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ENVIRONMENTAL STABILITY AND FISH COMMUNITY DIVERSITY[1]

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Abstract. Seasonal fluctuation of water level is the most critical environmental factor affecting the fish community of the Everglades marshes. During a 27-mo period of water-level stability, fish density decreased but biomass, average size of fish, species richness, and species diversity increased. These changes were accompanied by a functional shift from the dominance of small sized omnivorous species to the dominance of larger sized carnivorous fish. The changes resulted from immigration of large carnivorous species poorly adapted for survival in fluctuating marshes. Increased predation assumed the determining role in restructuring the community under environmentally stable conditions. The fish community of Everglades marshes oscillates between opposing tendencies of species domination, which depend on the degree of water level stability.

Key words: Diversity; environmental stability; Everglades; fish communities; Florida; marsh ecology; predation; wetlands.

INTRODUCTION

Numerous studies have investigated geographic differences between structural and functional components of various animal communities, generally using diversity indices to measure these differences. Although environmental stability often is discussed as a parameter affecting animal communities, the effect of environmental stability on an animal community has been studied very little under natural conditions. In this paper I show how relatively short-term variation of environmental stability affected the freshwater fish community of Everglades marshes.

Although the extensive freshwater marshes of the southern Florida Everglades have a comparatively equitable subtropical temperature regime, variation in rainfall produces a drastically seasonal hydroperiod. Generally, a wet season from June through October causes high water levels that recede in the dry season to the point where, by May, most surface water disappears and remnant populations of aquatic organisms are confined to localized pools. To persist, aquatic animals must be adapted to survive the exigencies of this periodic loss of surface water.

METHODS

The study was conducted in the marshes of Everglades National Park, Florida. Sampling was within an area of 5 km^2 approximately 14 km south of the northern park boundary. The marsh habitat, typical of the southern Everglades, was composed primarily of sawgrass (*Cladium jamaicensis*) and other herbaceous species such as *Eleocharis cellulosa*, *Rynchospora tracyi*, and *Panicum hemitomon*. Other important habitats near the study area included relatively deep water ponds and a canal.

The fish community was sampled with 10 Higer pull-up traps consisting of a sheet of 3-mm mesh nylon netting 1.5 m $\times$ 3.0 m that catches fish when pulled quickly to the surface (Kushlan 1974*a*). The trapping technique, while neither random nor highly accurate, produced results which quantitatively reflected changes in the fish community with time. A monthly trapping consisted of the catch from 10 traps on two consecutive nights. The average number of fish per trap, average number of grams (wet weight) per trap, and the average grams per individual for each species and for all species were calculated. The effect of seasonal variation was eliminated by averaging each parameter for each biological year, June through May. Species richness is the total number of species sampled during the year. Species diversity was measured by the Shannon-Weaver index, $H' = -\Sigma P_i \ln P_i$, where P_i is the proportion of a species in the sample. Biomass diversity was calculated using wet weight. H' was scaled such that one represents even distribution and zero represents extremely skewed distribution (Fager 1972).

RESULTS

The typical wet season-dry season pattern prevailed during most years of the study (Fig. 1). However, starting in the 1968–69 biological year surface water remained high for 27 consecutive months. Fish collections in the biological years of 1968–69, 1969–70, and 1970–71 reflected this stabilized water level. A return to the typical pattern of water level fluctuation in 1970–71 was reflected in the data from 1971–72. Yearly differences in water conditions can be contrasted in a gross way by the differences in the annual mean water level, which was somewhat

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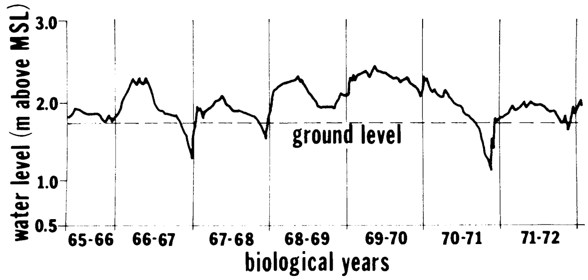

FIG. 1. Water level fluctuation in the southen Everglades 1965–1972. Biological years run from June in one calendar year through May the following calendar year. The 27-mo period of high water levels occurred from 1968–69 into 1970–71.

higher than typical in 1968–69 and substantially higher in 1969–70 (Fig. 2).

High water conditions and concurrent elimination of dry intervals had a substantial impact on fish populations. Average fish density fell during the high water period, but high density returned in 1971–72 after restoration of the fluctuating regime (Fig. 2). Because high annual mean fish density depends in part on fish concentrating during the dry season, low density during the prolonged high water might have been caused only by lack of such dry season concentration. However, low density continued through the 1970–71 dry season (Fig. 2) during which fish concentration did occur when water levels dropped. This demonstrates that the decline in mean density reflected decreased abundance of fish in the community. Size of fish varied inversely with mean fish density (Fig. 2). During the period of extended high water, mean fish size increased from the typical value of < 1 g per fish to > 5 g per fish. Total fish biomass did not change greatly, except in 1970–71, when it increased when the average size of fish was greatest.

The structure of the fish community also changed during prolonged high water. The number of species sampled and species diversity increased. In contrast, the more functional index, biomass diversity, declined (Fig. 3) reflecting the dominance of a few species of relatively large fish. The different pattern of biomass diversity shows that the changes were more complicated than the mere redistribution of relative abundances.

To determine more precisely the functional components of such changes, I partitioned the fish community into three groups based on size and general trophic information (Table 1). Species richness of various trophic groups varied differently during the study period. Large carnivorous species increased during the high water period followed by a decrease in 1971–72 after conditions returned to normal (Fig. 4). The number of species of small omnivorous and herbivorous fish that form the basis

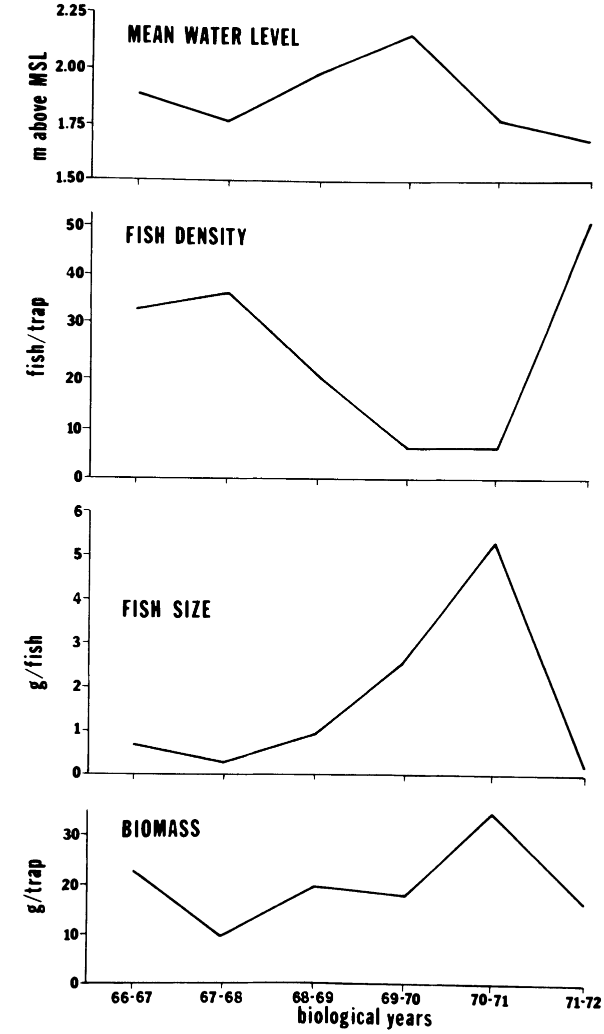

FIG. 2. Changes in average water level, and in the biomass, density, and size of fish in southern Everglades marshes.

of the Everglades food web remained constant except for 1970–71 when the least killifish (*Heterandria formosa*), one of the most abundant small fish in the Everglades during normal conditions, was not found in samples. The number of species of small carnivores, which includes relatively rare species, fluctuated without apparent pattern. Thus, the major change in species richness was a threefold increase in the number of large carnivorous species sampled. This was also reflected in the density changes that occurred in each group (Fig. 4).

Changes in the contribution of the three trophic groups to the diversity indices further substantiated differences in the response of the three groups (Fig. 4). Species and biomass diversity of small omnivorous fish decreased during the high water period; whereas, both measures increased for large carnivorous fish. The species diversity of small carnivorous

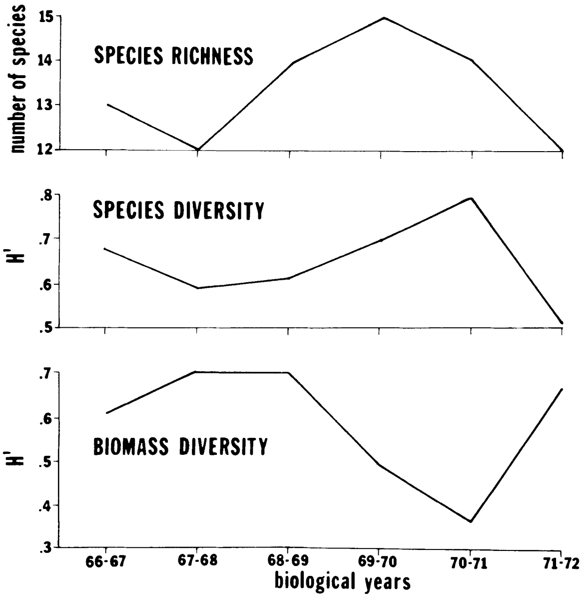

FIG. 3. Changes in species richness, species diversity, and biomass diversity of the Everglades fish community.

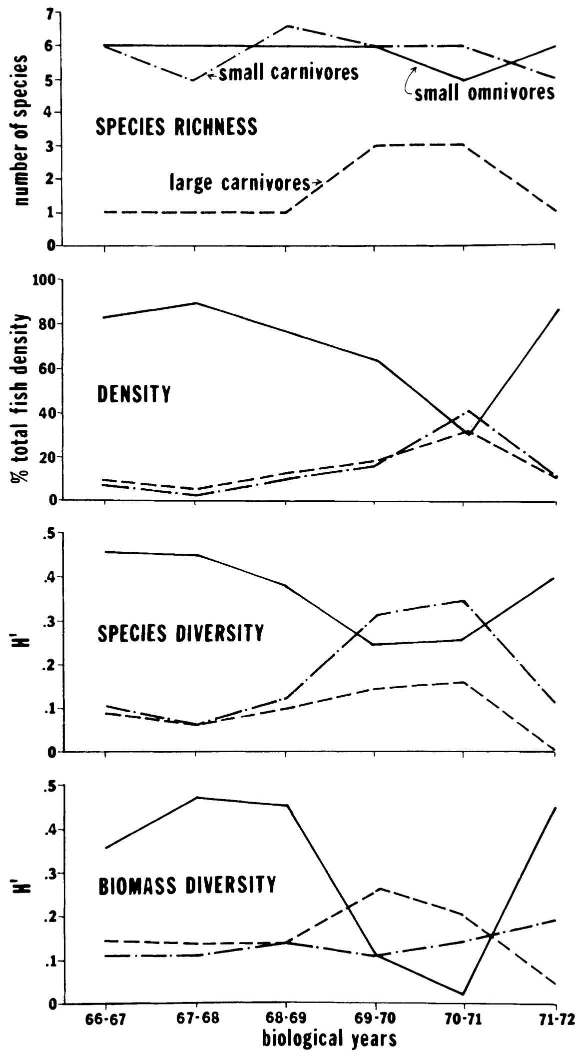

FIG. 4. Changes in species richness, density, species diversity, and biomass diversity of three trophic groups of the Everglades fish community.

fish increased although biomass diversity remained fairly constant. Thus, the overall increase in species diversity occurring during stabilized water condtions (Fig. 3) was accomplished by increased diversity of carnivorous species despite a drop in the diversity of omnivorous fish. This pattern, along with the similar but more energetically meaningful pattern of change in biomass diversity, demonstrates a functional shift within the fish community to the dominance of large carnivorous species at the expense of small omnivores during the period of stabilized water conditions. Return of these indices to their usual ranges in 1971–72, after typically fluctuating conditions were restored, further demonstrated that the changes were correlated with the period of water level stability.

TABLE 1. Functional groupings of component species of the Everglades fish community

Functional group	Species
Small omnivores and herbivores	*Gambusia affinis, Poecilia latipinna, Heterandria formosa, Cyprinodon variegatus, Adinia xenica, Jordanella floridae, Erymizon succetta*
Small, primarily carnivores	*Fundulus confluentus, F. chrysotus, F. seminolis, Lucania goodei, Notemigonus crysoleucas, Labidesthes sicculus, Notropis petersoni, N. maculatus*
Large carnivores	*Ictalurus natalis, Lepomis* sp., *Micropterus salmoides*

DISCUSSION

Changes within the fish community occuring with stabilization of the natural fluctuation of water level were substantial. In general, the diversity of small omnivorous species, which dominate the community in biomass and in numbers under normal conditions, decreased; whereas, the number of species, abundance, size, and diversity of large carnivorous fish increased. The overall result was a shift of the fish community to a predator dominated system, suggesting that decreased abundance and increased size of forage fishes were caused by increased predation pressure. The role of predators in increasing community species richness (Paine 1971) or decreasing prey species richness (Addicott 1974, Dodson 1974) has been documented in several animal communities.

In the present case, the impact of the increased influence of predatory species caused a decline in the numbers and diversity of small omnivorous species.

The changes also demonstrated a shift in the factors controlling the fish community under different regimes of environmental stability. Under fluctuating conditions, the predictable cycle of water loss limits the number and kinds of fish to those capable of repopulating the marshes after a dry period. Under stabilized water conditions, community control is exercised by the predation of larger species. The increased species richness during the stable period was the result of immigration of species into the marshes from ponds and canals, which under present conditions are the most stable habitats within the ecosystem. The larger carnivores, especially centrarchids, are characteristic of such stable habitats and are poorly adapted for survival in fluctuating environments. These species show a size-dependent ability to survive critical low-water conditions because larger individuals are more susceptible to stresses associated with dry periods (Kushlan 1974*b*). In that much of the change in the Everglades fish community occurred as a result of the increased dominance of carnivorous species, a group under normal conditions in the marshes composed of small or relatively rare fish, the overall effect was the addition of another trophic compartment to the community and its subsequent reorganization. The impact of such changes could be reflected throughout the ecosystem and may particularly affect those species groups that prey upon members of the Everglades fish community, especially wading birds that depend on the fish production of the marshes for successful nesting (Kushlan 1976).

Although changes in the relative abundance of all species, i.e., species diversity, demonstrated some aspects of the changes that occurred in the community, species diversity alone was not a good measure of the total change in the community. A more functional analysis is possible by categorizing species comprising a community along a functional basis (Root 1973) and measuring diversity in additional ways. Use of biomass (Wilhm 1968) and productivity (Dickman 1968) are obvious steps, and determining the species-specific influence on community productivity (Hurlbert 1971) is undoubtedly a worthwhile goal. However, given the present state of knowledge of the Everglades fish community, adding biomass diversity and categorizing species by general size and trophic parameters were the possible additional steps in the analysis of functional changes within the community. The changes were more clearly distinguished by considering both species and biomass diversity.

It might be noted that the short-term community changes found in this study are in many ways analogous to those occurring elsewhere on an evolutionary time scale. The climatic stability theory (Pianka 1966) postulates that the evolution of high faunal diversity occurs where environmental variability is low and is, of course, most often cited in reference to the latitudinal increases in species diversity from polar to tropical regions. In the present study, increased stability permitted an increase in species richness and species diversity, a change from environmental to biotic regulation of community structure, and the addition of another trophic compartment (cf. Orians 1969, Fleming 1973).

With increased stability, the marshes of the study area tended to change toward a shallow pond environment. These changes occurred as a result of a combination of successive wet years and localized increase of surface water flow due to artificial water manipulation. Increased flow during the typical dry season created a water level stability which, in these particular years, would probably not have occurred to such an extent without the discharge. However, the species of predatory fish that invaded the marshes and became dominant in the fish community during the period of water level stability inhabited the southern Everglades prior to the existance of either canals or water manipulation, being particularly associated with ponds within the marsh. Periods of water level stability undoubtedly occurred under more natural, premanipulation conditions, probably in association with hurricanes. Thus, the fish community of the southern Everglades naturally oscillates between tendencies toward predator domination and forage fish domination, depending on the degree of water level stability. It is apparent that the Everglades ecosystem evolved in response to the yearly cycle of water level fluctuation and the continued natural functioning of the system depends, within the limits of natural variability, upon the preservation of that cycle.

Acknowledgments

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