

# Fish as sources and sinks of nutrients in lakes

JEFF M. SEREDA\*, JEFF J. HUDSON\*, WILLIAM D. TAYLOR<sup>†</sup> AND ERIC DEMERS<sup>‡</sup>

\*Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada

<sup>†</sup>Department of Biology, University of Waterloo, Waterloo, ON, Canada

<sup>‡</sup>Department of Biology, Malaspina University-College, Nanaimo, BC, Canada

## SUMMARY

1. The release of total phosphorus (TP) and nitrogen (N in ammonium) was measured for the five most abundant fish species (>85% of biomass) in Mouse and Ranger Lakes, two biomanipulated, oligotrophic lakes in Ontario.
2. The specific release rate of both nutrients was significantly related to fish mass;  $\log_{10}$  TP release rate ( $\mu\text{g h}^{-1}$ ) =  $0.793 (\pm 0.109) [\log_{10} \text{wet mass (g)}] + 0.7817 (\pm 0.145)$ , and  $\log_{10}$  N release rate ( $\mu\text{g h}^{-1}$ ) =  $0.6946 (\pm 0.079) [\log_{10} \text{wet mass (g)}] + 1.7481 (\pm 0.108)$ .
3. When fish nutrient release was standardized for abundance (all populations, 1993–95) and epilimnetic volume, fish were estimated to contribute  $0.083 (\pm 0.061) \mu\text{g TP L}^{-1} \text{ day}^{-1}$ , and  $0.41 (\pm 0.17) \mu\text{g N L}^{-1} \text{ day}^{-1}$  in Mouse L., and  $0.062 (\pm 0.020) \mu\text{g TP L}^{-1} \text{ day}^{-1}$  and  $0.31 (\pm 0.08) \mu\text{g N L}^{-1} \text{ day}^{-1}$  in Ranger L.
4. In comparison, concurrent rates of total planktonic P regeneration were  $1.02 (\pm 0.45) \mu\text{g L}^{-1} \text{ day}^{-1}$  (Mouse L.) and  $0.85 (\pm 0.19) \mu\text{g L}^{-1} \text{ day}^{-1}$  (Ranger L.). Fish represented 8% of planktonic P release in Mouse L. and 7% in Ranger L.
5. Fish dry mass had mean elemental body compositions of 39.3% carbon, 10.9% nitrogen, and 4.0% phosphorus (all fish combined), with a mean molar C : N : P ratio of 27 : 6 : 1. This comprised about 55% and 23% of the total epilimnetic particulate P and N respectively.
6. Turnover times of P and N in fish were approximately 103 and 48 days respectively. In comparison, planktonic turnover times of particulate P in Mouse and Ranger Lakes were 4.3 and 4.4 days respectively. Given their high P content and low turnover rates, fish appear to be important P sinks in lakes.

*Keywords:* Fish, Nitrogen, Nutrient-Regeneration, Phosphorus, Plankton

## Introduction

The significance of nutrient release by fish for plankton communities is uncertain; many authors have suggested that nutrient release by fish is important (Brabrand, Faafeng & Nilssen, 1990; Mather *et al.*, 1995; Persson, 1997; Schaus *et al.*, 1997; Vanni, 2002) whereas others suggest it is a

small contribution (Kitchell, Koonce & Tennis, 1975; Hudson, Taylor & Schindler, 1999; Gido, 2002; Griffiths, 2006). Some of this difference in opinion arises from whether nutrients released by fish are compared to external loading or internal cycling. While nutrient regeneration by fish may be large relative to external sources of nutrients to lakes (e.g. Shostell & Bukaveckas, 2004), fish are an internal source of nutrients and internal cycling of nutrients (e.g. planktonic regeneration) in lakes is large relative to external loading (Hudson *et al.*, 1999).

Some recent studies have explored the role of fish as benthic-pelagic couplers, transporting and releasing

Correspondence: Jeff Sereda, W.P. Thompson Building  
112 Science Pl., University of Saskatchewan,  
Saskatoon, SK, Canada, S7N 5E2.  
E-mail: jeff.sereda@usask.ca

benthic nutrients into the pelagic zone (Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002; Vanni, 2002). This translocation of nutrients has been considered a source of 'new' nutrients for the plankton community (Vander Zanden & Vadeboncoeur, 2002). Benthic organisms comprise a significant proportion of the diet of many littoral zone fish species, particularly in small lakes. However, fish undergo ontogenetic (Winemiller, 1989), biomass-dependent (Schaus, Vanni & Wissing, 2002) and seasonal diet shifts due to prey availability (Mehner *et al.*, 1998). When planktivorous fish feed and release nutrients in the pelagic zone, they only recycle nutrients in the water column and do not provide new nutrients to the plankton community. More importantly, since there is usually no thermal barrier to horizontal movement of nutrients regenerated by littoral organisms, it is not clear that the involvement of motile organisms such as fish is required for nutrients to reach the plankton; water currents can bring nutrients into the pelagic zone and vice versa. Fish feeding on profundal benthos could also bring new nutrients into the epilimnion, but this is a much less likely migration and the net effect of fish movements between these zones could be to move nutrients out of the euphotic zone.

Nutrient release rates have been estimated through both bioenergetic models (Tarvainen, Sarvala & Helminen, 2002; Bunnell, Johnson & Knight, 2005) and direct measurements (Gido, 2002; Zimmer, Herwig & Laurich, 2006). However, parameters of consumption and growth, as well as the nutrient and energy content of both predator and prey, must be known for bioenergetic modelling (Kraft, 1992). These parameters are not known for many species, and must often be inferred from other closely related species. Regression models of nutrient release have been developed for single species from direct measurements (Shostell & Bukaveckas, 2004; Vanni *et al.*, 2006). These empirical relationships have been applied to fish populations to estimate nutrient release over multiple years. However, these relationships only capture the variability in release rates of a single species, and may not be applicable to other systems. Therefore, the development of an empirical relationship of nutrient release for multiple species would be useful for the rapid estimation of the total nutrients released by all fish in a given waterbody.

Fish may contain a substantial amount of P in their biomass which is unavailable to primary producers. Kitchell *et al.* (1975) found up to 75% of total phosphorus (TP) in the pelagic zone of Lake Wingra (Wisconsin) was in fish biomass. In addition, they estimated that 30–35% of the annual input of P into Lake Wingra was sequestered into fish biomass. Nakashima & Leggett (1980) estimated that the P content of pelagic fish in Lake Memphremagog was comparable to that of the seston, and much greater than that of the zooplankton. Kraft (1992) estimated that P sequestered by young-of-the-year yellow perch in Lake Memphremagog (Vermont/Quebec) was similar to P losses from algal sedimentation. Parmenter & Lamarra (1991) estimated that 40% of the total fish P may remain immobilized in bone and scales which, upon death of the fish, may be incorporated into the sediment and lost permanently from the water column. Such studies suggest that fish may be more important as sinks rather than sources of nutrients.

Our study had five objectives. (1) To determine the amount of phosphorus (TP) and nitrogen (ammonium-N) released by the five dominant fish species in Mouse and Ranger Lakes (Ontario) during the summers of 1993–95. (2) To develop empirical relationships of nutrient release of TP and N for multiple species that could be used for the rapid estimation of fish nutrient release in other systems. (3) To compare the release rates of fish to planktonic regeneration rates of P in both lakes. (4) To characterize the stoichiometry of direct P and N release from the fish assemblage. (5) To determine the quantity of nutrients (P and N) bound in fish and plankton, and to compare the P turnover rates of both.

## Methods

### *Study Lakes*

This study was conducted at Mouse and Ranger Lakes in south central Ontario. Each lake has a single basin, is oligotrophic, and is found on the Canadian Shield. These lakes undergo stratification during the summer, and share similar morphological and chemical properties (Table 1). Detailed physical and chemical properties are described in Hudson *et al.* (2001); McQueen *et al.* (2001) and Dillon *et al.* (2001).

	Area (ha)	Mean depth (m)	Max. depth (m)	Mean epilimnetic volume (10 <sup>8</sup> L)	TP (µg L <sup>-1</sup> )	TKN (µg L <sup>-1</sup> )
Mouse	9.9	4.9	9	2.87	6.1	255
Ranger	11.2	5.5	13	2.91	6.5	300

**Table 1** Physical and chemical properties of Mouse and Ranger Lakes (from Dillon *et al.*, 2001; McQueen *et al.*, 2001). TP and TKN (Total Kjeldahl Nitrogen) are mean epilimnetic concentrations (1993–95)

Mouse Lake was free of obligate piscivores from 1978 until late 1993, and was characterized by high densities (mean = 2008 ha<sup>-1</sup>) of small non-piscivorous fish (Demers *et al.*, 2001a). Fish biomass over 1993–95 was 26–43 kg ha<sup>-1</sup>. In late 1993 largemouth bass (*Micropterus salmoides* L.) and smallmouth bass (*Micropterus dolomieu* L.) were transferred from Ranger L. to Mouse L. as part of the Dorset Biomanipulation Project (McQueen *et al.*, 2001). Prior to bass removal in late 1993, Ranger L. was characterized by low densities (mean = 30 ha<sup>-1</sup>) of piscivores (largemouth bass and smallmouth bass) and abundant (mean = 230 ha<sup>-1</sup>) non-piscivores (Demers *et al.*, 2001a). Fish biomass over 1993–95 was 19–29 kg ha<sup>-1</sup>. Following biomanipulation, fish abundance in both lakes was dominated by golden shiners (*Notemogonus crysoleucas* M.), pumpkinseed (*Lepomis gibbosus* L.), yellow perch (*Perca flavescens* M.), largemouth bass, white sucker (*Catostomus commersonii* L.), and smallmouth bass. These six species represented, on average, 85% and 99% of the fish biomass in Mouse L. and Ranger L. respectively.

#### Measurements

The five most abundant fish species were collected during July and August 1993 (golden shiner, pumpkinseed, yellow perch and largemouth bass) and 1994 (white sucker). Fish collections in 1993 were completed prior to the transfer of piscivores from Ranger L. to Mouse L. Fish were collected from both lakes by shoreline seining or angling (largemouth bass only). A broad range in fish size was selected for each species to capture size-related differences in nutrient release. Captured fish were rinsed twice with lake water and transferred with a dip net into incubation containers with 2–36 L of lake water depending on fish size. Prior to fish introduction, incubation water was boiled then cooled to ambient temperature to limit ammonia uptake by microorganisms. Two control containers without fish (three for golden shiners and white sucker) were used for each fish species to monitor

changes in TP and N concentrations that were not attributable to fish. Incubation containers were kept under low light and noise levels, and were partly immersed in the lake to maintain ambient lake temperatures. Water temperature was monitored throughout the incubations. All incubations began 1–3 h after fish capture. Containers were sub-sampled (approximately 50 mL, once for TP and once for N analysis) at time 0 and subsequently at approximately 1, 2 and 4 or 5 h unobtrusively through outlet valves. At the end of each incubation the wet mass of each fish was recorded and then fish were sacrificed and stored at –20 °C for determination of C, N and P.

TP samples were first oxidized with potassium persulfate and then analysed using the molybdate blue colorimetric method (Parsons, Maita & Lalli, 1984). Ammonium samples were preserved according to Degobbis (1973) and then analysed within 2 weeks for ammonium nitrogen using the phenol-hypochlorite method (Wetzel & Likens, 1991). Our measurement of P as TP included all processes (egestion and excretion) that release P into the incubation container. However, our measurements of N only include processes that release NH<sub>4</sub><sup>+</sup> (e.g. excretion) and as a result do not include the release of N in other forms of dissolved or particulate organic N. Changes in the concentration of TP and NH<sub>4</sub><sup>+</sup> in each container were plotted as a function of time and modelled with linear or non-linear regression. The instantaneous release rate (µg h<sup>-1</sup>) of each fish was calculated by taking the derivative at the start of the incubation (i.e.  $t = 0$ ) (Wilhelm, Hudson & Schindler, 1999).

The contribution that the fish assemblage made to the nutrient supply of each lake was determined as follows. Fish abundance and biomass estimates were calculated as described by Demers *et al.* (2001a). Briefly, sampling was conducted at three to five equally spaced intervals from May to September using a series of active (beach seine and electrofishing) and passive (trap netting) sampling. All captured fish were identified to species and up to 500 individuals were measured (fork and total length). Size-stratified

sub-samples of up to 100 individuals were weighed (nearest 0.1 g), and scales or pectoral spines taken for age determination. Population estimates were calculated each May (1993–95), and also in August of 1994 and 1995, with Schnabel multiple-census mark-recapture experiments (Ricker, 1975). Confidence limits for biomass were calculated using the upper and lower limits of density because errors associated with density estimation represent the largest uncertainties in calculating biomass (Demers *et al.*, 2001b). These biomass and abundance estimates were then applied to a bioenergetics model (Hewett & Johnson, 1992) with daily estimates for young of the year (YOY), juvenile, and adult fish abundance, biomass, growth and mortality (Demers *et al.*, 2001b). Estimation of bioenergetic model parameters is described by Demers *et al.* (2001b).

The rate of release ( $\mu\text{g h}^{-1}$ ) of individual fish of a species (*n.c.* 10 fish/species) was regressed against fish mass. These relationships were then applied to the estimates of fish biomass and abundance ( $\pm 95\%$  CI) over 3 years (1993–95) to obtain lake-wide estimates of fish release. Biomass and abundance estimates were obtained from a separate study (Demers *et al.*, 2001b). Release rates of largemouth bass were used to estimate the release rate of smallmouth bass, the sixth most abundant species in both lakes. Release rates for larval fish were not directly measured, but were extrapolated from species specific regressions and were included in whole-lake release rate estimates. Confidence intervals (95%) were calculated for release rates predicted from species-specific regression (Zar, 1999). Release rates and associated 95% CI were summed for each size class of each species and then for all species combined to provide a total daily release rate ( $\pm 95\%$  CI) for the entire fish assemblage. Total daily release rates, and associated 95% CI were then summed for July and August and a mean daily release rate and CI was calculated. We assumed that fish were confined to the oxygenated epilimnetic waters during the summer months in both lakes. Therefore, daily nutrient release by the entire fish assemblage ( $\mu\text{g L}^{-1} \text{ day}^{-1}$ ) was standardized for the mean epilimnetic volume of each lake ( $2.87 \times 10^8$  in Mouse L. and  $2.91 \times 10^8$  L in Ranger L.).

Concurrent total epilimnetic planktonic regeneration rates of P were measured using radioisotope techniques for both Mouse and Ranger Lakes according to Hudson & Taylor (1996). Planktonic

regeneration rates were measured on three separate dates each summer (1993–95). Daily nutrient release rates by fish were compared on dates when planktonic regeneration rates were measured.

Elemental composition of each fish was determined using the following procedure. Fish were thawed and the dry mass of each fish was determined. Fish were dried at 80 °C, for 12–13 h (independent of fish mass). Fish had been kept frozen for 10 years and were already in a dehydrated state, hence only short drying times were required. Fish were first ground with a food processor, and then with a mortar and pestle. TP analysis was conducted with two to three sub-samples (0.0093–0.455 g) of homogenized tissue per fish. Sub-samples were acid digested with 3 mL of 70% nitric acid, neutralized with sodium hydroxide ( $4 \text{ mol L}^{-1}$ ), and brought up to 50 mL with de-ionized water. Samples were diluted, oxidized with potassium persulfate, and analysed for TP using the molybdate blue colorimetric method with a spectrophotometer (Parsons *et al.*, 1984). One to two replicates of dried tissue (0.100–0.300 g) from each fish were also analysed on a LECO CNS-2000 carbon–nitrogen analyzer (St-Joseph, MI, U.S.A.) to determine fish carbon and nitrogen content.

To estimate the quantity of C, N and P bound in fish biomass we determined fish dry mass for each size class of each species using species-specific dry mass to wet mass ratios. Mean percentages of C, N and P (species specific) were then multiplied by the dry mass of fish. Mass of each element was then summed, for each size class for each species, and then for all species combined. This provided the total mass of nutrients bound in fish biomass each day. Daily totals were then averaged over July and August.

Turnover rates of P and N were then determined. The quantity of P and N bound in fish biomass was divided by the daily quantity of the nutrient released. Turnover rates were calculated each day, for each size class, for each species. Daily turnover rates accounted for changes in biomass through estimates of growth and mortality. Turnover rates for all species were then averaged over July and August.

Epilimnetic particulate P (i.e. planktonic P) was determined according to Hudson *et al.* (2001). Epilimnetic total particulate nitrogen was determined on the same water with the identical filter size fractionation procedures that Hudson *et al.* (2001) used for determining particulate P concentrations. Particulate

nitrogen was measured as Kjeldahl nitrogen using the modified atrazine technique outlined by the Ontario Ministry of the Environment (reference E3188 – The determination of solids in liquid matrices by gravimetry, 19 August, 2004). With this technique, nitrogen samples were mineralized to ammonia using a hot acid/mercuric oxide digestion. Samples were then neutralized and analysed using phenate-hypochlorite colorimetry at 630 nm.

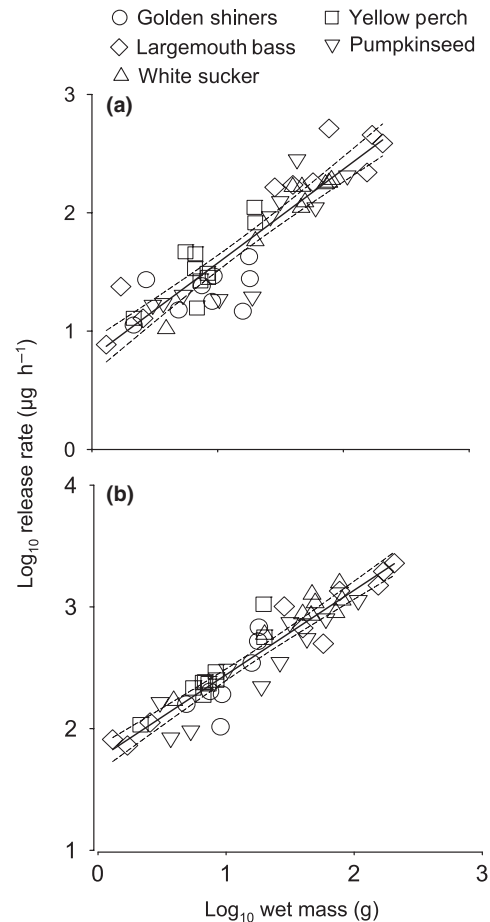
Statistical analysis was performed with Statistica Version 6.0 (Tulsa, OK, U.S.A.), and all statistical significance levels were set at  $P = 0.05$ .

## Results

Ambient lake temperatures during the measurements of nutrient regeneration by fish ranged from 22.8 to 25.9 °C. Temperature, TP and N concentrations in control containers did not change significantly ( $P > 0.05$ , model I linear regression) over the course of the incubations. The concentration of TP increased significantly over the course of all fish incubations ( $P < 0.05$ ,  $R^2 \geq 0.79$ ). Instantaneous release rates (at  $t = 0$ ) ranged from 7.69 to 515.6  $\mu\text{g TP h}^{-1}$  (Fig. 1), and inter-specific differences in P release rates were observed [ $F_{1,4} = 2.864$ ,  $P = 0.035$ , analysis of covariance (ANCOVA)].

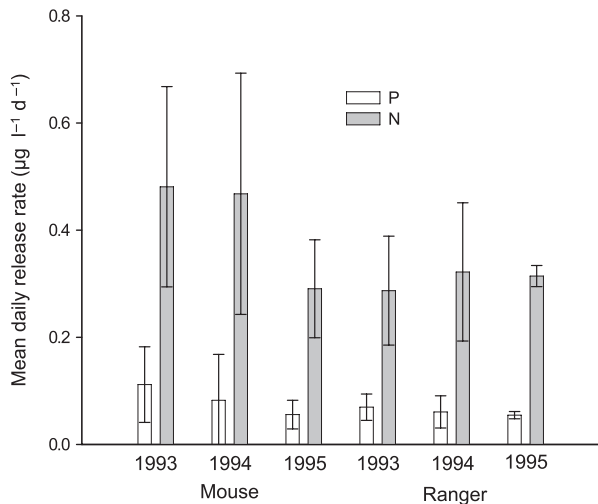
Ammonium concentrations (henceforth, N) also increased over time in all fish incubation containers ( $P < 0.05$ ,  $R^2 \geq 0.97$ ), except in two containers where a trend was not evident. The fish in these two containers were very small (<3 g) and increases in the concentration of N may have been undetectable, or offset by slight losses of N from the containers. The results from these two incubations were not included in subsequent analyses. Release rates of N across all species ranged from 72.6 to 2282  $\mu\text{g h}^{-1}$  (Fig. 1), but inter-specific differences in N release rates were non-significant ( $F_{1,4} = 1.817$ ,  $P = 0.14$ , ANCOVA).

Directly measured instantaneous release rates of P and N ( $\mu\text{g h}^{-1}$ ) for all fish were log-transformed and regressed (model I) against the log of fish wet mass (Fig. 1). Release rates of both nutrients increased with fish mass but at a decreasing rate (i.e. slope of each relationship is <1). The total contribution that fish made to the nutrient supply of each lake was calculated over the 3 years of study (Fig. 2). Total nutrient release for the six main species present in each lake (five species used in incubations, plus



**Fig. 1** (a) Release of TP by all fish in relation to their wet mass (g),  $n = 48$ ,  $R^2 = 0.82$ ,  $P < 0.001$ ,  $\log_{10}$  TP release rate ( $\mu\text{g h}^{-1}$ ) =  $0.793 (\pm 0.109) [\log_{10} \text{ wet mass (g)}] + 0.7817 (\pm 0.145)$ . Release rates of P across all species ranged from 7.69 to 515.6  $\mu\text{g h}^{-1}$ . (b) Release of N in the form of  $\text{NH}_4^+$  in relation to wet mass (g) for all fish,  $n = 46$ ,  $R^2 = 0.88$ ,  $P < 0.001$ ,  $\log_{10}$  N release rate ( $\mu\text{g h}^{-1}$ ) =  $0.6946 (\pm 0.079) [\log_{10} \text{ wet mass (g)}] + 1.7481 (\pm 0.108)$ . Release rates of N across all species ranged from 72.6 to 2282  $\mu\text{g h}^{-1}$ . Confidence intervals (95%) for each regression are shown.

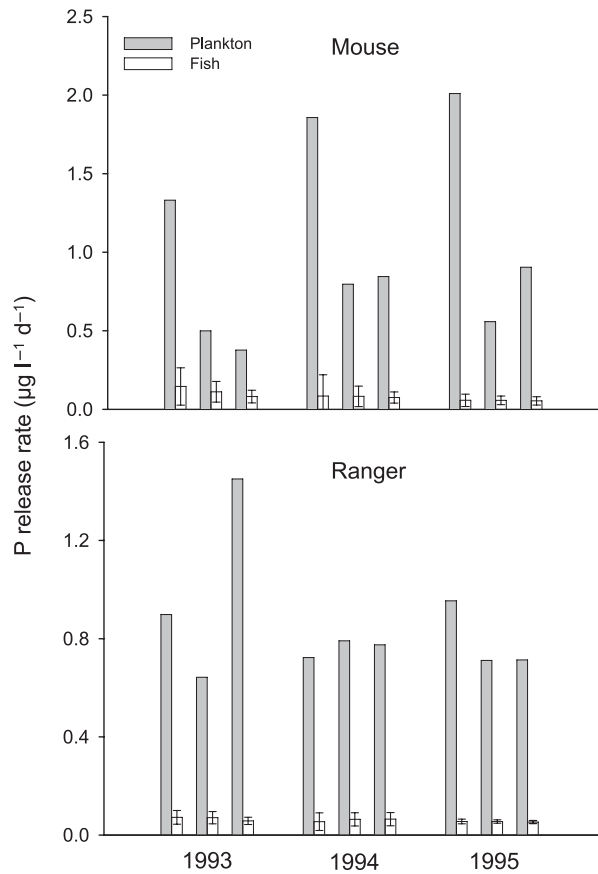
smallmouth bass) was 0.053–0.145  $\mu\text{g TP L}^{-1} \text{ day}^{-1}$  (mean =  $0.083 \pm 0.061$ , 95% CI) and 0.053–0.072  $\mu\text{g TP L}^{-1} \text{ day}^{-1}$  (mean =  $0.062 \pm 0.020$ , 95% CI) for Mouse L. and Ranger L. respectively. Nutrient release of N (1993–95) was 0.270–0.527  $\mu\text{g L}^{-1} \text{ day}^{-1}$  (mean =  $0.41 \pm 0.17$ , 95% CI) in Mouse L., and 0.240–0.355  $\mu\text{g L}^{-1} \text{ day}^{-1}$  (mean =  $0.31 \pm 0.08$ , 95% CI) in Ranger L. Total planktonic release rates of P were 0.38–2.01  $\mu\text{g L}^{-1} \text{ day}^{-1}$  (mean =  $1.02 \pm 0.45$ , 95% CI) (Mouse L.) and 0.64–1.45  $\mu\text{g L}^{-1} \text{ day}^{-1}$  (mean =  $0.85 \pm 0.19$ , 95% CI) (Ranger L.) and were much greater than P regeneration by the fish assemblage (Fig. 3).



**Fig. 2** Mean daily release of P and N ( $\mu\text{g L}^{-1} \text{day}^{-1}$ ) by the fish assemblages in Mouse and Ranger Lakes. Confidence intervals (95%) represent cumulative variance of release rates predicted from species specific regressions of nutrient release, CI surrounding fish abundance estimates, and variation between daily release rates (July 1 to August 31) of each year.

The molar ratio of ammonium to TP release (henceforth N : P release ratio) by all fish had a range of 4.3 : 1–54.1 : 1, with a mean of 18.1 : 1 (Fig. 4). White sucker had a significant negative relationship between the N : P ratio of released nutrients and wet mass ( $P = 0.02$ ), but this trend was not observed for other species or when all species were combined. Inter-specific differences in N : P ratios were observed ( $F_{1,4} = 2.895$ ,  $P = 0.034$ , ANCOVA), but not when two outlying golden shiner values (Fig. 4) were removed ( $F_{1,4} = 1.286$ ,  $P = 0.30$ , ANCOVA).

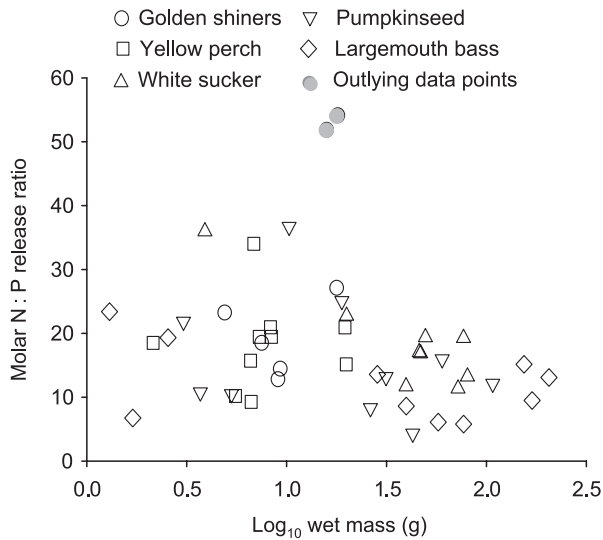
Fish wet mass ranged from 1.3 to 205.5 g, with a mean of 34.6 g. The dry mass of all fish ranged from 16.1% to 38.0% (mean = 22.8%) of initial wet mass. Carbon was 31.9–43.9% (mean = 39.3%) of dry mass (Fig. 5). The carbon content was negatively correlated with dry mass in largemouth bass ( $P = 0.0002$ ), and when data for all fish were combined ( $P = 0.008$ ). Nitrogen accounted for 9.6–12.2% (mean = 10.9%) of dry mass. The N content of pumpkinseed was negatively correlated with dry mass ( $P = 0.03$ ). Similar, but non-significant relationships were also found for largemouth bass and when data for all fish were combined ( $P = 0.06$  and  $0.09$  respectively). The phosphorus content of all fish ranged from 2.1% to 5.3% (mean = 4.0%) of dry mass. Phosphorus content was not correlated ( $P > 0.05$ ) with dry mass. The mean



**Fig. 3** Comparison of daily release rates of P by the fish assemblage ( $\mu\text{g L}^{-1} \text{day}^{-1}$ ) to regeneration rates of P by the plankton community in Mouse and Ranger Lakes. The 95% CI are shown for daily fish release rates. Planktonic regeneration rates are individual measurements and therefore, 95% CI are not shown.

molar C : N : P ratio across all species was 27 : 6 : 1. Inter-specific differences in body nutrient content were observed (ANCOVA);  $F_{1,4} = 6.973$ ,  $P = 0.0002$ ,  $F_{1,4} = 8.16$ ,  $P < 0.001$ ,  $F_{1,4} = 10.787$ ,  $P < 0.001$ , for C, N and P respectively.

Approximately 1.58 kg of C, 0.42 kg of N and 0.16 kg of P per hectare were bound in fish biomass in Mouse L. during 1993–95 (Fig. 6). For Ranger L. the corresponding amounts were 1.54 kg C, 0.42 kg N and 0.14 kg of P per hectare. Turnover rates of phosphorus and nitrogen bound in fish biomass were 96 and 47 days, and 110 and 49 days, for Mouse and Ranger Lakes respectively. Over the same period, planktonic biomass in the epilimnion contained approximately 1.51 kg N  $\text{ha}^{-1}$  and 0.13 kg P  $\text{ha}^{-1}$  in Mouse L., and 1.30 kg N  $\text{ha}^{-1}$  and 0.12 kg P  $\text{ha}^{-1}$  in Ranger L.



**Fig. 4** N : P released by fish (mol : mol) in relation to dry mass (g),  $n = 46$ ,  $R^2 = 0.06$ ,  $P = 0.10$ , range 4.3 : 1–54.1 : 1 (mean = 18.1 : 1). Outlying data points for golden shiners are indicated.

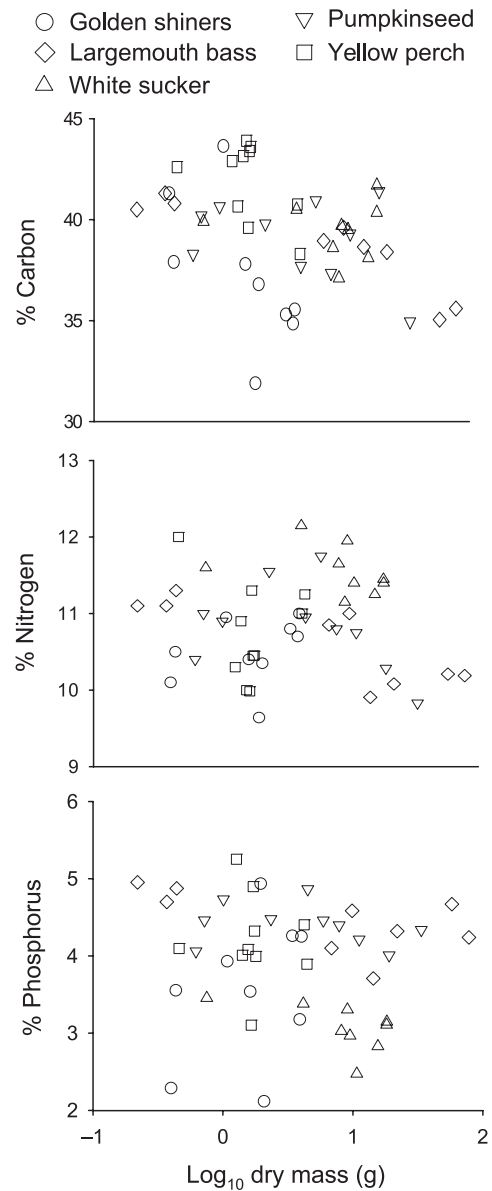
Turnover rates of phosphorus bound in planktonic biomass were on average 4.8 and 5.3 days for Mouse and Ranger Lakes respectively.

### Discussion

Our TP release rates may include some particulate matter that is unavailable to plankton, for example apatite from bone in the case of piscivores. We believe that most of the TP released would have been released as phosphate ( $\text{PO}_4$ ), or available via the action of exo- and ectoenzymes. For example, Brabrand *et al.* (1990) found that most (85–95%) of the P released by fish was in available form. However, it is possible that our rates of P regeneration may represent slight overestimates.

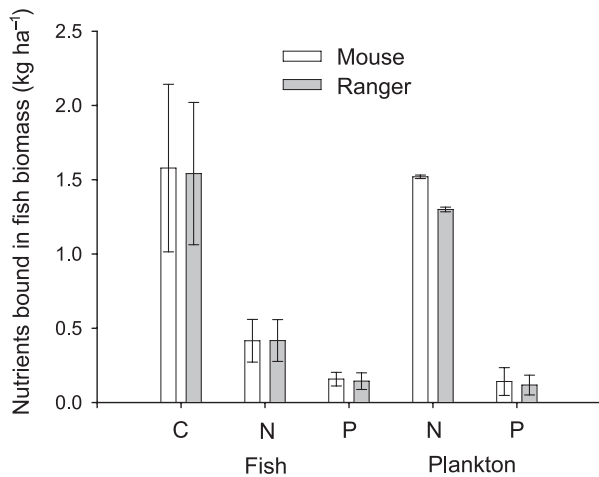
Unlike our measurements of TP, our measurements of N only measured the release of N as  $\text{NH}_4^+$  and may have underestimated total N release. Andre, Hecky & Duthie (2003) reported that approximately two-thirds of the total N regenerated by cichlids was in soluble form, of which 90% was  $\text{NH}_4^+$ . The remainder of the N was excreted in other soluble forms (e.g. urea) and egested as feces. As such, our measurements of N may have only accounted for approximately 60% of the total N released.

Handling stress may potentially increase fish release rates. However, Mather *et al.* (1995) concluded that handling stress had no significant affect on



**Fig. 5** Carbon, nitrogen and phosphorus content as a percentage of fish dry mass (g),  $n = 47$ . Each point represents a single fish. Note the log scale of the x-axis. Ranges of elemental composition were C 31.9–43.9% (mean = 39.3%), N 9.6–12.2% (mean = 10.9%) and P 2.1–5.3% (mean = 4.0%).

release rates or ratios. Egestion and excretion rates may be affected by the time elapsed since the fish fed (Tarvainen *et al.*, 2005). Glaholt & Vanni (2005) observed that P excretion rates peaked 2 h after feeding and then returned to a low and constant level. All incubations in this study were started 1–3 h after fish were captured. If fish had fed before capture, then our release rates may represent maximum rates



**Fig. 6** Mean mass (kg) of C, N and P per hectare bound in fish and plankton in Mouse and Ranger lakes from 1993 to 1995 (95% CI are shown). Carbon content of plankton was not measured.

because we calculated release rates at  $t = 0$ ; when the incubation started. However, the feeding history of the fish in this study is unknown. Assuming release rates were maximal, applying these rates to the population would overestimate the contribution by fish to the nutrient supply. For example, Schaus *et al.* (1997) observed daily excretion rates of gizzard shad (*Dorosoma cepedianum* L.) to be 82% of maximum. Alternatively, extended separation from food may have resulted in lower release rates, thereby potentially underestimating the contribution by fish to the nutrient supply. However, we believe that biases in either direction are minor for two reasons. First, our release rates overlap with other directly measured rates from the literature (Table 2). Secondly, Griffiths

(2006) presented a relationship of TP released ( $\text{g ha}^{-1} \text{ day}^{-1}$ ) by fish communities in relation to fish biomass ( $\text{kg ha}^{-1}$ ). This relationship was derived from eight studies, calculating areal nutrient loads by fish communities in 22 lakes. Fish biomass in our lakes was approximately  $20\text{--}40 \text{ kg ha}^{-1}$ , with areal loading estimates of  $1.2\text{--}2.5 \text{ g ha}^{-1} \text{ day}^{-1}$ . These values are similar to those presented by Griffiths (2006). Therefore, our estimates of fish nutrient release appear typical.

Mean daily release rates of P and N did not change substantially across 3 years of study in Mouse and Ranger lakes (Fig. 2). The general trend in Mouse L. was a declining mean daily release by the fish community. This is likely a result of decreased fish production following the addition of piscivores in late 1993 (Demers *et al.*, 2001b). From 1993 to 1995 changes in mean daily P and N release ( $\pm 95\%$  CI) by the fish community in Ranger L. were non-significant. Following the removal of piscivores, fish production increased in Ranger L. (Demers *et al.*, 2001a,b). The quantity of nutrients released is expected to increase with increased fish production. However, substantial increases in fish production did not occur in Ranger L. until after our study was completed (1996–97).

To test the usefulness of our two nutrient release relationships (Fig. 1) we applied our relationships to fish species used in other nutrient release studies that measured nutrient release directly (Table 3). Our predicted rates were comparable to those reported in these studies. However, extrapolation beyond the limits of fish mass in the regression resulted in large 95% CI relative to the predicted release rate. Therefore, expanding these relationships to include a

**Table 2** Comparison with other studies of fish release rates of N, P and N : P release ratios (by moles). Nutrients released were  $\text{NH}_4\text{-N}$  (N) and TP unless otherwise stated. All rates, except one (Tarvainen *et al.*, 2002) were determined by direct measurements of release

Species	Mean fish wet Mass (g)	Incubation Temperature ( $^{\circ}\text{C}$ )	Release Rate ( $\mu\text{g g}^{-1} \text{ h}^{-1}$ )		N : P Release (mols)	Type of Study	Reference
			N	TP			
All species	34.6	23–26	8.68–62.6	0.93–14.0	4.3–54.1	Field	This study
<i>Gymnocephalus cernuus</i> L.	9.84	16–17	5.9	1.4	25.2	Lab	Tarvainen <i>et al.</i> , 2005
<i>Rutilus rutilus</i> L.	0+ older	n/a	n/a	15–22.5 2.91–6.67	N/a	Model	Tarvainen <i>et al.</i> , 2002
<i>Lepomis Macrochirus</i>	1.96	18–22	12.0–15.6 (unfed) 34.5–47 (fed)	1.0–2.3 (unfed) (SRP) 1.2–5.7 (fed) (SRP)	18–35 (unfed) 18–101 (fed)	Lab	Mather <i>et al.</i> , 1995
<i>Dorosoma cepedianum</i>	18.7	18–22	15.2–15.5 (unfed) 5.9–101.3 (fed)	1.0–1.3 (unfed) 2.0–13.7 (fed)	33–35 (unfed) 3–35 (fed)	Lab	Mather <i>et al.</i> , 1995



**Table 3** Comparison of predicted TP and N (N in  $\text{NH}_4^+$ ) release rates with release rates from other studies. Release rates presented as a range represent observed rates for all fish in the study. Predicted rates were calculated with our empirical fish release relationships (Fig. 1), and the fish wet mass reported in each study. TP, SRP,  $\text{NH}_4\text{-N}$  and total ammonia nitrogen (TAN) were the release products measured from each study

Species	Fish wet mass (g)	Reported P release ( $\mu\text{g g}^{-1} \text{h}^{-1}$ )	Predicted TP Release ( $\mu\text{g g}^{-1} \text{h}^{-1}$ )	Reported N release ( $\mu\text{g g}^{-1} \text{h}^{-1}$ )	Predicted $\text{NH}_4\text{-N}$ Release ( $\mu\text{g g}^{-1} \text{h}^{-1}$ )	Study
<i>Gymnocephalus cernuus</i>	9.84*	1.4 (TP)*	$3.77 \pm 2.74$	15.9* ( $\text{NH}_4\text{-N}$ ) 24* (TAN)	$27.9 \pm 2.02$	Tarvainen et al., 2005
<i>Lepomis macrochirus</i>	1.96*	1.2–5.7 (SRP)	$5.26 \pm 2.81$	34.5–47.0 ( $\text{NH}_4\text{-N}$ )	$45.6 \pm 2.06$	Mather et al., 1995
<i>Dorosoma cepedianum</i>	2.2	2.0–13.7 (SRP)	$5.14 \pm 2.80$	5.9–101.3 ( $\text{NH}_4\text{-N}$ )	$44.0 \pm 2.02$	Mather et al., 1995
	18.7		$3.30 \pm 2.74$		$22.9 \pm 2.01$	
	23.27		$3.15 \pm 2.74$		$21.4 \pm 2.01$	
	48		$2.71 \pm 2.76$		$17.2 \pm 2.02$	
<i>Stizostedion vitreum</i> M.	3.3	n/a	$4.72 \pm 2.75$	30.1 (20 °C) (TAN)	$38.9 \pm 2.04$	Forsberg & Summerfelt, 1992
	5.6		$4.23 \pm 2.74$	45.2 (25 °C)	$33.1 \pm 2.03$	
<i>Cyprinus carpio</i> L.	390	1.2 (TP)	$1.76 \pm 2.77$	n/a	$9.05 \pm 2.03$	Lamarra, 1975
	780	1.0	$1.52 \pm 2.79$		$7.33 \pm 2.04$	
<i>Sander lucioperca</i> L.	11.7*	n/a	$3.64 \pm 2.74$	21.2 * (TAN)	$26.4 \pm 2.02$	Zakęś et al., 2001

Predicted release rates overlap with rates reported from other studies (\* mean).

broader range in fish mass would improve their predictive capabilities. Other multi-species nutrient release models have been developed by Schindler & Eby (1997). However, these models were derived from bioenergetic modelling and require knowledge of fish diet and prey nutrient content. Our relationships are derived from direct measurements of planktivorous, zoobenthivorous, and piscivorous fish (Demers et al., 2001b) and capture the variability in nutrient release derived from variations in diet for a broad range in fish size. Therefore, our empirical relationships of nutrient release may be useful for the rapid determination of nutrient release by fish in future studies.

Nutrient release by fish represents approximately 1–36% (mean 8%) of the planktonic regeneration rate in Mouse L. and 3–15% (mean 7%) of planktonic regeneration in Ranger L (Fig. 3). If we had included the P regeneration rates of the metalimnetic plankton ( $1.11 \mu\text{g P L}^{-1} \text{day}^{-1}$  in Mouse L. and  $0.97 \mu\text{g P L}^{-1} \text{day}^{-1}$  in Ranger L.: Hudson & Taylor, 1996), the relative contribution by fish would be even less. These observations are consistent with the results of other studies. For example, Griffiths (2006) reported fish to regenerate an average of 6% of the P regenerated by plankton (comparison of 13 lakes from 10 studies using the empirical model by Hudson et al. (1999). Nakashima & Leggett (1980) found that the P supplied by yellow perch in Lake Memphremagog only represented 0.06–0.17% of the seston daily

summer requirements. Gido (2002) estimated that benthic fish of Lake Texoma released a comparatively small amount of P ( $0.12 \mu\text{g P L}^{-1} \text{day}^{-1}$ ) relative to plankton ( $2.58\text{--}14.36 \mu\text{g P L}^{-1} \text{day}^{-1}$ ). In summary, fish are minor regenerators of P relative to plankton in the pelagic zone of Mouse and Ranger Lakes, and this appears to be generally true of lakes.

Across all species, nitrogen release rate declined relative to the phosphorus release rate with increasing fish wet mass (Fig. 4). The ratio of N released to total phosphorus released (N : P release ratio) was variable, 4.3 : 1 to 54.1 : 1 by moles. Our results overlapped with the results of other studies, which is not surprising given the broad range we found (Table 2). When all fish were combined, the mean N : P ratio was 18.1 : 1 ( $\pm 3.14$ , 95% CI). Some previous studies (Schaus et al., 1997; Levine & Schindler, 1999; Attayde & Hansson, 2001) have suggested that the low N : P ratio of nutrient regeneration by fish may favour algal communities dominated by Cyanobacteria. However, since the quantity of nutrient released is small relative to other sources, it probably has only a minor influence on plankton. In addition, our N : P ratios, as well as those of other studies (Table 2) overlap with the Redfield ratio and therefore would be unlikely to favour Cyanobacteria over other algae.

Fish biomass contains approximately  $0.16 \text{ kg P ha}^{-1}$  in Mouse L. and  $0.14 \text{ kg P ha}^{-1}$  in Ranger L. This represents approximately 55% and 54% of the

epilimnetic P (planktonic P and P bound in fish biomass) in Mouse and Ranger Lakes respectively. Average turnover time for P bound in fish biomass would be 103 days. Fish biomass contained approximately 0.42 kg ha<sup>-1</sup> of N in both Mouse and Ranger Lakes (Fig. 6). This represents approximately 22% and 24% of the epilimnetic N (planktonic N and N bound in fish biomass) in Mouse L. and Ranger L. respectively. Average turnover time for N bound in fish biomass would be 48 days. The plankton community accounted for approximately 45% of the epilimnetic P (planktonic P and P bound in fish biomass) or 0.13 kg P ha<sup>-1</sup> in Mouse L., and 46% of the epilimnetic P or 0.12 kg P ha<sup>-1</sup> in Ranger L. Planktonic regeneration rates of 1.02 µg L<sup>-1</sup> day<sup>-1</sup> (Mouse L.) and 0.85 µg L<sup>-1</sup> day<sup>-1</sup> (Ranger L.), would turn over the planktonic P pool every 4.8 and 5.3 days respectively. Other studies have reported similar planktonic P turnover times of 4–8 days in a variety of other pelagic environments (Dodds, Priscu & Ellis, 1991; Taylor & Lean, 1991; Thingstad, Skjoldal & Bohne, 1993; Van Den Broeck *et al.*, 2004; Flaten *et al.*, 2005). The slow turnover time of fish compared to plankton confirms that fish are important sinks for nutrients (Bartell & Kitchell, 1978; Griffiths, 2006).

Past studies have suggested that fish may be important suppliers of nutrients to the pelagic zone of lakes (Kraft, 1993; Schaus *et al.*, 1997; Vanni *et al.*, 2006). The effect of released nutrients on pelagic primary production will be influenced by the location of the fish in the lake at the time of release (Kraft, 1993). Fish may move nutrients from the benthic or littoral zones to the pelagic zone by feeding in the benthic or littoral zone and then swimming to and releasing nutrients in the pelagic zone. Conversely, fish could forage in the plankton at night and retreat to deeper water or nearshore structure during the day. The location of fish in Mouse and Ranger Lakes was determined by beach seining, trap netting, purse seining, electrofishing, angling, Miller trawling, telemetry, and snorkeling surveys (Demers *et al.*, 2001a; unpublished data). YOY golden shiner, pumpkinseed and yellow perch were observed to feed and remain in the pelagic zone. Therefore, these YOY recycled pelagic nutrients, and would not be expected to import nutrients to the pelagic. Meanwhile, older age-classes of fish were observed to feed and remain in the littoral zone. Therefore, evidence of fish feeding in the benthic and littoral zone and then movement to

the pelagic zone was not evident in Mouse and Ranger Lakes. Either way, one might expect the horizontal relocation of nutrients by water movements alone to be relatively large compared to the release of nutrients by fish.

In conclusion, we found fish to be minor contributors to the nutrient supply of both lakes, relative to the plankton community. On the other hand, fish biomass contained over 50% of the particulate P and approximately 25% of the particulate N in the epilimnion of Mouse and Ranger Lakes. While fish are rich in P, the nutrient content of fish and fish excretion does not deviate greatly from Redfield ratios and they are unlikely to cause stoichiometric effects. Other than as sinks, the greatest effect of fish on pelagic food webs is more likely to be through size-selective predation which may affect nutrient cycling through altered nutrient regeneration rates and sedimentation rates (Larocque *et al.*, 1996).

### Acknowledgments

Thanks to J. Almond, S. Leung, T. MacDonald and L. Lawton for field and lab assistance. Thanks to the Dorset Environmental Science Centre for providing assistance, laboratory space, equipment and accommodation. This research was supported by NSERC (Canada) funding to JJH, WDT and D. McQueen and a University of Saskatchewan scholarship to JMS.

### References

- Andre E.R., Hecky R.E. & Duthie H.C. (2003) Nitrogen and phosphorus regeneration by cichlids in the littoral zone of Lake Malawi, Africa. *Journal of Great Lakes Research*, **29**, 190–201.
- Attayde J.L. & Hansson L.A. (2001) The relative importance of fish predation and excretion effects on planktonic communities. *Limnology and Oceanography*, **46**, 1001–1012.
- Bartell S.M. & Kitchell J.F. (1978) Seasonal impact of planktivory on phosphorus release by Lake Wingra zooplankton. *Verhandlungen der Internationalen Vereinigung fuer Theoretische und Angewandte Limnologie*, **20**, 466–474.
- Brabrand A., Faafeng B.A. & Nilssen J.P.M. (1990) Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 364–372.

- Bunnell D.B., Johnson T.B. & Knight C.T. (2005) The impact of introduced round gobies (*Neogobius melanostomus*) on phosphorus cycling in central Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 15–29.
- Degobbi D. (1973) On the storage of seawater samples for ammonia determination. *Limnology and Oceanography*, **18**, 146–150.
- Demers E., McQueen D.J., Ramcharan C.W. & Perez-Fuentetaja A. (2001b) Did piscivores regulate changes in fish community structure? *Archiv für Hydrobiologie, Special Issues Advances in Limnology*, **56**, 49–80.
- Demers E., McQueen D.J., Popiel S.A., Rocchi A.M., Ramcharan C.W. & Perezfuentetaja A. (2001a) Changes in fish community structure. *Archiv für Hydrobiologie, Special Issues Advances in Limnology*, **56**, 23–48.
- Dillon P.J., McQueen D.J., Ramcharan C.W., Yan N.D., Demers E. & Hudson J.J. (2001) Changes in nutrient and ion chemistry. *Archiv für Hydrobiologie Special Issues Advances in Limnology*, **56**, 227–255.
- Dodds W.K., Priscu J.C. & Ellis B.K. (1991) Seasonal uptake and regeneration of inorganic nitrogen and phosphorus in a large oligotrophic lake: size-fractionation and antibiotic treatment. *Journal of Plankton Research*, **13**, 1339–1358.
- Flaten G.A.F., Skjoldal E.F., Krom M.D. et al. (2005) Studies of the microbial P-cycle during a Lagrangian phosphate-addition experiment in the Eastern Mediterranean. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **52**, 2928–2943.
- Forsberg J.A. & Summerfelt R.C. (1992) Effect of temperature on diel ammonia excretion of fingerling walleye. *Aquaculture*, **102**, 115–126.
- Gido K.B. (2002) Interspecific comparisons and the potential importance of nutrient excretion by benthic fishes in a large reservoir. *Transactions of the American Fisheries Society*, **131**, 260–270.
- Glaholt S.P. & Vanni M.J. (2005) Ecological responses to simulated benthic derived nutrient subsidies mediated by omnivorous fish. *Freshwater Biology*, **50**, 1864–1881.
- Griffiths D. (2006) The direct contribution of fish to lake phosphorus cycles. *Ecology of Freshwater Fish*, **15**, 86–95.
- Hewett S.W. & Johnson B.J. (1992) *Fish Bioenergetics Model 2*. University of Wisconsin Sea Grant Institute, Technical Report WIS-SG-92-250, Madison, WI.
- Hudson J.J. & Taylor W.D. (1996) Measuring regeneration of dissolved phosphorus in planktonic communities. *Limnology and Oceanography*, **41**, 1560–1565.
- Hudson J.J., Taylor W.D. & Schindler D.W. (1999) Planktonic nutrient regeneration and cycling efficiency in temperate lakes. *Nature*, **400**, 659–661.
- Hudson J.J., Taylor W.D., McQueen D.J. & Somers K.M. (2001) Phosphorus in pelagic food webs. *Archiv für Hydrobiologie, Special Issues Advances in Limnology*, **56**, 211–225.
- Kitchell J.F., Koonce J.F. & Tennis P.S. (1975) Phosphorus flux through fishes. *Verhandlungen der Internationalen Vereinigung fuer Theoretische und Angewandte Limnologie*, **19**, 2478–2484.
- Kraft C.E. (1992) Estimates of phosphorus and nitrogen cycling by fish using a bioenergetics approach. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2596–2604.
- Kraft C.E. (1993) Phosphorus regeneration by Lake Michigan alewives in the mid-1970s. *Transactions of the American Fisheries Society*, **122**, 749–755.
- Lamarra V.A. (1975) Digestive activities of carp as a major contributor to the nutrient loading of lakes. *Verhandlungen der Internationalen Vereinigung fuer Theoretische und Angewandte Limnologie*, **19**, 2461–2468.
- Larocque I., Mazumder A., Proulx M., Lean D.R.S. & Pick F.R. (1996) Sedimentation of algae: relationships with biomass and size distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1133–1142.
- Levine S.N. & Schindler D.W. (1999) Influence of nitrogen to phosphorus supply ratios and physicochemical conditions on cyanobacteria and phytoplankton species composition in the Experimental Lakes Area, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 451–466.
- Mather M.E., Vanni M.J., Wissing T.E., Davis S.A. & Schaus M.H. (1995) Regeneration of nitrogen and phosphorus by bluegill and gizzard shad: effect of feeding history. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 2327–2338.
- McQueen D.J., Ramcharan C.W., Yan N.D., Demers E., Perez-Fuentetaja A. & Dillon P.J. (2001) Objectives, methods, the physical-chemical setting. *Archiv für Hydrobiologie Special Issues Advances in Limnology*, **56**, 1–21.
- Mehner T., F. Mattukat, Bauer D., Voigt H. & Benndorf J. (1998) Influence of diet shifts in underyearling fish on phosphorus recycling in a hypertrophic biomanipulated reservoir. *Freshwater Biology*, **40**, 759–769.
- Nakashima B.S. & Leggett W.C. (1980) The role of fish in the regulation of phosphorus availability in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1540–1549.
- Parmenter R.R. & Lamarra V.A. (1991) Nutrient cycling in a fresh-water marsh – the decomposition of fish and waterfowl carrion. *Limnology and Oceanography*, **36**, 976–987.
- Parsons T.R., Maita Y. & Lalli C.M. (1984) *A Manual of Chemical and Biological Methods for Seawater Analysis*, 1st edn. Pergamon Press, Oxford.

- Persson A. (1997) Phosphorus release by fish in relation to external and internal load in a eutrophic lake. *Limnology and Oceanography*, **42**, 577–583.
- Ricker W.E. (1975) Computation and interpretation of biological statistics of fish populations. *Bulletin Fisheries Research Board of Canada*, **191**, p. 382.
- Schaus M.H., Vanni M.J. & Wissing T.E. (2002) Biomass-dependent diet shifts in omnivorous gizzard shad: implications for growth, food web, and ecosystem effects. *Transactions of the American Fisheries Society*, **131**, 40–54.
- Schaus M.H., Bremigan M.T., Garvey J.E. & Stein R.A. (1997) Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnology and Oceanography*, **42**, 1386–1397.
- Schindler D.E. & Eby L.A. (1997) Stoichiometry of fishes and their prey: implications from nutrient recycling. *Ecology*, **78**, 1816–1831.
- Schindler D.E. & Scheuerell M.D. (2002) Habitat coupling in lake ecosystems. *Oikos*, **98**, 177–189.
- Shostell J. & Bukaveckas P.A. (2004) Seasonal and interannual variation in nutrient fluxes from tributary inputs, consumer recycling and algal growth in a eutrophic river impoundment. *Aquatic Ecology*, **38**, 359–373.
- Tarvainen M., Sarvala J. & Helminen H. (2002) The role of phosphorus release by roach [*Rutilus rutilus* (L.)] in the water quality changes of a biomanipulated lake. *Freshwater Biology*, **47**, 2325–2336.
- Tarvainen M., Ventela A.M., Helminen H. & Sarvala J. (2005) Nutrient release and resuspension generated by ruffe (*Gymnocephalus cernuus*) and chironomids. *Freshwater Biology*, **50**, 447–458.
- Taylor W.D. & Lean D.R.S. (1991) Phosphorus pool sizes and fluxes in the epilimnion of a mesotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1293–1301.
- Thingstad F.T., Skjoldal E.F. & Bohne R.A. (1993) Phosphorus cycling and algal-bacterial competition in Sandsfjord, western Norway. *Marine Ecology Progress Series*, **99**, 239–259.
- Van Den Broeck N., Moutin T., Rodier M. & Le Bouteiller A. (2004) Seasonal variations of phosphate availability in the SW Pacific Ocean near New Caledonia. *Marine Ecology-Progress Series*, **268**, 1–12.
- Vander Zanden M.J. & Vadeboncoeur Y. (2002) Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, **83**, 2152–2161.
- Vanni M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **33**, 341–370.
- Vanni M.J., Bowling A.M., Dickman E.M., Hale R.S., Higgins K.A., Horgan M.J., Knoll L.B., Renwick W.H. & Stein R.A. (2006) Nutrient cycling by fish supports relatively more primary production as lake productivity increases. *Ecology*, **87**, 1696–1709.
- Wetzel R.G. & Likens G.E. (1991) *Limnological Analyses*, 2nd edn. Springer-Verlag, New York.
- Wilhelm F.M., Hudson J.J. & Schindler D.W. (1999) Contribution of *Gammarus lacustris* to phosphorus recycling in a fishless alpine lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1679–1686.
- Winemiller K.O. (1989) Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan Llanos. *Environmental Biology of Fishes*, **26**, 177–199.
- Zakęs Z., Demska-Zakęs K., Karczewski P. & Karpiński A. (2001) Selected metabolic aspects of pike-perch, *Stizostedion lucioperca* (L.) reared in a freshwater recirculation system. *Archives of Polish Fisheries*, **9**, 25–37.
- Zar J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice-Hall, London.
- Zimmer K.D., Herwig B.R. & Laurich L.M. (2006) Nutrient excretion by fish in wetland ecosystems and its potential to support algal production. *Limnology and Oceanography*, **51**, 197–207.

(Manuscript accepted 17 September 2007)