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Recovery of a Reservoir Fish Community from Drawdown Related Impacts

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Abstract.—Par Pond, a 10.5-km^2 reservoir in South Carolina, was drained over a period of 3 months to less than 50% of its former surface area and volume; it was maintained in that state for approximately 3.5 years. The drawdown resulted in significant reductions in fish abundance and number of fish species, changes in the relative abundance of fishes, and changes in the size structure of individual species of fish. An important factor contributing to these changes was complete loss of the original littoral zone. Within approximately 9 months of the refill of Par Pond to its former level, the fish community had recovered in terms of number of species and overall fish abundance, and had nearly recovered in terms of species composition. However, size structures after refill were different than before the drawdown: large individuals were fewer and small individuals greater in number. Factors contributing to the recovery of the Par Pond fish community included recolonization from refugia, high reproductive rates of resident species, and the shelter for small fishes provided by inundated terrestrial vegetation and rapidly regrowing aquatic vegetation. These results suggest that at least some reservoir fish communities are resilient to disturbances of their physical habitat and, in this respect, resemble stream fish communities.

Resilience, the ability of an ecological community to return to a preperturbation condition (Holling 1973), is an important criterion for assessing environmental impacts and ecological risks (Cairns and Niederlehner 1993). Among stream fish communities, there is substantial evidence of resilience to many types of perturbations as indicated by relatively quick recovery from catastrophic flooding (Matthews 1986), severe drought (Bayley and Osborne 1993), and experimental defaunation (Meffe and Sheldon 1990; Peterson and Bayley 1993). An important reason for this resilience is that potential colonists generally are nearby in relatively large numbers (e.g., in tributaries and adjacent reaches) and can quickly recolonize perturbed areas (Matthews 1986; Bayley and Osborne 1993; Peterson and Bayley 1993). In contrast, reservoirs are more insular, which may make reservoir fish communities less resilient than stream fish communities. Knowledge of the resilience of reservoir fish communities is important because it can be used to influence decisions concerning the need for mitigation following environmental perturbations.

One of the most important perturbations affecting reservoirs is changes in water level. Moderate fluctuations in water level that mimic natural cycles of change have been used to improve recreational fisheries in reservoirs (Bennett 1970), although the collateral effects of such management actions on small, ecologically important, littoral zone species are largely unknown. Large or untimely water level changes can be very detrimental (Estes 1972; Gaboury and Patalas 1984), with effects that are both direct (e.g., dewatering of eggs and larvae, reduced availability of spawning substrate [Lantz et al. 1967; Estes 1972]) and indirect (e.g., alterations in the type and quantity of littoral zone aquatic vegetation or changes in water chemistry [Nichols 1975; Gaboury and Patalas 1984]).

In this study, I investigated the effects of a drawdown of approximately 3.5 years' duration that temporarily eliminated the littoral zone in a 37-year-old reservoir with a stable fish community and historically stable water levels. My objectives were (1) to assess the effects of the drawdown on fish community structure and the size structure of individual species, and (2) to assess the extent and rate of recovery of the fish community following refill of the reservoir.

Methods

Study area and field methods.—Par Pond is a 10.5-km^2 reservoir on the Savannah River Site (SRS), a 780-km^2 former Department of Energy nuclear materials production site on the Atlantic coastal plain near Aiken, South Carolina. Par Pond was created in 1958 by impounding the upper reaches of Lower Three Runs Creek and pumping in water from the Savannah River. It served as a cooling reservoir for nuclear reactors until 1988. In spite of its use as a cooling reservoir and contamination with low levels of radionuclides, Par Pond historically has supported diverse and abun-

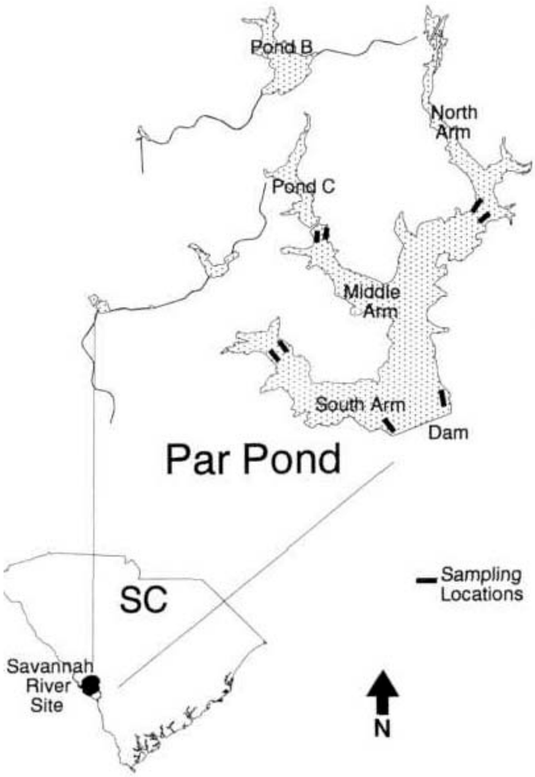

FIGURE 1.—Map of Par Pond showing locations of electrofishing sample sites.

dant assemblages of fish and other aquatic biota (Wilde 1985). In 1991 the water level of Par Pond was reduced from its artificially maintained level of 61 m above mean sea level (msl) to 55 m above msl because of a defect in the Par Pond dam. The drawdown began in June 1991, and the water level dropped to 55 m by September 1991, where it remained until the dam was repaired and Par Pond was refilled to its previous level in early 1995.

Par Pond was sampled during the drawdown (three times in 1991 and three times in 1992), during the refill (January 1995), and after refill was completed (May–June 1995, September–October 1995, and December 1996). Sample stations were in the north arm, middle arm, south arm, and near the dam (Figure 1). Fish were collected from each sample station by electrofishing approximately 600 m of shoreline (two 300-m segments) along the 1–2-m depth contour. Electrofishing was conducted from an aluminum boat by using a 4,000-W, 230-V DC generator with controlled frequency and pulse width. One pass was made through each sample station on each sample date, and attempts were made to collect as many fish as possible without regard to species or size. Captured fish were returned to the water after being identified, weighed, and measured (total length), except during the drawdown 1991 and drawdown 1992 samples, when fish were neither measured nor weighed for logistical reasons. Aggregate weights and length ranges usually were determined for small species present in large numbers (e.g., brook silverside *Labidesthes sicculus*).

Data analysis.—I used data from several earlier cove rotenone (Clugston 1973; Hogan 1978; Martin 1980) and electrofishing studies (Paller and Saul 1985) to provide information concerning the characteristics and stability of the Par Pond fish community prior to the drawdown. I primarily used data collected in 1984–1985 by Paller and Saul (1985) to represent predrawdown conditions, because their sampling methods were similar to mine, and they sampled the same general areas that I did. However, I also used the cove rotenone data for some analyses.

I separated fish community samples from Par Pond into seven time periods: predrawdown (1984–1985), drawdown 1991, drawdown 1992, refill 1995, spring postrefill 1995, fall postrefill 1995, and fall postrefill 1996. Refill, spring postrefill 1995, fall postrefill 1995, and fall postrefill 1996 were each represented by a single sampling event. Drawdown 1991 and drawdown 1992 were each represented by three sampling events (summer, fall, and winter in 1991, and spring, summer, and fall in 1992). The predrawdown period was represented by the 18 monthly sampling events (January 1984–June 1985) summarized in Paller and Saul (1985).

I assessed differences in fish community structure among time periods on the basis of species number, total number of fish caught, species rank abundance, and Schoener's (1968) proportional similarity index (PSI). I compared differences in species number and number of fish among time periods with the *T*-method for unplanned comparisons (Sokal and Rohlf 1981). This procedure controlled the experimentwise error rate (i.e., the error rate for the entire series of tests) and permitted plotting of "comparison intervals" around each mean ($P \leq 0.05$). There were four replicates (one per sample area) for each of the seven time periods ($N = 28$). For simplicity and because some of the historical data were presented only as means, I used the mean value within each period for periods with multiple sampling events (predrawdown, drawdown 1991, and drawdown 1992). Numbers of species and numbers of individuals were log transformed, $\log_{10}(X + 1)$, before analysis to reduce heterogeneity of variance (Sokal and Rohlf 1981).

I assessed changes in species rank abundance between the predrawdown sample period and the later periods with the Spearman rank correlation coefficient (Sokal and Rohlf 1981). I treated the correlations as ordinary product-moment correlation coefficients for statistical testing (Sokal and Rohlf 1981). I used the Bonferroni procedure (Marasciulo and McSweeney 1977) to maintain the probability value at 0.05 for the entire set of comparisons because the same data were tested several times. For periods with multiple sampling events, I summed over sampling events within each period to determine the species ranks.

I used the PSI to assess similarities between the predrawdown species assemblage (summed over sample events) and the assemblages collected during drawdown and after refill. I calculated proportional similarity (PS) as follows (Schoener 1968):

$$PS_{ij} = 1 - 0.5 \sum_{n=1}^{s} |p_{in} - p_{jn}|,$$

where PS_{ij} is the proportional similarity between samples i and j, s is the number of species, and p_{in} and p_{jn} are the proportions by number (n) for each species in samples i and j. Proportional similarity ranges from 0 (completely different) to 1 (identical). Values greater than 0.7 are often considered to indicate very similar fish assemblages (Pennington et al. 1983; Matthews 1986; Peterson and Bayley 1993).

Proportional similarity would be expected to vary over time even in the absence of anthropogenic disturbances because of sampling error and normal temporal variations in abundance. Although collected using cove rotenone rather than electrofishing methods, the best estimate of this variability that I had were the four samples collected in 1969, 1972, 1977, and 1980 (Clugston 1973; Hogan 1978; Martin 1980), when Par Pond water levels were constant. I calculated PS among these samples to determine the range of PSs characteristic of normal interannual variability. This range provided a basis against which I could compare the PSs calculated between the predrawdown electrofishing samples and the postrefill electrofishing samples.

To make this comparison, I drew 1,000 random samples of two (with replacement) from the six PS values calculated among the four cove rotenone samples, calculated the mean for each sample, and plotted the resulting distribution of means. As a measure of recovery, I used the mean of the predrawdown–postrefill fall 1995 PS and predrawdown–postrefill fall 1996 PS, and compared it to the preceding distribution of means. My criterion for deciding that recovery had occurred was that the predrawdown–postrefill mean PS fell within the upper 90% of the distribution of PS means for the rotenone samples. I chose a critical level of 90% rather than the more commonly used 95% because I believed that it was more serious to mistakenly assume that recovery had occurred than that it had not.

To determine whether size distributions within species had changed as a result of the drawdown, I categorized each species by total length into three groups of approximately equal range. I tested for differences in the proportions of fish in these length groups between the predrawdown and postrefill fall 1996 time periods with a chi-square contingency test (Zar 1984). The length-groups were 0-199, 200–399, and 400 mm or longer for largemouth bass (scientific names are given in Table 1); 0–149, 150–299, and 300–449 mm for lake chubsuckers; and 0–99, 100–199, and 200–299 mm for bluegill. The significance level was $P \leq 0.05$. I calculated size distributions for the predrawdown sample by summing over the monthly sampling events.

I conducted the statistical analyses with SYSTAT (Wilkinson 1989) and JMP (SAS Institute 1989) software.

Results

Par Pond Fish Communities

Seventeen species of fish were collected from Par Pond by electrofishing during the predrawdown period (Table 1). The most abundant by number were brook silversides (50.7%), bluegills (17.9%), and largemouth bass (15.6%). Other species collected in substantial numbers were lake chubsucker, coastal shiner, golden shiner, chain pickerel, yellow perch, and redbreast sunfish.

Comparisons between the predrawdown electrofishing samples and earlier samples collected with cove rotenone techniques during 1969, 1972 (Clugston 1973), 1977 (Hogan 1978), and 1980 (Martin 1980) (Table 2) must be approached cautiously because of method-related biases (Nielsen and Johnson 1983) and because the cove rotenone results were reported by weight rather than number. However, the cove rotenone samples consistently demonstrated that the most abundant species

TABLE 1.—Percent composition of fishes (by number) collected by electrofishing from Par Pond, South Carolina, before, during and after a drawdown event of 3.5 years' duration.

Species	Pre-drawdown 1984–1985	Drawdown 1991	Drawdown 1992	Refill 1995	Postrefill Spring 1995	Postrefill Fall 1995	Postrefill Fall 1996
Brook silverside *Labidesthes sicculus*	50.7	3.3	2.8	90.8	9.1	21.7	33.0
Bluegill *Lepomis macrochirus*	17.9	46.7	45.8	2.8	21.4	17.9	21.7
Largemouth bass *Micropterus salmoides*	15.6	16.7	22.2	2.8	20.6	8.3	2.6
Lake chubsucker *Erimyzon sucetta*	6.1	2.5	1.4	1.6	5.8	4.7	6.0
Coastal shiner *Notropis petersoni*	3.4		11.1		9.7	4.8	6.4
Golden shiner *Notemigonus crysoleucas*	1.8	3.3		0.2	14.8	13.2	8.4
Chain pickerel *Esox niger*	1.3	5.0	1.4	1.6	2.9	4.5	7.3
Yellow perch *Perca flavescens*	0.9				7.6	6.0	0.4
Redbreast sunfish *Lepomis auritus*	0.7	1.7			0.8	0.6	2.3
Black crappie *Pomoxis nigromaculatus*	0.4	0.8	1.4	0.2	0.4	1.4	0.4
Warmouth *Lepomis gulosus*	0.4	2.5			0.2	1.9	2.2
Bowfin *Amia calva*	0.2	0.8	1.4		0.8	0.4	
Spotted sunfish *Lepomis punctatus*	0.1	0.8			1.2	2.0	0.4
Yellow bullhead *Ameiurus natalis*	0.1						
Dollar sunfish *Lepomis marginatus*	0.1				4.7	1.2	5.8
Blueback herring *Alosa aestivalis*	<0.1	14.2	12.5			11.0	2.5
Gizzard shad *Dorosoma cepedianum*	<0.1					0.1	0.5
Mosquitofish *Gambusia affinis*						0.1	
Swamp darter *Etheostoma fusiforme*						0.1	
Flat bullhead *Ameiurus platycephalus*		1.7					

in Par Pond were bluegills, lake chubsuckers, largemouth bass, chain pickerel, other species of sunfishes, and yellow perch, all of which were also well represented in the 1984–1985 electrofishing samples. Brook silversides and other small species were not prominent in the cove rotenone samples because of their comparatively insignificant weight. Given the previously mentioned caveats, these comparisons suggest that the Par Pond fish assemblage was relatively stable prior to the drawdown; most species were persistent and the same

TABLE 2.—Percent composition (by weight) of fishes from Par Pond during 1969–1980. Data were obtained from various cove rotenone studies: 1969 and 1972 (Clugston 1973), 1977 (Hogan 1978), 1980 (Martin 1980).

Species	1969	1972	1977	1980
Blueback herring	0.1			0.1
Bluegill	25.3	13.7	25.1	30.5
Other sunfishes *Lepomis* spp.	13.1	13.7	10.8	15.0
Bullheads *Ameiurus* spp.	0.8	2.3	2.4	0.5
Bowfin	2.5	1.8	2.7	0.4
Chain pickerel	4.5	12.9	7.5	5.4
Black crappie	2.6	1.7	1.1	2.5
Lake chubsucker	15.4	42.3	33.8	19.7
Spotted sucker *Minytrema melanops*	2.2			
Golden shiner	0.4	5.2	5.0	7.3
Largemouth bass	22.8	5.6	8.0	17.4
Yellow perch	5.8	0.9	3.4	1.2
Miscellaneous fish	4.6		0.2	0.4

group of species appeared to share numerical dominance.

The drawdown resulted in a 50% reduction in reservoir surface area, a 65% reduction in reservoir volume (DOE 1994), and the loss of virtually all littoral zone emergent and submerged vegetation (Mackey and Riley 1996). Massive fish kills were not observed, but continuous attrition was indicated by ongoing observations of moderate numbers of dead fish of various species and sizes following drawdown (Whicker 1991). The cause of these deaths was uncertain. The average number of species collected from Par Pond declined significantly the first year of drawdown (drawdown 1991) and decreased still further the second year (drawdown 1992) (Figure 2). The number of individual fish also declined significantly, reaching levels approximately an order of magnitude lower than before drawdown (Figure 2).

Samples collected during refill (January 1995) indicated significant increases in the number of species and number of individuals, but both variables remained significantly lower than before drawdown (Figure 2). However, the spring postrefill sample, collected approximately 3 months after refill was completed, indicated that species number and number of individuals had increased to predrawdown levels. Most of the increase in number of individuals consisted of age-0 fish (as determined based on size). The fall postrefill 1995 sample indicated additional increases in numbers of

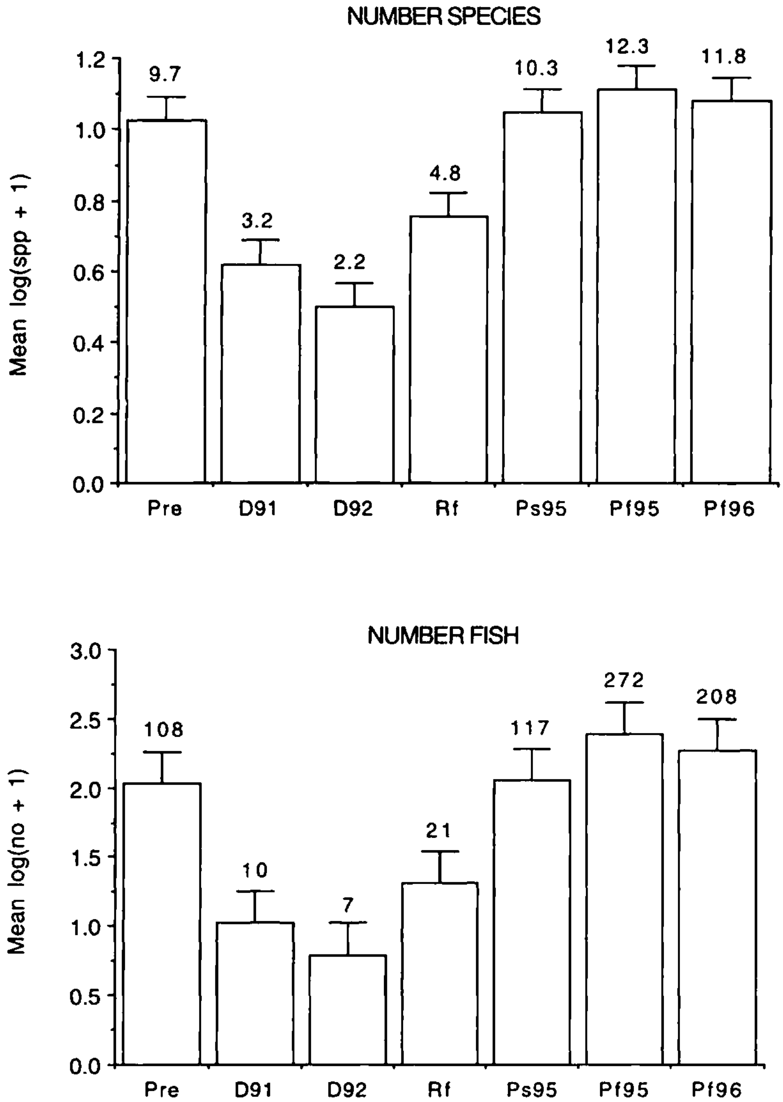

FIGURE 2.—Average log-transformed number of species and number of fish collected from Par Pond prior to the drawdown (Pre), during the drawdown in 1991 and 1992 (D91 and D92), during the refill (Rf), and in the spring 1995 (Ps95) and fall 1995 and 1996 (Pf95 and Pf96) following the refill. Means with nonoverlapping comparison intervals (Sokal and Rohlf 1981) are significantly different ($P \leq 0.05$). Numbers above the error bars are arithmetic means.

species and individuals, although neither was significantly greater than the predrawdown values. The fall postrefill 1996 sample was generally similar to the fall postrefill 1995 sample, although numbers declined slightly.

Species rank abundance correlations between the predrawdown and drawdown samples were significant ($P \leq 0.05$) but moderate (i.e., 0.59–0.60). The correlations between the predrawdown and refill samples (Spearman $r = 0.79$) and predrawdown and spring 1995 postrefill, fall 1995 postrefill, and fall 1996 postrefill samples (Spearman $r = 0.88$, 0.75, and 0.75, respectively) were higher, reflecting recovery of the Par Pond fish community toward its predrawdown state. Correlations of this magnitude were typical among interannual samples from the Par Pond fish community as indicated by the rank correlations among the cove rotenone samples (Spearman $r = 0.60$–0.95, average of 0.81), which were not punctuated by major disturbances. Such variability may be attributable to sampling error and interannual variations in the reproductive success of individual species.

Proportional similarity between the predrawdown sample and drawdown samples was relatively low (0.45 for drawdown 1991 and 0.43 for drawdown 1992) indicating, as did the rank abundance correlations, that community structure was altered by the drawdown. Proportional similarity between the predrawdown sample and the refill, spring postrefill 1995, fall postrefill 1995, and fall postrefill 1996 samples increased to 0.60, 0.58, 0.62, and 0.68 respectively, reflecting a return toward predrawdown community structure. The last of these values approached the 0.70 often considered to indicate high similarity between fish assemblages. The mean of the last two PSs was 0.65, which was higher than 15% of the means in the sampling distribution of mean PSs calculated from the cove rotenone data (PSs for the cove rotenone samples ranged from 0.58 to 0.82). This comparison indicated that the similarity between the predrawdown and fall postrefill samples was not significantly lower than between samples without an intervening disturbance.

Species size structure (i.e., distribution of length-classes) was affected by the drawdown. Prior to the drawdown, largemouth bass and lake chubsucker populations were dominated by large (≥300 mm TL) fish, although small individuals were also present (Table 3). Small fish appeared to have been largely eliminated by the drawdown and few remained by the time of refill. The fact that largemouth bass and lake chubsucker under 150 mm TL were nearly absent in the refill sample suggests that recruitment had been poor throughout the drawdown. In the months following refill, numbers of small individuals increased substantially and dominated the size structures of both species. The relative scarcity of large fish was responsible for statistically significant ($P \leq 0.05$) differences between the predrawdown and fall 1996 postrefill size distributions of both species.

Like largemouth bass and lake chubsuckers, the abundance of small bluegills decreased during the drawdown and increased following the refill, as indicated by the prominence of the 50–99-mm size-class in the 1995 postrefill sample (Table 3). The relative scarcity of 0–49-mm fish in these samples probably was related to sample timing. Unlike the situation with largemouth bass and lake chubsuckers, large bluegills (≥100-mm TL) increased rapidly in number and by fall 1996 were the dominant size-class, resulting in a statistically significant ($P \leq 0.05$) difference between the predrawdown and fall 1996 postrefill size distributions.

TABLE 3.—Length frequencies (%) of largemouth bass, lake chubsuckers, and bluegills sampled by electrofishing before and after the Par Pond drawdown.

Length interval (mm)	Predrawdown 1984–1985	Refill 1995	Postrefill Spring 1995	Postrefill Fall 1995	Postrefill Fall 1996
		Largemouth bass			
0–49	23	0	40	0	0
50–99	4	6	36	57	55
100–149	6	0	3	20	14
150–199	8	0	6	9	0
200–249	9	0	4	1	9
250–299	5	6	1	7	0
300–349	13	47	1	4	0
350–399	12	29	8	1	9
400–449	16	12	2	2	5
450–499	3	0	0	0	5
500–549	1	0	0	0	5
550–599	0	0	0	0	0
Number of fish	1,530	17	106	115	22
		Lake chubsucker			
0–49	1	0	23	0	0
50–99	4	0	0	22.6	2
100–149	3	0	30	34	12
150–199	4	10	13	15	36
200–249	5	10	10	22	20
250–299	16	0	13	5	14
300–349	35	80	0	2	16
350–399	30	0	7	2	0
400–449	1	0	3	0	0
450–499	1	0	0	0	0
500–549	1	0	0	0	0
Number of fish	598	10	30	65	50
		Bluegill			
0–49	46	12	19	1	2
50–99	31	24	65	49	9
100–149	9	24	11	48	42
150–199	4	0	6	1	28
200–249	5	41	0	1	14
250–299	6	0	0	0	4
Number of fish	1,754	17	110	248	180

Discussion

It is probable that reductions in numbers of species and changes in relative abundance observed in this study were a direct consequence of the drawdown. Drawdown apparently resulted in marked reductions in habitat size and quality, including the temporary loss of the littoral zone and its associated vegetation. Many of the species that declined during the drawdown (e.g., brook silverside, lake chubsucker, yellow perch, and dollar sunfish *Lepomis marginatus*) prefer littoral zone habitats with extensive aquatic vegetation (Pflieger

1975; Robison and Buchanan 1988). The temporary elimination of the littoral zone probably also was responsible for the loss of juveniles of larger species (e.g., largemouth bass), because juvenile fish use littoral zone aquatic vegetation as shelter from piscivores (Werner et al. 1983). Species richness declined significantly during the first year of the Par Pond drawdown, indicating that small, shelter-seeking species may be decimated quite quickly following the loss of cover. Hence, such species also may be affected by relatively short winter drawdowns conducted for management purposes.

Fish community structure in Par Pond recovered rapidly following refill. By fall 1996, remaining differences between predrawdown and postrefill community structure were within the range of normal interannual variability. Several factors contributed to the recovery of the Par Pond fish community. One was recolonization of new habitat by species reduced in numbers or temporarily eliminated from the main body of the reservoir (as represented by our sample sites). These species may have persisted in small refugia located in the headwater stream that feeds Par Pond and possibly in shallow coves where the regrowth of aquatic vegetation during the drawdown provided shelter from predaceous fish and birds. A second factor contributing to recovery was the highly successful reproduction following the refill that resulted in recruitment of large numbers of juvenile fishes. Also contributing to recovery was the habitat provided first by inundated terrestrial vegetation (including herbaceous vegetation and loblolly pine trees *Pinus taeda* 2 m or more in height) and subsequently by the rapid regrowth of aquatic vegetation in the reestablished aquatic habitat produced by the refill. Analysis of aerial photographs indicated approximately 120 ha of emergent aquatic vegetation in Par Pond at the end of the 1995 growing season (Mackey and Riley 1996), or about 40% as much as before the drawdown (1984–1990; Jensen et al. 1991).

Although species richness and abundance and, to a large extent, species composition returned rapidly to predrawdown levels once Par Pond was refilled, the size structure of individual species remained significantly different than before the drawdown. Predrawdown size structures of largemouth bass and lake chubsuckers were generally characteristic of relatively old and stable populations with a preponderance of large individuals. The postrefill size structures that developed in 1995 and 1996 were the reverse, with a preponderance of juveniles and relatively few large fish (Table 3). These size structures were probably the result of considerable mortality of larger fish during the drawdown, followed by highly successful reproduction following refill. Given their probable growth rates (Carlander 1969, 1977), it is likely that the size distributions of largemouth bass and other comparatively long-lived fishes will require at least several years to return to their predrawdown states. In contrast, large bluegills were abundant by fall 1996, presumably because of the relatively rapid growth rate of this species.

This study suggests that at least some southeastern reservoir fish communities are resilient to extensive and relatively long-term reductions of habitat volume and destruction of littoral zone habitat. If this is true of southeastern reservoirs in general, there may be little need for expensive restoration actions, such as artificial stockings, after drawdowns or other perturbations that temporarily alter habitat volume or disturb the littoral zone, even when such disturbances are severe. Exceptions may occur if water quality deteriorates during drawdown and results in complete fish kills, or if there are no refugia for future recolonists during the drawdown. The preceding recommendation parallels that of Bayley and Osborne (1993) for warmwater streams. They found that the short time period of natural recovery of fish communities in low-order streams indicates no need for stocking when undertaking restoration projects. Additional research is needed to determine whether high resiliency is characteristic of other reservoir fish communities, particularly in colder climates.

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