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Thomas M. Burton
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ZEBRA MUSSELS (DREISSENA POLYMORPHA) IN A GREAT LAKES COASTAL MARSH: POPULATION DYNAMICS AND EFFECTS ON THE INVERTEBRATES

By

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ABSTRACT

ZEBRA MUSSELS (DREISSENA POLYMORPHA) IN A GREAT LAKES COASTAL MARSH: POPULATION DYNAMICS AND EFFECTS ON THE INVERTEBRATES

By

Valerie J. Brady

I documented zebra mussel (*Dreissena polymorpha*) population dynamics in a Saginaw Bay, Lake Huron, coastal wetland and investigated the potential effects this filterer might have on marsh zooplankton and macroinvertebrate communities. This research was conducted during 1993, 1994, and 1995. Clusters of mussels over-wintered in the outer area of the emergent marsh and were the source of recruitment for the marsh population. Recruitment was primarily onto stems of the dominant emergent plant, three-square bulrush (*Scirpus americanus*). Peak larval production and settlement occurred between 300 and 350 m from shore in July and August, respectively. Disappearance of mussels from stems decreased abundance by up to 80% in this area by the end of September in 1994. Lack of recruitment closer to shore and high loss of mussels in the middle section of the marsh was probably due to very little water movement in the center and nearshore areas.

The ability of this population to impact the wetland invertebrate community was examined both experimentally and by comparing the pre-existing community to that present after the invasion. Zooplankton remains, particularly rotifer loricas, were observed in the feces of wetland mussels. Predation by mussels on rotifers and small *Bosmina* *longirostris* was experimentally confirmed for high mussel filtration capacities. Mussel filtration capacities more representative of the marsh population did not significantly reduce the abundance of any zooplankton. A laboratory experiment was designed to examine the potential for mussel competition with marsh Cladocera. After being cultured for 14 days in the presence of a range of mussel filtration capacities, *Ceriodaphnia dubia* abundances were significantly lower at higher filtration capacities. Negative effects of competition on *C. dubia* became apparent at mussel filtration capacities higher than those calculated for the marsh mussel population. A comparison of the Cladocera community before (1990) and after (1994) zebra mussels colonized the marsh showed no evidence of changes attributable to zebra mussels.

The wetland macroinvertebrate community showed more evidence of changes potentially related to zebra mussels than did the wetland zooplankton. The abundances of larval Tanytarsini increased on plant stems ($p = 0.03$) between 1990 and 1994 while at the same time decreasing in density in the sediment ($p = 0.08$), perhaps indicating a habitat shift. Abundances of tubificid oligochaetes were significantly higher ($p = 0.04$) in marsh sediments in 1994. No other groups had significant changes in abundance, nor was there a change in the number of taxa present between 1990 and 1994. These results indicate that zebra mussels are not having a major impact on coastal wetland invertebrates.

To those who introduced me
to the beauty and wonder
of the natural world:

Dorsey M. Ennis
Shelby and Lora Ennis
Mr. Charles Stuermer

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INTRODUCTION

The accidental introduction of zebra mussels (*Dreissena polymorpha* Pallas) into North America in 1986 (Hebert et al. 1989) has provided ecologists with the opportunity to investigate and understand a biological invasion in progress. The effects of an invading species depend both on the nature of the species and the structure of the invaded community (Lewin 1987). The zebra mussel's rapid and successful colonization of much of the United States and Canada can be attributed in part to their high fecundity of up to 1 million eggs released per summer by a single female (Snyder et al. 1994). These tiny planktonic (veliger) larvae are rapidly dispersed by water currents and accidental human transport (Cooley 1991). Zebra mussels typically suffer their highest mortality during the larval stage due to cannibalism by adult mussels and settlement onto inappropriate substrates (Stanczykowska 1977, MacIsaac et al. 1991). Low densities of adult mussels in newly colonized areas and an abundance of colonizable surfaces has allowed much higher survival in many areas (MacIsaac et al. 1991). Finally, the mesotrophic condition of many areas provided both juvenile and adult mussels with a large food resource (Snyder et al. 1994), supporting high fecundity. This match between the life history requirements of the invader and the characteristics of the invaded ecosystem (Lewin 1987) allowed *D. polymorpha* to reach very high densities in many areas of the Great Lakes.

Zebra mussels change aquatic ecosystems by altering the way food resources are allocated (Nalepa and Fahnenstiel 1995) and increasing the heterogeneity of benthic surfaces (Griffiths 1993). Mussels filter bacteria, phytoplankton, and other organic material and nutrients from the water column and deposit feces and pseudofeces in the sediment (Nalepa and Fahnenstiel 1995). This process shifts the base of the food chain from planktonic to benthic. Studies indicate that zebra mussels approximately 2.25 cm long filter particles ranging from 50 - 400 µm in length (MacIsaac et al. 1991). This particle size range, coupled with the mussel's high filtration capacity (1 L/mussel/day, Reeders et al. 1991) and high densities, suggests that food web changes could take place very rapidly. For example, Hebert et al. (1991) calculated that zebra mussels could filter the entire volume of Lake St. Clair twice daily in 1989. Increased water clarity and concomitant macrophyte growth were already apparent in Lake St. Clair by 1990, and populations in some places had reached 341,000/m^2 (MacIsaac et al. 1991, Griffiths 1993). The large decrease in Lake St. Clair phytoplankton would be expected to limit zooplankton populations. Hebert and colleagues (1991) hypothesized that only the importation of zooplankton from Lake Huron was keeping the Lake St. Clair phytoplankton population from collapsing. By 1994, Lake St. Clair had shifted from a planktonic to a benthic food web, with large changes observed in most trophic levels, including the behavior and abundances of some species of fish and waterfowl (Ross 1994). Increases were observed in some benthic invertebrates, but other species disappeared (Griffiths 1993).

Impacts of *D. polymorpha* on invertebrates have been investigated in many areas around the Great Lakes (Dermott et al. 1993, Griffiths 1993, Mackie 1991, Stewart and

Haynes 1994). However, the impacts of zebra mussels on littoral areas have received much less attention. It is important to determine the magnitude of zebra mussel effects on littoral zone food webs because of their importance to the overall functioning of lake ecosystems. Jude and Pappas (1992) found that 75% of Great Lakes fish species are dependent on coastal wetlands during some portion of their life history. Thirty two of 36 species collected by Stephenson (1990) were using Lake Ontario coastal marshes for reproduction. The wetlands provided abundant food resources (phytoplankton, zooplankton, and invertebrates) for the young fish, as well as protection from predators (Stephenson 1990). Brown et al. (1995) found that Lake Huron littoral zone fish assemblages were still predominantly composed of native species, indicating the importance of these areas for native fish production. Changes at the base of the food web have the potential to impact these populations which rely on Great Lakes coastal wetlands.

Zebra mussels could potentially alter the wetland invertebrate community in several ways. First, zooplankton, particularly the smaller, weaker groups, might suffer predation from zebra mussels (MacIsaac et al. 1991). Secondly, zebra mussels might compete with planktivores for food resources (Mackie 1991). Third, the shift in energy from the plankton to the benthos by *D. polymorpha* might benefit benthic invertebrates (Stewart and Haynes 1994, Izvekova and Lvova-Katchanova 1972). If these effects were on a sufficient scale, species higher up in the food web would also be affected.

A quantitative analysis of the invertebrate community in the most extensive remaining wetland complex in Lake Huron, the Saginaw Bay east coastal wetland (Prince and Flegel 1995, Wilcox 1995), was completed just before zebra mussels colonized this area (Brady 1992). This dataset provided the opportunity to investigate changes to this community caused by *D. polymorpha.* Zebra mussels were found in Saginaw Bay in 1990, and by 1992 reached densities of 60 to 120 thousand/m^2 on rocks in shallow areas (Pillsbury and Lowe 1994). Mussels were first observed on bulrush stems in the wetland in 1991, with one to five mussels per stem being common. My research was conducted from 1993 - 1995. The subsequent chapters 1) document the zebra mussel's colonization, survival, and population dynamics in a coastal wetland; 2) investigate the potential for zebra mussel predation on and competition with the marsh zooplankton community; and 3) compare the pre-invasion macroinvertebrate community to that present after zebra mussels became established. These results will indicate the invertebrate community changes that can be expected in shallow lake littoral zones as zebra mussels continue to spread.

CHAPTER ONE

THE SEASONAL AND SPATIAL LIMITS OF COLONIZATION

Introduction

Most research regarding zebra mussels (*Dreissena polymorpha* Pallas) in the Great Lakes has concentrated on the open waters of the lakes and bays. It is generally accepted that colonization in these areas is limited, at least in part, by the availability of hard substrates. Great Lakes coastal marshes, however, provide an almost unlimited amount of colonizable surface area in the form of emergent macrophytes. Macrophyte stems have been shown to be good substrates for larval settlement (Lewandowski 1982), yet the vegetation in many coastal marshes is destroyed each winter by ice scour. In addition, the water in these shallow littoral zones often freezes down to the sediment. These observations led us to two predictions: (1) mussels would not be able to maintain year-round populations due to a lack of suitable substrate in the winter, and (2) the summer populations often observed in these marshes were the result of recruitment from offshore communities. In this study we examined the above predictions and characterized the extent and abundance of the mussel population within a typical coastal marsh.

Site Description

Our study site was located in an extensive wetland complex along the southeastern shore of Saginaw Bay, Lake Huron (Figure 1). This site was characteristic of many of the exposed coastal marshes around Saginaw Bay, with emergent vegetation dominated by three-square bulrush (*Scirpus americanus* Pers.) extending 500 m from shore. Small patches of other emergent vegetation such as cattail (*Typha angustifolia* L.), arrowhead (*Saggitaria latifolia* Willd.), and spikerush (*Eleocharis smallii* Britton) were present (Prince and Burton 1994). A characterization of the submergent vegetation in this area is presented elsewhere (Suzuki *et al.* 1995).

The upper marsh sediments were primarily sand (85-97%) with much smaller portions of clay and silt (Suzuki *et al.* 1995). Water depth gradually increased bayward, but the slope was shallow and irregular. Depth at the outer edge of the emergent vegetation ranged from 75 to 110 cm during our study, while depths closer to shore were up to 30 cm shallower.

Methods

Larval and attached mussels were routinely sampled during the ice free seasons of 1993 and 1994 along a transect which bisected the marsh from shore to open water (500 m). Larvae were collected on 900 cm^2 sheets of tulle (bridal veil mesh) placed inside plastic mesh boxes. This material has been shown to be successful in attracting all stages of larval and juvenile mussels (S. J. Nichols, personal communication, National Biological Service). One box (n=5) was placed every 50 to 100 m along the transect (Figure 1). The tulle was collected and exchanged at 14 day intervals from May through October. Larvae,

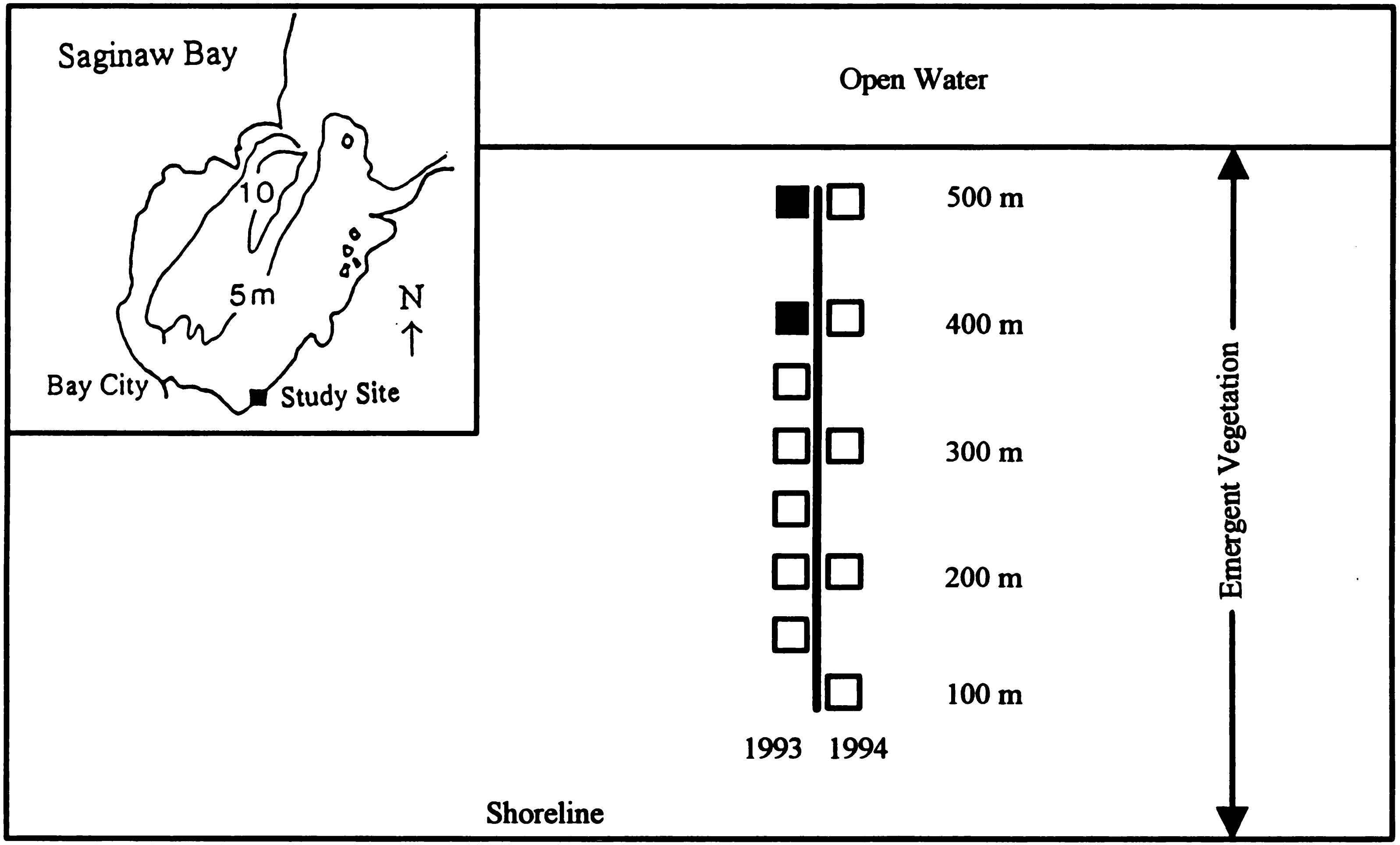


Figure 1. Location of study site in Vanderbilt Park Marsh, Saginaw Bay, Lake Huron. Boxes along transect show larval sampling locations in 1993 and 1994. Black boxes represent substrates lost during storms.

defined as mussels ≤ 0.5 mm, were washed from the tulle into a 60 µm sieve, preserved in ethanol, and enumerated under 15x magnification.

Attached mussels were sampled monthly by collecting 4 stems of *S. americanus* every 50 m along the transect. Mussels were scraped from the stems, preserved, and divided into 4 size classes (0.6-2.0 mm, 2.1-4.0 mm, 4.1-6.0 mm, and 6.1-8.0 mm). The abundance of each size class is generally expressed as number per stem throughout this paper. However, during peak abundance in 1994 we also determined stem densities along this transect using a 0.0625 m^2 quadrat, allowing calculation of areal mussel densities.

We used 3-dimensional contour plots with a distance-weighted least squares (DWLS) smoothing function (tension=0.10, cut=50, SYSTAT 1992) to display changes in zebra mussel density over time and space. We chose the DWLS function because the algorithm produces a true, locally weighted curve. This, along with the low tension setting, shows local irregularities more accurately than other methods such as linear or low order polynomial smoothing.

We examined the net loss/gain of attached mussels relative to distance from shore for each size class over the interval of August 25 - September 24, 1994. Net changes in the attached population represent both survival and migration, as we were unable to separate the two. August 25 was the first date with enough attached mussels to make such an analysis feasible.

In interpreting net loss/gain in the population, two assumptions were made: (1) growth rates were 2 mm/month, and (2) growth rates did not differ between size classes. These assumptions are consistent with other studies such as Dorgelo (1993) and Mackie

(1993) who found that growth rates for mussels of these sizes were from 1 to 3 mm/month. In addition water temperature in the marsh was very consistant during the chosen time interval. Furthermore, Neumann *et al.* (1993) determined that mussels between 4 and 7 mm displayed very similar growth rates.

In addition to routine sampling, we examined the potential for mussels to survive in the marsh over the winter. In November 1993 we placed clumps of live mussels inside 10 small (15 x 15 x 10 cm) mesh boxes. Each clump (druse) consisted of 500 to 1000 individuals. One box was anchored to the sediment every 50 m along the transect beginning at 100 m from shore and extending into open water. Maximum/minimum thermometers were attached to the boxes at 100, 350, and 550 m. Boxes were retrieved shortly after ice-out (early April 1994) and transported to the laboratory where the clumps were placed in aquaria at 12°C to initiate filtration. Live individuals were preserved in an open position by slowly adding ethanol over a period of several hours. Clusters were labeled as viable or nonviable and survival relative to distance from shore was examined.

To supplement this experiment with observations under natural conditions, we searched for clumps of living mussels in the early spring of both 1994 and 1995. In 1994 the area was qualitatively searched during the retrieval of the overwintering experiment. In 1995 we systematically searched a 3 m radius at 40 m intervals along the transect. Clusters found within this radius were again determined to be viable or nonviable, and survival was examined relative to distance from shore.

Results

In 1993, larvae were first collected in June, but the highest larval densities of 300/trap occurred in July following a water temperature increase from 20 to 27°C (Figure 2). Artificial substrates beyond 350 m were repeatedly destroyed by strong seiches, thus it was impossible to distinguish at what distance from shore peak abundance occurred. Larval abundance decreased dramatically by the end of July, and very low numbers were observed until September. Attached mussels were first noted in July, despite the fact that macrophytes had been available for colonization since June. Most of these individuals were in the smallest size class (0.6-2.0 mm) suggesting that they were recruits from the July larval peak. Maximum abundance of attached mussels occurred in August at 450 m from shore with nearly 100 individuals/stem (Figure 2). By November these densities had dropped to only 8/stem even though most of the *Scirpus* was still standing. Neither larvae nor attached mussels were found shoreward of 300 m in 1993.

In 1994, larvae were first collected in June and continued to be present in very low numbers through August. The larval peak of 470/trap occurred in July at 300 m from shore, and followed a sharp water temperature increase from 25 to 40°C (Figure 3). As in 1993, attached mussels were not found early in the year even though *Scirpus* stems were available for colonization. The highest abundance of attached mussels again occurred in August (77/stem) which, like the previous year, suggests recruitment from the July larval peak (Figure 3). Attached mussel abundance decreased to 15/stem by late September and remained at this density through November.

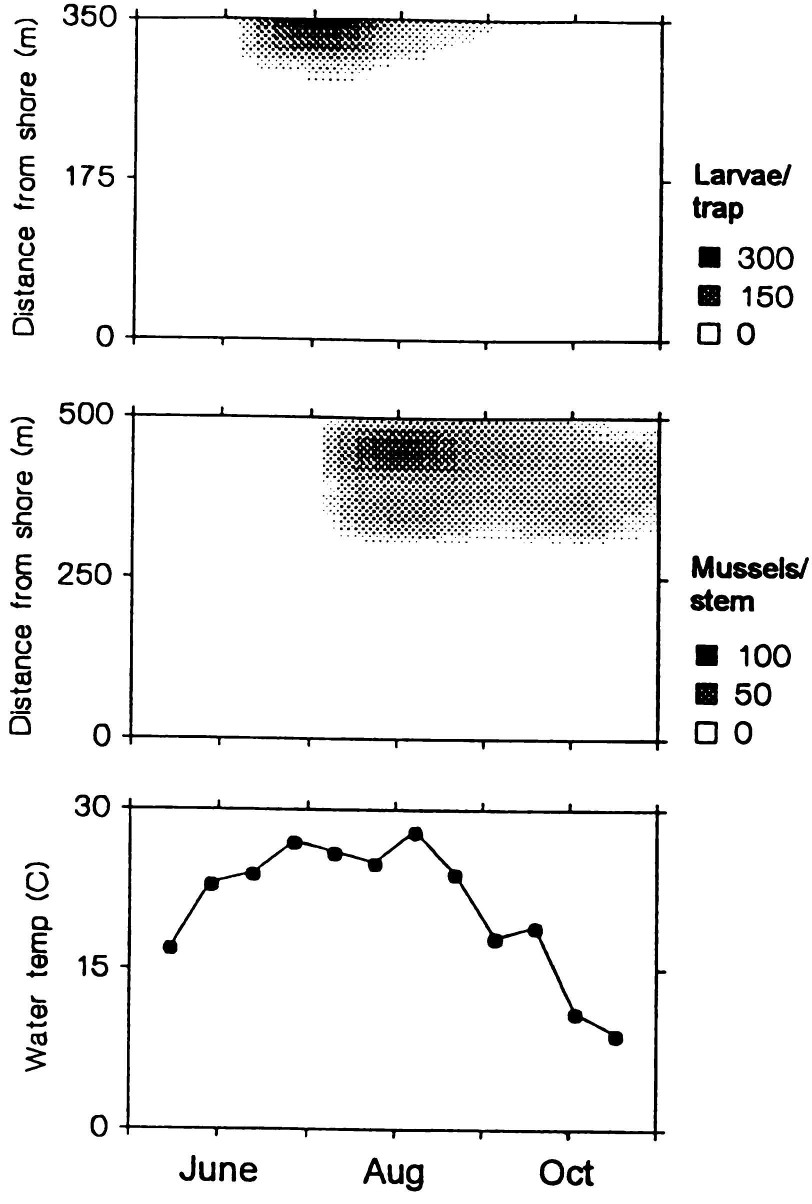


Figure 2. Seasonal and spatial distribution of larval and attached mussels from May-November, 1993. Note the difference in the Y-axis scale - larval sampling substrates beyond 350 m were lost during storms. Water temperatures were taken at 300 m.

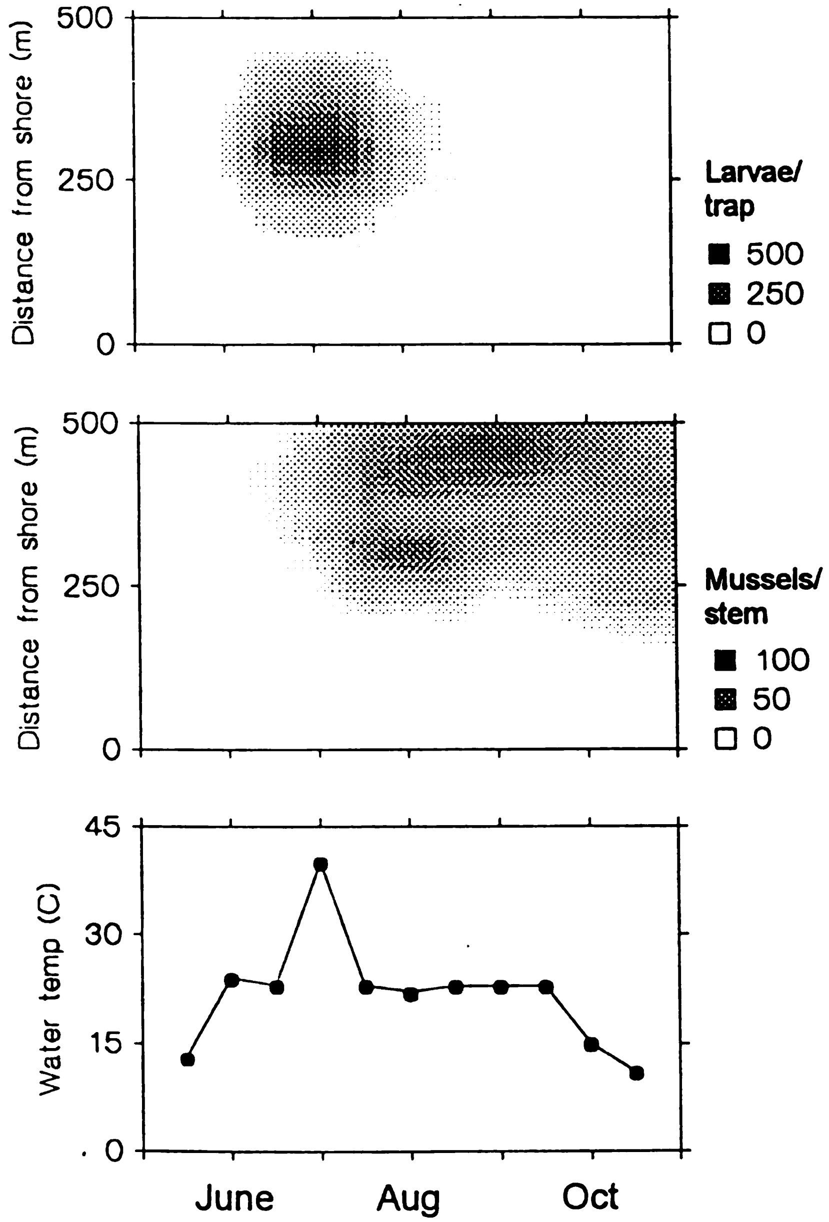


Figure 3. Seasonal and spatial distributions of larval and attached mussels from May-November, 1994. Water temperatures were taken at 300 m.

Attached mussel abundance in 1994 was greatest at 300 m from shore (77/stem) and remained fairly high bayward (Figure 3). As in 1993, neither larvae nor attached mussels were found in the shoreward half of the emergent vegetation. The areal density of mussels was highly correlated with *Scirpus* density (Figure 4, $\rho = 0.84$, $p < .001$). Highest overall densities occurred at 300 m from shore with nearly 55,000 mussels/m^2, due in part to the high density of bulrush in this area.

The relative losses or gains in the numbers of mussels on *Scirpus* stems from late Aguust to late September 1994 showed a strong spatial trend (Table 1), with disproportionately high losses in the middle of the marsh (300 - 400 m) for all size classes combined ($\chi^2 = 121.9$, $p < .005$). Losses were most pronounced for the 2.1-4 mm size class, followed by the 0.6-2 mm size class. We did not calculate relative losses or gains for mussels occurring closer to shore than 300 m because their abundances were very low.

Results of the 1993-94 overwintering experiment revealed surviving mussels in the outer third of the marsh. Clumps placed from 350 to 500 m from shore consisted almost entirely of live individuals, while mussels placed 100 to 300 m from shore exhibited complete mortality (Table 2). Shoreward of 300 m the mussels had obviously been frozen as the minimum temperature recorded was -8°C. Mussels past 350 m did not experience minimum temperatures below 0°C. Our search for naturally occurring clumps each spring confirmed the presence of viable mussels in the outer half of the marsh (Table 2). Using the range of individuals we have previously found in clusters, we estimated densities of up to 300 individuals/m^2 in spring 1995. This represents only 5 - 10% of the areal density of mussels found attached to stems the previous November.

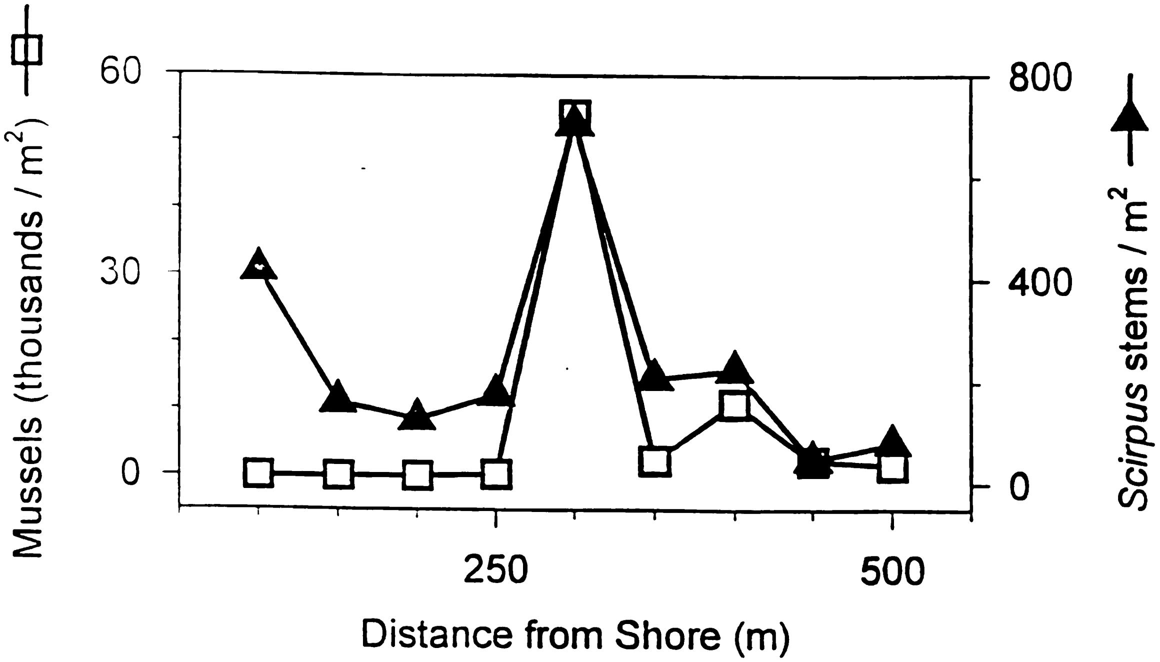


Figure 4. Attached mussel density during peak abundance, August 1994. The correlation between mussel density and *Scirpus americanus* density was 0.84 ($p < 0.001$).

TABLE 1. Net change in numbers of zebra mussels attached to bulrush stems between August and September 1994. Percent loss or gain, which includes both survival and / or migration, was calculated with the assumption of 2 mm growth per month.

Size class	Distance from shore (m)	Number per stem ± s.e.		% Loss or gain (survival ± migration)
		Aug 25	Sept 24	
0.6 to 2.0 mm	300	56.3 ± 14.5		
	350	7.2 ± 2.5		
	400	32.7 ± 12.7		
	450	28.0 ± 11.0		
	500	8.4 ± 4.6		
2.1 to 4.0 mm	300	17.3 ± 4.3	11.0 ± 4.4	-80
	350	3.4 ± 0.5	6.2 ± 2.1	-13
	400	13.7 ± 6.3	16.2 ± 8.3	-50
	450	21.7 ± 9.8	28.2 ± 10.8	+1
	500	11.4 ± 7.0	17.7 ± 7.1	+111
4.1 to 6.0 mm	300	3.0 ± 1.0	1.0 ± 0.4	-94
	350	1.2 ± 0.4	1.0 ± 0.4	-71
	400	3.0 ± 1.5	5.7 ± 4.1	-58
	450	1.3 ± 0.8	12.0 ± 6.2	-45
	500	0.6 ± 0.4	6.2 ± 3.1	-45
6.1 to 8.0 mm	300		1.0 ± 0.7	-67
	350		0.2 ± 0.2	-83
	400		0.5 ± 0.3	-83
	450		2.0 ± 0.9	+54
	500		1.5 ± 0.5	+150

TABLE 2. Clusters (druses) of viable mussels found after ice-out two consecutive winters. In 1993-1994, viability was assessed qualitatively. Thus, a plus indicates location of viable clumps while a minus indicates dead or absent clumps. In 1994 - 1995 we assessed viability quantitatively.

Distance from shore (m)	1993 - 1994		1994 - 1995	
	Experiment	Observation	Clusters / m^2	Individuals / m^2
50	-	-	0	0
100	-	-	0	0
150	-	-	0	0
200	-	-	0	0
250	-	-	0.07	35-70
300	-	-	0.20	106-212
350	+	+	0.25	124-247
400	+	+	0.30	150-300
450	+	+	0.18	88-177
500	+	+	0.04	18-35

Discussion

Originally, we anticipated poor winter survival of zebra mussels in this coastal wetland due to the senescence and ice scour of emergent bulrush - the primary substrate available for colonization. We hypothesized that ice cover would result in almost complete mortality of mussels each winter, and that summer populations would arise from settling mussels recruited from offshore colonies. Although a few of these small mussels might reach reproductive size by fall, freezing would again reset the cycle for the following year.

We now believe our hypothesis was incorrect. Our spatial analysis showed that peak recruitment in 1994 occurred from a spawning event within the wetland rather than from offshore waters. The most likely source of this recruitment was the overwintering clusters which contained the only adult mussels within the marsh. Reproductive size mussels (>6mm) were only found on bulrush stems after peak larval abundance, and they never occurred in any notable densities. Thus, we believe populations were not replenished each summer by offshore recruitment but were instead "seeded" by the adults within substrate independent clusters.

Our experiment suggested that clusters of mussels could over-winter in the marsh. These results may simply indicate that the temperature extremes could be tolerated since the boxes might have protected the clumps from ice scour. However, sampling in the spring of both 1994 and 1995 supported our findings because viable clusters of mussels were found under natural conditions in the outer half of the emergent zone. Using the regression developed by Assel (1976), we calculated a maximum littoral ice depth of 37 cm for Saginaw Bay in 1993-94, one of the most severe winters in the last two centuries (R.A. Assel, personal communication, Great Lakes Environmental Research Laboratory). This depth would indicate complete freezing to approximately 300 m from shore at our site, beyond which we noted surviving mussels. Taken collectively, these results suggest that zebra mussels are surviving even severe winters in the outer half of the marsh as clusters unattached to bulrush stems.

We found as many or more zebra mussels per m^2 in this littoral zone as have been reported from open waters. The density of attached mussels in the bayward half of the marsh ranged from about 1000 to 55,000 individual/m^2. These numbers are comparable to the averages reported for Lake St. Clair (Griffiths 1993) and nearshore Lake Erie (Dermott *et al.* 1993). Furthermore, densities were often higher than those reported for inner Saginaw Bay (Nalepa *et al.* 1995). However, total biomass may be lower in the littoral zone since mussel growth on the dominant substrate is seasonally limited by the availability of bulrush. Instead, adults can only accrue within the less abundant clusters. This results in a littoral population skewed toward the smallest size class (0.6-2.0 mm).

We did not anticipate the spatial distribution of mussels found during peak abundance periods, especially the lack of larvae and attached mussels in the nearshore 250 m of vegetation each year. This pattern may be the result of a unique form of stratification recently described for coastal wetlands. Suzuki *et al.* (1995) documented a conductivity gradient which divided a coastal marsh into two horizontally adjacent water masses - a nearshore zone and an offshore zone. The nearshore zone had approximately 60% higher ionic conductivity due to increased concentrations of Ca^{2+}, Mg^{2+}, and K^+. The stability of this stratification was maintained by the emergent vegetation, which impeded mixing from wind or wave energy. Data from an ongoing study indicate that this form of stratification also occurs at our site (Cardinale and Burton 1995). Thus, we hypothesize that as clusters of mussels spawned in the offshore half of the marsh, a lack of water movement at the stratification interface prevented the planktonic veligers from distributing into the nearshore zone.

There was clearly a positive relationship between net loss/gain in attached mussels and distance from shore. The net gain beyond 450 m was a function of immigration with attached mussel numbers more than doubling in some cases. The high net loss between 300 and 400 m suggests that attached mussels had low survivorship and/or were migrating away from this area. These two possibilities are not mutually exclusive since factors decreasing survivorship would also probably initiate migration. Previous studies have shown mussel survival to be positively correlated with colonizable surface area and food availability, but negatively correlated with vegetative senescence and turbidity (Lewandowski 1982, Stanczykowska 1977). At our study site bulrush densities were highest in the area of highest net loss, and the stems did not begin senescence until November - well beyond the time interval we considered. In addition, turbidity was highest at the bayward edge of the marsh due to increased wave exposure (Cardinale and Burton 1995). Therefore, differences in substrate and turbidity do not appear to explain our observations.

The other alternative, food availability, may be an important factor due to fluctuating algal concentrations caused by horizontal shifts in the stratification reported by

Suzuki *et al.* (1995). The stratification interface was shown to move between 250 and 350 m with increasing or decreasing water levels caused by periodic seiches. Although the offshore zone of the marsh had chlorophyll a concentrations similar to the eutrophic waters of Saginaw Bay, the nearshore zone had 80 to 90% lower planktonic algal biomass (Suzuki *et al.* 1995). Thus, the center of the marsh may be an area of constantly changing resource availability. If true, this would represent a less than ideal environment for mussels, particularly the smallest size classes.

CHAPTER TWO

POTENTIAL INTERACTIONS WITH WETLAND ZOOPLANKTON

Introduction

Zebra mussels (*Dreissena polymorpha* Pallas) have colonized lake littoral zones along with their settlement of hard substrates in deeper waters. Because survivorship is low and because littoral populations typically contain very few adults (Brady *et al.* 1995), there has been comparatively little study of the impacts from these young mussels. However, the addition of these invertebrate filterers to the coastal marsh food web could affect littoral zooplankton. Zebra mussels may compete with native filter-feeders for planktonic food resources. For example, Leach (1992) found that zebra mussels could greatly reduce ambient concentrations of chlorophyll a in offshore waters of Lake Erie. Lewandowski (1983) calculated that the densities and filtration capacities of small young mussels in the littoral zone of a Polish lake exceeded those of the adult mussels occurring in offshore colonies. In addition, *D. polymorpha* may also consume small or weak-swimming zooplankton and change community composition through direct predation. This potential has been demonstrated in laboratory experiments (MacIsaac *et al.* 1991) and in mesocosms (Shevtsova *et al.* 1986) for some zooplankton taxa.

The lack of research on the potential for zebra mussels to affect these coastal communities represents a large gap in our investigation of this invasion. In addition, while decreases in phytoplankton abundance have been linked to zebra mussels, this has not yet been demonstrated to have affected crustacean zooplankton populations in the Great Lakes. Thus, the purpose of this research was to determine whether zebra mussels in lakeshore marshes were likely to have a significant effect on the zooplankton community.

Brady and Burton (1995) determined that a Saginaw Bay coastal wetland contained a microcrustacean community with more than 35 taxa which reached densities of 350,000/m^3. This analysis was completed just prior to colonization of the wetland by *D. polymorpha* in 1991. In 1994 zebra mussel densities in this marsh reached 55,000/m^2 (Brady *et al.* 1995). The existence of this dataset provided the opportunity to compare the pre-existing community (1990) with the community that came to coexist with zebra mussels (1994). I tested the following hypotheses:

1. Zebra mussels are predators on small zooplankton, and
2. Zebra mussels are competitors for food resources with Cladocera and will have a negative impact on cladoceran populations.

Methods

1. Site Description

Field work was conducted in the most extensive wetland complex in Saginaw Bay (Lake Huron, Michigan), the Saginaw Bay east coastal wetland, which encompasses 6754 ha. (Wilcox 1995) (Figure 5). Emergent vegetation, dominated by three-square bulrush (*Scirpus americanus* Pers.), extended 500 m from shore. Other emergents included cattail (*Typha angustifolia* L.), arrowhead (*Saggitaria latifolia* Willd.), and spikerush (*Eleocharis smallii* Britton) (Prince and Burton 1994). Submergent vegetation was only abundant in shallow areas near the shore. Sediments were primarily sand, particularly

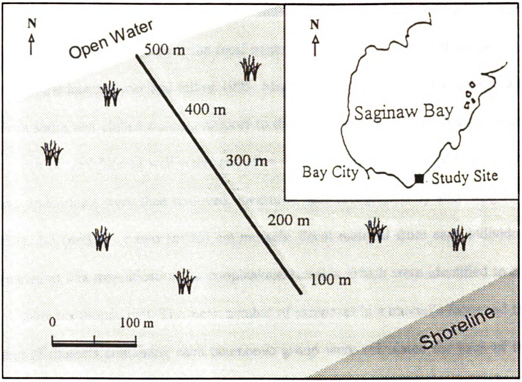


Figure 5. Location of the study site and sampling transect in Saginaw Bay, Lake Huron.

toward the bayward edge. Water depth gradually increased bayward, reaching 70 to 110 cm at the outer marsh edge.

2. Zooplankton Remains in Mussel Feces

To determine whether marsh zebra mussels (*Dreissena polymorpha*) were consuming zooplankton, I examined the fecal material from freshly collected mussels on eight dates in the late summer and fall of 1995. Mussels were collected between 400 and 500 m from shore and chilled during transport to the laboratory. Individual mussels were placed in cups of cool filtered well water and allowed to filter and expel fecal material for two hours. Individuals were then removed, measured, and categorized by shell length as one (n=28), 1.5 (n=53), or two (n=46) cm mussels. Fecal material from each individual was examined at 25x magnification for zooplankton remains, which were identified to the lowest possible taxonomic unit. The mean number of carapaces in a mussel's feces and the percentage of mussels containing each taxonomic group were calculated for each of the size classes.

3. Zooplankton Vulnerability to Mussel Filtration

Short-term experiments were performed to assess the vulnerability of various zooplankton taxa to zebra mussel predation. The experiments, which were conducted on site to minimize stress and damage to the zooplankton, took place on August 6 (experiment one), August 21 (experiment two), and October 15 (experiment three) of 1994. Experiments one and two exposed zooplankton to one (mean 822 mussels) or two (mean 1827 mussels) clumps of zebra mussels which had been retrieved from the outer section of the wetland. Experiment three exposed the zooplankton community to mussels attached to *S. americanus* stems (mean 219 individuals). Experimental vessels were two L plastic containers ($r = 0.075$ m, volume = $0.002\ m^3$). (Table 3). The marsh zooplankton community was concentrated for experiments one and two by filtering 500 L through 60 μm mesh and resuspending the zooplankton in 30 L of water, resulting in a concentration of 17 times over ambient densities. The concentrated zooplankton still had a lower density (about 100,000 individuals/m^3) than the ambient density of 200,000 zooplankton/m^3 in the marsh in October. Because the zooplankton were more abundant on October 15, they were not concentrated for experiment three. The collected zooplankton were homogenized with very gentle mixing in a large container. Two L of the homogenized zooplankton were added to each experimental vessel after being passed through a one mm sieve to remove any large invertebrate predators. Mussels in clumps (experiments one and two) or on bulrush stems (experiment three) were added to all containers except controls to begin each experiment (Table 3).

The mussels were allowed to filter for 1.5 (experiments one and two) or 3 hr (experiment three), and then were removed, preserved, enumerated, and measured for length to the nearest mm. The theoretical filtration capacity of the mussels in each container was calculated based on the published length-rate regressions of Bunt *et al.* (1993) and Reeders and Bij de Vaate (1990).

The regression from Bunt *et al.* (1993) was used for mussels ≤ 1 cm:

$$FC = 0.057 \times L^{1.82}$$

FC = filtration capacity in ml/ind/hr
L = mussel shell length in mm

Table 3. Experimental design used to investigate zooplankton vulnerability to zebra mussel filtration.

Exp. #	# of zebra Mussels	Zooplankton concentration	Duration (min)	Reps
	0	17 x		3,5
1, 2	823 ± 59[a]	by	90	3,3
	1827 ± 281[b]	Plankton tow		3,4
3	0	Ambient density	180	3
	219 ± 20[c]			14

[a] 1 mussel clump.

[b] 2 mussel clumps.

[c] Mussels attached to *S. americanus* stems.

and the regression developed by Reeders and Bij de Vaate (1990) was used for larger mussels:

$$FC = 15.63/(0.293 + 52.38e^{-0.367L})$$

FC = filtration capacity in ml/ind/hr
L = mussel shell length in mm

Filtration capacities for each size class were multiplied by the number in that class for each container and converted to $m^3/m^2/d$ assuming a 16 hr daylength. Mean filtration capacities were 2.74, 5.6, and 0.17 $m^3/m^2/d$ for one clump, two clumps, and mussels on stems, respectively. Integrating mussel sizes and densities into the single variable of filtration capacity allowed the results from the various experiments to be more easily compared and allowed for comparison with the mussel population in the wetland.

The zooplankton were filtered out of each container using 60 μm mesh, preserved in 95% ethanol, then size-fractionated into categories of small (60-125 μm), medium (126-250 μm), and large (251-1000 μm). These fractions were subsampled and one tenth of the zooplankton in each category were enumerated and identified. Means and standard errors for experiments one and two were calculated using the results from both experiments for each treatment (control, or one or two mussel clumps). Concentrations of each taxon in each size fraction were compared between the control and each mussel density using Mann-Whitney's rank sum. Finally, the percentage reduction in abundance of each taxon was calculated. Box plots were generated to compare the percent reductions created by mussels in clumps to those created by mussels attached to *S. americanus* stems.

4. Competition Between Mussels and *Ceriodaphnia dubia*

The potential for competition between zebra mussels and filtering Cladocera was investigated by culturing representative filter-feeder in the presence of various sizes and densities of mussels. *Ceriodaphnia dubia* was selected to represent the Cladocera because it is the planktonic filter feeder that was often abundant in the wetland. In addition, neonate *C. dubia* are 300 µm at birth, making them unlikely to be filtered out of the water by mussels. This allowed the effects of competition to be examined separately from those of predation. Finally, this species is easily cultured under laboratory conditions.

Ceriodaphnia dubia were collected from the marsh by plankton tow in October 1995 and maintained in mass culture. Cultures were fed both live algae (*Selenastrum capricornutum*) and a mixture of yeast, digested Trout Chow, and dried *Cerophyll* (YTC) obtained from the Michigan State University Aquatic Toxicology Laboratory. Zebra mussels were obtained from the River Raisin at the Monroe (Michigan) power generating facility in January 1996 and maintained in mass culture for several weeks. Cultures were exposed to a light cycle of 16 h light:8 h dark under "warm" UV lights. Temperature was 22 to 25°C. Mussels in mass culture were fed dried *Chlorella* (Nichols 1993). Water for both cultures and the experiment was well water filtered through an activated charcoal filter and then aerated overnight (initial assessment: pH 7.0, conductivity 533 µS/cm, alkalinity 160 mg $CaCO_3$/L).

The experiment was conducted in one L glass beakers. Cultures were fed a mixture of *S. capricornutum* and YTC at a density based on summer wetland phytoplankton production estimates of 1.7 mg carbon/L/d in mid-summer (based on unpubl. data from

Suzuki *et al.*). The amount of carbon in *S. capricornutum* and YTC was determined to be 39% and 34% by weight, respectively. These data were generated by the MSU Environmental Geochemistry Laboratory. Each type of food supplied half of the daily carbon estimate. Thus, each chamber received the equivalent of 2.2 mg *S. capricornutum*/L/day and 2.5 mg YTC/L/day based on calculations from the dry weights of each new batch of food. The food mixture was diluted in 250 mL flasks, each of which supplied two experimental chambers with 100 mL of food solution over 24 hr through a gravity-fed continuous microdrip system (Williamson *et al.* 1985). This continuous drip food supply system was used to minimize food depletion over each 24 hr period. Food flasks were stirred with magnetic stirrers set on low speed to prevent settling of food while minimizing damage to algal cells. Microtubing supplying the food had an internal diameter of 350 µm (2 mm total diameter). Food flasks were rinsed and refilled every 24 hr. Food supply tubes were rinsed in culture water every 48 hr and replaced if clogged.

One of the biggest threats to successful laboratory culture of *D. polymorpha* is the buildup of ammonia (Nichols 1993). Several steps were taken to reduce the possibility of toxic ammonia buildup. First, half of the culture water was gently pumped out of each chamber and replaced every 24 hr. The intake hose was covered with 60 µm mesh and held against the side of the container to prevent trapping zooplanktors against the screen and damaging them. Secondly, zeolite, a mineral which absorbs ammonia, was added at 30 g/chamber. Finally, an air tube plugged with cotton and adjusted to gently produce tiny bubbles was placed in each chamber to provide aeration. Ammonia and pH were checked occasionally in the chambers containing the highest mussel densities. Ammonia did not rise above 0.05 mg/L, while pH remained below 8.1 and was more commonly around 7.6.

The experiment began on February 8, 1996, with the addition of 20 adult female *C. dubia* (density 0.02/m^3) and the appropriate size and density of mussels to each chamber. Mussel sizes and densities were selected to cover a range of filtration capacities (0.04 to 0.93 m^3/m^2/d) so that regressions of filtration versus various *C. dubia* population variables could be developed (Table 4). The experiment was terminated after 14 days because fungal growth was beginning in several of the chambers.

At the end of the experiment, zebra mussels were removed and preserved. *Ceriodaphnia dubia* were filtered out of the culture water with a 60 µm mesh and preserved in chilled 10% buffered sugar formalin (Prepas 1978). The total number of *C. dubia* and the number of females with eggs were counted for each chamber. The lipid-ovary-egg (LOE) index (Tessier and Goulden 1982, Hoenicke and Goldman 1987) was used to qualitatively assess the nutritional status of a subsample of each population. Because the *C. dubia* were preserved for more than 48 hr before assessment, each sample was immersed in a Sudan IV dye solution for 2.5 min to stain the triglycerides (Bjorkman and Shapiro 1986). Four *C. dubia* in each of 3 size classes (600, 700, and 800 µm) were selected by locating the first four individuals in each size class with intact carapaces. All indexing was done at 30x magnification by the same person due to the subjective nature of the analysis (Tessier and Goulden 1982).

The effects zebra mussels had on *C. dubia* populations were determined using linear regressions. All dependent variables were $\log_{10}$ or $\log_{10}(x + 1)$ transformed to make

Table 4. Sizes, densities, and filtration capacities of zebra mussels cultured with *Ceriodaphnia dubia*.

Shell length (mm)	Number[a]	Density (#/m^2)	Filtration capacity (m^3/m^2/d)
0 (controls; n=6)	0	0	0[b]
5	25	3125	0.05
5	50	6250	0.11
8	50	6250	0.25
10	8	625	0.038
10	16	2000	0.12
10	30	3750	0.226
10	90	11,250	0.678
18	2	250	0.17[c]
18	4	500	0.34
18	11	1375	0.93
22	3	375	0.30
22	7	875	0.70
25	2	250	0.21
25	6	750	0.62

[a] Number per 1 L container.

[b] Based on length-rate regression of Bunt et al. (1993).

[c] Based on length-rate regression of Reeders and Bij de Vaate (1990).

the data approximately linear. A multiple linear regression was developed using the independent variables of zebra mussel size and density versus the dependent variable of *C. dubia* abundance. The validity of using the calculated filtration capacity as a way of integrating mussel size and density into a single variable was tested by comparing the simple linear regression of filtration capacity versus *C. dubia* abundance with the multiple linear regression. This was necessary because the sizes and densities of mussels that could be cultured in the laboratory did not overlap well with the size-density combinations that were found in the wetland (Brady *et al.* 1995). The use of this single independent variable provided a comparable regression, so filtration capacity was regressed separately against the mean LOE scores and the percentage of *C. dubia* with young. Data for all regressions passed tests for normality and homoscedasticity.

5. *In Situ* Effects of Mussels on Cladocera

The question of mussel competition with marsh Cladocera was investigated by comparing the pre-existing cladoceran community to that present after mussels had colonized the emergent vegetation. Data on the Cladocera of this coastal wetland had been collected in 1990 for another project (Brady and Burton 1995). To keep the data comparable, the cladoceran community was sampled in 1993 through 1995 in the same area using the same methods. All sampling was conducted along a single transect which bisected the emergent zone from near shore (100 m) to open water (500 m; Figure 5). Once a month from May through November a single sample of the epiphytic and planktonic Cladocera was collected every 100 m along the transect with a modified Gerking sampler (Mittelbach 1981). This sampler (21.5 cm ID) enclosed the emergent vegetation and water column to depth. At the laboratory, large vegetation within samples was rinsed to remove any Cladocera. Samples (n=5 on each date) were sieved (250 µm mesh) and preserved in 95% ethanol with rose bengal dye to aid in sorting (Mason and Yevich 1967). Each sample was later subsampled by dividing the sample into 6 equal parts using a calibrated box subsampling device. One sixth of each sample was examined under 10x magnification and all Cladocera removed. Cladocera were identified using keys in Brooks (1959), Balcer *et al.* (1984), and Dodson and Frey (1991). Numbers were converted to number per cubic meter based on water depth.

Brady *et al.* (1995) previously determined that zebra mussels only become abundant in the bayward 250 m of the marsh. The cladoceran community in this offshore area of the marsh was compared before and after the zebra mussel invasion. The offshore area was represented by samples collected from 400 and 500 m along the transect. Samples collected during 1994 were used to represent the community present after mussel colonization. The year 1994 was chosen because the mussels reached high densities in the bayward area of the wetland (Brady *et al.* 1995) and because the transect that year best matched the 1990 transect location. Only samples from August through November were used for each of the years because these were the only months in 1994 during which zebra mussels were present in fairly high numbers (Brady *et al.* 1995). Abundances of routinely-collected species, species richness, and the total density of the community were all compared between 1990 and 1994.

Because the nearshore area was not colonized by the mussels, I considered this area to be unimpacted by the invasion. This allowed differences in the communities before and after mussel colonization to be confirmed using BACI analysis as a conservative statistic (Stewart-Oaten *et al.* 1986). Samples considered to be from the "control" area were those collected at the 100 m and 200 m points along the transect (Figure 5) and samples collected from 400 m and 500 m were classified as "impact" area samples, providing an n of 8 for each of the areas each year.

6. Filtration Capacities

The potential for competition between the marsh mussel population and the cladoceran community was further investigated by comparing the theoretical filtration capacities of the two groups. The filtration capacity of the mussel population in the emergent marsh was estimated based on mussel population densities from 1993 and 1994 (Brady *et al.* 1995) and on samples collected each month during the ice-free seasons of 1995. Samples were collected similarly in all three years. Attached mussels were scraped from four *S. americanus* stems every 50 m along the transect, preserved in ethanol, and measured to the nearest mm. Numbers per stem were converted to areal density based on the density of *S. americanus* stems (1993: Brady unpubl. data; 1994: Brady *et al.* 1995; 1995: enumerated using a 0.025 m^2 quadrat). The potential filtration capacity of the mussel population was calculated in a manner similar to the calculations for the filtration vulnerability experiment.

The filtration capacities of the four most abundant filtering Cladocera (*Bosmina longirostris*, *Ceriodaphnia dubia*, *Chydorus* spp., and *Sida crystallina*) were calculated for each date. Filtration rates for each taxon were obtained from the literature (Table 5). No values could be located for *Sida crystallina*, so the filtration rate of

Table 5. Filtration rates used to estimate the filtration capacities of selected Cladocera.

Cladocera	Filtration rate (ml/ind/day)
Bosmina longirostris	0.8[a]
Ceriodaphnia quadrangularis	5.7[a]
Chydorus spp.	2.58[b]
Simocephalus vetulus	33[a]

[a] Webster and Peters 1978

[b] estimated from Lair 1991

Simocephalus vetulus was used as a surrogate. *Simocephalus vetulus* is another filter feeder and is similar in size to *S. crystallina*. Densities of Cladocera were recalculated as #/m^2 so that the filtration capacities would be comparable to those calculated for zebra mussels. Theoretical filtration capacities for each taxon on each date were calculated based on their densities in the bayward marsh area. These capacities were summed to obtain an estimate of the filtration capacity of the dominant filtering Cladocera. Finally, the percent of the outer marsh which could be filtered by these Cladocera on each date was calculated based on the average water depth in this area. The capacity of zebra mussels to filter this area was calculated similarly.

Results

1. Zooplankton Remains in Mussel Feces

Examination of mussel fecal material suggested that rotifers and other small zooplanktors might be vulnerable to mussel filtration. Rotifer loricas were the most common zooplankton remains found in zebra mussel feces for all three size classes of mussels examined (Table 6). Similar numbers of rotifers, *Bosmina longirostris*, and harpactacoid copepod remains in the feces of all three size classes of zebra mussels indicated that mussels one cm and larger were capable of consuming zooplanktors 60 to 250 µm from several very different groups.

Rotifers were the dominant zooplanktors in the 60 to 125 µm size class in the wetland and were an important component of the 126 to 250 µm size class (Figure 6). *Bosmina longirostris*, adult copepods and copepod nauplii comprised the rest of this size fraction. Other Cladocera, *B. longirostris*, and adult copepods dominated the largest size

Table 6. Mean number of zooplankton remains found in the feces of individual zebra mussels ± 1 standard error. Numbers in parentheses indicate the percentage of mussels with that group in their feces.

	Mussel shell length			
Taxon	1 cm (n = 28)	1.5 cm (n = 50)	2 cm (n = 43)	Total (n = 121)
Rotifera	7.1 ± 0.7 (89%)	8.4 ± 1 (94%)	9.0 ± 1.1 (98%)	8.3 ± 0.6 (94%)
Bosmina longirostris	1.5 ± 0.1 (7%)	1.4 ± 0.2 (22%)	2.0 ± 0.4 (23%)	1.7 ± 0.2 (19%)
Harpactacoida	1 ± 0 (7%)	1 ± 0 (10%)	1.3 ± 0.1 (33%)	1.2 ± 0.05 (17%)
Copepod nauplii	0 ± 0 (0%)	0 ± 0 (0%)	1 ± 0 (7%)	1 ± 0 (2%)
Ostracoda	0 ± 0 (0%)	1.5 ± 0.1 (4%)	2.3 ± 0.2 (14%)	2.1 ± 0.1 (7%)

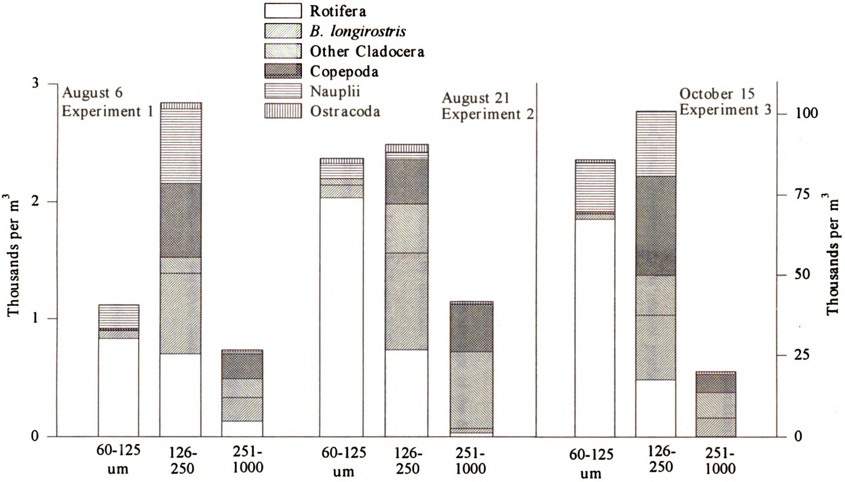


Figure 6. Composition of the marsh zooplankton community in 1994 during experiments assessing their vulnerability to zebra mussel filtration. The community has been size-fractioned.

fraction (251-1000 μm). *Bosmina longirostris* was the only cladoceran consistently present in all size fractions, and was typically more abundant on these dates than all other Cladocera combined. Composition of this community was determined in August and October of 1994 during tests of the vulnerability of small zooplankton to mussel filtration.

2. Zooplankton Vulnerability to Mussel Filtration

Vulnerability of small zooplankton to mussel predation was further tested by exposing this community to several levels of mussel filtration. There was substantial entrainment of small zooplankton from even short-term exposure to the high filtration capacity (2.74 or 5.6 $m^3/m^2/d$) of mussels in clumps. All rotifers ≤ 250 μm exposed to clumps of mussels were significantly reduced relative to the controls ($p < 0.05$), with reductions ranging from 64 to 81% (Table 7). The smallest of the *B. longirostris* (60 to 125 μm) were also significantly reduced by filtration from mussel clumps ($p < 0.05$). Abundances of copepod nauplii tended to be lower in the presence of mussel clumps, but the decreases were not significant. The lower filtration capacity (0.17 $m^3/m^2/d$) of mussels attached to *S. americanus* stems did not cause a significant decrease in the abundance of any zooplankton taxa, although rotifer and *B. longirostris* numbers in the 126 to 250 μm size fraction tended to be reduced relative to controls (Table 7). By contrast mean abundances of 60 to 125 μm rotifers and copepod nauplii were elevated in association with mussels on stems, suggesting that they had been added along with the mussels.

3. Competition between Mussels and *Ceriodapnia dubia*

The question of competition between zebra mussels and Cladocera was initially tested by comparing population densities of a representative species (*Ceriodaphnia dubia*)

Table 7. Percent decrease in zooplankton abundance (by size fraction) due to zebra mussel entrainment. Experiments were conducted in two L containers (r = 0.075 m) and lasted for 90 (experiments 1 and 2) or 180 (experiment 3) minutes.

					Rotifera (µm)		*B. longirostris* (µm)		Nauplii (µm)	
Exp	# of Mussels[a] (density #/m^2)	% Mussels > 1 cm	Filtration ($m^3/m^2/d$)[a]	Temp. (°C)	60 - 125	126 - 250	60 - 125	126 - 250	60 - 125	126 - 250
1, 2	823 ± 59 (47,850)	12	2.74 ± 0.42	24	77%**[b]	64%**	56%*	-10%[c]	24%	17%
	1827 ± 281 (106,220)	10	5.60 ± 0.31	24	81%**	72%*	73%**	13%	28%	1%
3	219 ± 20 (12,730)	0.7	0.17 ± 0.02	17	-21%	36%	[d]	25%	-82%	12%

* $p < 0.05$

** $p < 0.01$

[a] Data as means ± standard errors.

[b] All tests were Mann-Whitney rank sums.

[c] Negative percent reductions indicate increases relative to controls.

[d] Abundance too low to test for differences.

after culturing populations alone or in the presence of zebra mussels. The initial density of 20 *C. dubia* per beaker (0.02 ind/m^3) increased to 195 to 676 ind/beaker (0.195 to 0.676/m^3) in control beakers after 14 days, an increase of 10 to 30 fold. *Ceriodaphnia dubia* abundances in beakers containing mussels ranged from 0 to 291/beaker (0 to 0.291/m^3) after 14 days, representing a range from the complete loss of all individuals to an increase of 15 fold (Table 8, Figure 7).

The regression of *C. dubia* abundance on mussel filtration capacity produced a highly significant regression with a negative slope (Table 9), indicating that the population densities were significantly reduced by increasing levels of mussel filtration. This regression explained 64% of the variation in *C. dubia* numbers. The multiple regression using both mussel size and density as independent variables explained even more of the variation (82%) in population densities. Mussel size explained a larger percentage of this variation than did mussel density because of the higher filtration capacity of the larger mussels.

The percentage of *C. dubia* with eggs and the average lipid-ovary-egg (LOE) score both decreased with increased mussel filtration capacity (Table 8). Mean LOE scores began to decrease when mussel filtration reached 0.12 m^3/m^2/d and reproduction appeared to be affected at filtration capacities of 0.25 m^3/m^2/d and higher. When each of these variables were regressed separately on mussel filtration capacity, both regressions were highly significant at $p < 0.01$ and explained 44% (LOE score) or 57% (percent with young) of the observed variation, respectively. The significant negative slopes of these regressions indicated that the average nutritional state and the reproductive capacity of

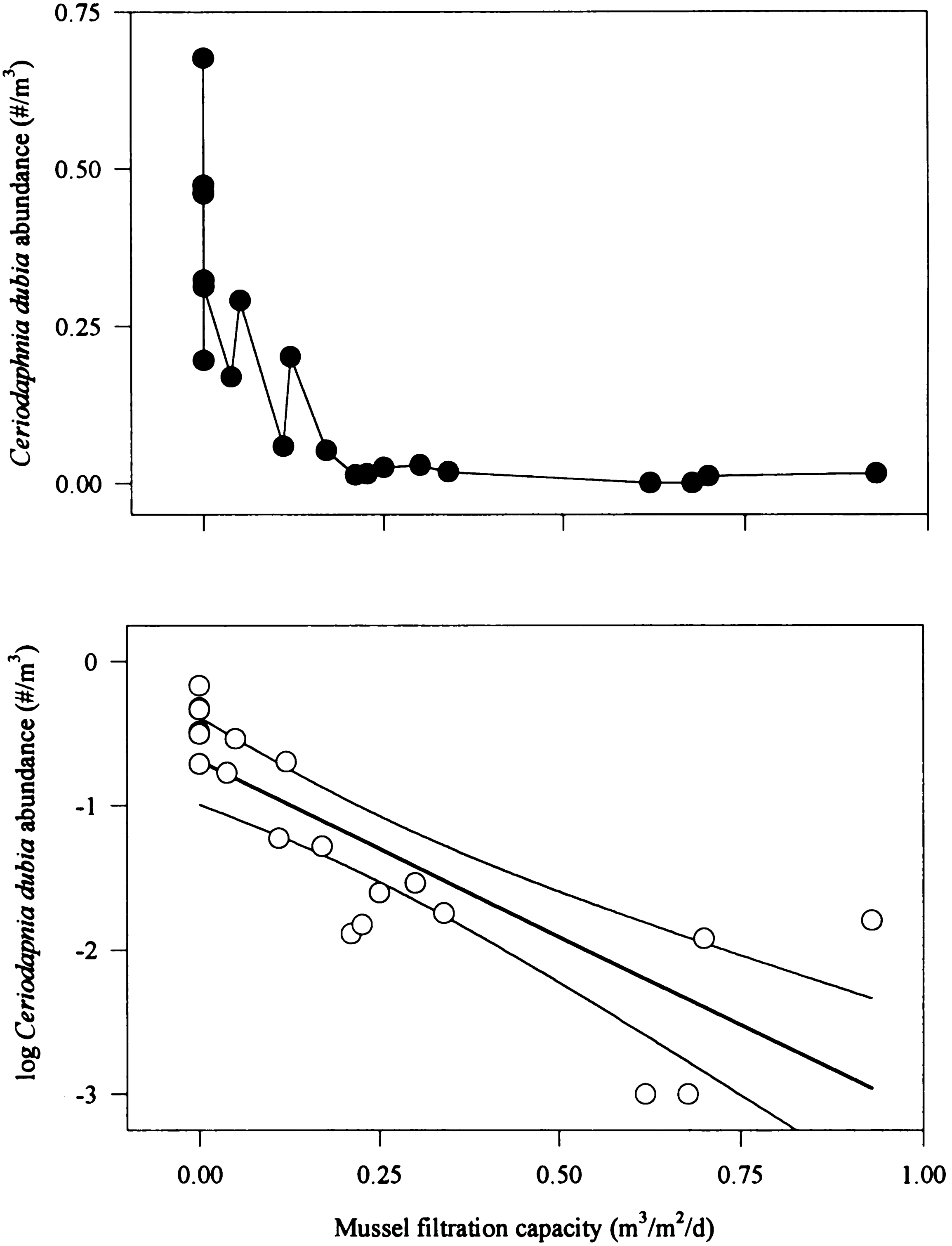


Figure 7. *Ceriodaphnia dubia* population size when cultured in the presence of a range of zebra mussel filtration capacities (top) and the regression (with 95% C.I.) based on the log of these abundances (bottom).

Table 8. Results of culturing *Ceriodaphnia dubia* with various sizes and densities of zebra mussels for 14 days. Initial *C. dubia* density was $0.02/m^3$.

Shell length (mm)	Mussels (#/L)	Mussel density (#/m^2)	Filtration capacity ($m^3/m^2/d$)[a]	*C. dubia* (#/m^3)	% *C. dubia* with eggs	Mean LOE score
0	0	0	0	0.676	12	5.58
0	0	0	0	0.474	17	3.58
0	0	0	0	0.461	8	3.67
0	0	0	0	0.195	15	4.67
0	0	0	0	0.323	24	4.75
0	0	0	0	0.313	24	4.75
5	25	3125	0.05[b]	0.291	20	4.08
5	50	6250	0.11	0.059	12	4.58
8	50	6250	0.25	0.025	4	3.14
10	8	1000	0.04	0.169	7	5.58
10	16	2000	0.12	0.201	4	2.4
10	30	3750	0.23	0.015	0	1.75
10	90	11250	0.68	0	0	[c]
18	2	250	0.17[d]	0.052	15	4.25
18	4	500	0.34	0.018	33	2.8
18	11	1375	0.93	0.016	0	3.0
22	3	375	0.30	0.029	21	3.75
22	7	875	0.70	0.012	0	1.33
25	2	250	0.21	0.013	8	4.18
25	6	750	0.62	0.001	0	[c]

[a] Mussels assumed to filter 16 h per day.

[b] Calculation for mussels ≤ 1 cm from Bunt et al (1993).

[c] Mean LOE could not be calculated.

[d] Calculation for mussels > 1 cm from Reeders and Bij de Vaate (1990).

Table 9. Regressions developed from *Ceriodaphnia dubia* population responses (y) to culturing for 14 days in the presence of zebra mussels (x).

C. dubia	Zebra mussel measurement			Probabilities			
response	x_1	x_2	r^2	p_r	p_1	p_2	Regression
abundance (#/m^3)	mussel shell length (mm)	mussel density (#/m^2)	0.82	<0.0001	<0.0001	0.0001	$\log(y + 1) = -0.0707x_1 - 0.0184x_2 - 0.261$
abundance (#/m^3)	filtration capacity ($m^3/m^2/d$)		0.64	<0.0001	<0.0001		$\log(y + 1) = -2.35x - 0.74$
mean LOE score	filtration capacity ($m^3/m^2/d$)		0.44	0.0011	0.0011		$\log(y + 1) = -0.556x + 0.556$
% with young	filtration capacity ($m^3/m^2/d$)		0.57	<0.0001	<0.0001		$\log(y + 1) = -1.45x + 1.17$

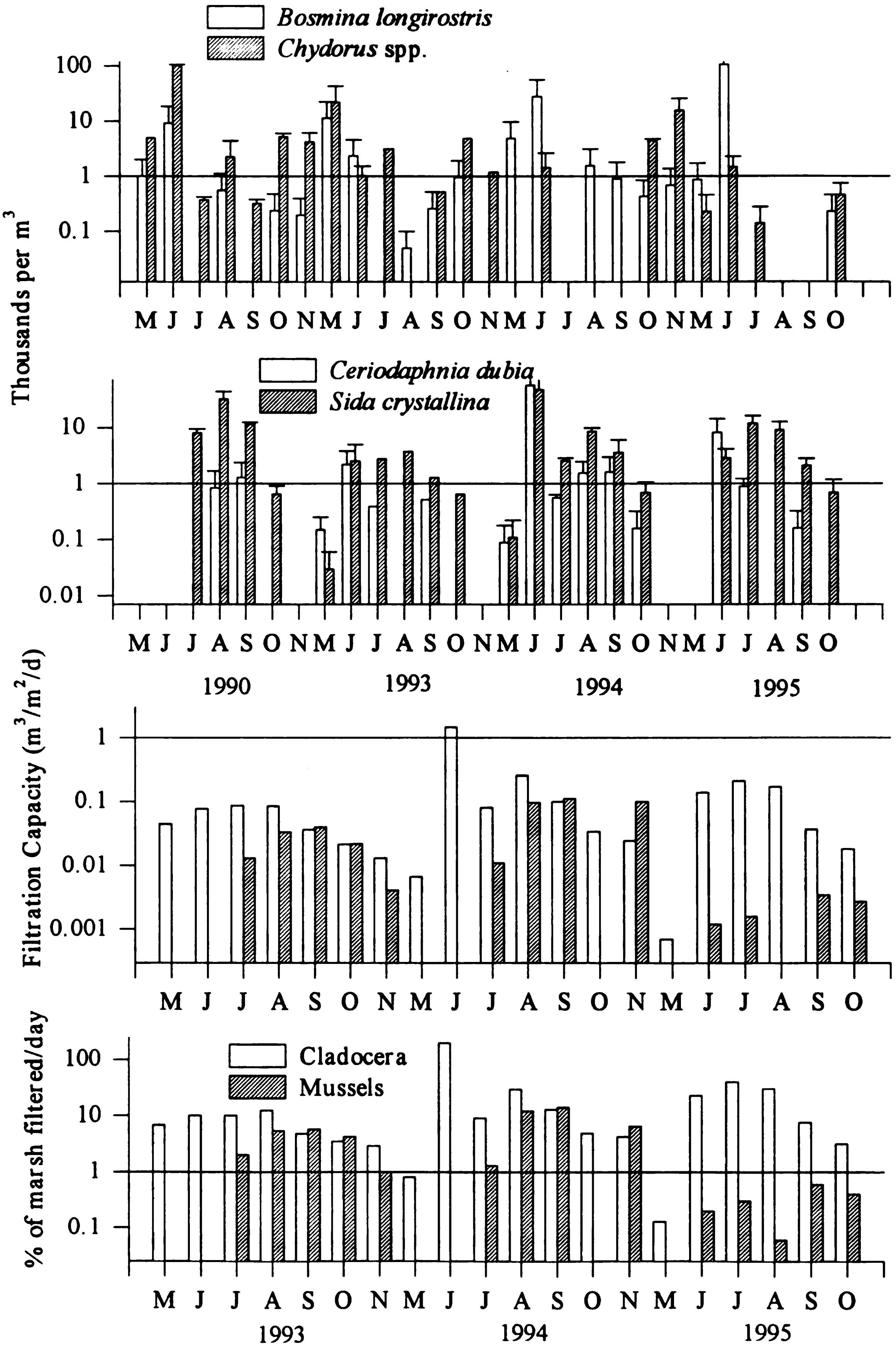
C. dubia populations were significantly reduced by increasing levels of mussel filtration. These decreases, in turn, resulted in the much lower densities of *C. dubia* cultured in the presence of high levels of mussel filtration.

4. Filtration Capacities

The potential for competition between wetland Cladocera and zebra mussels was also investigated by comparing the filtration capacities of these two groups. The four most abundant and common filter-feeding Cladocera were *Ceriodaphnia dubia*, *Chydorus* spp., *Bosmina longirostris*, and *Sida crystallina*. In the offshore area, *Bosmina longirostris* had yearly abundance peaks of 10,000 to 100,000/m^3 in May or June, but was more commonly between 100 and 1000/m^3 (Figure 8). *Ceriodaphnia dubia* typically reached densities of 100 to 1000/m^3 with a three year peak of 30,000/m^3 in June 1994. *Sida crystallina*, one of the largest Cladocera in the wetland, usually had highest concentrations from June through August, reaching 30,000 to 50,000/m^3 each year. *Chydorus* spp. reached their greatest concentrations in the spring or fall with densities approaching 100,000/m^3. Typical abundances were between 1000 and 10,000/m^3.

Filtration capacities of these species were calculated based on their densities in the offshore area. The total theoretical filtration capacity of the four cladoceran filter feeders ranged from 0 to 1.5 m^3/m^2/d (Figure 8). Zebra mussel filtration capacity reached 0.04 m^3/m^2/d in late August 1993 and 0.1 m^3/m^2/d in September 1994 (Figure 8). Mussel filtration capacity was much lower in 1995 and never exceeded 0.005 m^3/m^2/d. Thus, the maximum capacity of the four cladoceran species was 15 times greater than the maximum capacity calculated for *D. polymorpha*. In fact, cladoceran filtration capacity was greater

Figure 8. Top: Mean densities ± 1 standard error of selected Cladocera in the bayward area of the coastal marsh. Bottom: Filtration capacity of four species of Cladocera and zebra mussels and the percent of the marsh water column that each group could filter per day. In all graphs the Y-axis is a log scale.


Bosmina longirostris
Chydorus spp.
Thousands per m3
100
10
1
0.1
M J J A S O N M J J A S O N M J J A S O N M J J A S O
Ceriodaphnia dubia
Sida crystallina
10
1
0.1
0.01
M J J A S O N M J J A S O N M J J A S O N M J J A S O
1990
1993
1994
1995
Filtration Capacity (m3/m2/d)
1
0.1
0.01
0.001
M J J A S O N M J J A S O N M J J A S O
% of marsh filtered/day
Cladocera
Mussels
100
10
1
0.1
M J J A S O N M J J A S O N M J J A S O
1993
1994
1995

than that of mussels on almost all dates, the only exceptions occurring in the fall of 1993 and 1994. Calculations based on the average water depth in this area indicated that these four Cladocera were probably able to filter as much or more of the outer marsh per day as the zebra mussels (Figure 8). In June 1994 they could have filtered the entire water column almost 2 times per day. The highest mussel filtration (in August and September of 1994) would have only filtered one sixth of the water column per day, and this capacity was not routinely achieved by the mussels. More commonly, the mussel population would have been able to filter 1 to 10% of the marsh water column per day in 1993 and 1994 and less than 1% per day in 1995.

5. *In Situ* Effects of Mussels on Cladocera

To determine whether this level of mussel filtration had an effect on the wetland cladoceran community, I compared species richness, total abundance, and the abundance of the four abundant filtering species before and after mussels colonized the wetland. There was no difference in the number of cladoceran taxa or the total abundance of the Cladocera in the offshore area between the late summer and fall of the two years, 1990 and 1994 (Table 10). In the offshore area abundances of *Bosmina longirostris* were higher in 1994 and abundances of *Sida crystallina* were lower. However, these same changes also occurred in the nearshore area, indicating that some factor other than zebra mussel presence was probably the cause. These observations were statistically confirmed using BACI analysis. None of the BACI comparisons were significant for the number of taxa, total abundance, or individual abundances of the filterers *Ceriodaphnia dubia*, *Chydorus* spp., *Bosmina longirostris*, and *Sida crystallina*. This conservative statistic controlled for

Table 10. Means ± 1 standard error (n=8) of the number of Cladocera species and abundances of the dominant filtering species in both areas of the marsh for August through November of each year.

	Nearshore		Offshore	
	1990	1994	1990	1994
Number of species	26.8 ± 1.6	22.5 ± 3.1	24.8 ± 3.1	20.8 ± 1.9
Bosmina longirostris	536 ± 201	2143 ± 992	264 ± 161	1013 ± 376
Ceriodaphnia dubia	1808 ± 1496	14,469 ± 9348	709 ± 378	1113 ± 476
Sida crystallina	13,337 ± 8874	4846 ± 4379	14,892 ± 9278	4279 ± 2282
Chydorus spp.	2477 ± 593	1079 ± 1079	2589 ± 1424	1513 ± 1513
Total abundance	520,370 ± 143,910	223,095 ± 109,555	122,210 ± 53,080	77,030 ± 20,290

any changes occurring in both areas of the marsh by giving a significant rating only to large changes which occurred in only the impacted area.

Discussion

The densities that *Dreissena polymorpha* can reach in lake littoral zones (Brady *et al.* 1995, Lewandowski 1983) suggests the potential for them to affect the zooplankton community in these areas. Zebra mussels have been demonstrated to be very effective in removing small particles from the plankton and depositing them in the sediment (Stanczykowska 1977). Thus, this food resource becomes unavailable to planktonic filter feeders even if it is not efficiently assimilated by the mussels (Sprung and Rose 1988). In addition zooplankton may themselves make up some fraction of the particulate matter consumed by the mussels (Shevtsova *et al.* 1986).

1. Mussel Predation on Zooplankton

The presence of zooplankton remains in the fecal material of zebra mussels collected from the marsh suggested that mussels were consuming live zooplankton, particularly the smaller, weak-swimming taxa such as rotifers and *Bosmina longirostris*. Other researchers have noted that small, weak-swimming zooplankton are vulnerable to *Dreissena polymorpha* filtration (MacIsaac *et al.* 1991, Shevtsova *et al.* 1986). Rotifers were the most abundant zooplankton in the 60 - 125 µm size fraction of the wetland community (Figure 6). They are considered weak swimmers which are not capable of escaping from mussel filtration currents (MacIsaac *et al.* 1991). One of the smallest Cladocera present in the marsh, *Bosmina longirostris,* is also considered to be a weak swimmer (MacIsaac *et al.* 1991). The vulnerability of these zooplankton to zebra mussel filtration was confirmed in short-term experiments in which one or two clumps of mussels were able to reduce the abundance of rotifers and small *B. longirostris* by 55 to 80% in only 1.5 hr. Copepod nauplii and slightly larger *B. longirostris* (126 - 250 μm) were much less vulnerable to mussel predation, probably because they possess better swimming abilities than do rotifers of comparable size (MacIsaac *et al.* 1991). No zooplankton larger than 250 μm were affected. This may reflect both size selectivity on the part of the mussels (Ten Winkel and Davids 1982) and/or stronger escape swimming by the larger zooplankton.

These experiments exposed the zooplankton to very high levels of mussel filtration: mussels in a single clump had the capacity to completely filter the water twice during the 90 min experiment, while two clumps of mussels could filter all the water four times. In similar experiments Shevtsova *et al.* (1986) found that *D. polymorpha* 1.5-2.0 cm could remove 15% of juvenile cyclopoids, 63-65% of *B. longirostris*, and 90% of the dominant rotifer in 12 hr while not affecting larger species such as *Chydorus sphaericus* and *Sida crystallina*. MacIsaac *et al.* (1991) found that 2.25 cm mussels could significantly reduce the densities of several species of rotifers. They did not find any evidence of mussel consumption of *B. longirostris*, but the individuals they used were > 250 μm in size.

The vulnerability of rotifers and small *B. longirostris* to mussel filtration raised the question of whether mussels in the marsh could prey upon these zooplankton to a significant extent under natural conditions. Predation on rotifers has been suggested for western Lake Erie by MacIsaac *et al.* (1992), who determined that a 75% reduction in rotifer densities was likely due to direct predation by dense mussel communities. Mussel densities in the marsh ranged from 1000 to 55,000/m^2 during August of 1994 (Brady *et al.* 1995). The highest density was very close to the density of a single mussel clump in the filtration vulnerability experiments (48,000/m^2). The marsh population was not comprised primarily of mussels in clumps, however, as there were an average of < 0.5 clumps/m^2 (Brady *et al.* 1995). Instead, most mussels were attached to stems of the dominant emergent plant, three-square bulrush (*Scirpus americanus*). In addition, the mussels on bulrush stems were quite small, most < 6 mm (Brady *et al.* 1995). At least 10% of mussels in clumps, by contrast, had shell lengths ≥ 1 cm. Thus, the highest theoretical filtration capacity for the marsh population was only 0.1 m^3/m^2/d, much lower than the 2.74 m^3/m^2/d for a single clump in the experiment. Had the sizes of mussels been similar to the size distribution found in clumps, their filtration capacity would have been 10 times greater.

The filtration capacity for the marsh mussel population was more closely approximated by the third filtration vulnerability experiment. This experiment used mussels attached to bulrush stems at densities similar to those occurring in the wetland, leading to an average filtration capacity of 0.17 m^3/m^2/d. Although these smaller mussels were allowed to filter twice as long as the mussels in clumps, they would only have been able to filter about 1/3 of the water in the chamber by the end of the experiment. The much lower filtration capacity of these less numerous and smaller mussels was still greater than the highest capacity calculated for the marsh population. This mussel density did not cause significant reductions in the abundances of any zooplankton group. These results indicated that zebra mussels were unlikely to reduce the population size of even the vulnerable marsh rotifer community by direct predation, given the size structure and densities at which mussels occurred in the wetland.

2. Mussel Competition with Cladocera

Another mode of interaction between *D. polymorpha* and zooplankton is through competition for food. This potential has been suggested by evidence of phytoplankton reduction by zebra mussels in other areas around the Great Lakes. For example, zebra mussels in western Lake Erie caused an 80% reduction in planktonic diatoms (Holland-Beeton 1990) and a 50% decrease in chlorophyll a concentrations (Leach 1992), moving the lake into an oligotrophic classification based on its chlorophyll a levels.

I investigated mussel competition with a filtering Cladocera by culturing *Ceriodaphnia dubia* in the presence of various sizes and densities of mussels. *Ceriodaphnia dubia* neonates are too large (> 300 µm) to be filtered from the water by zebra mussels, removing predation as a possible factor in the experiment. Increasing levels of mussel filtration caused *C. dubia* population sizes to be significantly reduced, indicating competition between the zooplanktors and zebra mussels. An alternative explanation is that *C. dubia* populations were repressed by some substance released by the mussels, representing a toxic effect of mussels on the zooplankton. Ammonia is the most likely substance that could cause the observed density-dependent effect. However, ammonia levels remained ≤ 0.05 mg/L, well below the level of 2 mg/L that has been shown to cause reproductive impairment in *C. dubia* (Nimmo *et al.* 1989). Thus, competition for food between mussels and *C. dubia* was the most likely cause of the significant decrease in population density with increasing exposure to mussels. The large decrease in nutritional status of *C. dubia* with increasing exposure to mussel filtration indicates increasing food limitation for these cladoceran populations. These *C. dubia* populations also exhibited much reduced reproduction as mussel filtration capacity increased, indicating that food limitation was severe enough to greatly limit the ability of *C. dubia* to produce eggs. Taken together, the decreased survivorship, nutritional status, and reproduction of *C. dubia* indicates they were losing in the competition with zebra mussels for food.

The laboratory results indicating competition between zebra mussels and large filterers such as *Ceriodaphnia dubia* were not supported by field observations. A comparison of the densities and community composition of cladoceran filter-feeders before and after mussel colonization failed to yield any evidence of effects attributable to the invasion, perhaps because of the high variability associated with the field observations.

An alternative explanation, however, is that mussel filtration in the marsh was not great enough to have an observable effect on the Cladocera. The small size and relatively low numbers of mussels in the wetland (Brady *et al.* 1995) caused mussel filtration capacities to be low, rarely reaching 0.1 $m^3/m^2/d$. This is just below the level of filtration at which *C. dubia* abundances, nutritional status, and reproduction began to be reduced in the microcosm experiment. Instead, the filtration capacity of the four dominant cladoceran filterers equaled or exceeded that of the zebra mussels on most dates. At their greatest density, zebra mussels could only filter one sixth of the bayward section of the marsh per day, while these four Cladocera had the capacity to filter at least half of the water column per day on several occasions. In many of the offshore areas of the Great Lakes the opposite result has been found, with mussels representing a filtration capacity many times greater than that of the zooplankton and capable of filtering the water column many times over during a single day (MacIsaac *et al.* 1992). For example, offshore colonies of mussels in inner Saginaw Bay had the capacity to filter all of the water in less than a day in 1992 (Fanslow *et al.* 1995), while pelagic zooplankton required 37 days to filter the water column (Bridgeman *et al.* 1995). In contrast, marsh mussels required 17 to 70 days to filter the water column in 1993 and 14 to 196 days to accomplish this same task in 1995.

Summary and Conclusions

Zebra mussels have the capacity to both prey upon and compete with zooplankton. The presence of zooplankton exoskeletons within the fecal material of zebra mussels collected from a Saginaw Bay coastal emergent marsh suggested that these mussels were consuming live zooplankton. Experiments to assess the vulnerability of wetland zooplankton to mussel predation demonstrated that the filtration capacities of high densities of mussel clumps (2.74 to 5.6 $m^3/m^2/d$) could remove up to 80% of small rotifers and 73% of small *Bosmina longirostris*. However, the mussel communities naturally occurring in the wetland primarily consisted of mussels < 1 cm which were attached to bulrush stems. At these lower filtration capacities (0.17 $m^3/m^2/d$) more representative of the wetland population, there were no significant decreases in any zooplankton taxa. These results suggest that while mussels are capable of consuming small, weak-swimming zooplankton, the existing wetland mussel community will exert only minimal predatory pressure on the zooplankton.

The potential for mussels to compete with wetland filter feeders was investigated by culturing *Ceriodaphnia dubia* with zebra mussels across a range of filtration capacities. Regressions indicated that *C. dubia* population densities, reproduction, and average nutritional state were all significantly reduced with increasing levels of zebra mussel filtration. These negative effects of mussel competition with *C. dubia* began to be evident at mussel filtration capacities of 0.12 to 0.17 $m^3/m^2/d$. Thus, even fairly low levels of mussel filtration were sufficient to induce competition for food between mussels and *C. dubia* in the laboratory.

However, comparisons of the cladoceran community before and after mussels colonized this coastal wetland showed no evidence of changes attributable to the invasion. Species richness, total abundance, and the densities of four common species of filtering Cladocera were not different after mussels colonized the bayward area of the marsh. This was probably because the filtration capacity of the marsh mussel community was always lower than the levels at which competitive effects became apparent under experimental conditions. Instead, the combined filtration capacity of just four cladoceran species was almost always greater than that of the mussels.

These results indicate that the mussel population in this Saginaw Bay coastal marsh was having neither a large predatory nor a large competitive effect on the wetland zooplankton community. Mussel densities and filtration capacities would probably have to be 10 to 100 times greater than those seen thus far before effects on the zooplankton would become noticeable.

CHAPTER THREE

EFFECTS ON MACROINVERTEBRATES

Introduction

Zebra mussels (*Dreissena polymorpha* Pallas) have altered the way in which energy is transferred through the food web in many of the areas they have colonized (MacIsaac *et al.* 1992, Mackie 1991). In some instances researchers have been able to demonstrate that this has caused fairly substantial changes in the macroinvertebrate community. For example, benthic detritivores such as oligochaetes, chironomids, and amphipods, have been shown to increase (Dermott *et al.* 1993, Griffiths 1993, Stewart and Haynes 1994). These studies have typically been conducted in the offshore areas of lakes where zebra mussels form large shoals on the bottom substrate. Young mussels, however, often settle onto the vegetation in lake littoral areas, sometimes reaching high densities (Lewandowski 1982, 1983). Because these littoral zone studies were conducted in Europe long after zebra mussel colonization, researchers were unable to investigate whether zebra mussels had changed the macroinvertebrate community of these areas.

The macroinvertebrates of coastal wetlands around the Great Lakes may provide crucial food resources to many Great Lakes fish, waterfowl, and shorebirds. Fifty-one species of fish are associated with Lake Huron wetlands (Wilcox 1995). At least 28 species of waterfowl use Lake Huron wetlands for postbreeding foraging and as staging areas and migration stopovers (Wilcox 1995). Prince and Flegel (1995) estimated that 16 species of avifauna forage in emergent marshes while 9 species use them for breeding habitat. The macroinvertebrate food resources required by these groups are found in abundance in coastal wetlands. Duffy *et al.* (1991) reported invertebrate densities of 19,300/m^2 in northern Lake Huron wetlands, while Brady (1992) reported an estimated biomass of 3-4 g/m^2 in Saginaw Bay coastal marshes. Macroinvertebrates play an additional important role in these ecosystems by helping to process the abundant detrital matter which accumulates (Krieger and Klarer 1992). Given the importance of this invertebrate community and the fact that so few coastal wetlands remain around the Great Lakes (Krieger *et al.* 1992), major changes in the functioning of these ecosystems could have far-reaching impacts.

I completed a characterization of the macroinvertebrate community in a Great Lakes coastal marsh in 1990 (Brady 1992), just before the area was colonized by zebra mussels in 1991. This dataset provided the opportunity to examine the impacts that this large filter feeder might have on this community. Because other researchers (Griffiths 1993, Stewart and Haynes 1994) have reported increases in some benthic invertebrates, I hypothesized that detritivores would increase in abundance in the area colonized by mussels. An additional hypothesis was that there would be changes in the epiphytic invertebrate community due to the attachment of mussels to the wetland vegetation.

Methods

The study site was located in a large wetland complex that extended along the southeastern shore of Saginaw Bay, Lake Huron, Michigan (Figure 9). This location was

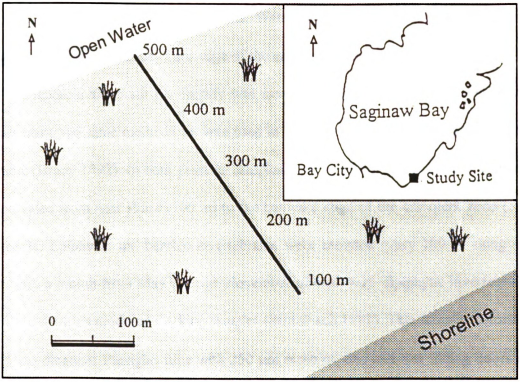


Figure 9. Location of the study site and sampling transect in Saginaw Bay, Lake Huron.

chosen because the macroinvertebrates of this area were studied in 1990 (Brady 1992), before zebra mussels had colonized the emergent marsh. Emergent vegetation, principally three-square bulrush (*Scirpus americanus* Pers.) extended approximately 500 m offshore. The marsh substrate was predominantly sand. Water depth gradually increased bayward, reaching 75 to 125 cm at the bayward edge of the emergent zone.

The macroinvertebrate community was sampled in 1993, 1994, and 1995 in the same area using the same methods as were used in 1990 to ensure that the data would be comparable (Brady 1992). In both years all samples were collected along a 400 m transect which extended from near shore (100 m) to the bayward edge of the emergent zone (500 m; Figure 9). Epiphytic and benthic invertebrates were sampled every 100 m along the transect once a month from May through November of each year. Epiphytic invertebrates were collected with a modified Gerking sampler (Mittelbach 1981). This sampler consisted of a 21.5 cm diameter Plexiglas tube with 250 μm mesh on one end and sliding doors on the other. The sampler was designed to enclose aquatic vegetation, the surrounding water column, and associated littoral invertebrates. The entire length of the water column from surface to bottom was included in each sample. Benthic invertebrates were sampled using a 4.5 cm diameter plexiglas tube which was used to collect a 15 cm long sediment core. One sample was taken with the modified Gerking sampler and two with the coring device at each of the five stations along the transect on each sampling date. The paired core samples were pooled for analysis.

Large vegetation was scrubbed, then examined with the unaided eye and any remaining invertebrates removed. These invertebrates were added to the rest of the

Gerking sample. The Gerking sample and the entire contents of the sediment cores were preserved separately in 95% ethanol containing rose bengal dye (Mason and Yevich 1967). Gerking samples were subsampled by dividing the sample into 6 equal parts using a calibrated box subsampling device. Sediment cores were sugar floated (Anderson 1959) then subsampled. One sixth of each sample was examined under 10x magnification for invertebrates. Invertebrate identification was based on Merritt and Cummins (1984), Thorp and Covich (1991), and Simpson and Bode (1980).

It was previously determined that zebra mussels only became abundant in the bayward 250 m of the marsh (Brady *et al.* 1995). Thus, samples collected at 400 and 500 m along the transect were used to investigate changes occurring after zebra mussels became part of the community. The macroinvertebrates in this offshore area of the marsh (n=2/date) were compared before (1990) and after (1994) zebra mussels colonized the emergent vegetation. The year 1994 was chosen as the comparison year because zebra mussels reached high densities in the bayward area of the wetland in 1994 (Brady *et al.* 1995) and because the transect that year best matched the 1990 transect location. Only samples from August through November were used for each of the years because these were the only months in 1994 during which zebra mussels were present in fairly high numbers (Brady *et al.* 1995). The epiphytic and benthic communities were considered to be separate and discrete entities and were analyzed separately. For each community, taxa richness and the abundances of species making up at least 10% of total community abundance were compared between years.

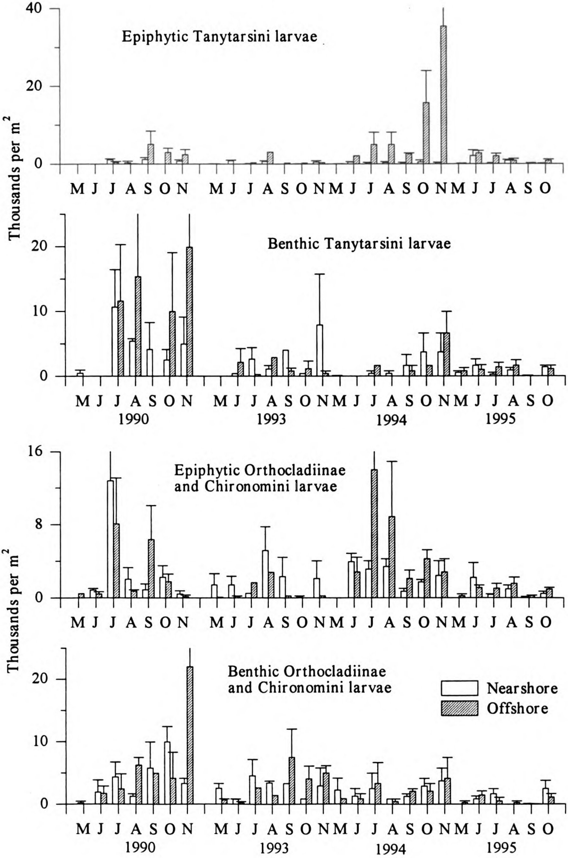
Because the nearshore area was not colonized by mussels, I considered this area to be unimpacted by the invasion. This allowed me to confirm changes seen in the before-after community comparison using a fairly conservative statistic, BACI analysis (Stewart-Oaten *et al.* 1986). BACI analyses are conservative because they compare the variability between the control and impact areas before and after the impact, thus controlling for changes that have occurred in both areas and should not be considered a result of the impact. Samples considered to be from the "control" area were those collected at the 100 m and 200 m points along the transect (Figure 9).

Results and Discussion

The earlier research in this Saginaw Bay coastal wetland documented 54 insect taxa, many of them Chironomidae, and 11 other macroinvertebrate groups (Brady 1992). These invertebrates reached abundances approaching 50,000/m^2 in both epiphytic and benthic communities (Brady 1992). In all years, the epiphytic community primarily consisted of chironomid larvae, larval Ephemeroptera, oligochaetes in the family Naididae, amphipods and isopods. The benthic community was made up of chironomid and mayfly larvae, both naidid and tubificid oligochaetes, nematodes, amphipods and isopods.

Abundance trends over time were observed for some of these taxa. Chironomid larvae in the tribe Tanytarsini were more abundant in the benthos than on plant stems in the offshore area in 1990 (Figure 10). This trend somewhat reversed in 1994 when epiphytic densities were greater than benthic abundances. Overall, larval densities in the benthos were lower in 1993 through 1995 than they were in 1990. Trends in the abundance of other larval chironomids were not particularly obvious, although benthic

Figure 10. Mean densities ± 1 standard error of epiphytic and benthic chironomid larvae from nearshore and offshore areas of a coastal marsh.


Epiphytic Tanytarsini larvae
Benthic Tanytarsini larvae
Epiphytic Orthocladiinae and Chironomini larvae
Benthic Orthocladiinae and Chironomini larvae
Thousands per m²
Thousands per m²
40
20
0
20
10
0
16
8
0
20
10
0
M J J A S O N M J J A S O N M J J A S O N M J J A S O
1990
1993
1994
1995
Nearshore
Offshore

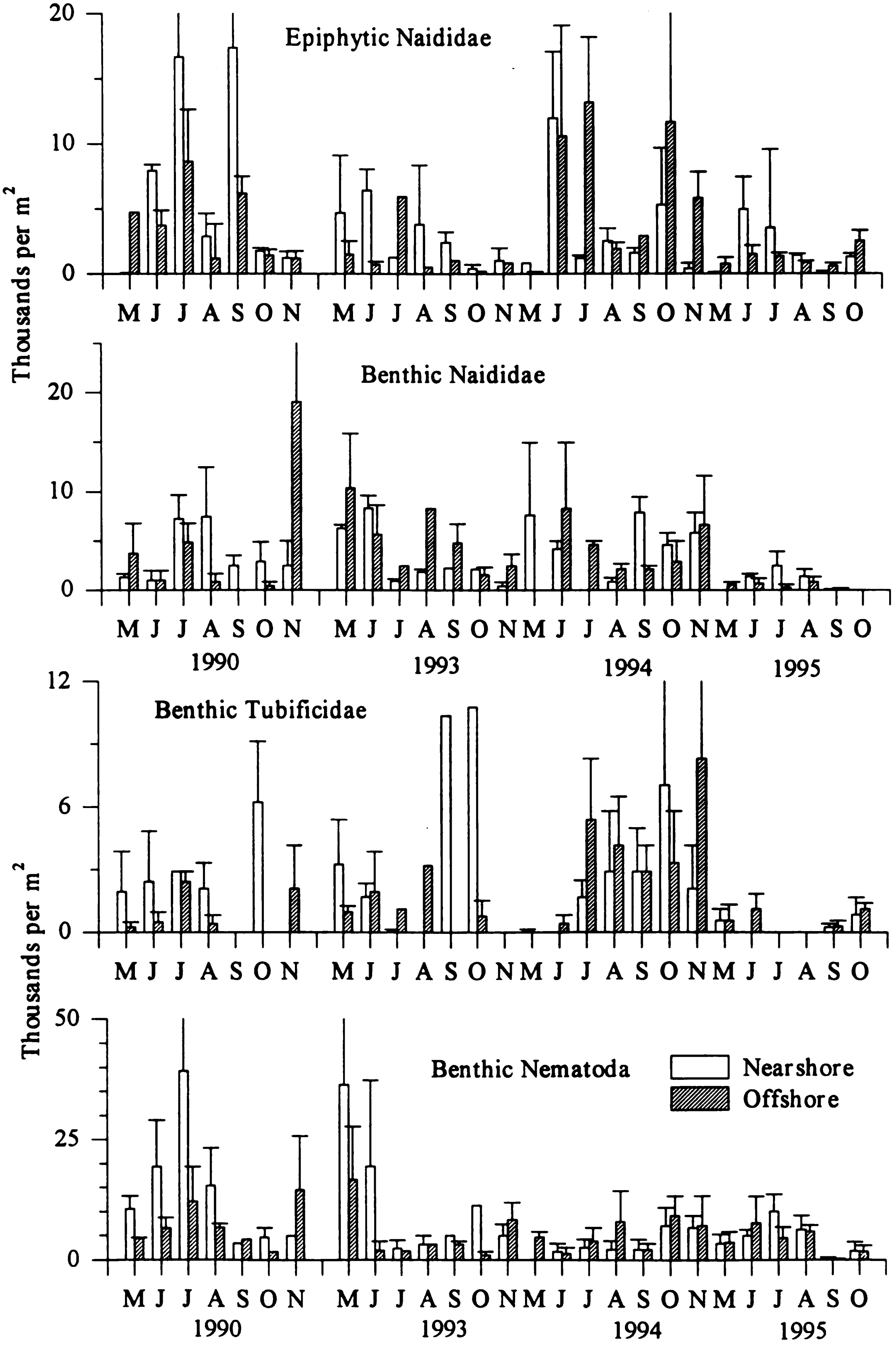
densities appeared slightly higher in 1990 than in subsequent years (Figure 10). There was no apparent trend in the abundances of epiphytic naidid oligochaetes (Figure 11). Densities of benthic Naididae were lower in 1995 than they had been in preceding years. Tubificid oligochaetes were primarily benthic; their densities were high in the offshore area of the marsh in 1994 (Figure 11). They also had high densities in the nearshore area in the fall of 1993. Benthic nematodes were generally less abundant in 1993 through 1995 than they were in 1990 (Figure 11).

Samples collected in the late summer and fall (August through November) of 1990 and 1994 were chosen for a comparison of the invertebrate community before and after zebra mussel colonization. This decision was based on zebra mussel densities from samples collected separately and on the ability to match sampling sites between 1990 and 1994. The choice was made before data on the macroinvertebrate community were analyzed to preclude these results from influencing the decision.

A comparison of the communities in each habitat, epiphytic and benthic, between the nearshore and offshore areas of the wetland revealed more similarities than differences. The most noticeable differences were that larval Tanytarsini were particularly abundant in the bayward area, and amphipods, isopods, and ephemeropteran larvae were more abundant nearshore (Figure 12).

Differences in the two nearshore habitats between 1990 and 1994 were compared to changes that had occurred in the two communities in the offshore area over this same time period. The number of taxa and community composition in both nearshore habitats were almost identical between years (Figure 12). There was an increase in the abundance

Figure 11. Mean densities ± 1 standard error of epiphytic and benthic oligochaetes and nematodes from nearshore and offshore areas of a coastal marsh.


Epiphytic Naididae
Benthic Naididae
Benthic Tubificidae
Benthic Nematoda
Thousands per m²
Thousands per m²
20
10
0
20
10
0
12
6
0
50
25
0
M J J A S O N M J J A S O N M J J A S O N M J J A S O
1990
1993
1994
1995
Nearshore
Offshore

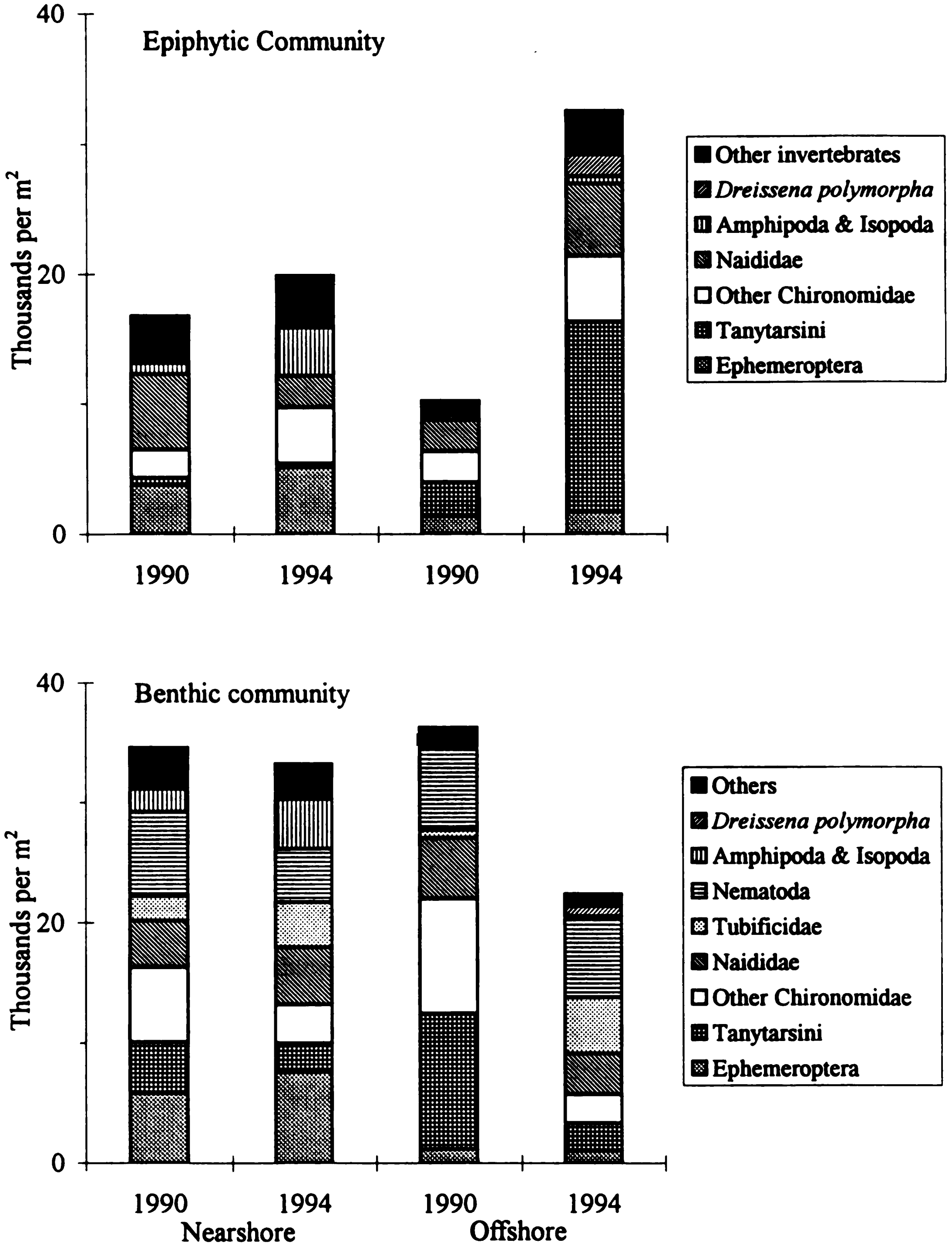


Figure 12. Community composition of the epiphytic (top) and benthic (bottom) macroinvertebrate communities in the nearshore and offshore marsh areas. Each bar represents 2 samples per month for Aug.- Nov. for an n=8.

of amphipods and isopods, a decrease in the numbers of epiphytic naidids, and a switch in chironomid larvae from higher abundance in the sediment to greater abundance on stems. In the offshore area there was no change in taxa richness in either community. In the epiphytic community chironomid larvae and naidid oligochaetes both increased in abundance. Zebra mussels only comprised about 5% of this community in 1994. Chironomid larval abundances decreased in the sediment between 1990 and 1994 and tubificid densities increased (Figure 12). Zebra mussels made up about 4% of the benthic community in 1994.

Some of the observed changes occurred in both areas of the wetland irregardless of the presence of zebra mussels. Because of this, BACI analysis was used to provide a conservative indication of the significant changes that occurred only in the "impacted" area in conjunction with zebra mussel colonization. BACI analyses indicated no significant differences for taxa richness or the abundances of most groups in the offshore area of the wetland following zebra mussel colonization (Tables 11 and 12). There was a significant increase in the abundance of epiphytic larval Tanytarsini ($p = 0.03$) and a marginally significant decrease in their abundances in the benthos ($p = 0.08$) (Figure 13). The change in tanytarsinid density between the two communities was similar: 12,000/m^2 more in the vegetation and 9000/m^2 less in the sediments. Other researchers have found increases in chironomid larvae, including Tanytarsini (Stewart and Haynes 1994), in association with zebra mussels. In an elegant series of experiments, Stewart (1996) demonstrated that chironomid larvae were responding to the presence and activity of living mussels rather than simply to the increased complexity created by their shells. Many larval tanytarsinids

Table 11. Means ± 1 standard error (n=8) of the number of macroinvertebrate taxa and abundances of the dominant epiphytic groups in both areas of the marsh for August through November of each year.

	Nearshore		Offshore	
	1990	1994	1990	1994
Number of taxa	21.5 ± 2.0	18.0 ± 0.9	15.0 ± 1.5	14.8 ±1.3
Chironomidae (other)	1393 ± 446	2064 ± 573	2245 ± 1406	4505 ± 1516
Tanytarsini	570 ± 254	327 ± 63	2591 ± 1021	14,598 ± 7475*
Naididae	3580 ± 1774	2114 ± 1107	2066 ±1102	2819 ± 1046
Caenis spp.	3746 ± 2843	5034 ± 1505	1384 ± 242	1736 ± 495

+ Indicates significance at $p < 0.1$ by BACI analysis.

* Indicates significance at $p < 0.05$ by BACI analysis.

Table 12. Means ± 1 standard error (n=8) of the number of macroinvertebrate taxa and abundances of the dominant benthic groups in both areas of the marsh for August through November of each year.

	Nearshore		Offshore	
	1990	1994	1990	1994
Number of taxa	11.8 ± 0.8	11.8 ± 0.9	7.5 ± 1.7	8.3 ± 1.3
Chironomidae (other)	5076 ± 1871	2176 ± 684	9323 ± 4234	2176 ± 764
Tanytarsini	4248 ± 642	2382 ± 818	11,292 ± 4278	2279 ± 1489+
Naididae	3833 ± 1212	4765 ± 1480	5076 ± 4665	3644 ± 1016
Tubificidae	2072 ± 1465	3730 ± 1122	622 ± 493	4662 ± 1236*
Nematoda	7044 ± 2785	4455 ± 1378	6733 ± 2782	6526 ± 1545
Caenis spp.	5801 ± 3142	7148 ± 2340	1140 ± 459	1036 ± 766

+ Indicates significance at $p < 0.1$ by BACI analysis.

* Indicates significance at $p < 0.05$ by BACI analysis.

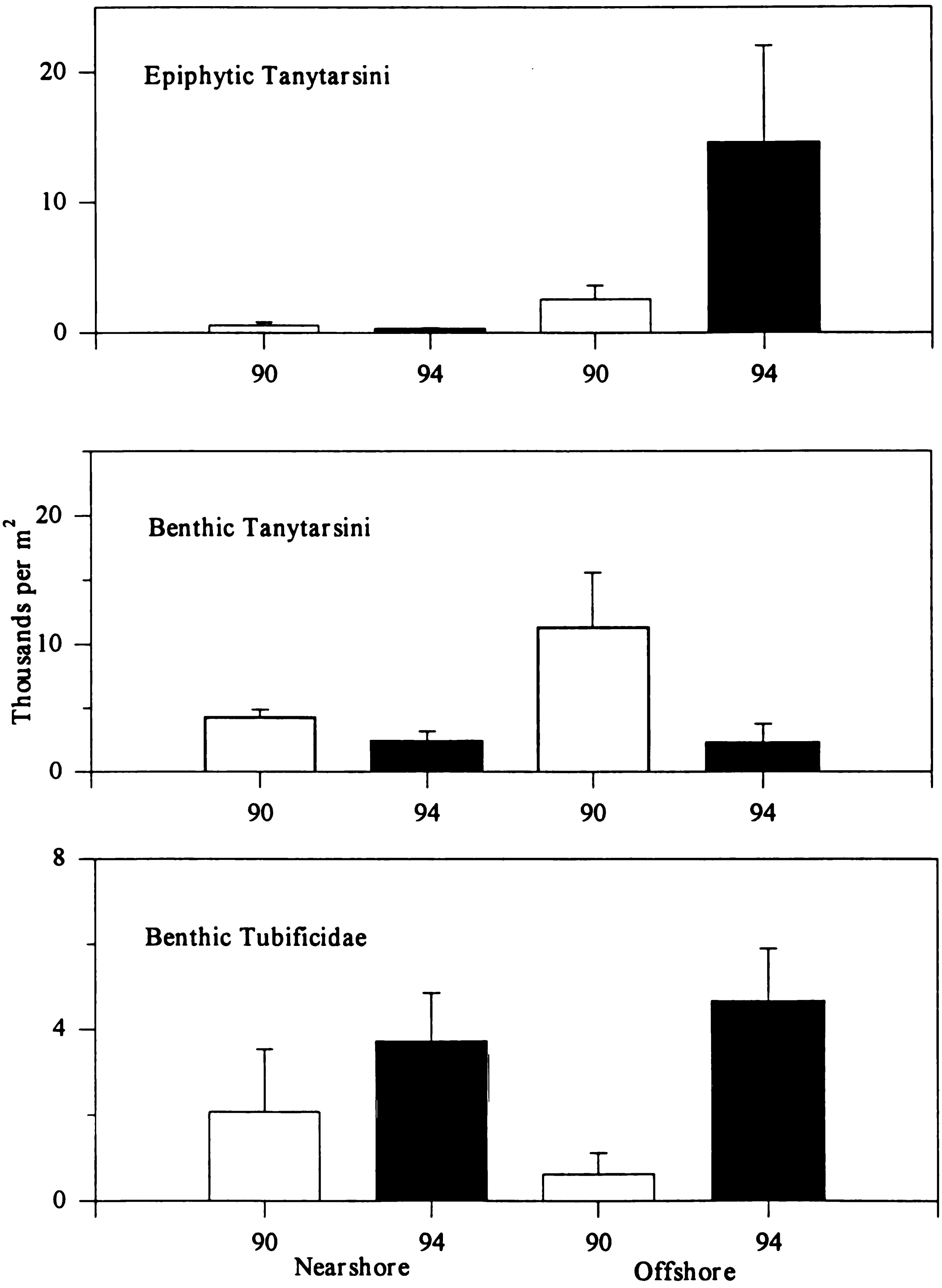


Figure 13. Densities of larval Tanytarsini and Tubificidae before and after zebra mussel colonization. Top: Epiphytic Tanytarsini; p= 0.03. Center: Benthic Tanytarsini; p= 0.08. Bottom: Benthic Tubificidae; p= 0.04.

are filterers, particularly *Rheotanytarsus*, a dominant genus in the offshore area (Cardinale *et al.* submitted). These larvae were the only other macroinvertebrate filter feeders present in the wetland prior to the arrival of the zebra mussel. Filtering larvae may be benefiting from the filtration currents created by the mussels. Collector-gathering larvae may be consuming mussel feces and psuedofeces, a nutritious and digestible food source for larval chironomids (Izvekova and Lvova-Katchanova 1972).

The only other significant change in macroinvertebrates in the offshore area following mussel colonization was an increase in the densities of tubificid oligochaetes in the sediment ($p = 0.04$) (Figure 13). Griffiths (1993) and Stewart and Haynes (1994) noted increases in oligochaete densities after mussels colonized Lake St. Clair and Lake Erie. Other researchers (Griffiths 1993, Izvekova and Lvova-Katchanova 1972, Stewart and Haynes 1994) have indicated that these detritivores respond positively to the presence of mussel fecal and pseudofecal material. The organic content of the sandy sediments in the offshore area of the marsh, although not measured, may have been fairly low prior to the arrival of zebra mussels. The addition of mussel fecal and pseudofecal material likely increased the organic content, providing these detritivores with an additional source of nutrition and resulting in the observed increases.

This shift in energy from planktonic to benthic by zebra mussels has been observed in many areas of the Great Lakes. The result has been a major alteration of the ecosystem in Lake St. Clair (Griffiths 1993). Abundances of benthic detritivores have increased, water clarity has increased greatly, leading to highly expanded macrophyte cover, and phytoplankton abundances have greatly decreased (Griffiths 1993). This has shifted the fish assemblage to a community typical for a littoral zone (Ross 1994).

As hypothesized, there were increases in benthic detritivores (tubificid oligochaetes) after mussels invaded the Saginaw Bay wetland. There was also a change in the epiphytic community with the apparent habitat shift of tanytarsinid larvae from benthic to epiphytic. The changes observed in the wetland were not as large nor as encompassing as those seen in Lake St. Clair or western Lake Erie (Dermott *et al.* 1993). This is not surprising because zebra mussels densities were much lower in the marsh than the 300,000 to 1 million/m^2 reported for these other areas (Dermott *et al.* 1993, Griffiths 1993). In addition the mussel population in the marsh was predominantly composed of mussels < 2 mm, resulting in much lower filtration capacities than those of similar densities of larger mussels. This lower level of impact is encouraging given the importance of coastal wetland food webs to Great Lakes fish and waterfowl.

SUMMARY AND CONCLUSIONS

Zebra mussels (*Dreissena polymorpha*) colonized a Saginaw Bay coastal wetland in 1991 and were studied in 1993 through 1995. The marsh mussel population consisted primarily of mussels attached to stems of the dominant emergent plant, three-square bulrush (*Scirpus americanus*). Much lower densities of mussels existed as substrate-independent clumps resting on the sediment, but these clusters contained most of the reproductive mussels in the marsh. The population varied both seasonally and spatially in 1993 and 1994. Mussel densities were low in the spring and early summer ($300/m^2$), represented only by the mussel clumps that had survived the winter in the bayward half of the wetland where the water was deep enough for them to avoid ice scour. Abundances did not increase until recruitment of young-of-the-year mussels onto bulrush stems in August. Recruitment only occurred in the outer 250 m of the 500 m wide emergent zone because there was little water movement to carry veligers into the nearshore area. Highest densities of larval and juvenile mussels were found between 300 and 400 m from shore, indicating that the substrate-independent clumps of mussels in the marsh rather than deeper water populations were serving as the source of the larvae. Mussel densities reached 100/bulrush stem with areal densities as high as $55,000/m^2$ near the center of the marsh in August 1994. These areas experienced high losses by September, however, and densities were much lower in the fall. Over the winter most of the remaining mussels on stems apparently succumbed due to senescence of the vegetation and ice scour. Thus, the marsh mussel population consisted primarily of mussels 2 mm and smaller that were abundant only in the bayward half of the wetland from August through November of each year.

I investigated whether this population was large enough to have an impact on wetland zooplankton or macroinvertebrates. The ability of these mussels to prey upon wetland zooplankton was investigated both observationally and experimentally. Observation of the remains of rotifers, *Bosmina longirostris*, copepod nauplii, and other zooplankton in the fecal material of wetland mussels suggested that these groups were experiencing predation. This was experimentally tested in short term experiments. Rotifers smaller than 250 µm and *B.* l*ongirostris* smaller than 125 µm were significantly reduced by just 90 min of filtration by zebra mussel clumps. Larger *B. longirostris* and taxa that were stronger swimmers, such as copepod nauplii, were not affected by this filtration. Mussels attached to bulrush stems represented a much lower filtration capacity than that of mussel clumps, but one that was more representative of the wetland population. Mussels on bulrush stems did not significantly reduce the abundances of any zooplankton taxa during 180 min of exposure.

The potential for competition between zebra mussels and filtering Cladocera was also tested experimentally. A common wetland species, *Ceriodaphnia dubia*, was cultured with zebra mussels for 14 days. Population densities of *C. dubia* decreased significantly with increasing levels of mussel filtration. The reproductive and nutritional status of these populations showed significant reduction with greater mussel filtration capacities. The effects of mussel competition began to be apparent at filtration capacities of 0.12 to 0.17 $m^3/m^2/d$ in this experiment. These levels were higher than the highest filtration capacities calculated for marsh mussel population. There was no evidence that wetland mussels were having a competitive effect on the marsh Cladocera. Comparisons of cladoceran species richness, total abundance, and the abundance of common taxa before and after mussel colonization showed no apparent changes attributable to the invasion. Instead, the combined calculated filtration capacities of the four abundant filtering Cladocera were usually higher than the filtration capacity of the mussel population.

The epiphytic and benthic macroinvertebrate communities were compared before and after zebra mussel colonization of the marsh. BACI analyses indicated several changes potentially attributable to zebra mussels. Larval chironomids in the tribe Tanytarsini were significantly more abundant on bulrush stems after mussels invaded the wetland. This was accompanied by an almost significant decrease in the densities of these larvae in the sediments. The magnitude of both changes was similar and resulted in no overall change in the numbers of these larvae in the marsh. These larvae may have benefited from filtration currents generated by the mussels attached to bulrush stems. These currents would have increased water circulation, thus bringing additional food to the larvae. It is also possible that some of the larvae may have been utilizing the fecal material of mussels as a source of food. Another difference occurring in conjunction with zebra mussel colonization was a significant increase in tubificid oligochaete abundance in the sediment, perhaps due to the use of mussel feces and pseudofeces as an additional source of nutrition.

In summary, zebra mussels were able to maintain a year-round reproducing population in the offshore half of this coastal emergent marsh. Their densities were low during most of the year, and high abundances consisted almost entirely of very small mussels. The filtration capacity of this population was insufficient to reduce the populations of even the vulnerable rotifer community through predation under experimental conditions. Although competition between Cladocera and mussels was demonstrated in the laboratory, there was no evidence of change in the wetland cladoceran community with the arrival of the mussels. Only two macroinvertebrate groups exhibited any changes potentially related to the zebra mussel invasion. Larval tanytarsinid chironomids shifted from a predominantly benthic to a primarily epiphytic habitat in conjunction with zebra mussel colonization. Benthic tubificids significantly increased in abundance in the sediment, perhaps benefiting from the input of mussel feces and pseudofeces. If the mussel population in this wetland is representative of populations in shallow coastal marshes, it appears unlikely that they will cause dramatic changes such as those seen in some of the open water areas around the Great Lakes.

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