16.5)	333.5 (14.3)	367.6 (15.1)	414.0 (26.7)			$L_{age} = 543(1-e^{(-0.172(age-0.213))})$			
Golden redhorse															
Boone	70	72.4 (2.0)	150.6 (4.1)	220.1 (4.7)	283.7 (4.6)	327.4 (3.5)	366.0 (4.2)	383.9 (8.7)	384.3 (4.8)	408.0 (2.0)		$L_{age} = 455(1-e^{(-0.271(age-0.422))})$	0.42	0.71	0.66
North Raccoon	4	79.8 (11.5)	157.1 (20.6)	236.4 (23.4)	291.7 (19.7)							$L_{age} = 676(1-e^{(-0.148(age-0.166))})$	(a)	(a)	(a)
Shell Rock	49	86.8 (2.4)	175.7 (3.9)	249.3 (5.4)	302.3 (6.4)	352.9 (9.8)	381.2 (5.9)	412.5 (12.5)				$L_{age} = 516(1-e^{(-0.236(age-0.224))})$	0.49	0.93	0.83
Wapsipinicon	73	70.9 (2.4)	153.9 (5.1)	228.1 (6.8)	277.8 (7.1)	315.6 (7.1)	345.2 (7.9)	353.7 (12.6)	367.1 (8.9)	407.0 (3.1)		$L_{age} = 431(1-e^{(-0.279(age-0.365))})$	0.44	0.87	0.84
Overall	196	77.3 (1.4)	160.5 (2.6)	231.1 (3.3)	285.4 (3.4)	326.0 (3.3)	360.9 (3.8)	374.9 (7.6)	373.9 (6.1)	407.7 (1.8)		$L_{age} = 437(1-e^{(-0.290(age-0.360))})$			
Shorthead redhorse															
Boone	55	82.5 (2.7)	185.0 (5.0)	262.7 (5.9)	305.6 (7.8)	354.6 (7.5)	394.5 (11.8)	421.0 (a)				$L_{age} = 509(1-e^{(-0.258(age-0.289))})$	0.48	0.72	0.84
North Raccoon	54	96.0 (2.7)	202.1 (5.4)	258.3 (6.5)	297.7 (20.6)	341.3 (28.2)	360.0 (a)					$L_{age} = 408(1-e^{(-0.371(age-0.249))})$	0.62	0.92	0.88
Shell Rock	145	76.8 (1.2)	177.4 (3.3)	230.6 (4.8)	272.3 (4.3)	317.2 (4.0)	341.2 (4.3)	345.5 (25.5)	348.0 (a)			$L_{age} = 376(1-e^{(-0.380(age-0.392))})$	0.53	0.75	0.81
Wapsipinicon	89	78.8 (1.5)	177.6 (3.7)	253.7 (5.5)	296.6 (4.9)	342.5 (4.8)	375.5 (6.6)	402.2 (13.1)	437.7 (23.7)	460.0 (a)		$L_{age} = 531(1-e^{(-0.219(age-0.205))})$	0.41	0.96	0.82
Overall	343	81.3 (0.9)	182.6 (2.1)	247.2 (2.9)	286.7 (3.2)	332.1 (3.2)	362.3 (4.5)	392.8 (12.7)	419.8 (25.6)	460.0 (a)		$L_{age} = 541(1-e^{(-0.194(age-0.043))})$			
Silver redhorse															
Boone	10	64.9 (7.3)	145.6 (14.8)	232.2 (19.8)	299.7 (29.6)	369.9 (39.9)	398.8 (24.9)	463.0 (38.0)				$L_{age} = 783(1-e^{(-0.133(age-0.377))})$	0.31	0.69	0.74
North Raccoon	8	62.2 (2.4)	145.9 (7.8)	216.8 (11.9)	274.2 (13.1)	332.3 (14.0)	376.6 (12.3)	413.8 (8.4)	447.1 (16.9)	481.7 (27.2)	518.2 (34.4)	$L_{age} = 706(1-e^{(-0.132(age-0.277))})$	0.25	0.59	0.76
Shell Rock	17	71.4 (5.5)	156.9 (12.8)	243.3 (13.7)	328.2 (23.1)	363.2 (37.8)	451.9 (2.0)	481.9 (8.7)	503.5 (11.1)	525.9 (8.9)	556.0 (a)	$L_{age} = 676(1-e^{(-0.183(age-0.464))})$	0.18	0.49	0.06
Wapsipinicon	12	58.7 (2.5)	124.1 (4.0)	199.4 (5.6)	274.3 (9.5)	336.7 (10.8)	381.5 (11.5)	436.2 (10.1)	471.1 (8.8)	513.8 (13.1)		$L_{age} = 877(1-e^{(-0.103(age-0.405))})$	0.26	0.63	0.74
Overall	47	63.5 (2.4)	142.2 (4.9)	220.2 (6.8)	285.4 (8.4)	342.1 (9.4)	386.5 (8.1)	431.1 (7.3)	466.9 (9.2)	505.8 (11.5)	530.6 (23.4)	$L_{age} = 734(1-e^{(-0.134(age-0.338))})$			
White sucker															
Boone	13	95.8 (6.2)	223.2 (21.2)	276.9 (13.9)	319.9 (19.7)	405.5 (4.5)						$L_{age} = 581(1-e^{(-0.231(age-0.145))})$	(a)	(a)	(a)

The lowercase letter "a" indicates that the values are not estimable.
Number in parenthesis for back-calculated lengths at age represents one standard error. L_{age} represents length for a given age; RCD, recruitment coefficient of determination; RVI, recruitment variability index.

Published in 2011 by John Wiley & Sons, Ltd.
River Res. Applic. **28**: 1567–1586 (2012)
DOI: 10.1002/rra

abundant species in the North Raccoon River, shorthead redhorse dominated the catostomid assemblage in the Shell Rock River, and highfin carpsucker, *Carpiodes velifer*, golden redhorse, and shorthead redhorse were the most abundant catostomids in the Wapsipinicon River (Table II).

Maximum age of catostomids varied from 3 to 11 years among species and was highly variable among reaches. On average, river carpsucker had the highest maximum age, followed by silver redhorse, *Moxostoma anisurum*, and quillback, *Carpiodes cyprinus* (Table II). Mean back-calculated lengths at age were highly variable among species and reaches. Carpsuckers and shorthead redhorse tended to grow fastest in the Wapsipinicon, North Raccoon, and Boone rivers and slowest in the Shell Rock River. Northern hogsucker, *Hypentelium nigricans*, golden redhorse, and silver redhorse tended to grow fastest in the Shell Rock River. Among species, silver redhorse and river carpsucker tended to have the highest theoretical maximum lengths (Table II).

Total annual mortality estimates varied from 0.18 to 0.62 among species and reaches (Table II). Northern hogsucker, golden redhorse, and shorthead redhorse had the highest average mortality estimates; whereas, silver redhorse and river carpsucker had the lowest estimates of *A*. Northern hogsucker, golden redhorse, and shorthead redhorse had the most stable recruitment (i.e., highest RCD and RVI values) across reaches (Table II). Silver redhorse and river carpsucker tended to have the most unstable recruitment of the eight catostomid species. As might be expected from RCD and RVI index values, year-class strength was highly variable among species, reaches, and years (Figure 3). Temperature and the number of days exceeding the 75th percentile in discharge explained little variation in year-class strength of catostomids (R^2 generally less than 0.30; Table III). The only model that explained a substantial amount of variation in year-class strength was for northern hogsucker in the Boone River. Although the models did not explain much variation in recruitment, all relationships between year-class strength and discharge were negative, except for white sucker in the Boone River. The direction of influence for temperature was highly variable among species and reaches.

Mixed-models of fish growth provided several insights on growth of catostomids. Growth increments declined with increasing age for all species and patterns were similar among river systems (Figure 4). In contrast, growth increments of catostomids were highly variable among years for all species-reach combinations (Figure 5). Unlike recruitment, growth of catostomids was closely related to discharge (Table IV). The best model across species and reaches was consistently the model with just the number of days where discharge exceeded the 75th percentile. More than 50%, and sometimes more than 70%, of the variation in growth was typically explained by discharge during the growing season. The relationship between discharge and growth was positive for all species, except silver redhorse in the North Raccoon River and golden redhorse in the Shell Rock River. Temperature added little explanatory power.

DISCUSSION

Nonwadable rivers remain one of the least studied ecosystems and catostomids are among the most poorly understood groups of fishes in North America (Cooke *et al.*, 2005; Flotemersch *et al.*, 2006). Only recently has research begun to examine fish assemblages and conceptualize the structure and function of temperate nonwadable river systems (Lyons *et al.*, 2001; Flotemersch *et al.*, 2006; Neebling and Quist, 2010). This study contributes to those efforts where the population demographics of catostomids in Iowa rivers were found to be highly variable among species and rivers. Although catostomids are common fishes that occur in a variety of habitats across North America, little has been reported on their basic life-history characteristics and population demographics making comparison among populations and species difficult. Nevertheless, a few studies have been published that allow results of the current study to be integrated with existing knowledge of catostomids. Grabowski *et al.* (2008) estimated total annual mortality for four catostomids in the Savannah River, South Carolina and Georgia, and found that mortality was around 40% for robust redhorse, *Moxostoma robustum*, and 46% for notchlip redhorse, *M. collapsum*. Mortality was higher for northern hogsucker ($A = 52\%$) and spotted sucker, *Minytrema melanops*, ($A = 57\%$). Reid (2009) found that total annual mortality was 23% for black redhorse, *Moxostoma duquesnei*, and 21% for shorthead redhorse in the Grand River, Ontario. Total annual mortality estimates for catostomids in Iowa were similar to those reported in the literature where mortality varied from 18% for silver redhorse in the Shell Rock River to 62% for shorthead redhorse in the North Raccoon River. On average, northern hogsucker, golden redhorse, and shorthead redhorse had the highest mortality (i.e., >40%), whereas carpsuckers and silver redhorse tended to have the lowest mortality (i.e., <30%).

Similar to mortality, quantifying recruitment variation is important for understanding the dynamics of fish populations. The RCD and RVI are relatively new techniques for indexing recruitment variability but have proven useful in providing insight on fish population dynamics. For example, Guy and Willis (1995) found that RVI values (minimum-maximum; 0.18–0.99) for black crappie, *Pomoxis nigromaculatus*, populations in small South Dakota lakes was related to lake and watershed morphology. Highly dendritic systems and lakes with high watershed to lake area ratios tended to have more stable recruitment compared with

systems with low watershed to lake area ratios or circular lakes. Reduced effects of wind and higher water during the spawning season were thought to have contributed to stable recruitment. Paukert and Willis (2004) used the RVI (0.09–0.92) to evaluate recruitment of largemouth bass, *Micropterus salmoides*, in Nebraska lakes and found that shallow lakes with high densities of emergent vegetation had stable largemouth bass recruitment. Quist (2007) found that RCD values for walleye, *Sander vitreus*, varied from 0.25 to 0.70 and RVI varied from 0.29 to 0.76 across eight reservoirs in Kansas. Isermann *et al.* (2002) provided estimates of RCD that varied from 0.01 to 1.0, and RVI that varied from –0.20 to 0.99 across 122 white crappie, *Pomoxis annularis*, populations in the US. Although patterns in

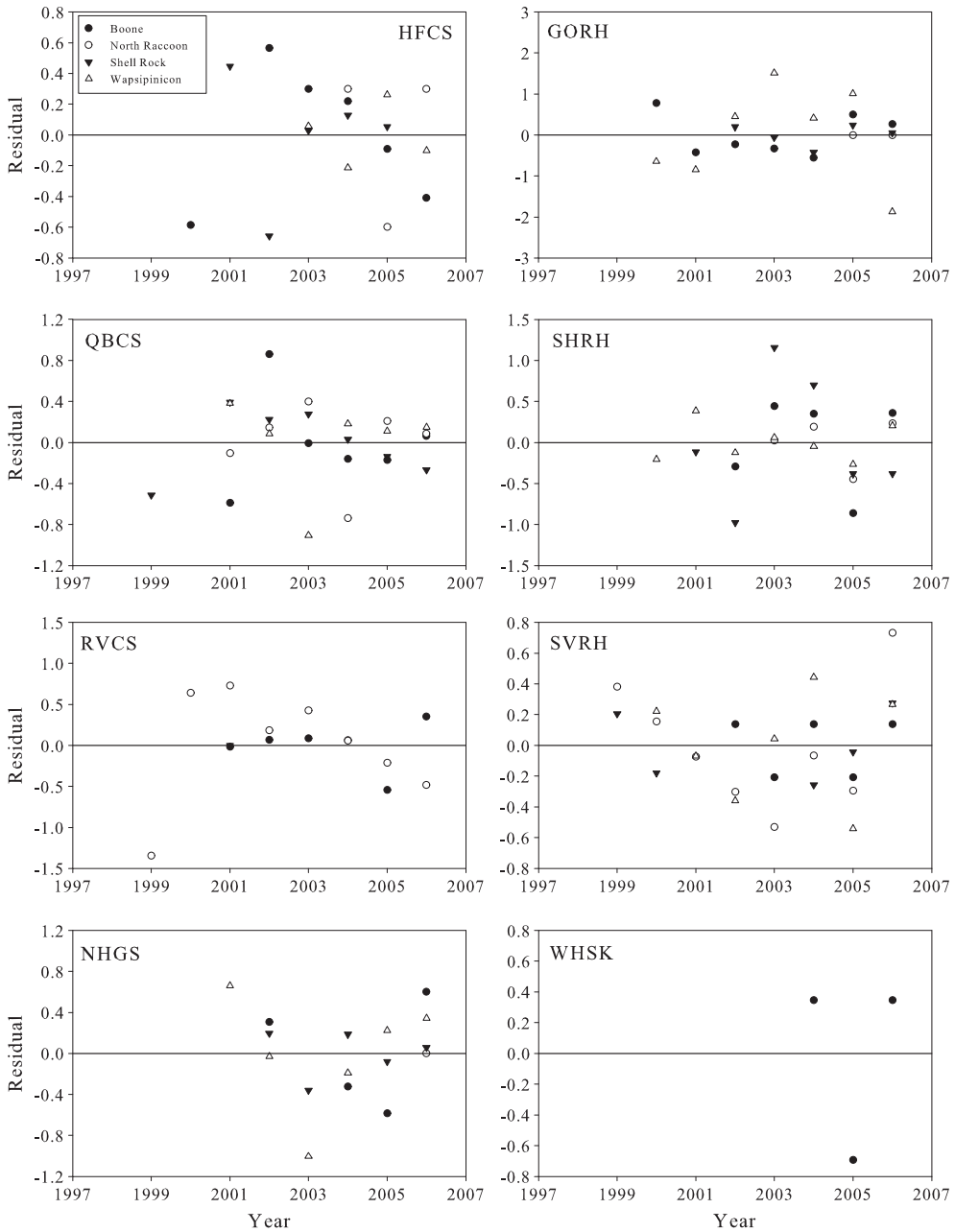

Figure 3. Residuals from catch curves regressions for catostomids sampled from four nonwadable river systems in Iowa, 2009. Species include highfin carpsucker (HFCS), quillback (QBCK), river carpsucker (RVCS), northern hogsucker (NHGS), golden redhorse (GORH), shorthead redhorse (SHRH), silver redhorse (SVRH), and white sucker (WHSK). Positive residuals indicate strong year classes, and negative residuals represent years with poor year-class strength.

Published in 2011 by John Wiley & Sons, Ltd.

DOI: 10.1002/rra

Table III. Multiple-regression models predicting year-class strength of catostomids sampled from four nonwadable rivers in Iowa, 2009

Species	Variable(s)	RSS	AIC_c	w_i	%Max w_i	ER	R^2
				Boone River			
Highfin carpsucker	**Q_{75}**	0.759	−11.456	0.584	100	1.000	0.22
	Temp	0.827	−10.685	0.397	67.9	1.471	0.15
	Q_{75} + Temp	0.728	−4.632	0.019	3.3	30.336	0.25
Quillback	**Q_{75}**	0.697	−7.523	0.873	100	1.000	0.39
	Temp	1.149	−3.523	0.118	13.5	7.390	<0.01
	Q_{75} + Temp	0.685	1.671	0.009	1.0	99.206	0.40
River carpsucker	**Temp**	0.334	−13.404	0.703	100	1.000	0.23
	Q_{75}	0.419	−11.594	0.284	40.5	2.471	0.04
	Q_{75} + Temp	0.293	−5.123	0.011	1.6	62.828	0.33
Northern hogsucker	**Q_{75}**	0.252	−9.269	0.987	100	1.000	0.72
	Temp	0.899	−0.367	0.012	1.2	85.754	<0.01
	Q_{75} + Temp	0.230	4.091	0.001	0.1	796.538	0.74
Golden redhorse	**Q_{75}**	0.177	−11.743	0.835	100	1.000	0.37
	Temp	0.282	−8.486	0.164	19.6	5.095	<0.01
	Q_{75} + Temp	0.156	1.373	0.001	0.1	704.841	0.45
Shorthead redhorse	**Temp**	1.179	1.531	0.514	100	1.000	0.07
	Q_{75}	1.199	1.649	0.485	94.3	1.061	0.06
	Q_{75} + Temp	1.169	15.472	0.001	0.1	>1000	0.08
Silver redhorse	(a)						
White sucker	**Temp**	0.617	4.348	0.596	100	1.00	0.14
	Q_{75}	0.702	5.127	0.404	67.8	1.476	0.03
	Q_{75} + **Temp**	0.606	34.245	<0.001	<0.1	>1000	0.16
				North Raccoon River			
Highfin carpsucker	**Q_{75}**	0.431	2.206	0.549	100	1.000	0.19
	Temp	0.461	2.603	0.451	81.9	1.219	0.14
	Q_{75} + Temp	0.423	32.087	<0.001	<0.1	>1000	0.21
Quillback	(a)						
River carpsucker	**Q_{75}**	2.483	−6.944	0.750	100	1.000	0.23
	Temp	3.230	−4.051	0.177	23.5	4.249	<0.01
	Q_{75} + Temp	2.355	−2.288	0.73	9.7	10.257	0.27
Northern hogsucker	(a)						
Golden redhorse	(a)						
Shorthead redhorse	**Temp**	0.210	−2.102	0.681	100	1.000	0.28
	Q_{75}	0.271	−0.584	0.319	46.8	2.135	0.07
	Q_{75} + Temp	0.206	27.770	<0.001	<0.1	>1000	0.30
Silver redhorse	Temp	0.131	−39.306	0.715	100	1.000	0.21
	Q_{75}	0.161	−37.038	0.230	32.2	3.108	0.03
	Q_{75} + Temp	0.130	−34.153	0.054	7.6	13.156	0.21
White sucker	(a)						
				Shell Rock River			
Highfin carpsucker	**Q_{75}**	0.562	−9.249	0.639	100	1.000	0.14
	Temp	0.652	−8.056	0.352	55.1	1.816	<0.01
	Q_{75} + Temp	0.502	−0.815	0.009	1.5	67.843	0.23
Quillback	**Q_{75}**	0.573	−18.595	0.602	100	1.000	0.10
	Temp	0.635	−17.567	0.360	59.8	1.671	<0.01
	Q_{75} + Temp	0.547	−13.059	0.038	6.3	15.924	0.14
River carpsucker	(a)						
Northern hogsucker	**Q_{75}**	1.322	−2.402	0.647	100	1.000	0.20
	Temp	1.547	−1.145	0.345	53.3	1.875	0.06
	Q_{75} + Temp	1.263	6.566	0.007	1.1	88.592	0.23
Golden redhorse	Temp	1.248	−6.981	0.551	100	1.000	0.21
	Q_{75}	1.309	−6.483	0.429	77.9	1.283	0.16
	Q_{75} + Temp	1.175	−0.324	0.019	3.6	27.903	0.25
Shorthead redhorse	Temp	2.810	3.629	0.589	100	1.000	0.09
	Q_{75}	3.089	4.387	0.404	68.5	1.460	<0.01
	Q_{75} + Temp	2.764	12.831	0.006	1.0	99.548	0.11

(Continues)

Table III. (Continued)

Species	Variable(s)	RSS	AIC_c	w_i	%Max w_i	ER	R^2
				Boone River			
Silver redhorse	Temp	1.083	−12.229	0.565	100	1.000	0.08
	Q_{75}	1.157	−11.568	0.406	71.9	1.392	0.01
	Q_{75} + Temp	1.081	−6.247	0.028	5.0	19.901	0.08
White sucker	(a)						
				Wapsipinicon River			
Highfin carpsucker	Temp	0.118	−5.582	0.538	100	1.000	0.08
	Q_{75}	0.124	−5.275	0.858	159.3	0.628	0.03
	Q_{75} + Temp	0.107	23.839	<0.001	<0.1	>1000	0.16
Quillback	Temp	0.801	−6.413	0.591	100	1.000	0.23
	Q_{75}	0.881	−5.649	0.403	68.3	1.465	0.15
	Q_{75} + Temp	0.799	2.903	0.006	0.9	105.389	0.23
River carpsucker	*A*						
Northern hogsucker	**Q_{75}**	0.172	−11.943	0.671	100	1.000	0.19
	Temp	0.211	−10.513	0.328	48.9	2.045	<0.01
	Q_{75} + Temp	0.164	1.723	<0.001	0.1	928.251	0.22
Golden redhorse	**Temp**	6.927	8.444	0.623	100	1.000	0.17
	Q_{75}	7.839	9.557	0.357	57.3	1.745	0.06
	Q_{75} + **Temp**	6.708	15.355	0.019	3.2	31.672	0.19
Shorthead redhorse	Temp	0.308	−19.574	0.548	100	1.000	0.05
	Q_{75}	0.324	−19.118	0.437	79.6	1.256	<0.01
	Q_{75} + Temp	0.308	−12.374	0.015	2.7	36.598	0.05
Silver redhorse	(a)						
White sucker	(a)						

The lowercase letter "a" indicates that the values are not estimable.
Independent variables include the number of days where discharge exceeded the 75th percentile (percentile estimated using data from 1955 to 2009; Q_{75}) and mean temperature during the growing season (i.e., 1 April to 30 September). Akaike's information criterion corrected for small sample size (AIC_c), Akaike weight (w_i), percent of the maximum w_i, (%Max w_i), and the evidence ratio (ER = max w_i/w_i) were used to evaluate candidate models. The AIC_c values were calculated from the number of model parameters, sample size, and the residual sum or squares (RSS). Bold variables indicate that the direction of influence was negative in the model. The coefficient of determination (R^2) is provided as an indication of model fit.

recruitment variation among species and reaches were not evident in our study, recruitment of catostomids appears to be more stable than for other species reported in the literature. Specifically, RCD was typically greater than 0.50 and often above 0.80, and RVI was generally greater than 0.60 across species and reaches. The current study contributes to the growing literature on patterns in recruitment variability of freshwater fishes; however, further research across a variety of systems and species is needed to better characterize general patterns in recruitment stability.

Several patterns were observed with regard to growth of catostomids in Iowa rivers. Mean back-calculated lengths at age of carpsuckers and shorthead redhorse were highest in the North Raccoon, Wapsipinicon, and Boone rivers, whereas growth of northern hogsucker, golden redhorse, and silver redhorse was highest in the Shell Rock River. These differences are probably because of the ecology of the study species and differences in habitat characteristics among reaches.

The trophic ecology of catostomids is highly diverse and displays elements of both similarity and dissimilarity among taxonomic groups. The diet of carpsuckers is typically dominated by plant material and detritus, and when benthic invertebrates are consumed, they are typically dipterans (primarily chironomids) and oligochaetes (Cahn, 1927; Buchholz, 1957; Beecher, 1979). Similar to carpsuckers, shorthead redhorse diets are often dominated by dipterans, oligochaetes, algae, and detritus (Jenkins, 1970; Becker, 1983; Sule and Skelly, 1985; Jenkins and Burkhead, 1994). In contrast, northern hogsucker, golden redhorse, and silver redhorse consume a high proportion of invertebrates and only small amounts of plant material (Cahn, 1927; Meyer, 1962; Minckley, 1963; Gatz, 1979; Smith, 1977; Becker, 1983; Jenkins and Burkhead, 1994). Not only are invertebrates a primary component of the diet, but those consumed include a diverse array of mollusks, insects (e.g., Diptera, Ephemeroptera, Trichoptera), and crustaceans (Cahn, 1927; Meyer, 1962; Gatz, 1979). Recent research in Iowa on the trophic ecology of catostomids supports the observations reported by previous researchers (Spiegel, 2010). Given differences in the ecology of the study species, dissimilarities in habitat and the corresponding macroinvertebrate assemblage may help explain differences in growth among reaches.

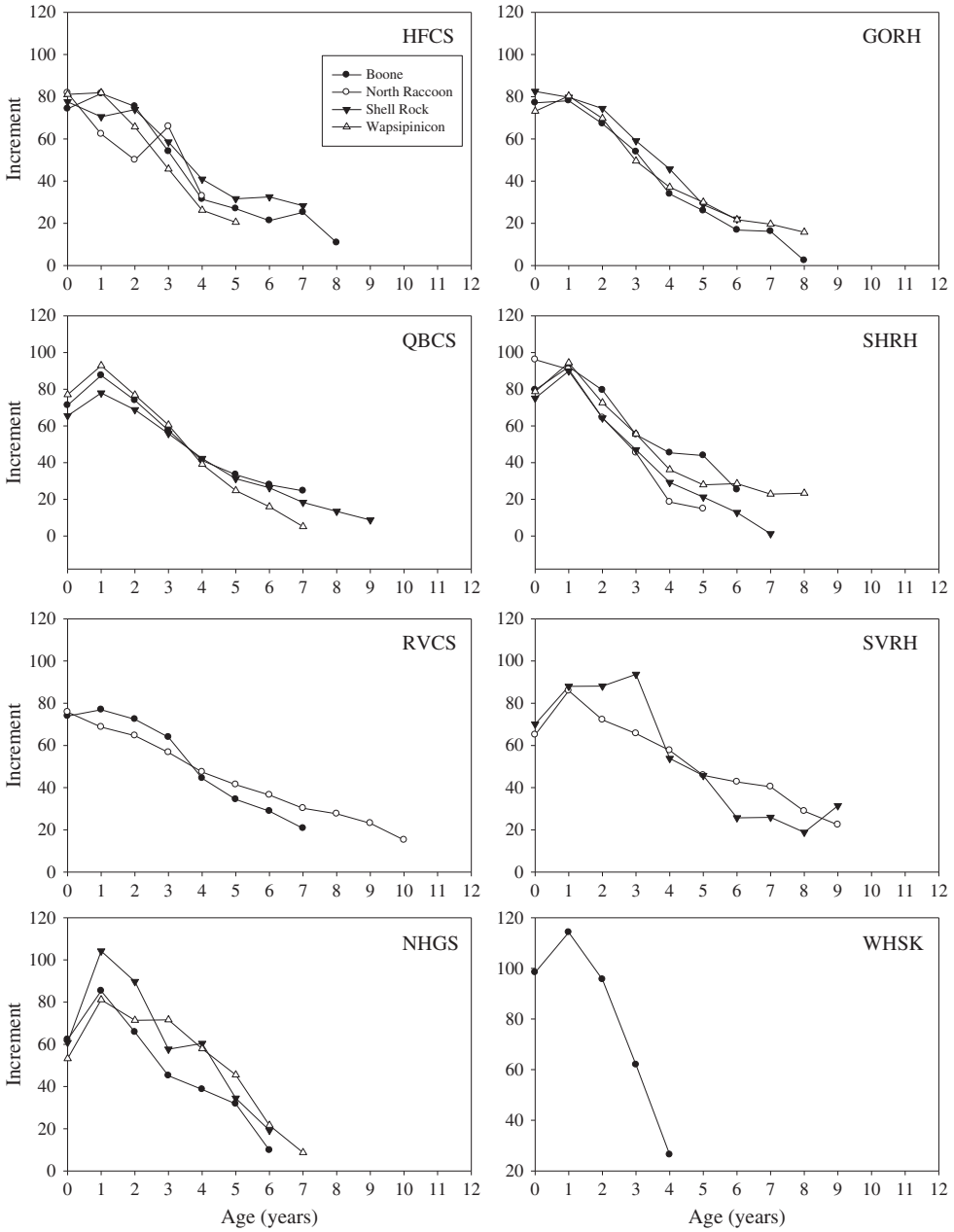

Figure 4. Growth increment (mm) estimates by age for catostomids sampled from nonwadable river systems in Iowa, 2009. Species include highfin carpsucker (HFCS), quillback (QBCK), river carpsucker (RVCS), northern hogsucker (NHGS), golden redhorse (GORH), shorthead redhorse (SHRH), silver redhorse (SVRH), and white sucker (WHSK).

Growth of carpsuckers and shorthead redhorse was highest in the Wapsipinicon, North Raccoon, and Boone rivers. Substrate in the North Raccoon and Wapsipinicon rivers, and to a lesser extent the Boone River, was dominated by sand and silt. Both silt and sand are considered poor substrate for maintaining diverse assemblages of macroinvertebrates (Ward, 1992; Allan, 1995). Although taxa specialized for life in sand and silt may be locally abundant (e.g., *Caenis* spp., *Hexagenia* spp.), chironomids and oligochaetes typically dominate macroinvertebrate assemblages and can often reach very high densities in fine substrate (Strommer and Smock, 1989; Quinn and Hickey, 1990; Ward, 1992). Consequently, fast growth of carpsuckers and shorthead redhorse in systems with a high proportion of fine substrate may be a reflection of the availability and importance of dipterans (particularly

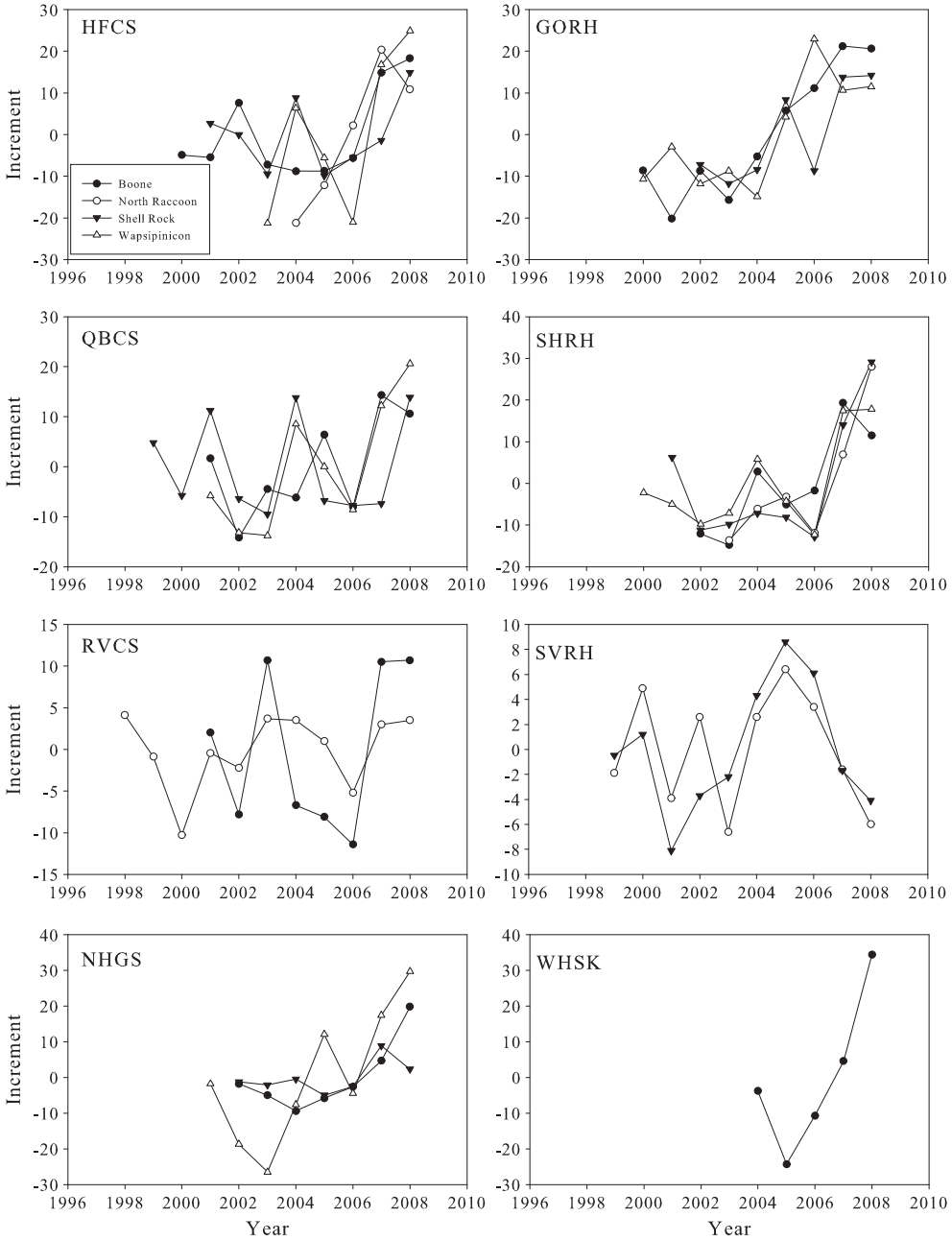

Figure 5. Growth increment (mm) estimates by year for catostomids sampled from nonwadable river systems in Iowa, 2009. Species include highfin carpsucker (HFCS), quillback (QBCK), river carpsucker (RVCS), northern hogsucker (NHGS), golden redhorse (GORH), shorthead redhorse (SHRH), silver redhorse (SVRH), and white sucker (WHSK).

chironomids) and oligochaetes in their diet. Northern hogsucker, golden redhorse, and silver redhorse grew fastest in the Shell Rock River, which had a much higher proportion of large rocky substrate than the other reaches. Unlike fine substrates that are often depauperate, rocky substrates maintain a high diversity of macroinvertebrates, particularly insects and mollusks (Ward, 1992; Downes *et al.*, 2000; Voelz and McArthur, 2000; Litvan *et al.*, 2008). In addition, taxa such as ephemeropterans, trichopterans, and plecopterans are often most abundant on rocky substrates (Ward, 1992). Fast growth of northern hogsucker, golden redhorse, and silver redhorse in the Shell Rock River likely reflects the diversity and availability of prey items, including taxa like ephemeropterans and trichopterans.

In addition to describing population characteristics of catostomids in Iowa rivers, a primary focus of this research

Table IV. Multiple-regression models predicting growth of catostomids sampled from four nonwadable rivers in Iowa, 2009

Species	Variable(s)	RSS	AIC_c	w_i	%Max w_i	ER	R^2
			Boone River				
Highfin carpsucker	Q_{75}	659.917	49.454	0.783	100	1.000	0.27
	Temp	900.689	52.253	0.193	24.7	4.054	0.01
	Q_{75} + **Temp**	646.651	56.471	0.023	2.9	33.402	0.29
Quillback	Q_{75}	317.430	41.447	0.939	100	1.000	0.54
	Temp	656.116	47.255	0.051	5.5	18.253	0.04
	Q_{75} + Temp	308.155	50.543	0.009	1.1	94.448	0.55
River carpsucker	Q_{75}	269.996	40.152	0.951	100	1.000	0.58
	Temp	594.296	46.463	0.040	4.3	23.473	0.08
	Q_{75} + **Temp**	269.952	49.484	0.009	0.9	106.273	0.58
Northern hogsucker	Q	195.992	37.325	0.971	100	1.000	0.66
	Temp	542.269	44.449	0.028	2.8	35.230	0.05
	Q_{75} + Temp	182.766	50.836	0.001	0.1	858.739	0.68
Golden redhorse	Q_{75}	411.969	42.525	0.884	100	1.000	0.48
	Temp	737.415	46.601	0.116	13.0	7.673	0.08
	Q_{75} + Temp	395.326	56.237	0.001	0.1	949.247	0.50
Shorthead redhorse	Q_{75}	503.963	43.936	0.884	100	1.000	0.44
	Temp	904.692	48.032	0.114	12.9	7.751	<0.01
	Q_{75} + Temp	480.595	57.604	0.001	0.1	928.741	0.47
Silver redhorse	(a)						
White sucker	Q_{75}	311.051	41.689	0.979	100	1.000	0.84
	Temp	1125.533	49.406	0.021	2.1	47.378	0.41
	Q_{75} + **Temp**	222.33297	69.674	<0.001	<0.1	>1000	0.88
			North Raccoon River				
Highfin carpsucker	Q_{75}	751.199	46.979	0.772	100	1.000	0.34
	Temp	1127.775	49.417	0.228	29.6	3.384	<0.01
	Q_{75} + Temp	679.8384	76.377	<0.001	<0.1	>1000	0.40
Quillback	(a)						
River carpsucker	Q_{75}	66.900	29.287	0.929	100	1.000	0.67
	Q_{75} + Temp	66.889	34.523	0.068	7.3	13.709	0.67
	Temp	192.423	40.908	0.003	0.3	333.864	0.06
Northern hogsucker	(a)						
Golden redhorse	(a)						
Shorthead redhorse	Q_{75}	347.027	42.346	0.961	100	1.000	0.71
	Temp	1005.435	48.728	0.039	4.1	24.320	0.17
	Q_{75} + **Temp**	346.714	72.340	<0.001	<0.1	>1000	0.71
Silver redhorse	**Q_{75}**	204.420	41.573	0.509	100	1.000	0.13
	Temp	209.378	41.837	0.446	87.7	1.141	0.11
	Q_{75} + Temp	197.177	46.415	0.045	8.9	11.253	0.16
White sucker	*A*						
			Shell Rock River				
Highfin carpsucker	Q_{75}	81.878	30.606	0.959	100	1.000	0.84
	Q_{75} + **Temp**	64.226	37.997	0.024	2.5	40.261	0.88
	Temp	224.085	38.661	0.017	1.8	56.103	0.58
Quillback	Q_{75}	230.350	41.370	0.904	100	1.000	0.73
	Q_{75} + **Temp**	224.885	47.130	0.051	5.6	17.813	0.74
	Temp	419.380	47.362	0.045	4.9	20.003	0.51
River carpsucker	*A*						
Northern hogsucker	Q_{75}	1582.099	54.297	0.816	100	1.000	0.36
	Temp	2333.219	57.405	0.172	21.1	47.730	0.05
	Q_{75} + **Temp**	1441.114	62.883	0.011	1.4	73.209	0.42
Golden redhorse	**Q_{75}**	1304.595	55.588	0.529	100	1.000	0.04
	Temp	1351.080	55.903	0.453	85.5	1.171	<0.01
	Q_{75} + Temp	1249.287	62.398	0.018	3.3	30.116	0.08
Shorthead redhorse	Q_{75}	823.403	49.072	0.857	100	1.000	0.48
	Temp	1308.926	52.780	0.134	15.7	6.386	0.18
	Q_{75} + **Temp**	815.634	58.329	0.008	0.9	102.386	0.49

(Continues)

Table IV. (Continued)

Species	Variable(s)	RSS	AIC_c	w_i	%Max w_i	ER	R^2
			Boone River				
Silver redhorse	Q_{75}	152.311	37.233	0.610	100	1.000	0.20
	Temp	169.670	38.313	0.336	58.3	1.715	0.11
	Q_{75} + Temp	149.087	43.019	0.034	5.5	18.048	0.22
White sucker	(a)						
			Wapsipinicon River				
Highfin carpsucker	Q_{75}	434.609	43.696	0.987	100	1.000	0.77
	Temp	1828.061	52.316	0.013	1.3	74.418	0.02
	Q_{75} + Temp	367.607	72.692	<0.001	<0.1	>1000	0.80
Quillback	Q_{75}	260.958	39.879	0.986	100	1.000	0.77
	Q_{75} + Temp	250.951	48.899	0.011	1.1	90.946	0.78
	Temp	1116.942	51.511	0.003	0.3	335.614	<0.01
River carpsucker	(a)						
Northern hogsucker	Q_{75}	91.043	31.958	0.706	100	1.000	0.25
	Temp	117.000	33.714	0.293	41.6	2.406	0.04
	Q_{75} + Temp	82.766	45.290	0.001	0.1	785.562	0.32
Golden redhorse	Q_{75}	1404.425	56.251	0.764	100	1.000	0.25
	Temp	1861.256	58.786	0.215	28.2	3.551	<0.01
	Q_{75} + **Temp**	1403.338	63.444	0.021	2.7	36.471	0.25
Shorthead redhorse	Q_{75}	309.869	42.650	0.968	100	1.000	0.69
	Q_{75} + **Temp**	308.370	49.807	0.027	2.8	65.808	0.69
	Temp	1000.013	53.195	0.005	0.5	194.861	<0.01
Silver redhorse	(a)						
White sucker	(a)						

The lowercase letter "a" indicates that the values are not estimable.
Independent variables include the number of days where discharge exceeded the 75th percentile (percentile estimated using data from 1955 to 2009; Q_{75}) and mean temperature during the growing season (i.e., 1 April to 30 September). Akaike's information criterion corrected for small sample size (AIC_c), Akaike weight (w_i), percent of the maximum w_i, (%Max w_i), and the evidence ratio (ER = max w_i/w_i) were used to evaluate candidate models. The AIC_c values were calculated from the number of model parameters, sample size, and the residual sum or squares (RSS). Bold variables indicate that the direction of influence was negative in the model. The coefficient of determination (R^2) is provided as an indication of model fit.

was to examine the influence of temperature and discharge on recruitment dynamics and growth over long periods. Temperature can directly influence the timing and duration of spawning, hatch of eggs, and growth of larval fishes, or through indirect mechanisms such as the production of prey (e.g., Blaxter, 1991). Nonetheless, temperature was not related to recruitment of catostomids in Iowa rivers. Similar to recruitment, temperature did not appear to have a major influence on growth. Although temperature undoubtedly influences growth and year-class strength of catostomids in Iowa, it is probably that variability in air temperature was not sufficient to noticeably influence growth or recruitment over the temporal scale examined in this study. Also, air temperature may have been a poor surrogate for water temperature, particularly given the high variation in temperature that is often observed in rivers (Allan, 1995).

The flow regime is generally considered to be the primary driver of ecological process in lotic systems (Poff *et al.*, 1997; Jacobson and Galat, 2006; Poff and Zimmerman, 2010; Carlisle *et al.*, in press). In large rivers, the interaction of a river and its floodplain is particularly critical for maintaining biodiversity and high levels of productivity (Junk *et al.*, 1989). For some species, the floodplain provides spawning habitat and prey items suitable for larval and juvenile fishes (e.g., Galat *et al.*, 1998; Sparks *et al.*, 1998). Consequently, high flows are often related to enhanced recruitment (Welcomme, 1979; King *et al.*, 2003). Phelps *et al.* (2010) examined abundance of age-0 sturgeon, *Scaphirhynchus* spp., in the middle Mississippi River and found that higher densities of sturgeon occurred in years with long periods of high water. Coutant (2004) suggested that recruitment of white sturgeon, *Acipenser transmontanus*, was positively associated with flooding of terrestrial habitats in rivers of the western North America. Quist and Guy (1998) found that year-class strength of channel catfish, *Ictalurus punctatus*, was highest during flood years in the Kansas River, Kansas, and Raibley *et al.* (1997) showed that strong year classes of largemouth bass were associated with flood years in the Illinois River. Although discharge did not explain a high proportion of the variation in year-class strength, all relationships (expect for one) were negative. Peterson and Jennings (2007) found that long periods of high discharge were inversely related to year-class strength of *Carpiodes* spp. in the Oconee River, Georgia.

Freeman *et al.* (2001) reported that high densities of age-0 catostomids in the Tallapoosa River, Alabama, were positively associated with persistence of shallow-water habitat in summer. As such, Peterson and Jennings (2007) argued that poor recruitment of age-0 *Carpiodes* spp. was due to reduced availability of shallow-water habitats during high flows. High flows may have other more direct effects on recruitment. Weyers *et al.* (2003) found that newly hatched robust redhorse and v-lip redhorse, *Moxostoma pappillosum*, had difficulty swimming to the surface to inflate their swim bladders in high velocities. These same fish experienced reduced growth during the larval phase because of increased expenditure of energy required to maintain position in the water column. Carpsuckers typically spawn in shallow habitats with low current velocities (e.g., Smith, 1977; Harlan *et al.*, 1987; Jenkins and Burkhead, 1994), and northern hogsucker and redhorse spawn in riffles, runs, or the tail end of pools over rocky substrate (Meyer, 1962; Curry and Spacie, 1984; Jenkins and Burkhead, 1994; Grabowski *et al.*, 2008). Thus, high flows may have a negative influence on catostomids by reducing or eliminating shallow-water habitats or by physically damaging eggs and larvae via movement of large substrates (e.g., Zhao *et al.*, 2009).

The most consistent pattern observed in this study was the association between discharge (i.e., days exceeding the 75th percentile in discharge) and growth. One of the primary concepts associated with floodplain rivers, and a central tenet of the FPC is that high flows increase production in river systems (e.g., Junk *et al.*, 1989). Growth of fishes is one expression of increased productivity. Consequently, a variety of studies have been conducted to evaluate the influence of flooding on growth of fishes, particularly in tropical rivers. Welcomme (1979) examined growth of two cichlid species in the Kaufe River, Zambia, and found that age-specific and sex-specific growth were positively related with a flood index and negatively related to measures of river drawdown. Bayley (1988) studied growth of 12 fish species and their response to flooding in the central Amazon. Detritivores did not show a response to flood, but growth of omnivorous species was approximately 60% faster during flood conditions. De Graaf (2003) found that growth of banded gourami, *Colisa fasciatus*, and snakehead, *Channa punctata*, in the River Brahmaputra, Bangladesh, was significantly higher in years with flooding. Similar results have been reported for myriad species across a diversity of tropical river systems (e.g., Dudley, 1974; Kapetsky, 1974; Smith, 1991; Perez and Fabre, 2009).

Compared with tropical systems, little research has been conducted to evaluate the influence of high flows on growth of fishes in large temperate rivers. Of the studies that have been conducted, nearly all have shown patterns consistent with those observed in tropical river systems. For example, Quist and Guy (1998) found that growth of channel catfish was positively related to flooding in the Kansas River, Kansas. Sommer *et al.* (2001) showed that growth of juvenile Chinook salmon, *Oncorhynchus tshawytscha*, was significantly faster in floodplain habitats than in main channel habitats in the Sacramento River basin, California. Similar results were reported by Jeffres *et al.* (2008) for Chinook salmon in the Cosumnes River, California. A number of studies have evaluated the effects of high flows on growth of fishes in the Mississippi River, particularly in response to flooding that characterized the system in the early and middle 1990s. Rutherford *et al.* (1995) found that growth of blue catfish, *Ictalurus furcatus*, channel catfish, freshwater drum, *Aplodinotus grunniens*, and gizzard shad, *Dorosoma cepedianum*, in the lower Mississippi River was not related to discharge. The authors suggested that channelization and construction of levees served to disconnect the river from its floodplain; therefore, high flows did not benefit fishes as would be expected from a functioning floodplain river system. Schramm and Eggleton (2006) argued that Rutherford *et al.* (1995) failed to consider the importance of temperature. When temperature was integrated with measures of floodplain inundation, Schramm and Eggleton (2006) found strong positive relationships between flooding and growth of blue catfish and flathead catfish, *Pylodictis olivaris*, in the lower Mississippi River. In the middle Mississippi River, Jones and Noltie (2007) concluded that growth of flathead catfish was enhanced following flood conditions. Gutreuter *et al.* (1999) found that growth of largemouth bass and bluegill, *Lepomis macrochirus*, species that typically exploit littoral habitats (i.e., similar to floodplain habitats), increased during a year with a warm-season flood in the upper Mississippi River. Growth of white bass, *Morone chrysops*, a pelagic species, did not respond to flooding.

With few exceptions, growth of catostomids of all ages was positively related to flooding across reaches in Iowa rivers. Like previous studies examining the effects of high discharge on growth, the specific mechanisms responsible for the observed patterns are unknown. Several studies suggest that catostomids directly access and use the floodplain, presumably to feed. Sullivan and Watzin (2009) sampled fish assemblages in main channel and in connected-floodplain habitats in Vermont streams and found that white suckers occurred at 25% of the floodplain sites. Grabowski and Isely (2006) used radio telemetry to monitor movement of robust redhorse in the Savannah River, South Carolina and Georgia. During high water conditions, robust redhorse actively used the floodplain. The authors commented that several individuals moved so far onto the floodplain that they were barely detectable from the main channel. In the Ocmulgee River, Georgia,

Grabowski and Jennings (2009) found similar results where robust redhorse often used floodplain habitats during high flows. In addition to providing access to high invertebrate and algal production typical of floodplain habitats, receding waters provide nutrients that enhance primary and secondary production in the main channel (e.g., Forsberg *et al.*, 1988; Gladden and Smock, 1990; Vegas-Villarrubia and Herrera, 1993; Bayley, 1995; Theiling and Tucker, 1999; Tockner *et al.*, 1999). Because catostomids diets are dominated by algae and invertebrates, enhanced production of these prey items in response to high flows may help explain the observed patterns.

This research provides basic information on the population demographics of catostomids. Such information is important for developing a better understanding of catostomid ecology and their role in aquatic systems. Basic demographic information is becoming increasingly important as the conservation status of species deteriorates and as scientists attempt to model the effects of different management activities on populations, assemblages, and ecosystems (e.g., Christensen and Pauly, 1992). In addition to providing information on the ecology of catostomids, this research contributes to the growing literature focused on the importance of floodplains to temperate river systems. Previous research on the growth response of fishes to discharge has focused almost exclusively on Great Rivers (e.g., Mississippi River) and (or) taxa that occupy high trophic levels, typically sport fishes (e.g., flathead catfish, largemouth bass; Gutreuter *et al.*, 1999; Schramm and Eggleton, 2006). Our findings fill an important gap in that the study systems were much smaller than those previously examined, and the focal taxa were nongame species that occupy low trophic levels. Future research both on the population demographics of catostomids and the interaction of fishes with their floodplain in temperate rivers is greatly needed to better understand the structure and function of river systems.

ACKNOWLEDGEMENTS

We thank L. Brown, N. Hogberg, and M. Mork for the assistance in the field and laboratory. We also thank S. Weisberg for helpful insight on statistical procedures. Helpful comments on a previous version of this manuscript were provided by C. Guy, T. Neebling, and two anonymous reviewers. This project was supported, in part, by Iowa State University, Iowa Department of Natural Resources, and the Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the University of Idaho, U.S. Geological Survey, Idaho Department of Fish and Game, U.S. Fish and Wildlife Service, and Wildlife Management Institute. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Allan JD. 1995. *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall: New York, NY.

Allen MS, Hightower JE. 2010. Fish population dynamics: mortality, growth, and recruitment. In *Inland Fisheries Management in North America*, *third edition*, Hubert WA, Quist MC (eds). American Fisheries Society: Bethesda, MD; 43–79.

Bayley PB. 1988. Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. *Environmental Biology of Fishes* **21**: 127–142.

Bayley PB. 1995. Understanding large river-floodplain ecosystems. *Bioscience* **45**: 153–158.

Becker GC. 1983. *Fishes of Wisconsin*. The University of Wisconsin Press: Madison, WI.

Beecher HA. 1979. Comparative functional morphology and ecological isolating mechanisms in sympatric fishes of the genus *Carpiodes* in northwestern Florida. *Ph.D. Dissertation*, Florida State University, Tallahassee.

Blaxter JHS. 1991. The effect of temperature on larval fishes. *Netherlands Journal of Zoology* **42**: 336–357.

Brunel T, Boucher J. 2007. Long-term trends in fish recruitment in the north-east Atlantic related to climate change. *Fisheries Oceanography* **16**: 336–349.

Buchholz M. 1957. Age and growth of river carpsucker in the Des Moines River, Iowa. *Proceedings of the Iowa Academy of Science* **64**: 589–600.

Bunn SE, Davies PM, Mosisch TD. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. *Freshwater Biology* **41**: 333–345.

Bunt CM, Cooke SJ. 2001. Post-spawn movements and habitat use of greater redhorse, *Moxostoma valenciennesi*. *Ecology of Freshwater Fish* **10**: 57–60.

Bruch RM, Campana SE, Davis-Foust SL, Hansen MJ, Janssen J. 2009. Lake sturgeon age validation using bomb radiocarbon and known-age fish. *Transactions of the American Fisheries Society* **138**: 361–372.

Burnham KP, Anderson DR. 2002. *Model Selection and Multi-model Inference*, 2nd edition. Springer-Verlag: New York, NY.

Cahn AR. 1927. An ecological study of southern Wisconsin fishes. *Illinois Biological Monographs* **11**(1): 1–151.

Carlander HB. 1954. *A History of Fish and Fishing in the Upper Mississippi River*. Upper Mississippi River Conservation Committee: Rock Island, IL.

Carlisle DM, Wolock DM, Meador MR. In press. Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment. *Frontiers in Ecology and the Environment*. DOI: 10.1890/100053

Christensen V, Pauly D. 1992. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* **61**: 169–185.

Cooke SJ, Bunt CM, Hamilton SJ, Jennings CA, Pearson MP, Cooperman MS, Markle DF. 2005. Threats, conservation strategies, and prognosis for suckers (Catostomidae) in North America: insights from regional case studies of a diverse family of non-game fishes. *Biological Conservation* **121**: 317–331.

Coutant CC. 2004. A riparian habitat hypothesis for successful reproduction of white sturgeon. *Reviews in Fisheries Science* **12**: 1064–1262.

Curry KD, Spacie A. 1984. Differential use of stream habitat by spawning catostomids. *American Midland Naturalist* **111**: 267–279.

De Graaf G. 2003. The flood pulse and growth of floodplain fish in Bangladesh. *Fisheries Management & Ecology* **10**: 241–247.

DeVries DR, Frie RV. 1996. Determination of age and growth. In *Fisheries Techniques*, second edition. Murphy BR, Willis DW (eds). American Fisheries Society: Bethesda, MD; 483–512.

Downes BJ, Lake PS, Schreiber ESG, Glaister A. 2000. Habitat structure, resources and diversity: the separate effects of surface roughness and macroalgae on stream invertebrates. *Oecologia* **123**: 569–581.

Dudley RG. 1974. Growth of tilapia of the Kafue floodplain, Zambia: predicted effects of the Kafue Gorge Dam. *Transactions of the American Fisheries Society* **103**: 281–291.

Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**: 753–762.

Flotemersch JE, Stribling JB, Paul MJ. 2006. *Concepts and Approaches for the Bioassessment of Non-wadeable Streams and Rivers*. EPA/600/R/06/127. U.S. Environmental Protection Agency: Washington, DC.

Forsberg BR, Devol AH, Richey JE, Martinelli LA, Dos Santos H. 1988. Factors controlling nutrient concentrations in Amazon floodplain lakes. *Limnology and Oceanography* **33**: 41–56.

Freeman MC, Bowen ZH, Bovee KD, Irwin ER. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. *Ecological Applications* **11**: 179–190.

Freund RJ, Littell RC. 1991. *SAS System for Regression, 2nd edition*. SAS Institute Inc.: Cary, NC.

Galat DL, Frederickson LH, Humburg DD, Bataille KJ, Bodie JR, Dohrenwend J, Gelwicks GT, Havel JE, Helmers DL, Hooker JB, Jones JR, Knowlton MF, Kubisiak J, Mazourek J, McColpin AC, Renken RB, Semlitsch RD. 1998. Flooding to restore connectivity of regulated, large-river wetlands—natural and controlled flooding as complimentary processes along the lower Missouri River. *Bioscience* **48**: 721–733.

Gatz AJ. 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* **21**: 91–124.

Gladden JE, Smock LA. 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. *Freshwater Biology* **24**: 533–545.

Grabowski TB, Isely JJ. 2006. Seasonal and diel movements and habitat use of robust redhorse in the lower Savannah River, Georgia and South Carolina. *Transactions of the American Fisheries Society* **135**: 1145–1155.

Grabowski TB, Jennings CA. 2009. Post-release movements and habitat use of robust redhorse transplanted to the Ocmulgee River, Georgia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **19**: 170–177.

Grabowski TB, Ratterman NL, Isely JJ. 2008. Demographics of the spawning aggregations of four catostomid species in the Savannah River, South Carolina and Georgia, USA. *Ecology of Freshwater Fish* **17**: 318–327.

Gulland JA. 1982. Why do fish numbers vary? *Journal of Theoretical Biology* **97**: 69–75.

Gutreuter SA, Bartels D, Irons K, Sandheinrich MB. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the upper Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 2282–2291.

Guy CS, Willis DW. 1995. Population characteristics of black crappies in South Dakota waters: a case for ecosystem-specific management. *North American Journal of Fisheries Management* **15**: 754–765.

Harbicht S. 1990. Ecology of the shorthead redhorse (*Moxostoma macrolepidotum*) (LeSuer) 1817 in Dauphin Lake, Manitoba. *M.S. Thesis*, University of Manitoba: Winnipeg, MB.

Harlan JR, Speaker EB, Mayhew J. 1987. *Iowa Fish and Fishing*. Iowa Department of Natural Resources: Des Moines, IA.

Isermann DA, McKibbin WL, Willis DW. 2002. An analysis of methods for quantifying crappie recruitment variability. *North American Journal of Fisheries Management* **22**: 1124–1135.

Jacobson RB, Galat DL. 2006. Flow and form in rehabilitation of large-river ecosystems: an example from the lower Missouri River. *Geomorphology* **77**: 249–269.

Jeffres CA, Opperman JJ, Moyle PB. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes* **83**: 449–458.

Jenkins RE. 1970. Systematic studies of the catostomid fish tribe Moxostomatini. *Ph.D. Dissertation*, Cornell University: Ithaca, NY.

Jenkins RE, Burkhead NM. 1994. *Freshwater Fishes of Virginia*. American Fisheries Society: Bethesda, MD.

Johnson DW. 2007. Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish. *Ecology* **88**: 1716–1725.

Jones BD, Noltie DB. 2007. Flooded flatheads: evidence of increased growth in Mississippi River *Pylodictis olivaris* (Pisces: Ictaluridae) following the great Midwest flood of 1993. *Hydrobiologia* **592**: 183–209.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. In *Proceedings of the International Large River Symposium*, Dodge DP (ed). Canadian Journal of Fisheries and Aquatic Sciences Special Publication **106**: 110–127.

Jurajda P. 1995. Effects of channelization and regulation on fish recruitment in a floodplain river. *Regulated Rivers: Research and Management* **10**: 207–215.

Kapetsky JM. 1974. Growth, mortality and production of five species fish species of the Kafue River floodplain, Zambia. *Ph.D. Dissertation*, University of Michigan: Ann Arbor, MI.

King AJ, Humphries P, Lake PS. 2003. Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**: 773–786.

Koch JD, Quist MC. 2007. A technique for preparing fin rays and spines for age and growth analysis. *North American Journal of Fisheries Management* **27**: 781–784.

Koch JD, Schreck W, Quist MC. 2008. Standardized removal and sectioning locations for shovelnose sturgeon fin rays. *Fisheries Management & Ecology* **15**: 139–145.

Litvan ME, Stewart TW, Pierce CL, Larson CJ. 2008. Effects of grade control structure on the macroinvertebrate assemblage of an agriculturally impacted stream. *River Research and Applications* **24**: 218–233.

Lyons J, Piette RR, Niermeyer KW. 2001. Development, validation, and application of a fish-based index of biotic integrity for Wisconsin's large warmwater rivers. *Transactions of the American Fisheries Society* **130**: 1077–1094.

Maceina MJ. 1997. Simple application of using residuals from catch-curve regressions to assess year-class strength in fish. *Fisheries Research* **32**: 115–121.

Markle DF, Cooperman MS. 2002. Relationship between Lost River and shortnose sucker biology and management of upper Klamath Lake. In *The 2001 Water Allocation Decisions in the Klamath Basin*, Braunworth B, Welch T (eds). Oregon State University Extension Publication: Corvallis, OR; 93–188.

Master L. 1990. The imperiled status of North American aquatic animals. *Biodiversity Network News (The Nature Conservancy)* **3**: 1–8.

McIntyre PB, Flecker AS, Vanni MJ, Hood JM, Taylor BW, Thomas SA. 2008. Fish distributions and nutrient cycling in streams: can fish create biochemical hotspots? *Ecology* **89**: 2335–2346.

Meyer WH. 1962. Life history of three species of redhorse (*Moxostoma*) in the Des Moines River, Iowa. *Transactions of the American Fisheries Society* **91**: 42–419.

Minckley WL. 1963. The ecology of a spring stream Doe Run, Meade County, Kentucky. *Wildlife Monographs 11*.

Minckley WL, Deacon JE (eds). 1991. *Battle Against Extinction: Native Fish Management in the American West*. The University of Arizona Press: Tucson, AZ.

Miranda LE, Bettoli PW. 2007. Mortality. In *Inland Fisheries Management in North America, third edition*, Hubert WA, Quist MC (eds). American Fisheries Society: Bethesda, MD; 229–277.

Mutel F. 2010. *A Watershed Year: Anatomy of the Iowa Floods of 2008*. University of Iowa Press: Iowa City, IA.

Natural Resources Conservation Service (NRCS). 2000. *Natural Resources Inventory: 1997 Summary Report*. U.S. Department of Agriculture: Ames, IA.

Neebling TE, Quist MC. 2010. Relationships between fish assemblages and habitat characteristics in Iowa's non-wadeable rivers. *Fisheries Management & Ecology* **17**: 369–385.

Needham JT, Watkins DW Jr, Lund JR, Nanda SK. 2000. Linear programming for flood control in the Iowa and Des Moines rivers. *Journal of Water Resources Planning and Management* **126**: 118–127.

Nilsson CC, Reidy A, Dynesius M, Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–408.

Paukert CP, Willis DW. 2004. Environmental influences on largemouth bass *Micropterus salmoides* populations in shallow Nebraska lakes. *Fisheries Management & Ecology* **11**: 345–352.

Perez A, Fabre NN. 2009. Seasonal growth and life history of the catfish *Calophysus macropterus* (Lichtenstein, 1819) (Siluriformes: Pimelodidae) from the Amazon floodplain. *Journal of Applied Ichthyology* **25**: 343–349.

Peterson RC, Jennings CA. 2007. Effects of river discharge on abundance and instantaneous growth of age-0 carpsuckers in the Oconee River, Georgia, USA. *River Research and Applications* **23**: 1016–1025.

Phelps QE, Tripp SJ, Hintz WD, Garvey JE, Herzog DP, Ostendorf DE, Ridings JW, Crites JW, Hrabik RA. 2010. Water temperature and river stage influence mortality and abundance of naturally occurring Mississippi River *Scaphirhynchus* sturgeon. *North American Journal of Fisheries Management* **30**: 767–775.

Poff NL, Zimmerman JKH. 2010. Ecological responses to altered flow regimes: a literature review to inform science and management of environmental flows. *Freshwater Biology* **55**: 194–205.

Poff NL, Allan JD, Bain MB, Karr J, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. *Bioscience* **47**: 769–784.

Puckridge JT, Sheldon F, Walker KF, Boulton AJ. 1998. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**: 55–72.

Quinn JM, Hickey CW. 1990. Magnitude of effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **24**: 411–427.

Quinn TP, Peterson NP. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 1555–1564.

Quist MC. 2007. An evaluation of techniques used to index recruitment variation and year-class strength. *North American Journal of Fisheries and Aquatic Sciences* **27**: 30–42.

Quist MC, Guy CS. 1998. Population characteristics of channel catfish from the Kansas River, Kansas. *Journal of Freshwater Ecology* **13**: 351–359.

Raibley PT, O'Hara TM, Irons KS, Blodgett KD, Sparks RE. 1997. Largemouth bass size distributions under varying annual hydrological regimes in the Illinois River. *Transactions of the American Fisheries Society* **126**: 850–856.

Reid SM. 2009. Age, growth and mortality of black redhorse (*Moxostoma duquesnei*) and shorthead redhorse (*M. macrolepidotum*) in the Grand River, Ontario. *Journal of Applied Ichthyology* **25**: 178–183.

Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**.

Rinne JN, Hughes RM, Calamusso B (eds). 2005. *Historical Changes in Large River Fish Assemblages of the Americas*. American Fisheries Society, Symposium 45: Bethesda, MD.

Rosenberg DM, McCully P, Pringle CM. 2000. Global-scale environmental effects of hydrological alterations: introduction. *Bioscience* **50**: 746–751.

Rutherford DA, Kelso WE, Bryan CF, Constant GC. 1995. Influence of physicochemical characteristics on annual growth increments of four fishes from the lower Mississippi River. *Transactions of the American Fisheries Society* **124**: 687–697.

SAS Institute. 2005. *The SAS System for Windows, version 9.1*. SAS Institute: Cary, NC.

Schramm HL Jr., Eggleton MA. 2006. Applicability of the flood-pulse concept in a temperate floodplain river ecosystem: thermal and temporal components. *River Research and Applications* **22**: 543–553.

Scoppettone GG, Vinyard G. 1991. Life history and management of four endangered lacustrine suckers. In *Battle Against Extinction: Native Fish Management in the American West*, Minckley WL, Deacon WL (eds). The University of Arizona Press: Tucson, AZ; 359–377.

Shoup DW, Wahl DH. 2009. Fish diversity and abundance in relation to interannual and lake-specific variation in abiotic characteristics of floodplain lakes of the lower Kaskaskia River, Illinois. *Transactions of the American Fisheries Society* **138**: 1076–1092.

Smith CG. 1977. The biology of three species of Moxostoma (Pisces: Catostomidae) in Clear Creek, Hocking and Fairfield counties, Ohio, with emphasis on the golden redhorse, *M. erythrurum* (Rafinesque). *Ph.D. Dissertation*, Ohio State University: Columbus, OH.

Smith MAK. 1991. Models of seasonal growth of the equatorial carp *Labeo dussumieri* in response to the river flood cycle. *Environmental Biology of Fishes* **31**: 157–170.

Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ. 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 325–333.

Sparks RE, Nelson JC, Yin Y. 1998. Naturalization of the flood regime in regulated rivers. *Bioscience* **48**: 706–720.

Spiegel JR. 2010. Summer food habits and gill raker morphology of seven catostomid species in Iowa rivers. *M.S. Thesis*, Iowa State University: Ames, IA.

Spiegel JR, Quist MC, Morris JE. 2010. Precision of scales and pectoral fin rays for estimating age of highfin carpsucker, quillback carpsucker, and river carpsucker. *Journal of Freshwater Ecology* **25**: 271–278.

Spink A, Sparks RE, Van Oorschot M, Verhoeven JTA. 1998. Nutrient dynamics in large river floodplains. *Regulated Rivers: Research and Management* **14**: 203–216.

Strommer JL, Smock LA. 1989. Vertical distribution and abundance of invertebrates within the sandy substrate of a low-gradient headwater stream. *Freshwater Biology* **22**: 263–274.

Sule MJ, Skelly TM. 1985. The life history of the shorthead redhorse, *Moxostoma macrolepidotum*, in the Kankakee River drainage, Illinois. *Illinois Natural History Survey Biological Notes* **123**.

Sullivan SMP, Watzin MC. 2009. Stream-floodplain connectivity and fish assemblage diversity in the Champlain Valley, Vermont, U.S.A. *Journal of Fish Biology* **74**: 1394–1418.

Swain DP, Sinclair AF, Hanson JM. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proceedings of the Royal Society B* **274**: 1015–1022.

Theiling CH, Tucker JK. 1999. Nektonic invertebrate dynamics and prolonged summer flooding on the lower Illinois River. *Journal of Freshwater Ecology* **14**: 499–510.

Tockner K, Pennetzdorfer D, Reiner N, Schiemer F, Ward JV. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology* **41**: 521–535.

Turner RE, Rabalais NN. 2003. Linking landscape and water quality in the Mississippi River basin for 200 years. *Bioscience* **53**: 563–572.

Vegas-Villarrubia T, Herrera R. 1993. Effects of periodic flooding on the water chemistry and primary production of the Mapire systems (Venezuela). *Hydrobiologia* **262**: 31–42.

Voelz NJ, McArthur JV. 2000. An exploration of factors influencing lotic insect species richness. *Biodiversity and Conservation* **9**: 1543–1570.

von Bertalanffy L. 1938. A quantitative theory of organic growth (Inquiries on growth laws. II). *Human Biology* **10**: 181–213.

Ward JV. 1992. *Aquatic Insect Ecology: 1. Biology and Habitat*. John Wiley and Sons, Inc.: New York, NY.

Wehmeyer LL, Weirich FH, Cuffney TF. 2011. Effect of land cover change on runoff curve number estimation in Iowa, 1832–2001. *Ecohydrology*. **4**: 315–321.

Weisberg S. 1993. Using hard-part increment data to estimate age and environmental effects. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 1229–1237.

Weisberg S, Spangler G, Richmond LS. 2010. Mixed effects models for fish growth. *Canadian Journal of Fisheries and Aquatic Sciences* **67**: 269–277.

Welcomme RL. 1979. *Fisheries Ecology of Floodplain Rivers*. Longman: London, UK.

Weyers RS, Jennings CA, Freeman MC. 2003. Effects of pulsed, high-velocity water flow on larval robust redhorse and v-lip redhorse. *Transactions of the American Fisheries Society* **132**: 84–91.

Zeug SC, Winemiller KO. 2008. Relationships between hydrology, spatial heterogeneity, and fish recruitment dynamics in a temperate floodplain river. *River Research and Applications* **24**: 90–102.

Zhao Y, Jones ML, Shuter BJ, Roseman EF. 2009. A biophysical model of Lake Erie walleye (*Sander vitreus*) explains interannual variations in recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **66**: 114–125.

Zohrer JJ. 2006. *Iowa Comprehensive Wildlife Conservation Plan*. Iowa Department of Natural Resources: Des Moines, IA.

Published in 2011 by John Wiley & Sons, Ltd.

River Res. Applic. **28**: 1567–1586 (2012)
DOI: 10.1002/rra