Ten-year Assessment of the Unique Fishery of the Okefenokee Swamp

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Abstract: The Okefenokee Swamp is the largest freshwater wetland in the United States; however, population dynamics of the fish assemblage within the swamp are poorly understood. Fish surveys from 1992–2001 indicate that two species, bowfin *(Amia calva)* and flier *(Centrarchus macropterus),* are the numerically dominant taxa of the eastern portion of the swamp, representing over 88% of all fishes collected. Results indicated that the fish assemblage was persistent and stable in terms of constancy of dominant species presence and their abundances. The four most abundant species, bowfin, flier, chain pickerel *(Esox niger),* and warmouth *(Lepomis gulosus),* had high relative conditions in all years. When combined with high catch-per-unit-effort and angler-preferable sizes, these results suggest that the eastern swamp has the potential to support an excellent flier and bowfin fishery, as well as a lesser fishery for chain pickerel and warmouth. Lack of traditional sport fishes and other fishes common to the area was likely attributable to the abiotic conditions of the swamp, specifically low pH levels. Managers should consider publicizing the unique and excellent fishery available in the eastern portion of the Okefenokee Swamp.

Key words: Okefenokee Swamp, fish assemblages, long-term monitoring, bowfin, and flier fishery

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The Okefenokee Swamp, located in southeastern Georgia and northern Florida, is the largest freshwater wetland in the United States (Laerm and Freeman 1986). This naturally acidic swamp contains a wide variety of vegetation types, consisting primarily of shrub, cypress, and pine species (Laerm and Freeman 1986). Rainfall and subsequent runoff feed its watershed, with the largest portion of the swamp draining from the northeast south and west into the Suwannee River, and the southeast portion draining into the St. Mary's River. In 1937, the U.S. Fish and Wildlife Service (USFWS) established the Okefenokee National Wildlife Refuge (ONWR) to protect the swamp as a refuge and breeding ground for migratory birds and wildlife. The National Wildlife Refuge System Improvement Act of 1997 recognized wildlife-dependent recreation activities on refuges including fishing and hunting. The ONWR contains approximately 80% of the swamp and is administered by the USFWS. Although the hydrology, geology, and flora of this relatively shallow, subtropical blackwater swamp have been and continue to be well studied, relatively little is known about the fish assemblage inhabiting this system.

Because of its inaccessibility and difficulty in surveying, the Okefenokee Swamp has been poorly studied by ichthyologists historically, and it was not until 1920 that the first published records of fishes inhabiting the swamp became available (Palmer and Wright 1920). This survey was the only major account of the fish assemblage in the swamp until Joshua Laerm and Byron J. Freeman published *Fishes of Okefenokee Swamp* in 1986. Laerm and Freeman (1986) identified 36 species of fish representing 14 families and provided life-history information and qualitative assessments of species' abundances and habitat use in the swamp. Despite the advances of these works, much about the fish populations and fishery dynamics of the Okefenokee Swamp remains unknown.

Considering the unique environment and the poorly-understood fish assemblage and fishery resources of the swamp, the USFWS and the Georgia Department of Natural Resources (GDNR) initiated an ongoing survey in 1992 in an effort to identify trends in the population dynamics of the fish assemblage. The goals of the monitoring are to (1) identify the major components of the fish assemblage, (2) identify changes in the fish assemblage over time, and (3) attain a better understanding of sport fishery dynamics of the swamp. Our objective was to summarize the fish assemblage of the eastern swamp from 1992 to 2001. We examined temporal trends in the assemblage through measures of similarity, persistence, stability, and catch-per-unit-effort (CPUE). We also examined trends in condition and proportional and relative stock densities of sport fish populations through time.

Study Area

The ONWR is a wilderness area occupying 1,477 km^2 of the Okefenokee Swamp, which drains approximately 285,120 ha of land (Laerm and Freeman 1986). The swamp is relatively shallow, with peat soil inundated by water during normal hydrological conditions (Laerm and Freeman 1986). Although certain areas of the swamp may have water depths of >2.5 m, the average depth is 0.6 m (Laerm and Freeman 1986). During drought conditions, water levels are significantly lower or absent in certain areas of the swamp. The swamp is a naturally acidic ecosystem with an average pH of 3.7 (Blood 1981).

Methods

Sampling Protocol

The USFWS and GDNR conducted annual fish surveys of the Okefenokee Swamp from 1992 through 2001. The USFWS sampled six sites in the eastern portion of the swamp, representing all available habitat types (canals, lakes, and prairies), were sampled during winter months (December to January) each year. The GDNR sampled the western portion of the swamp similarly; however, collection data were not available at the time of this analysis and thus were not used in this examination. Fish population structure and abundance were estimated by boat electrofishing surveys. Electrofishing was conducted using pulsed DC at 10–12 amps for approximately 60 min at each site. All fishes were counted, and a representative sample (usually the entire sample) of fishes for each site was measured (nearest mm total length), weighed (nearest g), and released near the vicinity of capture.

Fish Assemblage Data Analysis

Fish assemblage data were assessed for stability and persistence by combining data from all sites across sample years. An assemblage member was included in analysis if it was considered dominant, which we defined as those contributing at least 1% of the total collection and occurring in at least 50% of samples through the entire study period (sensu Grossman et al. 1990). Assemblage stability was assessed using both Horn's Index of Similarity (Krebs 1999) and the coefficient of variation (Grossman et al. 1990). Horn's Index of Similarity was used to quantify temporal differences in abundances of dominant species by combining all sites for all pairwise year combinations, with values ranging from 0 (no similarity) to 1 (complete similarity). We used the coefficient of variation (CV) to quantify variability in abundances of each dominant species (Grossman et al. 1990). CVs between sample sites (i.e., intra-annual CVs) were calculated for each year based on standardized abundances at each site (mean number per 60 min electrofishing) and averaged across years for each dominant species. Inter-annual CV was calculated across years based on yearly mean abundance for each dominant species. If there were large changes in dominant fishes across the sample period, we would predict that the inter-annual CVs would be greater than intra-annual CVs (Gido et al. 2000).

Relative condition factors (K_n) were calculated for the four numerically dominant species (Le Cren 1951) according to the formula:

$$K_n = (W/W'),$$

where W is weight of the individual and W' is the length-specific mean weight for the individual as predicted by a length-weight equation calculated for the entire population over the study period. Proportional stock densities (PSDs) were calculated for the numerically abundant sport fishes per sample year according to the formula:

$$\text{PSD} = \frac{\text{number of fish} \geq \text{minimum quality length}}{\text{number of fish} \geq \text{minimum stock length}} \times 100.$$

Table 1. Fish species collected from the eastern Okefenokee Swamp from 1992–2001.

Family	Scientific name	Common name
Lepisosteidae	*Lepisosteus platyrhincus*	Florida gar
Amiidae	*Amia calva*	bowfin
Esocidae	*Esox americanus*	redfin pickerel
	Esox niger	chain pickerel
Catostomidae	*Erimyzon sucetta*	lake chubsucker
Ictaluridae	*Ameiurus natalis*	yellow bullhead
	Ameiurus nebulosus	brown bullhead
Aphredoderidae	*Aphredoderus sayanus*	pirate perch
Fundulidae	*Fundulus cingulatus*	banded topminnow
	Fundulus lineolatus	lined topminnow
Poeciliidae	*Gambusia holbrooki*	eastern mosquitofish
Elassomatidae	*Elassoma okefenokee*	Okefenokee pygmy sunfish
Centrarchidae	*Centrarchus macropterus*	flier
	Enneacanthus gloriosus	bluespotted sunfish
	Enneacanthus obesus	banded sunfish
	Lepomis gulosus	warmouth
	Lepomis macrochirus	bluegill
	Lepomis punctatus	spotted sunfish
	Micropterus salmoides	largemouth bass
Percidae	*Etheostoma fusiforme*	swamp darter

Standardized values for minimum stock and quality lengths per species were from Gablehouse (1984). If standardized values were not available, minimum stock and quality lengths were derived according to Anderson and Weithman (1978), where minimum quality and stock lengths are defined as 20%–26% and 36%–41% of the world-record length for a given species. Traditional relative stock densities (RSDs) for the numerically abundant sport fishes for all years combined were calculated according to the methods above for preferred, memorable, and trophy lengths (defined as 45%–55%, 59%–64%, and 74%–80% of world-record lengths, respectively) per species (Gablehouse 1984). We chose the midpoint of these percentages for PSD and RSD classifications for bowfin *(Amia calva)* and flier *(Centrarchus macropterus)* collections to be conservative in our results given that there are virtually no reports of these methods of length-frequency analyses being applied to populations of these species.

Results

Fish Assemblage Structure

Sampling between 1992 and 2001 produced 6,213 fishes, representing 20 species from 11 families (Table 1). Bowfin, flier, chain pickerel *(Esox niger),* and

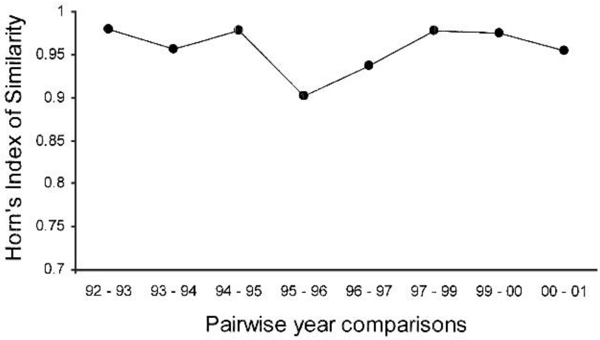

Figure 1. Pairwise year comparisons of the dominant fish assemblage of the eastern Okefenokee Swamp from 1992–2001 using Horn's Index of Similarity. Data from 1998 were not included because only sport fish species were collected.

Table 2. Coefficients of variation for the four dominant fish species collected from the eastern Okefenokee Swamp between 1992 and 2001.

	Coefficient of variation	
Species	Intra-annual	Inter-annual
Bowfin	97.9	81.7
Chain pickerel	103.1	51.1
Flier	125.3	80.5
Warmouth	128.4	71.5

warmouth *(Lepomis gulosus)* were considered dominant species and accounted for 44%, 44%, 4%, and 3%, respectively, of all fishes collected. The remaining 16 species were captured only sporadically throughout the study and when combined constituted only 5% of the total fishes collected; therefore, collection data for these species were considered unrepresentative of this portion of the assemblage and were not used in further analyses.

The mean Horn's Index of Similarity for all combinations of pairwise year comparisons was 0.86 (*SD* = 0.11), indicating that the fish assemblage was similar in terms of constancy of dominant species and their abundances during the duration of the study. Similarity of pairwise year comparisons was high for the entire study period ($\bar{x}$ = 0.96, *SD* = 0.03; Fig. 1). The mean CV across years for the four dominant species was 71.2% (*SD* = 14.2%), suggesting moderately fluctuating abundances between sample sites (Freeman et al. 1988). However, mean intra-annual CV ($\bar{x}$ =

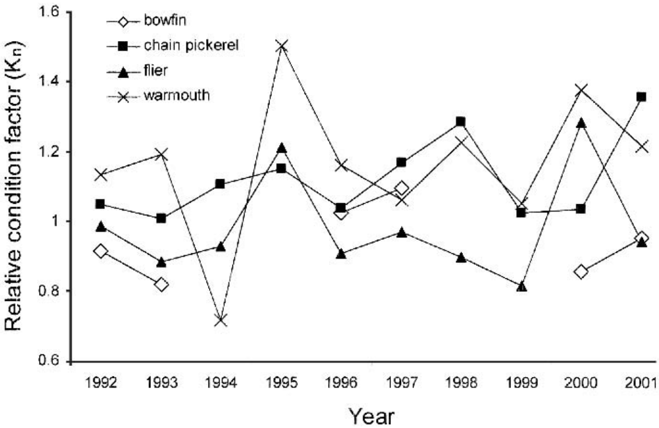

Figure 2. Mean relative condition for bowfin, chain pickerel, flier, and warmouth in the eastern Okefenokee Swamp from 1992–2001. Bowfin data absent in 1994, 1997, 1998, and 2001 because weights were not measured.

113.7%, *SD* = 15.4%) for these species was higher than inter-annual CV; therefore, there were no substantial changes in dominant fish populations across the sample period (Table 2).

Fish Abundance and Size Structure

Bowfin and flier were the most commonly collected dominant species throughout the study period (Table 3). In addition, bowfin and flier had the greatest CPUE of the four dominant fishes (Table 3). The mean relative condition factor for all years sampled for the four dominant species was 1.06 (*SD* = 0.20), with species-specific relative weights varying around 1.0 across years (Fig. 2).

Both PSDs and RSDs were calculated only for only bowfin and flier because small sample sizes prohibited their calculations for chain pickerel and warmouth (Table 4). Standardized stock, quality, preferable, memorable, and trophy size-class values for bowfin were according to Gablehouse (1984). Because to our knowledge there are no standardized size-class values published for flier, we generated these values using the maximum length reported for this species (International Game Fish Association 2001; Table 4). PSDs for both bowfin and flier were high (i.e., near 100) in all years calculated (Fig. 3). RSDs for bowfin and flier for all years combined further indicated that large (e.g., preferred and memorable size classes) individuals of both species were present in high abundance throughout the study period (Table 4).

Table 3. Mean total length (TL, mm) and CPUE (*N* per hour), range, and number of dominant species collected from the eastern Okefenokee Swamp from 1992–2001. Dashed lines (—-) indicate that no individuals were collected.

Species		1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Bowfin	TL	419	410	427	432	475	470	—-	—-	447	454
	Range	(285–735)	(285–755)	(140–800)	(272–642)	(310–777)	(220–730)	—-	—-	(165–795)	(320–684)
	CPUE	43.3	55.8	28.2	16.8	17.0	24.6	—-	181.5	215.7	90.6
	Total	*N*=260	*N*=308	*N*=169	*N*=67	*N*=85	*N*=123	—-	*N*=726	*N*=719	*N*=317
Chain pickerel	TL	389	373	317	360	374	261	249	360	360	361
	Range	(221–595)	(115–480)	(137–494)	(260–582)	(279–570)	(120–455)	(110–458)	(250–480)	(220–490)	(218–486)
	CPUE	6.2	2.5	5.5	10.5	2.8	1.6	5.5	6.8	7.2	3.7
	Total	*N*=37	*N*=14	*N*=33	*N*=42	*N*=14	*N*=8	*N*=33	*N*=27	*N*=24	*N*=13
Flier	TL	125	144	148	151	153	173	158	145	138	141
	Range	(82–200)	(85–205)	(51–200)	(69–195)	(77–212)	(95–210)	(55–210)	(80–220)	(60–203)	(59–215)
	CPUE	100.3	77.4	104.2	97.0	19.6	12.0	29.7	42.8	29.7	25.1
	Total	*N*=602	*N*=427	*N*=625	*N*=388	*N*=98	*N*=60	*N*=178	*N*=171	*N*=99	*N*=88
Warmouth	TL	160	173	223	180	199	111	133	130	145	142
	Range	(59–208)	(138–205)	(93–443)	(92–242)	(159–243)	(60–235)	(50–250)	(40–230)	(75–185)	(43–223)
	CPUE	3.0	1.3	3.8	1.5	3.8	0.8	2.8	7.0	7.8	10.9
	Total	*N*=18	*N*=7	*N*=6	*N*=6	*N*=23	*N*=4	*N*=17	*N*=28	*N*=26	*N*=38

Table 4. Mean relative stock densities (RSD) of quality, preferred, memorable and trophy size-classes of bowfin and flier in the eastern Okefenokee Swamp from 1992–2001. Record length for bowfin from Gablehouse (1984). Record length for flier from International Game Fish Association (2001). Standard deviation of RSD in parentheses.

		Stock		Quality			Preferred			Memorable			Trophy		
Species	Record length (mm)	mm	% of record length	mm	% of record length	RSD	mm	% of record length	RSD	mm	% of record length	RSD	mm	% of record length	RSD
Bowfin	914	210	23	356	39	87 (7.1)	457	50	35 (14.2)	558	61	10 (4.9)	695	76	1 (0.9)
Flier	292	67	23	114	39	89 (9.1)	146	50	53 (20.2)	178	61	16 (15.0)	222	76	0

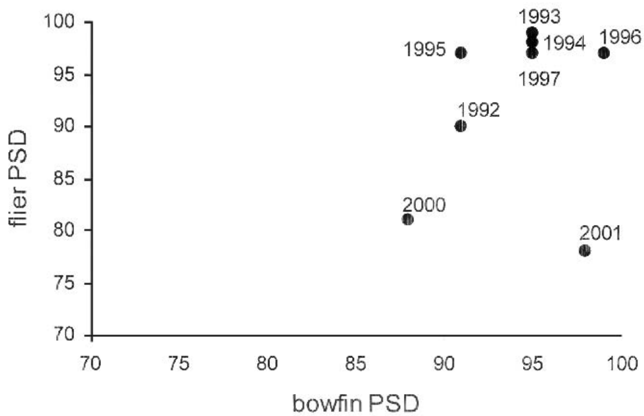

Figure 3. PSDs for bowfin and flier in the eastern Okefenokee Swamp from 1992 to 2001. Appropriate data not collected for bowfin in 1998 and 1999.

Discussion

Of the 36 species representing 14 families known to have occurred in the Okefenokee Swamp (Laerm and Freeman 1986), sampling between 1992 and 2001 produced 20 species from 11 families with bowfin, chain pickerel, flier, and warmouth considered dominant. Flier and bowfin represented the greatest proportion of all fishes collected during the study period. Historically, flier has been considered the most common centrarchid in the Swamp (Laerm and Freeman 1986), while bowfin has also been a dominant member of the Swamp assemblage in terms of abundance and biomass (Holder 1970). Our data support these assertions and indicate their continued assemblage dominance in the eastern Okefenokee Swamp.

Differences in effectively detecting both the presence of certain species and accurately representing their populations was likely influenced by both collection method and sampler bias. Small-bodied species, such as the fundulids, poeciliids, and certain centrarchids, were not effectively sampled by our collection methods, and it is likely that these species represented a greater proportion of the assemblage than was found in this study (see Freeman and Freeman 1985). Sampler bias also may have underrepresented certain large-bodied fishes. For instance, the absence of bowfin in collections in the 1998 collection resulted from sampler bias, as they were not collected because they were considered a "non-game" species by the 1998 sampling crew. A better representation of the true species abundance and population dynamics in the Okefenokee Swamp can be achieved by refining collection methods and standardizing sampling protocols for fish collections. Despite these shortcomings, we believe the population dynamics of certain species (i.e., the dominant species identified) were accurately described in this study.

The populations of dominant fishes in our study area were stable across the study period, as evident by the persistence (i.e., continued presence) and high assemblage similarity and stability among years. The dominant fish assemblage changed little between years as indicated by high pairwise year similarities. Intra-annual CVs for dominant species were greater than their inter-annual CV variation, indicating that although populations may differ among sampling sites, these differences did not substantially change over time. Therefore, populations of dominant species are considered stable within the eastern Okefenokee Swamp. Stability in these populations may result from evolutionary adaptation to the harsh environment of the swamp and the establishment of temporally stable populations under these conditions. However, this apparent stability may also be due to the relatively long lifespan of the dominant fishes in this study, as these species can live from 7–12+ years. Fluctuations in their populations therefore may not be detected as these species may have gone through only two or fewer generations during this ten-year sampling period. Further monitoring of these populations will likely provide additional insights into their dynamics over time.

Fishery Implications

Our results suggest that the four dominant species in our study, particularly bowfin and flier, may provide excellent angling opportunities in the eastern Okefenokee Swamp. For example, these species exhibited high relative condition factors over the ten-year study period. This may result from non-limiting resources for growth of both predator and prey species in the eastern Swamp. Unlike similar blackwater systems, the Okefenokee Swamp supports substantial secondary production that may exceed some comparable river and stream habitats (Freeman and Freeman 1985). In addition, the exclusion of certain taxa (e.g., cyprinids) due to high acidity and other environmental conditions (Laerm and Freeman 1986) and the resulting relatively low local species diversity may result in reduced interspecific competition for these resources. The interaction of these factors likely influences the relative condition patterns of both predator and prey populations in the eastern Okefenokee Swamp.

Our results suggest that there is the potential for a trophy fishery for bowfin and possibly flier in the eastern Okefenokee Swamp. Although no trophy-sized fliers were collected during this study, a high percentage of fliers sampled in every year were in the memorable size class. Thus, it is possible that trophy-sized fliers inhabit the swamp but were inefficiently sampled. Trophy-sized bowfins were present in all but two years sampled in the eastern swamp. Analysis of length-frequency distributions for these species indicated that large individuals of both species were common in all study years. Specifically, these species fall into the recommended RSD percentages for a "large individuals desired" fishery (Gablehouse 1984). Interestingly, fisheries with this objective commonly have low abundances of such species. This is the opposite of our results, as bowfin and flier were the most abundant species collected. Further, those bowfin and flier collected were usually of quality size or greater, with few small individuals being sampled. Our results may indicate a "best of both worlds" scenario for this fishery: high densities of quality-, preferred-, and memorable-sized individuals of both species in the eastern Okefenokee Swamp.

It should be noted that there are several limitations to the interpretation of the fish assemblage data collected in this area of the Okefenokee Swamp during this study. In addition to gear and sampler bias discussed earlier, sample sites examined were located in the eastern portion of the swamp limiting our ability to extrapolate results to the other areas of this system. Also, the calculation of PSDs and RSDs for fish populations is usually applicable specifically to small impoundments. Extrapolation of results to larger systems, such as the Okefenokee Swamp, may lead to inaccurate data interpretation. For example, bowfin and flier PSDs were high in all years, which according to Anderson and Weithman (1978) might be an indication of an unbalanced population in small impoundments resulting from successive years of low recruitment. Because our sample methods limited our ability to detect yearly reproduction of these species, we are unable to determine whether this might explain the PSD trends for bowfin and flier. However, the lack of variation in high PSDs for these species combined with the probability of at least one generation of bowfin and several generations of flier during the study period suggests that low recruitment might may not explain these trends. It is possible that high PSDs for bowfin and flier during the study may have resulted from the high production and species complexity (versus small impoundments) of the expansive Okefenokee Swamp.

In addition, the predator-prey link between bowfin and flier is assumed in this study though there are no diet data from the eastern swamp to support this. Bowfin are predominantly piscivorous in other parts of their range (Becker 1983, Robison and Buchanan 1988, Etnier and Starnes 1993) and will prey on heavily on fliers when they are sympatric (S.J. Herrington, unpub. data). Given the abundance of these species in this system, it is reasonable to expect that fliers constitute an important portion of bowfin diets and that these populations interact in predator/prey fashion. Lastly, basic life-history information and population structure (i.e., age and growth) of most species inhabiting the swamp, such as bowfin and flier, is unknown. Our results should therefore be interpreted cautiously with these limitations considered.

Despite these limitations, this study is the first known attempt to examine temporal trends in fish assemblage dynamics of the eastern Okefenokee Swamp. Furthermore, this study serves as a benchmark for both population dynamics and the fishery potential of bowfin, chain pickerel, flier, and warmouth within this system. These data suggest that populations of these species are persistent, stable, and in good overall condition within the eastern swamp. Furthermore, populations of bowfin and flier, which constitute the majority of all fishes collected, are characterized by high abundances of large-sized individuals.

Managers should consider emphasizing the unique members of this fishery, specifically bowfin and flier, and refrain from attempting to stock traditional sport fishes. Past attempts at stocking largemouth bass *(Micropterus salmoides)* and bluegill *(Lepomis macrochirus)* have failed to establish exploitable populations in the swamp. These species were both stocked in 1942, 1956, and 1965 to supplement their populations in the swamp. However, annual creel surveys conducted from 1970 to 1975 indicated a declining trend for largemouth bass from 2,374 fish in 1970 to 821 in 1975 (USFWS, unpub. data), and are currently uncommon in the system. Only one largemouth bass and four bluegills were captured during our sampling from 1992 to 2001, supporting this observation. The natural acidity of the Okefenokee Swamp likely prevents the successful establishment of these supplemental stocks. Graham (1993) found that stocked largemouth bass and bluegill failed to establish populations in naturally acidic lakes in New Jersey, despite extensive stocking efforts. Adults of both species can survive pH levels of 4.0 (Calabrese 1969), but are unable to reproduce successfully under such conditions (Stewart 1972). While local populations of largemouth bass and bluegill may be adapted to the high acidity of the swamp (Graham 1983), they have never been abundant (Laerm and Freeman 1986), and stocking of these species from populations poorly adapted to acidic conditions will likely continue to be unsuccessful.

Alternatively, a campaign to increase public interest in the unique fishery of the swamp should be considered. Anglers are currently targeting warmouth, chain pickerel, and flier (USFWS, unpub. data) as they readily take artificial and live bait and provide great sport when hooked. Unlike these target species, bowfin has never achieved popularity as a sport fish in the Okefenokee Swamp or in most other parts of their natural range. Although frequently caught by fisherman, they are commonly considered a "trash" or "nuisance" species and are implicated (without validation) in negatively affecting traditional sport fisheries (e.g., Holder 1970). Low-standing populations of traditional sport fish species such as largemouth bass and bluegill in the Okefenokee Swamp are likely the result of highly-acidic conditions rather than the detrimental effects of bowfin. Like flier, bowfin readily take artificial and live bait and put up a tremendous fight when hooked. Our study indicates that the eastern swamp provides the potential to catch an abundance of large-sized bowfin and flier. The sustainability of these populations to angling can be assessed by evaluating age and growth and mortality rates of these species as described above. Managers should therefore consider maximizing the potential of this unique fishery rather than focusing their efforts on stocking non-sustainable traditional sport fishes such as largemouth bass and bluegill in the Okefenokee Swamp.

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Literature Cited

Anderson, R. O. and A. S. Weithman. 1978. The concept of balance for coolwater fish populations. American Fisheries Society Special Publication 11:371–381.

Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Blood, E. C. 1981. Surface water hydrology and biogeochemistry of the Okefenokee Swamp watershed. Ph. D. dissertation, University of Georgia, Athens, Georgia.

Calabrese, A. 1969. Effects of acids and alkalies on survival of bluegills and largemouth bass. U.S. Bureau of Sport Fisheries and Wildlife Technical Paper 42.

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

Freeman, B. J. and M. C. Freeman. 1985. Production of fishes in a subtropical blackwater ecosystem: the Okefenokee Swamp. Limnology and Oceanography 30:686–692.

Gablehouse, D. W. Jr. 1984. A length-categorization system to assess fish stocks. North American Journal of Fisheries Management 4:273–285.

Gido, K. B., W. J. Matthews, and W. C. Wolfinbarger. 2000. Long-term changes in a reservoir fish assemblage: stability in an unpredictable environment. Ecological Applications 10:1517–1529.

Graham, J. H. 1993. Species diversity of fishes in naturally acidic lakes in New Jersey. Transactions of the American Fisheries Society 122:1043–1057.

Grossman, G.D., J.F. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes: a review. Environmental Management 14:661–671.

Holder, D.R. 1970. A study of fish movements from the Okefenokee Swamp into the Suwannee River. Proceedings of the Southeastern Association of Game and Fish Commission 18:247–255.

International Game Fish Association (IGFA). 2001. Database of IGFA angling records until 2001. IGFA, Fort Lauderdale, Florida.

Krebs, C. J. 1999. Ecological methodology, 2nd edition. Addison-Wesley Educational Publishers, New York, New York.

Laerm, J. and B. J. Freeman. 1986. Fishes of the Okefenokee Swamp. University of Georgia Press, Athens, Georgia.

Le Cren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in perch *Perca fluviatilus*. Journal of Animal Ecology 20:201–219.

Palmer, E. L. and A. H. Wright. 1920. A biological reconnaissance of the Okefenokee Swamp in Georgia: the fishes. Journal of the Iowa Academy of Science 27:353–357.

Robison, H. W. and T. M. Buchanan. 1988. Fishes of Arkansas. University of Arkansas Press, Fayetteville, Arkansas.

Stewart, R. W. 1972. Neutralization experiments. New Jersey Division of Fish, Game, and Shellfisheries, Freshwater Fisheries Laboratory, Miscellaneous Report 35, Lebanon, New Jersey.