

SEASONAL FISH POPULATION FLUCTUATIONS IN SOUTH FLORIDA SWAMP

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Abstract: We monitored fish populations in a southwest Florida cypress (*Taxodium distichum*) strand system through an annual wet season-dry season cycle. Populations increased from zero when the site was inundated to densities of 3-8 fish m^2 and biomass of .3-.4 g/ m^2 in late wet season. Two months after drydown began, fish became concentrated. In wet prairie and "pond" cypress habitats concentration continued until the sites went dry, but "bald" cypress populations reached high densities early, then stabilized until just prior to complete drydown, when they decreased drastically. Wet season populations were probably controlled by hydrologic factors, but predation was important in determining dry season density, biomass, and species composition.

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There have been a number of studies of fish populations in South Florida wetlands. Kolipinski and Higer (1969) and Kushlan et al. (1975) measured the density of small fishes in Everglades marshes. Kahl (1964), Kushlan (1972), and Browder (1976) investigated the relationship of fish density, water level fluctuation, and wading bird activity in marshes and ponds in the Big Cypress Swamp (Fig. 1). Carter et al. (1973) studied fish

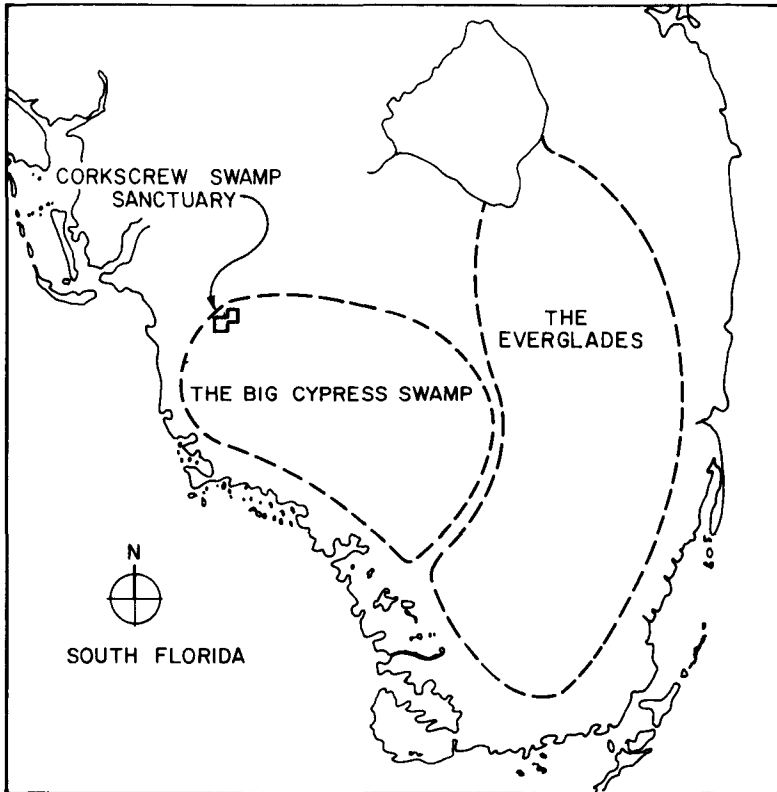


Fig. 1. Location of study site in relation to Big Cypress and Everglades ecosystems.

populations in canals and lakes in the Fahkahatchee Strand, a cutover and drained area of the Big Cypress. Results of these studies indicate that fish constitute a large portion of the animal biomass in these seasonally aquatic environments and function as a major food chain link for terrestrial as well as aquatic predator populations in South Florida. Fish are produced during the summer-fall wet season when the region is 90 percent aquatic habitat and are concentrated in drying pools during the winter-spring dry season when less than 10 percent of the area is inundated.

Our study emphasizes the interrelationship between fish populations and water levels in an undisturbed cypress "strand". A strand is essentially a shallow, slow-flowing forested river with lower elevation and hence longer hydroperiod (length of time inundated) than adjacent marshes. Fish which survive the dry season in the strand's deeper holes and sloughs serve as seed stock to repopulate the marshes when water levels rise. The sooner the fish begin to utilize the flooded marshes, the higher their populations can build before dry season and the greater their potential as a food source for predators. Kushlan (1972) and Browder (1976) showed that fish produced in the marshes and trapped in open water ponds the following dry season are an important concentrated food source for wading birds and other wildlife. Fish confined to the strand are not as available to predators because of the cover provided by logs, stumps, cypress knees, etc. and thus may be a more secure population reservoir.

Our study was designed to monitor species composition, density, and biomass of fish populations through a complete annual wet season-dry season cycle at Corkscrew Swamp. This work was supported by Rockefeller Foundation Grant No. RF-73029 administered through the University of Florida's Center for Wetlands. L. C. Duever helped extensively in manuscript preparation.

METHODS

Sampling sites were established along a transect at Corkscrew Swamp Sanctuary in 3 major habitats with distinct elevation and hydroperiod characteristics: "bald cypress," "pond" cypress (both are here considered *Taxodium distichum*), and wet prairie (Fig. 2). Predominant wet prairie plants are *Spartina* sp., *Panicum* sp. and *Utricularia* sp.

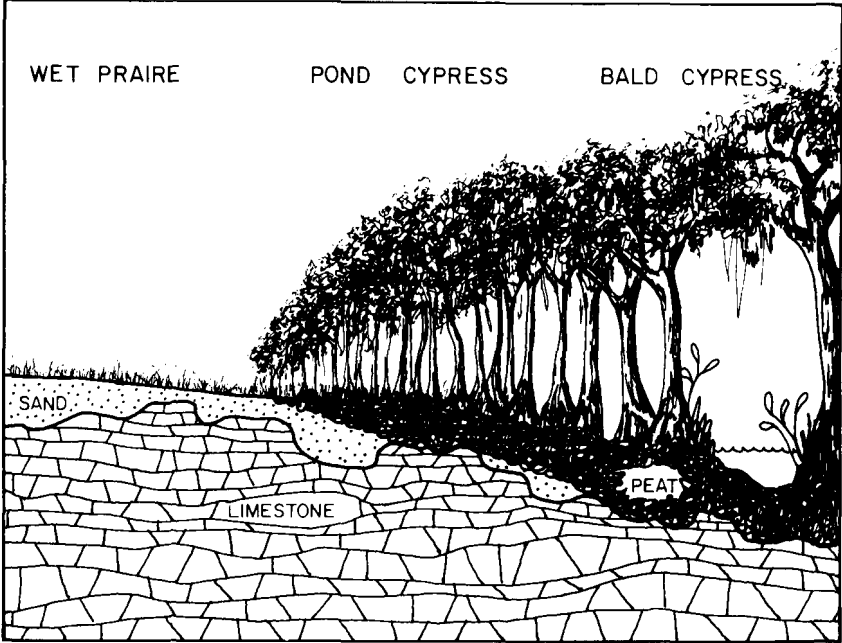


Fig. 2. Schematic representation of cypress strand habitats.

Our sampling device was a 1 m² Wegener Ring (Wegener et al. 1973). Three to 5 samples per habitat were taken on each date. To sample, we walked 10 steps perpendicular to the transect and threw the ring about 5 m ahead. If the ring was snagged by a log, cypress knee, or heavy undergrowth, the process was repeated until a clear landing was achieved. No attempt was made to aim the ring. There was some bias, since the sampling ring worked much better in open spots, but only the most heavily vegetated areas were altogether excluded. Because of its small diameter, the ring was inefficient at capturing large and/or fast-moving fish, but in swamps and marshes these are normally only a minor component of the community.

Fish were removed live from the Wegener Ring with a dip net and preserved in formalin, then identified, counted, and measured for standard length to the nearest mm in the lab. Biomass was calculated with length-weight regression equations developed by Browder (pers. comm.) from her work on Corkscrew Marsh.

During the 1975 dry season we rotenoned two small isolated pools (gator holes) in the "bald" cypress to assess total fish populations.

RESULTS

The wet prairie and "pond" cypress sites had been inundated for 5 mo when initial samples from these habitats were taken in November 1974. Water levels had been dropping for 2 mo and water depth averaged 7 cm in the wet prairie and 17 cm in the "pond" Cypress. Total fish biomass and density were relatively high then, but were even higher in December when water levels were lower (Fig. 3) All surface water was gone from the wet prairie 2 weeks after this sample, and the "pond" cypress went dry 4 weeks later. It is interesting that density and biomass values were highest during low water conditions, although it was still possible for fish to move into deeper habitats.

"Bald" cypress sampling began in December 1974 (Fig. 3). Total fish density and biomass were lower than in the wet prairie or "pond" cypress at this time. Little change was evident in January, but total biomass had decreased 90 percent by March. The water had dropped 50 cm during this period and was confined to the deeper pools, yet density was half what it had been in January.

There was no surface water at any of the sampling sites in April, but a few small pockets of water were left in the deepest spots in some "bald" cypress areas on the Sanctuary.

Sampling resumed 30 June 1975, when rains began to fill the "gator hole" in the "bald" cypress, but no fish were found until after heavy rains 12 and 13 July raised water levels enough to connect all ponds in the "bald" cypress. Fish were first observed in the gator hole on 14 July 1975, and 5 samples on 16 July yielded 5 mosquitofish (*Gambusia affinis*) and 1 least killifish (*Heterandria formosa*).

There were few fish in the early wet season samples and only small numbers in September and November.

Fish were concentrated in the wet prairie by December, but by January the water had dropped to 2.5 cm and density and biomass had declined slightly.

In the "bald" cypress, fish became concentrated by December, and density and biomass remained stable through February. During this period, the water receded completely from the "pond" cypress where the fish density had increased by a factor of 5 in January just prior to drydown, but there was no corresponding increase in the "bald" cypress fish population. Fish had disappeared almost entirely from the "bald" cypress by March. Again, as in 1975, continuing concentration of fish by descending water was not seen in the "bald" cypress.

We found mosquitofish to be the most abundant species in the cypress strand, normally constituting 55-85 percent of the population in the "pond" cypress and over 80 percent in the "bald" cypress. During drydown, when other species moved into the deeper waters of the "bald" cypress, mosquitofish became a less overwhelming component of the population, but throughout the year they accounted for over 40 percent of the fish biomass at both cypress sites. In the wet prairie, they represented only 30-55 percent of the population and 10-20 percent of the biomass.

Flagfish (*Jordanella floridae*) were the dominant species in the wet prairie, normally making up 25-60 percent of the population and 20-85 percent of the biomass. There were always a few in the "pond" cypress, but they never accounted for more than 20 percent of either population or biomass. Flagfish were found in the "bald" cypress only during drydown and they never amounted to as much as 10 percent of a sample there.

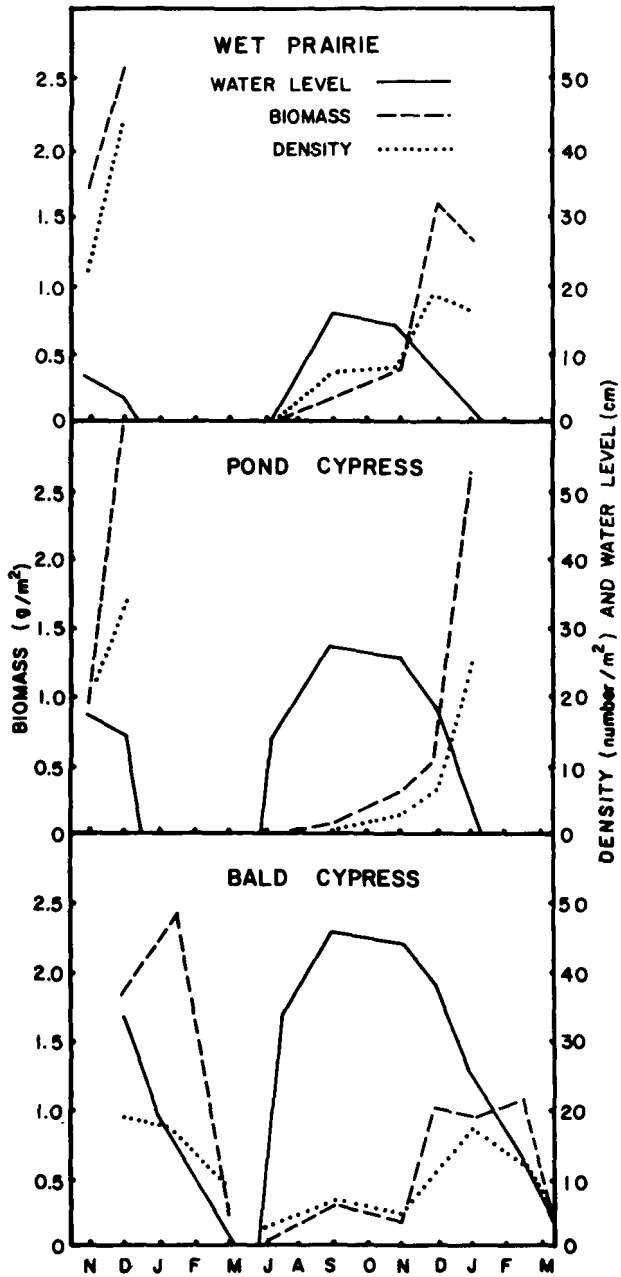


Fig. 3. Seasonal fluctuations in surface water levels and fish biomass and density.

Least killifish rarely constituted more than 20 percent of a sample by numbers or 10 percent by weight at any site. Most numerous in the wet prairie, they were seldom found in the "bald" cypress except during drydown, but at that time they constituted up to 40 percent of the population and 14 percent of the biomass. Their small size may have allowed them to outlive larger species and become relatively more numerous as the water became critically shallow.

The only other species we encountered frequently was the golden topminnow (*Fundulus chrysotus*). We usually found these in the wet prairie, but a few appeared in the "pond" cypress during drydown.

Species occurring sporadically included redear sunfish (*Lepomis microlophus*), sailfin molly (*Poecilia latipinna*), bluefin (*Lucania goodei*), brown bullhead (*Ictalurus nebulosus*), and a small unidentified sunfish. Rarely did any of these represent more than 15 percent of a sample either by numbers or by weight.

We measured wet season fish densities of 3-8/m² and biomass of .3-.4 g/m² (dry-weight, which was 20-25% of fresh weight) (Tables 1-3). Maximum dry season fish density was 16-43/m² and maximum biomass was 1-3 g/m². During the 1975-1976 drydown, maximum dry season concentrations were higher than wet season densities by a factor of 3-10 and biomass increased by a factor of 3-8. Neither drydown nor wet season fish densities or biomass differed significantly between habitats.

Thirteen species of fish, including 4 centrarchid species, bowfin (*Amia calva*), Florida gar (*Lepisosteus platyrhincus*), yellow bullhead (*I. natalis*), and 6 species of small forage fish were found in 2 residual pools in the "bald" cypress rotenone samples in April 1976. One pool was approximately 7 m² and 50 cm deep and had little cover; the other, about 80 m² and 50 cm deep, was cluttered with stumps, logs, litter, and emergent vege-

Table 1. Wet prairie fish density (D) number m⁻² and biomass (B) (g m⁻²).

	Mosquito-fish		Flagfish		Least Killifish		Golden Topminnow		Other Species		Total	
	D	B	D	B	D	B	D	B	D	B	D	B
11 11 74	6.6	.18	12.8	1.47	2.0	.04	.8	.04	0	0	22.2	1.73
12 9 74	14.2	.45	24.4	2.4	.04	1.0	.08	.6	.04	42.6	2.65	
1 31 75	a	a	a	a	a	a	a	a	a	a	a	a
3 17 75	a	a	a	a	a	a	a	a	a	a	a	a
7 16 75	a	a	a	a	a	a	a	a	a	a	a	a
7 31 75	0	0	0	0	2	.00	0	0	0	0	2	.00
9 17 75	2.5	0.01	3.3	.16	1.5	.01	0	0	.3	.01	7.5	.20
11 12 75	4.4	0.07	.8	.09	1.2	.02	.8	.03	.8	.18	8.0	.40
12 15 75	9.4	.30	4.8	.51	2.0	.04	1.6	.66	.8	.07	18.6	1.58
1 26 76	6.4	.49	4.8	.39	2.4	.02	.8	.18	1.8	.20	16.2	1.28
3 1 76	a	a	a	a	a	a	a	a	a	a	a	a
3 29 76	a	a	a	a	a	a	a	a	a	a	a	a

*No surface water.

Table 2. "Pond" cypress fish density (D) (number m⁻²) and biomass (B) (g m⁻²).

	Mosquito-fish		Flagfish		Least Killifish		Golden Topminnow		Other Species		Total	
	D	B	D	B	D	B	D	B	D	B	D	B
11 11 74	17.5	.75	1.0	.11	.3	.01	0	0	2.0	.10	20.7	.98
12 9 74	19.4	1.37	5.4	.63	1.0	.03	.32	7.0	.68	33.8	3.03	
1 31 75	a	a	a	a	a	a	a	a	a	a	a	a
3 17 75	a	a	a	a	a	a	a	a	a	a	a	a
7 16 75	a	a	a	a	a	a	a	a	a	a	a	a
7 31 75	0	0	0	0	0	0	0	0	0	0	0	0
9 17 75	1.3	.05	.3	.02	0	0	0	0	0	0	1.7	.07
11 12 75	2.4	.32	.2	.02	.2	.00	0	0	0	0	2.8	.34
12 15 75	3.8	.22	.2	.03	.6	.03	.4	.12	.2	.19	5.2	.58
1 26 76	19.8	1.53	2.3	.27	1.3	.04	0	0	1.8	.88	25.0	2.73
3 1 76	a	a	a	a	a	a	a	a	a	a	a	a
3 29 76	a	a	a	a	a	a	a	a	a	a	a	a

*No surface water

Table 3. "Bald" cypress fish density (D) (number m⁻²) and biomass (B) (g m⁻²)

	Mosquito-fish		Flagfish		Least Killifish		Golden Topminnow		Other Species		Total	
	D	B	D	B	D	B	D	B	D	B	D	B
11 11 74 ^a												
12 9 74	19.3	1.85	0	0	0	0	0	0	0	0	19.3	1.85
1 31 75	13.0	1.54	1.0	.13	1.3	.03	0	0	2.8	1.47	18.0	3.16
3 17 75	3.5	.13	0.8	.07	4.0	.03	0	0	.5	.6	8.8	.24
7 16 75	2.0	0.1	0	0	0	0	0	0	0	0	2.0	.01
7 31 75	3.4	.11	0	0	0	0	0	0	0	0	3.4	.11
9 17 75	5.5	.28	0	0	.3	.00	0	0	0	0	5.8	.29
11 12 75	5.4	.24	0	0	.6	.02	0	0	.8	.07	6.8	.34
12 15 75	11.0	1.01	0	0	0	0	0	0	.2	.02	11.2	1.03
1 26 76	15.2	.98	0	0	0	0	0	0	0	0	15.2	.98
3 1 76	11.0	.51	.4	.03	.2	.01	0	0	1.4	.54	13.0	1.09
3 29 76	1.8	.04	.3	.02	1.0	.02	0	0	.3	.05	3.3	.14

^aNo samples taken.^bNo dry weight available for bullhead

tation. The bare pool harbored no large predators and its species composition was similar to that found in the Wegener Ring samples: mostly small forage species. Biomass was 5 gm² and density was 140 fish/m². The fish population of the cluttered pool was very different. Over 80 percent of the biomass was made up of young-of-the-year predators capable of feeding on small forage fish. Warmouth (*L. gulosus*) and dollar sunfish (*L. marginatus*) constituted 38 percent of the population, but young Florida gar contributed significantly to the biomass. Golden topminnows, mosquitofish, flagfish, and least killifish made up 55 percent of the population, but were responsible for only 14 percent of the 1.8 g/m² biomass. Density in this pool was 2 fish/m².

DISCUSSION

Seasonal patterns of fluctuation

Kolopinski and Higer (1969) observed the interrelationships of fish populations and water levels in the Everglades marshes over a 2 year period. The first year's wet season water levels were low, the subsequent drydown undramatic and fish concentrations were minimal. The next year, wet season water levels were relatively high and there was a marked, though incomplete, drydown with pronounced concentrations. Milleson (1976) studied a marsh system with artificially controlled water levels. He found relatively low and stable fish populations when water levels were kept high, and large increases in density when the water was drawn down. Minor water level declines appeared to have little effect. A 7 yr study by Kushlan et al. (1975) suggested that maximum fish densities in Everglades marshes occurred when declining water levels reached a depth of about 25-30 cm. When water levels receded below this optimum depth, fish moved on to deeper areas. Few fish were stranded in the marshes during drydown. Since water rose above 30 cm at only one of our sites during the study period and was never deeper than 17 cm at our wet prairie site (when wet season conditions were within the normal range recorded for the sanctuary over the previous 15 yr), 30 cm cannot be a critical level for fish concentration at Corkscrew. A wet season with water levels in excess of about 10 cm for several months followed by a pronounced drydown appears to create conditions conducive to fish concentration in the strand habitats. In our study area, when water levels declined to 18-50 percent of their maximum wet season depth fish began to be concentrated. Increased fish densities became apparent within the first 2 mo of drydown even at sites which did not dry up completely until several months later. Kushlan (1972) also observed significant population increases in the first 2 months of a 5 month drydown in an Everglades "gator hole". High fish densities early in the dry season are probably a phenomenon of ponds or sloughs associated with extensive areas of shallower habitat. Such sites dry rapidly and force fish into low spots early, whereas locales with widespread deep water provide ample fish habitat until later in the dry season. Thus, drydown fish concentrations are probably more a function of reduction in inundated area than of simple decrease in water depth.

Our results suggest that mass long-distance (100 m) movements of fish into deeper habitats during drydown are not a regular phenomenon in natural Big Cypress communities. This is probably because physical features of the habitats limit fish movement. Irregular minor depressions are plentiful, but there are no clear channels through which

fish can swim freely. Vegetation and plan debris hinder mobility and trap fish in drying environments. Thus, density and biomass of both wet and dry season fish populations are dependent primarily on the productivity of the particular site and not of adjacent habitats from which fish may have migrated. A few fish do manage to find their way into deeper water, however. In both years of our study, densities of golden topminnow, least killifish, and bluefin killifish increased in the "pond" cypress as the adjacent wet prairie went dry. We did not detect higher density in the "bald" cypress as a result of a mass movement of fish from adjacent drying habitats, but the proportion of flagfish and least killifish sharply increased during drydown. Still, it appears that only a small percentage of the fish produced in the shallower habitats ever make it to the "bald" cypress.

No fish kills occurred in the "bald" cypress to account for the loss of fish observed prior to complete drydown during 1975 and 1976. Kushlan (1972) did record an almost complete fish kill in a Big Cypress gator pond when dissolved oxygen remained at 0.0 ppm for several days, but felt extremely dense fish concentration caused the low oxygen level and thus was the ultimate cause of the kill. We found no oxygen in a single early afternoon measurement taken from the middle of the water column in a meter-deep "gator hole" in March. However, even during the wet season when the water was flowing, dissolved oxygen levels remained surprisingly low (less than 2 ppm) for a habitat with so large and varied a fish population.

Species Composition

Virtually all studies of South Florida marsh and swamp fish populations have found small forage fish to be the predominant species in terms of both population and biomass. Both our data and those gathered by previous researchers indicate that mosquitofish, flagfish, and least killifish are the most common species and regularly represent more than 75 percent of the fish population (Carter et al. 1973, Kolipinski and Higer 1969, Milleson 1976, Tabb et al. 1976, Kahl 1964, Wegener et al. 1973, Kushlan 1972) and 85 percent of the biomass (Carter et al. 1973, Tabb et al. 1976). Sailfin mollies were encountered frequently in these studies, but they never made up more than 10 percent of the population.

Density

Our wet season fish densities are comparable to Kushlan et al. (1975) estimates for southern Everglades marshes and a Big Cypress gator pond (Kushlan 1972) and Wegener et al. (1973) figures for deeped marshes bordering Lake Tohopekaliga in south-central Florida, but are an order of magnitude less than densities measured by researchers working in other similar systems and using equivalent methods (Wegener et al. 1973, Carter et al. 1973, Milleson, 1976) (Table 4). There is no clear explanation for the wide range of wet season fish densities in South Florida. Year to year variability does not seem to be responsible for the discrepancies, since Kushlan et al. (1975) found relatively little variability in 7 years data. Neither do habitat differences offer a consistent explanation. We found similar densities in distinctly different Corkscrew habitats and these data were quite comparable to those reported from a variety of other environments (Kushlan 1972, Kushlan et al. 1975, Wegener et al. 1973). Wegener et al. (1973) and Milleson (1976) documented considerable differences in fish densities between habitats at 2 sites in the Kissimmee watershed. However, Milleson's density calculations for oxbows and canals are probably an underestimate, since he did not collect small fish. Fish communities were comparable at all sites, so species composition does not account for the site-to-site variability. Nor was there any apparent correlation between sampling methods and measured densities.

The great variety of dry season density estimates make more sense. Timing of sampling relative to the drydown process, fish kills, site topography, and predation probably all contribute to differences in data. Peak dry season concentrations at Corkscrew were similar to those Kushlan et al. (1975) observed in the Everglades but half of what Milleson (1976) recorded in the Kissimmee marshes (Table 4). Other researchers working in shallow ponds and canals have reported dry season densities an order of magnitude higher than ours (Carter et al. 1973, Tabb et al. 1976, Kushlan 1972). Permanently inundated deep-water sites generally have densities equal to or an order of magnitude lower than those found in marshes and swamps (Carter et al. 1973, Milleson 1976).

Biomass

Browder's (1976) estimates for wet season fish biomass in an undisturbed marsh-pond system are virtually identical to ours for a natural cypress strand (Table 4). Other

Table 4. Fish density and biomass in south Florida environments.

	Density (number m ⁻²)			Biomass (g m ⁻²)		
	Peak Wet Season	Peak Dry Season	Concentration Factor	Peak Wet Season	Peak Dry Season	Concentration Factor
Southern Everglades marshes (Kushlan et al., 1975)	4-10	20-50	2-9	---	---	---
Lake Tohopekalgia						
Shallow marsh	53	---	---	10	---	---
Deep marsh	5	---	---	10	---	---
(Wegener et al., 1973)						
Fahkahaatchee Strand						
Shallow canal	30	575	19	4	34	8
Deep canal	---	2-39	---	---	1-34	---
Lake	---	.6	---	---	3	---
(Carter et al., 1973)						
Kissimmee River						
Marsh	20-50	70-110	2-6	---	---	---
Barrow canal	1.1	1.2	1	31	54	2
Oxbow	.1	---	---	7	---	---
(Milleson, 1976)						
Corkscrew Marsh						
Pond edge	---	---	---	1-4	---	---
Pond	---	---	---	.3	13.6	45
(Browder, 1976)				.1	7.3	73
Pond						
(Kushlan, 1972)	12	859	71	---	---	---
Farm Ditch	---	890	---	---	110	---
(Tabb et al., 1976)	---	---	---	7-35	---	---
Lake Trafford (Horrel, unpubl. rep.)						
Corkscrew Swamp						
Wet prairie	8	31	4	.4	2.1	5
"Pond" cypress	3	29	10	.3	2.9	10
"Bald" cypress	6	17	3	.3	2.1	7
Residual pools	---	2-140	---	---	2-5	---
(This study)						

researchers working with canals (Carter et al. 1973, Milleson 1976) or lakes (Wegener et al 1973, Horrel, unpublished report, Milleson 1976) found wet season biomass to be 1-2 orders of magnitude higher. Our dry season biomass values are similar to several of Carter et al. (1973) Fahkahaatchee figures, but are generally about an order of magnitude less than data derived from previous studies of lakes and canals (Carter et al. 1973, Browder 1976, Milleson 1976, Tabb et al. 1976).

These data suggest that proximity to deep water is a factor contributing to high fish biomass and low density. This is not surprising since larger species (centrarchids, bullheads, and gar), although they rarely dominate numerically, generally make up the bulk of the fish biomass in permanent water situations (Milleson 1976, Carter et al. 1973). Wegener et al. (1973) found an order of magnitude more forage fish in shallow marshes without predatory fish than in deeper waters inhabited by large centrarchids. During a drydown following several years of continuously high water, Kushlan (1976) saw no fish concentrations. He felt this was due to development of a substantial population of piscivorous fish which thinned populations of the small forage species normally involved in high drydown concentrations. Fish were 17 times more dense in our bare residual pool than they were in our nearby wet season samples. Yet, in the cluttered pool with abundant predators, forage fish were not concentrated. Apparently, the extensive cover available in the cluttered pool enabled the larger fish to escape non-aquatic predators, and the larger fish simply ate the smaller fish. Hansen (pers. comm.) documented significant wading bird predation on larger (over 5 cm) fish in drawn down ponds at Corkscrew Swamp Sanctuary. He observed relatively little impact on the smaller forage species. Ogden et al. (1976) found that wood storks (*Mycteria americana*) fed more on the larger species and the larger individuals of a given species. He noted that where other foods are available wood storks do not feed heavily on mosquitofish, least killifish or (unless they are very concentrated) flagfish.

Concentration Factors

Maximum wet to dry season concentration factors in Corkscrew Swamp were similar to those calculated for Carter et al. (1973) Fakkahatchee site (biomass and density), Kushlan et al. (1975) Everglades marshes (density), and Milleson's (1976) Kissimmee marshes (biomasses and density), but were an order of magnitude lower than figures for Browder's (1976) isolated pond in Corkscrew Marsh (biomass) or Kushlan's (1972) Big Cypress gator hole (density) (Table 4). Both of these high concentration sites were open water areas in topographic depressions which held water significantly longer than the surrounding habitats. Tabb et al. (1976) found equally large dry season densities in farm ditches in the Big Cypress region. This suggests that such shallow man-made environments may be functioning like natural ponds or "gator holes" in fish concentration process.

Since human activities in South Florida are both eliminating the natural semi-permanent ponds through drainage and creating new ones through construction of ditches and excavations, the net gain or loss of these habitats is uncertain. Of greater significance is the proliferation of man-made deepwater habitats (canals and barrow pits) because these introduce a radically new environment to an ecosystem that has evolved in the context of a severe annual drought. Under pre-development conditions, South Florida probably had few permanent bodies of fresh water. Alligators (*Alligator mississippiensis*) did maintain numerous gator holes prior to the species' near extinction in the mid-1900s. But it is unlikely that water in these holes was ever as deep as that in present-day excavations. These numerous new deepwater habitats may be altering the composition of South Florida fish communities in favor of larger piscivorous species which reduce forage fish populations and thus affect non-aquatic predator populations.

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