

Research Article

Increased Chlorophyll *a*, phytoplankton abundance, and cyanobacteria occurrence following invasion of Green Bay, Lake Michigan by dreissenid mussels*

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Abstract

The invasion of freshwater ecosystems in North America by the zebra mussel, *Dreissena polymorpha* (Pallas, 1769), has repeatedly led to rapid changes in water clarity and phytoplankton abundance. Examining cases where a successful invasion has occurred but where rapid changes do not occur can help us understand the full range of responses of ecosystems to invasions. We re-sampled established sampling locations in Green Bay, Lake Michigan during four years of the post-invasion period. We determined Secchi depths, Chlorophyll-*a* concentrations, and phytoplankton composition and biovolume at five stations along a previously documented trophic gradient. Our data support the continued existence of a strong trophic gradient between lower and middle bay areas of Green Bay. Secchi depth did not significantly change following invasion at either lower bay or middle bay locations. Responses to invasion were stronger at middle bay than lower bay for both Chlorophyll-*a* and phytoplankton biovolume. Chlorophyll-*a* was significantly greater in the post-invasion period at both locations, while phytoplankton biovolume was significantly higher following invasion in middle bay. Along with these increases in abundance there was a significant shift to higher and more frequent dominance of the phytoplankton community by cyanobacteria. The increased phytoplankton abundance during the post-invasion period is likely explained by selective feeding and increased nutrient recycling by zebra mussels under high turbidity conditions in this highly productive embayment of Lake Michigan.

Key words: cyanobacteria, *Dreissena*, Green Bay, phytoplankton, zebra mussel

Introduction

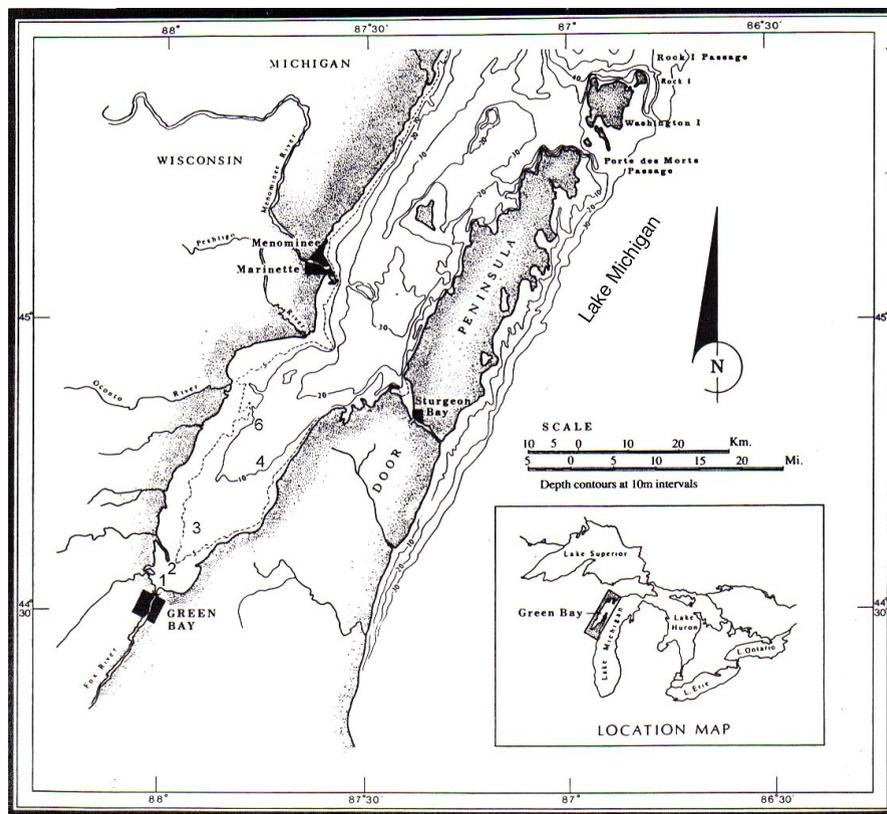
Invasion of the Laurentian Great Lakes by the zebra mussel *Dreissena polymorpha* (Pallas, 1769) during the 1980's and 1990's resulted in significant changes in many aquatic ecosystems. Numerous studies have demonstrated that water clarity increased relatively quickly following invasion while Chlorophyll-*a* (Chl-*a*) and phytoplankton abundance decreased (Lavrentyev et al. 1995; Idrisi et al. 2001; Barbiero et al. 2006; Depew et al. 2006). Zebra mussels have the capacity to filter large volumes of water and

can develop large populations, resulting in the ability to clear water rapidly (MacIsaac et al. 1992; Bunt et al. 1993). They are also able to filter a broad size range of particles, thereby enabling them to have effects on a wide variety of ecosystems (Bastviken et al. 1998).

The largest embayment of Lake Michigan is Green Bay, one of the most productive ecosystems in the Laurentian Great Lakes. Prior to invasion of the bay by zebra mussels in 1992 extensive studies documented a large effect of nutrient inflows from the Fox River, leading to a strong trophic gradient in the lower bay

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Figure 1. Map of Green Bay, Lake Michigan, USA showing the five stations (numbers 1, 2, 3, 4 and 6) sampled during 2000, 2004, 2005, and 2006.



(Richman et al. 1984; De Stasio and Richman 1998; Sager and Richman 1991). Early modeling studies predicted that zebra mussel filtering would lead to significant decreases in phytoplankton in the bay, especially in the well-mixed lower bay (Padilla et al. 1996). Anecdotal observations did not support these predictions following the invasion, and here we document actual changes in the bay by determining average summer values of water clarity as measured by Secchi depth, and abundances of Chl-*a* and phytoplankton following the invasion of Green Bay by *Dreissena polymorpha*.

Methods

Green Bay was sampled during the summers of 2000, 2004, 2005, and 2006 at five locations previously established along a trophic gradient before invasion by zebra mussels (Figure 1; Richman et al. 1984; De Stasio and Richman 1998; Sager and Richman 1991). Sites sampled along the trophic gradient range from shallow (mean depth = 2 - 3 m) inner bay hypereutrophic

conditions to the deeper (mean depth = 15 m) mesotrophic middle bay region. Samples were collected approximately biweekly each year between June and August. Water clarity was determined on each date using a black and white Secchi disk (20 cm diameter). For Chl-*a* and phytoplankton analysis, duplicate integrated samples were collected from the top 4 m of the water column using a submersible pump (or to just above the bottom at sites shallower than 4 m). Water for Chl-*a* determination was stored on ice in the dark until returned to the laboratory later the same day, while phytoplankton samples were preserved in 1% Lugol's solution. In the laboratory Chl-*a* concentration was determined using the acetone extraction procedure (Wetzel and Likens 1991). Replicate sub-samples for phytoplankton determination (15 - 50 ml) were examined using settling chambers viewed on an inverted Zeiss microscope or on permanent slides made by filtering subsamples onto membrane filters (0.45 μm pore size) under low vacuum. Filters were cleared with immersion oil, sealed with Permunt and enumerated at 100-

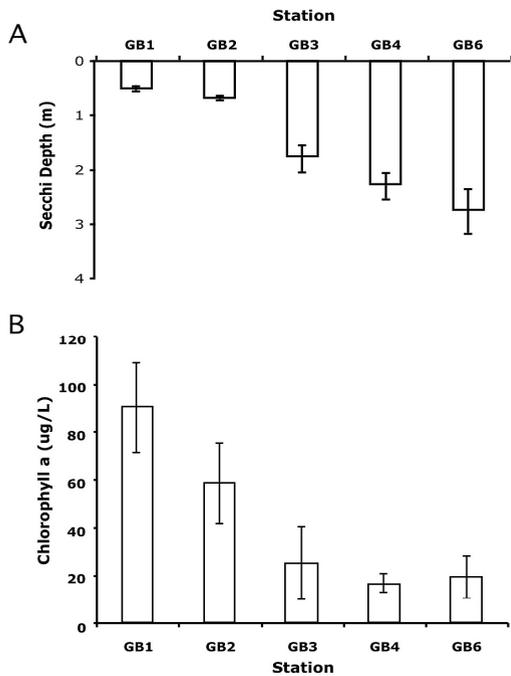


Figure 2. Secchi depth (A) and epilimnetic Chlorophyll *a* concentration (B) during 2006 (summer mean +/- 1 standard error) at stations sampled along the trophic gradient in Green Bay, Lake Michigan, USA.

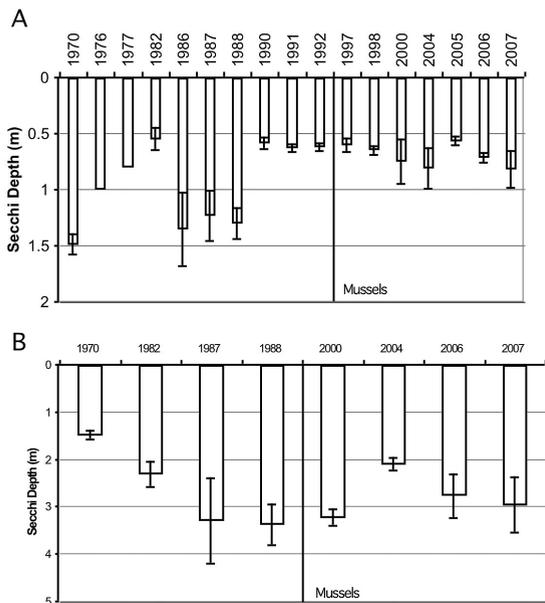


Figure 3. Secchi depth (summer mean +/- 1 standard error) at A) lower bay (station GB 2) and B) middle bay (station GB6) for pre-invasion years (years to the left of the vertical line) and post-invasion years (years to the right of the vertical line) in Green Bay, Lake Michigan, USA.

500 X magnification. Cell linear dimensions were determined using an ocular micrometer and used to estimate cell biovolume based on published relationships between linear size and volume (Wetzel and Likens 1991).

Comparisons were conducted between published and unpublished data from the studies of Richman and Sager prior to invasion (Richman et al. 1984; De Stasio and Richman 1998; Sager and Richman 1991) with data collected in this study. Examination for heteroscedasticity and normality, data transformations, Analysis of Variance and post hoc tests were performed using SPSS® (Statistical Package for the Social Sciences, version 13.0).

Results

A clear trophic gradient was observed along the five sites in each year during the post-invasion period. Data from 2006 exemplify the trends observed in other years (Figure 2). Water clarity increased significantly along the trophic gradient in 2006, with Secchi depths near 0.5 m in the lower bay and values approaching 3 m in the middle bay (Figure 2a; ANOVA $F_{4,15}=10.80$, $P<0.001$). There was not a significant difference between Secchi depths at GB1 and GB2, but both of these were significantly different than the other three stations (Fisher's LSD *post hoc* test, $P<0.01$). Chlorophyll *a* concentration also demonstrated a strong trophic gradient. Average Chl-*a* concentration was significantly higher in the lower bay sites (GB1 and GB2) than in the other locations (Figure 2b; ANOVA $F_{4,38}=33.33$, $P<0.001$).

Comparing across time, there was a significant effect of time on Secchi depth overall for the lower bay (Figure 3a; $F_{14,69}=5.303$, $P<0.0001$) but average Secchi depth was not significantly different in the post-invasion period than prior to invasion (LSD *post hoc* test, $P>0.05$). The same results were obtained for the middle bay station (Figure 3b) with no significant difference observed between pre- and post-invasion time periods.

Average Chl-*a* was significantly greater during the post-invasion years than during the pre-invasion time period (Figure 4). At the lower bay station (GB2) there was a significant effect of time on Chl-*a* concentration ($F_{6,13}=21.42$, $P<0.0001$) and summer average Chl-*a* concentrations in 2000, 2005 and 2006 were all significantly greater than during the pre-invasion

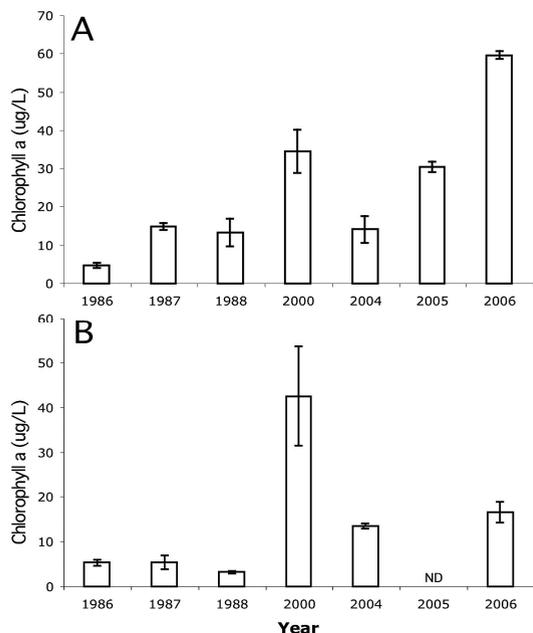


Figure 4. Epilimnetic Chlorophyll *a* concentration (summer mean \pm 1 standard error) at A) lower bay (station GB 2) and B) middle bay (station GB6) for three pre-invasion years (1986, 1987 and 1988) and four post-invasion years (2000, 2004, 2005, 2006) in Green Bay, Lake Michigan, USA. No data are available from middle bay in 2005.

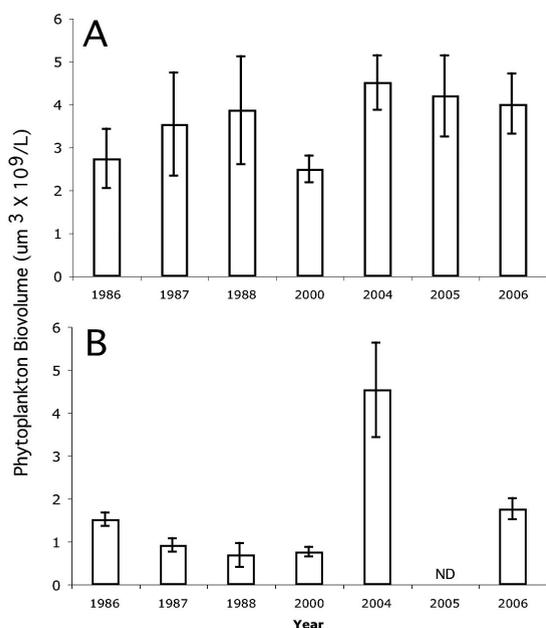


Figure 5. Total phytoplankton biovolume concentration (summer mean \pm 1 standard error) at A) lower bay (station GB 2) and B) middle bay (station GB6) for three pre-invasion years (1986, 1987 and 1988) and four post-invasion years (2000, 2004, 2005, 2006) in Green Bay, Lake Michigan, USA. No data are available from middle bay in 2005.

years (LSD *post hoc* test, $P \leq 0.01$). Chlorophyll concentration in 2004 was not significantly greater than that observed before invasion by zebra mussels. A similar result was obtained for the middle bay location (GB6) with a significant overall effect of time ($F_{5,25}=17.28$, $P < 0.0001$) on Chl-*a* concentration. Dramatic blooms of the cyanobacterium *Aphanizomenon* occurred in July 2000, leading to extremely high average biomass and variability. Overall, all post-invasion years at middle bay were significantly higher in Chl-*a* than all pre-invasion years (LSD *post hoc* test, $P < 0.01$).

Total biovolume of phytoplankton based on counts also increased following invasion, especially in the middle bay region (Figure 5). There were significant increases in phytoplankton biovolume over time at station GB6 ($F_{5,17}=2.88$, $P < 0.046$), reaching extreme levels in 2004 due to persistent diatom blooms. Biovolume also tended to increase at station GB2, but there was not an overall significant effect of time at this location ($F_{6,18}=0.45$, $P < 0.836$).

Changes in phytoplankton community dominance patterns were also evident following colonization by zebra mussels (Figure 6). Prior to 1992 the phytoplankton community of lower Green Bay was dominated by chlorophyte taxa as measured by biovolume. The percent of biovolume attributed to chlorophytes was significantly lower in the post-invasion years ($F_{7,15}=36.44$, $P < 0.001$), consistent with the abundant literature on the ability of zebra mussels to feed heavily on chlorophyte taxa. All post-invasion years demonstrated significantly lower percentages of chlorophytes compared to all pre-invasion years (LSD *post hoc* test, $P < 0.001$). Concurrent with this decrease in chlorophyte dominance were increases in percentage composition of both diatoms and cyanobacteria (diatoms: $F_{7,15}=4.56$, $P = 0.007$; cyanobacteria: $F_{7,15}=2.441$, $P = 0.07$). Following invasion, the phytoplankton community had clearly switched to dominance by cyanobacteria and diatoms instead of chlorophytes.

Discussion

Our comparison of published and unpublished data from Green Bay prior to invasion by zebra mussels with data from four years following invasion by zebra mussels demonstrate that Secchi depths have not changed between the two periods and that chlorophyll and phytoplankton

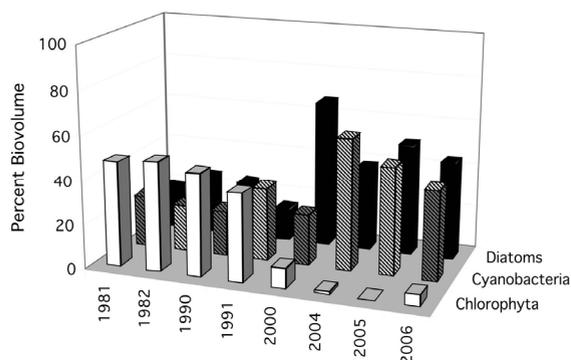


Figure 6. Relative biovolume concentration (average summer percent biovolume) of three major phytoplankton taxa in lower bay (station GB2) for four pre-invasion years (1981, 1982, 1990 and 1991) and four post-invasion years (2000, 2004, 2005, 2006) in Green Bay, Lake Michigan, USA.

abundance have increased following the invasion (Figures 4 and 5). In addition, phytoplankton community composition has shifted significantly. Chlorophytes have decreased in importance while cyanobacteria and diatoms have increased in both absolute and relative abundance (Figure 6).

Based on these findings it is clear that the responses in Green Bay have been different than those reported in other ecosystems in the Great Lakes to invasion by *Dreissena polymorpha*. Numerous studies have documented increased water clarity following invasion by zebra mussels (e.g. Barbiero and Tuchman 2004; Fahnenstiel et al. 1995; Idrisi et al. 2001) as well as decreases in phytoplankton abundance (e.g. Lavrentyev et al. 1995; Idrisi et al. 2001; Barbiero et al. 2006; Caraco et al. 1997, 2006; Hall et al. 2007). These results from other ecosystems raise the question of why the invasion of Green Bay by dreissenids has resulted in the opposite pattern, no increase in water clarity and a shift towards greater phytoplankton abundance.

Two direct factors that could explain the documented changes include 1) low zebra mussel abundance in Green Bay and therefore no strong grazing effect on phytoplankton, and 2) increased nutrient loadings to the bay during the same time as the invasion. However, neither of these appears to be the case in Green Bay. Zebra mussel abundances in middle bay have reached

over 250,000/m² (Kraft 1993) and druses occur in patches of soft bottom areas even in the lower bay (Reed et al. 2004). These abundances are higher than those observed in other ecosystems that have shown strong effects. In terms of nutrient loading, the International Joint Commission has designated Green Bay as an Area of Concern and consequently a Remedial Action Plan was enacted to reduce phosphorus loading during the 1990s. As a result, annual phosphorus loading decreased approximately 30% between the pre- and post-invasion years (Klump et al. 1997). In light of these facts, an alternate explanation is necessary for the observed phytoplankton changes.

At least four other factors may help explain the increases in phytoplankton. Lower Green Bay is a shallow, well-mixed environment with high concentrations of suspended solids that have resulted in light limitation of algae (Sager and Richman 1991). High turbidity and suspended sediment loads have been shown to affect feeding and energetics of zebra mussels, indicating that the lower bay may not present good growth conditions for mussels (e.g. Alexander et al. 1994). However, this explanation is not entirely satisfactory because of the significant declines in chlorophytes observed, a preferred food of zebra mussels (Bastviken et al. 1998; Vanderploeg et al. 2001).

The selective nature of feeding by zebra mussels may also help explain the observed patterns. Although the feeding abilities and preferences of zebra mussels are apparently complex (Sarnelle et al. 2005), a number of recent studies have shown that cyanobacteria are selectively shunted into pseudofeces and thereby gain an advantage over other phytoplankton following invasions (e.g. Vanderploeg et al. 2001; Raikow et al. 2004; Bierman et al. 2005). The observed increased dominance of Green Bay phytoplankton by cyanobacteria following invasion is consistent with this mechanism. A third factor is that zebra mussels may have increased the recycling rate of nutrients in the bay, as has been observed elsewhere (e.g. Arnott and Vanni 1996). If recycling rates have increased, then there is the possibility for increased productivity rates. This suggestion is consistent with our recent findings that primary productivity rates are as high or higher in the post-invasion period than they were prior to invasion. Our ongoing studies of phytoplankton productivity should help address this aspect of the ecosystem.

The three parameters examined in this study each give a partial view of the changes in water quality in Green Bay following invasion by dreissenid mussels, and not all showed significant changes following invasion. The relationships between Secchi depth, chlorophyll abundance and phytoplankton biovolume or community structure are complex, therefore differences in responses are not unexpected. For instance, Secchi depth may not be as responsive as chlorophyll to changes because of the known non-linear relationship between these parameters, especially at high chlorophyll values (Carlson 1980). In addition, water transparency is more closely related to the total number of particles in the water (and thus the total surface area of particles) than the biomass of chlorophyll (Edmondson 1980). Our results show that there was not a significant difference in Secchi depth following invasion (Figure 3) but that the direction of the trend was towards decreased water transparency. Such non-significant results for Secchi depth measurements, while chlorophyll and phytoplankton biovolume significantly increased, could be explained by these non-linear relationships between Secchi depth and the other parameters.

In a similar way, it is not surprising that the changes in chlorophyll were more definitive than those for phytoplankton biovolume. Our biovolume estimates employed published relationships between linear dimensions of phytoplankton cells and biovolume estimates whereas chlorophyll values were direct measurements of biomass. Also, chlorophyll content of phytoplankton cells is known to vary based on community composition, position in the water column, and seasons, each separately from biovolume changes (Felip and Catalan 2000). Therefore, a likely factor explaining differences in the responses of chlorophyll and biovolume could be the dramatic shift in phytoplankton community composition observed following invasion. Increased dominance of cyanobacteria and diatoms could change the average chlorophyll content per biovolume in the system compared to pre-invasion conditions. The ecological consequences of these changes will rely on how higher trophic levels have responded to such shifts in the phytoplankton community.

One observation that supports this possibility is that we have observed decreases in zooplankton biovolume in the bay, resulting in decreased grazing on phytoplankton. The increases we have documented for phytoplankton

abundance are consistent with these data. It is not clear at this time what has caused the decreased abundance of zooplankton. One possibility is that predation by fish on zooplankton has increased. However, it is also possible that the higher concentrations of cyanobacteria and lower abundance of chlorophytes represent poor feeding conditions for crustacean zooplankton, which may have caused the zooplankton to decline. If this is the case, there should have been decreases in energy flow and trophic transfer efficiencies following invasion. Further studies reconciling observations at higher levels of the food web with our findings are clearly called for in this highly productive embayment of Lake Michigan.

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