Population Demographics of Hiodon tergisus (Mooneye) in the Lower Tallapoosa River

Authors: Katechis, Costas T., Sakaris, Peter C., and Irwin, Elise R.

Source: Southeastern Naturalist, 6(3) : 461-470

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/1528-7092(2007)6[461:PDOHTM]2.0.CO;2

Population Demographics of *Hiodon tergisus* (Mooneye) in the Lower Tallapoosa River

Costas T. Katechis[1], Peter C. Sakaris[1,3], and Elise R. Irwin[2,*]

Abstract - We describe age structure, growth, and fecundity of *Hiodon tergisus* (Mooneye) from the lower Tallapoosa River, AL. Mooneye (N = 49, 214–316 mm total length, 79–284 g) were aged using otoliths, and a von Bertalanffy growth model was derived for the species ($L_\infty = 316$, $K = 0.285$, $t_o = -0.7$). Growth rates of Mooneye differed between the Tallapoosa River population and a previously studied population from the northern extent of the species' range (Assiniboine River, MB, Canada). In addition, fecundity of Mooneye from the Tallapoosa River was similar to the northern population, ranging from 5321 to 7432 eggs per female. Because the species is declining throughout its range in Alabama, we recommend that managers use our findings in conservation efforts. Future studies should investigate how hydrology influences the spawning success and early growth and development of Mooneye in regulated systems. More information about this species is needed regarding their early life history, including early growth, survival, and habitat use.

Introduction

Hiodon tergisus Lesueur (Mooneye) biology has been documented at northern latitudes in the Great Lakes region and Canada (Glenn 1975a, 1975b, 1976, 1978, 1980; Glenn and Williams 1976; Johnson 1951). However, in the southern extent of their range, Mooneye have been rarely studied (Jandebeur 1972, Wallus and Buchanan 1989), and life-history characteristics of Mooneye have not been reported in the Mobile River Basin (AL), where they are becoming increasingly rare (Boschung and Mayden 2004). Age structure, growth, and fecundity information are important for developing conservation and management strategies for fish species of concern.

A life-history study of Mooneye is needed within the Mobile River Basin of Alabama. Boschung and Mayden (2004) recommended that the status of Mooneye be listed as special concern, primarily because abundance of the species has dramatically declined, especially in the Mobile River Basin. Habitat fragmentation and altered flow and water-quality regimes resulting from dam construction, land-use activities, and the introduction of exotic species have been implicated as major causes for the reduction of fish diversity and distribution in Alabama rivers (Freeman et al. 2005). Mooneye

[1]Alabama Cooperative Fish and Wildlife Research Unit, 3301 Forestry and Wildlife Building, Auburn University, AL 36849. [2]United States Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, 3301 Forestry and Wildlife Building, Auburn University, AL 36849 [3]Current address - Southern Polytechnic State University, Department of Biology, Chemistry, and Physics, Marietta, GA 30060. [*]Corresponding author - irwiner@auburn.edu.

populations presumably only existed in the Cahaba River of the Mobile Basin (Boschung and Mayden 2004), but we recently encountered a population in the lower Tallapoosa River within the historical range of the species.

Fecundity of Mooneye has been estimated for northern populations (Glenn and Williams 1976, Johnson 1951), but little fecundity information exists for southern populations (Wallus and Buchanan 1989). Fecundity of Mooneye in the Mobile River Basin has not been documented. Although otoliths have been the preferred structures for aging a variety of fishes (Erickson 1983), scales have been the only structures used for aging Mooneye.

The goal of this project was to describe the life history of Mooneye in the lower Tallapoosa River, Alabama. Specific objectives were to develop methodology for using otoliths to age Mooneye and evaluate the age structure, growth, and fecundity of this species. In addition, we compared growth rates and fecundity with a northern population from the Assiniboine River, MB, Canada.

Methods

Study species

Mooneye is a silvery, insectivorous fish that has unusually large eyes with adipose eyelids and an anal fin posterior to its dorsal fin origin (Mettee et al. 1996). The anal fin has 26 to 29 rays, and the dorsal fin has 11 or 12 rays. Spawning generally occurs in late April and early May, and fish typically spawn in clear, large tributaries over rocks and gravel shoals (Boschung and Mayden 2004). Etnier and Starnes (1993) reported that adult Mooneye exhibit upstream spawning migrations into clear rivers in Tennessee. Female Mooneye lack oviducts; therefore, eggs are released into their body cavities prior to being shed. Habitats of Mooneye include tailwaters of locks and dams (Mettee et al. 1996), deep pools, backwaters of medium to large rivers, and lakes and impoundments (Page and Burr 1991). Mooneye are distributed from the St. Lawrence River (Canada) to the Mobile River Basin, including the Mississippi River drainage and the Hudson Bay Basin (Page and Burr 1991). In the Mobile basin, Mooneye have been collected below the fall line in the Alabama, Cahaba, Coosa, and Tallapoosa rivers (Mettee et al. 1996).

Field methods

Adult Mooneye were collected from the Tallapoosa River below Thurlow dam near Tallassee and Ft. Toulouse, AL (Fig. 1). Sampling was conducted in spring, summer, and fall of 2002 and in spring and summer of 2003 using boat electrofishing. Fish were euthanized in tricaine methanesulfonate (300 mg/L, MS-222), placed on ice, and then brought to the laboratory for processing.

Laboratory methods

Total length (TL, mm) and weight (g) were recorded, and the sex of each fish was determined. Saggital otoliths were extracted by cutting into the dorsal surface of the head posterior to the eye using a scalpel. Otoliths were then removed with forceps, dried, and placed in vials with appropriate labels.

Three 2-gram sub-samples of mature eggs were removed from anterior, middle, and posterior sections within the body cavity of gravid females. Ten randomly selected eggs from each sub-sample were measured using a calibrated ocular micrometer to the nearest 0.01 mm to determine diameter (10X, Olympus dissecting microscope, Model SZH - ILLK). After egg diameters were measured, all eggs within the body cavity were removed, weighed (i.e., total egg weight) and manually counted for fecundity estimation (i.e., fecundity = total number of eggs in the body cavity of a female). Because the body cavities of all gravid females were entirely full with eggs, we assumed that females did not deposit their eggs before they were collected. Eggs were placed into labeled jars with 5–10 percent formalin for preservation (Murphy and Willis 1996). Eggs contained little connective tissue; therefore, Gilson's fluid was not needed to facilitate the disintegration of connective tissue (Murphy and Willis 1996).

For aging, otoliths were burned on a hotplate (Model # HP - 46825, Thermolyne Corporation, Dubuque, IA) for 30–60 seconds on medium heat until they were light brown (Buckmeier et al. 2002). Otoliths were then mounted in crystalbond mounting wax (40-8150, Aremco Products, Inc., Valley Cottage, NY) similar to the methods described by Nash and Irwin (1999) for mounting *Pylodictis olivaris* Rafinesque (flathead catfish) otoliths. After the crystalbond hardened, otoliths were ground to the nucleus with wet sand paper (600 grit). During grinding, otoliths were frequently viewed under a dissecting microscope (5–25X) to determine when the nucleus was visible. After reaching the nucleus, a fiber optic light source was used to illuminate the

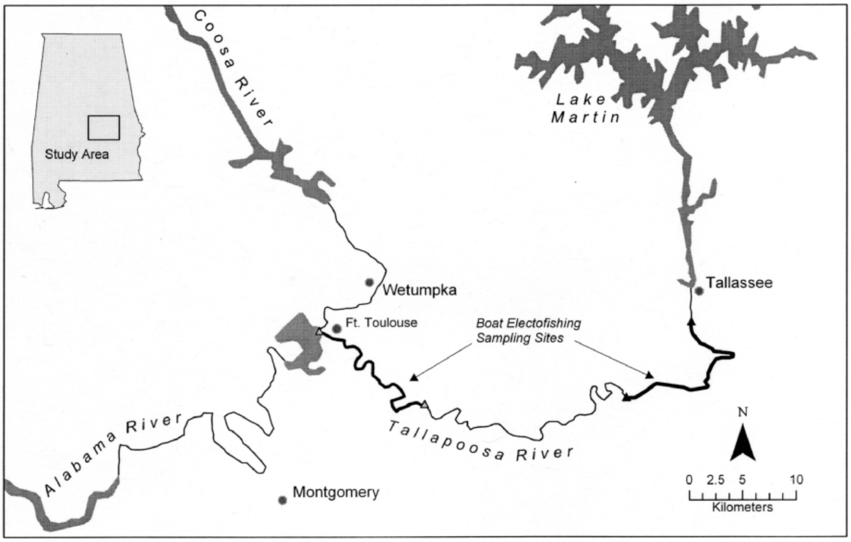

Figure 1. Study area and boat electrofishing sampling sites on the Tallapoosa River near Tallassee and Ft. Toulouse, AL.

sectioned otolith and facilitate the discrimination of annuli. A drop of mineral oil was applied to the otolith's surface to enhance the visibility of annuli. Two technicians, with numerous years of experience, recorded the number of annuli with knowledge of only fish ID number and date of collection. All discrepancies in age between readers were reconciled with concert reads (i.e., mutual examination; Buckmeier et al. 2002). We also attempted to use scales to age Mooneye ($N \approx 20$), but annuli were not distinct and interpretation of age was difficult due to the presence of false annuli. After final ages were determined, we used an image-analysis system to measure otolith radii (mm) from the nucleus to each annulus and the outer edge of each otolith (Image-Pro Plus®, Media Cybernetics, Inc., Silver Spring, MD). Total lengths at previous ages were back-calculated using the direct proportion method (DeVries and Frie 1996).

Statistical analysis

A von Bertalanffy (1938) growth model ($L_t = L_\infty * [1 - e^{-k(t - t_o)}]$) was derived for Mooneye using SAS (Statistical Analysis System, version 8, SAS Institute, Inc., Cary, NC). Regression analyses were used to evaluate relations between: 1) Log_{10} (Wt) and Log_{10} (TL), 2) otolith radius and TL, 3) TL and Log_{10} (age), and 4) Fecundity and TL. Relations were considered significant at the $\alpha = 0.05$ level. Analysis of covariance (ANCOVA) was used to compare the slopes and elevations of TL-to-log (age) regressions between Mooneye populations from the Assiniboine River (MB, Canada; Glenn 1975a) and the Tallapoosa River. We used analysis of variance (ANOVA) to compare egg diameter among posterior, middle, and anterior sections within the body cavity of Mooneye.

Results

A total of 49 Mooneye (214–316 mm, 79–284 g) were collected from the lower Tallapoosa River. The majority of Mooneye were collected during March and April of 2002 and 2003 (40/49 [82%] of the sample; Table 1). Catch per unit of effort was also highest during these months ranging from 0.61 to 1.34 fish per shocking hour (Table 1). Catch rates were very low in May, June, and July of 2002 and 2003 (8/49 [16%] of the sample), and only one fish was collected in fall 2002 (Table 1).

Ages of Mooneye ranged from 2 to 9 years. We collected 31 males, 12 females, and six fish with undeterminable sex. A relation between Log_{10} (WT) and Log_{10} (TL) was significant ($P < 0.01$); Log_{10} (TL) accounted for 85% of the variability in Log_{10} (WT) ($r^2 = 0.85$; Fig. 2). Total length of Mooneye was positively related to otolith radius ($r^2 = 0.54$, $P < 0.01$). Back-calculated lengths-at-age indicated that fish growth varied among year classes (Table 2). The von Bertalanffy growth model predicted the following lengths (mm) at age: 121 at age-one, 170 at age-two, 206 at age-three, 233 at age-four, 254 at age-five, 269 at age-six, 281 at age-seven, and 290 at age-eight ($L_\infty = 316$, $K = 0.285$, $t_o = -0.7$, $P < 0.01$).

A positive linear relation between mean TL and Log $_{10}$ (age) was significant ($P < 0.01$); Log $_{10}$ (age) explained 99.8% of the variability in TL of

Table 1. Sampling periods, effort, and catch per unit of effort for Mooneye (N = 49) collected from the lower Tallapoosa River (Alabama) below Thurlow Dam.

Year	Month	N	Effort (shocking hours)	CPUE (no. fish/hr)
2002	March	6	9.88	0.61
	April	20	14.87	1.34
	May	1	6.31	0.16
	June	1	12.36	0.08
	July	1	7.93	0.13
	October	0	1.84	0.00
	November	1	1.27	0.79
2003	March	10	9.25	1.08
	April	4	5.70	0.70
	May	5	13.57	0.37
	June	0	5.46	0.00
	July	0	1.99	0.00

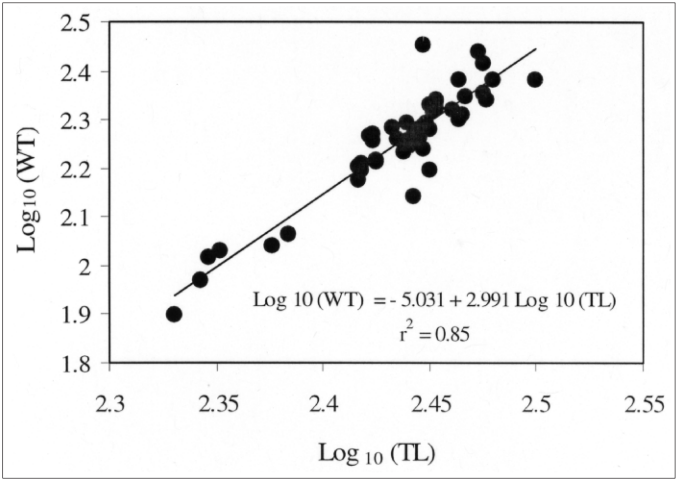

Figure 2. Log $_{10}$ (WT)-to-Log $_{10}$ (TL) regression for Mooneye (n = 49) collected below Thurlow Dam on the Tallapoosa River (AL).

Table 2. Back-calculated mean total lengths (mm) at age for Mooneye (year classes 1993–2001) collected from the lower Tallapoosa River (Alabama) below Thurlow Dam.

Year class	N	1	2	3	4	5	6	7	8	9
2001	4	142	220							
2000	2	163	237	283						
1999	7	139	201	251	275					
1998	20	128	190	235	268	280				
1997	6	121	174	215	251	280	292			
1996	7	100	157	194	226	253	280	288		
1995	1	91	145	190	220	250	270	294	316	
1994	1	88	138	180	207	232	256	280	300	
1993	1	83	113	147	168	202	228	251	269	291
Total	49									
Grand mean		117	175	212	231	250	265	278	295	
S.D.		28.2	40.7	43.4	37.3	29.7	24.8	19.1	24.0	

Mooneye from the Tallapoosa River (Fig. 3). For Mooneye from the Assiniboine River (Glenn 1975a), mean total length was also positively related to Log $_{10}$ (age) ($r^2 = 0.998$, $P < 0.01$; Fig. 3). The slope of the TL-to-Log $_{10}$ (age) regression for Mooneye in the Assiniboine River (slope = 227.0) was higher (ANCOVA: $t = 6.20$, $P < 0.01$) than the slope for the Tallapoosa River population (slope = 192.3). Elevations of TL-to-Log $_{10}$ (age) regressions were similar between the populations (Tallapoosa intercept = 117.2; Assiniboine intercept = 110.2; ANCOVA: $t = 1.93$, $P = 0.08$).

On 17 April and 24 April 2002, three gravid females (271–299 mm TL, 192–260 g) were collected when water temperatures were 20 and 22 ºC, respectively. In 2003, five gravid females (264–316 mm TL, 183–274 g) were collected from 13 March to 1 May when water temperatures ranged from 12 to 17 ºC. Ages of gravid females ranged from 3 to 8 years (mean ± SD = 5.3 ± 1.7). Fecundity ranged from 5321 to 7432 total eggs (mean ± SD = 6412 ± 847), and total egg weight ranged from 23.9 to 60.0 g per female (mean ± SD = 42 ± 11). Fecundity was positively related to total length of Mooneye ($r^2 = 0.67$, $P = 0.01$). Egg diameter ranged from 2.16 mm to 2.77 mm; no significant differences were recorded among anterior (mean ± S.D. = 2.47 mm ± 0.24), middle (mean = 2.50 mm ± 0.22), and posterior (mean = 2.49 mm ± 0.20) sections within the body cavities of the fish (ANOVA: $F = 0.02$, $P = 0.98$).

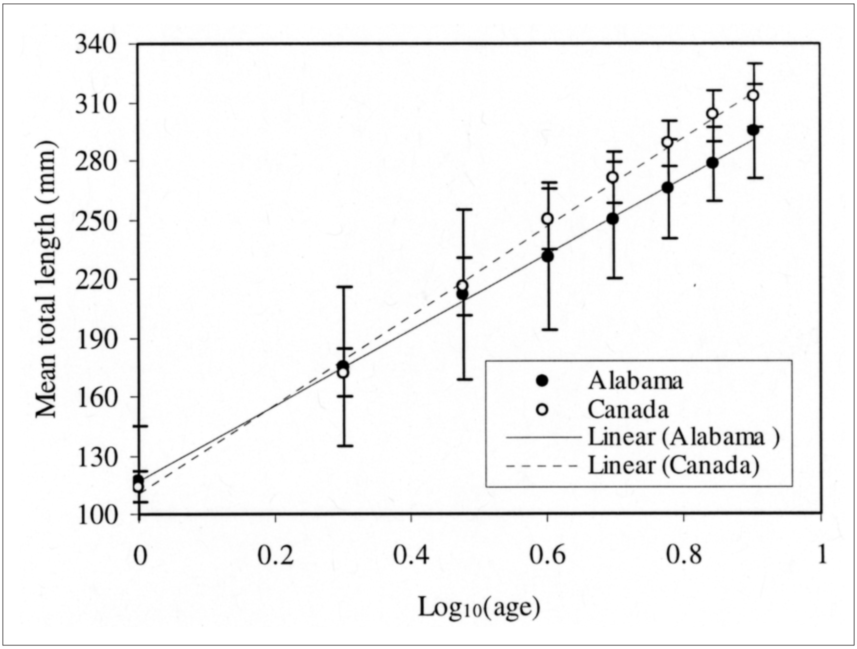

Figure 3. Mean TL-to-Log $_{10}$ (age) regressions for Mooneye (n = 669) collected in the Assiniboine River (Canada, Glenn 1975a) and for Mooneye collected in the Tallapoosa River (AL; error bars = S.D.).

Discussion

Our results demonstrated that Mooneye in the Assiniboine River (Canada) grew faster than fish in the lower Tallapoosa River (Alabama). Because our sample consisted mostly of Mooneye undergoing spawning migrations, our results were slightly biased with larger and possibly faster growing fish at younger ages (ages 2 and 3). For example, mean back-calculated lengths at ages 2 and 3 were 175 and 212 mm TL, respectively (Table 2); in contrast, mean lengths of age-2 and age-3 fish from the original sample were 224 and 267 mm TL, respectively. Glenn and Williams (1976) reported that only 23% of Mooneye were mature at age 3 in the Assiniboine River. Therefore, we probably did not account for a large proportion of immature two- and three-year-old fish, which likely resulted in the overestimation of Mooneye growth in the Tallapoosa River system. However, fish growth still appeared to be faster in the Assiniboine River than in the Tallapoosa River. Faster growth in the northern population could have been related to system-specific (biotic and abiotic) factors (e.g., food resource levels and water quality). However, we hypothesize that growth of Mooneye varies along a latitudinal gradient. Because our analysis was limited to only two populations, Mooneye should be studied across their range to determine if latitudinal variation in growth rate truly exists. Latitudinal variation in growth rate has been observed in other fishes (Brown et al. 1998, Conover and Present 1990, Conover et al. 1997, Schultz et al. 1996); fish from northern populations have exhibited inherently higher growth rates than their southern counterparts to counteract the negative effect of a shortened growing season (i.e., countergradient variation in growth).

Longevity was similar between northern and southern populations. Maximum age in the Assiniboine and Tallapoosa rivers was 9 years. Northern fish were aged using scales, which may underestimate the ages of older fish (Donald et al. 1992, Glenn 1975a). Fecundity appeared to be similar between northern and southern populations. Fecundity of Mooneye ranged from 4956 to 8912 ova per female in the Assiniboine River and 5321 to 7432 ova per female in the lower Tallapoosa River. Wallus and Buchanan (1989) also reported similar fecundity estimates for Mooneye, ranging from 3037 to 7773 eggs per female in the Tennessee and Cumberland river systems. However, more fecundity data should be collected from Mooneye in the Tallapoosa River to conduct a reliable comparative test among the populations.

Glenn and Williams (1976) reported that the mean diameter of ripe ova of Mooneye was 1.98 mm in the Assiniboine River. Mean diameter of eggs of Mooneye from the Tallapoosa River ranged from 2.16 to 2.77 mm, which was similar to the egg diameters reported for Mooneye in the Tennessee and Cumberland river systems (2.0–2.5 mm; Wallus and Buchanan 1989). Glenn and Williams (1976) found no significant differences among diameters of eggs removed from anterior, middle, and posterior portions of the same ovary, which was consistent with our findings. Our results indicated that all eggs in our gravid females were ripe (i.e., fully mature), and these fish were in close proximity to spawning. Because all eggs were at the same maturity level, Mooneye were probably complete spawners releasing all of their eggs at one time.

In early spring, Mooneye were typically collected from habitats that appeared to be conducive for spawning (i.e., clear, flowing water, over rocky or coarse substrate; Boschung and Mayden 2004). Furthermore, forty-four of 49 fish (90%) were age-3 or older, indicating that most of our fish were probably mature individuals either beginning or ending their spawning runs. Wallus and Buchanan (1989) also suggested that Mooneye undergo spring spawning migrations to flowing areas of the Tennessee River. Glenn and Williams (1976) reported that spawning began after May 8 and was completed by June 12 in the Assiniboine River. We did not collect any juvenile fish (age-0 or age-1 fish); immature fish were probably occupying other habitats while spawning fish moved into the sampling area.

Conservation and management implications

Fluctuating flows below dams may have negative impacts on Mooneye populations, due to increased temperature variation, decreased prey abundance (i.e., aquatic insects), and increased sedimentation and turbidity that can strand larvae and smother eggs (Cereghino and Lavandier 1998, Cushman 1985, Freeman et al. 2001). Irwin and Freeman (2002) proposed a plan for adaptively managing regulated systems, which included providing periods of stable flow during the spawning season that would potentially enhance survival and development of fish larvae and juveniles (Freeman et al. 2001). Moderate discharges are believed to facilitate egg transport downstream and larval transport and feeding, whereas high and low flows are considered detrimental to recruitment (Rulifson and Manooch 1990). Mooneye eggs are buoyant and non-adhesive and develop as they drift in the current (Boschung and Mayden 2004); therefore, this species probably requires moderate discharges and stable flow conditions for successful egg development. Future studies should investigate how hydrology influences the spawning success and early growth and development of Mooneye in regulated systems. In addition, flow requirements for successful recruitment of Mooneye should be identified. More information about this species is needed regarding their early life history, including early growth, survival, and habitat use.

Mooneye populations may also be negatively affected by the presence of predator species, specifically striped bass that have been landlocked due to dam construction (Boschung and Mayden 2004). Several Mooneye were observed in stomachs of striped bass from the Tallapoosa River (P.C. Sakaris, pers. observ.), indicating that Mooneye may be vulnerable to striped bass predation, especially during the spawning season. Because Mooneye are declining throughout their range in Alabama, we recommend that managers use our findings in conservation efforts.

Acknowledgments

This research was funded by the Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fisheries. We thank G. Turner, S. Herrington, B. Ricks, and T. Piper for their contributions to this paper. The cooperators of the Alabama Cooperative Fish and Wildlife Research Unit are: Alabama Agricultural Experiment Station, Auburn University; Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fisheries; the Wildlife Management Institute; and the US Fish and Wildlife Service.

Literature Cited

Boschung, H.T., and R.L. Mayden. 2004. Fishes of Alabama. Smithsonian Books, Washington, DC.

Brown, J.J., A. Ehtisham, and D.O. Conover. 1998. Variation in larval growth rate among striped bass stocks from different latitudes. Transactions of the American Fisheries Society 127:598–610.

Buckmeier, D.L., E.R. Irwin, R.K. Betsill, and J.A. Prentice. 2002. Validity of otoliths and pectoral spines for examining ages of channel catfish. North American Journal of Fisheries Management 22:934–942.

Cereghino, R., and P. Lavandier. 1998. Influence of hydropeaking on the distribution and larval development of the Plecoptera from a mountain stream. Regulated Rivers: Research and Management 14:297–309.

Conover, D.O., and T.M.C. Present. 1990. Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia 83:316–324.

Conover, D.O., J.J. Brown, and A. Ehtisham. 1997. Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. Canadian Journal of Fisheries and Aquatic Sciences 54:2401–2409.

Cushman, R.J. 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. North American Journal of Fisheries Management 5:330–339.

DeVries, D.R, and R.V. Frie. 1996. Determination of age and growth. Pp. 483–508, *In* B.R. Murphy and D.W. Willis (Eds.). Fisheries Techniques, 2nd Edition. American Fisheries Society, Bethesda, MD.

Donald, D.B., J.A. Babaluk, J.F. Craig, and W.A. Musker. 1992. Evaluation of the scale and operculum methods to determine age of adult goldeyes with special reference to a dominant year-class. Transactions of the American Fisheries Society 121:792–796.

Erickson, C.M. 1983. Age determination of Manitoban walleyes using otoliths, dorsal spines, and scales. North American Journal of Fisheries Management 3:176–181.

Etnier, D.A., and W. C. Starnes. 1993. The Fishes of Tennessee. The University of Tennessee Press, Knoxville, TN.

Freeman, M.C., Z.H. Bowen, K.D. Bovee, and E.R. Irwin. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecological Applications 11(1):179–190.

Freeman, M.C., E.R. Irwin, N.M. Burkhead, B.J. Freeman, and H.L. Bart, Jr. 2005. Status and conservation of the fish fauna of the Alabama River system. American Fisheries Society Symposium 45:557–585.

Glenn, C.L. 1975a. Annual growth rates of Mooneye, *Hiodion tergisus*, in the Assiniboine River. Fisheries Research Board of Canada 32:407–410.

Glenn, C.L. 1975b. Seasonal diets of Mooneye, *Hiodion tergisus*, in the Assiniboine River. Canadian Journal of Zoology 53:232–237.

Glenn, C.L. 1976. Seasonal growth rates of Mooneye (*Hiodion Tergisus*) in the Assiniboine River. Fisheries Research Board of Canada 33:2078–2082.

Glenn, C.L. 1978. Seasonal growth and diets of young-of-the-year Mooneye (*Hiodion tergisus*) in the Assiniboine River, Manitoba. Transactions of the American Fisheries Society 107(4):587–589.

Glenn, C.L. 1980. Seasonal parasitic infections in Mooneye, *Hiodion tergisus* (LeSueur), from the Assiniboine River. Canadian Journal of Zoology 58:252–257.

Glenn, C.L., and R.R.G. Williams. 1976. Fecundity of Mooneye, *Hiodion tergisus*, in the Assiniboine River. Canadian Journal of Zoology 54:156–161.

Irwin E.R., and M.C. Freeman 2002. Proposal for adaptive management to conserve biotic integrity in a regulated segment of the Tallapoosa River, Alabama, USA. Conservation Biology16(5):1212–1222.

Jandebeur, T.S. 1972. A study of the fishes of the Elk River drainage system in Alabama and Tennessee. M.Sc. Thesis. University of Alabama, AL. 153 pp.

Johnson, G.H. 1951. An ecological investigation of the Mooneye *Hiodion tergisus* (LeSueur). M.Sc. Thesis. University of Western Ontario, London, ON, Canada.

Mettee, F.M., P.E. O'Neil, and J.M. Pierson. 1996. Fishes of Alabama and the Mobile Basin. Oxmoor House, Inc., Birmingham, AL. 820 pp.

Murphy, B.R., and D.W. Willis (Eds.). 1996. Fisheries Techniques, 2nd Edition. American Fisheries Society, Bethesda, MD.

Nash M.K., and E.R. Irwin. 1999. Use of otoliths versus pectoral spines for aging adult flathead catfish. American Fisheries Society Symposium 24:309–316.

Page, L.M., and B.M. Burr. 1991. A Field Guide to Freshwater Fishes. Houghton Mifflin Co., New York, NY.

Rulifson, R.A., and C.S. Manooch III. 1990. Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. North American Journal of Fisheries Management 10:397–407.

Schultz, E.T., K.E. Reynolds, and D.O. Conover. 1996. Countergradient variation in growth among newly hatched *Fundulus heteroclitus*: Geographic differences revealed by common-environment experiments. Functional Ecology 10:366–374.

Von Bertalanffy, L. 1938. A quantitative theory of organic growth. Human Biology 10:181–213.

Wallus R., and J.P. Buchanan. 1989. Contribution to the reproductive biology and early life ecology of Mooneye in the Tennessee and Cumberland Rivers. American Midland Naturalist 122(1):204–207.