J. DOUGLAS OLIVER
Effects of Biogenic and Simulated Nutrient Enrichment on Fish and Other Components of Okefenokee Swamp Marshes
(under the direction of BERNARD C. PATTEN)

Biogenic and simulated nutrient enrichment increased levels of various ecological components of Okefenokee Swamp marshes. Fertilization by wading birds and an artificial experimental source increased stores of phosphorus in diverse links of the food web. Simulation modeling lent support to the hypothesis that birds mediated such changes that persisted after they abandoned this ecosystem.

To simulate nutrient enrichment from birds, I placed pots of enriched agar inside clear enclosures. In the laboratory, pots released a mean of 45 mg NH_4-N d^{-1} and 11 mg PO_4-P d^{-1} into water. In the marsh, mesocosms containing pots had higher stocks of zooplankton (primarily _Diaphanosoma_ _brachyurum_) than controls. These results demonstrate that simulation of enrichment remaining after birds left can cause significant effects on zooplankton primary consumers in the marshes.

Evidence was presented for residual enrichment by a biotic component of the ecosystem itself, the birds. One to two years after they abandoned the marsh, it showed continued nutrient effects. Elevated available phosphorus in sediments contributed to enhanced levels of phytoplankton. Planktivorous fish were greater in biomass than at reference sites. These results and the zooplankton data suggest residual enrichment effects of birds on sediments, and indirectly on plankton and fish.

I measured the trophic transfer to *Leptolucania ommata* and *Gambusia affinis*, *in situ*. Both fishes ate mainly insect larvae (such as Chironomidae) and Cladocera. Consumption by both species in summer (26.31 mg m^{-2} d^{-1}) supports a hypothesis that invertebrate prey production must be substantial in such blackwater marshes.

Trophic model dynamics were checked by seasonal data before, during and after simulated nutrient input from birds. The model reasonably estimates effects of enrichment on benthic detritus, aquatic macrophytes and phytoplankton, and conservatively estimates the increase of zooplankton and fish. Simulated levels decreased after simulated abandonment, and the decreases generally followed field trends. The model indicates that nesting birds can have considerable effects on aspects of an ecosystem not normally associated with them.

On the applied side, wetlands have been suggested for natural sewage treatment. Results described here indicate a sizeable capacity to buffer pulses of sewage nutrients, by time-delayed release.

INDEX WORDS: Fish, Okefenokee Swamp, Marsh, Mesocosm,
Phosphorus, Plankton, Simulation Model

EFFECTS OF BIOGENIC AND SIMULATED NUTRIENT ENRICHMENT ON FISH AND OTHER COMPONENTS OF OKEFENOKEE SWAMP MARSHES

by

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Soli Christo Gloria

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CHAPTER 1

INTRODUCTION

> "By enriching adjacent waters with the biogenous elements contained in their droppings, birds significantly affect the scale of the organic cycle in the areas of their nesting sites. Fish-eating birds are not, therefore, a closed side branch in the network of the biocoenosis, and they do not, as it previously seemed, remove from the hydrosphere the organic matter which they transform" (Golovkin and Zelikman 1965).

Fish can interact with higher order consumers such as wild aquatic birds, via nutrients. First, it is clear that an increase in abundance of fish that are subject to avian predation might increase the birds, by means of enhanced macronutrient/biomass transfer (Lack 1954, Browder 1978, Furness 1982). Second and more controversial is whether or not a reverse stimulation takes place, i.e. whether or not natural aggregations of birds increase abundances of fish, via fertilization resulting from excretion (suggested by Wheeler 1945). In the first case, ingestion is responsible for the effects of fish on birds, whereas in the second, the reverse process of egestion would be indirectly responsible for the effect of birds on fish.

Nutrient effects are not usually considered to extend between widely diverse ecosystem components such as from birds to fish, via guano and the intervening food web. Nevertheless, this dissertation proposes that such effects can be significant, even continuing after birds have left the system. In the process of investigating these ideas, new information is brought to light on various aquatic components of the captivating marshes of Okefenokee Swamp.

Okefenokee Swamp is the largest entirely freshwater wetland in the United States. It extends over some 1800 km^2, and 21 percent of this area is aquatic macrophyte marshland (Finn and Rykiel 1979). Various researchers have shown that the Okefenokee ecosystem is not high in available nutrients (such as phosphorus and nitrogen, Auble 1982). It is underlain by nutrient poor sand and clay and is ombrotrophic, or rain-fed (Rykiel 1977). Thus, an exogenous source of nutrients might be expected to have considerable effect on the ecosystem.

Stinner (1983) demonstrated that nesting wading birds significantly enriched a marsh near Mack's Island in Okefenokee Swamp. They brought in food for their young from a radius of up to 20 km. Resulting concentrations of guano caused levels of nutrients such as phosphorus (P) to increase significantly in aquatic macrophytes and in water. Biomass of macrophytes also increased.

I hypothesized that such enrichment would move up through the food web and cause increases in nutrient stores of various trophic levels. In particular, the sediment complex, phytoplankton, zooplankton, insect larvae and fish were expected to increase. This general theme is investigated in this dissertation. Such trophic effects from the "bottom-up" in the ecosystem may be significant to the development of a theory of indirect effects (Kerfoot 1987).

In order to detect possible enhancement of fish in the bird rookery relative to other sites, a quantitative fish trapping method was needed. Finally we were successful with a 1-m x 1-m portable drop trap (Freeman et al. 1984). This method, which recovered 90% of tagged marsh fish, was adopted as standard.

Wading birds did not return to the rookery marsh from 1981 until 1984. The reason for abandonment is unknown, but may have been because of unusually low water levels in 1981. Since the rookery site was no longer active, I examined the abandoned site for possible nutrient effects that might be residual. All data for this dissertation were collected prior to the return of birds. (However, nesting wading birds were in the rookery site again later. Mack's Island rookery had "high usage" in 1984, 700 nesting wading birds in 1985, 30000 in 1986, and 6000 in 1987 (Okefenokee Nat. Wildl. Refuge, 1984-1987)).

Although several components were shown to be affected by wading birds, an important food web link, zooplankton, had not been quantified in the abandoned rookery, so it was quantified in mesocosms. A new gradual chemical release device was used to artificially enrich experimental mesocosms with P and nitrogen (N) in situ, to determine if zooplankton could be indirectly enhanced by these nutrients. These mesocosm experiments were also designed as an independent confirmation that such macronutrients could limit production in the Okefenokee marsh ecosystem. Results of this mesocosm experiment are given in Chapter 2.

Chapter 3 describes direct and indirect nutrient effects of birds on diverse components, such as the sediment complex, phytoplankton and fish. Evidence that nutrients could significantly affect the marsh ecosystem (Stinner 1983) even after birds had abandoned the site (Chapter 3), led me to model nutrient effects before, during and after enrichment by the birds. By doing so, not only is it possible to simulate the sequence of changes to various trophic levels, but to address questions that are otherwise impossible to answer after birds have left. For example, by how much might guano enrichment have increased the biomass of Okefenokee marsh fish, relative to unenriched marshland? Chapter 5 addresses such effects in light of the ecosystem simulation model.

In order to build an appropriate trophic model of the marsh, I needed to find answers to two questions about Okefenokee fish feeding, in Chapter 4:

1) What taxa are Okefenokee marsh fish eating, i.e. what trophic links are appropriate?

2) How much are typical marsh fish eating (consumption rates), i.e. what are the magnitudes of trophic flows?

Finally, the system model brings together results of all chapters formally (Chapter 5), and Conclusions distills them (Chapter 6).

Other researchers have demonstrated that nutrient elements such as P can have considerable effects on an aquatic ecosystem. Eutrophication has been well documented (e.g., Edmondson 1972, Wetzel 1975) and enhancement of production of phytoplankton (DeCosta et al. 1983), zooplankton (Vanni 1987) and fish (Hall et al. 1970) are commonly seen. In fact, southern farm ponds are often artificially fertilized to increase fish production for man's harvest (Swingle 1956, Stickney 1979). Fertilization also can cause increased nutrients in sediments (Schindler et al. 1977, Richardson and Marshall 1986) and in shallow, marshy land, can cause increased biomass and P concentration of macrophytic vegetation (Dolan et al. 1981).

Furthermore, it has been documented that bird guano can result in elevated levels of various aquatic components. Guano can fertilize phytoplankton (Leah et al. 1978, Devol et al. 1984) and zooplankton (Golovkin and Zelikman 1965, Zelikman and Golovkin 1972). In some countries, man deliberately raises domestic ducks in conjunction with pond fish in order to increase fish production (via guano or uneaten duck food, Huet 1971, Woynarovich 1979, Chen 1983).

Thus, it might not be surprising if natural populations of wading birds could increase natural populations of phytoplankton, zooplankton, and fish.

On the other hand, no one has documented indirect enhancement of higher trophic levels (such as fish) by wild populations of birds. In fact, Schaefer's classic (1970) paper showed that Peruvian anchoveta recruitment increased when abundance of guano birds decreased, a situation that he attributed to intense predation by these fish-eating birds. Furthermore, natural nutrient enrichment of the anchoveta fishery is primarily due to deep-water upwelling rather than to guano (Lack 1954, Parsons et al. 1984). At St. Brandon's Islands, large guano inputs accompanied a highly productive fishery relative to other islands of the western Indian Ocean, but Wheeler (1945) did not know if guano fertilization was rapid enough to overcome tidal dissipation to allow a causal link. Onuf et al. (1977) stated that enrichment of mangroves by egrets and pelicans increased mangrove biomass and N content which then caused increased consumption by lepidopteran and coloeopteran insects, but they did not report any further effects on any higher trophic levels. The present dissertation suggests that wild birds not only enhance primary producers and zooplankton primary consumers, but also secondary-tertiary consumers such as fish. Evidence is also presented for indirect time-delayed mediation of such enrichment by birds, via slow movement from sediments (benthic detritus, Chapters 3 and 5).

Patten (1982) has emphasized the importance of time-delayed indirect effects in the ecosystem (e.g., effects of enrichment by birds on fish, via intermediate components). His mathematical analyses (Higashi and Patten 1986) suggest that such indirect effects can exceed direct effects (e.g., possibly the effects of zooplankton on fish, Fig. 2 of Chapter 5). Although this dissertation is not a test of such theory, it does support the notion that indirect effects such as the effect of birds on plankton and fish can be significant in the ecosystem.

Many authors have presented other evidences that indirect effects can be highly significant. Aside from previously cited references, the following are some trophically mediated examples from various aquatic systems. Kerfoot (1987) stated that increases of fish density in a Vermont lake increased Mesocyclops zooplankton because positive effects along indirect pathways were greater than direct (negative) predation by the fish. He pointed out, however, that the balance between the two path strengths was sensitive enough to fish density that the overall interaction could easily shift from positive to negative, at high fish density.

Dungan (1987) showed that on a rocky intertidal surface, algal grazing by a limpet (Collisella) freed space on the surface, thus indirectly increasing the abundance of a barnacle (Chthamalus), and thus also its predator (the gastropod, Acanthina). In return, the predatory gastropod indirectly increased the limpet by removing the barnacle, thus increasing the limpet's food and space.

Moss (1976) stated that high levels of artificial P and N fertilization of ponds caused changes in the epiphytic diatom community that could be "directly ascribed to fertilization and some [indirectly] to a change in... the host macrophyte." He believed that shading by increased phytoplankton indirectly caused a reduction in biomass of epiphytic diatoms. Furthermore, at high fertilization, the presence of fish caused increased biomass of epiphytes, probably indirectly through predation of grazing invertebrates. Papers from the recent book by Kerfoot and Sih (1987) cite and review other indirect effects in aquatic ecosystems.

The effects of nutrients on aquatic systems are more than a matter of academic analysis. Possible practical significance involves use of wetlands for treatment of sewage and other wastes. Many authors (e.g., Dolan et al. 1981, Winchester and Emenhiser 1983, Fritz and Helle 1984, Ewel and Odum 1984) have discussed the application of secondarily treated sewage to wetlands for the purpose of an inexpensive natural tertiary treatment (largely via nutrient movement to sediments, Nichols 1983, Dierberg and

Brezonik 1984). The present dissertation examines similar nutrient additions from birds and artificial devices (Chapters 2 and 5), and their effects on wetland ecology. Long-term return toward initial natural states is also considered (Chapter 5), and may be of future use for analysis of the return of former sewage-treatment wetlands toward their natural conditions.

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CHAPTER 2

A SYSTEM FOR EXAMINING THE RESPONSE OF AQUATIC ECOSYSTEMS TO GRADUAL CHEMICAL INPUTS, AND FIELD APPLICATION IN OKEFENOKEE SWAMP, GEORGIA

[1] J. Douglas Oliver. 1985. Archiv fur Hydrobiologie 102: 415-423.

Introduction

Ecologists sometimes want to add a chemical to aquatic ecosystems and analyze responses. The primary purpose of the present study is to describe a system that introduces sustained and standardizable chemical inputs to aquatic ecosystems on an areal basis. The second purpose is to determine responses of an Okefenokee Swamp marsh (particularly the plankton) to nitrogen and phosphorus inputs that simulate enrichment from a bird rookery. The third purpose is to quantify the input system's N and P releases into water.

Laboratory microcosms are useful in ecological research, but artificial. On the other hand, field experiments are more natural, but less controllable; when a chemical is added to a field site it may become dispersed rapidly unless the whole area is treated. Furthermore, adding a chemical continuously is difficult and usually it is necessary to pulse the system.

Mesocosm experimentation offers a promising compromise between microcosm and field methodologies (Odum 1983, Grice & Reeve 1982, Odum 1984). A mesocosm is enclosed so area or volume can be quantified and so any chemical treatment is contained within a reasonably natural environment. Mesocosms should be large enough so that the ratio of wall area to enclosed area or volume is minimized, yet small enough to be replicated and nondestructively sampled. Personal observation and another worker's (S.A. Schoenberg of the University of Georgia) experience suggest that such a mesocosm should enclose about 2 m^2.

Initially, a standard medical intravenous setup was connected to a carboy, in an attempt to obtain constant release of dissolved chemical. However the rate of dripping could not be maintained for more than a few hours, so this setup was discarded. Alternatively, clay pots were filled with nutrient-enriched agar for releasing N and P. Fairchild et al. (1983) developed this technique for examining the response of algae that attached to pots in a lake, but also noted significant releases of NO_3-N and PO_4-P into the surrounding water.

In some previous studies, effects of natural nutrient inputs from bird guano on aquatic systems have been documented and sometimes effects on plankton have been noted. Golovkin & Garkavaya (1975) reported an increase in phosphate, organic nitrogen and nitrate in marine waters adjacent to bird colonies. This stimulated the development of planktonic algae and this affected the next link in production, the zooplankton (*Calanus* sp.) (Where N and P were added in organic form directly over an inundated rock ledge, the algae that predominated were flagellates whereas guano that was first allowed to mineralize resulted in an increase in diatoms.) Similarly, Manny et al. (1975) looked at the effect of more than 6000 migrant Canada geese (*Branta canadensis*) on Wintergreen Lake, Michigan. They found that these birds "were the chief cause of hypereutrophic primary productivity conditions". Leentvar (1967) showed that gulls' (Larus ridibundus) guano increased phosphate concentration in a Dutch acid oligotrophic fen and that unicellular flagellates (Chlamydomonas) appeared in increasing numbers. McColl & Burger (1976) found that Franklin's gulls (Larus pipixcan) nesting among cattails (Typha) in shallow Minnesota pools caused large increases in N and P in the immediate vicinity of the gulls, but possible effects on biota were not examined.

Methods

To calculate release rates of N and P into water that approached natural input rates into Okefenokee Swamp, natural daily inputs had to be calculated first. Stinner (1983) showed that wading birds, predominantly white ibis (Eudocimus albus), added 4.6 g m^{-2} yr^{-1} total phosphorus via guano, to a rookery that was located in a macrophytic marsh in Okefenokee Swamp. She found that the major input occurred from about May to August. It follows that the average input of P was approximately 4.6 g m^{-2} /100 d = 46 mg P m^{-2} d^{-1}, i.e. about 92 mg d^{-1} into a 2 m^2 area. Since Stinner (1983) did not measure N input, this was estimated assuming an N/P ratio of 1.29 g N /0.39 g P (Manny et al. 1975), to calculate 152 mg N m^{-2} d^{-1}, i.e. 304 mg N d^{-1} into 2 m^2. This guano N probably changes to NH_4-N through time (Leentvaar 1967).

To get artificial release rates of N and P into water (through clay pot walls) that approached the natural input rates mentioned above, I modified pots of Fairchild et al. (1983). Each of their release experiment pots had been an 8.8 cm O.D. (245 mL) clay flower pot inverted and sealed to a Petri dish, filled with 2% agar containing 0.1 M $NaNO_3$ or K_2PO_4 and sealed by a rubber stopper. Fairchild et al. were in the process of testing release rates but thought that such a pot might release about 1 mmole N (14 mg) and 1 mmole P (31 mg) d^{-1} (pers. comm. 1983). Because simulation of rookery input implied higher release values and implied NH_4-N instead of NO_3-N, I chose larger, 15 cm O.D. (1 L) clay pots and filled them with 0.2 M $(NH_4)_2HPO_4$ in 2% agar.

Mesocosms were constructed of a frame of 10 cm x 15 cm-mesh steel fencing, covered on both sides by 0.15-mm nylon-reinforced plastic film (Almac Plastics, Md.), stapled together where it extended beyond the fencing. Ends of the enclosure were joined by twisting wire ends together, then sealing the plastic by duct tape. They were partially flattened for carrying ready-made to the field. Enclosures were secured by 5 cm x 5 cm wooden stakes and cord. Fish were eliminated by shocking at high voltage. Enclosures were located at a site approximately 200 m east of the entrance to the Suwannee River sill (an earthen dam that borders the west side of Okefenokee Swamp). This area (mean depth 0.52 m) is similar to the rookery described by Stinner (1983). Vegetation is dominated by the spatterdock (Nuphar). The area is virtually devoid of guano input from nesting birds.

A plastic tube of 6.4 cm I.D. was used to collect a top to bottom sample from each of the three mesocosms containing a pot (experimentals) and from each of the three without pots (controls). Between 1 and 6 L (the amount depending inversely on relative concentration of plankton were filtered through 64 μm mesh for zooplankton, and preserved in buffered formalin and sucrose. Another 30-200 mL were passed through a glass fiber filter (1.2 μm retention), frozen and later analyzed fluorometrically for phytoplankton chlorophyll a, according to Holm-Hansen et al. (1965) and Turner Designs (1983). A third sample was put on ice, then analyzed by standard persulfate digestion and Technicon II Autoanalyzer. To determine temperatures that biota and pots experienced, bottom water temperature was measured by oxygen/temperature probe. Sampling was repeated approximately every three weeks from May 16 - August 29, then pots were replaced so there would continue to be a relatively undepleted source of N and P. To see whether or not net community productivity was increased by N and P, dusk-dawn-dusk oxygen profiles were measured on three occasions (Hall & Moll 1975).

To estimate release rates of N and P in the laboratory, 15 L of deionized water and one 0.2 M $(NH_4)_2HPO_4$ pot were put into each of four replicate carboys. Every 24 h (± 0.3 h), water was stirred and one, two, four, eight and 16 days after initiation, the water in each was sampled by a top to bottom core tube. Carboys were refilled to 15 L daily. Because release rates are probably dependent on temperature, water temperatures were monitored.

The experiment was repeated for two days using blackwater from Okefenokee Swamp to determine if its chemical composition influenced release rates. Such blackwater is high in dissolved organic compounds such as fulvic acids (Beck & Reuter 1974) and low in pH (4).

Results

Neither total N nor P water concentrations were significantly different in experimental mesocosms than in controls (Table 1). Water column chlorophyll a and diel O_2 fluctuation also were not significantly different.

On the other hand, there were more zooplankton in experimental mesocosms than in controls (Fig. 1, Mann-Whitney U = 146, $P < 0.025$). This is largely due to an increased abundance of Diaphanosoma brachyurum (Cladocera: Sididae) in experimentals (U = 155, $P < 0.005$).

In the laboratory, release of NH_4-N into deionized water decreased through time, with an average release of 45 mg NH_4-N d^{-1} (Fig. 2). Release of PO_4-P into deionized water declined over the initial two days but then appeared to increase, with an overall average of 11 mg d^{-1}. Blackwater caused greater release rates of NH_4-N and PO_4-P from pots than did deionized water, at least during the initial two days of release. Average water temperature during release into deionized water was 21.6°C (range 17.3-25.2°C, n = 44). Average water temperature during blackwater release was 21.9°C (range 18.3-24.8°C, n = 8).

Discussion

Release was substantial for at least 16 d, thus the modified clay pot is successful as a chemical source for aquatic mesocosms. This conclusion is consistent with Fairchild et al. (1984) who found considerable release from 245 mL pots for at least 23 d. They illustrated release rates of PO_4-P into distilled water (0.05 M K_2HPO_4 pots; 150 μmole d^{-1} = 5 mg PO_4-P d^{-1}) which were similar to rates shown in the present paper (1-L 0.2 M $(NH_4)_2HPO_4$ pots; 11 mg PO_4-P d^{-1}). Likewise, their release rates of N from 0.5 M $NaNO_3$ pots (average of 5000 μmole NO_3-N d^{-1} = 70 mg NO_3-N d^{-1}) were similar to those that I observed from 0.2 M $(NH_4)_2PO_4$ pots (releasing 45 mg NH_4-N d^{-1}). (I have averaged release rates of Fairchild et al. (1984), above. They found that release rates in general declined through time as nutrients in pots decreased, although PO_4-P release from 0.05 M K_2HPO_4 pots appeared to increase somewhat for the initial several days).

Release rates from 0.2 M $(NH_4)_2HPO_4$ pots into deionized water, though substantial, were less than N and P added by guano of wading birds to 2 m^2 of rookery. As mentioned in Methods, such birds added about 92 mg TP d^{-1} and 304 mg TN d^{-1} to such an area. However these rates of guano input are maximal since they were from the center of the most heavily nested part of Okefenokee that was discovered, and they do not consider later processes such as losses of chemical from the area by diffusion and by slow water movements, and possible non-availability of some of the N and P due to low solubilities. Furthermore, release from pots into Okefenokee mesocosms was probably greater than my deionized release data would suggest, since pots in the field experienced higher temperatures (Table 1 & Results) and much more water (about 1000 L) for the dissolution of chemical than did laboratory pots, and since release into blackwater was shown to be higher than into deionized water. Thus the mesocosm system appeared to be simulating effects of addition of N and P at rates approaching those of a wading bird rookery, but at some distance from the center of nesting.

Although $(NH_4)_2HPO_4$ pots released substantial amounts of N and P, these amounts did not result in increases in N in the water column nor in significant increases in P within mesocosms. This lack of effect on mesocosm water concentrations may have been due to natural loss to system components such as adsorption to sediments. This is supported by the low equilibrium phosphate concentration (4 μg PO_4-P L^{-1}) in sediments at the site and time of the mesocosm study (Chapter 3), and suggests that P added to mesocosms was to some extent adsorbed by sediments. Other workers have suggested such loss of nutrients to be important in enclosures (Twinch & Breen 1978) and in natural wetlands (e.g., Nichols 1983).

Pots resulted in higher densities of zooplankton and in particular of Diaphanosoma brachyurum which eats phytoplankton and bacteria. However neither chlorophyll a, a measure of phytoplankton abundance, nor diel oxygen production, a measure of net community production, were increased. Perhaps zooplankton were increased via some phytoplankton stimulation due to pots, then they kept the phytoplankton in check via increased phytoplanktivory. (Lynch & Shapiro [1981] have shown that enclosures containing large herbivorous zooplankton had lower phytoplankton biomass than those in which such zooplankton were removed. Similarly, Timms & Moss [1984] found that a shallow wetland's chlorophyll a concentration was decreased if Cladocera were present). An alternative explanation for the experimental mesocosm's increased zooplankton without increased phytoplankton is that zooplankton may have increased due to possible stimulation of bacteria by pots.

The use of pots in 2-m^2 clear enclosures was an effective means of applying chemicals to an aquatic ecosystem. Release was gradual and pots could be left in position for at least two to three weeks before replacement. Pots were inexpensive i.e. less than US$10.00 each, sturdy, made of readily available materials, and capable of being built easily and quickly (four were constructed via 0.5 man-hr effort). The enclosure part of the mesocosm system also proved to be cost-effective ($25.00), portable and sturdy. Inorganic nutrients were added to aquatic mesocosms, and presumably other chemicals such as selected algicides and pesticides could be added via the pot/enclosure system, to test their environmental impacts in the field.

Comparative ecosystem ecology could be investigated using the technique. Various vegetated aquatic areas and shallow lakes could receive 2-m^2 enclosures and pots of standardized concentration to compare responses (to a pollutant, for example) that vary with latitude or habitat type.

Summary

A mesocosm system for examining the response of aquatic ecosystems to gradual chemical input has been described. Clear 2-m^2 enclosures made of plastic film and steel fencing were placed in an Okefenokee Swamp marsh. Half of these enclosures contained 1-L porous clay pots filled with 0.2 M $(NH_4)_2HPO_4$-enriched agar to simulate N and P fertilization by birds. Diel O_2 fluctuation, chlorophyll a and total N and P concentrations in water were not significantly different in experimental mesocosms than in controls (Table 1), but abundance of zooplankton (primarily Diaphanosoma brachyurum) was increased (Fig. 1). In the laboratory, pots released an average of 45 mg NH_4-N d^{-1} and 11 mg PO_4-P d^{-1} into deionized water and more than this into Okefenokee blackwater (Fig. 2).

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Table 1. Average water parameters in mesocosms with and without $(NH_4)_2HPO_4$ pots. Depth shown in cm, temperature in °C, and oxygen fluctuation in mg L^{-1}. Nitrogen, phosphorus and chlorophyll concentrations shown in μg L^{-1}. Samples were taken between June 5 and August 29, 1983. Parentheses show (minimum-maximum range, n).

	With Pots	Without Pots
Depth	52.3 (42.0- 61.0, 15)	52.0 (45.0- 67.0, 15)
Bottom Temp.	25.8 (23.1- 27.8, 26)	25.5 (23.1- 28.0, 26)
Total N	1330.3 (993.9-2008.9, 14)	1342.0 (773.7-2083.8, 14)
Total P	20.2 (0.0- 119.1, 14)	12.2 (0.0- 39.6, 14)
Chl. a	25.9 (4.3- 61.9, 13)	22.9 (3.1- 64.7, 13)
Diel O_2 Fluct.	1.8 (1.5- 2.5, 8)	1.3 (-1.2- 3.5, 8)

Fig. 1. Zooplankton in Okefenokee Swamp. Stars represent densities in mesocosms with $(NH_4)_2HPO_4$ pots (see text), circles in mesocosms without pots. Bars represent ±S.E. N = 3 for each datum except n = 2 on August 11. Note log scales on ordinates.

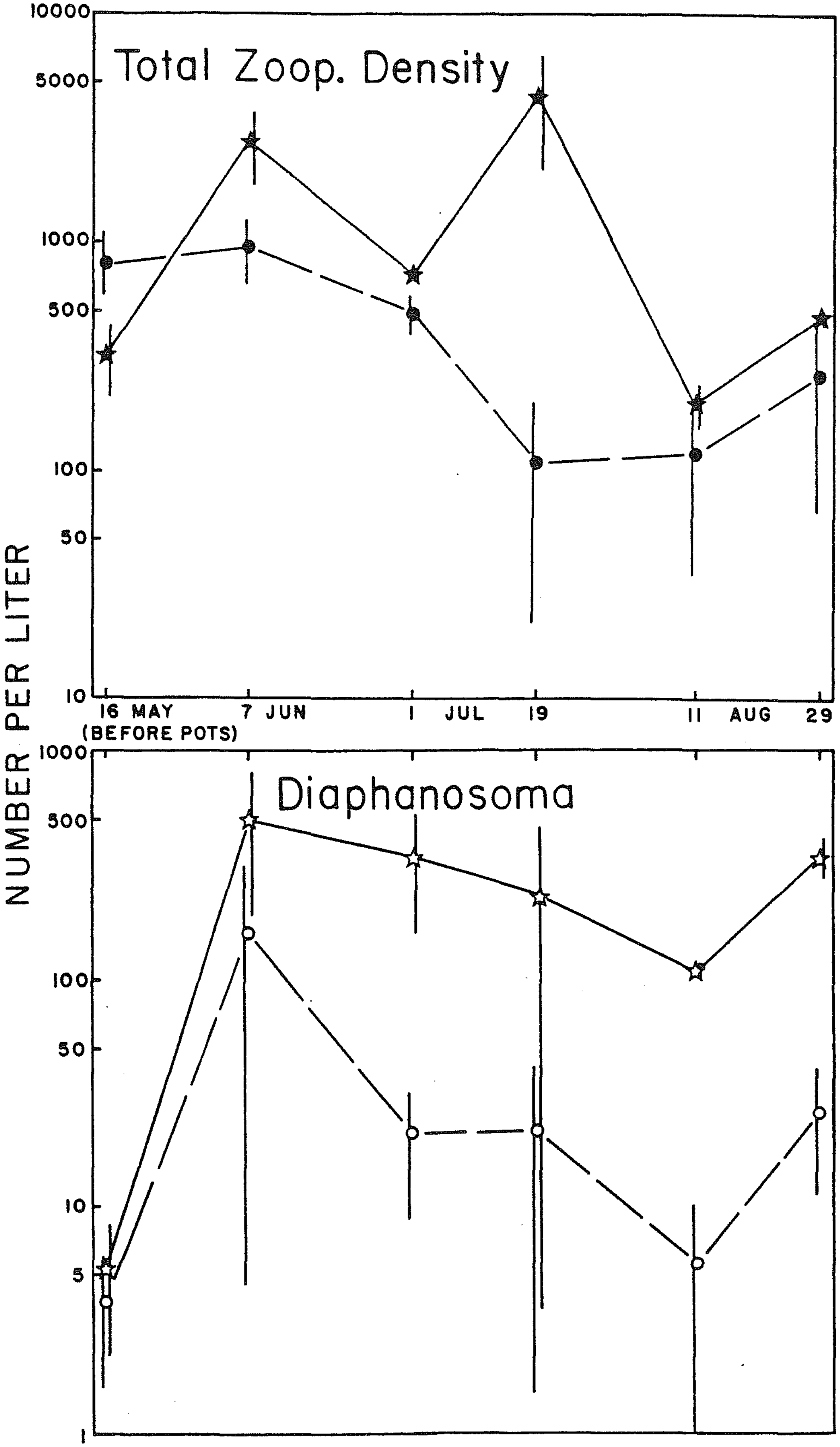
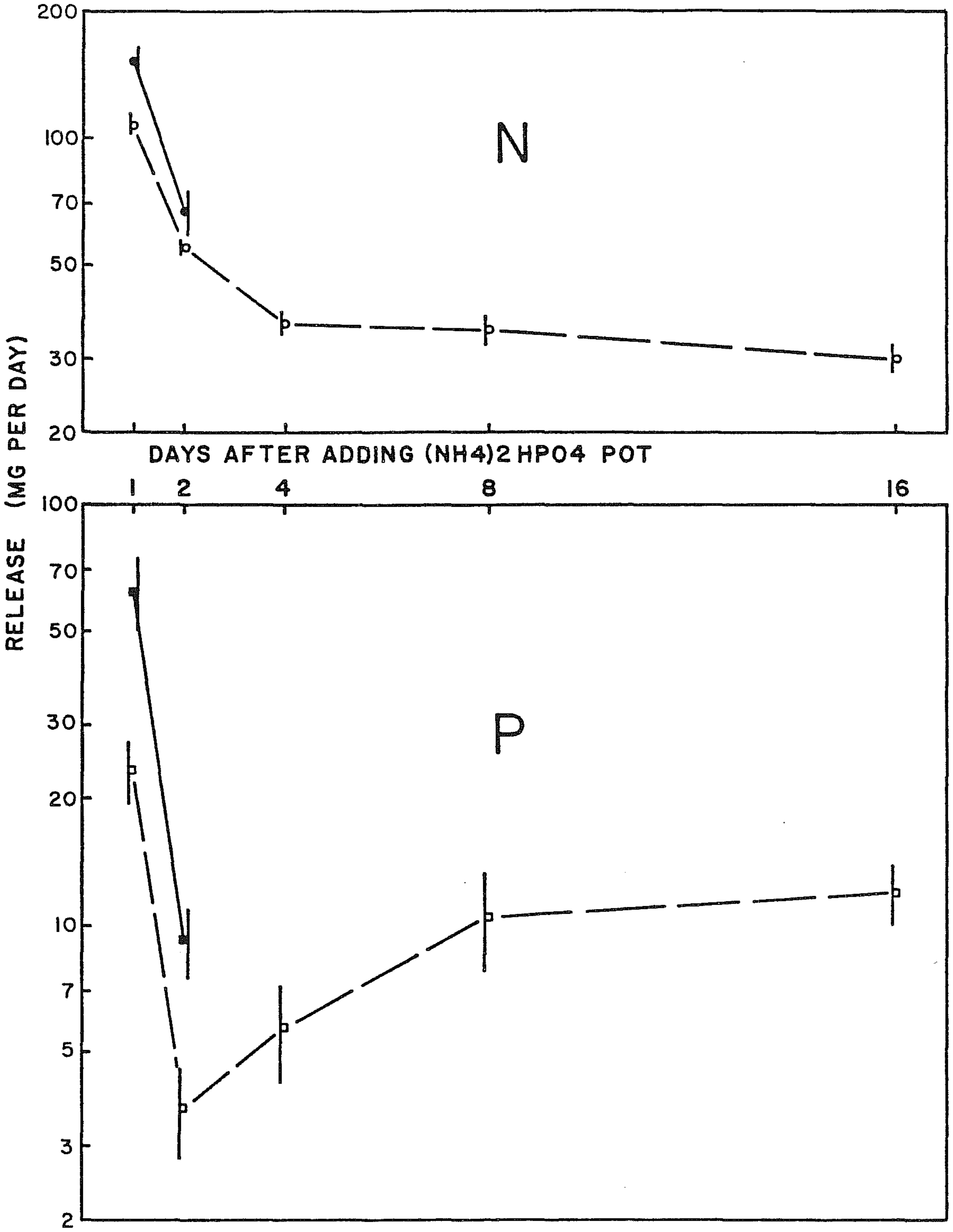

Total Zoop. Density
10000
5000
1000
500
100
50
10
16 MAY
(BEFORE POTS)
7 JUN
1 JUL
19
11 AUG
29
NUMBER PER LITER
Diaphanosoma
1000
500
100
50
10
5
1

Fig. 2. NH_4-N and PO_4-P released by pots through time. Solid symbols represent values in Okefenokee blackwater, open symbols in deionized water. Bars represent ±S.E., $n = 4$ for each datum. Log scales on ordinates.


200
100
70
50
30
20
N
DAYS AFTER ADDING (NH4)2 HPO4 POT
1
2
4
8
16
RELEASE (MG PER DAY)
100
70
50
30
20
10
7
5
3
2
P

CHAPTER 3

RESIDUAL INFLUENCE OF MACRONUTRIENT ENRICHMENT ON THE AQUATIC FOOD WEB OF AN OKEFENOKEE SWAMP ABANDONED BIRD ROOKERY[1]

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[1] J. Douglas Oliver and Steven A. Schoenberg. To be submitted to Oikos.

Introduction

Okefenokee Swamp, a large (1800 km^2) wetland in southeastern Georgia and adjacent Florida, has blackwaters that are not high in available nutrients (Auble 1982). However, guano enriched at least one part of Okefenokee, a now abandoned ibis (Eudocimus albus) rookery, for at least 11 years (Stinner 1983). Other workers have documented guano effects on aquatic ecosystem nutrients and plankton, but not residual effects after birds had left, nor effects on higher trophic levels such as fish. McColl and Burger (1976) found that Franklin's gulls (Larus pipixcan) nesting among cattails (Typha) in shallow Minnesota pools caused large increases in aquatic P and N in the immediate vicinity of the gulls. Similarly, Manny et al. (1975) found that more than 6000 migrant Canada geese (Branta canadensis) were the chief cause of hypereutrophic primary productivity in Wintergreen Lake, Michigan. Leentvar (1967) showed that guano of gulls (Larus ridibundus) increased phosphate concentration in a Dutch acid oligotrophic fen and that unicellular flagellates (Chlamydomonas) appeared in increasing numbers. Golovkin and Garkavaya (1975) reported an increase in phosphate, organic nitrogen and nitrate in marine waters adjacent to bird colonies. This stimulated the development of planktonic algae and this affected the next link in production, the zooplankton (Calanus sp.) In some countries, people deliberately raise domestic ducks in conjunction with pond fish in order to cause increased production of the latter (via guano or uneaten duck food, Huet 1971, Woynarovich 1979, Chen 1983). Thus, natural populations of birds can increase natural populations of phytoplankton and zooplankton, and it might not be surprising if they could increase fish.

On the other hand, no one has documented enhancement of higher trophic levels (such as fish) by wild populations of birds. Although Wheeler (1945) indicated that St. Brandon's Islands had large guano inputs and a highly productive fishery relative to other islands of the western Indian Ocean, he did not know if guano fertilization was rapid enough to overcome tidal dissipation to allow a causal link. Onuf et al. (1977) stated that enrichment by egrets and pelicans increased mangrove consumption by lepidopteran and coleopteran insects, but they did not report any further effects on any higher trophic levels. The present paper suggests that wild birds not only enhance primary producers and zooplankton primary consumers, but also secondary consumers such as fish. Evidence is also presented for indirect time-delayed mediation of enrichment by birds, via slow macronutrient movement from sediments.

Despite the importance of blackwater systems worldwide, there have been few descriptions of effects of impinging enrichment. Based on the conclusion of Fittkau et al. (1975) that available nutrients are usually low, enrichment effects should be substantial. For example, Rai and Hill (1980) stated that in Amazonian lakes, dissolved nutrients (such as P and N) were generally much less abundant in blackwaters than in whitewaters and should be considered limiting factors in the blackwaters. Schmidt (1976) indicated that additions of P, N and trace elements resulted in only "relatively unimportant" phytoplankton growth stimulation in an Amazonian whitewater lake, but resulted in considerable stimulation of Rio Negro blackwaters. However, Devol et al. (1984) showed that P + N addition resulted in several-fold increases in phytoplankton from an Amazonian lake, whether or not blackwater humic and fulvic acids were also present. In spite of the presence of organic compounds that attenuate light and thus might affect production, blackwaters may be limited by macronutrients, according to these few studies.

Although such short-term bioassays are available for nutrient effects, there has been even less study of residual responses after enrichment of blackwaters has ceased. In clearwater systems such as Lake 304 in Ontario, Schindler (1974) showed that after two years of enrichment and large phytoplankton responses, cessation of P enrichment brought phytoplankton back to pre-enrichment levels within one year. In Lake Washington after diversion of sewage P and other nutrients, winter phosphate and summer phytoplankton declined to equilibrium levels in about three years (Edmondson and Lehman 1981). In a blackwater system, a cypress wetland, Dierberg and Brezonik (1983) found that addition of secondarily-treated sewage caused increased nutrients in water, and that 1.7 years after the cessation of sewage pumping, total P in water still had not returned to natural levels. They concluded that sediments and vegetation on the swamp floor released P to overlying water long after the addition of nutrients. In summary, residual nutrients and their biotic effects can remain significant in clearwater systems for about one to several years after enrichment, but to our knowledge, only one previous paper has examined such effects in blackwaters.

In the present study, we have taken advantage of a natural change in nutrient conditions to examine the effects of residual nutrients on a blackwater system. We hypothesized residual indirect positive effects of bird guano on phytoplankton, zooplankton and fish biomass in the recently abandoned wading bird rookery. Input by the birds was expected to cause sediments to have more P available to the overlying water, which might then result in higher standing stocks of phytoplankton, and higher densities of fish than at sites that lacked such a rookery. We examined another link in this food chain, zooplankton, after we fertilized enclosures at macronutrient levels representing residual enrichment after birds had left.

Site Descriptions

Our sites are all shallow ($\leq$1.2 m depth), vegetated marshes within Okefenokee National Wildlife Refuge, Georgia. They have blackwater containing humic and fulvic acids, with a pH of 3.8 (e.g., Beck, Reuter and Perdue 1974). Floating and submerged macrophytes (Nuphar luteum, Utricularia spp., Cabomba pulcherrima) dominate the rookery site at Mack's Island (R, Fig. 1). During each spring-summer period from at least 1970-1981, 2000-30000 wading birds (predominantly Eudocimus albus), nested in shrubs and trees adjacent to this site. In 1979-1980, Stinner (1983) found significant increases in macronutrients in the water column and in aquatic macrophytes. She estimated that the total amount of phosphorus addition by the birds, 4.6 g m^{-2} yr^{-1}, was comparable to crop field fertilization. In 1981, following a severe drought in much of the southern United States, the birds did not return, terminating the nutrient input at this site.

For comparison with the rookery, we chose a control site (RC) 1.6 km away, because it has similar depth and floating and submersed vegetation (e.g., Nuphar luteum, Utricularia spp.) We also compared R with two Okefenokee marshes of different vegetation. Little Cooter Prairie (LCP) is a shallower ($\leq$0.5 m) site in which floating and submerged macrophytes (Nymphaea odorata, Utricularia spp.) accompany emergents (Eriocaulon compressum, Rhynchospora inundata, Orontium *aquaticum*, Greening and Gerritsen 1987). Mizell Prairie (MP) is even shallower, and during the course of our study, it frequently had no standing water. It is dominated by sedge (*Carex walteriana*) with an understory of *Sphagnum*. These three comparison sites have lacked bird rookeries for at least 15 years.

Methods

We characterized sediment nutrient availability to the overlying water column by determining the equilibrium phosphate concentration (Taylor and Kunishi 1971). First, we collected 2-3 samples of sediment from each site, then combined 2.5 g wet subsamples with 25 ml of 0.01 *M* $CaCl_2$ containing 0-320 μg PO_4-P l^{-1}. Mixtures were vortexed every five minutes for 30 minutes and centrifuged (4500 x *g*). We determined supernatant concentrations by the ascorbate method (Anonymous 1973) and calculated equilibrium phosphate concentration (that concentration at which phosphate was neither adsorbed nor desorbed) at each of four sampling times between January and August, 1983.

We measured levels of several components at six-weekly intervals from late 1982 to late 1983. Phosphate concentrations from the bottom of the water column were averaged over all sampling dates. To estimate phytoplankton biomass, we sampled whole water by an integrating tube, passed it through

Whatman GF/C filters, ground filters in 90% acetone, and quantified chlorophyll a fluorometrically (Turner 1983). Fish collected by 1-m^2 drop traps (n = 5-12/site) were preserved in buffered formalin (Freeman et al. 1984); biomass is expressed as wet weight.

We conducted enclosure experiments at RC to determine if levels of nutrients equivalent to those left by birds would stimulate zooplankton prey available to fish. Clay pots filled with $(NH_4)_2HPO_4$-enriched agar (Fairchild et al. 1985, Oliver 1985) continually enriched each of three 2-m^2 corrals. Three other corrals were unenriched controls. In order to directly assess the enrichment effect on zooplankton, we removed fish by electroshocking. Zooplankton were quantified by filtering integrated water column samples through 64 µm mesh and preserving in buffered formalin and sucrose.

Results

As hypothesized, levels of several components of the food web were elevated at the abandoned rookery. Sediment nutrient availability, phytoplankton, zooplankton and fish were higher than at reference sites during at least the early part of the second year following abandonment.

Sediment nutrient availability measurements helped reveal long-term effects of former rookery activities on the ecosystem. Across all sample dates, equilibrium phosphate concentrations were significantly greater at R than at RC (two-way nonparametric ANOVA, $p < 0.001$, Zar 1984). RC can be considered a valid reference site, because equilibrium phosphate concentration at RC was not significantly different than that at other Okefenokee sites, LCP and MP (Fig. 2). These results indicate that about 1-2 years after birds abandoned the rookery, nutrient availability at R was still greater than at other sites. As may be expected from the greater available phosphorus in sediments, R water had a higher mean (and SE) value of 37.7 µg/L PO_4-P (8.1), compared to 18.2 (5.8) at RC, 7.9 (3.9) at LCP, and 7.5 (2.1) at MP, for samples taken at various times between November 20, 1982 and October 9, 1983; however these means are not significantly different. It is possible that phytoplankton rapidly assimilated much of the released phosphate which thereby stimulated their growth.

In fact, greater nutrient availability at the rookery site accompanied greater biomass of phytoplankton (Fig. 3). The trend over all sampling dates is clear: Chlorophyll a was greater at R than at RC. Seasonal patterns at the two sites were similar, increasing together in summer, then decreasing in late fall and winter. However, the factor by which the chlorophyll a level at R exceeded that at RC declined after March 1983; the mean R:RC ratio from July 1982 to March 1983 was 6.6, but after March was only 3.9. Thus, despite year to year changes in absolute levels of phytoplankton, there was some indication that greater levels in the abandoned rookery were approaching those in the control.

As with phytoplankton primary producers, primary consumers showed greater abundance in enriched than in unenriched marshland. Enrichment experiments had 4.4 times as many zooplankton as controls (Fig. 4, Mann-Whitney U = 146, p <0.025). These increases were largely a result of 6.5 times as many Diaphanosoma brachyurum, a phytoplanktivorous cladoceran, in experimentals (U = 155, p <0.005). In Okefenokee blackwater, zooplankton increased in response to macronutrient enrichment.

Levels of planktivorous fish were elevated in the abandoned rookery, then declined. We sampled fish from October 1982 through October 1983, i.e. 1.1-2.1 years after birds had left R. Fig. 5 indicates that fish biomass was greater in R than in RC or LCP from October 1982 until about February 1983. Specifically, biomass of Leptolucania ommata was significantly greater at R than at the other sites in October 1982 and in January and February of 1983 (Scheffe multiple contrasts and nonparametric contrasts, p <0.05 at each date). Gambusia affinis was greater at R than at other sites in October 1982. Enneacanthus gloriosus was greater there in February. Biomass of "other genera" was also significantly greater, in October and January. Total biomass of all fish was significantly greater at R, in October and January (p <0.05 for all of the above). Thus, most ichthyofauna showed some significant residual elevation at the rookery in the early samples that followed abandonment.

Fish biomass did not exhibit significant differences among sites at later dates (more than 1.5 years after birds ceased fertilization). For example, the large mean biomass of "other genera" at RC in October 1983 (Fig. 5) resulted from one unusually large fish in one of the traps; fish weight at RC was not significantly greater than at the other two sites (nonparametric contrast, $p > 0.05$). These data suggest that the effect of enrichment on higher order consumers rapidly diminishes. This contrasts with the slower diminution of algal primary producers.

Discussion

The suggestion that blackwater systems are severely nutrient-limited is supported by the results of this study. However, instead of describing changes due to an external anthropomorphic influence, we have documented effects of nutrients from avifauna, which differ in being part of the system itself. Analysis of sediment nutrient availability suggests that excess nutrients are deposited into sediments and delay the recovery of the system from enrichment for at least two years. More importantly, our observations indicate a stimulation of higher trophic levels, including zooplankton and fish. Therefore, it is reasonable to hypothesize that the influx of macronutrients from birds could provide an indirect, positive feedback mechanism which enhances their production as well.

Nesting wading birds evidently did raise the equilibrium phosphate concentration of sediments at the rookery site, by means of guano. A (positive) interaction arrow in Fig. 6 indicates this nutrient effect of wading birds on Okefenokee's microbially rich sediment complex (Murray and Hodson 1984), with no direct effect on the birds. Water column PO_4-P was not significantly greater at R than at other sites, but this may have been due to the several-fold higher levels of phytoplankton present. Higher phytoplankton and equilibrium phosphate concentrations are consistent with enhanced macronutrient availability.

Some of the increased sediment phosphate availability at R must have been taken up by phytoplankton, and probably contributed to the elevated biomass of phytoplankton there. The most common nutrient limitation in freshwaters is phosphorus, and phytoplankton can take up PO_4-P very rapidly (Wetzel 1975). In Okefenokee marshes, sediments have a high N:P ratio of 64:1 and P is likely to be limiting (Flebbe 1982). A linkage between sediments and phytoplankton, via residual nutrient transfer, is illustrated (Fig. 6).

Many of the dominant zooplankton found in Okefenokee marshes (e.g. Cladocera) are phytoplanktivorous. When we fertilized corrals continuously at levels below those that wading birds added to the Rookery during nesting (about 30% and 19% of nesting P and N, respectively; Oliver 1985), representing residual enrichment sometime after the birds had left, zooplankton biomass increased significantly. Abundance of the phytoplanktivorous cladoceran Diaphanosoma brachyurum was especially elevated. The residual enrichment from nesting birds appears to indirectly increase biomass levels of consumers through stimulation of algal resources (Fig. 6, phytoplankton --> zooplankton).

Because zooplankton and zooplanktivorous invertebrates comprise a major portion of the diet of fish in Okefenokee marshes (about 50% by weight, Chapter 4), it was reasonable that enrichment from sediments would lead to greater abundance of fish than in non-rookery sites. During the early samples, 1.1-1.5 years after birds left, biomass of various fish taxa were significantly greater in R relative to reference sites. Biomass declined to levels comparable to other sites thereafter. The increased weight of fish at R was mainly a result of greater levels of "other genera" (mostly the zooplanktivorous species Centrarchus macropterus, Fundulus chrysotus, and Etheostoma fusiforme.) Our data support the hypothesis that residual nutrients enhance the fish component (at the expense of zooplankton, Fig. 6).

Fish biomass at the rookery site declined relatively soon, 1.5 years after abandonment by birds, while sediment available P and phytoplankton were still elevated. Perhaps very high levels of enrichment during the active rookery (Stinner 1983) had contributed to earlier higher levels of fish. One and a half years after birds abandoned the site, macronutrient levels were still high enough to sustain elevated sediment equilibrium phosphate concentration and phytoplankton, but apparently not enough to sustain the fish production/biomass ratio of active rookery years.

The direct connections between components that are described above suggest some indirect influences in the ecosystem. To show these influences, we multiply the positive signs of consecutive direct interactions together, to yield indirect interactions (Levins 1975). The product of a positive interaction from wading birds to sediments, followed by a positive interaction from sediments to phytoplankton thus becomes a positive indirect effect (Fig. 6, dashed arrow from wading birds to phytoplankton). This effect is in accord with intuitive and known effects of P or N enrichment by birds on phytoplankton (Manny et al. 1975, Leentvaar 1967, McColl and Burger 1976). The remaining solid arrows of Fig. 6 are resolved into the remaining dashed arrows via similar multiplications, resulting in the elucidation of residual indirect positive effects of nesting wading birds on the zooplankton and fish communities.

Indirect effects between ecosystem components, via intermediate components, are increasingly recognized as potentially important within an ecosystem (Vandermeer 1980, Dethier and Duggins 1984). Patten (1982) has emphasized the importance of indirect effects (e.g., effects of enrichment by birds on fish). His mathematical analyses (Higashi and Patten 1986) have suggested that such indirect effects can exceed direct effects (e.g., possibly the effects of zooplankton on fish). Although the present paper is not a test of such theory, it does support the notion that indirect effects such as the effect of birds on plankton and fish can be significant in an ecosystem.

Would wading birds have benefitted from any stimulation of fish densities that they had indirectly caused? Was there a significant positive feedback from fish to birds, to close a cycle in the wetland ecosystem (Fig. 6)? White ibis eat a substantial fraction of the weight of their diet as fish, about 20% in southern Florida (Kushlan and Kushlan 1975), so there could have been a significant trophic pathway from fish to birds. Furthermore, most consumed fish are about 2 cm long (Kushlan 1979) and this size is common in Okefenokee marshes (Chapter 4). Wading birds did not appear to forage in the neighborhood of the rookery itself (Stinner 1983); foraging white ibis generally prefer shallower marshes (5-10 cm, Kushlan 1979). Ibis from R foraged up to 20 km away (Stinner 1983). Many wetlands within this radius are linked by water to the rookery site. It is possible that fish populations increased by nutrients from nesting birds dispersed into surrounding marshes where wading birds from the rookery ate them. However, because of the low probability of such distant encounters, a measurable positive feedback seems unlikely. In other aquatic ecosystems, water birds do eat a significant portion of the resident fish (e.g., Schaefer 1970). Thus, a positive feedback might be significant in other systems if bird rookeries are adjacent to feeding grounds.

In Okefenokee blackwater marshes, results suggest that residual levels of macronutrients left by nesting wading birds affected several trophic levels. Equilibrium phosphate concentration of the sediment complex was elevated at the abandoned rookery, and levels of phytoplankton were correspondingly elevated. These field results are corroborated by results from laboratory experiments, which indicated that sediments from the abandoned rookery released more PO_4-P to overlying water than sediments from other Okefenokee marshes, and overlying phytoplankton were then increased to greater levels (Schoenberg and Oliver in press). Experimental enrichment of Okefenokee corrals corresponding to levels left after birds had abandoned the site caused elevation of zooplankton primary consumers. Lastly, biomass of various fish taxa showed significant elevation in biomass at the rookery site, from the beginning of the study until 1.5 years after abandonment by birds. These results suggest that residual levels of nutrients left by nesting wading birds affected Okefenokee blackwaters, and that diverse components of the system (such as wading birds, the sediment complex, plankton and fish) were linked through direct and indirect macronutrient/biomass transfers.

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Fig. 1. Map of marsh sites mentioned in the text. Solid lines on the enlarged map delineate the Okefenokee Swamp watershed, its enclosed islands and watercourses.

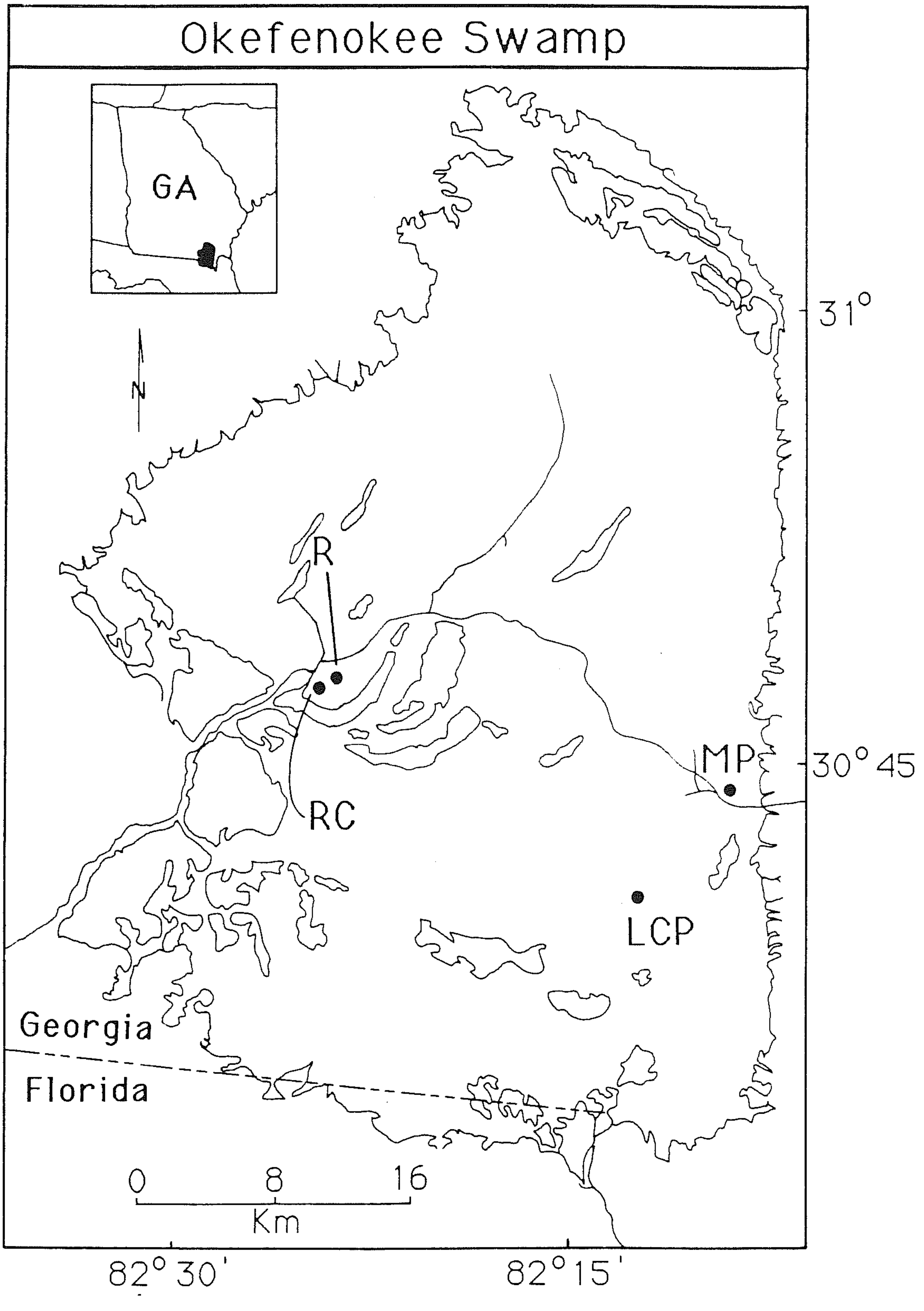

Okefenokee Swamp
GA
N
31°
R
RC
MP
30°45'
LCP
Georgia
Florida
0
8
16
Km
82°30'
82°15'

Fig. 2. Equilibrium phosphate concentrations at R, RC, LCP, and MP sites. N = 3 for each datum except n = 2 for LCP and MP. Vertical bars denote ±S.E.

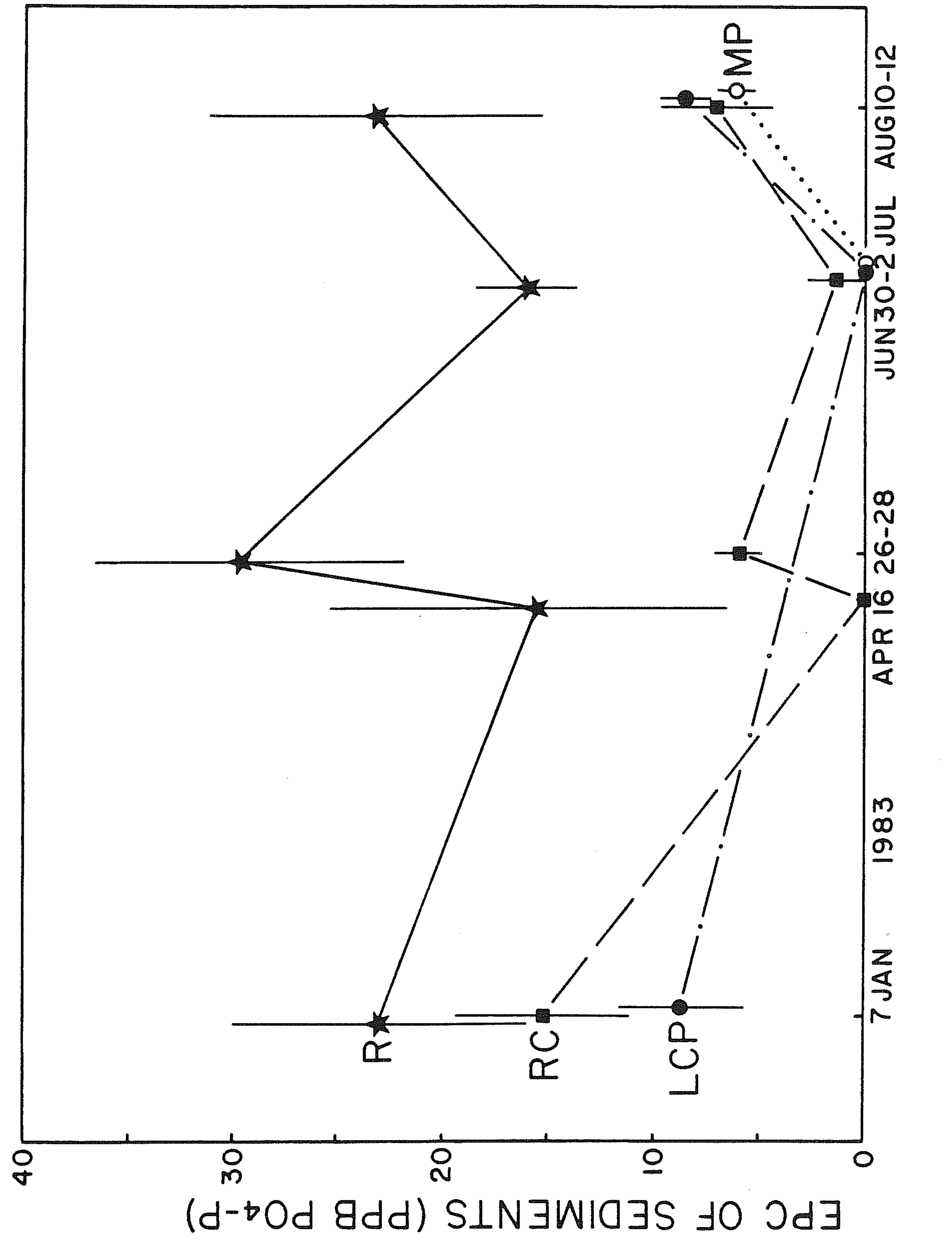

EPC OF SEDIMENTS (PPB PO4-P)
0
10
20
30
40
7 JAN
1983
APR 16
26-28
JUN 30-2 JUL
AUG 10-12
R
RC
LCP
MP

Fig. 3. Phytoplankton chlorophyll _a_ concentrations in the water column at R and RC. N = 2 for each datum. Bars (and parenthetical numbers) represent range.

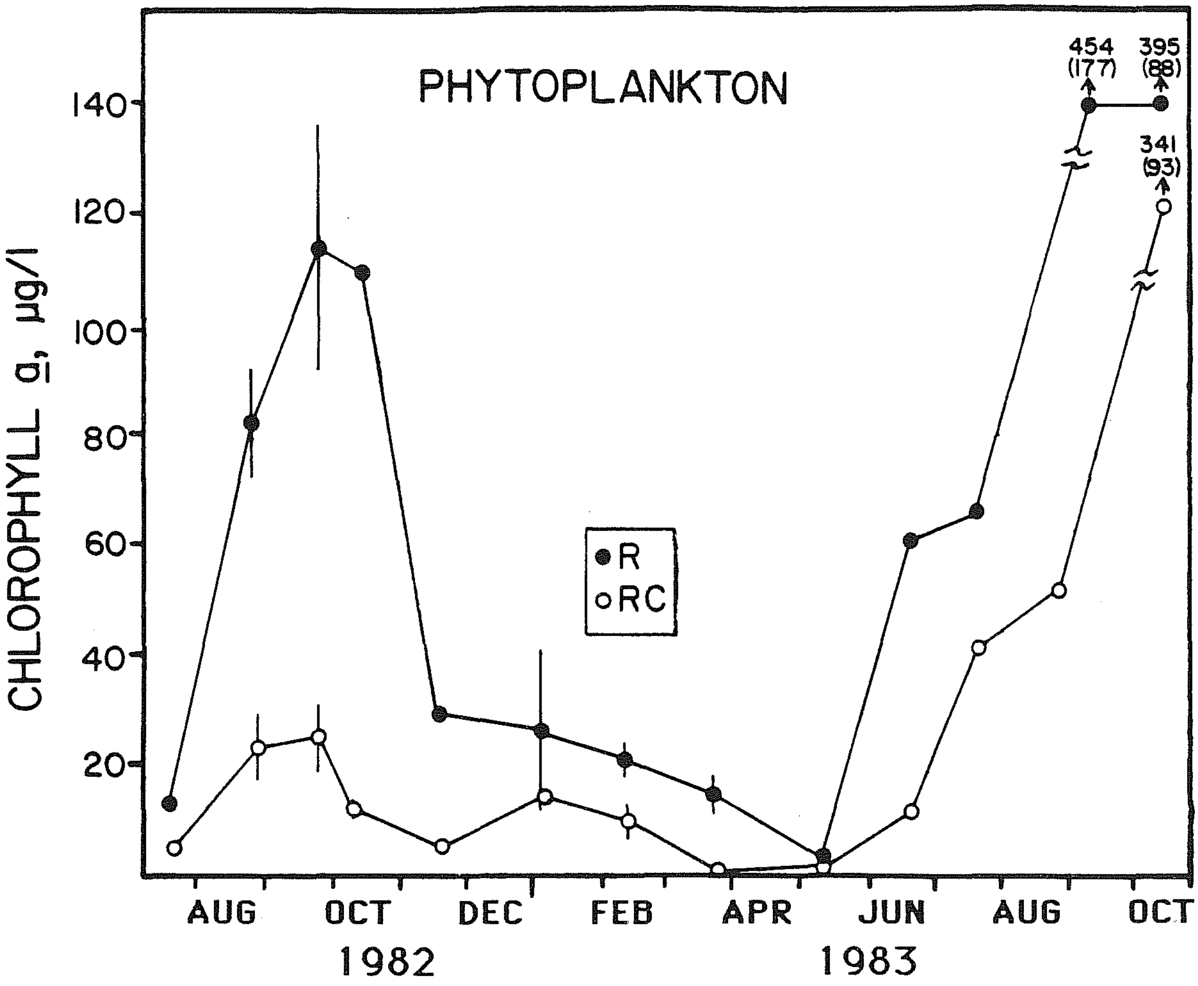

PHYTOPLANKTON
CHLOROPHYLL a, µg/l
140
120
100
80
60
40
20
● R
○ RC
454
(177)
395
(88)
341
(93)
AUG
OCT
DEC
FEB
APR
JUN
AUG
OCT
1982
1983

Fig. 4. Zooplankton densities in corrals receiving artificial enrichment of N and P (stars) versus no enrichment (circles), 1983. N = 3 for each datum except n = 2 on August 11. Bars represent ±S.E. Note log scales on ordinates. Modified from Oliver (1985).

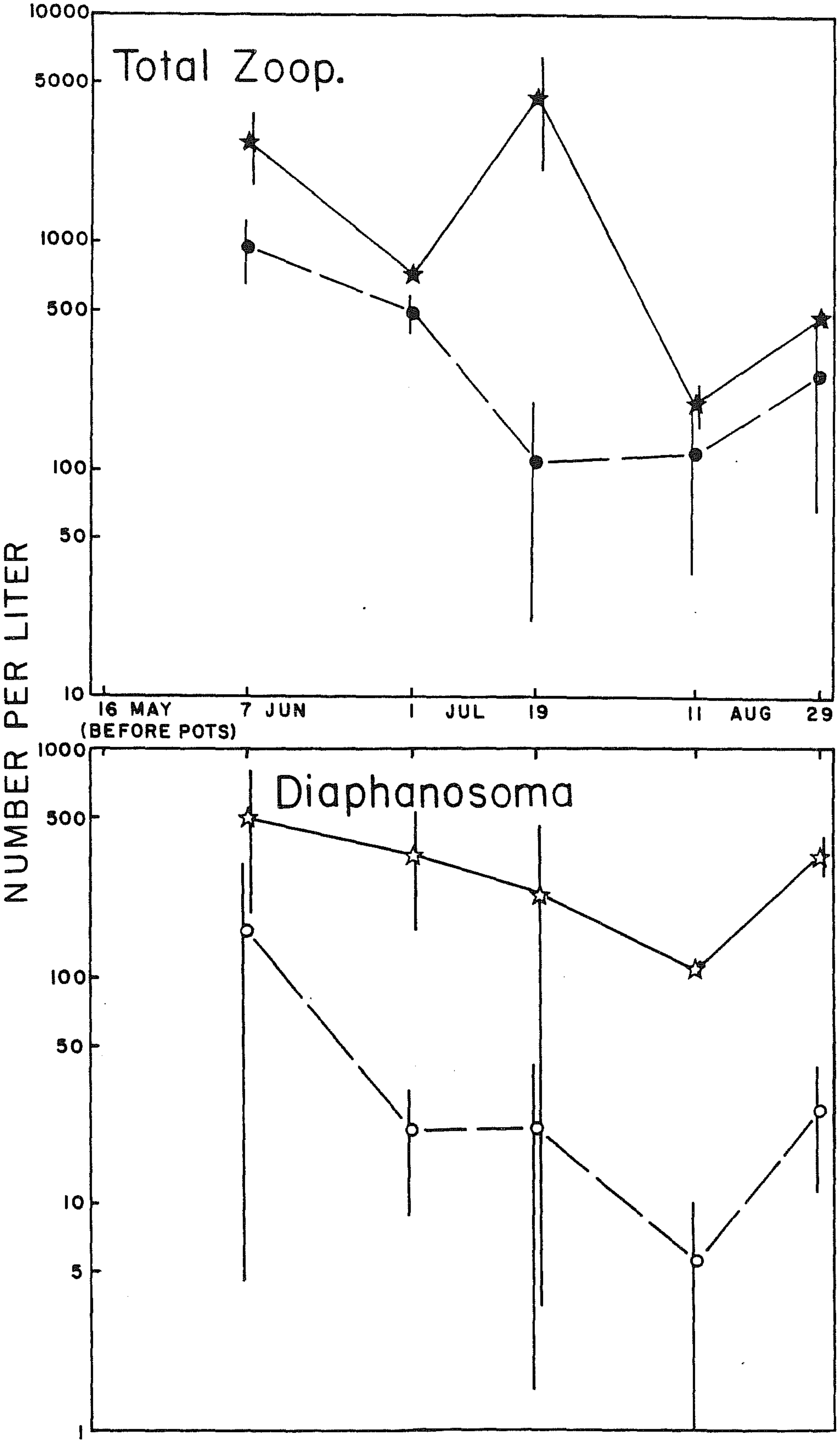

Total Zoop.
Diaphanosoma
NUMBER PER LITER
10000
5000
1000
500
100
50
10
16 MAY
(BEFORE POTS)
7 JUN
1
JUL
19
11
AUG
29
1000
500
100
50
10
5
1

Fig. 5. Fish biomass (wet g m^{-2}) in R contrasted with two other Okefenokee sites (RC and LCP). Each value is an average over n = 8, except that n = 6 in October 1982 at LCP, n = 7 in November at R and RC, n = 12 in January 1983 at RC, n = 7 in February at LCP, n = 5 in June at R, n = 7 in August-September at R, and n = 7 in October 1983 at RC. A plus sign indicates that biomass at R is significantly greater, a negative significantly less than at other sites ($P < 0.05$). See text.

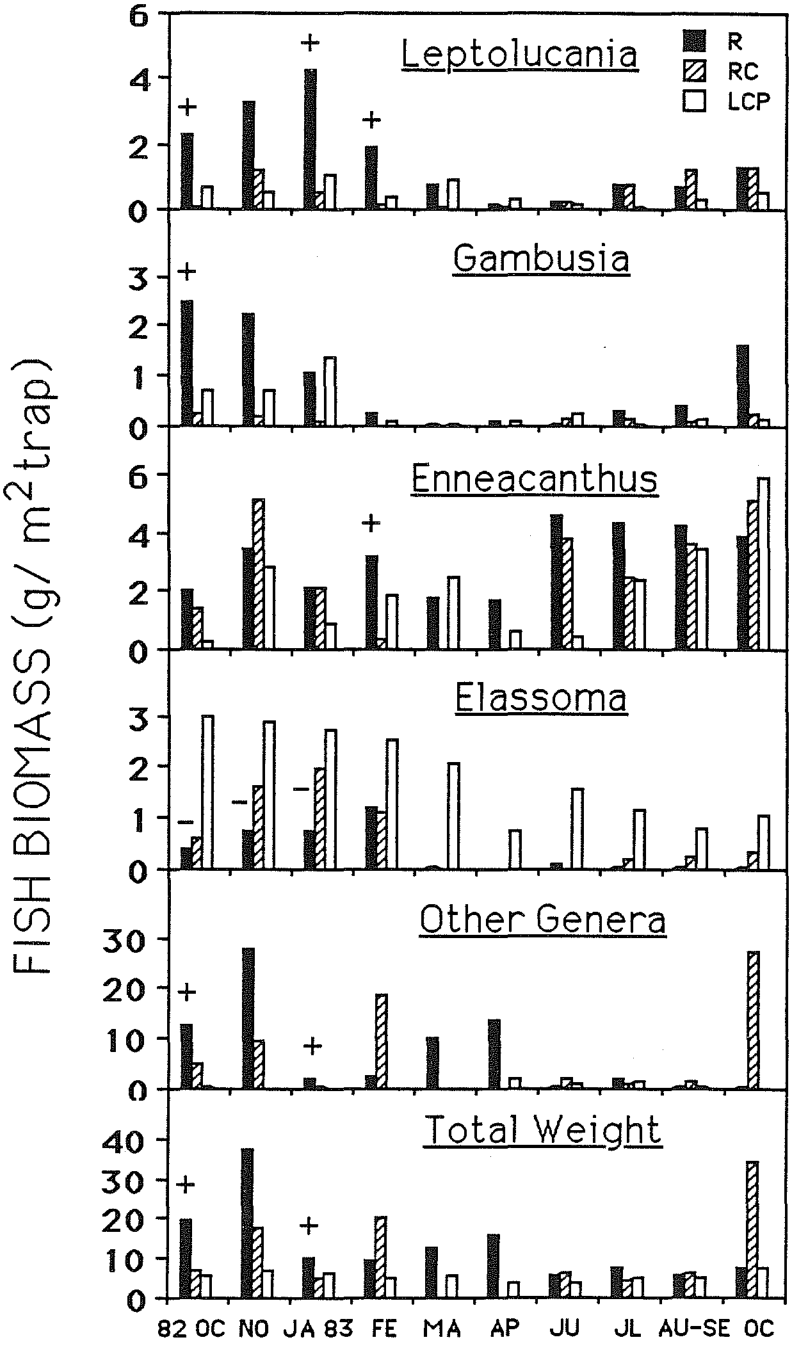
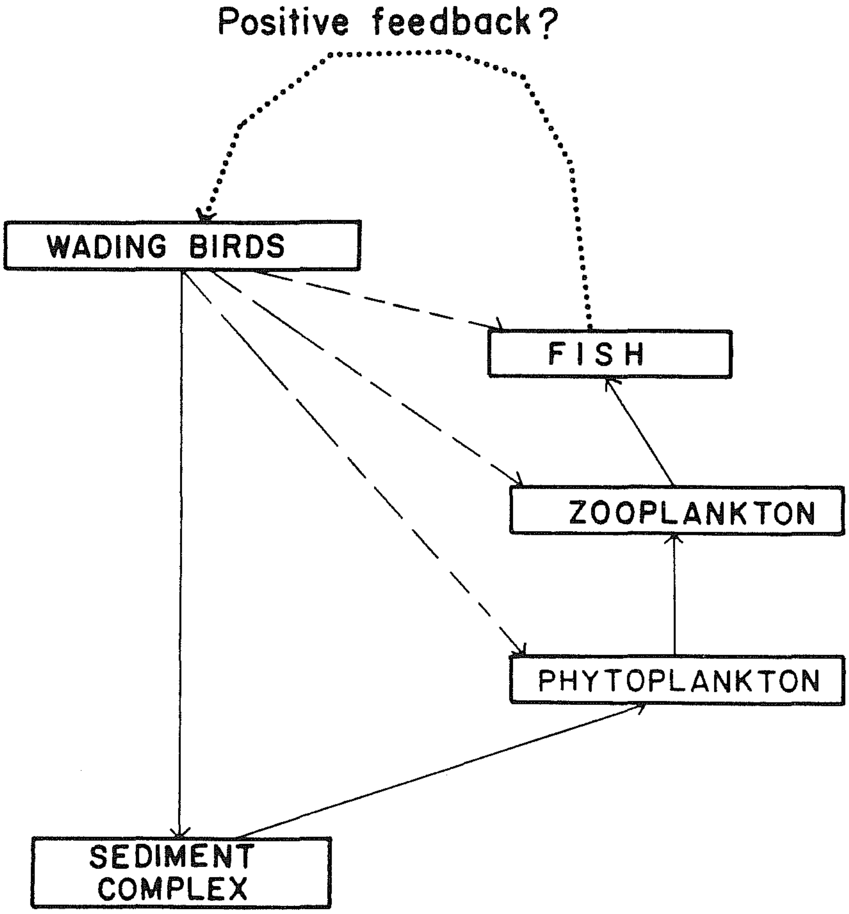

FISH BIOMASS (g/ m^{2}trap)
Leptolucania
Gambusia
Enneacanthus
Elassoma
Other Genera
Total Weight
R
RC
LCP
+
−
0
1
2
3
4
6
10
20
30
40
82 OC
NO
JA 83
FE
MA
AP
JU
JL
AU-SE
OC

Fig. 6. Interactions via macronutrient transfer in an aquatic ecosystem (Okefenokee Swamp marsh). Solid arrows indicate positive direct relationships, dashed arrows show indirect relationships, and a dotted arrow indicates a possible relationship. See text.


Positive feedback?
WADING BIRDS
FISH
ZOOPLANKTON
PHYTOPLANKTON
SEDIMENT COMPLEX

CHAPTER 4

CONSUMPTION, EVACUATION RATES AND DIETS OF PYGMY KILLIFISH, *LEPTOLUCANIA OMMATA*, AND MOSQUITOFISH, *GAMBUSIA AFFINIS* (OSTEICHTHYES: ATHERINIFORMES) IN OKEFENOKEE SWAMP[1]

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[1] J. Douglas Oliver. Submitted to Brimleyana, 9/3/87.

Introduction

Researchers know relatively little about fishes of freshwater wetlands and their feeding (Weller 1981). They have examined diets of fishes from wetlands, but most often from salt and estuarine marshes (e.g., Wetzel 1969, Harrington and Harrington 1961, Kjelson et al. 1975). To my knowledge, there are no previous studies on consumption or evacuation rates of any fish in any salt or freshwater wetland.

The purposes of this study are to determine the diets and rates of consumption and evacuation under field conditions, for two of the most abundant fishes of a marsh on the west side of Okefenokee Swamp, Georgia, a large freshwater wetland. Consumption and evacuation rates will be used for a model of this marsh, and represent the first feeding dynamics for the fish species, *Leptolucania ommata* and *Gambusia affinis*. To quantify dynamics at the ecosystem level and to estimate minimum invertebrate prey production, I then use measures of daily food consumption to estimate area-based consumption (consumption per m^2) by these fish. Such invertebrate production estimates may help to resolve whether blackwater habitats have low secondary productivity, as suggested for tropical blackwaters (Janzen 1974, Fittkau et al. 1975, Araujo-Lima et al. 1986), or substantial productivity (Freeman and Freeman 1985). Methods are field-based to obviate elaborate laboratory feeding studies and to obtain data under natural conditions.

The two fishes examined are *L. ommata*, the pygmy killifish, and *G. affinis*, the mosquitofish, small members of the Atheriniformes. *L. ommata* lives in quiet, densely vegetated freshwaters from southern Georgia and Alabama to Florida (McClane 1955, Laerm et al. 1980). *G. affinis* is native to southern coastal United States but has been introduced to warm waters around much of the world, primarily to consume juvenile mosquitos (Hess and Tarzwell 1942, Hurlbert and Mulla 1981). In marshes on the west side of Okefenokee Swamp, *L. ommata*, *G. affinis*, *Enneacanthus gloriosus* and *Elassoma okefenokee* are by far the most numerous fishes (R and RC sites, Chapter 3). The individuals in this study are adults of common length distribution (*L. ommata* of 13-20 mm, *G. affinis* of 15-25 mm standard length).

The study site is a shallow subtropical marsh which has large daily temperature fluctuations. It lies approximately 200 m east of the entrance to the Suwannee River sill (an earthen dam that borders the west side of Okefenokee Swamp). This blackwater area (mean depth 43 to 113 cm) had floating and submersed macrophytic vegetation (mainly *Nuphar luteum* and *Utricularia* spp.) Daily water temperature ranges were 4-20°C during the winter experiments, and 26-37°C during summer experiments.

Methods

I obtained evacuation rates by two related methods, simultaneously. This allowed comparison of results obtained by both (cf. single method analysis, e.g., Sainsbury 1986). In the first ("tank") method, the decline in gut contents of fish held without food was converted to evacuation rate (Staples 1975, Garcia and Adelman 1985). Clear immersed tanks at the edge of the marsh tracked ambient water temperatures and light levels. Okefenokee water was filtered into them through a mesh (<64 µm) to remove potential food items. At 4-h intervals, large fish captured by seine were placed into different tanks than smaller fish so they would neither frighten nor consume the latter. I preserved about half the fish quickly in buffered formalin and preserved the rest approximately 4 h later, for comparison of gut contents. In the "field" method, the decline in gut contents between field samples of adjacent periods during non-feeding times of day yielded a second measure of evacuation rates. (See FEEDING DYNAMICS for an example of evacuation analyses).

In the laboratory, lengths of foods in foreguts were converted to weights. (Foreguts were analyzed because their contents declined consistently with time in tanks, whereas hindguts continued to receive food from foreguts in some cases). I examined foregut contents under a dissecting microscope and measured lengths of food items. Length-weight regressions in Dumont et al. (1975) yielded dry weights of Ostracoda, Harpacticoida, nauplii and most Cladocera. Hall et al. (1970) gave macrothricid weights. Insect head capsule widths were converted to weights (Smock 1980). Ruttner-Kolisko (1977) and J. Gerritsen and H.S. Greening (pers. comm.) gave rotifer length-weight conversions. A regression by Gerritsen for Okefenokee Swamp (pers. comm.) derived cyclopoid weights. Maximum carapace widths of araneids were converted to weights (Barber 1983, Edgar 1971). Weights of Acari were estimated from the regression of Oribatei by Persson and Lohm (1977). An unpublished length-weight regression yielded weights of *Gambusia affinis* in foreguts. Foregut content (S) was expressed in relative units, i.e., mg dry food(g dry fish)$^{-1}$, assuming 20% dry to wet weight conversion for fish (e.g., Lagler et al. 1977).

I calculated evacuation rates, daily food consumption and area-based consumption for both fishes. Area-based consumption equals the dry weight equivalent of fish biomass (Chapter 3) times calculated daily food consumption (Staples 1975, adjusted in Elliott and Persson 1978; Persson 1982, Garcia and Adelman 1985).

Analyses and Results

DIETS

Chironomids and Cladocera dominated the diet of *Leptolucania ommata*. Major foods were non-tanypode Chironomidae, tanypode Chironomidae, unidentified Insecta and Cladocera (Table 1). Oribatid mites, not usually found in fish guts (B.J. Freeman of the University of Georgia, pers. comm.), were eaten by both *L. ommata* and *G. affinis*.

In *Gambusia affinis*, insects strongly predominated in the diet, but other arthropods and some fish were eaten. In summer, Tanypodinae and odonate larvae were significant foods (Table 1). Cladocera, Cyclopoida and Araneae composed more of the diet in summer than in winter. In both winter and summer, non-tanypode Chironomidae and unidentified Insecta were dominant food items. *G. affinis* showed some cannibalism (in summer, about 3%).

FEEDING DYNAMICS

Gambusia affinis

The balance between consumption and evacuation may be inferred from diel changes in foregut content (solid lines on Fig. 1). When the slope of the line is positive, consumption rate is greater than evacuation rate during the specified time period; when negative, consumption is less than evacuation.

Analysis of evacuation rates is based on comparisons of gut content trends obtained by field vs tank methods. During certain periods, (such as 10:55 AM until 2:55 PM,) fish in the field actively fed, resulting in an increase in their foregut contents (Fig. 1). For such periods, it is necessary to use fish held in food-free tanks (dashed lines) for calculating evacuation rates. At other times (6:50 PM until 10:50 PM), foregut contents declined in field fish and in tank-held fish. For these periods, field fish were unconfined and egesting in their natural environment and provide the better estimate of evacuation rate. Evacuation rate,

$$r = \frac{\ln(S_o+1)-\ln(S_t+1)}{t} ,$$

in which S_o is relative foregut content before and S_t is relative foregut content after time t (adapted from Elliott and Persson 1978; 1 added to allow logarithmic transformation of zeros). The same equation applies for determining evacuation in tank-held fish. When evacuation data were missing for a period, evacuation rate was presumed to be an average of rates before and after that period. Finally, the various rates during the day were weighted by time to produce an average evacuation rate (Table 2).

Evacuation rates for each of the time periods were used in calculating consumption over each of these periods. Each such evacuation rate was combined with average foregut content before and after the period to yield consumption during the period (adapted from Elliott and Persson 1978):

$$C_t = \frac{((S_t+1)-(S_o+1)e^{-rt})rt}{1-e^{-rt}} .$$

Daily food consumption, ΣC_t, is the sum of consumption rates over each period. For G. affinis in summer, the graph of consumption vs time (bottom panel of Fig. 1) indicates that peak consumption occurred in the afternoon.

G. affinis from winter samples showed feeding trends similar to summer but at lower levels. Evacuation rate and daily food consumption were lower in February than in August (Table 2). There was a single feeding peak in late afternoon, as in summer. Low daily food consumption combined with low fish biomass to produce very low area-based consumption.

Leptolucania ommata

L. ommata showed diel feeding patterns similar to G. affinis. Foregut content in summer peaked in late afternoon (Fig. 2). Consumption showed one daily peak, in the afternoon. In winter (March 1984), L. ommata also consumed maximally in the afternoon, as other species-season combinations had done.

L. ommata had seasonal feeding dynamics similar to G. affinis. Evacuation rate in summer was 0.279 h^{-1}, similar to the 0.262 h^{-1} calculated for G. affinis in summer (Table 2). Evacuation rate in winter was also similar in the two species, 0.143 and 0.157 h^{-1}, respectively. In both species, daily food consumption increased from winter to summer by a factor of about 4 (3.85 for L. ommata, 4.62 for G. affinis).

An inconsistency in a third set of L. ommata data appeared resolvable. In winter 1985 (February), estimated evacuation rate was 0.345 h^{-1} and daily food consumption was 214.1 mg g^{-1} d^{-1}, values that were higher than in summer. Closer analysis revealed that if one unusually large insect had not been present in each of two foreguts (out of 3 foreguts examined), rates would have been much lower, 0.074 h^{-1} and 39.0 mg g^{-1} d^{-1}. Thus L. ommata rates from February 1985 are considered anomalous and those from March 1984 are taken as more appropriate winter values.

Discussion

Diets, evacuation and consumption by the two fishes in wetlands were similar to values reported for fishes in other types of habitats. The diet of *Leptolucania ommata* in the Okefenokee marsh was mainly chironomid larvae and other insects as well as Cladocera. Similarly, in the nearby St. Johns River system, *L. ommata* ate mainly chironomids, Cladocera and Copepoda (McLane 1955).

Gambusia in Okefenokee consumed mainly insects and Cladocera. They ate chironomids, odonates, other insects and various Cladocera (Table 1). *G. affinis* at Gulf Breeze, Florida, ate mostly insects, copepods, algae and plant detritus (Wetzel 1971). (Probably the two latter food categories were different than at Okefenokee because the Gulf Breeze fish were from a different type of environment, a salt-marsh canal). *G. affinis* in shallow areas of Wheeler Reservoir, Alabama, ate mostly Entomostraca (presumably Cladocera or Copepoda), Chironomidae, and juvenile insects (*Anopheles*) (Hess and Tarzwell 1942). Thus, *Gambusia* in Okefenokee fed primarily on the same kinds of foods that they ate in other nearby regions.

However the Okefenokee site was unusual in being a freshwater marsh, and it had some unusual fish foods. The two fishes in this algal, detrital system ate oribatid mites, which are often associated with such substrates

(Pennak 1978). Nevertheless, Oribatei were a minor component of their diets (Table 1).

The two fishes fed on similar kinds of foods. This may not be surprising since I captured them in the same areas and observed them feeding at about the same depth, near the surface. These fishes may minimize competition between their similar trophic niches by some temporal partitioning of food resources. G. affinis appears to do some feeding at night (Fig. 1; Maglio and Rosen 1969) whereas L. ommata appears to confine feeding to daylight (Fig. 2). That G. affinis may feed at night is consistent with their possession of open cephalic canals containing "neuromasts almost if not, in contact with the surface film. Disturbances on the surface caused by trapped insects would probably be sensed ... rapidly" (Rosen and Mendelson 1960). G. affinis may minimize competition for food by maintaining activity at night (Wetzel 1971) and feeding even when light levels are low.

Both fishes showed peak consumption rates at about the same time of day, the afternoon. Afternoon usually had bright sunlight and the highest temperatures of the day, and these factors may have contributed to increased consumption. Increased temperatures usually result in increased consumption by fish that are heat-tolerant (Reddy 1975, Mann 1978, Smagula and Adelman 1982, Garcia and Adelman 1985) and high illumination may make feeding more effective, particularly in a vegetated, blackwater environment like an Okefenokee macrophytic marsh.

Evacuation rates of the two fishes were alike, and similar to rates reported for other fishes. Foregut evacuation rates were 0.143 and 0.279 h^{-1} for L. ommata in winter and summer, respectively. Similarly, rates for G. affinis were 0.157 and 0.262. Doble and Eggers (1978) reported rates of 0.109 and 0.267 h^{-1} for Oncorhynchus nerka small juveniles in winter and summer. Persson (1982) found rates of 0.129 and 0.499 h^{-1} for Rutilus rutilus held at 12 and 24°C in the laboratory. Thus, evacuation rates for L. ommata and G. affinis appear to be well within the range of values reported for various fishes.

Consumption measures of Gambusia and Leptolucania in Okefenokee Swamp are in the same range as estimates for other fishes. Daily food consumption by L. ommata was 24.2 and 93.1 mg g^{-1} d^{-1} (dry weights), in winter and summer, respectively. Values for G. affinis were 32.1 and 148.3 mg g^{-1} d^{-1}. Doble and Eggers (1978) found that Oncorhynchus nerka juveniles ate 15.3 and 44.1 mg g^{-1} d^{-1} in Lake Washington in winter and summer, respectively. Garcia and Adelman (1985) reported that Cyprinus carpio in the Mississippi River consumed 204 mg g^{-1} d^{-1} in summer (assuming a fish dry to wet ratio of 20%). Thorpe (1977) reported summer consumption by Perca fluviatilis in Loch Leven to be 54 mg g^{-1} d^{-1} (dry weights, assuming fish dry to wet ratio of

20% and prey wet to dry ratio of 6; Freeman and Freeman 1985) but this was an underestimate (Elliott and Persson 1978). Basimi and Grove (1985) reported that summer consumption by small Pleuronec-tes platessa off the coast of Wales was 43 mg g^{-1} d^{-1} (assuming the same ratios). Food consumption rates of L. ommata and G. affinis from the Okefenokee wetland obviously fall within the range of fish from other types of environments.

As expected, area-based consumption by the two fishes was low in winter and higher in summer. Leptolucania ommata in the Okefenokee marsh consumed 0.71 and 22.99 mg m^{-2} d^{-1} in winter and summer, respectively. Gambusia affinis ate less because of their lower biomass; they consumed 0.33 and 3.32 mg m^{-2} d^{-1} in winter and summer, respectively. In comparison, in a small New Zealand lake with only one fish species, Staples (1975) reported that Philypnodon breviceps in summer consumed 203 mg m^{-2} d^{-1} (assuming a wet to dry ratio of 6), but this value was an underestimate (Elliott and Persson 1978). In a New Zealand stream where trout and eels were also present (Hopkins 1970, in Staples 1975), the maximum reported area-based consumption by P. breviceps was equivalent to 74 mg m^{-2} d^{-1}.

Consumption data support a hypothesis that invertebrate prey production in Okefenokee blackwater marshes is substantial. Consumption values in spring and fall are usually between winter and summer values (e.g., Staples

1975, Doble and Eggers 1978). Thus, averaging winter and summer consumption values may give a reasonable estimate of average daily food consumption for the whole year. Such averaging of consumption values (from Table 2) yields estimates of 58.7 and 90.2 mg g^{-1} d^{-1} for _L. ommata_ and _G. affinis_, respectively. When each of these values is multiplied by average dry biomass per m^2 (Chapter 3) for each of these fishes, consumption by both _L. ommata_ and _G. affinis_ is calculated to be 7.37 mg m^{-2} d^{-1}. Assuming a wet to dry conversion of 6, invertebrate prey production would have to be at least 160 kg ha^{-1} yr^{-1} (wet weight), just to meet consumption needs of these fish. At a recently abandoned bird rookery on the west side of Okefenokee, guano fertilization apparently increased standing stocks of several trophic levels, including fish (Chapter 3): Average annual biomass estimates of _L. ommata_ and _G. affinis_ were elevated. Invertebrate production may have been substantial, at least 730 kg ha^{-1} yr^{-1}, just to meet consumption by these fish. This estimate of invertebrate prey production is on the same order as the 680 kg ha^{-1} yr^{-1} estimated for a marsh on the east side of Okefenokee Swamp (Freeman and Freeman 1985).

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Table 1. Percent of total dry diet (and standard error) attributable to various foods in winter and summer. Numbers of foreguts (in brackets) are about equally represented from all parts of diel cycle.

Food category	*Leptolucania ommata*				*Gambusia affinis*			
	March, 1984 [27]		August, 1984 [30]		February, 1985 [12]		August, 1984 [23]	
Chydoridae	4.66	(1.54)	2.23	(0.53)	0.02	(0.01)	0.29	(0.11)
Macrothricidae	1.06	(0.45)	0.52	(0.21)	0.02	(0.02)	0.20	(0.08)
Other Cladocera	9.44	(3.04)	5.71	(2.39)	0.10	(0.06)	1.51	(0.63)
Ostracoda	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.05	(0.02)
Harpacticoida	0.30	(0.16)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
Cyclopoida	0.61	(0.56)	1.26	(0.47)	0.00	(0.00)	0.76	(0.27)
Nauplii	0.05	(0.05)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)
Rotifera	0.00	(0.00)	0.02	(0.01)	0.00	(0.00)	0.00	(0.00)
Non-tanypode Chironomidae	46.56	(20.64)	43.63	(23.20)	4.76	(4.76)	9.73	(4.96)
Tanypodinae	35.67	(21.92)	20.72	(14.65)	0.00	(0.00)	13.59	(7.80)
Hemiptera	0.00	(0.00)	3.67	(3.67)	0.00	(0.00)	3.44	(1.30)
Odonata	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	15.50	(12.00)
Unidentified Insecta	1.65	(1.65)	21.87	(19.23)	94.25	(55.05)	35.44	(14.13)
Araneae	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	15.91	(7.72)
Oribatei	0.00	(0.00)	0.35	(0.29)	0.84	(0.57)	0.61	(0.28)
Other Acari	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.02	(0.01)
Fish (*G. affinis*)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	2.94	(2.94)
TOTAL	100.00		100.00		100.00		100.00	

Table 2. Evacuation rates and food consumption. Food in mg, fish in g dry weight.

Species	Season	Sampling dates	Foregut evacuation rate, r (h^{-1})	Daily food consumption, ΣC_t (mg g^{-1} d^{-1})	Fish biomass (g m^{-2})	Area-based consumption (mg m^{-2} d^{-1})
L. ommata	Winter	February 11, 1983			0.0292	
		March 7-8, 1984	0.143	24.2		0.71
	Summer	August 29, 1983			0.2468	
		August 19-20, 1984	0.279	93.1		22.99
G. affinis	Winter	January 4-5, February 11, 1983*			0.0103	
		February 16-17, 1985	0.157	32.1		0.33
	Summer	August 29, 1983			0.0224	
		August 19-20, 1984	0.262	148.3		3.32

* No *G. affinis* were captured in February 1983, so biomass is averaged over January and February.

Figure 1. Foregut content and food consumption of G. affinis in summer. In upper panel, filled circles and solid lines show diel content trends in field fish; open squares and dashed lines show changes in content of fish held in food-free tanks. In lower panel, filled circles and solid lines show trends in consumption during each time period; open circle and dotted lines show presumed trend based on difference between the final (4:30 PM) and initial (8:50 PM) consumption values.

Gambusia affinis
AUGUST

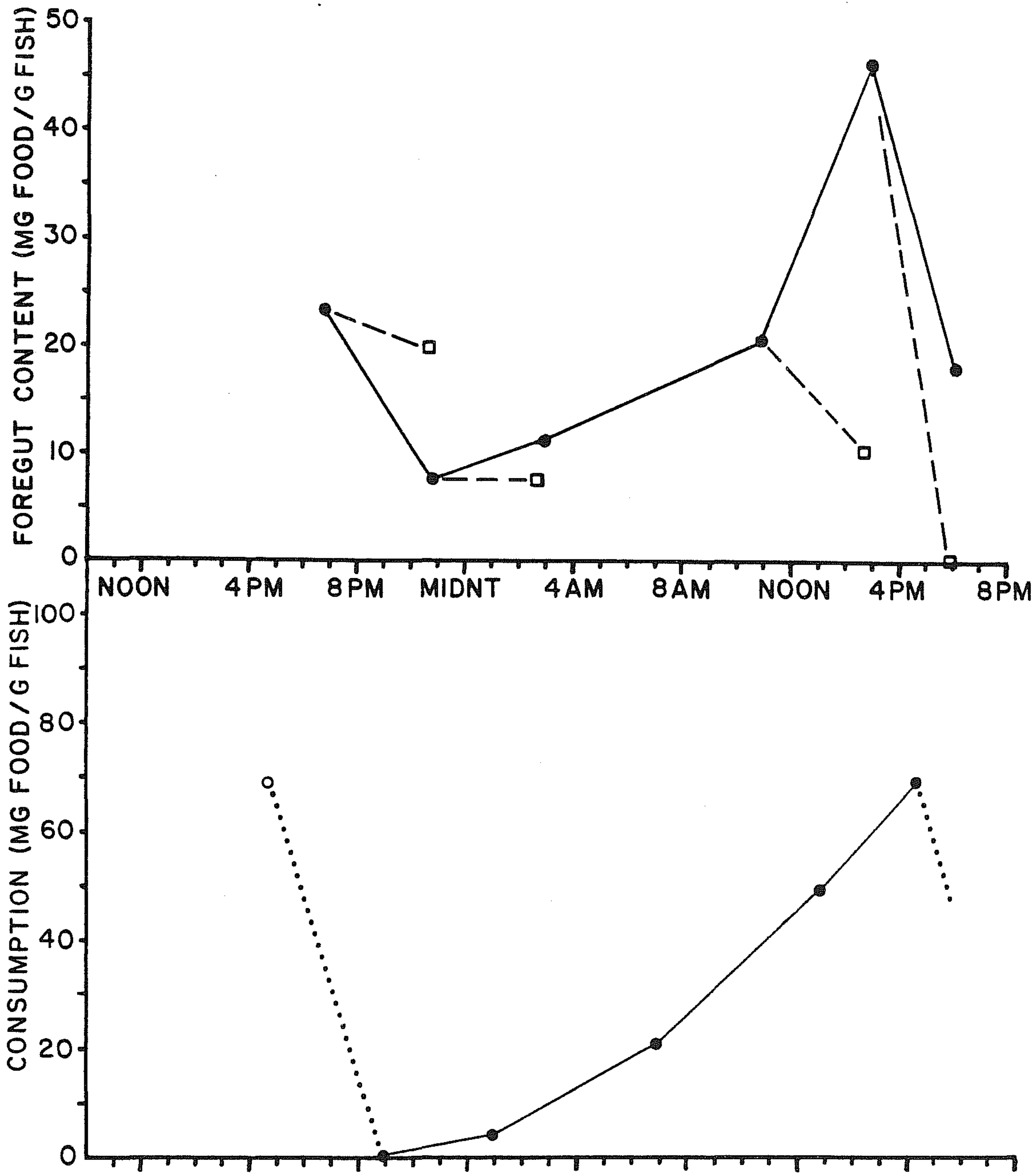
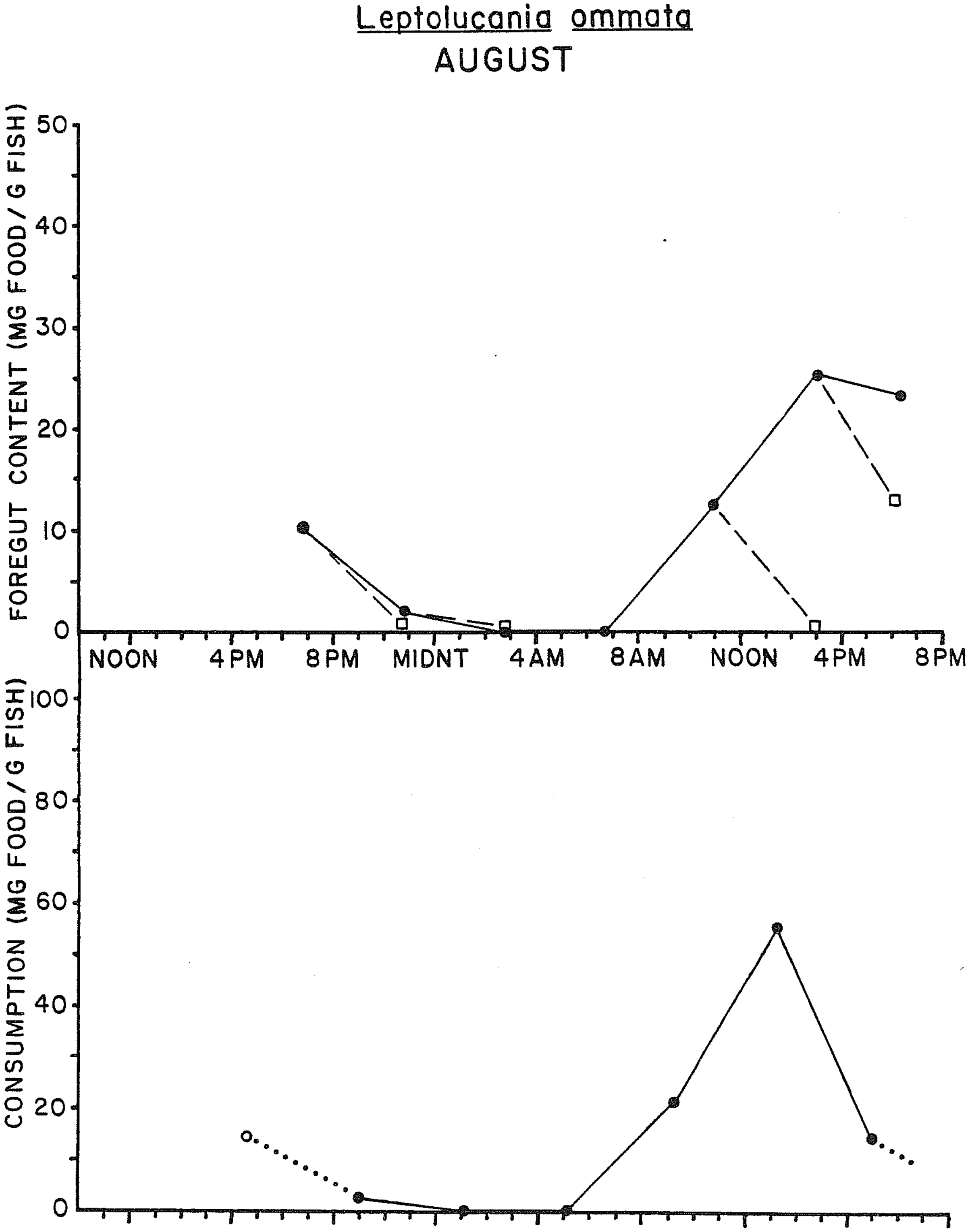


Figure 2. Foregut content and food consumption of <u>L. ommata</u>. (See Fig. 1 legend for details).


Leptolucania ommata
AUGUST
FOREGUT CONTENT (MG FOOD/G FISH)
0
10
20
30
40
50
NOON
4PM
8PM
MIDNT
4AM
8AM
NOON
4PM
8PM
CONSUMPTION (MG FOOD/G FISH)
0
20
40
60
80
100

CHAPTER 5

OKEFENOKEE MARSHLAND BEFORE, DURING AND AFTER NUTRIENT ENRICHMENT BY A BIRD ROOKERY[1]

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[1] J. Douglas Oliver and Tarzan Legović. Accepted by Ecological Modelling, 10/19/87.

Introduction

Nutrient enrichment can increase the biomass of various trophic levels of an aquatic system. A well known example is addition of sewage to freshwater which results in increased phytoplankton and therefore increased production of zooplankton (Wetzel 1975). In some instances, nutrients are added deliberately, e.g., to southern farm ponds to increase the biomass of plankton and thus increase the biomass of centrarchid fishes (Swingle 1956). In an abandoned bird rookery of Okefenokee Swamp, Oliver and Schoenberg (Chapter 3) found indications that long-term nutrient release from bird guano also increased biomass of various trophic levels. We constructed a model of the marsh ecosystem to investigate the effect of such a natural influx of nutrients on plankton, fish, insects and macrophytes, and to estimate the unmeasured increase in fish during the active rookery.

Various workers have used models to examine the effects of nutrient enrichment on freshwater wetlands. Patten (1975) modeled an Oklahoma reservoir cove, then simulated a ten-fold increase in phosphorus (P) from land. According to the model, this increased phytoplankton to 1.35 times nominal levels, submerged macrophytes to 1.24, dead plants to 1.27, particulate organic matter to 1.12, zooplankton to 1.14, deposit-feeding and carnivorous insects to 1.01 and fishes to 1.001 times unenriched levels. Bayley and Odum (1976) estimated model coefficients for an Everglades marsh, then showed that resulting levels of sawgrass resembled those in the field. Simulated P inputs resulted in buildup of the sawgrass. Mitsch (1976) simulated diversion of sewage inflow from a shallow Florida lake, which resulted in reduction of water hyacinths to 0.5 and benthic detritus to 0.3 times eutrophied levels. Dixon and Kadlec (1975, in Howard-Williams 1985) modeled effects of wastewater on a wetland and indicated that, according to the model, most detrital components increased for at least 10 years. Mitsch (1983) simulated effects of application of treated wastewater to a north Florida cypress dome, which resulted in simulated understory plants increasing to 1.5-4.0 and peat increasing to 1.2-2.8 times nominal levels. See Costanza and Sklar (1985) for a recent review of models of freshwater wetlands. Although such models cover a wide range of situations, we know of no previously published marsh simulation models that included a fish compartment.

In this paper, our goal is to obtain a deeper understanding of the effects of birds on Okefenokee marshland. Specifically, we are interested in projecting the effects of increased nutrient inputs (principally P) from guano on dynamics of levels of benthic detritus P, phytoplankton, zooplankton, insects, fish and aquatic macrophytes. In the first step we construct the model, simulate the dynamics of model components for a marsh that lacked birds (control site, Fig. 1) and compare model dynamics with existing data. We then apply the model to an active rookery site, characterized by increased nutrient input, and compare model macrophyte results with field data from the active rookery. Finally, we use the model to project a transition phase from active rookery back to control (i.e., the rookery site after abandonment by birds) and compare model results to existing data collected there. Since density of fish was not measured when the rookery was active, we use the model to estimate the increase in density of fish due to nutrient increase (evidence of which had been seen as increased fish biomass in the abandoned rookery, Chapter 3).

Area of Study

Okefenokee Swamp, the largest entirely freshwater wetland in the United States (1800 km^2), should be highly affected by added guano. Because it lies in a sandy watershed, its blackwater is low in minerals (Auble 1982), and its nutrient inputs come mainly via rain (Blood 1981). Thus, Okefenokee has unusually low nutrient inputs (Table 2) unless birds are nesting. Furthermore it is shallow (0.5 m depth at our sites), and many of its organisms feed partly on a benthic layer of peaty detritus. Since most guano P is not soluble (Stinner 1983), most should become detritus to help feed these detritivores. For these reasons, effects of added nutrients from a rookery should be important.

The sites we model are subtropical, vegetated marshes within the Okefenokee National Wildlife Refuge (Fig. 1).

Floating and submerged macrophytes (Nuphar luteum, Utricularia spp., Cabomba pulcherrima) dominate the rookery site (30° 47' N, 82° 25' W). For at least 11 consecutive spring-summer periods, 2000-30000 wading birds, predominantly white ibis (Eudocimus albus), had nested in shrubs and trees adjacent to this site. In 1979-1980, Stinner (1983) found significant increases in macronutrients in aquatic macrophytes during nesting. She estimated that the total amount of phosphorus addition by the birds, 4.6 g m^{-2} yr^{-1}, was comparable to crop field fertilization. In 1981, following a drought in much of the southern United States, the birds did not return, at least not for several years.

We chose a control site similar to the rookery site but not affected by nesting wading birds. This site (Fig. 1) is located 1.6 km from the rookery. It has similar depth and floating and submersed vegetation (e.g., Nuphar luteum, Utricularia spp.) but has lacked rookeries for at least 15 years.

Methods

Phosphorus is most often the limiting nutrient in freshwater systems (Wetzel 1975) and is a major nutrient in guano (e.g., Manny et al. 1975). In Okefenokee marshes, Flebbe (1982) observed very low levels of dissolved inorganic P, and peat N:P ratios of 64:1. Furthermore, Auble (1982) noted ratios of C:P = 900:1 during litter decomposition, which suggests that P was in especially low concentration. Therefore, we used phosphorus as the measure of all components and flows.

Model components (Fig. 2) were chosen on the basis of their relevance to fish. Almost all fish were small (<60 mm standard length) and ate similar foods, so we lumped all fish species into one compartment (X_6). The most numerous Okefenokee marsh fishes (Leptolucania ommata and Gambusia affinis) predominantly eat carnivorous insects (e.g., odonates and tanypode chironomids), detritivorous insects (e.g., non-tanypode chironomids) and zooplankton (e.g., cladocerans, Chapter 4). Thus, we included carnivorous insects (X_4), detritivorous insects (X_5), and zooplankton (X_3) in the model. The latter component eats phytoplankton (X_2) and benthic detritus (X_7). Aquatic macrophytes (X_8, e.g., Nuphar advena) are mostly rooted and thus also receive nutrients (P) from benthic detritus. We used soluble reactive phosphorus (SRP, X_1) as a measure of P in water, because it represents the most important form for phytoplankton (Wetzel 1975). These eight components constitute the system of interest.

This system has several sources and sinks for P (Table 1). Wading birds (I_B) are a large source of P when present (Stinner 1983). Precipitation (I_D) is the largest source when the bird rookery is not present (Blood 1981), and it is taken to be constant throughout the year (Fig. 3a, data from Schlesinger 1978). Cypress trees (I_C, Taxodium ascendens) in nearby swamp forests provide a small amount of P in the form of needles and this is modeled as constant. Adult insects (I_A) provide a very small source as eggs every May-June and a small sink when adults fly away during April-September. Annual buildup of peat is negligible (see CONTROL SITE (WITHOUT BIRDS)), thus outflowing water (O) is the major sink for nutrients from Okefenokee Swamp (Rykiel 1977). Outflow P comes basically from benthic detritus since the peaty detritus is flocculent, easily disturbed and is the largest component in the system (Table 2). Flows to sinks were modeled by linear, donor-dependent formulations.

In years when nesting birds are present, field data show that they input P during warm months (Fig. 3b, from Stinner 1983). Because field data were from a particular year's nesting with that year's minor details of timing of P input, and because we preferred a generalized input for simulation of many years, we used a step function as an approximation of this variable seasonality. This allowed some simplicity, standardization and generality in the model.

We modeled most flows between system components nonlinearly (i.e., levels of both donor and recipient components determine such flows). Michaelis-Menten functions control some flows. For instance, phytoplankton take up soluble reactive P (SRP) based on a half-saturation level of SRP (Bowie et al. 1985). Growth of aquatic macrophytes is logistic because of competition for space (Table 3). A sine function of day of year represents temperature and modifies most within-system flows (Table 4).

Food threshold and satiation values constrain predation flows. Because predators (e.g., odonates) could drive their prey to extinction in a single day in southern systems that lacked refuges (Benke 1972), threshold levels were essential and were incorporated into the model. Food satiation levels were also added as a natural constraint on feeding (Wiegert et al. 1981).

Other major flows included herbivorous and detritivorous ingestion, and absorption by macrophytes from benthic detritus. Egestion went to benthic detritus (and to SRP from zooplankton, Le Borgne 1973). Uningested dead organisms passed to benthic detritus. All modeled flows are shown in Fig. 2, and all parameters used are given in Tables 1, 3 and 4.

OVERVIEW:

Flow	Type	Reference
Loss of benthic detritus from system	Linear, donor-dependent	Rykiel 1977
Phytoplankton uptake of SRP	Michaelis-Menten	Bowie et al. 1985
Macrophyte uptake of benthic detritus P	Michaelis-Menten and logistic	Greening and Gerritsen pers. comm., Wetzel 1975, Twilley et al. 1985

Feeding by zooplankton and detritivorous insects	Michaelis-Menten	Bowie et al. 1985
Natural mortalities	Linear, donor-dependent	Jorgensen 1979
Decomposition of detritus P to SRP	Linear, donor-dependent	Auble 1982
All carnivory	Threshold/satiation	Benke 1972, Wiegert et al. 1981

Timing of simulations is based on field information. We simulated 11 years of bird effects because birds nested for at least this long (Stinner 1983). The eleventh year was chosen as the active rookery benchmark. For the control (without birds), the eleventh year of simulation was also chosen as benchmark. Because we examined residual nutrient effects in the field 1.1-2.1 years after abandonment, we ran abandoned rookery simulations by resetting birds to zero, component values to those after 11 years of rookery simulation, and simulating for a further 2.1 years. We modeled in FORTRAN (Appendix) on an IBM microcomputer.

Results and Discussion

CONTROL SITE (WITHOUT BIRDS)

First we simulated the control site, with low constant P inputs due only to precipitation, cypress litter, and insect eggs. Since without birds, buildup of system components is negligible (e.g., 1 cm of peat / 20 years at other Okefenokee marsh sites = 10 mg P m^{-2} yr^{-1} = 1.8% of total inputs, Cohen et al. 1984), the initial output was set equal to the inputs above:

$$O = I_A + I_C + I_D$$

Under this steady state condition with regard to nutrient exchange between the system and its environment (Table 1), and starting with initial values as in Table 2, all components came into nominal state within one simulated year. (By nominal state we mean an unperturbed, reference state for the control site. It is not an equilibrium state but a periodic state with a period of one year). Since initial states were our best estimates and were close to the modeled nominal states, it is not surprising that any small internal adjustments in states and flows were complete within one year. After 11 years, all components were within 60% of their field- and literature-derived initial states (Table 5).

Modeled nominal states of macrophytes had about the same values as field data (data from Stinner 1983, assuming 40% of biomass is aboveground; Fig. 4a). Low seasonality of modeled macrophytes was a result of the low temperature coefficient derived from the literature (THET78, Table 3).

Simulated values of SRP overlapped field data (Fig. 4b). Data were quite variable, due mainly to a considerable error in measuring such low values of SRP. In simulations, the low concentrations of SRP during the warmer part of the year (April-October) were not unreasonable, because of accelerated phytoplankton growth. During the cold season, simulated SRP values were up to 6.0 times as great.

The modeled nominal states of phytoplankton were similar to field data. Although nominal levels were greater than data from October 1982-August 1983, high field values in October 1983 caused average data to be 1.19 times as great as average simulated states (Fig. 4c). Simulated levels did not show as much variability as field data from season to season or from year to year.

Zooplankton nominal states showed some overlap with levels of zooplankton seen in enclosures at the control site (Fig. 5a, data from Oliver 1985). Although no data from cold seasons are available for comparison, available data indicate that simulated levels of zooplankton are generally low. This suggests that, as with the previously discussed biota, effects of seasonality are minimized in the model. Part of this low seasonality is a result of high predation on zooplankton levels that began to rise above threshold level (see OVERVIEW).

Nominal simulations of insects showed some seasonal effects. Temperature-dependent rates of ingestion resulted in high levels of carnivorous and especially detritivorous insects in spring and summer (Fig. 5b). A temperature-dependent release from predation by carnivorous insects and fish may have caused the increasing levels seen in winter.

No field data on insect dynamics are available for comparison with simulations, but levels are reasonably close to the field-based initial states of Table 2.

The nominal simulation of fish showed low seasonality (Fig. 5c). This was at least partly a result of low seasonality of the zooplankton resource. The slight increases in fish biomass from June-October were expected because of accelerated growth of food organisms (zooplankton and insects) during this warmer period. The fish simulation overlapped field data. The observed variability in fish data lacked seasonal trends and was at least partly due to high variability in the marsh.

The nominal simulation of benthic detritus was notably constant throughout a year (634-644 mg P m^{-2}). Seasonal changes in benthic detritus are not known, but are thought to be low because of large mass and probable low rate of turnover of this compartment. Thus, relative constancy of the simulated nominal state may be generally reasonable.

ACTIVE ROOKERY

Simulation of the active rookery started with the same initial conditions as the control except that contributions of 8000 birds increased P input to the system (Fig. 3b). This resulted in elevated levels of a number of components.

Simulated levels of rookery macrophytes averaged 4.5 times as great as simulated control levels (Fig. 6a).

Simulated rookery levels were generally greater than field data (1.35 times as great). Although field data showed variability, they did not show seasonality. The rookery macrophyte simulation was consistent with this lack of seasonality.

Field data for other components during the active rookery period are lacking, so we contrast simulated rookery components with simulated control components. Simulated guano input greatly increased benthic detritus P (Fig. 6b) because most guano went to the bottom of the shallow marsh (based on Stinner's BRDSRP data, Table 4). Simulated levels of benthic detritus P in the rookery increased during the nesting season (May-August), then gradually declined during the rest of the year as linear donor-dependent outflow continued. Over the entire eleventh year, rookery levels were 8.9 times nominal levels, on average. Thus simulation showed benthic detritus to be the largest storage for added P in our system. Field results have tended to confirm high increases (Richardson and Marshall 1986, Heliotis and DeWitt 1983, Howard-Williams 1985) and to suggest that the peat sediment is "the critical unit in removing and storing nutrients" (Ewel and Odum 1984).

Simulated addition of guano caused a slight decrease in SRP, contrary to expectation (to 0.87 times control level). This decrease was a result of increased phytoplankton, and thus increased SRP uptake, during enrichment (Fig. 6c). Simulated SRP in the rookery decreased during the warm season, consistent with the control simulation (Fig. 4b) and with seasonal decreases in nature (Wetzel 1975). As mentioned above, simulation of enrichment by birds resulted in increased phytoplankton (to 9.4 times nominal levels, Fig. 6c). Seasonal phytoplankton dynamics also became more pronounced because of simulated guano P input from May-August.

Simulated enrichment caused an insignificant zooplankton increase (to 1.03 times nominal levels, Fig. 7a). This smallness of effect was due to strong limitations on predation on zooplankton by threshold and satiation values (see OVERVIEW). Such limitations are biologically reasonable (Wiegert et al. 1981) and necessary to prevent extinction of simulated zooplankton.

Similarly, threshold and satiation levels were necessary to prevent extinction of simulated insects (in agreement with experimental observations of Benke 1972), but also tended to decrease effects of added nutrients (Fig. 7b). Simulation of addition of P from birds (4600 mg P m^{-2} yr^{-1}) thus had little effect on detritivorous or carnivorous insects. This result is consistent with Moss (1976) who found that fertilization of macrophyte dominated ponds (.09 g P m^{-2} $week^{-1}$ x 12 fertilization weeks yr^{-1} = 1100 mg P m^{-2} yr^{-1}, plus nitrogen) had little effect on total benthic invertebrate biomass. Simulated rookery insects showed spring peaks, as expected for such emergents.

Because the fish component feeds on zooplankton and insect components, rookery-caused elevations in the latter were passed on to fish (Fig. 7c). In nature, increased food availability can result in an increase in fish (e.g., in fertilized ponds, Swingle 1956); we simulate this by donor-dependent feeding (OVERVIEW and Appendix). Over all simulated seasons, fish increased to 1.42 times nominal levels.

The fact that most simulated components increased when bird P was added to the system was consistent with the literature. For instance, Dolan et al. (1981) found that secondarily treated effluent caused aquatic macrophytes in a central Florida marsh to have higher biomass and higher P concentration. They also found that of 38030 mg P m^{-2} added to the marsh during its first year of treatment, 74% ended up in peaty soil and litter. Similarly, when Richardson and Marshall (1986) added 2200 mg P m^{-2} yr^{-1} plus nitrogen to a Michigan aquatic peatland, they found increases in net primary productivity and P storage by <u>Carex</u> spp. These aquatic macrophytes removed 61% of P addition in the first year, while the litter-microorganism compartment sorbed 22%. Richardson and Marshall concluded that algae quickly absorbed significant amounts of P added to the system, but long-term storage was controlled by soil adsorption and peat accumulation. Our model is consistent with these findings because it incorporates donor-dependent fluxes and data on low guano solubility (BRDSRP, Table 4).

ABANDONED ROOKERY

After the eleventh year of rookery simulation, inflow of guano P was stopped and the components changed back toward nominal conditions. P input to the system declined while linear donor control of losses from components brought them down toward a new lower steady state. This resulted in a simulation of residual nutrient effects.

Simulated aquatic macrophytes were almost as high as those found when the birds were present. Average states after 1.1-2.1 years were 0.91 times those in the active rookery simulation (Fig. 8a, cf. Fig. 6a). However, levels were declining because of a decline in simulated benthic detritus P after birds left (Fig. 9a).

We compared simulated levels of abandoned rookery macrophytes with field data. Field data were based on abandoned rookery macrophyte densities (Greening and Gerritsen 1987 and pers. comm.), times: I) concentration of P in active rookery macrophytes (Stinner 1983); and II) concentration of P in control macrophytes (Fig. 8a). The average simulated levels were 2.04 times these field levels. Simulated levels would have been lower (i.e., closer to field data) if simulated mortality rate (MU87) had been higher. The relatively low rate was maintained because it was based on our best field information on macrophytes (Table 4).

Abandoned rookery simulation did not alter soluble reactive phosphorus greatly (values close to control levels, Fig. 8b cf. 4b). The simulated values overlapped field data marginally but were somewhat lower. As with other SRP field data, the high observed temporal variability lacks seasonal trends and can be considered a result of error in measurement of low values.

Dierberg and Brezonik (1983) found that secondarily treated sewage added to cypress domes caused increased nutrients in surface water and that 1.7 years after the cessation of sewage pumping, total P in water still had not returned to natural levels. They concluded that sediments and vegetation on the swamp floor released P to overlying water long after the addition of nutrients. These results contrast with our lack of increased SRP in active and abandoned rookery simulations. In our model, increased guano causes a higher release of SRP, thus higher levels of phytoplankton, which then results in phytoplankton driving down levels of SRP.

Simulated phytoplankton in the abandoned rookery gradually decreased to levels between rookery and control simulations (3.7 times nominal levels, i.e. 0.39 times rookery levels, Fig. 8c cf. 6c). As P in the modeled abandoned rookery decreased, very high rookery levels of phytoplankton could no longer be supported. Simulated levels of abandoned rookery phytoplankton were greater than corresponding field data by a factor of 1.26. Simulated phytoplankton followed generally expected seasonal trends of greater levels in warmer seasons.

Simulation of zooplankton in the abandoned rookery was virtually the same as simulations for the rookery and control (average of .212 cf. .213 and .206 mg P m^{-2}, respectively). As in the latter simulations, nonlinear limits on predation by carnivorous insects and fish, although necessary (for reasons discussed above), strongly damped zooplankton behavior, both seasonally and with respect to enrichment. In experimental systems, Oliver (1985) and others have shown significant increases in levels of zooplankton as a result of P and N enrichment. Thus, the degree of increase during active and abandoned rookery simulations was less than expected.

Residual P in the rookery also had relatively little effect on insects (Fig. 9b cf. 7b). Simulated states were close to simulated control and rookery states, which differed little from each other because of the nonlinear limits on predation.

Simulated levels of abandoned rookery fish were almost as high as simulated levels of rookery fish (0.95 times as high). However, simulated levels were not as high as field data (0.54 times as high) and were especially lower in the first two months of the year-long comparison (Fig. 9c). Nevertheless, simulated levels of abandoned rookery fish were not significantly different from corresponding field data.

Simulated levels of benthic detritus were still elevated 1.1-2.1 years after abandonment (Fig. 9a). Average levels were 3.7 times nominal (cf. Fig. 6b). Field results are consistent with these data: The equilibrium phosphate concentration of benthic detritus was 3.7 times as great in the abandoned rookery as in the control, 1.4-2.0 years after abandonment (Chapter 3). Benthic detritus continued to decrease as phosphorus loss to outflow brought this compartment, the major storage for P in the system, back toward normal unenriched levels. Long term simulation of abandonment projected levels of benthic detritus that were 1.1 times simulated levels in the control, 9 years after abandonment.

Our simulation indicated that the biggest sink for guano P in the system was benthic detritus. Reviews of Heliotis and DeWitt (1983) and Howard-Williams (1985) agreed with this conclusion by indicating that sediment accumulation was the major long-term sink for P added to wetlands.

Conclusions

The model simulated major components of Okefenokee Swamp marshes reasonably well. Because it incorporated known initial conditions and constants without birds, it simulated this situation best. Simulation of P input from an active wading bird rookery (to 8.9 times nominal input) resulted in mean increases in benthic detritus to 8.9 times nominal levels, aquatic macrophytes to 4.5, phytoplankton to 9.4, zooplankton to 1.03, detritivorous insects to 1.04, and fish to 1.42, while soluble reactive P decreased to 0.87 and carnivorous insects to 0.97 times nominal levels. As expected, increases in benthic detritus and phytoplankton were highest because these components were proximal to the nutrient input (Fig. 2). Increase in macrophytes was next highest, in agreement with field observations (e.g., Dolan et al. 1981). The fish increase of 42% should be regarded as a minimum estimate of unknown increase in the active rookery.

Simulation of the marsh after birds abandoned it resulted in gradual declines of most components toward nominal levels. After 1.1-2.1 years, mean levels of benthic detritus decreased to 3.7 times nominal levels, macrophytes to 4.1, phytoplankton to 3.7, detritivorous insects to 1.01, and fish to 1.35, while SRP increased to 0.95, zooplankton remained at 1.03 and carnivorous insects at 0.97 times nominal levels. Because the simulated increase in fish in the abandoned rookery appeared less than its increase in the field, simulated fish increases should be considered minimum estimates of nutrient effects.

The results of simulations in this study and of observations in the field (Chapter 3) indicate that nesting wading birds can have considerable nutrient effects on an aquatic ecosystem. Birds can increase components of the system that are not normally associated with them, such as benthic detritus and fish. The analysis of the system has shown significant nutrient links between aerial biota and such aquatic components.

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TABLE 1.
Sources and sinks of phosphorus.

Name	Meaning	Value	Source
I_A	Adult insects	X_4 egg deposition	
		= X_4 x 2% yr^{-1}	Waters 1969
		x yr(61 depos. d)$^{-1}$ = .0031 mg P m^{-2} d^{-1} X_4 emergence	Benke 1972
		= .450 g dry m^{-2} emerg. (1.5 g dry wt m^{-2})$^{-1}$	" "
		x(.4 m^2 emerg. area) m^{-2}	" "
		(154 emerg. d)$^{-1}$ = .00078 d^{-1} (X_5 egg depos. and emerg. are yr-round & unquantified; depos. and emerg. are considered to balance)	" "
I_B	Wading birds	2000-30000 bird, typically 8000; 4600 mg P m^{-2}yr^{-1}	Stinner 1983
		(8000 bird)$^{-1}$ x yr(105 nesting d)$^{-1}$ =.0055 mg P m^{-2}d^{-1}bird^{-1}	" "
I_C	Cypress litter	133 mg P m^{-2} yr^{-1} x 10% forest to marsh transfer x yr(365 d)$^{-1}$ =.036 mg P m^{-2} d^{-1}	Schlesinger 1978
I_D	Precipitation	570 mg P m^{-2} yr^{-1} x yr(365 d)$^{-1}$ =1.56 mg P m^{-2} d^{-1}	Blood 1981
O	Outflow	Outflow balances above flows (when no birds) =I_D + I_C + I_A =(570+.036x365+.0031x61 mg P m^{-2}yr^{-1} -9.4 mg P m^{-2}x.00078 d^{-1} x 154 emerg. d yr^{-1}) = 1.6 mg P m^{-2} d^{-1}	

TABLE 2.
Initial states based on initial simulation day (August 29).

Name	Meaning	Value	Source
X_1	Soluble reactive P	5 μg P L^{-1} x 1000 L m^{-3} x .48 m depth = 2.4 mg P m^{-2}	pers. obs. 1982-3 " " " "
X_2	Phytoplankton	17.6 mg chl a m^{-2} x .6 mg TP(mg chl a)$^{-1}$ = 10.6 mg P m^{-2}	" " " " Bowie et al. 1985
X_3	Zooplankton	28 mg dry wt m^{-2} x 1% TP wt(dry wt)$^{-1}$ = .28 mg P m^{-2}	pers. obs. Khan and Siddiqui 1971
X_4	Carnivorous insects	(2700 total chiron. m^{-2} x 10% tanyp. (total chiron.)$^{-1}$ x .402 mg dry wt ind^{-1} + 830 mg dry odon. m^{-2}) x 1.0% TP wt(dry wt)$^{-1}$ = 9.4 mg P m^{-2}	H.S. Greening pers. comm. 1986 Smock 1980 Benke 1972 and pers. obs.; Allen et al. 1974
X_5	Detritivorous insects	2700 total chiron. m^{-2} x 90% non-tanyp. (total chiron.)$^{-1}$ x.402 mg dry wt ind^{-1} x 1.0% TP wt(dry wt)$^{-1}$ =9.8 mg P m^{-2}	Greening pers. comm.; pers. obs. Smock 1980 Allen et al. 1974
X_6	Fish	6.54 g wet wt m^{-2} x 5.9 mg P(g wet wt)$^{-1}$ = 38.6 mg P m^{-2}	Chapter 3 Jorgensen 1979
X_7	Benthic detritus	3 cm depth x 10^{4} cm^{2} m^{-2} x 1 g wet wt cm^{-3} x .058 g dry(g wet)$^{-1}$ x .36 mg P(g dry)$^{-1}$ = 630 mg P m^{-2}	pers. obs. " " " " J.Gerritsen & Greening pers. comm. 1986
X_8	Aquatic macrophytes (> 1 cm diam)	108 mg P m^{-2} aboveground x total plant biomass (40% aboveground)$^{-1}$ = 270 mg P m^{-2}	pers. obs. Wetzel 1975

TABLE 3.
Literature-based values for nonlinearities.

Name	Meaning	Value	Source
F1ON2	Limit on phyto. by SRP	$X_1/(KM12+X_1)$	this table
F2ON3	Limit on zoop. by phyto.	$X_2/(KMTO35+X_2)$	" "
F3ONP	Limit on predation on zoop. by their density (parenthetic expression followed by "+" subscript means set to zero if negative)	$(1-(X_{3satiat}-X_3)_+$ $(X_{3satiat}-X_{3refuge})^{-1})_+$ $=(1-(2 \times X_{3init}-X_3)_+$ $(2 \times X_{3init}$ $-.5 \times X_{3init})^{-1})_+$ $=(1-(.56\ mg\ P\ m^{-2}-X_3)_+$ $(.42\ mg\ P\ m^{-2})^{-1})_+$	Wiegert et al. 1981 our estimate Table 1
F4ONP	Limit on predation on carn. insects by their density	$(1-(X_{4satiat}-X_4)_+$ $(X_{4satiat}-X_{4refuge})^{-1})_+$ $=(1-(2 \times X_{4init}-X_4)_+$ $(2 \times X_{4init}$ $-.5 \times X_{4init})^{-1})_+$ $=(1-(18.8\ mg\ P\ m^{-2}-X_6)_+$ $(14.1\ mg\ P\ m^{-2})^{-1})_+$	Wiegert et al. 1981 Table 1
F5ONP	Control on predation of detritiv. insects by their density	$(1-(X_{5satiat}-X_5)_+$ $(X_{5satiat}-X_{5refuge})^{-1})_+$ $=(1-(2 \times X_{5init}-X_5)_+$ $(2 \times X_{5init}$ $-.5 \times X_{5init})^{-1})_+$ $=(1-(19.6\ mg\ P\ m^{-2}-X_5)_+$ $(14.7\ mg\ P\ m^{-2})^{-1})_+$	Wiegert et al. 1981 Table 1
F7ON35	Limit on zoop. and detritiv. insects by their benthic detritus food	$EDIFRC*X_7/(KMTO35+ EDIFRC*X_7)$	Table 3 and this table
F7ON8	Control on macrophytes by benthic detritus	$EXTRCP*X_7/(KM78+ EXTRCP*X_7)$	" " " "
F8ON8	Limit on macrophytes by their density	$(K8-X_8)/K8$	this table
K8	Max. density of macrophytes	130 g dry aboveground m^{-2} x total plant biomass (40% aboveground)$^{-1}$	Control, Greening and Gerritsen pers.comm., Wetzel

		x.00394 g P(g dry wt)$^{-1}$ =1300 mg P m^{-2}	1975, Twilley et al. 1985
KM12	Half-saturation value of SRP	.02 mg PO_4-P L^{-1} x 480 L m^{-2} =9.6 mg P m^{-2}	Bowie et al. 1985 pers. obs.
KM78	Half-saturation value of benthic detritus for limit on macrophytes	405 mg P m^{-2}	our estimate
KMTO35	Half-saturation value of food (phyto. and benthic detritus) on zoop. and detritiv. insects	.5 mg dry wt L^{-1} x 1% P(dry wt)$^{-1}$ x 480 L m^{-2} =2.4 mg P m^{-2}	Bowie et al. 1985

TABLE 4.
Literature-based constants.

Name	Meaning	Value	Source
AMTSRP	Fraction of rain P which is SRP	.072	Rykiel 1977
AVTO4	Average transfer (feeding) rate to carn. insects	Production/Biomass$_{X4}$ (1-EPS47)$^{-1}$ =5 yr^{-1} (1-.55)$^{-1}$ =11.1 yr^{-1} x yr(365 d)$^{-1}$ =.030 d^{-1}	 this table Benke 1972 this table
BRDBEG	Day of yr on which birds begin to nest (and to add P); based on 0 d = January 1	135 d	Stinner 1983
BRDFIN	Day of yr on which birds finish nesting (and adding P)	239 d	" "
BRDSRP	Fraction of bird guano P which is SRP	2.6 mg SRP L^{-1} x.75 L x(9000 mg guano x8.3%TP)$^{-1}$ =.0026	" " " "
DEPBEG	Day of yr on which carn. insects begin to deposit eggs	120 d	Benke 1972
DEPFIN	Day on which carn. insects finish depositing eggs	180 d	" "
EDIFRC	Fraction of benthic detritus which is edible by zoop. & detritiv. insects	.01	S.A.Schoenberg pers. comm. 1986
EPS3	Fraction of ingestion by zoop. which is egested or excreted	.6	Leidy and Ploskey 1980
EPS47	Fraction of ingestion by carn. insects	1 - growth/ingestion = 1 - 45% =.55	 Benke 1972

	which is egested or excreted		
EPS57	Fraction of ingestion by detritiv. insects which is egested or excreted	.8	Strayer and Likens 1986
EPS67	Fraction of ingestion by fish which is egested or excreted	.642	Klekowski et al. 1970
EXTRCP	Fraction of benthic detritus P which is extractable by macrophytes	2.62μg extractable P cm^{-3} (136 μg TP $cm^{-3})^{-1}$ =.0193	Christiansen et al. 1985
FRAC44	Fraction of food of carn. insects which is carn. insects	high, .25	Benke 1972
INTOFS	Invertebrate to fish P ratio (for calculating trophic transfer to fish)	1% TP(dry $wt)^{-1}$ in invertebrates (3% TP(dry $wt)^{-1})^{-1}$ in fish =.33	Khan and Siddiqui 1971, Allen et al. 1974, Nakashima and Leggett 1980
K17	Transfer from SRP to benthic detritus	At equilibrium without biota, F17 $\sim$ F71, K17 x X_1 $\sim$ K71 x X_7, K17 $\sim$ .0022 d^{-1} x 630 mg P m^{-2}/X_1 but 630 mg P m^{-2} $>X_1>0$ X_1 $\sim$ 300 mg P m^{-2} so K17 = .005 d^{-1}	this table Table 1
K71	Decomposition of detritus P (to SRP)	.82 yr^{-1} x yr(365 $d)^{-1}$ =.0022 d^{-1}	Auble 1982
K7O	Outflow constant from benthic detritus	1.6 mg P m^{-2} d^{-1} (630 mg P $m^{-2})^{-1}$ =.0025 d^{-1}	Table 2 Table 1
LVBEG	Day of yr on which carn. insects begin to leave marsh	90 d	Benke 1972

LVFIN	Day on which insects finish leaving	243 d	Benke 1972
MU27	Natural mortality rate of phyto.	.12 d^{-1}	Bowie et al. 1985
MU37	Natural mortality rate of zoop.	.02 d^{-1}	" " " "
MU47	Natural mortality rate of carn. insects	.002 d^{-1}	Jorgensen 1979
MU57	Natural mortality rate of detritiv. insects	.002 d^{-1}	" "
MU67	Natural mortality rate of fish	.005 d^{-1}	" "
MU87	Natural mortality rate of macrophytes	(aboveground turnover time x fraction aboveground + belowground turnover time x fraction belowground)$^{-1}$ =(88.49 d x.4 + 4 yr(365 d yr^{-1})x.6)$^{-1}$ =.0011 d^{-1}	Greening and Gerritsen pers. comm., M.E.Cochran pers. comm. 1986
TAU12	Max. transfer rate from SRP to phyto.	.5 d^{-1}	Bowie et al. 1985
TAU23	Max. transfer rate from phyto. to zoop.	Max. total transfer rate to zoop. x (phyto. dry wt/ total dry wt eaten) x 1% P/phyto. dry wt (total P eaten)$^{-1}$ =.8 d^{-1} x(100%-(40% detritus dry wt)) x 1% P (40% x .036%P + 60% zoop. dry wt x 1%P)$^{-1}$ =.78 d^{-1}	Khan and Siddiqui 1971 Bowie et al. 1985 this table
TAU34	Max. transfer rate from zoop. to carn. insects	AVTO4 x (1-FRAC44)/2 x(1/$F3ONP_{init}$) =.034 d^{-1}	this table Table 4
TAU36	Max. transfer rate from zoop. to fish	WNCONS x INTOFS x(correction of observed consumption rate to max. rate)(conversion of	this table

		winter rate to standard rate)	
		x 7.6% zoop. wt (total food wt)$^{-1}$ =.0282 d^{-1} x .33	Chapter 4
		x(1/$F3ONP_{init}$) x	Table 4
		(THETO6**(20.0°C-12.3°C)) x .076 =.0039 d^{-1}	this table
TAU44	Max. transfer rate from carn. insects to carn. insects	AVTO4 x FRAC44	
		x(1/$F4ONP_{init}$) =.023 d^{-1}	Table 4
TAU46	Max. transfer rate from carn. insects to fish	WNCONS x INTOFS	this table
		x(correction of observed consumption rate to max. rate)(conversion of winter rate to standard rate)	
		x 44.6% carn. insect wt (total food wt)$^{-1}$ =.0282 d^{-1} x .33	Chapter 4
		x(1/$F4ONP_{init}$) x (THETO6**(20.0°C-12.3°C)) x .446 =.0227 d^{-1}	Table 4
TAU54	Max. transfer rate from detritiv. insects to carn. insects	AVTO4 x(1-FRAC44)/2	
		x(1/$F5ONP_{init}$) =.034 d^{-1}	" "
TAU56	Max. transfer rate from detritiv. insects to fish	WNCONS x INTOFS x(correction of observed consumption rate to max. rate)(conversion of winter rate to standard rate)	
		x 47.8% detritiv. insect wt(total food wt)$^{-1}$ =.0282 d^{-1} x .33	Chapter 4
		x(1/$F5ONP_{init}$) x (THETO6**(20.0°C-12.3°C)) x .478 =.0242 d^{-1}	Table 3
TAU73	Max. transfer rate from benthic detritus to zoop.	Max. total transfer rate to zoop. x detritus dry wt/total dry wt eaten	
		x.36 mg P/g dry detritus (total P eaten)$^{-1}$	Table 1
		=.8 d^{-1}	Bowie et al. 1977

		x 40% of total dry x.036% P (40% x.036%P +60% phyto. dry wt x 1%P)$^{-1}$ =.019 d^{-1}	Hilbricht-Ilkowska 1977
TAU75	Max. transfer rate from benthic detritus to detritiv. insects	Production/Biomass$_{X5}$ (1-EPS57)$^{-1}$ x(1/F7ON35$_{init}$) =7-30 yr^{-1} say 15 yr^{-1} (1-.8)$^{-1}$ x (1/.724) x yr(365 d)$^{-1}$ =.28 d^{-1}	this table chironomids, Smock and Gilinsky 1985
TAU78	Max. transfer rate from benthic detritus to macrophytes	.047 d^{-1}	our estimate
TEMP	Water temp.	Avg. temp. - amplitude x sin(2 pi(d of yr)yr/365d +phase shift) =18.7^{o}C - 9.5 x SIN(2(3.142)T/365+.599)^{o}C	calibration
THET12	Temp. adjustment coefficient for transfer from SRP to phyto.	1.068	DiToro and Matystik 1980
THET71	Temp. adjustment coefficient for transfer from detritus to SRP	1.05	Bowie et al. 1985
THET78	Temp. adjustment coefficient for transfer from detritus to macrophytes	(Uptake rate in summer (Uptake rate in winter)$^{-1}$) **(1/(summer temp.-winter temp.))=(287%P x 10^{-3} d^{-1} (157%P x 10^{-3} d^{-1})$^{-1}$) **(1/(30^{o}C-4.5^{o}C)) =1.024	Twilley et al. 1977 " " "
THETO6	Temp. adjustment coefficient for transfer to fish	((Summer consumption (winter consumption)$^{-1}$) **(1/(summer temp.-winter temp.)) =(.1207 d^{-1}(.0282 d^{-1})$^{-1}$) **(1/(30.9^{o}C-12.3^{o}C)) =1.081	Chapter 4

THTINV	Temp. adjustment coefficient for transfer to invertebrates	1.052	Robinson et al. 1983
WNCONS	Winter average consumption by most numerous fish (*Leptolucania ommata* and *Gambusia affinis*)	$(.0242\ d^{-1}+.0321\ d^{-1})/2$ $=.0282\ d^{-1}$	Chapter 4
ZPSRP	Fraction of P egestion+excretion which is SRP	.48	Le Borgne 1973

TABLE 5.
Comparison of initial states to states after 11 simulated years without birds (in mg P m^{-2}).

Component	Initial state (from Table 1)	State after 11 yr	Percent change from initial
SRP	2.40	1.77	-26.3
Phytoplankton	10.60	16.92	+59.6
Zooplankton	0.28	0.21	-26.1
Carn. insects	9.40	5.12	-45.5
Detritiv. insects	9.80	9.62	-1.8
Fish	38.60	35.15	-8.9
Benthic detritus	630.00	635.77	+0.9
Aquatic macroph.	270.00	257.76	-4.5

Fig. 1. Map of the marsh sites mentioned in the text. Solid lines on the enlarged map delineate the Okefenokee watershed, its enclosed islands and watercourses.

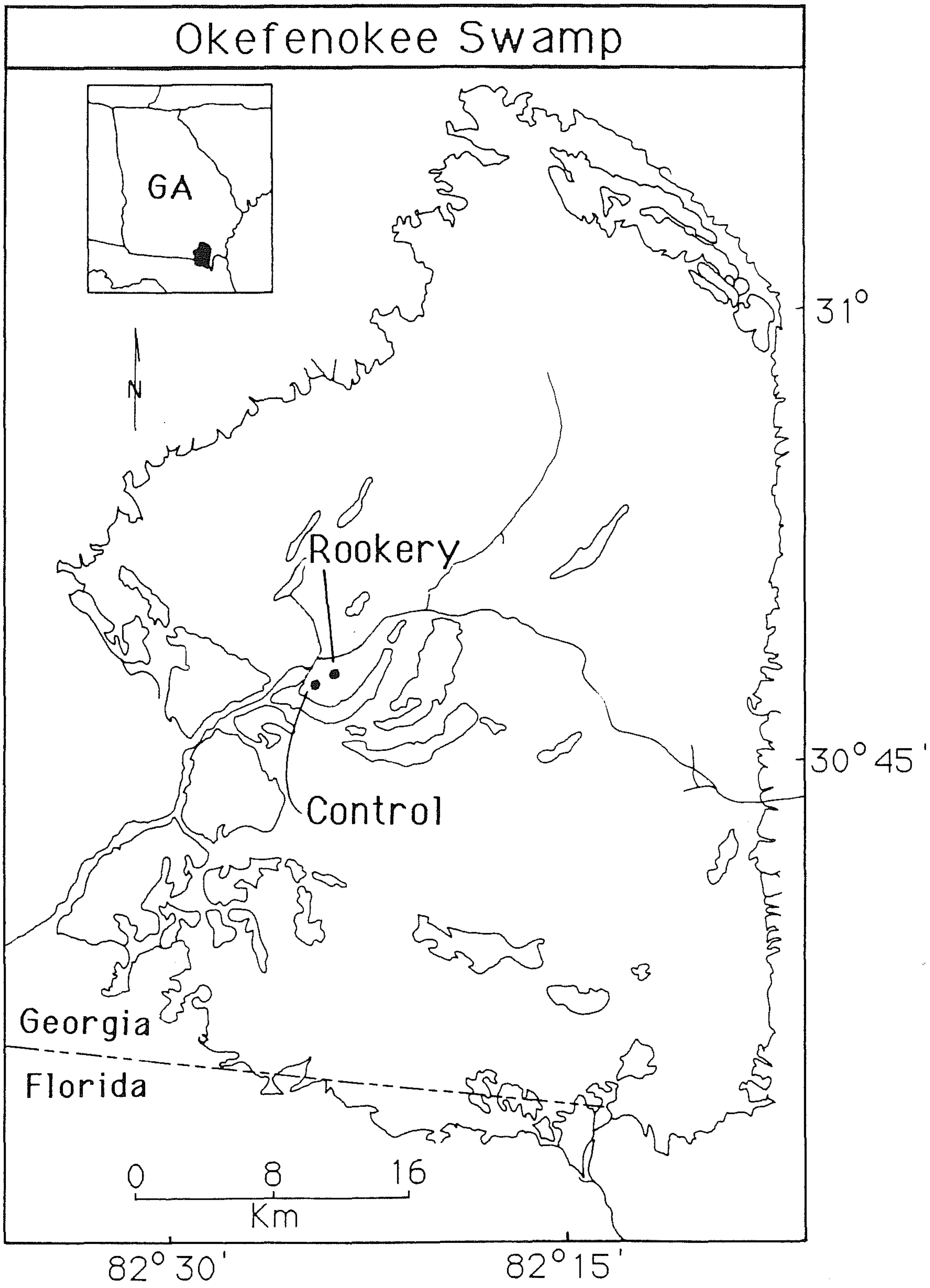

Okefenokee Swamp
GA
N
Rookery
Control
31°
30° 45'
Georgia
Florida
0
8
16
Km
82° 30'
82° 15'

Fig. 2. An Okefenokee marsh system and its interacting environment. Rectangles are major system components and "clouds" are sources and sinks of phosphorus.

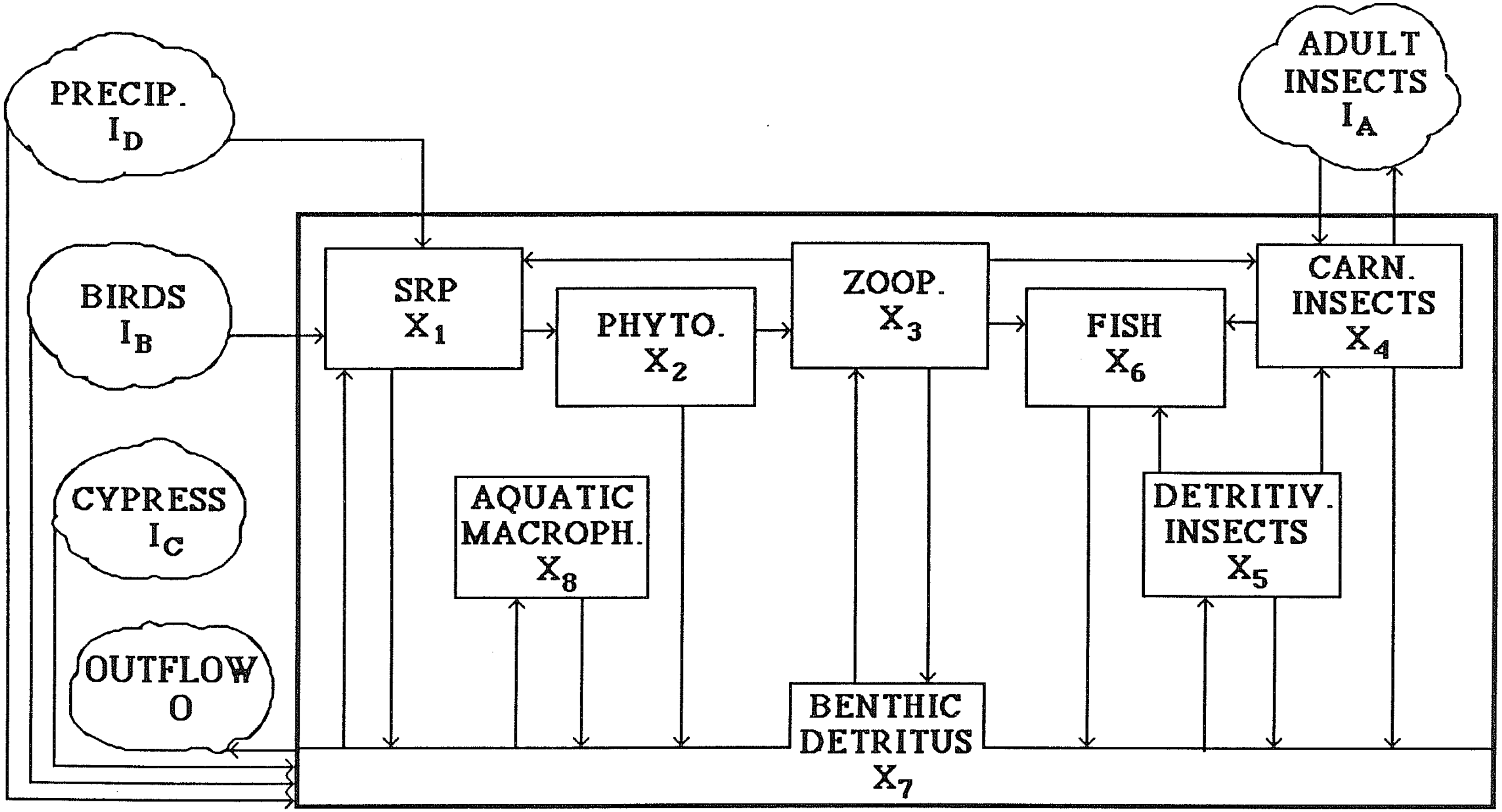

PRECIP.
I_D
BIRDS
I_B
CYPRESS
I_C
OUTFLOW
O
ADULT INSECTS
I_A
SRP
X_1
PHYTO.
X_2
ZOOP.
X_3
FISH
X_6
CARN. INSECTS
X_4
AQUATIC MACROPH.
X_8
DETRITIV. INSECTS
X_5
BENTHIC DETRITUS
X_7

Fig. 3. P inputs to Okefenokee Swamp via rain and birds. Although wading bird data represent input from a normal nesting of 8000 birds, the step function is similar (but lower or higher) when smaller or larger numbers of birds are simulated.

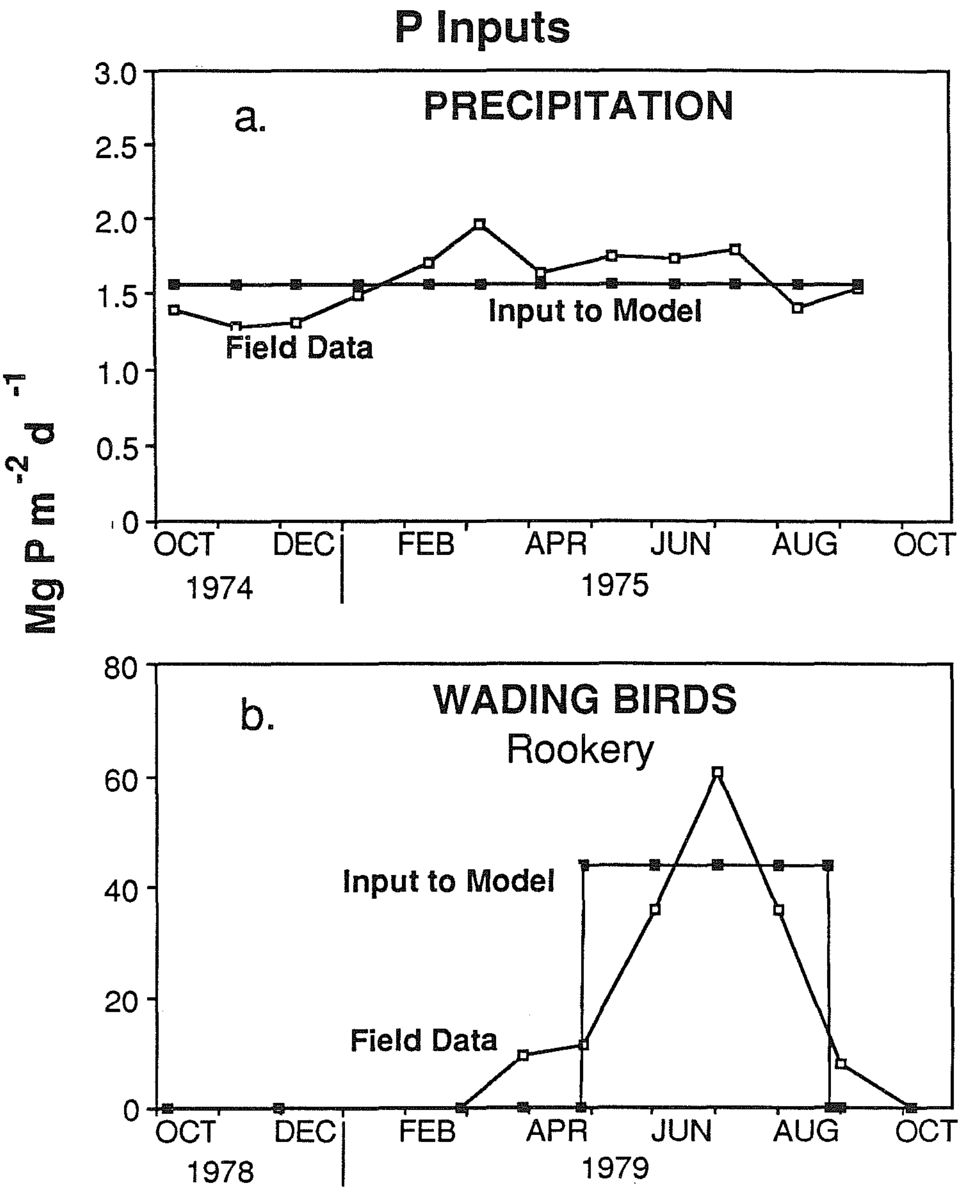

P Inputs
a.
PRECIPITATION
Input to Model
Field Data
3.0
2.5
2.0
1.5
1.0
0.5
0
OCT
DEC
FEB
APR
JUN
AUG
OCT
1974
1975
Mg P m^{-2} d^{-1}
b.
WADING BIRDS
Rookery
Input to Model
Field Data
80
60
40
20
0
OCT
DEC
FEB
APR
JUN
AUG
OCT
1978
1979

Fig. 4. Primary producer and SRP dynamics when no birds are present. Bars show ±S.E. for macrophytes and range of duplicate values for phytoplankton.

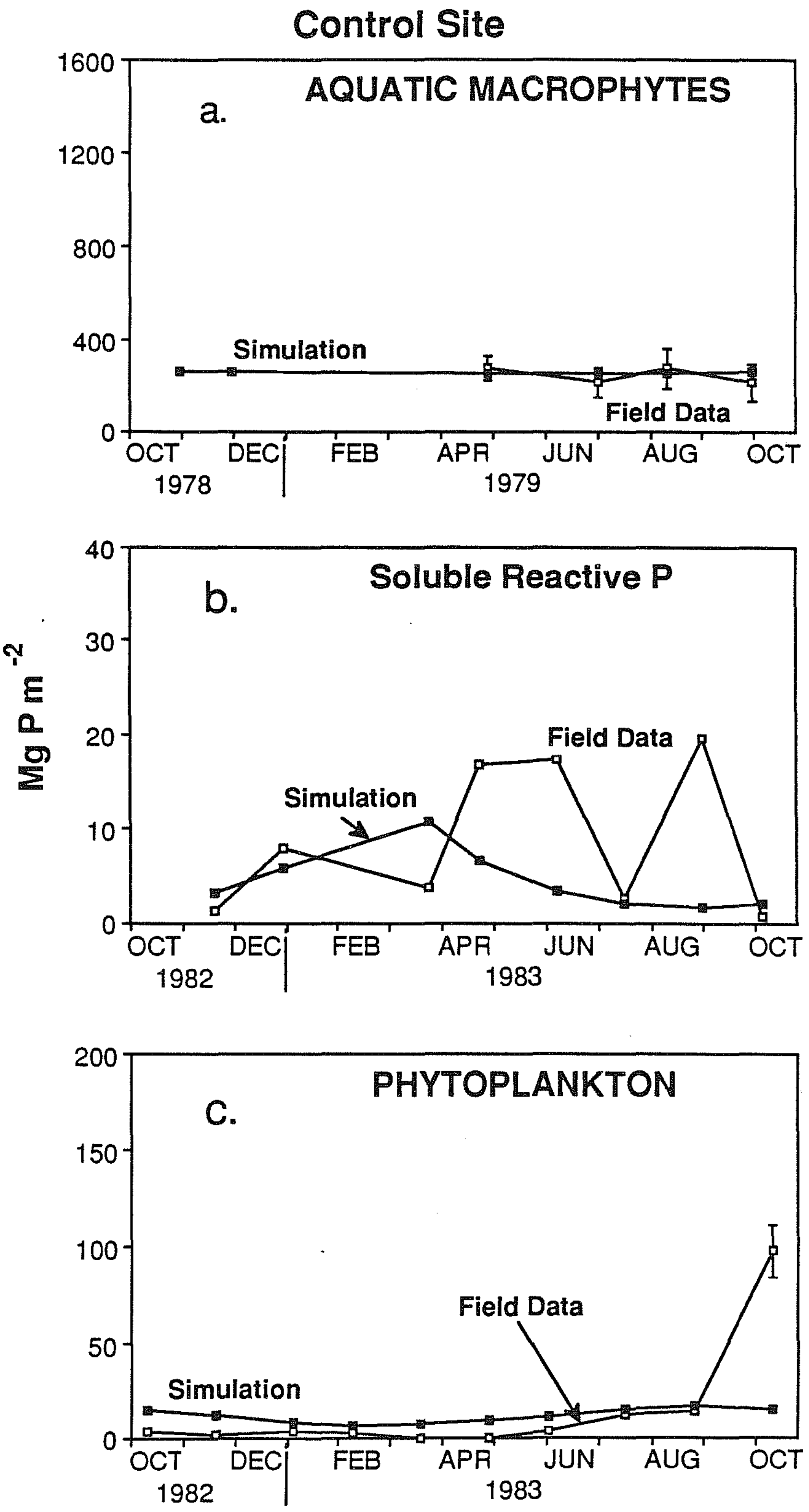

Control Site
a.
AQUATIC MACROPHYTES
1600
1200
800
400
0
Simulation
Field Data
OCT
DEC
FEB
APR
JUN
AUG
OCT
1978
1979
Mg P m^{-2}
b.
Soluble Reactive P
40
30
20
10
0
Field Data
Simulation
OCT
DEC
FEB
APR
JUN
AUG
OCT
1982
1983
c.
PHYTOPLANKTON
200
150
100
50
0
Field Data
Simulation
OCT
DEC
FEB
APR
JUN
AUG
OCT
1982
1983

Fig. 5. Animal dynamics when no birds are present. Bars show ±S.E.

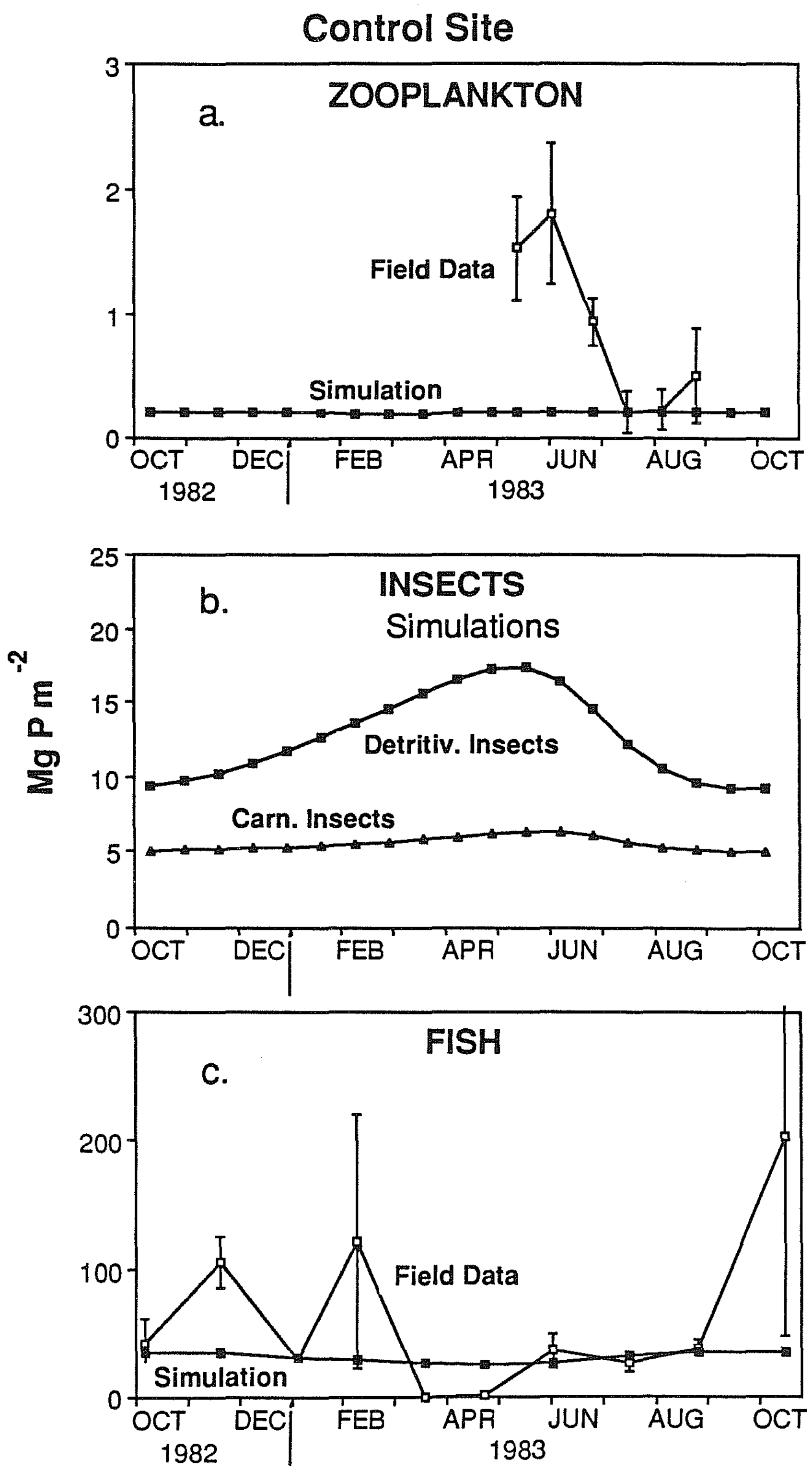

Control Site
a.
ZOOPLANKTON
Field Data
Simulation
b.
INSECTS
Simulations
Detritiv. Insects
Carn. Insects
c.
FISH
Field Data
Simulation
Mg P m^{-2}
0
1
2
3
5
10
15
20
25
100
200
300
OCT
DEC
FEB
APR
JUN
AUG
OCT
1982
1983

Fig. 6. Primary producer and benthic detritus dynamics in the active rookery compared with dynamics without birds. (In Fig. a and c, controls correspond to simulated cases in 4a and 4c).

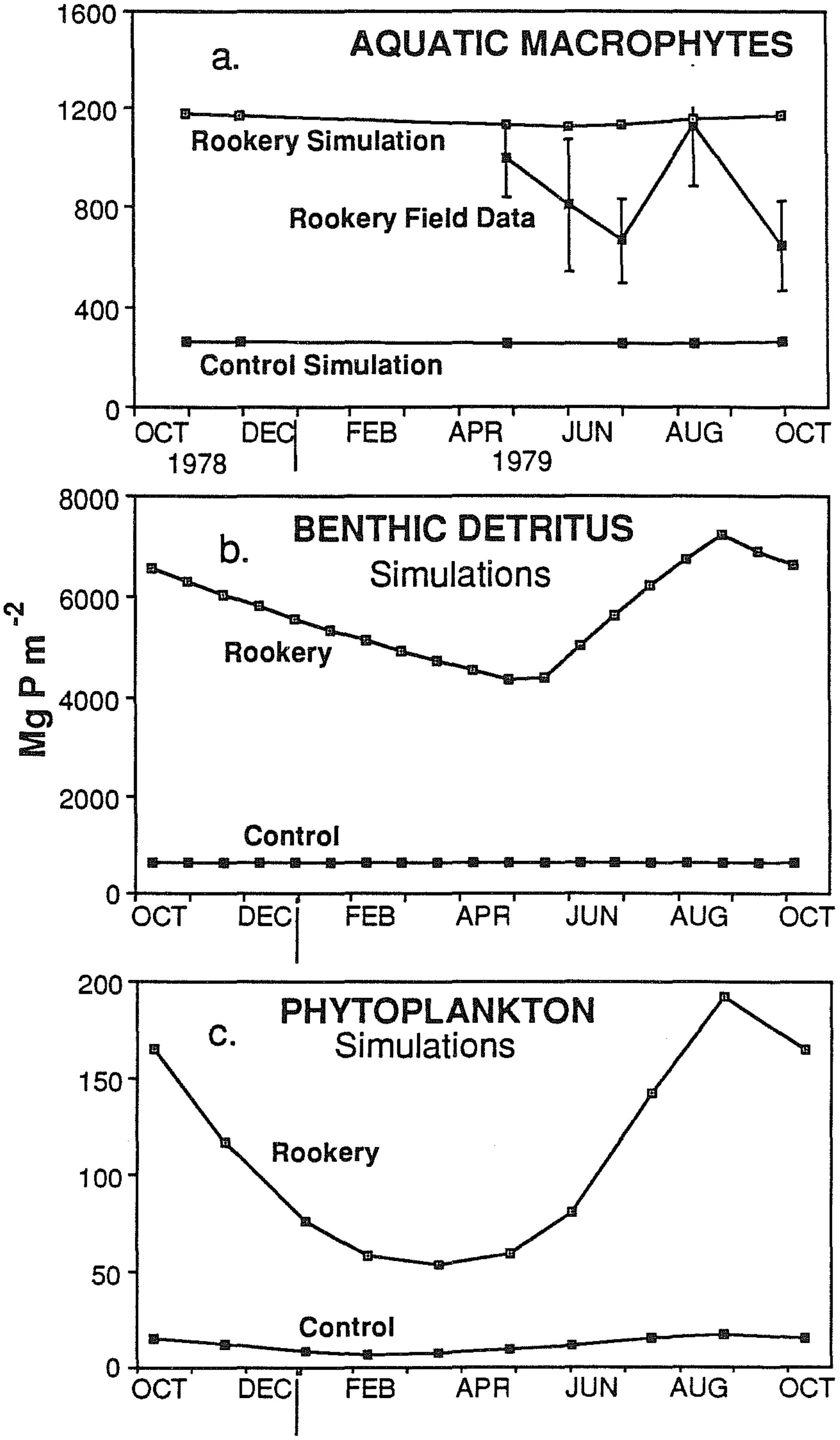

a.
AQUATIC MACROPHYTES
Rookery Simulation
Rookery Field Data
Control Simulation
1600
1200
800
400
0
OCT
DEC
FEB
APR
JUN
AUG
OCT
1978
1979
Mg P m^-2
b.
BENTHIC DETRITUS
Simulations
Rookery
Control
8000
6000
4000
2000
0
OCT
DEC
FEB
APR
JUN
AUG
OCT
c.
PHYTOPLANKTON
Simulations
Rookery
Control
200
150
100
50
0
OCT
DEC
FEB
APR
JUN
AUG
OCT

Fig. 7. Animal dynamics in the active rookery compared with dynamics without birds.

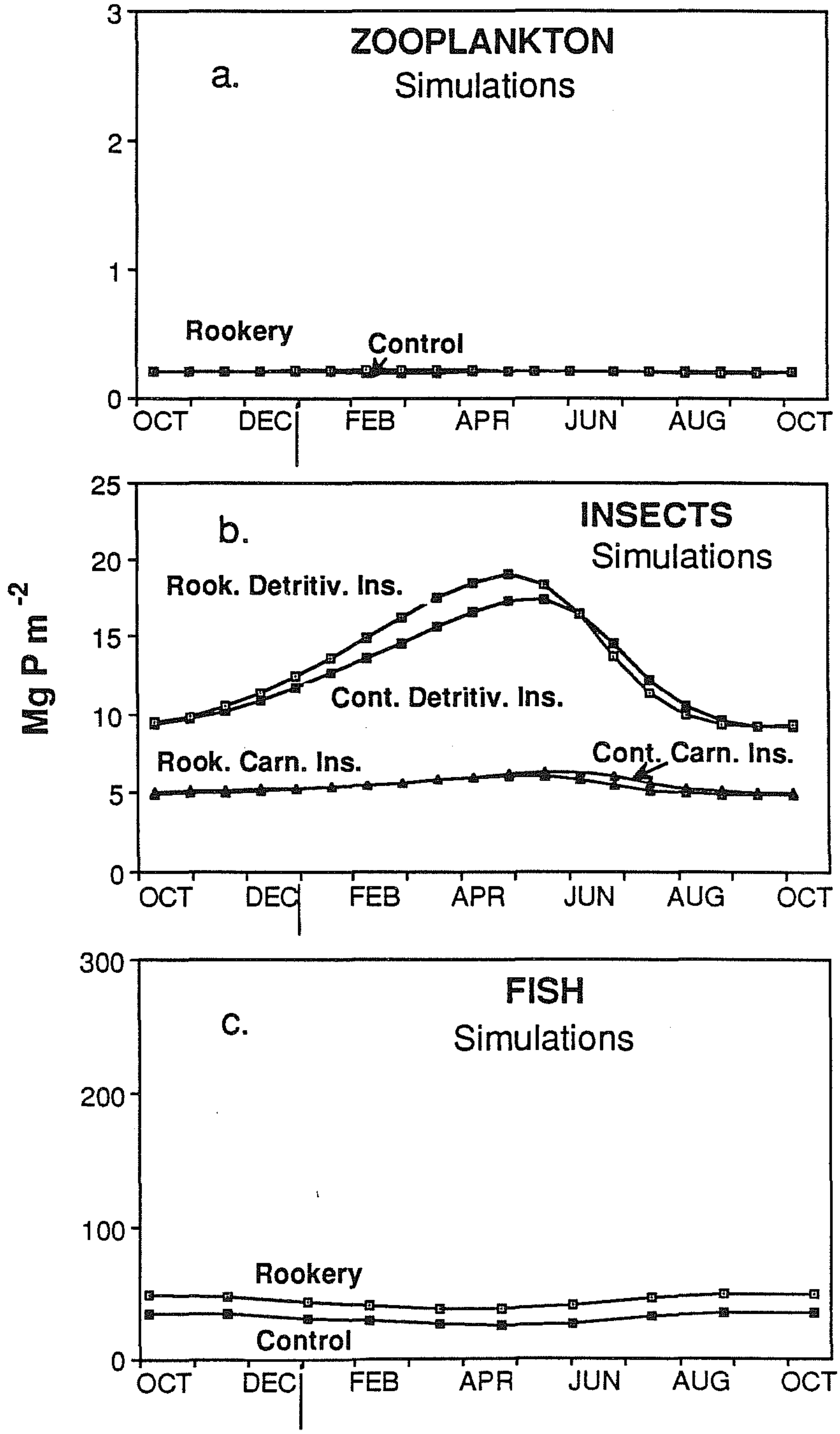

Mg P m $^{-2}$
a.
ZOOPLANKTON
Simulations
Rookery
Control
0
1
2
3
OCT
DEC
FEB
APR
JUN
AUG
OCT
b.
INSECTS
Simulations
Rook. Detritiv. Ins.
Cont. Detritiv. Ins.
Rook. Carn. Ins.
Cont. Carn. Ins.
0
5
10
15
20
25
OCT
DEC
FEB
APR
JUN
AUG
OCT
c.
FISH
Simulations
Rookery
Control
0
100
200
300
OCT
DEC
FEB
APR
JUN
AUG
OCT

Fig. 8. Primary producer and SRP dynamics in the abandoned rookery. In a, field data are based on abandoned rookery macrophyte densities times P concentrations in macrophytes of I) active rookery and II) control sites. (Nesting birds left the site in August 1981, thus graphs represent dynamics 1.1-2.1 years after abandonment).

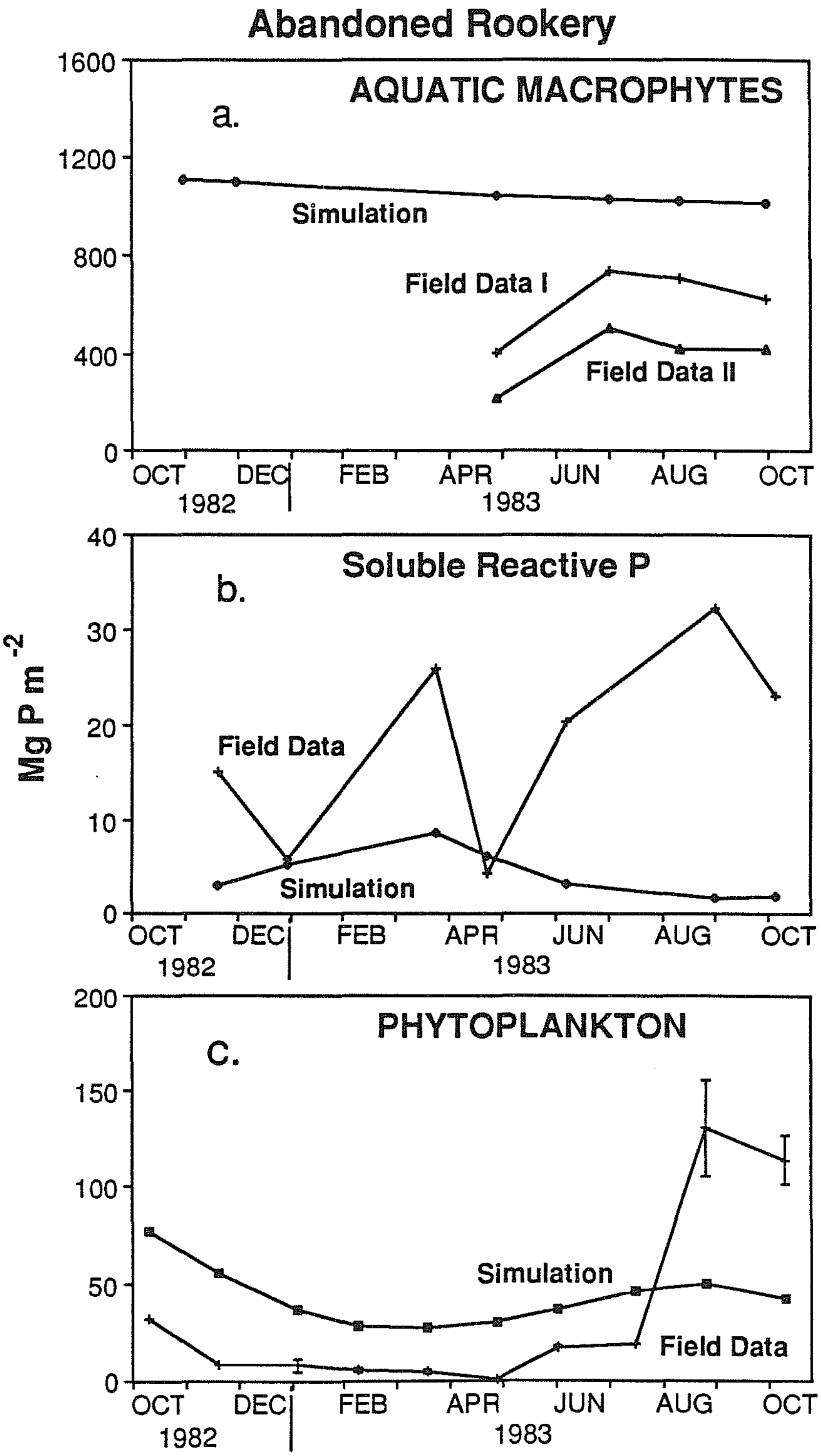
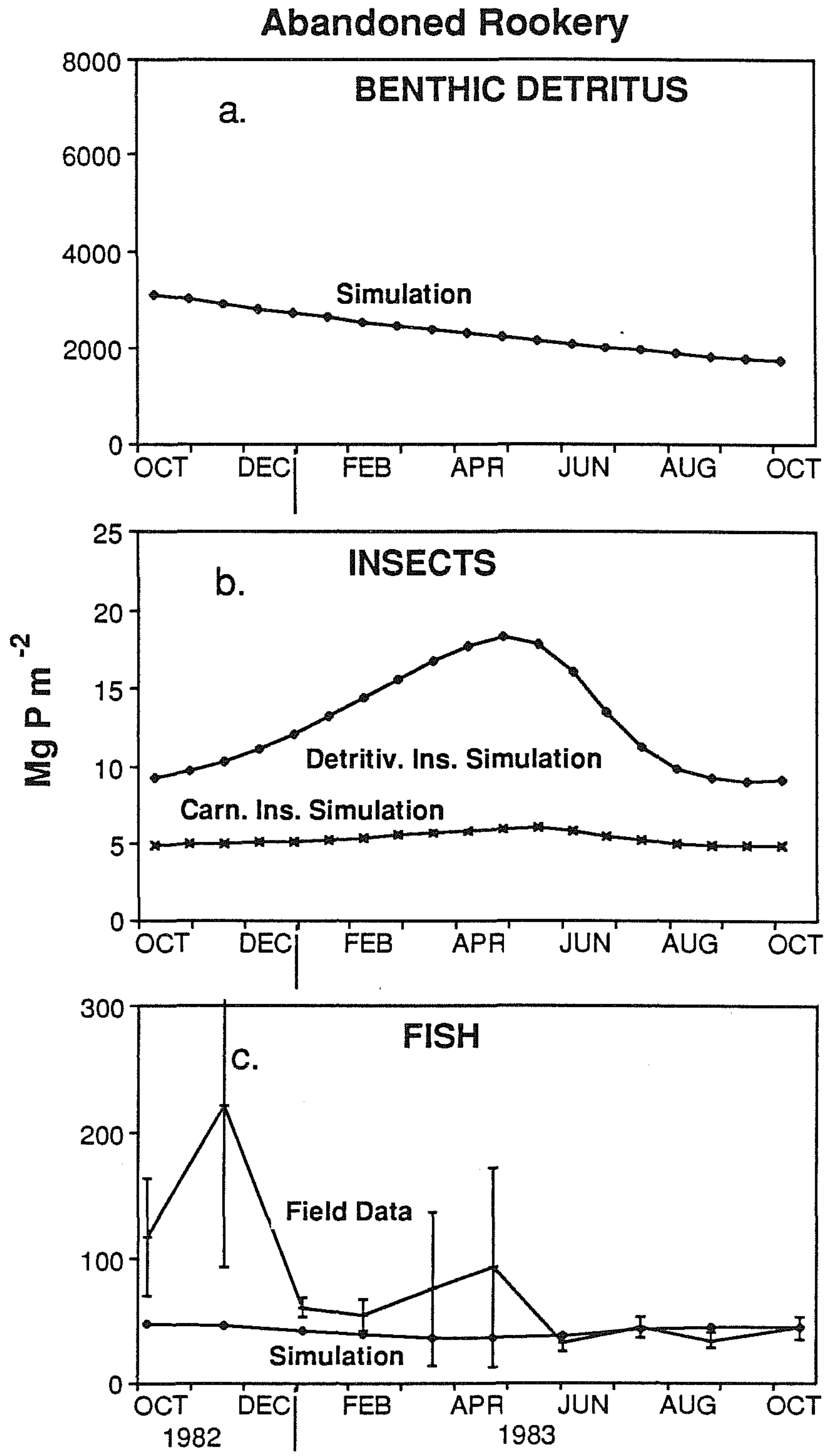

Abandoned Rookery
a.
AQUATIC MACROPHYTES
Simulation
Field Data I
Field Data II
0
400
800
1200
1600
OCT
DEC
FEB
APR
JUN
AUG
OCT
1982
1983
Mg P m -2
b.
Soluble Reactive P
Field Data
Simulation
0
10
20
30
40
OCT
DEC
FEB
APR
JUN
AUG
OCT
1982
1983
c.
PHYTOPLANKTON
Simulation
Field Data
0
50
100
150
200
OCT
DEC
FEB
APR
JUN
AUG
OCT
1982
1983

Fig. 9. Detritus and animal dynamics in the abandoned rookery.


Abandoned Rookery
a.
BENTHIC DETRITUS
Simulation
8000
6000
4000
2000
0
OCT
DEC
FEB
APR
JUN
AUG
OCT
b.
INSECTS
Detritiv. Ins. Simulation
Carn. Ins. Simulation
25
20
15
10
5
0
Mg P m -2
c.
FISH
Field Data
Simulation
300
200
100
0
1982
1983

CHAPTER 6

CONCLUSIONS

The preceding chapters support a hypothesis of biogenic and simulated nutrient enrichment causing increased levels of various ecological components of an Okefenokee Swamp marsh. Enrichment by wading birds and an artificial experimental source caused increased stores of phosphorus in diverse links of the food web. Simulation modeling of such eutrophication produced similar increases in components, lending increased support to a hypothesis that an aerial component, wading birds, caused broad-scale changes to the aquatic ecosystem that persisted for some years after the birds abandoned the site.

To chemically simulate nutrient enrichment from birds, I developed a convenient standardized system for testing effects of chemical inputs on ecosystems in remote regions. Clay flower pots filled with chemically-enriched agar (Fairchild et al. 1984) inside 2-m^2 clear plastic enclosures provided sturdy, easily constructed and easily maintained experimental mesocosms in an Okefenokee Swamp macrophytic marsh. One-L pots filled with 0.2 M $(NH_4)_2HPO_4$-enriched agar released an average of 45 mg NH_4-N d^{-1} and

11 mg PO_4-P d^{-1} into deionized water in the laboratory, with higher release into Okefenokee Swamp blackwater. Marsh mesocosms containing pots had higher stocks of zooplankton (primarily Diaphanosoma brachyurum) than controls. These results demonstrate that simulation of enrichment levels remaining after birds had left can cause significant effects on zooplankton primary consumers in the marshes.

Evidence was presented for residual nutrient enrichment of diverse components of a blackwater marsh, by a biotic component of the ecosystem itself. Thousands of nesting white ibis (Eudocimus albus) that foraged over a 20-km radius imported macronutrients to a rookery within Okefenokee Swamp. One to two years after the birds abandoned it, this marsh showed continued nutrient effects. Elevated available phosphorus in sediments, as measured by equilibrium phosphate concentration, contributed to enhanced biomass of phytoplankton in the overlying water column. Planktivorous fish were greater in biomass than at reference sites. These results and the zooplankton data demonstrate that this blackwater ecosystem was macronutrient limited, and manifested residual enrichment effects of wading birds on sediments, and a positive effect of sediments on phytoplankton. Results also suggest further indirect positive effects of birds on higher trophic levels (zooplankton and fish), via macronutrient transfers.

To calculate the trophic transfer to fish, for a simulation model of the Okefenokee marshes, I measured feeding dynamics of Leptolucania ommata and Gambusia affinis, in situ. Both fishes ate mainly insect larvae (such as Chironomidae) and Cladocera. Evacuation rates ranged from 0.143 (L. ommata in winter) to 0.279 h^{-1} (L. ommata in summer). Daily food consumption ranged from 24.2 (L. ommata in winter) to 148.3 mg g^{-1} d^{-1} (G. affinis in summer; dry weight). Maximum consumption by both species was estimated at 26.31 mg m^{-2} d^{-1} in summer. Such values support a hypothesis that invertebrate prey production must be substantial in such blackwater wetlands.

Field measurements and data from the literature were used to construct a trophic model of Okefenokee Swamp marshland. Seasonal data were used to check dynamics of the model before, during and after simulated nutrient input from wading bird guano. The model gives reasonable estimates of the effects of enrichment on benthic detritus, aquatic macrophytes and phytoplankton, and conservative estimates of the increase of zooplankton and fish stocks. Simulated levels of the above components decreased toward nominal states after simulated abandonment by birds, and the rates of decrease generally followed field trends that were measured. The model indicates that nesting wading birds can have considerable effects on aspects of an aquatic ecosystem that are not normally associated with them (such as benthic detritus and fish).

In the model, zooplankton were not sensitive to enrichment or its withdrawal, and this at first seemed inconsistent with the zooplankton sensitivity (elevation) observed in enriched mesocosms. However, zooplanktivorous fish were present in the model and not in mesocosms, and they contributed to the lower levels of zooplankton in the simulations. Thus the observed lower enrichment effects in the model were not unreasonable.

The above conclusions help to address some topics from the Introduction. First, wading birds can recycle and import substantial quantities of nutrients to an aquatic ecosystem, and these nutrients can enhance higher trophic levels, even after the birds have left. Second, by enhancing higher trophic levels, such birds might increase their own food supplies, thereby having a positive indirect influence on themselves, via the ecosystem. This consideration remains speculative but intriguing, and could make worthwhile future research on indirect effects in food webs. Third, results support the general importance of indirect effects in aquatic ecosystems. For instance, indirect effects of birds on phytoplankton (via sediments) were substantial, and supported the notion that time-delayed indirect effects can be significant in themselves and important to other components of an ecosystem.

Another interesting finding is that, contrary to a common belief, biotic production in blackwaters is substantial, and that enrichment can readily increase it. Rather than demonstrating low production as a result of low light penetration or low pH (Janzen 1974, Fittkau et al. 1975, Araujo-Lima et al. 1986), the unenriched blackwater system evidenced substantial invertebrate production, as determined from levels of predation by fishes (Chapter 4). Furthermore, residual enrichment from wading birds apparently stimulated primary producers, invertebrates and fish to even greater levels of productivity. Such results help to bolster the hypothesis of Freeman and Freeman (1985), that such blackwaters have substantial secondary productivity.

The marsh ecosystem took up much of the biogenic fertilization from birds, and released it only gradually. Sediment available P and simulated benthic P were elevated for years (Chapters 3 and 5). These results support the conclusions of others (e.g., Ewel and Odum 1984, Dolan et al. 1981, Richardson and Marshall 1986, Howard-Williams 1985) that wetlands can indeed absorb wastes, primarily via sediments. On the applied side, wetlands have been suggested for natural treatment of sewage. The results described here indicate a sizeable capacity to buffer pulses of sewage nutrients, by time-delayed release to downstream ecosystems.

APPENDIX

FORTRAN MODEL OF MARSHLAND ON THE WEST SIDE OF OKEFENOKEE SWAMP

Note especially the dynamical equations of state, delimited by lines of asterisks. See Chapter 5 for an explanation of the program, including components and flows (Fig. 2) and variable names (in Tables).

```
C  PROGRAM OKE-- SIMULATION OF WEST SIDE MARSHES OF OKEFENOKEE
C     J.D. OLIVER AND T. LEGOVIC (1987)
C     OUTPUTS OF TIME ARE PLACED IN TIME() FOR PLOTTING
      REAL TIME(140), VAR(140,10)
      REAL NESTIM, MU27, MORT27, MU37, MORT37,
     +   MU67, MORT67, MU87, MORT87, MU47, MORT47, MU57, MORT57
      REAL INSEGP, LVBEG, LVFIN
      REAL KM12, KMTO35, KM78, K3P, K4P, K70, K71, K8
      REAL K3PMNA, K4PMNA, LV
      REAL K17, K5P, K5PMNA
C     START ON T = 240 = AUG 29 = DAY OF INIT. CONDITIONS
      T = 240.
      WRITE(*,10)
C     INPUT # OF BIRDS,DT,# SIMULATION YRS,# DT'S BETWEEN PRINTING
      READ(*,*) XOB, DT, YRS, INTERV
      WRITE(9,20) XOB, DT, YRS, INTERV
C     INIT. CONDITIONS OF VARIABLES
      X1 = 2.4
      X2 = 10.6
      X3 = 0.28
      X6 = 38.6
      X8 = 270.
      X4 = 9.4
      X7 = 630.
      X5 = 9.8
C     INPUT PARAMETERS
      EPS3 = 0.6
```

```
      EPS67 = 0.642
      EPS47 = 0.55
      EPS57 = 0.8
      K17 = 0.005
      K8 = 1300.
      K70 = 0.0025
      K71 = 0.0022
      KM12 = 9.6
      KM78 = 405.
      KMTO35 = 2.4
      MU27 = 0.12
      MU37 = 0.02
      MU67 = 0.005
      MU87 = 0.0011
      MU47 = 0.002
      MU57 = 0.002
      TAU12 = 0.5
      TAU23 = 0.78
      TAU36 = 0.0039
      TAU34 = 0.034
      TAU4IA = 0.00078
      TAU46 = 0.0227
      TAU44 = 0.023
      TAU73 = 0.019
      TAU78 = 0.047
      TAU75 = 0.28
      TAU56 = 0.0242
      TAU54 = 0.034
      THET12 = 1.068
      THET71 = 1.05
      THET78 = 1.024
      THETO6 = 1.081
C     THTINV= METAB. TEMP. COEF. USED AS FOOD-TO-INVERT. TEMP. COEF.
      THTINV = 1.052
C     TOTAL P FROM RAIN = 570 MG M**-2 YR**-1
      RAINP = 570.
C     FIDSYS = FLOW FROM ID (PRECIP.) TO THE SYSTEM
      FIDSYS = RAINP/365.
C     FRACTION OF RAIN P WHICH IS SRP
      AMTSRP = 0.072
      FID1 = AMTSRP*FIDSYS
C     REMAINING P GOES TO DETRITUS, X7
      FID7 = (1.0 - AMTSRP)*FIDSYS
C     EXTRCP = ESTIMATED PLANT-EXTRACTABLE P / DETRITUS P
      EXTRCP = 0.0193
      EDIFRC = 0.01
C     P IN DEPOSITED CARN. INSECT EGGS = 9.4 MG M**-2 * 2% /YR
      INSEGP = 0.19
C     CARN. INSECTS DEPOSIT EGGS FROM T = DAY DEPBEG TO DEPFIN
      DEPBEG = 120.
      DEPFIN = 180.
```

```
      DEPDAY = DEPFIN - DEPBEG + 1.
      FIASYS = INSEGP/DEPDAY
C     INSECTS LEAVE FROM LVBEG TO LVFIN
      LVBEG = 90.
      LVFIN = 243.
      BRDBEG = 135.
      BRDFIN = 239.
C     P PER BIRD = 0.0055 MG M**-2 D**-1
      PPERB = 0.0055
      BRDSRP = 0.0026
      CYPRSP = 13.
      FIC7 = CYPRSP/365.
C     ALPH3P= REFUGE LEVEL BELOW WHICH X3 FREE FROM PRED. = .5*X3
      ALPH3P = 0.14
C     K3P= LEVEL OF X3 THAT SATIATES ITS PREDATORS' FEED RATES=2*X3
      K3P = 0.56
      K3PMNA = K3P - ALPH3P
      ALPH4P = 4.7
      K4P = 18.8
      K4PMNA = K4P - ALPH4P
      ALPH5P = 4.9
      K5P = 19.6
      K5PMNA = K5P - ALPH5P
      ZPSRP = 0.48
      PI = 3.1416
C     INITIALIZE COUNTER FOR PRODUCTION OF X6 TO 0
      PROD6 = 0.
C     CALCULATE # OF ITERATIONS OF FORMULA TO RUN
      TMAX = YRS*365.
      ITERAT = IFIX(TMAX/DT) + 1
C     INITIALIZE COUNTERS IPRINT, N, & NV, USED IN PLOTTING
      IPRINT = 0
      N = 0
      NV = 9
      WRITE(9,60)
C     RUN ITERATIONS OF FORMULA
      DO 2 I=1, ITERAT
C     CHECK WHETHER IT IS BIRD NESTING TIME OR NOT
      NESTIM = 0.
      IF(T .GE. BRDBEG .AND. T .LE. BRDFIN) NESTIM = 1.
      DEP = 0.
      IF (T .GE. DEPBEG .AND. T .LE. DEPFIN) DEP = 1.
      LV = 0.
      IF (T .GE. LVBEG .AND. T .LE. LVFIN) LV = 1.
C     CALCULATE AVERAGE DAILY TEMP. & TEMP.- 20 C
      TEMP = 18.7 - 9.50*SIN(2.*PI*T/365. + 0.599)
      TEMN20 = TEMP - 20.
      EDIBL7 = EDIFRC*X7
      EXTRC7 = EXTRCP*X7
      F1ON2 = X1/(KM12 + X1)
      F2ON3 = X2/(KMTO35 + X2)
      F3ONP = DIM(1.0, DIM(K3P,X3)/K3PMNA)
```

```
      F8ON8 = (K8 - X8) /K8
      F4ONP = DIM(1.0, DIM(K4P,X4)/K4PMNA)
      F7ON35 = EDIBL7 /(KMTO35 + EDIBL7)
      F7ON8 = EXTRC7 /(KM78 + EXTRC7)
      F5ONP = DIM(1.0, DIM(K5P,X5)/K5PMNA)
      FIB1 = PPERB*XOB*NESTIM *BRDSRP
      FIB7 = PPERB*XOB*NESTIM *(1.0 - BRDSRP)
C     FLOW FROM IA TO X4 = EGGS TO MARSH SYS. DURING DEPOSITION
      FIA4 = FIASYS*DEP
      F12 = TAU12*X2*THET12**TEMN20 *F1ON2
      F17 = K17*X1
      F23 = TAU23*X3*THTINV**TEMN20 *F2ON3
      F36 = TAU36*X6*THETO6**TEMN20 *F3ONP
      F34 = TAU34*X4*THTINV**TEMN20 *F3ONP
      F4IA = TAU4IA*X4*LV
      F46 = TAU46*X6*THETO6**TEMN20 *F4ONP
      F44 = TAU44*X4*THTINV**TEMN20 *F4ONP
C     F7O = LOSS FROM BENTHIC DETRITUS TO OUTFLOW
      F7O = K7O*X7
      F71 = K71*X7*THET71**TEMN20
      F73 = TAU73*X3*THTINV**TEMN20 *F7ON35
      F78 = TAU78*X8*THET78**TEMN20 *F8ON8 *F7ON8
      F75 = TAU75*X5*THTINV**TEMN20 *F7ON35
      F56 = TAU56*X6*THETO6**TEMN20 *F5ONP
      F54 = TAU54*X4*THTINV**TEMN20 *F5ONP
      EGES3 = (F23 + F73)*EPS3
      EGES31 = ZPSRP*EGES3
      EGES37 = (1.0 - ZPSRP)*EGES3
      EGES67 = (F36 + F46 + F56)*EPS67
      EGES47 = (F34 + F44 + F54)*EPS47
      EGES57 = F75*EPS57
      MORT27 = MU27*X2
      MORT37 = MU37*X3
      MORT67 = MU67*X6
      MORT87 = MU87*X8
      MORT47 = MU47*X4
      MORT57 = MU57*X5
      IF(I .EQ. 1) GO TO 1
C     EULER FORMULA FOR CALCULATING CHANGES IN X'S
C*********************************************************************
      DX1 = DT*(FID1 + FIB1 + EGES31 + F71 - F12 - F17)
      DX2 = DT*(F12 - F23 - MORT27)
      DX3 = DT*((F23 + F73)*(1.0 - EPS3) - F36 - F34 - MORT37)
      DX6 = DT*((F36 + F46 + F56)*(1.0 - EPS67) - MORT67)
      DX8 = DT*(F78 - MORT87)
      DX4 = DT*(FIA4 + (F34 + F44 + F54)*(1.0 - EPS47) - F4IA - F46
     +        - F44 - MORT47)
      DX7 = DT*(FID7 + FIB7 + FIC7 + F17 + EGES37 + EGES67 + EGES47
     +        + EGES57 + MORT27 + MORT37 + MORT67 + MORT87 + MORT47
     +        + MORT57 - F7O - F71 - F73 - F78 - F75)
      DX5 = DT*(F75*(1.0 - EPS57) - F56 - F54 - MORT57)
C*********************************************************************
```

```
      DPROD6 = DT*(F36 + F46 + F56)*(1.0 - EPS67)
      X1 = X1 + DX1
      X2 = X2 + DX2
      X3 = X3 + DX3
      X6 = X6 + DX6
      X8 = X8 + DX8
      X4 = X4 + DX4
      X7 = X7 + DX7
      X5 = X5 + DX5
      PROD6 = PROD6 + DPROD6
      T = T + DT
C     AFTER END OF YEAR, DAY = 0 + DT
      IF(T .GT. 365.) T = DT
      IPRINT = IPRINT + 1
      IF(IPRINT .LT. INTERV) GO TO 2
1     WRITE(9,100) T, TEMP, F75, F56, F73, F54,
     +   F34
C     INFO. FOR "PLOTER" SUBROUTINE
      N = N + 1
      TIME(N) = T
      VAR(N,1) = X1
      VAR(N,2) = X2
      VAR(N,3) = X3
      VAR(N,4) = X4
      VAR(N,5) = X5
      VAR(N,6) = X6
      VAR(N,7) = X7
      VAR(N,8) = X8
C     PLOT ANNUAL PRODUCTION OF X6 AS X9
      VAR(N,9) = PROD6
      INTEGT = IFIX(T)
      IF(INTEGT .EQ. 240) PROD6 = 0.
      IPRINT = 0
2     CONTINUE
10    FORMAT(27H ENTER X0B, DT, YRS, INTERV, /, /)
20    FORMAT(1H ,/, 35H THIS RUN'S SIMULATED # OF BIRDS IS , F8.0,
     +  1H;, 24H THE VALUE OF DELTA T IS , F8.3, /,
     +  29H  THE FINAL VALUE OF TIME IS , F8.3, 4H YRS ,/,
     +  28H  PRINTING INTERVAL IS EVERY ,I5, 10HTH DELTA T ,
     +  /)
60    FORMAT(1H ,/, 39H  DAY     TEMP       F75          F56       ,
     +               34H    F73          F54          F34    , /)
100   FORMAT(F7.1, F7.1, 5F12.5)
      CALL PLOTER(VAR,NV,N,TIME)
      STOP
      END
      SUBROUTINE PLOTER(VAR,NV,N,TIME)
C     PLOTTING SUBPROGRAM
C     INPUT NUMBER OF VARIABLES, NUMBER OF OUTPUT VALUES, & TIME
      REAL MIN,MAX
      DIMENSION PICT(60),MIN(10),MAX(10),VAR(140,10),TIME(140)
```

```
      DATA DASH/1H-/,PLUS/1H+/,BLNK/1H /
C     INITIALIZE ALL 51 COLUMNS OF OUTPUT TO BLANKS
      DO 50 K=1,51
50    PICT(K)= BLNK
      DO 100 JM=1,NV
      MIN(JM)=VAR(1,JM)
      MAX(JM)=VAR(1,JM)
      DO 100 I=2,N
      IF(VAR(I,JM).LT.MIN(JM)) MIN(JM)=VAR(I,JM)
      IF(VAR(I,JM).GT.MAX(JM)) MAX(JM)=VAR(I,JM)
100   CONTINUE
      DO 500 JM=1,NV
      WRITE(9,98)JM,MIN(JM),MAX(JM)
98    FORMAT(1H ,/, 9HVARIABLE= ,I5,4X, 8HHAS MIN= ,F14.5,5X,8HHAS
     +MAX= ,F14.5 )
C     CALCULATE RANGE OF VAR VALUES & DIST=1/50TH OF RANGE
      RANGE=MAX(JM)-MIN(JM)
      DIST=RANGE/50.
      DO 500 I=1,N
      DO 400 J=1,50
      RJ=J-1
      PICT(J)=DASH
C     Z = HISTOGRAM BAR OF APPROPRIATE SIZE
      Z = MIN(JM) + DIST*RJ
      IF(VAR(I,JM).LE.Z) GO TO 800
400   CONTINUE
800   PICT(J)=PLUS
      WRITE(9,99) TIME(I),VAR(I,JM),(PICT(K),K=1,51)
99    FORMAT(1H ,F8.1,F10.3,2X,51A1)
      DO 150 L=1,51
C     REINITIALIZE 51 COLUMNS TO BLANKS
150   PICT(L) = BLNK
500   CONTINUE
      RETURN
      END
```