

Nutrient excretion by fish in wetland ecosystems and its potential to support algal production

Kyle D. Zimmer¹

Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle,
St. Paul, Minnesota 55108

Brian R. Herwig

Minnesota Department of Natural Resources, Division of Fish and Wildlife-Fisheries Research, 2114 Bemidji Avenue,
Bemidji, Minnesota 56601

Leah M. Laurich²

Department of Zoology, Miami University, Oxford, Ohio 45056

Abstract

We used both direct measurement and bioenergetic methods to examine nitrogen and phosphorus (P) excretion by fathead minnows in two wetlands over 2 yr. We also assessed the potential importance of nutrient flux from fish by comparing excretion estimates to empirically derived estimates of algal P demand. Population-level estimates of P excretion across the four lake-years were high relative to other published studies, peaking at $11.7 \text{ mg m}^{-3} \text{ d}^{-1}$ and occurring when fish densities exceeded 69 fish m^{-3} . Excretion rates peaked in late summer during maximal algal demand, and P excretion by fish exceeded algal demand in two of the four wetland-years. Detritus was a major diet component (up to 90% by mass), making fish excretion a major nutrient flux from wetland sediments to the water column. Consumer-driven effects could have strong influences on nutrient dynamics in prairie wetlands, ecosystems historically thought to be constrained largely by abiotic factors.

Fish populations can have strong influences on ecological processes and the structure of aquatic ecosystems, and one common pattern is higher phytoplankton abundance and elevated water-column nutrients in the presence of dense populations of benthivorous and planktivorous fish (Hanson and Butler 1994; Vanni et al. 1997). Although this relationship is well documented, the mechanisms responsible and their relative importance are not always clear.

In a general sense, there have been three (not necessarily exclusive) models proposed to explain the positive relationship between benthivorous–planktivorous fish and nutrient concentrations and algal abundance (Vanni and Layne 1997). In the first model, nutrient excretion by sediment-feeding

fishes increases nutrient levels and facilitates higher algal abundance (Brabrand et al. 1990; Schindler et al. 1993). In a second model, fish predation changes zooplankton community structure, which modifies zooplankton nutrient cycling and stimulates phytoplankton growth (Sterner et al. 1992). In the final model, algal abundance increases because fish predation reduces the abundance of large-bodied zooplankton, which are effective grazers on phytoplankton (Carpenter et al. 1985). In the first model, fish consumption and subsequent excretion result in internal loading of nutrients that stimulates algal growth. However, the degree to which fish populations influence nutrient cycling is variable (Schindler and Eby 1997), as is the specific role of fish, with some populations serving as potential sinks (Kraft 1992) and others as sources of nutrients (Carpenter et al. 1992).

Several studies have assessed the importance of fish in nutrient cycling in lakes (Brabrand et al. 1990; Persson 1997b) and reservoirs (Schaus et al. 1997), yet effects of fish on nutrient cycling in wetland ecosystems are virtually unknown. Fathead minnows (*Pimephales promelas*) are usually the dominant species of fish in wetlands of the Prairie Pothole Region (PPR) of the United States and Canada (Zimmer et al. 2000). The degree to which fish populations influence nutrient cycling is probably species and ecosystem dependent and is influenced by the type of prey, density, and size structure of the fish population (Kraft 1992; Schindler and Eby 1997). The characteristics of fathead minnow populations indicate that these fish may have strong influences on nutrient cycling in PPR wetlands.

The diet of fathead minnows is extremely flexible, but benthic macroinvertebrates and detritus are readily con-

¹ Present address: Department of Biology, University of St. Thomas, Mail OWS 390, 2115 Summit Avenue, St. Paul, Minnesota 55105.

² Present address: Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, Minnesota 55108.

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Table 1. Characteristics of the two study wetlands. Values for total phosphorus, total nitrogen, N:P ratios, Chl *a*, and turbidity are averages across the 2 yr of the study.

	Surface area (m^2)	Mean depth (m)	TP ($mg\ L^{-1}$)	TN ($mg\ L^{-1}$)	N:P ratio (mass)	Chl <i>a</i> ($\mu g\ L^{-1}$)	Turbidity (NTUs)
Bellview	130,338	1.61	0.14	3.2	23	72.8	17.5
Stammer	91,314	1.27	0.08	2.8	35	27.0	9.4

sumed (Duffy 1998). Detritus is often a considerable proportion of the diet and can be an important source of energy for these fish (Lemke and Bowen 1998). Consumption of benthic invertebrates and detritus, and subsequent excretion of nitrogen (N) and phosphorus (P) in the water column, can represent a major nutrient flux from sediments to the water column, promoting higher levels of primary production in the water column (Vanni 1996; Schindler and Eby 1997). Nutrients originating from detritus may be especially important, as these nutrients would normally not cycle rapidly back into the water column (Vanni 1996). Additionally, consumption of detritus allows minnow populations to remain high despite low abundance of aquatic invertebrates (Zimmer et al. 2002). These factors, coupled with an absence of piscivorous fish and absence or low numbers of potential competitors in many PPR wetlands, facilitate extremely high minnow densities and production rates. Duffy (1998) observed minnow biomass as high as $48.2\ g\ m^{-2}$ ($43\ \text{fish}\ m^{-2}$) and daily net production rates of $1.35\ g\ m^{-2}\ d^{-1}$ in four South Dakota wetlands. Finally, young-of-the-year (YOY) fish appear to have strong potential to affect nutrient dynamics as a result of metabolic allometry, with mass-specific metabolic rates inversely related to fish size (Post 1990; Kraft 1992), and fathead minnow populations are typically dominated by YOY fish. Payer and Scalet (1978) reported that 194 adult minnows in a South Dakota wetland increased to 126,000 YOY fish in 3 months and that YOY fish accounted for 99% of total annual production.

Understanding the influences of minnows on nutrient cycling in PPR wetlands is especially important because some wetlands contain populations of these fish while others are fishless (Zimmer et al. 2000). Zimmer et al. (2002) found that phytoplankton abundance averaged sixfold higher in wetlands with minnows compared to fishless sites, whereas large-bodied zooplankton were 26-fold more abundant in fishless wetlands. Although it seems certain that reduced grazing pressure played some role in generating higher algal abundance in wetlands with fish, the role of fish-mediated nutrient cycling has not been assessed. Algae in these systems appear to be phosphorus limited the majority of the time (Zimmer et al. 2003), and so increased algal abundance could also be driven by increased P availability via fish excretion (Reinertsen et al. 1986; Persson 1997a; Attayde and Hansson 1999).

Here we examine the influence of fathead minnows on nutrient cycling (i.e., excretion of N and P) in two PPR wetlands over 2 yr using both bioenergetic modeling and direct estimates from fish in the field. These data were coupled with estimates of fish densities to (1) estimate P excretion rates of fish at the ecosystem scale, (2) estimate the proportion of algal primary production that could be supported by

fish excretion, and (3) compare P excretion rates of zooplankton and fish.

Methods

We assessed excretion rates of fathead minnows in two wetlands over 2 yr using two techniques: bioenergetics modeling (Hewett and Johnson 1987; Kraft 1992) and direct estimates from fish in the field (Schaus et al. 1997). The two wetlands used in this study were located in the PPR of west-central Minnesota and were part of a larger study involving 18 wetlands. The larger study was designed to assess the utility of stocking walleye (*Sander vitreus*) as a biomanipulation tool, and it had six wetlands in each of three treatments: wetlands stocked with adult walleye, wetlands stocked with walleye fry, and undisturbed sites (see Herwig et al. [2004] for details). In this study we used two wetlands containing fathead minnow populations for bioenergetic modeling: one site was left undisturbed (Stammer wetland) and one site was stocked with adult walleye (Bellview wetland). Stammer was also used for direct estimates of fish excretion. Fathead minnows and brook sticklebacks (*Culea inconstans*) were the only fish present in both wetlands prior to walleye stocking in Bellview in May of 2001, but fathead minnows represented more than 80% of the fish biomass in both sites. Characteristics of the two wetlands are summarized in Table 1.

Density estimates for juvenile (20–40 mm total length [TL]) and adult fathead minnows (>40 mm TL) were obtained using $1\ m^2$ pop nets (Dewey et al. 1989). Larval fathead minnow (<20 mm TL) densities were estimated using an ichthyoplankton push net (0.5-m diameter, 0.8-mm mesh) concurrently with adult and juvenile estimates. Twelve pop-net samples were taken at random locations in depths ranging from approximately 0.1 to 1.0 m from mid-May to mid-September of each year, with samples collected every other week during 2001 and every third week during 2002. Pop nets were allowed to sit undisturbed on the sediments for 1 h and were then triggered remotely via a trip cord. Captured fish were enumerated and total lengths were determined for 480 fish in each wetland on each date. Although our sampling was restricted to depths of approximately 1.0 m and less, we have found no difference in minnow density across variable depths in these ecosystems (Zimmer et al. unpubl. data). Larval minnow densities were estimated by towing an ichthyoplankton net for 120 s along three fixed transects established in each wetland. Captured minnows were preserved in 95% ethanol and were later enumerated and total lengths determined for up to 100 fish per wetland on each date.

We estimated the total number and mass of larval, juve-

nile, and adult fish by multiplying the density estimates for each size of fish by the surface area of each wetland, and we then converted this estimate to fish m^{-3} based on wetland volume. The volume and surface area of each wetland were estimated by mapping lake edges and depth profiles with a GPS and analyzing these data with Surfer software (Golden Software 1997).

Fathead minnows spawn fractionally and are capable of producing multiple cohorts each year; therefore, standard aging methods cannot be used to identify cohorts in populations (Duffy 1998). Thus, we used modal-length distributions to track the growth of individual cohorts during the sampling season (Jearld 1983). Mean lengths were then determined for each cohort on each date and converted into mean weights via length-weight regressions developed for these populations. Individual growth of fish in each cohort was determined from the weight change between sampling dates.

Bioenergetics modeling of nutrient dynamics requires information on fish diet, nutrient and energy content of the fish, and energy and nutrient content of the prey. Diets were determined for 10 fathead minnows in each of the three size classes from each wetland on three dates (June, July, August) during 2001 and 2002. Larval fish were collected using an ichthyoplankton net, whereas juvenile and adult fish were collected with a beach seine. Collected fish were initially preserved in 10% formalin, then transferred to 95% ethanol. Only the anterior one third of the intestinal tract was analyzed because items lower in the intestinal tract are severely masticated and difficult to identify (Duffy 1998). Invertebrate prey were identified to the lowest feasible taxon, and the biomass of each prey item was determined from length-weight regressions (Smock 1980; McCauley 1984; Zimmer et al. unpubl. data). Energy and nutrient content of invertebrate prey were taken from the literature (Cummins and Wuycheck 1971; Nakashima and Leggett 1980; Penczak 1985). We used values for the most closely related taxonomic group when species-specific data were not available. N and P content of detritus were determined from detritus extracted from guts of 75 fish frozen after collection in the field. Mass of detritus in fish guts was determined by weighing detritus on preweighed, precombusted, acid-washed GF/F filters (0.7- μ m nominal pore size). Duplicate GF/F filters were collected from each fish; one filter was analyzed for N content and the other for P content. N content was determined using a Perkin-Elmer CHN analyzer, while P content was determined via persulfate digestion followed with ascorbic acid colorimetry (APHA 1989).

Use of the bioenergetic model requires constructing energy and nutrient budgets via the energy mass-balance equation $G = C - (R + S + F + U)$, where G is observed growth, C is energy ingested, R is energy used in metabolism, S is specific dynamic action, F is egestion, and U is excretion (Hewett and Johnson 1987). Values of variables in the equation are based on a number of physiological parameters that are species specific, and we used values developed for adult and juvenile fathead minnows by Duffy (1998). Adult-derived parameters do not model larval fish metabolism accurately because of metabolic allometry (Post 1990). Thus, we used the parameters derived by Post (1990) for

larval yellow perch (*Perca flavescens*), one of the few species with larval parameters, to model our larval fathead minnows (Hanson et al. 1997). While yellow perch and fathead minnows are within different families and differ both morphologically and ecologically, patterns of metabolic allometry should be similar among fish species. Thus, we expect physiological parameters for larval yellow perch to be a reasonable approximation for currently undeveloped parameters specific to larval fathead minnows.

Consumption, allocation to growth, and excretion of both P and N can be estimated similarly with the mass-balance equation $C = G + F + U$, where C is mass of nutrients consumed, G is nutrients allocated to growth, F is nutrients lost in feces, and U is nutrients lost in urine (Kraft 1992). We used P and N assimilation efficiencies of 0.72 and 0.80, respectively (Nakashima and Leggett 1980) and a value of 0.10 for F (Duffy 1998). Nutrient modeling also requires data on fish body nutrient content, and we estimated N and P content of 50 fathead minnows of variable size collected over the course of the study. N content was determined with a Perkin-Elmer CHN analyzer and P via combustion at 500°C and sulfuric acid digestion, followed by ascorbic acid colorimetry (Sterner and George 2000). Water temperature for modeling was measured hourly in both study sites using temperature loggers suspended approximately 1 m below the surface of each wetland. All modeling was performed with Fish Bioenergetics 3.0 (Hanson et al. 1997), and the program was used to estimate N and P excretion rates of individual fish.

Direct estimates of excretion were collected in Stammer on 14 June, 15 July, and 2 September 2002 between 11:00 h and 14:00 h. On each date, fish were collected with a beach seine and immediately transferred to a plastic bag containing 1 liter of water collected from Stammer. The wetland water was prefiltered with precombusted, acid-washed GF/F filters to remove particles that might either produce or absorb dissolved P or NH_3 . Samples were also collected from the filtered wetland water to determine the initial concentration of total dissolved P and NH_3 in the wetland water. We randomly selected fish to span the entire range of sizes observed on each date. The number of fish deployed in each bag varied with fish size, but in most cases we used one fish per bag. The bags were left open and upright in the shade, and the fish were left in the bags for 60 min. The fish were removed from the bag at the end of the time period and measured for TL, and TL was then converted to fish mass based on length-weight regressions.

After fish removal, two water samples were collected from each bag by filtering the water through a precombusted, acid-washed GF/F filter. The samples were placed on ice and frozen within 2 h of collection. In the lab, one sample was analyzed for NH_3 (hereafter N) using the fluorometric method (Holmes et al. 1999) and the other for total dissolved P (hereafter P) using high-temperature persulfate oxidation followed by ascorbic acid colorimetry. Excretion of N and P were defined as the difference between initial and final nutrient concentrations. Total excretion values for each bag were then corrected for the number of fish in the bag and expressed as P and N excretion $fish^{-1} h^{-1}$. Mass-specific N:P ratios of excretion rates were also determined.

We used analysis of covariance (ANCOVA) to test for significant effects of time (month of experiment) and body size on N and P excretion rates and N:P ratios of excretion. The N, P, and N:P data were log transformed to increase homoscedasticity of residuals. Tukey multiple comparison tests were used to determine which dates differed when significant effects of time were observed. ANCOVA results and estimated slopes and intercepts were then used to predict P excretion rates of the average-sized adult, juvenile, and larval fish on the dates whole-wetland population estimates were conducted. Average excretion rates for the three sizes of fish were then multiplied by the estimated fish density for population level estimates of P excretion $\text{m}^{-3} \text{ h}^{-1}$. These estimates were scaled to excretion $\text{m}^{-3} \text{ d}^{-1}$ to compare with our estimates of algal primary production demand for P (described below). We limited our comparison of fish excretion rates to algal nutrient demand to P because our previous work has indicated that phytoplankton in these systems are strongly P limited (Zimmer et al. 2003).

Fathead minnows feed throughout the day, but feed very little during the night (Duffy 1998). Excretion rates of fish have been shown to decline rapidly when consumption slows (Mather et al. 1995), and so our daylight estimates overestimate excretion rates during the night. Diel feeding habitats of gizzard shad are similar to those of fathead minnows, and Schaus et al. (1997) found that 82% of peak excretion rates equaled the average excretion rate over a 24-h period. Thus, we assumed our daylight estimates were peak daily rates and adjusted them to 82% to approximate the average rate over a 24-h period. These rates were scaled by a factor of 24 to estimate total P excretion over a 24-h period.

We used methods similar to that of Vanni and Headworth (2003) to estimate the proportion of algal primary production demand for P in our study sites potentially supported by excretion by fathead minnows. First, we used two empirical models to estimate primary production ($\text{mg carbon [C]} \text{ m}^{-3} \text{ d}^{-1}$), allowing us to compare the similarity of estimates from the two methods. The first method predicted primary production via total phosphorus (TP) in the water column (Smith 1979; eq. 6), and the second used water temperature and chlorophyll *a* (Chl *a*) concentrations in the water column (Morin et al. 1999; lake phytoplankton subset equation). Water-column TP was determined using persulfate oxidation and ascorbic acid colorimetry, while Chl *a* was estimated using acetone extraction followed by fluorometric analysis (APHA 1989). Primary production rates were estimated by both methods on five dates in both years in both lakes. Production rates were then divided by the C:P mass ratios of seston on each date to assess the amount of P required ($\text{mg m}^{-3} \text{ d}^{-1}$) to sustain production. Seston C:P ratios were estimated on the same dates we estimated primary production by filtering lake water on acid-washed GF/F filters. One filter was analyzed for P via persulfate oxidation and ascorbic acid colorimetry while the other was analyzed for C content using a Perkin-Elmer CHN analyzer.

Zooplankton were sampled on the same dates we estimated primary production. Samples were collected using a vertical column sampler (Zimmer et al. 2000), and an image analysis system was used to determine the average body size for cyclopoid and calanoid copepods and all cladoceran gen-

era on each date in each wetland. Mean body lengths were then converted to body mass using length-weight regressions (Smock 1980; McCauley 1984; Zimmer et al. unpubl. data). Average weights and density estimates of zooplankton were then coupled with the empirical model of Wen and Peters (1994) to estimate P excretion rates of zooplankton at the community level.

Results

Densities of juvenile and larval fish were substantially higher in 2001 compared to 2002 in both wetlands, while adult densities were similar between years (Fig. 1). Reduced recruitment of YOY fish in 2002 was likely caused by an abnormally cold spring, as water temperature reached the point at which fathead minnows initiate spawning (18°C) 16 d later in 2002 relative to 2001. Overall, both lakes in both years were dominated by juvenile and larval fish, with adult densities seldom exceeding two fish m^{-3} . In contrast, larval and juvenile densities fluctuated dramatically and exceeded a summed total of 65 fish m^{-3} in August 2001 in both Stammer and Bellview. Peak biomass was observed on the same dates, with 15.6 g m^{-2} in Bellview and 6.3 g m^{-2} in Stamer.

ANCOVA indicated significant effects of body mass and month on direct estimates of P excretion rates ($p = 0.020$ and $p < 0.001$, respectively) but no significant interaction ($p < 0.305$). Multiple comparison tests indicated all three intercepts were significantly different (all $p < 0.05$; Table 2), with highest rates for a given body size in September and lowest rates in June (Fig. 2). Wetland water temperature increased from 21°C to 25°C from June to July, but then dropped to 23°C in September. Thus, increased excretion rates from June to July were likely driven by the higher water temperature, but temperature cannot explain the increase in September. Results for N were nearly identical, with significant effects of body mass and time, but no interaction ($p < 0.001$, $p < 0.001$, and $p = 0.192$, respectively). Multiple comparison tests again indicated all three intercepts were significantly different (all $p < 0.05$; Table 2), with September rates the highest and June rates the lowest (Fig. 2). In contrast, N:P ratios showed significant effects of body size ($p = 0.035$) and a time–body size interaction ($p = 0.044$), but no effect of time ($p = 0.162$). The only difference detected with multiple comparison tests was the June intercept being significantly lower than that for July or September (Fig. 2).

Direct and bioenergetic estimates of excretion rates were similar for fish larger than 1 g wet mass for both P and N (Fig. 3). However, estimates for both nutrients differed for smaller fish, with the bioenergetic estimate consistently lower than the direct estimate for both P and N. The differences in estimates for smaller fish were pronounced; the bioenergetic estimate was often an order of magnitude lower and in some cases indicated no P excretion by the fish.

Slopes and intercepts of directly measured P excretion for June and July (Table 2) were subsequently used to estimate excretion rates of average-sized larval, juvenile, and adult fish on dates on which we estimated fish densities. The June

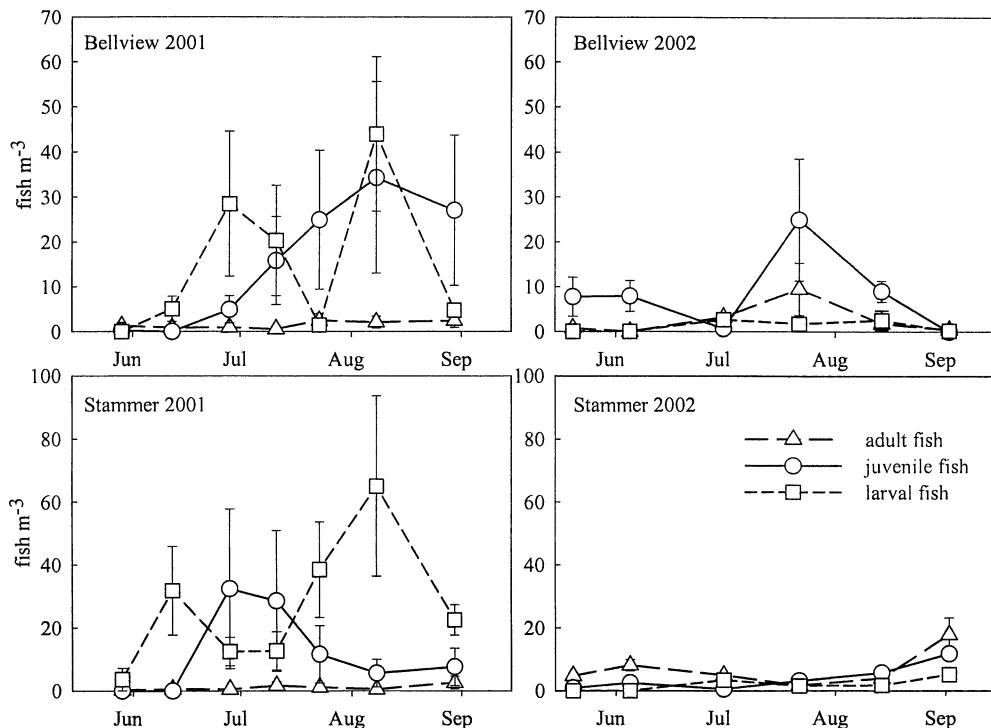


Fig. 1. Density estimates for adult, juvenile, and larval fish in both wetlands in both years (± 1 SE).

equation was used for the month of June and the July equation for July through September. We chose to not use the September equation for predicting population-level excretion rates because the cause of the higher estimates during September were not known, whereas the difference in excretion rates between June and July were likely due to differences in water temperature. Thus, we used the more conservative July equation for late-summer months.

Estimates of algal P demand for primary production were

Table 2. ANCOVA estimates of slope and intercepts (1 SE) for log N, log P, and log N:P excretion with fish wet mass and date (June, July, or September) as main effects. Slopes and intercepts with common superscript letters within log P, log N, and log N:P did not differ across dates as determined by Tukey multiple comparison tests.

	June	July	September
<i>log P</i>			
Slope	0.12 (0.02) ^a	0.14 (0.02) ^a	0.18 (0.03) ^a
Intercept	0.83 (0.04) ^a	0.92 (0.03) ^b	0.99 (0.04) ^c
R ²	0.68	0.52	0.50
<i>log N</i>			
Slope	0.12 (0.02) ^a	0.11 (0.03) ^a	0.15 (0.03) ^a
Intercept	2.14 (0.01) ^a	2.28 (0.03) ^b	2.35 (0.04) ^c
R ²	0.69	0.35	0.46
<i>log N:P</i>			
Slope	0.00 (0.01) ^a	-0.03 (0.01) ^a	-0.02 (0.02) ^a
Intercept	1.31 (0.02) ^a	1.36 (0.02) ^b	1.36 (0.02) ^b
R ²	0.02	0.12	0.06

similar between the TP and Chl *a* models, with estimates differing by just 2–3 mg P m⁻³ on nearly half the dates (Fig. 4). The greatest discrepancy occurred in Stammer in 2001, when the Chl *a* model estimates were consistently 4–5 mg P m⁻³ higher than the TP model. Direct estimates of fish P excretion were higher than the bioenergetics estimates on almost all dates, although both methods estimated the same pattern of maximum excretion in late summer, when fish communities were dominated by juvenile and larval fish (Fig. 4). On dates of maximum excretion, the direct method indicated that fish excretion supplied 84% (Bellview, 2001), 104% (Stammer, 2001), 38% (Bellview, 2002), and 124% (Stammer, 2002) of algal demand for P. Averaged across the summer, fish excretion supplied 36% (Bellview, 2001), 71% (Stammer, 2001), 11% (Bellview, 2002), and 51% (Stammer, 2002) of algal demand for P. Zooplankton P excretion rates in both wetlands were similar to excretion estimates for fish (Fig. 4). However, zooplankton excretion tended to peak earlier in the summer, whereas fish excretion peaked in late summer, when algal primary production was also maximal. The exception to this pattern was Bellview in 2002, when a dramatic increase in *Daphnia* densities resulted in a sharp increase in zooplankton excretion in late summer. The importance of the excreted P by fish during times of peak excretion in late summer is likely increased by the large proportion of detritus in the diet at those times. The bioenergetic model indicated that detritus comprised over 50% of the diet by mass during times of peak excretion rates in three of the four wetland-years and peaked at 92% of diet in Stammer in September 2001.

Comparison of fish density estimates for the three size

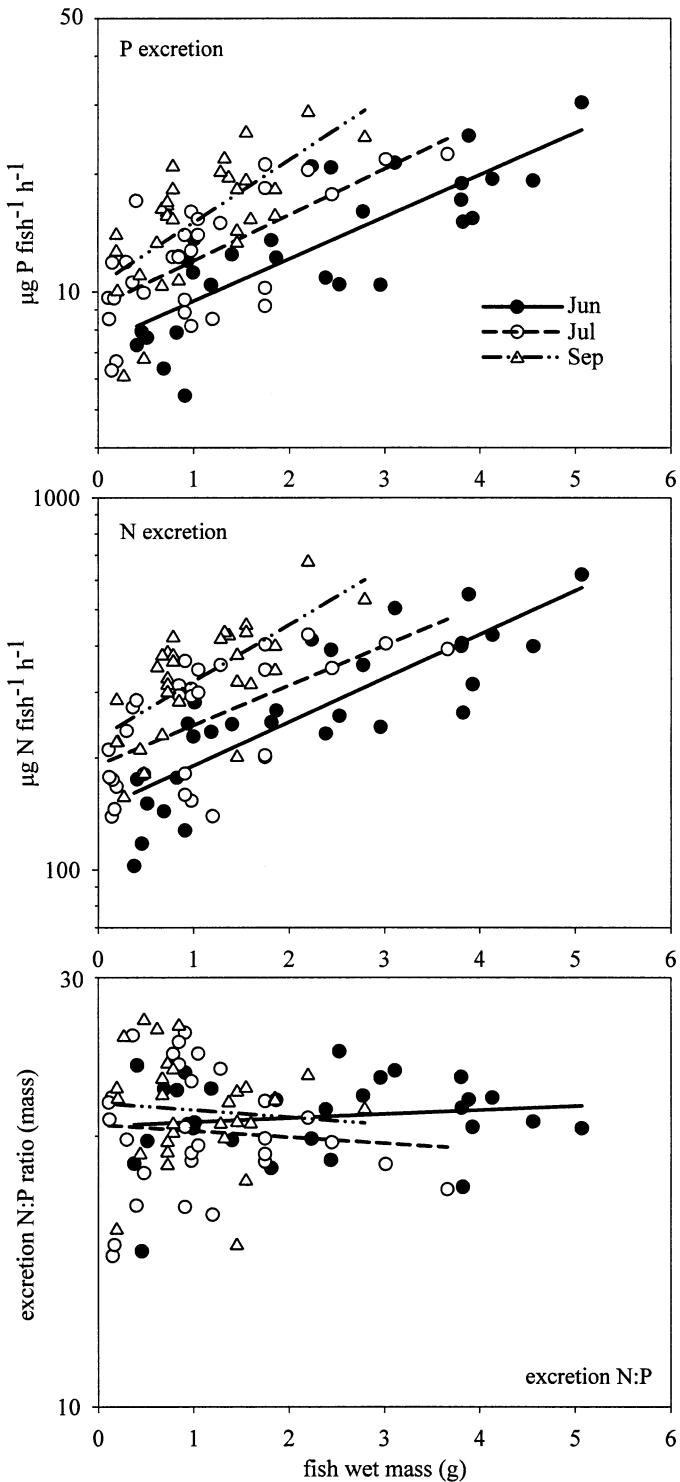


Fig. 2. Effects of fish mass and sampling date (June, July, or September) on P excretion, N excretion, and N:P excretion ratios. Results of ANCOVA for these data are summarized in Table 2.

classes of fish (Fig. 1) with the P excretion estimates at the population level (Fig. 4) shows that peak excretion rates over the course of the summer were consistently associated with peak densities of larval and juvenile fish. Similarly, the average excretion rate of the fish population during the summer

for the four wetland-year combinations showed a strong positive relationship with average larval fish density ($r^2 = 0.90$, $p = 0.04$, $n = 4$), a weaker positive relationship with juveniles ($r^2 = 0.65$, $p = 0.19$, $n = 4$), but no relationship with adult numbers ($r^2 = 0.20$, $p = 0.55$, $n = 4$).

Discussion

Consumers can influence the abundance of primary producers through both top-down effects associated with predation (Carpenter et al. 1985) and bottom-up effects associated with influences on resource availability (Carpenter et al. 1992; Vanni and Layne 1997), yet most studies of fish influences on aquatic ecosystems have focused on top-down effects on primary production. Our results add to the growing body of literature indicating that fish-driven nutrient cycling may also have strong influences on freshwater ecosystems (Schindler et al. 1993; Persson 1997b; Schaus et al. 1997). Our bioenergetics estimates were consistently lower than our direct estimates, likely because of the use of model parameters developed for a different fish species. Thus, we focus our discussion on excretion rates obtained using the direct method. It is worth noting, however, that estimates of N and P excretion using Duffy's (1998) parameters for larger fathead minnows were similar to the direct estimates of similar-sized fish. This result supports previous work indicating that direct and bioenergetic/mass-balance methods generate similar estimates of excretion (reviewed by Vanni 2002).

Comparison of excretion rates with demand rates for primary production is one way to assess the importance of consumer-driven nutrient recycling (Vanni 2002), and our results indicate that fathead minnows potentially can have strong bottom-up influences on phytoplankton abundance in prairie wetlands. Our estimates of maximum percent of algal nutrient demand supplied by fish ranged from 38% to 124% for P and are among the highest reported in the literature (Table 3). Reports of algal P demand supported by fish excretion range from 126% in a stream ecosystem (Vanni et al. 2002), to 36% for shad in an Ohio reservoir (Schaus et al. 1997), and to 5% and 36% for two Wisconsin lakes (Schindler et al. 1993). Our two empirical methods produced similar estimates of phytoplankton demand for P, but both methods may have underestimated total demand in the water column, because they fail to account for bacterial and periphyton P demand (Vanni 2002). High P demand by bacteria and periphyton in these shallow ecosystems may reduce the response of phytoplankton to high rates of P excretion from fish, as some of the excreted P is sequestered by these other pools. However, from May 2001 (minimum fish excretion rates) to August 2001 (maximum fish excretion rates) phytoplankton Chl *a* increased from 23 to 100 $\mu\text{g L}^{-1}$ in Bellview and from 15 to 47 $\mu\text{g L}^{-1}$ in Stammer. Thus, even though some excreted P ends up in other ecosystem pools, excretion by fish in these systems is great enough to have strong influences on algae.

The relative importance of fish-mediated nutrient cycling can also be assessed by comparing flux rates of nutrients from fish to other potentially important flux rates, such as internal loading from sediments or external loading from wa-

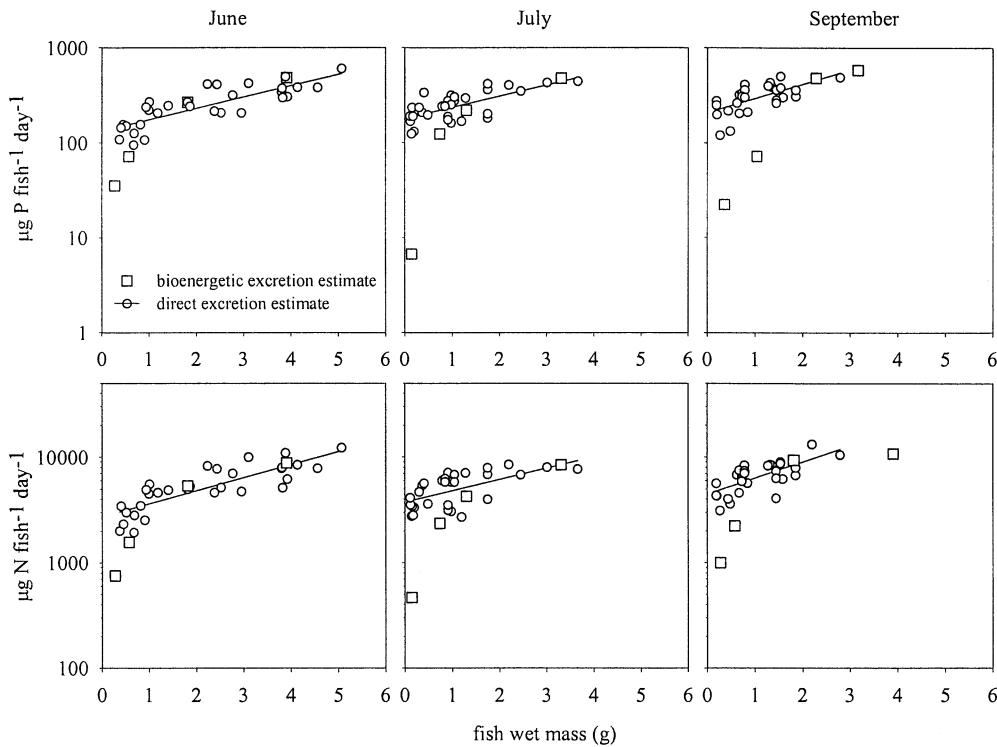


Fig. 3. Comparison of bioenergetic model and direct estimates of P and N excretion rates in June, July, and September of 2002 in Stammer wetland. Values for the bioenergetics estimates are model estimates for average-sized fish observed in each cohort on each date.

tersheds (Vanni 2002). We did not assess these factors in our two study sites, but Davis et al. (1981) estimated watershed P loading rate of $0.31 \text{ g m}^{-2} \text{ yr}^{-1}$ in Eagle Lake Marsh, an Iowa prairie wetland with an agricultural watershed. Similarly, a modeling approach indicated P loading rates of 0.44, 0.66, and $9.16 \text{ g m}^{-2} \text{ yr}^{-1}$ for three prairie wetlands in northwest Iowa (U.S. EPA 2002). Our estimate of P excretion by fish from June through August totaled 0.13, 0.25, 0.39, and 0.54 g m^{-2} for our study sites in 2001 and 2002. Thus, nutrient transport by fish from wetland sediments to the water column over a 3-month period was similar to watershed loading over an annual basis for three of the four above estimates of watershed loading. Equally as important as the overall rates is the fact that nutrient loading from watersheds likely comes in a pulsed fashion in response to major rain events and spring snow melt, whereas fish excretion represents a more constant flux that peaks in late summer, when primary production is also maximal.

Estimates of N:P excretion ratios were similar between the bioenergetic and direct methods and averaged 22 (by mass) across all fish and were higher than most values reported for fish (reviewed by Schaus et al. 1997; Vanni 2002). This is likely driven by the relatively high N:P ratios of the ingested detritus (17), similar to other high N:P ratio prey, such as copepods. The high N:P excretion ratio could have strong influences on competitive interactions among algal species, favoring species with higher demand for N relative to P (Sterner et al. 1992). Higher N:P excretion ratios could also shift the competitive advantage away from N-fixing cyanobacteria in wetlands with minnows populations (Elser

1999). Interestingly, blooms of N-fixing *Aphanizomenon* are relatively common in fishless wetlands and were a prominent feature in biomanipulated wetlands, but we have never observed such a bloom in wetlands dominated by fathead minnows (Zimmer et al. pers. obs.). Neither body size nor date showed strong relationships with N:P excretion ratios, but there was substantial variability in our direct estimates of N:P ratios. This variability is likely driven by differences in the N:P ratios of prey items of individual fish used in our experiments (Schindler and Eby 1997).

Excretion rates of zooplankton and fish were similar in our two study sites, and both are comparable to the higher range of rates reported in previous studies (Table 3). Zooplankton densities are sharply reduced in wetlands with minnows compared to fishless sites (Zimmer et al. 2002). Thus, it may seem that the addition of fish to a wetland food web simply substitutes zooplankton excretion with fish excretion, with no overall change in nutrient dynamics or ecosystem consequences. The key difference, however, is that zooplankton largely recycle water-column nutrients, while the detritus-feeding minnows translocate nutrients from the sediment pools to the water column (Vanni and Headworth 2003). Translocation of nutrients can increase the overall nutrient supply rate in the water column by “tapping” a new nutrient source (Brabrand et al. 1990; Schindler et al. 1993), making nutrient translocation by fish more comparable to nutrient sources such as watersheds or lake sediments than to zooplankton excretion (Schaus and Vanni 2000). Thus, nutrient dynamics and flux rates likely differ dramatically between wetlands with and without fish, with much greater

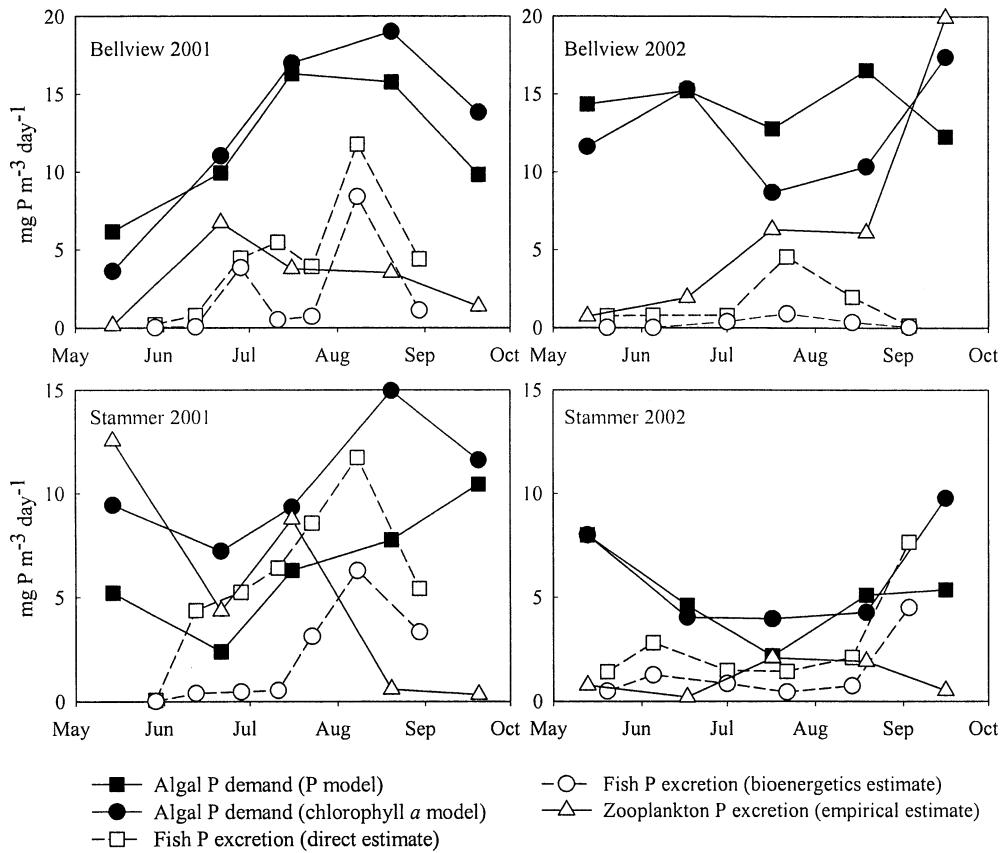


Fig. 4. Estimates of algal P demand for primary production using the total P and chlorophyll *a* models, estimates of fish P excretion rates from both the bioenergetics model and the direct method, and estimates of zooplankton excretion using the empirical model based on community composition and body size.

Table 3. Comparison of published estimates of phosphorus (P) excretion rates of zooplankton and fish with estimates obtained in this study. Estimates for zooplankton and fish from this study are the average rates from May through September of both 2001 and 2002 in each wetland. Data from previous studies were extracted from Vanni (2002).

Location	Taxonomic identity	Excretion rate (mg P m⁻² d⁻¹)	Source
Zooplankton			
Bellview wetland	Assemblage	8.19	This study
Stammer wetland	Assemblage	4.09	This study
Lake Washington	Assemblage	4.00	Lehman 1980
Latvian Lakes	Assemblage	3.03	Gutelmakher and Makartseva 1990
West Long Lake	Assemblage	0.83	Schindler et al. 1993
Peter Lake	Assemblage	0.16	Schindler et al. 1993
Fish			
Rio Las Marías	Assemblage	7.17	Vanni et al. 2002
Stammer wetland	Fathead minnow (<i>Pimephales promelas</i>)	5.62	This study
Acton Lake	Gizzard shad (<i>Dorosoma cepedianum</i>)	5.46	Schaus et al. 1997
Bellview wetland	Fathead minnow (<i>Pimephales promelas</i>)	4.73	This study
Peter Lake	Assemblage	2.30	Schindler et al. 1993
Lake Gjersjøen (May–Oct)	Roach (<i>Rutilus rutilus</i>)	1.21	Brabrand et al. 1990
Lake Finjasjön	Roach (<i>Rutilus rutilus</i>), bream (<i>Abramis brama</i>)	0.53	Persson 1997b
West Long Lake	Assemblage	0.15	Schindler et al. 1993

flux rates from benthic to pelagic pools when fish are present.

The amount of detritus in fish diets in this study varied within each wetland over the course of the summer, as well as within a wetland from one year to the next. Consumption of detritus during the 3 months of the study period ranged from 149.1 to 2,293 kg ha⁻¹ (wet mass), and detritus on average represented 48% of the fish diets by mass. Temporally, three of the four wetland-years had peak consumption of detritus in late summer, the same time during which fish excretion rates and phytoplankton densities are also maximum (Zimmer et al. 2001; Herwig et al. 2004). The shallow depths of our study sites (1.6-m and 1.3-m mean depths) may seem to reduce the importance of fish transporting nutrients from benthic to pelagic pools. However, Schaus and Vanni (2000) found that algal abundance in 0.75-m-deep mesocosms was twofold higher when detritivorous shad were allowed to feed on lake sediment compared to when they were forced to feed in the water column, indicating that benthic–pelagic nutrient transport by fish is important in depths similar to those observed in our study sites.

Our estimates for maximum areal minnow density and biomass (all sizes of fish) of 107 fish m⁻² and 252 kg ha⁻¹ were similar to estimates in other prairie wetlands. Duffy (1998) reported that standing stock biomass of fathead minnows in three South Dakota wetlands exceeded 300 kg ha⁻¹, with a maximum biomass of 482 kg ha⁻¹ and density of 43 fish m⁻². Similarly, Zimmer et al. (2001) observed peaks of 369 kg ha⁻¹ and densities of 570 fish m⁻² in one Minnesota wetland. High densities of fathead minnows in these ecosystems are facilitated by lack of piscivorous fish, low interspecific competition for food resources, and a nearly unlimited supply of detritus as a food resource. Consumption of detritus may be especially important, as it weakens the link between abundance of invertebrate prey and abundance of minnow predators (Schaus and Vanni 2000), resulting in consistently high densities of minnows, with strong influences on nutrient cycling. Consistently high estimates of minnow densities across multiple ecosystems indicate that the strong bottom-up influences of these fish may be widespread among prairie wetlands.

Our estimates of fish excretion at the population level likely represent the greatest uncertainty in this study. Propagation of errors from those associated with estimates of excretion rates for individual fish with errors in estimating fish density would result in extremely wide error bars on the estimates in Fig. 4. However, examination of Figs. 1 and 4 shows that our population-level estimates of excretion are driven by fish density. This, coupled with the fact that other studies have estimated similar densities of minnows in other wetland ecosystems (Duffy 1998; Zimmer et al. 2001), lends credence to our estimates of excretion. Nonetheless, we view our excretion and production estimates as approximations in a first attempt to compare algal nutrient demand to supply rates from fish.

Recent studies have shown that prairie wetlands follow a pattern of alternative regimes (*sensu* Scheffer et al. 1993), existing in either a clear-water state dominated by submerged macrophytes or a turbid-water state dominated by phytoplankton (Zimmer et al. 2003; Herwig et al. 2004).

Fathead minnow predation on zooplankton is thought to be the primary stabilizer of the turbid state in these systems, promoting high phytoplankton abundance and preventing establishment of submerged macrophytes (Zimmer et al. 2003). However, results from this study indicate that minnows may also facilitate consistent, high algal abundance via strong bottom-up influences. The relative importance of bottom-up and top-down influences of minnows in these systems is unclear, but it seems likely that both are important for maintenance of high algal abundance and stabilization of the turbid state. Nutrient availability likely sets the upper boundary on phytoplankton abundance, whereas grazer pressure from zooplankton determines the realized level (Stephen et al. 1998). Thus, the addition of minnows to a wetland food web increases the upper boundary and realized level of algal abundance by translocating nutrients from benthic to water-column pools and by virtually eliminating zooplankton grazing. The net result is that algal densities are higher and more stable than would be possible with either bottom-up or top-down influences associated with fish operating individually. In turn, higher, more consistent densities of algal abundance increase the overall stability of the turbid-water state.

Many discussions and studies concerning ecosystem characteristics, nutrient dynamics, and nutrient flux rates in wetland ecosystems have centered on the importance of watershed and groundwater inputs, internal loading from sediments, redox potentials, and influences of hydroperiod (Detenbeck et al. 2002; Euliss et al. 2004). The above processes undoubtedly have strong influences on nutrient dynamics in prairie wetlands, but the work presented here indicates that biotic effects associated with consumer recycling can be important as well. We argue that consideration of such biotic processes would improve our understanding of nutrient dynamics and ecosystem properties in prairie and perhaps other wetland ecosystems and could help explain broader patterns of ecosystem characteristics.

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