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# The impact of introduced round gobies (*Neogobius melanostomus*) on phosphorus cycling in central Lake Erie

David B. Bunnell, Timothy B. Johnson, and Carey T. Knight

**Abstract:** We used an individual-based bioenergetic model to simulate the phosphorus flux of the round goby (*Neogobius melanostomus*) population in central Lake Erie during 1995–2002. Estimates of round goby diet composition, growth rates, and population abundance were derived from field sampling. As an abundant introduced fish, we predicted that round gobies would influence phosphorus cycling both directly, through excretion, and indirectly, through consumption of dreissenid mussels, whose high mass-specific phosphorus excretion enhances recycling. In 1999, when age-1+ round gobies reached peak abundance near 350 million ( $2.4 \text{ kg}\cdot\text{ha}^{-1}$ ), annual phosphorus excretion was estimated at 7 t ( $1.4 \times 10^{-3} \text{ mg P}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ). From an ecosystem perspective, however, round gobies excreted only 0.4% of the phosphorus needed by the benthic community for primary production. Indirectly, round gobies consumed <0.2% of dreissenid population biomass, indicating that round gobies did not reduce nutrient availability by consuming dreissenids. Compared with previous studies that have revealed introduced species to influence phosphorus cycling, round gobies likely did not attain a sufficiently high biomass density to influence phosphorus cycling in Lake Erie.

**Résumé :** Un modèle bioénergétique basé sur l'individu nous a servi à simuler le flux de phosphore de la population de gobies à taches noires, *Neogobius melanostomus*, du centre du lac Érié en 1995–2002. Les estimations de la composition du régime alimentaire, du taux de croissance et de la densité de population du gobie à taches noires sont tirées d'échantillonnages de terrain. Comme c'est un poisson introduit abondant, nous avons prédit que les gobies à taches noires influenceraient le cycle du phosphore directement par leur excrétion et indirectement par leur consommation de moules dreissenidées dont l'excrétion de phosphore élevée en fonction de la masse favorise le recyclage. En 1999, au moment où les gobies à taches noires d'âge 1+ ont atteint leur abondance maximale de près de 350 millions d'individus ( $2,4 \text{ kg}\cdot\text{ha}^{-1}$ ), l'excrétion annuelle de phosphore a été estimée à 7 t ( $1,4 \times 10^{-3} \text{ mg P}\cdot\text{m}^{-2}\cdot\text{jour}^{-1}$ ). À l'échelle de l'écosystème, cependant, les gobies à taches noires excrètent seulement 0,4 % du phosphore requis pour la production primaire de la communauté benthique. Indirectement, les gobies à taches noires consomment moins de 0,2 % de la biomasse de la population de dreissenidés, ce qui indique qu'ils ne réduisent pas la disponibilité des nutriments par leur consommation de dreissenidés. Contrairement à ce qui se passe dans des études antérieures où des espèces introduites peuvent influencer le recyclage du phosphore, les gobies à taches noires n'atteignent vraisemblablement pas des densités de biomasse nécessaires pour influencer le recyclage du phosphore dans le lac Érié.

[Traduit par la Rédaction]

## Introduction

The role of zooplankters, benthic macroinvertebrates, and fish consumers as nutrient recyclers has gained increased attention (see review by Vanni 2002). These consumers can directly affect nutrient concentrations by consuming critical nutrients, sequestering some, and excreting the remainder as dissolved phosphorus (e.g.,  $\text{PO}_4$ ) for immediate uptake by primary producers (e.g., Lehman 1980; Braband et al. 1990).

In addition, selective feeding by consumers and the resultant change in relative abundance of their prey can indirectly influence nutrient cycling should the prey species differ in rates or ratios of nutrient excretion (e.g., Shapiro and Wright 1984; Vanni et al. 1997). Overall, zooplankters and other invertebrates likely contribute more to nutrient recycling than fishes because these invertebrates are generally smaller and possess a greater population biomass and higher mass-specific excretion rate than fishes (e.g., Hudson et al. 1999).

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In some circumstances, however, fishes can have considerable impact on nutrient recycling (Vanni 2002). For example, fishes can consume prey in one habitat and excrete those nutrients in another, thereby providing new nutrients to a particular habitat of a lake (e.g., Braband et al. 1990; Schaus et al. 1997). In some cases, nutrient recycling by fishes can exceed the external nutrient input to the lake or reservoir (Braband et al. 1990; Schaus et al. 1997; Gido 2002). Successful introductions of fishes also may have considerable impact on nutrient recycling because they can attain high biomasses (e.g., Eck and Wells 1987) and can influence the composition of the food web (e.g., Brooks and Dodson 1965).

Despite the increasing frequency of fish introductions in the past century (see Rahel 2000) and their potential direct and indirect effects on lake nutrient cycling, relatively few studies have examined these effects. One example of a direct effect on phosphorus cycling is trout introduced into fishless oligotrophic Sierra Nevada lakes in North America. Their phosphorus excretion was estimated to be equivalent to the atmospheric deposition of phosphorus to the lakes (Schindler et al. 2001). Another study estimated phosphorus excretion and egestion by alewife (*Alosa pseudoharengus*) in Lake Michigan during the 1970s to be comparable with the phosphorus cycling by the zooplankton community (Kraft 1993). The introduction of northern pike (*Esox lucius*) into an experimental Canadian lake provided an example of fish indirectly influencing nutrient cycling. The pike eliminated all of the minnows, which in turn increased the biomass of large-bodied cladocerans and resulted in higher concentrations of dissolved phosphorus and nitrogen in the water column (Elser et al. 2000). Hence, introduced fishes can both directly and indirectly influence nutrient cycling in lake ecosystems.

In addition to the alewife, the Laurentian Great Lakes have experienced several fish introductions in the past century that may have influenced nutrient cycling. In this paper, we sought to determine whether the round goby (*Neogobius melanostomus*) population has influenced phosphorus recycling in Lake Erie since its introduction in 1993. This benthic molluscivore underwent an exponential increase in abundance over the next 5 or so years, attaining extremely high densities (40–100 fish·m<sup>-2</sup> (Vanderploeg et al. 2002; Steinhart et al. 2004)) in preferred rocky and cobble substrates (Jude and DeBoe 1996). Our field sampling in the central basin of Lake Erie revealed round gobies to rank among the top three species, in terms of biomass, during August bottom trawl surveys of 1997–2000. Ironically, another introduced species, the zebra mussel (*Dreissena polymorpha*), may have facilitated the success of the round goby (Vanderploeg et al. 2002). Zebra mussels are the primary prey item of larger (>70 mm) round gobies (Ray and Corkum 1997; French and Jude 2001) and enhance the habitat for other benthic macroinvertebrates (e.g., amphipods and isopods) that are the primary prey item of smaller round gobies (French and Jude 2001).

Unlike round gobies, the effects of zebra mussels on nutrient cycling in the Great Lakes have been fairly well described. Owing to their high biomass and filtering capacity, zebra mussels can have dramatic impacts on nutrients (Heath et al. 1995; Mellina et al. 1995; Arnott and Vanni 1996),

bacteria (Cotner et al. 1995), and phytoplankton (Madenjian 1995). Zebra mussel excretion of dissolved phosphorus and nitrogen can be a considerable source of nutrient regeneration in the Great Lakes (Heath et al. 1995; Arnott and Vanni 1996). In recent years, quagga mussels (*Dreissena bugensis*), another introduced species and a congener to zebra mussel, also have become widespread and dominate much of the dreissenid community in Lake Erie (Vanderploeg et al. 2002). Because we do not yet know the effect of quagga mussels on nutrient recycling, we will assume that their effects are the same as those of zebra mussels and will collectively refer to these exotic mussels as dreissenids.

Because round gobies have become abundant in Lake Erie and consume dreissenids, which are important nutrient recyclers, we hypothesized that round gobies may be directly and indirectly influencing nutrient cycling in Lake Erie. Using a mass balance bioenergetic modeling approach, we calculated the phosphorus excreted by round gobies (direct effect) in the Lake Erie central basin, where we have annual estimates of round goby abundance, diet, growth, and mortality. As one of the few fishes that exploit dreissenid mussels as prey, round gobies can provide a “new” source of phosphorus to benthic primary producers by releasing phosphorus bound in mussel tissue. At the same time, however, their consumption of dreissenid mussels also may indirectly influence phosphorus recycling. We used model results to evaluate whether the newly available phosphorus excreted by gobies is offset by the phosphorus that would have been excreted by those dreissenid mussels had they not been consumed (herein referred to as potential excretion). Even more simply, we compared the modeled annual consumption of dreissenids by round gobies with estimates of dreissenid standing stock biomass to determine whether round gobies may be imposing a measurable top-down influence on dreissenids. In total, providing annual estimates of round goby excretion and consumption of dreissenid mussels will contribute to a greater understanding of the role of exotic species in altering nutrient dynamics in central Lake Erie.

## Methods

Our general approach was to use the mass balance approach of Kraft (1992) to estimate consumption, excretion, and accumulation of phosphorus by individual round gobies in the central basin of Lake Erie. To estimate this phosphorus flux, we incorporated annual field-based estimates of round goby growth, diet, population abundance, and mortality into an individual-based model, which allowed us to monitor the daily consumption and excretion of phosphorus by individual fish of varying size within a yearly cohort. Conventional bioenergetic model simulations use one fish of average size to represent the cohort. Because many of the equations in the bioenergetic model are size dependent (and many are nonlinear), we used an individual-based model to preserve the observed variation in size among individuals, which in turn should provide more realistic estimates of the bioenergetics of the population. We extrapolated the flux of the simulated individuals in the individual-based model to the number of individuals estimated in the population to calculate the annual rates of phosphorus flux by the population.

### Study site

Lake Erie, the shallowest and most productive of the Laurentian Great Lakes, has three distinct basins that vary in depth and productivity. We focused on the central basin of Lake Erie, which is intermediate in depth (mean = ~18 m) and productivity to the western basin (shallow, most productive) and eastern basin (deep, least productive). Unlike the western basin, the central basin is deep enough to stratify during summer. Nearly every year in the central basin, oxygen concentrations in the hypolimnion become hypoxic (<2 mg·L<sup>-1</sup>) during late summer (Bertram 1993). Since 1995, concentrations of total phosphorus have increased in the central basin (Charlton and Milne 2004), despite relatively constant phosphorus loadings (D. Dolan, Department of Mathematics, University of Wisconsin-Green Bay, Green Bay, WI 54311 USA, unpublished data), which has led to increasingly hypoxic conditions. If internal phosphorus recycling is responsible for these higher phosphorus concentrations, then it is possible that the introduction and success of round gobies may be influencing phosphorus dynamics in the central basin.

### Population sampling

For annual estimates of individual round goby growth rates, population abundance, and diet composition, round gobies were sampled with a bottom trawl (10.4-m head rope, 1.3-m vertical opening, 15.2-m roller sweep, and 6-mm cod-end liner) that effectively sampled a variety of substrates (silt, mud, shale, rocks, and boulders). Sampling occurred at least four times annually between May and October 1995–2002 (gobies were first sampled in Lake Erie in 1994). For each month of sampling, trawls sampled two to nine standardized transects in the central basin. Along each transect, replicate trawls were completed at each of four depth strata: 5 m (5–9.99 m), 10 m (10–14.99 m), 15 m (15–19.99 m), and 20 m (≥20 m). Trawls at sites <5 m depth were not possible. The duration of the trawls ranged from 2 to 15 min (mean = 9.6 min), and the distance covered by the trawl was calculated by multiplying the minutes trawled by the trawling speed of 2.5 kn. Multiplying the distance covered by the width of the trawl estimated the area swept for each trawl. For each trawl, at least 30 round gobies were randomly selected for measurement of total length (TL) (nearest millimetre) and at least five fish per estimated size-class (<40 mm, between 40 and 100 mm, and >100 mm) were frozen from each site for later measures of age, diet, and sex. Round goby ages were estimated from scales; aging by scales was validated by otoliths (C.T. Knight, unpublished data). Age-0 round gobies were rarely captured in the trawls, as they had not yet grown to a size large enough to be sampled. Hence, all references to round gobies in this paper will refer only to those at least 1 year of age.

All diet items were enumerated and identified to genus. Fish prey were measured in length and their wet weight was estimated from length–weight regressions (Ohio Division of Wildlife 2003). For all other prey items, a mean wet weight was applied, which was calculated from a compilation of lengths and weights from prey items collected between 1990 and 1996 in Lake Erie. We categorized diet items into one of six categories: dreissenid mussels, other mollusks (75% of which were other bivalves), Chironomidae, other benthos

(45% of which were Amphipod and 22% of which were Trichoptera), zooplankton (58% ostracods, 17% copepods, and 12% *Bythotrephes longimanus*), and fish (27% clupeids and 22% round gobies). We used wet mass to determine the proportion of each diet category as a function of habitat, season, year, and size. Habitat was defined as either nearshore (between 5 and 15 m depth) or offshore (≥15 m depth). We chose 15 m as a cutoff because the percentage of non-mud habitat differed considerably between nearshore (72%) and offshore (26%) (Haltuch and Berkman 1998), which may affect prey assemblages. Seasons for the diet analyses were partitioned as spring (May–June), summer (July–August), and autumn (September–October); winter diets were estimated as the interpolation between the diet proportions of autumn and spring. We divided the diets of round gobies into three size-classes, which approximated age-classes: <70 mm TL (through autumn of age-1 fish), 70–110 mm TL (between autumn of age-1 and age-2), and >110 mm TL (age-3+ fish). When fewer than three stomachs were available for a given season, size, habitat, and year combination (occurred for 7% of the inshore and 39% of the offshore combinations), we substituted the average of all other years with similar seasons, sizes, and habitats.

Round goby density was estimated as a function of depth strata, sex, age, and year. To determine the length distribution in each trawl, we multiplied the proportion of measured fish in each centimetre length bin by the total catch. To determine the sex ratio in each catch, we calculated a sex–length key by pooling all fish that were measured and identified to sex across all years and calculating the sex ratio for each centimetre length bin. Similarly, to determine a sex-specific age–length key, we pooled all fish that were identified to sex and aged in all years. With these probabilities in hand, we calculated the density of round gobies in each trawl as a function of age and sex. To estimate density of round gobies at each depth strata, we calculated the mean density, with 90% confidence limits, across all sites and months within each depth strata. For each depth strata, we multiplied the mean density (and confidence limits) by its total area in the central basin (estimate by Haltuch and Berkman 1998) to estimate population abundance. In our models, we assumed that this abundance represented the number of fish on 1 June of each year.

To estimate total annual mortality, we used a catch-curve analysis. We calculated the total abundance of each age-class for each sex in each year. The negative slope of the log<sub>e</sub>-transformed data (without the age-0 or age-4 gobies, as they were so rare that including them biased the slope) estimated  $z$ .

### Individual-based model

We used an individual-based model to simulate the phosphorus flux by individuals from representative “groups” of the round goby population. For each year, 1995–2002, we ran two replicate individual-based model simulations for each group of round gobies, which comprised a particular sex (male or female), age (1, 2, 3, or 4), and habitat (nearshore or offshore). Because age-4 females were never sampled in either habitat, that group of simulations was not run. Within the individual-based model, we monitored the grams of phosphorus that each individual had consumed, mobilized to

**Table 1.** Grand mean mass and SD of round gobies in the central basin of Lake Erie at initiation of each model run (i.e., 1 January) across simulated years 1995–2002.

Age (years)	Males		Females	
	Grand mean mass (g) across years	SD of grand mean across years	Grand mean mass (g) across years	SD of grand mean across years
1	2.97	0.0	2.97	0.0
2	11.70	1.06	9.45	0.68
3	33.71	2.32	24.21	2.85
4	67.16	2.70	—	—

Note: No simulations were run for age-4 females.

new tissue (i.e., growth), and excreted. At the initiation of each model run, 1 January each year, 1000 fish were drawn from a normal distribution of masses, where the mean and standard deviation were estimated from aged fish collected in the field (Table 1). Each day, each fish consumed a diet whose proportional contents were determined by the field-based observations (a function of year, habitat, season, and fish size) and grew according to a bioenergetics subroutine (see next section). The amount of prey consumed was set by the  $p$  value, the proportion of maximum consumption. For all groups of fish, we used the  $p$  value that allowed fish to grow at the same rate in the simulation as fish sampled from the field. The daily probability of survival equaled  $s^{1/365}$ , where  $s$  was the sex-specific annual survival rate.

As batch spawners, mature gobies were assumed to spawn four times each year. We assumed spawning to begin when temperatures warmed to 12 °C (Moiseyeva and Rudenko 1996). Assuming a 21-day spawning interval (Kulikova 1985; L. Corkum, Department of Biological Sciences, University of Windsor, Windsor, ON N9B 3P4, Canada, personal communication), gobies were modeled to spawn 20 May, 17 June, 15 July, and 5 August each year (using the average daily temperature over the years 1994–2002). Females were assumed to mature at age 2 and males at age 3. Because batch spawners do not expel all gonadal tissue each spawning event (i.e., structural and immature tissue), we assumed that 75% of the gonadal tissue was released each event. With a gonadal mass estimated at 1.35% of somatic mass for mature males (Belanger 2002) and 9.1% for mature females (MacInnis and Corkum 2000; Belanger 2002), males and females expelled 1% and 6.8%, respectively, of body mass at the end of each spawning day.

#### Mass balance approach to estimate phosphorus flux

With the mass balance, we assumed that phosphorus consumed ( $C_p$ ) was used to build new tissue (i.e., somatic or gonadal growth ( $G_p$ )), egested as organic fecal waste, or excreted ( $U_p$ ) as soluble inorganic waste. Because egestion was assumed to be 28% of phosphorus consumed (Nakashima and Leggett 1980), phosphorus excretion was estimated as (Kraft 1992)

$$(1) \quad U_p = (0.72C_p) - G_p$$

To estimate  $C_p$  and  $G_p$ , we required wet mass estimates of round goby consumption and growth as well as estimates of the phosphorus concentrations of round gobies and their prey. Daily estimates of  $C_p$  and  $G_p$  were generated from the bioenergetics subroutine of the individual-based model, which included parameters derived for round gobies (Lee 2003)

and equations from the Wisconsin bioenergetics model (Hanson et al. 1997). The bioenergetics model balances energy consumed with energy used in metabolism, growth, excretion, and egestion, given a known growth rate, temperature regime, diet composition, and energy density of predator and prey. As previously described, growth and diet composition were estimated from round gobies sampled in central Lake Erie. Daily temperature was represented as the average water temperature collected from four municipal water intake sites across the central basin: (i) Cleveland, Ohio (8046 m offshore, 13.0 m depth), (ii) Painesville, Ohio (366 m offshore, 3.7 m depth), (iii) Wheatley, Ontario (426 m offshore, 6.4 m depth), and (iv) Elgin, Ontario (1250 m offshore, 9.8 m depth). Estimates of energy density for the six prey categories were compiled from the literature (Table 2). In categories with multiple taxa, we used their average proportional abundance of the primary taxa to weight the values (Table 2). Energy density of round gobies in Lake Erie was modeled to increase with size (G.W. Kim, Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 1314 Kinnear Road, Columbus, OH 43212, USA, and T.B. Johnson, unpublished data) according to

$$(2) \quad J \cdot g \text{ wet mass}^{-1} = 2942.86 \times \text{mass}^{0.08646}$$

Grams of phosphorus consumed ( $C_p$ ) were estimated by multiplying daily consumption (grams) of each prey item by its phosphorus concentration that was estimated from the literature (Table 2). Similarly, grams of phosphorus into growth ( $G_p$ ) were estimated by multiplying daily growth of the round goby by its phosphorus concentration (Table 2), which we estimated from 30 round gobies (two or three fish per centimetre size-class, sizes ranged from 3 to 16 cm TL) sampled from the central basin of Lake Erie during May–June 2002.

To estimate the phosphorus concentrations of round gobies, we removed the contents of the stomach and intestines from each fish and the remaining tissue was dried at 60 °C until a constant mass (nearest 0.001 g) was reached. The tissue was then homogenized with either a mortar and pestle or a Retsch ZM 100 tissue grinder (Newtown, Pennsylvania) and then dried again for 3 days at 60 °C. For each of three replicate samples (0.3–1.0 mg each) per fish, phosphorus was converted to soluble reactive phosphorus with a hydrochloric acid digestion (Stainton et al. 1974) and then estimated with a Lachat FIA+ QuikChem 800 series autoanalyzer (Loveland, Colorado) (samples run by M. Vanni, Department of Zoology, Miami University, Oxford, OH 45056, USA). Because phosphorus concentrations did not increase with

**Table 2.** Literature-compiled estimates of energy density and phosphorus concentrations for the six prey categories of round gobies in the central basin of Lake Erie.

Category	Energy density (J·g wet mass <sup>-1</sup> )	Reference(s)	Phosphorus concentration (g P·g wet mass <sup>-1</sup> )	Reference(s)
Dreissenid mussels	2427 <sup>a</sup>	Schneider 1992	0.0015 <sup>a</sup>	Arnott and Vanni 1996
Other mollusks	2427 <sup>b</sup>	Cummins and Wuycheck 1971	0.0015 <sup>b</sup>	Arnott and Vanni 1996
Chironomidae	2745	Cummins and Wuycheck 1971	0.0019	Penczak 1985
Other benthos	3969 <sup>c</sup>	Cummins and Wuycheck 1971	0.0019 <sup>c</sup>	Penczak 1985
Zooplankton	3235 <sup>d</sup>	Cummins and Wuycheck 1971; Vijverberg and Frank 1976	0.001 <sup>e</sup>	Cummins and Wuycheck 1971; Vijverberg and Frank 1976
Age-0 fish	2500	Post 1990; T.B. Johnson and G.W. Kim, unpublished data	0.005	Kraft 1992; this study

<sup>a</sup>Zebra mussel soft tissue only, as shells are not digested by round gobies. Assumed that quagga and zebra mussels are equal.

<sup>b</sup>Assumed equal to dreissenid mussels.

<sup>c</sup>Weighted average of Amphipoda and Trichoptera.

<sup>d</sup>Weighted average of Ostracoda (assuming average crustacean), cyclopoids, and *Bythotrephes longimanus* (assuming average Cladocera).

<sup>e</sup>Weighted average of Ostracoda (assuming  $p = 0.1\%$  of dry mass), cyclopoids, and *B. longimanus* (assuming average Cladocera).

round goby size ( $F_{[1,28]} = 3.17$ ,  $r^2 = 0.10$ ,  $p = 0.09$ ), we used a mean phosphorus concentration of 0.00585 g P·g wet tissue<sup>-1</sup> for all round gobies.

We compiled the 28 different individual-based model results each year to calculate the round goby population contribution to phosphorus cycling. For each day in each model run, we added the phosphorus consumed, mobilized into growth of new tissue, and excreted across the surviving fish. When fish were losing mass (i.e., growth was negative), we set phosphorus growth to zero so as not to overestimate phosphorus excretion (Kraft 1992). Within each group of ages, sexes, and habitats, we then calculated the mean daily phosphorus flux across the two replicates. To extrapolate the individuals in the individual-based model to the population, we used an extrapolation coefficient, which equaled the number of surviving fish on 1 June in the individual-based model divided by our field-based estimate of round goby abundance. For each day of the model, we then divided the relevant model output (e.g., number of individuals, phosphorus excretion) by the extrapolation coefficient to extrapolate the dynamics of the modeled individuals to the central basin population.

## Results

### Population sampling

Because age-0 round gobies had not recruited to the bottom trawl, our population estimates include only age-1+ fishes. Estimates of mean annual abundance of age-1+ round gobies in the central basin of Lake Erie varied between 1995 and 2002. After round gobies were first sampled in 1994 (C.T. Knight, unpublished data), the population increased considerably until it reached a peak in 1999 of nearly 350 million fish (Fig. 1a). Across all years, mean densities of round gobies were greater in the nearshore habitat (mean = 307 individuals·ha<sup>-1</sup>, range = 34–583) than in the offshore habitat (mean = 81 individuals·ha<sup>-1</sup>, range = 7–201). However, round gobies in the offshore habitat comprised at least 46% of the total population size in six of the eight years (Fig. 1b) because of the larger area of offshore habitat. With regard to sizes of gobies sampled during the survey, the average TL of the more than 32 000 individuals measured (range = 1798–6279 fish across years) equaled

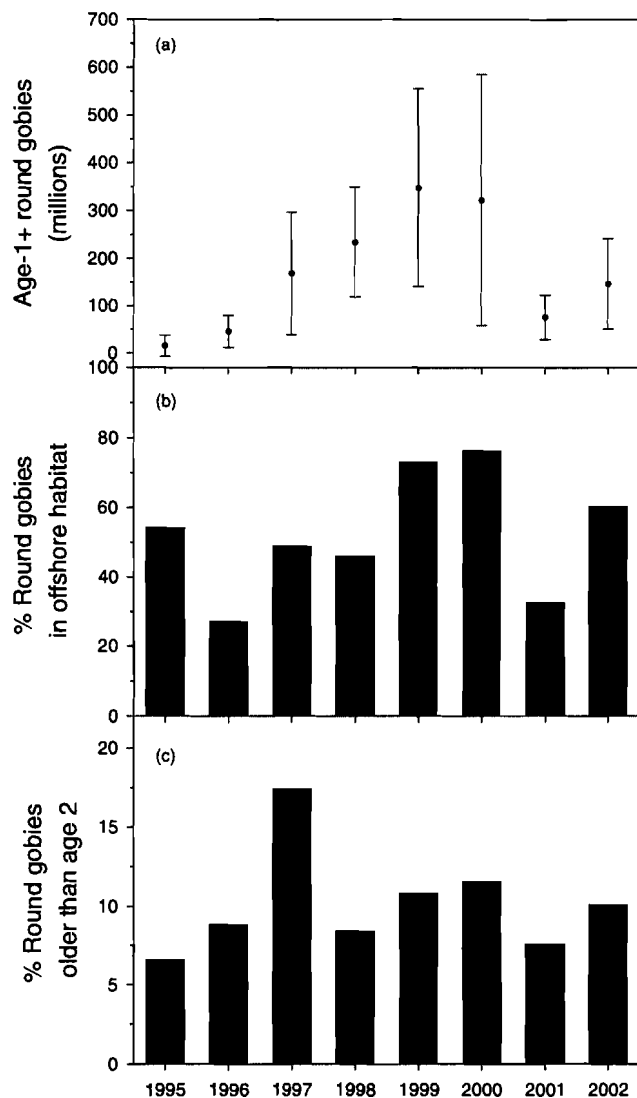
75 mm. The majority of individuals were between 30 and 79 mm TL in each year (range = 57.9%–69.0% of measured fish across years, mean = 63.4%), and <1% of individuals were <30 mm TL. The size distributions of gobies in each trawl were used to assign putative ages and sexes to the gobies for the population model. With respect to age-classes, the vast majority of round gobies were predicted to be age 1, as only 7.5%–17% of the age-1+ population was age 2 or older (Fig. 1c). This was a result of the length–age key that found at least 74% of round gobies between 30 and 79 mm TL to be age 1.

With regard to sex, males were estimated to be slightly more than 50% of the population in each year (range 50.3%–58.5%). This was a result of the sex–length key that found a high bias towards males at larger sizes. Females slightly dominated the sex ratio among fishes smaller than 80 mm TL (mean = 54.3% of the population). Males, however, predominated among fishes of larger sizes: 57% of fish 80–89 mm, 63% of fish 90–99 mm, 79% of fish 100–119 mm, more than 90% of fish 120–159 mm, and 100% of fish larger than 160 mm. Annual survival rates derived from catch-curve analyses also revealed differences between males and females. From 1995 to 2002, average annual survival for males was 58% (range = 35%–70%) compared with 19% for females (range = 14%–23%).

### Individual-based population simulation of phosphorus flux

Using the population densities, diets, and rates of growth and survival derived from field sampling, we simulated individual round gobies (ages 1–4 of males and ages 1–3 of females in both nearshore and offshore habitat) during 1995–2002 to determine population rates of consumption and excretion. This model did not include age-0 round gobies from when they were hatched (May–August) until 31 December because our field samples did not collect age-0 round gobies. The interannual growth pattern of round gobies exhibited a general trend across years. Using 1998 as an example, all ages and sexes of simulated round gobies lost weight during winter (December–April) and began gaining weight in May (Fig. 2). The largest weight gains, however, occurred during autumn (October–November). Given

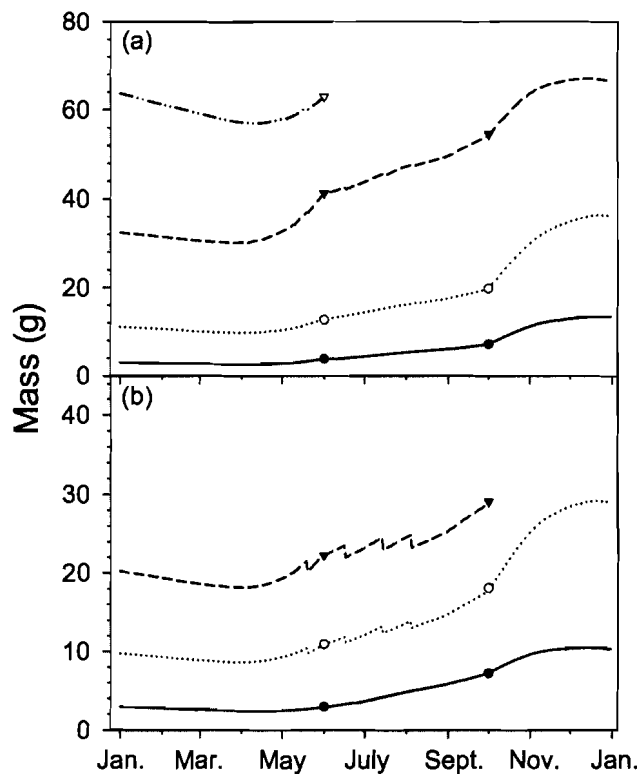
**Fig. 1.** Interannual population dynamics of age-1+ round gobies in the central basin of Lake Erie estimated from bottom trawls during May–October of each year. (a) The 90% confidence intervals around the annual mean abundance; (b) percentage of round gobies that were estimated to occur in the offshore habitat (i.e.,  $\geq 15$  m depth) in each year; (c) percentage of round gobies (includes ages 1–4) that were estimated to be older than age 2 in each year.



that mean sizes of round gobies sampled 1 June and 1 October in the field were used to calibrate the growth rates of round gobies in the model, the growth trajectory of simulated gobies passed through the mean sizes of field-sampled gobies on those dates, as expected (Fig. 2).

Estimated annual consumption by age-1+ round gobies was influenced largely by their annual abundance. Consumption of prey peaked at nearly 25 000 t in 1999 (Fig. 3) (range of 9981 – 39 795 using 90% confidence interval from mean population abundance). Dreissenid mussels dominated the diet in each year, ranging from 40.8% in 1997 to 57.2% of the diet in 1998. The second most abundant prey item varied across years: chironomids (1995, 1998, 2000, and 2002),

**Fig. 2.** Comparison of mean masses estimated from round gobies in the Lake Erie central basin during June and October 1998 (symbols) with daily mass of round gobies in the model simulation (lines). Open triangles are age-4 fish, solid triangles are age-3 fish, open circles are age-2 fish, and solid circles are age-1 fish. (a) Males; (b) females. Note the difference in the scales on the y axes.

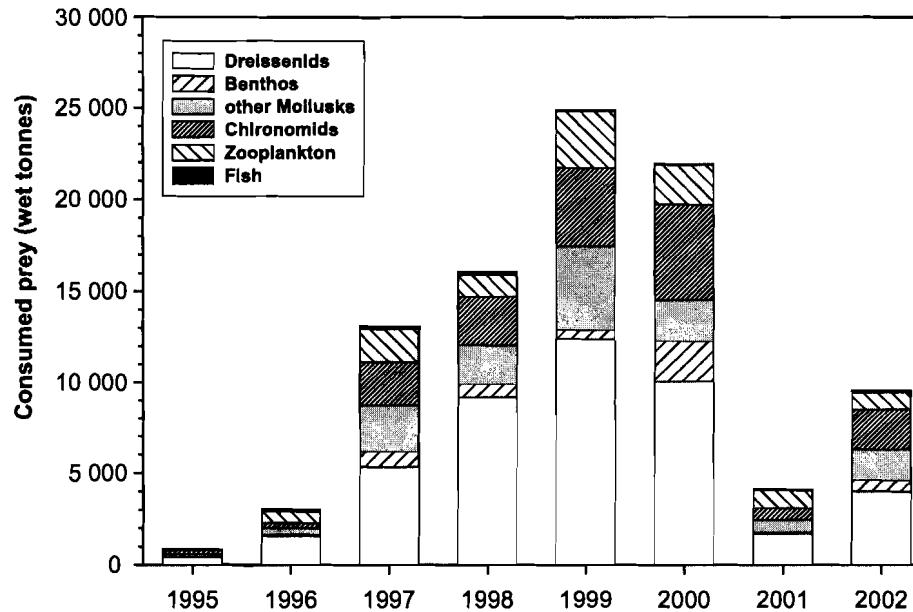


mollusks other than dreissenids (1997 and 1999), and zooplankton (1996 and 2001).

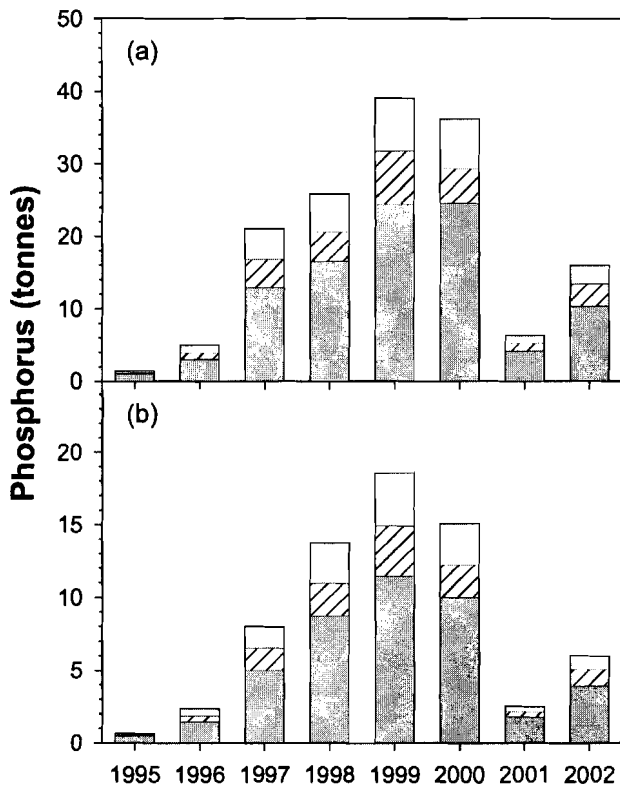
Interannual variation in round goby population abundance drove interannual changes in the contribution of round gobies to phosphorus cycling in the lake. The average amount of phosphorus bound in age-1+ round goby population biomass was as low as 0.8 t in 1995 and peaked at 23.9 t in 1999, when mean round goby abundance was highest. Annual tonnes of phosphorus consumed by age-1+ round gobies reached a maximum of 39 t (15.7–62.3 t, 90% confidence interval) in 1999 (Fig. 4a). Tonnes of phosphorus mobilized into new round goby tissue (i.e., growth) were slightly higher in 2000 (mean = 24.5 t·year<sup>-1</sup>, 4.7–44.3 t, 90% confidence interval) than in 1999 (mean = 24.4 t·year<sup>-1</sup>, 9.8–39.1 t, 90% confidence interval) (Fig. 4a). Excretion of dissolved phosphorus was highest in 1999, at 7.3 t·year<sup>-1</sup> (3.0–11.7 t, 90% confidence interval) (Fig. 4a). Finally, excretion that could be attributed to round goby consumption of dreissenid mussels (i.e., newly available phosphorus) also was highest in 1999 (mean = 3.5 t·year<sup>-1</sup>, 1.5–4.5 t, 90% confidence interval) (Fig. 4b).

Within a given year, phosphate excretion varied seasonally. Because consumption rates (i.e., *p* value) in the model were changed on 1 June and 1 October, abrupt changes in excretion occurred on those dates. Although these sudden changes likely are not representative of nature, the model

**Fig. 3.** Estimated mean annual consumption of six different prey items by the age-1+ round goby population in the Lake Erie central basin during 1995–2002.



**Fig. 4.** Annual phosphorus dynamics of age-1+ round gobies in the Lake Erie central basin. The shaded bars depict phosphorus mobilized into new tissue, the hatched bars depict phosphorus excreted, and the open bars depict phosphorus egested. The height of each bar represents the total phosphorus consumed. (a) Phosphorus consumed from all prey items; (b) phosphorus that can be attributed to consumption of dreissenid mussels. Note the different scales on the y axes.

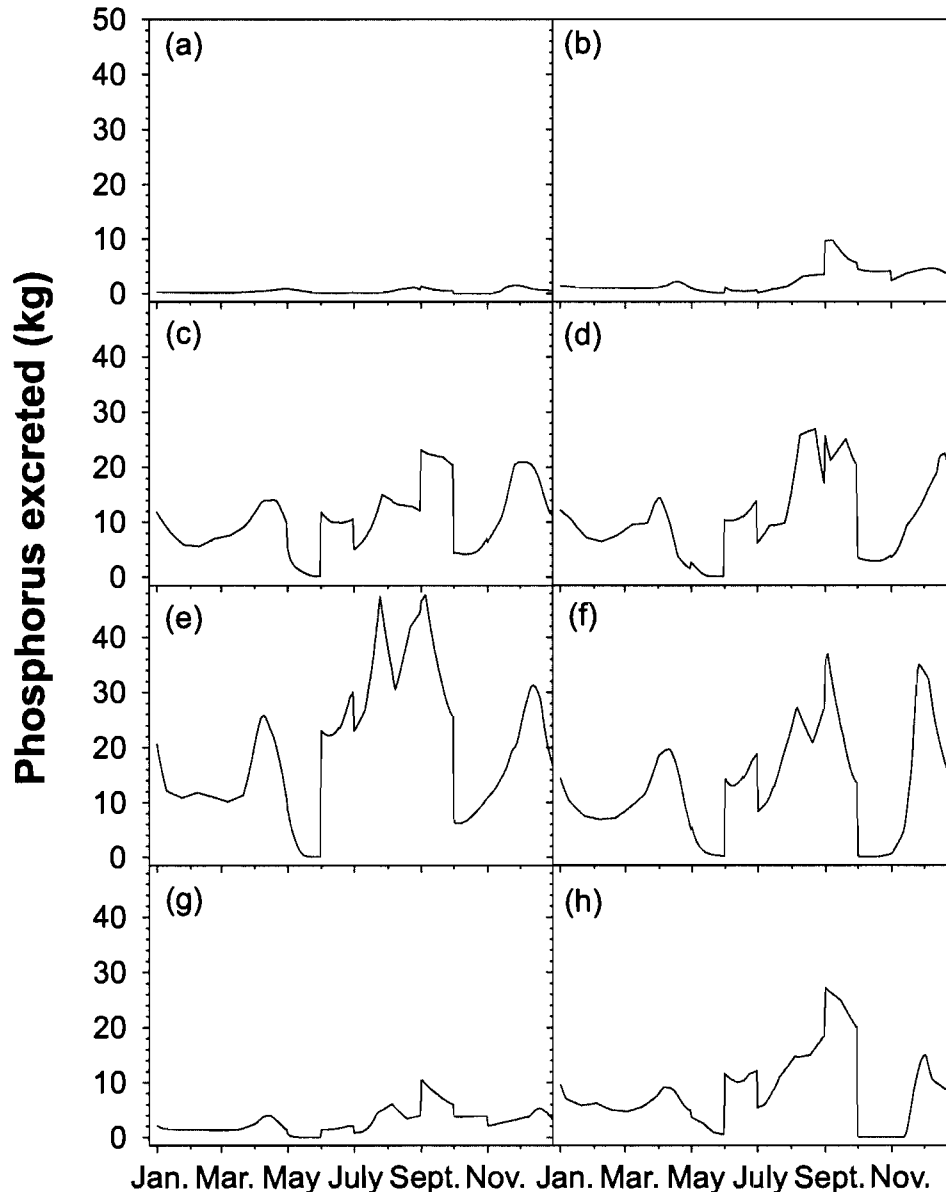


can reveal relative changes in excretion through the year. Most of the phosphorus was excreted between 1 June and 1 October, when warm water temperatures and moderate growth rates resulted in high consumption and residual phosphorus for excretion (Fig. 5). Another pulse of excretion occurred around December in most years, when end-of-the-year growth had begun to taper off but temperatures remained sufficiently warm for consumption to continue. During the coldest months of January and February, however, consumption and excretion remained very low. During April, another pulse of phosphorus was excreted by the round gobies as consumption increased with the warming spring temperatures.

To determine the indirect effects of round gobies on phosphorus regeneration, we first estimated how much potential dreissenid excretion was lost because of round goby consumption of dreissenid mussels. To estimate potential excretion by dreissenids, we assumed a phosphorus excretion rate of  $3.16 \times 10^{-5} \text{ g} \cdot \text{g dry mass}^{-1} \cdot \text{h}^{-1}$  (Arnott and Vanni 1996; estimated for zebra mussels in Lake Erie during summer), an 85% water composition for soft tissue (Schneider 1992), and that dreissenids were open (i.e., filtering and excreting) for  $19 \text{ h} \cdot \text{day}^{-1}$  (Walz 1978). Because we know zebra mussel excretion estimates for the summer months only, we estimated potential excretion from June through September of each year. The mean potential excretion by dreissenid mussels ranged from  $142 \text{ g P} \cdot \text{day}^{-1}$  when round gobies were not abundant in 1995 to more than  $4249 \text{ g P} \cdot \text{day}^{-1}$  in 1999 when round gobies reached their peak abundance (Table 3). In each year, however, the new phosphorus excreted by round gobies, owing to their dreissenid mussel consumption, exceeded the phosphorus that would have been excreted by those mussels had they not been consumed (Table 3; Fig. 6). Taking into account the lost potential excretion from consumed dreissenids reduced the new phosphorus available to primary producers by an average of 60%.



Fig. 5. Dissolved inorganic phosphorus excreted by the age-1+ round goby population in the Lake Erie central basin as a function of day of year. (a–h) Years 1995–2002, respectively.



Finally, we compared the estimated consumption of dreissenid biomass with the standing stock biomass of dreissenids to evaluate whether round gobies could be indirectly modifying phosphorus recycling by influencing the biomass of dreissenids in the central basin. Because we could not find a time series of dreissenid biomass from 1995 to 2002, we used a mean dreissenid biomass of  $878 \text{ g}\cdot\text{m}^{-2}$  (wet mass with shell), which was estimated across 19 sites in the central basin during 1998 (Jarvis et al. 2000). Assuming that 57% of the total wet mass was tissue (Johannsson et al. 2000; i.e., digestible), we approximated a basin-wide biomass abundance of  $7.5 \times 10^6 \text{ t}$  of dreissenid tissue. In 1998, when round gobies were near their peak in abundance, our model estimated that 9171 t of dreissenid tissue was con-

sumed, which translated to just over 0.1% of dreissenid standing stock biomass.

## Discussion

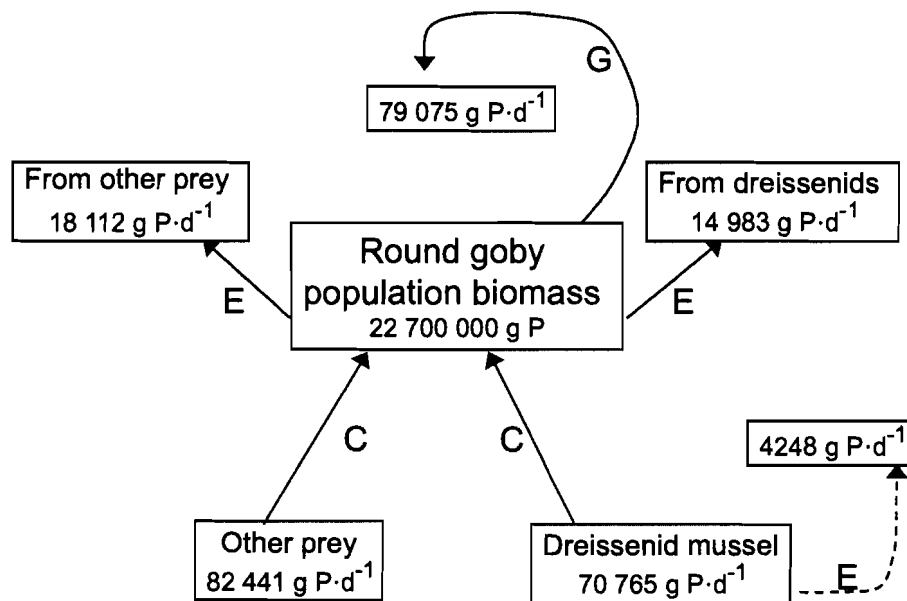
Since round gobies became established in Lake Erie, they have attained population abundance estimates as high as 350 million (age 1 and older) in the central basin. Phosphorus cycling by the population followed the general trend of the population abundance: increasing consumption, accumulation, and excretion of phosphorus from 1995 through 1999 and then a subsequent reduction in 2000–2002. At their peak in 1999, round gobies excreted more than 7 t of phosphorus. Because dreissenid mussels predominated their diets, most

**Table 3.** Annual indirect effect of round goby consumption of dreissenid mussels on available phosphorus to primary producers during June–September in the central basin of Lake Erie.

Year	Wet tissue of dreissenids consumed (t·day <sup>-1</sup> )	Wet phosphorus of dreissenids consumed (g·day <sup>-1</sup> )	Phosphorus excreted by round gobies from dreissenids (g·day <sup>-1</sup> )	Potential excretion by dreissenids that was consumed (g·day <sup>-1</sup> )	Net gain of new phosphorus (g·day <sup>-1</sup> )
1995	2	2 365	181	142	39
1996	6	9 370	1 208	563	645
1997	15	22 957	4 343	1378	2 965
1998	33	50 019	9 045	3003	6 042
1999	47	70 765	14 983	4249	10 734
2000	35	51 911	8 083	3117	4 966
2001	6	8 789	1 239	528	711
2002	12	17 286	5 052	1038	4 014

**Note:** Net gain of new phosphorus equals phosphorus excreted by round gobies from their consumption of dreissenid mussels minus the potential phosphorus excretion by dreissenid mussels that were consumed.

**Fig. 6.** Phosphorus dynamics associated with the age-1+ round goby population in the central basin of Lake Erie during June–September 1999, the year in which round gobies were most abundant. Solid arrows with their respective labels (G, growth; E, excretion; C, consumption) represent phosphorus rates from round gobies. The broken arrow from the box that represents consumed dreissenid mussels indicates the predicted phosphorus that would have been excreted by those dreissenids had they not been consumed by round gobies (i.e., potential excretion).



of the phosphorus excreted by round gobies can be considered newly available to the benthic community, as relatively few native predators consume and excrete the phosphorus bound in dreissenid tissue. Indirectly, however, consumption of dreissenid mussels also will reduce phosphorus available to primary producers because dreissenids are one of the most important phosphorus recyclers in Lake Erie (Arnott and Vanni 1996). Taking into account the lost potential excretion by dreissenids that were consumed reduced our estimate of new phosphorus available to primary producers (via round goby consumption of dreissenids) by an average of 60% across all years. In addition, our model results suggested that consumption of dreissenids was not sufficient to reduce their basin-wide biomass: round gobies were estimated to con-

sume only around 0.1% of the estimated dreissenid standing stock biomass in 1998.

#### Round goby excretion rates in comparison with fishes in other systems

Compared with previous studies that have estimated fish phosphorus cycling, excretion by the round goby population in central Lake Erie was low (Table 4). Fish excretion rates, standardized by surface area, have ranged from 0.01 to 5.46 mg P·m<sup>-2</sup>·day<sup>-1</sup> in previous studies. During 1995–2002, our estimates of round goby excretion ranged only 0.03–1.35 µg P·m<sup>-2</sup>·day<sup>-1</sup>, at least an order of magnitude smaller than all other published studies. This result could be the result of a low mass-specific excretion rate by individual round

**Table 4.** Summary of phosphorus excretion rates estimated for populations or assemblages of fishes in various lakes and reservoirs sorted as a function of fish biomass.

Lake or reservoir	Taxonomic grouping	Area (ha)	Mean depth (m)	Biomass (kg·ha <sup>-1</sup> )	Excretion rate (mg P·m <sup>-2</sup> ·day <sup>-1</sup> )	Mass-specific excretion rate (µg P·g <sup>-1</sup> ·h <sup>-1</sup> )	Source
Lake Erie, central basin	Round goby ( <i>Neogobius melanostomus</i> ) <sup>a</sup>	1 506 321	18	2	0.0014 <sup>b</sup>	0.0–1.0 <sup>b</sup>	This study
Sierra Nevada lakes (unstocked)	Trout <sup>a</sup>	1–13		3–17	0.01		Schindler et al. 2001
Sierra Nevada lakes (stocked)	Trout <sup>a</sup>	3–23		14–21	0.02		Schindler et al. 2001
Lake Pend Orielle	Kokanee salmon ( <i>Oncorhynchus nerka</i> ) <sup>a</sup>	35 300	164	16	0.02		Chipps and Bennett 2000
Lake Köyliönjärvi	Roach ( <i>Rutilus rutilus</i> )	1250	3	38	0.86		Tarvainen et al. 2002
Lake Michigan	Alewife ( <i>Alosa pseudoharengus</i> ) <sup>a</sup>	5 780 000	85	69	0.57 <sup>c</sup>		Kraft 1993
Lake Memphremagog, south basin	Young-of-the-year yellow perch ( <i>Perca flavescens</i> )	4371	7	70	0.14–2.06		Kraft 1992
West Long Lake	All fish	4	10	139	0.44		Schindler et al. 1993
Lake Texoma	Benthivores	36 000	8	192	0.96		Gido 2002
Peter Lake	All fish	2	8	199	3.18		Schindler et al. 1993
Union Lake	Common carp ( <i>Cyprinus carpio</i> ) <sup>a</sup>			200	0.52–1.07	0.5–10.0	Lamarra 1975
Lake Finjasön	Roach ( <i>Rutilus rutilus</i> ), bream ( <i>Abramis brama</i> )	1100	3	229	0.53		Persson 1997
Lake Gjersjoen	Roach ( <i>Rutilus rutilus</i> )	270	23	300	1.2–2.9	2.5–7.7	Braband et al. 1990
Lago Paranoá, Riacho Fundo	Tilapias ( <i>Oreochromis niloticus</i> , <i>Tilapia rendalli</i> ) <sup>a</sup>	446		341–791	0.88–2.04	0.5–1.6	Starling et al. 2002
Acton Lake	Gizzard shad ( <i>Dorosoma cepedianum</i> )	253		417	5.46	2.2–21.4	Schaus et al. 1997

<sup>a</sup>Introduced species.<sup>b</sup>In 1999, the year in which round gobies were most abundant.<sup>c</sup>Annual average. Value of 2.19 in Vanni (2002) was an average of July–October.

gobies or a relatively low population biomass density. Several studies have directly measured mass-specific phosphate excretion by fishes and have found it to range from 0.5 to 21.4  $\mu\text{g P}\cdot\text{g wet mass}^{-1}\cdot\text{h}^{-1}$  (Table 4). We derived mass-specific excretion rates from our simulated round gobies and found them to range from 0 to 2  $\mu\text{g P}\cdot\text{g wet mass}^{-1}\cdot\text{h}^{-1}$  across all years. Zero excretion generally occurred in early May as growth resumed following weight losses during winter, and the highest excretion rates occurred during summer and autumn as water temperatures warmed and consumption increased. In general, round gobies in our model were excreting phosphorus at a lower rate than some direct measures but within the range of others (Table 4). Hence, the extremely low population excretion by round gobies is not fully explained by an extremely low mass-specific excretion rate.

A low round goby population biomass density, compared with previous studies, could be another explanation for the low population excretion. Among other species caught in the bottom trawls during our field sampling, round gobies were ranked either second or third in terms of mean biomass captured during August of 1997–2000 when their population was at its peak. As the population abundance declined in 2001 and 2002, however, their August biomass ranking declined to sixth and fourth, respectively. Among native species during 1997–2000, round goby biomass ranked below yellow perch (*Perca flavescens*) in each year and below freshwater drum (*Aplodinotus grunniens*) only in 1998. Among nonnative species, round goby biomass exceeded that of rainbow smelt (*Osmerus mordax*) during August 1998–2000. Thus, the trawl samples revealed round gobies to be an important component of the central Lake Erie benthic community, especially during 1997–2000. When considering the area of central Lake Erie, however, the highest annual mean biomass density was only 2.4  $\text{kg}\cdot\text{ha}^{-1}$  (230 individuals $\cdot\text{ha}^{-1}$ ) in 1999. Most of the previous studies that have estimated fish excretion have focused on populations or assemblages with biomass densities  $>10 \text{ kg}\cdot\text{ha}^{-1}$ , and those with the highest excretion rates have biomass densities ranging from 199 to 417  $\text{kg}\cdot\text{ha}^{-1}$  (Table 4). Although round goby biomass was relatively high among species in the central basin, its biomass in comparison with other studies that have estimated fish excretion rates is extremely low. Hence, this relatively low round goby biomass density is likely responsible for the comparatively low population excretion rate.

Given the relatively low biomass density estimate, we consider the possibility that our sampling underestimated the round goby population size. First, we were not able to sample round gobies in depths  $<5 \text{ m}$ . Because this depth strata represents  $<2\%$  of the area of the central basin of Lake Erie (Haltuch and Berkman 1998), round gobies would have to attain extremely high densities for this omission to have a measurable impact on the total population density. Assuming that round goby density is influenced by habitat, we can assume that round goby density in 0–4.99 m depth is similar to that in 5–9.99 m depth owing to similar habitat composition (0–4.99 m: 40.7% glacial till, 36.2% sand–gravel, 17.2% bedrock, 5.9% sand–mud; 5–9.99 m: 51.1% glacial till, 24.5% sand–gravel, 15.8% bedrock, 8.6% sand–mud (Haltuch and Berkman 1998)). In 1999, when round gobies were most abundant, this assumption increased our total population es-

timate by only 2%, which is not nearly enough to push the biomass estimates up into the range of most other previous studies.

We also know that our population estimate was low because it did not include age-0 round gobies, which were not large enough to be collected in our bottom trawl. In terms of effects on phosphorus cycling, our model partially addressed the missing age-0 fishes, however. Age-1 round gobies in our model were simulated from 1 January to 31 December; field samples provided the abundance of age-1 round gobies on 1 June, and we used annual survival rates to back-calculate the abundance of that cohort to 1 January. Hence, we modeled round gobies that were only 6 months of age in all years, meaning that only the very youngest of gobies (i.e., 4–6 months of age) were not simulated in the model. Nonetheless, several studies have revealed the age-0 age-class to contribute a significant percentage of the overall population phosphorus recycling (e.g., 25%–50% (Kraft 1992, 1993; Chipps and Bennett 2000)). In our study, age-1 round gobies (which included fish as young as 4–6 months of age) also contributed more to phosphorus cycling than any other age-class. Undoubtedly, if our field sampling had provided estimates of age-0 round goby abundance and a bioenergetic model parameterized for larval round gobies were available, those model simulations would have revealed a higher population excretion rate for round gobies in the central basin of Lake Erie. Even if that rate were doubled (sensu Kraft 1993), however, the population excretion rate still would have been the lowest measured among other fish excretion studies.

#### Potential ecosystem effects in the Lake Erie central basin

Despite a low population excretion rate in comparison with other studies, we still wanted to evaluate the potential ecosystem-level effects of round gobies on the phosphorus cycling in the central basin of Lake Erie. One measure of the impact of phosphorus excretion by round gobies is to compare their excretion with the phosphorus required by primary producers. Before making this comparison, however, we needed to make some assumptions about whether the excreted phosphorus remained within the benthic habitat or diffused into the entire water column. The ultimate fate of these ions is dependent on a suite of factors, including whether or not the basin is stratified and the direction and magnitude of the prevailing winds and currents. Indeed, understanding the hydrodynamics is critical for the prediction of the ecosystem impact of dreissenid mussels on the phytoplankton community in the Great Lakes, as the mussels must rely on turbulent diffusion or “sinking” of phytoplankton to supply their food (e.g., MacIsaac et al. 1999; Ackerman et al. 2001). To maximize the potential impact of round goby excretion, we will assume that the phosphorus remains in the benthic habitat; if we had assumed that the phosphorus diffused into the entire water column, then we would have minimized the effects of round goby excretion because the phosphorus would diffuse into a much larger volume of water. At 2 m depth, the net benthic community photosynthetic rate in Lake Erie is  $\sim 30 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  (R.E. Hecky, Biology Department, University of Waterloo, Waterloo, ON N2L 3G1, Canada, personal communication). Dividing by the Redfield ratio of carbon to phosphorus (106:1), we estimated that  $\sim 730 \mu\text{g P}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  is required to sustain benthic primary produc-

tion. Because we could not sample 2 m depth areas, we will use our nearshore (between 5 and 15 m depth) round goby density estimate as a surrogate to calculate an areal excretion rate of round gobies at 2 m depth. In 1999, when the round goby abundance was at its peak, nearshore excretion was only  $2.7 \mu\text{g P}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ , which is about 0.4% of the phosphorus required for benthic primary production. Thus, even in the scenario where round goby excretion was maximized by minimizing the volume of water in which the phosphorus diffused, round gobies were predicted to contribute little to primary production.

Another way to evaluate the impact of fish excretion is to compare it with the amount of phosphorus that enters the system from the watershed. In some reservoirs, phosphorus excretion by fishes can exceed the external phosphorus loading into the system during some parts of the year (Braband et al. 1990; Schaus et al. 1997; Gido 2002), although the biomass of those fish or fish assemblages ranged from 192 to  $417 \text{ kg}\cdot\text{ha}^{-1}$ . The annual excretion by the round goby population peaked at 7.3 t in 1999, but that represented only 0.6% of the total phosphorus externally loaded to the central basin in that year (D. Dolan, Department of Mathematics, University of Wisconsin-Green Bay, Green Bay, WI 54311, USA, unpublished data). During 1997–2000, phosphorus recycled by round gobies was only 0.3%, on average, of the external phosphorus load to the basin. This analysis is another indication of the limited direct impact of round gobies on the Lake Erie phosphorus cycle.

We also evaluated the indirect effect of round gobies on phosphorus recycling through their consumption of dreissenid mussels. Since their invasion in the late 1980s, the filtering capacity of zebra mussels has been suggested to contribute to reductions of phytoplankton and increased water transparency in Lake Erie (e.g., MacIsaac et al. 1992; Madenjian 1995). With regard to nutrient regeneration, their high nutrient excretion rates also can have considerable lake-wide impacts. Arnott and Vanni (1996) estimated phosphorus recycling by zebra mussels to be greater than all other sources, including zooplankton, sediment release, macrophytes, and external inputs. Because round gobies consumed up to 12 379 t of dreissenid tissue per year during our study period, we determined whether the “new” nutrients released from round goby consumption of dreissenid tissue was offset by a reduction in excretion of those mussels. Despite dreissenid mussels having a mass-specific excretion rate that is two orders of magnitude higher than round gobies (zebra mussels:  $1.02 \mu\text{mol P}\cdot\text{g dry mass}^{-1}\cdot\text{h}^{-1}$  (Arnott and Vanni 1996); round gobies:  $0.04 \mu\text{mol P}\cdot\text{g dry mass}^{-1}\cdot\text{h}^{-1}$  (this study)), excretion by round gobies that was attributed to consumption of dreissenids was 2.8 times higher, on average, than the potential excretion by those dreissenids. This result is a consequence of the wet mass of the round goby population being at least 100 times greater than the mass of the dreissenid mussels that were consumed on any given day. Nonetheless, taking the potential excretion into account diminishes the amount of new phosphorus that round gobies excrete from consuming dreissenid tissue.

Owing to the importance of dreissenid mussels in the phosphorus recycling in Lake Erie (Arnott and Vanni 1996), we also were interested in whether the round goby predators

were making an impact on the population dynamics of dreissenid mussels. Unfortunately, we could not find a time series of dreissenid biomass in the central basin to determine whether increasing round goby densities coincided with reductions in dreissenids. In 1998, however, we were able to compare the consumption estimate of dreissenids by round gobies with an estimate of dreissenid biomass in the central basin (Jarvis et al. 2000). Even with a relatively high population density by round gobies in 1998, we found that they consumed about 0.1% of the dreissenid biomass in the basin. This result, coupled with sonar estimates that reveal increases in dreissenid percent cover within the central basin (Haltuch et al. 2000), suggests that round goby consumption is not having a basin-wide impact on the population dynamics of dreissenid mussels. As a result, round gobies do not appear to be indirectly affecting phosphorus cycling by reducing the biomass of dreissenids in the central basin.

#### **Predictions regarding the impact of introduced species on phosphorus cycling**

Our results revealed round goby to have a negligible impact on the phosphorus available to primary producers in the central basin of Lake Erie. This result is counter to several previous studies that have documented a considerable effect by introduced species on phosphorus cycling in lakes and reservoirs. In the 1970s, alewife excretion and egestion of phosphorus in Lake Michigan was estimated to be equivalent to phosphorus recycling by zooplankton (Kraft 1993). Excretion by tilapia in Lago Paranoá, Brazil, was estimated to be 9%–21% of the external phosphorus load (Starling et al. 2002), and excretion by trout in several Sierra Nevada lakes was estimated to be equivalent to the lake's atmospheric deposition of phosphorus (Schindler et al. 2001). Several factors may influence the impact of an introduced species on phosphorus cycling, including its population biomass density and the food web structure to which the fish are introduced.

In the case of tilapia in Lago Paranoá and alewife in Lake Michigan, both of these species attained high biomass densities ( $>300$  and  $69 \text{ kg}\cdot\text{ha}^{-1}$ , respectively) compared with round gobies in Lake Erie ( $\leq 2.4 \text{ kg}\cdot\text{ha}^{-1}$ ), which likely explains the greater effect of nonnative alewife and tilapia in those systems. The food web within which the fish is introduced also may determine whether the fish influences nutrient cycling. Trout introduced into oligotrophic Sierra Nevada lakes had a considerable impact on phosphorus cycling (Schindler et al. 2001) despite reaching biomass densities that were relatively low compared with other fish excretion studies (Table 4). In most of these systems, the trout were introduced into systems that were historically without fish, so it is not surprising that they would have a measurable impact on phosphorus cycling. These salmonids recycled phosphorus through their consumption of zooplankton but also provided new sources of phosphorus by feeding on benthic and terrestrial prey that were not consumed by native organisms (Schindler et al. 2001). Conversely, the effect of zooplanktivorous kokanee salmon (*Oncorhynchus nerka*) on phosphorus cycling in Lake Pend Oreille was influenced by another species, *Mysis relicta* (opossum shrimp) (Chipps and Bennett 2000). In this food web, *Mysis* and kokanee both compete for zooplankton, but *Mysis* appear to have gained a competitive advantage,

which contributes to their greater effects on phosphorus recycling (Chipps and Bennett 2000).

Overall, fish likely have the greatest impact on phosphorus cycling when introduced into systems with simple food webs (i.e., fishless Sierra Nevada lakes). If introduced into more complex food webs, their effects on phosphorus cycling will depend on the outcome of competitive or predatory interactions (i.e., Lake Pend Orielle). If the fish are successful enough to reach extraordinarily high biomass densities (i.e., alewife in Lake Michigan or tilapia in Lago Paranoá), then that biomass alone will have some impact on the phosphorus cycles in lakes. Despite their ability to take advantage of abundant dreissenid mussels as a prey resource, round gobies in the central basin of Lake Erie did not attain sufficiently high biomass densities to influence phosphorus cycling. It remains to be determined whether their population has been limited by piscivores in the lake, as round gobies have become prevalent in the diets of smallmouth bass (*Micropterus dolomieu*), yellow perch, white bass (*Morone chrysops*), walleye (*Stizostedion vitreum*), and burbot (*Lota lota*) in Lake Erie (C.T. Knight, unpublished data).

In conclusion, Lake Erie remains a dynamic ecosystem whose nutrient dynamics are difficult to understand owing to its interannual variability in external nutrient inputs and the seemingly constant stream of invaders. With the success of introduced dreissenid mussels, whose filtering has contributed to water clarity and facilitated the resurgence of benthic algae and invertebrates, Lake Erie is believed to have shifted from a pelagic- to a benthic-dominated system (Johannsson et al. 2000). From an ecosystem perspective, dreissenid mussels can increase dissolved nutrient concentrations in the water column through excretion (Heath et al. 1995). As a benthic fish, the round goby has been contributing to the increasing biomass of the benthic habitat, but heretofore, its ecosystem impacts were unknown. Our model results indicated that round goby effects on phosphorus cycling in the central basin of Lake Erie are minimal. Directly, their excretion contributes little (0.4%) to benthic primary production. Their population excretion estimates were lower than those of any previously published studies, a result of their comparatively low population biomass density. Indirectly, round gobies consumed far less than 1% of the dreissenids in central Lake Erie, indicating that round gobies have not been influencing phosphorus cycling by reducing the abundance of the dreissenid population, the most important nutrient recycler in the lake (sensu Arnott and Vanni 1996). In our view, future research regarding round goby ecosystem effects should focus on their role as couplers of the benthic and pelagic food web. If round gobies remain prevalent in the diets of pelagic piscivores, then they will serve as a vector to move energy and nutrients concentrated in the benthic habitat up into the pelagic habitat.

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