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NOTE

Zooplankton Grazing During the Zebra Mussel (*Dreissena polymorpha*) Colonization of Saginaw Bay, Lake Huron

Thomas B. Bridgeman,[1,4] Gary L. Fahnenstiel,[2] Gregory A. Lang,[3] and Thomas F. Nalepa[3]

[1]*Cooperative Institute for Limnology and Ecosystems Research*
University of Michigan
2200 Bonisteel Blvd.
Ann Arbor, Michigan 48109

[2]*Lake Michigan Field Station*
Great Lakes Environmental Research Laboratory
U.S. Department of Commerce
National Oceanic and Atmospheric Administration
1431 Beach St.
Muskegon, Michigan 49441

[3]*Great Lakes Environmental Research Laboratory*
U.S. Department of Commerce
National Oceanic and Atmospheric Administration
2205 Commonwealth Blvd.
Ann Arbor, Michigan 48105-1593

ABSTRACT. *Weight-specific zooplankton filtering rates were determined at three sites in Saginaw Bay during the period of maximum zooplankton abundance prior to and after the establishment of zebra mussel colonies (June 1991 and June 1992). Biomass-specific filtering rates were similar in both years (inner bay: 0.24–0.33 mL μg dry wt.$^{-1}$ d^{-1}; outer bay: 1.27–1.83 mL μg dry wt.$^{-1}$ d^{-1}), but large decreases in zooplankton biomass resulted in a decrease, on average, of 58% in community filtering rates between years. As part of a large-scale monitoring program, zooplankton abundance and biomass estimates were also recorded at 13 sites during May-August of both years. Mean biomass in the inner bay was 40% lower in 1992 than in 1991, and in the outer bay, mean biomass was 70% lower in 1992 than in 1991. Zooplankton community composition was the same in both years. We estimated the time required to clear the water volume of the inner bay during the May–June period to be 17 days in 1991 and 37 days in 1992. For these two periods, decreased zooplankton numbers and community filtering rates indicate that grazing by zooplankton was likely not responsible for noted declines in phytoplankton abundance and productivity.*

INDEX WORDS: *Lake Huron, zooplankton, grazing, zebra mussels.*

INTRODUCTION

The colonization of the Laurentian Great Lakes by the zebra mussel *Dreissena polymorpha* in the 1980s and early 1990s has been well documented (Hebert *et al.* 1991, Leach 1993). In most affected areas, the introduction of the zebra mussel has coincided with decreases in phytoplankton abundance and increases in water clarity (Leach 1993, Holland 1993). While the phytoplankton decrease has been widely attributed to the large filtering capacity of zebra mussels (Leach 1993, Holland 1993), the relative importance of grazing by herbivorous zooplankton following colonization by zebra mussels is not well known. In attributing declining chlorophyll levels almost exclusively to zebra mussels, the considerable impact of zooplankton grazing on controlling phytoplankton abundance may be underestimated.

[4]Present address: Dept. of Biology, Univ. of Michigan, Ann Arbor, MI 48109

For example, in western Lake Erie, correlations between grazing by species of *Daphnia* and volume of edible algae present were noted for years before and after the proliferation of zebra mussels (1988–1989). In July–August of both years, a decline in *Daphnia* abundance was followed by a rebound in edible algae, suggesting that edible algae density was controlled by *Daphnia* grazing even after zebra mussels became abundant (Wu and Culver 1991).

Saginaw Bay, a shallow, productive region of Lake Huron ecologically similar to western Lake Erie, was identified as a probable site of future zebra mussel colonization, and efforts to monitor benthic and pelagic communities began in May 1990. The first heavy colonization of zebra mussels occurred in late summer 1991, and by the springs of 1992 and 1993, zebra mussels were clearly established throughout the hard substrate regions of Saginaw Bay (Nalepa *et al.* 1995). During this time period (1991–93) phytoplankton abundance and productivity declined dramatically in Saginaw Bay (Fahnenstiel *et al.* 1995a,b). In this study, we focused on assessing the grazing impact of the zooplankton community for periods before (June 1991) and after (June 1992) zebra mussels became abundant in the bay. Weight-specific filtering rates were determined by experiment and combined with ambient zooplankton biomass data to estimate community filtering rates. Comparison of zooplankton grazing and biomass estimates of 1991 and 1992 allowed us to determine the role of zooplankton grazing relative to decreased chlorophyll levels in 1992 compared to 1991.

This work was part of a larger Saginaw Bay ecosystem study. Specific results for water quality parameters (chlorophyll concentration, water clarity, and total phosphorus concentration) are reported in Fahnenstiel *et al.* (1995a). Phytoplankton productivity estimates are reported in Fahnenstiel *et al.* (1995b). Results for dissolved and particulate nutrients are reported in Johengen *et al.* (1995). Population recruitment, density, and size structure of the zebra mussel are reported in Nalepa *et al.* (1995). Zebra mussel filtering and clearance rates are reported in Fanslow *et al.* (1995).

METHODS AND MATERIALS

Zooplankton grazing experiments were conducted at three sites in Saginaw Bay in June of 1991 and June 1992 (Fig. 1). Two of the sites were in the inner bay (Stations 4 and 14) and one was in the outer bay (Station 24). The inner and outer regions of the bay are divided roughly by a line extending between Sand Point and Point Lookout.

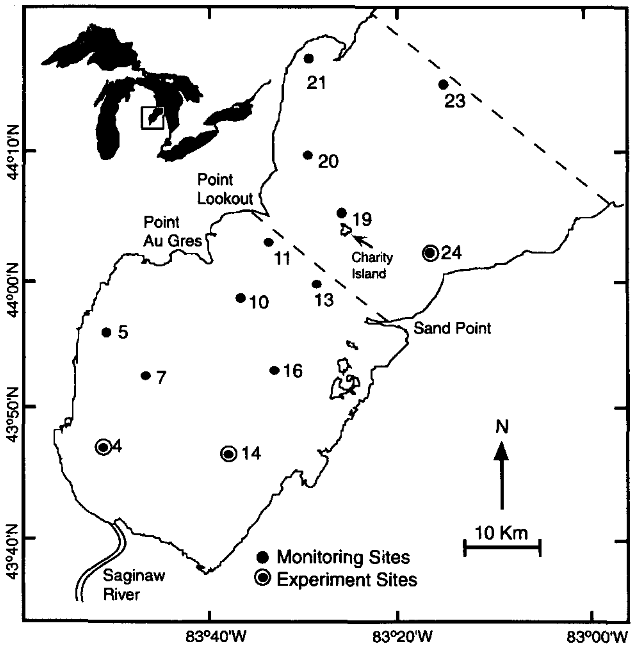

FIG. 1. Location of sampling sites in Saginaw Bay, Lake Huron. Dashed lines differentiate inner bay from outer bay and outer bay from Lake Huron.

The inner bay is relatively shallow (mean depth = 5 m), eutrophic, and more influenced by inputs from the Saginaw River outflow. The outer bay is deeper (mean depth = 14 m), more oligotrophic, and more characteristic of Lake Huron water.

All sampling for grazing experiments was conducted after dusk with incubations initiated in darkness to minimize shock to the organisms. Collections for determining zooplankton community structure associated with the zooplankton grazing experiments were made by vertical hauls through the photic zone using a metered 153 μm mesh zooplankton net (0.5 m diameter). Samples were narcotized and then preserved in sugar formalin (Haney and Hall 1973).

Weight-specific zooplankton filtering rates were determined at each site by a series of incubations in which 10-L carboys containing ambient phytoplankton were exposed to grazing by varying concentrations of zooplankton (Carrick *et al.* 1991, Lehman 1980). Surface water (0–2 m) was collected, prescreened (<153 μm), and stored in a large 200-L tank (tank 1). Live zooplankton were collected by vertical hauls with a 153-μm plankton net and solid net bucket. To avoid mortality, animals were handled carefully and quickly transferred to a second 200-L tank (tank 2) which was partially filled with prescreened (<153 μm) water. For each treatment, prescreened water (tank 1) was added to each 10-L carboy, and then water containing concentrated zooplankton (tank 2) was added to each carboy in varying amounts to create treatments of 0×, 1×, 2×, 3×, and 4× times the ambient zooplankton density. In June 1991, one treatment at each site was replicated, whereas in June 1992, two treatments at each site were replicated. To minimize differential effects between treatments due to zooplankton excretion, phosphate (1 μmol L^{-1} final concentration) was added to each carboy to maintain constant algal growth rates across zooplankton treatments. After mixing, 200 mL were removed from each carboy for initial measurements of chlorophyll.

All treatments were incubated for 24 h at ambient light and temperature in a solar-simulated shipboard incubator equipped with rotating racks and color screening selected to match the subsurface spectral characteristics of Saginaw Bay (Lohrenz *et al.* 1992). 200 mL were removed for determinations of final chlorophyll at the end of the experiment. The remaining water in each carboy was screened with a 153-μm mesh and the zooplankton narcotized and preserved. Zooplankton biomass in the treatments was determined by enumerating subsamples and subsequently converting to dry weight using species-specific conversion values for Lake Michigan (Hawkins and Evans 1979; G. L. Pernie, personal communication, Great Lakes Environmental Research Laboratory). For broad comparisons of community composition, zooplankton species were grouped into three major categories: calanoid copepods, cyclopoid copepods, and cladocerans.

Chlorophyll concentrations were determined by collecting samples on glass fiber filters (Whatman GF/F). Samples were ground and extracted in 90% acetone, and analyzed fluorometrically.

The algal net growth rate (r) was estimated by

$$r = \ln (N_t/N_o)/t$$

where, N_o and N_t are initial and final chlorophyll concentrations, and t is the duration of the incubation. Net growth rate was then plotted against zooplankton biomass and a linear regression was made to determine weight-specific zooplankton filtering rate (slope) and algal intrinsic growth rate (intercept) after Scavia and Fahnenstiel (1987).

Zooplankton abundance and biomass were also measured throughout Saginaw Bay as part of a larger zooplankton monitoring program (Nalepa *et al.* in prep.). Samples for determining bay-wide zooplankton abundance and biomass were collected monthly from eight inner bay sites and five outer bay sites in Saginaw Bay (Fig 1). Replicate samples were collected by vertical hauls from 1 m above the bottom to the surface using a 63-μm mesh net (0.5 m diameter). Samples were narcotized and then preserved in sugar formalin (Haney and Hall 1973). Early trials using inside/outside flowmeters indicated high flow efficiency through the net. We assumed the ability of the 153-μm mesh net and the 63-μm net to collect crustacean zooplankton to be equivalent. Small-sized zooplankton (<100 μm) were excluded from the analysis.

RESULTS

Zooplankton Filtering Rates

Ambient conditions and experimental results of the zooplankton grazing experiments are presented in Table 1. Weight-specific zooplankton filtering rates from the inner bay were similar between sites and between years (t-test for comparison of slopes; $p>0.05$). Filtering rates at Station 4 were 0.24 and 0.27 mL μg dry $wt.^{-1}$ d^{-1} in 1991 and 1992, respectively, and filtering rates at Station 14 were 0.28 and 0.33 mL μg dry $wt.^{-1}$ d^{-1} in the 2 years. At these stations the most abundant zooplankton was the cladoceran, *Bosmina.* At the outer bay site, Station 24, weight-specific filtering rates were significantly higher than values from the inner bay sites (t-test for comparison of slopes; $p<0.05$) due to the dominance of large calanoid copepods. The filtering rate at this site was lower in 1992 than in 1991, but the difference was not significant (t-test for comparison of slopes; $p>0.05$).

Zooplankton community filtering rates were used for broad comparisons of the impact of zooplankton grazing between years and sites. Community filtering rates were calculated by multiplying experimentally-determined weight-specific filtering rates by corresponding ambient zooplankton biomass (mg dry wt. m^{-3}) measured during the experiments. Community filtering rates at all three sites were less in June 1992 than in June 1991 (Table 1). At Station 4, the community filtering rate was 88% lower in 1992 than in 1991 due to a 10-fold decrease in zooplankton biomass. At Station 14, the community filtering rate was 3% lower in 1992 than in 1991.

Community filtering rates for the outer bay site, Station 24, were higher than rates at both inner bay sites, mainly as a result of higher weight-specific filtering rates. The community filtering rate at Station 24 was 83% lower in 1992 than in 1991 as a result of decreased biomass and weight-specific filtering rate estimates.

TABLE 1. Ambient conditions and experimental results for zooplankton grazing experiments at two inner Saginaw Bay sites (Stations 4 and 14) and one outer Saginaw Bay site (Station 24). Standard errors are in parentheses.

Site	Chlorophyll Concentration (mg m^{-3})	Abundance (per m^3)	Biomass (mg dry wt. m^{-3})	Weight-Specific Filtering Rate (mL μg dry $wt.^{-1}$ d^{-1})	Community Filtering Rate (L d^{-1} m^{-3})
Station 4					
21 June 1991	3.40 (0.06)	140,106	336	0.24 (0.07)	80.6
24 June 1992	7.54 (0.16)	15,251	37	0.27 (0.07)	10.0
Station 14					
20 June 1991	3.97 (0.58)	152,816	399	0.28 (0.16)	111.7
24 June 1992	0.55 (0.06)	143,120	330	0.33 (0.16)	108.9
Station 24					
20 June 1991	1.90 (0.04)	239,389	535	1.83 (0.36)	979.1
23 June 1992	2.21 (0.09)	53,758	131	1.27 (0.60)	166.4

Zooplankton Abundance and Biomass (Monitoring Data)

Mean abundance of zooplankton was significantly lower in May–August 1992 than in May–August 1991 in both the inner and outer bay (paired-sample t-test; inner bay: $p = 0.026$, df = 31; outer bay: $p = 0.004$, df = 19; Fig. 2a,b). Means in the inner bay were 67,837/m^3 and 36,760/m^3 in 1991 and 1992, respectively, while means in the outer bay were 53,693/m^3 and 15,629/m^3 in the 2 years. Seasonal patterns differed between the 2 years. In 1991, zooplankton abundance was highest in May and June and decreased dramatically in July and August in both the inner and outer bay. Zooplankton abundance in 1992 was low throughout the May–August period in both the inner and outer bay and more similar to values from the July–August period of 1991.

Trends in zooplankton biomass reflected those of abundance (Fig. 2c,d). Mean biomass of zooplankton was significantly lower in summer 1992 than in summer 1991 in both the inner and outer bay (paired-sample t-test; inner bay: $p= 0.036$, df = 31; outer bay: $p = 0.006$, df = 19). Means in the inner bay were 130 mg dry wt. m^{-3} and 78 mg dry wt. m^{-3} in 1991 and 1992, respectively, while means in the outer bay were 112 mg dry wt. m^{-3} and 33 mg dry wt. m^{-3} in the 2 years.

For comparisons of community composition, zooplankton were grouped into three large groups—calanoid copepods, cyclopoid copepods, and cladocerans. In terms of biomass, zooplankton composition in May–August 1991 and May–August 1992 were not significantly different (t-test; inner bay: $p>0.65$, df = 32; outer bay: $p>0.24$, df = 20; Fig 3). In the inner bay, cladocerans dominated the community (60% in 1991, 55% in 1992), followed by cyclopoid copepods (34% in 1991, 38% in 1992) and calanoid copepods (6% in 1991, 7% in 1992). In the outer bay, the community structure was more evenly distributed among the three groups. In 1991, cladocerans, cyclopoid copepods, and calanoid copepods comprised 46%, 27%, and 27% of the total biomass, respectively. In 1992, the same groups comprised 41%, 40%, and 19%, respectively.

DISCUSSION

Our estimates of zooplankton community filtering rates are similar to those reported in previous studies in Saginaw Bay and southern Lake Huron, suggesting that we have accurately estimated zooplankton filtering rates in Saginaw Bay. We found community filtering rate estimates that ranged from 10.0 to 979.1 L d^{-1} m^{-3} for June 1991 and June 1992, with a median value of 110.3 L d^{-1} m^{-3}. In the May–June period of 1981, Ross and Munawar (1988) reported a community filtering rate of 30.4 L d^{-1} m^{-3} in outer Saginaw Bay. In a study of zooplankton grazing in southern Lake Huron, McNaught *et al.* (1980) reported community filtering rates for May–June of 1975 that ranged from 9.1 to 76.5 L d^{-1} m^{-3}.

In the two periods in which filtering rates were measured, phytoplankton abundance and productivity declined dramatically in Saginaw Bay. In inner

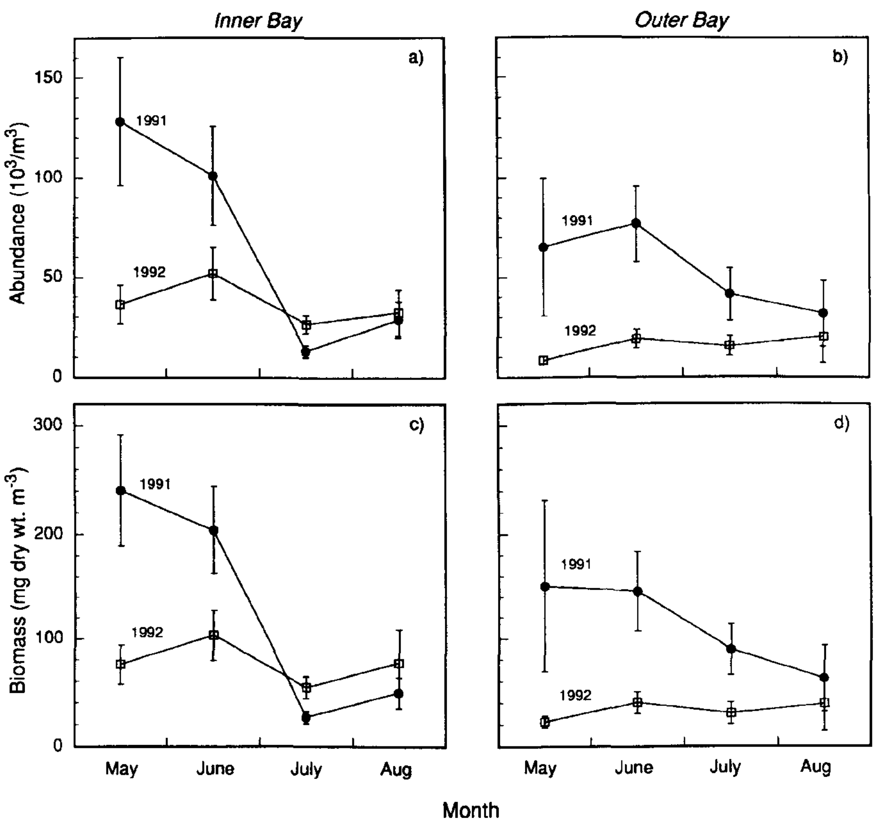

FIG. 2. Monthly mean abundance (a) and biomass (c) of zooplankton from inner Saginaw Bay monitoring sites, and monthly mean abundance (b) and biomass (d) of zooplankton from outer Saginaw Bay monitoring sites during May–August 1991–1992. Error bars represent 1 standard error.

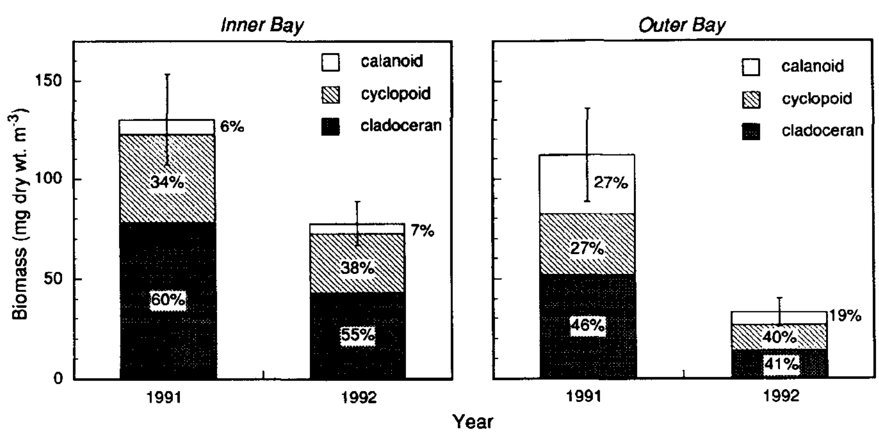

FIG. 3. Mean biomass and composition of zooplankton in inner and outer Saginaw Bay averaged over the May–August study period for 1991–1992. Error bars represent 1 standard error of mean total biomass.

Saginaw Bay, chlorophyll concentrations averaged 15 mg m^{-3} in spring 1991 and decreased to 3 mg m^{-3} by fall 1991 (Fahnenstiel *et al.* 1995a). Chlorophyll values remained low throughout 1992 and averaged 6 mg m^{-3}. Chlorophyll concentrations from the May–June period of 1992 were 71% lower compared to the same period in 1991. These lower chlorophyll values were accompanied by decreased total phosphorus concentrations and increased water clarity. Phytoplankton productivity also decreased by 47% from 1991 to 1992 (Fahnenstiel *et al.* 1995b).

This dramatic decline in phytoplankton abundance and productivity corresponded to the period of zebra mussel colonization in Saginaw Bay. The first heavy colonization of zebra mussels occurred in late summer 1991 when large populations of settled veligers were first noted (Nalepa *et al.* 1995). By fall 1991, a large population of juvenile zebra mussels (<5 mm) was present at many sites in the inner bay and outer bay. By fall 1992, overall mean density of zebra mussels on hard substrates in the inner bay was 33,800/m^2. This pattern of decreased phytoplankton abundance after colonization by zebra mussel has been largely attributed to mussel filtering activities (Leach 1993, Holland 1993, Nichols and Hopkins 1993). We have attempted to assess the relative role of zooplankton in contributing to the decline in phytoplankton abundance that occurred during the zebra mussel colonization.

Zooplankton grazing was likely not responsible for the dramatic decline in phytoplankton abundance in Saginaw Bay in 1992. The large decrease in phytoplankton abundance occurred at a time when zooplankton abundance and biomass and zooplankton community filtering rates were also decreasing (Fig. 2, Table 1). Mean biomass in the inner bay was 40% lower in summer (May–August) 1992 than in summer 1991. Zooplankton community filtering rates in June 1992 were, on average, 58% lower than rates in June 1991. Because weight-specific filtering rates were relatively similar in 1991 and 1992, the decreased community filtering rates were attributed to decreased zooplankton biomass.

A comparison of zooplankton clearance rates and phytoplankton growth rates suggests that zooplankton grazing was not likely the principal loss controlling phytoplankton abundance in 1992. Zooplankton clearance rates, or turnover rates, were calculated as the inverse of the product of the experimentally-determined, weight-specific zooplankton filtering rates measured in June 1991 and June 1992, and the inner and outer bay zooplankton biomass estimates averaged over the May–June period. These biomass estimates, derived from the zooplankton monitoring program (Nalepa *et al.* in prep.), were used because they represent a much greater spatial and temporal coverage of Saginaw Bay during 1991 and 1992 than did our three sites sampled in June of each year. The monitoring data was limited to the May–June period to coincide with the June filtering rate experiments, and because this period reflects maximum biomass values; the resulting estimates of zooplankton clearance rates are thus considered to be maximum rates.

Based on zooplankton biomass and filtering rates, it was estimated that zooplankton were capable of clearing the entire water volume of the inner bay every 17 days in May–June 1991 and every 37 days in May–June 1992, and clearing the water volume of the outer bay every 4 days in May–June 1991 and every 25 days in May–June 1992. Phytoplankton growth rates in inner Saginaw Bay in the May–June period averaged approximately 0.25 d^{-1} in both 1991 and 1992 (Fahnenstiel, unpubl. data). Thus, in 1992 phytoplankton biomass doubled approximately every three days and zooplankton cleared the water column of phytoplankton only every 25–37 days.

Not only did zooplankton grazing represent a small loss relative to phytoplankton growth rates, but a comparison of potential clearance rates of zooplankton and zebra mussels supports the findings of Fanslow *et al.* (1995) that zebra mussels were responsible for the dramatic declines in phytoplankton abundance in Saginaw Bay. Similarly-calculated clearance rates were estimated for zebra mussels in Saginaw Bay based on measured weight-specific zebra mussel filtering rates and population biomass (Fanslow *et al.* 1995). It was estimated that the zebra mussel population was capable of filtering the water volume of the inner bay every 0.8 days in April–October 1992 and every 0.5 days in May–June 1992. Because both zooplankton and zebra mussel filtering rates were determined from changes in phytoplankton abundance (chlorophyll), they are directly comparable. It is important to note that the filtering impact of zebra mussels increased from approximately zero in 1991 to a point at which all phytoplankton could be removed from the water column in less than one day in 1992. Thus, zebra mussels and not zooplankton were the dominant grazers of phytoplankton in 1992 and were more likely responsible for the dramatic decline in phytoplankton abundance observed in 1992.

Although decreases in zooplankton abundance and biomass were coincident with the colonization of zebra mussels in Saginaw Bay (Fig. 2), the role of zebra mussels in causing this decrease is not clear. Zooplankton abundance decreased in all regions of Saginaw Bay, including the outer bay where zebra mussels were much less prevalent (Nalepa *et al.* 1995). Water quality parameters (chlorophyll, water clarity, and total phosphorus) from the outer bay sites were similar after heavy zebra mussel colonization (1992–1993) to values before heavy colonization (1990–1991), suggesting little direct zebra mussel affect (Fahnenstiel *et al.* 1995a). Thus, the unexpected decline in zooplankton abundance at these outer bay sites cannot be easily related to the zebra mussel colonization. It is likely that other factors, e.g., changes in algal food quality and predation levels, contributed to decreases noted at sites in the outer bay and also possibly at other sites. Detailed analysis of the zooplankton monitoring data (Nalepa *et al.* in prep.) should provide information on the cause and duration of reduced zooplankton abundances in Saginaw Bay.

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