Effects of Stress on Largemouth Bass Reproduction

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Abstract.-Although largemouth bass Micropterus salmoides are frequently subjected to sublethal stressors (e.g., angling), the associated effects on their reproductive success have not been assessed. We examined the reproduction of largemouth bass that were subjected to the stress of exhaustive exercise, air exposure, culling, live-well conditions, and weigh-in procedures. Age-0 largemouth bass produced from parents subjected to stress were smaller (total length, 31 ± 0.4 mm [mean \pm SE]) and weighed less (0.59 \pm 0.04 g) than controls that were not stressed (35 \pm 0.4 mm; 0.76 \pm 0.03 g). Adults that were stressed had offspring with later swim-up dates than did controls. Our results provide evidence that stress before spawning has the potential to negatively affect largemouth bass reproductive success.

Largemouth bass Micropterus salmoides are frequently subjected to significant capture and handling stress as a result of intensive culture and angling (Carmichael et al. 1984; Gustaveson et al. 1991; Cooke et al. 2000, 2002a, 2002b). Stress can significantly disrupt the reproductive processes of fish (Pottinger 1999; Schreck et al. 2001). Although stress induced by capture and handling during parental care and postspawning periods has been shown to have negative effects on the reproductive success of wild centrarchids (Kieffer et al. 1995; Philipp et al. 1997; Cooke et al. 2000), information on the effects of stress on largemouth bass before spawning is limited. Studies with other species suggest that stress encountered during early stages of the reproductive cycle have the potential to negatively effect fish reproduction. For example, Campbell et al. (1992, 1994) and Contreras-Sanchez et al. (1998) showed that exposure

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of cultured rainbow trout *Oncorhynchus mykiss* to acute and chronic stressors before spawning resulted in a significant delay in ovulation, reduction in egg size, sperm count, progeny survival, and smaller swim-up fry compared with controls. In addition, studies have linked ovarian atresia in wild fish with the stress of capture and transport (De Montalembert et al. 1978; Wallace et al. 1993; Barry et al. 1995). Although the mechanisms by which stress exerts effects on fish reproductive processes are not fully understood, studies have shown associations with elevated levels of plasma cortisol and depression of gonadal steroids (Pankhurst and Dedual 1993; Clearwater and Pankhurst 1997; Suski et al. 2003).

Largemouth bass are ideal for studying the inhibitory effects of capture and handling stress on reproductive processes given the continued growth in popularity of angling for this species, including the common practice of catch and release (Quinn 1996) and competitive angling events (Gustaveson et al. 1991; Schramm et al. 1991a, 1991b; Wilde et al. 1998). However, the ultimate consequences of stress in terms of overall reproductive success have received little attention. Measurements of hormone concentrations involved in reproduction and other metrics such as gamete quality and quantity have been used to assess the effects of acute and chronic stress on fish reproduction (See Pankhurst and Van Der Kraak 1997, 2000; Schreck et al. 2001). However, it is the quantity and quality of viable progeny produced that ultimately show the effect of stress on reproductive fitness (Campbell et al. 1994). Therefore, we sought to determine how reproduction by largemouth bass was affected by sublethal stress (i.e., exhaustive exercise, air exposure, culling, live-well conditions, and weighin procedures) before spawning. We compared the

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TABLE 1.—Average total length, weight, number, and age (± 1 SE) of adult and age-0 largemouth bass in ponds stocked with stressed and nonstressed (control) adult largemouth bass. Comparisons for all response variables between treatments were analyzed with mixed–model, nested analysis of variance except number, which was compared with a one-way analysis of variance.

	Stressed		Control		Contrasts	
Variable	Mean	SE	Mean	SE	$F_{1,6}$	P-value
		Adult larg	emouth bass	6		
Male length (mm)	357	4	363	8	0.11	0.75
Male weight (g)	597	39	641	90	0.13	0.72
Female length (mm)	385	12	386	15	0.01	0.94
Female weight (g)	866	76	944	104	0.19	0.66
		Age-0 larg	emouth base	5		
Length (mm)	31	0.43	35	0.38	40.94	< 0.01
Weight (g)	0.59	0.03	0.76	0.04	10.84	< 0.01
Number	214	54	444	239	0.88	0.38
Age (d)	48	0.63	50	0.58	3.64	0.05

age (measured in days), number, size, and weight of age-0 largemouth bass produced from adults that were subjected to stress with those that were not.

Methods

Adult largemouth bass (total length, 373 ± 6.3 mm [mean \pm SE]; weight, 762 \pm 53.8 g) were collected from local ponds, lakes, and reservoirs via electrofishing during late winter 2001 and held in an earthen pond for at least 2 months before spawning. Spawning readiness was determined by visual observations of adult largemouth bass behavior and pond water temperatures (Swingle 1956; Kramer and Smith 1962). The holding pond was drained on 9 April 2001, and adult fish were sorted into eight water flow-through raceways to create equal groups between treatments, based upon weight, total length (TL), and gender (Table 1). Gender of largemouth bass was judged from external characteristics (Parker 1971; Benz and Jacobs 1986). Our accuracy rate in correctly sexing fish was high (98%) as determined via dissections at the completion of the experiment. The misidentified fish were two females; one was in the stressed group and the other in the control group. Fish were allowed to acclimate in these raceways for 24 h before being subjected to a suite of stressors (i.e., exhaustive exercise, air exposure, culling, live-well conditions and weigh-in procedures) designed to simulate tournament angling practices (Cory Suski, Queen's University, unpublished data). Our observations indicated that spawning began on 10 April in other experimental ponds.

Fish were first individually introduced into a large circular tank (1.52 m in diameter, 0.3 m deep)

and chased manually for 90 s. Manual chasing is a standard methodology in fish physiology research to simulate exhaustive exercise (e.g., Kieffer 2000). Water temperature (19.2°C) and dissolved oxygen (9.0 mg/L) in the chase tank were kept constant. Fish were then exposed to air (26.2 \pm 0.3°C) for 60 s before being introduced to live wells (19.7 \pm 0.12°C), where they were held at a density of five fish per live well for 6 h. Live wells were circular tanks (0.91 m in diameter) containing 100 L of water that were housed in an indoor experimental laboratory. Live wells were operated with water flowing through at about 1 L/min. Throughout the 6-h experiments, fish were exposed to a series of disturbances including brief air exposures (<3 s) and manual disturbances to simulate the addition of fish, wave action, culling, and other live-well disturbances. During the livewell component of the experiment, water quality characteristics varied (as has been observed empirically, e.g., Hartley and Moring 1993; Kwak and Henry 1995). Water temperature increased during the early morning hours but thereafter remained relatively stable (19.9 \pm 0.4°C). Water temperature (20.2°C) at the end of the live-well retention was similar ($t_6 = -0.5$, P = 0.6) to those in the ponds $(20.1 \pm 0.08^{\circ}C)$. Live-well dissolved oxygen concentrations (5.4 \pm 0.90 mg/L) were allowed to fluctuate naturally and at some times allowed to approach hypoxic conditions. Dissolved oxygen in the live-wells was highest (maximum = 9.1 ± 0.04 mg/L) before the addition of fish, but decreased naturally as fish were added, reaching its lowest level of 2.3 mg/L at 2 h after the beginning of the experiment. When dissolved oxygen levels were particularly low, water in the live wells was agitated using an air infusion pump. At the termination of live-well retention, fish were held in a water-filled bag (20 L) for 120 s to simulate the movement of fish from the boat to the weigh-in site. The contents of the bag were then emptied into a laundry basket, to simulate weigh-in, where the fish were unrestrained. Fish were then weighed and measured. The air exposure period lasted 120 s, and fish were then introduced to experimental ponds.

Following the stress procedures, eight 0.04-ha ponds were each stocked with five female and five male adult largemouth bass of equal size and weight. We employed a completely randomized design where four of these eight ponds were stocked with stressed largemouth bass randomly selected from those fish that had experienced stress; the remaining four ponds were stocked with nonstressed control fish. Each pond was subsequently stocked with 2,500 fathead minnows Pimephales promelas (48 \pm 0.7 mm TL; 0.9 \pm 0.4 g) and had natural invertebrate populations as forage. Fish were then allowed to spawn and forage under natural conditions. Water temperature was not different between ponds stocked with control fish and those stocked with stressed fish ($t_6 = 0.8$, P = 0.4). Ponds were drained after 69 d and all adult and age-0 largemouth bass were removed and enumerated.

The timing of draining was chosen to ensure that age-0 largemouth bass had developed past the fry stage because relative year-class strength is commonly set by high mortality during the first few weeks of life (Parkos and Wahl 2002). At least 200 randomly selected age-0 largemouth bass from each pond were weighed, measured, and frozen whole. If fewer than 200 individuals were produced in a pond all individuals were collected. Because recruitment among adult largemouth can be variable among ponds we used a mixed model, nested analysis of variance (ANOVA). Individuals within ponds were nested within the stressed and nonstressed treatments. The F-values and probabilities were determined from the type III sums of squares to compare length and weight of age-0 largemouth bass from ponds stocked with stressed and nonstressed adults. By using a nested ANOVA we separated the variance components attributable to both stress and pond effects (Sokal and Rohlf 1969). We also compared length frequency distributions of age-0 largemouth bass produced from stressed and nonstressed adults using a Kolmogorov-Smirnov test. The number of age-0 largemouth bass produced by stressed and nonstressed adults was compared with an ANOVA. An alpha level of 0.05 was used for all statistical tests.

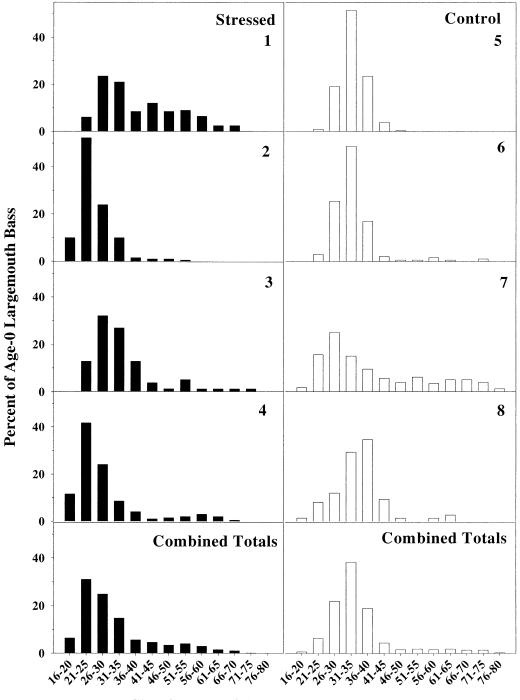
Sagittal sections of otoliths from randomly selected age-0 largemouth bass produced from adults in stressed (N = 20 per pond) and nonstressed (N= 20 per pond) treatments were prepared via the methods outlined by Miller and Storck (1982). Some otoliths were found to be unreadable and were excluded (12%). The daily growth rings from the remainder were counted three times by two independent readers to reduce reader error. To prevent bias, otoliths were examined in random order, and no two counts of the same otolith were consecutive (Miller and Storck 1982). Mean ring counts from both readers for each fish were then compared. Otolith ring counts that differed by less than 3 d were accepted (70%) and averaged for the two readers. The length frequencies of fish used for age determination were similar to those at the draining for both the control (Kolmogorov-Smirnov; D = 0.11, P = 0.68) and treatment (D = 0.12, P= 0.44) groups. We compared the age at the time of draining between offspring produced from stressed adults with those produced from controls with a mixed-model nested ANOVA.

Results

Age-0 largemouth bass produced from parents subjected to stress were smaller and weighed less than controls (Table 1). Length and weight differences (means, 4.0 mm TL and 0.2 g) at the time of draining appear small, but the relative differences were high: 11% percent of total length and 26% of body weight. Length frequency distributions of age-0 largemouth bass at draining also were variable among individual ponds within a treatment (Figure 1). However, when length frequencies were combined across ponds they differed between treatments (D = 0.38, P < 0.01). Length frequency distributions of the cohort produced from parents that experienced stress was skewed toward smaller size-classes compared with controls (Figure 1). Numbers of age-0 largemouth bass recruited to each pond were highly variable, resulting in no difference between treatments (Table 1). Daily ring counts from age-0 largemouth bass otoliths (N = 49 per treatment) indicated that swim-up for progeny of individuals subjected to stress was 2 d earlier than for the nonstressed group (Table 1).

Discussion

Largemouth bass exposed to stress during the later stages of gonadal development may delay the



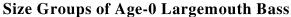


FIGURE 1.—Length frequency distribution by 4-mm size increments of age-0 largemouth bass produced in eight ponds (panels 1–8) by adults that were either subjected to stress (panels 1–4) or were not stressed (controls; panels 5–8). The two bottom panels represent fish combined across the four ponds within each treatment type.

swim-up date of offspring and negatively affect the size of young produced. Our results are consistent with previous studies that report delayed ovulation for rainbow trout that are stressed during late ovarian development (Campbell et al. 1992; Contreras-Sanchez et al. 1998). Stressed fish in these experiments also produced smaller offspring (Contreras-Sanchez et al. 1998). The effects of stress on offspring will most likely vary with the severity and duration of the stressor, the gonadal maturation stage of the adults (Campbell et al. 1992, 1994; Contreras-Sanchez et al. 1998; Schreck et al. 2001), and the reproductive costs and strategies of the fish species or subspecies (Booth et al. 1995). Our experiment indicates that periods of stress during later stages of gonadal development may have negative effects on individual largemouth bass reproduction.

Delays in swim-up date and smaller progeny resulting from stress could have negative population consequences. Smaller larval and juvenile fishes within a cohort have a number of disadvantages such as an increased risk to starvation and predation (Miller et al. 1988; Rice et al. 1987) leading to lower survival (Ludsin and DeVries 1997; Garvey et al. 1998). Size-specific mortality can have important consequences for later recruitment when interspecific and intraspecific competition is strong and resources are limiting (Werner and Gilliam 1984; Rice et al. 1987; Garvey et al. 1998). The delays in swim-up date in our experiments were small compared with the variation observed among natural populations, but may have contributed to the differences in size between treatments. Earlier-hatched largemouth bass typically are larger than those hatched later and often retain this advantage throughout the first growing season (Isely et al. 1987; Maceina et al. 1988; Ludsin and DeVries 1997; Sammons et al. 1999). Thus, individuals that are spawned earlier and that are larger generally continue to grow and survive better than their counterparts that are spawned later and are smaller (Von Geldern and Mitchell 1975). In addition, size is positively correlated with the switch to piscivory (Olson 1996; Keast and Eadie 1985), which in turn, dramatically increases growth and condition (Ludsin and DeVries 1997). Smaller-sized young may result directly from physiological processes during gonad and larval development or from behavior changes posthatch related to altered energy reserves and activity patterns. Size differences have the potential to affect size-specific mortality rates, which suggests that stress may negatively affect individual largemouth bass fitness. Additional experiments will be required to test whether the differences in size we observed remain throughout the first year of life, reduce overwinter survival, and affect later recruitment.

Several authors have reported deleterious effects of parental stress on the survival of progeny (Weiner at al. 1986; Mount et al. 1988; Campbell et al. 1992, 1994). In contrast, our results for largemouth bass and those of Contreras-Sanchez et al. (1998) for rainbow trout suggest that stress during late periods of gonad maturation have no effects on progeny survival. The period of maturation when fish are exposed to a stressor appears important (Campbell et al. 1992, 1994). The single exposure to a sequence of acute stressors in our experiment occurred a few days before spawning and, thus, was probably too late to affect fecundity (Philipp et al. 1985; Gross et al. 2002). Stressors experienced during earlier stages of gonadal development, however, may lower fecundity (De Montalembert et al. 1978; Clearwater and Pankhurst 1992) and progeny survival (Weiner et al. 1986; Mount et al. 1988; Campbell et al. 1992, 1994). The effect of stress on progeny survival for largemouth bass during earlier stages of gonadal development should be investigated.

The delay in swim-up date and smaller progeny produced by stressed adult largemouth bass has implications for angling and successful broodstock management. The regime of acute stressors used in this experiment was similar to the experiences of fish taken during angling, particularly competitive fishing events (see Suski et al. 2003). Our results suggest stressors similar to those that occur in competitive tournaments can have small effects on growth and timing of spawning. Future research should include manipulative controlled experiments that examine additional mechanisms for these differences, as well as the potential for cumulative effects of multiple captures. Largemouth bass are also frequently disturbed during the spawning season in hatcheries (Carmichael et al. 1984). If additional work confirms our findings, then protection of potential spawners from stressors or attempts to minimize physiological disturbance before spawning would be warranted.

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References

- Barry, T. P., J. A. Malison, A. F. Lapp, and L. S. Procarione. 1995. Effects of selected hormones and male cohorts on final oocyte maturation, ovulation, and steroid production in walleye (*Stizostedion vitreum*). Aquaculture 138:331–347.
- Benz, G. W., and R. P. Jacobs. 1986. Practical field methods of sexing largemouth bass. Progressive Fish-Culturist 48:221–225.
- Booth, R. K., J. D. Kieffer, K. Davidson, A. T. Bielak, and B. L. Tufts. 1995. Effects of late-season catchand-release angling on anaerobic metabolism, acidbase status, survival, and gamete viability in wild Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 52:283–290.
- Campbell, P. M., T. G. Pottinger, and J. P. Sumpter. 1992. Stress reduces the quality of gametes produced by rainbow trout. Biology of Reproduction 47:1140– 1150.
- Campbell, P. M., T. G. Pottinger, and J. P. Sumpter. 1994. Preliminary evidence that chronic confinement stress reduces the quality of gametes produced by brown and rainbow trout. Aquaculture 120:151– 169.
- Carmichael, G. J., J. R. Tomasso, B. A. Simco, and K. B. Davis. 1984. Characterization and alleviation of stress associated with hauling largemouth bass. Transactions of the American Fisheries Society 113: 767–777.
- Clearwater, S. J., and N. W. Pankhurst. 1992. Effects of capture stress on plasm cortisol and gonadal atresia in red gurnard *Chelidonichthys kumu*. New Zealand Marine Sciences Society Review 34:9.
- Clearwater, S. J., and N. W. Pankhurst. 1997. The response to capture and confinement stress of plasm cortisol, plasma sex seteroids, and vitellogenic oocytes in the marine teleost, red gurnard. Journal of Fish Biology 50:429–411.
- Contreras-Sanchez, W. M., C. B. Schreck, M. S. Fitzpatrick, and C. B. Pereira. 1998. Effects of stress on the reproductive performance of rainbow trout (*Oncorhynchus mykiss*). Biology of Reproduction 58:439–447.
- Cooke, S. J., D. P. Philipp, J. F. Schreer, and R. S. Mc-Kinley. 2000. Locomotory impairment of nesting male largemouth bass following catch-and-release angling. North American Journal of Fisheries Management 20:968–977.
- Cooke, S. J., J. F. Schreer, K. M. Dunmall, and D. P. Philipp. 2002a. Strategies for quantifying sublethal effects of marine catch-and-release angling:insights from novel freshwater applications. Pages 121–134 *in* J. A. Lucy and A. L. Studholme, editors. Catch

and release in marine recreational fisheries. American Fisheries Society, Symposium 30, Bethesda, Maryland.

- Cooke, S. J., J. F. Schreer, D. P. Philipp, and D. H. Wahl. 2002b. Physiological impacts of catch-and-release angling practices on largemouth bass and smallmouth bass. Pages 489–512 in D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.
- De Montalembert, G., B. Jalabert, and C. Bry. 1978. Precocious induction of maturation and ovulation in northern pike (*Esox lucius*). Annales de Biologie Animale Biochimie Biophysique 18:969–975.
- Garvey, J. E., N. Dingledine, N. Donovan, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size, food origin, and winter severity. Canadian Journal of Fisheries and Aquatic Sciences 55:2414–2424.
- Gross, T. S., C. M. Wieser, M. S. Sepulveda, J. J. Wiebe, T. R. Scoeb, and N. D. Denslow. 2002. Characterization of annual reproductive cycles for pondreared Florida largemouth bass *Micropterus salmoides floridanus*. Pages 205–212 in D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.
- Gustaveson, W. A., R. S. Wydoski, and G. A. Wedemeyer. 1991. Physiological response of largemouth bass to angling stress. Transactions of the American Fisheries Society 120:629–636.
- Hartley, R. A., and J. R. Moring. 1993. Observations of black bass (Centrarchidae) confined during angling tournaments: a cautionary note concerning dissolved oxygen. Aquaculture and Fisheries Management 24:575–579.
- Isely, J. J., R. L. Noble, J. B. Koppelman, and D. P. Philipp. 1987. Spawning period and first-year growth of northern, Florida, and intergrade stocks of largemouth bass. Transactions of the American Fisheries Society 116:757–762.
- Keast, A., and J. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Transactions of the American Fisheries Society 114:204– 213.
- Kieffer, J. D. 2000. Limits to exhaustive exercise in fish. Comparative Biochemistry and Physiology 126A: 161–179.
- Kieffer, J. D., M. R. Kubacki, F. J. S. Phelan, D. P. Philipp, and B. L. Tufts. 1995. Effects of catchand-release angling on nesting male smallmouth bass. Transactions of the American Fisheries Society 124:70–76.
- Kramer, R. H. and L. L. Smith, Jr. 1962. Formation of year-classes in largemouth bass. Transactions of the American Fisheries Society 91:29–41.
- Kwak, T. J., and M. G. Henry. 1995. Largemouth bass mortality and related causal factors during live-release fishing tournaments on a large Minnesota lake. North American Journal of Fisheries Management 15:621–630.

- Ludsin, S. A., and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. Ecological Applications 7: 1024–1038.
- Maceina, M. J., B. Murphy, and J. J. Isely. 1988. Factors regulating Florida largemouth bass stocking and hybridization with northern largemouth bass in Aquilla Lake, Texas. Transactions of the American Fisheries Society 117:221–231.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fish: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657–1670.
- Miller, S. J., and T. Storck. 1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. Transactions of the American Fisheries Society 111: 527–530.
- Mount, D. R., C. G. Ingersoll, E. D. Gulley, J. D. Fernandez, T. W. LaPoint, and H. L. Bergman. 1988. Effect of long-term exposure to acid, aluminum, and low calcium on adult brook trout (*Salvelinus fontinalis*): survival, growth, fecundity, and progeny survival. Canadian Journal of Fisheries and Aquatic Sciences 43:275–280.
- Olson, M. 1996. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology 76:1758– 1771.
- Pankhurst, N. W., and M. Dedual. 1993. Effects of capture and recovery on plasma levels of cortisol, lactate, and gonadal steroids in a natural population of rainbow trout. Journal of Fish Biology 45:1013– 1025.
- Pankhurst, N. W., and G. Van Der Kraak. 1997. Effects of stress on reproduction and growth of fish. Society for Experimental Biology Seminar Series 62:73–93.
- Pankhurst, N. W., and G. Van Der Kraak. 2000. Evidence that acute stress inhibits ovarian steroidogenesis in rainbow trout in vivo, through the action of cortisol. General and Comparative Endocrinology 117:225–237.
- Parker, W. D. 1971. Preliminary studies on sexing adult largemouth bass by means of an external characteristic. Progressive Fish-Culturist 33:55–56.
- Parkos, J. J., III, and D. H. Wahl. 2002. Towards an understanding of recruitment mechanisms in largemouth bass. Pages 25–45 *in* D. P. Philipp and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society Symposium 31, Bethesda, Maryland.
- Philipp, D. P., C. Kaminski, and G. S. Whitt. 1985. A comparison of the embryonic development of northern, Florida, and reciprocal F₁ hybrid largemouth bass in different thermal environments. Illinois Natural History Survey Bulletin 33:261–273.
- Philipp, D. P., C. A. Toline, M. F. Kubacki, D. B. F. Philipp, and F. J. S. Phelan. 1997. The impact of catch-and-release angling on the reproductive success of smallmouth bass and largemouth bass. North American Journal of Fisheries Management 17: 557–567.

- Pottinger, T. G. 1999. The impact of stress on animal reproductive activities. Pages 130–177 *in* P. H. M. Balm, editor. Stress physiology in animals. CRC Press, Boca Raton Florida.
- Quinn, S. 1996. Trends in regulatory and voluntary catch-and-release fishing. Pages 152–162 in L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium 16, Bethesda, Maryland.
- Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 126:850– 856.
- Sammons, S. M., L. G. Dorsey, P. W. Bettoli, and F. C. Fiss. 1999. Effects of reservoir hydrology on reproduction by largemouth bass and spotted bass in Normandy Reservoir, Tennessee. North American Journal of Fisheries Management 19:78–88.
- Schramm, H. L., Jr., M. L. Armstrong, A. J. Fedler, N. A. Funicelli, D. M. Green, J. L. Hahn, D. P. Lee, R. E. Manns, Jr., S. P. Quinn, and S. J. Waters. 1991a. Sociological, economic, and biological aspects of competitive fishing. Fisheries 16(3):13– 21.
- Schramm, H. L., Jr., M. L. Armstrong, N. A. Funicelli, D. M. Green, D. P. Lee, R. E. Manns, Jr., B. D. Taubert, and S. J. Waters. 1991b. The status of competitive sport fishing in North America. Fisheries 16(3):4–12.
- Schreck, C. B., W. Contreras-Sanchez, and M. S. Fitzpatrick. 2001. Effects of stress on fish reproduction, gamete quality, and progeny. Aquaculture 197:3– 24.
- Sokal, R. R., and J. F. Rohlf. 1969. Biometry. Freeman, New York.
- Suski, C. D., S. S. Killen, M. B. Morrissey, S. G. Lund, and B. L. Tufts. 2003. Physiological changes in largemouth bass caused by live-release angling tournaments in southeastern Ontario. North American Journal of Fisheries Management 23:760–769.
- Swingle, H. S. 1956. Appraisal of methods of fish population study, part IV. Determination of balance in farm fish ponds. Transactions of the North American Wildlife Conference 21:298–322.
- Von Geldern, J. C., and D. Mitchell. 1975. Largemouth bass and threadfin shad in California. Pages 436– 449 in R. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Wallace, R. A., S. M. Boyle, H. J. Grier, K. Selman, and T. R. Petrino. 1993. Preliminary observations on oocyte maturation and other aspects of reproductive biology in captive female snook, *Centropomus undecimalis*. Aquaculture 116:257–273.
- Weiner, C. S., C. B. Schreck, and H. W. Li. 1986. Effects of low pH on reproduction of rainbow trout. Transactions of the American Fisheries Society 115:75–82.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured

populations. Annual Review of Ecology and Systematics 15:393-426.

- Wilde, G. R. 1998. Tournament-associated mortality in black bass. Fisheries 23(10):12–22.
- Wilde, G. R., D. W. Strickland, K. G. Ostrand, and M. I. Muoneke. 1998. Characteristics of Texas black bass fishing tournaments. North American Journal of Fisheries Management 18:972–977.