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POPULATION FLUCTUATIONS OF EVERGLADES FISHES.—Fluctuating marsh ecosystems are found throughout the tropics and subtropics, but their fish populations are little understood (Beadle, 1974; Lowe-McConnell, 1975). In such marshes seasonal variation in rainfall and discharge cause considerable variation in the depth and extent of water cover, and many of these marshes become dry each year. The subtropical Everglades of southern Florida have marked wet and dry seasons, and thus, physical and biological constraints on fish populations that are similar to more tropical systems. The seasonal water level cycle appears to be the dominating influence on the fish community of the Everglades (Kushlan, 1976a). During the usual dry season, South Florida marsh fishes become densely concentrated in ponds (Kushlan, 1974a, 1976b), but little is known about population fluctuations of the fishes during the rest of the year outside of ponds. A question basic to understanding seasonal tropical marshes is how water level fluctuations affect individual fish species. In this paper I describe the effect of water level changes on population levels of fishes in the marshes of the Everglades on both a seasonal and long-term basis.

Study area.—The study was conducted in the southern Everglades, a shallow marsh 0.5 to 1 m deep in the wet season. During the typical dry season the marsh dries and water becomes confined to ponds. Sawgrass marsh, composed primarily of *Cladium jamaicense*, is the most characteristic plant community (Loveless, 1959). Interspersed are slightly deeper mixed species marshes composed of *Eleocharis cellulosa, Panicum hemitomon, Rhynchospora tracyi* and *Pontedaria latifolia.*

Methods.—The study was conducted from June 1966 through May 1972. Ten permanently positioned pull-up traps were located in sawgrass and mixed-species marsh communities. The traps were sheets of 3 mm mesh nylon netting, about 1.5 m × 3 m, supported by galvanized pipe. The trap and trapping procedures are described in detail elsewhere (Higer and Kolipinski, 1967; Kushlan, 1974b). The netting and pipe were pulled quickly to the surface, entrapping the fish in the water column above. The traps produced comparable results per unit effort that reflected changes in the fish populations they trapped. Sampling was conducted on two successive nights, generally once each month throughout the study. Fish were removed from the traps and placed in 10% formalin. They were later identified, counted and all fish of a given species were weighed together. The average number of fish per trap per month and average weight of individual fish per month were calculated. Water levels were measured continuously 4 km from the trap site.

Results.—The typical yearly pattern of water level fluctuation begins with a rapid increase in water depth at the beginning of the rainy season in June. When water levels rise, higher areas of marsh become inundated progressively. Water levels peak typically in fall and begin decreasing in winter (November) as the dry season begins. Water levels fall at an increasing rate through the spring (March–May) as continued low rainfall and high evapotranspiration cause additional loss of surface water. During May, marshes usually dry and remaining water is usually confined to ponds. In this paper a hydrologic year runs from June, the beginning of the rainy season, through May.

Typical seasonal cycles occurred during 4 of 6 hydrologic years during the study (66–67, 67–68, 70–71, 71–72). Two consecutive years of the study (68–69, 69–70) had high water conditions during the usual dry season. In those years high rainfall and discharge maintained water levels. Although water fell moderately in spring of each year, it did not reach ground level in the marshes at the study site. As a result the typical yearly drying did not occur those years. The water cycle returned to normal in 1970–71.

Twenty-two of the 96 fish species native to south Florida (Kushlan and Lodge, 1974) are found in Everglades marshes. Nineteen of these were sampled by the traps during the study (Table 1) including two, *Lepomis punctatus* and *L. marginatus*, that were often represented by small individuals and were combined for

TABLE 1. FISHES CAUGHT IN THE SOUTHERN EVERGLADES 1966–72, EXPRESSED AS THE PERCENTAGE OF MONTHS EACH SPECIES WAS CAUGHT DURING THE HYDROLOGIC YEAR.

Species (abbreviation)	Year					
	66–67	67–68	68–69	69–70	70–71	71–72
Gambusia affinis (G. a.)	100	100	100	100	100	100
Poecilia latipinna (P. l.)	100	100	33	100	40	100
Cyprinodon variegatus (C. v.)	100	100	88	14	20	100
Fundulus confluentus (F. cf.)	83	92	75	86	40	80
Heterandria formosa (H. f.)	67	85	12	57	60	80
Lucania goodei (L. g.)	50	69	37	100	100	20
Lepomis spp.[1] (L.)	100	77	100	86	100	60
Jordanella floridae (J. f.)	100	100	100	71	0	80
Labidesthes sicculus (L. s.)	83	46	87	86	100	60
Fundulus chrysotus (F. ch.)	17	23	0	0	0	60
Adinia xenica (A. x.)	42	31	13	0	0	0
Fundulus seminolis (F. s.)	8	8	12	29	60	0
Notropis petersoni (N. p.)	8	0	25	0	60	100
Notropis maculatus (N. m.)	0	0	25	14	0	0
Notemigonus crysoleucas (N. c.)	0	0	13	0	40	0
Ictalurus natalis (I. n.)	0	0	0	28	40	0
Micropterus salmoides (M. s.)	0	0	0	43	60	0
Erymizon sucetta (E. s.)	0	0	0	29	20	20

[1] Includes *Lepomis punctatus* and *L. marginatus*.

analysis. Species not trapped in the study but occurring in the marshes included *Elassoma evergladei* and, less frequently, *Lepisosteus platyrhincus* and *Amia calva*, the latter two being primarily deep water species.

Gambusia affinis was found every month sampled (Table 1). *Poecilia latipinna, Cyprinodon variegatus, Fundulus confluentus, Heterandria formosa, Lucania goodei, Lepomis* spp. and *Labidesthes sicculus* were also found each year. These, together with *Jordanella floridae* and *Fundulus chrysotus,* can be considered to be the fundamental elements of the Everglades marsh fish fauna (Table 1).

As a result of varying abundances over the study period, not all species were caught each year (Fig. 1). The number of species caught was highest in the middle of the study and decreased thereafter from 15 to 12. During this period, *Jordanella floridae* and *Fundulus chrysotus* were lost and *Notemigonus crysoleucas, Micropterus salmoides, Ictalurus natalis* and *Erymizon sucetta* appeared in the samples (Table 1). During the middle part of the study the average number of species caught each month declined (Fig. 1), despite the increase in total number of species caught during the year. Thus some species tended to be sampled only intermittently.

The usual annual pattern of population fluctuation of the common Everglades fishes can be illustrated by the fluctuations observed in a single hydrologic year having typical water conditions, such as 1966–67. The generalized pattern is exhibited by combining data for all species (Fig. 2). Populations were relatively small at the beginning of the wet season (June), because of dry season mortality, and increased to a peak at the beginning of the drying period in December–January. A second peak occurred during the dry season in April as fish were becoming concentrated in relatively deep areas of marsh such as the trap sites. Fluctuations of *G. affinis, P. latipinna* and *F. confluentus* were similar to this generalized pattern. *C. variegatus* population was highest in winter and remained stable in the dry season. *H. formosa* showed a second peak in April but declined in May. The density of *Lepomis* spp. was highest in summer. *J. floridae* had fall, winter and dry season peaks, the last being the strongest. Yearly fluctuations of other species are more difficult to interpret because of small numbers captured per month.

Considerable population fluctuations occurred over the term of the study (Fig. 3). In general, populations were high during the early and late parts of the study but declined during 1969 to 1971. During this same period the av-

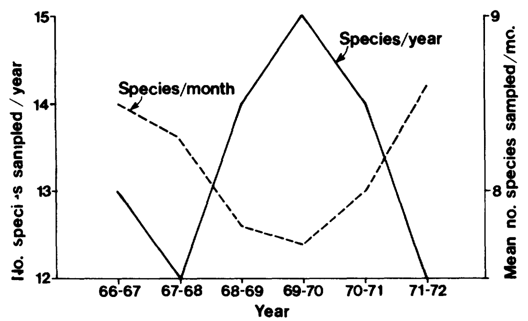

Fig. 1. Changes in the numbers of species trapped per year and the average number of species trapped per month each year.

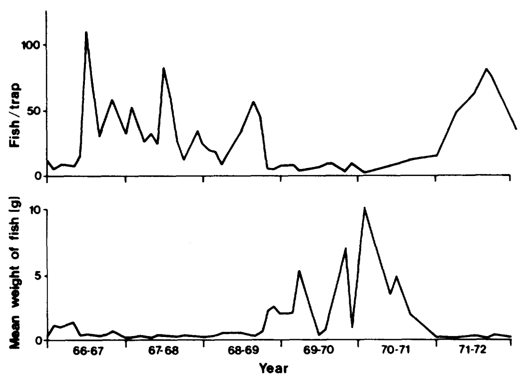

Fig. 3. Fluctuation in the number of fish per trap and the mean weight of individual fish caught in the Everglades, 1966–67 to 1971–72. Hydrologic years shown begin in June and end the following May.

erage weight of fish caught increased (Fig. 3). These population changes can be correlated with hydrologic conditions: populations declined and sizes increased during and immediately after the period of extended high water levels.

The change in water conditions affected various species differently (Fig. 4). Populations of *G. affinis, P. latipinna, C. variegatus, F. confluentus, H. formosa, J. floridae, F. chrysotus* and *A. xenica* decreased during the extended wet period ending in 1969–70. Populations remained depressed during 1970–71 and returned to normal levels after the dry year of 1970–71. Populations of *L. goodei, Lepomis, L. sicculus, F. seminolis, N. maculatus, N. crysoleucas, I. natalis, M. salmoides* and *E. sucetta* increased during the period without dry seasons. *N. petersoni* increased its population level in the year following the end of the wet period.

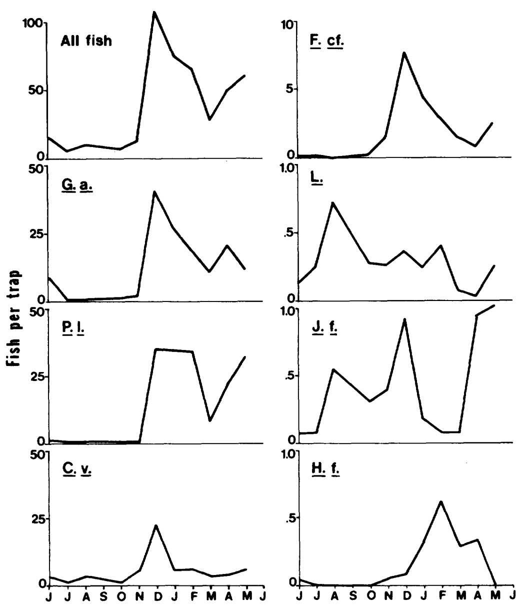

Fig. 2. Monthly fluctuations in the number fish per trap for all fish combined and for 7 common species of fishes in the Everglades in 1966–67. Abbreviations refer to species listed in Table 1.

Discussion.—Water fluctuation is a principal factor affecting fish populations in Everglades marshes, both seasonally and annually. Seasonally, populations in the marsh were high after the dry season in winter and when water levels declined in the spring (Fig. 2). The highest densities occur in the marsh when water depths decline to about 0.3 m (Kushlan, Ogden and Higer, 1975). Even higher densities are found in ponds and pools (Kushlan, 1976b). This pattern is similar to other tropical and subtropical marshes (Zaret and Rand, 1971; Matthes, 1964; Mago, 1970; Lowe-McConnel, 1964, 1975). When water levels increase and the marshes reflood, fishes move out of dry season refugia, often to spawn (Lowe-McConnel, 1964; Mago, 1970). A similar pattern of reproductive strategies probably occurs in the Everglades. *G. affinis,* for example, is ovoviviparous and able to spawn quickly when water returns, thereby increasing its population rapidly in the early wet season. Species such as *F. confluentus* have behavioral and physiological adaptations for spawning in the dry season and eggs that hatch

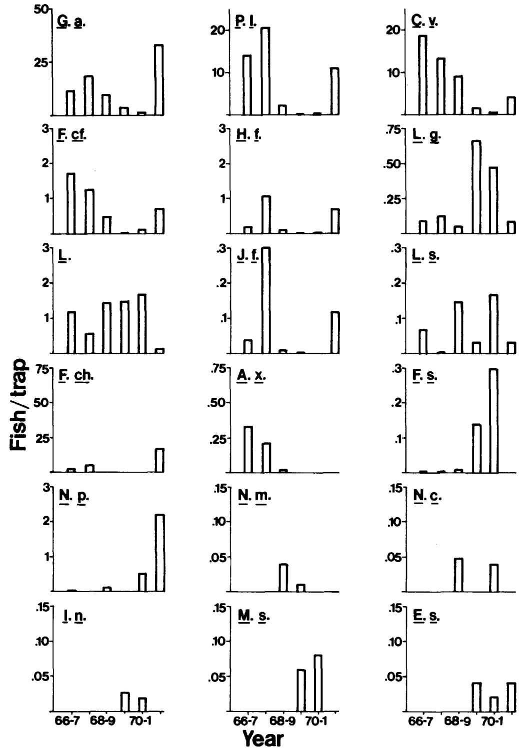

Fig. 4. Mean number of fish caught per trap each year. Abbreviations refer to species listed in Table 1.

on reflooding (Harrington, 1959; Kushlan, 1973). However adaptations such as these are not as common in the Everglades as in the tropics because the basically temperate ichthyofauna of south Florida has occurred in a subtropical marsh system for a relatively short time.

Annual differences in fish populations also show the effects of hydrologic conditions (Fig. 3). The decline in density and increase in average size of fish in 1969–70 and 70–71 corresponded to a period when the annual dry season did not occur. The average weight of animals increased about 20 times during that period, from approximately 0.5 g/animal to 10 g/animal (Fig. 3). Most of this was from increases in the number and size of the larger species of fish trapped, particularly *I. natalis*, *Lepomis* spp. and *M. salmoides* (Table 1). Both *I. natalis* and *M. salmoides* were sampled only during 1969 and 1970, and the average size of *Lepomis* spp. increased during this period from about 4 g/animal in 1966 and 1967 to a peak of about 31 g/animal in 1970. Such increases in the number and size of larger species represent increases in the predator component of the aquatic animal community. Coincident decreases in the total number of fish, especially small fish, may be due, at least in part, to increases in the number and size of predatory species.

The Everglades appears to be a dynamic system composed of species differentially adapted to fluctuating water conditions. The various fishes responded differently to extended high water, with some species increasing and others decreasing in abundance (Fig. 4). Other components of the Everglades marsh system are also affected differentially by extended high water. Apple snails (*Pomacea paludosa*), for example, increase in abundance during periods of extended high water (Kushlan, 1975), while crayfish (*Procambarus alleni*) and prawns (*Palaemonetes paludosus*) decrease (Kushlan and Kushlan, 1979, 1980).

Thus the population levels of the aquatic animals of the Everglades are determined by the recent history of physical conditions and biologic interactions. Biological interactions include not only competitive and predatory relationships among fishes and invertebrates but also relations with other carnivores (Kushlan, 1974c, 1976b). These biologic interactions both within and outside of the fish community determine its structure relative to recent water conditions. Such complex relationships are probably typical of fluctuating-water marsh ecosystems in other areas and emphasize the need for detailed study of the adaptive strategies of species occurring in tropical and subtropical marshes.

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MIXED SPECIES BROODS IN LAKE MALAWI CICHLIDS: AN ALTERNATIVE TO THE CUCKOO THEORY.—Ribbink (1977) described the guarding of mixed species broods by certain Lake Malawi cichlids. Three different species, *Haplochromis polystigma* Regan, *H. macrostoma* Regan and *Serranochromis robustus* Regan, were observed playing the role of foster parent, and in each case the foreign fry belonged to the small semipelagic species *H. chrysonotus* Boulenger. On the basis of these observations it was implied that *H. chrysonotus* behaved as an aquatic 'cuckoo,' introducing its young into the broods of other species rather than guarding them itself.

Further consideration of the facts in conjunction with more recent field observations suggest that 'cuckoo' behavior is not the most likely explanation for the mixed brood phenomenon among Lake Malawi cichlids.

Ribbink noted that female *H. chrysonotus* with eggs or fry in their mouths were common in