

**Effects of a Natural Fish Kill on the Water Quality,
Plankton, and Fish Population of a Pond in the
Big Cypress Swamp, Florida**

JAMES A. KUSHLAN

Made in United States of America
Reprinted from TRANSACTIONS OF THE AMERICAN FISHERIES SOCIETY
Vol. 103, No. 2, April 1974
pp. 235-243

Effects of a Natural Fish Kill on the Water Quality, Plankton, and Fish Population of a Pond in the Big Cypress Swamp, Florida¹

JAMES A. KUSHLAN
Department of Biology
University of Miami
Coral Gables, Florida 33124

ABSTRACT

A naturally occurring fish kill took place during the southern Florida dry season when receding water levels forced aquatic organisms out of shallow swamps and into a small pond. Physico-chemical parameters of water quality varied greatly from their usual range as did the abundance of phytoplankton which reached a peak of 2.5×10^9 cells per liter. The fish kill had no effect on the long-term limnological characteristics of the pond, as water quality returned to normal range within 2 months and phytoplankton disappeared within 1 month after the fish kill. The species of fish in the pond showed a range of susceptibility to low oxygen concentration and other aspects of the fish kill. They were classified into three categories based upon their survival: *Notemigonus crysoleucas*, *Lucania goodei*, and all centrarchids were eliminated rapidly; *Fundulus chrysotus*, *Poecilia latipinna*, *Heterandria formosa*, and *Ictalurus natalis* were either eliminated late in the fish kill or survived in numbers lower than measurable by methods used in this study; *Lepisosteus platyrhincus*, *Gambusia affinis*, *Jordanella floridae* and the prawn *Palaemonetes paludosus* survived the fish kill in moderate densities of 0.6 to 6 individuals/m². In three species of *Lepomis*, larger fish died before smaller ones. Six of 22 species of fish and only 0.6% of the previous fish population survived the fish kill.

The mass mortality of fish and other aquatic organisms is a recurring phenomenon in southern Florida especially in the canals of the Everglades and Big Cypress Swamp. The causes of such fish kills have been studied in detail by B. P. Hunt (unpublished data). Fish kills also occur in natural, unaltered localities in southern Florida but have received little attention. The purpose of this paper is to describe the effects of a naturally occurring fish kill on the physical and chemical parameters of water quality, on phytoplankton, and on the populations of fish in a pond in the Big Cypress Swamp of southern Florida. The effect of plant zonation in the pond on fish mortality is also considered.

Southern Florida has a rainy season from May through October followed by a 6-month dry period. During the dry season, water levels in the Everglades and Big Cypress Swamp fall and in doing so, concentrate fish from the broad shallow marshlands into deeper areas such as canals and ponds. It is during this period that most natural fish kills take

place. The fish kill described in this paper occurred during the final week of the dry season of 1970. It began at 0800 hr on 14 May 1970 when dying fish were first noted. At this time the pond was shrinking in size with no surface water connection to adjacent swamps. It ended on 24 May 1970 when the onset of the spring rainy season elevated the water level in the pond 0.27 m within a 24-hr period.

Some data are available as to the cause of the fish kill. Prior to the kill, concurrent with decreasing water level and increasing fish density, the pond experienced a gradual depletion of dissolved oxygen, from 5.24 mg/liter on 5 May to 3.70 mg/liter on 11 May. Undoubtedly the daily oxygen minima declined in a similar manner. At 1000 hr on 14 May, two hours after fish first began dying, oxygen was 1.30 mg/liter and carbon dioxide was 11.2 mg/liter. Neither of these levels is extreme for the pond, as similar values have been recorded previously over short periods in the early morning, but oxygen concentration usually increases rapidly during the morning. Although both physiological (Moore 1942) and behavioral (Lagler, Bardach, and Miller 1962: 242) adaptations of fish enable them

¹ Based upon portions of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science, University of Miami, Coral Gables, Florida.

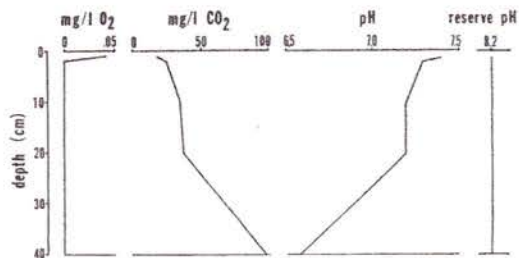


FIGURE 1.—Profile of O₂, CO₂, and pH in central area of pond at 1100 hr on 17 May 1970.

to survive temporarily lowered oxygen levels, the progressive decline in oxygen and increasing density of fish over a period of days may have surpassed the ability of more susceptible species to tolerate the stressful conditions. This progressive depletion of oxygen was probably in part responsible for initiating the fish kill, although other factors may also have been involved concurrently. Prior to the initiation of mortality, levels of most other parameters of water quality were similar to those measured at the same water level in other years as shown by comparison with 22 April 1969, a year when no fish kill occurred. After the initial mortality, significant changes occurred in the pre-existing levels of physico-chemical parameters, in plankton, and in fish populations in the pond.

STUDY SITE

The pond is located in the southeastern Big Cypress Swamp of southern Florida (25°44' 50" N. lat., 80°56'50" W. long.). It has a high-water surface area of 1520 m² and is composed of a peripheral zone of emergent grass, *Panicum* spp. (1150 m²), and a central area which during high water supports submerged *Najas flexilis*. The pond is surrounded by willows (*Salix caroliniana*) and bald cypress (*Taxodium distichum*). During average high water, mean depth is 0.82 m and maximum depth is 1.50 m. For most of the year the water in the pond is continuous with that of the surrounding cypress and willow swamps and fluctuates in response to variation in rainfall, evapotranspiration, and overland flow from the Big Cypress drainage system to the north.

METHODS

The fish kill took place during an extensive study of the ecology of the pond (Kushlan 1972). During the kill those procedures previously employed for measuring changes in fish populations and water quality were continued. Visits to the pond were made on 5, 6, 9, 11, 13, 14, 15, 17, 18, 19, 21, 24, 25, 27, 28 May and 3, 5, and 11 June 1970. The density of fish was measured in number per m² by six quantitative sampling devices. Larger species of fish were caught in two pull-up traps which sampled a surface area of 4 m². Both large and small fish were caught in four drop traps which sampled a surface area of 1 m². The two pull-up traps and two "free-fall drop traps" were situated in the central area of the pond, while two "modified Kahl traps" were located in the peripheral emergent zone. These traps are described in detail elsewhere (Kushlan 1974). Each trap was used once per day between 1300 and 1500 hr. The density of larger fish (centrarchids except *Elassoma* and *Enneacanthus*, ictalurids, *Lepisosteus*, *Notemigonus*) was computed by averaging the density as determined by the catch in all traps for each of the two plant zones, multiplying the density in each zone by the proportion of the pond area occupied by that zone, and summing the result:

$$d = \frac{1}{4}(P_1 + P_2 + FD_1 + FD_2)C + \frac{1}{2}(KD_1 + KD_2)E$$

where d is the average density of fish in the pond; P_1 and P_2 are the numbers of fish per m² in two pull-up traps; FD_1 , FD_2 are the numbers of fish per m² in two free-fall drop traps; KD_1 and KD_2 are the numbers of fish per m² in the modified Kahl drop traps; and C and E are the proportion of the pond occupied by central area and the emergent zone, respectively. The density of smaller fish was determined in the same manner with only the four drop traps. These calculations generate an estimate of the average density for the pond. The standard length of fish that died in a 250-m² quadrant-shaped area which

TABLE 1.—Concentration of dissolved oxygen and temperature in the pond during the fish kill

Item	Plant zone	Sample depth	14 May			15 May		17 May		
			1000	1500	2000	0500	1100	1100	1400	1900
Oxygen (mg/liter)	Emergent	1 cm	—	—	—	0.21	0.35	0.00	0.20	0.00
	Emergent	6 cm	0.76	0.56	0.00	0.00	0.00	0.00	0.00	0.00
	Central area	1 cm	—	3.00	2.20	0.22	0.41	0.05	0.38	0.17
	Central area	6 cm	1.30	2.29	0.00	0.00	0.00	0.00	0.00	0.00
Temperature (C)	Emergent	3 cm	29	29	28	28	29	30	32	29
	Central area	3 cm	29	30	28	28	30	30	32	28

included both plant zones was measured on the first, second and fourth day of the fish kill. This provided additional data on fish not sampled by the traps and on the size distribution of dead fish. Qualitative samples were also taken by dip net and cast net.

Plankton samples were collected in 1-liter plastic bottles, concentrated in a Foerst continuous flow centrifuge, and fixed in 10% formalin. Plankton larger than 20 μ were counted in a Sedgwick-Rafter cell with a Whipple ocular micrometer (Welch 1948). For plankton smaller than 20 μ , a known volume of concentrate was placed on a slide and 10 random fields on each of five slides were counted at 430 \times . From these counts the number of organisms per liter was determined by standard procedures (Welch 1948).

Chemical analyses were performed according to the procedures of the Hach Chemical Company with the Hach Engineering Kit Colorimeter except for the following: dissolved oxygen, the Rideal-Steward modified Winkler method (Welch 1948); carbon dioxide (Welch 1948); chloride, Mohr method (A.P.H.A. 1965); pH and reserve pH, Hellige color comparator; conductivity, YSI model 31 conductivity bridge; hardness (Mackereth 1963); total phosphate, treated by persulfate oxidation (Menzel and Corwin 1965); and total organic matter (Gonyea and Hunt 1970). Dissolved inorganic phosphate samples were filtered through a 0.45- μ millipore filter.

RESULTS

Changes in Water Quality

During the first days of the fish kill oxygen increased in the central area during daylight but decreased at night (Table 1). In the emergent zone, however, oxygen concentration decreased during the day, and by 2000 hr

had been completely depleted in the subsurface water of both zones. Anaerobic conditions prevailed throughout the pond until 27 May, except at the surface where the presence of oxygen probably was due to diffusion from the atmosphere. Oxygen was undoubtedly also being produced by the photosynthesis of algae and submerged plants but any such contribution below the surface was not detected.

Levels of carbon dioxide also changed drastically. On 14 May it increased from 11.2 mg/liter at 1000 hr at 6 cm depth in the central area to 20.8 mg/liter at 2000 hr. It remained between 20 and 40 mg/liter at this depth in both plant zones until 21 May. The concentration from the surface to 1 cm depth was equal to or less than that at 6 cm depth and showed a diurnal fluctuation. For example, on 17 May concentrations at the surface in the central area were:

1100 hr	16.8 mg/liter
1400 hr	10.2 mg/liter
1900 hr	37.6 mg/liter

After 16 May the concentrations found in the water of the emergent zone were greater than those of the central area. In comparison to the above data for the central area, concentrations on 17 May in the emergent zone were 34.6 mg/liter at 1100 hr and 18.2 mg/liter at 1400 hr.

Concentrations of oxygen and carbon dioxide varied with depth during the fish kill (Fig. 1). On 17 May oxygen (0.05 mg/liter) was present only at the surface. The extent of the oxygenated layer was not determined, as the sampling equipment could not sample less than the top 1 cm. Lewis (1970) in laboratory experiments found this layer to be only a few mm deep. Carbon dioxide in-

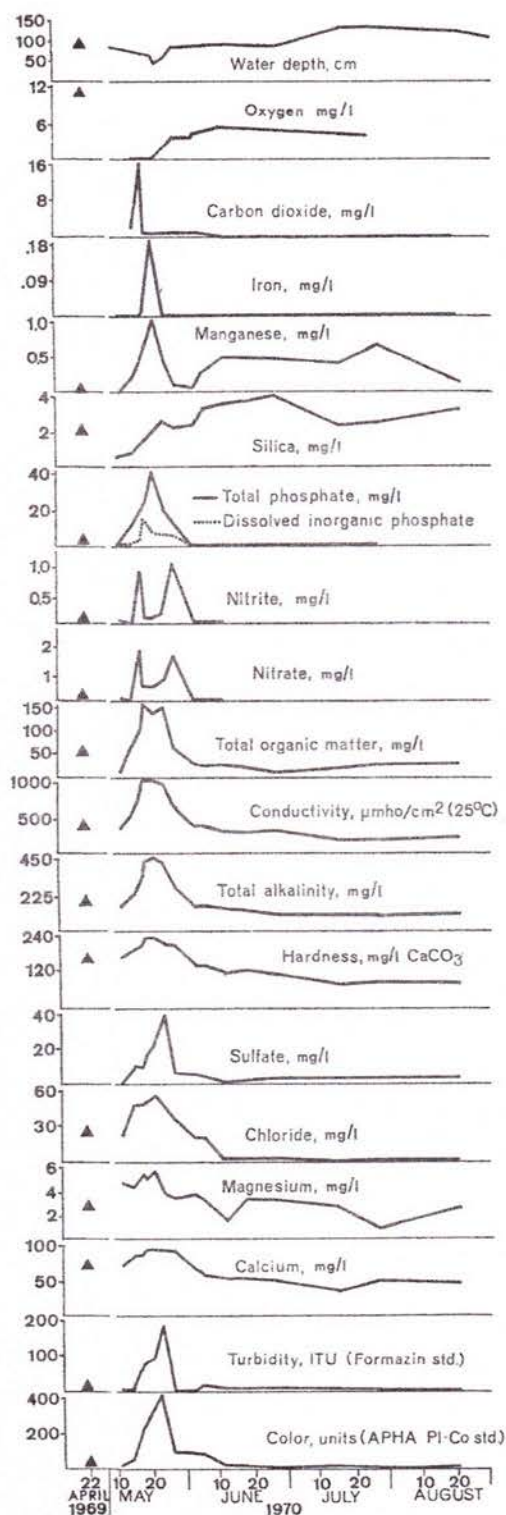


TABLE 2.—Abundance of phytoplankton in pond, May–June 1970

Date	Number of organisms, cells/liter $\times 10^3$				Total
	Chlorophyta		Cyanophyta	Bacillariophyceae	
	$> 20\mu$	$< 20\mu$			
5 May	18.5	0	18.5	0	37
17 May	1,140	14,000	60.6	51.8	14,800
19 May	670	14,600	21.9	135	15,300
21 May	460	114,000	13.0	83.3	115,000
24 May	1,110	2,500,000	6.6	120	2,500,000
27 May	325	8,970	0	15.0	9,310
3 June	1.3	1,000	1.3	10.6	1,010
5 June	0	40	4.0	1.2	45
11 June	0	0	0.4	0.4	0.8
18 June	0	0	0	0	0
27 June	0	0	0	0	0

creased from 16.8 mg/liter at the surface to 98 mg/liter at the bottom. The pH decreased with depth although reserve pH remained constant at 8.2, approximately that found at other times of the year, indicating that the lowered pH was caused in large part by dissolved gases rather than the release of organic or other acids into the water by decomposing animal material.

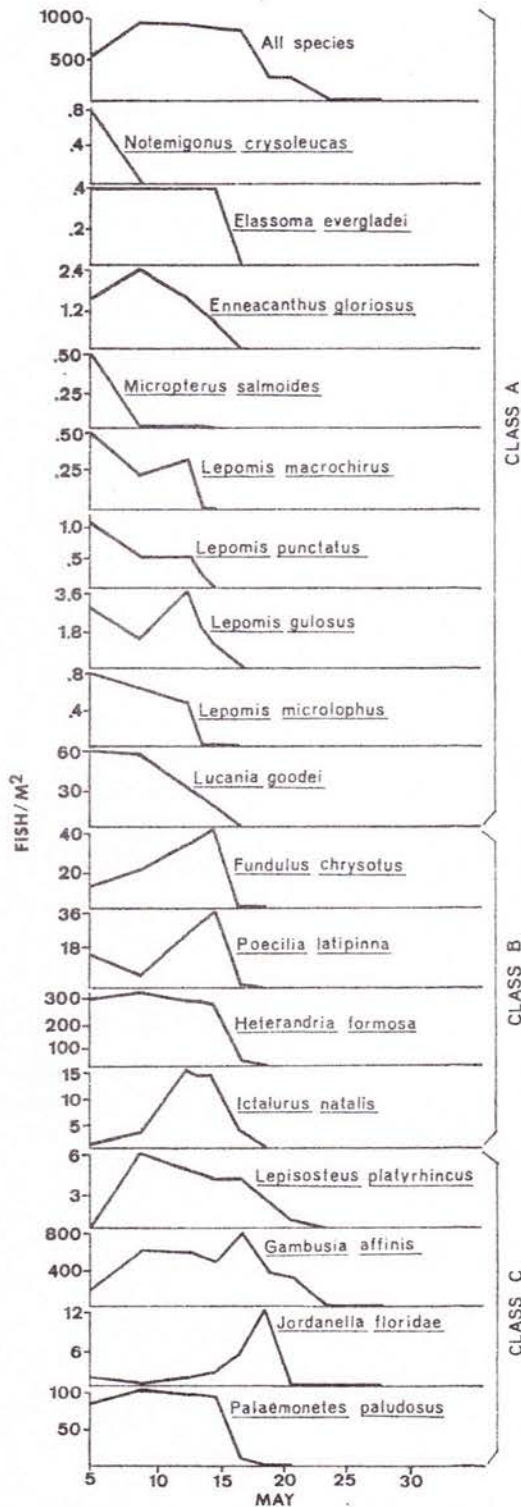
Levels of other physico-chemical parameters of water quality measured also fluctuated markedly during the fish kill (Fig. 2). Despite such severe fluctuations, the effects of the fish kill on water quality were relatively short-lived. By August all parameters measured were within their usual high water range, and with the exception of oxygen and silica, all were below their range during the fish kill.

Changes in Plankton

During the fish kill the concentration of plankton in the pond increased markedly. Zooplankton did not occur in the pond during the fish kill, and phytoplankton was first found on 5 May when both chlorophytes and cyanophytes were present. Samples prior to this date showed none present. By 17 May diatoms were also found. The abundance of plankton fluctuated markedly over the 2-month period of May–June 1970 (Table 2), the highest concentration occurring on 24 May

←

FIGURE 2.—Fluctuation of physico-chemical parameters of water quality in the pond, May through August 1970. Comparative data of some parameters for 22 April 1969 are indicated by triangles.



when 2.5×10^9 cells per liter were sampled. The dominant form was *Chloromonas* sp. (Chloromonadales) followed by *Tetraselmus* sp. (Volvocales). The sharp drop after that date reflected dilution due to rising water levels and also the decay of the bloom. By 18 June plankton was again absent.

Changes in Fish Population

Six of 22 species of fish survived the fish kill. Only *Lepisosteus platyrhincus*, *Gambusia affinis*, and *Jordanella floridae* maintained densities sufficient for quantitative sampling. *Heterandria formosa* and *Poecilia latipinna* survived the fish kill in low numbers, as did the uncommon *Amia calva*. The prawn, *Palaemonetes paludosus*, also survived. Maximum density measured for the entire pond prior to the fish kill was 970 individuals/m² on 9 May 1970 or an estimated total population of 1.4×10^6 fish and prawns in the pond. Over the first two days of the fish kill 10% of the population died, most of which were larger fish. On 24 May 1970 the total density was only 8 individuals/m², representing a total population of 8,500 fish and prawns. Approximately 0.6% of the previous population survived the fish kill.

The 16 most abundant species of fish and the prawn, *Palaemonetes paludosus*, are categorized according to the effect of fish kill on their populations (Fig. 3). Class A species were extremely susceptible and showed no survival. They were either completely eliminated by the second day of the fish kill (15 May) or were present in relatively small numbers at that time and were eliminated by the fourth day of the fish kill (17 May). This group includes all centrarchids found in the pond, some of which, *Lepomis macrochirus*, *Micropterus salmoides*, and *L. punctatus*, suffered severe mortality on the first

←

FIGURE 3.—Fluctuation in the average density of aquatic organisms in the pond during May-June 1970. Species are classified into three categories based upon their survival during the fish kill. Class A species were completely eliminated early in the fish kill. Class B species exhibited poor survival. Class C species exhibited moderate survival.

TABLE 3.—Comparison of the mean standard lengths of fish that died on different days during the fish kill, 14–17 May 1970

Species	14 May			15 May			17 May			Dates compared	P
	Sample size	Mean length	Standard deviation	Sample size	Mean length	Standard deviation	Sample size	Mean length	Standard deviation		
<i>Lepomis gulosus</i>	237	10.96	2.32	34	9.32	2.10	239	8.32	2.40	t	14–15 <.01 15–16 .021 14–17 <.01
<i>Lepomis microlophus</i>	48	10.92	1.85	3	9.17	3.06	0	—	—	t	14–15 .13
<i>Lepomis punctatus</i>	112	8.71	1.79	16	7.75	1.65	0	—	—	t	14–15 .047
<i>Lepomis macrochirus</i>	52	10.87	1.40	13	7.88	2.10	0	—	—	t'	14–15 <.01
<i>Micropterus salmoides</i>	27	17.76	4.40	6	15.16	4.82	0	—	—	t	14–15 .22
<i>Ictalurus natalis</i>	10	9.50	2.75	5	10.10	2.40	131	10.70	2.33	t	14–15 .69 15–17 .54 14–17 .12

day of the fish kill, their density decreasing by 94%, 67%, and 60%, respectively. The density of *Lepomis gulosus*, on the other hand, declined only 45% on the first day, 14 May, and the species was not eliminated until 17 May. These data indicate that *L. gulosus* is the best adapted of the centrarchids to these conditions.

Class B species were highly susceptible and showed poor survival. Each maintained a relatively high density through 15 May but was either eliminated or reduced to very low numbers late in the fish kill. *Fundulus chrysotus*, *Poecilia latipinna*, and *Heterandria formosa* suffered only slight mortality prior to 15 May. The density of the three species declined by 99%, 94%, and 86% respectively, between 15 and 17 May. *P. latipinna* and *H. formosa* survived the fish kill in very low numbers as they were caught on 19, 21, and 24 May after intensive qualitative sampling. Similarly, the density of *Ictalurus natalis* declined only 3% and 4% on the first and second day of the fish kill, but by 17 May density had decreased by 75% of the initial figure.

Class C species were moderately susceptible and measurable numbers survived the fish kill. The density of *Lepisosteus platyrhincus* declined 79% through the entire fish kill to 0.8 fish/m². *Gambusia affinis* and *Jordanella floridae* both maintained a moderate population level. By the end of the fish kill, the density of *Gambusia affinis* was 5.8/m², 1% of its peak, whereas the density of *J. floridae* was 0.65/m², 6% of its peak. Neither suffered severe mortality until 5 days after the beginning of the fish kill. The freshwater prawn, *Palaemonetes paludosus*, suffered only slight mortality during the first 2 days of the fish

kill, but its density declined 86% from 15 to 17 May, to 0.65/m².

Other species of fish collected in small numbers during the fish kill included *Cyprinodon variegatus*, *Fundulus confluentus*, and *Erimyzon succeta*, none of which apparently survived the fish kill. *Ictalurus nebulosus* was collected on 15 May and is probably in the same survival class as *I. natalis*. *Amia calva* was found as late as 24 May and therefore survived the fish kill.

Size-Related Mortality

For all five species of centrarchids analyzed, the mean standard length of individuals dying on the first day was larger than that of individuals dying the following days (Table 3). This difference was significant (t, t' tests $P < .05$) for three species, *Lepomis gulosus*, *L. macrochirus* and *L. punctatus*. The data for these species support the hypothesis, based upon direct observation, that on the average, larger centrarchids died before smaller ones. Data for the other species of centrarchids analyzed suggest this pattern, but differences were not statistically significant. Observation of small fish such as *Gambusia affinis* and *Fundulus chrysotus* suggests that larger fish of these species died first but I have no data on this. It is notable that the data for *Ictalurus natalis* shows a different pattern but the size differences were not significant.

Role of Plant Zones During the Fish Kill

During the fish kill, mortality occurred differentially in the two plant zones. An indication of the effect of plant zones was shown by an experiment conducted on 5 and

TABLE 4.—Dates during May 1970 when the density of various species became zero in each plant zone of the pond

Species	Central area	Emergent zone
<i>Elassoma evergladei</i>	5	17
<i>Enneacanthus gloriosus</i>	13	17
<i>Micropterus salmoides</i>	15	14
<i>Lepomis macrochirus</i>	15	14
<i>Lepomis punctatus</i>	15	14
<i>Lepomis gulosus</i>	17	14
<i>Lepomis microlophus</i>	17	14
<i>Lucania goodei</i>	17	17
<i>Fundulus chrysotus</i>	17	19
<i>Poecilia latipinna</i>	17	19
<i>Heterandria formosa</i>	17	19
<i>Ictalurus natalis</i>	19	17
<i>Lepisosteus platyrhincus</i>	— ^a	—
<i>Gambusia affinis</i>	—	—
<i>Jordanella floridae</i>	21	—
<i>Palaeomonetes paludosus</i>	19	—

^a Dash indicates that the species survived in the zone.

6 May 1970. In the late afternoon of 5 May, the 1-m² drop traps in both the emergent zone and central area were left in the water overnight with equal numbers of nine species of fish within them. By 0830 on 6 May, all individuals of *Micropterus salmoides*, *Lepomis microlophus* and *Lepomis punctatus* in the emergent zone trap were dead. *Lepisosteus platyrhincus*, *Ictalurus natalis*, and *Lepomis gulosus* survived in the emergent zone trap as did the smaller fish, *Gambusia affinis*, *Heterandria formosa*, *Fundulus chrysotus*, and all individuals of these same species which had been placed in the trap in the central area. These results indicated that conditions during this period of lowering water became critical at night for some species in the emergent vegetation prior to becoming critical in more open areas. It is apparent that at least 3 days prior to the beginning of the fish kill, conditions in the emergent zone were such that some species were unable to remain there throughout the night without being adversely affected.

During the fish kill, the larger species of centrarchids and *Ictalurus natalis* were eliminated from the emergent zone prior to being eliminated from the open area (Table 4). With two exceptions the remaining fish, all smaller species, were first eliminated from the central area and were either eliminated from the emergent zone later or survived there. *Gambusia affinis* survived in both zones while *Lucania goodei* disappeared in both zones on the same day. In both cases densities remained higher in the emergent zone for a longer period of time.

DISCUSSION

Water Quality

Lowering water level results typically in the increase of most physical and chemical parameters of water quality in the ponds of southern Florida wetlands (Kushlan 1972). However levels of the physico-chemical parameters of water quality measured during the fish kill fluctuated drastically from the normal levels of 11 May 1970. Some of this change may have been due to the continued water level decline totaling 0.13 m from 14 to 24 May. Unfortunately data from a similar decline without a fish kill are not available for comparison. Certainly much of the rise was caused by factors associated with the fish kill. The independent effects of these factors cannot be determined with certainty without a great deal more experimental and observational data. Some probable contributing factors can be noted however.

The prolonged oxygen depletion undoubtedly had significant effects on the levels of some constituents, particularly those normally bound in an oxidized state in the bottom sediments. The appearance of iron may be attributable to the release of ferrous ions into the water, and since manganese, silicate, phosphate, and bicarbonate are also released under reducing conditions, some of these materials may have been released from the sediment. Since under anaerobic conditions decomposition proceeds to intermediate organic states rather than to mineralization (Ruttner 1969: 200), this may account in part for the high levels of organic matter found in the pond.

The phytoplankton bloom may also have affected water quality. The double peaks of concentration of nitrate, nitrite, and total organic matter may be influenced by phytoplankton. Although in all three the first peak corresponds to the initial decay of the dead fish, the second peak of total organic matter (which includes that of the plankton) corresponds to the peak of the plankton bloom, and the second nitrogen peaks correspond to the decay of the plankton bloom. It is notable that the maximum total organic concentration of 147 mg/liter is high even for southern Florida waters (see Gonyea and Hunt 1970).

The peaks of turbidity and color were correlated with the peak of the plankton bloom. The role of bacteria is an additional unknown quantity, although characteristics such as a lowered capacity to accumulate phosphate under anaerobic conditions (Pomeroy 1970: 176) may be significant.

Plankton

The plankton bloom is notable for its extraordinarily high concentration. While plankton blooms generally achieve densities measured in millions of cells per liter, the peak found here was 2.5 billion cells per liter. Most of this number is attributed to phytoplankton less than 5μ in diameter, predominantly *Chloromonas* sp., a group characteristically found in waters where nutrients are elevated (N. Richardson, personal communication). Kolipinski (1969) also discovered phytoplankton concentrations over 1 billion cells per liter during a fish kill in southern Florida. This bloom was dominated by an unidentified alga whose description fits that of the one found in this study.

Fish Population

Although the fish kill had no long-term effect on either water quality or plankton, its impact on fish was both drastic and of long duration. The 99.4% reduction in fish density in the pond assumes importance when one realizes that this represents the productivity not of the pond alone but of many hectares of surrounding marsh and swamp from which the fish emigrate due to declining water levels. The dry season following that of the fish kill showed a marked reduction in the larger species of fish (Kushlan 1972).

The categorization of fish based upon survival during the fish kill reflects the ability of each species to tolerate conditions which are periodically encountered in dry seasons especially during drought years in southern Florida. As a result, the categorization is in part a reflection of adaptability of each species for survival in the rigorous water system of the southern Florida wetlands. This categorization, although based upon observations during the fish kill, is confirmed by observations throughout the Everglades and

Big Cypress Swamp where lowered water levels and high densities of fish lead to progressive mortality. The centrarchids are invariably among the first to succumb, and the position of *L. gulosus* as being the best able to survive is borne out.

The susceptibility of southern Florida centrarchids to lowered oxygen levels and other stresses emphasizes the significance of size-related mortality shown in this family. Smaller fish are probably able to survive less severe conditions than those encountered in this study, and this may be an important factor in the survival of these species in the shallow marshlands of southern Florida. The relationship between size of fish and resistance to oxygen depletion has been little studied in natural situations. Moore (1942) found that small fish in submerged cages were less tolerant of low oxygen levels than were larger fish. This, of course, would be expected since metabolic rate per gram body weight is greater in smaller than in larger vertebrates. However both field observations (Carter and Beadle 1931) and experimental results (Lewis, 1970) have shown that small fish are able to utilize oxygen at the air-water interface. The use of this layer by small fish during fish kills was noted as long ago as 1934 by Hutchinson (Allee et al. 1949). Its use was important to several small species in this study and probably accounts for the size-related mortality shown by centrarchids.

Class B species which showed poor survival in this study would probably survive less severe conditions, as each possesses physiological or behavioral adaptations which permit survival in oxygen-poor water. *Fundulus chrysotus*, *Poecilia latipinna*, and *Heterandria formosa* have upturned mouths which enable them to obtain oxygen from the surface while swimming in normal fashion, as shown by Lewis (1970) for *Fundulus notatus* and other species. *Ictalurus natalis* is physiologically adapted to survive oxygen depletion, as members of the genus possess a hemoglobin which exhibits a high affinity for oxygen and a very small Bohr effect (Lagler et al. 1962: 240-241). During the fish kill individuals swam at the surface of the water while rapidly moving their opercula. This may be a mecha-

nism which brings oxygen at the surface deeper into the water where it can be utilized.

Class C species that exhibited moderate survival also show distinct adaptations. Both *Lepisosteus platyrhincus* and *Amia calva*, the only other large species to survive, are physostomous (Potter 1927; Johansen 1970: 372). *Gambusia affinis* can survive in oxygen depleted water by virtue of its upturned mouth (Lewis 1970), but in addition Odum and Caldwell (1955) described it as gulping air. *Jordanella floridae* also has an upturned mouth. The prawn, *Palaeomonetes paludosus*, appears to survive in part because it swims at the surface of the water and probably utilizes the oxygen there.

Two points are raised by an examination of the classification and known adaptations of the species. First, those small fish and the prawn that survived the fish kill in moderate numbers had basically the same mechanism for survival—utilization of the oxygenated surface layer—as did several species which showed poor survival. The differential survival of similarly adapted species indicates that some probably possess other mechanisms as well. Secondly, the populations of all species, even though possessing mechanisms for survival, sustained drastic mortality late in the fish kill. There are two possible explanations. Disease may have played a part particularly in the decline of larger fish. Both *Ictalurus natalis* and *Lepisosteus platyrhincus* exhibited severe dilation and hemorrhaging of the blood vessels of the tail and fins, a condition which may be due to microbial infection. This was first noted in both species on 17 May, the first day of severe decrease in density. A second factor may have been the appearance of a surface film on the water from 17 to 24 May. Such a film might interfere with the diffusion of atmospheric oxygen into the water and consequently affect those species utilizing this source. The severe mortality of *Gambusia affinis* from 17 to 24 May and of *Jordanella floridae* from 19 to 21 May may be due in part to the film.

ACKNOWLEDGMENTS

I thank B. P. Hunt, O. T. Owre, D. L. Schneider, N. Richardson, C. R. Hare, M. C.

Kolipinski, R. H. Hofstetter for their suggestions during the study and W. Fernandez, C. Senna, H. Alexander and R. L. Paterson for assistance with field work and my wife, M. S. Kushlan, for making the illustrations.

LITERATURE CITED

- ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT. 1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia. 837 p.
- AMERICAN PUBLIC HEALTH ASSOCIATION. 1965. Standard methods for the examination of water and waste water. 12th Ed. New York. 769 p.
- CARTER, G. S., AND L. C. BEADLE. 1931. The fauna of the swamps of the Paraguayan Chaco in relation to its environment. II. Respiration in the fishes. J. Linn. Soc. Lond. 37: 327-368.
- GONYEA, W. J., AND B. P. HUNT. 1970. Organic matter in fresh waters of southern Florida. Quart. J. Fla. Acad. Sci. 32: 172-184.
- JOHANSEN, K. 1970. Air breathing in fishes, p. 361-411. In W. S. Hoar and D. J. Randall (eds.) Fish physiology. Vol. IV. Academic Press, New York. 532 p.
- KOLIPINSKI, M. C. 1969. Gar infested by *Argulus* in the Everglades. Quart. J. Fla. Acad. Sci. 32: 39-49.
- KUSHLAN, J. A. 1972. An ecological study of an alligator pond in the Big Cypress Swamp of southern Florida. M. S. Thesis, Univ. of Miami, Coral Gables, Florida. 197 p.
- . 1974. Quantitative sampling of fish populations in shallow, freshwater environments. Trans. Amer. Fish. Soc. 103(2): 348-352.
- LAGLER, K. F., J. E. BARDACH, AND R. R. MILLER. 1962. Ichthyology. John Wiley and Sons, New York. 545 p.
- LEWIS, W. M., JR. 1970. Morphological adaptations of cyprinodontoids for inhabiting oxygen deficient waters. Copeia 1970: 319-326.
- MACKERETH, F. J. H. 1963. Some methods of water analysis for limnologists. Freshwater Biol. Ass., Sci. Publ. 21. 70 p.
- MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol. Oceanogr. 10: 280-282.
- MOORE, W. C. 1942. Field studies on the oxygen requirements of certain fresh-water fishes. Ecology 23: 319-329.
- ODUM, H. T., AND D. K. CALDWELL. 1955. Fish respiration in the natural oxygen gradient of an anaerobic spring in Florida. Copeia 1955: 104-106.
- POMEROY, L. R. 1970. The strategy of mineral cycling. Ann. Rev. Ecol. Syst. 1: 171-190.
- POTTER, G. E. 1927. Respiratory function of the swim bladder in *Lepisosteus*. J. Exp. Zool. 49: 45-67.
- RITTNER, F. 1969. Fundamentals of limnology. Univ. of Toronto Press, Toronto, Canada. 295 p.
- WELCH, P. S. 1943. Limnological methods. McGraw-Hill, New York. 381 p.