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EFFECTS OF BIOMANIPULATION ON NUTRIENT CYCLES IN CENTRAL FLORIDA LAKES VIA NUTRIENT EXCRETION AND BIOTURBATION BY GIZZARD SHAD

ST. JOHNS RIVER WATER MANAGEMENT DISTRICT

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Effects of Biomanipulation on Nutrient Cycles in Central Florida Lakes via Nutrient Excretion and Bioturbation by Gizzard Shad

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Final Report

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Executive Summary

Gizzard shad (*Dorosoma cepedianum*) can have a major influence on nutrient cycling and fish communities in lakes, particularly in hypereutrophic systems, where it can be the dominant fish species. Gizzard shad can release large quantities of nutrients from sediments into the water column, and the feeding and excretion activities of this species can greatly increase phytoplankton biomass and decrease water clarity. Biomanipulation, or the removal of benthic feeding fishes to improve water quality, has been used by lake managers as a tool to improve water quality in many lakes in Europe and North America. The St. Johns River Water Management District has undertaken a large-scale removal of gizzard shad from Lake Apopka (over 6.4 million kilograms of gizzard shad removed during 1993-2007), Lake Dora, and Lake Griffin as a means to reduce lake phosphorus and phytoplankton concentrations, and improve water clarity. To date, water clarity has improved substantially (Coveney et al. 2005), but Lake Apopka has not yet shifted to a clear-water state that is stable and dominated by native macrophytes, as has been observed in some other systems following a reduction of benthivorous fishes.

Although fish manipulations have been conducted in a number of systems (e.g., Meijer et al. 1999, Søndergaard et al. 2000, Jeppesen et al. 2007), it is less well understood how these manipulations will impact lake nutrient cycles and which mechanisms are most important to water clarity. For example, by its feeding activities, gizzard shad can feed on a combination of benthic and planktonic food sources. Thus the impact of this species on lake ecosystems may be as a result of either mode of feeding. When zooplankton are abundant, gizzard shad have been shown to feed extensively on this food item, but shad can also switch to benthic feeding when zooplankton are rare. In feeding on sediment detritus and its associated microflora and benthic

invertebrates, this species can translocate nutrients from sediments to the water column both through excretion and by stirring up the sediments (bioturbation). The impact of this species on the ecosystem components may thus be a combination of its effects due to its planktivory, excretion, and/or bioturbation.

To better understand the impact of this large-scale fish removal on lake nutrient cycles, and the mechanisms important in this impact, we conducted four types of studies in Upper Ocklawaha River Basin (UORB) lakes:

1) Direct measures of nutrient excretion by Lake Apopka gizzard shad across the range of water temperatures and fish sizes observed in this system (2004-2005).
2) Comparisons of nutrient excretion rates by gizzard shad from Lakes Apopka, Dora, Eustis, and Griffin (2005-2006).
3) Mechanistic tank microcosm studies manipulating fish density, size and/or sediment access to determine the relative importance of nutrient excretion vs. bioturbation (2006-2007).
4) Preliminary studies of gizzard shad diet in Lakes Apopka and Dora using gut content analysis from a limited number of dates (2007).

Direct measures of nutrient excretion by Lake Apopka gizzard shad found that both N and P excretion were significantly impacted by fish wet mass and temperature. The N:P of nutrient excretion by gizzard shad was lower than has been reported for other systems, likely due to the higher temperatures in this system and the stronger influence of temperature on P excretion rates. Mass coefficients were significantly less than 1, indicating that larger fish had lower mass-specific rates of excretion, compared to smaller fish.

Using the mean monthly lake temperature between 1993 and 2005, we estimated that 454 mt (1,000,000 lbs) of gizzard shad >200g in a typical year excreted 45.8 mt of N and 7.8 mt of P. Across years, seasons of high gizzard shad removal impacted lake nutrient cycling by preventing the release of over 14 mt of P per year. Combined with direct P removal (via fish tissues), this yielded a total P effect (direct removal of P plus reduced excretion) of over 18 mt/year in the 3 years of highest fish removal. This impact on lake P cycles varied substantially from year to year, but can be substantial, especially during years of reduced external nutrient inputs.

Cross system comparisons of excretion during 2005 and 2006 found that N excretion, but not P, varied significantly among lakes. Individual regressions were developed to predict P excretion in Lakes Apopka, Griffin, and Dora, where extensive fish removals were conducted. Using length frequency distributions from each of these systems during 2002-2007 fish harvests coupled with predictions of P excretion for each system, we found that the impact on nutrient cycling per pound of fish removed was somewhat higher in Lakes Apopka and Griffin than in Lake Dora. This is due to both the harvest of larger fish in lake Dora, which have lower mass-specific rates of excretion and the slightly lower P excretion rates measured in Lake Dora, for fish of equivalent mass. Phosphorus excretion reduction effects of harvest in these systems (2002-2007) ranged from 3.6-13.0 mt/year for Lake Apopka, 1.5-1.9 mt/year for Lake Dora and 2.1-8.9 mt/year for Lake Griffin. The per hectare effect on P excretion in these three systems ranged from 0.29-2.35 kg P per hectare per year.

We also compared the nutrient based effects of different gill net mesh sizes in Lake Apopka during 2007. Smaller gizzard shad were susceptible to the 3.5-in stretch mesh gill nets, tend to have higher mass-specific excretion rates and tend to be more detritivorous (Gu et al. 1996, Catalano et al. 2007). The amount of P cycling prevented by an equivalent biomass removal using 3.5-in nets was 9.8% greater than for 4-in stretch mesh nets. This sized based effect on nutrient cycling and the 3.5-4-in mesh gill nets' inability to sample smaller sizes of gizzard shad suggests that it may be advantageous to consider both the effectiveness of particular harvesting strategies on reducing fish biomass and the resulting impact on reductions in nutrient release, in combination with other considerations (bycatch, cost, etc.).

Tank microcosms enabled us to separate the effects of excretion from those of biomanipulation by manipulating the density of fish, sediment access, and the presence of phytoplankton, comparing the responses across experiments. Gizzard shad typically only stimulated phytoplankton biomass and total and particulate nutrient concentrations when fish could feed directly on sediments. In most cases, there was an increased proportion of nutrients (both N and P) in particulate form, indicating that gizzard shad can have some impact on turbidity of the water column via bioturbation, in addition to excretion effects. Increases in turbidity, total and particulate nutrients, were highest with high fish biomass, as was expected. Tanks where sediments were manually disturbed with a paddle had a modest increase of total dissolved P concentrations, even though turbidity and chlorophyll were substantially elevated over control tanks. In this system, gizzard shad appear to be important in the excretion of nutrients, the resuspension of phytoplankton, and to some extent the release of dissolved P directly from sediment via bioturbation. In other systems where benthivores such as common carp (*Cyprinus carpio*) extensively disturb sediments, there may be a greater impact of bioturbation, especially if pore water nutrients remain mobilized in the water column or if sediment particles limit light availability to aquatic plants.

Our preliminary diet analyses for Lakes Apopka and Dora indicate that, for the time periods measured, gizzard shad diet was composed mostly of sediment detritus (mean of 97.5%

detritus), with zooplankton/zoobenthos and algae on average comprising only 0.3% and 2.2%, respectively of the ash free dry mass of items in the foregut. Although this sampling was only a brief snapshot of the feeding history of this species, other investigators (Gu et al. 1996, Catalano et al. 2007) have also observed that gizzard shad can rely heavily on detritus as a part of a mixed diet in these systems. Thus, in these systems, the role of gizzard shad appears to include a lesser amount of nutrient recycling within the water column via planktivory, while primarily transporting nutrients from sediments to the water column via detritivory.

Overall, our results indicate that nutrients released by gizzard shad can have a substantial impact on lake systems via nutrient excretion and bioturbation effects. Gizzard shad reductions are most likely to be effective in systems where anthropogenic nutrient inputs have been successfully reduced. A critical challenge for lake managers is to define criteria for a successful restoration effort and identify systems where biomanipulation is most likely to be successful, especially in the long term. Future studies aimed at determining how to best maximize the success of biomanipulation programs and determining ways to effectively shift the system to a stable clear water state would help to achieve this goal.

Cooperators and Acknowledgments

This study would not have been possibly without extensive support from many individuals who helped with one or more aspects of this project. Although this paper was written by a sole author, I have chosen to use the phrasing “we” throughout the text in acknowledgement of the contributions made to this study by others. From the St. Johns River Water Management District, Walt Godwin, Mike Coveney, Ed Lowe, and Larry Battoe helped to conceptualize this project and provide valuable ideas and feedback. Walt Godwin, Randy Roth, Brian Sparks, Shannon Curtis, Jim Peterson, Paul Ek, Don Nickerson, and Ellen Bailey provided extensive support in the field. Walt Godwin and Brian Sparks provided help with data analysis and by providing other supporting data to help interpret this study within a meaningful context. Olivia Thomas conducted experimental gill net sampling and surveys of commercial gill nets for SJRWMD. Without SJRWMD’s financial and logistical support, this project would not have been possible.

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Chapter 1 – Impact of a Large Scale Removal of Gizzard Shad on Nutrient Cycles in Lake Apopka, FL.

Introduction

Numerous studies have shown that benthic-feeding fishes can have important direct and indirect effects on lake ecosystems, such as stimulating phytoplankton (Lamarra 1975, Schaus and Vanni 2000), increasing nutrient concentrations (Lamarra 1975, Brabrand et al. 1990), and increasing turbidity (Meijer et al. 1990, Breukelaar et al. 1994, Tarvainen et al. 2005). These effects can be manifested directly via excretion or indirectly through mechanisms such as bioturbation (Vanni 2002). Some studies have found that the excretion of nutrients by benthic-feeding fishes can be of greater magnitude than other well recognized nutrient sources, such as external loading or nutrient release from sediments (Brabrand et al. 1990, Persson 1997b, Schaus et al. 1997, Schindler et al. 2001, Shostell and Bukaveckas 2004) and can be enhanced in more eutrophic systems (Drenner et al. 1996, Vanni et al. 2006). Thus, effective eutrophication control must consider both external inputs of nutrients and internal effects of these species, such as translocation of nutrients from benthos to the water column and subsequent stimulation of phytoplankton (Vanni et al. 2005).

As a result, lake managers have begun to utilize the removal of these fishes more frequently as a tool to improve water quality (i.e, Hansson et al. 1998, Meijer et al. 1999, Søndergaard et al. 2000, Jeppesen et al. 2007). This practice simultaneously removes nutrients sequestered in fish tissues and prevents the nutrient excretion and bioturbation that otherwise would have occurred. In many cases, these biomanipulations have significantly improved water quality (i.e., Moss et al. 1996, Søndergaard et al. 2000), although in some systems, the effect can be more short lived or less effective than was desired (Persson et al. 1993, Hansson et al. 1998), especially if the harvested species increases in abundance (Kim and DeVries 2000, Irwin et al. 2003). Ideally, the removal of dominant benthic-feeding fishes linked with reduction in external nutrient inputs seeks to shift lake systems from a turbid stable state dominated by phytoplankton productivity to a clear-water stable state with much greater macrophyte abundance and greater water transparency that persists over time (Scheffer et al. 1993, Scheffer 1998, Carpenter 2005).

In lakes and reservoirs of the midwestern and southern U.S., the omnivorous gizzard shad (*Dorosoma cepedianum*) often dominates the fish assemblage (i.e., Stein et al. 1995, Gido and Matthews 2000), especially in eutrophic to hypereutrophic systems (Bachmann et al. 1996, DiCenzo et al. 1996, Allen et al. 2000). This species can feed on zooplankton and phytoplankton (Mundahl 1988, Gu et al. 1996, Mitchell et al. 1996), but often relies extensively on benthic detritus as a food source (i.e., Mundahl and Wissing 1987, Gido 2001, Schaus et al. 2002, Higgins et al. 2006), enabling this species to maintain a high biomass even when zooplankton is rare. High gizzard shad biomass can simultaneously suppress zooplankton abundance and supply nutrients to stimulate phytoplankton in the absence of grazer control (Schaus and Vanni 2000, Schaus et al. 2002). Mesocosm experiments and cross-lake studies have shown that this species can increase water column nutrient concentrations (Schaus and Vanni 2000) and support higher phytoplankton biomass (Aday et al. 2003), with a greater proportion of phytoplankton productivity supported in more eutrophic systems (Vanni et al. 2006).

These effects are especially important because gizzard shad can translocate nutrients from sediments to the water column, providing a “new” source of nutrients (Dugdale and Goering 1967, Shapiro and Carlson 1982, Caraco et al. 1992) to lake phytoplankton. By feeding on benthic food sources, gizzard shad can increase total water column nutrients (Schaus and Vanni 2000), unlike nutrients recycled via planktonic feeding, which merely recycle nutrients already present within the water column. In a field enclosure experiment, gizzard shad only stimulated phytoplankton and water column nutrients when it could feed on sediments (Schaus and Vanni 2000). Thus, this species appears to be an ideal candidate for biomanipulation efforts in temperate and subtropical systems.

In three Florida Lakes (Denham, Griffin, and Apopka), the St. Johns River Water Management District (SJRWMD) has previously conducted extensive gizzard shad removals to reduce algal biomass and improve water quality. In Lake Denham, removal of ~80% of the harvestable gizzard shad biomass using haul seines led to increased Secchi depths and reduced Chlorophyll and total P (Godwin et al. 1993). In Lake Griffin, increased water clarity coincided well with the removal of 79% of the harvestable gizzard shad biomass in 2002 and following substantial external P loading reductions beginning about 1999 (Godwin et al. 2006). In Lake Apopka, eutrophication control measures have included reductions in external input (Coveney et al. 2005), wetland filtration (Coveney et al. 2002), and gizzard shad removal using commercial gill nets (Godwin et al. 2006). While the mechanisms for the observed improvements in water quality are likely due to several of the methods utilized, the timing of the response suggests that fish removal has an important impact on water quality.

To better understand the impact of the large-scale fish removal in Lake Apopka, we sought to quantify the effects of this biomanipulation on lake nutrient cycles. To do so, we determined the N and P excretion rates of Lake Apopka gizzard shad across the range of fish sizes and lake temperatures observed and used these rates to estimate the amount of N and P excretion prevented by the large-scale removal of gizzard shad. In doing so, we could examine the seasonality of the nutrient effect and compare the magnitude of this effect with those of other management techniques utilized in this system.

Methods

We directly measured N and P excretion of 229 gizzard shad, using methods with short time intervals similar to those used by other investigators (i.e., Brabrand et al. 1990, Mather et al. 1995, Gido 2002). This method provides results similar to bioenergetics modeling and also avoids the decrease in excretion that is observed during longer incubation times (Mather et al. 1995, Vanni 2002). Excretion measurements were conducted during 8-17 June 2004 (N=72), 20-22 Dec. 2004 (N=30), 21-23 March 2005 (N=23), 23-26 May 2005 (N=47), and 6 July – 7 August 2005 (N=57). All measurements were conducted between 0900 and 1500 hours, and always at least 2 hours after sunrise, during times when fish actively feed (Pierce et al. 1981). Excretion rates were measured across the range of fish sizes observed in this system (1.5-657.1g wet mass), and across the range of temperatures (14.0-33.5 °C) typically encountered in this system (Appendix 1). NH_4-N and PO_4-P were measured for all dates, whereas other N and P fractions were also measured during June 2004.

Water was collected from Lake Apopka and was filtered through a 1 μm pore size glass fiber filter to remove algae, which could take up excreted nutrients. Filtered water (2-20L, volume dependent on fish size) was placed in new polyethylene liners placed within plastic containers and was held at lake temperature overnight, until the containers were placed onto the boat for excretion measurements. Fish were collected via electrofishing from the northwestern quadrant of the lake, including nearshore and offshore areas and the first 200m of the Apopka-Beauclair canal. Collected fish were placed in an aerated livewell for 5-30 minutes to allow fish time to recover from any handling stress. Fish were then transferred to the containers of prefiltered water for excretion measurements. This water was maintained within 1°C of the lake temperature for the duration of the excretion measurement. After 5 minutes, an initial water sample was collected from the chamber, and 30 minutes after the initial sample, a final water sample was collected. Differences in nutrient concentrations were also measured in control buckets, which were handled in an identical manner, but without the addition of fish.

Excretion samples were immediately placed on ice and were kept there until filtration in the lab (typically within 2-3 hours). Gizzard shad were then sealed in plastic bags and placed on ice until these fish could be weighed and measured in the lab. Excretion samples were filtered through a 1 μm pore size glass fiber filter to remove fecal matter and any other particulates, and a subsample was preserved to a pH<2 using sulfuric acid. Samples were then packed in ice and shipped to PPB labs (Gainesville, FL) for N and P analyses using standard EPA methods. From these samples, the excretion rate could be determined by difference, correcting for volume, and expressed as mg N or P fish^{-1} hr^{-1}.

During June 2004, we measured total N and P on unfiltered samples, and used filtered samples to analyze for total dissolved N and P, NH_4-N, NO_x and PO_4-P. NO_x was extremely low, thus it was eliminated after June 2004. Measurements on unfiltered samples proved to be too variable because feces were distributed within the container in a heterogeneous manner and total nutrients varied strongly depending on the amount of feces removed with each water sample (initial or final). As a result, we focused solely on NH_4-N and PO_4-P after June 2004, and this report will only present the results for NH_4-N and PO_4-P, as the other data are unreliable. In addition, nearly all other investigators measuring excretion rates (i.e., Brabrand et al. 1990, Mather et al. 1995, Schaus et al. 1997, but see Gido 2002) have used these two fractions as the relevant measures, as these forms are readily excreted by freshwater fish and are readily taken up by phytoplankton.

During June 2004, we also sampled an additional 14 fish using gill nets, but this technique qualitatively appeared to stress the fish and cause additional scale loss, even with extremely short net sets (<10 min). Gido (2002) reported that gillnetting did not appear to cause undue stress in smallmouth buffalo and river carpsucker, but these species are more hardy than gizzard shad, and we observed noticeable stress in gillnetted gizzard shad. To determine any potential effect of gillnetting on excretion by gizzard shad, we compared log transformed excretion rates (NH_4-N and PO_4-P) and N:P ratios of gillnetted gizzard shad (N=14) with gizzard shad collected by electrofishing (N=72) during June 2004, using ANCOVA, with log wet mass as a covariate. Because there was a moderately significant difference between the PO_4-P excretion measurements using these two sampling techniques (P=0.071), we chose to be conservative and only used fish sampled using electrofishing for our analyses, as this appeared to cause much less stress to fish.

Excretion data for NH_4-N and PO_4-P (mg $fish^{-1}$ hr^{-1}) and the N:P ratio (by mass) from the 229 fish collected using electrofishing were analyzed using stepwise multiple regression (SPSS version 15), with fish wet mass (g) and temperature (°C) as independent variables, with $\alpha = 0.05$ as the criterion for entry into the model and $\alpha = 0.1$ for removal from the model. Excretion rates and wet mass were log transformed prior to analysis because this was necessary to normalize the variance.

To extrapolate up to the effect of the large scale fish removal on a whole lake basis, we calculated the hourly N and P excretion rates of a 290.6g fish, which is the mean weight of all gizzard shad we collected >200g wet mass (i.e., those susceptible to 4-in stretch mesh gill nets).

These excretion rates were then multiplied by 0.82, because Schaus et al. (1997) observed that the average excretion throughout a 24-hour period is 82% of the peak (daytime) excretion rates and we are aware of no other comparable data in the literature. These hourly excretion rates per fish were converted to daily and monthly rates and multiplied by 1.56 million fish, which is the number of fish of this size in 454,000 kg of fish (1,000,000 pounds), in order to estimate the amount of nutrient cycling prevented by a typical annual gizzard shad harvest. Monthly mean temperatures were then used to predict seasonal effects of a typical fish harvest on an annual basis. Finally, mean monthly temperature and annual harvest data since 1993 were then used to estimate the amount of N and P recycling (both on a monthly and an annual basis) that was prevented by the gizzard shad harvest each year between 1993 and 2005. Because fish harvest occurred annually prior to (Table 1-1) and following (Table 2-2) our 2004-2005 excretion measurements, we are confident that these excretion measures are typical of the population throughout this fish removal.

Results

Measurement of Excretion Rates

Excretion of N by Lake Apopka gizzard shad was best predicted by the equation:

$$\log N \ (\mathrm{mg\ fish^{-1}\ hr^{-1}}) = 0.007 * \mathrm{Temp.}\ (^\circ\mathrm{C}) + 0.665 * \log \text{wet mass (g)} - 1.189$$

(P<0.001, $r^2 = 0.741$, Table 1-2) and excretion of P was best predicted by the equation:

$$\log P \ (\mathrm{mg\ fish^{-1}\ hr^{-1}}) = 0.053 * \mathrm{Temp.}\ (^\circ\mathrm{C}) + 0.649 * \log \text{wet mass (g)} - 3.041$$

(P<0.001, $r^2 = 0.610$, Table 1-2). Excretion of both N and P showed significant positive correlations with fish size and lake temperature (Fig. 1-1 and 1-2, Table 1-2). The correlation with fish mass was much tighter for N than for P, however, the impact of temperature on N excretion was much less than the impact of temperature on P, as the temperature coefficient was more than seven times higher for P (Table 1-2). For the N and P excretion regression coefficients, the 95% confidence intervals were within 15% of the values for these coefficients (Table 1-2).

Mass-specific excretion of N and P typically decreased with increasing mass, as is indicated by mass coefficients that were significantly <1 in the above equations (the upper 95% confidence intervals were less than 1, Table 2). For example, at 30°C, a 50g gizzard shad would excrete 1.415 mg N hr^{-1} and 0.448 mg P hr^{-1}, whereas a 500g gizzard shad would excrete 6.544 mg N hr^{-1} and 1.998 mg P hr^{-1}, thus a 10-fold increase in mass would yield a 4.62-fold increase in N excretion and a 4.56-fold increase in P excretion.

The N:P excreted by gizzard shad in Lake Apopka was best predicted as:

$$N{:}P \text{ (by mass)} = -1.297 * \text{Temp. } (^{\circ}C) + 42.919$$

($P<0.001$, $r^2 = 0.233$, Table 2). During summer, high water temperatures greatly increased P excretion rates, with a more modest effect on N excretion. Thus, summertime N:P was very low (typically <5 by mass), whereas the N:P was much higher when water temperatures were cooler (Fig. 1-3). This may have important implications for water quality, as low N:P supply ratios have been correlated with dominance by blue-green algae (Smith 1983, but see Xie et al. 2003).

Estimation of Nutrient Release

We estimated the monthly amount of nutrient release prevented by the removal of 1 million pounds of gizzard shad (454,000 kg), a typical annual harvest, on a seasonal basis. On an annual basis during a typical year, a million pounds of gizzard shad >200g would recycle 45.8

mt of N and 7.8 mt of P (Fig. 1-4). Based on a multiplicative error associated with our predictions of excretion based on temperature and wet mass, the 95% confidence intervals associated with our lakewide predictions should be ±21.5% and ±21.4% of our predictions for N and P, respectively. The predicted annual rate of P release exceeds external loading during years with low rainfall, and is about ⅓ of the P inputs from farms during a typical year (Table 3). On a seasonal basis, P excretion by gizzard shad is likely to be more important between spring and fall (Figure 1-5), especially during periods with reduced external loading. Across years, the estimated impact on lake nutrient cycles varied substantially based on fish harvest (Table 1-1, Fig. 1-5). Between 1993 and 2005, the gizzard shad harvest removed 38.5 mt of P in fish tissues (Table 1-1) and prevented the release of 558.1 mt of N and 99.9 mt of P via excretion (Table 1-1, Figure 1-5). During the 3 years where gizzard shad harvest was highest, the cumulative effect of removal of P in fish tissues and reduction in P release exceeded 18 mt of P on an annual basis (Table 1-1).

Table 1-1 – Gizzard shad harvest data for Lake Apopka, during 1993-2005, taken from data recorded by various fishing companies involved with this project. 1993-1997 fish harvest data have previously been reported by Crumpton and Godwin (1997). The cost of the fish harvest reflects the cost paid by SJRWMD as a subsidy to companies harvesting the fish. During years where the cost is $0, no subsidies were paid and fish were sold at market value, but harvests were subsequently lower. The amount of N and P removed by fish harvesting is based on estimated N content of 2.1% and P content of 0.7% (Davis and Boyd 1978). The total effect includes both the N and P removed in fish tissues and the reduction in N and P cycling caused by gizzard shad removal.

Year	Harvest (kg)	Cost	Direct N Removal (kg)	Direct P Removal (kg)	N Excretion Prevented (kg)	P Excretion Prevented (kg)	Total N Effect (kg)	Total P Effect (kg)
1993	408,388	$0	8,576	2,859	41,039	7,243	49,615	10,102
1994	764,942	$85,000	16,064	5,355	78,754	14,822	94,818	20,177
1995	288,520	$43,426	6,059	2,020	29,522	5,558	35,581	7,578
1996	268,560	$85,310	5,640	1,880	26,922	4,483	32,562	6,363
1997	581,542	$150,496	12,212	4,071	58,964	10,021	71,176	14,092
1998	760,230	$253,378	15,965	5,322	77,903	14,687	93,868	20,009
1999	223,365	$78,789	4,691	1,564	22,591	3,802	27,282	5,366
2000	139,462	$56,949	2,929	976	14,076	2,419	17,005	3,395
2001	79,243	$0	1,664	555	7,871	1,226	9,535	1,781
2002	238,227	$0	5,003	1,668	23,858	3,894	28,861	5,562
2003	700,404	$286,116	14,708	4,903	71,704	13,570	86,412	18,473
2004	562,187	$316,504	11,806	3,935	56,803	9,704	68,609	13,639
2005	476,775	$337,729	10,012	3,337	48,074	8,501	58,086	11,838
Total	5,491,845	$1,693,697	115,329	38,445	558,081	99,930	673,410	138,375

Table 1-2 – Results of stepwise multiple regression analysis predicting gizzard shad NH_4-N and PO_4-P excretion rates and N:P, based on Log wet mass (g), and Temperature (°C). Wet mass had no significant impact on N:P ($P>0.7$). R^2 values for the regressions were 0.741, 0.610, and 0.233 for NH_4-N and PO_4-P excretion rates and N:P, respectively.

	Coefficient	95% Lower Confidence Interval	95% Upper Confidence Interval	P-Value
Log NH_4-N				
Intercept	-1.189	-1.364	-1.014	<0.001
Log Wet Mass	0.665	0.613	0.717	<0.001
Temperature	0.007	0.003	0.011	0.001
Log PO_4-P				
Intercept	-3.041	-3.327	-2.754	<0.001
Log Wet Mass	0.649	0.563	0.734	<0.001
Temperature	0.053	0.046	0.060	<0.001
N:P by Mass				
Intercept	42.919	34.680	51.157	<0.001
Temperature	-1.297	-1.605	-0.989	<0.001

Table 1-3 – Impacts on the P cycle by gizzard shad and other important reductions or sources of nutrients to Lake Apopka. Direct removal refers to cases where nutrients are directly removed, such as through the removal of fish tissue or via wetland filtration. Reduction in P supply refers to reduced P inputs or recycling as a result of management strategies utilized by SJRWMD. Mean annual loading or recycling by several of the important sources of nutrients is provided for comparison of the magnitude of these effects.

	Mean Direct Removal of P (mt yr^{-1})	Mean Reduction in P supply (mt yr^{-1}) (Range)	Mean Annual Supply (mt yr^{-1})
Gizzard Shad	2.96	7.69 (1.23-14.82)	
Wetland Flow-way [a]	2.37		
Reduction in Farm Loading (1968-1992 vs. 1993-2002) [b]		37.5	
Farms (drought years 2000-2001) [b]			0.51
Farms (typical years 1993, 1995, 1997-1999, 2002) [b]			17.26-27.82 (range)
Farms (high loading years 1994, 1996) [b]			45.07
Atmosphere [b]			5.36
Springs/tributaries/Other [b]			3.61

[a] Erich Marzolf – SJRWMD, Personal Communication

[b] Coveney et al. (2005)

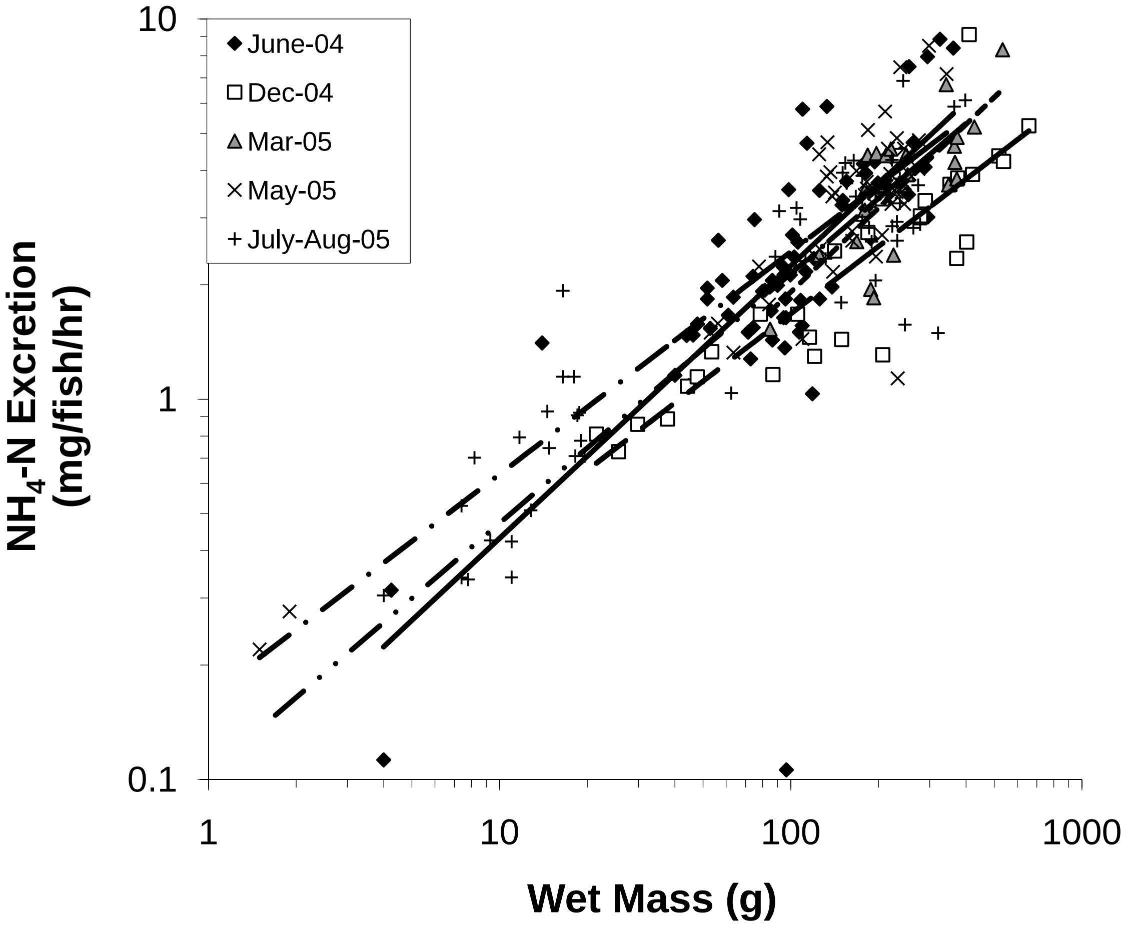

Fig. 1-1 – Excretion of NH_4-N by Lake Apopka gizzard shad during June 2004-Aug. 2005, expressed on a whole-fish basis. Trend lines are included for each sampling period (June ’04 ———, Dec ’04 — — —, Mar ’05 - - - - - -, May ’05 — - — - —, July-Aug ’05 — - - — - -). N excretion was significantly affected by log mass (P<0.001) and Temperature (P=0.001).

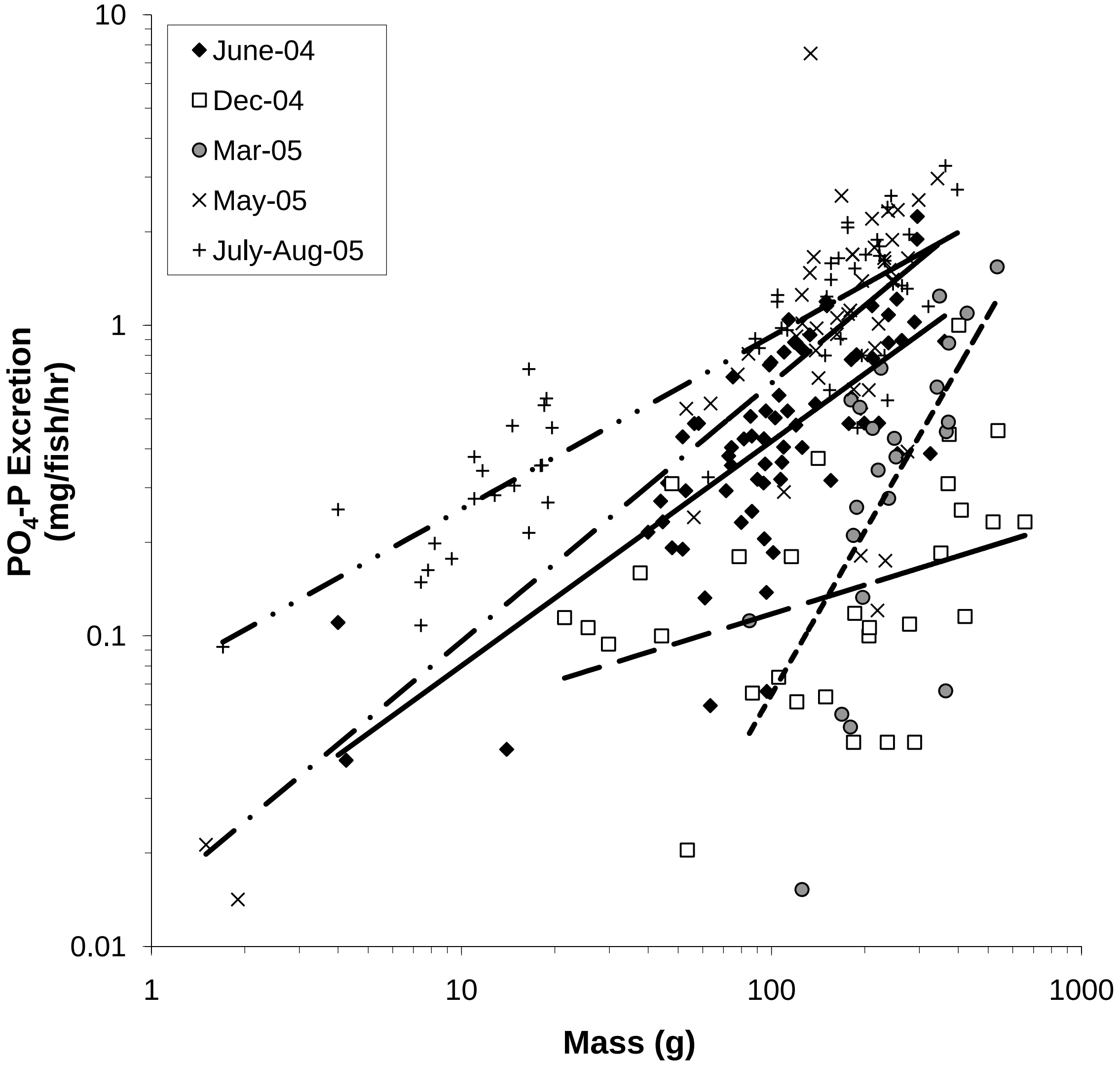

Fig. 1-2 – Excretion of PO_4-P by Lake Apopka gizzard shad during June 2004-Aug. 2005, expressed on a whole-fish basis. Trend lines are included for each sampling period (June ’04 ———, Dec ’04 — — —, Mar ’05 - - - - - -, May ’05 — - — - —, July-Aug ’05 — - - — - -). P excretion was significantly affected by log wet mass ($P<0.001$) and Temperature ($P<0.001$).

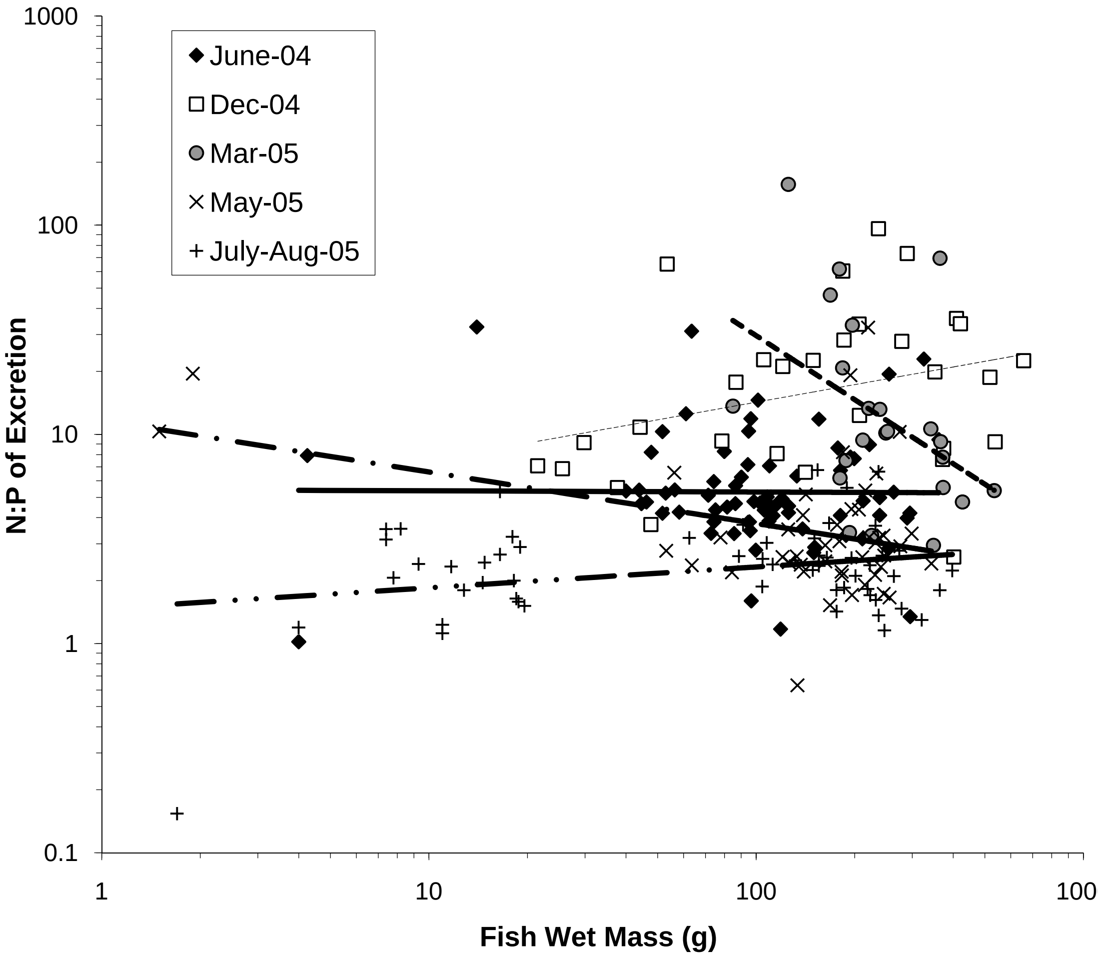

Fig. 1-3 – N:P of Excretion by Lake Apopka gizzard shad during June 2004-Aug. 2005. Trend lines are included for each sampling period (June '04 ————, Dec '04 — — — —, Mar '05 - - - - - - - - -, May '05 — - — - — -, July-Aug '05 — - - — - -). The N:P of excretion was significantly affected by temperature (P<0.001), but not log wet mass (P>0.7).

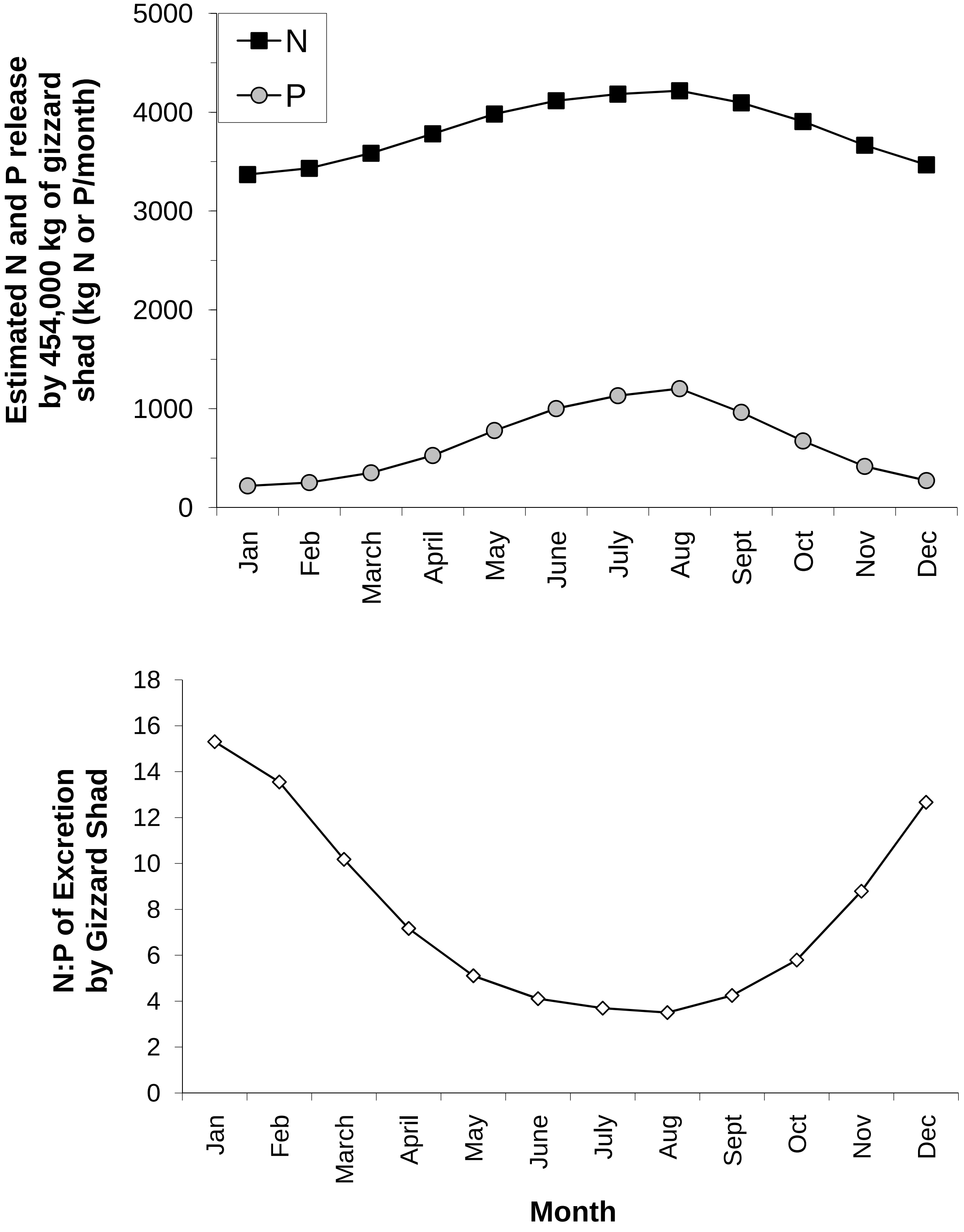

Figure 1-4 – Monthly N and P release (top panel) by 454,000 kg of gizzard shad in a typical year, based on mean monthly lake temperatures between 1993 and 2005 (Appendix 1). N:P of nutrients released (bottom panel) ranged from 3.5 (August) to 15.3 (January), based on temperature effects on P excretion.

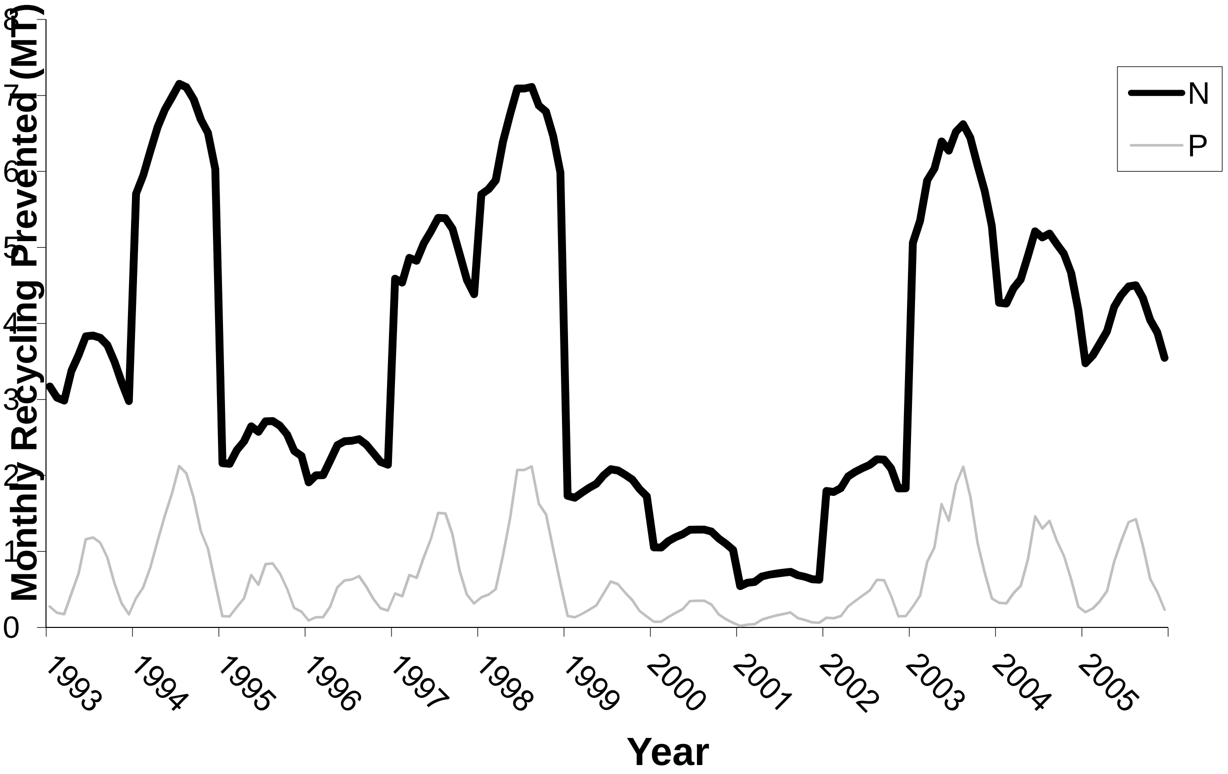

Fig. 1-5 – Simulated monthly N and P recycling prevented by the actual harvest of gizzard shad (Table 1-1). Effects of shad harvesting are assumed to occur only during that calendar year, thus large jumps can occur between Dec. and Jan., even though the actual effects are more likely smoothed. Increased levels in summers occur due to the increase in N and especially P excretion that is observed with increasing temperature. Cumulative amounts of nutrient release prevented by the fish harvest totaled 558.1 mt of N and 99.9 mt of P across years (Table 1).

Discussion

Excretion Measurements

Our trends were consistent with those of other investigations of nutrient excretion by gizzard shad (Schaus et al. 1997, Gido 2002, Higgins et al. 2006), as N and P excretion were significantly affected by fish size and temperature, with decreasing mass-specific excretion rates with increasing fish size. The fish measured in this study were also substantially larger than those reported by Schaus et al. (1997) and Higgins et al. (2006) and slightly larger than those reported by Gido (2002), broadening the applicability of these findings. Similar to studies in Acton Lake (Schaus et al. 1997), P excretion was much more strongly influenced by temperature, whereas N was more strongly influenced by fish mass. In addition, the N:P ratios excreted by Lake Apopka gizzard shad were much lower than those reported elsewhere for this species (Schaus et al. 1997, Gido 2002, Higgins et al. 2006), possibly due to the effect of high temperatures on P excretion or possible differences in food quality or lake productivity (Higgins et al. 2006). Because of the strong effect of temperature on P excretion, the effect of this species on lake nutrient cycles may be more pronounced in warmer climates.

Understanding the Role of Gizzard Shad in Lake Apopka

The role of this species in Lake Apopka is modified by several factors, including diet, biomass, growth rates and population size structure. Clearly, the impact of this species is proportional to the biomass of the population, and the degree to which water quality improvements can be made is somewhat dependent on the degree to which SJRWMD can decrease the population of gizzard shad. While current data exist for harvest rates (Table 1-1), it is much more difficult to assess the impact that this harvest has had on the resident gizzard shad population, as the confidence intervals surrounding biomass estimates often are quite large. For example, 1995 and 1996 gizzard shad population biomass estimates for Lake Apopka (Schramm & Pugh 1997a,b) range from 37 to 233 kg ha^{-1}, depending on the year and the method they used, and they acknowledge that these biomass estimates are lower than expected for a hypureutrophic system. A recent study (Vanni et al. 2006) has reported effective sampling of gizzard shad populations in Ohio reservoirs with acoustic surveys using side-scan and vertical-scanning sonar. This method appears to be especially effective, because similar to Lake Apopka, these systems are shallow and the offshore biomass is predominantly comprised of gizzard shad. More effective quantification of the population biomass would provide a better understanding of the effectiveness of the gizzard shad harvest on fish removal and reduction in nutrient release. Our estimates necessarily limit the impact of each year's harvest to that year, but better measures of seasonal changes in biomass could determine the time frame during which the population biomass remained reduced, as well as the degree to which population growth can counteract this harvest (Catalano et al. 2007).

Another factor that may substantially modify the role of gizzard shad in this system is the degree to which it utilizes benthic materials in its diet. Gu et al. used a multiple stable isotope approach to determine that Lake Apopka gizzard shad derive 40% of dietary carbon from zooplankton, with the remainder presumably of detrital origin. Likewise, current investigations by Catalano et al. (2007) have documented that Lake Dora gizzard shad between 100-250 mm TL rely heavily on a benthic diet. Our preliminary studies of gizzard shad gut contents (Chapter 4) have also documented that gizzard shad rely heavily on sediment detritus, but that its long term nutrition likely includes a combination of benthic and planktonic food items (Catalano et al. 2007), of which the organisms (zooplankton and benthic invertebrates) would be more easily digestible. Clearly, quantification of the degree to which this species feeds on benthic material would provide a better understanding of the proportion of excreted nutrients which are translocated from the benthos, rather than merely recycled within the water column.

The impacts of the harvesting method can also have important consequences for the success of a biomanipulation effort. Clearly, techniques should be utilized which are most effective at removing large quantities of fish within a fairly short time period. Within that framework, different types of gear can be more or less size selective, which is important because of the effects of mass on excretion rates (Hall et al. 2007). If a technique predominantly removes only large fish, the nutrient based effect could be substantially lower than if an equivalent biomass of smaller fish was removed. Other factors to consider are the degrees to which reproduction by the population can be reduced by biomanipulation, as this may help provide better long term success. It is also valuable to have information on the degree to which this species can increase growth rates (Schaus et al. 2002) or reproduce earlier (Schaus et al. 2002, Catalano et al. 2007) in response to reduced population biomass, as these factors may offset some of the gains made by the fish harvest.

Impact on Lake Nutrient Cycles

The overarching goal of this study was to quantify the effects of a large-scale fish removal on nutrient recycling. In doing so, we can evaluate its relevance in the context of other fluxes of nutrients and other management efforts. Overall, the amount of N and P recycled by fish is substantial relative to many of the other nutrient sources in this system (Table 1-3). The major effect of fish removal seems to be through the reduction in nutrients excreted by this species, as that exceeds the amount removed in fish tissues by a factor of 2.5, with a mean annual fish effect (nutrients removed and excretion prevented) of 10.6 mt yr^{-1}. During years of high gizzard shad harvest, the total annual fish effect is around 18-20 mt P yr^{-1}, which is comparable to P inputs from farms in a typical year (all except 1994 and 1996). These estimates provide an initial measure of the effect of the gizzard shad removal in relation to other management efforts and some of the other important sources of P to the system. They are also somewhat conservative, as they do not account for other effects, such as bioturbation of sediments. Our estimates could be further refined by using the actual size distribution of fish removed from the system (instead of the mean mass of fish >200g) to hone these measures. Studies of the nutrient effect across systems during 2006 (Chapter 2) utilized this approach and found similar whole-lake measures of nutrient effect (estimates were within 0.5% and 8% of the Chapter 1 measures) in Lake Apopka during 2002-2005.

Clearly, the largest improvement in P supply has been through the management of farm nutrients. Successful eutrophication control typically begins with reductions in external nutrient inputs, especially P. However, nutrients released by benthic-feeding fish, such as gizzard shad can potentially offset the expected improvements in water quality following reductions in P input. Vanni et al. (2005) argue that effective lake management must consider both external loading and fish populations that can translocate nutrients from the sediments into the water column. Without effective control of external nutrient inputs, it is unlikely that any eutrophication control program will be successful in the long term. However, provided that cuts in external loading can occur, biomanipulation of benthic-feeding fish can be an important tool to improve water quality (Hansson et al. 1998), by removing nutrients bound in fish tissue, by preventing excretion that would otherwise maintain high production despite reductions in external nutrient inputs, and by preventing bioturbation of sediments.

This multi-pronged management approach has sought to improve water quality and restore the system on all fronts, including reductions in external nutrient loading, biomanipulation, removal of suspended solids through wetland filtration, and replanting of native vegetation. Ideally, the improvements in water clarity will enhance the growth of macrophytes, which can maintain the system in a stable clear-water state, as is predicted by the multiple-stable-states model (Scheffer et al. 1993). To attain this level, European investigators have found that successful water quality improvement is typically attained when ~80% of the fish population is removed (Hansson et al. 1998, Søndergaard et al. 2000). Historic records (Schelske et al. 2005) indicate that Lake Apopka formerly supported substantial wetlands in the surrounding areas, extensive growth of macrophytes, lower TP and Chl a, and higher water transparency, as well as larger production of game fishes. Thus there is the potential to return the system to this clear water stable state. A challenge for the future will be to identify ways to speed the recovery of systems impacted by eutrophication (Carpenter 2005).

Chapter 2 – Biomanipulation Effects on Nutrient Release by Gizzard Shad in Central Florida Lakes

Introduction

Gizzard shad can dominate the fish biomass lakes and reservoirs of the midwestern and southern U.S. (Miranda 1983, Stein et al. 1995), especially in eutrophic systems where it tends to be more abundant (Bachmann et al. 1996, DiCenzo et al. 1996). It is thought to impact the rest of the food web via a complex interaction between "top-down" and "bottom-up" processes (Stein et al. 1995). It can impact higher trophic levels by competing with other fish as larvae, but it is also an important food item to many piscivores. However, it can grow rapidly in many systems, and thus may outgrow vulnerability to most gape limited piscivores (Johnson et al. 1988). These impacts on upper trophic levels can potentially "cascade" to impact lower trophic levels, but gizzard shad can also directly impact lower trophic levels via "bottom-up" means.

Gizzard shad can feed on abundant zooplankton (Mitchell et al. 1996, Yako et al. 1996, Schaus et al. 2002) and then switch to organic detritus when zooplankton are rare. In doing so, it can suppress zooplankton and transport nutrients from benthic to pelagic habitats via excretion and bioturbation (Vanni 2002), greatly contributing to the internal "loading" of nutrients within the system (Schaus et al. 1997, Vanni et al. 2005), and increasing nutrient concentrations and phytoplankton abundance (Schaus and Vanni 2000). The impact on lake nutrient cycles can vary substantially based on gizzard shad abundance, diet, and/or lake trophic status (Vanni et al. 2005, Higgins et al. 2006). Because of the potential importance of this source of nutrients, it would be useful to document the effects of this species on lake nutrient cycles and compare these effects across systems.

As omnivores, the role of gizzard shad in the system depends greatly on diet, which ranges from highly detritivorous (Mundahl and Wissing 1987, Higgins et al. 2006) to mixed (Gu et al. 1996, Thorpe et al. 1998, Gido 2001, Schaus et al. 2002) to primarily planktivorous (Mitchell et al. 1996). When gizzard shad feeds primarily on benthic food items, it is capable of transporting nutrients from benthic to pelagic habitats, providing a "new" source of nutrients to lake phytoplankton (Dugdale and Goering 1967, Caraco et al. 1992). By feeding on benthic food sources, gizzard shad can increase total water column nutrients (Schaus and Vanni 2000), unlike nutrients recycled via planktonic feeding, which are already present within the water column. When feeding on a mixed diet, the proportion of nutrients translocated between habitats will depend on the proportion of the diet that is comprised of benthic materials.

Some investigators have undertaken extensive removals of omnivorous and benthivorous fishes as a means to improve water quality in lakes (Meijer et al. 1990, Horpilla et al. 1998, Meijer et al. 1999, Drenner and Hambright 1999, Søndergaard et al. 2000). Removal of these fishes can decrease phytoplankton and nutrient concentrations, increase water clarity, and/or increase the abundance of larger zooplankton (Hansson et al. 1998, Meijer et al. 1999, Godwin et al. 2006). In some cases, the effect of fish removal has been shown to impact the system primarily via reductions in internal nutrient loading, rather than via increased zooplankton (Horpilla et al. 1998). Reductions of fish stocks are typically more successful in smaller systems with more extensive fish removals, especially of omnivores and benthivores (Hansson et al. 1998, Meijer et al. 1999, Drenner and Hambright 1999, Søndergaard et al. 2000). Ideally, an intense manipulation can shift the system from a highly productive phytoplankton dominated system to a stable clearwater phase, with decreased phytoplankton, increased zooplankton and increased macrophyte abundance (Scheffer et al. 1993, Scheffer 1998).

Because of its abundance and its omnivorous diet, gizzard shad is a good candidate for biomanipulation efforts to improve lake water quality. The St. Johns River Water Management District (hereafter SJRWMD), has removed approximately 5.4 million kg of gizzard shad from Lake Apopka, Florida between 1993 and 2005 (Table 1-1). SJRWMD has also conducted extensive fish removals from Lakes Denham, Dora, and Griffin, so it is possible to compare the nutrient effects of fish harvests among Florida lakes. We measured nutrient release rates of gizzard shad in four central Florida lakes (Apopka, Dora, Eustis, and Griffin), three of which have undergone, or are currently undergoing, intensive fish removal projects. These rates were then used to quantify the magnitude of the nutrient effect across these systems and determine means to optimize the effectiveness of biomanipulations in reducing internal nutrient release.

Methods

During March 2005 and during 2006, we measured nutrient release by 168 gizzard shad collected from Lakes Apopka (N = 58), Dora (N = 46), Eustis (N = 38) and Griffin (N = 26), using methods similar to those of other studies (Brabrand et al. 1990, Schaus et al. 1997, Gido 2002) and Chapter 1. These sample sizes in each lake are comparable to some published studies of fish excretion (Schaus et al. 1997, Gido 2002), but much lower than our sample size during our previous study in Lake Apopka (Chapter 1). Fish used in the excretion measurements spanned the range of sizes available in each system during the sampling periods (7.7-860.0g wet mass; mean fish mass for each system ranged from 192.6 in Lake Griffin to 251.5 g in Lake Apopka). Gizzard shad from Lakes Apopka and Dora were sampled during March 2005, and the Apopka fish (N = 23) were also included as a portion of the measurements reported in Chapter 1. During 2006 we compared excretion rates of gizzard shad from all four lakes during Jan/Feb, May, and July/Aug, and we sampled fish from all except Lake Griffin during March. Lake temperatures during the excretion measurements ranged from 15.6-31.8 ˚C, which is typical of the seasonal ranges observed in these systems (Appendix 1). All measurements were conducted between 0900 and 1500 hours, and always at least 2 hours after sunrise, during times when fish actively feed (Pierce et al. 1981).

Fish were collected using a boat mounted electrofisher and were placed into an aerated holding tank for a maximum of 30 minutes. Fish were then transferred individually to polyethylene lined containers, each of which contained 4-24L of lake water that had been prefiltered using a 1 μm pore size glass fiber filter to remove phytoplankton, which could take up excreted nutrients. A water sample was taken 5 minutes after the addition of fish and then 30 minutes later, with sample bottles immediately placed on ice and kept there until filtration in the lab (typically 2-3 hours). Initial and final water samples were also taken from control containers to which fish had not been added. Upon return to the lab, all samples were filtered through a 1 μm pore size glass fiber filter to remove particulates, and a subsample was preserved to pH<2 using sulfuric acid. Samples were shipped to PPB labs (Gainesville FL) for NH_4-N and PO_4-P analysis using standard EPA methods. Excretion measures were quantified as the difference in NH_4-N and PO_4-P concentrations after 30 minutes, corrected for container volume and converted to hourly rates.

To determine whether there were between-lake differences in N and P excretion rates we analyzed log transformed excretion data using ANCOVA (SPSS 15, General Linear Model), comparing lake as the factor, with log wet mass and temperature as covariates. To estimate the effect on nutrient cycling in each system, we also constructed regression equations for each lake, using multiple regression (SPSS 15) with log mass and temperature as independent variables.

Coefficients for each system could then be compared to published equations for this species in other systems, in order to determine the applicability of these results to other systems.

For lakes where the SJRWMD has recently conducted fish removals (Lakes Apopka, Dora, and Griffin), we sought to predict the effect of fish removals on nutrient cycling, especially the reduction in P excretion caused by the fish removal. To do this, we combined a length-frequency distribution from commercial gill nets sampled for SJRWMD in each lake-year (annual sample sizes were N=300-1400 fish for lake Apopka, N=501-682 for lake Dora, and N=100-650 for Lake Griffin) with a length-mass regression for gizzard shad collected by gill nets and/or electrofishing from each lake (N=132 fish for Apopka, N=719 for Dora and N=323 for Griffin). This enabled us to estimate the wet mass of a fish in each 1cm size group and determine the proportion of harvested biomass from each size grouping. By combining length-frequency and mass data with our estimates of excretion from each system and mean monthly temperatures from each lake (Appendix 1), we could approximate how the biomanipulation in each system impacted phosphorus cycling (reduction in excretion). For dates where we did not have temperature data (i.e., the remainder of 2007) we substituted mean monthly temperatures from years that we had data (Appendix 1).

In addition, because Lake Apopka was fished in 2007 with 3.5-in stretch mesh gill nets, and in other years and in other lakes 4-in mesh nets were used, and because the size distributions harvested varied with gear (Fig. 2-4), we were able to compare the impacts of the two types of net sizes on the amount of nutrient cycling prevented by the fish harvest. We also compared the size distributions of fish caught in different mesh sizes from experimental gill nets set in Lakes Apopka and Griffin during 2007 to examine the degree to which commercial gill nets impact various size classes in these systems.

Results

Overall, gizzard shad N and P excretion showed similar trends to the 2004-2005 data (Chapter 1), with mass strongly influencing N excretion rates and a substantial temperature effect on P excretion (Fig. 2-1, 2-2). The ANCOVA model for N explained much more of the among-fish variability (R^2=0.646) than did the model for P (R^2=0.395). There was a significant effect of lake on N excretion (P=0.037) but not P excretion (P=0.237), with significant overall effects of log wet mass and temperature for both N and P ($P \leq 0.001$ for all comparisons). The N:P ratio (Fig 2-3) showed no significant effect of lake (P=0.306) or log wet mass (P=0.931), but had a significant temperature effect (P=0.001), as was observed for Lake Apopka gizzard shad during 2004-2005 (Chapter 1).

The four lakes differed substantially in their within-lake regression coordinates (Table 2-1) and in the suitability of using this model in each system. Lakes Apopka and Dora had significant overall excretion models for NH_4-N and PO_4-P, whereas only NH_4-N could be predicted from excretion rates in Lake Eustis and only PO_4-P could be predicted for Lake Griffin (Table 2-1). For Lake Dora, the data appeared to be quite consistent with trends observed for Lake Apopka (Chapter 1) and Acton Lake (Schaus et al. 1997). Because we did not obtain a significant overall regression for NH_4-N in Lake Griffin, we restricted our estimations of lakewide nutrient effects to PO_4-P. This focused our lakewide predictions of the effects of fish removals for lakes where we had robust regressions with coefficients or trends similar to other predictions of nutrient excretion by gizzard shad (Schaus et al. 1997, Higgins et al. 2006, Chapter 1). To enhance our predictions of nutrient cycling for Lake Apopka, we combined our measures from this study with those from our previous measures in Lake Apopka (Chapter 1) to increase the sample size to 264 fish and improve the R^2 of that regression (from R^2=0.514 to R^2=0.601, Table 2-1).

Overall, the fish removals ranged from 19.1-121.6 kg gizzard shad per hectare per year, with typical harvests of 30-60 kg/ha/year (Table 2-2). The size distribution of the harvest from Lake Apopka was fairly consistent across years, with most fish 30-37 cm in total length (Fig. 2-4). The only exception to this was in 2007, when the fishermen were allowed to use 3.5-in stretch mesh nets and harvested fish that were typically 27-33 cm. The harvest in Lake Dora removed much larger fish than in other systems (typically 30-40 cm), with a shift toward somewhat smaller sizes during the second year of harvest (Fig. 2-5). However, larger fish excrete less per gram than do smaller fish. Thus, even though the fish removals in Lake Dora were greater per hectare than most other harvests (except the massive harvest of Lake Griffin gizzard shad in 2002 and the Lake Apopka harvest in 2003), the nutrient effect was still equivalent to that of the other lakes (Table 2-2). The harvests from Lake Griffin also showed a marked shift downward in size after the initial harvest (Fig. 2-6), from 34-42 cm during 2002 to 32-38 cm during following years. Differences in nutrient effects of harvest across lake-years are most strongly tied to differences in harvest rate, with some effects of mean fish size, due to the higher excretion per gram of the smaller fish, and more modest effects of minor temperature differences across years.

Experimental gill net samples from Lake Apopka (Fig 2-7) and Lake Griffin (Fig. 2-8) demonstrated that there was a substantial proportion of the gizzard shad population that was invulnerable to the typical 4-in commercial gill net mesh sizes. Smaller mesh sizes successfully harvested smaller fish (Table 2-3). Because smaller fish sizes represent additional harvest and because they have higher mass-specific rates of excretion, it seems prudent to attempt to remove this segment of the population as well. However, overall catch rates from smaller mesh sizes were much lower in biomass caught per unit of time, as compared to larger mesh sizes (Table 2-3). If these trends are consistent in the much larger commercial nets, increases in the amount of nutrient release prevented by harvesting smaller fish would be strongly offset by a marked reduction in overall harvest. However, it may be possible to have commercial fishers use nets of differing mesh size, and thus target different size classes of fish either simultaneously or sequentially.

Table 2-1 – Results of multiple regression analysis for each of the UORB lakes, in order to predict gizzard shad NH_4-N and PO_4-P excretion rates and N:P in each system, based on Log wet mass (g), and Temperature (°C). The Apopka All Fish model includes not only fish from this study, but also those from Chapter 1.

	N	Overall Model P-Value	Overall Model R^2	Coefficient	95% Lower Confidence Interval	95% Upper Confidence Interval	Coefficient's P-Value
Apopka (March 2005 and 2006)							
Log NH_4-N	58	<0.001	0.309				
Intercept				-0.650	-1.366	0.066	0.074
Log Wet Mass				0.514	0.265	0.764	<0.001
Temperature				-0.002	-0.011	0.008	0.735
Log PO_4-P	58	<0.001	0.514				
Intercept				-4.895	-6.361	-3.429	<0.001
Log Wet Mass				1.295	0.785	1.805	<0.001
Temperature				0.072	0.052	0.091	<0.001
N:P by Mass	58	0.002	0.202				
Intercept				169.552	61.634	277.469	0.003
Log Wet Mass				-41.544	-79.113	-3.974	0.031
Temperature				-2.620	-4.038	-1.202	0.000
Dora (March 2005 and 2006)							
Log NH_4-N	46	<0.001	0.910				
Intercept				-1.613	-1.832	-1.394	<0.001
Log Wet Mass				0.786	0.708	0.864	<0.001
Temperature				0.016	0.010	0.023	<0.001
Log PO_4-P	46	<0.001	0.470				
Intercept				-1.960	-2.515	-1.405	<0.001
Log Wet Mass				0.574	0.376	0.772	<0.001
Temperature				0.016	0.001	0.032	0.041
N:P by Mass	46	0.246	0.063				
Intercept				-0.247	-32.321	31.826	0.988
Log Wet Mass				8.610	-2.823	20.042	0.136
Temperature				-0.330	-1.234	0.574	0.466
Eustis (2006)							
Log NH_4-N	38	<0.001	0.506				
Intercept				-0.817	-1.904	0.270	0.136
Log Wet Mass				0.572	0.285	0.860	<0.001
Temperature				-0.001	-0.022	0.020	0.921
Log PO_4-P	38	0.170	0.096				
Intercept				-1.451	-3.028	0.125	0.070
Log Wet Mass				0.393	-0.024	0.810	0.064
Temperature				0.018	-0.013	0.049	0.236
N:P by Mass	38	0.008	0.240				
Intercept				1.931	-21.347	25.210	0.867
Log Wet Mass				3.999	-2.159	10.157	0.196
Temperature				-0.257	-0.715	0.201	0.263

Table 2-1 Continued

	N	Overall Model P-Value	Overall Model R^2	Coefficient	95% Lower Confidence Interval	95% Upper Confidence Interval	Coefficient's P-Value
Griffin (2006)							
Log NH_4-N	26	0.298	0.100				
Intercept				-0.263	-1.405	0.879	0.639
Log Wet Mass				0.317	-0.094	0.729	0.124
Temperature				0.005	-0.012	0.021	0.568
Log PO_4-P	26	0.002	0.411				
Intercept				-2.919	-4.519	-1.319	0.001
Log Wet Mass				0.759	0.183	1.335	0.012
Temperature				0.042	0.018	0.065	0.001
N:P by Mass	26	0.095	0.185				
Intercept				95.650	-11.984	203.284	0.079
Log Wet Mass				-18.308	-57.068	20.452	0.339
Temperature				-1.734	-3.313	-0.156	0.033
Apopka – All Fish (2004-2006)							
Log NH_4-N	264	<0.001	0.722				
Intercept				-1.165	-1.336	-0.995	<0.001
Log Wet Mass				.655	0.604	0.705	<0.001
Temperature				0.007	0.003	0.011	0.001
Log PO_4-P	264	<0.001	0.601				
Intercept				-3.062	-3.339	-2.786	<0.001
Log Wet Mass				0.670	0.588	0.753	<0.001
Temperature				0.053	0.046	0.059	<0.001
N:P by Mass	264	<0.001	0.233				
Intercept				46.555	33.331	59.780	<0.001
Log Wet Mass				-1.391	-5.315	2.533	0.486
Temperature				-1.342	-1.648	-1.035	<0.001

Table 2-2 Impacts on the P cycle of the gizzard shad harvests during 2002-2007 in Lakes Apopka and Griffin and during 2005 and 2006 in Lakes Dora and Beauclair. Direct removal refers to the removal of P contained in fish tissues. The total P effect is the sum of direct P removal and P excretion prevented. All data are expressed as both a whole lake effect (kg/yr) and also a per hectare effect (kg/ha/yr), to provide whole lake information and also effectively compare lakes of different sizes.

	Gizzard Shad Harvest (kg)		Direct P Removal (kg)		P Excretion Prevented (kg)		Total P Effect (kg)	
Year	(kg/yr)	(kg/ha/yr)	(kg/yr)	(kg/ha/yr)	(kg/yr)	(kg/ha/yr)	(kg/yr)	(kg/ha/yr)
				Apopka				
2002	238,227	19.1	1,667	0.13	3,590	0.29	5,257	0.42
2003	700,404	56.2	4,903	0.39	12,974	1.04	17,877	1.43
2004	562,187	45.1	3,935	0.32	9,640	0.77	13,575	1.09
2005	476,775	38.2	3,338	0.27	8,109	0.65	11,447	0.92
2006	558,291	44.8	3,908	0.31	9,760	0.78	13,669	1.10
2007	401,202	32.2	2,808	0.23	7,359	0.59	10,167	0.82
				Dora/Beauclair				
2005	124,877	53.8	874	0.38	1,532	0.66	2,406	1.04
2006	135,083	58.2	946	0.41	1,895	0.82	2,841	1.22
				Griffin				
2002	462,665	121.6	3,239	0.85	8,935	2.35	12,174	3.20
2003	102,816	27.0	720	0.19	2,172	0.57	2,892	0.76
2004	176,137	46.3	1,233	0.32	3,605	0.95	4,838	1.27
2005	112,953	29.7	791	0.21	2,259	0.59	3,049	0.80
2006	147,340	38.7	1,031	0.27	3,243	0.85	4,274	1.12
2007	114,960	30.2	805	0.21	2,402	0.63	3,207	0.84

Table 2-3 Comparison of catches from the 2007 experimental gill net sampling from Lakes Apopka and Griffin. The % of biomass <28cm value refers to the proportion of the catch that is of a size class that typically weighs <210g and is too small to be harvested by 4-in stretch mesh commercial gill nets.

Stretched Mesh Size (inches)	Number of Fish Sampled	Mean TL (mm)	Total mass (kg)	Mean WM (g)	% of Biomass <28cm
			Apopka		
2.5	101	219	10.80	106.9	79.4%
3	55	278	12.77	232.2	28.3%
3.5	123	335	49.57	403.0	0.6%
4	117	348	53.54	457.6	0.0%
4.5	136	360	69.17	508.6	0.0%
5	50	376	30.10	602.0	0.0%
			Griffin		
2.5	41	260	6.72	164.0	59.6%
3	119	283	26.17	219.9	31.3%
3.5	141	306	40.74	289.0	6.4%
4	62	327	22.66	365.5	0.5%
4.5	32	347	14.13	441.4	0.0%
5	7	388	4.34	620.1	0.0%

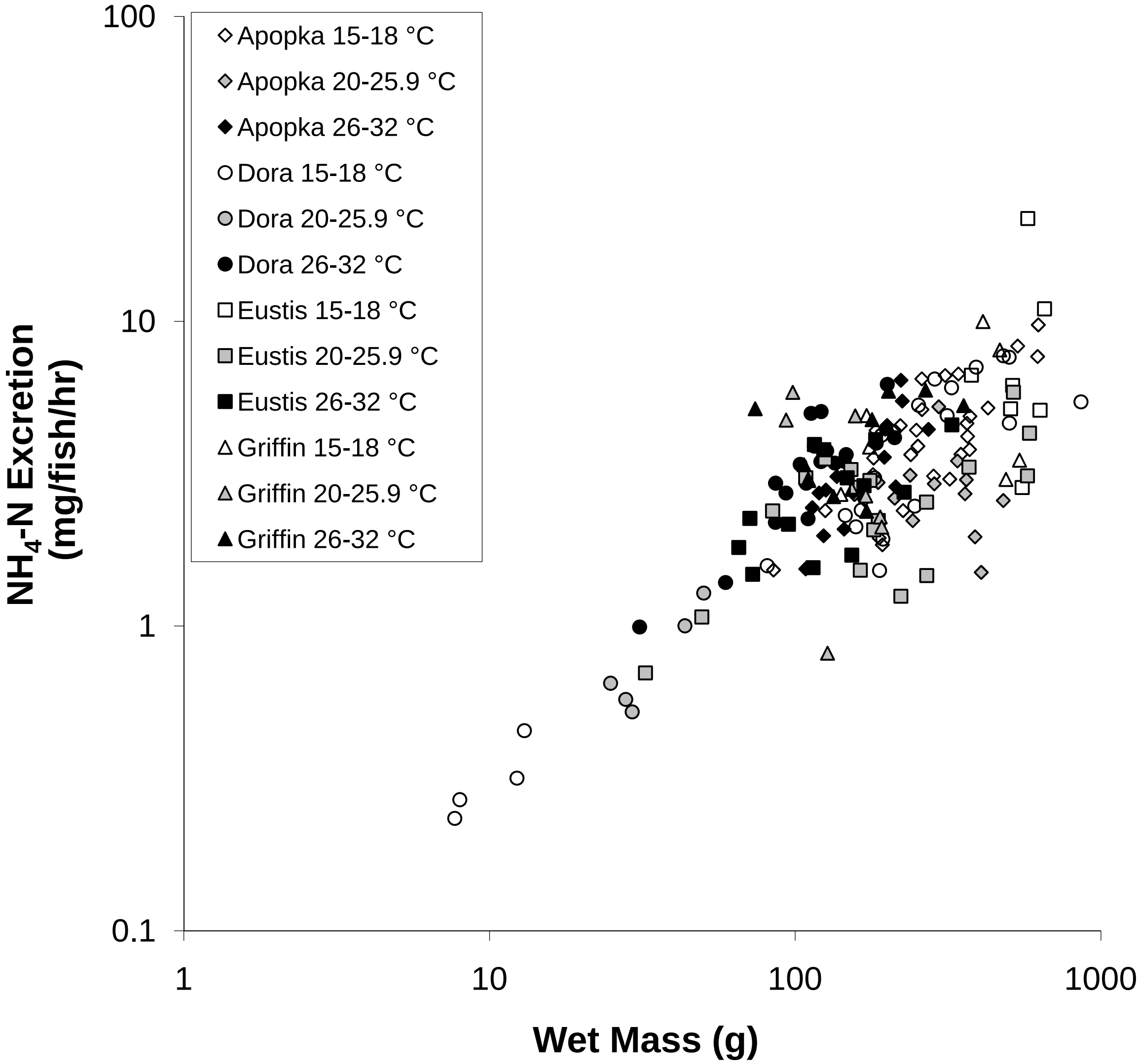

Fig 2-1 Excretion of NH_4-N by gizzard shad from Lakes Apopka (diamond), Dora (circle), Eustis (square) and Griffin (triangle). For all lakes, measurements are grouped by water temperature into 15-18 °C (white), 20-25.9 °C (gray), and 26-32 °C (black) groupings. ANCOVA results indicated significant differences among lakes (P=0.037), and significant effects of log wet mass (P<0.001) and temperature (P=0.001).

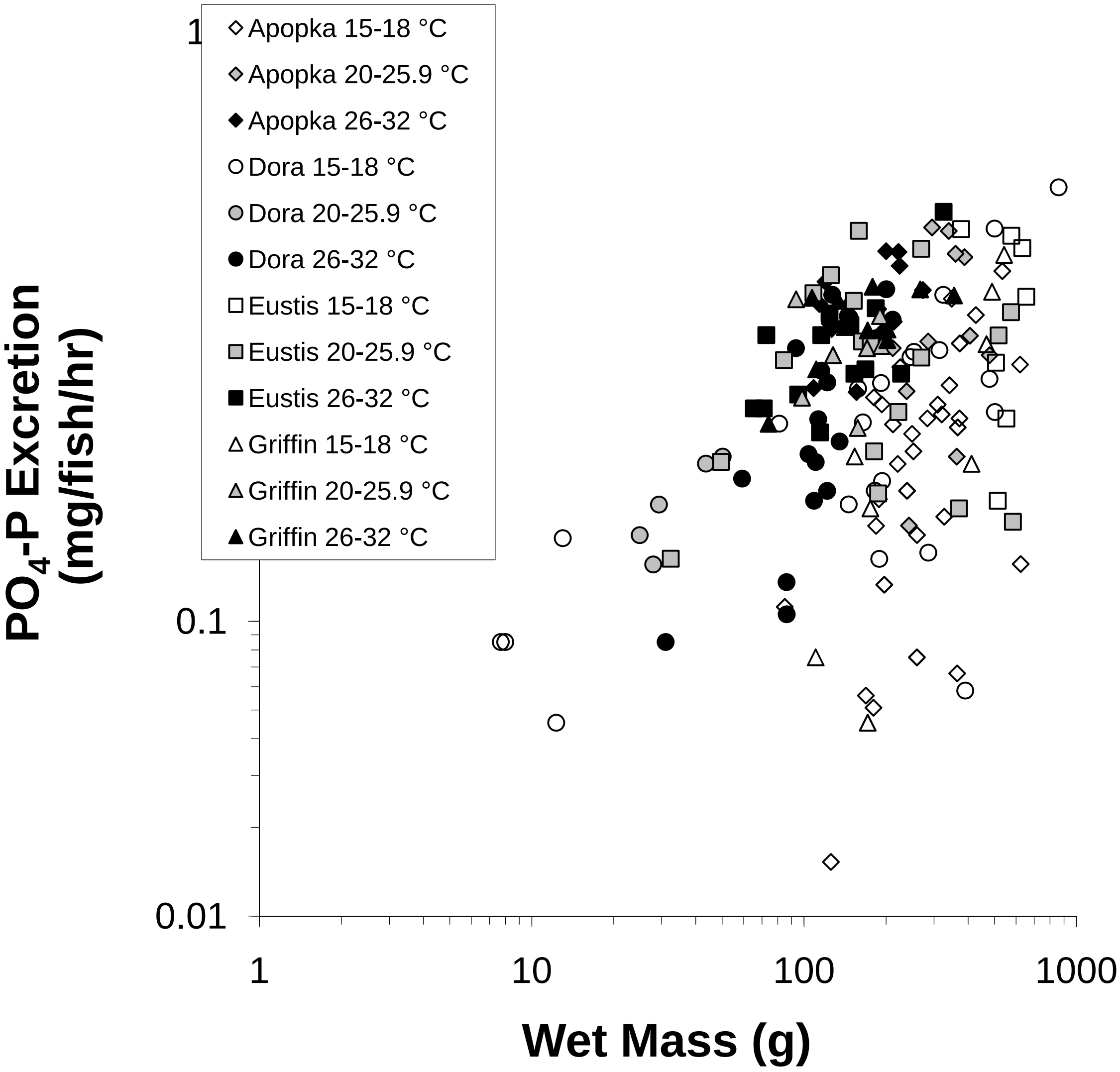

Fig 2-2 Excretion of PO_4-P by gizzard shad from Lakes Apopka (diamond), Dora (circle), Eustis (square) and Griffin (triangle). For all lakes, measurements are grouped by water temperature into 15-18 °C (white), 20-25.9 °C (gray), and 26-32 °C (black) groupings. ANCOVA results indicated no significant differences among lakes (P=0.237), with significant effects of log wet mass (P<0.001) and temperature (P<0.001).

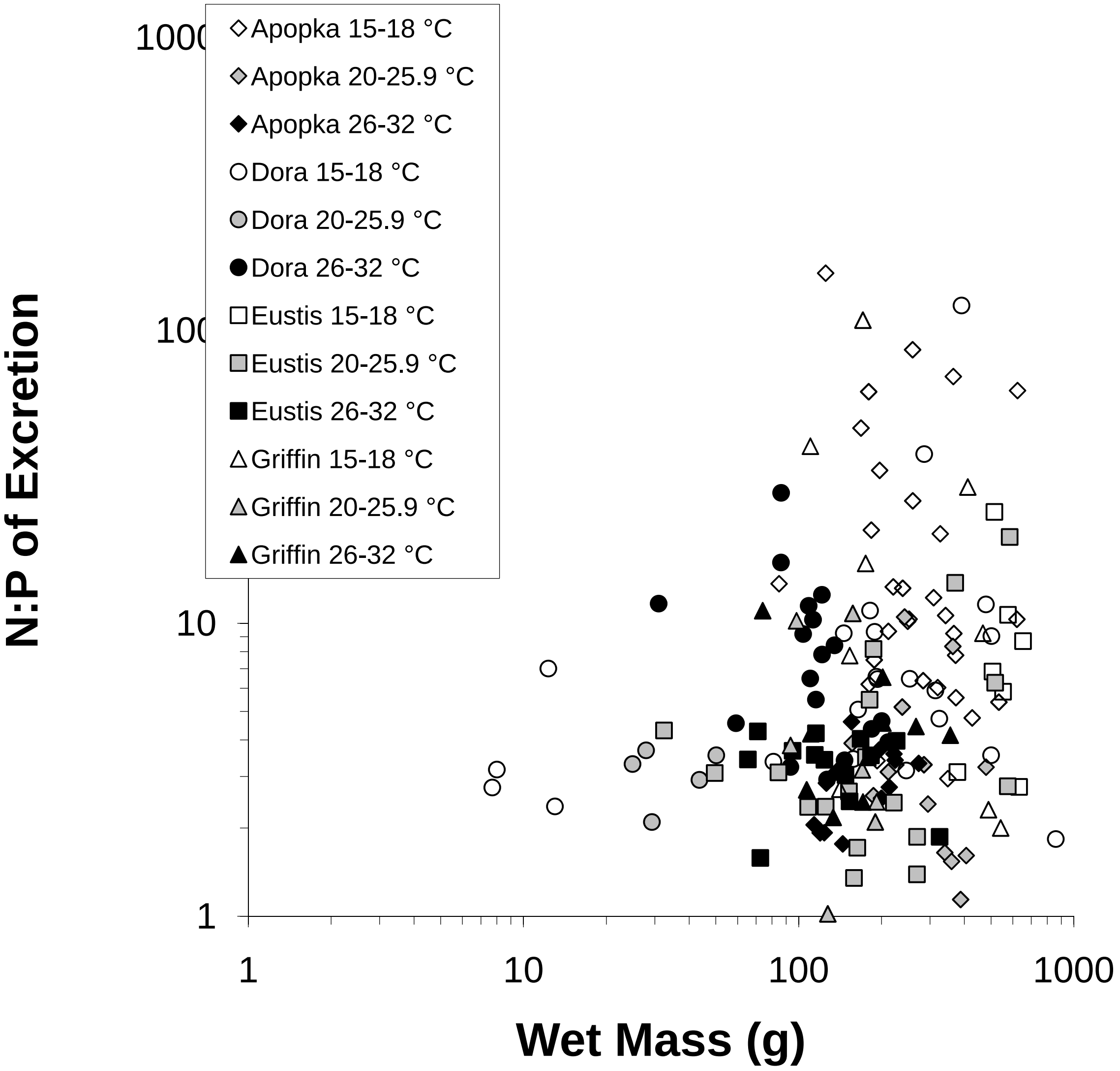

Fig 2-3 N:P ratio of excretion by gizzard shad from Lakes Apopka (diamond), Dora (circle), Eustis (square) and Griffin (triangle). For all lakes, measurements are grouped by water temperature into 15-18 °C (white), 20-25.9 °C (gray), and 26-32 °C (black) groupings. ANCOVA results indicated no significant effects of lake (P=0.306) or log wet mass (P=0.931), but there was a significant temperature effect (P=0.001).

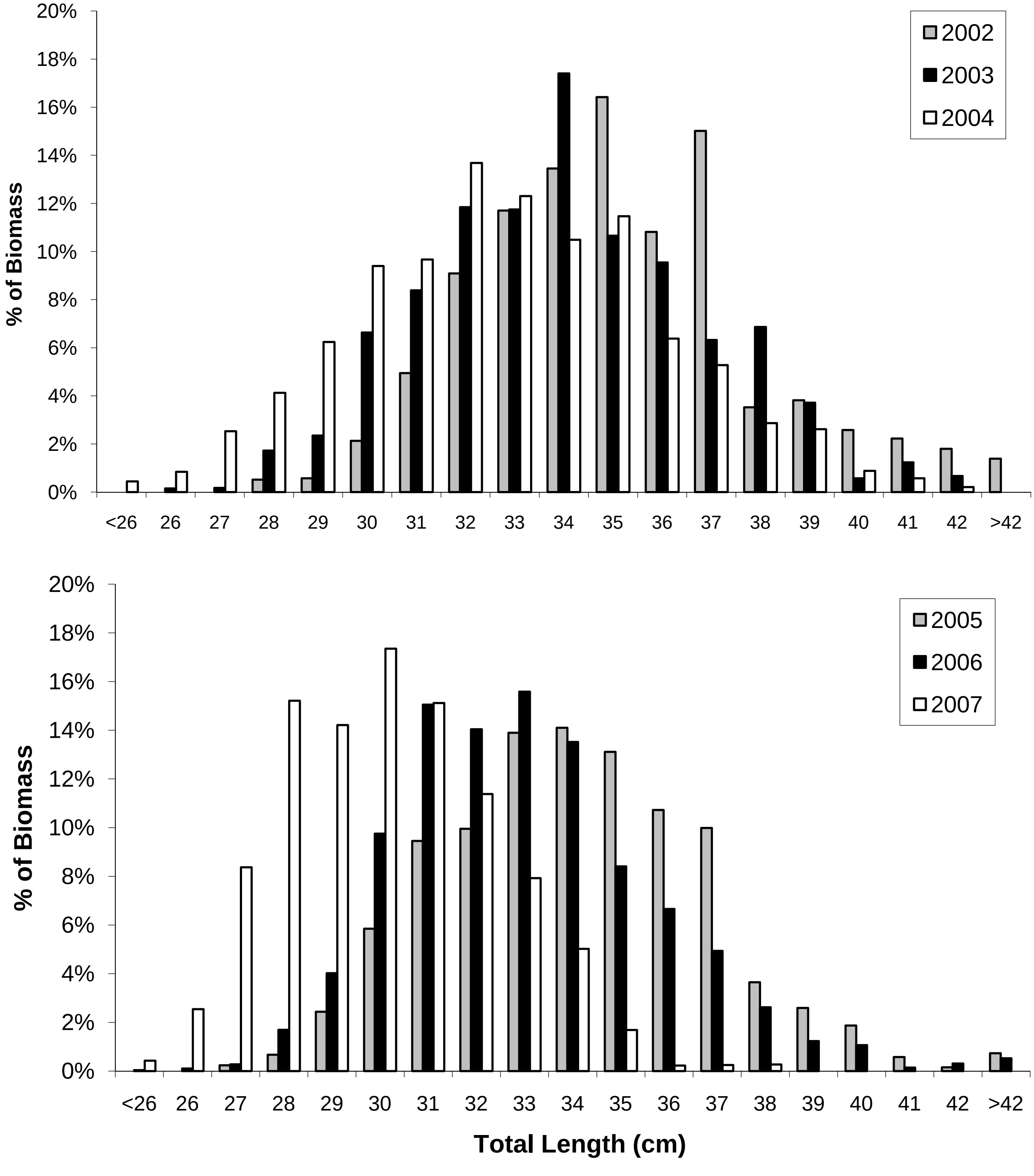

Fig 2-4 Length frequency distributions for samples of gizzard shad harvested from Lake Apopka during 2002-2004 (Top Panel) and 2005-2007 (bottom panel) using commercial gill nets. Data were collected by an observer from selected commercial gill nets.

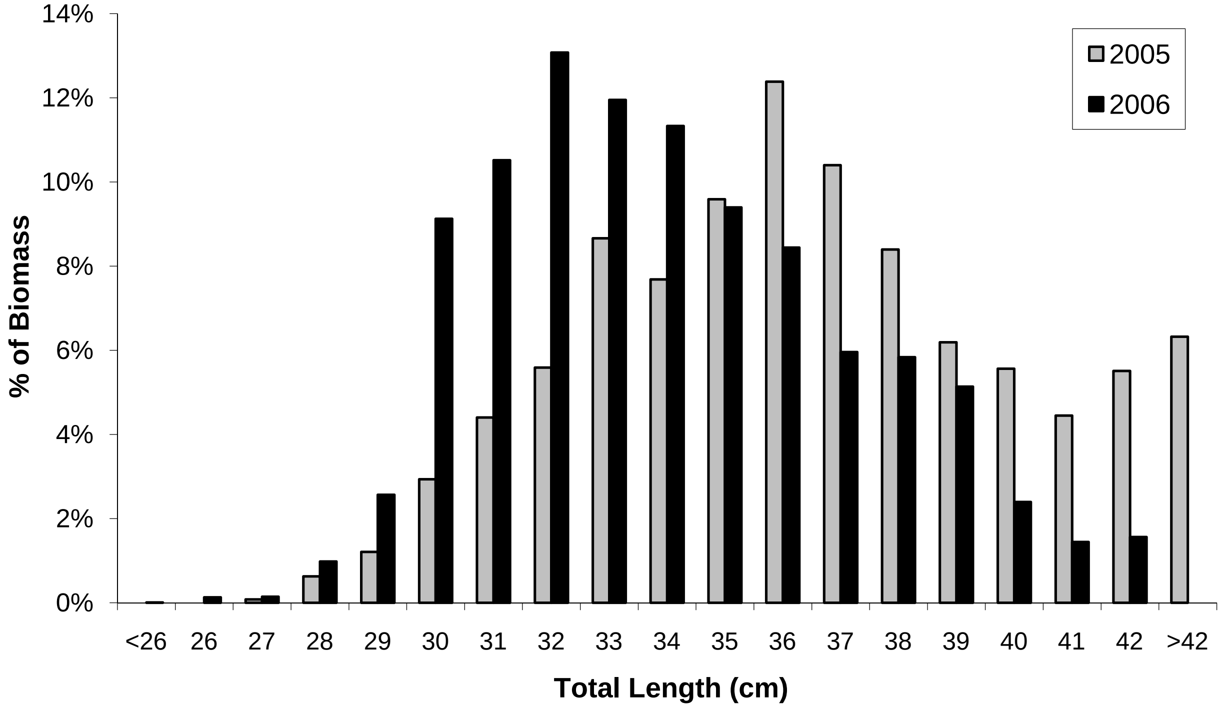

Fig 2-5 Length frequency distributions for samples of gizzard shad harvested from Lakes Dora and Beauclair during 2005 and 2006 using commercial gill nets. Data were collected by an observer from selected commercial gill nets.

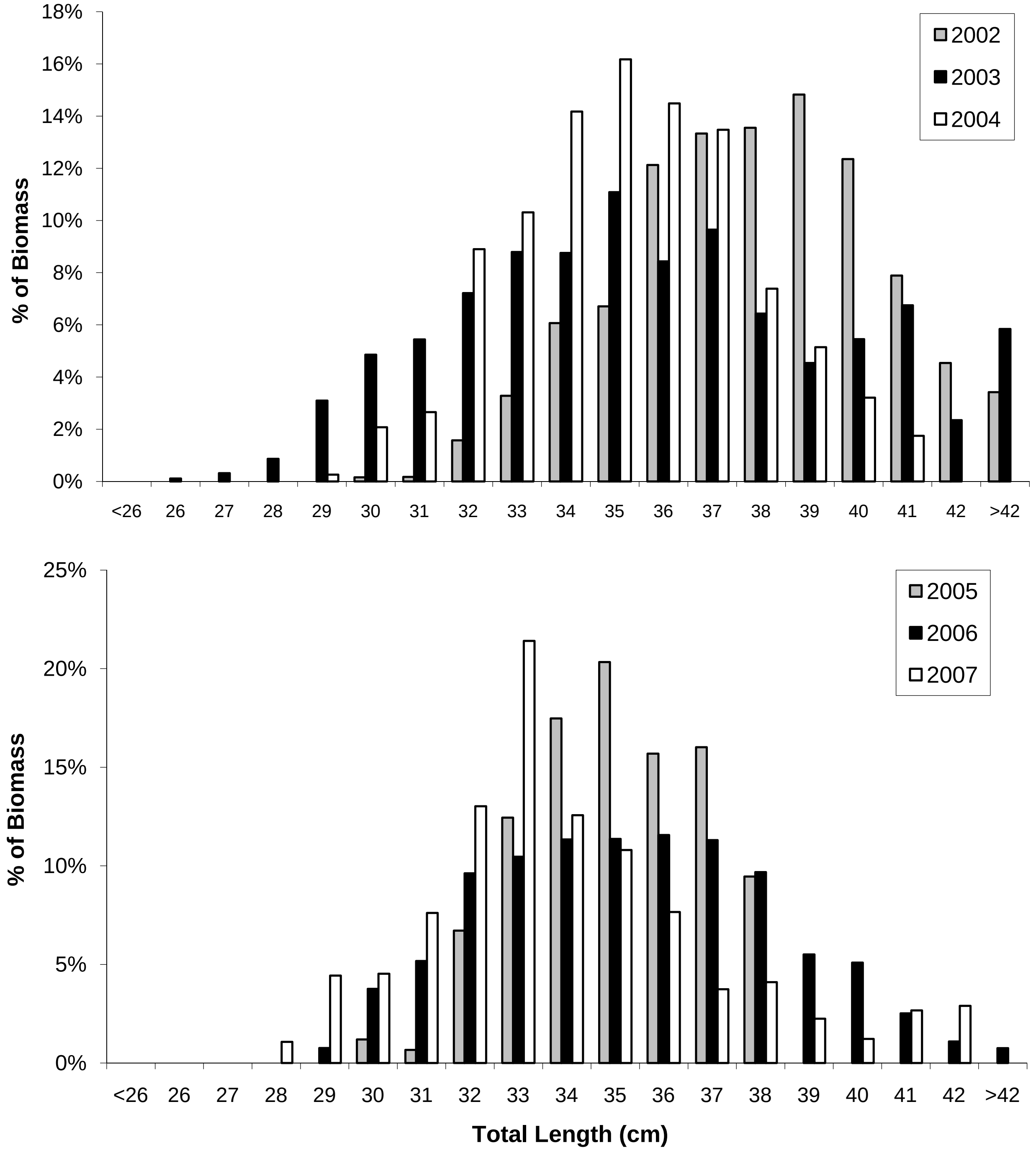

Fig. 2-6 Length frequency distributions for samples of gizzard shad harvested from Lake Griffin during 2002-2004 (Top Panel) and 2005-2007 (bottom panel) using commercial gill nets. Data were collected by an observer from selected commercial gill nets.

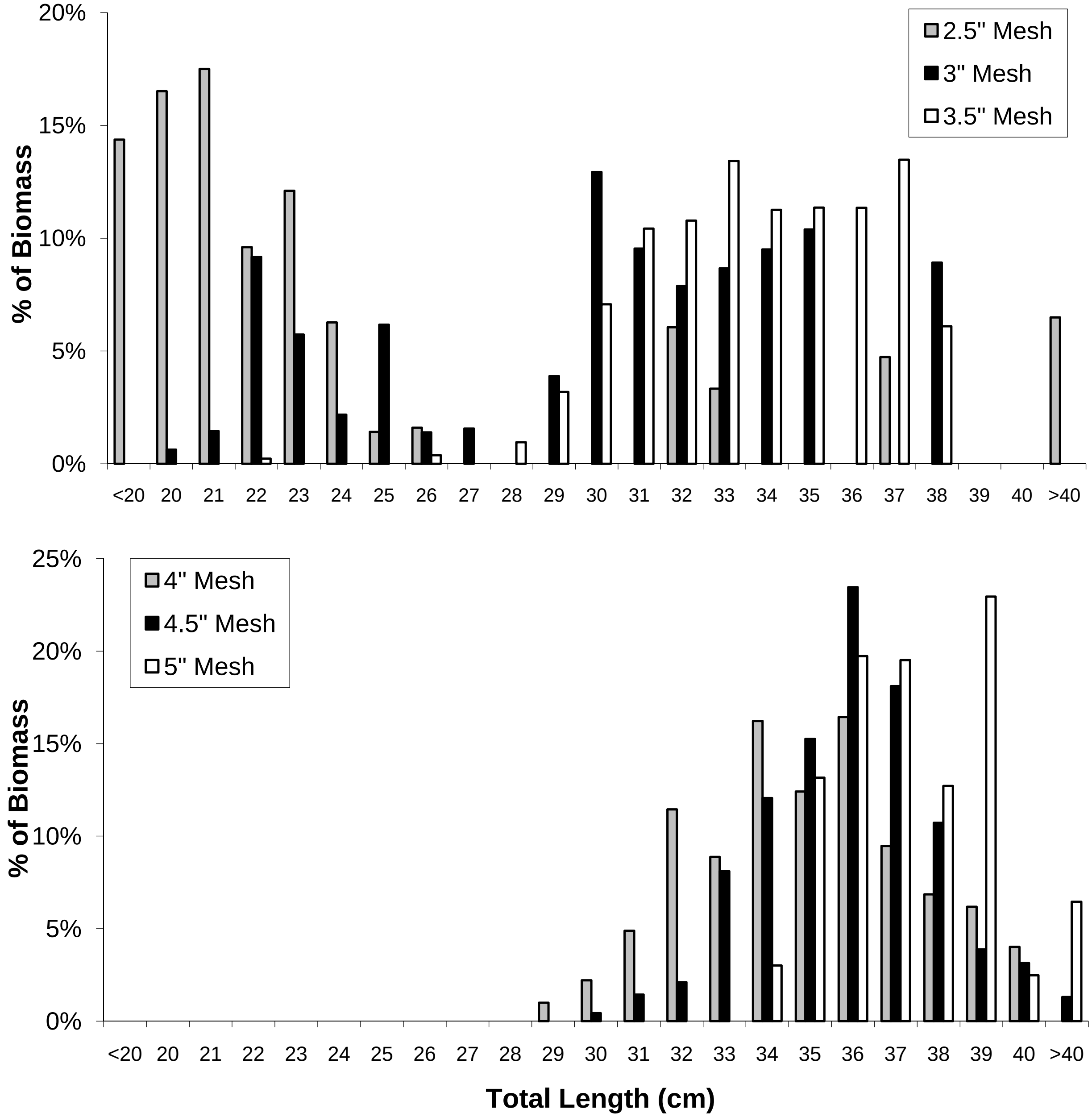

Fig. 2-7 Length frequency distributions from SJRWMD 2007 Lake Apopka experimental gill net panels with mesh sizes of 2.5-3.5-in stretch mesh (top panel) and 4-5-in stretch mesh (bottom panel). Each mesh size sampled 50-136 fish. All data are expressed as % of the total biomass collected in that mesh size, to facilitate comparisons.

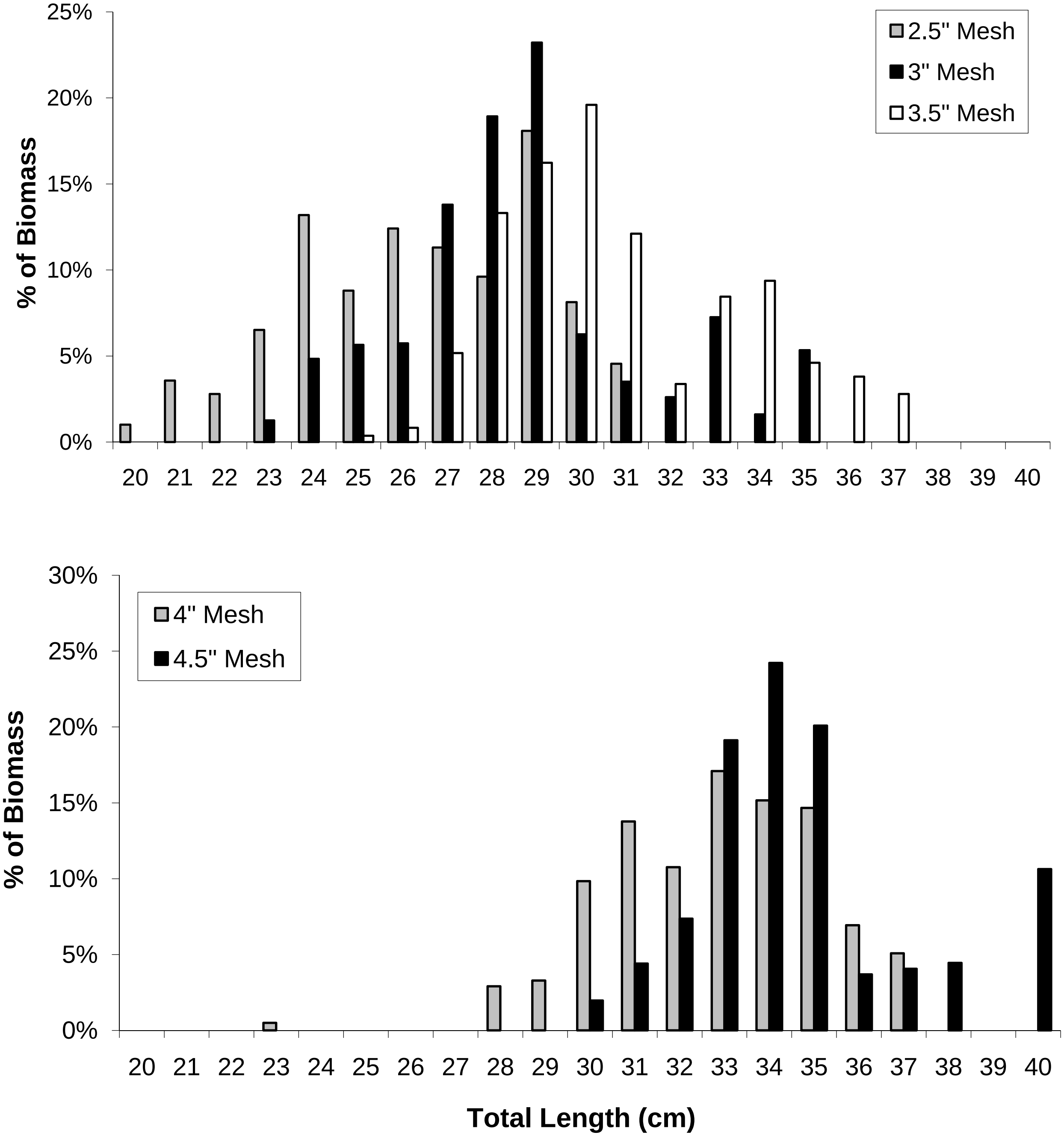

Fig. 2-8 Length frequency distributions from SJRWMD 2007 Lake Griffin experimental gill net panels with mesh sizes of 2.5-3.5-in stretch mesh (top panel) and 4-4.5-in stretch mesh (bottom panel). 5-in stretch mesh panels are not included because this mesh size only caught 7 fish (all >35cm), whereas all other size panels sampled 32-142 fish. All data are expressed as % of the total biomass collected in that mesh size, to facilitate comparisons of mesh sizes.

Discussion

It is clear that nutrient impacts of biomanipulation can vary substantially across systems and with differences in gear. The potential benefits to lake nutrient cycles can be influenced greatly by many factors, including well established metabolic effects of temperature and body size (i.e., Schmidt-Nielsen 1975, Hall et al. 2007) and also effects of diet, growth rate, fecundity, and the proportion of the population removed by the manipulation. Predictions of the potential benefits to nutrient dynamics within a particular system will depend on an understanding of these factors and how they may impact the population over the short term and in the long term.

Our length-frequency data strongly suggest that it is advisable to select mesh sizes that are effective overall in terms of harvesting fish, but allow the removal of smaller size classes, as these fish have higher mass-specific rates of excretion (Schaus et al. 1997). Two clear cases of this are the 2006 harvest from Lake Dora and the 2007 harvest from Lake Apopka. In Lake Dora, the second year of harvest removed only 8% more fish (53.8 kg/ha in 2005 vs. 58.2 kg/ha in 2006), but the amount of P excretion prevented by the second harvest was 24% higher (Table 2-2). This occurred with only a modest shift in size structure (from 32-42 cm TL in 2005 to 30-39 cm TL in 2006, Fig. 2-5). Likewise, the 2007 Lake Apopka gizzard shad harvest removed smaller fish sizes (Fig. 2-4). Even though the overall harvest was lower in 2007, it followed several years of intense fish removal, so it is difficult to predict how mesh size would affect overall harvest. Our limited experimental gill net data from 2007 indicate that the amount of biomass caught by 3.5-in nets was similar to that caught by 4-in mesh nets (Table 2-3). Based on the length-frequency distributions observed in 2006, if we assume that these two mesh sizes remove a similar overall fish biomass that differs somewhat in size, then the overall nutrient release prevented by the 3.5-in net harvest was 9.8% higher than the same biomass harvested by

4-in nets. By increasing the vulnerability of small gizzard shad, it may be possible to increase the overall fish harvest and increase the nutrient effect per kg of fish removed. Ideally, biomanipulations seek to reduce all size classes of gizzard shad, because many populations are dominated numerically by small size classes that can avoid capture by commercial gill nets.

We typically observed a stronger effect of temperature on P excretion (Lake Dora being the exception to this trend), as compared to N excretion, as indicated by larger temperature coefficients for P than for N (Table 2-1). This can greatly impact the N:P ratio of nutrient excretion by fish, with lower N:P ratios typically observed during warmer seasons (Schaus et al. 1997, this study, Chapter 1). Low N:P supply ratios have generally been observed to promote dominance by cyanobacteria (Smith 1983, but see Xie et al. 2003). Thus, the nutrient based impact of this species may be at least partially responsible for the observed blooms of *Microcystis* in Lake Apopka, especially during midsummer. Overall, we would predict that nutrient based effects of this species (high P excretion and a low N:P) should be greater at warmer latitudes and during warmer seasons. However, Jeppesen et al. (2007) predicted that biomanipulations may be less effective at warmer latitudes because of the longer growing season and factors such as increased omnivory and increased risk of algal blooms, which may offset the gains made by fish reductions. Interestingly, several of the factors which may confound biomanipulation efforts in warmer systems (high omnivory, longer growing season) are also linked to the importance of this species in the nutrient cycles of southern lakes and reservoirs. Clearly, more research on biomanipulation efforts in tropical and subtropical systems is needed (Jeppesen et al. 2007).

Others have observed that nutrient excretion by gizzard shad can vary with the nutrient content of food, with higher rates of nutrient excretion in systems with higher nutrient contents of food sources (Higgins et al. 2006). Gizzard shad can feed selectively on high N detrital foods (Mundahl and Wissing 1987, Higgins et al. 2006), most likely by some type of physical sorting that removes the higher density particles (sand, etc.) from the less dense particles that are more enriched in organic material (Smoot 1999). As omnivores, shad can also ingest zooplankton when it becomes available (Yako et al. 1996), but the importance of this food source can vary substantially among systems and over time (Gu et al. 1996, Thorpe et al. 1998, Schaus et al. 2002). Likewise, in Florida lakes, size can have a substantial impact on planktivory by this species (Gu et al. 1996, Catalano et al. 2007), with high zooplanktivory by very small (<100mm TL) and very large gizzard (>300mm TL) shad and increased nutritional importance of detritivory for fish of medium size (100-300 mm TL). Differences in diet are likely important to excretion, as stoichiometry theory predicts that with all else being equal, excretion rates should increase with food nutrient content (Sterner 1990, Vanni et al. 2002).

Overall, the effectiveness of the biomanipulation effort will depend on the proportion of the population biomass removed and the extent to which the population remains depressed over time. Several reviews of European biomanipulations indicate that removing 80% of the fish biomass (planktivores, omnivores or benthivores) increases the likelihood of success for the fish removal project (Hansson et al. 1998, Meijer et al. 1999, Søndergaard et al. 2000, Jeppeson et al. 2007). Thus, some authors have recommended that biomanipulation will be most effective in smaller lakes where there is an increased likelihood of removing 80% of the fish biomass (Meijer et el. 1999, Jeppesen et al. 2007). Long term success can be affected by the capacity of the population to recover from decreases in biomass, and gizzard shad have mechanisms such as increased growth rate (Schaus et al. 2002) and decreased age at maturity (Schaus et al. 2002, Catalano et al. 2007) that could promote population recovery within several years.

However, it has also been well documented that this species only tends to dominate in highly eutrophic systems (Bachmann et al. 1996, DiCenzo et al. 1996, Allen et al. 2000). The multiple stable states hypothesis (Scheffer et al. 1993, Scheffer 1998) predicts that a substantial reduction in external nutrient loading coupled with biomanipulation could shift the system to a clearwater state dominated by macrophytes, which resists the change toward phytoplankton dominance and cyanobacterial blooms. Gizzard shad have been found to be less abundant in lakes with lower water column chlorophyll and/or with abundant macrophytes (Allen et al. 2000, Michaletz and Bonneau 2005). If the system can be shifted to a clear water system dominated by macrophytes, it is possible that the reduced productivity of the system could counteract the tendency of this species to proliferate, potentially maintaining the system as a macrophyte dominated shallow lake system similar to what was historically documented in Lake Apopka (Schelske et al. 2005). At the least, a substantial fish reduction could increase the time interval between large scale fish removal projects. Decisions about whether or not to utilize biomanipulation efforts should consider not only the duration, cost and the likelihood of bycatch, but also the likelihood of achieving the objectives of an 80% fish reduction and a shift to a stable, clearwater state dominated by macrophytes.

Chapter 3 – Impact of Gizzard Shad on Lake Nutrient Dynamics via Excretion and Bioturbation in Tank Microcosms

Introduction

Fish have many important effects on the structure and functioning of aquatic ecosystems. These effects can occur via direct means, such as consumptive interactions, or through indirect means, such as the changes that occur in subsequent trophic levels via the trophic cascade. Many experimental studies have examined the effects of shifts in fish biomass and/or community composition on zooplankton and phytoplankton abundance (i.e., Hrbáček et al. 1961, Hurlbert et al. 1972, Carpenter et al. 1987, Vanni et al. 1990, Persson 1997a). Results from these types of studies have provided direct support that reductions in planktivorous and omnivorous fishes can reduce phytoplankton biomass. As a result, many lake managers have utilized this approach in combination with reductions in external nutrient loading as a means to improve water quality (i.e., Hansson et al. 1998, Meijer et al. 1999; Søndergaard et al. 2000).

The removal of planktivorous fish can potentially increase the abundance of large zooplankton and reduce nutrient recycling by planktivores (Vanni et al. 1997, Vanni and Layne 1997). Reductions in omnivorous fish that feed on benthic organisms and/or detritus can also improve water quality by reducing the nutrients transported from benthic to pelagic habitats via excretion and/or bioturbation (Vanni 2002). In the same way that lake managers seek to reduce external nutrient inputs (i.e., Vollenweider 1976, Coveney et al. 2005), the removal of benthivores can reduce internal “loading” of nutrients (Dugdale and Goering 1967, Shapiro and Carlson 1982, Caraco et al. 1992). Indeed, many of the successful biomanipulation efforts have utilized the removal of omnivorous or benthivorous fishes (Hansson et al. 1998, Meijer et al. 1999, Søndergaard et al. 2000, Jeppesen et al. 2007). Likewise, the effect of these species has been shown to be stronger in more productive systems (Drenner et al. 1996, 1998, Vanni et al. 2006). Thus if omnivore removal can shift the system toward a clear water state (Scheffer et al. 1993, Scheffer 1998), it is possible to favor the dominance of other species.

To better understand nutrient based effects of benthic feeding fishes, some investigators have sought to measure the amount of nutrient excretion by these species (Lamarra, 1975, Brabrand et al. 1990, Persson 1997, Schaus et al. 1997, Gido 2002). Studies have generally found that these species can be important sources of nutrients. However, few studies have explicitly examined the effects of bioturbation by benthic feeding fishes as an important mechanism for nutrient transport from the sediments to the water column (Haertel-Borer et al. 2004), even though many investigators have indicated that this mechanism is potentially important to phytoplankton and water quality (i.e., Havens 1991, Drenner and Hambright 1999, Vanni 2002).

Although other investigators have sought to examine the effect that fish-induced bioturbation can have on phytoplankton and nutrient dynamics (Lamarra 1975, Havens 1991, 1993, Drenner et al. 1998, Schaus and Vanni 2002), these have generally not experimentally separated the mechanisms of excretion and bioturbation (Threlkeld 1994). Lamarra (1975) used a paddle to stir limnocorrals once per week in an attempt to simulate bioturbation. Haertel-Borer et al. (2004) used short term (6 hr) experiments with filtered salt marsh water and manipulated sediment access to separate the effects of nutrient excretion by fishes and shrimps from the bioturbation effects of these species. We used an approach similar to that of Haertel-Borer et al. (2004) to quantify the effects of excretion and bioturbation by gizzard shad, an omnivorous fish that is abundant in eutrophic systems in the midwestern and southern U.S. (Bachmann et al. 1996). We hypothesized that gizzard shad would substantially impact water column nutrients, turbidity, suspended solids, and phytoplankton (measured as Chl *a*) only when it could feed directly on sediments. We hypothesized that smaller fish would have a greater impact than an equivalent biomass of large gizzard shad. We also hypothesized that the effect on water column nutrients would be a combination of excretion based effects and those of bioturbation.

Methods

We conducted four mechanistic tank experiments during 2006 and 2007 which sought to separate the effects of nutrient excretion from that of bioturbation. Although this type of experiment does not perfectly duplicate conditions found in ecosystems (Carpenter 1996), the ability to manipulate variables of interest and conduct well replicated trials allows insight into the mechanisms important in ecosystems (Drenner and Mazumder 1999). The 2006 experiments utilized lake sediments and a natural assemblage of phytoplankton and zooplankton. The experiments manipulated fish density and sediment access, using nets suspended above the surface of the sediments (Havens 1991, 1993; Schaus and Vanni 2002). The first of the 2006 experiments also had some tanks where the sediments were manually disturbed two times per day using an oar (Lamarra 1975), in order to roughly simulate biomanipulation of sediments without excretion. The 2007 experiments repeated this general approach (manipulating fish density and sediment access), except that they contained well water instead of a natural phytoplankton assemblage, in order to simulate Haertel-Borer's (2004) approach of measuring changes where phytoplankton could not take up nutrients that had been released via excretion and/or bioturbation. By comparing trends across experiments and estimating the proportion of the change that could be accounted for via fish excretion (Chapters 1 and 2), we sought to separate the effects of excretion and bioturbation and evaluate the relative importance of each mechanism.

All experiments were conducted in 440 gallon (1670L; 1.54 m diameter x 1 m depth) blue polyethylene tanks (Aquatic Eco-Systems, Apopka FL) held on the SJRWMD restoration area on the north end of Lake Apopka. The March 2006 experiment was conducted in a sunny location, whereas the other three experiments (May 2006, March 2007 and May 2007) were conducted under extensive shade of trees or a tarp, in order to prevent large daily temperature fluctuations during the warmer months. Each tank was filled with 4-6cm of surface sediments collected from the north end of Lake Apopka, using an Eckman dredge (March 2006) or a Ponar dredge (May 2006, March 2007 and May 2007). A plastic tarp was positioned over the surface of the sediments, so that the addition of water would minimize sediment disturbance. During 2006, tanks were filled by pumping a natural assemblage of phytoplankton from the Apopka-Beauclair Canal (March 2006) or a nearby canal that fed into the Apopka-Beauclair Canal (May 2006), both of which contained natural assemblages of zooplankton and phytoplankton. In 2007, tanks were filled using well water from the restoration site. Investigations prior to our 2007 experiments indicated that gizzard shad could thrive in this water, as ionically it was quite similar to surface waters, with concentrations of all ions similar to those of surface waters, except for higher concentrations of zinc (SJRWMD, unpublished data). After filling the tank with either canal or well water, the tarp was slowly pulled out of the tank. Typically, any tanks that had slightly elevated turbidity, due to sediment disturbance caused by tarp removal, returned to low turbidity levels within one day.

In all experiments, water samples were collected using a swing arm water sampler (Forestry Suppliers, Inc.) rinsed with water from that tank prior to collecting the water sample or a grab sample. In all cases, the sample bottle was immersed below the surface and was allowed to fill as the sampler was depressed to approximately ½ the depth of each tank, thus collecting an integrated sample of the top ½ of the water column. The collected water was used to fill three 250mL polyethylene sample bottles for nutrient analyses. Water was sampled every 2-3 days during 2006 and every day during 2007, with initial samples taken prior to the introduction of fish. A portion of the water samples collected for nutrients was retained unfiltered for total nutrient analyses. The remainder was filtered through a 1µm pore size glass fiber filter to remove particulates. The unfiltered sample and one of the two filtered samples from each tank were preserved to pH <2 using sulfuric acid. All samples were placed on ice and were shipped overnight to PPB/Advanced Analytical labs in Gainesville, FL, where they were analyzed for relevant nutrient fractions, which were total N (TN) and total P (TP), total dissolved N and P (TDN and TDP, respectively), PO_4-P, NH_4-N, and NO_x) using standard EPA methods. Particulate N and P were estimated by the difference between total N and P and total dissolved N and P, respectively.

Turbidity measurements were collected in the same way, and were analyzed using a nephelometric turbidity meter to the nearest 0.1 NTU. During the May 2006 experiment, turbidity was measured on additional dates to ensure a reading every 1-2 days. Chlorophyll and suspended solids samples were collected in a similar manner to that of nutrient samples, and an appropriate volume of water (typically 100-500mL, depending on algal concentrations) was filtered onto a 1µm pore size glass fiber filter (dried and preweighed for suspended solids). Chlorophyll samples were then frozen until analysis and suspended solids samples were dried overnight at 60 °C and the filter was weighed to the nearest 0.01 mg. Chlorophyll was extracted following grinding of the filters in 5mL of alkaline acetone in the dark and was centrifuged for 5 minutes at 3000 RPM to separate the acetone solution from the glass fibers. Chlorophyll was then analyzed spectrophotometrically at 750 and 655 nm before and after acidification, following the methods of Wetzel and Likens (2000).

Temperature and oxygen were measured each sampling date using a YSI probe. During all experiments, oxygen concentrations remained above 4.5 mg/L. Zooplankton were collected 1-2 times per experiment during 2006, by using the swing arm sampler and measuring out 2L of water, filtering it through an 80 µm mesh screen and preserving the zooplankton using 10% formalin. The 2007 experiments did not include zooplankton sampling because the tanks were filled with well water, thus zooplankton were not expected to be present except for a very small number that may have been collected with sediments.

The March 2006 experiment used 16 tanks; four were fishless, four had one gizzard shad added (mean wet mass 273.2g, range 185.7-370.8g), four had 2-3 gizzard shad added (mean wet mass of 249.7g per fish, range 147.2-378.2g), and four had sediments that were manually disturbed with an oar two times per day. Gizzard shad were collected from the north end of Lake Apopka and the Apopka-Beauclair Canal using a boat mounted electrofisher. Gizzard shad were first placed in a 440 gallon stock tank, and were then added to the tanks. Fish were collected and added to the tanks four days after setting the tanks up, and the experiment ran for six days following the addition of fish. Temperatures ranged 18.7-25.4 °C during the course of the experiment. During this experiment, eleven fish died and were replaced with fish of equivalent size from the stock tank with additional gizzard shad collected from the same locations. High mortality has been observed in this species (i.e., Drenner et al 1986, Threlkeld 1987, Threlkeld and Drenner 1987), and our concerns led us to move the next tank study to a location where they would be more shaded and thus less impacted by temperature fluctuations.

The May 2006 experiment used 16 tanks. Five tanks had one gizzard shad each (mean wet mass of 209.0g, range 174.1-279.9g) with direct access to feed on and disturb sediments. Five tanks had one gizzard shad each (mean wet mass of 190.1g, range 91.8-327.5g) that was prevented from feeding on sediment by a mesh net (0.6 cm openings) suspended 10cm above the sediment surface. Three tanks were fishless and open to the sediments, and three tanks were fishless with a mesh net. Gizzard shad were added one day after setting the tanks up, as there was little change in the turbidity in the days before the start of the previous experiment, and the experiment ran for ten days following the addition of fish. Temperatures ranged 24.7-27.8 °C during this longer experiment, and six fish died and were replaced with fish of equivalent size.

For the March 2007 experiment, we repeated the experimental design of the May 2006 experiment, using five tanks with one fish per tank (mean wet mass of 186.7g, range 151.1-212.9g) that had sediment access, five tanks with fish and a net (mean wet mass of 249.3 g, range 140.0-472.0g, with the mean skewed upwards by the one large fish), three fishless tanks with sediment access and three fishless tanks with a net preventing sediment access. Instead of canal water, the tanks were filled with well water, thus limiting nutrient uptake to the few phytoplankton found in or on the sediments. Gizzard shad were added the day after setting the tank up and the experiment ran only three days. Haertel-Borer et al. (2004) also used a short duration experiment (6 hr) to examine these mechanisms and our previous studies indicated that treatments typically diverged during a three day time frame. Temperatures ranged 16.7-18.8 °C during the experiment, and we had no fish mortality.

For the May 2007 experiment, we manipulated fish size (small vs. large, with fishless controls), as has been done previously (Schaus and Vanni 2002), but also crossed those treatments with access or no access to the sediments in a 2x3 factorial design, with each treatment run in triplicate (18 total enclosures). Mean wet masses of large gizzard shad were 344.6g (range 203.1-600.4) where fish could feed on sediments and 265.4g (range 227.1-308.0g) where the net was present. In the small gizzard shad treatments, the mean wet masses were 186.7g (range 130.9-258.8g) where fish could feed directly on sediments and 177.0 (range 136.0-216.4g) where the net was present. Two fish were added per enclosure to attempt to roughly equal the fish biomass in tanks with large gizzard shad (which had 1 fish per tank), given the ranges of fish sizes available at the time and our desire to transfer fish to the tanks with minimal handling. This was also a shorter duration experiment designed to tease out the mechanisms of excretion vs. bioturbation. Temperatures ranged 21.6-24.9 °C. We had only one fish die during the experiment (it was replaced with a fish of similar size) and one die right at the conclusion of the experiment (it was not replaced).

Data were analyzed using ANOVA for each response variable (turbidity, suspended solids, chlorophyll, total N (TN), total P (TP), total dissolved N (TDN), total dissolved P (TDP), particulate N, particulate P, NH_4-N, NO_x, and PO_4-P) on the average of all samples taken after fish introduction. This was done in place of repeated measures ANOVA because of the short duration of the experiment. For the March 2006 experiment, we used a simple ANOVA contrasting the four treatments. For May 2006 and March 2007 we used a 2x2 factorial ANOVA and considered sediment access * fish interaction effects as the test of our hypothesis. For May 2007 we used a 2x3 factorial ANOVA, looking for sediment access * fish interactions and also comparing differences between the different sizes of fish using a Tukey post hoc test. All comparisons used $\alpha=0.05$ as the level of statistical significance, and all statistical results are reported in Table 3-1.

We examined the effects of excretion vs. bioturbation in two ways. The March 2006 experiment provided a very rough approximation of the potential effects of bioturbation, as the paddle treatment only contained bioturbation effects, and no fish excretion. For the 2007 experiments with well water, changes in dissolved nutrient accumulation could be compared between treatments with and without sediment access, as the water contained minimal phytoplankton that could take up excreted nutrients. All tanks containing fish would be subject to fish excretion, but bioturbation would only occur in tanks where fish could stir up sediments. However, Mather et al. (1995) observed that excretion rates of unfed fish (those in treatments with a net) would decrease, especially for P. Thus, we estimated the proportion of the change in total dissolved P concentration that could be accounted for by excretion, using our estimates of N and P excretion for Lake Apopka and the mean temperature during each experiment, correcting for the decrease in feeding using Mather et al. (1995) and our estimates of mean % gut fullness. Percent gut fullness was estimated by comparing the mean dry mass of food in gizzard shad foreguts at the conclusion of the March 2007 experiment with the mean dry mass in guts of field-collected fish used for our gut content analyses (Chapter 4).

Results

In the March 2006 experiment (Fig. 3-1 through 3-4), there were large increases in turbidity, particulate and total nutrients, in tanks with fish. As expected, the high fish treatment had a larger mean effect on these measures, but never differed significantly from the low fish treatment. Both fish treatments and the paddle treatment were significantly elevated over that of the fishless treatments for Chl *a*, Turbidity, TP, and Particulate N and P (Table 3-1). TDN showed no significant differences among treatments, and Tukey's test did not identify treatments that differed significantly for PO_4. For all other response variables (suspended solids, TN, NH_4, and TDP), the fishless and low treatments did not differ significantly and the low, paddle, and high fish treatments did not differ significantly, but the high fish and paddle treatments differed significantly from the fishless tanks.

In the May 2006 experiment (Fig. 3-5 through 3-8), most parameters decreased over time. Higher levels of turbidity, suspended solids, and chlorophyll a were observed in the treatment where fish could access the sediments, but these parameters decreased overall. Significant fish*net interactions were observed for Chl *a* and turbidity (Table 3-1). There were significant fish and net main effects for TN and a significant net effect was observed for suspended solids. There were significant fish effects for total P, TDN, particulate P, and NH_4-N. TDP, particulate N and PO_4 had no significant effects among treatments, although the former two had marginally significant fish effects ($0.05<X<0.1$, Table 3-1).

Zooplankton in the 2006 tank experiments (Fig. 3-9) only differed significantly among treatments during the May 2006 experiment, and no significant differences were observed in March 2006 (Table 3-1). In May 2006, fish had a significant effect on rotifers, such that rotifers were higher in the presence of fish. Copepods were significantly lower with the presence of a net, and cladocerans showed no significant differences among treatments. Total zooplankton showed significant effects of fish and net, but the interaction term was only marginally significant ($P=0.071$, Table 3-1).

In March, 2007, there were strong increases in turbidity, total, and particulate nutrients in the treatment where fish could access sediments. TDN, TDP, NH_4-N and PO_4-P also showed slight increases over time, but these were not as pronounced as the trends for turbidity and for particulate and total nutrients. There were significant fish*net interaction effects on turbidity, suspended solids, total N, total P, particulate N, and particulate P (Table 3-1, Fig. 3-10 to 3-13). All other comparisons did not differ significantly.

In May 2007, (Fig 3-14 to 3-17), both small and large fish treatments that could feed on sediments showed marked increases in turbidity, total and particulate nutrients. Significant fish*net interaction effects were observed for turbidity, suspended solids, NH_4-N, TN, TDN, and particulate N (Table 3-1). A significant fish effect was observed for TP, and a significant net effect was observed for NO_x. All other comparisons showed no significant differences and no strong trends. For all parameters, we never observed a significant difference between the small and large fish size treatments (Tukey's test, $P>0.1$ for all comparisons).

Comparing across experiments to examine bioturbation, we observed that TDP typically showed a clearer pattern than PO_4-P, thus it was easier to compare responses of treatments over time, in order to estimate the proportion of the effect that was due to excretion vs. bioturbation. In the 2006 experiments, where there were at least marginally significant effects of TDP, excretion by gizzard shad could account for nearly all of the net change in TDP that was observed (Table 3-2), even with our corrections for reduced excretion rate due to reduced feeding activity. The mass of foods observed in guts of fish that could feed directly on sediments averaged 46.8% of those field collected from Lake Apopka and the Apopka-Beauclair Canal, so we divided our estimates of excretion by tank gizzard shad in half, as excretion rates have been shown to decrease with time since feeding (Mather et al. 1995) and decreased ration size (Glaholt and Vanni 2005). In May 2006, the gizzard shad treatments both increased in TDP whether or not gizzard shad could feed on sediments, although the magnitude of the increase was 45% higher if fish could feed on sediments (Table 3-2). The difference between our estimates of excretion by gizzard shad and the observed increases in TDP could be explained by nutrients released via bioturbation.

Table 3-1 Statistical results for all comparisons during the 2006 and 2007 tank experiments. P-values are shown, therefore values less than 0.05 (in bold) are considered statistically significant. Parameters measured include turbidity (Turb.), suspended solids (SS), chlorophyll *a* (Chl *a*), total nitrogen (TN), total dissolved nitrogen (TDN), particulate nitrogen (Part. N), total phosphorus (TP), total dissolved P (TDP), particulate P (Part. P), ammonia N (NH_4-N), nitrates and nitrites (NO_x), phosphate P (PO_4-P), total rotifers (Rotif.), total copepods (Copep.), total cladocerans (Clad.), and total zooplankton (Total ZP).

Effect	Turb.	SS	Chl *a*	TN	TDN	Part. N	TP	TDP	Part. P	NH_4-N	NO_x	PO_4-P	Rotif.	Copep.	Clad.	Total ZP
March 2006																
Treatment	**0.001**	**0.007**	**0.001**	**0.001**	0.068	**0.001**	**0.001**	**0.006**	**0.001**	**0.015**		**0.015**	0.373	0.118	0.507	0.364
May 2006																
Fish*Net	**0.038**	0.127	0.763	0.334	0.643	0.469	0.880	0.957	0.739	0.577		0.634	0.409	0.246	0.971	0.071
Fish	**0.004**	0.060	**0.001**	**0.001**	**0.031**	0.083	**0.002**	0.051	**0.015**	**0.026**		0.239	**0.001**	0.440	0.530	**0.018**
Net	**0.001**	**0.011**	**0.001**	**0.001**	0.693	0.564	0.057	0.315	0.054	0.360		0.341	0.717	**0.002**	0.400	**0.023**
March 2007																
Fish*Net	**0.019**	**0.002**		**0.020**	0.277	**0.012**	**0.038**	0.920	**0.004**	0.355	0.506	0.694				
Fish	0.051	0.070		0.051	0.237	**0.046**	0.176	0.828	0.224	0.481	0.267	0.830				
Net	**0.004**	**0.014**		**0.040**	0.613	**0.015**	**0.048**	0.618	**0.022**	0.786	0.990	0.863				
May 2007																
Fish*Net	**0.043**	**0.044**	0.868	**0.007**	**0.016**	**0.027**	0.215	0.430	0.497	**0.003**	0.115	0.634				

Fish Treatment	**0.018**	**0.001**	0.831	**0.001**	**0.003**	**0.004**	**0.001**	0.093	**0.004**	**0.001**	0.723	0.494
Net	**0.001**	**0.001**	0.622	0.064	0.430	**0.001**	0.114	0.433	0.207	**0.026**	**0.001**	0.898

Table 3-2 Trends in total dissolved P (TDP) over the first 3-6 days of each 2006 experiment, where significant treatment effects were observed for TDP. Net changes in TDP are the amount of change relative to the appropriate fishless treatment (with or without a net). The amount of TDP increase that can be potentially accounted for by P excretion by gizzard shad is calculated using our excretion estimates from Chapter 2 for all Lake Apopka gizzard shad, the mean temperatures in tanks and the mean wet mass for fish in each treatment. These estimates were divided in ½, because gut contents for fish recovered from tank experiments averaged ~½ the mass of diet samples from field collected fish and because excretion rates can vary with time since feeding (Mather et al. 1995) and ration (Glaholt and Vanni 2005).

Experiment	Treatment	Change in TDP (µg/L/day)	Net Increase in TPD (µg/L/day)	P Excretion Effect of Gizzard Shad (µg/L/day)
March 2006	Fishless	-0.92		
	Low Fish	0.87	1.79	3.43
	High Fish	4.19	5.11	8.49
	Paddle	0.13	1.05	
May 2006	Fish/No Net	11.93	5.46	4.81
	Fish/Net	9.44	3.76	[a]
	No Fish/No Net	6.47		
	No Fish/Net	5.68		

[a] Excretion measures could not be estimated for fish that were prevented from feeding on sediments, as our excretion measures from Chapters 1 and 2 were from field collected fish that has access to sediment detritus.

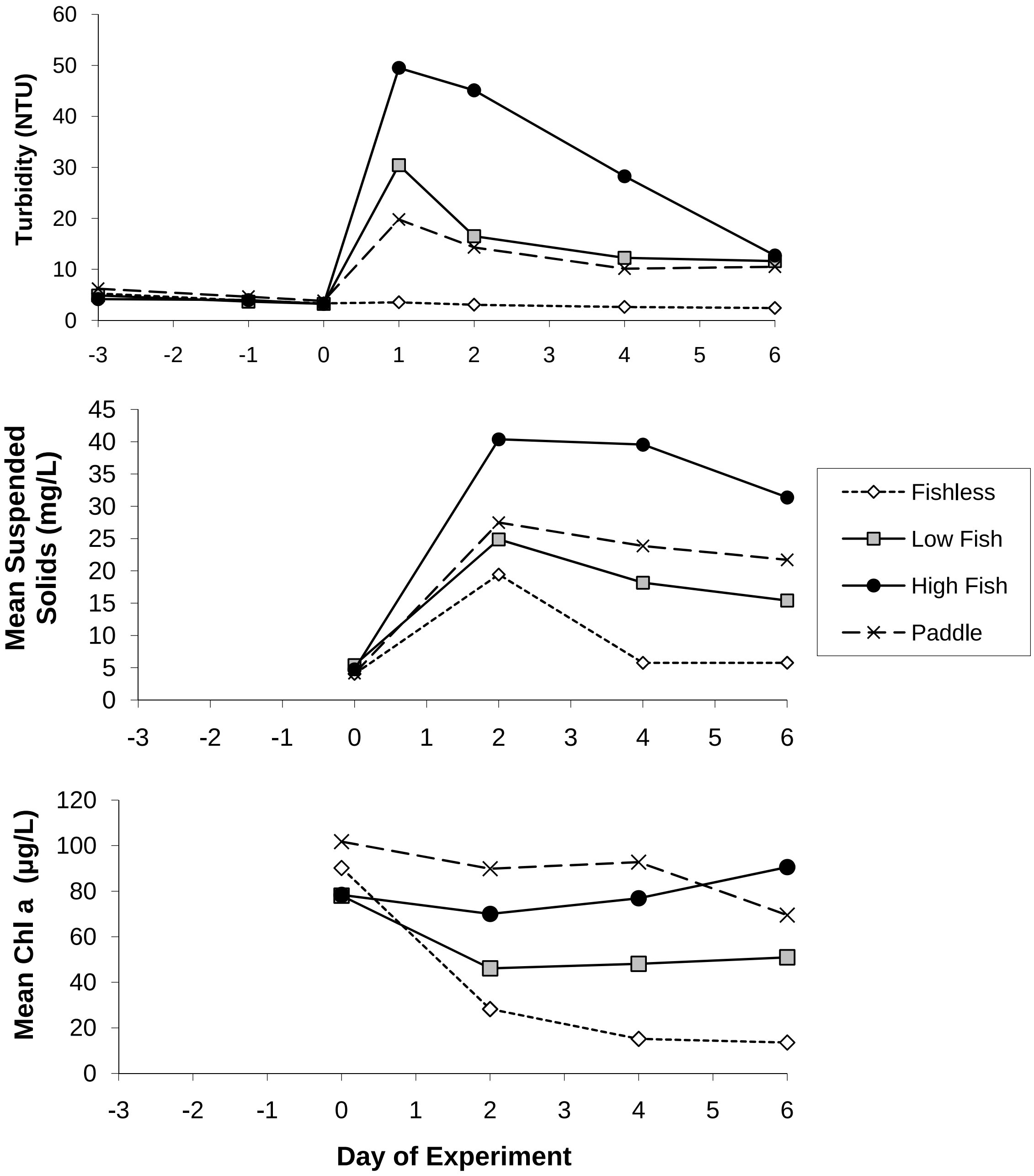

Fig 3-1 Turbidity (top panel), suspended solids (middle panel) and chlorophyll a (bottom panel) from the March 2006 tank experiment. There were significant treatment effects on turbidity (P=0.001), suspended solids (P=0.007) and chlorophyll a (P=0.001).

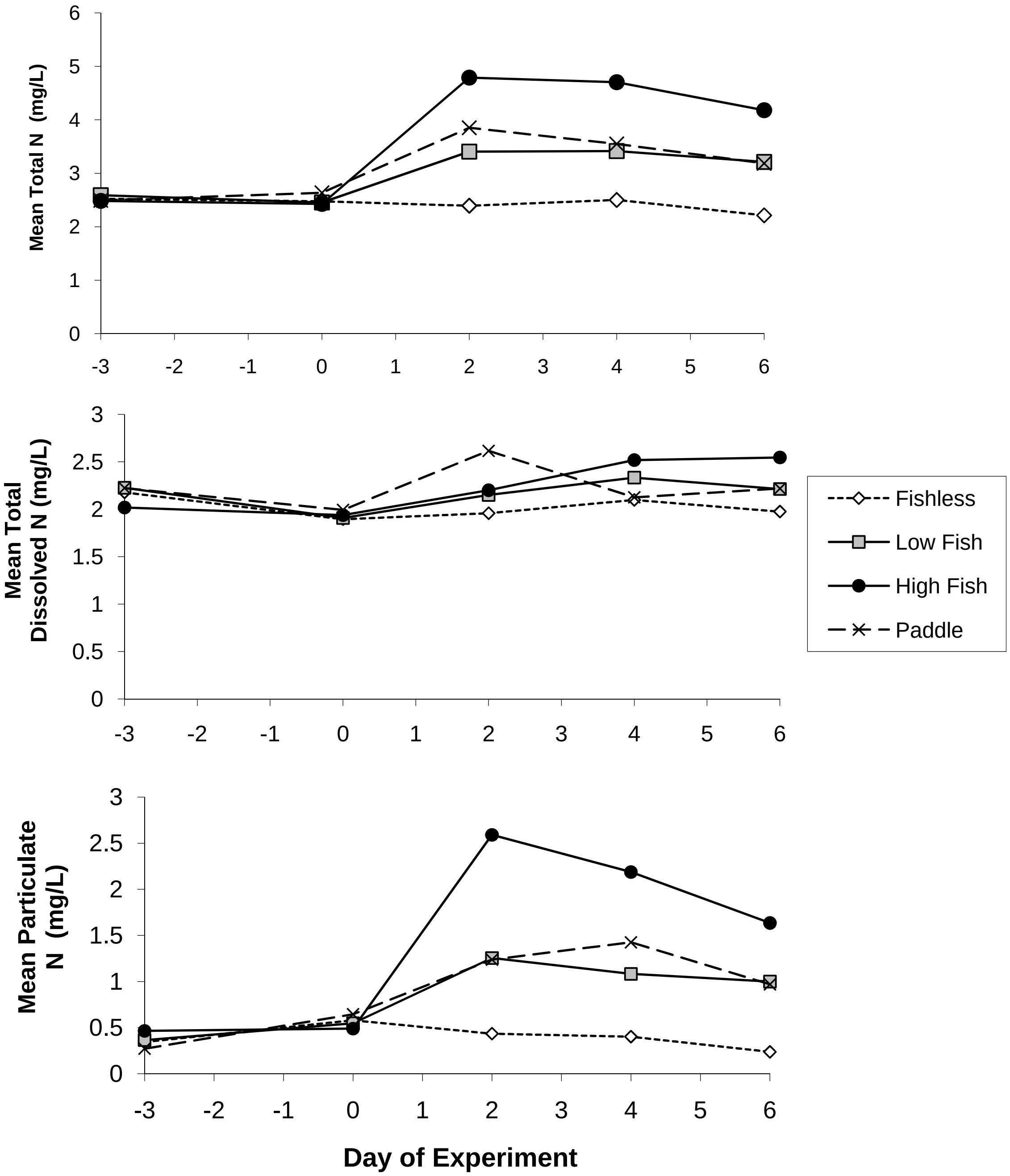

Fig 3-2 Total N (top panel), total dissolved N (middle panel) and particulate N (bottom panel) from the March 2006 tank experiment. There were significant treatment effects on total N (P=0.001) and particulate N (P=0.001), but not total dissolved N (P=0.068).

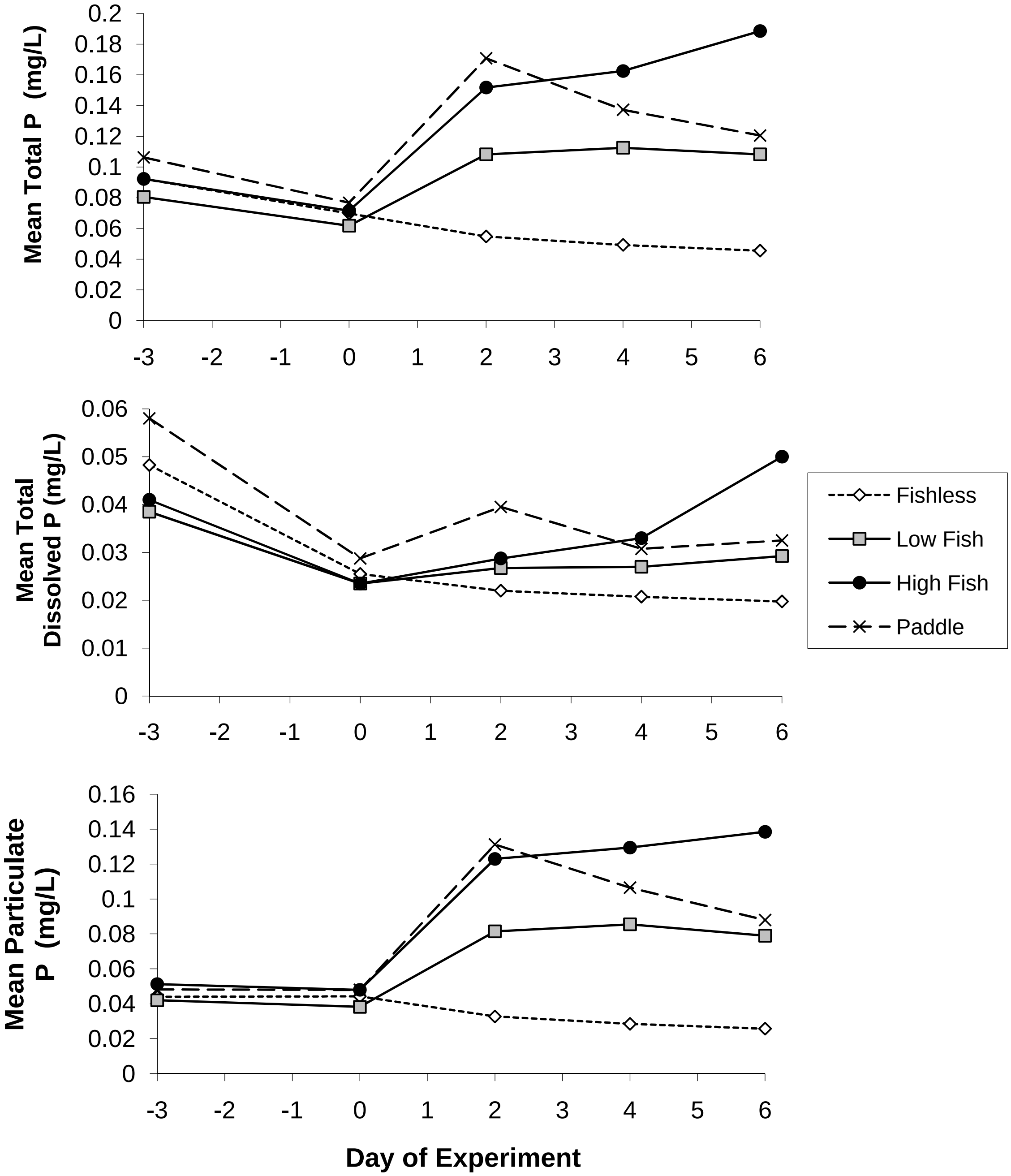

Fig 3-3 Total P (top panel), total dissolved P (middle panel) and particulate P (bottom panel) from the March 2006 tank experiment. There were significant treatment effects on total P (P=0.001), total dissolved P (P=0.006) and particulate P (P=0.001).

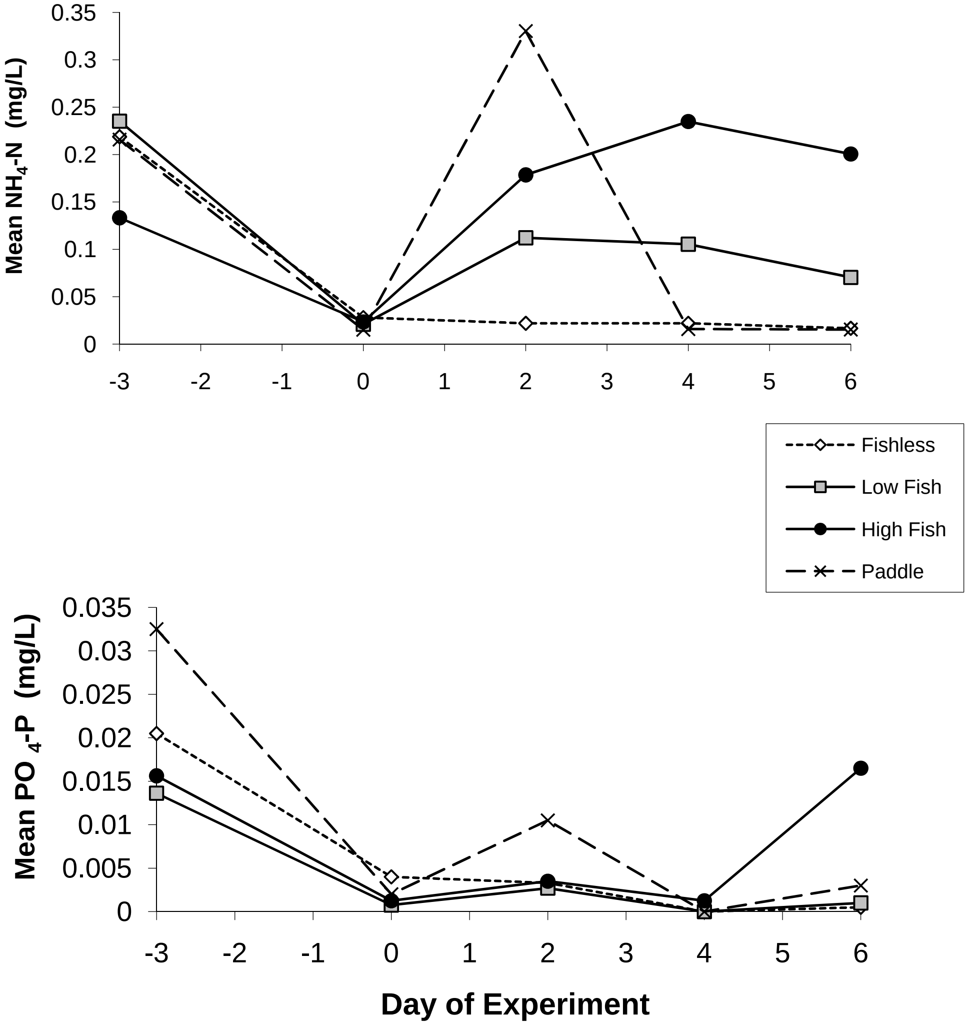

Fig 3-4 NH_4-N (top panel), and PO_4-P (bottom panel) from the March 2006 tank experiment. There were significant treatment effects on NH_4-N ($P=0.015$) and PO_4-P ($P=0.015$).

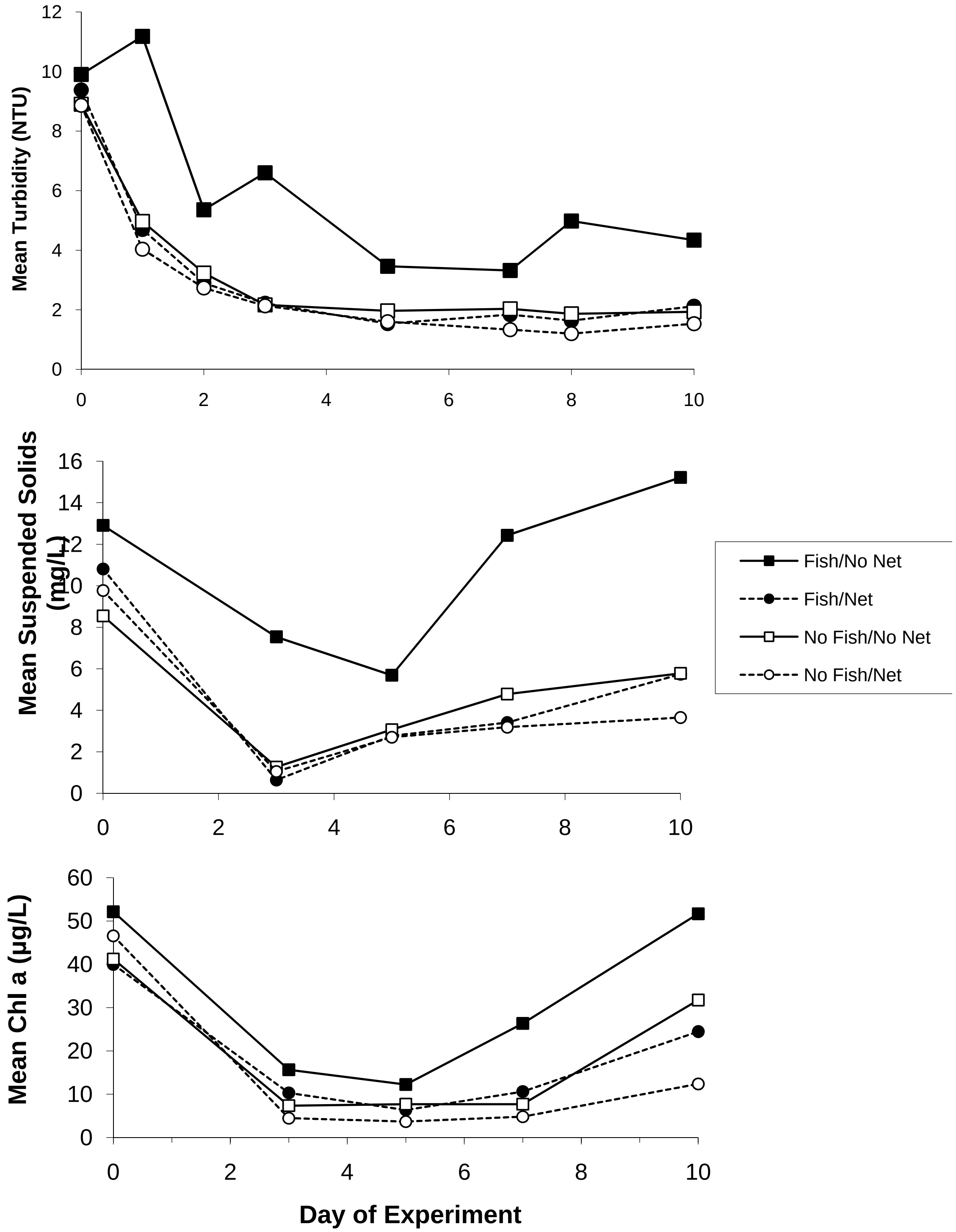

Fig 3-5 Turbidity (top panel), suspended solids (middle panel) and chlorophyll a (bottom panel) from the May 2006 tank experiment. There was a significant fish*net interaction effect for turbidity (P=0.038), a significant net effect on suspended solids (P=0.011) and significant fish and net effects on chlorophyll a (P=0.001 for both).

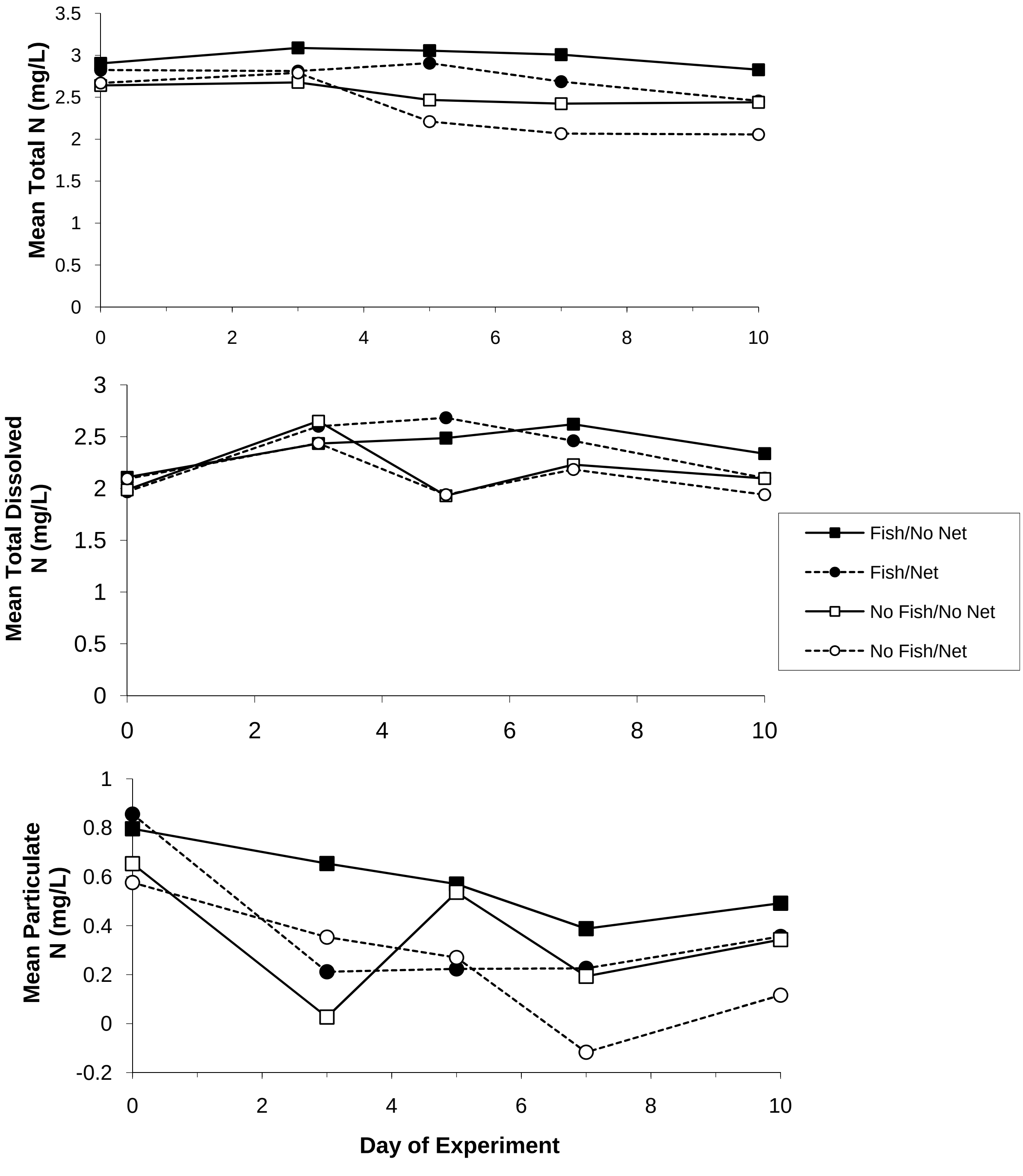

Fig 3-6 Total N (top panel), total dissolved N (middle panel) and particulate N (bottom panel) from the May 2006 tank experiment. There were significant fish and net effects on total N (both P=0.001) and there was a significant fish effect on TDN (P=0.031).

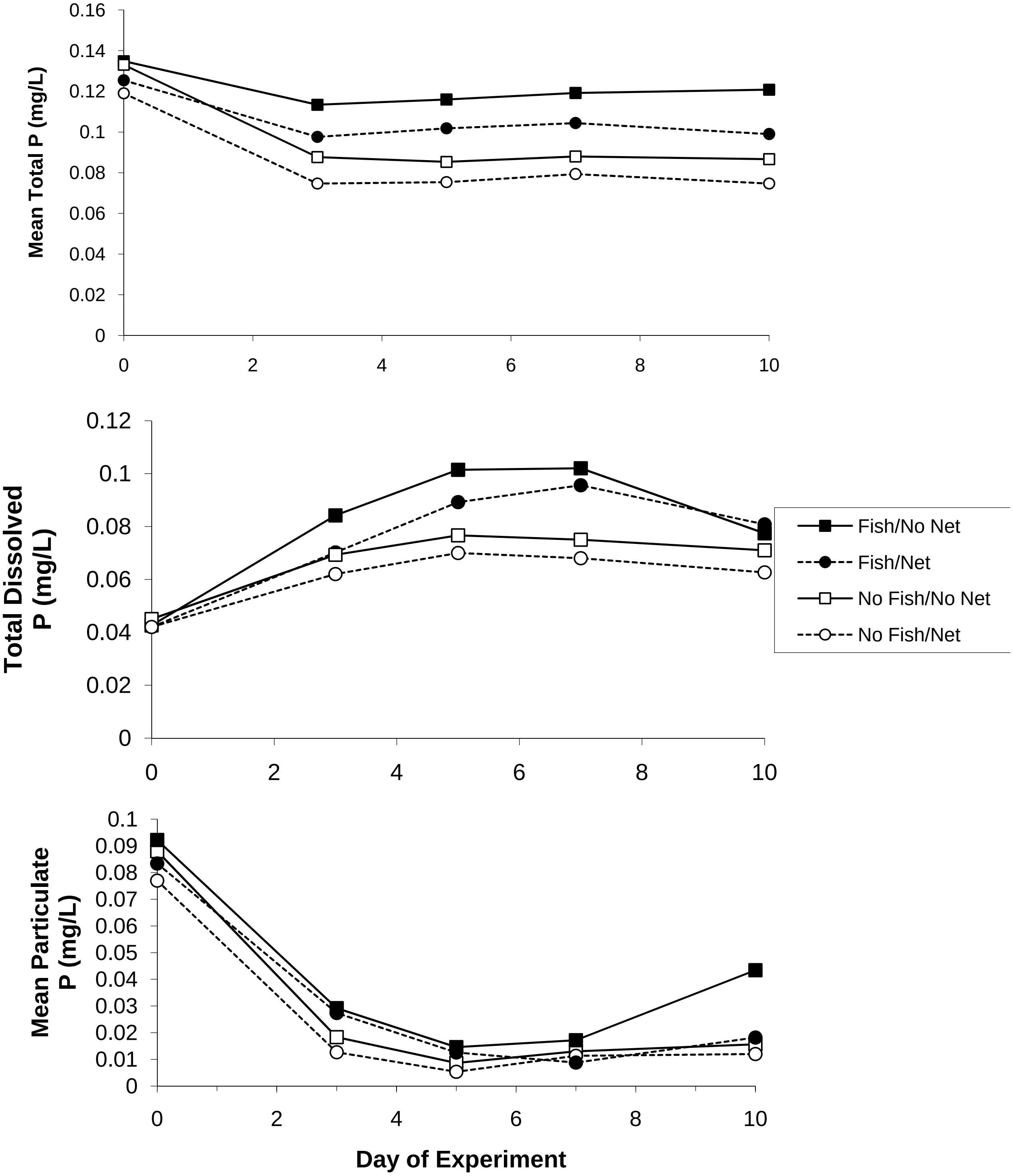

Fig 3-7 Total P (top panel), total dissolved P (middle panel) and particulate P (bottom panel) from the May 2006 tank experiment. There were significant fish effects on total P (P=0.002) and particulate P (P=0.015), and the fish effect on TDP was marginally significant (P=0.051).

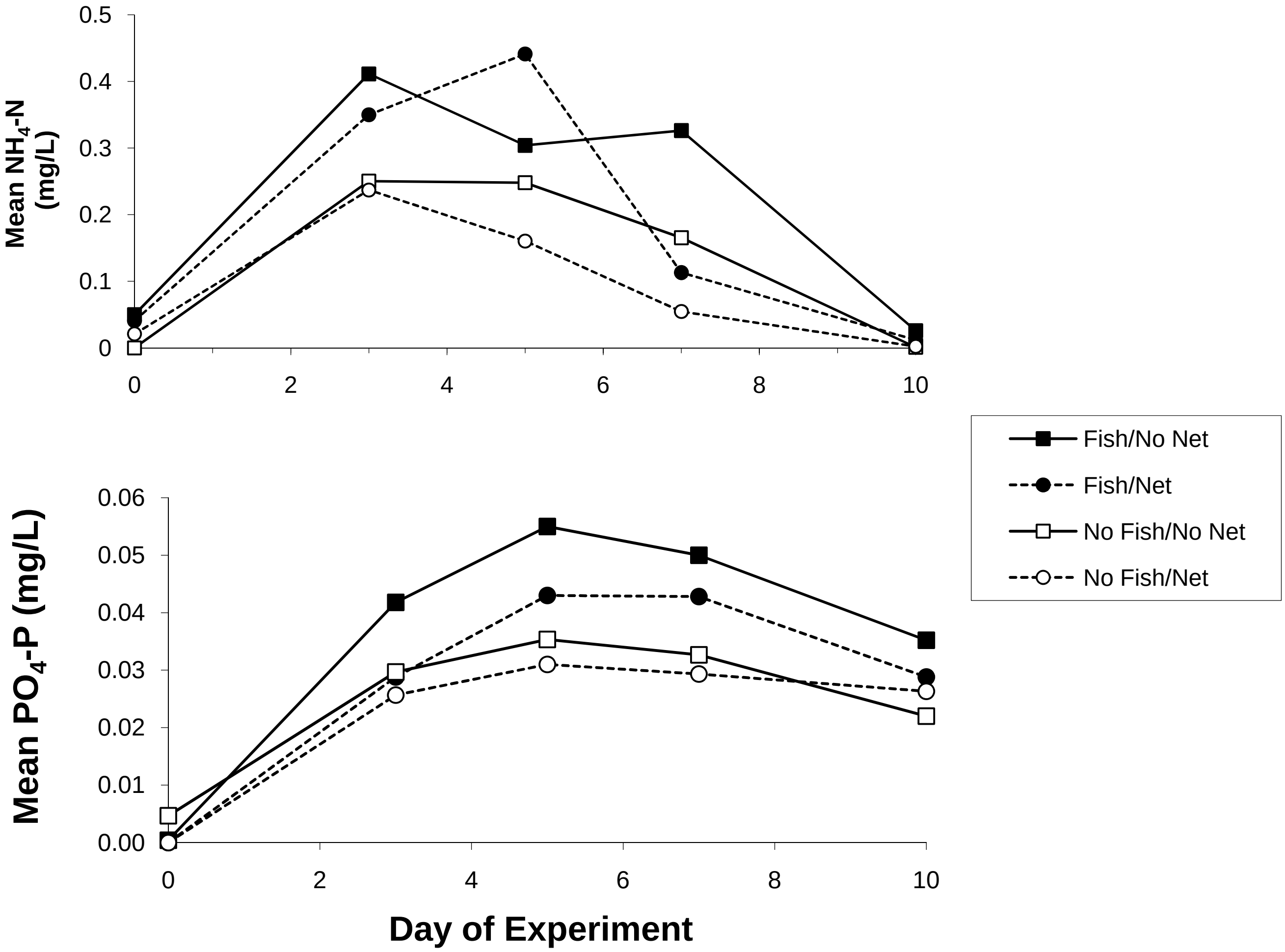

Fig 3-8 NH_4-N (top panel), and PO_4-P (bottom panel) from the May 2006 tank experiment. There was a significant fish effect on NH_4-N (P=0.026), but not PO_4-P.

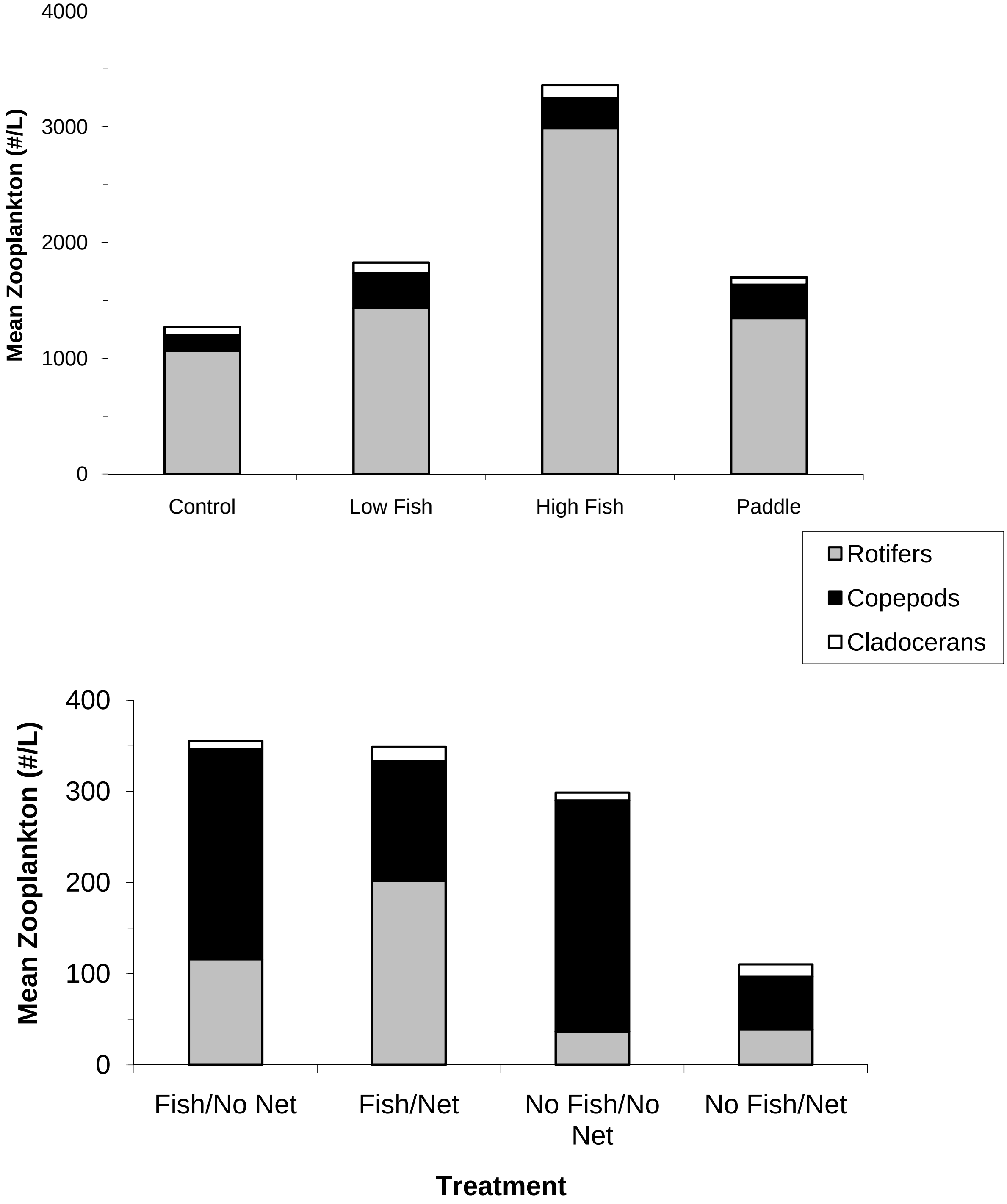

Fig 3-9 Zooplankton data from the March 2006 (top) and May 2006 (bottom panel) tank experiments. During March 2006, no significant treatments were seen for all zooplankton groups and total zooplankton (P>0.1 for all comparisons). In May 2006, there was a significant effect of fish on rotifers (P=0.001), a significant effect of net on copepods (P=0.002), and significant effects of fish (P=0.018) and net (P=0.023) on total ZP.

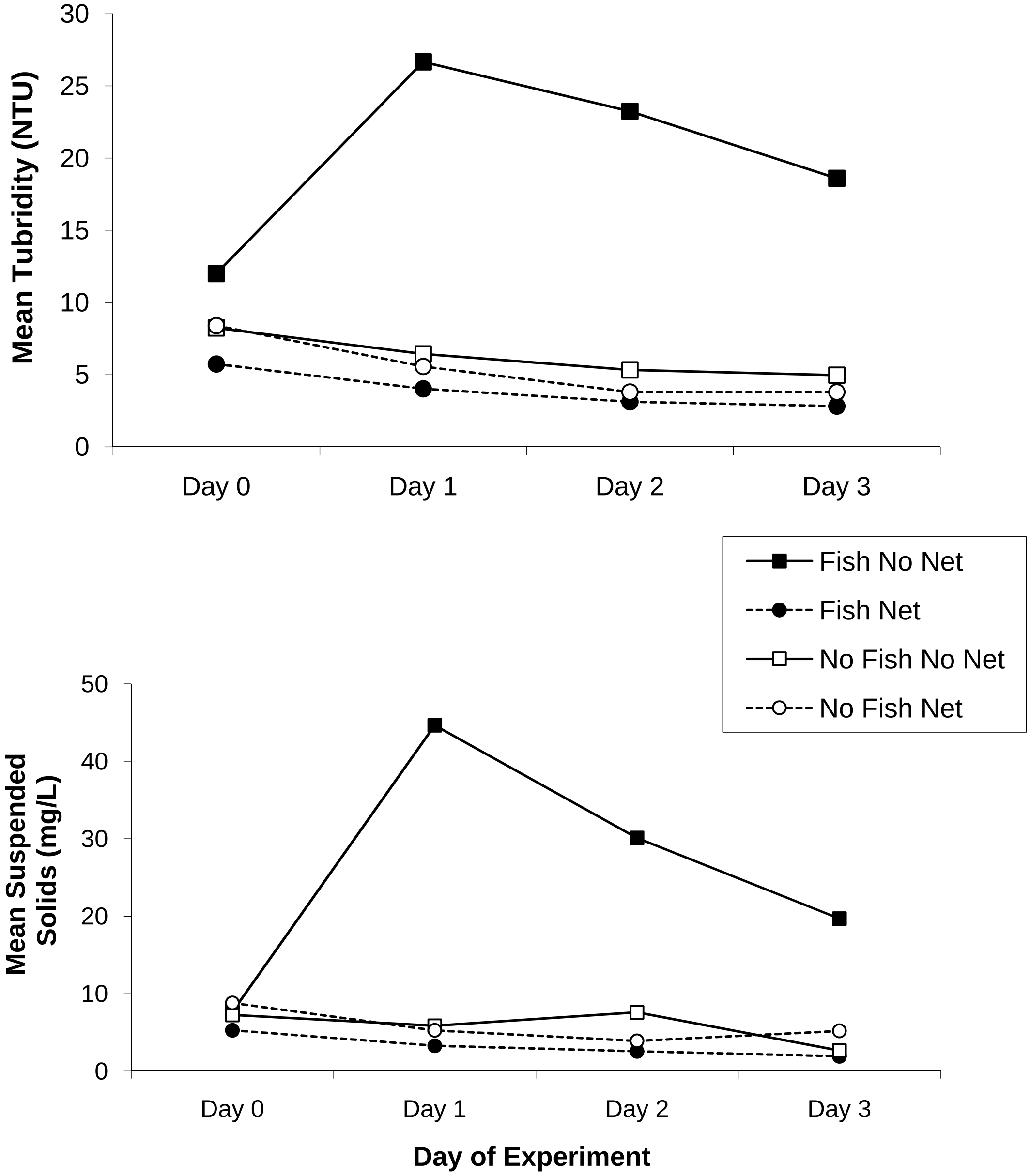

Fig 3-10 Turbidity (top panel), suspended solids (middle panel) and chlorophyll a (bottom panel) from the May 2007 tank experiment. There was a significant fish*net interaction effect for both turbidity (P=0.019) and suspended solids (P=0.002).

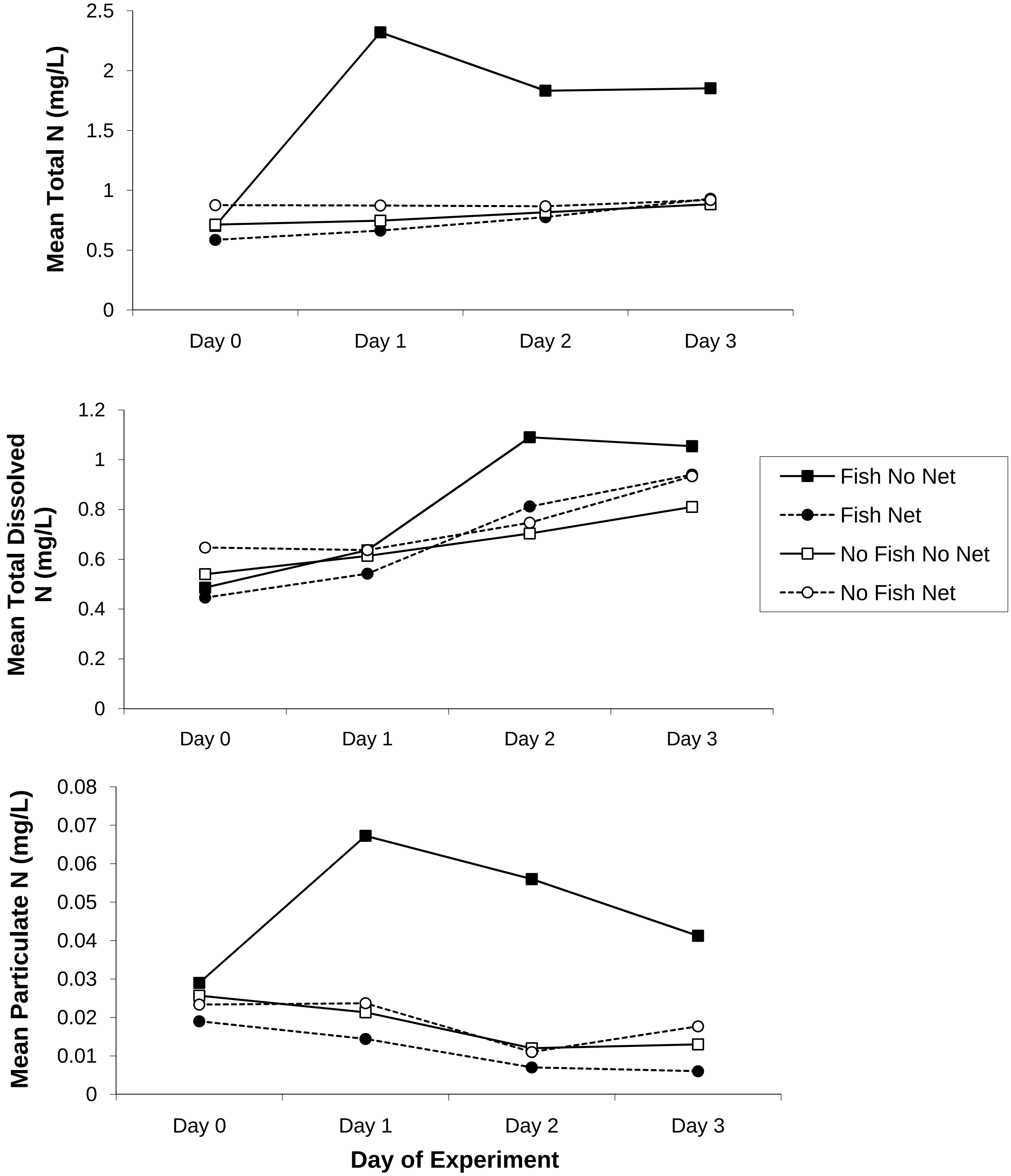

Fig 3-11 Total N (top panel), total dissolved N (middle panel) and particulate N (bottom panel) from the March 2007 tank experiment. There were significant fish*net interaction effects for total N (P=0.020) and particulate N (P=0.012), but not total dissolved N (P=0.277).

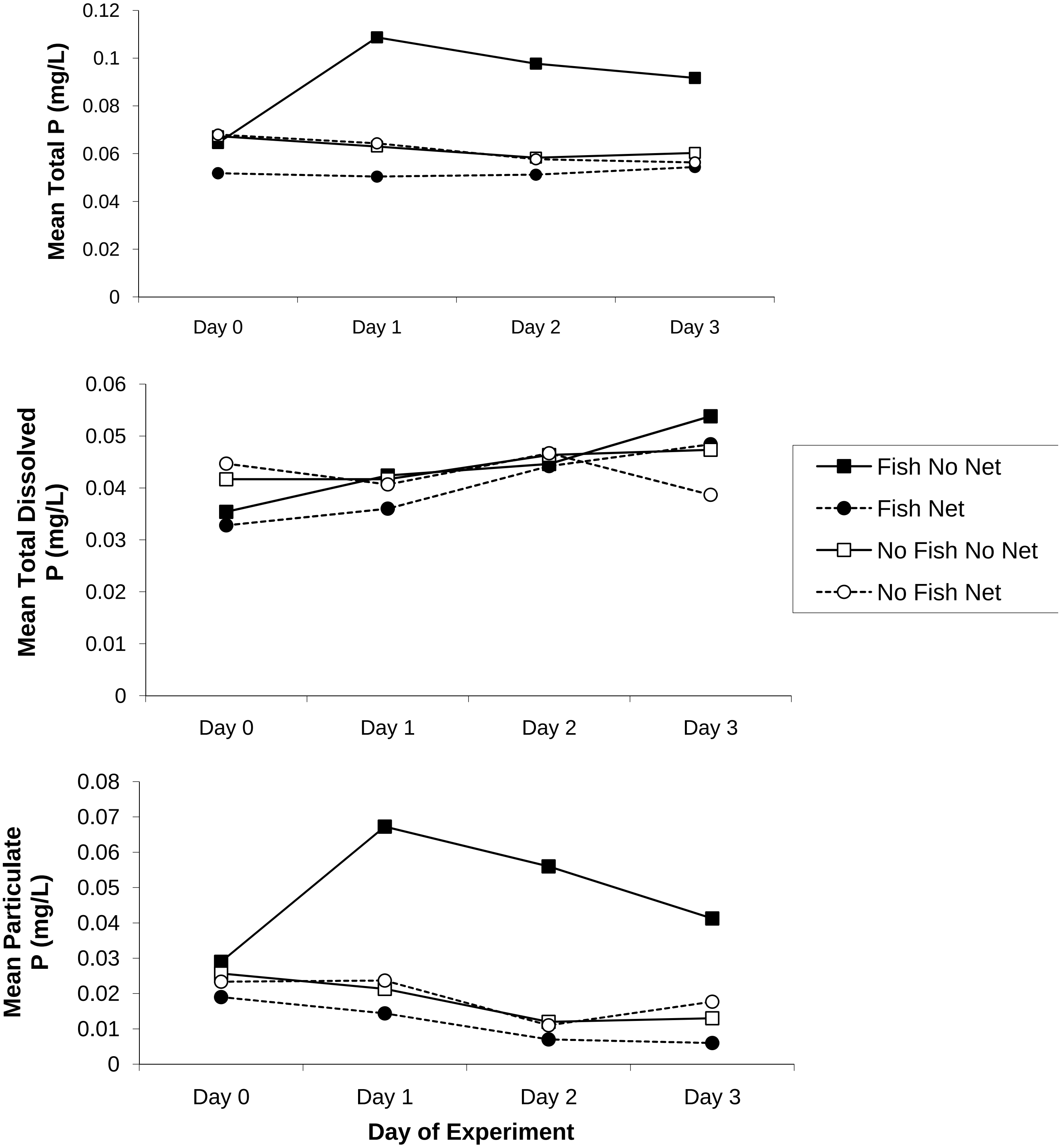

Fig 3-12 Total P (top panel), total dissolved P (middle panel) and particulate P (bottom panel) from the March 2007 tank experiment. There were significant fish*net interaction effects on total P (P=0.038), and particulate P (P=0.004), but not total dissolved P (P=0.920).

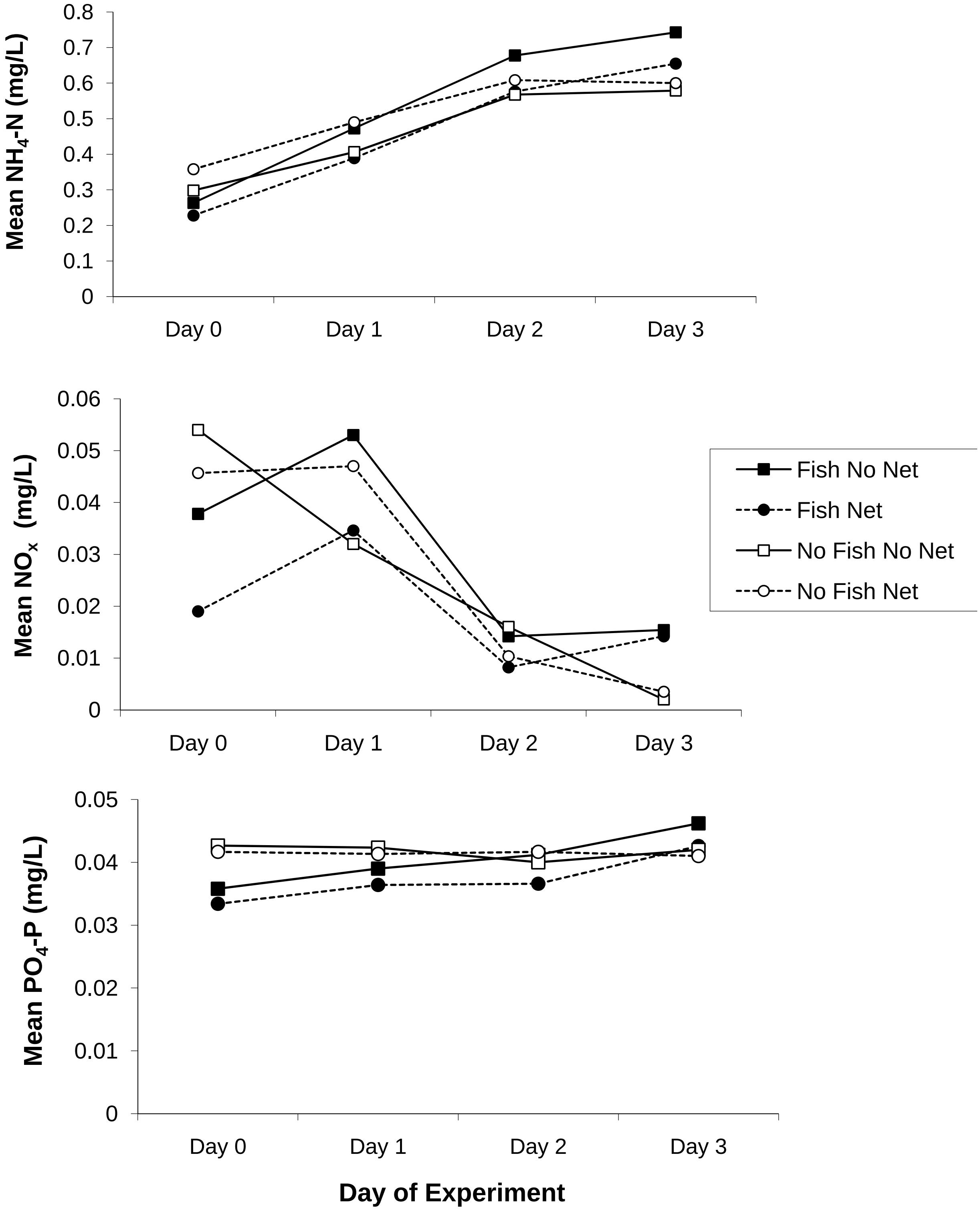

Fig 3-13 NH$_4$-N (top panel), NOx (middle panel), and PO$_4$-P (bottom panel) from the May 2007 tank experiment. No significant treatment or interaction effects were observed for these soluble nutrients.

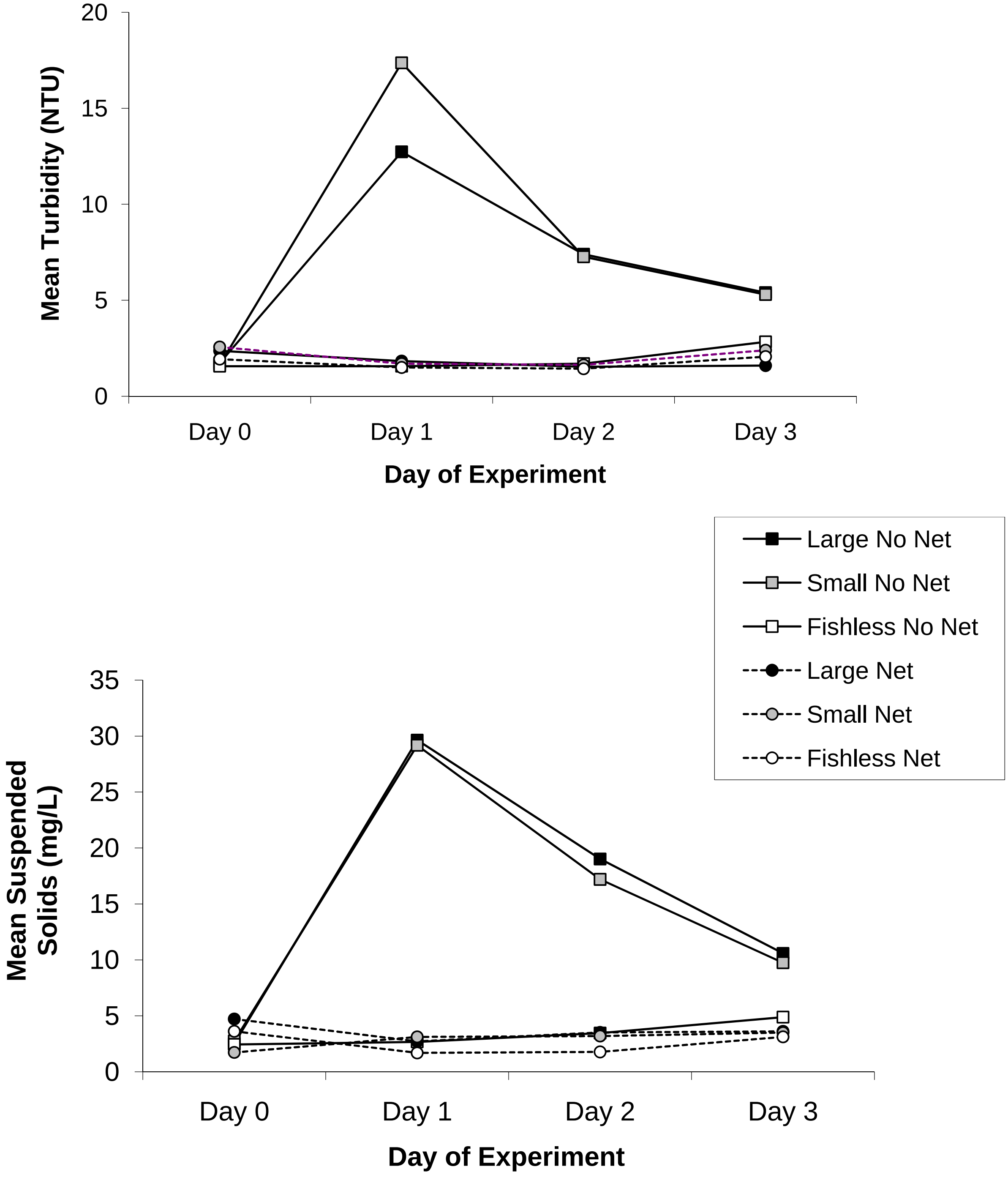

Fig 3-14 Turbidity (top panel), suspended solids (middle panel) and chlorophyll a (bottom panel) from the May 2007 tank experiment. There was a significant fish*net interaction effect for both turbidity (P=0.043) and suspended solids (P=0.044).

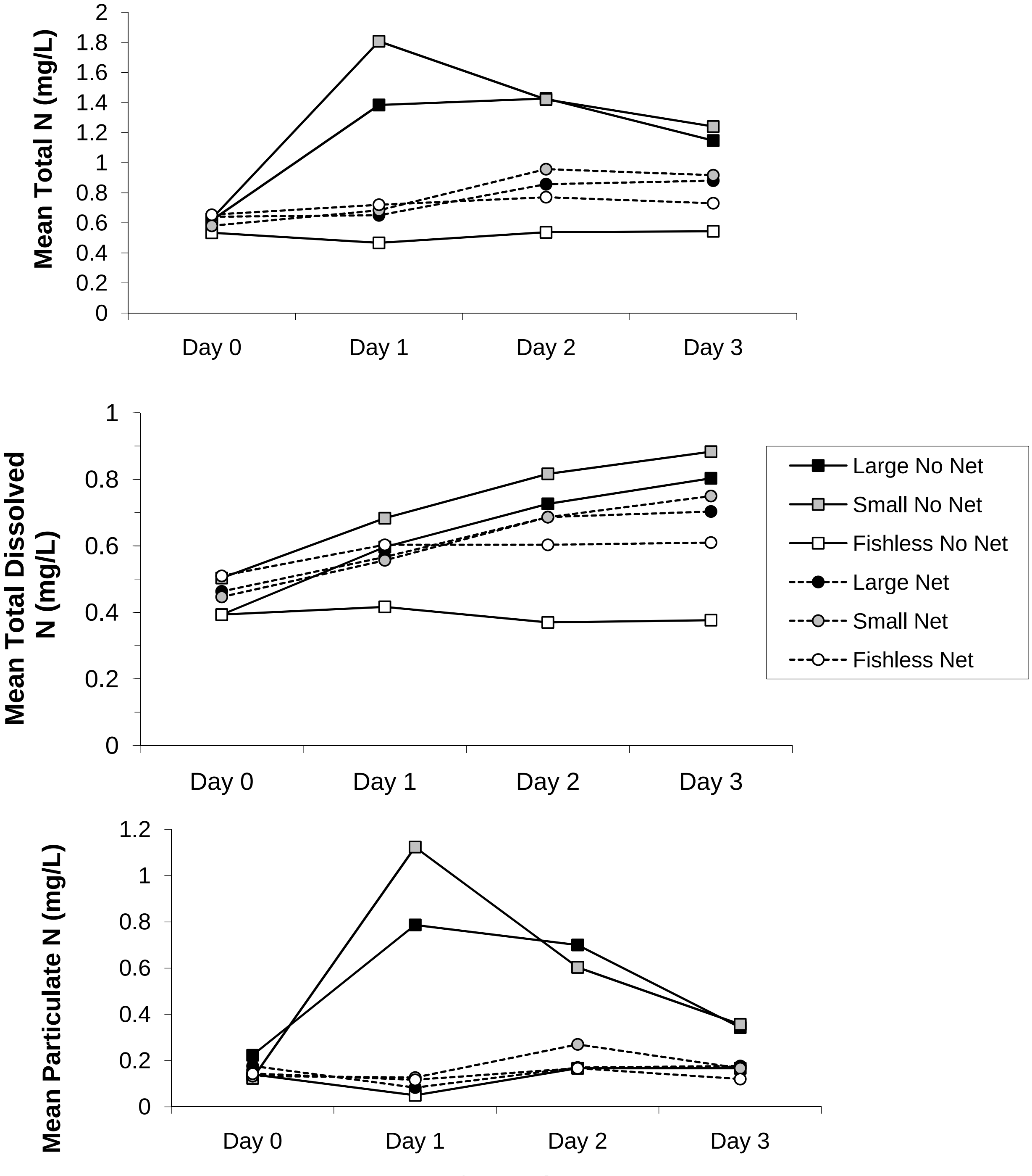

Fig 3-15 Total N (top panel), total dissolved N (middle panel) and particulate N (bottom panel) from the May 2007 tank experiment. There were significant fish treatment*net interaction effects for total N (P=0.007), total dissolved N (P=0.016), and particulate N (P=0.027).

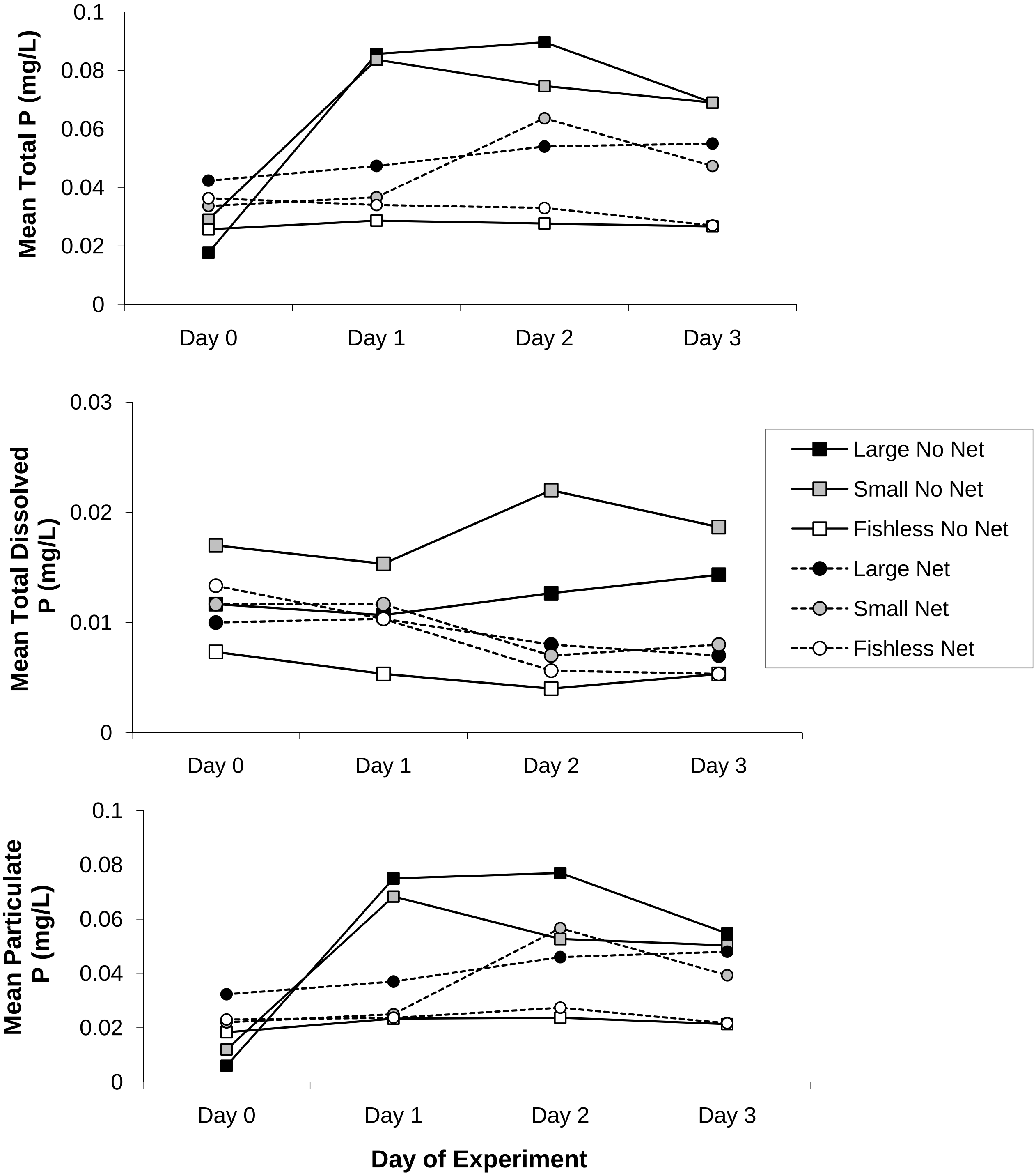

Fig.3-16 Total P (top panel), total dissolved P (middle panel) and particulate P (bottom panel) from the May 2007 tank experiment. There were significant fish treatment effects on total P (P=0.001), and particulate P (P=0.004), but not total dissolved P (P=0.093).

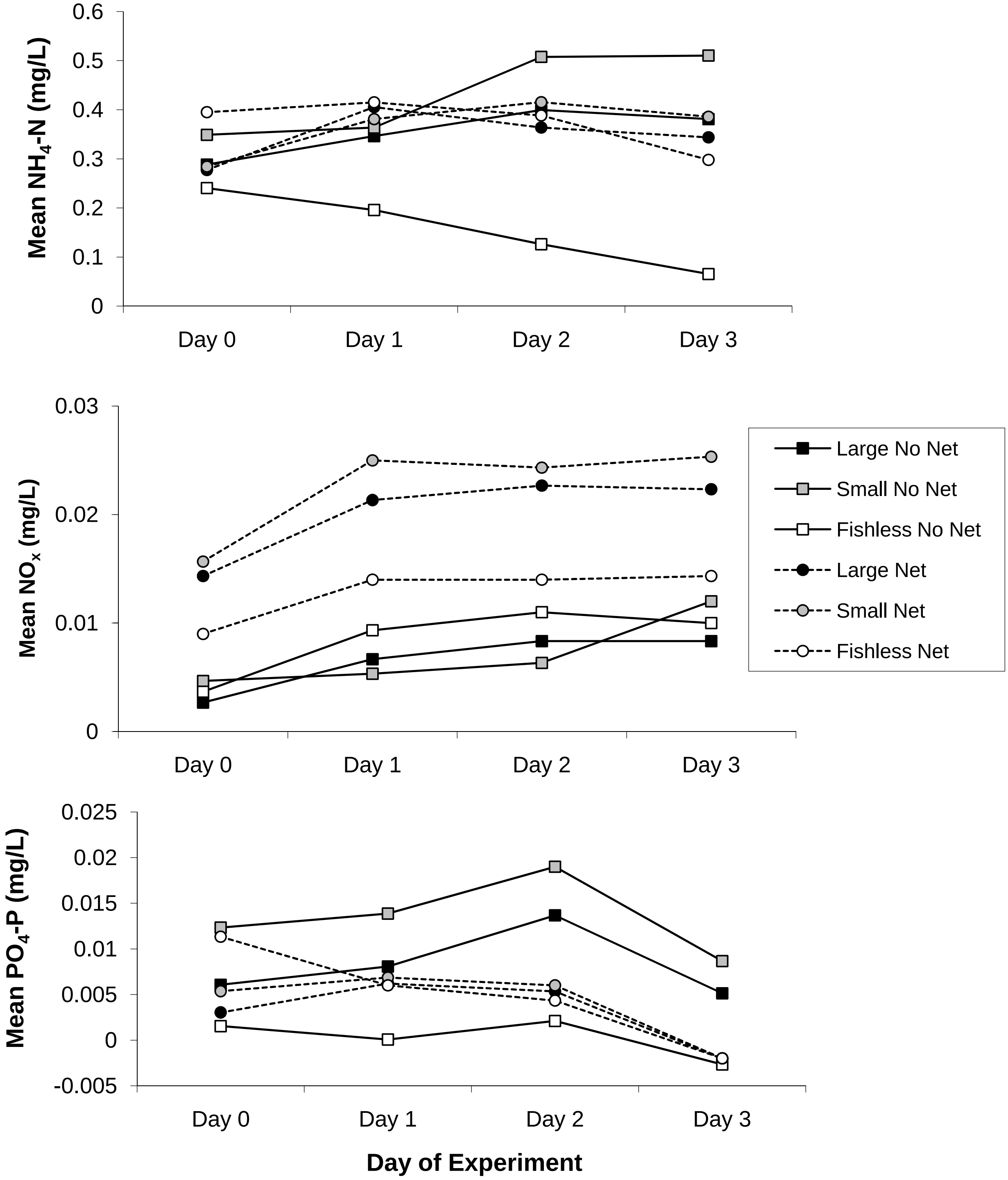

Fig 3-17 NH_4-N (top panel), NO_x (middle panel) and PO_4-P (bottom panel) from the May 2007 tank experiment. There was a significant fish treatment*net interaction effect on NH_4-N (P=0.003) and a significant net effect on NO_x (P=0.001).

Discussion

Tank microcosm results followed patterns observed in several other enclosure studies (Havens 1991, 1993, Schaus and Vanni 2002, Matshzaki et al. 2007). Fish generally impacted turbidity, suspended solids, total, and particulate nutrients only when they could actively feed on sediment detritus. In most cases, there was an increased proportion of nutrients (both N and P) in particulate form, indicating that gizzard shad can have some impact on turbidity via bioturbation, in addition to excretion effects. Increases in turbidity, total and particulate nutrients were highest with high fish biomass during the March 2006 experiment. In some cases, we observed a significant net effect, as has been previously observed (Schaus and Vanni 2002). This is important because our experimental design controls for the presence of a net and the ways that it can potentially impact nutrients and planktonic organisms (by providing an attachment site for attached algae, by providing a refuge from predation for copepods, etc.), whereas the experimental design of other investigators has not always appropriately controlled for these effects (i.e., Havens 1991, 1993, Roozen et al. 2007).

Dissolved P concentrations increased during the 2006 experiments regardless of whether fish could feed directly on sediments, indicating the importance of excretion on the nutrient based effect. The P excreted by gizzard shad could account for more than the observed increase in March 2006 and nearly all of the TDP during May 2006. The remainder would be expected to come from bioturbation. In the March 2006 study, the tanks that had the sediments manually disturbed with a paddle increased the concentrations of turbidity substantially and also significantly increased TDP over the control treatment. This provides evidence that bioturbation can be one of the effects that gizzard shad have on this system, especially as Lake Apopka sediments are easily resuspended (Schelske 1997). In addition to Lamarra’s (1975) study, which found no effect of stirring sediments once per week, Ogilvie and Mitchell (1998) also conducted an enclosure experiment where sediments were stirred, in order to simulate wind resuspension, but certainly their findings would be applicable to the stirring up of the sediments by benthic feeding fishes. They found that phytoplankton and nutrient levels were increased for several days following sediment disturbance, whereas suspended solids typically returned to baseline levels within 1 day (Ogilvie and Mitchell 1998).

In other systems where benthivores such as common carp (*Cyprinus carpio*) extensively disturb sediments (Matsuzaki et al. 2007), there may be an even greater impact of bioturbation of sediment particles, and also if pore water nutrients are released and remain mobilized in the water column. Matsuzaki et al. (2007) manipulated carp abundance and sediment access in enclosures that contained macrophytes. They observed that increased turbidity and suspended solids where carp could feed on the bottom decreased the abundance of macrophytes. This is critical because biomanipulation attempts to shift the system to an alternative clear water state with increased macrophyte cover, but sediment particles resuspended by benthic feeding fishes can suppress macrophytes. In this system, the importance of bioturbation in releasing nutrients to the water column is still not fully understood, but this study demonstrates the importance of both excretion and bioturbation mechanisms.

Another potentially important mechanism of benthic feeding fishes is the resuspension of phytoplankton that sediment out or are meroplanktonic. Roozen et al. (2007) found that a major effect of benthivorous fishes was to physically resuspend phytoplankton, especially taxa such as diatoms and green algae, that have a high sedimentation velocity. Our 2006 experiments show mixed support for this hypothesis. During March 2006, the paddle treatment maintained high concentrations of phytoplankton, likely by simply keeping phytoplankton up in the water column. In the fishless enclosures, chlorophyll concentrations declined rapidly, whereas treatments with fish and the paddle treatment maintained high chlorophyll *a* concentrations throughout the experience. However, during our May 2006 experiment, the chlorophyll *a* concentrations declined even where fish could feed on sediments, and only later increased in the treatment where fish can feed on sediment. This indicates a bit of a time lag prior to the increase in phytoplankton, indicating that it probably is increasing in response to nutrients released via excretion and/or bioturbation.

Gido (2003) conducted an enclosure/exclosure experiment using gizzard shad to determine the impact of this species on benthic invertebrates. At high fish density, gizzard shad could suppress the densities of chironomids and ostracods, but not in the experiment using typical gizzard shad densities (175-213 kg/ha). Effects were thought to be due to sediment disturbance rather than via direct consumption. Likely, gizzard shad could impact other sedimentary organisms via their feeding activities and sediment processing, but this mechanism is not well understood as few studies have examined it.

Overall, benthivores can impact lake systems in a variety of ways, including suspension of sediment and/or phytoplankton, subsequent shading of macrophytes, release of nutrients from pore waters or from sediment particles, and direct excretion of nutrients derived from sediment organisms or detritus. Because of these varied effects, several investigators have stressed the importance of focusing on the removal of benthivores and omnivores during biomanipulation efforts (Hansson et al. 1998, Meijer et al. 1999). In addition, several investigators have stressed the need to conduct strong manipulations (Hansson et al. 1998, Meijer et al. 1999, Søndergaard et al. 2000), which can restrict the manipulations to smaller systems (Meijer et al. 1999, Jeppesen et al. 2007). If these recommendations are considered and if external loading of nutrients can be reduced, then biomanipulation efforts can be a practical and cost effective means of improving water quality (Hansson et al. 1998, Meijer et al. 1999, Horpilla et al. 1998).

Chapter 4 – Preliminary Diet Analysis of Lake Apopka Gizzard Shad

Introduction

Understanding the diets of organisms is critical to fully understand their role in ecosystems. For organisms with specialized diets, this can be more straightforward. However, for omnivores and detritivores, it is much more difficult to quantify the importance of different food sources, and thus their potential impacts in ecosystems. This is especially the case for omnivores who ingest detritus, as detritus often represents a poorer quality food source (Mundahl and Wissing 1987), leading some to infer that it is less important than high quality food sources that are more easily digested and assimilated. Despite this, detritus is used extensively by some species (i.e., Goulding 1981, Bowen 1981, 1983, Winemiller 1990, Deegan et al. 1990). Even omnivores that rely on benthic macroinvertebrates have been found to use detritus to supplement their diets, especially when organisms are rare (Ahlgren 1990).

The difficulty quantifying the diets of facultative omnivores is enhanced because of diet flexibility across systems and over time. As a result, some investigators have used stable isotopes to quantify diet over longer time intervals (Peterson et al. 1985, Peterson and Fry 1987). The advantage of this method is that it measures food actually assimilated, and integrates feeding history over long time scales. One disadvantage is that it can be difficult to interpret intermediate isotopic values in cases where multiple food sources could potentially contribute to a mixed diet. In these cases, isotopic analysis can benefit from the utilization of gut content analysis to clarify potential food sources that may contribute to an organism’s nutrition.

In lakes and reservoirs of the southern and Midwestern U.S., the gizzard shad, *Dorosoma cepedianum* can often dominate fish communities, especially in eutrophic to hypereutropic systems (Bachmann et al. 1996). This species relies exclusively on zooplankton as larvae, and then develops gut adaptations, such as a gizzard and a long and convoluted intestine while a juvenile (Heinrichs 1982). From this point on, it can increase its reliance on detritus as a food source, and can switch from zooplankton, its preferred food item, to organic detritus associated with sediments when zooplankton are rare (Heinrichs 1982, Schaus et al. 2002). In some lakes, gizzard shad rely heavily on detritus (Mundahl and Wissing 1987, Higgins et al. 2006), whereas in other systems, planktonic food sources contribute much more to the diet (Mundahl 1988, Gu et al. 1996, Mitchell et al. 1996). The ability to switch to planktonic prey can increase growth rates (Schaus et al. 2002), and allow this species to capitalize on temporally variable prey, while still relying on a ubiquitous reserve food source.

The role of gizzard shad can vary substantially in lakes based on the composition of its diet. When planktonic foods comprise the majority of the diet, this species primarily recycles nutrients within the water column and does not contribute greatly to internal "loading" of nutrients. However, when it feeds extensively on organic detritus associated with sediments or on benthic macroinvertebrates, it can transport nutrients from benthic to pelagic habitats via its excretion and bioturbation. Nutrient translocation between habitats by fishes can potentially be important to productivity in a number of systems (i.e., Bray et al. 1981, Meyer and Schultz 1985, Kline et al. 1990, Vanni 2002, Haertel-Borer et al. 2004). Preliminary analysis of gizzard shad diets in Lakes Apopka and Dora were completed as a part of this study to examine the role of this species within the nutrient dynamics of these systems.

Methods

To provide a preliminary measure of gizzard shad diet, we conducted gut content analysis on 38 gizzard shad from Lake Apopka (N = 26 fish) and Lake Dora (N = 12 fish) following methods modified from Ahlgren and Bowen (1992) and Schaus et al. (2002). Gizzard shad (39.4-587.2g wet mass) were collected from Lake Dora on May 4th, 2007 and 30 May 30th, 2007, and were collected from Lake Apopka and the portion of the Apopka-Beauclair Canal adjacent to Lake Apopka on Jan. 24th, 2007 and May 4th, 2007, using an airboat mounted electroshocker. All fish were placed immediately on ice and frozen for later diet analysis. In the lab, individual fish were thawed and the entire digestive tract was removed. Contents of the foregut between the gizzard and the pharynx were extruded and dispersed in <1mL of deionized water. A subsample of this material (approximately ⅓ of the sample) was transferred to a Sedgewick-Rafter zooplankton counting cell for direct counts of zooplankton, and the remainder of the material was filtered onto a preweighed 1µm pore size glass fiber filter, and frozen for later chlorophyll analysis. Four of the chlorophyll filters (3 from lake Dora and 1 from Lake Apopka) were simultaneously dropped in preparation for chlorophyll analysis, thus these fish could only be used for zooplankton measures and not chlorophyll measures.

Contents of the Sedgewick-Rafter cell were examined; zooplankton were identified to the lowest taxonomic unit and enumerated. Contents of the Sedgewick-Rafter cell were then rinsed into a preweighed aluminum weighing boat and dried to a constant mass at 60 ˚C. The sample was then ignited in a muffle furnace at 550 ˚C in order to remove all organic material prior to reweighing. The proportion of organic material was then estimated as ash free dry mass (AFDM), the proportion of mass lost on ignition. Control weighing boats were used to correct for the mass loss on ignition of boats without a sample. The total mass of zooplankton was determined by measuring the lengths of zooplankton (and widths for rotifers) observed in the guts using an ocular micrometer. Measurements were converted to dry biomass using published equations for zooplankton dry mass (Dumont et al. 1975, Bottrell et al. 1976, Culver et al. 1985), volumetric conversions (Bottrell et al. 1976, Ruttner-Kolisko 1977), and wet-dry mass ratios (Dumont et al. 1975, Bottrell et al. 1976).

The subsample frozen on the glass fiber filter was dried to a constant weight at 60 ˚C (typically this took 2-3 hours). This subsample was then analyzed for chlorophyll by spectrophotometry following extraction in 90% alkaline acetone, following the methods of Wetzel and Likens (2000). The mass of chlorophyll was then used to estimate the dry mass of phytoplankton and meroplankton using a Chlorophyll:Biomass ratio of 204:1 (Canfield et al. 1985). From the estimates of algal and zooplankton/zoobenthos biomass and from the proportion of the subsample that was AFDM, we were able to calculate the percent of AFDM in each sample that was comprised of zooplankton and phytoplankton, and thus estimate the contribution of these items to the diet. Percent detritus was determined by difference (Ahlgren and Bowen 1992) between total AFDM and the mass that was comprised of phytoplankton and zooplankton/zoobenthos. Diet composition across the range of sizes observed was examined statistically using regression on arcsine square root transformed % of AFDM data for % zooplankton, % algae, and % detritus.

Results

All fish demonstrated qualitative evidence of consuming detritus, as plant fibers and amorphous detrital particles were observed in all subsamples analyzed for zooplankton, and detritus comprised an average of 97.5% of the mass of the foregut contents. Most fish also demonstrated at least some evidence of planktivory, as 36 of 38 fish contained some zooplankton/zoobenthos in the gut contents and measurable quantities of chlorophyll were observed in 25 out of 34 fish. Zooplankton/zoobenthos typically comprised <1% of the organic matter in the guts, with a mean of 0.29% of the diet (Fig. 4-1). Cladocerans were most frequently observed, both numerically (35.4%) and by biomass (53.3%), with ostracods and copepods also comprising at least 15% of the individuals and biomass of zooplankton/zoobenthos. Rotifers comprised 21.4% of the zooplankton counted in the guts, but these amounted to <0.5% of the zooplankton/zoobenthos biomass measured in guts because of their very small sizes. Algae typically comprised <5% of the organic material in the guts (Fig. 4-1), with a mean of 2.18%. Across the sizes of fish examined, there was no significant effect of fish size on % zooplankton in the diet (P=0.099). However, there was a weak but statistically significant decrease in algal consumption (P=0.027, R^2=0.143) and a weak but statistically significant increase in detritus consumption (P=0.012, R^2=0.183) with fish size, but this was based on a comparison with a small sample size from a limited number of dates. Overall, one fish had detritus comprising only ~77% of the diet and a second had 89% detritus in the foregut. All other fish had >95% detritus in their foreguts. Our results demonstrated little planktivory, however, the limitations of the study greatly restrict the widespread applications of these findings.

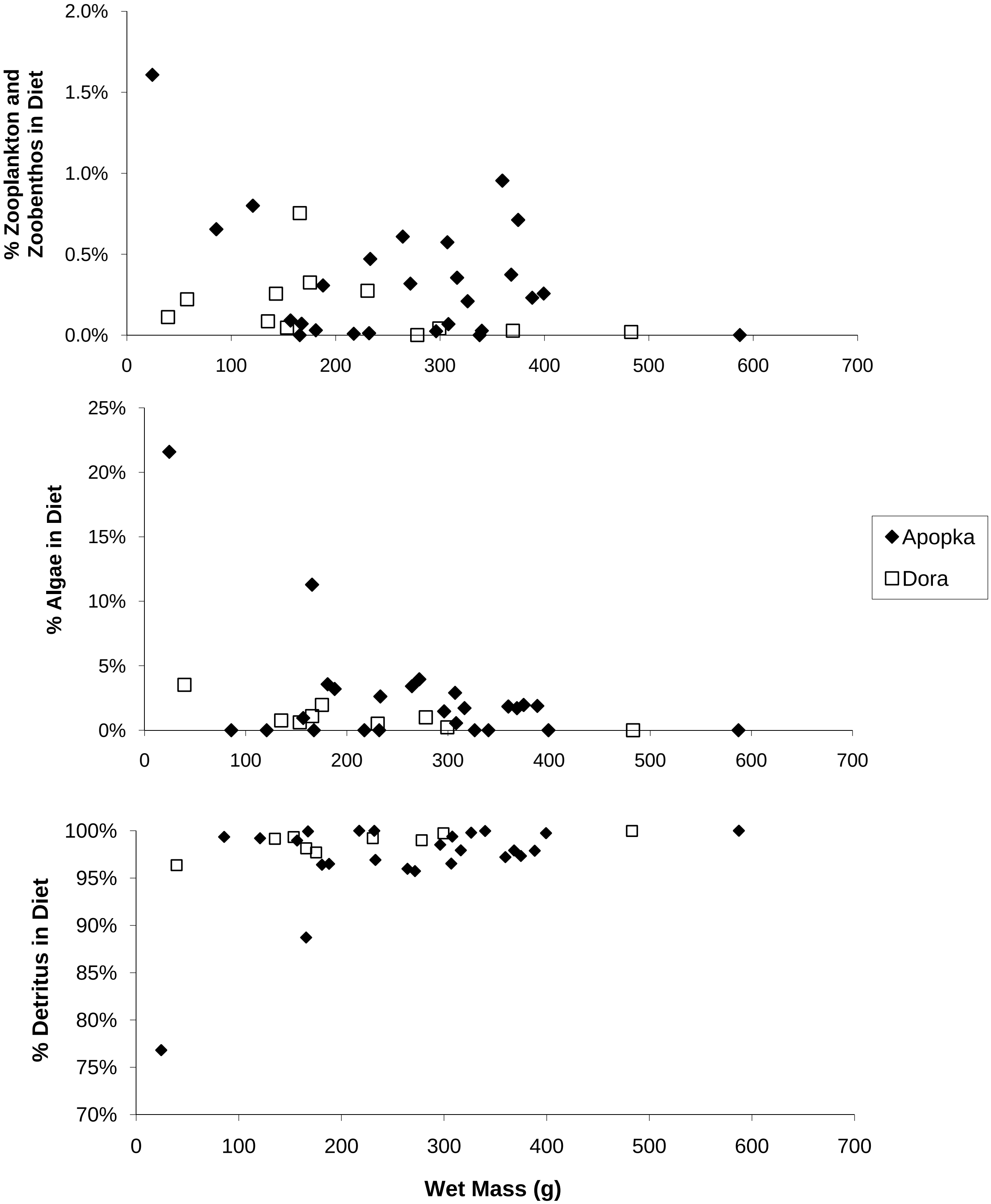

Fig. 4-1 Quantification of zooplankton and zoobenthos (top panel), algae (middle panel), and detritus (bottom panel) in the diet. Mean % zooplankton/zoobenthos was 0.29%, mean algae was 2.18% and mean detritus was 97.51% of AFDM in gizzard shad foreguts.

Discussion

Our results indicated that gizzard shad rely on a mixed diet comprised primarily of organic detritus, with some algal materials, and zooplankton/zoobenthos. These results must be interpreted with caution, as they come from a fairly limited sample size and represent a snapshot of feeding during the times when the fish were collected. During the times we sampled the fish, detritus comprised the majority of the food occurring in the guts. Many of the organisms observed in the guts are frequently associated with sediments or littoral areas (i.e., Ostracods, *Alona*), and many algae in Lake Apopka are meroplanktonic, and thus could be from either benthic or pelagic habitats. The importance of planktonic foods in the long term nutrition of this species will depend on the frequency with which these items are included in the diet, which can depend on periodic peaks of algae and/or zooplankton abundance. Regardless, the vast majority of AFDM in these fish came from organic detritus.

One other factor that can increase the importance of planktonic foods in the diet of gizzard shad is that these items are more easily digested than sediment detritus and decaying plant materials. These items are also more likely to be higher in carbon, nitrogen, and phosphorus than sediment foods, but we did not explicitly measure this. For example, if zooplankton and algae averaged ~50% carbon, but sediments averaged ~10% carbon (Schaus et al. 2002), this could increase the importance of planktonic foods 5-fold over their proportional mass in the diet. However, Mundahl and Wissing (1988) found that Acton Lake (OH) gizzard shad had a high assimilation efficiency for C and N when feeding on low quality detrital food sources and that shad could selectively ingest the fraction of the sediments enriched in organic material and nutrients. Smoot (1999) demonstrated that low density sediment materials in this system were higher in carbon and nutrients than were the higher density sediments. Thus some sort of physical sorting mechanism that removes the denser particles may allow this species to more efficiently feed on detritus and rely extensively on it.

Stable isotope analysis has also helped to shed insight on the longer term nutritional history of this species and other species. This technique is particularly effective because it integrates feeding history over the time scale of tissue turnover and measures foods actually assimilated, and not just consumed. In Lake Apopka, Gu et al. (1996) used stable C and N isotopes to estimate that gizzard shad derives approximately 40% of its diet from zooplankton, with the remainder presumed to be comprised of detritus. In Lake Dora, Catalano et al. (2007) used stable S isotopes to determine that gizzard shad in that system shift from planktonic foods at small sizes to extensively rely on benthic detritus at sizes 100-250mm TL, and then shift back to more extensive reliance on planktonic foods at sizes from 250-450mm TL. Our analysis demonstrated no evidence of a shift back to planktonic sources, but our analysis relied on limited sample sizes, which could have missed a seasonal pulse of planktivory in the diets.

In other systems, gizzard shad have been shown to have a diet that can rely extensively on detritus but take advantages of peaks in zooplankton abundance (Gido 2001, Schaus et al. 2002). Typically isotope analysis has shown that this species exhibits a diet that is mixed between sediments and other potential food sources (Thorpe et al. 1996, Mitchell et al. 1996). Even in systems such as Oneida Lake, where gizzard shad rely extensively on zooplankton, the isotopic signals are still intermediate between that of zooplankton and sediments, but closer to the signal of planktonic foods (Mitchell et al. 1996). Gizzard shad have also been shown to shift substantially between food sources, due to this species' omnivorous food habits and shifts of the availability of preferred food items. (Thorpe et al. 1998, Gido 2001, Schaus et al. 2002).

A better understanding of gizzard shad diets helps to better understand the role of this species in nutrient dynamics of the system. In systems where gizzard shad relies heavily on zooplankton, it would primarily recycle nutrients within the water column, whereas when it relies heavily on benthic food sources, shad can transport nutrients from benthic to pelagic habitats, thus providing phytoplankton with a “new” source of nutrients that would not directly be available to them (Vanni 2002). In systems where gizzard shad feed on a mixed diet, it is important to quantify the proportion of the diet that is from benthic sources, in order to better quantify the role of this species. Future studies could evaluate the diet of this species across a gradient of productivity or across latitudes to determine the degree to which gizzard shad diets vary in their reliance on planktonic vs. benthic sources and whether this shows predictable trends.

In Lakes Apopka and Dora, it appears as though sediment detritus makes a substantial contribution to the diet of gizzard shad, even though some of its diet does come from pelagic sources, (Gu et al. 1996, Catalano et al. 2007, this study). Even if the planktonic nutrients are more easily digested and assimilated, gizzard shad still show strong evidence of feeding on benthic materials and benthic species (Catalano et al. 2007). Thus, shad are more likely to be important in internal loading of nutrients via excretion and in bioturbation of sediments via their feeding activities. Also, the large scale biomanipulation efforts that have been conducted in Lakes Apopka, Dora, Griffin, and Denham may make a substantial impact on internal loading of nutrients, especially when nutrient excretion is higher, when smaller fish can be effectively captured (because smaller fish excrete more per gram), and when fish biomass can be greatly suppressed by the biomanipulation. If anthropogenic nutrient inputs to these systems can be greatly reduced, then biomanipulation offers the potential to further reduce internal nutrient loading, allowing the potential for these systems to shift to a stable clear water state.

Recently, improvements in water quality have been observed in some, but not all of the systems that SJRWMD has conducted extensive gizzard shad removals on (Godwin et al. 1993, Godwin et al. 2006, but see Catalano et al. 2007). These improvements have the potential to impact lake systems through several means, including direct nutrient removal (Godwin et al. 2006, Chapter 1), reduction in internal nutrient loading (Chapters 1-2), reduction in planktivory (Schaus and Vanni 2000, Schaus et al. 2002), decreased competition with larval game fish, and shifts to a stable clear water state (Scheffer 1998). A challenge for the future is to identify systems where fish reductions have a strong potential for success (Håkanson et al. 2003, Jeppesen et al. 2007) and the least chance for negative impacts (Catalano et al. 2007).

References Cited

Aday D.D., R.J.H. Hoxmeier, and D.H. Wahl. 2003. Direct and indirect effects of gizzard shad on bluegill growth and population size structure. Transactions of the American Fisheries Society 132:47-56.

Ahlgren, M.O. 1990. Nutritional significance of facultative detritivory to the juvenile white sucker (*Catostomus commersoni*). Canadian Journal of Fisheries and Aquatic Sciences 47:49-54.

Ahlgren, M.O. and S.H. Bowen. 1992. Comparison of quantitative light microscopy techniques used in diet studies of detritus-consuming omnivores. Hydrobiologia 239:79-83.

Allen, M. S., M. V. Hoyer, and D. E. Canfield, Jr. 2000. Factors related to gizzard shad and threadfin shad occurrence and abundance in Florida lakes. Journal of Fish Biology 57:291-302.

Bachmann, R.W., B.L. Jones, D.D. Fox, M. Hoyer, L.A. Bull, and D.E. Canfield, Jr. 1996. Relations between trophic state indicators and fish in Florida (U.S.A.) lakes. Canadian Journal of Fisheries and Aquatic Sciences 53:842-855.

Bottrell, H.H., A Duncan, Z.M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology 24:419-456.

Bowen, S.H. 1981. Digestion and assimilation of periphytic detrital aggregate by *Tilapia mossambica*. Transactions of the American Fisheries Society 110:239-245.

Bowen, S.H. 1983. Detritivory in neotropical fish communities. Environmental Biology of Fishes 9:137-144.

Brabrand, Å., B.A. Faafeng, and J.P.M. Nilssen. 1990. Relative importance of phosphorus supply to phytoplankton production: Fish excretion versus external loading. Canadian Journal of Fisheries and Aquatic Sciences 47:364-372.

Bray, R.N., A.C. Miller, and G.G. Gessey. 1981. The fish connection: A trophic link between planktonic and rocky reef communities? Science 214:204-205.

Breukelaar, A.W., E.H.R.R. Lammens, and J.G.P.K Breteler. 1994. Effects of benthivorous bream (*Abramis brama*) on sediment resuspension and concentrations of nutrients and chlorophyll *a*. Freshwater Biology 32:113-121.

Canfield, D.E. Jr., S.B. Linda, and L.M. Hodgson. 1985. Chlorophyll-biomass-nutrient relationships for natural assemblages of Florida phytoplankton. Water Resources Bulletin 21:381-391.

Caraco N.F., J.J. Cole, and G.E. Likens. 1992. New and recycled primary production in an oligotrophic lake: Insights for summer phosphorus dynamics. Limnology and Oceanography 37:590-602.

Carpenter, S.R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677-680.

Carpenter, S.R. 2005. Eutrophication of aquatic ecosystems: Bistability and soil phosphorus. Proceedings of the National Academy of Sciences of the United States of America 102:10002-10005.

Carpenter, S.R., J.F. Kitchell, J.R. Hodgson, P.A. Cochran, J.J. Elser, M.M. Elser, D.M. Lodge, D. Kretchmer, X. He, and C.N. von Ende. 1987. Regulation of lake primary productivity by food web structure. Ecology 68:1863-1876.

Catalano, M.J., J.R. Dotson, L. DeBrabandere, M.S. Allen, and T.K. Frazer. 2007. Biomanipulation impacts on gizzard shad population dynamics, lake water quality, and a recreational fishery. Final Report. St. Johns River Water Management District, Palatka, Florida.

Coveney, M.F., E.F. Lowe, L.E. Battoe, E.R. Marzolf, and R. Conrow. 2005. Response of a eutrophic shallow subtropical lake to reduced nutrient loading. Freshwater Biology 50:1718-1730, and erratum, Freshwater Biology 50:2167.

Coveney, M.F., D.L. Stites, E.F. Lowe, L.E. Battoe, and R. Conrow. 2002. Nutrient removal from eutrophic lake water by wetland filtration. Ecological Engineering 19:141-159.

Crumpton, J.E. and W.F. Godwin. 1997. Rough fish harvesting in Lake Apopka, summary report, 1993-1997. Special Publication SJ97-SP23. St. Johns River Water Management District, Palatka, FL.

Culver, D.A., M.M. Boucherle, D.J. Bean, and J.W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Canadian Journal of Fisheries and Aquatic Sciences. 42:1380-1390.

Davis, J.A. and C.E. Boyd. 1978. Concentration of selected elements and ash in bluegill (*Lepomis macrochirus*) and certain other freshwater fish. Transactions of the American Fisheries Society 107:862-867.

Deegan, L.A., B.J. Peterson, and R. Porter. 1990. Stable isotopes and cellulase activity as evidence for detritus as a food source for juvenile gulf menhaden. Estuaries 13: 14-19.

DiCenzo, V.J., M.J. Maceina, and M.R. Stimpert. 1996. Relations between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. North American Journal of Fisheries Management 16:888-895.

Drenner, R.W., K.L. Gallo, R.M Baca, and J.D. Smith. 1998. Synergistic effects of nutrient loading and omnivorous fish on phytoplankton biomass. Canadian Journal of Fisheries and Aquatic Sciences 55:2087-2096.

Drenner, R. W., and K. D. Hambright. 1999. Review: Biomanipulation of fish assemblages as a lake restoration technique. Archiv für Hydrobiologie 146:129-165.

Drenner, R.W. and A. Mazumder. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: Comment. Ecology 80:1081-1085.

Drenner, R.W., J.D. Smith, and S.T. Threlkeld. 1996. Lake trophic status and the limnological effects of omnivorous fish. Hydrobiologia 319:213-223.

Drenner, R.W., S.T. Threlkeld, and M.D. McCracken. 1986. Experimental analysis of direct and indirect effects of an omnivorous filter-feeding clupeid on plankton community structure. Canadian Journal of Fisheries and Aquatic Sciences 43:1935-1945.

Dugdale, R.C. and J.J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnology and Oceanography 12:196-206

Dumont, H.J., I Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of cladocera, copepoda, and rotifera from the plankton, periphyton, and benthos of continental waters. Oecologia 19:75-97.

Gido, K.B. 2001. Feeding ecology of three omnivorous fishes in lake Texoma (Oklahoma-Texas). Southwestern Naturalist 46:23-33.

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.

Gido, K.B. 2003. Effects of gizzard shad on benthic communities in reservoirs. Journal of Fish Biology 62:1392-1404.

Gido, K.B. and W.J. Matthews. 2000. Dynamics of the offshore fish assemblage in a southwestern reservoir (Lake Texoma, Oklahoma-Texas). Copeia 2000:917-930.

Glaholt, S.P. Jr. and M.J. Vanni. 2005. Ecological responses to simulated benthic-derived nutrient subsidies mediated by omnivorous fish. Freshwater Biology 50:1864-1881.

Godwin, W.F., L. Battoe, M. Coveney, E. Lowe, R. Roth, M. Schaus, and B. Sparks. 2006. Manipulation of omnivorous fish stocks as a restoration component for Ocklawaha basin lakes. Proceedings of the Florida Lake Management Society 17:P4-P5.

Godwin, W.F., S.G. Coyne and E.A. Gisondi. 1993. An evaluation of methods for removal of rough fish as a restorative technique for Lake Apopka. Technical Memorandum No. 3. St

Johns River Water Management District, Palatka, FL.

Goulding, M. 1981. The fishes and the forest: Explorations in Amazonian natural history. University of California Press.

Gu, B., C.L. Schelske, and M.V. Hoyer. 1996. Stable isotopes of carbon and nitrogen as indicators of diet and trophic structure in a shallow hypereutrophic lake. Journal of Fish Biology 49:1233-1243.

Haertel-Borer, S.S., D.M. Allen, and R.F. Dame. 2004. Fishes and shrimps are significant sources of dissolved inorganic nutrients in intertidal salt marsh creeks. Journal of Experimental Marine Biology and Ecology 311:79-99.

Håkanson, L., V.V. Boulion, and A.P. Ostapenia. 2003. The influence of biomanipulations (fish removal) on the structure of lake foodwebs, case studies using the LakeWeb-model. Aquatic Ecology 37:87-99.

Hall, R.O., Jr., B.J. Koch, M.C. Marshall, B.W. Taylor, and L.M. Tronstad. 2007. How body size mediates the role of animals in nutrient cycling in aquatic ecosystems. Pages 286-305 *in* A.G. Hildrew, D.G. Raffaelli, and R. Edmonds-Brown, eds. Body size: The structure and function of aquatic ecosystems. Cambridge University Press.

Hansson, L.A., H. Annadotter, E. Bergman, S.F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P-Å Nilsson, M. Søndergaard, and J. Strand. 1998. Biomanipulation as an application of food-chain theory: Constraints, synthesis, and recommendations for temperate lakes. Ecosystems 1:558-574.

Havens, K.E. 1991. Fish-induced sediment resuspension: Effects on phytoplankton biomass and community structure in a shallow hypereutrophic lake. Journal of Plankton Research 13:1163-1176.

Havens, K.E. 1993. Responses to experimental fish manipulations in a shallow, hypereutrophic lake-the relative importance of benthic nutrient recycling and trophic cascade. Hydrobiologia 254:73-80.

Heinrichs, S.M. 1982. Ontogenetic changes in the digestive tract of larval gizzard shad, *Dorosoma cepedianum*. Transactions of the American Microscopical Society 101:262-275.

Higgins, K.A., Vanni, M.J. and Gonzalez, M.J. 2006. Detritivory and the stoichiometry of nutrient cycling by a dominant fish species in lakes of varying productivity. Oikos 114:419-430.

Horppila, J., H. Peltonen, T. Malinen, E. Luokkanen, and T. Kairesalo. 1998. Top-down or bottom-up effects by fish: Issues of concern in biomanipulation of lakes. Restoration Ecology 6:20-28.

Hrbáček, J. M. Dvořakova, V. Kořínek, and L. Procházkóva. 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Internationale Vereingung für Theoretische und Angewandte Limnologie, Verhandlungen 14:192-195

Hurlbert, S.H., J.B. Zedler and D.A. Fairbanks. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Science 175:639-641.

Irwin, B.J., D.R. DeVries, and G.W. Kim. 2003. Responses to gizzard shad recovery following selective treatment in Walker County Lake, Alabama, 1996-1999. North American Journal of Fisheries Management 23:1225-1237.

Jeppesen, E., and coauthors. 2007. Restoration of shallow lakes by nutrient control and biomanipulation - the successful strategy varies with lake size and climate. Hydrobiologia 581:269-285.

Johnson, B. M., R. A. Stein, and R. F. Carline. 1988. Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. Transactions of the American Fisheries Society 117:127-141.

Kim, G. W., and D. R. DeVries. 2000. Effects of a selectively reduced gizzard shad population on trophic interactions and age-0 fishes in Walker County Lake, Alabama. North American Journal of Fisheries Management 20:860-872.

Kline, T.C. Jr., J.J. Goering, O.A. Mathisen, and P.H. Poe. 1990. Recycling of elements transported upstream by runs of Pacific Salmon: I. δ^{15}N and δ^{13}C evidence in Sashin Creek, Southeastern Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:136-144.

Lamarra, V.A., Jr. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Internationale Vereingung für Theoretische und Angewandte Limnologie, Verhandlungen 19:2461-2468.

Mather, M.A., M.J. Vanni, T.E. Wissing, S.A. Davis, and M.H. Schaus. 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

Matsuzaki, S.S., N. Usio, N. Takamura, and I. Washitani. 2007. Effects of common carp on nutrient dynamics and littoral community composition: Roles of excretion and bioturbation. Fundamental and Applied Limnology 168:27-38.

Meijer, M.-L., I. de Bois, M. Scheffer, R. Portielje, and H. Hosper. 1999. Biomanipulation in shallow lakes in the Netherlands: An evaluation of 18 case studies. Hydobiologia 408/409:13-30.

Meijer, M-L., M.W. de Haan, A.W. Breukelaar, and H. Buiteveld. 1990. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? Hydrobiologia 200/201:303-315.

Meyer, J.T. and E.T. Schultz. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnology and Oceanography 30:146-156.

Michaletz, P.H. and J.L. Bonneau. 2005. Age-0 gizzard shad abundance is reduced in the presence of macrophytes: Implications for interactions with bluegills. Transactions of the American Fisheries Society 134:149-159.

Miranda, L.E. 1983. Average ichthyomass in Texas large impoundments. Proceedings of the Texas Chapter of the American Fisheries Society 6:58-67.

Mitchell, M.J., E.L. Mills, N. Idrisi, and R. Michener. 1996. Stable isotopes of nitrogen and carbon in an aquatic food web recently invaded by *Dreissena polymorpha* (Pallas). Canadian Journal of Fisheries and Aquatic Sciences 53:1445-1450.

Moss, B., J. Stansfield, K. Irvine, M. Perrow, and G. Phillips. 1996. Progressive restoration of a shallow lake: A 12-year experiment in isolation, sediment removal and biomanipulation. Journal of Applied Ecology 33:71-86.

Mundahl, N.D. 1988. Nutritional quality of foods consumed by gizzard shad in western Lake Erie. Ohio Journal of Science 88:110-113.

Mundahl, N.D., and T. E. Wissing. 1987. Nutritional importance of detritivory in the growth and condition of gizzard shad in an Ohio reservoir. Environmental Biology of Fishes 20(2):129-142.

Mundahl, N. D., and T. E. Wissing. 1988. Selective and digestive efficiencies of gizzard shad feeding on natural detritus and two laboratory diets. Transactions of the American Fisheries Society 117:480-487.

Ogilvie, B.G. and S.F. Mitchell. 1998. Does sediment resuspension have persistent effects on phytoplankton? Experimental studies in three shallow lakes. Freshwater Biology 40:51-63.

Persson, A. 1997a. Effects of fish predation and excretion on the configuration of aquatic food webs. Oikos 79:137-146.

Persson, A. 1997b. Phosphorus release by fish in relation to external and internal load in a eutrophic lake. Limnology and Oceanography 42:577-583.

Persson L., L. Johansson, G. Andersson, S. Diehl, and S.F. Hamrin. 1993. Density dependent interactions in lake ecosysytems: Whole lake perturbation experiments. Oikos 66:193–208.

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320.

Peterson, B.J., R.W. Howarth, and R.H. Garritt. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science 227:1361-1363.

Pierce, R.J, T.E. Wissing and B.A. Megrey. 1981. Aspects of the feeding ecology of gizzard shad in Acton lake, Ohio. Transactions of the American Fisheries Society 110:391-395.

Roozen, F.C.J.M., M. Lürling, H. Vlek, E.A.J. Van der Pouw Kraan, B.W. Ibelings, and M. Scheffer. 2007. Resuspension of algal cells by benthivorous fish boosts phytoplankton biomass and alters community structure in shallow lakes. Freshwater Biology 52:977-987.

Ruttner-Kolisko, A. 1977. Suggestions for biomass calculation of planktonic rotifers. Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie 8:71-76.

Schaus, M. H. and M. J. Vanni. 2000. Effects of omnivorous gizzard shad on phytoplankton and nutrient dynamics: Role of sediment feeding and fish size. Ecology 81:1701-1719.

Schaus, M.H., M.J. Vanni, and T.E. Wissing. 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., M. J. Vanni, T. E. Wissing, M. T. Bremigan, J. E. Garvey, and R. A. Stein. 1997. Nitrogen and phosphorus excretion by detritivorous gizzard shad (*Dorosoma cepedianum*) in a reservoir ecosystem. Limnology and Oceanography 42:1386-1397.

Scheffer, M. 1998. Ecology of shallow lakes. Kluwer Academic Publishers, Dordrecht.

Scheffer, M., S.H. Hosper, M-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8:275-279.

Schelske C.L., E.F. Lowe, L.E. Battoe, M. Brenner, M.F. Coveney and W.F. Kenney. 2005. Abrupt Biological Response to Hydrologic and Land-use Changes in Lake Apopka, Florida, USA. Ambio 34:192-198.

Schelske, C.L. 1997. Sediment and phosphorus deposition in Lake Apopka. Special Publication SJ97-SP21, St. Johns River Water management District, Palatka, Florida.

Schindler, D.E., R.A. Knapp, and P.R. Leavitt. 2001. Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. Ecosystems 4:308-321.

Schmidt-Nielsen, K. 1975. Animal physiology, adaptation, and environment. Cambridge University Press.

Schramm, H.L. Jr. and L.L. Pugh 1997a. Gizzard shad stock estimation for Lake Apopka, Florida, 1995. Special Publication SJ97-SP10, St Johns River Water Management District.

Schramm, H.L. Jr. and L.L. Pugh 1997b. Gizzard shad stock estimation for Lake Apopka, Florida, 1996. Special Publication SJ97-SP11, St Johns River Water Management District.

Shapiro, J. and R.E. Carlson. 1982. Comment on the role of fishes in the regulation of phosphorus availability in lakes. Canadian Journal of Fisheries and Aquatic Sciences 39:364.

Shostell, J. and P.A. Bukaveckas. 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.

Smith, V.H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221:669-671.

Smoot, J.C. 1999. A field study of sedimentary microbiota as food for detritivorous gizzard shad, *Dorosoma cepedianum*, in Acton Lake: A biomarker approach. Doctoral Dissertation. Miami University, Oxford, Ohio.

Søndergaard, M., E. Jeppesen, J. P. Jensen, and T. Lauridsen. 2000. Lake restoration in Denmark. Lakes and Reservoirs: Research and Management 5:151-159.

Stein, R.A., D.R. DeVries, and J.M. Dettmers. 1995. Food-web regulation by a planktivore: Exploring the generality of the trophic cascade hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 52:2518-2526.

Sterner, R. W. 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. American Naturalist 136:209–229.

Tarvainen, M, A-M Ventela, H. Helminen, and J. Sarvala. 2005. Nutrient release and resuspension generated by ruffe (*Gymnocephalus cernuus*) and chironomids. Freshwater Biology 50:447–458.

Thorpe, J.H., M.D. Delong, K.S. Greenwood, and A.F. Casper. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. Oecologia 117:551-563.

Threlkeld, S.T. 1987. Experimental evaluation of trophic-cascade and nutrient-mediated effects of planktivorous fish on plankton community structure. Pages 161-173 *in* W.C. Kerfoot and A. Sih, eds. Predation – Direct and indirect impacts on aquatic communities. University Press of New England, Hanover.

Threlkeld, S.T. 1994. Benthic-pelagic interactions in shallow water columns: An experimentalist’s perspective. Hydrobiologia 275/276:293-300.

Threlkeld, S.T. and R.W. Drenner. 1987. An experimental mesocosm study of residual and contemporary effects of an omnivorous, filter-feeding, clupeid fish on plankton community structure. Limnology and Oceanography 32:1331-1341.

Vanni, M.J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics 33:341-370.

Vanni, M.J., K.K. Arend, M.T. Bremigan, D.B. Bunnell, J.E. Garvey, M.J. González, W.H. Renwick, P.A. Soranno, and R.A. Stein. 2005. Linking landscapes and food webs: Effects of omnivorous fish and watersheds on reservoir ecosystems. BioScience 55:155-167.

Vanni, M.J., Bowling, A.M., Dickman, E.M., Hale, R.S., Higgins, K.A., Horgan, M.J., Knoll, L.B., Renwick, W.H., and Stein, R.A. 2006. Nutrient cycling by fish supports relatively more primary production as lake productivity increases. Ecology 87:1696-1709.

Vanni, M.J., A.S. Flecker, J.M. Hood, and J.L. Headworth. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: Linking species identity and ecosystem processes. Ecology Letters 5:285-293.

Vanni, M.J. and C.D. Layne. 1997. Nutrient recycling and herbivory as mechanisms in the “top-down” effect of fish on algae in lakes. Ecology 78:21-40.

Vanni, M.J., C.D. Layne, and S.E. Arnott. 1997. “Top-down” trophic interactions in lakes: Effects of fish on nutrient dynamics. Ecology 78:1-20.

Vanni, M.J., C. Luecke, J.F. Kitchell, Y. Allen, J. Temte, and J.J. Magnuson. 1990. Effects on lower trophic levels of massive fish mortality. Nature 344:333-335.

Vollenweider, R.A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell’Instituto Italiano di Idrobiolodia dott Mario de Marchi 33:53-83.

Wetzel, R.G. and G.E. Likens. 2000. Limnological Analyses. Springer, New York.

Winemiller, K. 0. 1990. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs 60:331-367.

Xie, L.Q., P. Xie, S.X. Li, H.G. Tang, and H. Liu. 2003. The low TN:TP ratio, a cause or a result of *Microcystis* blooms? Water Research 37:2073-2080.

Yako, L.A., J.M. Dettmers, and R.A. Stein. 1996. Feeding preferences of omnivorous gizzard shad as influenced by fish size and zooplankton density. Transactions of the American Fisheries Society 125:753-759.

Appendix 1 – Mean Monthly Temperature Data (°C) for Lakes Apopka, Dora, and Griffin

Month	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean
								Apopka								
Jan	18.1	15.6	15.9	12.6	19.1	15.9	18.1	16.4	10.5	16.3	13.6	16.8	14.2	16.1	18.4	15.84
Feb	15.2	18.2	15.6	15.6	18.4	16.7	17.2	16.3	15.3	15.8	17.1	16.6	16.0	16.8	14.3	16.34
Mar	14.4	21.5	20.7	15.7	22.7	17.9	19.5	21.1	16.5	17.5	23.0	19.5	18.6	20.3	18.2	19.14
Apr	22.0	24.5	23.6	21.5	22.2	23.0	21.7	23.9	23.4	22.6	24.6	21.1	21.3	23.8	22.5	22.78
May	25.8	26.6	28.4	26.8	25.1	26.5	23.5	25.8	25.6	24.4	28.2	25.1	26.2	24.8	25.4	25.88
Jun	29.8	28.1	26.8	28.1	27.0	29.5	27.0	28.8	26.9	25.9	27.0	29.1	28.5	27.3	26.9	27.78
July	30.0	29.6	30.0	28.3	29.1	29.5	29.4	28.9	27.9	27.1	29.4	28.2	30.0	29.4	28.7	29.03
Aug	29.5	29.3	30.1	28.8	29.0	29.7	29.0	28.9	28.8	29.2	30.3	28.8	30.3	29.4		29.36
Sept	27.9	27.9	28.7	27.0	27.4	27.5	27.2	27.6	25.0	29.1	28.6	27.1	27.9	28.1		27.64
Oct	24.1	25.4	25.9	24.0	23.3	26.8	25.2	23.0	23.0	25.7	25.1	25.5	23.7	24.6		24.66
Nov	19.2	23.8	20.3	20.8	18.9	23.8	21.1	19.2	20.0	17.4	21.5	22.3	21.0	19.9		20.66
Dec	14.2	19.1	18.6	19.7	16.3	19.0	17.8	14.5	19.4	17.5	16.3	15.4	15.5	19.0		17.31
								Dora								
Jan		12.5	15.7	15.3	21.2	18.8	19.5	17.9	15.1	17.1	14.7	15.1	14.9	17.0	18.8	16.69
Feb	17.2							17.7	18.8		17.5	17.5	17.7	18.8	15.5	17.59
Mar		24.5	20.8		23.4	22.5	19.6	21.6	20.9		22.7	20.0	19.7	21.6	18.0	21.28
Apr	22.6							22.9	25.8		23.4	23.4	21.6	24.1	19.9	22.96
May		27.7		29.3	27.9	28.2	26.6	28.2	27.5	27.4	28.5	26.8	25.5	26.9	23.7	27.25
Jun	29.5							30.5	29.3		29.9	29.8	28.2	29.3	27.7	29.28
July		30.2	29.4	31.4	29.8	29.8	31.1	30.7	29.2	28.1	30.0	30.9	30.0	30.4	28.7	29.98
Aug								30.5	31.1		31.4	31.3	31.6	30.3		31.03
Sept	29.0	28.0	30.2	27.8	29.3	27.3	27.1	29.6	27.4	30.6	28.7	27.9	29.1	29.1		28.65
Oct								23.0	24.0		25.1	25.0	23.6	24.1		24.13
Nov	19.0	24.6	24.2	20.4	20.2	24.5	20.7	21.5		18.3	21.4	21.4	21.5	19.7		21.34
Dec							20.1	18.0	22.5		16.1	15.2	16.3	18.8		18.14

Appendix 1 continued

Month	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean
								Griffin								
Jan						16.4	19.0	17.2	14.9	16.1	13.1	15.1	14.9	15.8	18.8	16.13
Feb				15.7	19.8	15.5	16.6	15.9	18.3	16.7	16.5	16.9	17.3	16.5	14.7	16.7
Mar					22.2	18.8	19.4	20.9	18.6	20.3	22.9	19.1	18.8	21.1	19.4	20.14
Apr			23.9	25.0		23.6	24.6	23.3	24.8	24.3	23.8	22.2	22.3	24.5	21.5	23.65
May						27.0	25.3	27.0	27.4	26.4	28.1	26.2	25.7	26.9	23.8	26.38
Jun				29.1	29.5	31.0	28.2	29.0	29.0	27.9	29.1	29.4	28.4	29.6	28.7	29.08
July			30.4			30.3	31.3	30.5	29.1	28.9	29.7	29.3	30.4	30.7	29.0	29.96
Aug			29.9	29.0	28.5	30.7	30.0	30.0	30.1	28.9	28.9	29.5	30.2	30.6	31.4	29.82
Sept				28.1		28.4	27.8	29.0	27.0	29.4	28.3	27.5	27.7	29.2		28.24
Oct			25.4	25.6	23.5	27.0	24.6	22.3	25.1	26.1	25.3	26.0	23.0	24.6		24.88
Nov			17.0		17.4	24.1	19.5	19.7		20.0	22.7	22.2	21.0	20.0		20.36
Dec			14.9	15.9	14.4	19.7	19.0	17.2	22.4	15.7	15.2	16.7	15.4	18.9		17.12

Appendix 2 – Gizzard Shad Excretion Data from Direct Measurements During 2004-2006.

Time Period	Lake	Wet Mass (g)	NH_4-N (mg/fish/hr)	PO_4-P (mg/fish/hr)	N:P (by mass)	Temp (°C)
Jun-04	Apopka	74.2	2.104738	0.353894	5.947368	28
Jun-04	Apopka	58.2	2.052988	0.483056	4.25	28
Jun-04	Apopka	125.5	3.53894	0.83817	4.222222	28
Jun-04	Apopka	99.7	2.121996	0.759088	2.795455	28
Jun-04	Apopka	98.4	3.557566	0.74504	4.775	28
Jun-04	Apopka	14	1.406038	0.04313	32.6	28
Jun-04	Apopka	133.1	5.885816	0.9313	6.32	28
Jun-04	Apopka	113.7	4.712378	1.043056	4.517857	28
Jun-04	Apopka	150	3.240924	1.192064	2.71875	28
Jun-04	Apopka	155.4	3.743826	0.316642	11.82353	28
Jun-04	Apopka	75.1	2.967344	0.681454	4.35443	28
Jun-04	Apopka	72.8	1.276648	0.379544	3.363636	28
Jun-04	Apopka	109.8	5.792686	0.819544	7.068182	28
Jun-04	Apopka	105.8	2.5878	0.595194	4.347826	28
Jun-04	Apopka	85.6	1.707948	0.508934	3.355932	28
Jun-04	Apopka	40	1.155884	0.21565	5.36	28
Jun-04	Apopka	294.8	7.956956	1.892674	4.204082	28
Jun-04	Apopka	194.1	4.209476	0.540154	7.793103	28
Jun-04	Apopka	90.1	1.992606	0.319162	6.243243	28
Jun-04	Apopka	238.4	4.432988	1.080308	4.103448	28
Jun-04	Apopka	96.3	1.63894	0.138016	11.875	28
Jun-04	Apopka	289.3	4.079094	1.02443	3.981818	28
Jun-04	Apopka	263.2	4.731004	0.894048	5.291667	28
Jun-04	Apopka	71.4	1.500924	0.293284	5.117647	28
Jun-04	Apopka	46.2	1.475046	0.310536	4.75	28
Jun-04	Apopka	199.3	3.706574	0.484276	7.653846	28
Jun-04	Apopka	107	1.500924	0.319162	4.702703	28
Jun-04	Apopka	52.9	1.535428	0.293284	5.235294	28
Jun-04	Apopka	138.6	1.974356	0.55878	3.533333	28
Jun-04	Apopka	295.5	3.012828	2.240308	1.344828	28
Jun-04	Apopka	108.1	1.820086	0.362292	5.02381	28
Jun-04	Apopka	109.4	1.561306	0.405422	3.851064	28
Jun-04	Apopka	221.8	4.321232	0.484276	8.923077	28
Jun-04	Apopka	86.4	2.052988	0.439926	4.666667	28
Jun-04	Apopka	254.8	7.493444	0.38626	19.4	28
Jun-04	Apopka	94.3	2.225508	0.310536	7.166667	28
Jun-04	Apopka	94.5	1.63894	0.4313	3.8	28
Jun-04	Apopka	325.4	8.845354	0.38626	22.9	28
Jun-04	Apopka	44.6	1.086876	0.232902	4.666667	28
Jun-04	Apopka	4.25	0.314735	0.039756	7.916667	28
Jun-04	Apopka	96.6	0.106016	0.06626	1.6	28
Jun-04	Apopka	61	1.663126	0.13252	12.55	28

Time Period	Lake	Wet Mass (g)	NH_4-N (mg/fish/hr)	PO_4-P (mg/fish/hr)	N:P (by mass)	Temp (°C)
Jun-04	Apopka	95.4	1.364956	0.357804	3.814815	28
Jun-04	Apopka	212.2	3.762452	0.782292	4.809524	28
Jun-04	Apopka	74.3	1.543858	0.404186	3.819672	28
Jun-04	Apopka	177.6	4.153784	0.482658	8.606061	28
Jun-04	Apopka	181	3.934394	0.58504	6.725	28
Jun-04	Apopka	112.7	2.166702	0.53008	4.0875	28
Jun-04	Apopka	86.5	1.431216	0.251788	5.684211	28
Jun-04	Apopka	95.9	1.835402	0.53008	3.4625	28
Jun-04	Apopka	253.5	3.451736	1.213958	2.843373	28
Jun-04	Apopka	47.8	1.576988	0.192154	8.206897	28
Jun-04	Apopka	361.6	8.381842	0.888398	9.434783	28
Jun-04	Apopka	4	0.112642	0.110433	1.02	28
Jun-04	Apopka	101.3	2.703408	0.185528	14.57143	28
Jun-04	Apopka	94.8	2.126946	0.205406	10.35484	28
Jun-04	Apopka	238.5	4.373174	0.87756	4.983333	28
Jun-04	Apopka	43.9	1.470972	0.271666	5.414634	28
Jun-04	Apopka	102.8	2.365482	0.503576	4.697368	28
Jun-04	Apopka	79.9	1.92154	0.23191	8.285714	28
Jun-04	Apopka	63.5	1.85528	0.059634	31.11111	28
Jun-04	Apopka	180.8	3.173842	0.775178	4.09434	28
Jun-04	Apopka	120	2.345604	0.477072	4.916667	28
Jun-04	Apopka	150.9	3.334728	1.155454	2.886076	28
Jun-04	Apopka	125.6	1.835402	0.404186	4.540984	28
Jun-04	Apopka	211.1	3.6565	1.155454	3.164557	28
Jun-04	Apopka	81.5	1.934792	0.43069	4.492308	28
Jun-04	Apopka	118.7	1.033656	0.881258	1.172932	28
Jun-04	Apopka	188.1	2.647306	0.80443	3.290909	28
Jun-04	Apopka	51.7	1.835402	0.437316	4.19697	28
Jun-04	Apopka	51.7	1.959884	0.190138	10.30769	28
Jun-04	Apopka	56.4	2.618054	0.482658	5.424242	28
Dec-04	Apopka	21.5	0.809424	0.114464	7.071429	14
Dec-04	Apopka	25.6	0.727664	0.106288	6.846154	14
Dec-04	Apopka	29.8	0.85848	0.094024	9.130435	14
Dec-04	Apopka	37.7	0.887096	0.159432	5.564103	14
Dec-04	Apopka	44.2	1.081472	0.099968	10.81818	14
Dec-04	Apopka	47.7	1.145088	0.308992	3.705882	14
Dec-04	Apopka	53.5	1.332688	0.02044	65.2	14
Dec-04	Apopka	78.6	1.671992	0.179872	9.295455	14
Dec-04	Apopka	86.8	1.160992	0.065408	17.75	14
Dec-04	Apopka	105.5	1.671992	0.073584	22.72222	14
Dec-04	Apopka	115.9	1.455328	0.179872	8.090909	14
Dec-04	Apopka	120.7	1.295896	0.06132	21.13333	14
Dec-04	Apopka	141.4	2.45376	0.372608	6.585366	14
Dec-04	Apopka	149.5	1.435904	0.063616	22.57143	14

Time Period	Lake	Wet Mass (g)	NH_4-N (mg/fish/hr)	PO_4-P (mg/fish/hr)	N:P (by mass)	Temp (°C)
Dec-04	Apopka	184	2.744576	0.04544	60.4	14
Dec-04	Apopka	185.6	3.335296	0.118144	28.23077	14
Dec-04	Apopka	206.3	3.36256	0.099968	33.63636	14
Dec-04	Apopka	207	1.30816	0.106288	12.30769	14
Dec-04	Apopka	236.5	4.371328	0.04544	96.2	14
Dec-04	Apopka	278.8	3.035392	0.109056	27.83333	14
Dec-04	Apopka	289.6	3.326208	0.04544	73.2	14
Dec-04	Apopka	352	3.670992	0.184704	19.875	14
Dec-04	Apopka	371.5	2.344704	0.308992	7.588235	14
Dec-04	Apopka	374.2	3.81696	0.445312	8.571429	14
Dec-04	Apopka	401.9	2.59008	0.99968	2.590909	14
Dec-04	Apopka	409.6	9.096672	0.253968	35.81818	14
Dec-04	Apopka	421.1	3.901872	0.11544	33.8	14
Dec-04	Apopka	518.4	4.3632	0.232704	18.75	14
Dec-04	Apopka	537.7	4.218448	0.458112	9.208333	14
Dec-04	Apopka	657.1	5.23584	0.232704	22.5	14
Mar-05	Apopka	84.9	1.5264	0.111936	13.63636	18
Mar-05	Apopka	125.4	2.39136	0.015264	156.6667	18
Mar-05	Apopka	168.5	2.59488	0.055968	46.36364	18
Mar-05	Apopka	179.7	3.139296	0.05088	61.7	18
Mar-05	Apopka	180.4	3.556512	0.574944	6.185841	18
Mar-05	Apopka	183.7	4.37976	0.210672	20.78947	18
Mar-05	Apopka	188.2	1.943616	0.259488	7.490196	18
Mar-05	Apopka	192.8	1.846944	0.544416	3.392523	18
Mar-05	Apopka	196.9	4.424112	0.133056	33.25	18
Mar-05	Apopka	211.9	4.368672	0.465696	9.380952	18
Mar-05	Apopka	220.7	4.545408	0.34176	13.3	18
Mar-05	Apopka	225.4	2.39136	0.727584	3.286713	18
Mar-05	Apopka	238.8	3.647952	0.2772	13.16	18
Mar-05	Apopka	249.1	4.390848	0.432432	10.15385	18
Mar-05	Apopka	252	3.891888	0.376992	10.32353	18
Mar-05	Apopka	341.9	6.715584	0.632256	10.62162	18
Mar-05	Apopka	348.3	3.65904	1.241856	2.946429	18
Mar-05	Apopka	364.7	4.623696	0.066528	69.5	18
Mar-05	Apopka	366.4	4.191264	0.454608	9.219512	18
Mar-05	Apopka	371.9	3.792096	0.487872	7.772727	18
Mar-05	Apopka	372.9	4.87872	0.875952	5.56962	18
Mar-05	Apopka	427.3	5.194752	1.093632	4.75	18
Mar-05	Apopka	534.2	8.29008	1.541664	5.377358	18
May-05	Apopka	1.5	0.219728	0.021264	10.33333	28
May-05	Apopka	1.9	0.276432	0.014176	19.5	28
May-05	Apopka	53.1	1.495568	0.538688	2.776316	28
May-05	Apopka	56.2	1.580624	0.240992	6.558824	28
May-05	Apopka	63.6	1.325456	0.559952	2.367089	28

Time Period	**Lake**	**Wet Mass (g)**	**NH_4-N (mg/fish/hr)**	**PO_4-P (mg/fish/hr)**	**N:P (by mass)**	**Temp (°C)**
May-05	Apopka	77.8	2.23272	0.694624	3.214286	28
May-05	Apopka	84.3	1.77408	0.809424	2.191781	28
May-05	Apopka	109.7	1.438864	0.290608	4.95122	28
May-05	Apopka	120.4	2.388656	0.92144	2.592308	28
May-05	Apopka	125.3	4.401936	1.252944	3.513274	28
May-05	Apopka	125.7	2.4808	1.013584	2.447552	28
May-05	Apopka	133	3.847536	1.474704	2.609023	28
May-05	Apopka	133.7	4.737632	7.498736	0.631791	28
May-05	Apopka	136.9	3.953056	1.65968	2.381818	28
May-05	Apopka	139	3.409888	0.82984	4.109091	28
May-05	Apopka	139.8	2.16184	0.978144	2.210145	28
May-05	Apopka	141.8	3.49272	0.676368	5.163934	28
May-05	Apopka	162.6	2.761104	0.935456	2.951613	28
May-05	Apopka	162.7	2.608384	1.056112	2.469799	28
May-05	Apopka	168.2	3.983232	2.610224	1.526012	28
May-05	Apopka	176.7	4.013856	1.086624	3.693878	28
May-05	Apopka	179.6	3.440064	1.116512	3.081081	28
May-05	Apopka	182.4	3.726736	1.689856	2.205357	28
May-05	Apopka	182.8	3.575856	1.689856	2.116071	28
May-05	Apopka	184.2	5.10048	0.620928	8.214286	28
May-05	Apopka	194	3.47024	0.181056	19.16667	28
May-05	Apopka	195.5	3.515504	0.799664	4.396226	28
May-05	Apopka	196.2	2.368816	1.388096	1.706522	28
May-05	Apopka	206	2.700752	0.618608	4.365854	28
May-05	Apopka	211	5.703264	2.202848	2.589041	28
May-05	Apopka	214.8	3.3948	1.780384	1.90678	28
May-05	Apopka	215.6	4.556576	0.844928	5.392857	28
May-05	Apopka	219.8	3.907792	0.120704	32.375	28
May-05	Apopka	221.6	3.259008	1.010896	3.223881	28
May-05	Apopka	230.9	3.500416	1.644592	2.12844	28
May-05	Apopka	231.6	4.857696	1.59984	3.036364	28
May-05	Apopka	233	1.134432	0.174528	6.5	28
May-05	Apopka	237.8	7.46112	2.3316	3.2	28
May-05	Apopka	240.5	3.503808	1.507968	2.323529	28
May-05	Apopka	244.9	4.556576	1.388096	3.282609	28
May-05	Apopka	245.3	3.259872	1.88496	1.729412	28
May-05	Apopka	246.2	3.69656	1.403184	2.634409	28
May-05	Apopka	255.6	3.907792	2.353728	1.660256	28
May-05	Apopka	274.6	4.028496	0.392288	10.26923	28
May-05	Apopka	275.7	4.797984	1.644592	2.917431	28
May-05	Apopka	298.5	8.493696	2.530656	3.356322	28
May-05	Apopka	343	7.155648	2.966976	2.411765	28
July-Aug-05	Apopka	1.7	0.014176	0.092144	0.153846	31
July-Aug-05	Apopka	4	0.304784	0.255168	1.194444	31

Time Period	Lake	Wet Mass (g)	NH_4-N (mg/fish/hr)	PO_4-P (mg/fish/hr)	N:P (by mass)	Temp (°C)
July-Aug-05	Apopka	7.4	0.33968	0.10808	3.142857	30.1
July-Aug-05	Apopka	7.4	0.524512	0.148848	3.52381	33.5
July-Aug-05	Apopka	7.8	0.335808	0.162816	2.0625	31
July-Aug-05	Apopka	8.2	0.701712	0.198464	3.535714	33.5
July-Aug-05	Apopka	9.3	0.42528	0.1772	2.4	31
July-Aug-05	Apopka	11	0.422464	0.3772	1.12	31
July-Aug-05	Apopka	11	0.340224	0.276432	1.230769	31
July-Aug-05	Apopka	11.7	0.793856	0.340224	2.333333	33.5
July-Aug-05	Apopka	12.8	0.510336	0.28352	1.8	32.2
July-Aug-05	Apopka	14.6	0.928528	0.474896	1.955224	33.5
July-Aug-05	Apopka	14.8	0.74424	0.304784	2.44186	33
July-Aug-05	Apopka	16.5	1.14528	0.21474	5.333333	30.9
July-Aug-05	Apopka	16.5	1.927936	0.722976	2.666667	33.5
July-Aug-05	Apopka	18	1.145745	0.353625	3.24	30.9
July-Aug-05	Apopka	18.2	0.7088	0.3544	2	32.2
July-Aug-05	Apopka	18.5	0.907264	0.552864	1.641026	33.5
July-Aug-05	Apopka	18.8	0.92144	0.581216	1.585366	32.2
July-Aug-05	Apopka	19	0.777975	0.268755	2.894737	30.9
July-Aug-05	Apopka	19.6	0.7088	0.467808	1.515152	32.2
July-Aug-05	Apopka	62.5	1.037568	0.32424	3.2	30.9
July-Aug-05	Apopka	88.6	2.368816	0.90528	2.616667	31
July-Aug-05	Apopka	91.3	3.123216	0.844928	3.696429	33.5
July-Aug-05	Apopka	104.4	2.233024	1.191952	1.873418	31
July-Aug-05	Apopka	104.7	3.183568	1.252304	2.542169	33
July-Aug-05	Apopka	107.8	2.972336	0.98072	3.030769	31
July-Aug-05	Apopka	112.4	2.308464	0.965632	2.390625	31.5
July-Aug-05	Apopka	131.9	2.33864	0.935456	2.5	33
July-Aug-05	Apopka	149	1.795472	0.799664	2.245283	31
July-Aug-05	Apopka	150.8	3.937968	1.237216	3.182927	33
July-Aug-05	Apopka	154.1	4.179376	0.618608	6.756098	31.5
July-Aug-05	Apopka	155.6	3.69656	1.403184	2.634409	31.5
July-Aug-05	Apopka	155.6	3.726736	1.58424	2.352381	31.5
July-Aug-05	Apopka	164.6	4.239728	1.644592	2.577982	33.5
July-Aug-05	Apopka	167.2	3.409888	0.90528	3.766667	31.5
July-Aug-05	Apopka	176.1	3.862528	2.142496	1.802817	32.2
July-Aug-05	Apopka	176.2	2.94216	2.067056	1.423358	32.2
July-Aug-05	Apopka	185.8	2.821456	1.523888	1.851485	31
July-Aug-05	Apopka	189.5	2.595136	0.467728	5.548387	30.1
July-Aug-05	Apopka	195.6	2.051968	0.799664	2.566038	31
July-Aug-05	Apopka	201.3	3.560768	1.689856	2.107143	31.5
July-Aug-05	Apopka	219.3	3.440064	1.886	1.824	31
July-Aug-05	Apopka	222.8	4.254816	1.795472	2.369748	33
July-Aug-05	Apopka	223.2	2.851632	1.674768	1.702703	31
July-Aug-05	Apopka	231.6	2.927072	0.799664	3.660377	33

Time Period	Lake	Wet Mass (g)	NH_4-N (mg/fish/hr)	PO_4-P (mg/fish/hr)	N:P (by mass)	Temp (°C)
July-Aug-05	Apopka	232.1	2.610224	1.614416	1.616822	31
July-Aug-05	Apopka	236.8	3.802176	0.573344	6.631579	30.1
July-Aug-05	Apopka	236.9	3.274096	2.398992	1.36478	31.5
July-Aug-05	Apopka	243.2	6.870448	2.611392	2.630952	31
July-Aug-05	Apopka	246.8	1.569152	1.35792	1.155556	33
July-Aug-05	Apopka	263.7	2.821456	1.342832	2.101124	31
July-Aug-05	Apopka	274.1	3.651296	1.312656	2.781609	33
July-Aug-05	Apopka	278.3	2.881808	1.96144	1.469231	31
July-Aug-05	Apopka	320.7	1.492224	1.150256	1.297297	31.5
July-Aug-05	Apopka	364.2	5.875632	3.26424	1.8	31
July-Aug-05	Apopka	397.8	6.10848	2.734272	2.234043	31
Mar-05	Dora	193.4	1.929312	0.299376	6.444444	18
Mar-05	Dora	253.2	5.300064	0.820512	6.459459	18
Mar-05	Dora	314.0	4.900896	0.8316	5.893333	18
Mar-05	Dora	324.4	6.049152	1.2816	4.72	18
Mar-05	Dora	285.9	6.459264	0.17088	37.8	18
Mar-05	Dora	81.0	1.57728	0.468096	3.369565	18
Mar-05	Dora	390.7	7.068384	0.058176	121.5	18
Mar-05	Dora	860.0	5.439456	2.966976	1.833333	18
Mar-05	Dora	501.7	4.630848	0.51264	9.033333	18
Mar-05	Dora	145.8	2.304864	0.249312	9.244898	18
Mar-05	Dora	181.8	3.060288	0.2772	11.04	18
Mar-05	Dora	164.4	2.401536	0.473184	5.075269	18
Mar-05	Dora	191.6	4.224528	0.643104	6.568966	18
Mar-05	Dora	157.9	2.116608	0.615648	3.438017	18
Mar-05	Dora	188.7	1.521312	0.162816	9.34375	18
Mar-05	Dora	245.9	2.472624	0.787248	3.140845	18
Jan-Feb-06	Apopka	259.5	6.472752	0.07544	85.8	15.6
Jan-Feb-06	Apopka	309.4	6.63872	0.543168	12.22222	15.6
Jan-Feb-06	Apopka	620.9	7.661248	0.742672	10.31579	15.6
Jan-Feb-06	Apopka	259.8	5.12992	0.196144	26.15385	15.6
Jan-Feb-06	Apopka	327	4.571664	0.22632	20.2	15.6
Jan-Feb-06	Apopka	624.3	9.732912	0.156352	62.25	15.6
Jan-Feb-06	Apopka	283.5	3.10464	0.487872	6.363636	15.6
Jan-Feb-06	Apopka	320.2	3.033664	0.503248	6.028169	15.6
Jan-Feb-06	Dora	479.3	7.700336	0.664496	11.58824	15.6
Jan-Feb-06	Dora	500.7	7.62216	2.14984	3.545455	15.6
Jan-Feb-06	Dora	13	0.453632	0.191376	2.37037	15.6
Jan-Feb-06	Dora	7.7	0.233904	0.085056	2.75	15.6
Jan-Feb-06	Dora	8	0.269344	0.085056	3.166667	15.6
Jan-Feb-06	Dora	12.3	0.316848	0.045264	7	15.6
Jan-Feb-06	Eustis	576.5	21.73293	2.032576	10.69231	15.6
Jan-Feb-06	Eustis	653.9	10.98254	1.263168	8.694444	15.6
Jan-Feb-06	Eustis	506.5	5.160096	0.7544	6.84	15.6

Time Period	**Lake**	**Wet Mass (g)**	**NH_4-N (mg/fish/hr)**	**PO_4-P (mg/fish/hr)**	**N:P (by mass)**	**Temp (°C)**
Jan-Feb-06	Eustis	377.3	6.653808	2.142496	3.105634	15.6
Jan-Feb-06	Eustis	514.3	6.155904	0.256496	24	17.9
Jan-Feb-06	Eustis	632.3	5.105013	1.84704	2.763889	17.9
Jan-Feb-06	Eustis	552.8	2.84752	0.487413	5.842105	17.9
Jan-Feb-06	Griffin	542.1	3.500416	1.750208	2	17.9
Jan-Feb-06	Griffin	171.2	4.9036	0.045264	108.3333	17.9
Jan-Feb-06	Griffin	175.1	3.862528	0.241408	16	17.9
Jan-Feb-06	Griffin	153.3	2.806368	0.362112	7.75	17.9
Jan-Feb-06	Griffin	110.3	3.032688	0.07544	40.2	17.9
Jan-Feb-06	Griffin	467.1	8.051792	0.870464	9.25	17.9
Jan-Feb-06	Griffin	141.1	2.700752	0.995808	2.712121	17.9
Jan-Feb-06	Griffin	411.6	9.979248	0.341968	29.18182	17.9
Jan-Feb-06	Griffin	489.4	3.026576	1.31128	2.308108	17.9
Mar-06	Apopka	479.6	2.580048	0.799664	3.226415	21.7
Mar-06	Apopka	406.2	1.500178	0.931145	1.611111	21.7
Mar-06	Apopka	285.2	2.927072	0.890192	3.288136	21.7
Mar-06	Apopka	237.8	3.123216	0.60352	5.175	21.7
Mar-06	Apopka	242.5	2.217936	0.211232	10.5	21.7
Mar-06	Apopka	363.2	3.0176	0.362112	8.333333	21.7
Mar-06	Apopka	387.7	1.96144	1.720032	1.140351	21.7
Mar-06	Apopka	294.9	5.237792	2.169384	2.414414	21.7
Mar-06	Apopka	339.5	3.478832	2.110752	1.648148	21.7
Mar-06	Apopka	359.5	2.71584	1.765296	1.538462	21.7
Mar-06	Dora	29.3	0.522487	0.249093	2.097561	24.2
Mar-06	Dora	27.9	0.574128	0.155936	3.681818	24.2
Mar-06	Dora	24.9	0.648784	0.196144	3.307692	23.9
Mar-06	Dora	43.6	1.001295	0.342909	2.92	23.9
Mar-06	Dora	50.2	1.28248	0.362112	3.541667	23.9
Mar-06	Eustis	517.4	5.844544	0.93264	6.266667	20.6
Mar-06	Eustis	187	2.217936	0.271584	8.166667	20.6
Mar-06	Eustis	370.3	3.31936	0.241408	13.75	20.6
Mar-06	Eustis	180.8	2.067056	0.3772	5.48	20.6
Mar-06	Eustis	269.4	1.463536	0.784576	1.865385	20.6
Mar-06	Eustis	268.9	2.549216	1.834192	1.389831	20.6
Mar-06	Eustis	575	3.1088	1.119168	2.777778	20.6
Mar-06	Eustis	584	4.290144	0.217616	19.71429	20.6
May-06	Dora	59.2	1.389248	0.304784	4.55814	26.7
May-06	Dora	31	0.99232	0.085056	11.66667	26.7
May-06	Dora	86.2	2.18776	0.135792	16.11111	26.7
May-06	Dora	108.7	2.94216	0.256496	11.47059	26.4
May-06	Dora	110.2	2.248112	0.347024	6.478261	26.7
May-06	Dora	93.3	2.730928	0.844928	3.232143	26.4
May-06	Dora	86.3	2.94216	0.105616	27.85714	26.7
May-06	Apopka	272.9	4.416944	1.328992	3.323529	26.4

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May-06	Apopka	108.3	1.538976	0.618608	2.487805	26.7
May-06	Apopka	123.9	1.976528	1.025984	1.926471	27.2
May-06	Apopka	156.3	2.700752	0.694048	3.891304	25.6
May-06	Apopka	211.6	2.625312	0.844928	3.107143	25
May-06	Apopka	186.8	2.957248	1.146688	2.578947	25
May-06	Eustis	49.5	1.070288	0.347312	3.081633	24.7
May-06	Eustis	32.4	0.701712	0.163024	4.304348	25.6
May-06	Eustis	108.3	3.062864	1.297568	2.360465	24.4
May-06	Eustis	158.8	2.851632	2.11232	1.35	24.4
May-06	Eustis	125.3	3.530592	1.493712	2.363636	24.4
May-06	Eustis	152.2	3.259008	1.222128	2.666667	24.4
May-06	Eustis	84.4	2.383904	0.769488	3.098039	24.4
May-06	Eustis	221.7	1.252304	0.512992	2.441176	24.4
May-06	Eustis	163.3	1.523888	0.890192	1.711864	24.4
May-06	Eustis	175.6	3.002512	0.860016	3.491228	24.4
May-06	Griffin	93.4	4.737632	1.238121	3.826468	25.6
May-06	Griffin	157.3	4.888512	0.45264	10.8	24.4
May-06	Griffin	127.6	0.814752	0.799664	1.018868	24.4
May-06	Griffin	98.2	5.839056	0.573344	10.18421	24.4
May-06	Griffin	189.8	2.278288	1.086336	2.097222	24.4
May-06	Griffin	170.2	2.670576	0.844928	3.160714	24.4
May-06	Griffin	192	2.11232	0.860016	2.45614	24.4
Jul-Aug-06	Griffin	178.4	4.755888	1.365552	3.482759	30.3
Jul-Aug-06	Griffin	202	5.88744	0.900432	6.538462	30.3
Jul-Aug-06	Griffin	171.2	2.378064	0.969696	2.452381	30.5
Jul-Aug-06	Griffin	202.4	4.456032	0.9772	4.56	30.3
Jul-Aug-06	Griffin	110.7	3.00144	0.715728	4.193548	30.9
Jul-Aug-06	Griffin	106.9	3.379712	1.252304	2.698795	30.9
Jul-Aug-06	Griffin	133.5	2.655488	1.222128	2.17284	30.8
Jul-Aug-06	Griffin	74	5.160096	0.467728	11.03226	31.7
Jul-Aug-06	Griffin	355.6	5.28496	1.274608	4.146341	31.8
Jul-Aug-06	Griffin	266.9	5.937808	1.336784	4.44186	31.8
Jul-Aug-06	Eustis	325.3	4.567536	2.448576	1.865385	29.4
Jul-Aug-06	Eustis	124	3.786432	1.108224	3.416667	28.8
Jul-Aug-06	Eustis	167.9	2.886	0.715728	4.032258	28.4
Jul-Aug-06	Eustis	183.2	4.086576	1.1544	3.54	28.4
Jul-Aug-06	Eustis	227.1	2.747472	0.69264	3.966667	28.9
Jul-Aug-06	Eustis	153.1	1.708512	0.69264	2.466667	28.8
Jul-Aug-06	Eustis	72.6	1.478624	0.935456	1.580645	28.7
Jul-Aug-06	Eustis	71.1	2.255656	0.52808	4.271429	28.8
Jul-Aug-06	Eustis	147.9	3.062864	1.010896	3.029851	28.7
Jul-Aug-06	Eustis	95.1	2.157584	0.588432	3.666667	28.6
Jul-Aug-06	Eustis	115.6	3.937968	0.935456	4.209677	28.7
Jul-Aug-06	Eustis	65.4	1.81056	0.52808	3.428571	29

Time Period	Lake	Wet Mass (g)	NH_4-N (mg/fish/hr)	PO_4-P (mg/fish/hr)	N:P (by mass)	Temp (°C)
Jul-Aug-06	Eustis	114.4	1.554064	0.437552	3.551724	28
Jul-Aug-06	Dora	200.1	6.210672	1.339104	4.637931	30.55
Jul-Aug-06	Dora	112.7	4.987008	0.484848	10.28571	30.9
Jul-Aug-06	Dora	121.6	5.056272	0.646464	7.821429	30.75
Jul-Aug-06	Dora	121.4	3.4632	0.277056	12.5	31.1
Jul-Aug-06	Dora	103.8	3.393936	0.369408	9.1875	31
Jul-Aug-06	Dora	211.3	4.1492	1.05616	3.928571	30.7
Jul-Aug-06	Dora	146.8	3.651296	1.071248	3.408451	31
Jul-Aug-06	Dora	184.1	3.983232	0.914333	4.356436	31.1
Jul-Aug-06	Dora	144.7	3.47024	1.086336	3.194444	31
Jul-Aug-06	Dora	126.8	3.756912	1.28248	2.929412	31.6
Jul-Aug-06	Dora	134.9	3.424976	0.407376	8.407407	31
Jul-Aug-06	Dora	115.5	3.892704	0.709136	5.489362	31.2
Jul-Aug-06	Apopka	221.9	6.403968	1.789344	3.578947	29.5
Jul-Aug-06	Apopka	195.8	3.57864	0.969696	3.690476	29.4
Jul-Aug-06	Apopka	144.6	2.07792	1.177488	1.764706	29.4
Jul-Aug-06	Apopka	199.9	4.548336	1.800864	2.525641	30.7
Jul-Aug-06	Apopka	213.3	2.862912	1.03896	2.755556	31.1
Jul-Aug-06	Apopka	224.1	5.47232	1.606517	3.406326	29.5
Jul-Aug-06	Apopka	113.8	2.444256	1.191952	2.050633	29.5
Jul-Aug-06	Apopka	119.7	2.730928	1.418272	1.925532	29.75
Jul-Aug-06	Apopka	136.9	3.09304	0.995808	3.106061	30.05
Jul-Aug-06	Apopka	155.6	2.761104	0.599144	4.608411	31.45
Jul-Aug-06	Apopka	126.1	2.79128	0.98072	2.846154	30.25

Appendix 3 – Nutrient Data For all Tank Experiments During 2006-2007 (mean of all dates after the addition of fish).

Tank	Treatment	NH_4-N (mg/L)	PO_4-P (mg/L)	NO_x (mg/L)	Total N (mg/L)	Total P (mg/L)	Total Dissolved N (mg/L)	Total Dissolved P (mg/L)	Particulate N (mg/L)	Particulate P (mg/L)
March 2006										
1	No Fish	0.025	0.0020		2.193	0.033	1.923	0.018	0.270	0.015
2	Low Fish	0.176	0.0005		3.097	0.088	2.460	0.025	0.637	0.063
3	Low Fish	0.085	0.0005		3.163	0.097	2.183	0.031	0.980	0.065
4	High Fish	0.201	0.0023		4.990	0.164	2.417	0.025	2.573	0.139
5	High Fish	0.172	0.0167		3.510	0.136	2.453	0.052	1.057	0.084
6	High Fish	0.400	0.0030		6.083	0.210	2.810	0.034	3.273	0.176
7	Low Fish	0.110	0.0005		4.127	0.137	2.230	0.023	1.897	0.114
8	No Fish	0.026	0.0002		2.240	0.041	2.090	0.020	0.150	0.022
9	Paddle	0.096	0.0057		3.517	0.137	2.150	0.030	1.367	0.107
10	Paddle	0.128	0.0033		3.630	0.144	2.270	0.034	1.360	0.110
11	High Fish	0.045	0.0063		3.650	0.160	2.003	0.038	1.647	0.123
12	No Fish	0.004	0.0005		2.330	0.059	1.993	0.022	0.337	0.037
13	No Fish	0.026	0.0023		2.710	0.066	2.033	0.024	0.677	0.042
14	Paddle	0.180	0.0057		3.807	0.169	2.533	0.041	1.273	0.129
15	Low Fish	0.014	0.0033		2.990	0.117	2.053	0.032	0.937	0.085
16	Paddle	0.077	0.0033		3.167	0.121	2.323	0.032	0.843	0.089
May 2006										
1	No Fish/No Net	0.153	0.028		1.804	0.083	2.303	0.067	0.253	0.016
2	No Fish/No Net	0.247	0.034		1.685	0.092	2.420	0.080	0.010	0.012
3	No Fish/Net	0.155	0.037		1.352	0.083	1.978	0.076	0.210	0.008
4	Fish /Net	0.318	0.075		2.084	0.134	2.600	0.126	0.228	0.008
5	No Fish/Net	0.094	0.031		1.506	0.081	2.283	0.067	0.040	0.014
6	No Fish/Net	0.091	0.017		1.601	0.064	2.115	0.055	0.218	0.009
7	No Fish/No Net	0.098	0.028		1.905	0.086	1.958	0.072	0.563	0.014
8	Fish/No Net	0.322	0.057		2.099	0.125	2.128	0.108	0.770	0.017
9	Fish/Net	0.280	0.019		1.953	0.086	2.468	0.063	0.135	0.023
10	Fish/Net	0.143	0.022		1.795	0.088	2.480	0.073	0.130	0.015

Tank	Treatment	NH_4-N (mg/L)	PO_4-P (mg/L)	NO_x (mg/L)	Total N (mg/L)	Total P (mg/L)	Total Dissolved N (mg/L)	Total Dissolved P (mg/L)	Particulate N (mg/L)	Particulate P (mg/L)
11	Fish/No Net	0.330	0.042		2.196	0.107	2.620	0.091	0.313	0.016
12	Fish/Net	0.211	0.036		2.065	0.104	2.365	0.081	0.395	0.023
13	Fish/No Net	0.397	0.055		2.433	0.133	3.000	0.105	0.240	0.028
14	Fish/No Net	0.184	0.051		2.339	0.121	2.258	0.082	0.810	0.039
15	Fish/No Net	0.102	0.023		2.162	0.101	2.340	0.071	0.498	0.031
16	Fish/Net	0.193	0.028		2.026	0.092	2.390	0.077	0.385	0.015
					March 2007					
1	Fish/No Net	0.604	0.038	0.013	1.603	0.081	0.880	0.047	0.723	0.034
2	Fish/Net	0.592	0.046	0.019	0.880	0.058	0.830	0.053	0.050	0.005
3	Fish/No Net	0.481	0.027	0.011	1.113	0.069	0.720	0.029	0.393	0.040
4	Fish/Net	0.517	0.034	0.013	0.733	0.048	0.717	0.037	0.017	0.011
5	Fish/Net	0.475	0.033	0.016	0.630	0.041	0.660	0.038	-0.030	0.003
6	Fish/Net	0.530	0.031	0.021	0.800	0.046	0.777	0.035	0.023	0.011
7	No Fish/Net	0.619	0.037	0.032	0.980	0.056	0.850	0.035	0.130	0.021
8	No Fish/No Net	0.444	0.028	0.005	0.687	0.041	0.650	0.031	0.037	0.010
9	No Fish/Net	0.680	0.048	0.005	1.093	0.073	0.920	0.050	0.173	0.023
10	No Fish/No Net	0.613	0.055	0.011	1.037	0.088	0.777	0.057	0.260	0.031
11	Fish/Net	0.586	0.048	0.026	0.907	0.067	0.840	0.051	0.067	0.016
12	Fish/No Net	0.908	0.052	0.035	3.880	0.157	1.173	0.057	2.707	0.100
13	No Fish/No Net	0.496	0.042	0.035	0.723	0.053	0.700	0.047	0.023	0.006
14	No Fish/Net	0.399	0.039	0.024	0.587	0.049	0.547	0.040	0.040	0.009
15	Fish/No Net	0.500	0.038	0.045	1.410	0.091	0.690	0.045	0.720	0.046
16	Fish/No Net	0.661	0.055	0.034	2.237	0.141	1.170	0.056	1.067	0.085
					May 2007					
1	No Fish/No Net	0.172	0.001	0.010	0.533	0.027	0.400	0.005	0.133	0.021
2	No Fish/No Net	0.114	-0.002	0.007	0.480	0.025	0.387	0.004	0.093	0.021
3	Large/No Net	0.263	0.000	0.007	0.793	0.046	0.537	0.005	0.257	0.041
4	Small/No Net	0.344	0.000	0.007	1.380	0.072	0.623	0.007	0.757	0.065
5	Small/Net	0.365	0.003	0.032	0.753	0.039	0.587	0.009	0.167	0.030
6	Large/No Net	0.358	0.001	0.008	2.073	0.133	0.803	0.009	1.270	0.124

Tank	Treatment	NH_4-N (mg/L)	PO_4-P (mg/L)	NO_x (mg/L)	Total N (mg/L)	Total P (mg/L)	Total Dissolved N (mg/L)	Total Dissolved P (mg/L)	Particulate N (mg/L)	Particulate P (mg/L)
7	Large/Net	0.249	0.001	0.016	0.683	0.038	0.533	0.005	0.150	0.033
8	No Fish/No Net	0.101	0.000	0.014	0.533	0.031	0.377	0.005	0.157	0.026
9	No Fish/Net	0.312	0.001	0.009	0.680	0.028	0.510	0.005	0.170	0.022
10	Large/Net	0.469	0.009	0.022	0.910	0.057	0.777	0.014	0.133	0.043
11	No Fish/Net	0.356	0.001	0.022	0.743	0.031	0.643	0.004	0.100	0.028
12	Small/Net	0.437	0.007	0.025	0.873	0.043	0.743	0.011	0.130	0.032
13	Small/No Net	0.501	0.021	0.004	1.573	0.065	0.863	0.024	0.710	0.041
14	Small/No Net	0.537	0.021	0.012	1.513	0.090	0.897	0.025	0.617	0.065
15	Large/No Net	0.506	0.025	0.008	1.090	0.066	0.787	0.024	0.303	0.042
16	No Fish/Net	0.433	0.006	0.012	0.797	0.035	0.663	0.012	0.133	0.023
17	Large/Net	0.395	0.000	0.028	0.793	0.061	0.647	0.006	0.147	0.055
18	Small/Net	0.381	0.001	0.017	0.930	0.066	0.663	0.007	0.267	0.059

Appendix 4 – Turbidity, Suspended Solids, Chlorophyll and Zooplankton Data For all Tank Experiments During 2006-2007

(mean of all dates after the addition of fish).

Tank	Treatment	Turbidity (NTU)	Suspended Solids (mg/L)	Chlorophyll *a* (µg/L)	Rotifers (#/L)	Copepods (#/L)	Cladocera (#/L)	Total Zooplankton (#/L)
				March 2006				
1	No Fish	2.52	9.38	16.48	298.1	208.1	67.5	573.8
2	Low Fish	13.35	15.85	40.99	557.8	322.1	18.8	898.6
3	Low Fish	11.35	15.28	37.42	649.8	311.4	0.0	961.1
4	High Fish	36.00	51.17	77.52	533.8	166.9	54.4	755.0
5	High Fish	20.55	22.17	51.68	7148.1	345.0	235.0	7728.1
6	High Fish	66.02	57.70	97.12	1386.9	128.8	58.1	1573.8
7	Low Fish	40.47	32.50	65.71	2216.9	189.4	286.9	2693.1
8	No Fish	2.23	6.22	12.70	412.5	112.5	172.5	697.5
9	Paddle	15.11	24.18	63.71	1097.5	342.5	68.1	1508.1
10	Paddle	15.19	26.53	85.54	1237.5	247.5	0.0	1485.0
11	High Fish	13.02	17.32	90.21	2887.5	398.1	93.8	3379.4
12	No Fish	3.30	12.07	23.39	1161.0	6.8	40.5	1208.3
13	No Fish	3.65	13.63	26.06	1739.0	173.0	119.0	2031.0
14	Paddle	13.26	24.92	114.05	1331.3	237.5	155.6	1724.4
15	Low Fish	5.69	14.30	49.45	2305.0	386.3	63.8	2755.0
16	Paddle	11.20	21.77	72.84	1718.8	331.3	25.0	2075.0
				May 2006				
1	No Fish/No Net	2.50	3.17	14.79	26.3	191.3	0.0	217.5
2	No Fish/No Net	2.59	2.95	12.86	62.5	250.0	18.8	331.3
3	No Fish/Net	1.99	2.10	4.59	6.3	84.5	6.0	96.8
4	Fish /Net	2.33	2.10	7.60	57.5	68.8	0.0	126.3
5	No Fish/Net	2.09	3.02	5.60	58.1	46.9	28.1	133.1
6	No Fish/Net	2.17	2.81	8.77	51.9	42.5	6.3	100.6
7	No Fish/No Net	2.70	5.05	13.20	21.3	318.8	6.9	346.9
8	Fish/No Net	4.13	5.95	18.63	166.3	183.8	8.8	358.8

Tank	Treatment	Turbidity (NTU)	Suspended Solids (mg/L)	Chlorophyll *a* (µg/L)	Rotifers (#/L)	Copepods (#/L)	Cladocera (#/L)	Total Zooplankton (#/L)
9	Fish/Net	2.69	4.33	13.45	345.0	292.5	0.0	637.5
10	Fish/Net	2.76	4.20	17.88	274.4	188.1	6.9	469.4
11	Fish/No Net	3.50	5.09	23.39	78.8	187.5	0.0	266.3
12	Fish/Net	2.09	3.58	11.78	195.0	35.0	33.8	263.8
13	Fish/No Net	6.13	11.08	31.91	117.9	244.0	0.0	361.9
14	Fish/No Net	9.39	22.10	26.31	66.3	162.5	36.3	265.0
15	Fish/No Net	4.89	6.89	32.08	150.0	375.0	0.0	525.0
16	Fish/Net	2.26	1.50	15.04	136.9	71.3	40.6	248.8
March 2007								
1	Fish/No Net	12.63	22.47					
2	Fish/Net	3.83	2.67					
3	Fish/No Net	13.03	14.34					
4	Fish/Net	3.07	2.43					
5	Fish/Net	2.37	1.73					
6	Fish/Net	2.73	1.37					
7	No Fish/Net	4.93	3.28					
8	No Fish/No Net	4.23	2.37					
9	No Fish/Net	6.60	6.58					
10	No Fish/No Net	10.00	12.58					
11	Fish/Net	4.60	4.69					
12	Fish/No Net	51.60	73.32					
13	No Fish/No Net	2.50	1.14					
14	No Fish/Net	1.63	4.50					
15	Fish/No Net	14.10	15.78					
16	Fish/No Net	22.50	39.94					
May 2007								
1	No Fish/No Net	1.77	3.55	18.71				
2	No Fish/No Net	1.43	3.21	14.43				
3	Large/No Net	2.27	7.37	26.73				
4	Small/No Net	8.73	16.89	28.87				

Tank	Treatment	Turbidity (NTU)	Suspended Solids (mg/L)	Chlorophyll *a* (µg/L)	Rotifers (#/L)	Copepods (#/L)	Cladocera (#/L)	Total Zooplankton (#/L)
5	Small/Net	1.77	2.79	22.99				
6	Large/No Net	17.00	39.15	29.94				
7	Large/Net	1.63	3.27	18.18				
8	No Fish/No Net	2.90	4.25	19.25				
9	No Fish/Net	2.23	2.29	15.50				
10	Large/Net	1.43	2.69	27.26				
11	No Fish/Net	1.43	2.79	14.97				
12	Small/Net	1.87	3.04	25.13				
13	Small/No Net	12.23	21.78	9.62				
14	Small/No Net	8.97	17.43	19.78				
15	Large/No Net	6.27	12.71	6.95				
16	No Fish/Net	1.33	1.50	20.31				
17	Large/Net	1.90	3.87	15.50				
18	Small/Net	2.10	3.97	19.25				