THE IMPACT OF ZEBRA MUSSELS (DREISSENA POLYMORPHA)
ON PELAGIC FOOD WEBS

DISSERTATION

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By

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* * * * *

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ABSTRACT

Using an ecosystem approach, I investigated the role of turbulent mixing in zebra mussels’ impact on zooplankton and phytoplankton in western Lake Erie by estimating the flux of phytoplankton to benthic mussels. Zebra mussels, like other benthic suspension feeders, depend on water movements for food transport. Hydrodynamic transport processes (currents and turbulent mixing characteristics within the water column) affect the rate of delivery of organic matter produced in the pelagic zone to benthic mussels. Most food is transported horizontally in the low flow water near the mussel bed and vertically settling seston becomes potential food only when it enters this near-bed boundary layer. Thus, the delivery of phytoplankton to the benthos determines zebra mussel growth and population dynamics and the actual impact of benthic zebra mussels on pelagic food webs.

To evaluate the long-term population dynamics of a hard substrate mussel population I quantitatively sampled the Peach Point Reef mussel population at a 3 m site from 1990 through 1998. The zebra mussel population grew from 10,000 m$^{-2}$ in March 1990 to the maximum observed density of 81,850 m$^{-2}$ in May 1992. By May 1994 and again in May 1998 the mussel population appeared to have stabilized at 20-22,000 m$^{-2}$. Quagga mussels were first observed in 1991, but were rare at the 3 m site through 1994. By 1998 quagga mussels had increased in abundance until they represented 33% of the Peach Point Reef mussel population. The mean-sized individual zebra mussel generally increased in both shell length and biomass as the population aged during 1991 to 1994.
Most shell growth occurred from May to September and there was little increase in mean shell length during the September to May overwinter, prespawning period. Mean mussel biomass was always higher in the May than in September of the same year. Mussels in bottom cages in the boundary layer added only 10% to 20% as much soft-tissue biomass as those farther up in the water column providing evidence that mussel growth depends on the rate of delivery of pelagic algae and on competition with other mussels in the colony.

I also indirectly tested the effects of turbulent transport on mussels by measuring the relative abundance and soft tissue mass for populations found on bedrock and cobble, sand, and mud. Larger substrate size and shallower water are characterized by higher turbulent mixing levels. Populations on sand and mud had much lower densities and biomasses than populations on cobble and rock. I conclude that the impact of zebra mussels on pelagic phytoplankton (and consequently on zooplankton) has been less than predicted because mussel grazing and growth are limited by turbulent mixing characteristics within the water column.

Potentially zebra mussels and herbivorous zooplankters have impacts on the phytoplankton community of a lake; both are filter feeders that selectively graze similar-sized phytoplankters. Zooplankton have a fairly uniform habitat and can move within it to encounter food while adult zebra mussel experience a more variable habitat and are sedentary. Additionally, sedentary adult mussels compete with each other for algae. I found that 20-60 mussels in a clump had grazing rates 30% of predicted based on the same size and number of mussels feeding separately. At the high densities found in natural zebra mussel populations, adult zebra mussel grazing impact should be greatly reduced compared to predictions based on grazing rates for individual mussels. Zebra mussel filtration did not overwhelm phytoplankton production even in late summer when
algae were less abundant and large-bodied cladocerans had been replaced by smaller-bodied herbivorous zooplankters.

Zebra mussel feeding was restricted by reduced delivery of algae into the less-turbulent “concentration boundary layer” and by competition within the mussel colony for algae. I measured the relative magnitude of algal consumption by zooplankton in situ and by mussels in the lab relative to lake algal abundance and photosynthesis. Although seasonal phytoplankton successional patterns typical of north temperate lakes without zebra mussels have persisted after mussels became established in western Lake Erie, total phytoplankton biomasses were lower and Cyanobacteria rarer. However, changes in nutrient concentrations can account for shifts in algal species composition. Based on a comparison of primary productivity and algal standing crop phytoplankton were capable of reproducing once or twice a day.

Grazing by free swimming, large-bodied crustacean zooplankton was sufficient to explain seasonal changes in algal abundance without considering zebra mussel impact at all. Even when seasonally abundant (maximum of 750 L$^{-1}$ during August 1993), zebra mussel veligers grazed pelagic algae at an insignificant rate (generally 1 - 3% with a maximum of 7.1%) relative to other zooplankton. Thus, potentially only the benthic adult zebra mussel stage with its larger biomass could be significantly impacting phytoplankton. Grazing by sedentary adult zebra mussels present in high densities was insufficient to overwhelm phytoplankton production.
DEDICATION

To my family
for all their continued encouragement,
support, and sacrifices
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INTRODUCTION

Aquatic ecosystems are intricate and dynamic; any major alteration in an existing ecosystem can have a significant impact on other communities of that ecosystem (Paine 1974, 1980). The accidental introduction of the European zebra mussel, *Dreissena polymorpha* into the Laurentian Great Lakes some time after 1985 represents yet another perturbation that may eventually spread either naturally or through inadvertent human transfer to most other inland waters of the U. S.

A significant amount of research (MacIsaac et al. 1992, Holland 1993, Bunt et al. 1993; Leach 1993, Madenjian 1995) suggests that the colonization and development of a large, actively-filtering zebra mussel population in a lake, reservoir, or river has a major impact on dynamics of phytoplankton and zooplankton communities as well as indirect effects on the stability of the fish community. *Dreissena*’s potential use of phytoplankton biomass may cause a decreased abundance of zooplankton prey for forage fish as well as for young-of-year piscivorous species. Alterations in the pelagic food web in Lake Erie may have long term effects on the quality of commercial and sport fisheries, particularly walleye and yellow perch. Rapid mussel colonization of water intake pipes of commercial and public facilities necessitates expensive cleanup procedures. Furthermore, zebra mussels accumulate toxic chemicals in their bodies (Bruner et al. 1994), and the degree to which they consume algae containing these compounds may cause major shifts in the patterns of contaminant movement through aquatic systems. Thus, *D. polymorpha* may
alter the ecological, economic, and human health character of aquatic systems into which they are introduced.

*D. polymorpha*’s high fecundity, its free-swimming planktonic veliger larvae, and lack of natural predators permit widespread dispersal and rapid colonization of suitable substrate where they settle, attach, and develop into benthic filter-feeding adults (Morton 1969, Stanczykowska 1977, Hebert et al. 1989, Sprung 1989). Zebra mussels exist in high density clusters of individuals of many sizes attached to one another and preferentially to shallow-water, hard substrates (Wiktor 1963, Morton 1969, Kornobis 1977, Stanczykowska 1977, Lewandowski 1982, Stanczykowska et al. 1988, Reeders et al. 1989, Mackie et al. 1989). Thus, the rocky, shallow, nutrient-rich, thermally-unstratified western basin of Lake Erie is an ideal locale to study their interaction with the pelagic community.

To assess the impact of zebra mussels on the pelagic food web dynamics it is necessary to compare the roles of zebra mussels and zooplankters. Both are filter feeders that selectively graze similar-sized phytoplankters. However, adult zebra mussels are benthic, sedentary, have longer generation times, more biomass, and tie up nutrients for longer time periods than do the mobile, short-lived, smaller, more rapid nutrient recycling zooplankters. Thus, evaluation of the impact of *D. polymorpha* on zooplankton and phytoplankton requires a thorough knowledge of seasonal, size-specific zebra mussel grazing rates as well as the effects of turbulent mixing processes on the delivery of algae to benthic zebra mussels.

Using mussel density estimates and water clearance rates, others have estimated that zebra mussels could clear the entire western basin of Lake Erie of algae in three days (MacIsaac et al., 1992). Such assessments result in overestimates of mussel impact on pelagic algae because they assume that currents and turbulent mixing give zebra mussels...
equal access to algae from the entire water column and ignore refiltration of previously
processed water.

The quantity of food available to adult mussels is ultimately dependent on factors
affecting the delivery of pelagic phytoplankton assemblages to benthic zebra mussels.
Zebra mussels, like other benthic suspension feeders, depend on water movements for
food transport. Most food is transported horizontally in the low flow water near the
bottom (boundary layer) (Muschenheim, 1987). Vertically settling seston becomes
potential food when it enters this boundary layer. A strong food concentration gradient
develops with a localized depletion zone nearest the bed when marine filter-feeding
organisms remove seston faster than it is replaced (Buss and Jackson, 1981, Wright et al.,
1982; Wildish and Kristmanson, 1984, Frechette and Bourget, 1985a,b; Peterson and
Black, 1987; Frechette et al., 1989; Peterson and Beal, 1989).

Hydrodynamic sorting also occurs with denser inorganic particles more abundant
closer to the bed and lighter organic particles more abundant above the bed (Muschenheim
1987). Thus, the vertical feeding height (e.g., position of the recurrent siphon height
above the bottom) attained by an organism (Jumars and Nowell 1984, Monismith et al.
1990) and the orientation of a bivalve's siphons (Monismith et al. 1990) can determine the
quantity and quality of its food supply and its rate of growth (Frechette and Bourget
1985b, Frechette et al. 1989). Local food depletion and high population densities are
associated with reduced growth in the benthic suspension-feeding bivalves Mercenaria
(Peterson and Beal 1989) and Mytilus edulis (Kautsky 1982). Thus, the availability of
food for benthic filter feeders is determined by turbulent mixing and differential flow
within the boundary layer. Hydrodynamic conditions may have a more pronounced impact
on mussel growth and distribution in freshwater than in marine systems because
freshwater ecosystems such as Lake Erie lack the effects of strong tidal mixing seen in
marine systems. On a windless day, MacIsaac et al. (1992) measured a zone of chlorophyll a depletion extending from the bottom up to 1.5 m above zebra mussel beds in the western basin of Lake Erie.

I investigated the importance of turbulent mixing on zebra mussel impact on zooplankton and phytoplankton using an ecosystem approach to estimate the flux of phytoplankton to benthic mussels. My research goals were to evaluate turbulent mixing processes affecting the flux of phytoplankton to zebra mussels and the impact of zebra mussel grazing on the pelagic community. I tested the following four hypotheses to evaluate my goals.

**Goal 1:** Determine the role of turbulent mixing in benthic-pelagic interactions and the delivery of algae to benthic zebra mussels.

**Hypothesis 1:** Delivery of seston to mussels varies with flow rate, seston concentration and composition, topographic roughness, and location

**Goal 2:** Determine the relative influence of zebra mussels and zooplankton on the seasonal dynamics of phytoplankton.

**Hypothesis 2:** Zebra mussel grazing rates vary with mussel body size, seston (algae and suspended particulate matter) composition, and temperature.

**Hypothesis 3:** Competition among zebra mussels determines individual grazing rates.

**Hypothesis 4:** Zooplankton grazing influences seasonal variation in phytoplankton more than does grazing by adult mussels or larvae (veligers).

My dissertation is organized into three chapters: Chapter 1 evaluates zebra mussel *in situ* competition for algae within the boundary layer (Goal 1, Hypothesis 1); Chapter 2 examines factors affecting adult zebra mussel grazing (Goal 2, Hypotheses 2, 3); and Chapter 3 evaluates both adult and veliger zebra mussel competition with zooplankton based on grazing estimates, primary productivity, phytoplankton species composition and
abundance changes, and turbulent mixing processes (Goals 1 and 2, Hypotheses 1, 2, 3, 4). Below, a brief description of each chapter highlights approaches used and major findings.

Chapter 1. Population dynamics and growth of *Dreissena polymorpha* in western Lake Erie: implications for assessing the impact of zebra mussels on pelagic food webs (Goal 1, Hypothesis 1)

To evaluate the long-term population dynamics of a hard substrate mussel population I quantitatively sampled the Peach Point Reef mussel population at a 3 m site from 1990 through 1998. I evaluated population demographics by species for zebra mussels (*D. polymorpha*) and quagga mussels (*D. bugensis*). Starting from 10,000 m\(^{-2}\) in Mar. 1990 the zebra mussel population grew to an observed peak of 81,850 m\(^{-2}\) in May 1992. By May 1994 and again in May 1998 the mussel population dropped to 20-22,000 m\(^{-2}\). Quagga mussels were first observed in 1991, but were rare through 1994. By 1998 quagga mussels represented 33% of the Peach Point Reef mussel population. Most shell growth occurred from May to Sept. and there was little increase in mean shell length during the overwinter, prespawning period. Mean mussel biomass was always higher in May than in Sept. of the same year.

Zebra mussels' growth may be dependent on currents and the amount of turbulent mixing bringing phytoplankton to them. Small differences in flow rate, topographic differences, and zebra mussel feeding height may allow some zebra mussels to obtain more food than others. If mixing delivers phytoplankton equally well to all depths in the thermally unstratified western basin, then zebra mussel growth should not vary with water
depth. I tested this by measuring mussel shell and soft tissue mass growth when mussels were suspended in cages at various depths in the water column.

At both high and low mussel densities and at two locations, zebra mussels farther up in the water column added more shell length, were heavier for their length, and were more likely to add soft tissue body mass than animals at or near bottom. Mussels in bottom cages in the boundary layer added only 10% to 20% as much soft-tissue biomass as those farther up in the water column, even though there was no vertical thermal stratification and light was adequate for photosynthesis throughout much of the water column. Attached mussels appear to be limited in their growth by the rate of delivery of pelagic algae to the bottom and their growth rate differences result from competition with other mussels in the colony and lower food delivery rates at depth.

I further tested the effect of turbulent transport on mussels by measuring the relative abundance and soft tissue mass for populations found on bedrock and cobble, sand, and mud using SCUBA. Larger substrate size and shallower water are characterized by higher turbulent mixing levels. I compared population densities and biomasses at 13 locations representing both hard and soft substrates at a variety of depths.

Not all environments were equally satisfactory for mussels; mussel populations on sand and mud had much lower densities and biomasses than populations on bedrock, cobble, and gravel. No mussels were found on sand at depths of 3 or 6 m nor on mud at 18 m. Biomasses of mussel populations on mud at depths of 9 and 12 m were 1/4 to 1/2 those of populations on hard substrate and at shallower depths at the same location. Therefore, turbulent transport contributes to the differential growth and survival of zebra mussels.
Chapter 2. Estimating zebra mussel impact on pelagic food webs: the role of size-specific grazing rates (Goal 2, Hypotheses 2, 3)

In Western Lake Erie, I measured zebra mussel grazing rates under near natural conditions using a flow-through system that allows zebra mussels to filter ambient lake water with natural seston pumped through the experimental and control cages during a 24 hour period. To test for the effect of intraspecific competition on individual grazing rates I measured whether grazing rate varied for mussels feeding in clumps as compared to that predicted based on the same size and number of mussels feeding individually. I also evaluated the effects of flow rate, reproductive condition, and environmental influences such as sediment resuspension on zebra mussel grazing.

Although mussel grazing rate (mg seston • mg⁻¹ mussel • h⁻¹) increased with mussel size, mussel grazing was less effective in the presence of silt (e.g. from storms). Mussels of all sizes removed more seston at higher seston delivery rates. Zebra mussels in clumps had grazing rates 30% of those predicted based on the same size and number of mussels feeding individually.

Simple linear extrapolation of clearance rates for individual mussels to the whole water column of a lake (MacIsaac et. al, 1992) inappropriately ignores hydrodynamic conditions affecting algal delivery to densely-packed zebra mussels. The magnitude of the impact of zebra mussels' grazing on the pelagic community may depend on their occurrence in dense clusters; some mussels within a cluster may feed efficiently while others are deprived. Thus, the actual grazing impact of mussels in the lake will be lower than estimated from individual clearance rates due to intraspecific competition and slow delivery rates of algae.
Chapter 3. An ecosystem approach to examining the effects of zebra mussels on Lake Erie pelagic function (Goals 1 and 2, Hypotheses 1, 2, 3, 4)

The existing seasonal dynamics of phytoplankton of western Lake Erie alter the quality and quantity of food available to zebra mussels, and to all other consumers of planktonic production. Determining the impact of zebra mussels thus requires a careful measure of seasonal population dynamics of phytoplankton, zooplankton, as well as both adult and veliger zebra mussels.

I used direct microscopic enumeration to evaluate the seasonal population dynamics of phytoplankton, zooplankton, and D. polymorpha's veliger larvae. I measured nutrients (ammonia, nitrate, and total reactive phosphate) available to algae and used size-fractionated in situ $^{14}$C-uptake to estimate phytoplankton growth (Elser et al. 1986). I compared the relative impact of zooplankton community and veliger larvae feeding activity to that of attached zebra mussels. I measured the uptake of radioactively labeled ($^{32}$P) aquatic yeast by indigenous zooplankters and veligers using an in situ incubation chamber deployed at different depths in the lake (Haney 1973, 1985).

Although seasonal phytoplankton successional patterns typical of northern temperate lakes without zebra mussels have persisted after mussels became established in western Lake Erie, total phytoplankton biomasses were lower and Cyanobacteria rarer. Changes in nutrient concentrations can account for shifts in algal species composition from previous higher abundances. Prior to the midsummer “clear-water” phase (Lampert et al. 1986) zooplankton grazing rates were sufficient for zooplankton to process a volume of water equivalent to the entire water column in 2-3 days. Seasonally, grazing by large-bodied crustacean zooplankton like Daphnia alone can exceed the production of algae.
without considering zebra mussel impact at all. Even when seasonally abundant, zebra mussel veligers grazed pelagic algae at an insignificant rate relative to other zooplankton. Zooplankton have a fairly uniform habitat and can move within it to encounter food while adult zebra mussel experience a more variable habitat and are sedentary. Thus, benthic zebra mussels are dependent on the delivery of pelagic algae to them. Zebra mussel filtration did not overwhelm phytoplankton production even in late summer when algae were less abundant and only smaller-bodied zooplankters were present.
CHAPTER 1

POPULATION DYNAMICS AND GROWTH OF DREISSENA POLYMORPHA IN WESTERN LAKE ERIE: IMPLICATIONS FOR ASSESSING THE IMPACT OF ZEBRA MUSSELS ON PELAGIC FOOD WEBS

INTRODUCTION

The colonization and development of a large, actively filtering zebra mussel population may have a major impact on dynamics of pelagic phytoplankton and zooplankton communities as well as indirect effects on the stability of the fish community. The potential diversion of phytoplankton biomass from pelagic zooplankton to benthic zebra mussels may cause a decreased abundance of zooplankton prey for forage fish as well as for young-of-year piscivorous species.

Based primarily on the reported high filtration rates by zebra mussels (Stanczykowska 1977) and the ability of mussels to rapidly develop large population densities on hard substrate, researchers initially predicted large and wide-spread zebra mussel impact in North American inland waters. By comparing lake volume and zebra mussel population clearance rates, early investigators calculated the rate at which a mussel population could theoretically process the entire lake volume (e.g. Hebert et al. 1991). For example, using zebra mussel size frequency distributions and a size-specific filtering rate equation by Reeders et al. (1989), MacIsaac et al. (1992) calculated that zebra mussel populations in western Lake Erie could filter the entire 7 m water column
3.5 or more times daily. Therefore, based on theoretical lake clearance predictions, benthic zebra mussels were expected to have a large impact on pelagic algae (MacIsaac et al. 1992).

In reality, zebra mussels' impact is dependent upon currents and turbulent mixing characteristics within the water column that affect the rate of delivery of organic matter produced in the pelagic zone. Thus, the delivery of algae to the benthos determines zebra mussel growth and population dynamics and the actual impact of benthic zebra mussels on natural algal populations is not yet known. However, early studies following successful zebra mussel colonization in western Lake Erie report both decreases in phytoplankton abundance and increased water transparency (Wu and Culver 1991, Holland 1993). However, they disagree on whether or not the decline can be attributed solely to zebra mussel impact on pelagic algae. Holland (1993) cited the theoretical whole lake clearance predictions (MacIsaac 1992, Bunt et al. 1993) to explain the phytoplankton decline. Wu and Culver (1991) using in situ measurements of zooplankton grazing concluded that, when seasonally abundant, grazing of edible algae by large-bodied crustacean zooplankton can produce a clear-water phase characterized by increased Secchi transparency. However, in August when large-bodied cladoceran abundances were low, zebra mussel grazing did not prolong the clear-water phase. Secchi transparency in both nearshore and offshore sites in western Lake Erie actually decreased in August while adult zebra mussel abundances increased (Wu and Culver 1991).

Zebra mussel impact on particulate matter may depend on depth and their restriction to life on the bottom where boundary layers affect mixing. Several researchers report the development of a concentration boundary layer above beds of suspension feeding bivalves (Wildish and Kristmanson 1984, Frechette et al. 1989,
Monismith et al. 1990, O’Riordan et al. 1993). A concentration boundary layer is a zone of depletion above mussel beds where mussel filtration removes suspended particulate matter faster than vertical mixing and horizontal advection replenish it. Therefore, a mussel’s position within the population relative to other mussels may allow some mussels to obtain more food than others (Peterson and Beal 1989, Pullen and LaBarbera 1991, O’Riordan et al. 1993, O’Riordan et al. 1995).

Zebra mussel impact can be measured indirectly by evaluating mussel survival and growth since only food consumed in excess of an organism’s needs for survival and maintenance is available for growth. Zebra mussels’ growth may be dependent on currents and the amount of turbulent mixing bringing phytoplankton to them. Research on marine mussels illustrates factors affecting benthic mussels’ access to food: small differences in flow rate, topographic differences, and feeding height may allow some mussels to obtain more food than others (Kautsky 1982, Wildish and Kristmanson 1984, Peterson and Beal 1989, Frechette et al. 1989, Monismith et al. 1990, O’Riordan et al. 1993).

In my study I evaluated the impact of zebra mussel population dynamics on the pelagic community and the role of turbulent mixing processes on the flux of pelagic phytoplankton to benthic zebra mussels. Algal abundance varies widely in space and time, so I chose to use zebra mussels at fixed locations as integrators of the physical and biological processes affecting their access to food within the natural lake environment. I tested the importance of turbulent mixing on the impact of zebra mussels on the lake using three spatial scales: 1) competition within the mussel bed for food, 2) within the water column where turbulent mixing affects algal delivery rates and 3) within different regions of the lake where transport processes vary.
At the smallest scale, I studied the dynamics of a shallow water, hard substrate zebra mussel population and its impact on seasonal and annual patterns of algal population dynamics. In my medium scale experiments I studied the effect of turbulent mixing on the growth of caged zebra mussels suspended at various depths above the lake bottom in both thermally unstratified and stratified lakes relative to algal concentration gradients. At the largest scale, I made a comparative study of the effects of regional differences in transport processes delivering algae to benthic zebra mussels by comparing mussel populations at a series of habitats with graded levels of advection and turbulent mixing. At all three scales, I found that turbulent mixing processes within the lake determined the impact of zebra mussels on pelagic algae.

MATERIALS AND METHODS

Study Sites

Lake Erie

Our permanent study sites were off South Bass Island, western Lake Erie, near the F. T. Stone Laboratory field station (Figure 1). Peach Point Reef is located off the north side of South Bass Island and extends northeast toward the U.S. Coast Guard west channel navigational buoy for Put-In-Bay, OH. Peach Point Reef consists of honeycombed dolomite slabs, cobble, and rock rubble. Our smallest scale population dynamics study site on Peach Point Reef was located at 3 m depth where natural zebra mussel colonies formed continuous mats 3 to 5 cm thick.

Our shallow water study site for the medium scale water column cage experiments was located at another 3 m site 12 to 15 m off the northwest side of Gibraltar Island in Hatchery Bay (N 41° 40.00', W 82° 49.69'). It had a hard, dolomite rubble bottom where natural zebra mussel colonies formed continuous mats 3 to
5 cm thick. Our nearby 12 m site was located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef (N 41° 40.27’, W 82° 49.60’) and had mainly soft, mud substrate with scattered rocks. At the 12 m site zebra mussels were initially restricted to the hard substrate (July 1991), but by late Sept 1991 mussels had bridged open areas by forming chains across the mud. By July 1992 mussels had spread to form a continuous mat 2-3 cm thick.

**Hargus Lake**

We did a comparative water column cage experiment at Hargus Lake, a man-made reservoir located in south central Ohio east of Circleville, OH (N 39° 37.36’, W 82° 53.15’). Hargus Lake has an area of 54 ha and develops strong thermal stratification each year. Our study site was located east of the earthen dam at a depth of 12 m. Hargus Lake has a muddy, soft bottom with hard substrates limited to submerged trees and man-made structures. In August 1992 juvenile zebra mussels were found attached to littoral zone vegetation in Hargus Lake. Adult zebra mussel densities were low (1-2 mussels • m⁻²) and restricted to individuals 23 mm or larger attached to boulders lining the dam or to submerged trees located between 1.5 and 4.3 m. No mussels were found on soft substrate. Juvenile mussels (3-10 mm) were attached to the concrete spillway in densities of 40 mussels • m⁻² and to some rocks in adjacent Hargus Creek. During our 1993 experiments zebra mussel densities remained low (4 mussels • m⁻²) and were restricted to hard substrate or littoral zone vegetation at depths above the metalimnion.

For our largest scale, I made a comparative study of the effects of regional differences in algal transport processes on zebra mussel populations in western Lake Erie. I surveyed zebra mussel populations along a south-to-north transect across Gull
Island Shoal from our anchorage at N 41° 39.76', W 82° 41.56'; at three locations at the mouth of the Sandusky River near Bay Point Shoal (N 41° 30.59', W 82° 41.88'), (N 41° 30.51', W 82° 42.37'), (N 41° 30.74', W 82° 41.61'); at Starve Island Deep (N 41° 37.51', W 82° 49.34'); and at two locations on Niagara Reef (N 41° 40.44', W 82° 58.80') (Figure 1).

**Smallest Scale Studies: Intraspecific Competition within the Mussel Bed**

I assessed competition by comparing mussel numerical density over time with changes in shell length-soft tissue mass relationships. I collected mussels from Peach Point Reef at 3 m by retrieving randomly selected, mussel-encrusted rocks either by free diving or if large quantities were needed, by using SCUBA. From 1991 to 1994 during early September and late May I removed replicate, quantitative samples from 6 - 11 randomly selected Peach Point Reef rocks to determine zebra mussel population density, length-frequency distribution, and soft tissue mass. From each rock I removed all mussels within one 25 cm² quadrat. I then pooled all the excess, non-quadrat mussels taken from sample rocks collected on that date. From the pooled animals I selected a representative size range of 50-100 mussels and determined a date-specific, shell length-dry soft tissue mass relationship. Freezing and subsequent thawing of mussels permitted easier removal of soft tissue body mass. For each mussel I measured shell length using dial vernier calipers (to nearest 0.1 mm) and removed soft tissue mass from the shell. I dried the soft tissue at 65 °C for 24 hours prior to weighing (to nearest 0.1 mg).

For each replicate quadrat I measured the length of every mussel and then estimated size-specific individual soft tissue mass using the date-specific, length-dry mass regression. I calculated population density (mussels • m⁻²) and estimated total
population soft tissue mass (g dry mass • m\(^{-2}\)) for each sample date from the mussel
length-frequency distribution and estimated size-specific masses.

To evaluate the long-term population dynamics of a hard substrate mussel
population I again quantitatively sampled the Peach Point Reef mussel population four
years later in late May 1998. I evaluated population demographics as above by species
for zebra mussels (*D. polymorpha*) and quagga mussels (*D. bugensis*).

**Phytoplankton Dynamics**

To evaluate the impact of zebra mussels on seasonal and annual patterns of algal
population dynamics I monitored phytoplankton community composition and biomass
from April to Oct in 1991 and 1992 at a 5 m station in Hatchery Bay west of our 3 m
study site. Weekly I collected replicate integrated whole water column samples (0 to 3
m) using a 5 cm diameter PVC pipe that was lowered vertically into the water, stoppered,
and emptied into a bucket. I preserved a 500 ml subsample from each replicate whole
water column sample with acid Lugol’s solution for later evaluation of phytoplankton
species composition using the Utermohl sedimentation technique (Lund et al. 1958).
Each preserved phytoplankton sample was allowed to settle for at least one week in 250
ml graduated cylinder and then concentrated to 30 ml by using a modified J-shaped glass
pipet to draw off the upper liquid. I used an inverted microscope (400x) to identify,
count, and measure individual algae. To estimate phytoplankton volume for each taxon
I used equations for one or more appropriate geometric shapes (Kellar et al. 1980) and
used an ocular micrometer to measure linear dimensions of representative phytoplankters
(at least 50 for common genera and all encountered for rare genera). Using the
abundance and the mean calculated volume for each taxon I estimated algal volume
(ml • m\(^{-3}\)). Assuming a specific gravity of 1.0 for phytoplankters, I converted algal
volume to biomass (g wet weight • m\(^{-3}\)).
I evaluated how seasonal variation in turbulent mixing processes as well as phytoplankton dynamics affect the quantity and quality of suspended particulate matter (seston) delivered to benthic zebra mussels. During 1992 I measured seston concentration for each replicate integrated whole water column sample as well as for replicate water samples collected at specific depths in the water column. During July, August, and Sept. 1992 I used a submersible pump equipped with a pair of deflecting bottom plates that only permitted water to be drawn in laterally to collect replicate water samples at 0.5 m intervals from 0.5 to 2.5 m depths at a 3.5 m location adjacent to our 3 m cage experiment site. I determined total seston concentration by filtering a 500 ml subsample from each replicate and two 500 ml distilled water blanks through preweighed membrane filters (0.45 μm pore size). After drying at 65° C for 24 hr each filter was reweighed (to nearest 0.1 mg). I calculated total seston concentration as the mean mg dry mass · L⁻¹ of two replicates. To evaluate food quality I determined the relative inorganic and organic fractions in the seston. I ashed the filters at 550° C for 30 minutes and calculated the organic fraction of the seston as ash-free dry mass (difference between the total dry seston mass and final ash mass).

**Seasonal Lake Parameters**

To detect thermal stratification within the lake and variations in dissolved oxygen levels with depth, I measured water temperature and dissolved oxygen using an electrical thermistor thermometer equipped with a dissolved oxygen electrode (YSI). I measured water transparency using a 20 cm Secchi disk as an indirect measure of factors affecting phytoplankton abundance.
Medium Scale Experiments: Turbulent Mixing Effects in the Water Column

I studied the effect of turbulent mixing on the shell and soft tissue growth of caged zebra mussels suspended at various depths above the lake bottom in both thermally unstratified and stratified lakes.

Basic Procedures for Cage Experiments

Using a size range of mussels representative of the size range of animals in the natural population at that time, I marked each individual mussel with a numbered, colored, plastic tag (2.5 mm diameter) so that I could track shell growth and soft tissue mass changes of individual animals. Mussels less than 5 mm were not used because of the danger of gluing the valves shut while attaching a tag with cyanoacrylate gel adhesive. I measured the initial shell length of each marked mussel (nearest 0.1 mm). I estimated initial biomass of each marked mussel using length-dry soft tissue mass regressions generated for a representative size range of mussels collected at the same time and location as marked mussels. I suspended replicate, representative groups of marked and measured mussels in rigid, cylindrical, polyethylene mesh cages (10 cm diameter, 27 cm length, 2 mm mesh opening) placed at different depths on anchored, buoyed growth lines (Figure 2). At the end of each experiment (2 to 3 months) I determined survival of marked mussels and evaluated caged zebra mussel growth through measured changes in shell length and soft tissue mass for each individual.

Zebra Mussel Survival and Growth in a Thermally-unstratified Lake

In 1991 I placed a replicate group of 66-72 measured and tagged mussels in each cage (equivalent to a density of 2500 mussels m⁻²). I placed 16 cages on four lines at 0.5 m intervals above the bottom in two locations: Lines 1, 2, and 3 at our 3 m site and
Line RC at the 12 m site (Table 1). The duration of experiments ranged from 78 to 126 d (Table 1).

To evaluate whether mussel shell growth rates for different sized mussels varied while avoiding disturbing caged mussels I also held 97 marked and measured individuals from the same lake population as Line 3 caged mussels in the laboratory in a 40 L glass aquarium equipped with a continuous flow-through supply of Lake Erie water pumped from 0.25 m above the bottom. I measured shell lengths of all individuals in the lab mussel population (LAB) every two weeks from 14 July to 28 Sept. I calculated LAB mussel shell growth rate (μm • d⁻¹) as shell length added (μm) during the period between each two successive sampling dates (d). Lake water, pumped from 0.25 m above the lake bottom (1.5 to 2 m depth depending on lake level), provided natural seston and maintained mussels at ambient lake temperatures.

In 1992 I repeated our cage experiments, but tested the effect of zebra mussel density on growth (Table 1). During a 60 day period at both the 3 m and 12 m sites I placed replicate groups of mussels in cages at two densities: Low density, 34 mussels per cage (1250 mussels • m⁻² = LOW) and High density, 68 mussels per cage (2500 mussels • m⁻² = HIGH). All eight growth lines had cages at 0.0 m, 0.5 m, 1.0 m, 1.5 m above the bottom; the two lines at the 12 m site each also had cages at 2.0 m above the bottom.

**Zebra Mussel Survival and Growth in a Thermally-stratified Lake**

To evaluate the effect of thermal stratification on zebra mussel impact potential I investigated the effects of variations in turbulent mixing on zebra mussel shell growth and soft tissue mass changes in in situ cage experiments in Hargus Lake. Insufficient mussels were available in Hargus Lake in 1993 to conveniently collect enough for our growth experiments, so I obtained permission from the Ohio Department of Natural
Resources, Division of Wildlife, to use Lake Erie zebra mussels in Hargus Lake. For the three growth lines at the 12 m site I selected cage suspension depths of 2, 4, 6, and 8 m to bracket the metalimnion. I placed a replicate group of 34 measured and uniquely tagged mussels in each cage (equivalent density = 2500 mussels \( \cdot \) m\(^2\)). Hargus Lake experiments began 25 April and all cages were retrieved on 2 Sept. 1993 (131 d).

**Largest Scale Study: Regional Differences in Transport Processes**

Hard substrates preferred by zebra mussels are in the minority in western Lake Erie (bedrock 5.9%, gravel 9.4%) with mud (58.5%) and sand (26.2%) making up most of the surface sediments (Herdendorf 1970). Sites with mud characteristically represent regions with the lowest turbulent mixing, followed by sand, then gravel, and finally, bedrock with the highest turbulent mixing. Therefore, variations in depth, substrate type, and topographic roughness may vastly affect the rates of transport processes within the lake and, ultimately, the distribution and impact of zebra mussels in western Lake Erie. To evaluate the role of regional differences in the delivery of algae to zebra mussel populations I measured the densities, length-frequency distributions, and soft tissue masses of zebra mussel populations located in different habitat types in western Lake Erie. I selected 19 August 1993 for the survey because I anticipated that most mussels would have completed spawning earlier and the majority of the newly settled mussels would be large enough to count and measure. Since larger substrate size and shallower water are characterized by higher turbulent mixing levels I selected six anchorage locations that provided access to a representative variety of depths (1 to 18 m) and substrate types (bedrock, cobble, sand, and mud).

Divers using SCUBA collected three to six replicate, quantitative zebra mussel samples at each collection site. Divers placed a 64 cm\(^2\) metal quadrat on a randomly selected area and then collected all mussels within the quadrat. Divers recorded bottom
substrate characteristics and depth at each collection site. I held bagged mussels on ice until samples could be stored frozen for later analyses. After counting and measuring shell length of all mussels in each replicate, I measured dry soft tissue mass of 25 to 35 mussels from each sample. I developed a separate length-dry soft tissue regression for each collection site using the individual size-specific mussel soft tissue masses pooled from all replicates from the same substrate type and depth. I then estimated mean population density (individuals • m$^{-2}$) and soft tissue mass (g dry mass • m$^{-2}$) using quantitative counts, length frequency distributions, and the site-specific length-dry soft tissue mass regressions.

**General Statistical procedures**

Smallest Scale Studies

I log-transformed mussel lengths and dry soft tissue masses prior to calculating regressions. I used the General Linear Model (GLM) Analysis of Variance (ANOVA) (SAS Institute Inc., 1989) to test for significant seasonal and annual differences in length-dry soft tissue mass regressions for the hard substrate population on Peach Point Reef. I used GLM Analysis of Covariance (ANCOVA) (SAS Institute Inc., 1989) to test for significant effects of time on the biomass of a mean mussel. For ANCOVAs I use the term “mean” to refer to the mussel shell length representing the grand mean for the sample populations tested. In the results section I have specified the value of the mean covariate used because mean mussel shell length varied in different analyses depending on the size distribution of the mussels present in the sample populations under comparison.

Medium Scale Experiments

In the mussel cage experiments I tested for significant treatment effects (e.g., density, depth, location) on mean zebra mussel shell growth using Least Squares Means
(LSmeans) adjusted for the covariate initial shell length (GLM, ANCOVA). When I tested for significant treatment effects on changes in mean zebra mussel dry soft tissue mass I used final shell length as the covariate. When the ANCOVA F test indicated significant differences in treatment effects, I compared least-squares means (LSmeans) to identify where differences occurred.

Large Scale Study

In our survey of zebra mussel populations on different substrates I also used GLM Analysis of Variance (ANOVA) to test for significant differences in mussel populations’ densities and soft tissue masses for different collection sites and I again compared LSmeans to identify where differences occurred.

RESULTS

Smallest Scale Studies: Intraspecific Competition within the Mussel Bed

Zebra mussel impacts have been predicted to be maximal for populations settled on preferred hard substrates. Thus, the population dynamics of zebra mussels living on hard substrate at Peach Point Reef should reflect a successful population integration of the effects of competition with adjacent individuals for food and variations in algal delivery rates. If the benthic zebra mussel population is impacting pelagic algae, then as zebra mussel density increases (assuming that all sites have an equal probability of receiving settling veligers), I would expect phytoplankton to decline and seasonal successional patterns to be altered. Therefore, in these smallest scale studies I evaluated seasonal and annual changes in both the zebra mussel population and the phytoplankton community. To test whether zebra mussel size distribution and individual soft tissue mass values were altered I monitored the density, biomass, and size structure of the mussel population on Peach Point Reef from March 1990 through May 1994.
Based on a single quantitative sample I estimated the population density in March 1990 to be 10,000 mussels $\cdot$ m$^{-2}$. By September 1991 the density had risen to 68,000 mussels $\cdot$ m$^{-2}$ (Table 2). Mussel population density increased rapidly to a peak of 81,850 m$^{-2}$ in May 1992 (Table 2). Densities in Sept 1991, Sept 1992, and May 1993 did not differ. All other densities comparisons were significantly different (ANOVA, $p=0.0001$). In 1992 and 1993 population densities were higher in May and lower in September. During the overwinter periods, population densities changes varied yearly; from September 1991 to May 1992 mussel population densities increased significantly by almost 14,000 mussel $\cdot$ m$^{-2}$ ($p=0.022$) while the September 1993 to May 1994 population densities decreased by a similar amount ($p=0.045$).

The mean-sized individual in the hard substrate zebra mussel population at Peach Point Reef generally increased in both shell length and biomass as the population aged during 1991 to 1994 (Table 2, Figure 3 a-f). Most shell growth occurred from May to September and there was little increase in mean shell length during the September to May overwinter, prespawning period. Mean mussel biomass was always higher in the May than in September of the same year.

The 1998 mussel population demographics reflect the integration of long-term, small scale effects on a hard substrate, shallow water mussel population dynamics. In 1998 the total mussel population density and biomass were lower than in all previous May populations (Figure 4a) and mean mussel shell length and biomass were lower than in 1994 (Table 2). Although I observed quagga mussels in other samples taken during 1991 to 1993, quagga mussels were rare ($<0.1\%$) and did not appear in my Peach Point Reef 3 m site quantitative samples until May 1994 when they represented $<0.5\%$ of the population and were $<15$ mm in shell length. By May 1998 quagga mussels represented
33% of the 3 m Peach Point Reef population, were present in all size classes, and were similar in mean shell length and biomass to zebra mussels (Table 2, Figure 4b).

From 1991 to 1994 the zebra mussel population’s shell size distributions generally did not differ in May from those of the previous September (Figure 3a-f). However, late settlement, early secondary mussel recruitment, or favorable growth conditions prior to May sampling may be responsible for shifts in smaller size class densities from Sept 1991 to May 1992 (Figure 3a,b). There was a general decrease in the densities of all size classes from September 93 to May 94 (Figure 3e,f). Although the summer periods from May to September in 1992 and 1993 showed a shift in densities distribution toward larger sizes (10 - 18 mm) there were fewer animals in the largest size classes ( > 20 mm) in September than in May of both years suggesting increased post-spawning mussel mortality.

Changes in zebra mussel population biomass reflect zebra mussel consumption and reproductive condition. The significant increases in zebra mussel population biomass during the overwinter and early spring periods from September to May in all years (p < 0.005) probably reflect mussel preparation for spawning. Zebra mussel population biomasses (Table 2) were significantly higher in the May than in the September in both 1992 (p=0.0026) and 1993 (p=0.0004). In 1992 and 1993 mussels large enough to reproduce (> 10 mm) had lower biomasses in September than in May with the greatest decrease in biomass occurring in mussels >18 mm (Figure 3b,c,d,e).

In order to evaluate seasonal and annual changes in the Peach Point Reef mussel population I compared changes in biomass of standard length mussel (mean shell length =13.9 mm) from May to September in all years (Figure 5, Table 3). The bimodal changes in biomass of the standard mussel suggest that the hard rock population had at least two spawning episodes as evidenced by the sharp decline in biomass from mid to
late June followed by a recovery period in which biomass stabilized or increased and second, smaller decline in biomass that occurred from mid July through mid August. Standard mussel biomass was lowest in September when phytoplankton biomass was increasing.

The presence or absence of thermal stratification can affect mixing within the water column and thus, the delivery of pelagic algae to benthic zebra mussels. I monitored lake temperatures to determine whether or not thermal stratification had occurred. During our 1991 growth experiments water temperatures in Lake Erie ranged from 16 to 27 °C while 1992 temperatures ranged from 18.7 to 24.1 °C (Figure 6a). During 1992 I found no evidence of thermal stratification; water temperature generally differed by less that 0.1 °C from surface to 5 m (range 0.0 to 0.6 °C). In 1992 dissolved oxygen levels at our 5 m Lake Erie site were high, ranging from 6.8 to 9.8 mg • L⁻¹. On any date dissolved oxygen levels generally differed by less than 0.4 mg • L⁻¹ from surface to 3 m (range 0.1 to 0.6 mg • L⁻¹).

Food available to zebra mussels varied seasonally in Lake Erie during 1991 and 1992. Variations in phytoplankton biomass showed a pattern typical of a north temperate lake (Figure 6b). In both 1991 and 1992 there were spring maxima followed by a clear-water phase in late June and a subsequent recovery in late summer (Figure 6b). In 1991 diatoms were most abundant in spring and fall, cryptophytes reached a peak in early July while chlorophytes and cyanophytes peaked in late summer (Figure 7). Spring and early summer phytoplankton patterns in 1992 were similar to 1991 except that spring diatom peaks occurred later in 1992 possibly due to lower water temperatures later in the 1992 season (Figures 6, 7, 8). In 1992 there was an early August peak in phytoplankton and cyanophytes were rare (Figure 8).
In both 1991 and 1992 Lake Erie Secchi disk transparency at my 5.0 m site ranged from 2.0 m to the bottom suggesting that light was adequate for photosynthesis throughout the entire water column (Figure 9a). However, Secchi depth transparency, while often varying inversely with photosynthesis, also integrates the effects of turbulent mixing and sediment resuspension within the water column. Therefore, total suspended particulate matter in the water column and the relative inorganic and organic fractions in the seston more accurately reflect quality and quantity of food potentially available for delivery to benthic zebra mussels. During 1992 at our 5 m site in Hatchery Bay, western Lake Erie total seston concentration varied greatly, ranging from a 2.4 to 5.8 mg · L⁻¹, reflecting seasonal variation in phytoplankton species composition as well as local variation in turbulent mixing events such as storms or seiches (Figure 9b). Assuming that only the organic component of the seston was utilized for zebra mussel growth, then the presence of a larger organic fraction represents a higher “quality“ food. During 1992 the organic component of the whole water column seston samples ranged from 0.7 to 3.5 mg · L⁻¹ (Figure 9b). During July the organic component varied between 20% and 62% of the total suspended particulate matter with a mean of 48% while during August the organic fraction was consistently lower, ranging from 21% to 36% of the total seston with a mean of only 27%.

Based on seston concentration variation with depth, a thermally well-mixed water column may not be homogeneous in terms of food quality and quantity. When I measured seston concentration at specific depths in the water column adjacent to our cage experiment (3 m site), the organic component of the seston generally ranged between 24% and 32% of the total suspended particulate matter with no consistent pattern with depth. On 9 July the organic component varied little with depth ranging from 24% to 29% while on 11 Aug the organic fraction decreased with increasing lake depth ranging
from 32% at 0.5 m below the surface to 24% at 0.5 m above the bottom. On 15 September when the total seston concentration was the lowest of the three dates sampled the organic seston varied the most ranging from 24% at 0.5 m below the surface to a high of 50% midway in the 3 m water column.

Medium Scale Experiments: Turbulent Mixing Effects in the Water Column

Cage Experiments

Growth

General Trends

The specific length-frequency distribution of a zebra mussel population as well as its location may affect its impact on the phytoplankton. In all my zebra mussel cage experiments, mussel shell growth and soft tissue mass changes were allometric. Therefore, measurement of the effects of location on mussels in cages was evaluated on the regressions of shell growth and biomass against length. Size-specific shell growth patterns seen in all cage experiments can be illustrated by 1991 Line 3 mussels. For example, in cages from Line 3 in the 1991 (Figure 10) smaller mussels added more shell length than did larger mussels at the same depth, but the amount of shell length added for a given size mussel increased with increasing height above the bottom (Figure 10). Animals suspended in cages at the bottom added the least amount of shell length and in some cases lost shell.

Growth line mussels were measured only at the beginning and end of the experiment, therefore, it was not possible to detect seasonal variation in shell growth using the caged mussels. However, the mussels in Line 3 cage experiments and the mussels held in the lab (LAB) came from the same initial pooled mussel sample collected from the Peach Point Reef population. Therefore, to evaluate whether mussel shell
growth rates for different sized mussels varied while avoiding disturbing caged mussels I used shell growth of the LAB mussels which were measured six times. At the end of the experiment LAB mussels did not differ significantly in their total shell growth from that of Line 3 caged mussels in the bottom cage (0.0 m) (Figure 10). LAB mussel shell growth rates decreased with increasing mussel size (Figure 11). However, growth rates were not constant during the experiment; all size classes of LAB mussels showed increasing growth rates until mid August. Subsequent growth rates generally declined with an abrupt decrease after mid September even though algae were available for growth since phytoplankton biomass was increasing in Hatchery Bay (Figure 6).

In subsequent analyses, covariance estimates are evaluated for a mussel of mean length. At the end of the experiment caged mussels from Line 3 had higher soft tissue mass (=biomass ) when suspended farther above the bottom (ANCOVA, p =0.0001, mean final shell length = 19.7 mm, mean final dry soft tissue mass =20.6 mg, n = 287) (Figure 12). All mussels 0.5 m or higher above the bottom were heavier for their size than when initially collected from Peach Point Reef (Figure 12). Caged mussels added more biomass with increasing height above the bottom ( ANCOVA, p =0.0001, mean initial shell length = 15.7 mm, mean added biomass = 11.3 mg dry mass, n = 287) (Figure 13). Although caged mussels at the bottom (0.0 m) added little or actually lost mass during the experiment (Figures 12,13). At the end of the experiment mussels in the bottom cage (0.0 m, at a density of 2500 m⁻²) were heavier for their size than mussels collected from the Peach Point Reef population (at a density of 68,000 m⁻²) (Figure 12) (ANCOVA, p=0.0002, mean final shell length = 19.7 mm, mean final biomass = 20.6 mg dry mass, n= 357).
Zebra Mussel Survival and Growth in a thermally-unstratified Lake

Survival of caged mussels in thermally-unstratified Lake Erie 1991 and 1992 was high, ranging from 94 to 99% in both years with no detectable patterns. However, both shell growth and soft tissue changes were strongly influenced by the position of caged mussels within the water column.

Shell Growth

Zebra mussels farther up in the water column added more shell length than mussels at or near the bottom, regardless of duration or location, (1991: ANCOVA, 
\[ p=0.0001, \text{mean initial shell length} = 15.2 \text{ mm} \]) (Figure 14a). I saw the same pattern in 1992 (Figure 14b). In 1992 at the 3 m site mussels at low density (1250 mussels \( \cdot \text{m}^2 = \text{LOW} \)) in cages at both 0.0 m and 0.5 m above the bottom added more shell length than did caged mussels at high density (2500 mussels \( \text{m}^2 = \text{HIGH} \)) at the corresponding depths (ANCOVA, \[ p<0.0006, \text{mean initial shell length} = 15.7 \text{ mm} \]) (Figure 14b). At the 12 m site HIGH mussels in bottom cages added more shell length than did LOW mussels (\[ p=0.02 \]). At both locations caged mussels 1.0 m and 1.5 m above the bottom added similar amounts of shell lengths at both densities. However, at 12 m LOW mussels in cages 2.0 m above the bottom added less shell length than did HIGH mussels at the same depth (\[ p=0.03 \]).

Final Biomass

Zebra mussels farther up in the water column had higher final soft tissue mass (biomass) for their size than did mussels at or near the bottom (ANCOVA, \[ p=0.0001, \text{mean final shell length} = 19.9 \text{ mm in 1991, 19.5 in 1992} \]). In both 1991 and 1992, mussels in all bottom cages lost biomass during the experiments. Although mussels in bottom cages had lower final biomasses than when they were initially collected, they
were heavier for their size than mussels collected from the natural population on Peach Point Reef (at a density of 68,000 m\(^{-2}\)) at the end of the experiment (p=0.0002).

**Added Biomass**

In both 1991 and 1992 in Lake Erie caged zebra mussels at or near the bottom added less soft tissue body mass (biomass) than animals suspended farther up in the water column (ANCOVA, p=0.0001, mean initial shell length = 15.2 mm in 1991, 15.7 mm in 1992)( Figure 15a,b). In both years and at both sites the amount of biomass added by caged mussels increased with increasing height above the bottom (Figure 15a, b). In 1991 caged mussels at or near the bottom had lower added biomass than mussels suspended farther up in the water column regardless of the starting date or duration of the experiment (p=0.0001). At the 3 m site 97.5 to 100% of caged mussels 0.5 m or farther up in the water column added biomass while only 80% of mussels in bottom cages added biomass.

In 1992 caged mussels at lower density and higher up in the water column added more biomass at both the 3 m and 12 m sites. In 1992 at my 3 m site only 43.5 % of HIGH mussels and 67.9% of LOW mussels in bottom cages added biomass whereas all the LOW mussels suspended 0.5 m or higher above the bottom and 95 % of HIGH mussels suspended at 0.5 m added biomass (Figure 15b). For caged animals at or near the bottom, HIGH mussels had lower added biomass than LOW mussels at the same depth (p = 0.0001). Both HIGH and LOW mussels suspended in cages at 1.0 m and 1.5 m above the bottom added soft tissue mass and in similar amounts.

At the 12 m site only 69 % of mussels in bottom cages added soft tissue mass while 94.1 to 100 % of animals farther up in the water column did. HIGH Mussels in cages 1.0 m above the bottom added more soft tissue mass than did caged LOW mussels.
at the same depth (p <0.03). For all other depths caged mussels did not differ in added soft tissue mass.

HIGH mussels in bottom cages at the 3 m site lost soft tissue mass and differed significantly from other bottom caged animals at both locations (p=0.0001). LOW Mussels in cages 0.5 m above the bottom at the 3 m site had significantly more added soft tissue mass than did other caged mussels at the same depth at both locations (p=0.0001). At the shallow site mussels 1.0 and 1.5 m above the bottom added significantly more biomass than did mussels at the 12 m site (p=0.0001).

Zebra Mussel Survival and Growth in a Thermally-stratified Lake

In contrast to Lake Erie during 1991 and 1992 experiments, Hargus Lake in 1993 was strongly thermally-stratified throughout our cage experiments with the metalimnion established between 3 and 7 m. Secchi transparency ranged from 1.1 to 2.5 m during our cage experiments suggesting that photosynthesis was generally limited to the epilimnion and the degree of turbulent mixing would have limited algae delivery to caged mussels in the hypolimnion. Epilimnion water temperatures ranged from 10.6 to 30°C while epilimnetic dissolved oxygen levels ranged from 5.7 to 11.7 mg • L⁻¹. Conversely, mussels at 8 m experienced a narrow range of cold water temperatures (5 to 8°C) and not only a wider range of dissolved oxygen levels (0.1 to 9.2 mg • L⁻¹), but a prolonged period of low dissolved oxygen. From 2 June to 1 September dissolved oxygen levels from 6 to 12 m ranged from 0.1 to 1.8 mg • L⁻¹ with levels of less than 2 mg • L⁻¹ occurring from 4 to 12 m from early July to early August. Mussels within the metalimnion at 4 and 6 m experienced the widest fluctuation in both temperature and dissolved oxygen levels.
In Hargus Lake, overall caged mussel survival was only 43%. Mussels’ survival generally decreased with increasing depth ranging from 99% for epilimnetic mussels at 2 m to 1% for metalimnetic mussels at 6 m. Overall survival at 4 m was low (52%) due to variation in survival on different growth lines: mussel survival for Lines 2 and 3 was 78%, but no mussels survived at 4 m on Line 1. Line 1 mussels may have experienced localized, unfavorable conditions within the metalimnion while animals at 4 m on the other two lines did not. Survival was lowest at 6 m where only one mussel on all three growth lines survived (1%). However, the shells of caged animals at 6 m showed some shell growth indicating that these animals survived for part of the experimental period and may have died as the result of a combination of low dissolved oxygen levels and high temperatures during midsummer. Mussel survival at 8 m in the hypolimnion ranged from 9 to 43% with overall survival of 25%.

While all surviving caged mussels showed some increase in shell length (mean initial shell length = 15.1 mm, mean added shell length = + 5.2 mm, n = 174), their location within the water column affected the relative amount of shell growth. At my 12 m site surviving mussels higher up in the water column added significantly more shell length than did mussels below them (ANCOVA, p=0.0001). In the epilimnion mean added shell length of mussels at 2 m was 6.9 mm while at 4 m mussels only had mean shell growth of 4.0 mm. In the hypolimnion at 8 m, surviving mussels’ mean shell growth of 0.3 mm did not differ significantly from zero.

Location of surviving caged mussels within thermally-stratified Hargus Lake affected their mean final soft tissue mass (=biomass). Final mussel biomass differed significantly with depth (ANCOVA, p = 0.0001, mean final shell length= 20.3 mm, mean final biomass = 20.7 mg dry mass, n = 174). Mussel final biomass (18.7 mg) was lowest at 2 m and was significantly less than both the mussel final biomass at 4 m

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(p=0.0006) and at 8 m (p = 0.0001). However, the mussel final biomass at 4 m (22.6 mg) and 8 m (25.4 mg) did not differ significantly primarily reflecting the differences in the number of surviving mussels (higher at 4 m) and their size distribution at the two depths (all sizes survived at 4 m, while only very small or very large mussels survived at 8 m). Caged zebra mussels in the warmer, well-mixed epilimnion were more likely to add soft tissue mass (=biomass) during the experiment than caged mussels in the hypolimnion (ANCOVA, p = 0.0001, mean initial shell length = 15.1 mm, mean added biomass = 9.2 mg dry mass, n = 174).

**Largest Scale Study: Regional Differences in Transport Processes**

Prior to 1993 most of the research on zebra mussel impact in western Lake Erie focused on areas around islands and reefs, and in nearshore areas because of the availability of hard substrate where mussel impacts were expected to be maximal. Little was known about zebra mussel colonization of other substrates and how well those populations were doing in the open waters of the lake. Based on the results of my growth experiments and monitoring of the hard substrate population on Peach Point Reef I anticipated that zebra mussel populations distributions and impacts would vary with substrate type and water depth, reflecting local factors affecting the delivery of algae to benthic mussels and, hence, the potential effect of mussels on phytoplankton. I compared estimated population densities and biomasses at 13 locations representing both hard and soft substrates at a variety of depths.

The zebra mussel populations near Gull Island Shoal (Figure 1) occupied the greatest variety of substrates and were found at depths ranging from 1 to 12 m (Table 4). At 1 m depth I found only a few newly settled mussels (1-3 mm) in small cracks in the bedrock. At other Gull Island Shoal locations the mean mussel shell length and biomass were maximal at 3 m and generally decreased with increasing depth. Smaller
mean shell length and lower mean biomass was also associated with the presence of mud or sand substrate. I found no mussels on sand locations at 3 and 6 m near Bay Point Shoal and none on mud at 18 m at Starve Island Deep.

Larger substrate size (bedrock, boulders, cobble) and shallower water (3 - 9 m) are characteristic of locations with higher turbulent mixing levels and had much higher densities and biomasses than populations on sand and mud (Table 4). I found that location (substrate type and depth) had a significant effect on both estimated densities and biomasses of zebra mussel populations (ANOVA, p=0.0001). Estimated mean population densities for mussels 3, 6, 9, 12 m near Gull Island Shoal and at 4 m on a limestone slab at Niagara Reef did not differ significantly. The mussel population density on gravel at 4 m at Niagara Reef was 75% lower than that of adjacent mussels on the side of a slab (p=0.01). The locations at the mouth of the Sandusky River near Bay Point Shoal had both the highest and lowest mussels densities in my survey (Table 4). The mean population density of mussels on the side of a boulder at 3 m near Bay Point was almost double that of mussels on the adjacent mud-sand substrate and both were significantly higher than any other locations (p=0.0001).

Estimated mean population biomasses varied more with location than did densities (Table 4). The mussel population on the side of a boulder at 3 m near Bay Point Shoal at the mouth of the Sandusky River had a higher biomass than any other location (p=0.0001). Although biomass estimates were similar for mussel populations at 4 m on a slab at Niagara Reef and at 3 m on mud-sand near Bay Point Shoal, the population density of the Bay Point mussels was twice that of the Niagara Reef mussels. Similarly, population biomass estimates for mussels on a limestone slab at 3 m and a boulder at 9 m near Gull Island Shoal did not differ significantly from biomass estimate for mussels on gravel at 4 m on Niagara Reef. However, the population densities at the
two Gull Island collection sites were almost three times that of the Niagara Reef population. Biomass estimates may be more reliable indicators of mussel population success than density estimates since population biomass represents the integrated results of mussel consumption, survival, and growth.

In preparing the shell length-dry soft tissue mass regressions (Table 5) I actually measured both parameters for 948 mussels. These mussels ranged in size from 2.8 to 32.6 mm and the mean sized individual had a shell length of 14.5 mm (SE = 0.19 mm) while mean biomass was 9.8 mg (SE = 0.30 mg) and ranged from 0.1 to 60 mg dry mass.

To allow me to test for the effect of habitat on size distribution differences among habitats, I compared the regressions of the lengths of all 6501 mussels surveyed on 19 August 1993 and their estimated dry mass for a location effect (ANCOVA, p = 0.0001, mean shell length = 11.1 mm, mean biomass = 3.0 mg dry mass), I found that biomass of a mean-sized mussel differed significantly at all locations except for mussels from Gull Island Shoal at 9 m on rock and Niagara Reef at 4 m on gravel. At Gull Island Shoal locations, mean biomass of a 11.1 mm mussel increased from 2.4 mg on a slab at 3 m to 3.3 mg on the side of a boulder at 6 m and then generally decreased with increasing depth from 3.0 mg on a rock at 9 m to 2.7 mg on adjacent mud-sand bottom to a minimum of 2.2 mg at 12 m (p=0.0001). At Bay Point Shoal a 11.1 mm mussel at 4 m on the side of a boulder had a mean biomass of 3.6 mg while on adjacent mud-sand bottom mean biomass was only 3.4 mg (p=0.0001). At Niagara Reef a mean size mussel on limestone slab had a mean biomass of 3.0 mg while adjacent mussels in gravel had a greater mean biomass of 4.0 mg (p=0.0001). However, differences may be due to the fact that the Niagara Reef mussel population found on gravel had a skewed size
frequency distribution with more larger and heavier mussels and fewer mussels less than
10 mm than did the population on the adjacent slab.

Although I did not survey my permanent study sites on the same date as the other
1993 survey sites I compared the mussel population densities and biomasses from 3 m
on Peach Point Reef from 9 September 1993 (Table 2) and at the 12 m open channel site
at the U.S. Navigational Buoy (Red Can) on 31 July 1993 (Table 4) with the 14 August
1993 survey mussel populations. Both of my permanent study sites had higher mussel
population densities (p <0.02) and soft tissue masses (p <0.008) (Tables 2, 4) than all
other surveyed mussel sites except the 3 m boulder collection site at Bay Point Shoal.
There was no difference in mussel population densities between either of my permanent
study sites and the 3m mud-sand site at Bay Point Shoal (Tables 2, 4). While the mussel
population biomass at the 12 m Red Can site (mud substrate with scattered rocks) did not
differ from that at the 3m mud-sand site at Bay Point Shoal, the Peach Point Reef 3m site
had a higher population biomass (p=0.0001). In addition to experiencing increased
turbulent mixing due to its location at the mouth of the Sandusky River, the Bay Point
Shoal site may have higher algal availability due to nutrient loading from the adjacent
watershed. The higher densities and biomasses of mussel populations at Peach Point
Reef and Bay Point Shoal suggest that increased turbulent mixing may be more important
than substrate type or depth in determining zebra mussel population characteristics.

DISCUSSION

Smallest Scale Studies: Intraspecific Competition within the Mussel Bed

My observed zebra mussel population densities were higher than those reported
for European mussel populations that generally stabilize at 100-1100 individuals • m⁻²
(Kornobis 1977, Stanczykowska 1977, Stanczykowska et al. 1988, Reeder et al. 1989,
Bij de Vaate 1991). In European lakes zebra mussel population density may exceed 100,000 • m^2 in favorable environments (Wiktor 1963, Mackie et al. 1989). By May 1994 it was not clear whether the Peach Point Reef mussel population had stabilized, but finding similar densities again in 1998 suggests that it has. European zebra mussels generally live only a maximum of 5 to 7 years so there may have been insufficient time since initial colonization for stabilization to occur (Stanczykowsa 1977). However, it is clear that the shallow water, hard substrate zebra mussel population on Peach Point Reef is no longer expanding and almost one-third of the population has been replaced by quagga mussels. The source of quagga mussels is unknown, but they probably came from adjacent deep water areas. Wilson et al. (1999) report quagga mussel dispersal in the Great Lakes seems to be characterized by a gradual diffusion from its point of introduction. In late Oct. 1993 both mussel types were present in a qualitative sample taken from hard substrate at 8 m off the northern end of Peach Point Reef, but zebra mussels were overwhelmingly, numerically dominant. Significantly, the quagga mussels included individuals large enough to have spawned during summer 1993 (mean= 14.7 mm, range 5.5 to 30.6 mm) (R. A. Pontius and A. Stoeckmann, unpubl. data). Whether or not the quagga mussels will out-compete the zebra mussels at this shallow water site is unknown. Others report that quagga mussels densities increase with depth and frequently exceed zebra mussels in abundance at depth >10 m (Dermott and Munawar 1993, Mills et al. 1993) while zebra mussels are predominant in depths from 2-10 m (Stanczykowska 1977). Mitchell et al. (1996) found high quagga densities at a shallow site at Nanticoke in Lake Ontario and suggest primacy of settlement may determine which mussel will be predominate rather than depth or water temperature. The invading mussels will rapidly colonize available hard substrate (Morton 1969, Lewandowski 1982) including the shells of native bivalves (Mackie 1991, Haag et al.
Zebra mussels appear to have invaded the Great Lakes prior to quagga mussels in most locations (Mills et al. 1993). Therefore, if primacy of settlement is the important factor, then zebra mussels should continue to dominate the 3 m Peach Point Reef site. However, if competition for food rather than space is driving the dynamics of the Peach Point Reef mussel populations, then the consequences of interspecific competition are unclear. It is not yet known whether or not the grazing impact of the two mussels differ or whether any other differences will affect the impact of benthic mussel populations on pelagic algae.

Phytoplankton and zebra mussel population dynamics may also limit zebra mussel impact in a lake. Phytoplankton populations species composition and biomasses change seasonally, providing a variable food quality for grazers. A mussel population is also dynamic; population density, biomass, and size structure change during the year due to variation in the timing of reproductive events, environmental factors, and the accessibility of food. Therefore, what impact, if any, have changes in the mussel population had on pelagic algae? If zebra mussels have an effect on pelagic algae as others have predicted, changes in the mussel population should be reflected in phytoplankton dynamics even when taking seasonality into account. Seasonal phytoplankton successional patterns typical of northern temperate lakes without zebra mussels (Kalff and Knoechel 1978, Sommer et al. 1986, Lampert et al. 1986, Vanni and Temte 1990) have persisted after mussels became established and expanded on Peach Point Reef. Diatom abundance increased in the fall when mussel population densities were highest. Zebra mussel grazing did not overwhelm phytoplankton production as predicted nor did zebra mussels prolong the clear-water phase.
Medium Scale Experiments: Turbulent Mixing Effects in the Water Column

Most food is transported horizontally in the low flow water near the bottom (Muschenheim 1987). Vertically settling seston becomes potential food only when it enters this boundary layer. A strong food concentration gradient develops with a localized depletion zone nearest the bed when filter-feeding organisms remove seston faster than vertical mixing and horizontal advection replenish it (Wildish and Kristmanson 1984, Frechette et al. 1989, Monismith et al. 1990, O’Riordan et al. 1993). Several researchers document a decrease in phytoplankton concentration near benthic filter feeders in field experiments (Buss and Jackson 1981, Frechette and Bourget 1985a,b, Peterson and Black 1987, Frechette et al. 1989, Peterson and Beal 1989) as well as in laboratory experiments (Wright et al. 1982, Wildish and Kristmanson 1984). Hydrodynamic sorting also occurs with denser inorganic particles more abundant closer to the bed and lighter organic particles more abundant above the bed (Muschenheim 1987). Thus, the vertical feeding height attained by an organism (Jumars and Nowell 1984, Monismith et al. 1990) and the orientation of a bivalve's siphons (Monismith et al. 1990) can determine the concentration and quality of its food supply and its rate of growth (Frechette 1985b, Frechette et al. 1989). Local food depletion and high population densities are associated with reduced growth in the benthic suspension-feeding bivalves Mercenaria (Peterson and Beal 1989) and Mytilus edulis (Kautsky 1982). Roughness (form drag) associated with mussel shells and the formation of aggregate colonies (hummocks) may increase mixing in these depleted bottom layers and thus, increase the supply of food to the mussel bed (Frechette et al. 1989). In western Lake Erie MacIsaac et al. (1992) measured a zone of phytoplankton depleted water extending 1.25 m about zebra mussel beds. MacIsaac et al.(1999) found
that chlorophyll a concentrations were similar above 1.85 m from the lake bed, decreased closer to the lake bed, and were lowest adjacent to the bottom suggesting the development of a concentration boundary layer above mussels. In the present study the concentration boundary layer extended less than 1.0 m above the bed yet the growth of caged mussels within the concentration boundary layer was significantly lower than that of mussels out of the concentration boundary layer.

Zebra mussel growth is an indirect measure of mussel impact. Food consumed must first provide energy for an animal’s maintenance costs to ensure survival. Stoeckmann (personal communication) found that Lake Erie zebra mussel maintenance cost may be 94% or more of consumption leaving little energy available for growth. While growth may be both somatic and reproductive, I directly measured only somatic growth in my experiments. Changes in reproductive condition reflecting production of gametes and spawning are reflected indirectly in both mussel survival and biomass data. In poikilotherms maintenance costs vary with temperature and food quantity and quality. The quantity and quality food available to zebra mussels is dependent on mixing characteristics within the water column transporting food to the mussel beds as well as competition with adjacent mussels for food. In thermally-unstratified western Lake Erie, summer temperature variations were small, therefore, the rate of seston transport to benthic zebra mussels and intraspecific competition were more important in determining mussel growth.

The underlying assumption that benthic mussels have access to algae in the entire water column and would have the same quantity of food as mussels suspended higher up in the water column is inappropriate. Overall, caged zebra mussels’ growth patterns with depth were similar even when starting date and duration of the experiment varied; growth of mussels in cages at or near the bottom was only one-third of that of mussels
higher up in water column. At higher density (2500 m$^{-2}$), caged mussels at or near the bottom grew less than mussels at lower density at the same depth while mussels higher up in the water column had similar growth regardless of density. Mussels in bottom cages were more likely to lose biomass during experiment and had lower final biomasses than mussels in cages above them, but had higher final biomasses and growth than the natural lake population. Benthic mussels may have either less food available or lower quality food than mussel suspended in cages higher up in the water column, but my results suggest that competition with adjacent mussels for available food resources is an important factor in limiting mussel growth.

The initial decrease in shell growth rates of mussels (LAB) of all sizes in August may be due to high water temperatures and low food availability (Walz 1979). In laboratory experiments, Walz (1978a, b) found that at higher temperatures, larger mussels required relatively greater concentrations of food than did smaller mussels. However, all sizes of my experimental mussels (LAB) showed declining growth rates in mid-September when phytoplankton abundance was increasing due to fall diatom production. Sprung (1995) reports that shell growth only occurred at temperatures above 20$^\circ$C and that mussels show declining growth rates in late summer below 20$^\circ$C. Bij de Vaate (1991) reports zebra mussel growth during periods of rising, but not falling temperatures. Adult mussels lost weight during the overwinter period ending in March and did not resume growth when phytoplankton production increased in the spring (Walz 1978b).

The survival and growth of caged mussels in thermally-stratified Hargus Lake were strongly influenced by their location within the water column; the degree of turbulent mixing within the water column affects not only algal production and distribution with the lake, but the metabolic environment of the caged mussels. In
Hargus Lake I saw the effects of temperature on survival and growth where some mussels survived at 8 m, but none survived at 6 m. The zebra mussels collected from Lake Erie in late April had probably begun gametogenesis (unpublished data) before I placed them in Hargus Lake. Sprung (1989) reports that spawning generally begins at 12 °C, but may occur at lower temperatures. Water temperatures at 8 m did not rise above 8 °C during my experiment while temperatures at 6 m were between 10 and 12 °C during July. It is likely that mussels at 6 m spawned while those at 8 m did not.

There are energy costs associated with spawning; Haag and Garton (1992) report that spawning in Lake Erie mussels is associated with 50% drop in body mass. If mussels at 8 m did not spawn, the reproductive reserves may have served as additional energy resources that enabled some of the larger mussels at 8 m to survive. Survival of larger mussels at 8 m may also reflect the fact that mussels at the lower temperatures have lower maintenance costs (Walz 1978a) and larger mussels have lower metabolic rates (Quigley et al. 1993).

**Largest Scale Study: Regional Differences in Transport Processes**

Mussel populations at several of my survey locations had similar population densities perhaps reflecting development of stable population size or just the simple geometry of packing a maximum number of differently-sized individuals in a given space combined with self-thinning due to competition with adjacent mussels for food (Hughes and Griffiths 1988). However, I could not determine from my single survey date data whether or not western Lake Erie mussel population densities had stabilized in these locations.

Differences in biomass at my survey sites suggest that not all locations represent equally successful habitats for zebra mussels. Hard substrate mussel populations and populations that gain feeding height above bottom may be able to access more food or
minimize the effects of sediment resuspension and refiltration of food-depleted water. Less optimum substrates may be mud or sand and lower biomasses may be related to variation in food availability or in food quality. Soft sediments generally represent a low energy environment characterized by less turbulent mixing in the water column and lower transport of food to mussels. Decreased food quality may reflect decreased organic content due to refiltration of water depleted by adjacent mussels or by the presence of lower energy value dead or senescent phytoplankton cells. During storm events, soft sediment may be resuspended increasing the proportion of inorganic material in the water column. In the aftermath of a storm zebra mussels may have to use more energy handling a lower quality seston containing inedible material and requiring increased pseudofeces production thus, leaving less energy available for growth than mussel population on hard substrates. However, sand may provide a unstable environment lacking substrate large enough for stable attachment and thus, requiring animals to use more energy to maintain position. When mussel clusters are moved about in a sand environment mussels may obtain less food as they are alternatively shifted to face substrate and water column.

Although densities were similar in several of my survey locations, population biomasses differed greatly reflecting differences in food transport to mussel beds due to variation in water currents or vertical mixing within the water column that could replenish food depleted bottom water (Peterson and Beal, 1989). For any specific location the relative position of mussels within the densely packed clumps may determine their feeding success and growth (Pullen and LaBarbera 1991). Mussels may gain an advantage in feeding by being raised slightly above the surrounding terrain or settling in a higher energy environment. A higher energy environment may have greater horizontal advection or turbulent mixing in the overlying water column, thus, enhancing food
transport to locally-depleted bottom water above mussel beds. Additionally, the nearshore region at the river mouth characteristically represents a highly productive area due to nutrient-enriched water from agriculture runoff in the watershed.

Stanczykowska (1977) reports that larger and heavier zebra mussels are associated with lower density and more eutrophic zones. In contrast, I found that the heaviest mussels were also at the highest density, but their location in an area of river discharge suggests that water currents may enhance food transport to mussels. Similarly, Bij de Vaate (1991) observed that zebra mussels in areas experiencing greater water currents (e.g., areas receiving IJssel River discharge) had greater maximum shell lengths than did mussels in other areas of the same lake and that mussels were generally heavier in higher flow environments (Bij de Vaate et al. 1992). Neuman et al. (1993) also found increased shell growth in higher flow environments. Smit et al. (1993) reported that water movements had a greater effect on mussel growth in shallow, eutrophic Dutch lakes than did food concentration. Increased flow may increase vertical mixing in the water column and the transport of suspended particulate matter to beds to suspension feeding bivalves (O’Riordan et al. 1993; Lenihan et al. 1996). The higher densities and biomasses of mussel populations at Peach Point Reef and at the Sandusky River mouth suggest that increased turbulent mixing may be more important that substrate type or depth in determining zebra mussel population demographics.

**Implications for zebra mussel impact assessments**

Researchers making zebra mussel lake clearance calculations have generally worked in shallow, thermally unstratified lake environments using densities of mussel populations found on hard substrates. There they assume a well-mixed, homogenous water column in which algae are completely accessible to benthic mussels and extrapolate clearance rate values or equations from European mussels (Stanczykowska 1977, Kryger
and Riisgard 1988, Reeders et al. 1989) to the entire volume of the lake ignoring physical and biological factors affecting the delivery of pelagic algae to the local benthos.

Furthermore, current impact assessments ignore patchiness in the environment and generally assume a uniform distribution of mussels across the lake bottom and extrapolate density estimates from very small total areas of the lake bottom to the entire lake. However, in my limited, one day Lake Erie survey I found that zebra population densities and soft tissue masses varied on different substrate types and at different depths. Furthermore, both soft tissue biomass and size-frequency distributions varied for populations of similar sizes. High density colonies of zebra mussels are typically found in generally well-oxygenated areas and at depths < 0 m (Morton 1969, Lewandowski 1982). Preferred habitats include almost any hard substrate, but may also include aquatic macrophytes, Dreissena adults, and native mollusks (Lewandowski 1982). Less than 14% of western Lake Erie is hard substrate and most of the western basin west of the Bass Islands consists of large mud flats (Herdendorf 1970). Although the mud flats represent less favorable habitat for the development of large mussel populations, these regions of lower turbulent mixing may serve as source of phytoplankton that can be transported to areas with larger mussel populations. Horizontal advection can transport algae long distances via currents from areas where algae production is higher to areas where mussels do deplete local resources. Therefore, availability of preferred hard substrate and the heterogeneity of the lake bottom need to be included in modeling efforts in order to obtain a more real world estimate of mussel impact.

Zebra mussel filtration varies with food quality and quantity (Stanczkowska et al. 1976, Stanczkowska 1977). In field measurements of filtration rates Reeders et al. (1989) found that seston concentration is more important in determining filtering rates in
zebra mussels than is temperature. In the range of 5 to 20°C Reeders et al. (1993) found that mussel filtration rates and pseudofeces production were determined by seston concentration. *D. polymorpha* has a maximum filtration capacity at low food concentrations and a maximum ingestion capacity at high food concentrations (Sprung and Rose 1988). Many of the current impact estimates use the size-specific filtration rate equation generated by Reeders et al. (1989) or Kryger and Riisgård (1988). Reeders’ equation is based on zebra mussel filtration behavior in shallow, turbid, hypereutrophic polder lakes in the Netherlands. The hypereutrophic Dutch lakes used in the actual in situ zebra mussel filtration studies have a mean depth of <2.0 m (Lake Woldewijd 1.5 m, 2600 ha; Lake Veluwemeer 1.4 m, 3400 ha) (Reeders et al. 1989, Reeders and Bij de Vaate 1990). Even the large, eutrophic Lake IJsselmeer has a mean depth of only 4.5 m while in the smaller, eutrophic Lake Markermeer depth varies from 2.5 to 4.5 m (Bij de Vaate 1991). In these lakes there is sufficient wind-driven turbulent mixing of the shallow water column and low zebra mussel densities (< 1000 m⁻²) that it is unlikely that a thick concentration boundary layer would develop. Thus, in these unique environments the assumption of a homogenous water column in which turbulent mixing is constantly replenishing seston above mussel beds may be justified, but of questionable value to understanding north temperate lakes.

Generally seston concentrations for shallow, hypereutrophic Dutch lakes far exceed those reported in North America lakes today as well as the higher seston concentrations previously reported in western Lake Erie in the late 1960s. The shallow, hypereutrophic Dutch lakes used in zebra mussel filtration rate studies had seston concentrations ranging from 5 to 79 mg L⁻¹ in 1985 and 17 to 36 mg L⁻¹ in 1988 (Reeders and Bij de Vaate 1990). In 1970 even the eutrophic, shallow western basin of
Lake Erie (mean depth of 7.4 m) had mean seston concentration of 5.3 mg L\(^{-1}\), ranging from 3.3 to 7.1 mg L\(^{-1}\) (Munawar and Munawar 1976). At the same time Lake Erie’s eastern and central basin mean seston concentrations were much lower, 2.4 mg L\(^{-1}\) and 3.2 mg L\(^{-1}\), respectively. During 1992 at my western Lake Erie 5 m site mean seston concentration was 4.0 mg L\(^{-1}\) and ranged from 2.4 to 6.1 mg L\(^{-1}\). In Lake Huron the shallow (mean depth 5.1 m), nutrient-rich inner Saginaw Bay had seston concentrations ranging from 2.5 to 18.7 mg L\(^{-1}\) in 1992 and 1.0 to 7.0 mg L\(^{-1}\) during 1993. While in the deeper (mean depth 13.7 m), colder, more nutrient-poor outer Saginaw Bay seston concentrations ranged from 1.5 to 2.8 mg L\(^{-1}\) in 1992 and 0.6 to 6.3 mg L\(^{-1}\) during 1993 (Fanslow et al. 1995). Only after storm events did maximum seston concentrations approach those reported for the Dutch lakes. In the hypereutrophic lakes in the Netherlands pseudofeces production increases linearly with increasing seston concentration (Reeders and Bij de Vaate 1990). A large portion of the seston consists of material that zebra mussels find refractory resulting in increased pseudofeces formation as the mussels process inedible material (>90% of excreted solids are as pseudofeces) (Reeders and Bij de Vaate 1990, 1992). Thus, zebra mussel filtration behavior in shallow, hypereutrophic Dutch lakes may not be representative of mussel behavior in North American lakes.

Bioenergetics models are potentially valuable in estimating zebra mussel impact, but have been limited by difficulties in obtaining appropriate, contemporaneous baseline data for energy budget parameters in the model, and by some of the simplifying, underlying assumptions. Modifying a fish bioenergetics model and using a variety of sources of data, Schneider (1992) produced the first zebra mussel bioenergetics model. Other researchers modified the bioenergetic model by incorporating more recent zebra
mussel data for model parameters (Madenjian 1995) and by investigating the effect of different zebra mussel population length-frequency distributions on model predictions (Young et al. 1996). Stoeckmann (1997) further improved bioenergetic modeling efforts by directly measuring energy budget variables on zebra mussels in western Lake Erie rather than relying on limited data available from other sources and species. However, all these modeling efforts assume a homogeneous, well-mixed water column with all phytoplankton production completely accessible to sedentary zebra mussels and ignore factors affecting the transport of pelagic algae to benthic mussels. Additionally, zebra mussel bioenergetics models are still limited by the lack of current primary productivity data. Madenjian (1995) had to modify $^{14}$C primary productivity data from the 1970s using data on phytoplankton abundance from the early 1980s to approximate primary production available to zebra mussels and Stoeckmann (1997) made similar approximations.

With a better understanding of zebra mussel biology and ecology and an increased awareness of the effects of hydrodynamic processes on the delivery of algae to benthic zebra mussels, progress is being made in making more realistic estimates of mussel impact on pelagic ecosystems. MacIsaac et al. (1999) consider hydrodynamic transport processes in the development of a model to provide a better mechanism to estimate zebra mussel impacts in western Lake Erie. Bailey et al. (1999) in assessing their models of zebra mussel impact acknowledge the importance of scaling issues when they express concerns about extrapolating from individual filtration rates in small containers to lake-wide processes. Additionally, they appropriately identify the need to consider the role of vertical and horizontal transport processes occurring within the lake on development of future models of mussel impact on lake ecosystems. Clearly, the results of my study provide evidence supporting the viewpoint that any evaluation of the
impact of mussels on pelagic food web dynamics has to incorporate a fundamental understanding of the role of physical-biological coupling within the system.
CHAPTER 2

ESTIMATING ZEBRA MUSSEL IMPACT ON PELAGIC FOOD WEBS: THE ROLE OF SIZE-SPECIFIC GRAZING RATES

INTRODUCTION

Aquatic ecosystems are intricate and dynamic; any major alteration in an existing ecosystem can have a significant impact on other communities of that ecosystem. The impacts of the accidental introduction of the European zebra mussel, Dreissena polymorpha, through increased grazing, benthic biomass, and nutrient excretion are potentially very great, but estimating impact accurately is very contentious.

Most estimates of zebra mussel impact on the pelagic community are calculated by extrapolations of a combination of laboratory-based filtration (clearance) rates and field-based population density estimates which are then used to calculate the time required for the entire water volume to be filtered (Reeders et al. 1989, Hebert et al. 1991). MacIsaac et al. (1992) and Bunt et al. (1993) estimated that zebra mussels could potentially clear the entire western basin of Lake Erie of algae several times daily. However, such assessments overestimate mussel impact because they assume that currents and turbulent mixing give benthic zebra mussels access to algae from the entire water column and that mussels do not refilter water that has been previously cleared of particles. Comparisons of published clearance rates for D. polymorpha are limited by the
lack of data on seston, mussel biomass, and mussel density, which further complicate impact projections in field populations.

Previous estimates of filtration rates for *D. polymorpha* vary and are based on a closed laboratory system in which the mussel filters an enriched supply of food that it depletes exponentially over a short time period. These clearance rates are commonly measured indirectly as the volume of water completely cleared of particles by an individual in a given time period (Coughlan 1969). Furthermore, these lab-based estimates of *Dreissena* clearance rates vary widely (5 - 180 ml • ind⁻¹ • hr⁻¹ for a 22 mm shell length mussel), use a variety of inorganic materials or algal monocultures as food, and are almost exclusively for adults in a narrow size range (Morton 1971, see review in Walz 1978a Dorgelo and Smeenk 1988, Reeders et al. 1989). Kryger and Riisgård (1988) have generated a clearance rate regression equation for *Dreissena* over a range of body sizes, using laboratory determinations of clearance rate on *Chlorella*. They found filtration rates varied 50-fold over the range of body sizes used. Unlike other researchers, Stanczykowska et al. (1975, 1976) and Stanczykowska (1977) measure in situ zebra mussel grazing rates (mass of seston removed • ind • d⁻¹) using natural seston and ambient temperature for a range of body sizes.

Filtration rates of *D. polymorpha* vary with temperature, seston concentration, and food size. In field measurements of clearance rates Reeders et al. (1989) found that suspended matter content was more important in determining filtering rates in zebra mussels than was temperature; temperature sets only the gross level of seasonal filtration rate. However, zebra mussel grazing rates vary with quality and quantity of seston available (Stanczykowska et al. 1975, 1976, Stanczykowska 1977). Stanczykowska (1977) found that blooms of larger phytoplankton forms can inhibit filtration activity.
D. polymorpha has a maximum filtration capacity at low food concentrations and a maximum ingestion capacity at high food concentrations (Sprung and Rose 1988).

D. polymorpha feeds on phytoplankton and bacteria by filtering out all particulate matter and then rejecting inappropriately sized or inorganic material combined with mucus to form pseudofeces that are ejected via the incumbent siphon (Ten Winkel and Davids 1982, Sprung and Rose 1988). One way that adult zebra mussels can impact the pelagic food web is through selection of specific size ranges of phytoplankton and rejection of inappropriate sizes via pseudofeces formation. Size-selective grazing by Dreissena adults may decrease the abundance of appropriate sized phytoplankton otherwise suitable for smaller zooplankton or for zebra mussels' own larvae.

My assessment of the impact of D. polymorpha on pelagic communities requires knowledge of seasonal, size-specific zebra mussel grazing rates. Therefore, I have measured size-specific grazing rates using a flow-through system delivering ambient lake water and seston over 24 h (adapted from Stanczykowska et al. 1975, 1976, Stanczykowska 1977). Because the flow is continuous, food is constantly replenished, so grazing estimates are near their theoretical maxima. I used this system to evaluate the effects of density, flow rate, reproductive condition, and environmental influences such as temperature, seston concentration, and sediment resuspension on size-specific zebra mussel grazing.

However, improved size-specific grazing rate estimates are not sufficient to evaluate mussel impact on pelagic food webs. Natural populations of zebra mussels typically exist as densely-packed aggregates (druses) of individuals of many sizes attached to one another and the substrate. Some mussels on the surface of a druse may feed efficiently while others within are deprived (Peterson and Beal 1989, Pullen and Labarbera 1991). In this study, I tested for the effect of intraspecific competition on
individual grazing rates by measuring whether grazing rate varied for mussels feeding in clumps as compared to that predicted based on of the same size and number of detached mussels feeding individually. I combined estimates of size-specific grazing rates for separated individuals and clumps of mussels with population demographics to re-evaluate mussel impact on the western Lake Erie pelagic food web.

MATERIALS AND METHODS

Study Site

Lake Erie

All mussels used in size-specific grazing experiments were collected from the 3 m permanent population dynamics study site on Peach Point Reef (Chapter 1, Figure 1). Mussels used in the experiment to test for sex differences in mussel grazing rates were collected using an otter trawl from 8 m in Stone Cove on the northwest side of South Bass Island. I used the lakeside facilities of F. T. Stone Laboratory field station for the laboratory grazing experiments.

Basic Grazing Experimental Setup

At Lake Erie, I measured size-specific zebra mussel grazing rates under near natural conditions using a flow-through system modified from Stanczykowska et al. (1975, 1976), Stanczykowska (1977). A 1 L Imhoff cone was equipped with a lid and both inflow and outflow tubing attached to L-shaped glass tubes to form each grazing chamber (Fig. 16). Although I placed mussels on a plastic mesh screen (3 mm opening), mussels were free to move about in the upper 1/3 of the cone. A small glass vial was attached to the lower end of each cone to collect sedimenting seston and any feces or pseudofeces produced by the mussels. Natural lake seston drawn from 15 cm above the lake bottom was pumped into a 20 L central supply reservoir and allowed to overflow
uniformly into a 400 L aquarium in which the cones were suspended. Using a suction holder I attached the inlet tube for each cone to the inside of the supply reservoir so that the tube opening was 1-2 cm below the rim. The overflowing lakewater supply reservoir thus provided both a continuous supply of natural seston to the chambers and held the mussels at ambient lake water temperatures. I used two calibrated ten-channel peristaltic pumps (Manostat Corp.) to pump lake water from the supply reservoir through the 20 chambers. The flow rate through the chambers could be set using the variable speed pumps (100 to 490 ml • h⁻¹). I collected all lake water pumped through each chamber in separate 20 L buckets. I used a 24 h duration for all experiments to avoid the effects of diurnal variation in mussel grazing activity associated with different starting times. To prevent algal growth during the 24 h experiment I minimized lighting by using covered, opaque collection buckets, shades to prevent direct sunlight exposure, and subdued artificial lighting when necessary.

Generally mussels were collected from the Peach Point Reef 3 m site the same day as the experiment. Occasionally mussels attached to rocks were held for 2-3 days in large wall aquarium (400 L) receiving continuous flow through lakewater. For each experiment mussels were gently removed from rocks, separated from each other, and rinsed with lakewater to remove mud and rock debris. After discarding any detached mussels with damage to byssus or shell I pooled mussels taken from all the rocks collected. At this time I froze a size range of mussels from the pooled population for use in the population dynamics portion of my research (Chapter 1, Table 3). Next I selected at least 25% more mussels than I needed for my experiment and sorted them into size classes and treatment groups and held them in filtered (Whatman GF/C), aerated lake water for 5-6 h before the experiment to detect any additional damaged mussels and to allow time for any production of feces or pseudofeces associated with feeding prior to
the experiment. At the end of the 24 h experiment the animals were removed from each chamber and held in individual containers of filtered lakewater (250 ml) for 5-6 h to release any feces associated with grazing during the experiment. I then removed the mussels and froze them for later determination of soft tissue mass (methods in Chapter 1). I allowed 12 h for any feces, pseudofeces, and sedimenting seston produced during the experiment to settle from the grazing chamber into the collection vial at the bottom of the Imhoff cone. Using tared, 0.45 μm pore size membrane filters for each chamber and replicate distilled water blanks I filtered the combined contents of each vial and the corresponding container of water in which mussels had been held post-experimentally. All filters were dried at 65 °C for 24 h before reweighing. To determine whether mussel activity altered the relative organic and inorganic fractions of seston sedimenting out of the grazing chamber I ashed the filters containing feces, pseudofeces, and sedimenting seston at 550°C for 30 minutes and calculated the organic fraction of the seston as ash-free dry mass.

I measured the volume of water collected during the 24 hour period, typically 7 to 8 L at 300 ml • h⁻¹ flow rate, and determined the seston concentration (mg dry mass • L⁻¹) for both experimental and control (no mussels) buckets by filtering well-mixed, replicate subsamples (250 to 500 ml) and distilled water blanks through tared, 0.45 μm pore size membrane filters. All filters were dried at 65 °C for 24 h before reweighing.

I calculated grazing rate (mg dry mass • ind • d⁻¹) as mg dry mass of seston removed by individual mussels (or clumps) during 24 h (Stanczykowska et al. 1975, Stanczykowska 1976, 1977). In this continuous, flow-through system the mean seston concentration of the controls (no mussels) represents concentration of seston available to mussels feeding in all chambers. After adjusting for any small differences in the volume
of lakewater passing through each chamber the difference between the mass of all seston available for grazing and the seston remaining in each experimental treatment (mussels) collection bucket represented the mass of seston removed by mussels feeding in the experimental chambers during the 24 h period. Daily clearance rates (L • ind • d⁻¹) were calculated from grazing rates by dividing by the mean control seston concentrations.

Zebra mussels typically occur in high densities and as natural aggregations of many individuals of different sizes. Depending on a mussel’s location within a clump, its ability to orient its inhalant siphon and obtain food may be restricted or refiltration may be increased. My experimental design allowed detached mussels greater access to seston than they would normally experience in a lake. Therefore, I needed to adjust the number of mussels relative to the flow rate through the experimental chambers so that I had enough mussels in each chamber to obtain a measurable depletion of seston and still reflect the size-frequency distribution of the lake mussel population. In my 1991 experiments I thus sorted mussels into non-overlapping size classes based on shell length and measured grazing rates for different mussel densities in five different size classes, e.g. the 15-20 mm size class = 15 mm ≤ shell length (SL) < 20 mm included mussels between 15.0 and 19.9 mm shell length. Based on my 1991 preliminary grazing experiments I set the number of mussels of each size class used in 1992 and 1993 experiments as follows: 5-10 mm size class, 25 mussels between 5 and 9.9 mm; 10-15 mm size class, 15 mussels between 10 and 14.9 mm; 15-20 mm size class, 10 mussels between 15 and 19.9 mm, and 20-25 mm, 5 mussels between 20 and 24.9 mm.

In a typical experiment I used 20 grazing chambers four of which had no zebra mussels and served as controls and the remainder were four replicates for each of four size classes. I used a random number generator to determine grazing chamber treatment
assignment. I used the General Linear Model (GLM) Analysis of Variance (ANOVA) (SAS Institute Inc. 1989) to test for significant treatment effects (e.g., mussel density, seston delivery rate, clay, reproductive condition).

Grazing Experiments

Density: Competition for space and food

To test for the effect of intraspecific competition on individual grazing rates I tested whether grazing rates for mussels of the same size varied with mussel density. I measured grazing rates for 22 mm detached mussels at different densities (0, 5, 10, 20, 40 mussels • chamber⁻¹, equivalent to 0 to 8,500 • m⁻²) with 4 replicates.

Density: ‘Clump Effect’

To evaluate the role of intraspecific competition and refiltration in using grazing rates to predict larger scale clearance rates of a mussel population in a lake, I measured whether grazing rate varied for mussels feeding in clumps as compared to that predicted based on of the same size and number of mussels feeding individually.

In 1992 and 1993 I measured size-specific grazing rates for detached mussels in 4 size classes at densities reflecting natural distributions and for attached mussels in clumps (10-15 g wet mass, 20-60 mussels per clump). At the end of the experiment I separated the clumps of zebra mussels and measured the lengths of all animals present before determining the soft tissue mass. I calculated size-specific grazing rates of separated individuals and for clumps of mussels. To estimate the effect of competition among individuals in clumps for seston I used the size-specific grazing rates I measured for each size class of separated individuals and the size frequency distribution of individuals in the clumps to predict a grazing rate for the clump as a whole. I then compared the predicted grazing rate for the clump to that actually observed for detached mussels during the same experiment.
Population Clearance Impact Estimates

I estimated the impact of zebra mussel population clearance rates for the hard substrate mussel population from Gull Island Shoal (Figure 1) using both population size-frequency and biomass estimates. To estimate August 1993 Gull Island population impacts I used the results of my September 1993 grazing experiments rather than my July 1993 experiments because I was able to measure grazing rates for post-spawning mussels including smaller, juvenile mussels 5-10 mm in the September experiment while in my July 1993 grazing experiment some mussels were still capable of spawning and there were not enough smaller-sized mussels available to measure grazing rates. I combined mussel soft tissue dry mass estimates for each Gull Island Shoal depth (Chapter 1, Table 5) with the clearance rate soft tissue dry mass regression from 16-17 September 1993 zebra mussel grazing experiment (individual size classes and clumps) to calculate a zebra mussel population clearance rate at each depth. I also calculated a population clearance rate estimate by sorting Gull Island Shoal mussels size-frequency distributions into the same size classes I had used in my experiments. Population clearance rate was estimated using the frequency of mussels in each size class and the mean individual size class clearance rates. For mussels < 5 mm or > 25 mm I used the mean clearance rate of the adjacent size class.

Factors affecting size-specific mussel grazing

Seasonal variations in seston composition

To test for seasonal differences in size-specific mussel grazing rates I measured grazing rates for detached mussels in four size classes at ambient temperature and seston concentrations from May to Sept. With this system I also tested how algal delivery rate, reproductive condition, and environmental influences such as sediment resuspension affected size-specific zebra mussel grazing.
In the lake, mussel grazing rates are dependent upon factors affecting the delivery of phytoplankton to benthos. To evaluate the effect of differences in algal delivery rates I measured size-specific grazing rates for mussels in four size classes when water was pumped through the chamber at different rates. Because each pump controlled ten chambers I could set up my 20 chambers so that half of the replicates for each size class and control had lake water pumped through at one selected flow rate and the other ten chambers at a different flow rate, thus, altering the amount of available seston.

**Food Quality and Refiltration**

The quality and quantity of seston may affect grazing rates. Reeders et al. (1989) found that suspended matter content was important in determining zebra mussel clearance rates. Sediment resuspension associated with storm activity can alter the proportion inorganic and organic content of the seston and alter food quality and force mussels to refilter water previously cleared of particles. Mussels encountering increased levels of sediment may either cease filtering or continue filtering and increase pseudofecal production rates to remove excess inorganic material. I tested the effect of altering food quality through sediment resuspension by additions of clay during grazing experiments to simulate the effects of storm activity. I used a Y connector to split the inflow of lakewater so that I could fill two supply reservoirs simultaneously. I allowed the mussels to grazing undisturbed for 12 hours and then simulated storm activity by pulsing clay additions to only one of the supply reservoirs. After removing the supply hose from one 20 L reservoir I added 1 g reagent grade bentonite suspended in 150 ml lakewater. After 5 minutes I returned the supply hose to the reservoir and allowed the reservoir to return to normal use. I repeated pulsing 1 g samples of bentonite 5 more times at two hour intervals.
Reproductive Condition

Mussel soft tissue mass varies seasonally with growth, gametogenesis, and spawning. Haag and Garton (1992) report that in Lake Erie mussels, spawning is associated with a 50% drop in body mass. Although the physical act of spawning may limit mussel grazing activity, grazing may also be increased near spawning to meet associated energy demands. To test for the effect of reproductive condition on mussel grazing rates I measured individual grazing rates for individual mature mussels (22 mm) with only one mussel in each chamber. At the conclusion to the experiment I removed a small portion of gonadal tissue from each mussel prior to determining soft tissue dry mass. I examined the sample microscopically to determine the sex of each mussel and staged spawning condition. I used a gametogenic index to assess reproductive condition using a staging scale of 1 to 5 with stage 1 mussels having immature gametes and stage 4 “ripe” mussels having 50% fully mature gametes, e.g., sperm with tails or eggs with germinal vesicle, and stage 5 “spent” mussels with few mature gametes remaining (Borcherding 1991, Nicols 1993).

RESULTS

Density Effects: Competition for space and food

I measured individual grazing rates for single, mature mussels (n =14, mean size: 22.4 mm shell length, 55.8 mg dry soft tissue mass) during 23-24 June 1992 (19 °C). Mean individual mussel grazing rate was 8.4 mg seston • mussel⁻¹ • h⁻¹ (SE=1.25), equivalent to a clearance rate of 3.0 L • mussel⁻¹ • d⁻¹ (mean control seston concentration = 2.8 mg • L⁻¹). Even at these high grazing and clearance rates, mussels
consumed only 33% of the available seston and removed a mean of 51% of the organic matter present.

In nature, mussels rarely feed without competition for food with adjacent individuals so I tested the effect of density on grazing rates. During 21-22 Aug. 1991 (23 °C) I measured grazing rates for mussels (mean size 22 mm shell length, 16.9 mg dry soft tissue mass) at different densities (0, 5, 10, 20, 40 mussels • chamber⁻¹, equivalent to 0 to 8,500 • m⁻²). These mussels were detached from each other and free to move around the upper one-third of the grazing chamber. I observed a general trend of decreasing mean grazing rate with increasing density (Figure 17). Clearance rates generally declined with increasing density from a mean of 0.40 L • mussel⁻¹ • d⁻¹ for 5 mussels per chamber to 0.06 L • mussel⁻¹ • d⁻¹ when 40 mussels were present (Figure 17). Mean clearance rates for 5 mussels per chamber were significantly higher than clearances rates for 20 or 40 mussels per chamber (p=0.0336, p=0.0011). Mussels at all densities consumed 40% of the available seston and removed 30 to 44% of the organic matter present. However, mean mass-specific grazing rate (mg seston • mg mussel soft tissue⁻¹ • d⁻¹) did not vary significantly with density suggesting that observed differences in grazing rates were due to the number of individuals present rather than physiological differences in mussels.

Density: ‘Clump Effect’

During May, July, and Aug. 1992 and June, July, and Sept. 1993 I measured size-specific grazing rates for detached mussels in 4 size classes and at densities reflecting natural distributions. Simultaneously I measured grazing rates for attached mussels in clumps. Results from 12-13 August 1992 experiment (Table 6) are typical. Mean grazing rates for detached mussels increased with increasing mussel size. Using
mean size class grazing rates of detached mussels and the size-frequency distribution for individuals in the clumps, I calculated a predicted grazing rate for the clump as a whole and compared it to the observed clump grazing rate. The observed grazing rate was lower than the predicted rate in all cases (Table 6).

In experiments from May to September 1992 and 1993 I found that the mean grazing impact of mussel in clumps of 20-60 mussels was only 30% (range 21 to 47%) of what I predicted if the same sized mussels had been feeding detached from each other and free to move about the chamber (Table 7). In both years’ experiments, the greatest difference between observed and predicted grazing rates occurred in May or June and the least difference in August or September.

Population Clearance Impact Estimates

To extrapolate results of my clump experiments to field populations I used size-frequency distributions and population density estimates from my August 1993 survey of mussel populations in western Lake Erie (Chapter 1) and my observed size-specific mussel grazing rates. I estimated maximal clearance rates for four hard substrate field populations (Table 8) using both a shell length and a biomass approach (Figure 18). Although Gull Island Shoal had similar mussel population densities at different depths, 20,000 m², the population biomass differed significantly with depth (Chapter 1, Table 4). Therefore, I had expected that the biomass approach would produce the best estimate. Although clearance rates for both approaches were similar, those based on mussel biomass were always higher than those based only on mussel shell lengths (Table 8). The two estimates differed the least for the 3 m population perhaps reflecting the presence of a greater proportion of smaller and lighter, newly settled mussels < 3 mm (Table 4). The biomass based estimates take into account the actual individual mussel biomass while the shell length method grouped mussels by size class. However, since
other researchers are more likely to have mussel size-frequency distributions, the size
class approach may be more useful since it is easier to obtain field-based mussel size
frequency distributions than biomass estimates. In addition the shell length approach to
estimating population clearance rates parallels the method I used to predicted clump
grazing rates. Using the 30.8% value obtained from our grazing rate experiments with
small clumps as a correction factor for density or ‘clump effect’ on the Gull Island Shoal
population clearance estimates, I obtained corrected, much lower clearance estimates
ranging from 0.4 to 0.7 m³ • m⁻² • d⁻¹ (Table 8). However, these should still be
considered maximal estimates, because densities of 20,000 • m⁻² result in much larger
clumps of individuals competing for seston than 20-60 mussels in grazing experiment
clumps. In addition, mussels' access to seston is affected by environmental influences
such as sediment resuspension, water depth, topographic roughness, and by turbulent
mixing characteristics within the water column, all of which affect the rate of delivery of
particulate matter to zebra mussels.

Seasonal variations in seston composition

Difficulties in identifying the effects of seasonal variations in temperature and
seston concentration are compounded by changes in mussel body mass associated with
preparation for spawning in adult mussels. Because my grazing experiments used
ambient lakewater it was not possible to separately test the effect of varying temperature
and seston concentration on mussel grazing rates. From May to September, lake
temperatures ranged from 15 to 26.5 °C and temperature in the incubation aquarium
holding the grazing chambers was never more than 0.5 °C higher than lake temperature.
Mean seston concentration through the chambers ranged from 1.14 to 4.71 mg • L⁻¹
while whole water column lake mean seston concentrations ranged from 2.4 to 5.0 mg •
in 1992 at the sheltered Hatchery Bay 5 m site and from 1.3 to 7.9 mg • L⁻¹ in 1993 at the open channel 12 m site. Lower seston values measured in experimental control chamber most likely reflects the fact that chamber received water pumped from 0.15 m above the bottom. Although the separate effects of temperature, seston, and mussel condition could not be distinguished I did observe general trends in seasonal variation in size-specific mussel grazing rates. Mussels in all size classes had generally higher mean grazing rates in May and June than in late summer (Figure 19). Mussels > 15 mm, those that were large enough to potentially spawn, showed the greatest variation in seasonal grazing rates. Mussels <10 mm were only present in early spring and late summer and showed the least variation in grazing rates. Obviously, during the course of the season mussels in one size class could grow into another size class.

Mussels in all size classes showed a general pattern of increasing grazing rate with increasing seston concentration (Figure 20). Although regressions differed significantly, the large variation in the grazing response of mussels to different seston levels make it impossible to separate out the effect of seston concentration from concurrent changes in mussel biomass. Clearly mean grazing rates generally increased with increasing mussel soft tissue mass (Figure 21). However, mussels < 10 mm showed little variation, while mussels in the other three size class generally had a wider variation in both grazing rates and body mass. Mussels > 15 mm showed a decline in biomass from a seasonal high in the late spring (Figure 22). These biomass changes are probably associated with spawning. Haag and Garton (1992) report a 50 % drop in mussel soft tissue mass following spawning. Changes in mean soft tissue mass for mussels 20-25 mm in 1992 and 1993 are most likely spawning related (Figure 22). In fact, a smaller August biomass drop may also reflect a smaller spawning event in both

The quantity of food available to adult mussels is ultimately dependent on factors affecting the delivery of pelagic phytoplankton assemblages to benthic zebra mussels. Zebra mussels depend on water movements for food transport. Natural lake seston concentrations vary seasonally with phytoplankton successional patterns and the degree of turbulent mixing in the water column as well as with the impact of zooplankton grazing. To model the effect of delivery rate on size-specific mussel grazing rates I set each pump to a different flow rate allowing half of the experimental and control chambers to receive one seston concentration and half to receive another lower concentration. However, during my first flow rate experiment (27-28 July 1992), a large number of mussels spawned so I repeated the experiment on 29-30 July 1992 with different mussels collected at the same time as those used in the first experiment. During the second experiment no spawning occurred. During the first experiment spawning was widespread and occurred at both flow rates. Despite spawning, all mussels at the higher flow rate, 305 ml • h⁻¹, had significantly higher clearance rates than mussels at the lower flow rate, 212 ml • h⁻¹ (p=0.0067, r² =0.889). During the second, non-spawning experiments mussels in all size classes at the higher flow rate, 297 ml • h⁻¹, also had higher clearance rates than mussels at the lower flow rate, 148 ml • h⁻¹ (p=0.00187, r² =0.847).

Food Quality and Refiltration

During the 14-15 July 1992 grazing experiment, incoming lake seston was highly turbid due to high waves and wind associated with rain during half of the experiment. Mean control seston concentration was low (1.14 mg • L⁻¹), but contained almost 80%
organic material. Clearance rates were high for all size classes, pseudofeces were produced by mussels in all size classes, and mussels removed almost half of the available seston and 80% of the inorganic material.

The largest seston concentration (4.71 mg • L⁻¹) in my grazing experiments occurred 21-22 July 1992 when halfway through the experiment a large barge anchored adjacent to the field station was moved, disturbing bottom sediments at the pump inlet and causing highly turbid water with numerous pieces of broken macrophytes to be pumped into the grazing chambers. Vials attached to the lower end of the grazing chambers to collect pseudofeces, feces, and sedimenting seston were over half full of pseudofeces when normally very few pseudofeces were produced. Vials from control (no mussel) chambers had no pseudofeces and contained only 58% inorganic material, while vials from cages with mussels of all size classes contained 80% inorganic material reflecting increased pseudofeces production.

Prompted by my observed mussel responses to these two events I tested the effect of added clay on mussel size-specific grazing rates in an experiment 3-4 August 1992 by adding clay in pulses to only half of the experimental and control cages. Added clay significantly increased mussel clearance rates (p=0.0001, r² =0.98). All mussels >10 mm receiving clay had higher clearance rates than mussels of the same size that did not receive clay.

Reproductive Condition

During 23-24 June 1992 (19 °C) I measured grazing rates for individual large (mean size 22.4 mm, 55.8 mg dry soft tissue mass) mussels feeding one mussel per chamber. Based on post-experimental examination of gonadal tissue, the 8 female and 6 male mussels were fully mature, at stage 4 gametogenic index (50% + mature gametes),
and had not yet spawned. All mussels had high grazing rates (mean = 8.4 (±1.25) mg • mussel\(^{-1}\) • d\(^{-1}\)) and grazing rate did not differ with sex of the mussel. These high grazing rates, equivalent to 3 L • mussel\(^{-1}\) • d\(^{-1}\) at mean seston concentration= 2.8 mg • L\(^{-1}\)) may reflect either high food demands associated with large body mass and preparation for spawning, or lack of intraspecific competition for incoming seston, or both.

During an experiment on 27-28 July 1992 mussels > 15 mm spawned during grazing experiments during which I was varying flow rate and I observed mature gametes in 40-50% of the collecting vials attached to the bottom of the chambers. Because it appeared that spawning may have affected grazing measurements, I repeated, the flow rate experiment on 29-30 July using mussels drawn from those collected for the earlier experiment and held in the lab aquarium attached to rocks. Mussels did not spawn during the second experiment. Mussels that had spawned had significantly lower clearance rates than those in the same size class that did not spawn during the second experiment using the same flow rate (ANCOVA, p=0.0055, r\(^2\) = 0.923). Haag and Garton (1992) found that in Lake Erie local mussel populations had synchronous mass spawning episodes during a relatively short time period. Therefore, it is probable that the mussels used during the 29-30 July experiment had also spawned during 27-28 July.

DISCUSSION

Estimates of the impact of zebra mussels on the plankton of Lake Erie and their potential impact in other inland water have varied tremendously based on limited data and understanding of how pelagic zone phytoplankton are transported to benthic zebra mussels. Previous researchers have used several different clearance rate approaches to
estimate zebra mussel population filtration impact on pelagic algae. The first approximation that has gained considerable attention in the popular press was based on the fact that zebra mussels were reported to have high densities and high individual filtration rates. These early estimates combined a single clearance rate value of 0.8 L • ind⁻¹ • d⁻¹ reported by Stanczykowska et al. (1975) with density estimates. The next level of approximation for zebra mussel impact estimates recognized that mussel filtration rates were size-specific and used the clearance rate regression equation developed by Kryger and Riisgard (1988) with size frequency data from the lake of interest (MacIsaac et al. 1992, Bunt et al. 1993). Kryger and Riisgard (1988) measured individual clearance rates for Chlorella in the lab for mussels of different sizes. They published equations for both their clearance rate-dry soft tissue mass and a dry soft tissue mass-shell length regressions.

To compare impact estimates made with these two approaches with my clearance rates derived from size-specific mussel grazing rates (Table 8) and to illustrate the problems associated with extrapolating individual clearance rates to a lake population impact, I used my size-frequency distribution and population density estimate from August 1993 (Chapter 1) with the single value approach and the size-specific approach using equations of Kryger and Riisgard (1988). For the Gull Island Shoal mussels at 3 m at a density of 18,094 m⁻² (Table 8), using the single value approach (clearance rate of 0.8 L • ind • d⁻¹) the estimated population clearance impact is 14.4 m³ • m⁻² • d⁻¹ or assuming that the entire water column is accessible to benthic mussels without refiltration this is equivalent to theoretically turning over the entire 3 m water column nearly 5 times daily. If I use both of Kryger and Riisgard’s (1988) equations to convert my shell length measurements to dry mass and then to individual clearance rates, the estimated
population clearance impact for the 3 m mussel population at Gull Island Shoal becomes 41.8 m$^3$ • m$^{-2}$ • d$^{-1}$ or almost 14 times per day. However, if I use my own site-specific regression equation to calculate mussel dry mass and then use the clearance rate equation of Kryger and Riisgard (1988), the estimated population impact is much lower at 26.9 m$^3$ • m$^{-2}$ • d$^{-1}$ (turnover rate of 7 d$^{-1}$). Contrast these values (14.4 to 41.8 m$^3$ • m$^{-2}$ • d$^{-1}$) with those I obtained for the 3m population of Gull Island Shoal using shell length based clearance rates, 2.2 m$^3$ • m$^{-2}$ • d$^{-1}$, and biomass based clearance rates, 2.3 m$^3$ • m$^{-2}$ • d$^{-1}$ both would be equivalent to less than one turnover per day. After applying the density effect I observed with my clump experiments (Table 7) in which a clump of 20 to 60 mussels had a mean clearance rate that was only 30.8% of that predicted on individual clearance rates, my estimated maximal clearance impact for the mussel population at 3 m on Gull Island Shoal drops to around 0.4 to 0.7 m$^3$ • m$^{-2}$ • d$^{-1}$ (Table 8) and theoretically would take 4 to 5 days to turnover the 3 m water column. All of these estimates, including my own maximal estimate, are overestimates of mussel impact potential based on the assumption benthic zebra mussels have access to phytoplankton in the entire water column and can avoid processing water that has already been filtered by other mussels. Reeders et al. (1989) calculate zebra mussel community grazing rates at 490 x 10$^6$ m$^3$ • d$^{-1}$ in shallow (<4.5 m) Lake IJsselmeer and 140 x 10$^6$ m • d$^{-1}$ in Lake Markermeer (depth ranges from 2.5 to 4.5 m (Bij de Vaate 1991). These community grazing rates are estimated to turnover each of these shallow lakes' volumes in 11 and 18 days. However, Reeders' approach has restricted application since it is based on zebra mussel filtration behavior in shallow, turbid, hypereutrophic polder lakes in the Netherlands with a mean depth of < 2.0 m (Lake Woldewijd 1.5 m,
2600 ha; Lake Veluwemeer 1.4 m, 3400 ha) (Reeders et al. 1989, Reeders and Bij de Vaate 1990). In these lakes there is sufficient wind driven turbulent mixing of the shallow water column and low zebra mussel densities (≤ 1000 m\(^{-2}\)) that is unlikely that a concentration boundary layer would develop. Thus, these shallow polder lakes are unique environments where the assumption of a homogenous water column in which turbulent mixing is constantly replenishing seston above mussel beds may be justified, but of questionable value in modeling zebra mussel behavior in more typical north temperate lakes. These clearance rate approaches ignore the fact that algae can reproduce as many as several times per day and turbulent mixing characteristics within the water column will affect the rate of delivery of particulate matter to benthic zebra mussels. The continued persistence of typical seasonal patterns of algal abundance and species succession in Lake Erie shows that predictions that mussels could remove all the algae from the lake several times per day do not reflect what is actually occurring in lakes.

More recently several researchers have measured clearance rates for North American mussel populations in short term, fixed volume experiments using microspheres (Lei et al. 1996), mixed natural algal assemblages (Horgan and Mills 1997), or natural seston (Fanslow et al. 1995). Fanslow et al. (1995) estimated mussel population clearance rates of 0.9 and 6.4 m\(^3\)·m\(^{-2}\)·d\(^{-1}\) and estimated that mussels could potentially clear the volume of the shallow, inner Saginaw Bay, Lake Huron between 0.2 and 1.3 times per day. However, the problem still remains that a linear extrapolation of clearance rates from short term, closed system measurements to the whole water column of a lake for a full day inappropriately assumes mussels are grazing continuously from a volume that flows by without refiltration and without a decline in the mass of algae extracted from the water per unit time, conditions never met in nature. In all cases, clearance rate estimates based on closed system measurements are limited to the
volume of water immediately surrounding the zebra mussels, and fail to take into account
the turbulent mixing phenomena necessary to bring seston from the pelagic zone to the
benthos in natural ecosystems.

Current impact assessments ignore patchiness in the environment and generally
assume a uniform distribution of mussels across the lake bottom and extrapolate density
estimates from very small total areas of the lake bottom to the entire lake. My approach to
estimating maximal mussel population impact incorporates intraspecific competition with
size-specific grazing rates and size-frequency distribution of field mussel populations on
a variety of substrates and at various depths (Chapter 1) is an improvement over the other
approaches, yet still overestimates the impact of mussel filtration of pelagic algae. My
grazing chamber flow-through system delivers seston continuously and comes closer to
providing zebra mussels with seston without depletion or refiltration of previously
processed water. Ackerman (1999) working in a recirculating flow chamber found that
mussels at low flow condition could deplete seston from a 4-5 cm zone around them and
that their ability to orient and extend their siphons allowed them to adapt to various algal
delivery rates. However, in natural populations of zebra mussels in densely-packed
clusters of individuals of many sizes attached to one another and the substrate, some
mussels within a cluster may feed efficiently while others are deprived because their
ability to orient and extend their siphons is restricted by their position within the clump.
The magnitude of the impact of zebra mussels’ grazing on the pelagic community may
depend on their occurrence in these clusters (Peterson and Beal 1989, Pullen and
LaBarbera 1991). I found that clumps of zebra mussels were unable to remove all the
organic or inorganic seston delivered, and that binding together in clumps makes mussels
at least 70% less efficient at removing available seston, hence the impact of zebra mussel
grazing on Lake Erie seston is much less than had been predicted.
Generally field measured individual mussel clearance rates are lower than those derived from laboratory studies (see review in Kryger and Riisgard 1988). Only this study and those of Reeders et al. (1989) and Stanczykowska (1977) report in situ measurements of individual zebra mussel clearance rates. Reeders et al. (1989) made in situ clearance rate measurements by allowing 22 mm mussels to feed for a short time period on natural seston and reports clearance rates of 15-170 ml • ind⁻¹ • h⁻¹. However, the high seston concentrations (5 to 79 mg • L⁻¹) used by Reeders et al. (1989) for their clearance rate measurements restrict the application of their work to other lakes. Their seston concentrations far exceed those reported in North America lakes today as well as the high seston concentrations (3.3 to 7.1 mg • L⁻¹) previously reported in western Lake Erie in the late 1960s (Munawar and Munawar 1976). In 1970 even the eutrophic, shallow western basin of Lake Erie (mean depth of 7.4 m) had mean seston concentration of 5.3 mg • L⁻¹ (Munawar and Munawar 1976). In this study natural seston concentration through the grazing chamber ranged from 1.2 to 4.1 mg • L⁻¹. My study and those of Stanczykowska (1977) both measured zebra mussel grazing rates in flow-through chambers receiving ambient lakewater with natural phytoplankton assemblages. Seston concentrations reported by Stanczykowska (1977) for a variety of lakes used in grazing experiments ranged from 2.6 to 6.3 mg • L⁻¹ while in my experiments seston varied from 1.1 to 4.7 mg • L⁻¹. Using five (Stanczykowska, pers. comm.) 22 mm mussels in each in situ grazing chamber Stanczykowska (1977) reports grazing rates for 22 mm mussels from 0.36 to 0.96 L • ind⁻¹ • d⁻¹ during May through August experiments. I obtained comparable clearance rates for 20-25 mm mussels at a density of 5 mussels per chamber.
Doering and Oviatt (1986) used field mesocosm experiments to assess the accuracy of 8 laboratory-derived filtration models in predicting the removal of suspended particles or biosedimentation by the bivalve *Mercenaria mercenaria*. They found that only the four models using natural suspensions of seston accurately reflect natural processes; the four models using dye or monocultures overestimate bivalve removal of particulate material. Thus, laboratory methods used in determining zebra mussel filtration rate may be critical. Any overestimation of filtration rate may exaggerate the impact of zebra mussels on the phytoplankton community or may produce an underestimate of the role of other grazers (Doering and Oviatt 1986). Thus, accurately identifying variables affecting individual size-specific filtration rates are critical in evaluating the relative impact of zebra mussel and zooplankton grazing interactions with phytoplankton assemblages.

Although the effect of seasonally varying environmental factors such as temperature and seston concentration can not be separated in my study, the work of others (Morton 1971, Walz 1978a, Reeders et al. 1989, Reeders and Bij de Vaate 1990) suggests that for the range of ambient temperature (15 to 26.5 °C) in my experiments that temperature did not affect grazing rates. In field measurements of filtration rates Reeders et al. (1989) found that suspended matter content was more important in determining filtering rates in zebra mussels than was temperature (seasonal range 7 to 20 °C); temperature only set the gross level of seasonal filtration rate. In contrast, Lei et al. (1996) found that mussel clearance rates in lab experiments using plastic microspheres increased with increasing temperature between 8 and 20 °C, but decreased between 20 and 23 °C.
Clearance rates for *D. polymorpha* vary with quality and quantity of seston available (Stanczykowska et al. 1975, 1976, Stanczkowska 1977). Horgan and Mills (1997) found that even smaller mussels (9-11 mm) could clear a wide range of natural seston particles (10-150 μm) and that clearance rates were similar across that range. Stanczykowska (1977) found that blooms of larger phytoplankton forms can inhibit filtration activity. Sprung and Rose (1988) found that zebra mussels has a maximum filtration capacity at low food concentrations and a maximum ingestion capacity at high food concentrations. Similarly, in my study it appears that zebra mussels are effectively integrating a wide variety of environmental (temperature, seston concentration, delivery rates) and metabolic parameters (body mass, reproductive condition) in their grazing activity and that mussels respond to these environmental parameters with changes in clearance rates.
CHAPTER 3

AN ECOSYSTEM APPROACH TO EXAMINING THE EFFECTS OF ZEBRA MUSSELS ON LAKE ERIE PELAGIC FUNCTION

INTRODUCTION

With the arrival of a large, actively filtering population of zebra mussel, *Dreissena polymorpha*, to the inland waters of the U. S., the scientific community responded quickly to assess the impact of the invaders on the existing aquatic ecosystem (Mackie et al. 1989, Hebert et al. 1989, Leach 1993). Zebra mussel impacts in North American inland waters were expected to be high and ecosystem-wide due in part to their high fecundity, free-living planktonic larvae, and lack of natural predators in their new environments. The colonization and development of a significant zebra mussel population in a lake, reservoir, or stream may have a major impact on phytoplankton and zooplankton community dynamics as well as indirect effects on fish community stability. *Dreissena*'s potential diversion of phytoplankton biomass from zooplankton to the benthos may cause a decreased abundance of zooplankton prey for forage fish as well as for young-of-year piscivorous species.

Potentially zebra mussels and herbivorous zooplankters would have similar impacts on the phytoplankton community of a lake; both are filter feeders that selectively graze similar-sized phytoplankters. However, adult zebra mussels are benthic, sedentary, have longer generation times, have more biomass, and tie up nutrients in
pseudofeces and shells for longer time periods than the planktonic, mobile, short-lived, smaller, rapidly excreting zooplankters (Figure 23). In reality, sedentary adult zebra mussels have restricted access to pelagic phytoplankton and their impact is dependent upon physical transport mechanisms such as settling, turbulent mixing characteristics within the water column, advection, and resuspension that affect the rate of delivery of organic matter produced in the pelagic zone. Thus, an evaluation of the impact of *D. polymorpha* on pelagic communities of Western Lake Erie requires a thorough knowledge of the phytoplankton and zooplankton community dynamics as well as coupling of physical and biological processes (Figure 23).

I investigated the importance of turbulent mixing on zebra mussel impact on zooplankton and phytoplankton using an ecosystem approach to estimate the flux of phytoplankton to benthic mussels. My research goals were to evaluate turbulent mixing processes affecting the flux of phytoplankton to zebra mussels and the impact of zebra mussel grazing on the pelagic community. In this chapter, I present results of measurements of seasonal variation in the state variables shown in Figure 23 (phytoplankton, zooplankton, nutrients, and zebra mussels) and the rates of photosynthesis (primary production) and the transfer of materials between the compartments (zooplankton grazing, and both zebra mussel larval and adult grazing), incorporating the effects of variation in physical forcing functions (light, temperature, dissolved oxygen, and turbulent mixing) (Figure 23). I measured all components and processes on the same time scale and at the same location in western Lake Erie.

**Background**

**State Variables: Phytoplankton and Zooplankton**

Prior to the introduction of zebra mussels, western Lake Erie had a stable pattern of seasonal succession of phytoplankton and zooplankters, typical of many temperate
mesotrophic and eutrophic lakes (see Sommer et al. 1986). The seasonal succession patterns of the pelagic community in western Lake Erie are well documented (Munawar and Munawar 1976, Vollenweider et al. 1974, Watson and Carpenter 1974, Vanni and Temte 1990, Makarewicz 1993a,b). Winter algal populations are low (Culver 1980, Phipps 1987). Increased nutrient and light availability in late winter lead to rapid algal growth and a spring diatom peak. The early summer phytoplankton community is dominated by small, rapidly growing algae which are grazed by zooplankters. High zooplankton grazing rates result in a rapid decrease in phytoplankton abundance followed by a late June or early July 'clear-water' phase (Lampert et al. 1986, Lampert 1988). The more predator-resistant, large, green algae occur in mid-summer along with cyanobacteria that may form blooms. Diatoms, rich in lipids, increase during late summer and reach another maximum in fall. Rotifers are abundant in early spring shortly followed by copepods in early summer. Larger-bodied cladocerans reach peak abundance in late June and early July and, then, after rapidly overgrazing their food supply cause the clear-water phase. Then, the large cladocerans are replaced by smaller Cladocera during the rest of the summer (Culver et al. 1985, Phipps 1987). The existing seasonal dynamics of the pelagic communities of western Lake Erie alter both the quality and the quantity of phytoplankton available to all grazers. Therefore, any effect of Dreissena on phytoplankton may be detected within the seasonal variation of the established phytoplankton and zooplankton communities.

**Material Transfer: Zebra mussel and zooplankton grazing**

Zebra mussels and herbivorous zooplankters potentially compete because they both consume nanoplanckton (< 64 μm). Sprung and Rose (1988) found that zebra mussels adults filter food particles > 0.7 μm from water with maximum retention efficiency for particles of 5 μm in diameter, but particles up to 35 μm were filtered from
the water. Ten Winkel and Davids (1982) found that zebra mussels positively select spherical algae 15-45 μm in size in both the mantle cavity and stomach and reject smaller or larger sized particles. In their lab experiments with mixtures of Asterionella and Cryptomonas, zebra mussels had a strong positive selection for Cryptomonas. Fragmented, long diatoms were found in the stomachs, but were less abundant there than were spherical particles. Although larger-sized rejected particles were found in pseudofeces, the contents of pseudofeces were highly variable. In contrast, starved mussels were nonselective; they consumed lake water natural algae in all sizes up to 750 μm. Size-selective grazing on small particles by Dreissena adults may decrease the abundance of small phytoplankton that are the only appropriately-sized food for smaller zooplankton or for zebra mussels' own larvae. Depletion of small-sized phytoplankton by zebra mussels may actually favor the large-bodied cladocerans allowing them to maintain their domination in western Lake Erie in June since these larger zooplankters organisms can consume larger-sized phytoplankton while smaller zooplankters can not (Gliwicz 1977, Phipps 1987, Fulton 1988).

Potentially both zebra mussel benthic adults and larvae are competitors with zooplankters for pelagic algae. D. polymorpha has a free-swimming veliger larva (70 -290 μm) that lives in the freshwater plankton for 10 to 33 days, depending on water temperature, and then settles to the bottom (Stanczykowska 1977, Sprung 1989). Veliger larvae are most abundant in western Lake Erie during July and August (peak 500 L⁻¹, Haag and Garton (1992) when phytoplankton levels are low, especially small algae. Zebra mussel larvae feed only on particles between 1 and 4 μm in diameter, primarily picoplankton consisting of bacteria, cyanobacteria, and small flagellates (Sprung 1989). Although no published veliger grazing rates on natural phytoplankton are available, MacIsaac et al. (1992) estimated veliger grazing rates from 2.87 μm bead ingestion rates
in the laboratory, and report bead clearance rates of 0.247 to 0.420 ml • ind⁻¹ • d⁻¹.

Veliger impact can be expected to vary seasonally with abundance, but their short time in
the pelagic community may restrict them to a minor impact on phytoplankton compared
to adult *Dreissena* and zooplankton.

*D. polymorpha* feeds on phytoplankton and bacteria by filtering out all particulate
matter and then rejecting inappropriately sized or inorganic material combined with
mucus to form pseudofeces that are ejected via the incumbent siphon (Ten Winkel and
Davids 1982, Sprung and Rose 1988). Rejected pseudofeces and feces accumulate on *D.
polymorpha* colonies, removing N and P from the water column (Stanczykowska and
Planter 1985). Thus, adult mussels may indirectly impact phytoplankton assemblages by
altering nutrient dynamics in the lake. Stanczykowska and Planter (1985) show that only
a small portion of the N and P filtered is retained in the mussel's body (11-12.8% N;
0.84-0.92% P). Mussel soft tissue N levels were fairly constant, but P levels showed
seasonal variation; higher levels were associated with gametogenesis in the spring.
Accumulation of N and P in the shells of mussels was N: 2-3 times and P: 4-5 times
lower than in the body mass. *D. polymorpha* accumulates N and P in amounts similar to
aquatic macrophytes in these same lakes. Some of the N and P filtered by the zebra
mussel is tied up with mucus in pseudofeces. Pseudofeces composition varies with
quality and concentration of the seston. However, mussels expel 50-80% of the filtered
N and about 40% of the P as feces and pseudofeces (Stanczykowska and Planter 1985).
Sedimentation of mucus-laden pseudofeces and feces may act as a sink for N and P
preventing a rapid recycling of nutrients used by phytoplankters. In contrast,
zooplankton excretory products may be immediately available to phytoplankton (Lehman
1980). The long term consequences of N and P accumulations in pseudofecal deposits
and in empty shells of mussel colonies is not known. Heath et al. (1995) found
increased levels of dissolved organic phosphorus in enclosures when zebra mussels were present. Similarly, Gardner et al. (1995) report enhanced ammonium regeneration in bottle experiments when zebra mussels were present. Heath et al. (1995) and Gardner et al. (1995) conclude that the mussel's excretion of phosphorus and ammonium into the water column may account for enhanced phytoplankton growth in enclosures.

Most estimates of zebra mussel impact on the pelagic community are based on extrapolations of laboratory measured filtration rates of individual mussels, multiplied by field-derived population density estimates which are then used to calculate the time for the entire water volume to be filtered (Reeders et al. 1989). For example, Reeders et al. (1989) calculate zebra mussel population clearance rates at 490 x 10^6 m^3 • d^-1 in Lake IJsselmeer and 140 x 10^6 m^3 • d^-1 in Lake Markermeer during August-October. These population clearance rates suggest mussels filter a volume equal to the volume of each of these shallow lakes' volumes in 11 and 18 days, respectively. Performing similar calculations for western Lake Erie (volume: 25 km^3, mean depth: 7.4 m, zebra mussel density: 1000 to 10,000 • m^2, filtration rate: 0.8 L • ind^-1 • d^-1) produces estimates ranging from about 9 days to less than 1 day to turn over a volume equivalent to the entire volume of the western basin of Lake Erie. While attention-getting, such calculations ignore the dynamics of zebra mussel grazing, assuming mussels can filter the water without reprocessing the water they and their neighbors had already cleared, and add little to our assessment of the relative impact of zebra mussel's grazing on the pelagic communities.

An assessment of the impact of D. polymorpha on pelagic communities requires knowledge of seasonal, size-specific filtering rates and food size selection. Filtration rates of D. polymorpha vary with temperature, seston concentration, and food size. In
field measurements of filtration rates Reeders et al. (1989) found that suspended matter content was more important in determining filtering rates in zebra mussels than was temperature; temperature set only the gross level of seasonal filtration rate. Thus, filtration rates for zebra mussels vary with quality and quantity of seston available (Stanczykowska et al. 1976, Stanczykowska 1977). Stanczykowska (1977) found that blooms of larger phytoplankton forms can inhibit filtration activity. *Dreissena* has a maximum filtration capacity at low food concentrations and a maximum ingestion capacity at high food concentrations (Sprung and Rose 1988).

The removal of phytoplankton from the water column by adult zebra mussels can be reflected in increased water transparency. However, increased water transparency can also be due to zooplankton grazing. Large filter-feeding zooplankters may significantly reduce phytoplankton biomass by grazing selectively on depressing small, edible phytoplankton species. Inedible algal species may then appear (McCauley and Briand 1979, Lampert et al. 1986, Lampert 1988). Zooplankters efficiently feed on nanoplanckton (<35 μm), bacteria, and detritus (Bogdan and Gilbert 1982, Lampert et al. 1986, Lampert 1988). Lampert et al. (1986) tested the impact of zooplankton grazing on phytoplankton through a series of enclosure experiments. In the absence of zooplankters, small algae are in higher densities than when zooplankters are present. In lake populations Lampert et al. (1986) found that filter-feeding zooplankton biomass is high enough to account for the clear-water phase; zooplankters then become food-limited, and a rapid population decline follows. Zooplankton size-selective feeding depresses edible phytoplankton species and nutrient limitations function to reduce algal biomass during the summer (Munch et al. 1984). Wu and Culver (1991), using *in situ* measurements of zooplankton grazing, concluded that, when seasonally abundant, large-bodied crustacean zooplankton's grazing of edible alga can produce a clear-water phase characterized by
increased Secchi transparency. However, they found that in August when large-bodied cladoceran abundances were low, zebra mussel grazing did not prolong the clear-water phase. Secchi transparency in both nearshore and offshore sites in western Lake Erie actually decreased in August while adult zebra mussel abundances increased (Wu and Culver 1991).

Phytoplankton loss rates due to herbivorous zooplankters may be overestimated unless edible and inedible species are considered (Jassby and Goldman 1974). Similar edible and inedible criteria may apply to Dreissena's food selection by both size and chemical "taste" (Morton 1971), hence phytoplankton loss rates due to filtering by zebra mussels may be overestimated as well. Doering and Oviatt (1986) used field mesocosm experiments to assess the accuracy of 8 laboratory-derived filtration models in predicting the removal of suspended particles or biosedimentation by the bivalve Mercenaria mercenaria. They found that only the four models using natural suspensions of seston accurately reflect natural processes; the four models using dye or monocultures overestimate bivalve removal of particulate material. Thus, laboratory methods used in determining zebra mussel filtration rate may be critical. Any overestimation of filtration rate may exaggerate the impact of zebra mussels on the phytoplankton community or may produce an underestimate of the role of other grazers (Doering and Oviatt 1986). Thus, accurately determining variables affecting individual size-specific filtration rates are critical in evaluating the relative impact of zebra mussel and zooplankton grazing interactions with phytoplankton assemblages.

Forcing Functions: Hydrodynamic transport processes

Hydrodynamic processes must be considered in any evaluation of benthic-pelagic interactions. Water flowing over the bottom develops a shear region (boundary layer) due to drag of the bottom on the flow (Wildish and Kristmanson 1979, Butman 1987).
The velocity of water movement in this boundary layer decreases to zero near the bed where viscous forces dominate (Figure 23, lower right). Mean flow velocity (Figure 23, u) reaches a maximum above the boundary layer in a turbulent, mixed region. The availability of food for benthic filter feeders is determined by vertical mixing and differential flow within the boundary layer.

The rate of exchange of natural seston across the boundary layer thus involves the interaction of physical and biological factors. Zebra mussels, like other benthic suspension feeders, depend on water movements for food transport. Most food is transported horizontally in the low flow water near the bottom (Muschenehmic 1987). Vertically settling seston becomes potential food when it enters this boundary layer. A strong food concentration gradient develops with a localized depletion zone nearest the bed (Figure 23) when filter-feeding organisms remove seston faster than it is replaced. Several researchers document a decrease in phytoplankton concentration near benthic filter feeders in the field (Buss and Jackson 1981, Frechette and Bourget 1985a,b, Peterson and Black 1987, Frechette et al. 1989, Peterson and Beal 1989) and laboratory experiments (Wright et al. 1982, Wildish and Kristmanson 1984). Hydrodynamic sorting also occurs with denser inorganic particles more abundant closer to the bed and lighter organic particles more abundant above the bed (Muschenehmic 1987). Thus, the vertical feeding height attained by an organism (Jumars and Nowell 1984, Monismith et al. 1990) and the orientation of a bivalve' siphons (Monismith et al. 1990) can determine the concentration and quality of its food supply and its rate of growth (Frechette 1985b, Frechette et al. 1989). Local food depletion and high population densities are associated with reduced growth in the benthic suspension-feeding bivalves Mercenaria (Peterson and Beal 1989) and Mytilus edulis (Kautsky 1982). Roughness (form drag) associated with mussel shells and the formation of aggregate colonies (hummocks) may increase
mixing in these depleted bottom layers and thus, increase the supply of food to the mussel bed (Frechette et al. 1989).

Vertical mixing, current velocity, and bottom roughness as well as the filtering action of benthic organisms all interact to determine the rate of seston replenishment to the boundary layer (Wildish and Kristmanson 1979, Frechette et al. 1989). Thus, assessment of phytoplankton removal by zebra mussels lying at the bottom of the boundary layer requires knowledge of the rate of vertical mixing of the water column, horizontal advection, the degree of turbulent mixing at the bottom boundary layer, the height at which bivalve filtration occurs, bottom topographical roughness and roughness due to zebra mussel shells as well as mechanisms of phytoplankton replenishment to the boundary layer.

Approach

Because so many factors influence the impact of zebra mussels on the pelagic food web, I used an ecosystem approach to assess the effects of benthic adults and plankton veligers on western Lake Erie pelagic dynamics. Shallow, eutrophic, and thermally-unstratified, the western basin of Lake Erie is an ideal locale to test predictions relating zebra mussel interaction with the pelagic communities. If zebra mussel were to have an effect anywhere, it should be in western Lake Erie. I examined not only the benthic and pelagic components (via measurement of the abundance of phytoplankton, zooplankton, zebra mussels, and nutrients as state variables), but also the processes that connect them (photosynthesis, zooplankton grazing, larval and adult zebra mussel grazing).

The existing seasonal dynamics of the pelagic communities of western Lake Erie alter the food available to zebra mussels, and to all other consumers of planktonic production, both in quality and quantity. Determining the impact of zebra mussels
relative to other grazers, thus requires a careful evaluation of seasonal phytoplankton dynamics and the influence of zooplankton and photosynthesis upon those dynamics. Algae can replace their biomass as often as once per day, and even grazing by crustacean zooplankton alone can exceed the production of algae. Therefore, I studied the dynamics of algal production (not just their abundance) to determine the impact of grazers. To test for size-specific grazing impacts on phytoplankton I measured $^{14}\text{C}$ size-fractionated primary productivity and monitored seasonal changes in phytoplankton species composition, abundance, and biomass. I also compared pre- and post- zebra mussel phytoplankton and zooplankton communities to test whether or not typical seasonal successional patterns had been altered.

Zooplankton size-specific grazing is important in determining seasonal patterns in phytoplankton abundance and succession so I tested whether zooplankton grazing influences seasonal variation in phytoplankton more than does grazing by zebra mussels.

**MATERIALS AND METHODS**

**Study Sites**

I used the same Lake Erie study sites off South Bass Island that I described in Chapter 1 (Figure 1). To monitor phytoplankton and zooplankton dynamics in 1991 and 1992 I used the 5 m station in Hatchery Bay, but in 1993 I switched to the 12 m open channel site near the U.S. Coast Guard west channel buoy as more representative of the western basin. I continued monitoring the zebra mussel population at the 3 m site of Peach Point Reef as described in Chapter 1.

**General Considerations**

In my ecosystem approach (Figure 23) I wanted to evaluate the seasonal dynamics of the pelagic communities and benthic zebra mussels and also to assess the
relative impact of zebra mussel and zooplankton grazing on phytoplankton. Therefore, I combined frequent monitoring of nutrients (N, P, inorganic C), phytoplankton, zooplankton, and zebra mussel communities to detect seasonal changes in abundance with measurements of photosynthesis (primary productivity) and grazing impact estimates for zooplankters and zebra mussels (both adults and veligers). I measured $^{14}$C primary productivity, zooplankton community grazing (using $^{32}$P-labeled yeast), and zebra mussel grazing as close together in time as possible, generally within a 4 day period. I compared the relative impact of zebra mussel adult and veliger clearance rates and zooplankton community clearance rates on phytoplankton dynamics (seasonal changes in abundance and production). Protocols for the use, transport, storage, and disposal of radioactive ($^{14}$C and $^{32}$P) materials at both Lake Erie and main campus were approved by the Office of Radiation Safety, Ohio State University.

*State Variable: Phytoplankton Dynamics*

To detect changes in pelagic algae before and after zebra mussel introduction I compared species composition, abundance, and biomass in my algae samples from 1991 and 1992 (Chapter 1) with those collected by T. Phipps in 1986 from the 5 m Hatchery Bay site using an integrated whole water column tube sampler. I reanalyzed his 1986 samples using Utermöhl sedimentation techniques to identify, count, and measure individual algae from the preserved 1986 samples (Chapter 1).

*Photosynthesis*

Phytoplankton dynamics reflect seasonal variation due to the effects of nutrients, temperature and light changes on primary production and metabolism as well as grazing losses. In order to evaluate the effect of seasonal changes in phytoplankton composition on primary production in 1992 and 1993 I measured *in situ*, size-fractionated primary

Three times (July, August, and September) in 1992 I estimated primary productivity rates in Hatchery Bay at 5 depths (0.5 m intervals from 0.5 to 2.5 m) at a 3.5 m location adjacent to my 3 m cage experiment site. Water samples were collected at depth using a submersible pump (Chapter 1). In 1993 I estimated primary productivity twelve times from 22 May to 17 September at the 12 m site at 5 depths (2 m intervals from 2 to 10 m) collecting water with a 6.2 L clear Van Dorn sampler. Duplicate collections from each depth were pooled in a 20 L container and then poured through a supply bucket equipped with multiple outlet hoses that allowed me to simultaneously fill a large number of sample bottles at one time, rapidly moving hoses to new bottles as needed. At each sample depth I filled duplicate light and dark BOD bottles (mean volume = 308 ml) for primary productivity measurements as well as a single bottle for background and reagent blank. The BOD bottles were filled from the bottom and allowed to overflow continuously for three times their volume. Additional glass and polypropylene bottles were filled with the same water for later determination of pH, alkalinity, nutrients, seston concentration, and phytoplankton composition and abundance. All sample bottles were sealed and transferred to light-proof, insulated boxes for transport back to the lakeside lab facilities for inoculation with $^{14}$C.

I removed 3 ml of water from each BOD bottle to prevent overflow when adding $^{14}$C-sodium bicarbonate (ICN Biomedicals). The removed water was used to rinse $^{14}$C ampoules to transfer all radioisotope to a BOD bottle. Working rapidly under subdued light conditions I inoculated each BOD bottle with $^{14}$C-NaHCO$_3$ using a 1000 µL pipette equipped with a 5 cm polyethylene cannula so that radioisotope was added to the middle
of each bottle. I added 2 μCi $^{14}$C-NaHCO$_3$ to each bottle in 1992 and 5 μ Ci $^{14}$C-NaHCO$_3$ in 1993. Bottles were inoculated in the same sequence in which they were filled, the stopper secured with a safety clip to prevent leakage, and the bottle inverted three times to mix contents. I returned bottles to an insulated, light-proof box for transport to the field site. Using a series of metal frames ("spiders") that held the bottles horizontally I resuspended BOD bottles at the collection depths for a 4 h incubation, generally between 1030 and 1430 h. At the end of the incubation period I again held bottles in a light-proof, insulated box until aliquots could be filtered.

To estimate primary production of algae of different sizes (0.4 -14 μm, 14 - 43 μm, and >43 μm) I size-fractionated 100 ml aliquots from each bottle using three different combinations of polyester screens and track-etched polycarbonate filters (Poretics Corp.). I used vacuum filtration at least that 250 mm Hg to prevent cell rupture and loss of label $^{14}$C. After sequential filtration of each 100 ml aliquot through one of three size-fractionation combinations I placed rolled filters vertically in 20 ml liquid scintillation vials with 1 ml 0.1 N HCl for 4 hours. I then added 15 ml fluor (Cytoscin ES, water tolerant) and stored samples until radioassayed. During the incubation period I had also used the same procedure to size-fractionate the background (no $^{14}$C added) samples collected at each depth. After returning to the Columbus lab I measured $^{14}$C uptake of each filter using a single-label dpm program with a Beckman LS 5801 liquid scintillation counter equipped with external quench correction.

In 1992 and 1993 I estimated dissolved inorganic carbon available for primary production using pH, alkalinity (sulfuric acid titration with pH meter), and temperature of water samples collected from each depth and standard tables (Wetzel and Likens 1990). I calculated carbon assimilated (mg C m$^{-3}$ h$^{-1}$) (Wetzel and Likens 1990)
during the 4 h incubation for each bottle and then subtracted the mean dark bottle carbon assimilation at each depth from each of the light bottles from the same depth to obtain an estimate of photosynthesis at each depth. Dark bottle activities were < 10% of light bottle activities.

To estimate phytoplankton daily productivity I converted mean water column photosynthesis rates to areal daily rates (mg C • m⁻² • d⁻¹) for the 12 m water column. Photosynthesis rates for the 4 hour incubation period were expanded to diurnal values by assuming that 25% of daily productivity occurred during the 4 h midday period of the light day (Wetzel and Likens 1991). To estimate phytoplankton standing crop as organic carbon I converted mean water column phytoplankton volume (ml • m⁻³) to areal cellular organic carbon values for each date. Algal standing crop carbon content (mg C • m⁻²) was estimated from the mean water column cell volumes by assuming a wet weight density of 1.0 g • ml⁻¹ and a carbon to wet weight ratio of 0.1 (Vollenweider et al. 1974, Thompson et al. 1982, Reynolds 1990, Wetzel and Likens 1991). Phytoplankton turnover time (% • d⁻¹) was calculated from the photosynthesis: biomass ratio (areal daily productivity as mg C • m⁻² • d⁻¹ : algal standing crop (mg C • m⁻²)).

*Forcing Functions: Light, Temperature, and Dissolved Oxygen*

To evaluate the underwater light climate available for algal photosynthesis I measured the photosynthetically active radiation (PAR, 400-700 nm), using an underwater spherical quantum sensor connected to a Licor multichannel data logger. The meter was also equipped with a terrestrial quantum sensor that acted as a surface PAR reference (deck cell). PAR for each sensor was recorded for each depth in the vertical profile and underwater values adjusted to the average deck cell reading to correct for variations in incident light during the 15-20 minutes required to make the measurements.
I also measured Secchi disk transparency for comparison of light penetration and water clarity to pre-zebra mussel data.

During the primary productivity experiment incubation period I measured vertical profiles of temperature and dissolved oxygen (Chapter 1). I also evaluated how seasonal variation in turbulent mixing processes as well as phytoplankton dynamics affect the quantity and quality of suspended particulate matter available to grazers. During 1992 I measured total seston concentration and relative inorganic and organic factions on replicate integrated whole water column samples (Chapter 1) and for replicate water samples collected at specific depths in conjunction with primary production experiments in both 1992 and 1993.

State Variables: Nitrogen and Phosphorus

In 1993 I measured nitrogen and phosphorus on water samples collected with depth in conjunction with primary productivity experiments. I used ion specific electrodes (Orion Corp.) to measure ammonia nitrogen (µg NH₄-N • L⁻¹) and nitrate nitrogen (µg NO₃-N • L⁻¹). I measured soluble reactive phosphorus (µg PO₄-P • L⁻¹) on unfiltered samples using the acidified molybdate-stannous chloride method with a correction for turbidity (Rainwater and Thatcher 1960).

State variable: Zooplankton abundance and biomass

To evaluate seasonal and annual changes in zooplankton species composition, abundance, and biomass in 1991-1993 I collected zooplankton weekly using vertical hauls of a 112 µm mesh, metered net (0.5 m diameter). Samples were concentrated, immediately preserved with sucrose-formalin (Haney and Hall 1973), and stored in plastic containers for later analyses. I used a dissecting microscope (50x) to identify, count, and measure individual zooplankters from two subsamples (# • L⁻¹). To estimate
zooplankton biomass (μg dry mass) for each taxon I used an ocular micrometer to measure lengths (nearest 0.018 mm) of the first 20 individuals encountered in a sample for common taxa and all encountered for rare zooplankters. For cladoceran and copepod biomass I calculated dry mass using the length-weight regressions of Culver et al. (1985) and calculated a mean individual dry mass for each taxon. To estimate individual rotifer biomass I used published values (Dumont et al. 1975, Ruttner-Kolisko 1977, Markarewicz and Likens 1979) and unpublished values of dry mass of each rotifer taxon (Culver unpubl. data). I estimated the biomass (μg • L⁻¹) of each taxon as the product of the mean individual dry mass (μg) and the abundance (# • L⁻¹) for each sample.

To estimate veliger dry mass I generated my own length-dry mass equation using veligers collected with a 63 μm mesh net when they were abundant (19 July 1994). After separating all veligers with shells from the sample I used an ocular micrometer to measure the shell length of each individual as the greatest linear dimension parallel to the shell hinge. I then sorted veligers with the same shell length to the nearest ocular micrometer unit (18.2 μm = 1 unit) into nine groups (91-255 μm). Triplicate groups of measured veligers (25 to 70 individuals) were washed three times in distilled water to remove preservative and then transferred to a tared, platinum weighing pan. After drying at 65°C for 1 h I transferred pans to a desiccator (silica gel) where they were held for a total drying period of 24 h and then weighed using a Mettler UMT2 Ultramicrobalance. Using linear regression I developed a shell length-dry mass equation for zebra mussel veligers that I then used to estimate biomass of veliger in my zooplankton samples. For each sample I estimated the total veliger biomass (μg • L⁻¹) as the product of mean individual dry mass (μg) and abundance (# • L⁻¹).
Transfer Rates: Zooplankton Community and Veliger Grazing

Zooplankton grazing is important in determining seasonal patterns of phytoplankton abundance and success. To estimate the relative seasonal impact of grazing by the entire zooplankton community (crustaceans, rotifers, veligers) and by zebra mussel veligers alone, I measured zooplankton community and veliger clearance rates in 1993. I measured the uptake of radioactively labeled (32P) aquatic yeast (see below) by zooplankters and veligers from an in situ incubation system deployed at different depths in the lake (Haney 1973, 1985). The zooplankton community clearance rate is defined as the volume of lake water completely cleared of radioactive yeast particles by grazing activity of all zooplankters per day. Such a zooplankton community clearance rate is an index of actual grazing impact of zooplankters since the zooplankton community consists of many different-sized individuals with different feeding behaviors and selectivities, and phytoplankters vary widely in their susceptibility to herbivorous zooplankters.

The clear plexiglass in situ incubation system (Aquatic Research Instruments, Boise, ID) consisted of four 4.21 L cylindrical chambers surrounding a central core that contained the door release mechanism and allowed the device to be free standing when used with a support base (Figure 24). The incubation device was lowered into the lake at the 12 m site with all four doors open and then a messenger used to release the doors enclosing water in the chambers at the desired depth (2, 4, 6, 8, or 10 m). The closing of the upper door depressed the plungers on plastic syringes injecting radioactively labeled food into two of the chambers allowing duplicate measurements of zooplankton community and veliger individual clearance rates. One non-radioactive chamber was used for zooplankton analyses and the other for phytoplankton analyses as well as measurement of seston concentration. After allowing zooplankton to feed for 5 minutes
in situ I retrieved the incubation device and placed it on the support base with each chamber positioned over a wastewater container. I drained the two radioactive chamber contents through individual cylindrical ring screens (63 μm mesh) into separate catch buckets. Total feeding time from yeast injection to complete drainage of the chambers was 8 minutes. Using a minimal amount of water I transferred all zooplankters from each ring screen to separate liquid scintillation vials containing 1 ml of sugar-formalin. To determine radioactivity of food in each chamber I transferred one ml of radioactive filtrate from each catch bucket to separate scintillation vials. I placed the vials in a shielded box for transport to lakeside lab facilities where I then added fluor (Cytoscint ES, water tolerant) and stored samples in a shielded box until they could be returned to the main campus lab to determine $^{32}$P activity. I used a Beckman LS 5801 liquid scintillation counter to measure the radioactivity (counts per minute, cpm) of food accumulated in the zooplankters, and that available in each chamber. I calculated zooplankton community clearance rate (CR) as follows:

$$CR = \frac{A_Z}{A_C} \cdot \frac{1440 \text{ (min } \cdot \text{ d}^{-1})}{t}$$  

Equation 1

where,

CR = Zooplankton community clearance rate (ml $\cdot$ L$^{-1}$ $\cdot$ d$^{-1}$)

$A_Z$ = Zooplankton Community Activity (cpm $\cdot$ L$^{-1}$)

$A_C$ = Chamber Activity (cpm $\cdot$ mL$^{-1}$)

$\text{t}$ = Feeding time (min)

I drained one of the nonradioactive chambers through a third 63 μm mesh ring screen, transferred all zooplankters to a plastic storage container, and preserved them with sucrose-formalin. Subsequently I identified, enumerated, and measured all.
individual zooplankters in the sample to calculate the taxonomic composition, abundance, and biomass of the zooplankton characteristic of each depth. After draining the contents of the second non-radioactive chamber contents directly into a catch bucket I removed two 500 ml samples for seston determination and preserved another 500 ml sample with acid Lugol’s for later analyses of phytoplankton species composition, abundance, and biomass that had been available to grazers.

I repeated zooplankton community clearance rate experiments 12 times from 14 June to 17 Sept. 1993. To measure veliger clearance relative to total community clearance rates I measured individual veliger clearance rates during four experiments when I expected veligers to be abundant. I replicated 4 and 6 m depths and then sorted veligers from the replicate radioactive samples using a dissecting microscope. I measured shell lengths and sorted veligers into groups based on shell size and transferred groups containing a known number of measured veligers (29 to 96 individuals) to separate scintillation vials with fluor for radioisotopic analysis. I calculated size-specific individual veliger clearance rate (CR, ml • ind⁻¹ • d⁻¹) substituting individual veliger activity, (Aᵥ, cpm • ind⁻¹), for zooplankton community activity (Aᵥ) in Equation 1 above. Using linear regression I developed a shell length-clearance rate equation for zebra mussel veligers that I then used to estimate total veliger clearance rates. I combined the abundance of veligers in the 4.21 L chamber and their size frequency distribution with my size-specific veliger clearance rate equation to estimate the total veliger clearance rates for each depth in the four experiments.

To evaluate the impact of zooplankton community grazing on phytoplankton I estimated zooplankton community clearance impact and turnover time for each experiment. I converted mean water column zooplankton community clearance rates (L •
m$^{3} \cdot d^{-1}$) to areal daily clearance rates (m$^{3} \cdot m^{-2} \cdot d^{-1}$) for the 12 m water column. Turnover time was calculated as the time (d) to theoretically completely clear the 12 m$^{3} \cdot m^{-2}$ water column at the areal daily clearance rate on each date.

**Yeast Culture and $^{32}$P Labeling**

I obtained a dormant, axenic agar slant culture of the aquatic yeast *Rhodotorula* sp. from J. F. Haney, University of New Hampshire. Dr. Tien-Hsien Chang, Ohio State University, provided technical advice on yeast culture and reactivated the dormant culture. Dr. Chang has archived a stock of *Rhodotorula* cells (in 15% sterile glycerol at -80 °C) with his permanent yeast collection. *Rhodotorula* cells were spherical to slightly ovoid and small enough (2 - 4 μm in length) to be eaten by all zooplankters including small rotifers and veligers.

I cultured *Rhodotorula* sp. using the methods described by Haney (1970, 1973) and standard yeast culture protocols. I maintained stock cultures of *Rhodotorula* at room temperature by growing the yeast in phosphorus-deficient liquid nutrient medium with constant agitation with a shaker table to prevent cell clumping. Prior to labeling with $^{32}$P-phosphoric acid in 0.2 N HCl (ICN Biomedicals, Inc.) I determined stock culture cell density by counting a small subsample in a hemocytometer. Cells were centrifuged and resuspended in fresh phosphorus-deficient medium, $^{32}$P added (between 0.3 ml or approximately 250 μCi and 0.1 ml or approximately 1 mCi, depending on the age of the $^{32}$P stock solution), and the culture incubated at room temperature for 42 to 48 hours. Labeled cells were centrifuged, $^{32}$P medium removed, and cells rinsed. I repeated this process three times to remove all unincorporated $^{32}$P. Finally the stock culture of radioactively labeled *Rhodotorula* was resuspended in 3 ml fresh phosphorus-deficient
liquid medium and transported in a shielded, light-tight box to F. T. Stone Lab field station. Immediately prior to use I adjusted the labeled yeast suspension to an appropriate concentration with triple-distilled water so that the final concentration of labeled yeast cells in the chamber was approximately 1000 - 1200 cells • ml⁻¹.

Transfer Rates: Zebra Mussel grazing

In Chapter 2 I described methods used to evaluate the role of size-specific zebra mussel grazing rates and competition on the potential impact of zebra mussels on pelagic food webs as well as testing other factor affecting zebra mussel grazing rates. Zebra mussel grazing experiments were a major focus in 1991 and 1992. In 1993 measurements were limited to four size classes of mussels and for intact clumps of mussels to confirm that measured size-specific mussel grazing rates under conditions in 1993 were comparable to those found in 1991 and 1992 (Chapter 2).

To extrapolate results of my clump experiments to field populations I used size-frequency distributions and population density estimates from my August 1993 survey of mussel populations in western Lake Erie (Chapter 1) and my observed size-specific mussel grazing rates. I estimated maximal clearance rates corrected for the observed “Clump Effect”. The “Clump Effect” correction adjusts population clearance rate estimate for lower clearance rates of natural clusters of mussels during grazing experiments. To estimate a population clearance rate impact for mussels at 12 m at the Red Can in July 1993 and at 3 m on Peach Point Reef in the May and September 1993 I sorted mussels’ size-frequency distributions into the same four size classes I had used in my grazing experiments (Chapter 2). For each date I estimated maximal population clearance rate using the frequency of mussels in each size class and the mean individual size class clearance rates and “Clump Effect” correction (Table 7) from the 1993 grazing experiment closest to each date.
RESULTS

State Variable: Phytoplankton Dynamics

Biomasses of major phytoplankton taxa were lower in post-zebra mussel 1991-1993 than in pre-zebra mussel 1986 (Figure 25). In particular, at the same site Cyanobacteria were 70% lower in 1991 (Figure 26) than in 1986 (Figure 25) and rare in 1992 (Figures 27). In 1986 phytoplankton sampling stopped in July, but D. Culver (pers.comm.) reports that August 1986 had a major cyanophyte bloom that did not occur in August 1991-1993 (Figures 26, 27, 28). The large pyrrophyte, Ceratium, was more common in 1986 than in 1991-93 and did not appear in 1993 samples until late July (Figures 29, 30). In 1993 phytoplankton biomasses (Figure 28) at the 12 m open channel site were higher than those in 1991 and 1992 at the 5 m site (Figures 26, 27). Overall species diversity was higher in 1993 than in the other years. In 1993 phytoplankton were found throughout the water column (Figures 29, 30). Diatoms dominated the phytoplankton throughout the summer and their biomass was frequently highest at 8 or 10 m perhaps reflecting higher sinking rates (Figures 29, 30).

However, despite reduction in phytoplankton biomass, seasonal phytoplankton successional patterns typical of northern temperate lakes without zebra mussels have persisted in western Lake Erie after mussels became established. In all years there were spring maxima of diatoms (Bacillariophyta) followed by a clear-water phase in late June or early July when diatoms declined and a subsequent recovery in late summer. 1993 diatom biomass levels were similar to those in 1986 (Figures 25, 28). Diatoms made up over two-thirds of phytoplankton biomass from May to mid June in 1993 (Figure 29) and were the dominant taxon during much of the summer (Figure 30). In 1993 the clear-water phase was distinctly evident when total phytoplankton biomass dropped by 67% from June 12 to June 23 and diatom biomass decreased by 43% (Figure 29). In all
years small flagellates (Cryptophyta) were present throughout the sampling period and reached a peak in early July following the clear-water phase. Chlorophytes increased following the clear-water phase and are more abundant during July and August. Cyanobacteria were present at low levels in 1991 and 1993 and reached a peak in late summer.

Secchi transparency increased in 1991 and 1992 relative to 1986 at the same 5 m site (Figure 31a). Secchi depth in 1992 frequently indicated that light could penetrate to the bottom of the lake at the 5 m site. However, Secchi transparency was much less at the 12 m site in the spring of 1993 than in 1991 and 1992 at the 5 m site. Secchi depth transparency correlates negatively with the concentration of both inorganic and organic components of suspended particulate material in the water column. Variations in seston reflect seasonal variation in phytoplankton species composition (organic) as well as local variation in turbulent mixing events such as storms or seiches that alter the inorganic fraction of the seston. Seston thus represents all particulate matter available to herbivorous grazers and suspension-feeding mussels and the organic fraction approximates food availability. In 1992 mean total seston concentration in the water column varied greatly ranging from a 2.4 to 5.8 mg • L\(^{-1}\) while the organic fraction the organic component of the whole water column seston samples ranged from 0.7 to 3.5 mg • L\(^{-1}\) or 21 to 62% available particulate matter (Figure 31b). In 1993 at the 12 m open water site mean seston concentrations in the water column ranged from 1.3 to 7.9 mg • L\(^{-1}\) while the organic fraction ranged from 0.6 to 3.8 mg • L\(^{-1}\) ranging from 44 to 78% (Figure 31c). In 1993 vertical profiles of seston distribution with depth generally reflect a well-mixed water column with particulate matter throughout and a tendency for increased levels of particulate matter closer to the bottom (Figure 32). The effect of
storm activity on seston distribution was shown on 6 June by the overall high total seston concentration that resulted from increased turbulent mixing and then subsequent sedimentation (Figure 32).

*Photosynthesis*

Following the clear-water phase photosynthesis rates (Figure 33) and algal biomass (primary small flagellates and diatoms) were low and fairly uniform throughout the water column in early July 1992 at a 3.5 m site in Hatchery Bay, adjacent to Gibraltar Island (Figure 33). In Aug. 1992 I measured the highest photosynthesis rates in either year.

Photosynthesis rates in 1993 varied seasonally, were highest at 2 m, and decreased with depth (Figure 34). A marked drop in photosynthesis rates from 12 June to 23 June 1993 reflect a dramatic drop in diatom biomass associated with the clear-water phase (Figures 29, 34). The clear-water phase is also distinctly shown as an abrupt decline in June in the role of the larger size fraction of phytoplankton in total photosynthesis (Figure 35, dark bar predominant to small striped bar). Increases in photosynthesis rates at 4 and 6 m during July and August probably reflect increased in chlorophytes, and the presence of cyanobacteria (Figure 30). Generally, small phytoplankters < 14 μm contributed the most to photosynthesis throughout the season (Figure 35).

Phytoplankters could replace their biomass from once to more than twice daily during 1993 (Table 9). From mid June to early July photosynthesis to biomass ratios were lowest, but algae were still reproducing at least once a day.

*Forcing Functions: Light, Temperature, and Dissolved Oxygen*

Light, temperature, and dissolved oxygen function to set physiological metabolic rates of phytoplankton, zooplankton, and zebra mussels and may be limiting to growth.
Light intensity declines exponentially with depth and was <1-2% of surface values at > 8 m in 1993 (Figure 36). Similarly Secchi depth was fairly uniform and generally < 4 m. Light levels are usually considered to be adequate for photosynthesis at twice the Secchi depth. At light intensities > 200-600 μE • m⁻² • s⁻² photoinhibition can occur and at intensities < 100-200 μE • m⁻² • s⁻² photosynthesis is directly regulated by light (Reynolds 1984). In my experiments photosynthesis rates appear to be a function of underwater light climate (Figures 34, 36). On dates such as 30 June when the water column was well mixed due to storm activity and 1 m waves, light levels were <125 μE • m⁻² • s⁻² at all depths > 1.5 m and overall photosynthesis rates were comparable to those measured at 6 or 8 m on other dates. To test the effect of light on photosynthesis rates on 4 August I measured photosynthesis rates for water samples collected in upper water of the lake at lower depths and vice versa (water from 2 m was incubated at 10 m, 4 m water at 8 m, and vice versa). Water from 6 m was the only water resuspended at collection depth during the experiment. Light penetration on 4 August (Figure 37) was comparable to that available for photosynthesis in the 28 July and 9 August (Figure 36). The photosynthesis rates on 4 August (Figure 37) are similar to those obtained in normal experiments on 28 July and 9 August (Figure 34) suggesting that low photosynthesis rates were controlled by available light rather than by low algal biomass or nutrient availability (Figure 38). At high light intensities (> 200 μE • m⁻² • s⁻²) there appears to be photosaturation of photosynthesis at 2 on 12 June and 8 July (Figure 38).

Temperature depth profiles provide evidence for turbulent mixing affecting delivery of food to the benthos. During 1991 water temperatures in Lake Erie ranged from 16 to 27°C while 1992 temperatures ranged from 18.7 to 24.1°C (Figure 6a). In 1992 I found no evidence of thermal stratification; water temperature generally differed
by less than 0.1°C from surface to 5 m (range 0.0 to 0.6°C). From May to September 1993 water temperatures at the 12 m site ranged from 9.4 to 25.4°C (Figure 6a). There was little evidence of thermal stratification in 1993 since water temperature generally varied by < 1°C from 0 to 12 m with the maximum observed difference of 1.5°C from 0 to 12 m occurring in early June. In 1992 mean dissolved oxygen levels at our 5 m Lake Erie site were high, ranging from 6.8 to 9.8 mg • L⁻¹ (71 to 100% saturation) and were lowest in August. On any date in 1992 dissolved oxygen levels generally differed by less than 0.4 mg • L⁻¹ from surface to 3 m (range 0.1 to 0.6 mg • L⁻¹). From May to September 1993 mean water column dissolved oxygen at the 12 m site ranged from 6.1 to 12.8 mg • L⁻¹ (65 to 100% saturation). Dissolved oxygen levels were highest levels in May and declined throughout the summer with lowest levels in August. Dissolved oxygen levels varied more widely within the water column at the 12 m site in 1993 and were lowest at the bottom. However, dissolved levels from 0 to 12 m generally differed by less than 1 mg • L⁻¹ with a maximum observed difference of 1.87 mg • L⁻¹ at the end of July.

State Variables: Nitrogen and Phosphorus

Ammonia-nitrogen concentration was generally lowest during the spring and highest in August 1993 and ranged from 8 to 130 μg N • L⁻¹ (Figure 39). Nitrate-nitrogen showed an inverse pattern with highest values in spring and early summer and lowest values in August and September and ranged from 95 to 290 μg N • L⁻¹ (Figure 39). A storm from 0230 to 0800 h on July 8 probably caused increased nitrogen input due to sediment resuspension. Phosphate-phosphorus levels were lowest in spring and
ranged from 0.01 to 7.5 µg P • L⁻¹ (Figure 39). N:P ratios were high during spring and summer 1993 (>27:1).

State Variable: Zooplankton Abundance and Biomass

To test for changes in abundance and seasonal succession patterns in the zooplankton community (crustaceans, rotifers, veligers) I compared zooplankton communities in the 1986 pre-zebra mussel year with those during 3 years (1991-1993) post-zebra mussel introduction. Total zooplankton abundances at the same site in 1986 and 1991-1993 were similar in May through July (figure 40, note 1986 sampling stopped in July) and at a 12 m open water site except for one date (Figure 40, note scale change for 1993 data).

Zooplankters' grazing impact is a function of body size, therefore, it is important to consider which grazers are present during the year and when they are abundant. In the western Lake Erie zooplankton community body size ranged from 0.05 to 3.0 mm: large cladocerans (0.8 - 3.0 mm), small cladocerans (0.2 - 0.6 mm), adult copepods (1.0 - 1.5 mm), rotifers (0.1 - 0.5 mm), veligers (0.05 - 0.29 mm). Total mean cladoceran abundances were lower in 1991 (29 L⁻¹) and 1993 (28 L⁻¹) than 1986 (70 L⁻¹), but reached similar peak in abundance in 1992 (63 L⁻¹) (Figure 41). However, the dominant cladoceran taxa changed from 1986 to 1991-1993. Although both large (Daphnia) and small (Bosmina and Eubosmina) cladocerans were present in all years, Bosmina and Eubosmina were more abundant in the 1986 (38 L⁻¹) than in June and July of the other years, maxima of 7, 21, and 5 L⁻¹ in July 1991, 1992, and 1993, respectively. Daphnia had maximum abundance of 42 L⁻¹ in 1986 and 41 L⁻¹ in 1993, but in the intervening years maximum abundances were 22 in 1991 and 23 L⁻¹ in 1992.
Another large cladoceran, *Diaphanosoma*, was rare in 1986 (1 L⁻¹), but much more abundant (9, 21, and 13 L⁻¹) in 1991, 1992, and 1993, respectively, reflecting a shift in species composition among the cladocerans from smaller to larger-bodied grazers.

Copepods (copepodites and nauplii) were more abundant in post-zebra mussel invasion years 1991-1993 than in 1986 (Figure 42). Seasonal patterns were similar in all years with an early summer peak abundance followed by persistent lower population levels during the rest of the summer. Rotifer abundances appear to have been two-thirds higher in 1986 than in 1991-1992 and in most of 1993 (Figure 43). Veligers were not present in 1986 samples, but increased in abundance from 1991 to 1993 (Figure 44) adding a new and seasonally abundant group of grazers to the zooplankton community.

The apparent drop in rotifer abundance is probably a sampling artifact rather than a biologically significant change. 1986 samples were collected with a Schindler-Patalas trap with an unknown net size. However, generally Schindler-Patalas traps have nets < 50 μm so that they sample all sizes of zooplankters efficiently. In 1991-1993 I used a 112 μm net that collected Cladocera and copepods well, but smaller rotifer and veligers may not have been as adequately sampled. To illustrate the effect of net size on smaller zooplankter abundance estimates I have compared samples collected in 1993 at my 12 m site with the 112 μm net with those collected at the same site during zooplankton grazing experiments using a 63 μm net. I collected almost twice as many veligers using the 63 μm net than with the 112 μm net (Figure 45). Similarly, total zooplankton abundance was greater with the finer net, suggesting that my 1991-1993 abundances for rotifers were underestimated and that no biological significant change in rotifer abundance occurred after zebra mussels were introduced into Lake Erie. In fact, rotifers may have actually increased in abundance if the sampling underestimates rotifers by 40-50%.
Transfer Rates: Zooplankton and Veliger Grazing

Zooplankton community clearance rates varied both spatially and temporally (Figure 46). Zooplankton community clearance rates increased during June and July and then were lowest in August and September when they showed little variation with depth (Figure 46). The difference in zooplankton community clearance rates with depth may reflect variation in the distribution of the more mobile zooplankters trying to graze on phytoplankton, yet avoid fish and other visual predators. From mid-June through July, when larval fish were more common, zooplankton community clearance rates were lower at 2 m than at 4 and 6 m. On 5 August I measured zooplankton community clearance rates during the day (0830 to 1030 h) and again at night (2200 to 2330 h). I observed large numbers of juvenile fish feeding near the surface. During the 5 August day experiments community clearance rates were lower at 2 m than at 4 m while in the night experiments clearance rates at 2 m were not different from those at 4 m. I observed the seasonal maximum zooplankton community clearance rates on 14 July 1993.

The abundance of different zooplankton taxa present in clearance experiments varied seasonally (Figure 47, note scale differences). Cladocerans in general were present in lower numbers than other taxa (Figure 47). On 14 July zooplankton community grazing rates were maximal (476 ml • L⁻¹ • d⁻¹ at 4 m, mean for all depths: 410 ml • L⁻¹ • d⁻¹) and total zooplankton abundance was high (mean for all depths 440 L⁻¹). At this time the zooplankton community was numerically dominated by rotifers (174.4± 13.2 L⁻¹) and veligers (225.6 ± 46.7 L⁻¹) with cladoceran mean abundance for all depths only 14.3± 1.8 L⁻¹.

Abundance data can only give limited information about the impact of zooplankton grazing on phytoplankton dynamics. Abundance data are essentially a
“head count” and treat all zooplankters the same even though their body sizes differ by several orders of magnitude. Zooplankton grazing is greatly influenced by body size (Haney 1985, Knoechel and Holtby 1986). I used published methods for cladocerans, copepods, and rotifers and my own regression of veliger biomass on shell length (Figure 48) to calculate seasonal changes in the biomass of zooplankters present in 1993 community grazing experiments (Figure 49). Cladocerans now appear to have a relatively greater presence in the plankton, but their biomass was still less than veligers before mid-July.

Although veliger abundance and biomass were periodically high suggesting a significant impact on phytoplankton their actual grazing impact may be less depending on their distribution in the lake relative to phytoplankton. Most of the photosynthesis in the lake occurred at depths < 6 m (Figure 34), while veligers were most abundant deeper in the lake (Figure 50, 51). When seasonally abundant veligers often represented the majority of the community biomass (Figure 52, 53). Both high abundance and high biomass suggest a large impact for zebra mussel veligers.

To evaluate the impact of veliger grazing relative to total community grazing rates I regressed veliger clearance rate on veliger shell size (Figure 54). Veliger clearance rate increased with body size for mussels between 91 and 255 μm and ranged from 0.001 to 0.144 ml • ind⁻¹ • L⁻¹ (Figure 54). I used my regression with the veliger size frequency measurements from grazing chamber experiments to calculate veliger population clearance rates relative to measured total community clearance rate in the grazing chambers at each depth. Veliger clearance rate was generally 1 to 3% of total community clearance and had a maximum contribution of 7.1% on 5 August (Figure 55, note scale differences). Veliger grazing impact is thus insignificant relative to that of the entire zooplankton community even when veligers are seasonally abundant.
The estimated mean clearance rates for the entire zooplankton community on 14 July (observed maxima) were sufficient to theoretically turn over a volume of water equivalent to the entire 12 m water column in 2.4 days (Table 10). Estimated mean clearance rates for the entire zooplankton community in August and September when rotifers and veligers were abundant ranged from 13.0 to 24.0 days (Table 10).

_Zebra Mussel Dynamics and Hydrodynamic Transport Processes._

In Chapter 1 I studied the dynamics of a shallow water, hard substrate zebra mussel population at 3 m on Peach Point Reef and evaluated zebra mussel _in situ_ competition for algae within the boundary layer. I made a comparative study of the effects of regional differences in transport processes delivering algae to benthic zebra mussels by comparing mussel populations at a series of habitats with graded levels of advection and turbulent mixing.

_Transfer Rate: Zebra Mussel Grazing_

I estimated impact of the mussel population at 3 m on Peach Point Reef (Figure 1) in May and September 1993 and for the mussel population at 12 m at U.S. Coast Guard Navigational Buoy (Red Can) at the NE end of Peach Point Reef. Using the length-frequency distribution for each date and my 1993 June, July, and September size-specific individual clearance rates (Table 11) I calculated a predicted zebra mussel impact (Table 12). I applied the date-specific "Clump Effect" (Table 7), to obtain a maximal estimate of population clearance impact. My maximal estimate of Peach Point Reef mussel population clearance rate was 9.7 m³ • m⁻² • d⁻¹ on 21 May and 1.4 m³ • m⁻² • d⁻¹ (Table 12) on 9 September 1993. For 31 July 1993 at the 12 m site a maximal population clearance rate estimate was 4.7 m³ • m⁻² • d⁻¹. These are much higher than the maximal clearance rate estimates of 0.4 to 0.7 m³ • m⁻² • d⁻¹ I calculated for the hard substrate
populations at Gull Island Shoal (Table 8). The Peach Point Reef population had higher population densities, 62,000 m$^{-2}$ in May and 40,000 m$^{-2}$ in September, than either the Gull Island Shoal populations or the Red Can 12 m which all had similar densities of about 20,000 m$^{-2}$ (Tables 2, 4). These extrapolations to large scale processes (a field estimate of population clearance rate) from a small scale measurements (individual mussel clearance rate) appear to be sensitive to both density, size-distribution, and seasonal values selected for individual clearance rates.

DISCUSSION

State Variable: Phytoplankton Dynamics

Although total algal biomass was clearly less after zebra mussel introduction, seasonal phytoplankton successional patterns typical of north temperate lakes without zebra mussels persisted after mussels became established in western Lake Erie. Diatoms still form spring and fall peaks and are dominant in the plankton throughout much of the summer as was the case when Lake was much more eutrophic in the 1970s (Munawar and Munawar 1976). Clearly, predictions that mussels would completely 'clear up' the lake have not been substantiated.

Holland (1993) observed an 82 to 91% drop in April and May diatom abundance (frustules · ml$^{-1}$) from 1990 to 1992 in Hatchery Bay even though nutrient levels were adequate (Holland et al. 1995). However, at my 5 m sampling site in Hatchery Bay I found that diatom biomass (ml · m$^{-3}$) decreased < 30 % from April and May 1991 to April and May in 1992. Differences in our findings at the same sampling location may simply reflect differences in reporting methods: count versus biomass data. Count data treat all taxa the same and do not reflect differences in size. In 1993 at the 12 m open

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water site diatoms were the dominant taxa on a biomass basis from May to September. Makarewicz et al. (1999), sampling on a broader scale report only a 50% decrease in diatom biomass in post-zebra mussel years in western Lake Erie. Additionally they also found that some algal taxa, Chrysophyceae and Pyrrhophyta, were not significantly different in biomass from the pre-zebra mussel invasion period. Although a minor component of the pelagic algae, I found increases in Chrysophyceae in post-zebra mussel invasion period. 

*Ceratium* was less abundant in 1991 and 1992 than in 1986, other smaller pyrrhophytes were common in 1993 at the open water 12 m site. Makarewicz et al. (1999) report a post-zebra mussel invasion shift in cyanobacteria patterns with a spring increase and a summer decline rather than major late summer blooms. They attribute the shift to differences in dominant cyanobacteria taxa. Although cyanobacteria were rare in my post-zebra mussel invasion samples they also persisted without forming a late summer nuisance bloom like that reported in 1986.

Changes in nutrient concentrations can account for shifts in algal species composition from previous higher abundances. High N:P ratios (> 16:1) favor Chlorophyta in mid to late summer over nitrogen-fixing species of cyanobacteria. Makarewicz et al. (2000) found that ammonia and N:P ratios (>30:1) increased significantly in post-zebra mussel invasion years. They attribute increases in ammonia and soluble reactive phosphorus to zebra mussel excretion and decreases in particulate phosphorus fraction of nutrients due to zebra mussel filtration and the subsequent formation of phosphorus-rich feces and pseudofeces. In offshore sites in western Lake Erie decreased phytoplankton biomass was not accompanied by the expected increases in Secchi transparency (Makarewicz et al. 1999). They link decreased transparency to increases in turbidity in the spring due to resuspension of inorganic particulate matter in the well-mixed western Lake Erie. In 1992 Secchi transparency increased greatly over
1991. However, water temperatures in 1992 were lower throughout much of the spring and early summer than in 1991 and this may have resulted in either a temporal shift in phytoplankton patterns or decreased phytoplankton production with accompanying increased transparency (Figure 6a).

Photosynthesis

Prior to this study the last published $^{14}$C primary production estimates for western Lake Erie were made in 1970 (Glooschenko et al. 1974, Vollenweider et al. 1974). They do not report station depths, but since they were characterizing the entire western basin (mean depth = 7.4 m) I have assumed that my 1993 photosynthesis rates measured at 2 m at my 12 m open channel site are equivalent to their “near surface” samples (equal parts 1 m and 5 m depth water) and have converted my primary production rates to the same units. They report mean monthly near surface photosynthesis rates for all stations on their cruise in western Lake. Their mean monthly photosynthesis rates ranging from 15 to 48 mg C \( \cdot m^{-3} \cdot h^{-1} \) for May to September 1970 while my mean monthly photosynthesis rates ranged from 13 to 29 mg C \( \cdot m^{-3} \cdot h^{-1} \) for the same months in 1993. Comparing these values would suggest that seasonal photosynthesis was 13% to 39% less than in 1970. Millard et al. (1996) report that Lake Ontario phytoplankton photosynthesis measured from May to October in 1992 was 30% less than that measured in 1972. International efforts to reduce phosphorus loading from the drainage basins in the intervening years may explain much of the decline in phytoplankton in western Lake Erie, although turnover can be very rapid for a small pool of algae not competing for phosphorus or nitrogen. Throughout my 1993 experiments
algae replaced their biomass at least once per day even during the clear-water phase of late June and early July when large-bodied cladocerans were abundant (Table 9).

**State Variable: Zooplankton Abundance and Biomass**

Seasonal zooplankton successional patterns in the western Lake Erie have persisted after mussel introduction (Culver et al. 1985, Phipps 1987). In all years the sharp decline in cladoceran abundance in July followed the phytoplankton clear-water phase in late June when phytoplankton community contained algal species less edible by large cladocerans. Subsequently, smaller-bodied cladocerans such as *Bosmina* and *Eubosmina* increased in number in late summer. For cladocerans, seasonal successional patterns appear to be similar in all years. Total cladoceran abundances were lower in 1991 (29 L\(^{-1}\)) and 1993 (28 L\(^{-1}\)) than 1986 (70 L\(^{-1}\)), but reached a similar peak in 1992 (63 L\(^{-1}\)). However, a major shift in the dominant taxa within the cladocerans occurred with between 1986 and 1991-1993. In 1986 small-bodied cladocerans made up > 70% of the cladocerans in mid June and early July, while in 1991-1993 *Bosmina* and *Eubosmina* represented < 25% when present with *Daphnia*. Another large-bodied cladoceran, *Diaphanosoma*, was rare in 1986 (1 L\(^{-1}\)), but much more abundant (9, 21, and 13 L\(^{-1}\)) in 1991, 1992, and 1993, respectively, reflecting a shift in species composition among the cladocerans. Rotifers appear to have actually increased in abundance from 1986 to 1991-93. In 1993 there was a major bloom of colonial rotifers in mid-July when veliger and adult zebra mussel abundances were also high. MacIsaac et al. (1995) report that adult zebra mussels (6-22 mm) in laboratory experiments could clear both their own veliger larvae and rotifers from 4 L beakers. Larger mussels had higher clearance rates than smaller mussels and were more effective in clearing smaller
rotifers (89 μm) than veligers (144 μm). Other microzooplankters who are more effective swimmers, such as copepod nauplii, were able to escape predation. Settling veligers would actually be delivered within range of adult filtration, but generally are > 250 μm when this occurs and may be able to avoid predation by being too large for most adult mussels to ingest. Rotifers, although poor swimmers, generally do not overlap spatially with adult zebra mussels in the lake. Thus, since benthic adult mussels are dependent on turbulent mixing processes to delivery rotifers within pumping range of their inhalant siphon, in actual practice it is unlikely that predation by adult mussels will significantly impact pelagic rotifers.

*Transfer Rates: Zooplankton and Veliger Grazing*

Zooplankton grazing is a function of body size (Haney 1985). Large-bodied Cladocera contribute more to community grazing pressure than smaller Cladocera or copepods or rotifers (Haney 1973, Bogdan and Gilbert 1982, Lampert 1988, Wu and Culver 1991). Although the years post-zebra mussel introduction had fewer total cladocerans, suggesting decreased grazing impact, the differences in species composition among cladocerans present may be crucial to evaluating changes in zooplankton grazing impact on phytoplankton dynamics relative to that of zebra mussel grazing. In June and early July in 1986 there were more small-bodied cladocerans (*Rosmina* and *Eubosmina*) present than *Daphnia*. In 1991-1993 samples large-bodied cladocerans (*Daphnia* and *Diaphanosoma*) were more abundant than smaller cladocerans suggesting that cladoceran grazing impact has not dropped and the distinctive clear-water phase seen in late June reflect overgrazing by large-bodied cladocerans. Wu and Culver (1991) found that large cladocerans contributed more than 85% of the grazing rates measured in their *in situ* ³²P-labeled yeast clearance experiments and that grazing by *Daphnia* alone was sufficient to
overgraze edible phytoplankton and result in the clear-water phase. Wu and Culver (1991) report clearance rates for the large cladoceran (Daphnia and Diaphanosoma) portion of the zooplankton community of 156.7 ml L⁻¹ d⁻¹ at an abundance of 32.8 L⁻¹. Knoechel and Holthby (1986) report that even when Lake St. George was dominated by small cladocerans, larger cladocerans, such as Daphnia and Diaphanosoma, accounted for 33% of the community filtering rate. I found that zooplankton community grazing rates generally correlated with changes in the large cladoceran population that increased during June and reaching a maximum in mid July when the time for the zooplankton community to theoretically turnover the entire water column was fastest (2.4 d). After the middle of August, community grazing rates throughout the water column were low and turnover times slow (13 to 24 d). In August the zooplankton community in the experiments consisted of predominantly rotifers (>75%), small cladocerans, and very few veligers (2-6%).

Zebra mussel larvae are most abundant in western Lake Erie during July and August when phytoplankton levels are low, especially small algae. Sprung (1989) investigated the high mortality of European zebra mussel larvae. From cage experiments he found that predation was not the only cause of the high mortality. He postulates that starvation may be a major factor in the high larvae mortality since zebra mussel larvae consume primarily picoplankton, consisting of bacteria, cyanobacteria, and small algae in a very narrow size range (1 to 4 μm in diameter)

My clearance rates for veligers 91 to 242 μm measured using ³²P-labeled yeast ranged from 0.001 to 0.144 ml ind⁻¹ d⁻¹ while MacIsaac et al. (1992) using suspensions of beads obtained much higher clearance rates (0.247 to 0.420 ml ind⁻¹ d⁻¹) for similar sized veligers (100-240 μm). Sprung (1989) reports that veligers feed
on a narrow size range of particles between 1-4 μm therefore, both yeast cells (2-4 μm) and the unflavored beads (2.87 μm) were appropriately sizes for veligers. MacIsaac et al. (1992) estimated veliger gut passage time of 14 to 18 minutes and kept their bead exposure time to 5 minutes. Similarly, I used an 8 min veliger feeding period on 32P-labeled yeast so that labeled yeast cells would be retained in the gut. However, my study and theirs differ significantly in our estimates of the potential impact of veliger clearance rate on phytoplankton. MacIsaac et al. (1992), estimated veligers could clear 20% of the water column daily. I measured both the total zooplankton community clearance rates and the veliger clearance rates in situ so that I have been able to estimate potential veliger grazing impact relative to that of the entire zooplankton community. I measured maximum zooplankton community clearance rates on 14 July of 476 (±69.5) ml • L⁻¹ • d⁻¹ at 4 m and 468 (±112.3) ml • L⁻¹ • d⁻¹ at 6 m (Figure 55). Large cladocerans abundances for Daphnia and Diaphanosoma were 10.6 L⁻¹ at 4 m and 9.3 L⁻¹ at 6 m while veliger abundances were 76.2 L⁻¹ at 4 m and 144 L⁻¹ at 6 m. ml • L⁻¹ • d⁻¹ of total community clearance rate. Veliger clearance accounts for only 1.9% of the total community clearance rate at 4 m and for 3.2% at 6 m. The maximum veliger density I observed in 1993 occurred on 5 Aug 1993 night samples, when veligers were numerically dominant at 4 m (791 L⁻¹) and most of the other zooplankters consisted of small rotifers. At 4 m the total veliger clearance of 22.64 ml • L⁻¹ • d⁻¹ was only 7.1% of the total zooplankton community clearance rate (318.45 ml • L⁻¹ • d⁻¹). Additionally, veliger density varied greatly with depth (44 to 791 L⁻¹) and the proportion of the total community clearance impact due to veligers also varied widely 1.0% (2 m), 7.1% (4 m), 5.0% (6 m), and 1.4% (8 m). To further emphasize the effects of the high
variation in veliger distribution and abundance with the water column, 12 h earlier during day zooplankton community clearance experiments at the same site, 5 August veliger density at 4 m was only 90 L⁻¹ and a maximum of 161 veligers L⁻¹ at 6 m. In fact, although I measured zooplankton community grazing rates I had insufficient veligers in my daytime 5 August replicate samples to sort specimens for veliger clearance rate measurements. In addition, veligers were more commonly found at depths >6 m while most photosynthesis occurred at depths < 5 m. Thus, even when seasonally abundant, zebra mussel veligers grazed pelagic algae at an insignificant rate relative to other zooplankton.

Transfer Rate: Zebra Mussel Grazing

Initial concern about zebra mussels was that their reported high filtration capacity at high densities would divert energy flow from pelagic communities to the benthos, causing zooplankton to decline, impacting the forage basis for important sport fisheries in the Great Lakes. Initial estimates of zebra mussel impact were based on limited data and a lack of understanding about how hydrodynamic transport functions to deliver pelagic algae to benthic mussels through a coupling of physical and biological processes. The degree to which zebra mussels can deplete pelagic zone algae depends upon the rate of delivery of algae to the benthos and the development of a concentration boundary layer above the mussel beds.

Although benthic zebra mussels were viewed as competitors with zooplankton for the same sizes of pelagic phytoplankton, their location and high densities greatly reduce their actual impact on pelagic algae. Using 31 July 1993 zebra mussel population size distribution at the 12 m site and 14-15 July size-specific mussel grazing rates and the "Clump Effect" correction, I estimated a maximal zebra mussel population clearance
impact of 4.7 m³ m⁻² d⁻¹ (Table 12). Similarly, the zooplankton community clearance impact on 14 July was 4.9 m³ m⁻² d⁻¹ (Table 10). However, mobile zooplankters are up in the water column with immediate access to the algae while benthic adult mussels are sedentary and dependent on turbulent mixing processes to deliver sedimenting algae to them. Sedentary adult mussels compete with each other for algae since 20 to 60 mussels in a clump consumed an average of 70% less algae than the same-sized mussels feeding separately, suggesting that mussels in natural, high density aggregations in the lake would have far lower consumption impact than these estimates. Furthermore, mussels in bottom cages in the boundary layer added only 10% to 20% as much soft-tissue biomass as those farther up in the water column again providing evidence that mussel growth depends on the rate of delivery of pelagic algae to the benthos and on competition with other mussels in the colony (Chapter 1). While the actual magnitude of the real “clump” effect in natural benthic mussel population is not known, it seems likely that even my maximal estimate zebra mussel population clearance impact of 4.7 m³ m⁻² d⁻¹ is an overestimate by an order of magnitude, and possibly by several orders of magnitude.

A mussel’s location within the boundary layer can determine the quantity and quality of its food supply and its rate of growth (Frechette and Bourget 1985b, Frechette et al. 1989). Zebra mussel grazing activity can cause a localized zone of depletion near the mussel bed due to slow replenishment rates and the effects of refiltration (O’Riordan et al. 1993, 1995). Water exiting the mussels has had seston removed and fecal material added. Depending on the degree of mixing with the surrounding water, refiltration of previously filtered water and feces and pseudofeces can occur, diluting available seston and potentially lowering food quality. Energy spent in refiltration and processing lower
quality food may result in decreased energy available for growth and translate into lower individual and population biomass. Clusters of mussels thus have to compete with adjacent mussels for food decreasing the effective clearance rates of the entire group. In flume experiments with model bivalves O’Riordan et al. (1995) report refiltration fractions as high as 48% and increased refiltration at higher animal densities. The vertical feeding height (e.g., position of the incumbent siphon height above the bottom) attained by an organism (Jumars and Nowell 1984, Monismith et al. 1990) and the orientation of a bivalve’s siphons (Monismith et al. 1990) allow some mussels within a cluster to feed efficiently and others to be deprived, inefficiently filtering previously processed water. Caged zebra mussels higher up in the water column had more shell growth those at the bottom in high density colonies where competition for space and food was greater (Chapter 1). Peterson and Beal (1989) and Kautsky (1982) found that local food depletion and high population densities are associated with reduced growth in the benthic suspension-feeding marine bivalves. At the 12 m site the highest zebra mussel cages were located at 2 m above the bottom, a depth that corresponds to the 10 m photosynthesis incubation depth. Minimal photosynthesis occurred at 10 m depth and photosynthesis appeared to be light-limited. However, mussels feeding in cages at that depth still had enhanced growth over that of mussels at the bottom.

Although algal abundance was lower after zebra mussel introduction, zebra mussel grazing has not overwhelmed the phytoplankton community, providing further evidence that benthic zebra mussel impact has not been as great as predicted. The seasonal successional patterns of pelagic algae have persisted and reflect nutrient cycles and grazing by pelagic herbivorous zooplankters. Nutrient changes observed can account for lower nitrogen-fixing cyanobacteria in late summer. Small green algae forming much of the forage base for zooplankters are favored by the high N:P ratios I
observed. Increased water transparency has been credited to the filtration actions of zebra mussels removing particulate matter from the water (Reeders and Bij de Vaate 1990). Secchi depths have increased from pre-zebra mussel introduction years, transparency (light penetration) has been altered not only by changes in phytoplankton biomass in the water column, but also by changes in all suspended and dissolved material. However, nutrient loading to the basin has been altered and N:P ratios in the lake favor green algae (Chlorophyta) over forms of cyanobacteria that can fix nitrogen.

Clearly, neither zooplankton nor zebra mussel grazing has overwhelmed pelagic phytoplankton production. However, zebra mussels and zooplankters are not equally successful competitors for pelagic algae. Zooplankters by their mobility and location in the water column have better access to pelagic algae. Mussels in natural, high density aggregations in the lake would have far lower consumption impact since they are dependent on turbulent mixing process for algal delivery. The impact of zebra mussels on pelagic phytoplankton (and consequently on zooplankton) has been less than predicted because mussel grazing and growth are limited by turbulent mixing characteristics within the water column.

Alternative Energy Sources

If zebra mussels are not directly depleting pelagic phytoplankton and are dependent on transport processes to delivery pelagic algae to them, what other energy sources are supporting the large benthic biomass? Bacteria, protozoans, and benthic algae are several potential energy sources that zebra mussel may be utilizing that I did not evaluate in my study. Bacteria may potentially serve as an alternative energy source for zebra mussel adults and veligers (Sprung and Rose 1988, Silverman et al. 1996). Sprung and Rose (1988) found that adult zebra mussel could clear particles as small as
0.7 \mu m and Sprung (1989) reports that veliger feed almost exclusively on particles between 1-4 \mu m. Frischer et al. (2000) found that while mussel could use bacteria as food, it was more likely that mussels would use detrital or sediment bacteria than free-living forms. Cotner et al. (1995) found that mussels could selectively removed larger bacteria (> 0.9 \mu m) more effectively than smaller sized bacteria. Although Cotner et al. (1995) estimated that zebra mussels should have been able to clear the entire 3 m water column of bacteria in less than 1.6 days, the overall impact of mussel grazing on bacteria in the shallow, eutrophic inner Saginaw Bay, Lake Huron is unclear. Bacterial abundances did not decline as predicted with increasing zebra mussel abundance over a 3 year period. They speculate that either bacterial production exceeds grazing losses or mussels do not clear the entire 3 m water column as assumed or that both may be occurring. The production of feces and pseudofeces by zebra mussels may actually enhance microbial communities.

Protozoa may also provide an alternative energy source for zebra mussels. Lavrentyev et al. (1995) found that in bottle clearance experiments weak-swimming, non-flagellated protozoans were unable to escape the mussel’s inhalant siphon currents and were most susceptible to zebra mussel predation. However, it is unclear whether real world zebra mussels would experience similar success as protozoan predators.

Potentially benthic algae may also be utilized by benthic zebra mussels. Zebra mussels are known to graze a broad size range of planktonic algae preferentially 15-45 \mu m, but in all sizes up to 750 \mu m (Ten Winkel and Davids 1982). However, there are no published data currently available to indicate that zebra mussels consume benthic algal species. Following zebra mussel colonization, Lowe and Pillsbury (1995) report both increased benthic algal biomass and a taxonomic shift from predominantly diatoms
to chlorophytes due to increases in the amount of light available due to increased water clarity in the shallow, inner Saginaw Bay, Lake Huron.

Conclusions

The issue of zebra mussel impact on pelagic food webs becomes one of scale, and direct versus indirect effects. Extrapolations from small scale measurements (individual mussel clearance rate, growth, recruitment, and survival) to large scale processes (a field estimate of population clearance rate, lake-wide transport processes) must be done cautiously with full awareness of the limitations of the approach. One must not only identify spatial and temporal scales that separate benthic and pelagic interactions, but also consider the role of vertical and horizontal transport processes occurring within the lake that provide the actual coupling.

Free-swimming planktonic veligers are directly linked spatially and temporally to pelagic phytoplankton. Nevertheless, even when seasonally abundant, veligers’ clearance impact was insignificant relative to that of other zooplankters leaving only adult mussels to significantly impact pelagic algae. However, benthic adult mussels are not directly linked to pelagic processes since they are separated spatially and temporally from the pelagic phytoplankton production and dependent on the coupling of biological and hydrodynamic process to deliver food to them. Thus, the mussels’ impact is localized, at the level of the mussel bed, and only directly affecting seston within the benthic boundary layer.

Zebra mussel impact is restricted to the water adjacent to them. Even if they remove seston faster than it is replaced, their impact is localized and dependent on hydrodynamic processes to replenish seston removed from the boundary layer. Additionally, zebra mussels in high density natural aggregations compete with adjacent
mussels for food and refiltration of water previously filtered means mussels encounter a seston of degraded quality that includes not only settling pelagic algae but also pseudofeces and feces. Different location have different flow characteristics effecting the hydrodynamic transport of algae to the benthos. Mussel populations have a site-specific response to localized algal delivery rates so that some locations represent better environments than others. Thus, the hydrodynamic-seston interaction determines zebra mussel growth, recruitment, and mortality and, ultimately, the limited, indirect impact that benthic mussels have on pelagic food webs.
Table 1. Zebra mussel cage growth experiments: Variations in locations, incubation depths, mussel densities, and duration at 3 m and 12 m sites in western Lake Erie, 1991 and 1992, and at a 12 m site in thermally-stratified Hargus Lake, 1993. Replicate groups of individually tagged and measured mussels were placed in cylindrical, plastic mesh cages (10 cm diameter, 27 cm length) on buoyed lines (Figure 2) at densities equivalent to 1250 • m⁻² (LOW) and 2500 • m⁻² (HIGH).
<table>
<thead>
<tr>
<th>Year</th>
<th>Location</th>
<th>Site Depth</th>
<th>Cage Depths</th>
<th>Mussel Density</th>
<th>Start Date</th>
<th>Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>1991</td>
<td>Lake Erie</td>
<td>above lake bottom, m</td>
<td>3 0.0, 0.5, 1.0</td>
<td>2500</td>
<td>25 May</td>
<td>126</td>
</tr>
<tr>
<td></td>
<td>Line</td>
<td>NW off Gibraltar Is.</td>
<td>3 0.0, 0.5, 1.0</td>
<td>“</td>
<td>1 June</td>
<td>119</td>
</tr>
<tr>
<td></td>
<td></td>
<td>“</td>
<td>3 0.0, 0.5, 1.0, 1.5</td>
<td>“</td>
<td>12 July</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>RC</td>
<td>Red Can NE off Peach Point Reef</td>
<td>12 0.0, 0.5</td>
<td>“</td>
<td>3 July</td>
<td>88</td>
</tr>
<tr>
<td></td>
<td>LAB</td>
<td>Lab</td>
<td>in aquarium with flow-through Lake Erie water</td>
<td>“</td>
<td>14 July</td>
<td>76</td>
</tr>
</tbody>
</table>

| 1992 | Lake Erie| above lake bottom, m | 1,2,3 0.0, 0.5, 1.0, 1.5 | 1250          | 26 June     | 60       |
|      | LOW      | NW off Gibraltar Is. | 4,5,6 “           | 2500          | “           | “        |
|      | HIGH     | “           | 7 RED Can NE off Peach Point Reef | 12 0.0, 0.5, 1.0, 1.5, 2.0 | 1250        | “        |
|      | LOW      | “           | 8 RED Can NE off Peach Point Reef | 12 “           | 2500        | “        |

| 1993 | Hargus Lake| depth in lake, m | 1,2,3 2, 4, 6, 8 | 1250          | 25 April    | 131      |

Table 1
Table 2. Zebra Mussel demographics for mussel populations from 3 m on Peach Point Reef, western Lake Erie from 1991 to 1994. Population density (individuals • m⁻²) and soft tissue biomass (g dry mass • m⁻²) were estimated based on mean of replicate, quantitative samples (n) collected using randomly selected quadrats (25 cm² in 1991-1993; 64 cm² in 1994, 1998). Quagga mussels were observed in non-quantitative samples during 1991 to 1993. Quagga mussels represented < 0.5% of the mussel population in 1994, but 33% of mussel population in 1998. Regression parameters used to estimate population soft tissue mass for each date are given in Table 3.
<table>
<thead>
<tr>
<th>Date</th>
<th>Mean Shell Length (mm)</th>
<th>Minimum Shell Length (mm)</th>
<th>Maximum Shell Length (mm)</th>
<th>Population Density # · m⁻² (SE)</th>
<th>Population Biomass g · m⁻² (SE)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 September 1991</td>
<td>8.4 (0.09)</td>
<td>2.2 - 25.3</td>
<td>1.8 (0.05)</td>
<td>68,080 (4280)</td>
<td>128 (6)</td>
<td></td>
</tr>
<tr>
<td>21 May 1992</td>
<td>8.8 (0.09)</td>
<td>1.6 - 25.9</td>
<td>4.0 (0.13)</td>
<td>81,850 (5339)</td>
<td>329 (15)</td>
<td></td>
</tr>
<tr>
<td>14 September 1993</td>
<td>10.4 (0.08)</td>
<td>2.2 - 25.4</td>
<td>3.0 (0.50)</td>
<td>63,745 (4159)</td>
<td>192 (8)</td>
<td></td>
</tr>
<tr>
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<td>11.3 (0.09)</td>
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Table 2
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<td>2.4697</td>
<td>0.963</td>
<td>70</td>
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Table 3. Date-specific, shell length-dry soft tissue mass regression parameters for the zebra mussel population at 3 m on Peach Point Reef, western Lake Erie, from 1991-1994, 1998. For 1998 there are separate regressions parameters for zebra mussels and quagga mussels. \( W = aL^b \) where \( W = \) dry soft tissue mass (mg dry mass), \( L = \) shell length (mm). Date specific parameters: \( a, b \) = constants, \( r^2 = \) Coefficient of Determination, \( n = \) number of mussels, range = minimum and maximum shell lengths (mm) in sample. Sampling location is shown in Figure 1.

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Table 3 continued.

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<tr>
<th>Date</th>
<th>Water Temperature $^\circ$C</th>
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<th>b</th>
<th>$r^2$</th>
<th>n</th>
<th>Range in Lengths (mm)</th>
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Table 4. The effects of substrate type and depth on zebra mussel demographics for mussel populations in western Lake Erie on 19 Aug. 1993. Sampling locations are shown in Figure 1. Peach Point Reef 12 m site sampled on 31 July 1993. Population density (individuals • m⁻²) and soft tissue biomass (g dry mass • m⁻²) were estimated based on mean of replicate, quantitative samples collected using randomly selected 64 cm² quadrat at each location. n = number of samples. No mussels were collected at the three locations marked a. Regression parameters used to estimate population soft tissue biomasses are given in Table 5.
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<th>Location</th>
<th>Substrate</th>
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<th>Depth</th>
<th>Mean Shell Length mm (SE)</th>
<th>Minimum-Maximum Length mm</th>
<th>Mean Mussel Biomass mg (SE)</th>
<th>Population Density # • m$^{-2}$ (SE)</th>
<th>Population Biomass g • m$^{-2}$ (SE)</th>
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<td>3</td>
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<td>91 (19)</td>
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<td>5</td>
<td>6</td>
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<td>4.1 - 23.9</td>
<td>4.0 (0.45)</td>
<td>6,406 (910)</td>
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Table 4
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<th>r²</th>
<th>n</th>
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Table 5. Shell length-dry soft tissue mass regression parameters for zebra mussel populations on a variety of substrates and at different depths in western Lake Erie on 19 Aug. 1993. Peach Point Reef 12 m site sampled on 31 July 1993. $W = aL^b$ where $W =$ dry soft tissue mass (mg dry mass), $L =$ shell length (mm). Date specific parameters: $a$, $b =$ constants, $r^2 =$ Coefficient of Determination, $n =$ number of mussels, range = minimum and maximum shell lengths (mm) in sample. Sampling locations are shown in Figure 1.
<table>
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<th>Size Class</th>
<th>Abundance (# mussels)</th>
<th>Mean Individual Grazing Rate (mg • ind⁻¹ • d⁻¹ (SE))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clump 1</td>
<td>Clump 2</td>
</tr>
<tr>
<td>&lt; 5 mm</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>5 - 10 mm</td>
<td>14</td>
<td>27</td>
</tr>
<tr>
<td>10 - 15 mm</td>
<td>15</td>
<td>6</td>
</tr>
<tr>
<td>15 - 20 mm</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>20 - 25 mm</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>25 &gt; mm</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>35</strong></td>
<td><strong>41</strong></td>
</tr>
</tbody>
</table>

Table 6. Observed grazing rates for natural clumps of zebra mussels (10 g wet mass) and predicted grazing rates calculated using clump size frequency distribution and mean individual grazing rates (±SE) measured for detached mussels of the same size classes filtering independently. Individual grazing rates (IGR) were measured for separated mussels in four size classes between 5 and 25 mm shell length, e.g. the 15-20 mm size class = 15 mm ≤ shell length (SL) < 20 mm included mussels between 15.0 and 19.9 mm shell length. IGRs of adjacent size classes were used for clump predictions for mussels < 5 mm and 25 > mm. Data are from a 24 h experiment 12-13 Aug 1992: natural seston concentration = 2.07 mg • L⁻¹ and temperature = 24°C.
<table>
<thead>
<tr>
<th>Date</th>
<th>Seston mg L⁻¹</th>
<th>Observed(SE)</th>
<th>Predicted (SE)</th>
<th>% O : P</th>
</tr>
</thead>
<tbody>
<tr>
<td>27 - 28 May 1992</td>
<td>1.50</td>
<td>5.56 (0.620)</td>
<td>25.43 (0.623)</td>
<td>21.9</td>
</tr>
<tr>
<td>21 - 22 July</td>
<td>4.71</td>
<td>12.42 (3.195)</td>
<td>41.40 (1.610)</td>
<td>30.0</td>
</tr>
<tr>
<td>12 - 13 August</td>
<td>2.07</td>
<td>7.34 (0.284)</td>
<td>15.97 (0.861)</td>
<td>46.6</td>
</tr>
<tr>
<td>24 - 25 June 1993</td>
<td>3.42</td>
<td>13.58 (0.903)</td>
<td>67.16 (1.487)</td>
<td>20.2</td>
</tr>
<tr>
<td>13 - 14 July</td>
<td>1.73</td>
<td>14.23 (1.725)</td>
<td>44.96 (2.235)</td>
<td>31.7</td>
</tr>
<tr>
<td>16 - 17 Sept.</td>
<td>1.75</td>
<td>2.14 (0.600)</td>
<td>6.18 (0.174)</td>
<td>34.6</td>
</tr>
</tbody>
</table>

Mean 30.8

Table 7. Observed and predicted grazing rates for natural clumps of Lake Erie zebra mussels during 1992 and 1993. Data are observed and predicted clump means (± SE) calculated using date-specific individual grazing rates as per example in Table 6.
Table 8. Variation in estimated zebra mussel clearance rates as a function of depth and population density at Gull Island Shoal, western Lake Erie, August 1993. Population clearance rate estimates from this study based on biomass used regression of clearance rate (CR, L • ind⁻¹ • d⁻¹) on soft tissue dry mass (DM in mg) from 16-17 September 1993 zebra mussel grazing experiment (Figure 18). CR = 0.0453 + 0.0159 DM. Biomass at each depth was estimated for each measured individual using the depth specific regression parameters (Table 5). Population clearance rate estimates based on shell length used mussel size frequency distribution for each depth at Gull Island Shoal and mean individual clearance rates for separated mussels in four size classes between 5 and 25 mm shell length (5-10 mm: CR = 0.0309 L • ind⁻¹ • d⁻¹, 10-15 mm: CR = 0.1147, 15-20 mm: CR = 0.1992, 20-25 mm: CR = 0.3765). For Gull Island Shoal mussels < 5 mm or > 25 mm mean clearance rates of adjacent size classes were used. “Clump Effect” correction of 30.8% (Table 7) adjusts clearance rate estimate for lower clearance rates of natural clusters of mussels. Estimated population clearance rate using three other methods: Single value approach used clearance rate, 0.8 L • ind⁻¹ • d⁻¹, from Stanczkowska et al. (1975) and population density from this study. Kryger and Riisgard’s (1988) equation for clearance rate (CR, L • ind⁻¹ • d⁻¹) on soft tissue dry mass (DW in g) was used with biomass from this study. In last approach Kryger and Riisgard’s (1988) biomass-shell length regression equation was used with size-frequency distribution from this study and then their clearance rate equation was used to estimate population impact. CR = 6.814 DW⁰.⁸⁸ and DW = 1.54 • 10⁻⁵ SL⁻².⁴², where DW = soft tissue dry mass in g and SL = shell length in mm.
<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Mussel Density # ( \cdot ) m(^{-2})</th>
<th>Based on Shell Length</th>
<th>Based on Biomass</th>
<th>Corrected for &quot;Clump Effect&quot;</th>
<th>Single value Approach, Density from this study</th>
<th>Kryger and Riisgard</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>18094</td>
<td>2.2</td>
<td>2.3</td>
<td>0.7</td>
<td>14.5</td>
<td>CR = 6.814DM(^{0.88})</td>
</tr>
<tr>
<td>6</td>
<td>19938</td>
<td>1.2</td>
<td>1.8</td>
<td>0.4</td>
<td>16.0</td>
<td>DW = 1.54(\cdot)10(^{-5}) SL(^{2.42})</td>
</tr>
<tr>
<td>9</td>
<td>20312</td>
<td>1.7</td>
<td>2.2</td>
<td>0.5</td>
<td>16.3</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>21344</td>
<td>1.3</td>
<td>1.7</td>
<td>0.4</td>
<td>17.1</td>
<td></td>
</tr>
</tbody>
</table>

Table 8.
<table>
<thead>
<tr>
<th>Date</th>
<th>Photosynthesis g C m⁻² d⁻¹</th>
<th>Phytoplankton Biomass g C m⁻²</th>
<th>Photosynthesis: Biomass % d⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>8 May</td>
<td>1.60</td>
<td>1.40</td>
<td>114</td>
</tr>
<tr>
<td>15 May</td>
<td>0.64</td>
<td>0.34</td>
<td>189</td>
</tr>
<tr>
<td>22 May</td>
<td>1.14</td>
<td>1.01</td>
<td>113</td>
</tr>
<tr>
<td>12 June</td>
<td>2.81</td>
<td>2.24</td>
<td>125</td>
</tr>
<tr>
<td>23 June</td>
<td>1.02</td>
<td>0.74</td>
<td>138</td>
</tr>
<tr>
<td>30 June</td>
<td>0.21</td>
<td>0.20</td>
<td>103</td>
</tr>
<tr>
<td>8 July</td>
<td>1.00</td>
<td>0.90</td>
<td>112</td>
</tr>
<tr>
<td>15 July</td>
<td>2.68</td>
<td>1.60</td>
<td>168</td>
</tr>
<tr>
<td>21 July</td>
<td>2.40</td>
<td>1.08</td>
<td>222</td>
</tr>
<tr>
<td>28 July</td>
<td>2.67</td>
<td>1.55</td>
<td>172</td>
</tr>
<tr>
<td>9 August</td>
<td>2.77</td>
<td>1.64</td>
<td>168</td>
</tr>
<tr>
<td>18 August</td>
<td>1.59</td>
<td>0.91</td>
<td>175</td>
</tr>
<tr>
<td>23 August</td>
<td>0.73</td>
<td>0.50</td>
<td>146</td>
</tr>
<tr>
<td>17 September</td>
<td>1.27</td>
<td>0.72</td>
<td>176</td>
</tr>
</tbody>
</table>

Table 9. Temporal variation in mean photosynthesis (primary production, g C m⁻² d⁻¹), biomass (algal standing crop, g C m⁻²), and turnover rate at a 12 m site, western Lake Erie, 1993.
<table>
<thead>
<tr>
<th>Date</th>
<th>Zooplankton Estimated Clearance Impact</th>
<th>Turnover Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>14 June</td>
<td>1.7</td>
<td>6.9</td>
</tr>
<tr>
<td>22 June</td>
<td>2.0</td>
<td>6.1</td>
</tr>
<tr>
<td>30 June</td>
<td>2.0</td>
<td>5.6</td>
</tr>
<tr>
<td>7 July</td>
<td>2.6</td>
<td>4.6</td>
</tr>
<tr>
<td>14 July</td>
<td>4.9</td>
<td>2.4</td>
</tr>
<tr>
<td>20 July</td>
<td>2.9</td>
<td>4.1</td>
</tr>
<tr>
<td>5 August Day</td>
<td>3.0</td>
<td>4.0</td>
</tr>
<tr>
<td>5 August Night</td>
<td>3.0</td>
<td>4.0</td>
</tr>
<tr>
<td>17 August</td>
<td>0.7</td>
<td>17.6</td>
</tr>
<tr>
<td>30 August</td>
<td>0.9</td>
<td>13.2</td>
</tr>
<tr>
<td>9 September</td>
<td>0.9</td>
<td>13.0</td>
</tr>
<tr>
<td>17 September</td>
<td>0.5</td>
<td>24.0</td>
</tr>
</tbody>
</table>

Table 10. Temporal variation in mean estimated zooplankton community clearance impact (m³ · m⁻² · d⁻¹) and turnover time (d) at a 12 m site, western Lake Erie, 1993.
<table>
<thead>
<tr>
<th>Size Class</th>
<th>24-25 June</th>
<th>13-14 July</th>
<th>16-17 Sept.</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 5 mm</td>
<td>0.031</td>
<td>0.031</td>
<td>0.031</td>
</tr>
<tr>
<td>5 - 10 mm</td>
<td>0.279</td>
<td>0.404</td>
<td>0.031</td>
</tr>
<tr>
<td>10 - 15 mm</td>
<td>1.148</td>
<td>0.404</td>
<td>0.115</td>
</tr>
<tr>
<td>15 - 20 mm</td>
<td>0.904</td>
<td>0.975</td>
<td>0.199</td>
</tr>
<tr>
<td>20+ mm</td>
<td>0.904</td>
<td>1.371</td>
<td>0.377</td>
</tr>
</tbody>
</table>

Table 11. Individual clearance rates (ICR) for separated mussels in four size classes between 5 and 25 mm shell length during 1993 grazing experiments. Size class notation 15-20 mm = 15 mm ≤ shell length (SL) < 20 mm included mussels between 15.0 and 19.9 mm shell length. ICRs of adjacent size classes were used for mussels > 25 mm. September mean ICR for mussels 5 - 10 mm was used for mussels < 5 mm on all dates. Data are means from a 24 h experiment on each date.
<table>
<thead>
<tr>
<th>Location</th>
<th>Date</th>
<th>Depth</th>
<th>Based on Shell Length</th>
<th>Corrected for “Clump Effect”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peach Point Reef</td>
<td>21 May 1993</td>
<td>3</td>
<td>46.9</td>
<td>9.7</td>
</tr>
<tr>
<td></td>
<td>9 Sept 1993</td>
<td>3</td>
<td>4.0</td>
<td>1.4</td>
</tr>
<tr>
<td>Navigational Buoy:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red Can</td>
<td>31 July 1993</td>
<td>12</td>
<td>14.9</td>
<td>4.7</td>
</tr>
</tbody>
</table>

Table 12. Maximal zebra mussel population clearance rate impact estimates for two hard substrate mussel population in western Lake Erie, 1993. Estimates used size frequency distribution on each date and size-specific clearance rates of individual mussels (Table 11). “Clump Effect” correction (Table 7) adjusts population clearance rate estimate for lower clearance rates of natural clusters of mussels during grazing experiments on each date.
APPENDIX B

Figures
Figure 1. Locations of sampling sites, western Lake Erie. Insert shows primary study sites 1991-1994. Peach Point Reef extends northeast from Peach Point on the north side of South Bass Island towards the U.S. Coast Guard navigational buoy (solid dot •) near my 12 m in situ cage experiment site. The solid dot (●) in Hatchery Bay marks a 5 m sampling station west of my 3 m in situ cage experiment site. Other sites sampled only on 19 Aug. 1993.
Sampling Sites

Lake Erie
Figure 2. Arrangement of polyethylene mesh cages used in a typical zebra mussel growth experiment in Lake Erie. Cages were suspended from a buoyed line at 0.5 m intervals above the lake bottom.
Figure 3. Temporal changes in density and biomass of the zebra mussel population from 3 m on Peach Point Reef, western Lake Erie, 1991-1994. Population density (individuals • m^-2) and soft tissue biomass (g dry mass • m^-2) were estimated based on mean of replicate, quantitative samples collected using randomly selected 25 cm^2 quadrats on each date except 1994 when 64 cm^2 quadrats were used (Table 2). Regression parameters used to estimate population soft tissue biomass for each date are given in Table 3. Bars = size frequency distribution of mean population density within each size class (2 mm intervals, data plotted at midpoint, e.g. 7 mm for size class 6.0 ≤ shell length < 8.0 mm) for each date. Circles = size frequency distribution of mean population biomass within each size class for each date. Error bar is one standard error of mean (SE).
Figure 4. a) Shift in density distribution (individuals • m^-2) of the Peach Point Reef mussel population from 3 m, western Lake, from May 1992 to May 1998. Quagga mussels were < 0.5% in 1994, but represented 33% of May 1998 mussel population. b) Density of zebra and quagga mussel by size class in May 1998. Bars = size frequency distribution of mean population density within each size class (2 mm intervals, data plotted at midpoint. e.g. 7 mm for size class 6.0 ≤ shell length < 8.0 mm). Open bars = zebra mussel. Striped bars = quagga mussel.
Figure 4
Figure 5. Seasonal and annual changes in biomass of a mean-sized zebra mussel (shell length = 13.9 mm) from the Peach Point Reef zebra mussel population, 1991-1994. Data are adjusted means (± SE) from ANCOVA, covariate=shell length. Date specific, shell length-dry soft tissue mass regression parameters are given in Table 3.
Figure 5

Soft Tissue Mass (mg dry mass)

May June July Aug Sept Oct

1991 △
1992 □
1993 ○
1994 ▽
Figure 6. Seasonal variation in a) water temperature (°C) in 1991-1994 and b) total phytoplankton volume (ml • m⁻³) from April to October 1991 and 1992 based on integrated water column sample from 0 to 3 m taken at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Volume may be converted to biomass (g • m⁻³) by assuming a specific gravity for algae =1.0.
Figure 6
Figure 7. Seasonal changes in phytoplankton volumes (ml • m$^{-3}$) of abundant taxa from April to October of 1991 in an integrated water column sample from 0 to 3 m taken at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Volume may be converted to biomass (g wet weight • m$^{-3}$) by assuming a specific gravity for algae = 1.0.
Figure 8. Seasonal changes in phytoplankton volumes (ml • m⁻³) of abundant taxa from April to September of 1992 in an integrated water column sample from 0 to 3 m taken at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Volume may be converted to biomass (g wet weight • m⁻³) by assuming a specific gravity for algae =1.0.
Figure 9. a) Seasonal lake Secchi depths (m), 1991 (dash line) and 1992 (solid line), and b) 1992 mean total seston (●) and organic seston (○) concentrations (mg dry mass • L⁻¹) at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Seston concentrations are for integrated water column samples from 0 to 3 m.
Figure 9
Figure 10. Representative pattern of zebra mussel growth as added shell length (mm) for mussels of different sizes suspended in cages at different depths (0.5 m intervals) at a 3 m site. Data are from Line 3 1991 cage experiments in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. The 287 surviving Line 3 mussels had mean initial shell length = 15.7 mm and mean added shell length = 4.0 mm.
Figure 11. Zebra mussel shell growth rate (μm • d\(^{-1}\)) as a function of initial shell length for mussels held in a laboratory aquarium with a continuous, flow-through supply of Lake Erie water. Shell lengths of 97 uniquely marked mussels were measured biweekly from 14 July to 28 Sept. 1993. Mussels were collected from the population used in the Line 3 1991 cage experiments. Mussels were divided into 2 mm size classes, e.g., 8 < 10 mm, 10 < 12 mm. Data for July 14 are mean initial shell lengths and number of individuals (n) in each size class. For all other dates data are size class means (± SE). Shell growth rate (μm • d\(^{-1}\)) was calculated as shell length added (mm) during the period between each two successive sampling dates (d).
Figure 12. Representative pattern of zebra mussel final soft tissue mass (mg dry mass) for zebra mussels of different shell lengths (mm) suspended in cages at different depths (0.5 m intervals) at a 3 m site. Data are from Line 3 1991 cage experiments in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Small dashed line (labeled Initial PPR) represents regression of initial shell length and dry soft tissue mass for lake bottom mussels collected from 3 m hard substrate site on Peach Point Reef and placed in cages. Long dashed line (labeled Final PPR) represents the regression of shell length and dry biomass for mussels collected from the same location at the end of the experiment. The 287 surviving caged Line 3 mussels had mean final shell length = 19.7 mm and mean final soft tissue mass = 20.6 mg dry mass.
Figure 13. Representative pattern of zebra mussel growth as change in soft tissue mass (mg dry mass) for mussels of different shell lengths (mm) suspended in cages at different depths (0.5 m intervals) at a 3 m site. Data are from Line 3 1991 cage experiments in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. The 287 surviving Line 3 mussels had mean initial shell length = 15.7 mm, mean initial soft tissue mass = 9.2 mg dry mass, mean final soft tissue mass = 20.6 mg dry mass, and mean change in soft tissue mass = + 11.3 mg dry mass.
Figure 14. Growth as added shell length for caged zebra mussels of different sizes suspended in cages at different depths (0.5 m intervals) at a 3 m site and 12 m site during 1991 and 1992 cage experiments in western Lake Erie. Data plotted are adjusted least-squares means (± SE). a) In 1991 for 827 surviving mussels mean initial shell length = 15.2 mm, mean added shell length = 4.8 mm. The four lines had different durations: Line 1 25 May to 28 Sept. (126 d), Line 2 1 June to 28 Sept. (119 d), Line R 3 July to 29 Sept. (88 d), and Line 3 12 July to 28 Sept. (78 d). At the end of the experiment the top cage on Line 1 was missing and at the 12 m site only the two lowest cages of Line R remained. b) In 1992 for 1622 surviving mussels mean initial shell length = 15.7 mm, mean added shell length = 3.8 mm. In 1992 all lines were placed in lake on 26 June and retrieved on 25 Aug. (61 d). The 1991 experimental density and the 1992 high density treatment were equivalent to 2500 mussels • m⁻² (68-72 animals per cage). The 1992 low density treatment was equivalent to 1250 mussels • m⁻² (34 animals per cage).
Figure 14
Figure 15. Growth as change in soft tissue mass (mg dry mass) for caged zebra mussels of different shell lengths suspended in cages at different depths (0.5 m intervals) at a 3 m site and 12 m site during 1991 and 1992 experiments in western Lake Erie. Data plotted are adjusted least-squares means (± SE). (a) The four lines had different durations: Line 1 25 May to 28 Sept. (126 d), Line 2 1 June to 28 Sept. (119 d), Line R 3 July to 29 Sept. (88 d), and Line 3 12 July to 28 Sept. (78 d). At the end of the experiment the top cage on Line 1 was missing and at the 12 m site only the two lowest cages of Line R remained. In 1991 for 827 surviving mussels mean final shell length = 19.9 mm, mean change in soft tissue mass = 11.1 mg dry mass. 1991 experimental density (68-72 animals per cage) = 2500 mussels · m⁻². (b) In 1992 lines were placed in lake on 26 June and retrieved on 25 Aug. (61 d). In 1992 for 1622 surviving mussels mean final shell length = 19.5 mm, mean change in soft tissue mass = 10.7 mg dry mass. 1992 high density treatment (68 animals per cage) = 2500 mussels · m⁻² (68-72 animals per cage) and low density treatment (34 animals per cage) = 1250 mussels · m⁻².
Figure 15
Figure 16. Modified Imhoff cone used for 24 hour zebra mussel grazing experiments. Mussel were placed on the mesh screen and free to move around in upper part of chamber. Mussels received natural Lake Erie seston continuously pumped through the chamber by a multichannel peristaltic pump to individual collection buckets. Small vial collected feces, pseudofeces, and sedimenting seston.
Figure 17. Variation in mean zebra mussel grazing rates as a function of density (0, 5, 10, 20, 40 mussels • chamber⁻¹, equivalent to 0 to 8,500 • m⁻²), 21-22 Aug. 1991. Mean mussel size = 22 mm shell length, 16.9 mg dry soft tissue mass. Error bar represents one standard error of mean.
Figure 18. Clearance Rate (CR) as a function of soft tissue dry mass (DM in mg) derived from grazing rates of detached adult zebra mussels feeding on natural Lake Erie seston in flow-through grazing chamber experiment 16-17 Sept. 1993. Mean seston concentration of controls = 1.75 mg • L⁻¹.
Figure 19. Seasonal declines in mean size-specific zebra mussel grazing rates (mg • mussel⁻¹ • d⁻¹) in 1992 and 1993 zebra mussels experiments using a continuous flow-through supply of ambient lake seston. Grazing rates were measured for detached mussels in four size classes: 5 - 10 mm (●), 10 - 15 mm (triangle), 15 - 20 mm (□), 20 - 25 mm (○), where e.g., 5-10 mm size class = 5.0 ≤ shell length < 10.0 mm.
Figure 20. Variation in size-specific grazing rates (mg • mussel^{-1} • d^{-1}) at ambient seston concentration in 1992 and 1993 zebra mussels experiments using a continuous flow-through supply of lake seston. Mean grazing rates were measured for detached mussels in four size classes: 5 - 10 mm (●), 10 -15 mm (triangle), 15 - 20 mm (□), 20 - 25 mm (○), where e.g., 5-10 mm size class = 5.0 ≤ shell length < 10.0 mm.
Figure 21. Variation in size-specific grazing rates (mg · mussel⁻¹ · d⁻¹) with mussel soft tissue mass (mg dry mass) in 1992 and 1993 zebra mussels experiments using a continuous flow-through supply of ambient lake seston. Mean grazing rates were measured for detached mussels in four size classes: 5 - 10 mm (●), 10 - 15 mm (triangle), 15 - 20 mm (□), 20 - 25 mm (○), where e.g., 5-10 mm size class = 5.0 ≤ shell length < 10.0 mm.
Figure 22. Seasonal changes in mussel soft tissue mass (mg dry mass) for mussels used in 1991 - 1993 zebra mussel grazing experiments using a continuous flow-through supply of ambient lake seston. Data are means (± SE) for mussels in four size classes: 5 - 10 mm (●), 10 - 15 mm (triangle), 15 - 20 mm (□), 20 - 25 mm (○), where e.g., 5-10 mm size class = 5.0 ≤ shell length < 10.0 mm.
Figure 22
Figure 23. Model of Lake Erie food web. State variables (compartments of the model) include nutrients (nitrogen and phosphorus), pelagic phytoplankton and zooplankton (including zebra mussel veliger larvae), and fish, as well as benthic adult zebra mussels. Arrows represent rates of photosynthesis (primary production) and transfer of materials between compartments and incorporate the effects of variation in physical forcing functions (light, temperature, and hydrodynamic transport of dissolved and particulate components symbolized by the velocity profile in the benthic boundary layer).
Figure 24. Simplified schematic of the \textit{in situ} multichamber incubation system used to measure the uptake of radioactively labeled (\textsuperscript{32}P) aquatic yeast by zooplankters and veligers at different depths in the lake. Device has four 4.21 L cylindrical chambers surrounding a central core (not pictured) that contains a release mechanism for the four doors and allows the device to be free standing when used with a support base.
Figure 25. Seasonal changes in phytoplankton volumes (ml • m⁻³) of abundant taxa from May to August of 1986 in an integrated water column sample from 0 to 3 m taken at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Volume may be converted to biomass (g wet weight • m⁻³) by assuming a specific gravity for algae = 1.0.
Figure 26. Seasonal changes in phytoplankton volumes (ml • m⁻³) of abundant taxa from April to October of 1991 in an integrated water column sample from 0 to 3 m taken at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Data are means (±SE) of replicate samples. Volume may be converted to biomass (g wet weight • m⁻³) by assuming a specific gravity for algae = 1.0.
Figure 26

Phytoplankton Volume (ml \cdot m^{-3})

- △ Chlorophyta
- □ Cryptophyta
- ▼ Cyanobacteria
- ○ Pyrrhophyta

Bacillariophyceae

1991

April May June July Aug Sept Oct
Figure 27. Seasonal changes in phytoplankton volumes (ml • m⁻³) of abundant taxa from April to September of 1992 in an integrated water column sample from 0 to 3 m taken at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Data are means (±SE) of replicate samples. Volume may be converted to biomass (g wet weight • m⁻³) by assuming a specific gravity for algae =1.0.
Figure 28. Seasonal changes in phytoplankton volumes (ml • m⁻³) of abundant taxa from May to September of 1993 at a 12 m site NW of Gibraltar Island, in western Lake Erie. Data are water column means (±SE) of samples collected with a Van Dorn sampler at 2 m intervals from 0 to 10 m at a 12 m site in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. Volume may be converted to biomass (g wet weight • m⁻³) by assuming a specific gravity for algae =1.0.
Figure 28
Figure 29. Seasonal changes in the distribution of total phytoplankton volume (ml • m⁻³) with depth from May to June 1993 at a 12 m site NW of Gibraltar Island, in western Lake Erie. Pie charts show proportions of major taxa averaged for all depths. Samples were collected with a Van Dorn sampler at 2 m intervals from 0 to 10 m at a 12 m site in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. Volume may be converted to biomass (g wet weight • m⁻³) by assuming a specific gravity for algae =1.0.
Figure 29

Phytoplankton Volume (ml \cdot m^{-3})

Lake Depth (m)

- May 1
- May 8
- May 15
- May 22
- May 27
- June 6
- June 12
- June 23
- June 30

- Bacillariophyceae
- Cryptophyta
- Chlorophyta
Figure 30. Seasonal changes in the distribution of total phytoplankton volume (ml • m⁻³) with depth from July to September 1993 at a 12 m site NW of Gibraltar Island, in western Lake Erie. Samples were collected with a Van Dorn sampler at 2 m intervals from 0 to 10 m at a 12 m site in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. Pie charts show proportions of major taxa averaged for all depths. Volume may be converted to biomass (g wet weight • m⁻³) by assuming a specific gravity for algae =1.0.
Phytoplankton Volume (ml \cdot m^{-3})

Lake Depth (m)

- July 8
- July 15
- July 21
- July 28
- Aug 4
- Aug 9
- Aug 18
- Aug 23
- Sept 17

Legend:
- Chlorophyta
- Cyanophyta
- Pyrrophyta
- Bacillariophyceae
- Cryptophyta

Figure 30
Figure 31
Figure 32. Seasonal changes in the seston (mg • L⁻¹) distribution with depth from May to September 1993 at a 12 m site NW of Gibraltar Island, in western Lake Erie. Samples were collected with a Van Dorn sampler at 2 m intervals from 0 to 10 m at a 12 m site in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 32

Seston (mg L⁻¹) vs. Lake Depth (m)

- 8 May
- 10 May
- 15 May
- 22 May
- 23 June
- 12 June
- 21 July
- 28 July
- 17 Sept
- 23 Aug
- 18 Aug
- 9 Aug
- 30 June
- 4 Aug

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Figure 33. Seasonal variation in in situ photosynthesis (mg C • m⁻³ • 4 h⁻¹) with depth during July, August, and September 1992 at a 3.5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. Data are means (±SE) of duplicate photosynthesis estimates using the ¹⁴C uptake method.
Photosynthesis (mg C \cdot m^{-3} \cdot 4 h^{-1})

Lake Depth (m)

9 July

11 Aug

15 Sept 1992

Figure 33
Figure 34. Seasonal variation in in situ photosynthesis (mg C • m$^{-3}$ • 4 h$^{-1}$) with depth from May to September 1993 at a 12 m site NW of Gibraltar Island, in western Lake Erie. Samples were collected with a Van Dorn sampler at 2 m intervals from 0 to 10 m at a 12 m site in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. Data are means (±SE) of duplicate photosynthesis estimates using the $^{14}$C uptake method.
Photosynthesis (mg C \cdot m^{-3} \cdot 4 h^{-1})

Lake Depth (m)

Figure 34
Figure 35. Seasonal variation in size-fractionated in situ photosynthesis (mg C • m\(^{-3}\) • 4 h\(^{-1}\)) with depth from May to September 1993 at a 12 m site NW of Gibraltar Island, in western Lake Erie. Site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 36. Vertical profiles of light penetration measured as photosynthetically active radiation (μE • s⁻¹ • m⁻²) and Secchi depth (m) during May to September 1993 at a 12 m site NW of Gibraltar Island, in western Lake Erie. Secchi depth marked by ↓. Site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 36
Figure 37. a) In situ photosynthesis (mg C • m⁻³ • 4 h⁻¹) with depth for experiment on 4 August 1993 in which water collected at one depth was incubated at another depth. Water collected from 2 m was incubated at 10 m, 4 m water incubated at 8 m, and vice versa. Only 6 m water was incubated at collection depth. Samples were collected with a Van Dorn sampler at 2 m intervals from 6 to 10 m at a 12 m site in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. b) Vertical profile of light penetration measured as photosynthetically active radiation (μE • s⁻¹ • m⁻²) and Secchi depth (m) on 4 August 1993. Secchi depth marked by⊥.
Figure 37
Figure 38. *In situ* photosynthesis (mg C \( \cdot \) m\(^{-3} \cdot \) 4 h\(^{-1} \)) as a function of photosynthetically active radiation (\( \mu \)E \( \cdot \) s\(^{-1} \cdot \) m\(^{-2} \)) for 1993 experiments shown in Figure 34. Each line connects photosynthesis estimates for all depths on the same date. On 12 June and 8 July 1993 photosaturation occurred at 2 m.
Figure 39.  a) Seasonal changes in N : P (Nitrogen: Phosphorus), b) Soluble reactive phosphate ($\mu g$ P $\cdot$ L$^{-1}$), and c) Ammonia and Nitrate ($\mu g$ N $\cdot$ L$^{-1}$) during May to September 1993. Data are water column means for samples collected with a Van Dorn sampler at 2 m intervals from 0 to 10 m at a 12 m site in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 39
Figure 40. Seasonal and annual changes in total zooplankton abundance (number • L\(^{-1}\)) in pre-zebra mussel 1986 and post-zebra mussel 1991-1993. Data from 1986 are means for whole water column based on at depth samples were collected with Schindler-Patalas Trap. Data from 1991-1993 are means (±SE) for duplicate vertical hauls with a metered, 112 μm net. 1986, 1991, and 1992 samples collected at the same 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. 1993 samples were collected at a 12 m site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 40
Figure 41. Seasonal and annual changes in cladoceran abundance (number • L⁻¹) in pre-zebra mussel 1986 and post-zebra mussel 1991-1993. Data from 1986 are means for whole water column based on at depth samples were collected with Schindler-Patalas Trap. Data from 1991-1993 are means (±SE) for duplicate vertical hauls with a metered, 112 μm net. 1986, 1991, and 1992 samples collected at the same 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. 1993 samples were collected at a 12 m site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 41
Figure 42. Seasonal and annual changes in copepod (copepodites and nauplii) abundance (number • L⁻¹) in pre-zebra mussel 1986 and post-zebra mussel 1991-1993. Data from 1986 are means for whole water column based on at depth samples were collected with Schindler-Patalas Trap. Data from 1991-1993 are means (±SE) for duplicate vertical hauls with a metered, 112 μm net. 1986, 1991, and 1992 samples were collected at the same 5 m site in Hatchery Bay. 1993 samples collected at a 12 m site NW of Gibraltar Island, in western Lake Erie.
Figure 42
Figure 43. Seasonal and annual changes in rotifer abundance (number \( \cdot \) L\(^{-1} \)) in pre-zebra mussel 1986 and post-zebra mussel 1991-1993. Data from 1986 are means for whole water column based on at depth samples were collected with Schindler-Patalas Trap. Data from 1991-1993 are means (±SE) for duplicate vertical hauls with a metered, 112 μm net. 1986, 1991, and 1992 samples were collected at the same 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. 1993 samples collected at a 12 m site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 43
Figure 44. Seasonal and annual changes in veliger abundance (number • L⁻¹) in 1991-1993. Data from 1991-1993 are means (±SE) for duplicate vertical hauls with a metered, 112 μm net. 1991 and 1992 samples were collected at a 5 m site in Hatchery Bay, NW of Gibraltar Island, in western Lake Erie. 1993 samples were collected at a 12 m site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef.
Figure 45. The effect of net size on capture of small zooplankton illustrated using a, b) veliger and c, d) total zooplankton abundance (number \( \cdot \) L\(^{-1} \)) in 1993. Samples were collected at the same 12 m site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. The 112 \( \mu \)m net abundances are means (\( \pm \)SE) for duplicate vertical hauls with a metered net. 63 \( \mu \)m net abundances are means (\( \pm \)SE) zooplankton grazing chamber experiments.
Figure 45
Figure 46. Seasonal variation in zooplankton community clearance rate (ml \( \cdot \) L\(^{-1} \cdot \) d\(^{-1} \)) with depth at a 12 m site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. Clearance rates calculated from the uptake of \(^{32}\)P-labeled yeast using in situ multichamber incubation system with 63 \( \mu \)m net (Figure 24). Data was generally collected between 0830 and 1030 h. Night experiment on 5 August occurred between 2200 and 2330 h.
Figure 46
Figure 47. Seasonal changes in abundance (number • L⁻¹) of cladocerans, copepods, rotifers, and veligers present in 1993 zooplankton community grazing experiments. Data are means (±SE) for all depths and include all zooplankters in 4.21 L grazing chamber that were retained by 63 μm net.
Figure 48. Veliger biomass (μg dry mass) as a function of shell length (μm) for mussels 91 to 255 μm. Shell length was measured as greatest linear dimension parallel to shell hinge.
Figure 49. Seasonal changes in biomass (µg • L⁻¹) of cladocerans, copepods, rotifers, and veligers present in 1993 zooplankton community grazing experiments. Data are means (±SE) for all depths and include all zooplankters in 4.21 L grazing chamber that were retained by 63 µm net.
Figure 49
Figure 50. Seasonal changes in veligers and entire zooplankton community abundance (number • L⁻¹) with depth in June and July 1993 zooplankton community grazing experiments. Data include all zooplankters in 4.21 L grazing chamber that were retained by 63 µm net.
Figure 50
Figure 51. Seasonal changes in veligers and entire zooplankton community abundance (number • L⁻¹) with depth in August and September 1993 zooplankton community grazing experiments. Data include all zooplankters in 4.21 L grazing chamber that were retained by 63 μm net.
Figure 51

Abundance (number • L⁻¹)

Lake Depth (m)

Aug 5 Day

Aug 5 Night

Aug 17

Aug 30

Sept 9

Sept 17

○ All Zooplankton
● Veligers only
Figure 52. Seasonal changes in veligers and entire zooplankton community biomass (µg • L⁻¹) with depth in June and July 1993 zooplankton community grazing experiments. Data include all zooplankters in 4.21 L grazing chamber that were retained by 63 µm net.
Figure 52
Figure 53. Seasonal changes in veligers and entire zooplankton community biomass (μg • L⁻¹) with depth in August and September 1993 zooplankton community grazing experiments. Data include all zooplankters in 4.21 L grazing chamber that were retained by 63 μm net.
Biomass (μg L⁻¹)

Aug 17

Sept 17

Aug 5 Night

Sept 9

Aug 5 Day

Aug 30

Lake Depth (m)

Figure 53

All Zooplankton

Vegiers only
Figure 54. Veliger clearance rate (ml ind⁻¹ d⁻¹) as a function of shell length (µm). Shell length was measured as greatest linear dimension parallel to shell hinge. Clearance rates calculated from the uptake of ³²P-labeled yeast using in situ multichamber incubation system with 63 µm net.
Figure 55. Comparison of seasonal variations in veliger and total zooplankton community clearance rate (ml • L⁻¹ • d⁻¹) with depth at a 12 m site located in the open channel south of the U.S. Coast Guard west channel buoy at the northeast end of Peach Point Reef. Clearance rates calculated from the uptake of ³²P-labeled yeast using in situ multichamber incubation system with 63 µm net (Figure 24).
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