ZOOPANKTON IN WESTERN LAKE ERIE:
BEFORE AND AFTER ZEBRA MUSSELS

A Thesis
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By
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ABSTRACT

Zebra mussels (*Dreissena polymorpha*) constitute a threat to western Lake Erie's sport fisheries through their reported effects on phytoplankton and zooplankton. This project tested whether phytoplankton and zooplankton communities changed after the 1987 establishment of *Dreissena* into western Lake Erie.

Previous researchers predicted zebra mussel grazing would depress phytoplankton and zooplankton abundance in near-shore and shallow waters of Lake Erie. Spatial patterns of phytoplankton and zooplankton abundance from samples taken in 1995 did not coincide to those predicted to be produced under the influence grazing dreissenids. In addition, zooplankton biomass in 1995 after *Dreissena's* introduction was lower than estimates from 1970 but remains equivalent to estimates from 1983-84. Together these results indicate that pelagic phytoplankton and zooplankton may not be controlled just by zebra mussels but instead are simultaneously influenced by multiple factors, including those associated with external nutrient loading and lake size.
We tested whether crustacean production (mg m$^{-3}$ d$^{-1}$) has declined since *Dreissena*’s introduction into western Lake Erie. Because comparable crustacean production estimates from the 1970’s and 1980’s were unavailable, we used regressions, derived from current results, to back calculate historical productivity. Zooplankton production was highly correlated ($r^2 = 0.96-0.99$) to crustacean biomass and water temperature, providing an effective method to estimate historical production using only these two variables. Consequently, we estimated *pre-Dreissena*, crustacean productivity using historical biomass and water temperature data obtained from previous studies of western Lake Erie. Levels of crustacean production, 1995-6, were well below maximum 1970 and 1975 values, a period characterized by high phosphorus loading and no zebra mussels. Current zooplankton productivity does appear equivalent to that found near the Bass Islands in 1988-9, a period of reduced phosphorus and very low zebra mussel abundance. No evidence in this study indicates that zooplankton have dramatically declined since *Dreissena*’s colonization.
Dedicated to my parents.
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INTRODUCTION

Zebra mussels (*Dreissena polymorpha*) have changed western Lake Erie since their arrival in the late-1980's. High densities of zebra mussels, up to 340,000 ind m\(^{-2}\) (MacIsaac *et al.* 1991, Leach 1993), have reportedly altered benthic community composition and abundance, influenced internal nutrient dynamics, and may affect energy flow through the lake's pelagic ecosystem (see MacIsaac 1996 for review of zebra mussel ecosystem effects). Although zebra mussel effects have been carefully documented on small scales (i.e., in experimental tanks), it remains unclear what cumulative, large-scale impact *Dreissena polymorpha* may have on western Lake Erie.

Previous researchers predicted that reduced phytoplankton biomass from zebra mussel grazing would result in decreased zooplankton abundance and productivity (Holland 1993, MacIsaac *et al.* 1992). Crustacean zooplankton represent an important food source for larval and forage fish in western Lake Erie (Hartman *et al.* 1992, Wu and Culver 1992). Consequently, reduced zooplankton productivity would negatively
impact fish production and could seriously harm western Lake Erie's economically important sport fisheries (Wu and Culver 1994, MacIsaac et al. 1992).

This study was primarily aimed at evaluating whether phytoplankton and zooplankton have changed since zebra mussel colonization. Current spatial and temporal patterns phytoplankton and zooplankton can be compared to previously documented communities to test whether predicted *Dreissena* impacts are being realized. Zebra mussels were predicted to reduce phytoplankton and zooplankton in shallow, well mixed waters where their filtering activities would be most pronounced. In the first chapter of this thesis, I characterize spatial patterns of zooplankton and phytoplankton in western Lake Erie in relation to those predicted should zebra mussel grazing have as negative impact as some have suggested.

Zebra mussel reductions of phytoplankton and zooplankton biomass would negatively impact sport fisheries of western Lake Erie. To assess whether predicted declines in zooplankton are being realized, the second chapter directly compares zooplankton production (the amount of biomass fixed per unit time) before and after zebra mussels colonized western Lake Erie. Together, Chapters 1 and 2 provide strong evidence that pelagic ecosystem processes in western Lake Erie have not dramatically changed spatially or temporally due to high numbers of grazing zebra mussels.
CHAPTER 1

PHYTOPLANKTON AND ZOOPLANKTON RESPONSES TO
ZEBRA MUSSELS IN WESTERN LAKE ERIE

Introduction

Zebra mussels' (*Dreissena polymorpha*) colonization of Lake Erie has
created concern that these filter-feeding bivalves may compete with
crustacean zooplankton for algal primary production (Leach 1993, Dermott
phytoplankton declines in some areas of western Lake Erie have been
attributed to dramatic increases in zebra mussel abundance (Holland 1993,
Nicholls & Hopkins 1993). Declining phytoplankton could reduce
zooplankton abundance, and fewer zooplankton, as prey for larval and
forage fishes (Hartman *et al.* 1992, Wu and Culver 1992), could
compromise important lake sport fisheries (Wu & Culver 1994, MacIsaac *et
al.* 1992). However, whether zebra mussel grazing has reduced
zooplankton abundance within western Lake Erie remains unknown.
Zebra mussel grazing is predicted to vary spatially within western Lake Erie. Nearshore, shallow areas would be most affected by zebra mussel grazing due to higher densities of mussels relative to deeper, offshore areas (Nicholls & Hopkins 1993). Zebra mussel grazing impacts should vary between areas in the basin, not only due to differences in mussel densities, but also in response to spatial variability in water currents and water depth. Consequently, spatial patterns of phytoplankton and zooplankton should be influenced by this variability in zebra mussel grazing.

Before zebra mussels were introduced, western Lake Erie experienced dramatic alterations in nutrients available to phytoplankton for growth (Richards & Baker 1993, Dolan 1993). Changes in nutrient availability and nitrogen to phosphorus ratios have profound effects on the amount and type of phytoplankton (Tilman et al. 1986). Lake Erie total phosphorus loading has declined from peak levels in the early 1970's (Dolan 1993) whereas nitrogen inputs increased through the early 1980's (Richards & Baker 1993). External phosphorus and nitrogen loading from non-point sources now appear to be most related to water discharge from contributing rivers and streams (Fig. 1.1 & 1.2). Nitrogen to phosphorus ratios from 1985 to 1995 reflect annual variation in phosphorus loading and water discharge (Fig. 1.3) and remain higher than was typical during the 1960's and 1970's (Richards & Baker 1993).

The amount and type of plankton found in western Lake Erie changed in response to the nutrient alterations of the 1970's and 80's (Makarewicz
Large blooms of filamentous green and blue-green algae, once common in late summer in the 1970's (Munawar and Munawar 1976), are now rare. Summer phytoplankton during the 1990's has been composed primarily of cryptomonads, coccolid greens, and chrysophytes (D. A. Culver, The Ohio State University, unpublished data). Zooplankton abundance decreased between 1970 and 1984 due to the changes in phytoplankton abundance and composition (Makarewicz 1993b). Additional declines in zooplankton communities are expected in response to increased zebra mussel grazing in western Lake Erie (Holland 1993, Nicholls and Hopkins 1993).

Zooplankton communities have likely changed in two respects as a result of zebra mussel grazing in western Lake Erie. Spatial patterns of zooplankton abundance and composition likely reflect patchy zebra mussel distributions. In addition, current levels of zooplankton biomass should be less than those documented in the mid-1980's. This chapter therefore has two main objectives: 1) to characterize current spatial relationships between crustacean zooplankton and phytoplankton within western Lake Erie in relation to predicted zebra mussel grazing impacts and 2) to relate current phytoplankton and zooplankton abundance to previously documented communities.
Methods

Study Area

Phytoplankton and zooplankton samples were collected weekly from 13 sampling sites and monthly from an additional 14 sampling sites at four geographically distinct regions (Sandusky Bay, Maumee Bay, Bass Islands, and Offshore) in western Lake Erie by the Ohio Division of Wildlife between May 15 and July 24, 1995 (Fig. 1.4). Historical samples (1970 and 1983-84) had been collected from sites near most of those sampled in 1995, except 1995 sampling sites near Maumee Bay (Fig. 1.4). As a result of differences in depth, distance from shore, and primary substrate (Table 1.1), these regions vary in what impact grazing zebra mussels would likely have upon phytoplankton and zooplankton communities. Likewise, these regions also differ in what effects external nutrient loading and fish predation may have on phytoplankton and zooplankton.

Phytoplankton Sampling.

From phytoplankton samples, I assessed how early summer algal communities varied in response to regional differences in nutrient loading and possible zebra mussel effects. I collected phytoplankton samples with an integrated water sampler (2.5 cm plastic tube). Collected water was poured into a bucket from which a 250 ml sample taken, preserved with Lugol’s solution, and concentrated to 30 ml. All phytoplankton in two
transects across an Utermohl chamber were identified to genus and counted under a Wild inverted microscope at 400X (Lund et al. 1958). Cell biovolume (μm³ cell⁻¹) estimates were calculated from equations based on geometric dimensions measured for the first 20 individuals of each taxon. Each species’ concentration (cells l⁻¹) was multiplied by its average cell volume (μm³ cell⁻¹) to estimate wet biomass (mg l⁻¹) assuming a intra-cellular density of 1 mg·1 mm⁻³.

**Zooplankton Sampling**

I evaluated crustacean zooplankton responses to phytoplankton variability by examining zooplankton abundance and composition in different regions of western Lake Erie. Zooplankton was collected at phytoplankton sampling sites (Fig. 1.4) by vertical tows of a metered net (93 μm mesh). Filtration volume was determined by measuring, with a mechanical flow meter (General Oceanics model 2030R), the volume of water passing through the net. Samples were preserved with a 4% sugar and formaldehyde solution (Haney and Hall 1973) and stored. After diluting zooplankton samples to known volumes of 1000 to 5000 ml, all crustaceans in 5-10 ml subsamples were identified to species according to Balcer et al. (1984) and counted. Additional subsamples were counted until at least 100 individuals of one taxon were identified. Additionally, length measurements of the first 20 individuals encountered in each taxon were recorded to the nearest 0.05 mm. Biomass (mg m⁻³) of each taxon
was estimated as a product of its sample-specific mean dry weight and abundance. Dry weight (µg ind⁻¹) calculations were based on length-weight regressions (Culver et al. 1985).

**Historical Comparisons**

Historical results were used to assess whether predicted zebra mussel effects on pelagic processes in western Lake Erie are being realized. Sampling locations in 1970, 1983-84, and 1995 were dissimilar in number and location (Fig. 1.4). Zooplankton were collected in 1970 with an unmetered net (64 µm mesh) and in the 1983-84 study with a 0.5 m metered net (62 µm mesh). Zooplankton data for 1970 were based on Bean's (1980) size-frequency measurements of zooplankton from samples counted by Watson & Carpenter (1974). Phytoplankton biomass for 1970 (Munawar & Munawar 1976, 1982) was based on samples taken on the same dates and sites as the 1970 zooplankton samples. All phytoplankton and zooplankton results for 1983-4 were obtained from Makarewicz's (1987, 1993a, 1993b) analyses of U.S. E.P.A. cruises.

**Results**

**Phytoplankton dynamics in western Lake Erie, 1995**

Phytoplankton biomass varied temporally in western Lake Erie through early summer (Fig. 1.5). All regions exhibited a clear-water phase in mid-June with subsequent increases in phytoplankton biomass after that
decline. Although all four regions showed similar seasonal variation, large differences in magnitude existed among sampling regions. Lowest phytoplankton biomass consistently occurred in the offshore region during summer 1995. In fact, the offshore region's mean phytoplankton biomass was less (p < 0.05, ANOVA) than the other three regions (Table 1.2).

Phytoplankton biomass could vary with water depth because zebra mussel effects should be most pronounced in shallow water areas (Nicholls & Hopkins 1993, MacIsaac et al. 1991, MacIsaac et al. 1992). After grouping sampling sites by depth, I calculated mean biomass for shallow water (<7.5 m) and deep water (>7.5 m) sites on all sampling dates (Fig. 1.6). Phytoplankton biomass was not depressed in shallow water. On all sampling dates, shallow water phytoplankton biomass was equivalent to or greater than phytoplankton biomass at deep water sites. Mean summer phytoplankton biomass was significantly greater (p < 0.05, t-test) in shallow water (Table 1.3).

Zooplankton dynamics in western Lake Erie, 1995

Crustacean zooplankton increased in all regions through summer, but offshore areas produced considerably lower biomass than other regions on all dates (Fig. 1.7). Shallow water, bay areas (Sandusky and Maumee regions) exhibited the highest values of all regions through July.
Mean summer zooplankton biomass reflects these differences with less 
(p<0.05, ANOVA) biomass in the offshore region (Table 1.2).

If zebra mussels do divert energy from pelagic waters into benthic 
systems, then zooplankton should be depressed in areas of high zebra 
mussel abundance. Shallow water areas near bays and islands therefore 
should exhibit lower zooplankton biomass than areas relatively free of 
zebra mussels (e.g., deep water areas). Crustacean zooplankton biomass 
was relatively independent of depth as average zooplankton biomass for 
sites <7.5 m was equivalent to sites >7.5 m on all dates in 1995 (Fig. 
1.8). Mean zooplankton biomass is shallow water was greater (p<0.05, 
t-test) than deep water sites (Table 1.3).

Zooplankton taxonomic composition is strongly influenced by water 
quality within the St. Lawrence Great Lakes. Calanoid copepods are 
generally more abundant relative to cyclopid copepods and cladocerans in 
oligotrophic regions of the Great Lakes (Patalas 1972, Gannon & 
Stemberger 1978). Abundance ratios of calanoid copepods to cyclopid 
copepods plus cladocerans from western Lake Erie in 1995 reflect 
zooplankton compositional responses to water quality. Despite high 
variability due to seasonal changes in taxonomic composition, the mean 
summer abundance ratio was higher (p<0.05; ANOVA) in offshore than in 
other regions (Table 1.2).
Historical comparisons of phytoplankton and zooplankton in western Lake Erie.

Western Lake Erie mean phytoplankton biomass exhibits extensive temporal variation with a clear-water phase evident for both 1970 and 1995 (Fig. 1.9). 1995 phytoplankton biomass was lower than it was in 1970. 1983-84 data provide little information about phytoplankton summer dynamics because samples were collected only in April, July, and August.

Zooplankton biomass varied seasonally during 1970 and 1995 with biomass generally higher in 1970 than 1995 (Fig. 1.10). Seasonal results from 1983-84 are generally uninformative for zooplankton biomass due to the lack of sampling dates in mid-summer. The mean zooplankton abundance ratio for 1995 does not differ from typical ratios calculated for western Lake Erie in the mid-1980’s before the arrival of zebra mussels (Table 1.4).

Discussion

In contrast to Nicholls & Hopkins' (1993), who found zebra mussels have eliminated seasonal patterns of phytoplankton based on water intake samples, I show that phytoplankton continue to exhibit temporal trends of biomass in western Lake Erie during late spring and early summer. Such seasonal variation in phytoplankton biomass reflects the dynamic
interaction among reproducing phytoplankton, nutrient limitation, and grazers. Thus, in my view, zebra mussel grazing likely is not completely controlling seasonal phytoplankton biomass. Although zebra mussel grazing may influence algal biomass, it is likely that other factors, such as nutrient availability and pelagic herbivore grazing, continue to control seasonal dynamics of phytoplankton.

In addition to seasonal variation, western basin phytoplankton biomass exhibited strong spatial variability. Previous investigators suggested that in-shore and shallow water areas would be most affected by zebra mussel grazing activities (Nicholls & Hopkins 1993, MacIsaac et al. 1991, MacIsaac et al. 1992). Thus, higher phytoplankton biomass should occur offshore and in deeper water. Western Lake Erie phytoplankton biomass in 1995 (Fig. 1.5) did not fit this expectation. Current results provide little evidence that zebra mussel grazing precludes other factors, such as zooplankton grazing (Lampert et al. 1986, Scavia & Fahnenstiel 1987) and nutrient limitation (Vanni & Temte 1990) from coincidentally controlling phytoplankton biomass.

Previous researchers also predicted current patterns of zooplankton biomass should reflect _Dreissena polymorpha_’s spatial distributions (Nicholls & Hopkins 1993, Leach 1993). Near-shore and shallow water zones of the western basin, those areas supposedly most affected by zebra mussels, would therefore be expected to contain lower zooplankton biomass than off-shore and deeper regions. My spatial results do not
support hypotheses that zebra mussels have diverted energy from pelagic waters, thereby reducing zooplankton biomass. Instead, these results correspond better to observations from other large lake ecosystems that productivity tends to decline as the distance from nearshore areas increase (Patalas & Salki 1993). Reduced productivity of open water areas in large lakes likely results from limited horizontal movement of nutrients from nearshore zones to offshore areas (Patalas & Salki 1992, Patalas 1990).

Within Lake Erie, Patalas (1972) noted that calanoid abundance declined from the eastern basin into the highly productive western basin. In 1995, zooplankton composition significantly differed between the offshore, low phytoplankton region and the near-shore, high phytoplankton regions. This suggests that spatial differences in phytoplankton within western Lake Erie influence not only the biomass of zooplankton, but also the types of zooplankton found in different regions of the basin.

Following reductions in external nutrient loading in the 1970's, phytoplankton biomass dramatically declined in western Lake Erie (Makarewicz 1993a). Although seasonal dynamics of phytoplankton biomass were not clear due to limited sampling through summer 1983-84, phytoplankton levels were well below those reported in 1970. After zebra mussel colonization, phytoplankton declines were reported from several areas within western Lake Erie (Holland 1993, Nicholls & Hopkins 1993). Continued declines in phytoplankton biomass due to increases in zebra mussel abundance and hence grazing should yield phytoplankton
abundances far below those found in the 1983-84 pre-zebra mussel surveys. My historical comparisons provide little evidence that predicted zebra mussel grazing impacts are being realized. The lack of declining phytoplankton in western Lake Erie, despite high numbers of zebra mussels, is not surprising. Previous predictions (Maclsaac et al. 1992, Bunt et al. 1993) about zebra mussel grazing impacts rest upon assumptions, such as a totally mixed system, that do not likely hold for a large lake ecosystem like western Lake Erie.

Phytoplankton reductions in the 1970's were followed by decreased zooplankton biomass in the 1980's (Makarewicz 1993b). Continued decline of zooplankton biomass was expected after zebra mussel colonization in the late 1980's. My results do not indicate that significant reductions in zooplankton biomass have occurred since 1983-84. Differences in sampling location, frequency, and timing reduce the power of these historical comparisons of past and present results. However, zooplankton biomass is still at levels typical of pre-zebra mussel conditions in the western basin of Lake Erie. As ratios of nitrogen to phosphorus loading have increased since the 1970's, the relative increase in small chlorophyte, cryptophyte, and chrysophyte algae has no doubt increased the efficiency of energy transfer from photosynthesis to zooplankton.

Zooplankton composition within western Lake Erie has historically reflected the productive nature of its pelagic waters (Makarewicz 1993b). Mean summer ratios of calanoids to cyclopoid and cladoceran abundance
for western Lake Erie in the 1980's were typically much lower than values found for the central and eastern basins of the lake. Western Lake Erie's ratio for 1995 was similar to all values found for the basin between 1983 and 1987. This lack of zooplankton compositional change lends further support to my previous conclusions that increasing zebra mussels have not been accompanied by dramatic alterations in plankton dynamics in western Lake Erie.

Although zebra mussels may consume large quantities of phytoplankton in western Lake Erie (Madenjian et al. 1995), predicted changes of phytoplankton and zooplankton spatial and temporal patterns do not appear to have been realized. Although one can not conclude from these results alone that zebra mussels do not influence levels phytoplankton and zooplankton, increased abundance of zebra mussels in western Lake Erie does not appear to have reconfigured spatial patterns of algae and zooplankton. These results, together with the evidence from historical comparisons, suggest that zebra mussels' direct impact on large lake ecosystems may be less than previously postulated.
<table>
<thead>
<tr>
<th>Region</th>
<th>No. of stations</th>
<th>mean depth (m)</th>
<th>substrate</th>
<th>mean dist. from shore (km)</th>
</tr>
</thead>
<tbody>
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<td>w 4</td>
<td>8.62</td>
<td>sand and</td>
<td>3.12</td>
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<tr>
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<tr>
<td></td>
<td>m 7</td>
<td>9.13</td>
<td></td>
<td>13.71</td>
</tr>
<tr>
<td>Maumee</td>
<td>w 3</td>
<td>6.50</td>
<td>rock and</td>
<td>5.50</td>
</tr>
<tr>
<td></td>
<td>m 5</td>
<td>5.24</td>
<td>mud</td>
<td>4.25</td>
</tr>
</tbody>
</table>

Table 1.1: Geographical and physical characteristics of weekly (w) and monthly (m) sites of the four sampling regions in western Lake Erie, 1995. Substrate information obtained from Herdendorf (1971).

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandusky</td>
<td>47</td>
<td>1.09 (0.63)</td>
<td>0.43 (0.46)</td>
<td>0.21 (0.24)</td>
</tr>
<tr>
<td>Islands</td>
<td>31</td>
<td>0.84 (0.28)</td>
<td>0.33 (0.21)</td>
<td>0.12 (0.12)</td>
</tr>
<tr>
<td>Offshore</td>
<td>35</td>
<td>0.27 (0.28)*</td>
<td>0.04 (0.08)*</td>
<td>0.40 (0.44)*</td>
</tr>
<tr>
<td>Maumee</td>
<td>28</td>
<td>1.38 (1.41)</td>
<td>0.31 (0.32)</td>
<td>0.20 (0.31)</td>
</tr>
</tbody>
</table>

Table 1.2: Comparison of the mean phytoplankton (mg l^-1) and zooplankton biomass (mg l^-1) among four different regions of western Lake Erie, 1995. Also shown are the abundance ratios of calanoid copepodes to cyclopoid copepodes plus cladocerans for the same sites. *Significantly different (p <0.05, ANOVA) from other three regions.
<table>
<thead>
<tr>
<th>Water Depth</th>
<th>n</th>
<th>Phytoplankton Biomass (S.D.)</th>
<th>Zooplankton Biomass (S.D.)</th>
</tr>
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<tbody>
<tr>
<td>shallow (&lt;7.5 m)</td>
<td>72</td>
<td>1.18 (1.05)*</td>
<td>0.36 (0.37)*</td>
</tr>
<tr>
<td>deep (&gt;7.5 m)</td>
<td>118</td>
<td>0.67 (0.64)</td>
<td>0.25 (0.32)</td>
</tr>
<tr>
<td>all samples</td>
<td>190</td>
<td>0.87 (0.86)</td>
<td>0.29 (0.34)</td>
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Table 1.3: Annual means and standard deviations of phytoplankton (mg l\(^{-1}\)) and zooplankton (mg l\(^{-1}\)) biomass from western Lake Erie, 1995 sites separated on the basis of water depth. *Significantly greater (p <0.05, t-test).

<table>
<thead>
<tr>
<th>year</th>
<th>western basin</th>
<th>central basin</th>
<th>eastern basin</th>
<th>Source</th>
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<tbody>
<tr>
<td>1970</td>
<td>0.11</td>
<td>---</td>
<td>---</td>
<td>this study</td>
</tr>
<tr>
<td>1983</td>
<td>0.34</td>
<td>0.32</td>
<td>0.40</td>
<td>Makarewicz (1993b)</td>
</tr>
<tr>
<td>1984</td>
<td>0.35</td>
<td>0.60</td>
<td>0.50</td>
<td>Makarewicz (1993b)</td>
</tr>
<tr>
<td>1985</td>
<td>0.22</td>
<td>0.65</td>
<td>0.82</td>
<td>Makarewicz (1993b)</td>
</tr>
<tr>
<td>1986</td>
<td>0.31</td>
<td>0.95</td>
<td>0.85</td>
<td>Makarewicz (1993b)</td>
</tr>
<tr>
<td>1987</td>
<td>0.17</td>
<td>0.38</td>
<td>0.89</td>
<td>Makarewicz (1993b)</td>
</tr>
<tr>
<td>1995</td>
<td>0.24</td>
<td>---</td>
<td>---</td>
<td>this study</td>
</tr>
</tbody>
</table>

Table 1.4: Ratio of calanoid copepodites to cyclopoid copepodites plus cladocerans in Lake Erie for 1970, 1983-87, and 1995.
Figure 1.1: Recent trends in annual external phosphorus loading (bars) relative to annual water discharge (circles) to western Lake Erie from the Sandusky (shaded bars and closed circles) and Maumee (open bars and open circles) rivers. Data obtained from Baker (1995 a,b).

Figure 1.2: Recent trends in annual external nitrogen loading (bars) relative to annual water discharge (circles) to western Lake Erie from the Sandusky (shaded bars and closed circles) and Maumee (open bars and open circles) rivers. Data obtained from Baker (1995 a,b).
Figure 1.3: Annual N:P ratios for external nutrient loading from the Sandusky (closed circles) and Maumee (open circles) rivers. Nutrient loading data from Baker (1995a, b).
Figure 1.4: Location of sampling sites in western Lake Erie. May-July 1995 sampling sites (closed circles) were divided into four geographically distinct regions: (1) Sandusky Bay, (2) Bass Islands, (3) Offshore, and (4) Maumee Bay. Historical sampling sites, 1970 (open triangles) and 1983-84 (open squares), are shown in relation to 1995 sampling locations. Locations of 1970 sites were obtained from Bean (1980) and 1983-4 sites from Makarewicz (1988).
Figure 1.5: Seasonal variation of phytoplankton biomass (means +/- 1SE) in four regions in western Lake Erie, 1995.
Figure 1.6: Seasonal variation in phytoplankton biomass (means +/- 1SE) for deep, > 7.5 m (open circles) and shallow, < 7.5 m (closed circles) sites in western Lake Erie, 1995.
Figure 1.7: Seasonal variation in crustacean zooplankton biomass (mean +/- 1SE) in four regions of western Lake Erie, 1995. Biomass estimates include cladocerans, copepodes, and nauplii.
Figure 1.8: Comparison of crustacean zooplankton biomass (means +/- 1SE) for deep, >7.5 m (open circles) and shallow, <7.5 m (closed circles) sampling sites in 1995 for western Lake Erie. Biomass estimates include cladocerans, copepodites, and nauplii.
Figure 1.9: Seasonal variation in phytoplankton biomass for western Lake Erie in 1970 (closed diamonds), 1983-84 (closed triangles and squares respectively), and 1995 (open circles). See text for sources of historical data.
Figure 1.10: Seasonal variation in zooplankton biomass for western Lake Erie in 1970 (closed diamonds), 1983-84 (closed triangles and squares respectively), and 1995 (open circles). See text for sources of historical data.
CHAPTER 2

ZOOPLANKTON PRODUCTION IN WESTERN LAKE ERIE
BEFORE AND AFTER ZEBRA MUSSELS

Introduction

Zebra mussels (*Dreissena polymorpha*) represent a formidable threat to pelagic ecosystem productivity in Lake Erie (Bunt *et al.* 1993, Klerks *et al.* 1996). Since colonizing western Lake Erie in the late-1980's, zebra mussels have been deemed responsible for declining phytoplankton biomass and abundance (Holland 1993, Nicholls & Hopkins 1993, but see Chapter 1) and changing phytoplankton composition (Holland 1993). Previous researchers predicted that these changes in primary productivity, mediated by changes in zooplankton productivity, would translate into negative impacts on Lake Erie's sport fishery (Wu & Culver 1994, MacIsaac *et al.* 1992).

Predictions about zebra mussels' indirect impact on sport fish populations assume that zooplankton productivity is strongly related to levels of algal biomass, not an unwarranted assumption given the strong
empirical relationships between phytoplankton and zooplankton productivity (McCauley & Kalff 1981, Morgan 1980, Makarewicz & Likens 1979). Phytoplankton biomass does represent the pool of energy available for zooplankton consumption. As such, total secondary production is limited by the amount of primary production within a lake and by the efficiency with which zooplankton use this production (Edmondson and Winberg 1971).

Other lake factors, such as zooplankton community composition and water temperature, also influence secondary production (Nanazato & Yasuno 1985, Shuter & Ing 1997). Crustacean production represents the amount of energy fixed as growth and reproduction by all individuals in a community during a defined time period (Kimmerer 1987). As zooplankton abundance increases, more individuals contribute growth and reproduction to combined community production (Morgan 1980, Makarewicz & Likens 1979). Zooplankton taxonomic composition can dramatically affect production because grazing, growth, and reproductive rates vary widely among taxa (Mourelatos & Lacroix 1990, Richman & Dodson 1983, Wetzel 1983). As ectotherms, crustacean growth and reproductive rates also are tightly linked to water temperature (Orcutt and Porter 1982, Cooley et al. 1986, Vijverberg 1980).

Previous studies (MacIsaac 1996, Wu & Culver 1994, MacIsaac et al. 1992, but see Padilla et al. 1996) claimed diversion of energy flow by
zebra mussels in western Lake Erie from the pelagic to benthic ecosystem would reduce algae available for zooplankton, resulting in less food available for fish. One method to evaluate whether zooplankton production declined post-*Dreissena* colonization is through comparing current and historical levels of productivity. When making these comparisons, one needs to consider annual variability of zooplankton populations, spatial differences in productivity within the basin, and seasonal patterns of phytoplankton and zooplankton biomass and production in western Lake Erie (Chapter 1). These comparisons particularly depend upon the availability of non-biased historical sources of zooplankton production.

This study seeks to determine whether energy flow through crustacean zooplankton has declined since the introduction of zebra mussels. To do so, I present weekly phytoplankton and zooplankton data collected from western Lake Erie during 1995 and 1996. I then characterize how zooplankton production (P) relates to food availability, water temperature (*T*<sub>w</sub>), and zooplankton biomass (B). Finally, I compare 1995-6 with 1970's and 1980's (pre-zebra mussel invasion) zooplankton productivity in western Lake Erie, using relationships among P, B, and *T*<sub>w</sub> to hindcast historical crustacean productivity.
Methods

Zooplankton.

Zooplankton samples were collected frequently by the Ohio Division of Wildlife from a series of stations in western Lake Erie during 1995 and 1996 (Fig. 2.1). One zooplankton sample was collected from each site with vertical tows of a metered net (diameter = 0.5 m, mesh = 93 μm (1995) and 64 μm (1996)) pulled from near the lake bottom (< 1 m). Zooplankton was immediately placed in plastic collection bottles and preserved with a 4% sugar-formalin solution (Haney & Hall 1973).

I determined crustacean abundance and biomass in collected samples. After diluting zooplankton samples to a known volume (between 1000 and 5000 ml), all crustaceans in 5-10 ml subsamples were identified and counted. The first 20 individuals encountered of each taxon in each count were measured for length to the nearest 0.05 mm. Counting of additional subsamples continued until at least 100 individuals of one taxon was recorded. Biomass (g m⁻³) of each taxon was estimated as a product of its sample-specific mean dry weight and abundance. Dry weight (μg ind⁻¹) calculations were based on length-weight regressions specific to Lake Erie zooplankton (Culver et al. 1985).

Zooplankton secondary production estimates provide an index of crustacean growth and reproduction in the lake. I used the growth
increment summation method (Patalas 1970, Edmondson & Winberg 1971, Winberg 1971, Culver & DeMott 1978, see Appendix A for additional details) to estimate the amount of daily growth and reproduction of the most common crustacean taxa (Table 2.2):

\[ P = \sum_{i=1}^{n} \frac{N_i \times \Delta W_i}{DT_i} \]

where \( P \) is production in biomass per unit time, \( N_i \) is abundance in a size class, \( \Delta W_i \) is the change in biomass from one size class to the next, \( DT_i \) is the development time or duration of a size class, and \( n \) is the number of size classes (\( n = 7 \) for cladocerans and 12 for copepods). I calculated size-class abundance in each sample as the product of each taxon’s total abundance (ind m\(^{-3}\)) and its size-frequency distribution. Length-weight regressions (Culver et al. 1985) were used to calculate size-class biomass. Temperature-dependent development times (Table A.3) were used to estimate size-class duration. I calculated egg production by multiplying egg abundance by maximum egg weight and dividing by the egg development time. Each cladoceran species' daily \( P \) is a combined estimate of egg, juvenile, and adult biomass gain. Daily \( P \) estimates for copepods represent a combined total of egg, naupliar, and copepodite production.
Phytoplankton.

To examine how food availability influences daily zooplankton P, I estimated phytoplankton biomass from my zooplankton sampling sites. Algal samples were collected from the water column using an integrated water sampler (2.5 cm plastic tube) lowered to twice the Secchi depth at each sampling station. After thoroughly mixing collected water in a plastic bucket, 250 ml of water was fixed with Lugol’s solution. Water samples, allowed to settle 3-5 days, were concentrated to 30 ml and placed in glass vials. I determined algal biomass and composition using an inverted microscope (Lund et al. 1958, Wu & Culver 1994).

Water Temperature.

Water temperature ($T_w$) was used to estimate development times and to assess how zooplankton turnover rates (P:B) respond to physical conditions. In 1996, water temperature was recorded at all sampling stations with a YSI thermistor. Water temperature for all sites in 1995 was obtained from the Great Lakes Forecasting System (GLFS); courtesy of the GLFS lab, Dept. of Civil Engineering, The Ohio State University, Columbus, Ohio.
Historical comparisons.

I compared recent results with historical data to assess whether zooplankton productivity has decreased since the late-1980’s introduction of zebra mussels into western Lake Erie. By applying relationships among zooplankton production, biomass and water temperature described in this paper, I estimated historical levels of production using B and $T_w$ obtained from previous studies. Crustacean B and $T_w$ data were obtained for 1970 from Bean (1980); for 1975 from Culver & DeMott (1978); for 1984 from Makarewicz (1988) and Lesht & Rockwell (1987); and for 1988-9 from Wu (1991). The most significant difference between historical and current methods was the use of an unmetered net in 1970 which yields underestimates of zooplankton abundance (Welch 1948). To improve spatial comparability, I calculated production for 1995-6 using subsets of current sampling sites that were closest to each historical study’s sampling locations (Fig. 2.1 & 2.2).

Results

Zooplankton production and biomass varied extensively during summer 1995 and 1996. Biomass (dry weight) of cladocerans peaked at 1600 mg m$^{-3}$ in 1995 and 1800 mg m$^{-3}$ in 1996 whereas maximum copepod biomass was 750 mg m$^{-3}$ in 1995 and 600 mg m$^{-3}$ in 1996. Cladoceran production ranged from 0.06 to 600 mg m$^{-3}$ d$^{-1}$ in 1995 and
from 0.14 to 1800 mg m\(^{-3}\) d\(^{-1}\) in 1996. Copepod production varied between 0.03 & 300 mg m\(^{-3}\) d\(^{-1}\) in 1995 and 0.06 & 124 mg m\(^{-3}\) d\(^{-1}\) in 1996. Cladoceran P:B ratios ranged between 0.08 to 0.86 d\(^{-1}\) in 1995 and 0.19 to 0.92 d\(^{-1}\) in 1996 while copepod P:B ratios ranged 0.07 to 0.87 d\(^{-1}\) in 1995 and 0.09 to 0.81 d\(^{-1}\) in 1996.

Phytoplankton and water temperature exhibited seasonal variation in 1995 and 1996. Phytoplankton biomass varied between 0.01 & 5.15 g m\(^{-3}\) in 1995 and 0.03 & 7.24 g m\(^{-3}\) in 1996. Water temperature ranged from 10\(^{\circ}\)C in late-May to 28\(^{\circ}\)C in late July during 1995 and from 13.5\(^{\circ}\)C in late-May to 27.7\(^{\circ}\)C in August during 1996.

**Zooplankton production relationships to lake biotic and abiotic factors.**

Previous investigations have shown that food availability can directly influence herbivore production (Brylinsky 1980, Makarewicz 1985). My regressional results, however, show only weak or no relationships between total phytoplankton biomass and zooplankton P (Table 2.2, Appendix B). Crustacean production estimates were strongly related to zooplankton biomass in both 1995 and 1996 (Table 2.2, Appendix B). Despite the strength of these relationships, it is clear that crustacean productivity should also relate to water temperature. Crustacean P:B ratios were highly correlated to water temperature at all taxonomic levels (Table 2.2, Appendix B) in both 1995 and 1996.
I constructed multiple factor regressions to examine the relationship among P, B, and water temperature (Table 2.3). Due to the low correspondence of P to food availability, I eliminated phytoplankton biomass from this analysis. Relative to simple P versus B regressions, multiple regressions (P versus B & $T_w$) did improve the amount of variance explained in P (Table 2.3). More significantly, however, water temperature improved the multiple regression model's ability to predict production by reducing the simple regression model's bias to overestimate P at low $T_w$ and underestimate P at high $T_w$ (Fig. 2.3).

**Historical comparisons.**

Crustacean biomass and productivity has changed during the last two decades. Although the early 1970's represent a high nutrient loading period (Richards & Baker 1993), little difference was observed between 1970 and 1995-6 biomass and productivity (Figs. 2.4 & 2.5). Large differences between 1975 and 1995-6 in biomass and production were, however, evident at Locust Point (Figs. 2.4 & 2.5). Crustacean biomass and production in 1995 and 1996 do remain equivalent to levels found in a year (1984) from the post-nutrient reduction, pre-Dreissena period (Fig. 2.4 & 2.5). Similarly, little difference is evident between 1995-6 production
estimates (Fig. 2.5) from the Bass Island area and 1988-9 estimates, the latter being a period characterized by very low zebra mussel densities (MacIsaac et al. 1995).

Discussion

Evaluating the impact of *Dreissena* has typically involved comparing pre- and post-introduction characteristics of western Lake Erie (Holland 1993, Leach 1993, Nicholls and Hopkins 1993, MacIsaac et al. 1994). Historical comparisons are often limited by the amount and type of data collected before an ecosystem disturbance (Edmondson 1991). One underutilized method of improving historical comparisons is to use empirical relationships derived from current data to estimate parameters that previously went unrecorded or uncalculated. Regressional relationships among $P$, $B$, and $T_w$ described in our study provided a method by which to calculate historical productivity to be compared to current levels of zooplankton.

**Production relationships to lake biotic and abiotic factors.**

Total phytoplankton biomass appears to be a poor indicator of daily zooplankton production. The standing crop of phytoplankton in lake ecosystems reflects the combined effects of grazing (Lampert et al. 1986, Scavia & Fahnenstiel 1987), sinking rates (Sommer 1984, Reynolda and
Wiseman 1982), mixing processes (Forsberg 1985), and nutrient limitation (Vanni & Temte 1990). When grazing losses are the predominant factor controlling phytoplankton biomass, accumulation of zooplankton biomass results in subsequent declines of algal standing crops (Lynch & Shapiro 1981, Shapiro & Wright 1984). This results in a negative relationship, not the positive relationship commonly described between crustacean daily P and food availability on a seasonal basis (Brylinsky 1980). I found no relationship between zooplankton daily production and phytoplankton biomass. Because the utility of algal biomass, a widely reported historical parameter, in estimating zooplankton productivity appears low, I excluded phytoplankton from further analysis.

I did, however, find a strong relationship between zooplankton production and biomass in this study. Because production estimates incorporated crustacean abundance and size data which also were used to estimate community biomass, strong relationships may not be surprising. The relationship between production and biomass is influenced by water temperature (Morgan 1980, Shuter & Ing 1997), food availability (Brylinsky 1980, Makarewicz 1985, Orcutt & Porter 1983), and sometimes by mate limitation in copepods (Williamson & Butler 1987). Despite these confounding factors, P versus B relationships do provide a means by which
to approximate the relative magnitude of energy flow temporally and spatially within western Lake Erie, even when complete data to calculate production are unavailable.

Crustacean P:B ratios were strongly related to water temperature which perhaps reflects the use of temperature-dependent development times in production calculations. Shuter & Ing (1997), however, presented considerable evidence that suggested P:B versus $T_w$ relationships, derived with similar methodology, were not simply statistical artifacts. Given that crustacean zooplankton do in fact increase growth and reproductive rates as water temperature warms (Orcutt & Porter 1982, Cooley et al. 1986, Vijverberg 1980), $T_w$ needs to be considered when examining zooplankton turnover rates. Furthermore, my estimates of production made without including water temperature yielded biased results, illustrating the importance of including water temperature in production calculations.

Zooplankton productivity can be reliably estimated from crustacean biomass values and water temperature. Using regressions to estimate production increases comparability of results spatially and temporally, because results are standardized and calculation errors likely reduced. As such, relationships described among production, biomass, and water temperature provide a means, equivalent to more traditional methods, by which to estimate historical levels of productivity.
Historical comparisons.

Zooplankton productivity has changed in western Lake Erie during the last 25 years. Makarewicz (1993a, 1993b) concluded that phytoplankton and zooplankton declined in the open waters of western Lake Erie between the early 1970's and the mid-1980's. In addition to reduced abundance, crustacean composition also changed between 1970 and the 1980's and reflected declining productivity in the western basin (Chapter 1). My results from 1995-96 illustrate that current levels of zooplankton productivity remain at levels considerably lower than those found in the lake during 1975. 1970 crustacean productivity was likely underestimated due to the use of an unmetered net (Welch 1948) and yet was equivalent to or higher than 1995-6 levels of productivity (Fig. 2.5).

Previous researchers predicted dramatic zooplankton declines to coincide with increased zebra mussel abundance due to interspecific competition for phytoplankton in western Lake Erie. In my view, zooplankton productivity has not declined to levels below those common before Dreissena’s invasion. I found few differences among 1984, 88-89 and 1995-6. These results, together with the lack of zooplankton composition change in the western basin (Chapter 1), suggest that zebra mussels have not dramatically reduced western Lake Erie’s pelagic productivity and therefore do not likely pose a threat to the lake’s sport fisheries.
<table>
<thead>
<tr>
<th>Taxonomic Group</th>
<th>Common Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Copepoda</strong></td>
<td></td>
</tr>
<tr>
<td>Calanoida</td>
<td><em>Skistodiaptomus oregonensis</em>, <em>Leptodiaptomus sicilis</em>, <em>Leptodiaptomus ashandi</em>, <em>Leptodiaptomus minutus</em>, <em>Leptodiaptomus siciloides</em>, <em>Eurytemora affinis</em>, <em>Epischura lacustris</em></td>
</tr>
<tr>
<td>Cyclopoida</td>
<td><em>Mesocyclops edax</em>, <em>Acanthocyclops vernalis</em>, <em>Dacyclops bicuspidatus thomasi</em></td>
</tr>
<tr>
<td><strong>Cladocera</strong></td>
<td></td>
</tr>
<tr>
<td>Daphnidae</td>
<td><em>Daphnia galeata mendotae</em>, <em>Daphnia retrocurva</em></td>
</tr>
<tr>
<td>Bosminidae</td>
<td><em>Bosmina longirostris</em>, <em>Eubosmina coregoni</em></td>
</tr>
<tr>
<td>Sididae</td>
<td><em>Diaphanosoma</em> spp.</td>
</tr>
</tbody>
</table>

Table 2.1: Common crustaceans, taxa occurring in at least 3% of our zooplankton samples, during summers 1995-6 in western Lake Erie.
<table>
<thead>
<tr>
<th>Group</th>
<th>Year</th>
<th>Crustacean P vs Phyto B</th>
<th>Crustacean P vs B</th>
<th>Crustacean P:B vs T&lt;sub&gt;∞&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepoda</td>
<td>1995</td>
<td>0.09</td>
<td>0.96</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>0.08</td>
<td>0.86</td>
<td>0.57</td>
</tr>
<tr>
<td>Daphnidae</td>
<td>1995</td>
<td>0.00</td>
<td>0.97</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>0.04</td>
<td>0.93</td>
<td>0.41</td>
</tr>
<tr>
<td>Bosminidae</td>
<td>1995</td>
<td>0.05</td>
<td>0.96</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>0.09</td>
<td>0.96</td>
<td>0.47</td>
</tr>
<tr>
<td>Sigidae</td>
<td>1995</td>
<td>0.09</td>
<td>0.97</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>0.02</td>
<td>0.89</td>
<td>0.62</td>
</tr>
</tbody>
</table>

Table 2.2: Percent of variation in crustacean P and P:B explained by phytoplankton biomass (Phyto B), zooplankton biomass (B), and water temperature (T<sub>∞</sub>). Data reported as r² values for simple regressions calculated from 1995-6 western Lake Erie crustacean zooplankton data.
<table>
<thead>
<tr>
<th>Group</th>
<th>Year</th>
<th>n</th>
<th>α</th>
<th>β</th>
<th>ρ</th>
<th>$r^2$</th>
</tr>
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<tbody>
<tr>
<td>Copepoda</td>
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<td>191</td>
<td>0.0386</td>
<td>0.9599</td>
<td>1.0860</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>186</td>
<td>0.0432</td>
<td>0.8878</td>
<td>1.1010</td>
<td>0.94</td>
</tr>
<tr>
<td>Daphnidae</td>
<td>1995</td>
<td>172</td>
<td>0.0750</td>
<td>0.9548</td>
<td>1.0997</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>172</td>
<td>0.0532</td>
<td>0.9634</td>
<td>1.1073</td>
<td>0.96</td>
</tr>
<tr>
<td>Bosminida</td>
<td>1995</td>
<td>168</td>
<td>0.0587</td>
<td>0.9931</td>
<td>1.0685</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>148</td>
<td>0.0583</td>
<td>1.0133</td>
<td>1.0643</td>
<td>0.96</td>
</tr>
<tr>
<td>Sididae</td>
<td>1995</td>
<td>128</td>
<td>0.0373</td>
<td>0.9892</td>
<td>1.0740</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>114</td>
<td>0.0042</td>
<td>0.9587</td>
<td>1.1757</td>
<td>0.96</td>
</tr>
</tbody>
</table>

Table 2.3: Relationships among crustacean production, biomass, and water temperature described for western Lake Erie results. Parameters shown are from the multiple regression model, $production = α(zooplankton biomass)^β(ρ)^Tw$, fitted to western Lake Erie crustacean zooplankton data from 1995 and 1996.
Figure 2.1: Western Lake Erie sampling locations for 1995 and 1996. Zooplankton and phytoplankton samples were collected from weekly (closed circles) and monthly (open circles) locations between May 17 and July 24, 1995. Samples were collected from 1995 sampling sites and an additional three weekly (squares) locations between May 22 and September 4, 1996.
Figure 2.3: Test of the robustness of 1995 regressions of production as a function (A) only biomass and (B) biomass and water temperature over the range of temperatures encountered. Each data point represents the proportional difference, (estimate-prediction)/estimate, between one 1995 regresional prediction and 1996 data-based estimate of western Lake Erie crustacean daily production.
Figure 2.4: Comparison of historical and current levels of crustacean biomass from different areas in western Lake Erie. Locations of historical and current sampling sites are shown in Figure 2.2.
Figure 2.5: Comparison of historical and current levels of crustacean production from different areas in western Lake Erie. Location of historical and current sampling sites shown in Figure 2.2.
LIST OF REFERENCES


DeMott, W.R. 1976. Zooplankton productivity in western Lake Erie at Locust Point, Ohio. The Ohio State University, CLEAR Technical Report No. 58, 107 pp


APPENDIX A.

Production Calculations.

In this study, I used the growth increment summation method (Patalas 1970, Edmondson & Winberg 1971, Winberg 1971, Culver & DeMott 1978) to estimate the amount of daily growth and reproduction of each crustacean taxon:

\[ P = \sum_{i=1}^{n} \frac{N_i \times \Delta W_i}{DT_i} \]

where
P is production in biomass per unit time,
N\(_i\) is abundance in a size class,
\(\Delta W_i\) is the change in biomass from one size class to the next,
\(DT_i\) is the development time or duration of a size class,
and \(n\) is the number of size classes (\(n = 7\) for cladocerans and \(12\) for copepods).

To calculate production for each taxon using this method, one is required to have four main components:

1) a size-frequency distribution
2) abundance (no. \(1^1\))
3) length-weight regressions
4) temperature-dependent development times.

Each of these components are used together to estimate daily growth and reproductive output of crustaceans. Below I will perform sample
calculations to illustrate how this method was used in this study and to explicitly describe the various components and their sources.

Part 1. Size-frequency distribution:

To calculate production, one must first determine for each taxon the relative abundances of sizes in arbitrarily assigned size-classes. In this study, cladocerans were split into three juvenile and four adult size classes. Copepods were split into six naupliar, five copepodite, and one adult size class. Figure A.1 illustrates how size-classes and sizes were arranged when calculating size-frequency distributions. Three sizes were directly calculated from recorded measurements:

- neonate size (B1) = 5th percentile of all measurements of eggless individuals
- primipara size (C1) = 10th percentile of all egg carrying individuals
- max. adult size (C5) = 95th percentile of all individuals.

Additional sizes were calculated using B1, C1, C5. For example, size B2 = [(C1 - B1) + 3] + B1. Size-classes represent the interval between sizes. For example, juvenile size-class 1 (J1) extends from size B1 to size B2.

Copepod sizes were calculated similarly with sizes for:
- minimum nauplius = 5th percentile of all nauplii,
- maximum nauplius = 95th percentile of all nauplii,
- minimum copepodite = 5th percentile of all eggless copepodites,
- maximum copepodite = 95th percentile of all eggless copepodites,
- maximum adult = 95th percentile of all copepodites.

Given these size-classes (J1-A4), we calculated what percentage of measured sizes were found in each size-class to determine the size-frequency distribution, which yielded results shown in Figure A.2.

Multiplying the taxon's total abundance by this size distribution yields size-abundance distribution. For example, Figure A.3 illustrates what the size-abundance distribution would be if the abundance equaled 30 ind l⁻¹. Note that egg (E) abundance, in this case 12.2 egg l⁻¹, has been added in another size-class.

Part 2. Calculating biomass change from one size-class to the next.

At this point, one needs to determine the biomass gain from one size-class to the next. Since the sizes (Table A.1) separating each size-
class are known (B1-C5), one must calculate the mid-point size (MS) of each size class. For example,

\[(2) \quad \text{Juvenile size-class 1 midpoint size (MS1)} = \left[\frac{(B2-B1)}{2}\right] + B1.\]

Using MS1 in previously described length-weight regressions (Culver et al. 1985), one can calculate the weight at that size (Table A.2). After calculating midpoint sizes for all size classes, the biomass gain is simply the difference from one to the next (Table A.4).

For example, the biomass gain from J1 to J2 is:

\[(3) \quad \Delta W = MS2 - MS1.\]

Note that to calculate weight gained by eggs, we assumed maximum egg size to be the neonate size. One therefore calculates neonate weight, based on its length-weight regression, and assumes that this is the net female weight gain when an average egg is laid.


The final component necessary to calculate production is to estimate size-class duration. This is the amount of time which it takes the taxon to grow from one-size class to the next. Temperature-dependent development times (See Table A.3 for sources) allow one to estimate size-class durations. Embryonic and juvenile development times have been experimentally determined and can be directly applied to production calculations. We estimated adult development time in this study by applying a ratio described by Hall (1964). The ratio, adult size-class length change divided by the three times the juvenile size-class length change, was multiplied by the egg development time to yield an approximation of the adult size-class duration. If we again use *Daphnia retrocurva* as an example and let the water temperature \(T_w\) be 20°C, then development times for this example would be:

Egg Development Time
\[= \left\lfloor 65912 \times (T_w + 6.1)^{2.12} \right\rfloor + 24 = 2.73 \text{ days}\]

Juv. Develop. Time
\[= (31.68811) - (2.07378 \times T_w) + (0.03684 \times T_w^2) = 4.95 \text{ days}\]

Adult Develop. Time
\[= \left[\text{Egg DT} \times \left((MS6-MS5) + 3 \times (MS3-MS2)\right)\right] \times 4 = 1.42 \text{ days}.\]

With the calculation of size-abundance distributions, size-class weight change, and development times complete, the final step is to sum the components to calculate production (µg l⁻¹ day⁻¹). Sample calculations (Table A.5) show how different components are combined to estimate daily production.

Part 5. Automating production with computer spreadsheets.

Production can easily be calculated for crustaceans using computer spreadsheets if all necessary data are available. The most common limiting data were measurements of organisms. Rare organisms yield few measurements and thus inadequate data to calculate a size-frequency distribution for each sample. We, therefore, constructed a size-frequency library to facilitate calculation of production for rare taxa. Size-frequency distributions in the library were calculated for each taxon from all measurements recorded for each sampling date and from all measurements for the entire year. These alternate size-frequency distributions were used when required. Figure A.3 illustrates the decision making process forming the basis for spreadsheet production calculations using the size-library.
neonate size (B1) = 0.47 mm
B2 = 0.70 mm
B3 = 0.92 mm
primipara (C1) = 1.15 mm
C2 = 1.24 mm
C3 = 1.33 mm
C4 = 1.42 mm
Max. Adult (C5) = 1.51 mm.

Table A.1. Typical sizes found for *Daphnia retrocurva* during 1996.

<table>
<thead>
<tr>
<th>Midpoint</th>
<th>size (mm)</th>
<th>Biomass (µg ind⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MS1</td>
<td>0.59</td>
<td>1.76</td>
</tr>
<tr>
<td>MS2</td>
<td>0.81</td>
<td>4.22</td>
</tr>
<tr>
<td>MS3</td>
<td>1.04</td>
<td>8.41</td>
</tr>
<tr>
<td>MS4</td>
<td>1.21</td>
<td>12.76</td>
</tr>
<tr>
<td>MS5</td>
<td>1.29</td>
<td>15.22</td>
</tr>
<tr>
<td>MS6</td>
<td>1.38</td>
<td>18.33</td>
</tr>
<tr>
<td>MS7</td>
<td>1.47</td>
<td>21.82</td>
</tr>
</tbody>
</table>

Table A.2. Midpoint sizes calculated from *Daphnia retrocurva* sizes in Table A.1 and corresponding dry weights calculated from length-weight regressions.
<table>
<thead>
<tr>
<th>Taxa</th>
<th>Stage</th>
<th>Geographic locale</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cladocerans</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Daphnia galeata</em></td>
<td>E</td>
<td>Michigan</td>
<td>Hall 1964</td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>England</td>
<td>Munro and White 1975</td>
</tr>
<tr>
<td><em>Daphnia retrocurva</em></td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>England</td>
<td>Munro and White 1975</td>
</tr>
<tr>
<td><em>Bosmina longirostris</em></td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>Poland</td>
<td>Hillbricht-Ilkowska and Patalas 1967</td>
</tr>
<tr>
<td><em>Diaphanosoma</em> spp.</td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>Poland</td>
<td>Hillbricht-Ilkowska and Patalas 1967</td>
</tr>
<tr>
<td><em>Eubosmina</em> spp.</td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
<tr>
<td></td>
<td>J</td>
<td>Poland</td>
<td>Hillbricht-Ilkowska and Patalas 1967</td>
</tr>
<tr>
<td><strong>Copepods</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Eurytemora affinis</em></td>
<td>E</td>
<td>Netherlands</td>
<td>Vijverberg 1980</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>Netherlands</td>
<td>Vijverberg 1980</td>
</tr>
<tr>
<td><em>Leptodiaptomus</em></td>
<td>E</td>
<td>Nova Scotia</td>
<td>Cooley and Minns 1978</td>
</tr>
<tr>
<td><em>Skistodiaptomus</em></td>
<td>E</td>
<td>Ontario</td>
<td>Cooley and Minns 1978</td>
</tr>
<tr>
<td><em>Diacyclops</em></td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley 1978</td>
</tr>
<tr>
<td><em>Acanthocyclus</em></td>
<td>E</td>
<td>Aquarium</td>
<td>Robertson et al. 1974</td>
</tr>
<tr>
<td><em>Mesocyclops edax</em></td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley 1978</td>
</tr>
<tr>
<td>Calanoid copepods*</td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>Sweden</td>
<td>Nauwerck 1963</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
<tr>
<td>Cyclopoid</td>
<td>E</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>Germany</td>
<td>Spindler 1971</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>Lake Ontario</td>
<td>Cooley et al. 1986</td>
</tr>
</tbody>
</table>

Table A.3: Sources of temperature-dependent development times (E=egg, J=juvenile, N=nauplius, C=copepodite) used in production calculations for common taxa found in western Lake Erie. Source of zooplankton used in each study is listed under geographic locale. Note that when individual copepod taxa egg, nauplius, or copepodite development formulae were unavailable, the appropriate general calanoid or cyclopoid development times were used instead.
<table>
<thead>
<tr>
<th>Size-class change</th>
<th>ΔW(μg ind⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>E-B1</td>
<td>0.94</td>
</tr>
<tr>
<td>J1-J2</td>
<td>2.46</td>
</tr>
<tr>
<td>J2-J3</td>
<td>4.19</td>
</tr>
<tr>
<td>J3-A1</td>
<td>4.35</td>
</tr>
<tr>
<td>A1-A2</td>
<td>2.46</td>
</tr>
<tr>
<td>A2-A3</td>
<td>3.11</td>
</tr>
<tr>
<td>A3-A4</td>
<td>3.49</td>
</tr>
</tbody>
</table>

Table A.4. Differences in weights between consecutive size-classes used to estimate biomass gain of individuals passing from one size-class to the next.

<table>
<thead>
<tr>
<th>Size-class</th>
<th>Abundance (ind l⁻¹)</th>
<th>ΔW (μg ind⁻¹)</th>
<th>Develop. Time (days)</th>
<th>Production (μg l⁻¹ day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>12.2</td>
<td>0.94</td>
<td>2.73</td>
<td>4.20</td>
</tr>
<tr>
<td>J1</td>
<td>14.1</td>
<td>2.46</td>
<td>1.65</td>
<td>21.02</td>
</tr>
<tr>
<td>J2</td>
<td>4.5</td>
<td>4.19</td>
<td>1.65</td>
<td>11.43</td>
</tr>
<tr>
<td>J3</td>
<td>2.4</td>
<td>4.35</td>
<td>1.00*</td>
<td>10.44</td>
</tr>
<tr>
<td>A1</td>
<td>3.0</td>
<td>2.46</td>
<td>.355</td>
<td>20.79</td>
</tr>
<tr>
<td>A2</td>
<td>1.5</td>
<td>3.11</td>
<td>.355</td>
<td>13.14</td>
</tr>
<tr>
<td>A3</td>
<td>2.4</td>
<td>3.49</td>
<td>.355</td>
<td>23.59</td>
</tr>
<tr>
<td>A4</td>
<td>2.1</td>
<td></td>
<td></td>
<td>**</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>104.6</td>
</tr>
</tbody>
</table>

Table A.5. Calculation of production for *Daphnia retrocurva* using data presented in previous figures and tables. *Note that duration between size-class J3 and A1 represents the average of juvenile and adult development times and **size-class A4 yields no production since we assume that individuals in this size-class experience 100% mortality.
Figure A.1. Arrangement of sizes and size-classes used for cladoceran production calculations.

Figure A.2. Typical size-frequency distribution of western Lake Erie cladocerans found during this study.
<table>
<thead>
<tr>
<th>Abun.</th>
<th>E</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>12.1</td>
<td>14.1</td>
<td>4.5</td>
<td>2.4</td>
<td>3.0</td>
<td>1.5</td>
<td>2.4</td>
<td>2.1</td>
</tr>
<tr>
<td>B1</td>
<td>B2</td>
<td>B3</td>
<td>C1</td>
<td>C2</td>
<td>C3</td>
<td>C4</td>
<td>C5</td>
<td></td>
</tr>
</tbody>
</table>

Figure A.3. Size-abundance distribution (# l⁻¹) calculated from size-frequency distribution and total abundance.
Figure A.4: Flow-chart depicting the method used to calculate crustacean production.
Appendix B

Regressional Results.

<table>
<thead>
<tr>
<th>Group</th>
<th>Year</th>
<th>n</th>
<th>R</th>
<th>α</th>
<th>β</th>
<th>p-value</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>crustaceans</td>
<td>1995</td>
<td>189</td>
<td>0.01- 5.15</td>
<td>39.3</td>
<td>0.32</td>
<td>0.02</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>156</td>
<td>0.03- 7.24</td>
<td>26.8</td>
<td>0.47</td>
<td>&lt;0.01</td>
<td>0.11</td>
</tr>
<tr>
<td>Copepoda</td>
<td>1995</td>
<td>189</td>
<td>0.01- 5.15</td>
<td>12.2</td>
<td>0.46</td>
<td>&lt;0.01</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>156</td>
<td>0.03- 7.24</td>
<td>6.30</td>
<td>0.29</td>
<td>&lt;0.01</td>
<td>0.08</td>
</tr>
<tr>
<td>Cladocera</td>
<td>1995</td>
<td>178</td>
<td>0.01- 5.15</td>
<td>30.9</td>
<td>0.17</td>
<td>0.20</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>152</td>
<td>0.03- 7.24</td>
<td>16.8</td>
<td>0.47</td>
<td>&lt;0.01</td>
<td>0.08</td>
</tr>
<tr>
<td>Daphnidae</td>
<td>1995</td>
<td>171</td>
<td>0.01- 5.15</td>
<td>25.8</td>
<td>0.04</td>
<td>0.79</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>152</td>
<td>0.05- 7.24</td>
<td>15.3</td>
<td>0.36</td>
<td>0.01</td>
<td>0.04</td>
</tr>
<tr>
<td>Bosminidae</td>
<td>1995</td>
<td>167</td>
<td>0.01- 5.15</td>
<td>1.84</td>
<td>0.36</td>
<td>&lt;0.01</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>144</td>
<td>0.03- 7.24</td>
<td>1.38</td>
<td>0.40</td>
<td>&lt;0.01</td>
<td>0.09</td>
</tr>
<tr>
<td>Sididae</td>
<td>1995</td>
<td>128</td>
<td>0.01- 3.60</td>
<td>2.69</td>
<td>0.55</td>
<td>&lt;0.01</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>108</td>
<td>0.05- 7.24</td>
<td>0.52</td>
<td>0.21</td>
<td>&lt;0.01</td>
<td>0.02</td>
</tr>
</tbody>
</table>

Table B.1: Results of fitting the model, zooplankton production = \( \alpha \) (phytoplankton biomass)\(^\beta\), to western Lake Erie data from 1995 and 1996. R indicates range of phytoplankton biomass (g m\(^{-3}\)) used in each regression. We considered p-values <0.05 to indicate that \( \beta \) significantly deviates from zero.
<table>
<thead>
<tr>
<th>Group</th>
<th>Year</th>
<th>n</th>
<th>R</th>
<th>α</th>
<th>β</th>
<th>p-value</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepoda</td>
<td>1995</td>
<td>191</td>
<td>0.2 - 750</td>
<td>0.16$^*$</td>
<td>1.03$^*$</td>
<td>&lt;0.01</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>187</td>
<td>1.0 - 600</td>
<td>0.32</td>
<td>0.86</td>
<td>&lt;0.01</td>
<td>0.86</td>
</tr>
<tr>
<td>Daphnidae</td>
<td>1995</td>
<td>172</td>
<td>0.3 - 900</td>
<td>0.35</td>
<td>1.07</td>
<td>&lt;0.01</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>175</td>
<td>0.4 - 1700</td>
<td>0.34</td>
<td>1.04</td>
<td>&lt;0.01</td>
<td>0.93</td>
</tr>
<tr>
<td>Bosminidae</td>
<td>1995</td>
<td>168</td>
<td>0.2 - 400</td>
<td>0.21</td>
<td>1.04</td>
<td>&lt;0.01</td>
<td>0.96</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>173</td>
<td>0.1 - 50</td>
<td>0.20</td>
<td>1.05</td>
<td>&lt;0.01</td>
<td>0.96</td>
</tr>
<tr>
<td>Sididae</td>
<td>1995</td>
<td>128</td>
<td>0.3 - 550</td>
<td>0.16$^*$</td>
<td>1.05</td>
<td>&lt;0.01</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>132</td>
<td>0.2 - 150</td>
<td>0.12</td>
<td>1.10</td>
<td>&lt;0.01</td>
<td>0.89</td>
</tr>
</tbody>
</table>

Table B.2: Results of fitting the model, production = $\alpha$(zooplankton biomass)$^\beta$, to western Lake Erie crustacean zooplankton data from 1995 and 1996. R indicates range of zooplankton biomass (mg m$^{-3}$) used in each regression. We considered p-values <0.05 to indicate that $\beta$ significantly deviates from zero. Note that $^*$ indicates significant difference (p<0.05) between 1995 and 1996 model parameters.
<table>
<thead>
<tr>
<th>Group</th>
<th>Year</th>
<th>n</th>
<th>range of $T_w$ ($^{\circ}$C)</th>
<th>a</th>
<th>g</th>
<th>$p$-values</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepoda</td>
<td>1995</td>
<td>191</td>
<td>10-28</td>
<td>0.04*</td>
<td>1.08*</td>
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Table B.3: Results of fitting the model, production/biomass = $\alpha(\gamma)^{T_w}$, to western Lake Erie crustacean zooplankton data from 1995 and 1996. I considered $p$-values <0.05 to indicate that $\gamma$ significantly deviates from one. Note that * indicates significant difference ($p<0.05$) between 1995 and 1996 model parameters.
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<th>Model 2</th>
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Table B.4: Results of comparing taxonomic groups' parameters from models: (1) production = α(zooplankton biomass)^β and (2) P:B = α(γ)^Tw. P-values <0.05 indicate statistically significant difference between compared taxa's α, β or γ.