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J. Douglas Oliver

Liberty University, doliver@liberty.edu

Steven A. Schoenberg

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Residual influence of macronutrient enrichment on the aquatic food web of an Okefenokee Swamp abandoned bird rookery

J. Douglas Oliver and Steven A. Schoenberg

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We present evidence 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 fertilized a rookery with guano within Okefenokee Swamp, Georgia, USA. One to two yr after the birds abandoned it, this marsh showed continued enrichment 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. Experimental phosphorus and nitrogen fertilization of enclosures at a reference site (at levels representing residual enrichment after birds had left) caused zooplankton biomass to increase significantly. These results 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.

J. D. Oliver and S. A. Schoenberg, *Inst. of Ecology, Univ. of Georgia, Athens, GA 30602, USA (present address of JDO: P. O. Box 3162, 33 Lea Road, Stroud, Ontario, Canada L0L 2M0).*

Introduction

Okefenokee Swamp, an 1800 km² wetland in southeastern Georgia and adjacent Florida, has blackwaters (dark, humic-stained waters) that are not high in available nutrients (Auble 1982). However, guano enriched at least one part of Okefenokee, a now abandoned ibis (*Eudocimus albus* L.) rookery, for at least 11 yr (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* Wagler) nesting among cattails (*Typha*) in shallow Minnesota pools caused large increases in aquatic phosphorus (P) and nitrogen (N) in the immediate vicinity of the gulls. Similarly, Manny et al. (1975) found that more than 6000 migrant Canada geese (*Branta canadensis* L.)

were the chief cause of hypereutrophic primary productivity in Wintergreen Lake, Michigan. Leentvar (1967) showed that guano of gulls (*Larus ridibundus* L.) 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 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.

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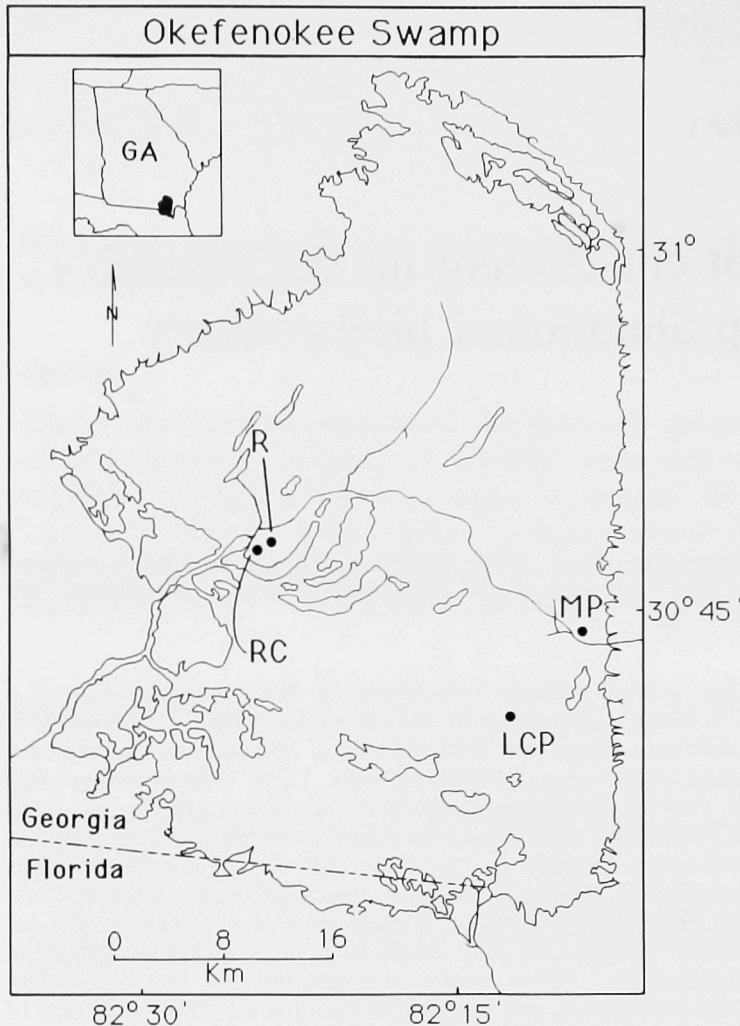


Fig. 1. Map of marsh sites (R is the abandoned rookery). Solid lines on the enlarged map delineate the Okefenokee Swamp watershed, its enclosed island and watercourses.

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 Lepidoptera and Coleoptera, 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. 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 white-water 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, USA, 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). After P input to Lake Erie, Canada-USA, decreased, levels of total P, soluble reactive P and phytoplankton declined significantly within 10 yr (El-Sharaawi 1987, Lam et al. 1987). In a Florida 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 yr 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.

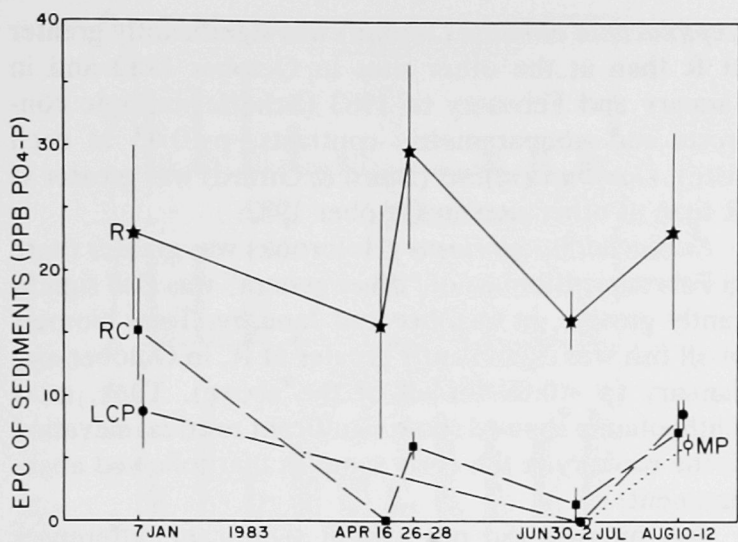


Fig. 2. Equilibrium phosphate concentrations at R, RC, LCP, and MP marsh sites. $N = 3$ for each date except $n = 2$ for LCP and MP. Vertical bars denote \pm SE.

Site descriptions

Our sites are all shallow (≤ 1.2 m depth), vegetated marshes within Okefenokee National Wildlife Refuge, Georgia. They have blackwater containing humic and fulvic acids, with a pH of about 3.8 (e.g., Beck et al. 1974). Floating and submerged macrophytes (*Nuphar luteum* L., *Utricularia* spp., *Cabomba pulcherrima* Harper) 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 P addition by the birds, $4.6 \text{ g m}^{-2} \text{ yr}^{-1}$, was comparable to crop field fertilization. After 1981, after 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 (≤ 0.5 m) site in which floating and submerged macrophytes (*Nymphaea odorata* Ait., *Utricularia* spp.) accompany emergents (*Eriocaulon compressum* Lam., *Rhynchospora inundata* Oakes, *Orontium aquaticum* L., 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* Bailey) with an understory of *Sphagnum*. These three comparison sites have lacked bird rookeries for at least 15 yr.

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 $0\text{--}320 \mu\text{g PO}_4\text{-P l}^{-1}$. Mixtures were vortexed every five minutes for 30 min and centrifuged ($4500 \times g$). We determined supernatant concentrations by the ascorbate method (Anonymous 1973) and calculated equilibrium phosphate concentration (that concentration at which phosphate was neither absorbed 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 ($n = 5\text{--}12/\text{site}$) 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 $((\text{NH}_4))_2\text{HPO}_4$ -enriched agar (Fairchild et al. 1985, Oliver 1985) continually enriched each of three 2-m^2 corrals. Three other corrals were unenriched controls. To directly assess the enrichment effect on zooplankton, we removed fish by electroshocking. Zooplankton were quantified by filtering integrated water column samples through $64 \mu\text{m}$ 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 after abandonment.

Sediment nutrient availability measurements helped reveal effects of former rookery activities on the ecosystem. Across all sample dates, equilibrium phosphate concentrations were significantly greater at R than at RC (Fig. 2, 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 yr after birds abandoned the rookery, nutrient availability at R was still greater than at other sites. As may be expected from the greater avail-

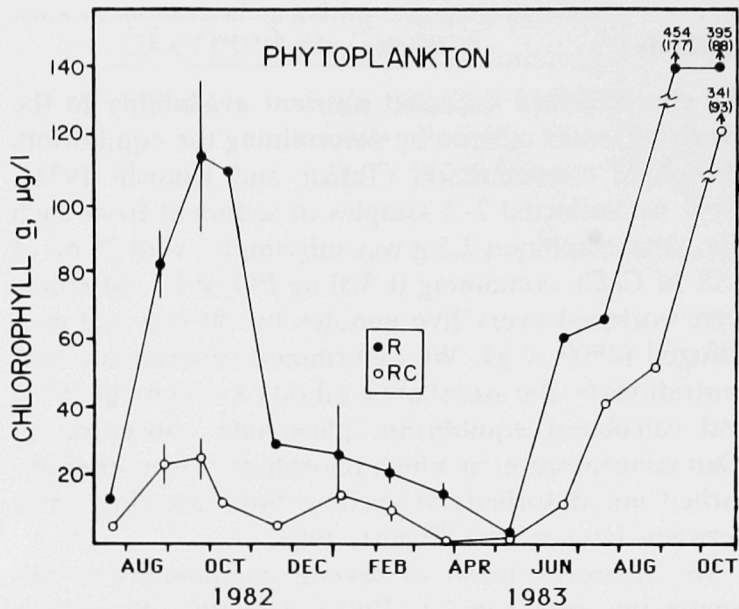


Fig. 3. Phytoplankton chlorophyll a concentrations in the water column at R and RC. N = 2 for each date. Bars (and parenthetical numbers) represent range.

able phosphorus in sediments, R water had a higher mean (and SE) value of $37.7 \mu\text{g l}^{-1} \text{PO}_4\text{-P}$ (8.1), compared with 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 20 November, 1982 and 9 October, 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 (Wilcoxon matched pair test, $p < 0.0005$). Seasonal patterns at the two sites were similar, increasing together in summer, then decreasing in late autumn 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 higher 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, Wilcoxon matched pairs, $p < 0.05$). These increases were largely a result of 6.5 times as many *Diaphanosoma brachyurum* (Liévin), a phytoplanktivorous cladoceran, in experimentals. 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 yr 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 (Jordan) 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* (Baird & Girard) was greater at R than at other sites in October 1982.

Enneacanthus gloriosus (Holbrook) 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 yr after birds

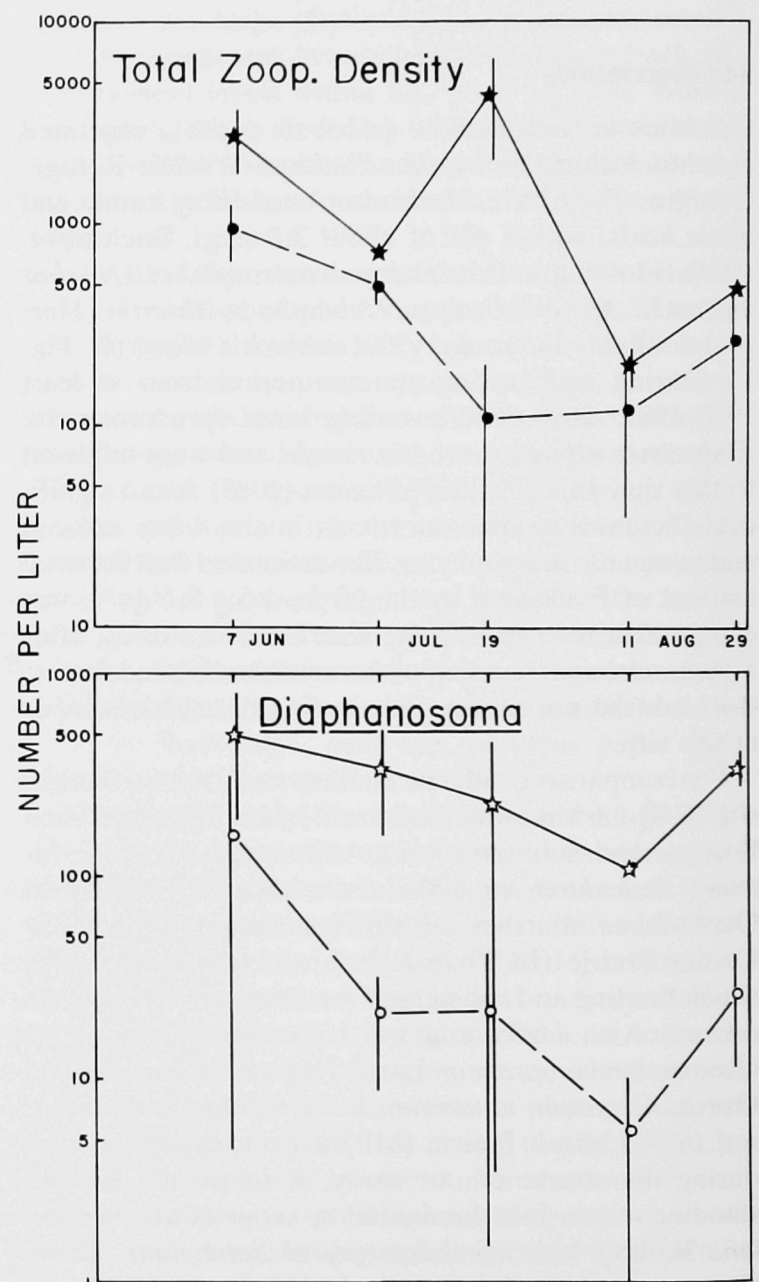


Fig. 4. Zooplankton densities in corrals receiving artificial enrichment of N and P (stars) versus no enrichment (circles), 1983. N = 3 for each date except n = 2 on 11 August. Bars represent \pm SE. Note log scales on ordinates. Modified from Oliver (1985).

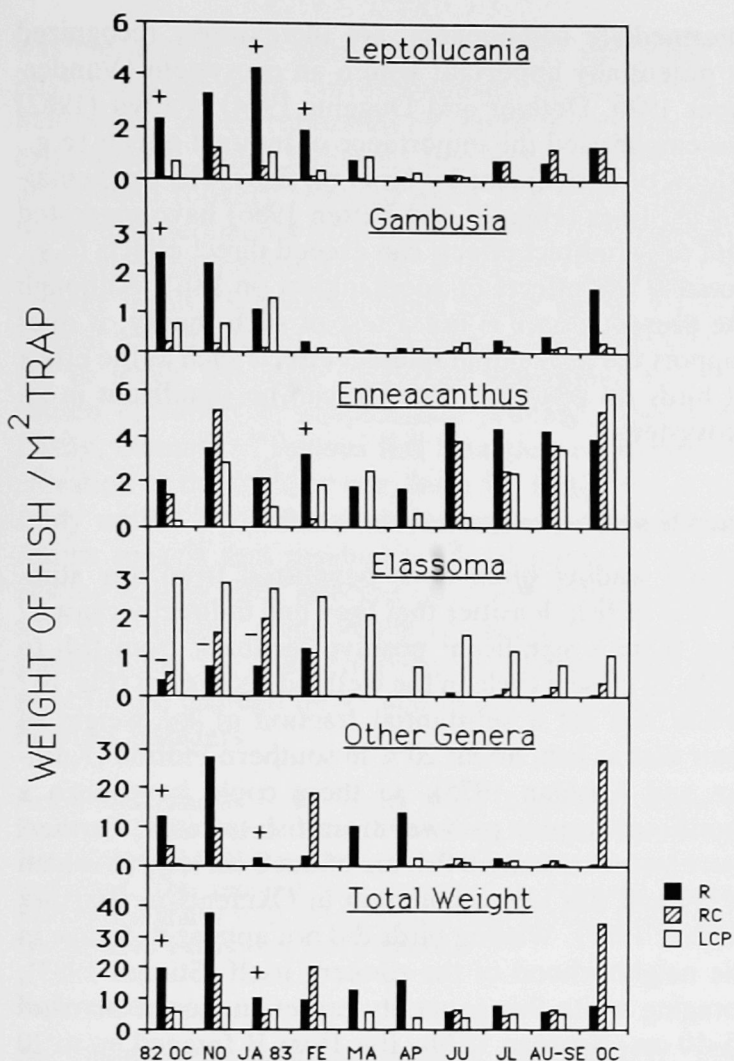


Fig. 5. Fish biomass (wet g m^{-2}) in R contrasted with two other Okefenokee sites (RC and LCP). Each value is an average over $n = 8$ traps, except that $n = 6$ in October 1982 at LCP, $n = 7$ in November at R and RC, $n = 12$ in January 1983 at RC, $n = 7$ in February at LCP, $n = 5$ in June at R, $n = 7$ 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 ($p < 0.05$).

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 biomass 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

Birds imported nutrients and affected the ecosystem

The suggestion that blackwater systems are severely nutrient-limited is supported by our results. However, instead of describing changes due to an anthropomorphic influence, we have documented effects of nutrients brought in from surrounding wetlands by avifauna. Analysis of sediment nutrient availability suggests that guano nutrients are deposited into sediments and delay

the recovery of the system from enrichment for at least two yr. More importantly, our observations indicate a stimulation of higher trophic levels, including zooplankton and fish, and suggest possible positive feedbacks to biota which we will discuss below.

Specific changes to system components

Nesting wading birds evidently did raise the equilibrium phosphate concentration of sediments at the rookery site, by means of guano (Fig. 2). 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). Water column $\text{PO}_4\text{-P}$ 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 $\text{PO}_4\text{-P}$ 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 in Fig. 6.

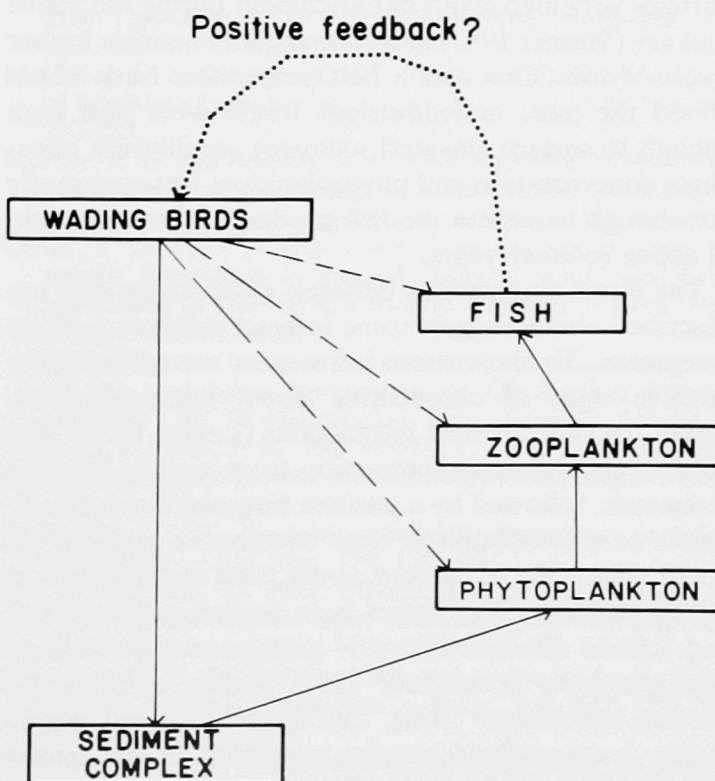


Fig. 6. Interactions via macronutrient transfer in an aquatic marshland (in Okefenokee Swamp). Solid arrows indicate positive direct relationships, dashed arrows show indirect relationships, and a dotted arrow indicates a possible relationship.

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, Oliver 1987), 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 yr 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* Lacépède, *Fundulus chrysotus* Gunther, and *Etheostoma fusiforme* Girard). 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 yr 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 (Leentvaar 1967, Manny et al. 1975, 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.

Possible positive feedbacks in the system

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 (Oliver 1987). 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 Swamp, even if there was no feedback from fish to birds, there may have been a positive feedback from fish to nutrients and plankton. Henrikson et al. (1980) indicated that a change in fish biomass could cause a corresponding change in the same direction in total P, N and phytoplankton, apparently via a change in turn-over rate of nutrients. These changes occurred even if input of nutrients to their system stayed constant. Similarly, in the Okefenokee abandoned rookery, the higher fish biomass observed at the beginning of our study may have contributed to increases in aquatic nutrient availability and phytoplankton, regardless of any possible effects on birds.

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 PO₄-P to overlying water than sediments from other Okefenokee marshes, and overlying phytoplankton were then increased to greater levels (Schoenberg and Oliver 1988). 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 at the rookery site, from the beginning of the study until 1.5 yr 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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