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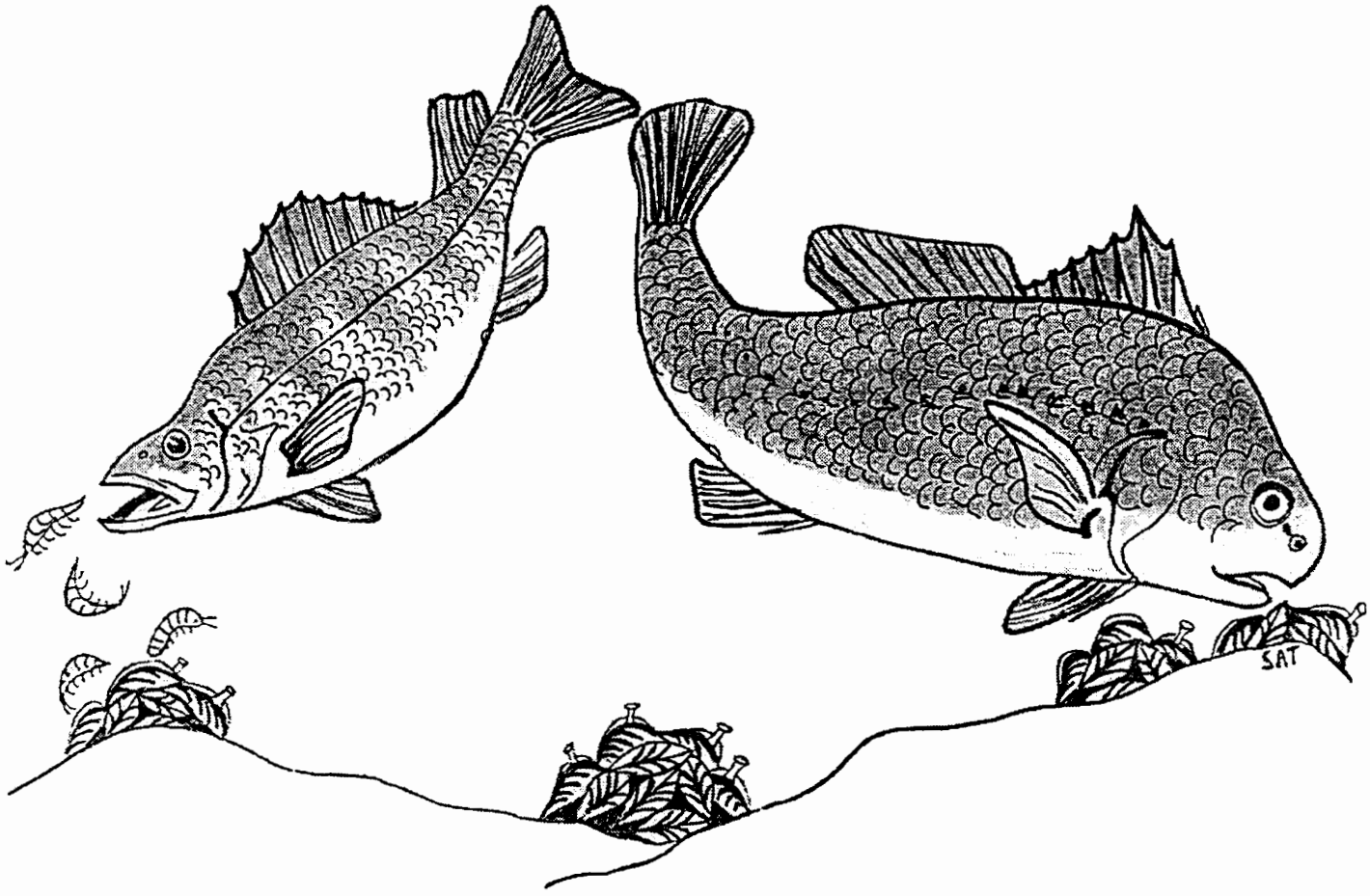
Zebra Mussel Effects On Diet and Growth of Adult Yellow Perch and Predatory Impact of Freshwater Drum On Zebra Mussels in Pond Enclosures

Sarah Ann Rautio



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ZEBRA MUSSEL EFFECTS ON DIET AND GROWTH OF ADULT YELLOW PERCH AND PREDATORY IMPACT OF FRESHWATER DRUM ON ZEBRA MUSSELS IN POND ENCLOSURES

by

Sarah Ann Rautio

A thesis

submitted in partial fulfillment

of the requirements for the

degree of

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IN BIOLOGICAL SCIENCES

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APPROVED BY:

11 Aug 94
Advisor Date

15 Aug. 1994
Date

12 Aug, 1994
Date

To George,

who often saw the worst of me in the last three years,

but always understood how much I loved what I was doing.

Acknowledgments

Those individuals who provided support and help with this study will always be remembered. My chief advisor, Dr. R. Douglas Hunter, whom I have come to know as an exemplary biologist, has shared his abilities, his ideas, and his time with me every step of the way. I will always be indebted to him for his suggestions, criticisms, and help during the exciting, as well as the grueling, hours of this project. I thank Dr. Thaddeus A. Grudzien and Dr. Keith A. Berven for serving as my committee members and for their constructive criticism of the thesis. They went great distances to do this.

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I would like to give very special thanks to Dr. Robert Kushler, who devoted an immeasurable amount of his time and energy to helping with statistical analyses. His enthusiastic interest in the data made its interpretation that much more enjoyable. Michael Janech will be remembered for his unconditional devotion to the tedious job of sorting benthic invertebrates from sediment. I never would have made it this far without him.

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ABSTRACT

Pond enclosure experiments were conducted for two years to test the effects of zebra mussel (Dreissena polymorpha) presence (6,000/m^2) on zoobenthos, and the diet and growth of yellow perch (Perca flavescens). Enclosures consisted of the following treatments: (1) yellow perch with zebra mussels; (2) yellow perch without zebra mussels; (3) zebra mussels only; and (4) no zebra mussels or fish. The hypothesis predicted higher growth rates for yellow perch with zebra mussels. In 1992, yellow perch with zebra mussels did not increase their wet biomass significantly more than yellow perch without zebra mussels ($X^2 = 0.015$, df = 1, $P = 0.90$). In 1993, however, yellow perch with zebra mussels either maintained or increased their wet biomass and yellow perch without zebra mussels lost weight. This difference in growth was highly significant ($X^2 = 55.63$, df = 1, $P < 0.001$). Although it was not possible to demonstrate a positive correlation between total dry weights of stomach contents and yellow perch growth, there was a significantly higher dry weight of amphipods and isopods in zebra mussel treatments. This suggests that crustaceans may have played a crucial role in the observed yellow perch growth difference. Diet analyses also provided significant evidence of reduced consumption of zooplankton by yellow perch with zebra mussels.

The benthic macroinvertebrate community tended to be dominated by Hirudinea and Diptera (mostly Chironomidae) regardless of the presence or absence of zebra mussels, yellow perch, or both. Other macroinvertebrate taxa appeared to respond to the presence of zebra mussels, some positively (triclads and oligochaetes), and at least or negatively (Gastropoda).

A concurrent experiment was conducted in the pond enclosures in 1992 to test the quantitative predator impact of freshwater drum (Aplodinotus grunniens) on zebra

mussels. The hypothesis predicted freshwater drum (standard length > 250 mm) would substantially reduce a population of zebra mussels. Two treatments, (1) freshwater drum and zebra mussels, and (2) freshwater drum and no zebra mussels were used. Evidence that freshwater drum were feeding on zebra mussels was unobtainable since these fish appeared to have become behaviorally stressed during the study, and subsequently did not feed on zebra mussels. They are not recommended for shallow pond studies such as this one.

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INTRODUCTION

Introduction of a nonindigenous organism can lead to profound changes in the structure and stability of a community. This is likely to occur if the organism is not predator-limited, has few competitors for food and space, and is capable of rapid reproduction and dispersal. Not only can such an exotic species become abundant in its new community, but it may displace or eliminate native species either directly by competitive interactions or indirectly through food chain effects or habitat alteration. The Eurasian zebra mussel, Dreissena polymorpha, first discovered in North America in 1988 (Hebert et al., 1989), poses such a threat to any North American freshwater lake and stream that is well-suited to colonization (shallow, temperate water bodies).

The success of zebra mussels in North America is partly attributable to their high fecundity and rapid dispersal. They have also been successful by filling a unique niche, since they lack competitors for substrate and food (freshwater ecosystems do not contain a great diversity nor high biomass of sessile, filter-feeding invertebrates). Unlike Europe, North America also lacks adequate control mechanisms from within existing aquatic communities. For example, diving ducks and coot wintering on the Rhine River, Germany, can consume 97% of the standing crop of zebra mussels every year (Suter, 1982). Europe also has several species of fish (nonindigenous to North America) that often consume large quantities of zebra mussels, such as roach (Rutilis caspicus, Rutilis heckeli, Rutilus frisii, and Rutilus frissi cutum), gustera, (Blicka bioerkna), and the Aral barbel (Barbus brachycephalus). North American predators are limited in numbers or have not yet responded to the onslaught of zebra mussels.

The ways in which high densities of zebra mussels are affecting the ecology of the Great Lakes are becoming increasingly evident. Substantial changes on an ecosystem scale have already been observed in the western basin of Lake Erie, Lake St. Clair, and Saginaw Bay

(Griffiths et al., 1991; Hebert et al., 1992; Leach, 1992; Skubinna et al., 1994), where water clarity and macrophyte density have increased markedly. These changes are the result of a diversion of energy from the pelagic to the benthic sector, driven by the collective filtration capacity of zebra mussels. Seston reduction is likely to have food web effects resulting in reduction in zooplankton biomass with implications for fish species that depend on zooplankton during important life stages, such as perch and walleye larvae. However, when zebra mussels remove seston from the pelagia, this energy is not lost to the ecosystem. Instead it is biodeposited onto surficial sediments when mussels reject undesirable and large food items in the form of pseudofeces, and, to a lesser extent, by production of feces. This additional energy diverted to the benthos can be utilized by benthic detrital-feeders and has been shown to improve the productivity of such benthic invertebrates as chironomid larvae (Izvekova and Lvova-Katchanova, 1972). Increased spatial heterogeneity through the addition of interstitial spaces in zebra mussel clusters could also encourage greater colonization by certain invertebrates, such as Amphipoda.

Examination of benthos in various regions in Europe and North America indicates a larger biomass of invertebrates when zebra mussels are present compared to times and areas in which they were not (Gizinski, 1982; Dermott et al., 1993; Griffiths, 1993; Stewart and Haynes, 1994). Those invertebrates that often respond by increasing population size include Oligochaeta, Tricladida, Amphipoda, Gastropoda, Hirudinea, and Chironomidae.

Zebra mussels and invertebrate responses to them pose potential benefits both to organisms who feed on the mussels and to those feeding on surrounding invertebrates, even within the same species. Local anglers in Lake St. Clair have found zebra mussels in the guts of very large yellow perch, Perca flavescens, (personal communication). This size of yellow perch, as well as those under twelve inches may also have access to additional food resources via other invertebrates that could increase their productivity in the benthos.

Larvae perch, on the other hand, may be negatively affected since they rely heavily on zooplankton.

Little is known about any of these interactions between zebra mussels and yellow perch. European experiences are not necessarily applicable to North America since the ecology and physico-chemical characteristics of the two regions differ. Since yellow perch are typically abundant in areas that are now heavily colonized by zebra mussels, and are valuable not only to the ecology of the Great Lakes, but also as a commodity to recreational and commercial fisheries, the impact zebra mussels will have on this species is of particular interest to many.

The work described in this thesis examines a portion of the interaction between zebra mussels and yellow perch. Adult yellow perch that were large enough to feed on benthic invertebrates, but too small to consume zebra mussels, were selected in order to test the precise impact a change in the benthic invertebrates could have on yellow perch. It is likely that the results of this study can be extrapolated to include other non-zebra mussel benthivores.

The objective of the study was to (1) determine if the growth rate of small adult yellow perch is different in the presence of zebra mussels than without zebra mussels and, if so, (2) how perch diet and benthic invertebrate composition may have influenced differential growth rates. We hypothesized (H_1) that moderate densities of zebra mussels ($6{,}000/m^2$) would increase the productivity of several benthic invertebrate taxa that are preferred food items of adult yellow perch, such as amphipods, gastropods, and chironomid larvae, and that this improvement in prey productivity would elicit a positive growth response in the test perch. The study took place over two years in order to test the effects of different years.

The focus of the above study represents only one portion of the total impact zebra mussels are likely to have on the ecology of freshwater ecosystems. Another response by native organisms could be one of a food-limited predator increasing in numbers if it is able to take advantage of a super-abundant food resource. One of the most likely species to benefit by feeding on zebra mussels is the benthivorous freshwater drum (Aplodinotus grunniens), which has molariform pharyngeal teeth for crushing shells. In select areas of Western Lake Erie, where zebra mussel density can be very high, this fish species has been shown to begin feeding on zebra mussels once it reaches 250 mm and to almost exclusively feed on them once it is over 375 mm, typically ingesting small (<5mm) mussels (French and Bur, 1991). The quantitative impact these fish have on a population of zebra mussels and the subsequent effect that zebra mussels have on growth of freshwater drum is not yet known. An additional objective of this study was to determine the first of these effects and test the hypothesis (H_2) that freshwater drum greater than 250 mm will significantly reduce a population of zebra mussels, particularly by feeding on small (< 5mm) individuals. This food web interaction, as well as those that occur between zebra mussels and yellow perch are summarized in Figure 1.

MATERIAL AND METHODS

Experiments were conducted in enclosures placed in a 0.2 hectare, one-meter deep pond. The pond is located on a small peninsula on the northwestern shoreline of Lake St. Clair at the outfall of the Clinton River (Figure 2), where it could be readily filled and emptied into Lake St. Clair that already supported a substantial zebra mussel population. The enclosures measured 1.8 x 1.8 x 1.5 m with sides of 0.63 cm mesh weathered galvanized hardware cloth and bottoms of fiberglass window screen uniformly covered with a mix of uninhabited sediment and large pea-stone gravel (to support zebra mussel clusters)

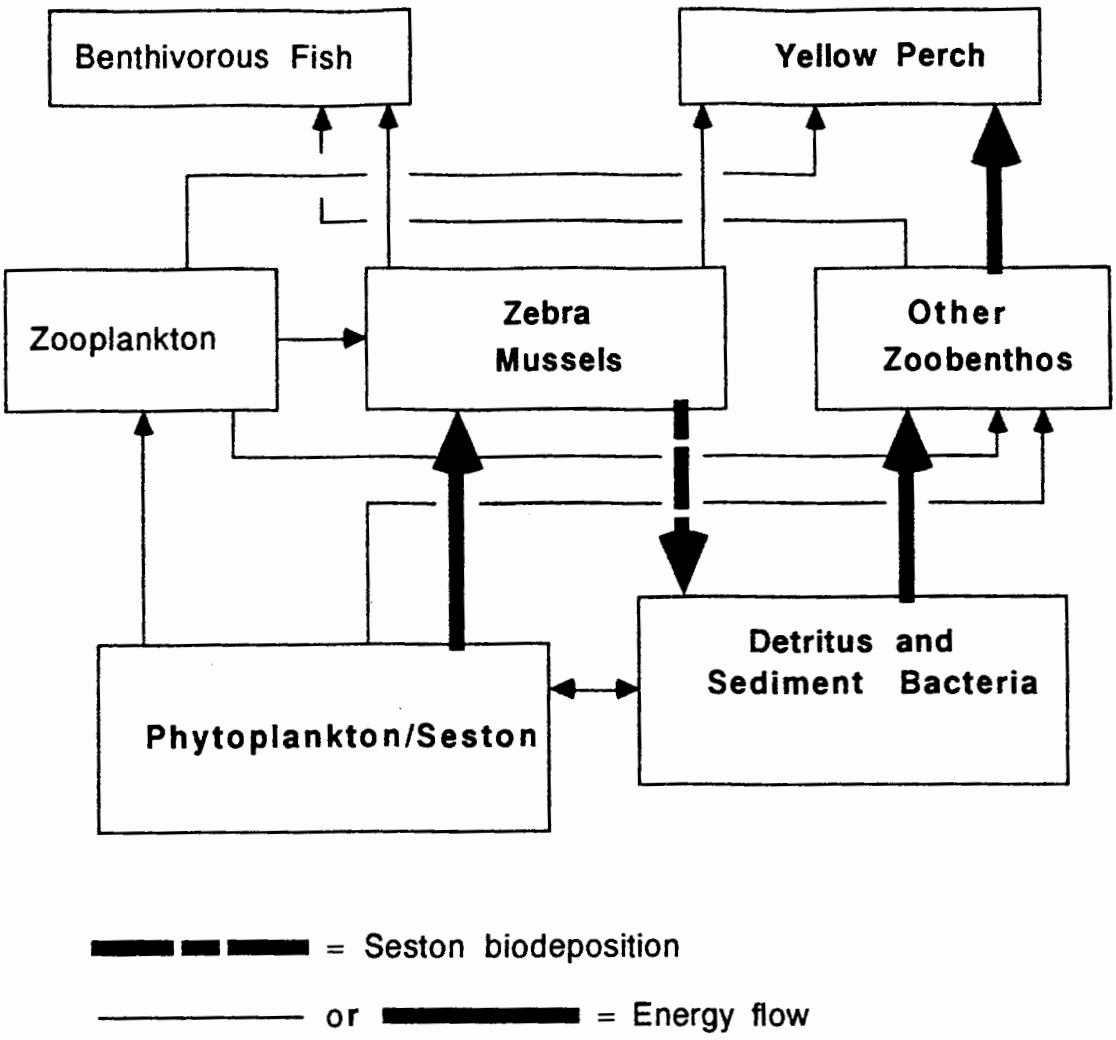


Figure 1. Role of zebra mussels in a lake food web. Bold arrows represent energy flow having indirect effects on yellow perch.

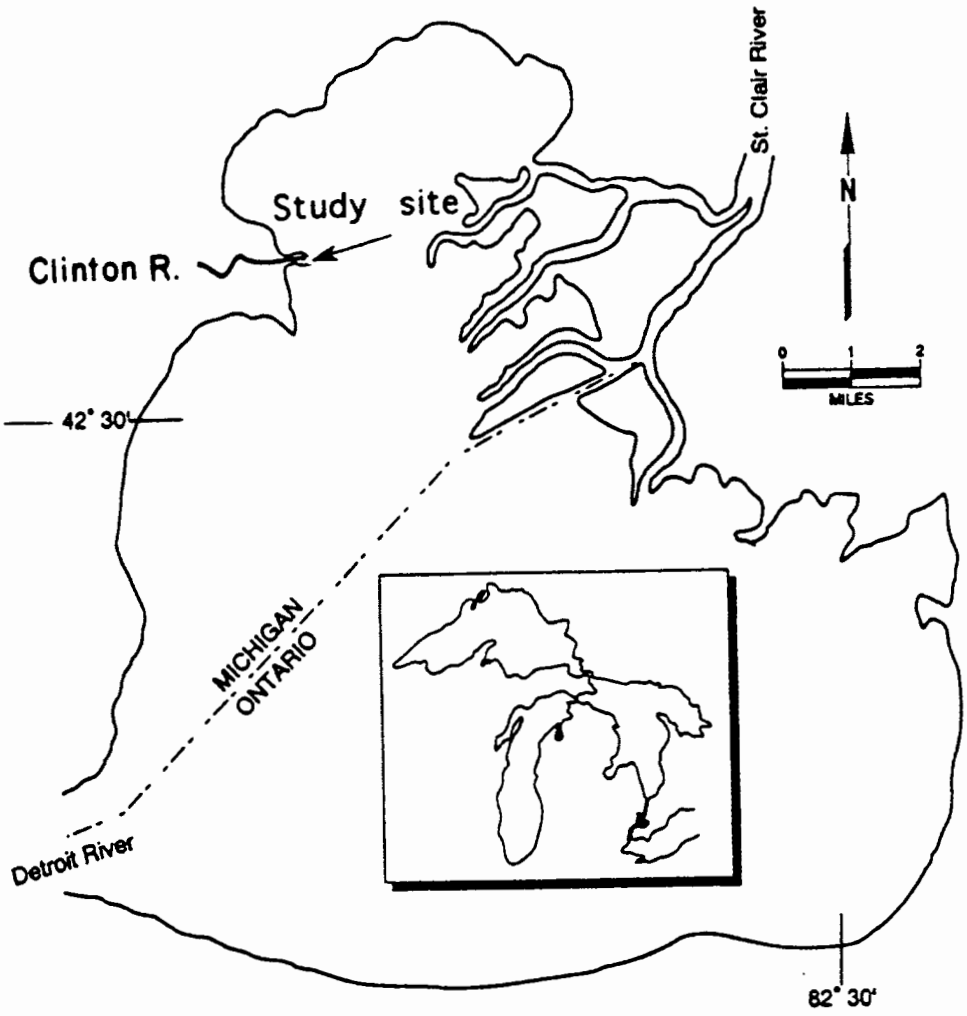


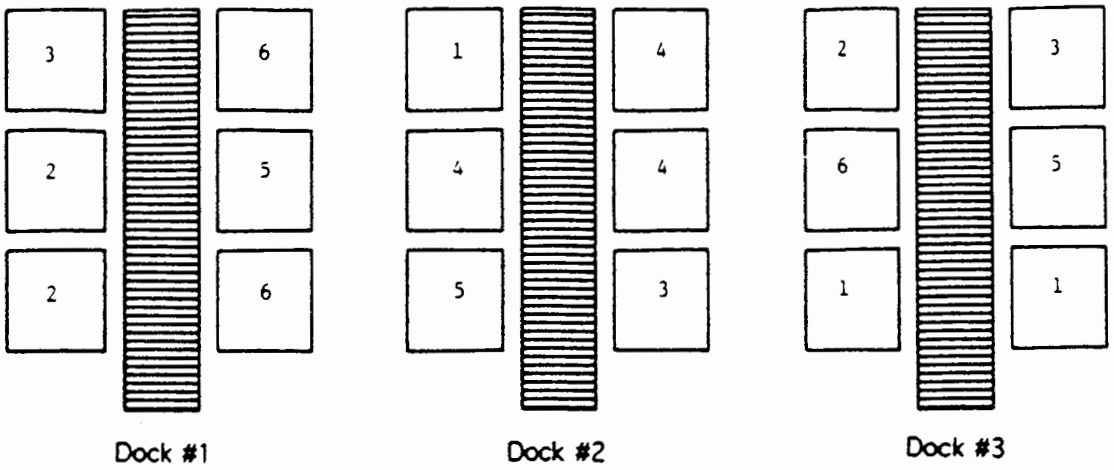
Figure 2. Location of the study site in Mt. Clemens, Michigan, in relation to Lake St. Clair.

to a depth of approximately 8 cm. The bottom of each enclosure was divided into 24 quadrats, from which we randomly selected eight to be the locations for plastic trays with the same sediment-stone mix as the surrounding quadrats.

In 1992, six treatments, with three replicates of each for which locations were randomly selected, were used: (1) zebra mussels; (2) yellow perch; (3) zebra mussels and yellow perch; (4) freshwater drum; (5) zebra mussels and freshwater drum; (6) no zebra mussels or fish (Figure 3). Zebra mussel clusters were uniformly added to the appropriate enclosures to give an arbitrarily chosen mean density of approximately 6,000/m^2. Treatments with fish contained six 120-150 mm perch/enclosure or four 335-435 mm drum.

In 1993, four treatments were used : (1) three replicates of zebra mussels; (2) six replicates of yellow perch; (3) six replicates of zebra mussels and yellow perch; (4) three replicates of no zebra mussels or fish (Figure 4). All replicate locations were randomly selected within a blocked design, which was developed to test location effects (Figure 4). The three blocks were selected based on location in the pond and water flow. Block one contained enclosures near the edges of the group in a corner of the pond. Block two contained inner enclosures that had reduced water flow. Block three contained enclosures near the opposite edges of the group towards the center of the pond. Zebra mussels were re-stocked at approximately 8,000/m^2 (higher to increase effects) and yellow perch size ranged from 120-130 mm.

Zebra mussel clusters were collected from Western Lake Erie. Yellow perch were collected by trawl, seine, or fyke net from Lake St. Clair. In 1992, some of the test yellow perch were collected with seines from Saginaw Bay. Freshwater drum were collected from Lake Erie commercial fishing nets in Sandusky Bay, Ohio. Individual fish were identified by removing a unique sequence of rays from the soft dorsal fin.



1= Yellow perch and zebra mussels
2= Yellow perch only
3= Zebra mussels only
4= No fish or zebra mussels
5= Freshwater drum and zebra mussels
6= Freshwater drum only

Figure 3. Randomly selected locations of the enclosures and treatments in the experimental pond in 1992. Enclosures are within two feet of each other at the sides of each dock and six feet of each other between docks.

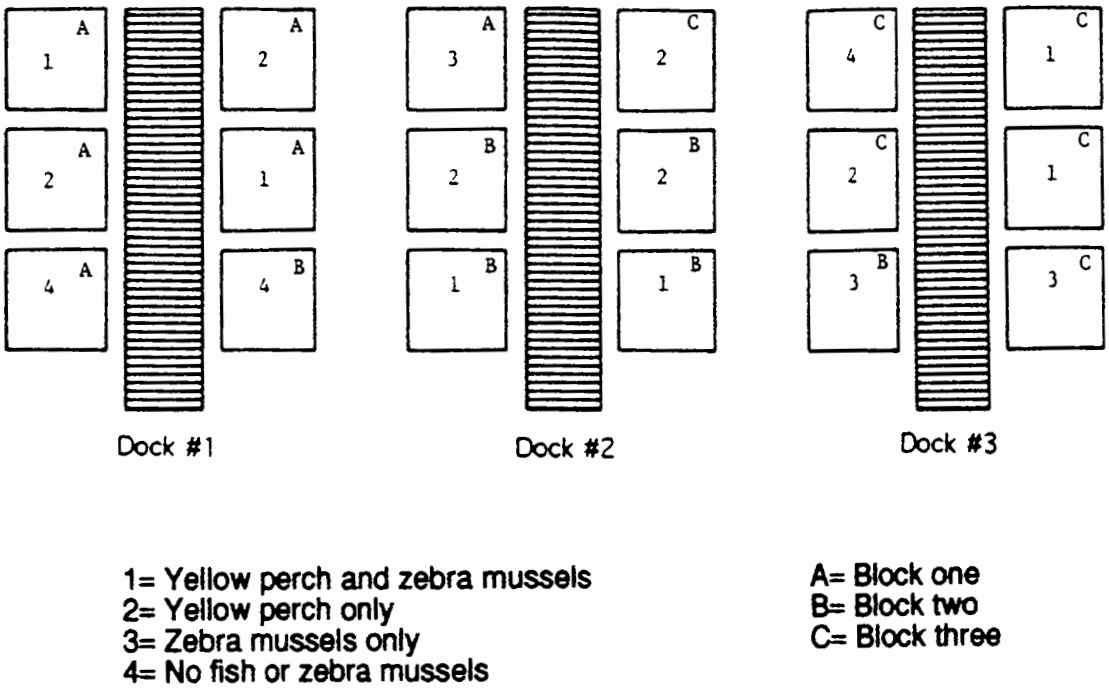


Figure 4. Randomly selected locations of the enclosures and treatments in the experimental pond in 1993. Enclosures are within two feet of each other at the sides of each dock and six feet of each other between docks. Block one is located at the northeastern corner of the pond and block three is located towards the center of the pond.

Yellow perch and freshwater drum were removed via an electroshocking backpack unit once/month from June through October of both years (except no freshwater drum in 1993), at which time standard length and wet weight of all fish were recorded. Stomachs of yellow perch were pumped for laboratory analysis by projecting a small stream of water from a squeeze bottle into the fish stomach and flushing out all stomach contents over a 153-micron sieve. (The effectiveness of this procedure was tested by pumping stomachs in October, followed by stomach removal to check for remaining food items.) Freshwater drum stomachs were sampled only in October of 1992. All stomachs were preserved in 5% buffered formalin.

Any fish that died during the study was promptly replaced with a new fish of similar size in order to maintain the proper fish density in every enclosure. Neither measurements nor stomach contents from these dead fish were used in analysis, unless the fish died soon after this information was taken (electroshocking mortalities usually occurred within an hour after electroshock).

Zebra mussel feeding by freshwater drum was determined by monitoring zebra mussel wet mass and mortality. On occasion, size distribution was determined. Zebra mussels and other zoobenthos were sampled by removing one tray from the same position in the bottom of every enclosure each month. Zoobenthos were removed from the sediment every other month by running the sediment through a 250-micron sieve. Benthic samples were split, stained with Rose Bengal, hand-picked and preserved in 5% buffered formalin. Samples were divided in half (1992) or into quarters (1993) using a Folsom splitter for all invertebrate removal except for oligochaetes and microzoobenthos (ostracods and macrothricids), which were picked from one-sixteenth of the sample due to their high concentration in the samples. The empty trays were then filled with fresh sediment, gravel,

and zebra mussels (where applicable) and returned to the enclosures to maintain homogeneous sediment and mussel density over the bottom of the enclosures.

All invertebrates from stomach and sediment samples were counted (heads were counted when whole bodies were not available) and identified as specifically as possible (usually to genus). At least ten individuals of every genus in every stomach sample of 1992 were measured using a stage micrometer (measurements accurate to the nearest 0.1 mm) and at least ten of every genus in every stomach sample of 1993 were measured, except for a small portion of stomachs collected in September and October. For zoobenthos samples, at least ten of every genus in at least one enclosure in every treatment of 1992 (except freshwater drum treatments) and 1993 were measured. (Usually all enclosures in a treatment but one were measured.)

Head-to-body regressions for Gammarus sp., Caecidotea sp., Oecetis sp., Polycentropus sp., and Chironomidae were formulated from the existing data (Appendix 1), so that heads for these frequently encountered invertebrates could be reliably converted to body lengths. Additional regressions from the data allowed shell-less Physella gyrina to be converted to a length with shell, as well as a regression that converted partially digested Ceriodaphnia sp. to a whole organism with its shell (Appendix 1).

Lengths of invertebrates that were not measured were estimated based on the mean size of that particular genus first from the rest of the yellow perch stomachs sampled from the same enclosure that month, or next from the rest of the enclosures in that treatment for that month. The above procedure accounted for virtually all the invertebrates contained in a sample that were not directly measured. Approximately 10-15 individual organisms for each year (accounting for less than 1% of the total organism lengths for that year) from an infrequently encountered genus did not have a length attached to them, so a grand mean size for that genus was assigned.

Invertebrate lengths were obtained so that all diet and benthos data could be converted to a dry weight. Published length and weight regressions for that genus or one of a closely related genus were used (Nalepa and Quigley, 1980; Culver et al., 1985; Meyer, 1989; Theiling, 1990). A dry weight regression for Physella gyrina was obtained from Hunter (unpublished data). Dry weight regressions for Coleoptera larvae and Hemiptera adults were formulated from existing data, and, since all adult Coleoptera were in the same family and within 1.0 mm in size of each other, one dry weight was determined and assigned to those individuals. See Appendix 1.

Zebra mussel growth was determined from changes in individual shell length and weight of individuals suspended in Plexiglas cages from a dock in the pond. Growth was monitored July, 1992, through October, 1992, and May, 1993, through October, 1993. Overall mortality was determined by counting all the dead and live zebra mussels in trays removed in October of each year. Zebra mussel reproduction was monitored through visual inspection for new settlement and veliger checks in zooplankton samples and in large volumes of pond water pumped through a 153-micron sieve.

Pond temperature, and bottom dissolved oxygen and ammonia concentration were regularly determined throughout the study to monitor conditions that could affect zebra mussel and fish condition. If bottom oxygen levels dropped below 6 ppm, an agitator was put into the pond until levels rose again. If ammonia levels rose sharply, zebra mussels were closely monitored to ensure their continuing survival throughout the study. Oxygen concentration was determined with an VWR oxygen meter and total ammonia was determined by the Nessler method using a Hach spectrophotometer.

An overall analysis of water quality was determined for each year, which included total nitrogen, total phosphorus, silica, total organic carbon, Ca^{2+} and Mg^{2+} concentrations, pH and conductivity. Nitrogen, phosphorus, silica, and total organic carbon analyses were

conducted by The Michigan Department of Natural Resources chemical analysis laboratory in Lansing, Michigan. Ca^{2+} and Mg^{2+} were determined via titration methods at the study site. Conductivity was measured using a conductivity meter and pH was determined with a Hach pH meter. Water transparency was determined weekly using a Secchi disk.

Qualitative zooplankton samples were taken usually once/week to monitor zooplankton density, species composition, and dry weight in the pond. Each sample consisted of a combination of three vertical plankton tows from three locations in the pond.

ANOVA was used to test differences in yellow perch growth, zebra mussel growth, stomach content biomass, and zoobenthos biomass using the following factors: zebra mussel, fish, enclosure, treatment, season, and year. Non-normalized data (yellow perch stomachs by month) were handled using the sum-rank test. In all cases, mean values cited in the text are given with the standard deviation. The details of the statistical methods were not determined until the completion of data collection and are presented in the results.

RESULTS

Zebra Mussel Growth and Survival

In 1992, fifty caged zebra mussels were placed into the pond on July 8. Forty-three survived up until their removal on October 23. Simple ANOVA was used to test zebra mussel change in length and weight from one date to the next. Zebra mussels significantly increased their length ($F_{(1,91)} = 9.25$, $P = 0.003$) and weight ($F_{(1,91)} = 47.83$, $P < 0.001$), but only grew from 7.04 ± 0.940 mm (mean $\pm$ s.d.) and 0.06 ± 0.021 g in July to 7.64 ± 0.953 mm and 0.11 ± 0.039 g in October. Corresponding growth rates for this period were 0.006 mm/day and 0.0005 g/day.

In 1993, fifty caged zebra mussels were placed into the pond on May 12. Forty-four survived up until their removal on October 4. These mussels also significantly increased

their length (ANOVA, $F_{(1,86)} = 1492.82$, $P < 0.001$) and weight (ANOVA, $F_{(1,86)} = 614.92$, $P < 0.001$), growing from 7.62 ± 0.678 mm (mean ± s.d.) and 0.06 ± 0.018 g to 15.86 ± 1.301 mm and 0.54 ± 0.129 g.

Zebra mussels either did not reproduce or veligers did not survive, since no new settlement was detected anywhere in the pond over the two years of the study. Weekly zooplankton samples using a 53-micron plankton net did not contain any veligers, and large volumes of water periodically pumped through a 153-micron sieves did not contain any veligers. Small ponds are subject to diurnal temperature fluctuation that is known to cause physiological stress to zebra mussels sufficient to prevent gonad maturation and spawning (Noordhuis, personal communication; Reeders and Bij de Vaate, 1990).

Zebra mussel mortality, as measured from the bottom of the pond by the number of dead zebra mussels in relation to the total count in a tray, was higher and more variable in 1992 (30% ± 15%)(mean ± s.d.) and lower and less variable in 1993 (17% ± 6%).

Yellow Perch Growth and Survival:

Most of the test yellow perch were retrieved each month and available for analysis. The number of yellow perch retrieved was distributed fairly evenly between treatments and enclosures. Yellow perch survival was moderate, with approximately fifty percent of the total original yellow perch used each year dying of either undetermined environmental stresses, or of stress induced by the effects of electroshocking (electrode touching the fish body and/or overexposure to high voltage). Logistic regression was used to assess differences (if any) in overall mortality rates and mortality by type of death (undetermined or electroshocking) between years, treatments, and enclosures.

Total mortality rates of yellow perch did not differ by year ($X^2 = 0.24$, df = 1, $P = 0.63$), by treatment ($X^2 = 0.47$, df = 1, $P=0.49$), or among enclosures ($X^2 = 20.75$, df = 15, P =

0.14). The frequency of yellow perch mortality by one causal agent, electroshocking, and not by any other means, was tested between treatments. The proportion of yellow perch deaths from electroshocking was significantly higher in enclosures without zebra mussels than in enclosures with zebra mussels ($X^2 = 11.79$, df = 1, $P < 0.001$), with no differences between years ($X^2 = 0.33$, df = 1, $P = 0.57$). This suggests yellow perch in enclosures without zebra mussels could have been in poorer condition, resulting in higher susceptibility to stress induced by electroshocking, however, the variation among enclosures in the same treatment was also significant ($X^2 = 30.27$, df = 15, $P = 0.01$). Significant differences between enclosures suggests electroshocking mortality was most likely enclosure-dependent (i.e., some enclosures were exposed to longer durations of electricity than others due to difficulty in retrieving fish from those particular enclosures).

Those perch that died during the study were replaced with new perch of similar size to maintain densities of six yellow perch/enclosure. Most of these "replacement" yellow perch would lose weight within the first month of introduction into the pond enclosures, while the residual yellow perch would continue to maintain similar growth patterns as previous months (usually maintaining or adding weight). For this reason, only those yellow perch present from the beginning of the experiment (provided that they lived long enough for at least one monthly measurement) were used to determine yellow perch growth for each year (May, 1992, or June, 1993). These yellow perch will be referred to as "original" yellow perch. (Note: Results were substantively the same when all yellow perch were used.)

In the statistical analysis of growth, weight and length residuals were visually inspected and no signs of deviation from normality were evident. Multiple measurements of the same fish were examined and found to be correlated with each other. It is important to take this into account when analyzing growth curve data. The program BMDP-5V (Dixon, 1990) made it possible to use different assumptions about the correlation structure

and test them against each other, so that the most appropriate one could be used. The following alternatives were considered: (1) assuming independence (ordinary regression analysis); (2) compound symmetry (standard "repeated measures ANOVA"); (3) random coefficients with independent errors; (4) random coefficients with serially auto-correlated errors; and (5) unstructured covariance matrix (multivariate regression). For the yellow perch weight and length data, likelihood ratio tests showed that alternative (4) was significantly better than the simpler models , (1) and (3).

Based on the chosen correlation model, BMDP-5V computed estimates of growth curve parameters (initial size and growth rate) using generalized least squares, and provided statistics for testing the effect of experimental factors (such as presence of absence of zebra mussels) on these parameters. This program handles unbalanced and missing data, which was important here since the yellow perch were not always retrievable by electroshocking and several original yellow perch died prior to the end of the experiment.

The results for 1992 and 1993 are clearly different (Figures 6 and 10), so a statistical test comparing the two years was not of interest. Thus, to simplify the analysis with respect to other factors, the data for the two years were analyzed separately.

Plots showing change in length and weight of all original fish used in the statistical analysis were developed for 1992 (Figures 7 and 8) and 1993 (Figures 11-14). In addition, a regression line that represents the typical growth (length and weight) of all the yellow perch in an enclosure of both treatments (with or without zebra mussels) was determined for each year using generalized least squares (Figures 5, 6, 9, and 10). Generalized least squares made it possible to determine the regressions while allowing the variances of each fish in an enclosure to be different and allowing for correlations over time. Typical yellow

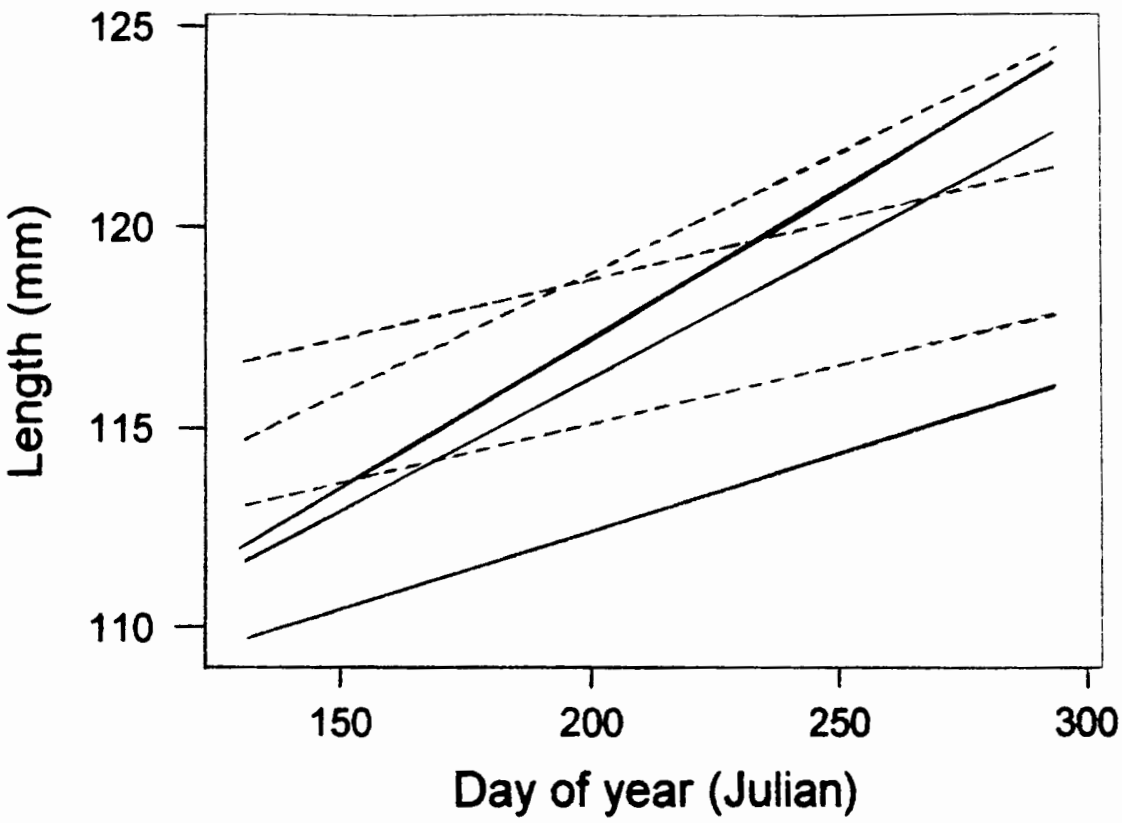


Figure 5. Estimated growth curves (change in standard length) for all original yellow perch by enclosure, 1992. Solid lines represent enclosures without zebra mussels and dashed lines represent enclosures with zebra mussels.

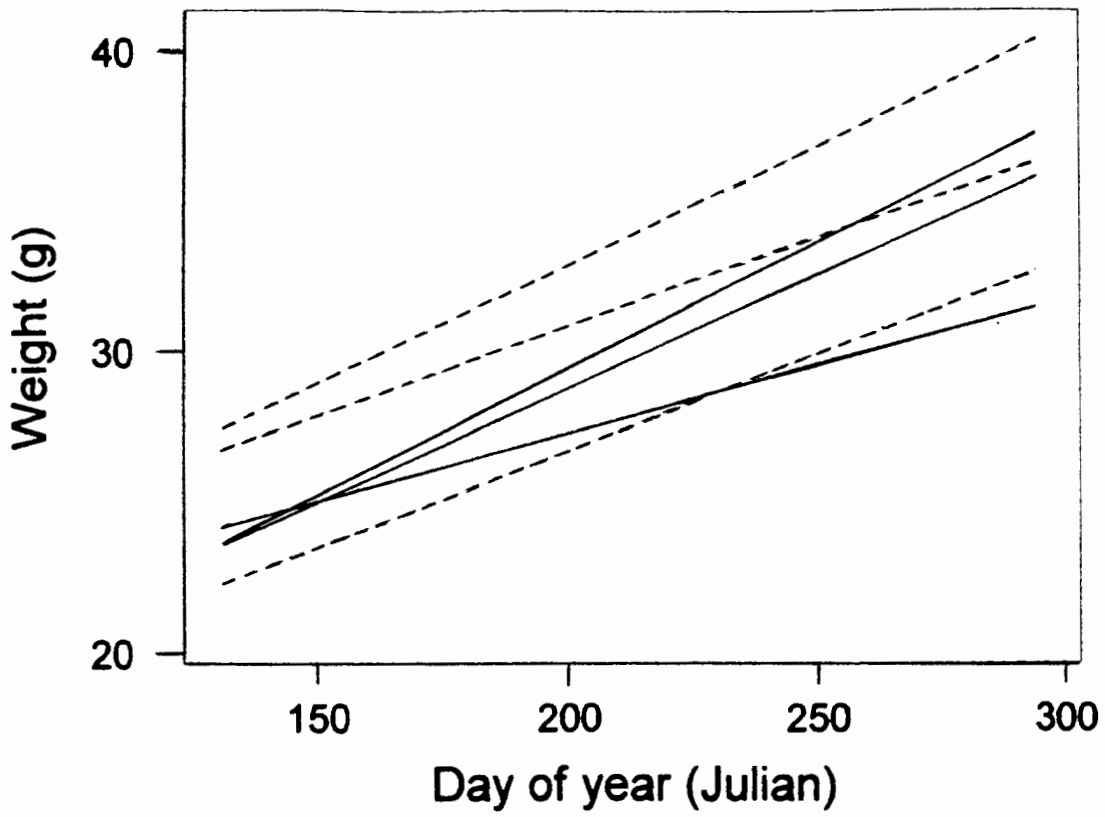


Figure 6. Estimated growth curves (changes in wet weight) for all original yellow perch by enclosure, 1992. Solid lines represent enclosures without zebra mussels and dashed lines represent enclosures with zebra mussels.

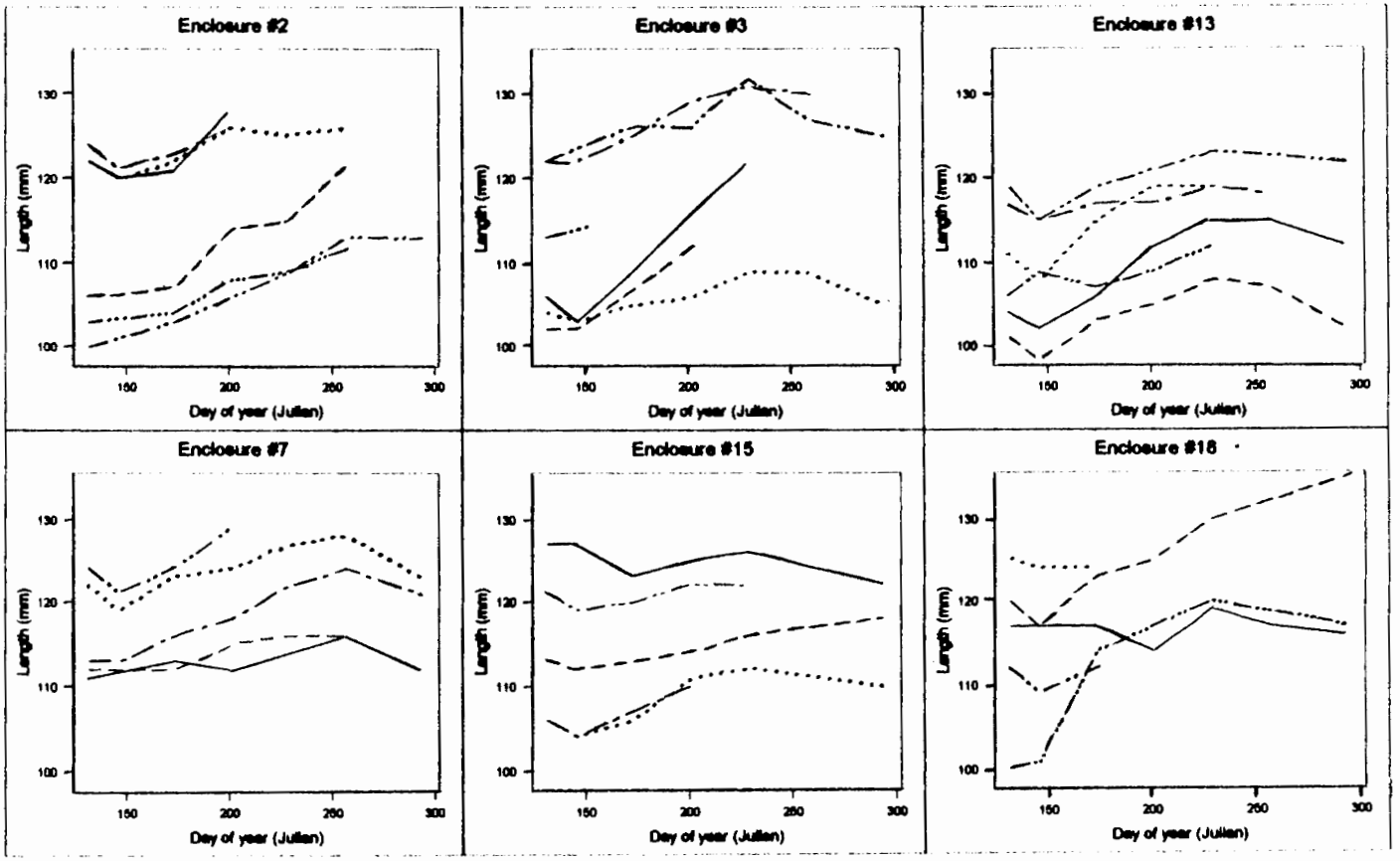


Figure 7. Actual growth curves (change in standard length) of each original yellow perch, by enclosure, 1992. Enclosures on the top row (nos. 2, 3, and 13) are without zebra mussels and those on the bottom row (nos. 7, 15, and 18) are with zebra mussels. Each line represents one fish.

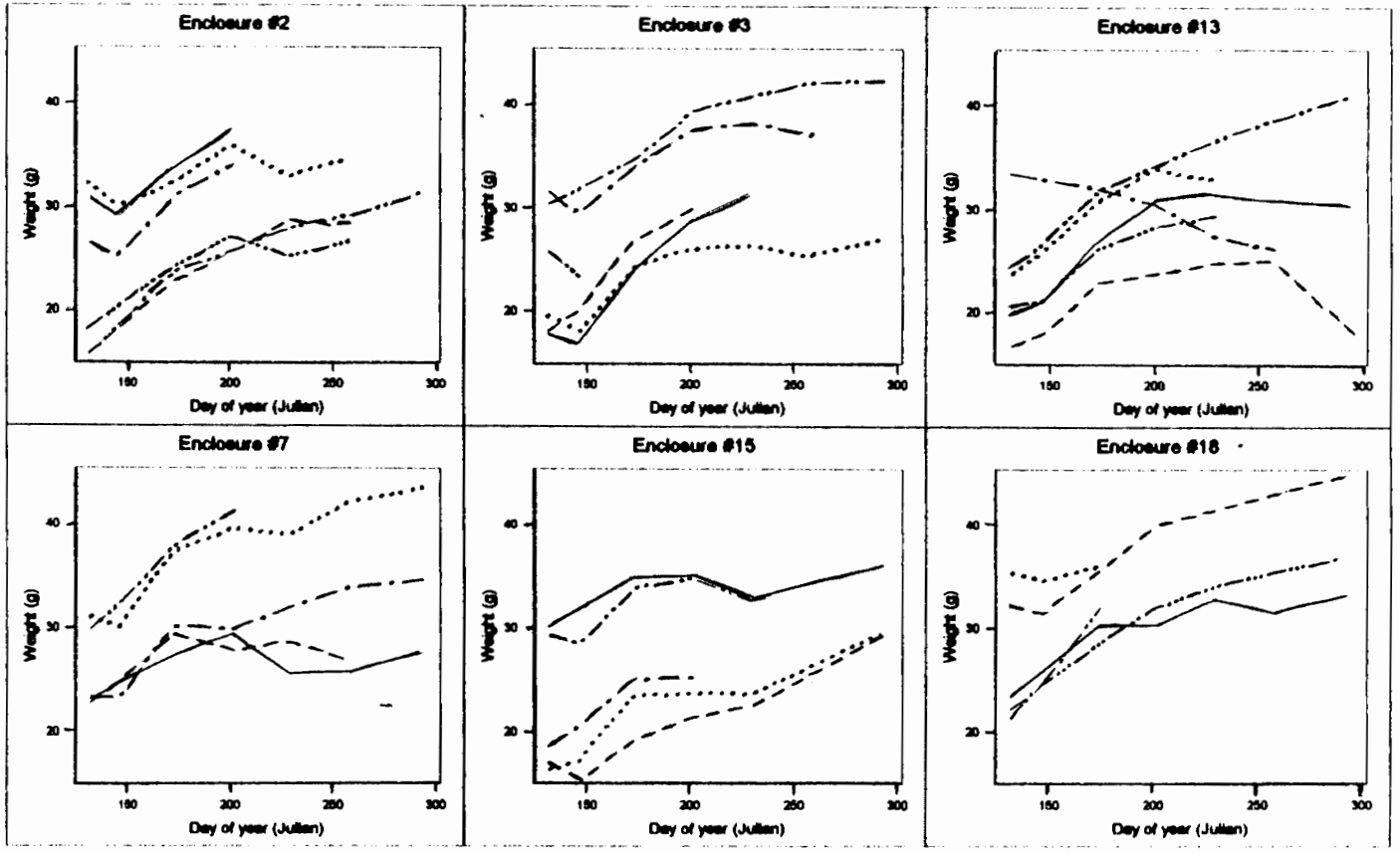


Figure 8. Actual growth curves (change in wet weight) of each original yellow perch, by enclosure, 1992. Enclosures on the top row (nos. 2, 3, and 13) are without zebra mussels and those on the bottom row (nos. 7, 15, and 18) are with zebra mussels. Each line represents one fish.

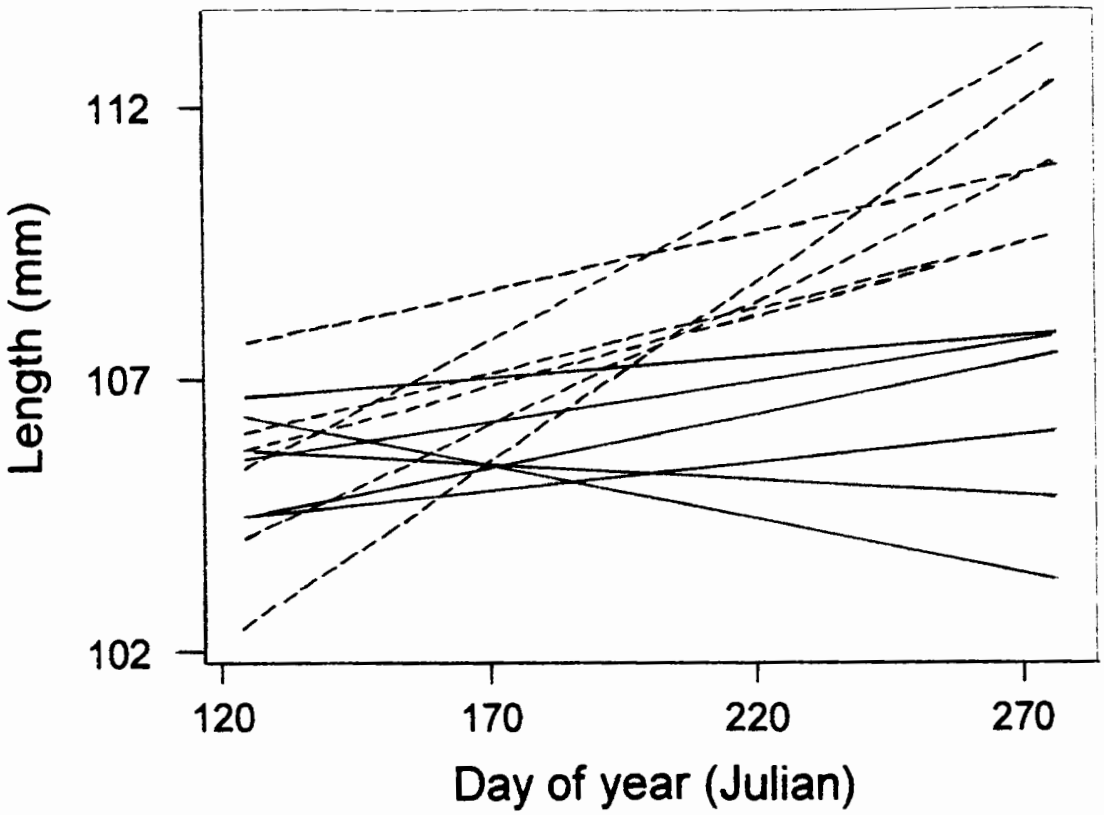


Figure 9. Estimated growth curves (change in standard length) for all original yellow perch by enclosure, 1993. Solid lines represent enclosures without zebra mussels and dashed lines represent enclosures with zebra mussels.

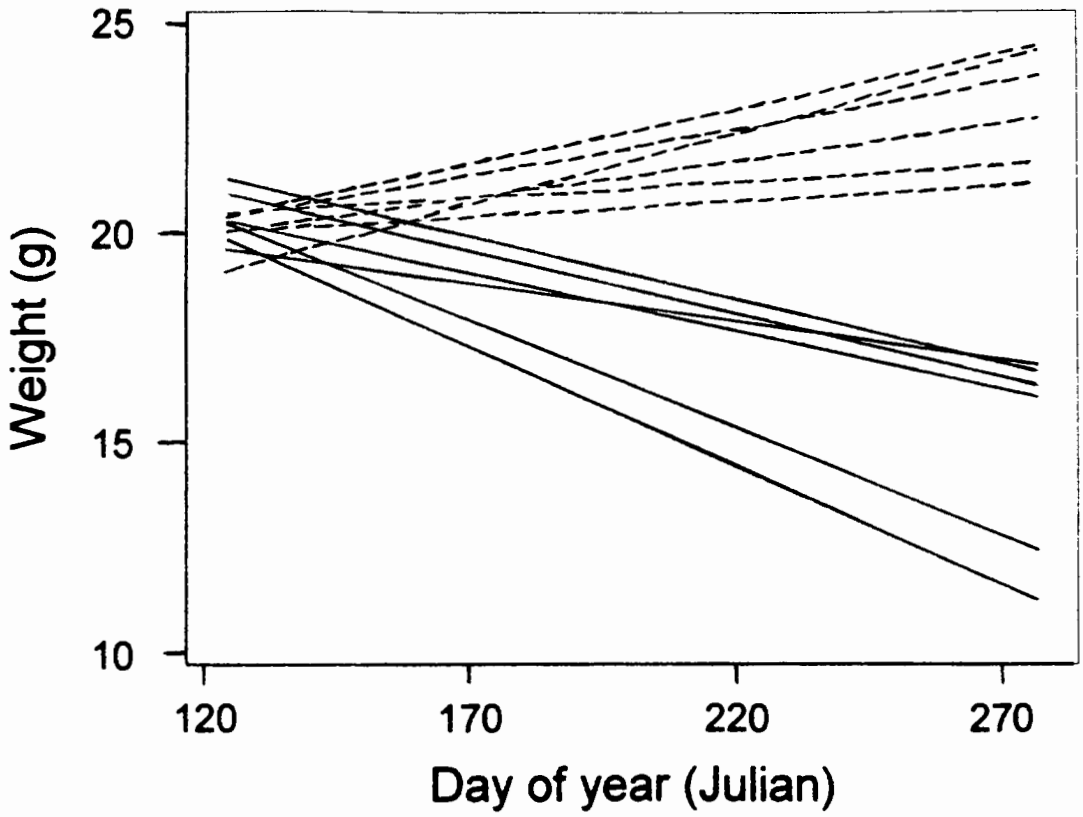


Figure 10. Estimated growth curves (change in wet weight) for all original yellow perch by enclosure, 1993. Solid lines represent enclosures without zebra mussels and dashed lines represent enclosures with zebra mussels.

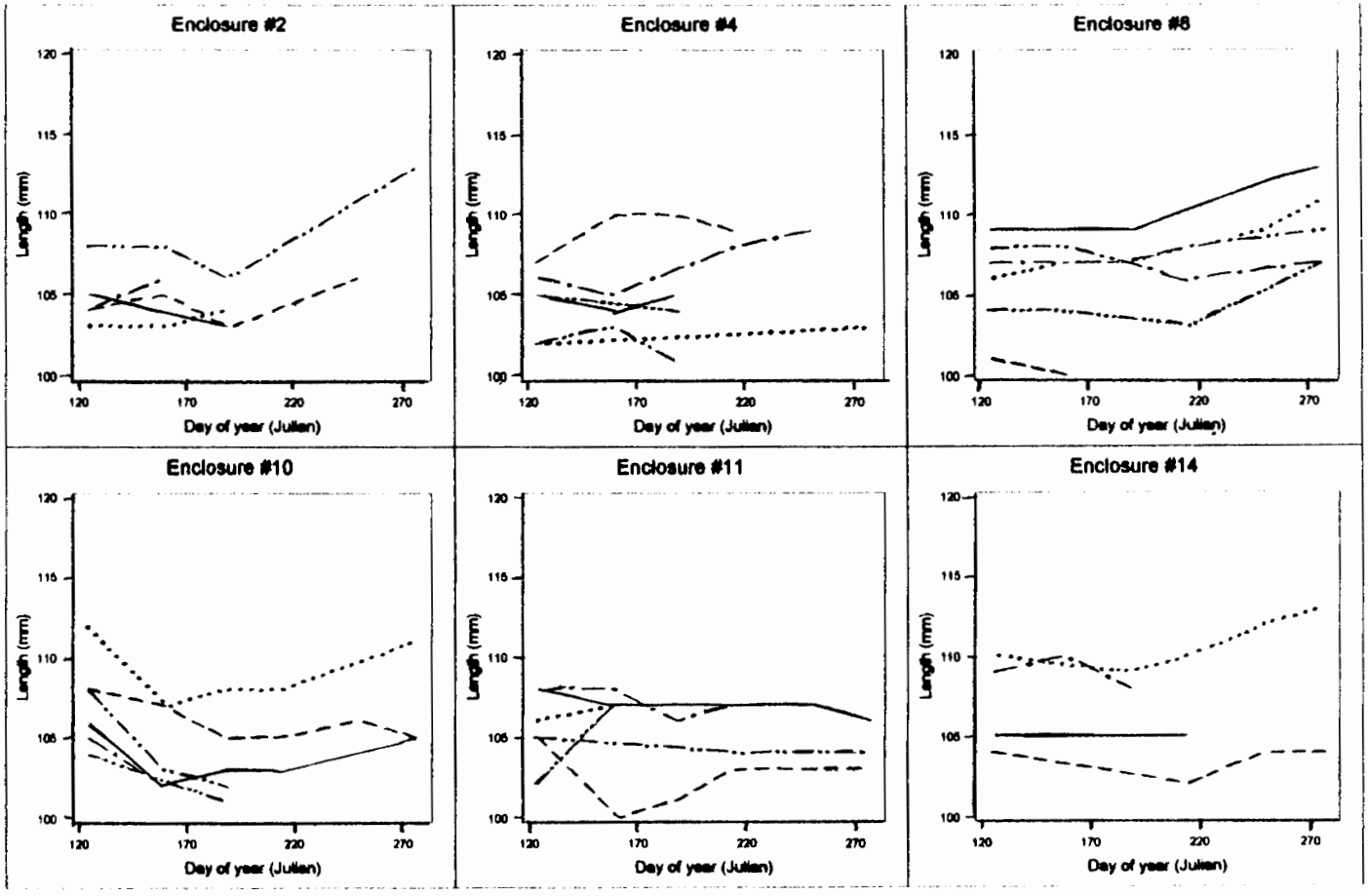


Figure 11. Actual growth curves (change in standard length) of each original yellow perch in enclosures without zebra mussels, 1993. Each line represents one fish.

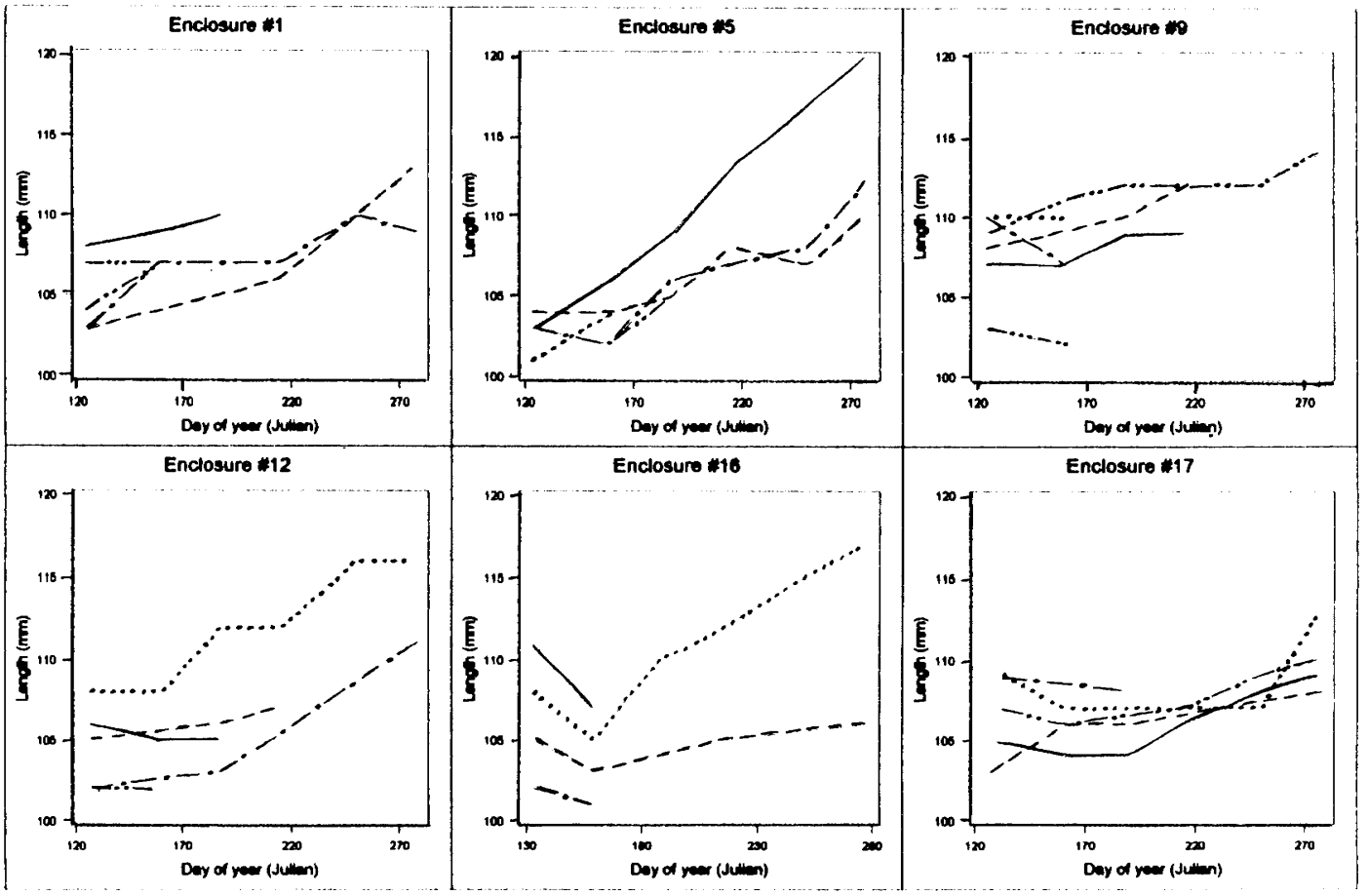


Figure 12. Actual growth curves (change in standard length) of each original yellow perch in enclosures with zebra mussels, 1993. Each line represents one fish.

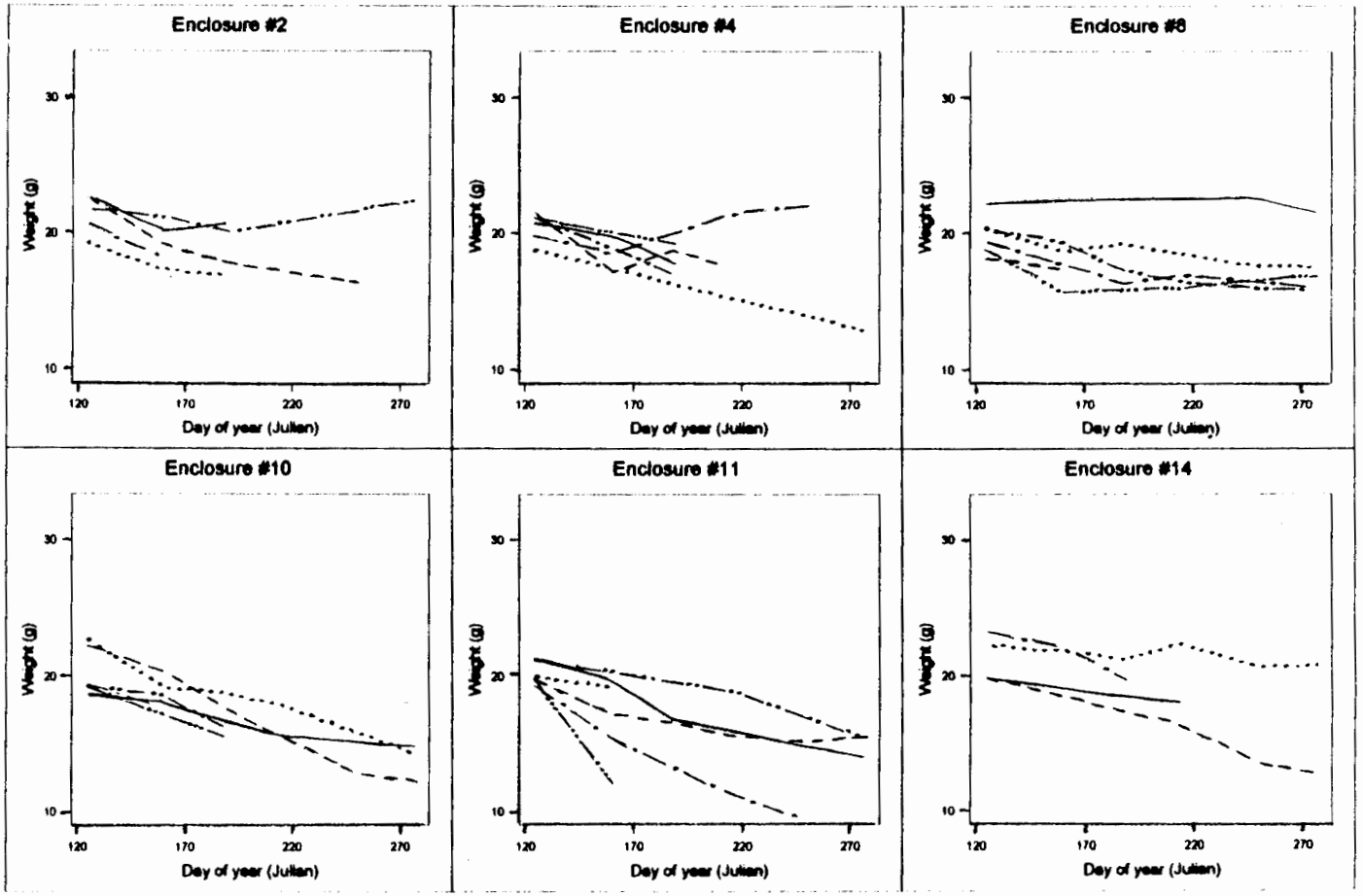


Figure 13. Actual growth curves (change in wet weight) of each original yellow perch in enclosures without zebra mussels, 1993. Each line represents one fish.

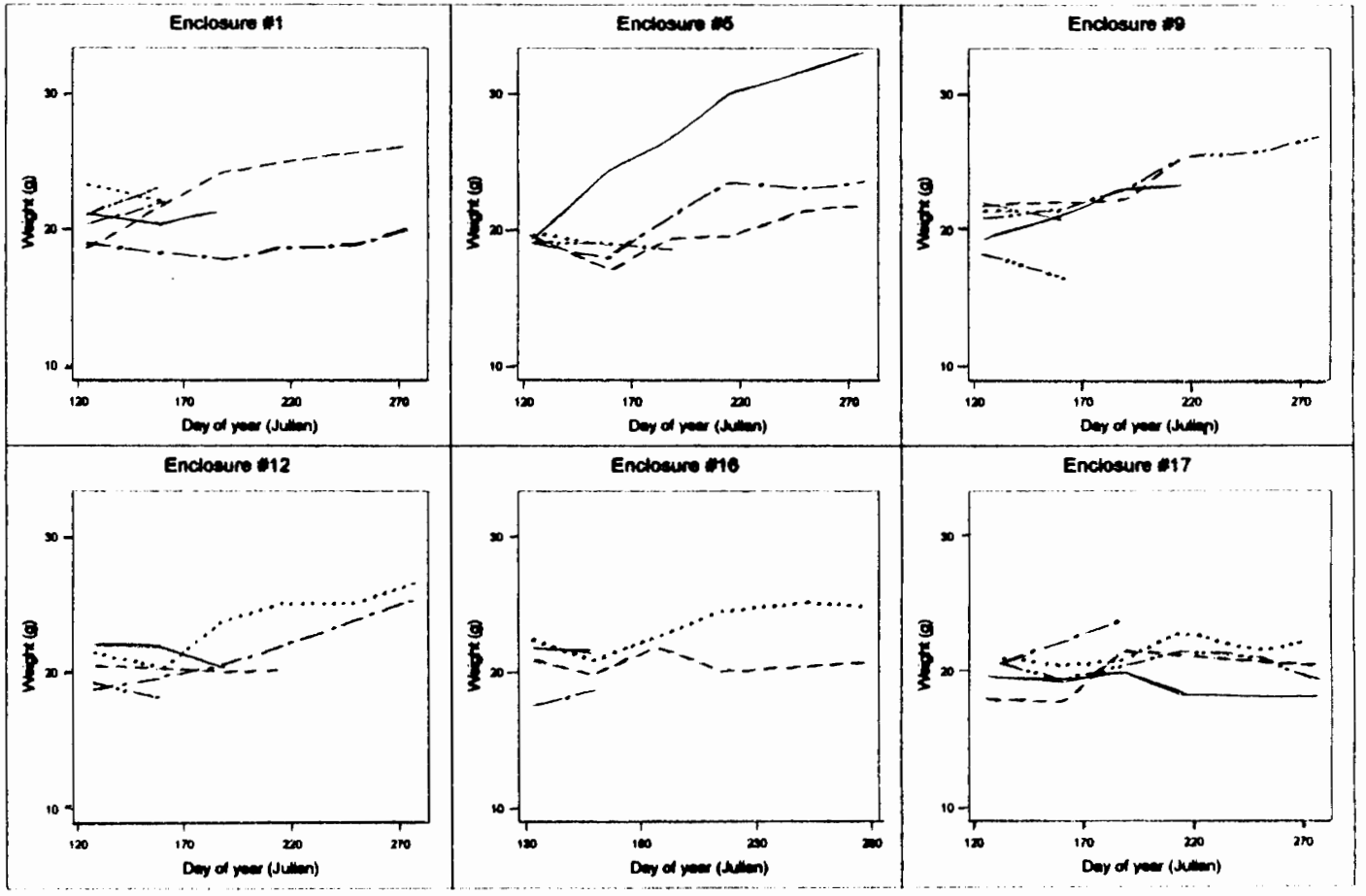


Figure 14. Actual growth curves (change in wet weight) of each original yellow perch in enclosures with zebra mussels, 1993. Each line represents one fish.

perch growth equations (mean initial size + or - growth/day) for each treatment were also formulated.

The above analysis of yellow perch growth for 1992 indicated initial lengths of yellow perch did not differ significantly by treatment ($X^2 = 0.82$, df = 1, P = 0.37), nor by enclosure ($X^2 = 2.71$, df = 5, P = 0.74), and initial weight of yellow perch did not differ significantly by treatment ($X^2 = 0.21$, df = 1, P = 0.64), nor by enclosure ($X^2 = 3.78$, df = 5, P = 0.58). Growth (change in length and weight) of perch in enclosures with zebra mussels was not significantly different from growth of yellow perch without zebra mussels ($X^2 = 0.94$, df = 1, P = 0.33 and $X^2 = 0.015$, df = 1, P = 0.90, respectively). Yellow perch growth curves (length and weight) among enclosures of the same treatment also did not differ significantly ($X^2 = 7.42$, df = 8, P = 0.49 and $X^2 = 8.43$, df = 8, P = 0.39, respectively). The typical growth equations for a yellow perch in an enclosure with zebra mussels in 1992 was: 113.26 mm (mean initial length) + 0.041 mm/day (rate) and 25.05 g (mean initial weight) + 0.066 g/day. The typical growth equations for a yellow perch in an enclosure without zebra mussels in 1992 was: 111.73 mm + 0.056 mm/day and 24.15 g + 0.068 g/day.

Initially, yellow perch in 1992 were significantly the same size between treatments, however, sizes of individuals within and between enclosures were somewhat variable. Initial yellow perch wet weight ranged from 16-32 g. Differential growth rates could have occurred among individuals, which may have led to potential bias towards enclosures with smaller fish (smaller fish grow faster). Growth analysis, using only those fish with initial weights below 25 g (approximately one half of the total fish analyzed) and covariance structure #3 (the program failed to converge for covariance structure #4), indicated no significant difference in weight change between treatments ($X^2 = 1.35$, df = 1, P = 0.25)

but significant differences in growth curves among enclosures within a treatment (X^2 = 31.58, df = 8, $P < 0.0001$).

The analysis of variance on growth of yellow perch (both length and weight) in 1993 indicated initial length of yellow perch did not differ significantly between treatments ($X^2 = 0.09$, df = 1, $P = 0.77$), but differed significantly among enclosures ($X^2 = 22.59$, df = 11, $P = 0.02$; see Figure 9) and initial weight of yellow perch did not differ significantly between treatments ($X^2 = 0.37$, df = 1, $P = 0.54$), nor among enclosures ($X^2 = 11.32$, df = 11, $P = 0.42$). The change in weight and length for yellow perch with zebra mussels was significantly higher ($X^2 = 55.73$, df = 1, $P < 0.001$ and $X^2 = 21.66$, df = 1, $P < 0.001$, respectively) than for yellow perch without zebra mussels. In 1993, yellow perch in enclosures with zebra mussels in nearly all cases increased their length and maintained or increased their weight. Yellow perch in enclosures without zebra mussels in nearly all cases maintained their length and lost weight. Yellow perch weight growth curves among enclosures of the same treatment were not significantly different ($X^2 = 23.11$, df = 20, $P = 0.28$), however, length growth curves among enclosures of the same treatment were significantly different ($X^2 = 41.81$, df = 20, $P = 0.003$). The typical growth equation for a yellow perch in an enclosure with zebra mussels in 1993 was: 105.27 mm (mean initial length) + 0.036 mm/day (rate) and 20.19 g + 0.0174 g/day, while that of a perch without zebra mussels was 105.45 mm + 0.004 mm/day and 20.39 g - 0.0174 g/day.

Since yellow perch were put into test enclosures after they completed spawning, it was not possible to identify their sex and distribute sexes evenly between enclosures and treatments. Female yellow perch typically grow faster than males, so it is possible for unequal sex ratios to affect results of the experiment. The growth analysis method described above with the addition of gender as an additional factor was used to determine if

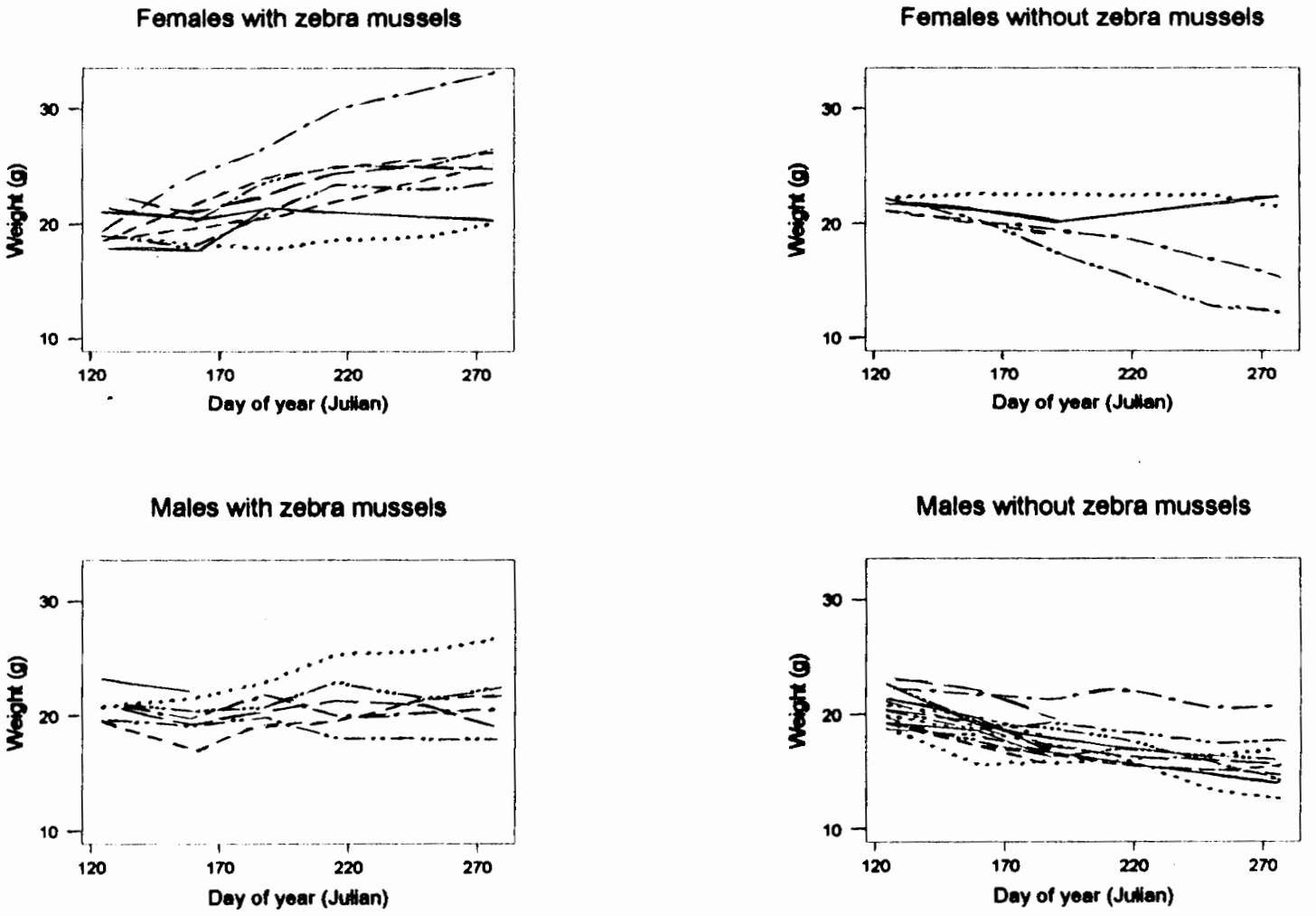


Figure 15. Yellow perch growth curves (change in wet weight) by gender and treatment type, 1993. Each line represents one fish.

this occurred. In 1992, it was difficult to tell whether the gender ratio influenced growth analysis results in 1992 since almost all fish that could be sexed at death or at the completion of the experiment were female. In 1993, those "original" yellow perch that could be sexed were included in analysis of growth by sex. Enclosures with zebra mussels had more female yellow perch than enclosures without zebra mussels, which could have influenced the results of growth analysis. Test results (covariance structure #3), however, indicate both females and males with zebra mussels experienced weight gain and both females and males without zebra mussels experienced weight loss, with the difference between treatments being more pronounced for females ($X^2 = 6.67$, df = 1, P = 0.01; Figure 15). A typical growth equation for a female with zebra mussels was: 19.32 g + 0.042 g/day, while that of a female without zebra mussels was 22.00 g - 0.038 g/day. A typical growth equation for a male with zebra mussels was 20.00 g + 0.010 g/day, while a male without zebra mussels was 20.04 g - 0.030 g/day.

Location of an enclosure in the pond could have influenced growth patterns, but was not testable during 1992 due to the lack of a blocked design and small sample size. Had this been testable in 1992, location effects would seem unlikely between enclosures that did not differ in growth. On the other hand, enclosure location effects on yellow perch growth could be tested in 1993 since enclosure location was used as a blocking factor (three blocks) when the treatments were assigned. Covariance structure #3 had to be used again (convergence failure with #4) with location as a factor. No significant location effects were detected (main effect $X^2 = 1.67$, df =1, P = 043; interaction with treatment $X^2 = 2.65$, df =1, P = 0.27; interaction with treatment and day/time $X^2 = 0.04$, df = 1, P = 0.98).

Diet Analysis

To maximize sample size, all yellow perch stomachs were used in diet analysis. Visual inspection of the results when the analysis was restricted to original perch stomachs indicated no change. Occasionally, a few yellow perch that were not retrieved by the electroshocking backpack unit on day one, would be retrieved the following day. These fish lengths and weights were included in growth analysis, but their stomach data were not used. All fish stomachs were pumped from perch within a three hour period after being shocked. Shocking always took place between 9:00 a.m. and 11:00 a.m. and stomachs were pumped immediately after shocking and in a random order. Pumping stomachs was a fairly effective means of stomach content removal. This procedure was periodically tested by pumping and then dissecting the stomachs of fish that died during the study period and those sacrificed at the end of each year. Little, if anything, was left behind in the dissected stomach unless the stomach was filled to a very high capacity, such as with fifty or more amphipods. In this case, the water pressure would not penetrate the contents entirely, leaving some organisms behind in the stomach. This was a problem in October, 1992, but appeared to be a consistent problem with every densely filled stomach that was encountered.

Since growth differences between yellow perch treatments in 1992 were not detected, it was believed that the amount of daphnids and "pond" invertebrates (Hydracarina, Hemiptera, and Coleoptera) was high enough throughout the pond to have made a significant contribution to the diets of the test perch, therefore masking any effects on perch growth due to differences in the zoobenthos. In Spring of 1993, approximately 200 juvenile and adult yellow perch were put into the pond outside the enclosures in an attempt to limit the availability of zooplankton and "pond" invertebrates. Reduction of the abundance of these invertebrates, would also model a lacustrial environment, where smaller

densities of daphnids and virtually no "pond" invertebrates are available to yellow perch as food.

For statistical analyses of perch diet, the following taxonomic groupings were used: zooplankton, Gastropoda, Trichoptera, Diptera (primarily Chironomidae larvae), Hirudinea (primarily Eropdellidae) Crustacea (Amphipoda and Isopoda), and other (Hydracarina, Hemiptera, Coleoptera, Tricladida, Oligochaeta). Yellow perch diet for 1992 and 1993 are summarized in Figures 16 and 17, which depict the mean dry weight of each taxonomic group/yellow perch stomach, by treatment and by month. In 1992, yellow perch with zebra mussels appear to have had a higher mean dry weight of invertebrates/stomach than yellow perch without zebra mussels in May, July, and October, however, the opposite appears to happen in September (Figure 16). Hirudinea and Crustacea appear to contribute to these higher mean dry weights. The highest consumption appeared to have occurred in July, September, and October. In 1993, the highest consumption appeared to have occurred in June and October. Diet appeared to be similar between treatments except in June, when it is higher in yellow perch stomachs with zebra mussels than yellow perch without zebra mussels (Figure 17). In June, all taxonomic groups except zooplankton appear to be higher in yellow perch stomachs with zebra mussels than yellow perch stomachs without zebra mussels. Zooplankton appears to be higher in yellow perch without zebra mussels in June. The diets are heavily dominated by Diptera in 1993, and Hirudinea in October, 1993.

Diet comparisons between the two treatments were made using the rank-sum test. The mean total biomass of invertebrates/yellow perch stomach for the whole year (1992 or 1993) and the total mean biomass of each taxonomic group/yellow perch stomach for the whole year (1992 or 1993) were tested by treatment. A significantly higher mean dry weight of "other" invertebrates in yellow perch without zebra mussels compared to yellow

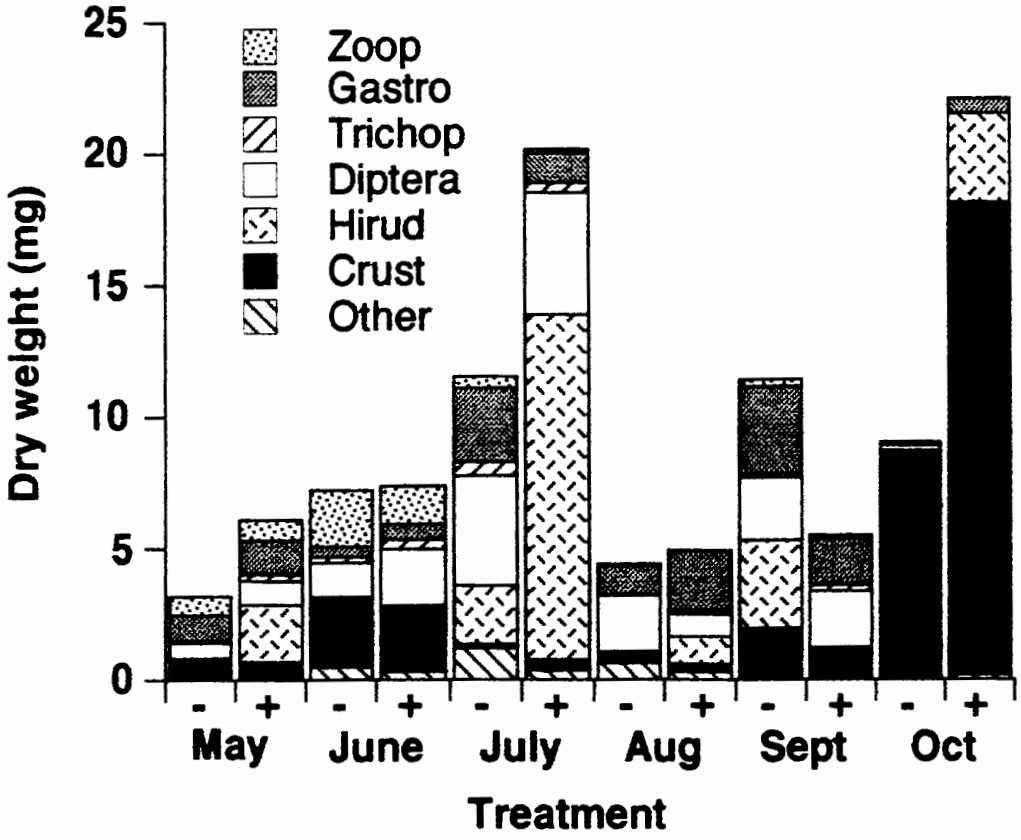


Figure 16. Mean yellow perch stomach content biomass in 1992 by taxonomic group, month, and treatment ("-" = yellow perch without zebra mussels and "+" = yellow perch with zebra mussels). Sample sizes from left to right = 13, 13; 16, 18; 12, 15; 13, 18; 6, 9; 11, 13.

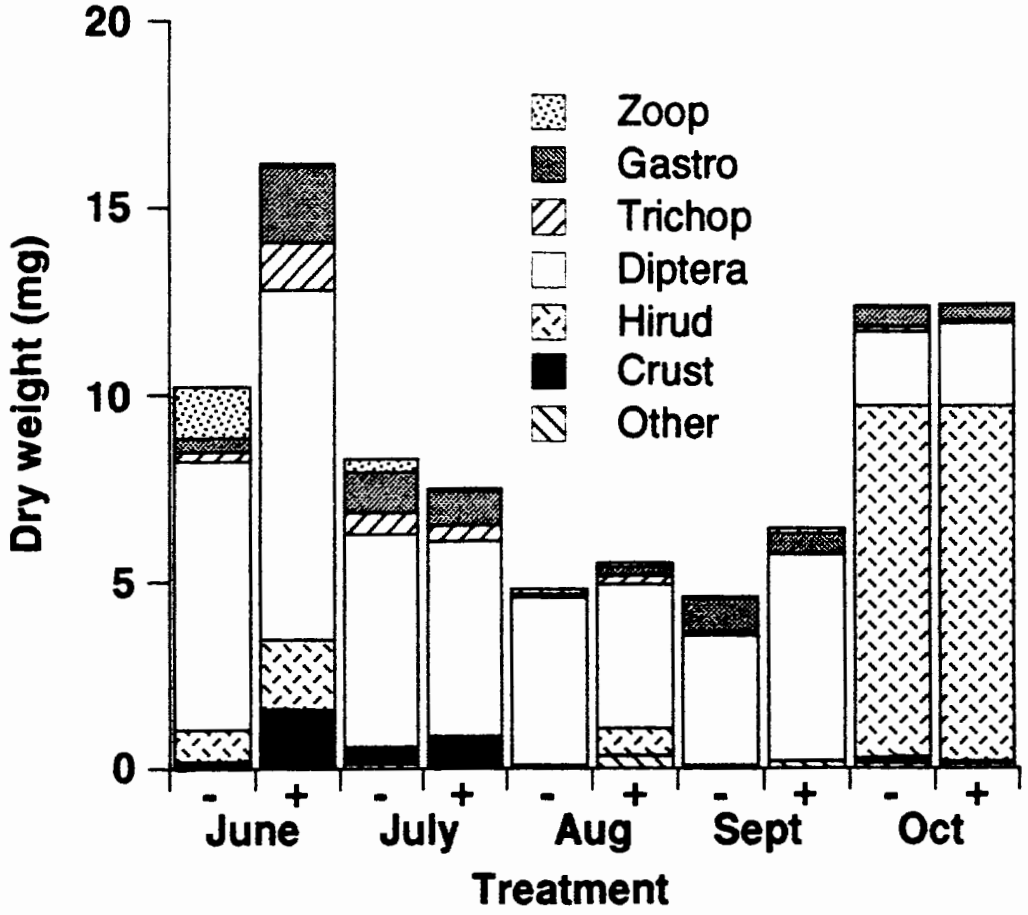


Figure 17. Mean yellow perch stomach content biomass in 1993 by taxonomic group, month, and treatment ("-" = yellow perch without zebra mussels and "+" = yellow perch with zebra mussels). Sample sizes in order across the horizontal axis = 14, 19; 22, 21; 23, 21; 22, 18; 26, 28.

perch with zebra mussels was detected in 1992 (P = 0.04; Table 1); and a significantly higher mean dry weight of zooplankton in perch without zebra mussels compared to yellow perch with zebra mussels was detected in 1993 (P = 0.03; Table 2). Treatments with zebra mussels often had a higher mean dry weight and higher maximum weights of certain invertebrates/stomach both in 1992 and 1993, specifically, higher Hirudinea, Crustacea and total dry weight in 1992 (Table 1) and higher Gastropoda, Trichoptera, Diptera, Crustacea, other, and total occurred in 1993 (Table 2). Due to the wide range of dry weights in the individual stomachs significant differences between treatments were not detected. Several of these same invertebrate groups were also more frequently encountered in stomachs of yellow perch with zebra mussels than in stomachs of yellow perch without zebra mussels (Table 1 and 2). The opposite scenario occurs with zooplankton.

Each taxonomic group, as well as the total dry weight/yellow perch stomach, by treatment, are represented in box plots (using medians) over time (monthly) in Figures 18 - 21. Diet comparisons between the two treatments for each month were made also using the rank-sum test. Testing by month was deemed appropriate since total food consumption by yellow perch appeared to differ by month (Figure 21, all groups), which appears to be negatively correlated with seasonal changes in water temperature (Figure 22). Although searching for significant differences among numerous tests can be misleading, several significant differences were found and are noteworthy, if only in a "practical" sense. For example, in July of 1992, perch without zebra mussels had a significantly higher dry weight of "other" invertebrates in their stomachs than perch with zebra mussels (Z = 2.73, df = 1, P = 0.006; Figure 21). In August, 1992, yellow perch with zebra mussels had a significantly higher dry weight of Trichoptera in their stomachs than perch without zebra mussels (Z = 1.56, df = 1, P =0.04; Figure 19), and in October, a higher dry weight of Gastropoda (Z = 1.13, df = 1, P = 0.05; Figure 18) and higher total dry weight/stomach

Table 1 . Descriptive statistics and results of nonparametric (rank-sum) tests on yellow perch stomach contents for all of 1992 [df=1 for all; , N=87 yellow perch stomachs from enclosures without zebra mussels (-), N=73 yellow perch stomachs from enclosures with zebra mussels (+)].

Food Type	ZM	% Freq.	Stom. Dry Wt. (Mean ± s.e.)	Maximum	Z-value	P-value
Zooplank.	-	78.08	0.679 ± 0.122	5.007	1.11	0.265
	+	87.36	0.498 ± 0.099	4.462		
Gastropoda	-	67.12	1.294 ± 0.265	11.182	0.30	0.758
	+	68.97	1.240 ± 0.233	6.990		
Trichoptera	-	52.05	0.191 ± 0.044	1.994	1.35	0.142
	+	41.38	0.233 ± 0.045	1.442		
Diptera	-	52.05	1.797 ± 0.339	16.919	1.32	0.169
	+	41.38	1.747 ± 0.567	35.285		
Hirudinea	-	8.22	0.744 ± 0.437	30.289	0.28	0.522
	+	5.75	3.290 ± 2.240	157.320		
Crustacea	-	68.49	2.279 ± 0.497	30.006	0.35	0.726
	+	77.01	3.610 ± 1.030	55.170		
Other	-	47.95	0.457 ± 0.088	3.627	1.99	0.038
	+	65.52	0.212 ± 0.048	2.314		
Total	-		7.441 ± 0.782	43.665	0.12	0.903
	+		10.830 ± 2.420	160.110		

Table 2 . Descriptive statistics and results of nonparametric (rank-sum) tests on yellow perch stomach contents for all of 1993 [df=1 for all; , N=107 yellow perch stomachs from enclosures without zebra mussels (-), N=107 yellow perch stomachs from enclosures with zebra mussels (+)].

Food Type	ZM	% Freq.	Stom. Dry Wt. (Mean +- s.e.)	Maximum	Z-value	P-value
Zooplank.	-	85.05	0.361 ± 0.106	7.920	2.18	0.029
	+	92.52	0.083 ± 0.016	1.078		
Gastropoda	-	47.66	0.570 ± 0.154	11.081	0.67	0.480
	+	59.81	0.711 ± 0.177	13.867		
Trichoptera	-	32.71	0.211 ± 0.059	5.230	0.08	0.925
	+	32.71	0.327 ± 0.133	11.058		
Diptera	-	87.85	4.388 ± 0.526	29.939	0.29	0.770
	+	85.05	4.808 ± 0.591	33.484		
Hirudinea	-	10.28	2.613 ± 0.956	61.494	0.22	0.662
	+	8.41	2.712 ± 0.948	54.616		
Crustacea	-	24.30	0.175 ± 0.048	3.402	0.06	0.938
	+	26.17	0.392 ± 0.128	9.732		
Other	-	34.58	0.085 ± 0.022	1.489	0.45	0.602
	+	40.19	0.175 ± 0.057	4.966		
Total	-		8.400 ± 1.070	63.58	0.53	0.599
	+		9.190 ± 1.090	56.25		

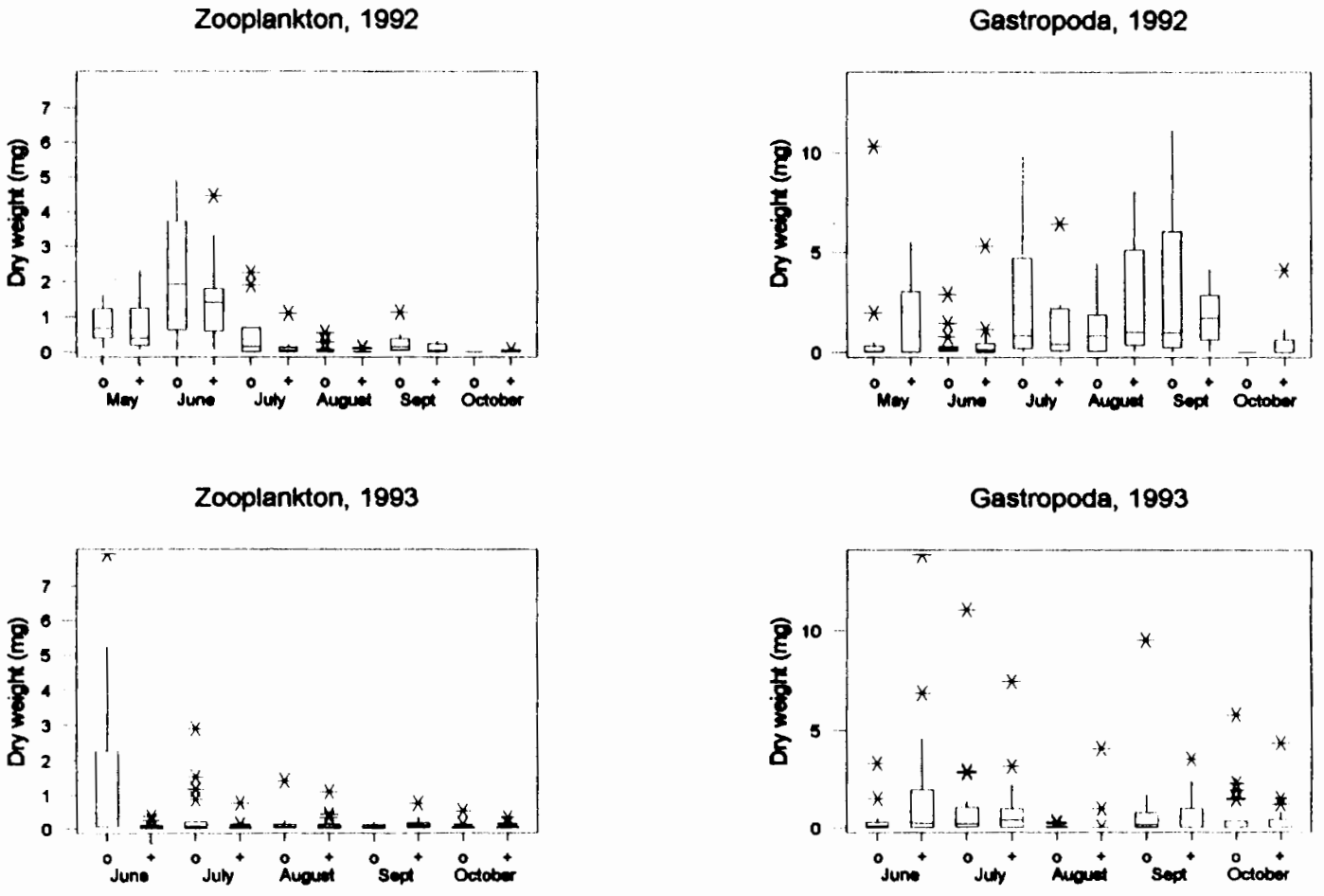


Figure 18. Box plots of yellow perch stomach biomass for zooplankton and Gastropoda, by month, 1992 and 1993. Horizontal lines inside boxes represent medians separating Q3 (top) from Q1 (bottom). Vertical lines at box tops and bottoms represent standard deviations and stars represent outliers.

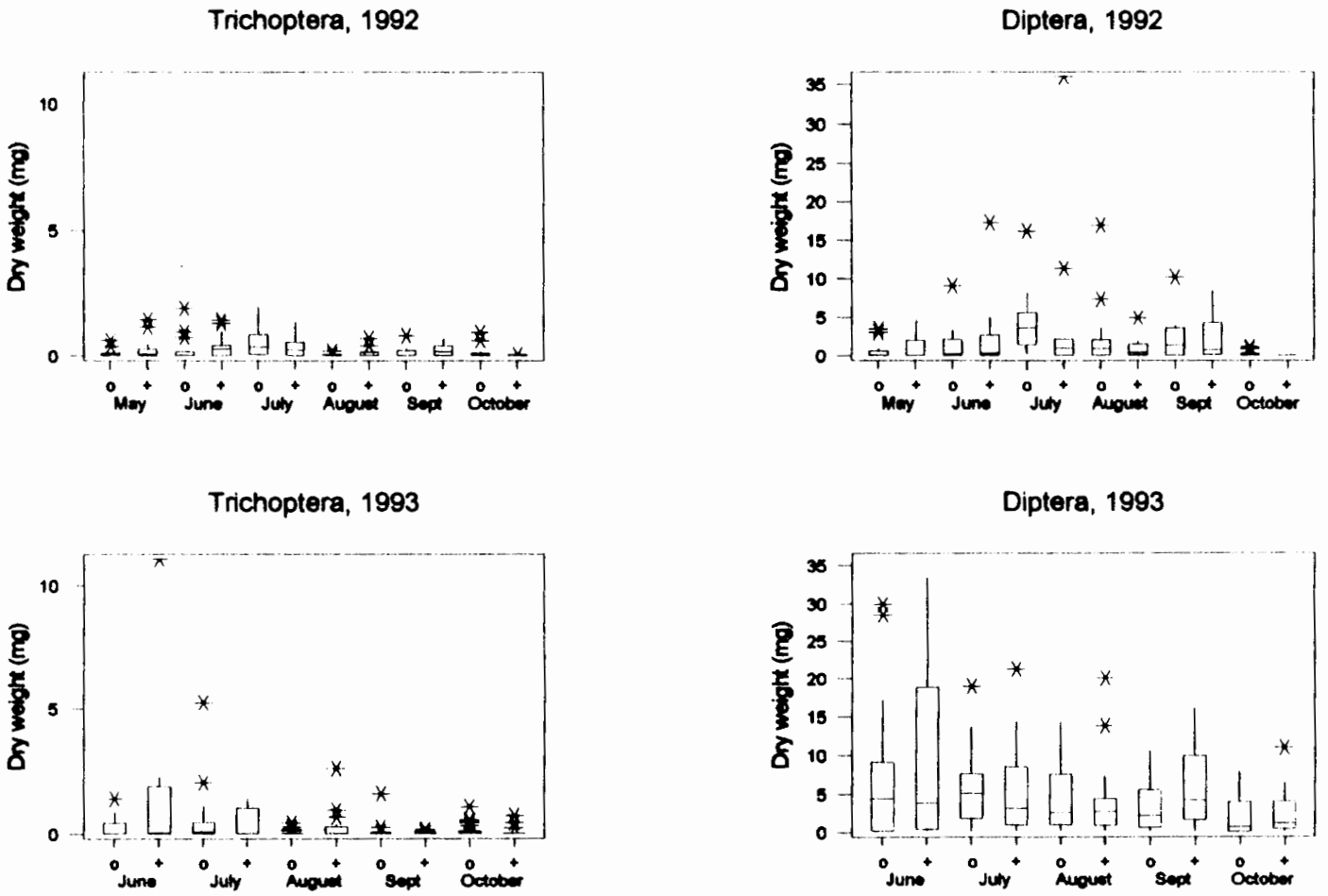


Figure 19. Box plots of yellow perch stomach biomass for Trichoptera and Diptera, by month, 1992 and 1993. Horizontal lines inside boxes represent medians separating Q3 (top) from Q1 (bottom). Vertical lines at box tops and bottoms represent standard deviations and stars represent outliers.

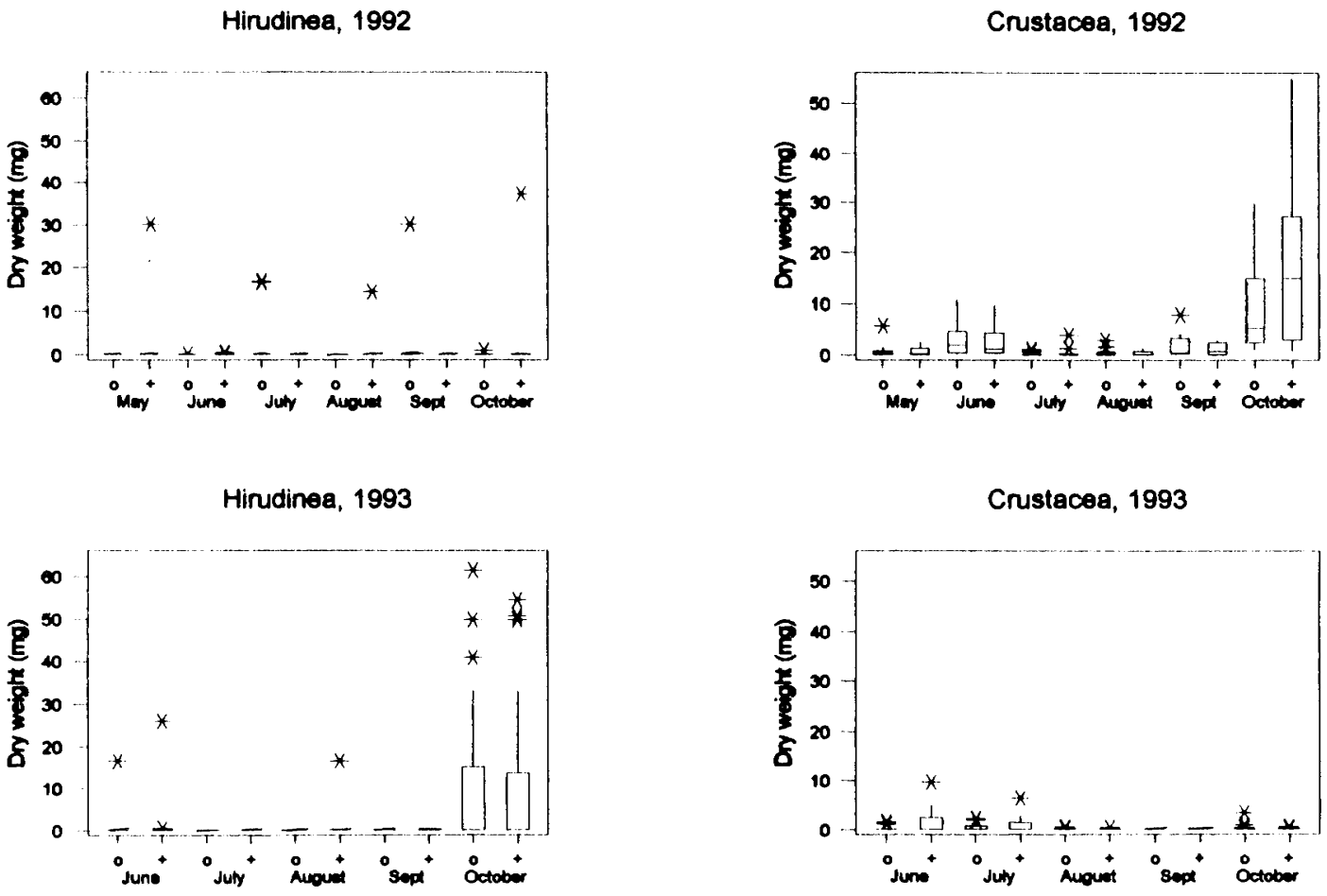


Figure 20. Box plots of yellow perch stomach biomass for Hirudinea and Crustacea, by month, 1992 and 1993. Horizontal lines inside boxes represent medians separating Q3 (top) from Q1 (bottom). Vertical lines at box tops and bottoms represent standard deviations and stars represent outliers.

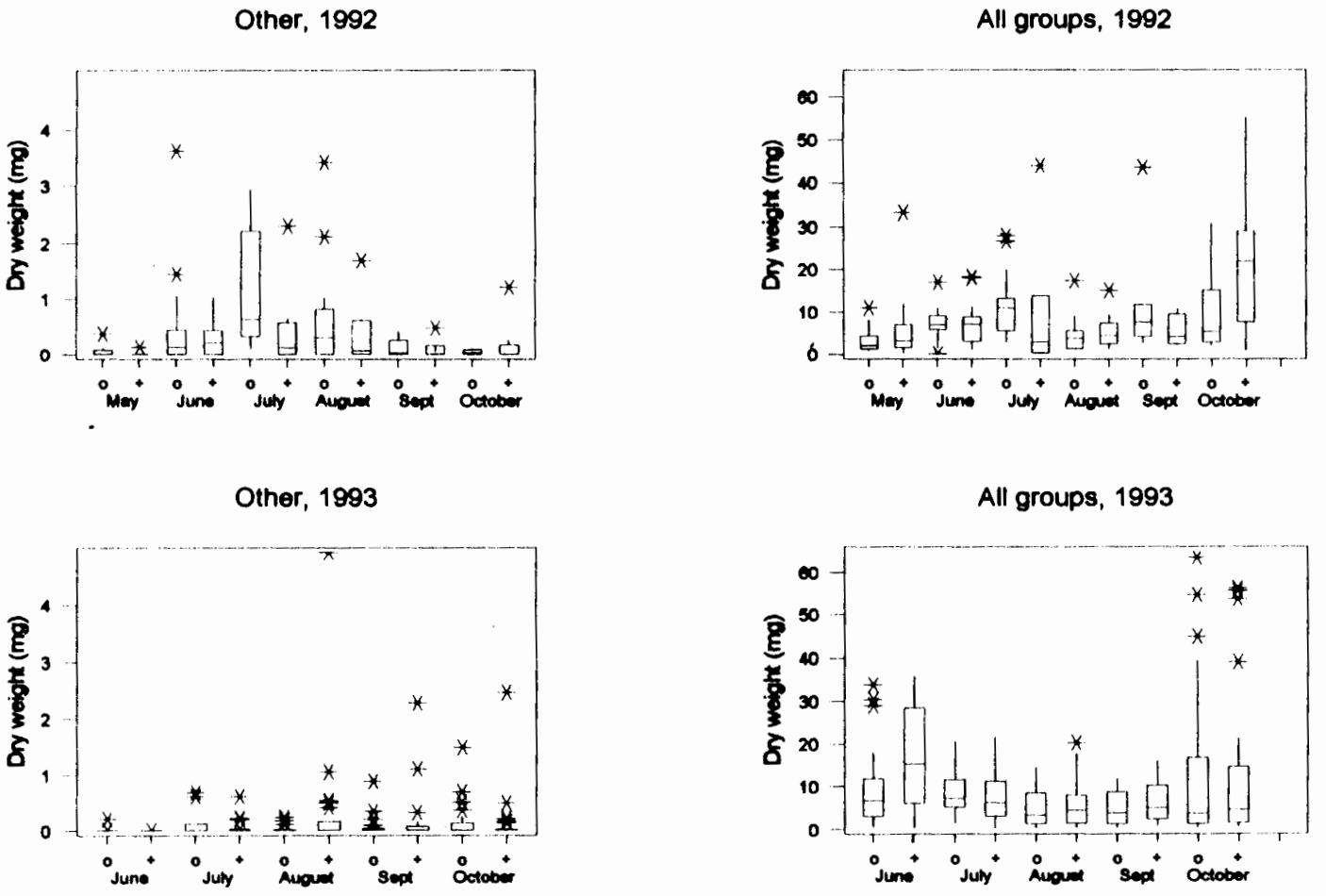


Figure 21. Box plots of yellow perch stomach biomass for "other" invertebrates and all invertebrate groups together, by month, 1992 and 1993. Horizontal lines inside boxes represent medians separating Q3 (top) from Q1 (bottom). Vertical lines at box tops and bottoms represent standard deviations and stars represent outliers.

($Z = 2.17$, df = 1, $P = 0.030$; Figure 21) than perch without zebra mussels. In June and July of 1993, perch without zebra mussels had a significantly higher dry weight of zooplankton/stomach ($Z = 2.84$, df = 1, $P = 0.005$ and $Z = 2.04$, df = 1, $P = 0.04$, respectively; Figure 18) than perch with zebra mussels; and in August of 1993, perch without zebra mussels had a higher mean dry weight/stomach of Gastropoda than yellow perch with zebra mussels ($Z = 1.62$, df =1, $P = 0.05$; Figure 18). In June of 1993, yellow perch with zebra mussels appeared to have had a higher mean dry weight of Crustacea in their diet than yellow perch without zebra mussels. This was not a significant difference at the 0.05 level, but its small P-value of 0.07 ($Z = 1.64$, df = 1) is worth noting.

Stomach data from both years was normalized by taking the cube root. Overall yellow perch diet was statistically examined using analysis of variance that assumed independence. A repeated measures analysis of variance was not necessary since individual diets were independent between months (i.e., a fish that ate a lot one month did not necessary eat as much the next). Data were unbalanced between enclosures since different numbers of fish were retrieved from each enclosure. A likelihood ratio test was used to compare analyses using treatment and enclosure separately as grouping factors. Just as much variation in diet occurred between enclosures as it did between treatments, so all the perch within a treatment were considered one group. Unbalanced data between seasons was handled by performing separate analyses on each season. Analyses were made on dry weight of stomach contents by season (Spring, Summer, and Fall) between treatments, including separate analyses on a group of invertebrates most likely to benefit from zebra mussel biodeposition (Amphipoda, Gastropoda, and Diptera).

Parametric testing (ANOVA) of stomach content dry weights using year, season, and treatment as factors, indicated a significantly higher mean total dry weight/perch stomach in Spring of 1993 than Spring of 1992 ($F_{(1,65)} = 4.92$, $P = 0.03$), but no significant difference

between treatments ($F_{(1,65)} = 1.42$, $P = 0.24$). Additional analyses indicate significant differences between enclosures ($F_{(17,51)} = 2.02$, $P = 0.03$) at this time, too. No significant differences in mean total dry weight/perch stomach were detected between year, season, treatment, or enclosure in Summer or Fall. When only Gastropoda/Crustacea/Diptera (invertebrates we predicted to benefit from zebra mussels) were considered, tests indicated a significantly higher dry weight/perch stomach of this invertebrate group in Spring of 1993 than Spring of 1992 ($F_{(1,65)} = 6.20$, $P = 0.02$) as well as a significant difference between enclosures ($F_{(17,51)} = 1.98$, $P=0.03$). No significant differences were detected in Summer. Significant differences in Fall occurred with a higher mean dry weight of this invertebrate group/perch stomach in Fall of 1992 than Fall of 1993 ($F_{(1,85)} = 27.81$, $P < 0.001$), a higher mean dry weight of this invertebrate group/perch stomach in the zebra mussel treatment than in the no zebra mussel treatment for both years (Fall) ($F_{(1,85)} = 6.65$, $P = 0.01$) and significant differences between all enclosures for both years ($F_{(17,71)} = 3.40$, $P < 0.001$). No interactions between treatment and year were detected.

Since consumption is correlated with yellow perch body size, an additional determination of stomach content biomass by treatment and by month was made after standardizing stomach content weight. To do this, total dry weight of stomach contents of an original yellow perch for a given month was divided by the length of that fish for that month. This did not appear to change any of the results.

The stomach dry weight of a particular fish was plotted against its growth (change in weight) from the previous month to determine if stomach content weight could be correlated with growth. There was no indication from visual inspection of the plot that yellow perch which grew more in 1993 also consumed more (Figure 23).

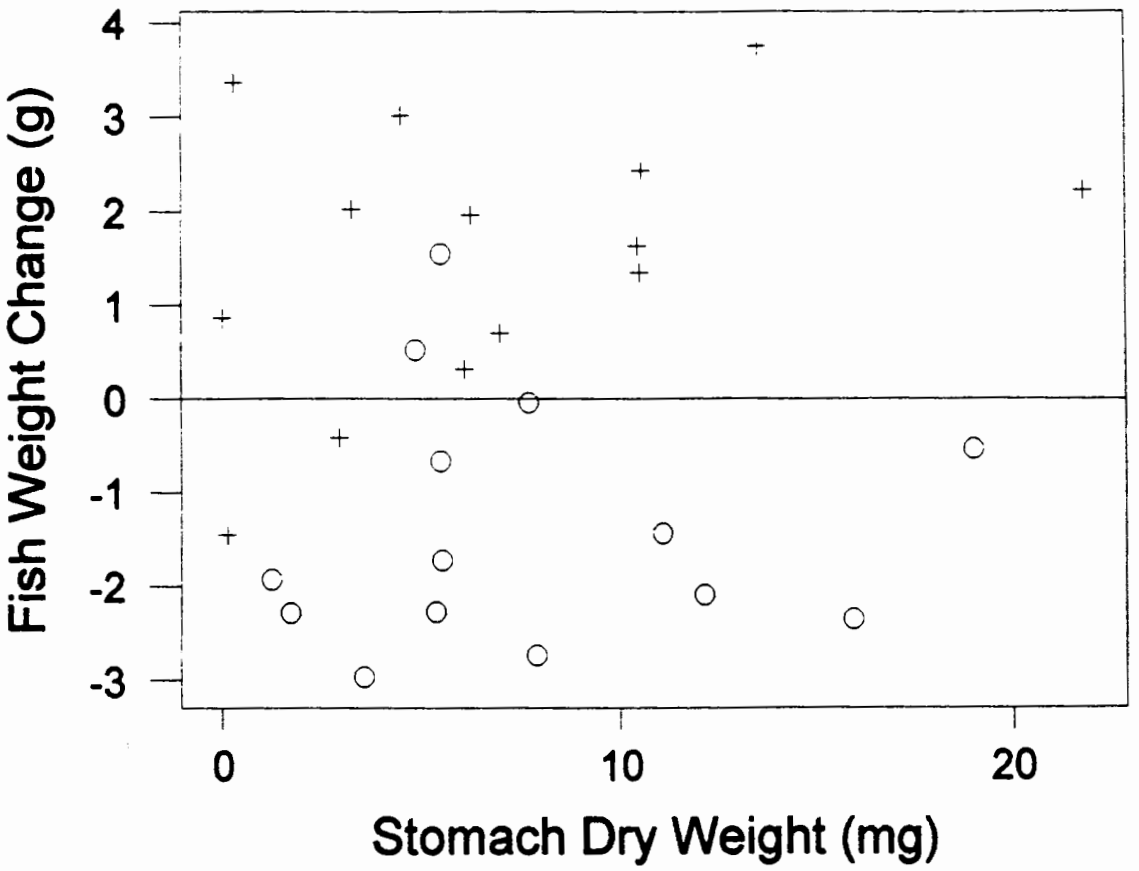


Figure 23. Yellow perch growth as weight change versus weight of yellow perch stomach contents, July, 1993. Stomachs of fish from enclosures without zebra mussels are shown with a "o" and those from enclosures with zebra mussels are "+".

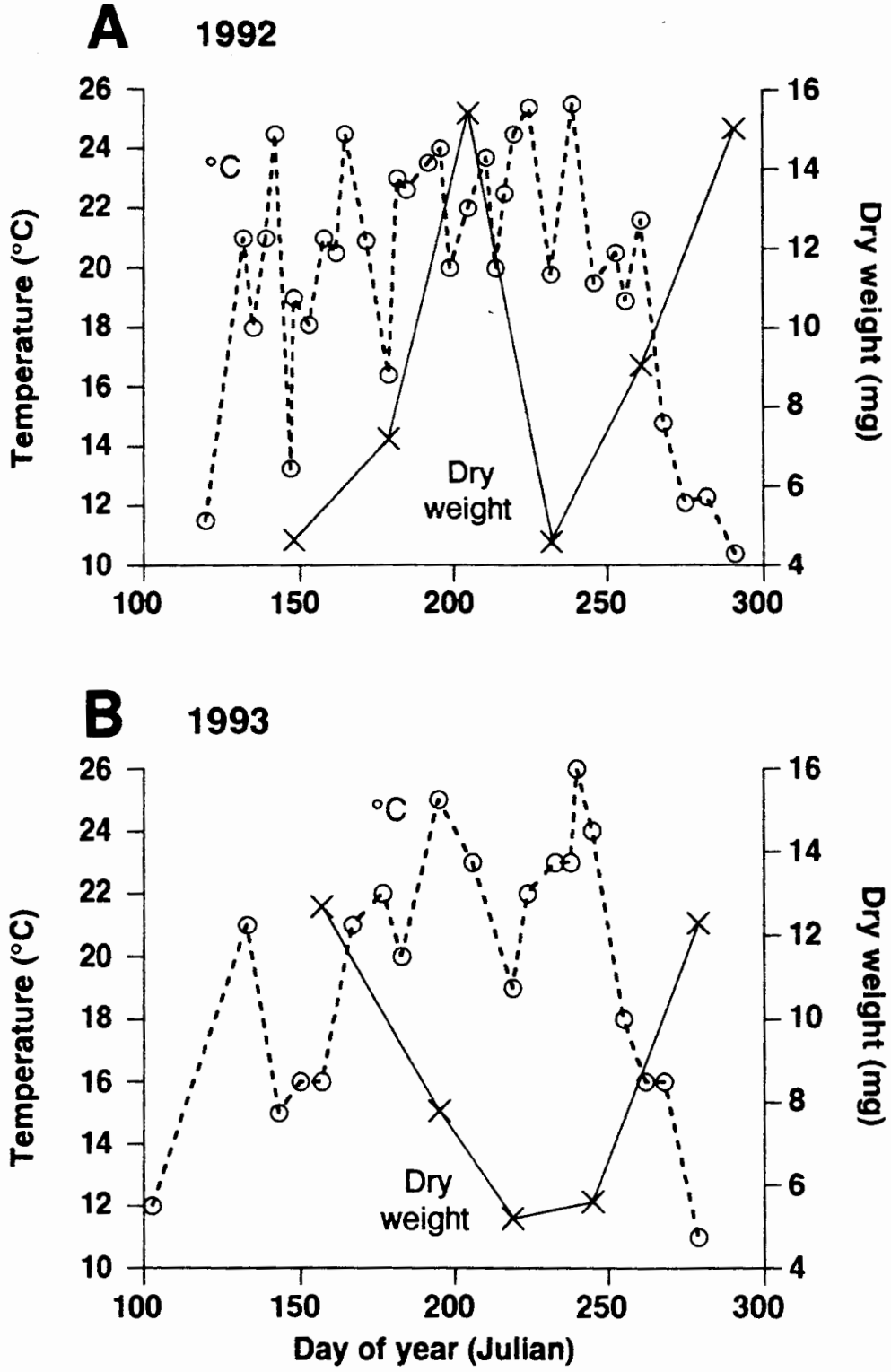


Figure 22. Pond water temperature (dashed line) for May-October, 1992 (A), and for April-October, 1993 (B). Monthly mean total dry biomass of all yellow perch stomach contents (solid line) is plotted for comparison.

Analysis of Zoobenthos

The following taxonomic groupings were used for analysis of zoobenthos: microzoobenthos (Ostracoda and Macrothricidae), Gastropoda, Trichoptera, Diptera (mostly Chironomidae), Hirudinea, Tricladida, Crustacea, and Oligochaeta. Total zoobenthic dry weight and dry weight by taxonomic group were determined for every enclosure and by treatment (except for freshwater drum enclosures) for Spring, Summer, and Fall of both years. On two occasions, samples had spoiled (one in Spring of 1992 and two in Summer of 1993). Only one enclosure from each treatment in Fall of 1993 was analyzed and was included in the overall analysis, but is not considered further due to its small sample size.

Zoobenthic mean dry weights in 1992 by invertebrate group, by treatment, and by season are represented in Figure 24. Note the large contribution by Diptera, Gastropoda, and Tricladida in Spring; dominance by Hirudinea, Diptera, Tricladida, Gastropoda, and Other in Summer; and dominance by Hirudinea, Diptera, Tricladida, and Oligochaeta in Fall. In 1993 (Figure 25), Spring and Summer were dominated by Diptera and Hirudinea. Other taxonomic groups were represented in smaller amounts but may be important in relation to perch prey preference and prey capture success. Variability in total dry weight among enclosures within the same treatment was common, as shown in Figure 26. Hirudinea, on the other hand, are often responsible for this variation since only a few leeches can add up to a large dry weight, while a sample even lacking one leech can be greatly skewed in the opposite direction. Their role in the analysis, however, is essential, since yellow perch have much to gain, nutritionally, from consuming leeches. Mean biomass of invertebrates by treatment is summarized, combining years, in Figure 27, and separately, in Figure 28, which removes two of the dominant groups, Diptera and Hirudinea, so differences between other groups are easier to recognize. Note how yellow perch without zebra mussels have a

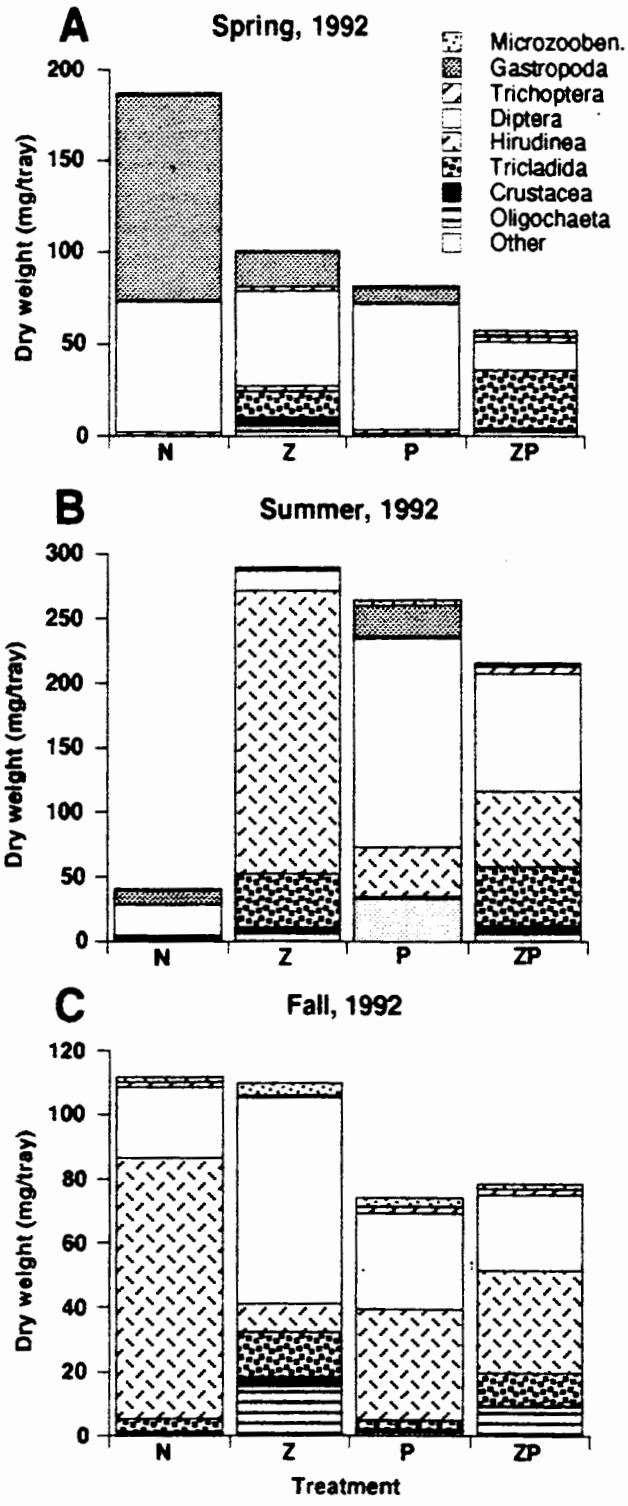


Figure 24. Zoobenthos biomass per tray, by taxonomic group and by treatment, Spring (A), Summer (B), and Fall (C), 1992. N = enclosures without zebra mussels or fish (N=3): Z = zebra mussel enclosures (N=3, minus one in Spring); P = yellow perch only enclosures (N=3); and ZP = yellow perch and zebra mussel enclosures (N=3).

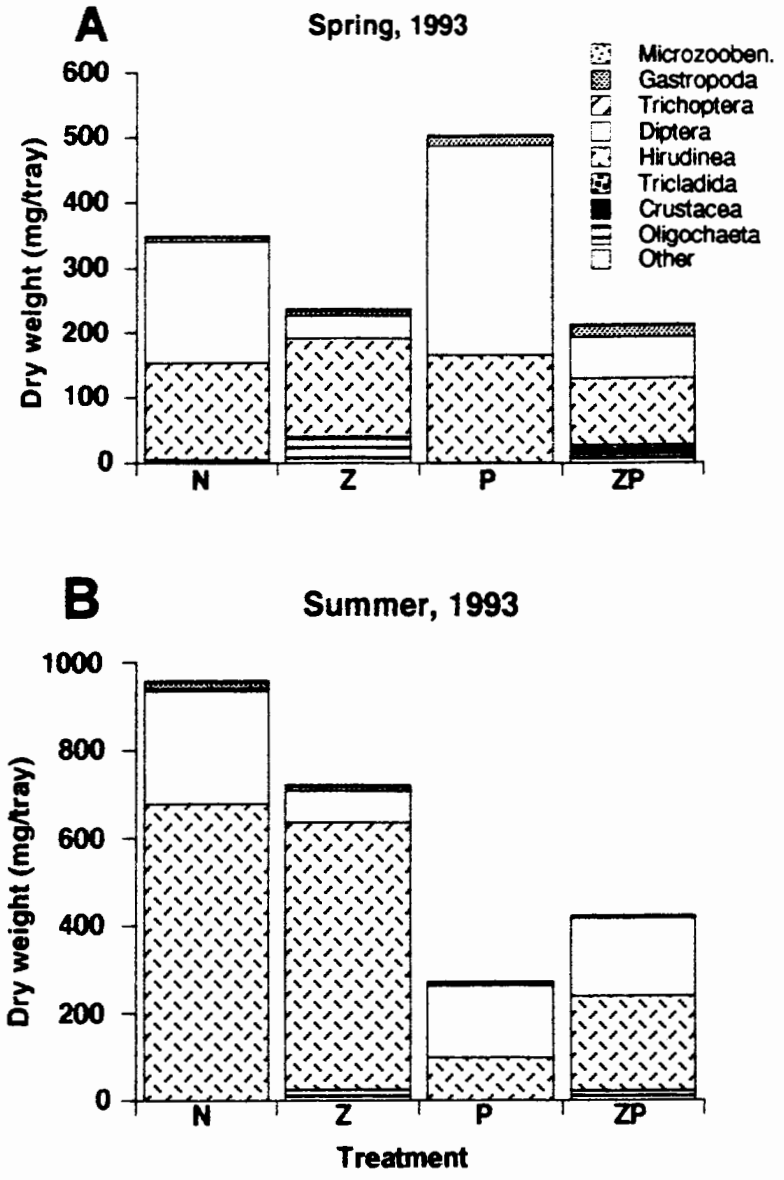


Figure 25. Zoobenthos biomass per tray, by taxonomic group and by treatment, Spring (A) and Summer (B), 1993. N = enclosures without zebra mussels or fish (N=3); Z = zebra mussel enclosures (N=3); P = yellow perch only enclosures (N=6); and ZP = yellow perch and zebra mussel enclosures (N=6, minus 2 in Spring).

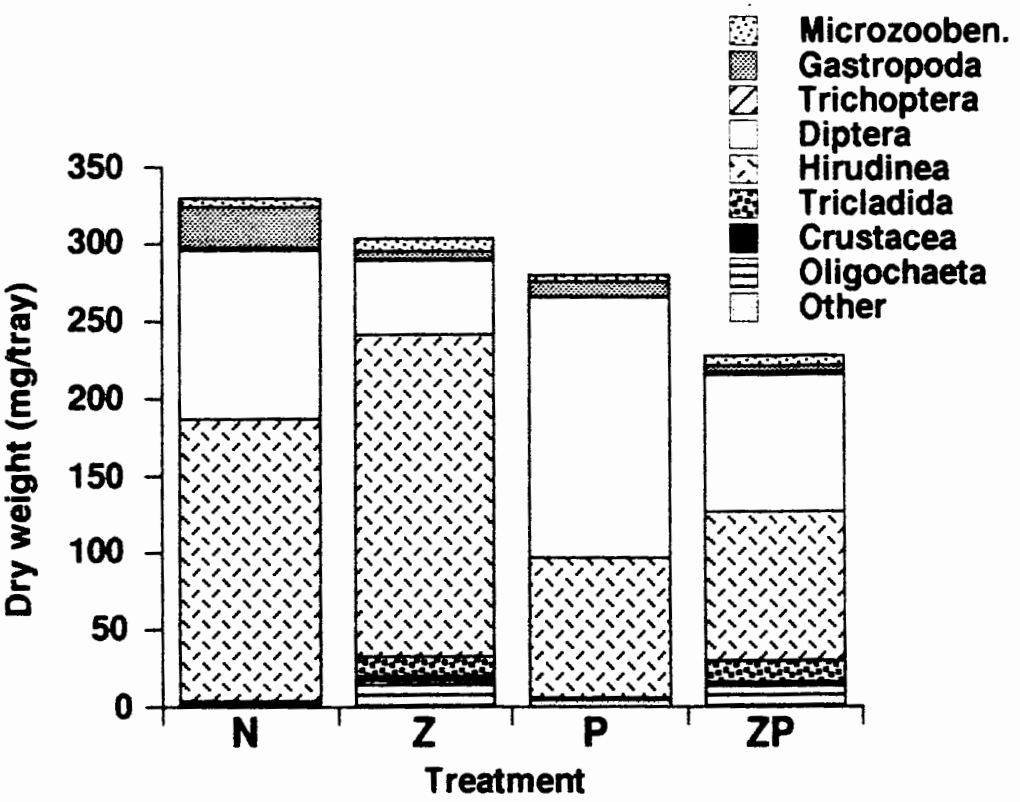


Figure 26. Combined 1992+1993 zoobenthos biomass per tray, by taxonomic group and by treatment. N = enclosures without zebra mussels or fish (N=9); Z = zebra mussel enclosures (N=8); P = yellow perch only enclosures (N=9); and ZP = yellow perch and zebra mussel enclosures (N=9).

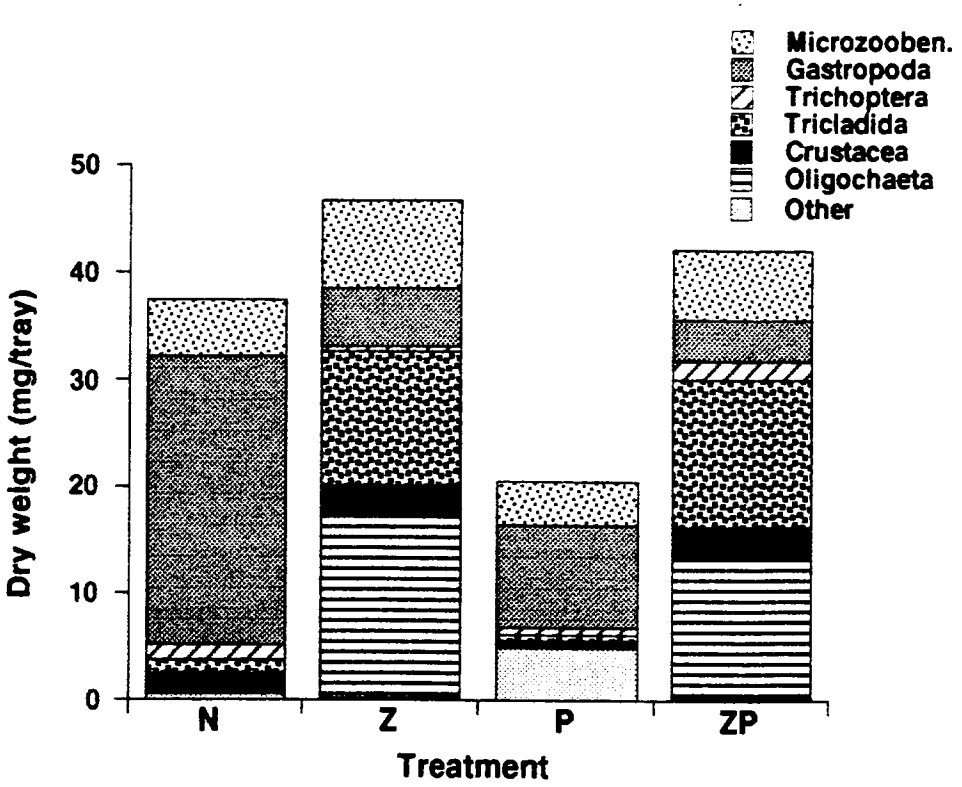


Figure 27. Combined 1992+1993 zoobenthos biomass per tray omitting Hirudinea and Diptera, by taxonomic group and by treatment. N = enclosures without zebra mussels or fish (N=6); Z = zebra mussel enclosures (N=6); P = yellow perch only enclosures (N=12); and ZP = yellow perch and zebra mussel enclosures (N=12).

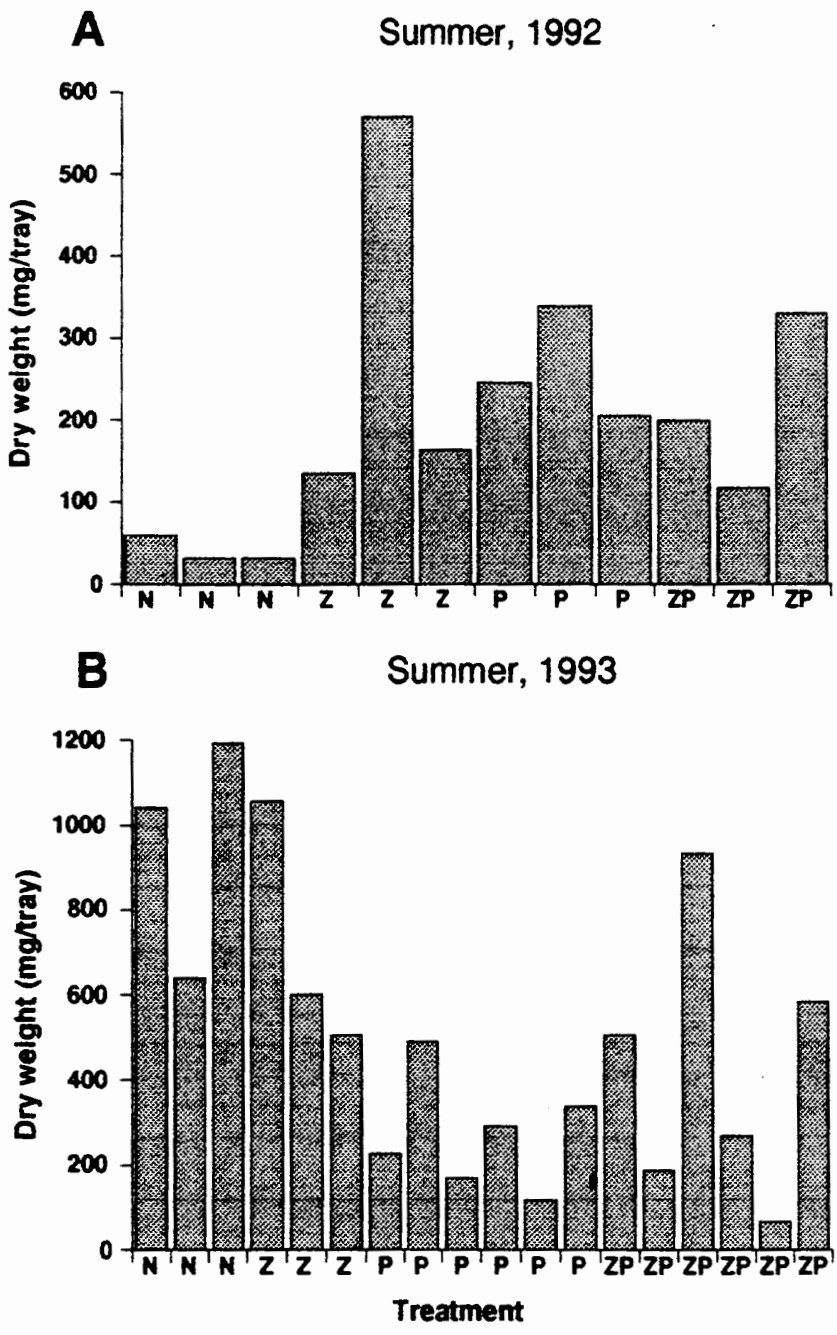


Figure 28. Total zoobenthos biomass per tray by enclosure and treatment; A is for Summer, 1992 and B is for Summer, 1993. Note the difference in the vertical scales.

bigger impact on the zoobenthos, relative to what is available without yellow perch, than yellow perch with zebra mussels.

The same statistical procedures used to analyze yellow perch diet were used to analyze zoobenthos, since the same assumptions applied to the data (i.e., seasons could be analyzed separately since there was no correlation between results for the same fish in different seasons.) Total invertebrate biomass and invertebrate biomass by group were analyzed.

Square root transformation of the data produced visually acceptable normality for most of the invertebrate groups. Parametric tests (ANOVA) of the zoobenthos using year, season, and treatment as factors indicated the following:

1. Trichoptera and Tricladida had a significantly higher dry weight in 1992 than in 1993 ($F_{(1,51)} = 31.11$ and 81.53, $P < 0.001$ and $P < 0.001$); microbenthos, Diptera, Hirudinea, Oligochaeta, and the total dry mass of zoobenthos were all significantly higher in 1993 than in 1992 ($F_{(1,51)} = 353.00$, 7.59, 37.41, 37.51, and 43.67, and $P < 0.001$, $P = 0.01$, $P < 0.001$, $P < 0.001$ and $P < 0.001$).
2. Gastropoda, Diptera, and "other" invertebrates had a significantly higher mean dry weight in enclosures without zebra mussels ($F_{(1,51)} = 9.65$, 4.75, and 4.17, $P = 0.003$, 0.03, and $P=0.05$). Tricladida, Oligochaeta, and Crustacea had a significantly higher mean dry weight in enclosures with zebra mussels ($F_{(1,51)} = 49.91$, 482.11, 10.45, $P < 0.001$, $P < 0.001$, and $P = 0.002$). Figure 29 shows zebra mussel effects on Crustacea.
3. The dry weight of Hirudinea was higher in enclosures that did not contain yellow perch ($F_{(1,51)} = 4.73$, $P = 0.03$).
4. Analyses performed on the years separately showed similar results.

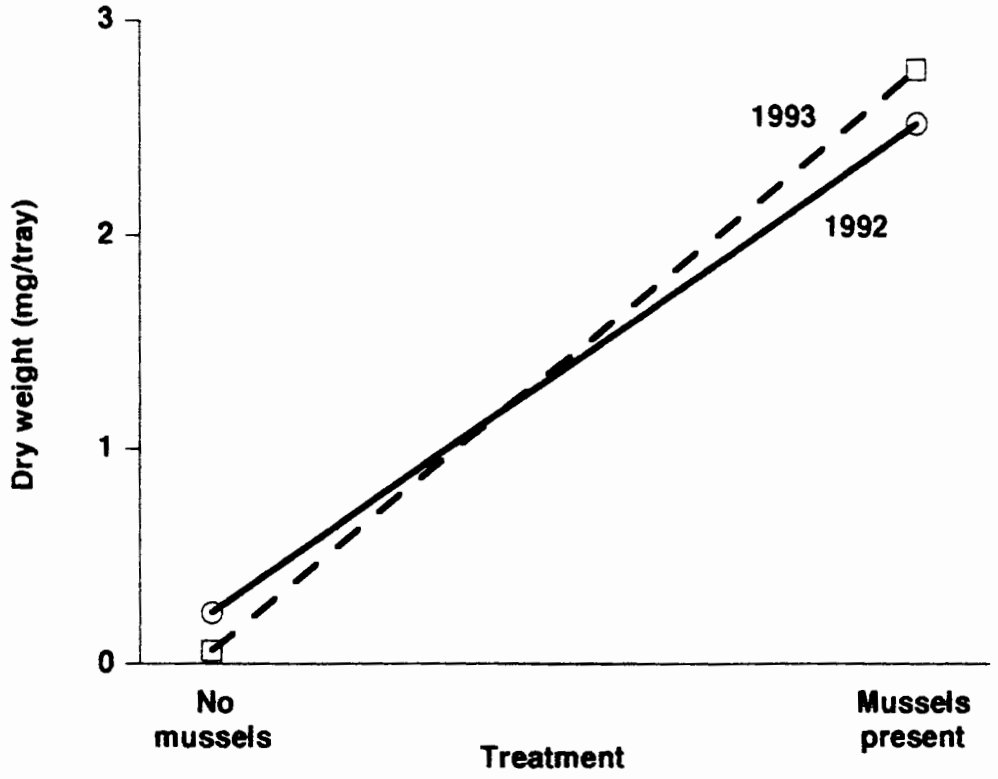


Figure 29. Interaction of mean dry weight per tray of Crustacea (Amphipoda and Isopoda) between treatments (with and without zebra mussels) and years (1992 and 1993). Although interaction effect is minimal, note significant difference in dry weight between treatments.

Drum Predation on Zebra Mussels

Freshwater drum growth between treatments with and without zebra mussels was not formally tested since mortality was high and all fish uniformly lost a large amount of weight. Approximately 40% of the original drum died during the season. Almost all of these deaths occurred soon after initial introduction into the enclosures or during a period of low oxygen concentration in late Summer. Many of the drum used as replacements for these fish also died and were continuously replaced. Drum without zebra mussels (N=8) had an initial mean size of 531.2 ± 105.31 g (mean ± s.d.) and an ending mean size of 405.0 ± 97.54 g, which translates into a 24% wet weight loss. Drum with zebra mussels (N=7) had an initial mean size of 765.7 ± 278.95 g and an ending mean size of 573.6 ± 225.25 g, which translates into a 25% wet weight loss.

Diet analysis of those fish whose stomachs were dissected in October (N=16), revealed no zebra mussels in the stomach, nor in the gut of any fish. Nine stomachs were empty and those that contained invertebrates (amphipods, isopods, gastropods, trichopterans, chironomids, zygopteran larvae, and adult beetles) were consistent between treatments.

Predation on zebra mussels by freshwater drum was determined by plotting zebra mussel wet weight at six separate time points for enclosures with and without freshwater drum, fitting a line to the data for each treatment, and comparing the slopes of these lines (Figure 30). The slope for the Dreissena + drum line is slightly greater than the "Dreissena only" line, which could be interpreted as zebra mussel reduction by drum predation. It is more likely to be a consequence of mortality. For example, a low zebra mussel biomass in October, 1992, in Enclosure # 17 (Dreissena + drum) of 102.52 g/tray compared to a zebra mussel wet biomass of 169.51 g/tray in Enclosure #16 (Dreissena only), was most likely due to high mortality in #17: 67.44% of the total compared to 34.22% in #16. Drum could have been selectively feeding on small zebra mussels (<= 5mm) which may not be

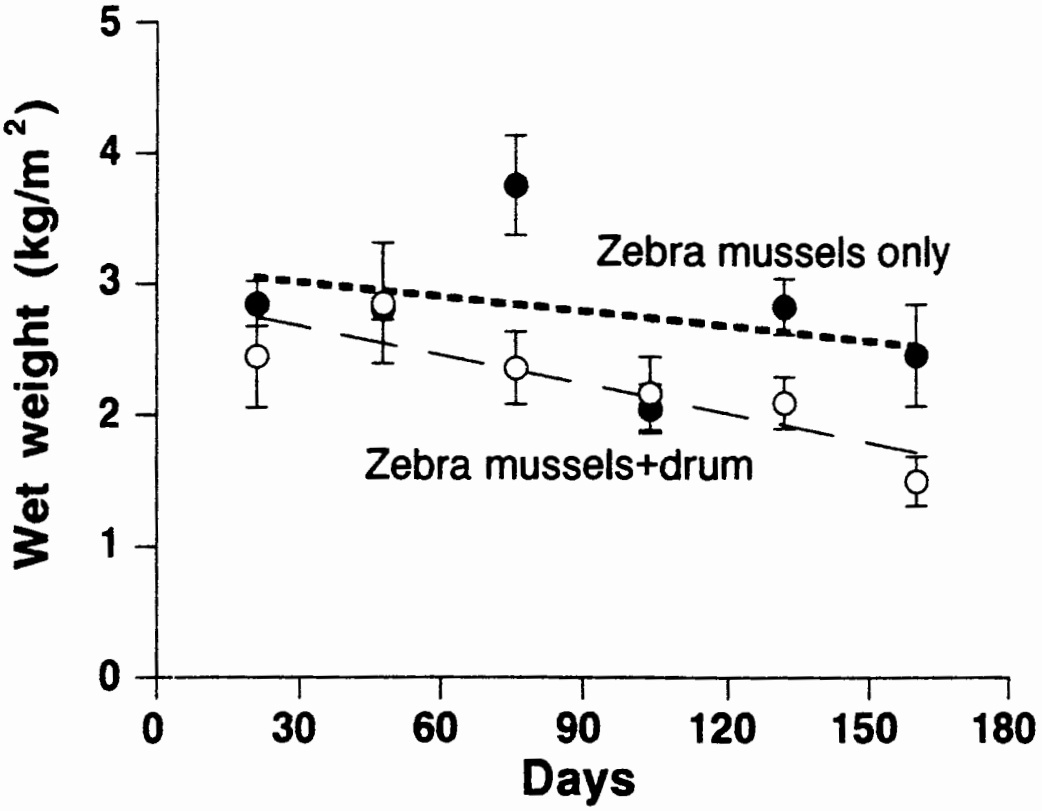


Figure 30. Change in zebra mussel wet biomass on a per m^2 basis, for enclosures with mussels only and enclosures with mussels and freshwater drum, May-October, 1992.

detectable in the total wet weight changes occurring in trays. Similar percentages of small mussels in both treatments were discovered when frequency distribution of zebra mussels from trays in July were determined. A tray from Enclosure #1 (Dreissena only) had a population of 2-5 mm juveniles of 7%, while a tray from Enclosure #5 (Dreissena + drum) had 6%, and a tray from Enclosure #9 (Dreissena + drum) had 7%.

Pond Water Quality

The pond temperature (mean ± s.d.) from April 30- October 7 of 1992 was 20 ± 4.3°C and the mean pond temperature from May 1- October 15 of 1993 was 19 ± 4.4° C. In 1992, oxygen concentrations usually ranged from 9-16ppm, except in September, when it dropped to 6ppm. Bottom ammonia levels ranged from a consistent 0.03-0.05 mg/L from May through July to 0.15-1.48 mg/L in August through October, with the maximum concentration occurring in October following significant zebra mussel mortality. In 1993, bottom oxygen concentrations ranged from 11-14 mg/L in May through mid-June, at which time they fell to as low as 4.6 mg/L in some places of the pond. Following this low, they rose again, only to reach another low of 3.3 mg/l in mid-July. Levels ranged between 8-11 mg/L for the rest of the year. Ammonia levels were variable over the season, ranging from 0.08-0.84 mg/L , with the highest levels occurring prior to June 15.

Trace amounts of nitrate+nitrite were detected in the pond, both years. The concentration of phosphorus was similar for both years (approximately 0.05 mg/L). In June, silica concentration was higher in 1992 (0.61 mg/L) than in 1993 (0.14 mg/L) and the total organic carbon was somewhat higher in 1993 (9.5 mg/L) than 1992 (7.5 mg/L), but the lack of repeated measurements makes it difficult to conclude anything significant about these differences. In 1992, Ca^{2+} ranged from a high of 102 mg/L in June to a low of

60 mg/L in August and Mg^{2+} ranged from a high of 44 mg/L in July to a low of 16 mg/L in June. In 1993, Ca^{2+} ranged from a high of 112 mg/L in May to a low of 48 mg/L in June, and Mg^{2+} was usually approximately 50 mg/L. Conductivity ranged from 50-200 µS/cm in 1992 and 160-330 µS/cm in 1993 and pH was 8-10 in 1992 and 8-10.5 in 1993. Secchi disk readings were usually to the bottom of the pond (approximately 1-m deep) in 1992 and averaged 0.75 ± 0.160 m (mean ± s.d.) in 1993.

In 1992, zooplankton was sampled from a combined three locations outside the enclosures, except on July 2, in which several locations were measured. Density ranged from 6.6 individuals/L in May to 127/L by August. On July 2, zooplankton density varied between an inshore and offshore location (Table 3), so there was a potential for near shore enclosures to have higher densities of zooplankton than offshore enclosures. On this same day, enclosures with zebra mussels only (no fish) had one-half the density of zooplankton as enclosures without zebra mussels (no fish)(Table 3). Zooplankton communities consisted primarily of Copepoda, rotifers, and Bosmina longirostris in May; Ceriodaphnia sp., Copepoda, Simocephalus sp., and Diaphanosoma sp. in June, July and August; and Bosmina longirostris and Copepoda in September and October.

In 1993, all zooplankton tows were taken within enclosures, since the possibility of treatment effects on this community seemed more probable. (We found possible evidence in the diet of yellow perch in 1992 that they were feeding on different amounts of zooplankton depending on the treatment.) Zooplankton density ranged from 0.5/L in April, to as high as 375/L by September. Zooplankton density was almost always higher in the treatment without zebra mussels, however, sometimes these differences were negligible (Table 3). Species composition was similar between treatments at almost any time point, however, the mean weights of certain dominant species on some dates were sometimes lower for zebra mussel treatments. Species composition in 1993 was very much dominated

Table 3. Zooplankton densities, 1992 and 1993. Pond = three pooled zooplankton tows from outside the test enclosures. Zm/no zm encls. = three pooled zooplankton tows from inside the three enclosures of the treatment.

Date	Location	Number/L	Date	Location	Number/L
			4-20-93	No zm encls.	2.3
				Zm encls.	0.5
5-11-92	Pond	6.6	5-12-93	No zm encls.	95.0
				Zm encls.	89.0
5-21-92	Pond	21.0	5-19-93	No zm encls.	8.5
				Zm encls.	13.0
5-28-92	Pond	14.0	5-27-93	No zm encls.	25.0
				Zm encls.	17.0
6-4-92	Pond	29.0	6-5-93	No zm encls.	15.0
				Zm encls.	13.0
6-14-92	Pond	9.8	6-15-93	No zm encls.	4.2
				Zm encls.	4.1
6-30-92	Pond-inshore	40.0	7-2-93	No zm encls.	59.0
	Pond-offshore	13.0		Zm encls.	34.0
	No zm encls.	7.2			
	Zm encls.	3.4			
7-23-92	Pond	40.0	7-22-93	Pond	113.0
8-24-92	Pond	127.0	8-24-93	No zm encls.	174.0
				Zm encls.	112.0
9-10-92	Pond	68	9-8-93	Pond	89.0
10-4-92	Pond	3.4	10-7-93	Pond	10.0

by copepoda through July, and later heavily dominated by Bosmina longirostris August-September. Daphnids were rarely present, and when they were, never in large numbers.

DISCUSSION

Results in 1993 clearly showed adult yellow perch grew better when zebra mussels were present than when they were not. The difference between treatments was highly significant and all the enclosures in a treatment behaved similarly. Differential yellow perch growth rates were most likely influenced by the quantity of zoobenthos available to them as prey.

Yellow perch in 1992 grew at faster rates than yellow perch in 1993 despite higher mean total benthic biomass in 1993 enclosures. Hence, one cannot argue that more zoobenthos prey was available to 1992 yellow perch, however, prey from pelagic and epiphyte zones may have been available in greater amounts in 1992 than in 1993. Such prey include Hydracarina, some Trichopteran larvae, pond insects (Hesperocorixa sp., Notonecta sp., Laccophilus sp.), and zooplankton. Diet analysis indicated a higher amount of "other" invertebrates (which included pond insects and Hydracarina) in stomachs in 1992 than in 1993. In 1993, not one adult insect or beetle was found in any stomach, and only a couple beetle larvae were found. These invertebrates did not always translate to a large dry biomass in the stomach, but may have had significant impacts on total caloric intake if perch were feeding on them in large amounts at times when stomachs were not sampled. The lack of pond insects in 1993 may have been correlated with the addition of adult perch to the area outside the enclosures.

Zooplankton community structure also differed between the two years, a likely result of addition of yellow perch to water outside the enclosures. Zooplankton species composition

(determined from plankton tows) in 1992 almost always consisted of substantial numbers of daphnids (large sized cladocerans, hence preferred perch prey), while in 1993, they were almost entirely absent. Yellow perch diet analysis showed significant numbers of Ceriodaphnia sp. in stomachs in 1992, while stomachs in 1993 rarely contained Ceriodaphnia sp. and generally had lower total amounts of zooplankters (usually Copepoda). Again, the total dry biomass contribution made by these organisms to the diet of perch is relatively small, but overall predation on them could have been underestimated since stomach samples were limited.

Other factors may have influenced higher yellow perch growth in 1992. Lower dissolved oxygen concentration and higher ammonia concentration in 1993 may have lowered yellow perch feeding rates in 1993. In 1993, oxygen dropped to a low in June of 4.6 mg/L and a low in July of 3.3 mg/L, at which times yellow perch likely reduced their feeding and did not gain much weight. This seems plausible since low dissolved oxygen often influences feeding and growth rates of fish, such as in channel catfish (Ictalurus punctatus), which Andrews et al. (1973) found to have lowered their food consumption and weight gain with decreasing concentrations of dissolved oxygen. Water temperature may have also influenced food consumption. Yellow perch in 1992 often consumed a higher mean total food biomass than yellow perch in 1993, and this higher consumption appeared to be related to temperature (Figure 22). 1992 appeared to have greater water temperature fluctuation, with a greater occurrence of lower temperatures, hence, higher consumption more often.

Since pond conditions (such as temperature, oxygen, and ammonia) were equivalent for treatments in 1993, something besides these factors encouraged greater growth of yellow perch in zebra mussel enclosures than that of yellow perch in enclosures without zebra mussels. Higher growth rates were predicted to be positively correlated with higher

diet dry weight. Sampling yellow perch diet once per month at one time during the day made it difficult to detect any correlations between the dry weight of the diet (its potential nutritional value) and yellow perch growth. Fish could have been feeding asynchronously; in fact the data seem to suggest this. No correlation between stomach dry weight and corresponding growth by month was detectable (Figure 23). In addition, yellow perch with similar stomach biomass showed very different growth responses. All the yellow perch in Figure 23 with empty stomachs had very different growth responses. Sampling more frequently to obtain diurnal samples was not a viable option since the same fish were used continuously throughout the experiment and any repeated electroshocking over short time periods would have been too stressful, and most likely, lethal. Observation of consistent and significantly large differences in consumption by fish between the two treatments would have been necessary to demonstrate significant differences in diet given the minimal sampling. The likelihood of this occurring is very improbable since variablility in feeding regime is certain to occur.

Despite the above sampling difficulties, some of the descriptive information on yellow perch diet can be useful in postulating explanations for differential yellow perch growth response. Yellow perch without zebra mussels consumed significantly more zooplankton than yellow perch with zebra mussels on some occasions. This feeding behavior could have been the result of higher densities of zooplankton in enclosures without zebra mussels, as suggested by zooplankton comparisons between treatments (Table 3), or the result of compensatory mechanisms due to a low benthic biomass. Also, even though the mean dry weight of most invertebrate groups in the diet did not differ significantly between treatments, it was often higher and more frequent for perch with zebra mussels than perch without zebra mussels (Table 1 and 2). Zebra mussel enclosures also contained those

individual perch that often fed on the largest amounts of these invertebrates (as indicated by the maximum of the range in Table 1 and 2).

Analysis of the zoobenthos revealed some information supportive of the differential yellow perch growth response between treatments in 1993. The total dry biomass of zoobenthos was significantly greater in 1993 than in 1992, which suggests that a higher amount of organic material could have been available to invertebrates, especially those invertebrates in enclosures with zebra mussels. Higher organic matter in surficial sediments in the second year of the study was likely since the first year's accumulation was present at the beginning of the second. Additionally in 1993, zebra mussel density was higher, mortality lower, and growth rate much higher than in 1992 (suggesting a greater amount of organic seston for feeding and, therefore, more biodeposited as pseudofeces and feces). Mean dry weights of Hirudinea and Crustacea were also significantly higher in 1993 than in 1992, suggesting a larger amount of organic material available to them as food.

Crustacea (Gammarus sp. and Caecidotea sp.) dry weight was significantly higher in zebra mussel enclosures than in enclosures without zebra mussels. According to diet analysis in June of 1993, these invertebrates were close to being significantly greater in the diet of yellow perch with zebra mussels than in the diet of yellow perch without zebra mussels in 1993 ($P = 0.07$). Even though their overall contribution to the diet was not great in terms of total dry biomass, their contribution could have been underestimated. Yellow perch have a strong preference for amphipods and isopods, as evidenced in diet analysis of perch in Saginaw Bay (Haas and Schaeffer, 1992), and this study (diets in October of 1992 primarily consisted of Crustacea only, while diets at any other time were more diverse in content). This is most likely due to the high capture success rate that yellow perch have for these invertebrates, since amphipods and isopods are easily accessible prey (epibenthic dwellers). If a yellow perch in an enclosure had these

crustaceans available as prey, it would most likely preferentially feed on them until their density was significantly reduced. If such feeding were of relatively short duration (days), stomach pumping on a monthly basis could easily miss detecting these organisms.

In addition to higher dry biomass of Crustacea, analysis of zoobenthos between treatments with and without zebra mussels indicates a significantly higher dry biomass of Oligochaeta and Tricladida in treatments with zebra mussels. These results are consistent with field observations. Dermott et al. (1993) found the amphipod, Gammarus fasciatus, to be significantly more abundant on zebra mussel colonized bedrock than on uncolonized bedrock in Lake Erie. Griffiths (1993) found a higher abundance of two tubificids, Potamothrix moldaviensis and Spirosperma ferox, and Gammarus sp., in 1992 in Lake St. Clair compared to 1983. No evidence from this study was found to indicate yellow perch fed on Oligochaeta nor Tricladida.

The hypothesis that zebra mussels increase productivity of Crustacea, Gastropoda, and Diptera is supported by significant effects on Crustacea only. It is not known why Gastropoda and Diptera did not respond as predicted. In fact, their biomass was significantly greater in no zebra mussel enclosures. The large variance in zoobenthos content among enclosures may have made it difficult to accurately assess zebra mussel effects on their productivity. Diptera could have been limited by competition from other benthic invertebrates. Izvekova and Lvova-Katchanova (1972) performed their chironomid experiments in a laboratory setting, where interspecific competition was not considered, so predictions of increased productivity of chironomids in the presence of zebra mussels may be overestimated.

Those benthic invertebrates that responded to zebra mussels had improved productivity either from feeding on biodeposited organic matter and/or from the increased habitat heterogeneity available due to interstitial spaces of zebra mussel clusters. It is difficult to

determine the magnitude of the effects that these two possible zebra mussels changes had on the zoobenthic community in this study due to the complexity of the experiment. Controlled laboratory experiments would be best-suited for such a study.

Many North American studies, such as those just referred, have examined zebra mussel effects on zoobenthos, but very few studies have attempted to assess zebra mussel impact on fish communities. Those that have examined population structure changes have done so in the field and with a high degree of speculation. MacLennan (1994) observed lower year-class strength in walleye (Stizostedion vitreum) in Lake St. Clair, and accounted lower catch success rate to changes in walleye movement patterns (i.e., walleye are moving into the shipping channel, where water is less transparent, since this species is light-sensitive). Culver et al. (1994) have based some of their predictions on yellow perch and walleye relative year-class strength data from Ohio Division of Wildlife. This field information can be informative, however, this pond study was unique in that it was an experiment that could be manipulated to produce co-occurring treatments that could be directly compared with each other. Time and water quality could be kept constant between treatments.

The results of such a study as this one can be applied to larger water ecosystems, such as Lake St. Clair, since the diet of primarily age-3 yellow perch from this study was similar to that of age-3 yellow perch in some areas of the Great Lakes. Yellow perch diet from this study was dominated in part by Diptera (primarily Chironomidae). Chironomidae in age-3 yellow perch from Saginaw Bay were shown to represent up to 95.4% of the mean total wet weight of the stomach in May of 1988 (Haas and Schaeffer, 1992).

Diet analysis of yellow perch from Lake St. Clair in June of 1993 (Synnestvedt, unpublished data) reveal a large percentage of Crustacea (93% occurrence of Amphipoda and 51% occurrence of Isopoda, ranging as high as 163 individuals/stomach), as well as the presence of large Oligochaeta (9% occurrence), which yellow perch typically do not eat.

Whether these fish have higher mean wet and dry biomass at the different year classes than previous years is presently being determined (Synnestvedt, personal communication). One notable discrepancy between the study pond and lacustrial benthos is that the pond did not contain Hexagenia sp., which, like other benthic invertebrates, would most likely benefit from zebra mussel biodeposition of organic matter. Large numbers of Hexagenia sp. were found in stomachs of yellow perch obtained from ten-minute bottom trawls in the northwestern section of Lake St. Clair in June of 1994, as well as large amounts of crayfish eggs (personal observations). A very large biomass of Orconectes sp. was present in Lake St. Clair at this time (at least one kilogram of crayfish was obtained from every ten-minute trawl at numerous locations). Crayfish success at this time may have been a consequence of their predation on zebra mussels, since they are known to feed on zebra mussels (MacIsaac, 1994). Response by yellow perch in zebra mussel-dense areas has been quite variable, as evidenced by yellow perch harvest from Michigan's Lake Erie noncharter sport fishery, which was 318,786 in 1988, peaked at 1,466,372 in 1989, dropped to 236,908 by 1992, and was up again to 451,826 in 1993 (Thomas and Haas, 1994).

At the moment, zebra mussel effects on planktivorous fish is unclear. Jennings (1994) reported significantly lower growth of fathead minnows (Pimephales promelas) in microcosm experiments when zebra mussel density was 3,000/m^2. Richardson and Bartsch found bluegill (Lepomis macrochirus) young-of-the-year growth and survival unaffected by a zebra mussel density of 2,000/m^2, however, mortality of zebra mussels in the Fall may have influenced the results.

Microcosm experiments are useful but do not consider predatory affects on population size. Increasing numbers of sight-feeding piscivores, such as Northern pike, muskellunge and large Centrarchids, may pose a predatory threat to yellow perch, as well as other potential prey. Reductions in larval and adult yellow perch are further complicated since

some reduction in species density can improve individual fish condition, and, perhaps produce larger year classes of yellow perch. Reports from local anglers both in Lake St. Clair and the Detroit River (personal communication), indicate some of the best yellow perch catch (size) than any year in decades.

Zebra mussel interactions with predatory fish may be quite different. The predicted interaction with freshwater drum was not detectable in this study, since the data suggested none of the drum fed on zebra mussels. This is most likely to have resulted from the freshwater drum not being large enough. Studies by French and Bur (1991) and personal observations of freshwater drum gut contents from Lake St. Clair seem to indicate only the very large (> 375mm) freshwater drum feed on significant amounts of zebra mussels (if any). Those large fish that were used may have failed to feed on zebra mussels due to the stress of shocking, handling, temperature, light, low oxygen, and/or high fish biomass/enclosure. The apparent sensitivity of this fish species makes it unsuitable for shallow pond studies.

Freshwater drum in Lake St. Clair and Western Lake Erie could potentially have an impact on the zebra mussel population, since they seem to prefer similar habitat. Monitoring freshwater drum size and density, as well as that of other predatory species, over the next decade, should give information in regard to their expected impact on zebra mussels as well as on their own population responses. Karatayev (1994) found that fish productivity in the zebra mussel infested Lukomskoe Lake in the Republic of Belarus doubled due to increased numbers of benthophagous fishes.

CONCLUSION

In 1992, yellow perch with zebra mussels grew similarly to yellow perch without zebra mussels. In 1993, yellow perch with zebra mussels maintained or gained weight and yellow

perch without zebra mussels lost weight. This differential growth response in 1993 was highly significant ($P < 0.0001$).

Results of yellow perch diet analysis suggest yellow perch with zebra mussels often fed on a larger dry weight of Crustacea (Amphipoda and Isopoda) and possibly Hirudinea (Eropdellidae) than yellow perch without zebra mussels. Yellow perch without zebra mussels fed on a significantly larger dry weight of zooplankton.

Tricladida, Oligochaeta, and Crustacea dry weights were significantly higher in enclosures with zebra mussels. Yellow perch without zebra mussels had a greater impact in reducing biomass of zoobenthos than did yellow perch with zebra mussels.

Yellow perch growth was higher in 1992 probably due to a greater availability of pelagic prey and lower oxygen concentration. Reasons for differential growth response in 1993, but not in 1992, were likely to have been 1) restrictions of yellow perch diet to the benthos in 1993 (most likely due to the addition of juvenile and adult yellow perch to the pond outside of the enclosures), 2) higher organic content in the surficial sediment of zebra mussel enclosures from two years worth of biodeposition, and 3) increased biodeposition rate in 1993, resulting from higher zebra mussel growth rate.

Freshwater drum lost weight, regardless of zebra mussels. Diet analysis, and inspection of changes in zebra mussel wet weight in zebra mussel enclosures with and without freshwater drum, revealed no predation on zebra mussels by freshwater drum. Predicted results were most likely not observed because the experiment lacked very large specimen and freshwater drum were likely stressed from crowded conditions, handling, and high temperatures and light penetration.

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Appendix 1. Regression coefficients used for estimation of body length from head length, shell length from tissue length, and dry weight from body length. Note: The regression coefficients used for a listed species are from the same species *or a closely related species (genetically or morphologically).*

		y-intercept	slope	conversion curve type	curve type	
Cladocera	Ceriodaphnia sp.	-0.10060	1.27600	tl-sl	lin	1
	"	0.00402	0.00198	bl-dw	log	2
	Chydorus sphaericus	0.01408	0.00198	bl-dw	log	2
	Eurycercus sp.	"	"	"	"	"
	Macrothrix laticornis	"	"	"	"	"
	Diaphanosoma sp.	0.00507	0.00105	"	"	"
	Bosmina longirostris	0.01774	0.00223	"	"	"
	Eubosmina coregoni	0.02191	0.00234	"	"	"
Copepoda	Cyclopoda	0.02191	0.00234	"	"	2*
	Calanoida	0.00647	0.00246	"	"	2*
Ostracoda	"	0.00163	0.00000	dw	lin	3
Crustacea	Gammarus sp.	-0.35700	6.31700	hd-bl	lin	1
	"	-4.82800	2.11200	bl-dw	ln	4
	Caecidotea sp.	-0.60280	5.43100	hw-bl	lin	1
	"	-5.80910	2.96300	bl-dw	ln	4
Gastropoda	Physella gyrinus	0.09210	1.28000	tl-sl	lin	1
	Lymnaea sp.	"	"	"	"	"
	Gyraulus sp.	"	"	"	"	"
	Physella gyrinus	-16.3460	4.88000	sl-dw	ln	5
	Lymnaea sp.	"	"	"	"	"
	Gyraulus sp.	"	"	"	"	"
Trichoptera	Oecetis sp.	0.61400	7.82200	hw-bl	lin	1
	"	-5.11600	2.27100	bl-dw	ln	4
	Setodes sp.	"	"	"	"	"
	Ceraclea sp.	"	"	"	"	"
	Agraylea sp.	-4.82830	2.02700	bl-dw	ln	4
	Oxyethira sp.	"	"	"	"	"
	Hydroptila sp.	"	"	"	"	"
	Orthotrichia sp.	"	"	"	"	"
	Polycentropus sp.	0.67500	9.02400	hw-bl	lin	1
	"	-7.60090	2.22500	bl-dw	ln	4
Diptera	Chironomidae	0.15040	12.6430	hw-bl	lin	1
	Chironomidae	-5.80910	3.07000	bl-dw	ln	4*
	Procladius sp.	"	"	"	"	"
	Tanypus sp.	"	"	"	"	"
	Clinotanypus sp.	"	"	"	"	"
	Ablabesmyia sp.	"	"	"	"	"

Diptera	Chironomus sp.	-5.80910	3.07000	bl-dw	ln	4*
	Cladopelma sp.	"	"	"	"	"
	Cricotopus sp.	"	"	"	"	"
	Microtendipes sp.	"	"	"	"	"
	Parachironomus sp.	"	"	"	"	"
	Dicrotendipes sp.	"	"	"	"	"
	Pseudochironomus sp.	"	"	"	"	"
	Endochironomus sp.	"	"	"	"	"
	Cryptochironomus sp.	"	"	"	"	"
	Tribelos sp.	"	"	"	"	"
	Tanytarsus sp.	"	"	"	"	"
	Paratanytarsus sp.	"	"	"	"	"
	Pupae	"	"	"	"	"
	Bezzia sp.	-4.96180	1.47300	bl-dw	ln	4**
Hydracarina	-	-4.96180	1.75200	bl-dw	ln	4
Coleoptera larvae	Peltodytes sp.	-6.21460	2.59300	bl-dw	ln	4
	Haliplus sp.	"	"	"	"	"
	Laccophilus sp.	"	"	"	"	"
	Dineutus sp.	"	"	"	"	"
	Hydroporus sp.	"	"	"	"	"
Coleoptera adults	Peltodytes sp.	0.27000	0.00000	dw	lin	1
	Haliplus sp.	"	"	"	"	"
	Laccophilus sp.	"	"	"	"	"
Hemiptera	Hesperocorixa sp.	0.35100	3.39800	hw-bl	lin	1
	Notonecta sp.	"	"	"	"	"
	Hesperocorixa sp.	-5.85050	2.21640	bl-dw	ln	1
	Notonecta sp.	"	"	"	"	"
Lepidoptera	Acentria sp.	-4.50090	2.07420	bl-dw	ln	6
Ephemeroptera	Caenis sp.	-3.54050	1.83700	bl-dw	ln	4**
Odonata	Coenagrionidae	-6.21460	2.56700	bl-dw	ln	4
Hirudinea	Eropdellidae	-3.03660	1.75900	bl-dw	ln	4
	Pisciolidae	"	"	"	"	"
Tricladida	Planaria sp.	-3.63440	1.85450	bl-dw	ln	6
Nematoda	-	0.00000	0.00001	bl-dw	lin	3
Oligochaeta	-	0.00000	0.00600	bl-dw	lin	3

1 = formulated from data from this study; Pearson correlation coefficients > 0.75.
2 = Culver (1985)
3 = Nalepa and Quigley (1980)
4 = Theiling (1990)
4* = formulated from data of Wiley (1981) by Theiling (1990)
4** = Hall et al. (1970), *in* Theiling (1990)
5 = formulated from data of Hunter; r = 0.94.
6 = Meyer (1989)