Phytoplankton Spatial and Temporal Distributions in Green Bay, Lake Michigan, Prior to Colonization by the Zebra Mussel (*Dreissena polymorpha*)

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Abstract. Spatial and seasonal patterns of change in phytoplankton composition, size structure, and standing stock along a trophic gradient in Green Bay, Lake Michigan, prior to the colonization of the bay by the zebra mussel (*Dreissena polymorpha*) are documented. Based on particle size distributions and microscope analysis of epilimnetic samples collected between June and October 1981 throughout Green Bay, at least two distinct regions can be identified. Lower bay waters are hypereutrophic and differ from all other regions throughout summer and fall. Upper bay regions are meso-oligotrophic and similar to Lake Michigan proper. These analyses demonstrate that the lower bay and upper bay regions undergo seasonal changes in epilimnetic algal communities similar to those which occur in separate lakes with differing trophic status. Recent reductions in nutrient loading to the lower bay region should produce a clear improvement in water quality, but the impact of colonization of the bay by zebra mussels is less clear given the abundance of filamentous and colonial phytoplankton in lower Green Bay.

INDEX WORDS: Green Bay, phytoplankton, zebra mussel, nutrient reductions, size distribution.

Introduction

Phytoplankton communities are highly dynamic systems that respond to seasonal changes in both abiotic and biotic factors (Reynolds 1984, Harris 1986). Investigations along gradients of physical conditions, nutrient concentrations, or biological communities provide one way of examining the importance of the factors affecting phytoplankton populations (e.g., Richman et al. 1984a, Sager et al. 1984, Sager and Richman 1991). A well-documented trophic gradient exists in Green Bay, Lake Michigan (Table 1; also see Richman et al. 1984a, 1984b; Sager et al. 1984; Conley 1983). The lower bay is considered hypereutrophic due to high loadings of phosphorus and nitrogen entering at the extreme southern end of the bay, primarily from the Fox River (Sager and Wiersma 1972). The presence of a natural shoal restricts circulation patterns such that most Fox River inputs remain in the extreme lower bay. Middle and upper bay regions are oligomesotrophic waters and are more similar to Lake Michigan due to frequent exchanges of lake and bay water (Miller and Saylor 1985).

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Earlier investigations of phytoplankton communities in Green Bay focused on specific, restricted groups of taxa such as diatoms (Holland and Claffin 1975) or cyanobacteria (Sager and Wiersma 1972), or emphasized primarily a size-structured analysis of the plankton (Richman et al. 1984a, 1984b; Sager and Richman 1991). Recent changes in the Green Bay ecosystem make it important to document in greater detail the spatial patterns and temporal dynamics of phytoplankton communities that occurred prior to those ecosystem changes.

Nutrient loadings to Green Bay were reduced in the early 1990s as a result of the Green Bay Remedial Action Program, mainly through reductions in point sources of phosphorus (Wisconsin Dept. of Natural Resources 1993). At the same time, a second major change in the Green Bay ecosystem occurred with the introduction and successful colonization by the zebra mussel (*Dreissena polymorpha*). Starting in 1992, zebra mussels were observed in increasing numbers in southern Green Bay, and densities of veligers reached 210,000/m³ by the summer of 1994, with massive accumulations of shells on the eastern shore occurring in 1996 (Kraft 1996). It is anticipated that both of these changes will have dramatic effects on the phytoplankton community structure and species composition in Green Bay (WI DNR 1993).

Reductions in nutrient loadings are expected to reduce the occurrence of massive blooms of cyanobacteria and enhance overall water quality in the lower bay, but it is not clear whether the impact of zebra mussels will help improve water quality. Studies in the other Great Lakes have shown that the effects of colonization by zebra mussels will be complex, involving both direct effects of grazing (Holland 1993, Fahnenstiel et al. 1995b, Fahnenstiel et al. 1995a, Lavrentyev et al. 1995, Nalepa and Fahnenstiel 1995) and indirect effects through increased nutrient recycling (Cotner et al. 1995, Heath et al. 1995, Arnott and Vanni 1996). One result of such complexities is that it is difficult to predict whether cyanobacteria blooms will decrease or increase in frequency and magnitude following such an invasion. There have not been any studies on the phytoplankton communities of Green Bay since these alterations of the ecosystem. However, in order to determine actual changes in the phytoplankton community of Green Bay in response to these system shifts, studies of phytoplankton abundance, community composition, seasonal dynamics, and spatial patterns throughout Green Bay prior to such changes are needed for comparison with future studies.

Here an analysis of the phytoplankton assemblages in Green Bay prior to nutrient reductions and establishment of zebra mussels is presented. This study includes both taxon-based and size-structured analyses of spatial patterns and seasonal dynamics of epilimnetic phytoplankton communities in Green Bay, Lake Michigan. To examine differences in community composition, principal component analyses of phytoplankton species and particle size distributions for sites throughout Green Bay is employed. This combination of analyses lays the groundwork for future studies on the phytoplankton of Green Bay.

**Materials and Methods**

Water samples were collected at established stations throughout Green Bay on six sampling dates in 1981: 21 to 23 June, 14 to 16 July, 6 to 8 August, 25 to 27 August, 17 to 19 Septem-
ber, and 23 to 24 October (Fig. 1). Conditions during 1981 were typical of the early and mid-
1980s in Green Bay (Richman et al. 1984a, 1984b; Sager and Richman 1991). Samples of
water from the surface (0.5 m) at each station were obtained using a Van Dorn Bottle. These
samples were used in particle size analyses. In addition, replicate surface samples (0.5 m) for
phytoplankton identification were collected during the June, July, and second August sam-
plings with an electric deck pump. All samples were preserved immediately, without being fil-
tered through a net, in 4% sucrose-Formalin.

Size distribution and abundance of particles in samples were measured with a Model B
Coulter Counter interfaced to a Digital PDP11/20 computer. Measurement of particles in the
range of particle volume from 30 to 300,000 µm³ (equivalent to 4 to 90 µm in spherical
equivalent diameter (s.e.d.)) was achieved by employing two aperture tubes (140 µm and
200 µm diameters). Data from each aperture tube were computationally combined into a
single continuous size distribution. Total biovolume for each sample was estimated as the
integral of the combined size frequency distribution.

Phytoplankton were identified with a Zeiss inverted microscope (400X to 1,000X oil
immersion) after samples settled for at least 1 week in counting chambers. Phytoplankton
abundance was recorded as relative abundance of each species observed in transects across
the counting chambers. Transects were continued until no new species were encountered. A
total of 222 taxa were identified in the study. To avoid overemphasis of extremely rare
species in the ordination analysis, only groups comprising more than 10% of the sample by
abundance were included in the analysis (218 total species).

Principal components analysis (PCA) was performed on both particle size data and phyto-
plankton community composition data. The SYSTAT 4.0 statistical package for personal

FIG. 1. Map of Green Bay, Lake Michigan indi-
cating locations sampled in 1981. Sampling sta-
tions and main region designations (lower, middle,
and upper bay) are identified.
computers was used to perform each ordination. To ordinate stations for each sampling date based on size distributions, and to avoid problems with inaccurate sizing of particles by the particle counter, abundance of particles in every fifth size channel (equal to one-half doubling of biovolume) was used to characterize each site. The PCA was based on the covariance matrices. Ordination of stations based on species composition employed the relative abundance of each species (ranked 0 to 4) and resulting correlation matrix for the PCA.

Results

Particle Size Structure

Principal components analysis on particle size data for each month sampled demonstrates that the size structure of the phytoplankton in lower Green Bay is always unique in comparison to other regions of the bay (Fig. 2). The first component axis on each date was generally determined by largesized particles (30 to 37 µm s.e.d.; positive abscissa values in Fig. 2) while the second component was controlled by smaller particle sizes (12 to 19 µm s.e.d.; positive ordinate values in Fig. 2). Station 1 is clearly separate from all other locations on every date. We therefore use this location (along with station 2 if sampled) to characterize the lower bay (LB).

![Figure 2](image)

**FIG. 2.** Principal components analysis of particle size data for each location during 1981. Total variance explained by the two factor axes is indicated in parentheses for each date. Lower bay station (open circles), middle bay stations (solid triangles), upper bay stations (large solid circles), and other intermediate stations (small solid circles) are indicated for each date sampled. See Figure 1 for station numbers in each region.
Other stations sampled fall at intermediate locations in the graphs, clearly illustrating the trophic gradient along Green Bay. Although middle bay (MB) and upper bay (UB) stations cluster together tightly in July, by August there are clear differences between LB, MB, and UB regions. Locations at MB and LB become more similar to each other in October, but are still distinguishable from UB sites. Upper bay waters (stations 28 to 31 in the northern and northwestern regions) remain tightly clustered throughout the season and are therefore easily distinguished from LB waters.

Analysis of individual size spectra for LB and UB regions during 1981 highlight the clear differences in both abundance and size structure of particles in those regions (Fig. 3). On each date sampled, a bimodal size distribution of particles was observed for LB samples, with peaks usually near 15 µm and 40 µm s.e.d. sizes. Biomass increases occurring during July were due to increases in large particles, which were followed by increases in abundance of smaller particles in August. Biovolume of large particles declined in both September and October, whereas that of small-sized particles decreased between September and October.

Patterns of size shifts in UB waters were not as clear as in the LB (Fig. 3). Biomodal size distributions were also observed at UB locations. In June and July, peaks occurred at sizes both smaller and larger than observed for LB water, but by late August sizes were similar between UB and LB.

Total volume of particles was higher in LB water than in the UB on every sampling date during 1981 (Fig. 4). Biomass in LB water increased three-fold during the summer, peaked in late August, and declined in October returning to early summer levels. Upper bay waters decreased after June and remained low through October.

**FIG. 3.** Biovolume-particle size distributions for lower bay (open symbols) and upper bay (solid symbols) water during 1981.
Phytoplankton Community Composition

Principal component analysis of the relative abundance of each taxon indicates that the LB phytoplankton community is easily distinguished from the UB community for each date sampled (Fig. 5). During June, the first principal component was positively related to diatoms (e.g., Fragilaria crotonensis, Asterionella formosa), while the second component was determined primarily by smaller diatoms (e.g., Stephanodiscus niagarae). First components during July and August loaded heavily on dinoflagellates (e.g., Peridinium cinctum, Ceratium hirundinella), with cyanobacteria and small diatoms the important species for the second component (e.g., Aphanizomenon flosaquae, Anabaena spiroides, Melosira granulata).

In each month studied, all stations were fairly widely separated in the analysis. As in the particle analysis, the trophic gradient is demonstrated by the positions of MB stations intermediate between LB and UB areas (Fig. 5). Overall, these results indicate that at least LB and UB are clearly different in both size structure and taxonomic composition from June through October based on the analysis of all the common phytoplankton taxa observed.

There were clear differences in phytoplankton community composition at LB and UB sites during summer 1981 (Table 2). A mixture of cyanobacteria, green algae, and diatoms was observed in the LB during June, but cyanobacteria were dominant during July and August. At UB locations, diatoms dominated in June, followed by a mixture of green algae, diatoms, and dinoflagellates in July and August.

Discussion

Data presented on phytoplankton size structure, abundance, and community composition together define distinct regions of Green Bay, Lake Michigan, that are consistent with a north-south trophic gradient in the bay (Holland and Claflin 1975, Richman et al. 1984a, Sager and Richman 1991). The lower bay is considered a hypereutrophic system with high nutrient loading from the Fox River whereas the upper bay demonstrates oligomesotrophic conditions, similar to Lake Michigan proper. The analyses presented here demonstrate that LB and UB regions undergo seasonal changes in epilimnetic algal communities similar to those which occur in separate lakes with differing trophic status.

Seasonal shifts in composition of phytoplankton communities of eutrophic lakes typically proceed from spring blooms of cryptophytes and diatoms, through complex mixed communities of green algae and diatoms during mid-summer. Late summer and fall blooms of cyanobacteria usually occur in these systems followed by winter diatom communities (Reynolds 1984, Sommer et al. 1986). Composition shifts in lower Green Bay follow these general
changes very closely (Table 2), although the shift to dominance by cyanobacteria occurred earlier in Green Bay than expected based on these general scenarios. Because the sampling program began in June, little can be said about the spring bloom.

Community composition changes in mesotrophic and oligotrophic lakes usually include shifts from large diatoms during spring to smaller diatoms, dinoflagellates, and cryptophytes during summer and fall (Reynolds 1984, Sommer et al. 1986). Changes in UB algae during 1981 followed this pattern remarkably closely (Table 2). Overall, these patterns of seasonal shifts in composition clearly illustrate the distinct characteristics of LB and UB regions. In the present study, seasonal biomass-size distributions in LB exhibited similar summer incre-

**FIG. 5.** Principal components analysis of phytoplankton composition for each location during 1981. Total variance explained by the two factor axes is indicated in parentheses for each date. Lower bay station (open circles), middle bay stations (solid triangles), upper bay stations (large solid circles), and other intermediate stations (small solid circles) are indicated for each date sampled. See Figure 1 for station numbers in each region.
ases in abundance of both large and small sized particles (Fig. 3), as expected for eutrophic systems (e.g., Sprules et al. 1983). Increased abundance of both relatively small filaments \textit{(Anabaena and Aphanizomenon)} and colonial algae \textit{(Microcystis, Coelastrum)} explain these trends (Table 2; also see Table 3 in Reynolds 1984). Size and abundance shifts in mesotrophic and oligotrophic lakes are less extreme, with decreases in size and abundance occurring during summer due to limiting nutrient conditions (Reynolds 1984, Sommer et al. 1986). Total algal biomass of the UB decreased during summer 1981 (Fig. 4) as expected in an oligotrophic system. Size distributions showed that mostly very small and very large particles occurred in early summer, whereas a range similar to that in the LB persisted though late summer and fall (Fig. 3). The mixture of small green algae and larger diatoms and dinoflagellates present in UB waters accounts for these trends (Table 2).

<table>
<thead>
<tr>
<th>Date</th>
<th>Lower Bay</th>
<th>Upper Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>21–24 June</td>
<td>\textit{Anabaena flos-aquae} \textit{Chroococcus limneticus} \textit{Oedogonium spp.} \textit{Pediastrum duplex} \textit{Asterionella formosa} \textit{Stephanodiscus niagarae} \textit{Synedra ulna}</td>
<td>\textit{Staurastrum paradoxum} \textit{Asterionella formosa} \textit{Fragilaria crotonensis} \textit{Stephanodiscus astrea} \textit{Tabellaria flocculosa}</td>
</tr>
<tr>
<td>14–16 July</td>
<td>\textit{Anabaena spiroides} \textit{Microcystis aeruginosa} \textit{Meloisa granulata} \textit{Aphanocapsa spp.}</td>
<td>\textit{Oedogonium spp.} \textit{Oocystis spp.} \textit{Staurastrum paradoxum} \textit{Asterionella formosa} \textit{Ceratium hirundinella} \textit{Peridinium cinctum}</td>
</tr>
<tr>
<td>25–27 August</td>
<td>\textit{Anabaena spiroides} \textit{Aphanizomenon flos-aquae} \textit{Microcystis aeruginosa} \textit{Aphanocapsa spp.} \textit{Meloisa granulata} \textit{Stephanodiscus astrea} \textit{Stephanodiscus niagarae} \textit{Coelastrum cambricum} \textit{Coelastrum microporum} \textit{Coelastrum reticulatum}</td>
<td>\textit{Chroococcus Rufescens} \textit{Coelastrum microporum} \textit{Oocystis gigas} \textit{Staurastrum paradoxum} \textit{Dinobryon sertulare}</td>
</tr>
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**Controls of Phytoplankton Structure and Abundance**

Composition and abundance of phytoplankton are determined by a balance between growth and loss processes. Population growth in general requires appropriate light, temperature, and nutrient conditions (Reynolds 1984, Harris 1986). Although LB is shallower than UB and therefore warms earlier, by June all sites provide sufficient light and temperature conditions for positive phytoplankton growth rates (Richman et al. 1984a, Sager et al. 1984, Sager and Richman 1991). By late summer, LB conditions cause light limitation of algal production due to the high nutrient loads and increased turbidity from sediment resuspension in the shallow lower bay areas (Sager et al. 1984). However, nutrients clearly are important in controlling phytoplankton growth processes throughout the bay, as mentioned above. High levels of nutrient loading to the LB from the Fox River and a general dilution of this loading along the length of the bay results in the gradient of nutrient and trophic status (Table 1, Fig. 4).
Because phosphorus is the major nutrient added in the LB and is diluted along the bay, a gradient of nutrient ratios occurs from LB to UB (Sager and Wiersma 1972). Low nitrogen and silica to phosphorus ratios (N:P and Si:P, respectively) occur in the LB, while higher N:P and Si:P ratios occur in UB locations. Data from the summer of 1980 given in Conley (1983) show that during July N:P values vary from approximately 1:1 in LB to over 40:1 in UB, while Si:P ranges from less than 10:1 in LB to over 50:1 in UB. Based on the predictions of resource ratio theory of competition (Tilman 1982; Sommer 1989a, 1989b), these conditions should lead to LB communities dominated by cyanobacteria and UB communities of green algae and diatoms. In addition, the nutrient data for 1980 show that Si concentrations are generally lower than 0.4 mg/L, except in LB in June and August when concentrations greater than 1 mg/L occurred. Given that many diatoms can become Si limited when concentrations drop below 0.5 mg/L (e.g., Schelske et al. 1986), if similar Si concentrations occurred in the following year (1981—this study year), it would support the abundance patterns of diatoms as given in Table 2 where diatoms were a major component in the LB in both June and August. These results and those of previous studies (Richman et al. 1984a, Sager et al. 1984) support these predictions and indicate an important role for nutrients in determining the growth potential of phytoplankton populations in Green Bay. Given these trends, experimental examination of the role of competition in determining phytoplankton community structure along the trophic gradient would be of interest.

Grazing losses have been shown to be important in controlling phytoplankton populations in general (e.g., Lehman and Sandgren 1985) and in Green Bay in particular (e.g., Sager and Richman 1991). Particle size distributions from both LB and UB presented here showed the presence of particles in the size range that the resident herbivorous zoo-plankton can ingest (< 35 µm s.e.d., Reynolds 1984); however, the LB community is of much lower quality due to the high abundance of both filamentous and colonial algae, some of which also are toxic (e.g., *Microcystis*; Richman and Dodson 1983). Grazing losses should be less important in LB compared to UB waters given these conditions. Determinations of community grazing rates and phytoplankton growth rates in LB and UB confirmed this conclusion. A higher proportion of the daily primary production was consumed by grazing in the UB (average of 60% grazed) than in the LB (average of 13%; Sager and Richman 1991). These studies demonstrate that the effectiveness of grazing in controlling phytoplankton populations can vary as a function of trophic status as suggested for other lakes (e.g., Persson et al. 1988), and can be more important in oligotrophic than in eutrophic systems.

**Zebra Mussels and Changes in Ecosystem Dynamics**

Recent studies on the effects of the introduction of the zebra mussel into the Laurentian Great Lakes indicate the potential for major changes in phytoplankton community structure and function in bays like Green Bay (Nalepa and Fahnenstiel 1995, Leach 1993, Holland 1993). In almost all studies, there was an initial drop in algal standing stock measured as chlorophyll a abundance (e.g., Leach 1993, Fahnenstiel et al. 1995a) and primary production (Fahnenstiel et al. 1995b). In the Saginaw Bay, Lake Huron, studies the conclusion was that the trophic status was not altered, rather the spatial partitioning of productivity switched to a more benthic dominated system (Fahnenstiel et al. 1995a, 1995b). This is thought to result from differences in the feeding characteristics and particle size selectivity of zebra mussels compared to crustacean zooplankton (Lavrentyev et al. 1995). These differences will undoubtedly be important for determining the impact of zebra mussels on the Green Bay ecosystem.

There are conflicting results on particle size-selection by zebra mussels based on laboratory studies and field studies. Although *Dreissena* can filter down to 0.7 µm particles, with maximum retention between 5 and 35 µm, its feeding abilities depend on the types of particles present and may be reduced when cyanobacteria such as *Microcystis* are in abundance (Lavrentyev et al. 1995). Because of the dominance of cyanobacteria in the pre-*Dreissena* colonization communities in lower Green Bay (Table 2), it appears that zebra mussels may have less of an effect than anticipated based on laboratory results. However, the fact that phytoplankton communities in lower Green Bay are limited by light because of low water
clarity due to the hyper-eutrophic conditions (Sager et al. 1984) indicates that increases in water transparency due to increased removal of particulate matter by *Dreissena* filtering could have significant impacts on algal communities in the lower bay.

In the upper bay, zooplankton have been shown to consume a major portion of the phytoplankton daily production (about 60%; Sager and Richman 1991). In this region of Green Bay, it would seem that additional filtering by *Dreissena* might be more important through indirect effects, such as reduction of zooplankton standing stock (e.g., Maclsaac et al. 1991) or increased recycling of nutrients (e.g., Arnott and Vanni 1996). Further studies on the phytoplankton assemblages of Green Bay will be necessary to determine the importance of these changes on the structure and function of this Great Lakes ecosystem.

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