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Journal

SIL Proceedings 1922-2010, 26(4)

ISSN

0368-0770

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Publication Date

1998-05-01

DOI

10.1080/03680770.1995.11900986

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Peer reviewed



Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen

ISSN: 0368-0770 (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/tinw19>

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To cite this article: Scott D. Cooper, Kenneth M. Mavuti, Sheila Wiseman, Orlando Samelle, Mary Gakungu & Nicola Pacini (1998) Effects of fish and phosphorus on small, turbid ponds in East Africa, Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen, 26:4, 1543-1550, DOI: [10.1080/03680770.1995.11900986](https://doi.org/10.1080/03680770.1995.11900986)

To link to this article: <https://doi.org/10.1080/03680770.1995.11900986>



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Effects of fish and phosphorus on small, turbid ponds in East Africa

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Introduction

The composition and abundance of freshwater organisms at different trophic levels are affected simultaneously by their predators and resources (POWER 1992, CARPENTER et al. 1985, MCQUEEN et al. 1989). Because the relative importances of resource-mediated, bottom-up effects and predator-mediated, top-down effects will likely depend on environmental conditions, it is important that limnologists examine these effects under a wide array of conditions so that they can quantify and predict the influences of abiotic and biotic factors on the outcome of consumer-resource interactions (LEIBOLD 1989, PERSSON et al. 1991, SARNELLE 1992).

To expand the range of conditions where top-down effects have been examined, we manipulated densities of planktivorous fish in small, turbid, savanna ponds in East Africa. Simultaneously, we examined bottom-up relationships among nutrients and the abundances of organisms at different trophic levels in these ponds in a related analysis (SARNELLE, COOPER, MAVUTI & WISEMAN, unpubl.). Very few studies have examined the effects of bottom-up and top-down interactions in tropical waters, particularly small ponds. Because domesticated livestock and wildlife often drink from, and wade in savanna ponds, and because these ponds are very shallow, these water bodies are often very turbid and high in nutrients. It is not known how high turbidity, high nutrient levels, and constantly high temperatures and solar radiation affect algal biomass and predator-prey interactions in such systems (ARCIFA et al. 1986, GROBBELAAR 1989, CUKER 1987, 1993). In addition, many tropical waters lack large cladocerans, such as *Daphnia*, that are central to the strong, top-down effects seen in many temperate waters (KERFOOT & LYNCH 1987, LEIBOLD 1989).

Study site

We studied 26 small ponds located along 14 km of the Nairobi - Tala Road, approximately 25 km east of Nairobi, Kenya, from January, 1990, to June, 1991 (ca. lat. 1° 17' S; long. 37° 8' E). These ponds were

created by road construction activities several decades ago and are similar to natural savanna ponds in the area. The native vegetation in this area is primarily *Acacia* scrub and grassland, and the major land use is livestock grazing; however, a small amount of subsistence farming occurs towards Nairobi. The climate is hot and semi-arid, with most rain falling in October and November (short rains) and again from March to June (long rains). The water from these ponds is drawn for domestic use, and is especially used for watering cattle. In addition, various wildlife species (gazelles, impala, kongoni, giraffe) use these ponds as watering holes.

These ponds vary greatly in degree of permanence, ranging from ponds which contain water for only a few weeks after rainstorms to ponds that contain water over several years. When filled with water, pond areas ranged from 8 to 9000 m², and maximum depths from 20 to >200 cm. None of the ponds have outlets and all primarily receive water inputs from their local basins.

In 1990-91, these ponds were highly turbid, and conductivity, alkalinity, total phosphorus and total nitrogen levels were high and increased as water levels declined during the dry seasons (Table 1). Soluble

Table 1. The range of values recorded for various physical, chemical, and biological factors for the Tala ponds from January, 1990, to June, 1991.

Factor	Range of values
Secchi Depth	0.5-70 cm
Suspended Solids	24-1076 mg/L
Conductivity	60-1100 µS/cm
Alkalinity	8-131 mg CaCO ₃ /L
pH	6.9-8.4
Surface Temperature (Day)	22-33°C
Total Nitrogen (TN)	52-167 µM
Total Phosphorus (TP)	1.1-25.7 µM
Molar TN/TP	15-80
Surface Dissolved Oxygen (Day)	2.5->20 mg/L
Chlorophyll <i>a</i>	0-836 µg/L
Fish Density	0-206/m ²

reactive phosphorus levels were often low, sometimes below the detection limits of our analytical technique ($<0.2\mu\text{M}$, $\bar{X} = 0.2\mu\text{M}$, $\text{SE} = 0.1$). Concentrations of nutrients and chlorophyll *a*, and densities of zooplankton, macroinvertebrates, and fish, varied greatly from pond-to-pond and through time within a pond. Daytime surface water temperatures were 1 to 5 °C higher than bottom water temperatures and, during the study period, daytime dissolved oxygen concentrations were often supersaturated (5.6 to $>20\text{ mg/L}$) in surface waters but near zero ($<1\text{ mg/L}$) just above the bottom.

The dominant fish in all ponds containing fish was a small species of *Barbus*; however, *Tilapia zillii*, *Labeo* sp., and *Poecilia reticulata* were also present in five ponds near the Athi River. Zooplankton assemblages in these ponds were dominated by copepods and/or rotifers, although the cladoceran, *Moina micrura*, and ostracods were commonly collected. The dominant pelagic macroinvertebrates collected in these ponds were planktivorous backswimmers, *Anisops* spp. Fairy shrimp (*Streptocephalus*), clam shrimp, and tadpoles (particularly *Xenopus*) were also collected in some of the ponds. Benthic and littoral macroinvertebrate assemblages were dominated by chironomids, oligochaetes, and the corixid *Micronecta*, although freshwater crabs (*Potamonautes* sp.), snails, and a variety of aquatic insects were also collected. Algal assemblages varied greatly from pond to pond and, depending on the pond, were dominated by cyanobacterial filaments, diatoms, flagellates, and colonial and unicellular chlorophytes. Most ponds consisted of open water overlying mud bottoms; however, littoral fringes dominated by *Cyperus* sp. with, in some cases, small amounts of *Typha domingensis* and *Scirpus* sp. were found around some of the ponds.

Experimental design and methods

Thirteen ponds were monitored for maximum depth, Secchi depth, total phosphorus, suspended particulates (inorganic solids and particulate organic matter), chlorophyll *a*, zooplankton, pelagic macroinvertebrates, and fish on 15 May, 1991. These ponds were then assigned to one of three treatments, including no fish control (Code: nn; 3 replicate ponds), fish control (Code: ff; 7 replicate ponds), and fish added (Code: nf; 3 replicate ponds) treatments. On 17 May, *Barbus* sp. were seined from a fish control pond and added to the three fish addition ponds in sufficient numbers to equal 4.4–5 fish/m² or 8.4–9.5 g of fish/m², which approximated the average fish biomass recorded from fish control ponds ($\bar{X} = 7.8\text{ g/m}^2$). Seven of these ponds (2 nn, 3 nf, 2 ff), matched by area, turbidity, and depth, were intensively monitored for fish, macroinvertebrates, zooplankton, chlorophyll *a*, suspended solids, total phosphorus, and Secchi depths on 20, 23, and 31 May, and 6 and 15 June. In

addition, the remaining no fish and fish control ponds were monitored for these parameters on 15–16 June. One “no fish control” pond dried up during the experiment, and was replaced by another pond lacking fish that had not been sampled before the experiment started. ANOVAs and ANCOVAs were performed on appropriately transformed data to examine treatment effects on response variables, and relationships among variables were examined through correlational and multiple regression techniques. Concentration, biomass, and abundance data were log (x) or log (x+1) transformed, and relative biomass data were angularly transformed, before analyses.

Secchi depths were measured with a 36 cm diameter Secchi disk, and dissolved oxygen and temperature with Winkler titrations and a thermometer, respectively, or with a YSI DO meter. Surface water was screened through 149 μm mesh for total phosphorus determinations and filtered through Gelman A/E filters for determinations of suspended solids and chlorophyll *a*. Total phosphorus concentrations were determined after digestion with persulfate (VALDERAMMA 1981). Filters for suspended solids were weighed after drying at 103 °C for one hour, cooled in a desiccator, then combusted at 550 °C for one hour and reweighed. Chlorophyll *a* was extracted in boiling methanol, and nonacidified and acidified extracts were read on a spectrophotometer at 665 and 750 nm.

Zooplankton were collected by pooling three samples from each pond taken with a 4.4 L water bottle (MAVUTI sampler; LITTERICK & MAVUTI 1985) and filtering the water through 45 μm mesh. Samples were preserved in 4 % buffered formalin. When ponds were very shallow, samples were taken with a bucket. Subsamples of zooplankton were counted and measured in a Sedgewick-Rafter cell at 40 \times on a compound microscope. Length measurements were made with a digitizer and converted to dry mass using published mean dry masses for soft-bodied rotifers (PAULI 1989), relationships between length and dry mass for microcrustaceans (DUMONT et al. 1975, BOTTRELL et al. 1978, CULVER et al. 1985) and relationships between length and volume converted to dry mass for loricate rotifers (PAULI 1989, RUTTNER-KOLISKO 1977). Zooplankton samples from nine ponds (3 nn, 3 nf, 3 ff) were analyzed for the premanipulation period, but zooplankton samples from all 13 ponds were analyzed for the last sample date.

Epibenthic and pelagic macroinvertebrates were sampled by taking standard sweeps with a D net (mesh size = 0.3 mm) from 10 sites in each pond. Macroinvertebrates were identified and counted in the field, and subsamples were preserved in 70 % ethanol for later measurements and to confirm identifications. Fish were sampled by taking hauls with a seine measuring 6 m long by 1 m high with 4 mm mesh. Each seine haul covered an area of 28 m², and from one to five hauls were taken from each pond.

Fish were identified, counted, and total lengths measured in the field. Subsamples of fish from each pond were weighed and measured in the laboratory to develop length-mass regressions for each fish species so that data on fish numbers and lengths could be converted to fish biomass. In addition, eight to ten *Barbus* were collected from each of 7 fish control ponds on 15 May, and ten *Barbus* were collected from each of three fish addition ponds on 20 May and from each of three fish addition and three fish control ponds on 31 May, 1991 (total = 97 ff fish, 60 nf fish). These fish were preserved in 4% buffered formalin for gut content analysis. Contents of the upper digestive tract (esophagus, stomach) of each fish were removed and prey items identified and counted under a dissecting microscope at 25 \times .

Results

Premanipulation data, 15 May. Ponds containing fish were deeper and had lower suspended solid concentrations than ponds lacking fish; however, there was no difference in total phosphorus and chlorophyll *a* concentrations, and Secchi depths, in ponds containing versus lacking fish (Fig. 1). Total zooplankton biomass, and the relative and absolute biomasses of rotifers and cyclopoid copepods, were higher in ponds containing versus lacking fish (one-way ANOVAs, $F_{1,7}$'s = 6.3 to 80.6, P 's = 0.02 to

<0.001). In contrast, the relative contribution of calanoid copepods to total zooplankton biomass tended to be higher in "no fish" than fish ponds ($F_{1,7} = 3.7$, $P = 0.09$). As a consequence, the body size of zooplankton was substantially lower in fish than in fishless ponds (Fig. 1). The density of *Anisops* spp. was greater in fish than fishless ponds, whereas corixids, primarily *Micronecta*, showed the opposite pattern (corixid \bar{X} (no./10 standard sweeps) ± 1 SE: fish = 0 ± 0 , no fish = 15.7 ± 9 ; one-way ANOVA, $F_{1,11} = 12.4$, $P = 0.005$). Ostracods were not collected in zooplankton samples from fish ponds, but were commonly found in ponds without fish (\bar{X} ($\mu\text{g/L}$) ± 1 SE = 9.8 ± 8.4). Values for response variables were similar for fishless ponds assigned to "fish addition" versus "no fish control" treatments.

Correlational analyses indicated that chlorophyll *a* concentrations were most closely related to total phosphorus concentrations (Pearson's $r = +0.66$, $P = 0.019$, $n = 12$), whereas inorganic suspended solids were negatively related to pond depth ($r = -0.67$, $P = 0.017$, $n = 13$). Particulate organic matter was positively related to total phosphorus concentrations ($r = +0.77$, $P = 0.004$, $n = 12$), and total zooplankton biomass was negatively related to suspended solids ($r = -0.83$, $P = 0.01$, $n = 9$) and positively

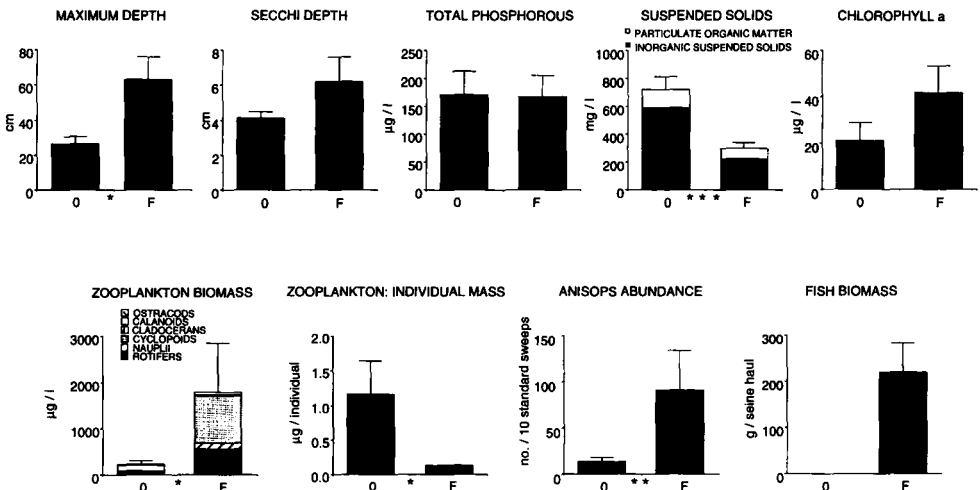


Fig. 1. Comparisons of values for response variables in ponds lacking (O) and containing (F) fish before fish manipulations began. Heights of histograms represent \bar{X} s + 1 SE for 6 ponds lacking fish and 7 ponds containing fish. Asterisks indicate significant differences between fish and no fish ponds (one-way ANOVAs on transformed data, $F_{1,11}$ tests; code: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

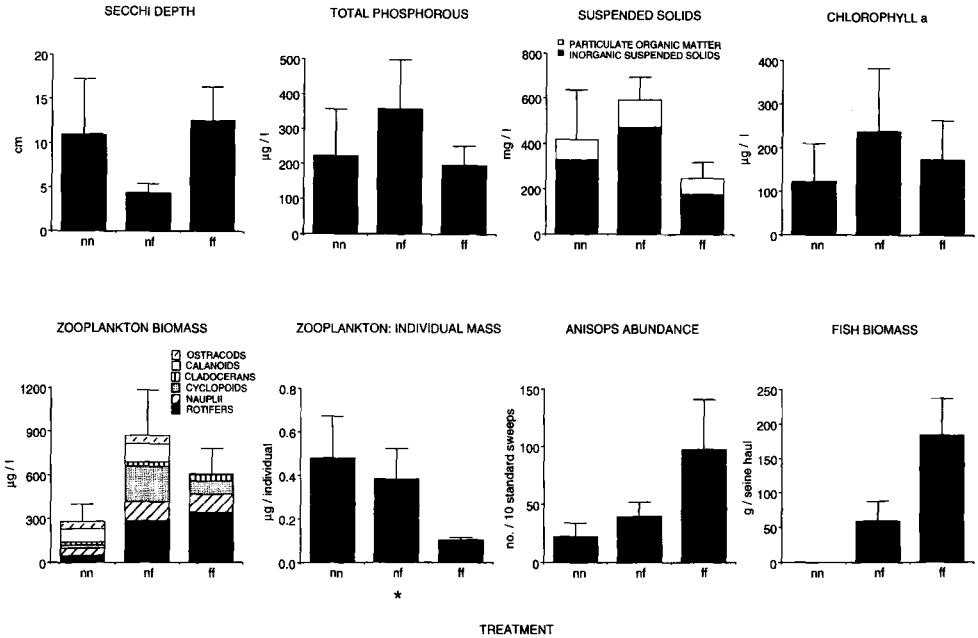


Fig. 2. Values of response variables for no fish control (nn, $n = 3$), fish addition (nf, $n = 3$), and fish control (ff, $n = 7$) ponds. Heights of histograms represent $\bar{X} + 1$ SE for ponds assigned to each treatment. Asterisks indicate significant effects of treatment (one-way ANOVA on transformed data, $F_{2,10}$ tests, code as in Fig. 1). Mean values for each pond throughout the experimental period were used as replicates in analyses. Analyses of values from only the last sampling date gave the same results.

related to chlorophyll *a* concentrations ($r = +0.70$, $P = 0.017$, $n = 9$).

Postmanipulation data, 17 May to 16 June. Pond volumes declined through time, and by the end of the experiment there were no significant differences in the areas, depths, or turbidities of ponds assigned to different treatments (Fig. 2, maximum depth $\bar{X} \pm$ SE: nn = 39 ± 14 , nf = 26 ± 1 , ff = 56 ± 14 cm; area $\bar{X} \pm$ SE: nn = 681 ± 213 , nf = 468 ± 154 , ff = 1503 ± 570 m²). Although fish densities in fish addition ponds were targeted to be similar to fish densities in fish control ponds, mean fish biomass in fish addition pools was at least three fold lower than in fish control pools (Fig. 2). Fish carcasses were not collected in fish addition ponds three days after fish additions; however, carcasses may have decomposed quickly or been eaten by birds.

There were no significant effects of fish treatment on Secchi depths; concentrations of total phosphorus, total suspended solids, inorganic sediments, particulate organic matter, and

chlorophyll *a*; total zooplankton biomass; and the densities of *Anisops* and corixids (Fig. 2). The relative and absolute biomasses of calanoid copepods and ostracods were significantly higher in fish addition and no fish control ponds than in fish control ponds (Scheffe's test, P 's < 0.05). The relative biomass of rotifers, on the other hand, tended to be higher in fish addition and fish control ponds than in ponds without fish (Fig. 3). As a consequence, zooplankton size in fish control ponds was less than in "no fish" ponds with fish addition ponds showing intermediate, but highly variable, values (Fig. 3). Relative rotifer biomass increased, and mean zooplankton size declined, in two of the three ponds to which fish were added, but not in the third fish addition pond where fish densities declined to low levels (Fig. 3). ANCOVAs indicated that premanipulation differences among ponds in the concentrations of total phosphorus and chlorophyll *a*, and in cladoceran biomass, were maintained through time and were not affected by fish manipulations.

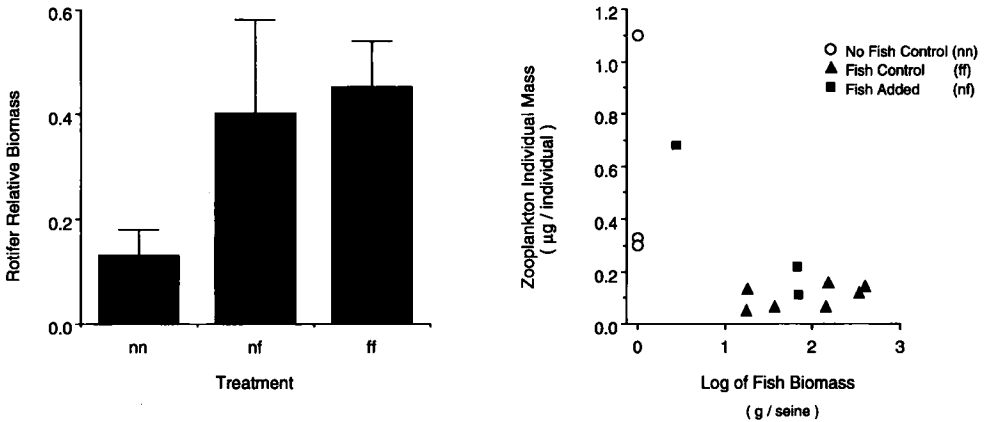


Fig. 3. Left: The proportion of total zooplankton biomass made up of rotifers (rotifer relative biomass) in ponds assigned to each experimental treatment, on the last sampling date. Treatment code and other designations as in Figs. 1 and 2. An analysis of covariance (ANCOVA) using treatment as the independent variable and premanipulation relative biomass of rotifers as the covariate revealed significant effects of the covariate ($F_{1,4} = 19.4$, $P = 0.012$) and treatment ($F_{2,4} = 13.1$, $P = 0.018$) on final rotifer relative biomass. Rotifer relative biomass was angularly transformed. Right: Plot of individual zooplankton mass, exclusive of nauplii, against $\log(x + 1)$ -transformed fish biomass for the final sampling date. Each data point represents a pond, and treatment codes are indicated on the plot. These data were best fit by the equation: zooplankton size = $0.60e^{(-0.83(\log(\text{fish biomass} + 1))}$, $r^2 = 0.48$. An ANCOVA using treatment as the independent variable and premanipulation individual zooplankton mass (log-transformed) as the covariate revealed effects of the covariate ($F_{1,4} = 9.8$, $P = 0.035$) and treatment ($F_{2,4} = 13.3$, $P = 0.017$) on final individual zooplankton mass (log-transformed).

Correlational and regression analyses indicated that total suspended solids, inorganic suspended sediment, particulate organic matter, and Secchi depth were related to pond depth, with shallow ponds being more turbid than deep ponds. By contrast, multiple regression analyses indicated strong positive relationships between total phosphorus concentrations and inputs of cattle fecal material ($r^2 = 0.62$), between chlorophyll *a* and total phosphorus concentrations ($r^2 = 0.86$), and between total zooplankton biomass and chlorophyll *a* concentrations ($r^2 = 0.75$, see below).

Although ostracods, copepods, and cladoceran ephippia were found in fish diets, chironomid larvae dominated the diets of *Barbus* sp. from both fish addition and fish control ponds (Fig. 4).

Discussion

Our results from small, turbid ponds on the savannas of East Africa indicated that the addition of small fish had effects on the relative biomass of rotifers and the size structure of zoo-

plankton assemblages (Fig. 3). It is unlikely, however, that these effects were owing to direct fish predation on large zooplankton, because large zooplankton, namely ostracods and calanoid copepods, were not affected by fish additions (Fig. 2). Furthermore, large zooplankton were relatively rare in the diets of *Barbus* collected from fish addition ponds (Fig. 4). Mean levels of phosphorus and chlorophyll were higher in fish addition than no fish control ponds, but this difference was not statistically significant. It is possible that increases in rotifer relative biomass were owing to increases in the rotifer's food supply. There were positive relationships among total phosphorus, chlorophyll *a*, and rotifer and microcrustacean biomass in this data set. Fish additions may augment pond nutrient pools through the decomposition of fish carcasses or through fish excretion (SCHINDLER 1992, THRELKELD 1988). Assuming that 0.5% of fish biomass was phosphorus (FINDLAY et al. 1994), we added from 280 to 370 µg/L of P, in fish biomass, to fish addition ponds. Phosphorus added to ponds in the form of fish could certainly have accounted

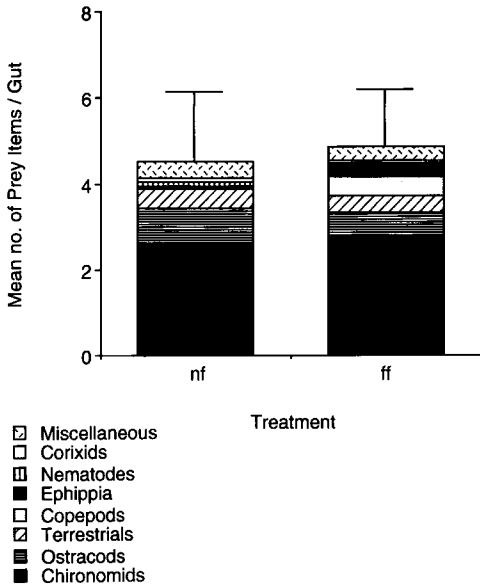


Fig. 4. Stacked histograms of the mean number of food items per *Barbus* gut for fish addition (nf) and fish control (ff) ponds. Ten fish were collected from each of 3 nf and 3 ff ponds on each of two dates, and eight to ten fish were collected from each of 4 additional ff ponds on one date (total = 60 nf fish and 97 ff fish). Mean numbers of prey in fish guts were calculated for each pond across both dates to obtain one value for each pond. Pond means, then, were averaged to obtain average fish diets for each treatment. Vertical lines above the histograms represent 1 SE for the mean total number of food items per gut.

for increases in P concentration in nf ponds as well as for mean differences in P concentration between nn and nf ponds. The subtle effects of fish additions on zooplankton assemblages seen here had no effects on total zooplankton biomass, phytoplankton biomass, total phosphorus concentrations, or water transparency.

Although the addition of fish did not appear to have direct effects on zooplankton, ponds with and without fish had quite different zooplankton assemblages at the beginning of the experiment (Fig. 1). Fishless ponds were dominated by calanoid copepods and ostracods, whereas fish ponds were dominated by rotifers and small cyclopoid copepods. Ponds initially lacking fish had recently refilled with water and were shallow and turbid, whereas ponds containing fish had contained water for over a year and a half and were clearer and deeper. It is

possible that the observed differences between fish and fishless ponds were owing to the direct effects of pond permanence, depth, or turbidity on zooplankton assemblage structure; however, all major zooplankton groups were present in most ponds and rotifers increased where fish were added to shallow, turbid ponds.

It is possible that our experiment was not run long enough with sufficient densities of fish to detect any direct effects on zooplankton assemblages or cascading effects to phytoplankton or nutrients. Where fish biomass had been increased to natural levels (Fig. 3), however, fish did have substantial effects on the relative abundances of zooplankton taxa and average zooplankton body size. Experiments conducted in large bags in a Brazilian reservoir showed that effects of planktivorous fish on zooplankton and phytoplankton were apparent within 2 to 3 weeks (ARCIFA et al. 1989). Our results indicate that *Barbus* did not prey substantially or have direct effects on zooplankton in ponds to which they were added (Figs. 2, 4).

We postulate that a likely explanation for the lack of convergence of the structure of zooplankton assemblages in fish addition and fish control ponds was differences in the turbidity of fish addition and fish control ponds. Fish addition and no fish control ponds were very turbid, and it is unlikely that visually-feeding fish would have direct effects on zooplankton in fish addition ponds because the fish would be unable to detect or capture prey at high turbidities (reviewed by CUKER 1993). By contrast, fish may have reduced or eliminated large zooplankton in clearer fish control ponds, leaving a zooplankton assemblage dominated by small-bodied species.

Correlational and regression analyses on both premanipulation and postmanipulation data indicate no relationships between fish biomass and nutrients, algal biomass, or water transparency. Although comparisons of zooplankton assemblages in ponds with and without fish indicate that fish may have effects on zooplankton assemblages in clearer ponds, there is no evidence that planktivorous fish have cascading effects below the primary consumer level. It seems likely that the lack of strong cascading effects in these ponds was related to the composition of zooplankton assemblages. Studies showing strong effects from the top to the bottom of food chains were conducted in systems containing large cladocerans, particu-

larly *Daphnia* (LEIBOLD 1989, SARNELLE 1992). The dominant taxa in our fish-free ponds, namely ostracods and copepods, generally do not appear to have strong effects on phytoplankton biomass. The only cladoceran commonly collected in these ponds, *Moina micrura*, was very small and was not affected by the presence or abundance of fish. The lack of fish effects on phytoplankton, nutrients, and water transparency, then, is probably owing to the absence of large cladocerans. The absence of large cladocerans in these ponds at the time of the experiment may have been owing to negative effects of suspended sediment on cladoceran feeding (KIRK & GILBERT 1990).

By contrast to the muted responses of this system to manipulations of consumers, our correlational analyses indicate that bottom-up effects in this system are very strong (SARNELLE, COOPER, MAVUTI & WISEMAN, unpubl.) Furthermore, we hypothesize that the effects of fish manipulation that we did see were related to nutrient inputs (see above). Multiple regression analyses showed strong, positive relationships between total phosphorus levels and fecal inputs by cattle, between phytoplankton biomass and total phosphorus levels, and between zooplankton and phytoplankton biomass. High biomasses of phytoplankton were recorded in these ponds despite their high turbidity, indicating that mixing was sufficient to allow phytoplankton populations to experience light levels necessary to grow to levels set by high nutrient concentrations (GROBBELAAR 1989). Chlorophyll *a* concentrations recorded from these ponds are among the highest recorded from any lake or pond.

There is also some indication that these bottom-up effects are transmitted, although weakly, to planktivores. There was a positive correlation between *Anisops* density and zooplankton biomass (Spearman's $r = +0.60$). Multiple regression analysis using log-transformed data from fish control ponds indicated that fish biomass was positively related to zooplankton biomass and total suspended solids and negatively related to chlorophyll *a* concentrations. The negative relationship between fish biomass and chlorophyll *a* concentration was probably related to the inverse relationship between phytoplankton biomass and nighttime dissolved oxygen levels (BOYD et al. 1978).

Because our study ponds occupied small, closed basins, the major source of nutrients to

these ponds was probably excretory products contributed by large, grazing mammals. Herdsmen used these ponds frequently to water their cattle, and wildlife occasionally visited these ponds. The positive relationships among cattle fecal input, total phosphorus, phytoplankton, zooplankton, and planktivores indicate that the productivity and biomass of trophic levels in savanna pond ecosystems are set by the use of these ponds by large grazing mammals. These relationships pose interesting questions regarding seasonal and interannual patterns in the use of these ponds by wildlife and pastoralists, and on the effects of changing land use patterns on pond productivity. These patterns indicate that large mammals can be important conduits of nutrients from terrestrial to aquatic environments.

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