Dreissenidae in Lake Ontario: Impact Assessment at the Whole Lake and Bay of Quinte Spatial Scales

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ABSTRACT. The total abundance in Lake Ontario of Dreissena polymorpha (Dreissenidae), the zebra mussel, and D. bugensis (Dreissenidae), the quagga mussel, was calculated by aggregating data from several surveys carried out in 1991 to 94. In 1993, there were between 3.0 × 10 and 8.7 × 1012 Dreissenidae mussels in Lake Ontario. A filtration model was constructed using depth-specific density estimates, a digital bathymetric map of the lake, and literature estimates of clearance rates for individual mussels. With reasonable estimates of both densities and filtration rates, the mean, area-weighted, turnover time of Lake Ontario water by dreissenid mussels was about 1 year. At the smaller spatial scale of the Bay of Quinte, the same model estimated turnover times of 0.05, 0.2, and 10 days for the lower, middle, and upper areas of the bay, respectively. Depth-specific secondary production estimates for dreissenids, combined with literature estimates of net primary production and energy transfer efficiencies, were incorporated into a food demand model that indicated about 1.25 gC/y mussel of food in Lake Ontario and a consumption efficiency of 50%. At the smaller spatial scale of the Bay of Quinte, the same model estimated one to two orders of magnitude less food per mussel and 62%, 130% and 115% consumption efficiency for the lower, middle and upper areas of the bay, respectively. Dreissenidae mussels may not have a huge impact on the Lake Ontario food web when considered at a whole-lake scale, but their potentially striking impact at the smaller spatial scale of embayments like the Bay of Quinte indicate that they may be locally important. When these effects are aggregated across several sub-systems, Dreissenidae mussels may have unpredictable, larger scale effects in the Lake Ontario ecosystem as a whole.

INDEX WORDS: Dreissenidae, zebra mussel, quagga mussel, density, whole-lake effects, scale-dependent effects, Lake Ontario, filtration model, food demand model.

INTRODUCTION

Two species of Dreissenidae mussel have invaded the Laurentian Great Lakes drainage basin. Zebra mussels (Dreissena polymorpha), first discovered in Lake St. Clair in 1988, were introduced in 1985 or 1986 (Hebert et al. 1989). They have since spread through the southern Great Lakes and several other basins and may eventually colonize most lakes and slow-flowing rivers of temperate North America (Strayer 1991). Quagga mussels (D. bugensis; Spidle et al. 1994) were discovered in 1991 (May and Marsden 1992) and have only recently been positively identified (Spidle et al. 1994). Currently, they occur from western Lake Erie through to Quebec City on the St. Lawrence River (Mills et al. 1993).

Parts of Lake Ontario were colonized by zebra and quagga mussels relatively early in their invasion, and there has been speculation about their whole-lake impact (e.g., Millard et al. 1996). Based on research in other large ecosystems (e.g., Lake St. Clair: Griffiths 1993; Lake Erie: MacIsaac et al. 1996; Hudson River: Strayer et al. 1996), the eco-
logical impact of Dreissenidae in Lake Ontario may be very significant and will be important to consider in developing lake management strategies (Millard et al. 1996). In spite of this, few data on dreissenid distribution, abundance, and secondary production in Lake Ontario have been reported. The goal of this study was to summarize the estimates of adult zebra and quagga mussel density and production in Lake Ontario in the early 1990s (1991 to 94), to use these data to estimate the number of dreissenid mussels in the entire lake, and infer from this their potential effect on the whole-lake ecosystem. To illustrate the variable effects of dreissenids with spatial scale, their influence on the Bay of Quinte ecosystem was also examined.

**METHODS**

**Abundance of Dreissenidae in Lake Ontario**

Adult Dreissenidae density data were compiled from field studies carried out in Lake Ontario from 1991 to 1994, inclusive (Table 1; Fig. 1). These studies included broad surveys of zoobenthos (WSA, BEAST) and large (OMNR) and small (CHASE) scale studies targeted specifically at Dreissenidae populations in Lake Ontario. Among and within the studies, there were several methods used to estimate densities. Particle sampling, where the number of mussels per unit of substrate surface area, the shape of the substrate particles, and the proportion of the bottom covered by the substrate are used to calculate the density of mussels per unit bottom area (Bailey et al. 1995), was used in the broad-scale OMNR study and the small-scale CHASE study. Core or air-life sampling from a given bottom area was used in the WSA and BEAST studies. In addition to particle sampling, visual estimates and quadrat harvesting by SCUBA were used in the OMNR study. Several sites were sampled by more than one method or in more than one year, allowing comparison of the estimates derived from different sampling techniques at the

<table>
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<th>Study Code; Author(s)</th>
<th>Year(s)</th>
<th>Estimation Technique(s)</th>
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<tr>
<td>BEAST; Reynoldson <em>et al.</em> (1995)</td>
<td>1991–93</td>
<td>sub-sampled box core</td>
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<td>CHASE; Chase (1998a)</td>
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**FIG. 1.** Locations in Lake Ontario of estimates of Dreissenidae mussel density in 1991 to 1994.
same place and time and among years at the same
place. All of the sampling programs were carried
out at least in the early to mid fall of the years sam-
ples. In the CHASE study, sampling of zebra mus-
sels at two Port Dalhousie sites to estimate sec-
ondary production was carried out repeatedly,
within and across years. Density data from that site
indicated that samples collected in the fall provide a
reasonable estimate of annual average density
(Chase and Bailey 1999a).

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Filtration Model
The potential of dreissenids in Lake Ontario to
alter food web dynamics through the removal of
phytoplankton and other suspended material was
assessed by estimating their filtering capacity in
comparison to the volume of lake water available
for filtration. The turnover time of the lake water
was estimated using (i) literature estimates of mus-
sel clearance rates in laboratory studies, (ii) depth-
specific mussel densities, and (iii) depth-specific
water volumes.

Whole-lake turnover time (T, the number of days
required for mussels to filter the water in Lake On-
tario) was estimated by an area-weighted average of
the s depth strata as:

\[ T = \sum_{i=1}^{s} p_i t_i, \]  

where \( p_i \) = proportion of total bottom area in stra-
tum \( i \) and \( t_i \) = turnover time for stratum \( i \) (days).

Turnover time for stratum \( i \), \( t_i \), was estimated by:

\[ t_i = \frac{v_i}{F_i}, \]

where \( v_i \) = volume of stratum \( i \) (L), and \( F_i \) = total
filtering capacity of mussels in stratum \( i \) (L/day).

The proportion of total bottom area in stratum \( i \),
\( p_i \), is:

\[ p_i = \frac{a_i}{\sum_{i=1}^{s} a_i} \]

where \( a_i \) = area of bottom in depth stratum \( i \) (m²).

The total filtering capacity of mussels in stratum
\( i \), was calculated as:

\[ F_i = X_i f_i, \]

where \( X_i \) = number of mussels in stratum \( i \) (mus-
sels) and \( f_i \) = filtering capacity of an average-sized
mussel (100 mL/hr/mussel).

The number of mussels in stratum \( i \) was esti-

\[ X_i = x_i a_i, \]  

where \( x_i \) = density of mussels in stratum \( i \) (mus-
sels/m²) and \( a_i \) = area of bottom in depth stratum
\( i \) (m²).

The density of dreissenid mussels in a given
depth stratum varies both spatially (e.g., among
substrate types, locations) and temporally (e.g.,
among seasons, day to day, year to year) within
years, along with temporal and spatial variation due
to the ongoing (in the early 1990s) invasion
process. Although density data from 189 sites in
Lake Ontario was assembled, coverage of the lake
both spatially and temporally was uneven (Fig. 1).
The available data allowed only crude estimates of
total numbers in the lake, but sensitivity analysis of
the lake-wide model showed that imprecision in the
nearshore density estimates, where mussel densities
are highest and most variable, did not markedly
change predictions of the model for the whole lake.

Area and volume data for the filtration model
were obtained from a digital bathymetric map of
Lake Ontario partitioned into 1-m depth intervals.
The value used for filtering capacity of an individ-
ual mussel (100 mL/h) was based on laboratory
measurements of Kryger and Riisgård (1988) and
their application to populations of settled mussels in
Lake Erie (MacIsaac et al. 1992). These determina-
tions are among the highest of recently published
estimates of dreissenid clearance rates (Kryger and
Riisgård 1988, Sprung and Rose 1988, Reeders
et al. 1989, MacIsaac et al. 1992, Bunt et al. 1993,
Roditi et al. 1996).

Food Demand Model
In addition to mussel abundance and filtering ca-
pacity, the impact of dreissenids on the Lake On-
tario ecosystem depends on secondary production
of the dreissenids in relation to the food supply
available. Net primary production (NPP) per mussel
and consumption efficiency of dreissenids was esti-
mated from (i) literature estimates of phytoplankton
production in Lake Ontario (Millard et al. 1996),
(ii) depth-specific estimates of dreissenid secondary
production (Chase and Bailey 1999b), and (iii) lit-
erature estimates of the efficiency of energy assimilation and use by the mussels (Stoeckmann and Garton 1997).

NPP per mussel, $Y$ (gC/y/mussel), for the whole lake was estimated by an area-weighted average of the $s$ depth strata as:

$$Y = \sum_{i=1}^{s} p_i y_i$$  \hspace{1cm} (6)

where $p_i =$ proportion of total bottom area in stratum $i$ \[3\] and $y_i =$ NPP per mussel in stratum $i$ (gC/y/mussel).

NPP per mussel in stratum $i$, $y_i$, was estimated by:

$$y_i = \frac{NPP}{x_i}$$  \hspace{1cm} (7)

where $NPP =$ net primary production (140 gC/m$^2$/y; Millard et al. 1996), and $x_i =$ density of mussels in stratum $i$ (mussels/m$^2$).

Whole-lake consumption efficiency ($CE$) was calculated as an area-weighted average of depth-specific consumption efficiencies:

$$CE = \sum_{i=1}^{s} p_i ce_i$$  \hspace{1cm} (8)

where $p_i =$ proportion of total bottom area in stratum $i$ \[3\] and $ce_i =$ consumption efficiency in stratum $i$.

Consumption efficiency in stratum $i$, $ce_i$, was estimated by:

$$ce_i = \left( \frac{SP_i \ast \frac{1}{pe} \ast \frac{1}{ae}}{NPP} \right)$$  \hspace{1cm} (9)

where $SP_i =$ secondary production of dreissenids in stratum $i$, $pe =$ dreissenid production efficiency (net production/gross production = 5%; Stoeckmann and Garton 1997), $ae =$ dreissenid assimilation efficiency (gross production/energy ingested = 72%) and $NPP =$ net primary production (140 gC/m$^2$/y; Millard et al. 1996). The numerator of this equation is the amount of food dreissenids require to generate the observed secondary production, and the denominator is the amount of food available.

The estimates of secondary production of dreissenids were from cohort production analysis of repeated sampling of these populations over several years. For the models in this study, dreissenid production estimates of 5 gC/m$^2$/y (1 to 5 m depth), 20 gC/m$^2$/y (6 to 15 m depth), and 1 gC/m$^2$/y (> 15 m depth were used).

**Modeling at the Bay of Quinte Spatial Scale**

After running both the filtration and food demand models for all of Lake Ontario, they were both re-run at the smaller spatial scale of the Bay of Quinte using bathymetric data from Minns et al. (1986) and dreissenid abundance data only from this area of the lake.

**RESULTS**

**Abundance of Dreissenidae in Lake Ontario**

Of the several sampling techniques used—(i) direct sampling of particles by hand, core or air-life, followed by mussel enumeration in the laboratory, (ii) visual estimates by divers of mussel numbers, and (iii) counts of mussels collected within quadrat frames by divers—sampling directly from particles required the most field and laboratory labor and should be the least biased. The OMNR surveys in 1991, 1993, and 1994 allowed some cross comparisons of these three techniques applied at the same sites in the same year. There was a significant correlation between particle and diver counts in 1991 ($r = 0.35$, $n = 39$, $p = 0.03$) and 1993 ($r = 0.50$, $n = 53$, $p < 0.001$), and for particle and frame counts in 1993 ($r = 0.63$, $n = 16$, $p = 0.009$), but not for diver and frame counts in 1993 ($r = 0.10$, $n = 16$, $p = 0.72$) or for particle and diver counts in 1994 ($r = 0.29$, $n = 25$, $p = 0.164$). Although there were some statistically significant correlations, no two methods were correlated enough to imply that the methods were providing redundant information (Fig. 2). Dreissenid density estimates were consistently highest using the particle technique, for which mussels were counted in the laboratory instead of in the field, as in the diver and frame techniques.

Throughout the sampling period of 1991 to 94, the highest densities of dreissenids were at sites in the western end of the lake and the Bay of Quinte region. In 1991, only zebra mussels were detected. By 1993, quagga mussels were collected from most sites, in numbers roughly an order of magnitude less than those of zebra mussels. The greatest mussel densities were found at intermediate sampling
Bailey et al.

depths (Fig. 3). In 1991 and 1993, sites 6 to 10 m deep generally had more mussels than those 1 to 5 or 11 to 25 m deep. Single particle samples from 30 and 74 m in 1993 both yielded no mussels. In 1994 samples from the shallower and more protected Bay of Quinte, dreissenid densities were greater in sites 1 to 5 m deep than those 6 to 15 m deep (but greater at 3 than at 2 m). Depth trends for zebra and quagga mussels appeared to differ. Whereas the numerically dominant zebra mussels were the most dense at depths of less than 10 m, quagga mussel densities were greatest the 11 to 15 meter sites (Fig. 3). Dreissenid densities increased between 1991 and 1993 in most of the 22 sites that were sampled in both of these years (Fig. 4). The median increase in individuals over this time period was 2,215 mussels/m² by particle count sampling and 1,660 mussels/m² by diver count sampling.

Total dreissenid abundance in Lake Ontario was estimated using density data from 1991 and 1993, the 2 years in which sites were sampled across a wide geographical area. Average densities were calculated for each 5 m depth stratum, multiplied by the corresponding area of lake bottom, and summed. Sampling technique and averaging method strongly affected the abundance estimates, which ranged over two orders of magnitude: $2.3 \times 10^{10}$ to $2.2 \times 10^{12}$ mussels in 1991, and $3.0 \times 10^{10}$ to $8.7 \times 10^{12}$ mussels in 1993. With the exception

**FIG. 2. Correlations between the density of Dreissenidae (mussels per m²) estimated in the same year and at the same site in Lake Ontario with two different techniques.**
of derived mean and median densities from the
diver counts, all estimation procedures indicated a
population increase from 1991 to 1993.

Impact of Dreissenidae on the
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**Filtration Model**

Using a liberal estimate of dreissenid densities in
Lake Ontario (1–15 m: 3,000 mussels/m\(^2\), >15 m:
100 mussels/m\(^2\)) from the studies assembled, the
whole-lake, area-weighted mean turnover time was
calculated to be 371 days (about 1 year). Turnover
times for individual depth strata ranged from 2 days
or less in shallow (< 15 m) water to over 2 years in
deep (> 200 m) water. If the depth-specific density
of mussels used in the model was varied, whole-
lake turnover time was related only to densities at
depths > 15 m; those at 1 to 15 m had virtually no
influence on turnover time (Fig. 5).
Food Demand Model

For Lake Ontario dreissenids at the same densities as those used in the Filtration Model (1–15 m: 3,000 mussels/m², > 15 m: 100 mussels/m²), the area-weighted mean net primary production per mussel was 1.25 gC/y/mussel. At depths < 20 m, estimated primary production per mussel was much less: 0.05 gC/y/mussel. Using liberal values of estimated mussel production from Bailey and Chase (1998b; 1–5 m: 5 gC/y/m²; 6–15 m: 20 gC/y/m²; > 15 m: 1 gC/y/m²), lake-wide consumption efficiency was about 50%. In other words, about half of all net primary production is being consumed by dreissenids. Depth-specific consumption efficiencies were 99% for 1 to 5 m, 400% for 6 to 15 m, and 20% for >15 m. Mean consumption efficiency was directly related to mussel production at depths both above and below 15 m (Fig. 6). Clearly, horizontal transport of food, although not part of these simple models, is at least partially responsible for the variability in consumption efficiency among depth strata in the lake.

Bay of Quinte Impact Assessment

Densities of dreissenids in the Bay of Quinte were substantially higher than those in the rest of Lake Ontario. As well, exchange of water among regions of the Z-shaped bay and between the bay and the main basin of Lake Ontario is restricted, especially for the upper regions and at shallow depths (Minns et al. 1986). Therefore, to more realistically assess impacts of dreissenids specifically to the Bay of Quinte water column above filtration and production models were applied separately to each of the upper, middle, and lower sections of the bay.

For the filtration model, densities of 65,000, 10,000, and 500 mussels/m² were used for the 1 to 5 m, 6 to 10 m, and > 15 m depth strata, respectively. These densities were similar to arithmetic mean densities observed at sites in the Bay of Quinte. For the food demand model, the value used for phytoplankton production was 250 gC/y/m² (Millard and Johnson 1986). Dreissenid production was set as in the whole-lake model at 5, 20, and 1 gC/y/m² for the 1–5 m, 6–10 m and > 15 m depth strata, respectively.

Turnover times due to dreissenid filtration in the lower, middle, and upper sections of the Bay of Quinte were estimated to be 10, 0.2, and 0.05 days, respectively, or three to five orders of magnitude lower than the estimated turnover time for the whole lake. Primary production per mussel was also much lower (by two to three orders of magnitude) in the Bay of Quinte than in the lake as a whole: 0.34, 0.03, and 0.01 gC/y/mussel for the lower, middle, and upper sections of the bay, while consumption efficiencies were 63%, 130%, and 115% for the lower, middle, and upper Bay of Quinte sections, respectively.

DISCUSSION

Abundance of Dreissenidae in Lake Ontario

In spite of the large amount of information assembled for this study, representing considerable field and laboratory efforts, the available data on dreissenid densities in 1991 to 1994 do not allow a precise estimate of the number of zebra and quagga mussels in Lake Ontario. Estimated whole-lake abundance for 1993 ranged from $3.0 \times 10^{10}$ to $8.7 \times 10^{12}$ individuals, depending on the sampling technique and averaging method used. Perhaps the most reliable estimates are those from the particle counts and arithmetic mean averaging, which resulted in the largest estimate.

Mussels were distributed very heterogeneously both within and among sampling sites, likely because of the spatial distribution of suitable (hard) substrate. As few samples were obtained from depths > 30 m deep (which comprises 78% of the total lake area), and no samples were included from
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along the U.S. shoreline, some caution must be associated with these numbers. Although profundal substrates tend to be fine sediments and thus not favorable for dreissenid colonization, clumps of mussels have been reported on soft substrate in western Lake Erie (Klerks et al. 1996; H. MacIsaac pers. comm.). If the same situation occurred in Lake Ontario, the above abundances estimates would be too low.

Impact of Dreissenidae on the Lake Ontario Ecosystem

The models presented here for assessing impacts of dreissenid filtering and production on suspended material concentration and phytoplankton production in Lake Ontario used maximum estimated densities of mussels and liberal assumptions for extrapolating processes involving individuals and small scales to populations and larger scales. Despite this liberal approach, on a lakewide basis the extant mussels do not appear capable of substantially altering water transparency. Turnover time, area-weighted for the whole lake, was about 1 year. In the shallowest depths (1–15 m), where mussel densities are the greatest, estimated turnover times were 2 days or less. Here, it is most likely that suspended material could be significantly reduced (under the simple but unrealistic assumption of no horizontal water exchange between depth layers). But these depths correspond to only 11% of the total lake bottom, with similar levels of planktonic primary production to offshore areas (Millard et al. 1996). The calculated whole-lake turnover time was strongly influenced by the mussel densities in the offshore regions, which available data indicate are very low. If it were even more simply assumed that complete instantaneous lake circulation existed, and turnover time was estimated as lake volume divided by total mussel filtering capacity, it would still take about 90 days for the mussels to filter all of the water in Lake Ontario.

The estimated consumption efficiencies, both depth specific and for the whole lake, suggest a potentially greater influence of dreissenids on water column trophic dynamics than do the filtration model or the phytoplankton production per mussel estimates. The lakewide consumption efficiency estimate implies that about one half of the total phytoplankton productivity is diverted into dreissenid production, a significant amount considering that less than 10 years ago this diversion did not exist. In the 6 to 15 m stratum, the estimated consumption efficiency was almost 400%, which indicates the obvious potential for depletion of the local food supply. On the other hand, the consumption efficiency calculations are highly dependent on the assumed dreissenid production per m². The values used (5, 20, and 1 gC/m²/y for depths 1–5, 6–15, and > 15 m, respectively) are almost certainly maximum secondary production rates for nearshore and overestimates for the offshore (> 15 m) areas.

In the Bay of Quinte, the situation appears quite different. In all sections of the bay, and especially the comparatively shallow upper section, estimated turnover times (0.01 to 10 days) suggest the potential for significant removal of suspended matter by dreissenids. The amount of food available per mussel was orders of magnitude smaller than in Lake Ontario as a whole, and consumption efficiency was estimated as well over 100% for the middle and upper parts of the bay.

These conclusions about the whole-lake impact of Dreissenidae on Lake Ontario must take such smaller-scale effects into account for two reasons. First of all, even if on a lake-wide basis the effect of dreissenids, through either their filtering or food consumption, is modest, relatively isolated embayments may be drastically changed by their presence. Secondly, and less predictably, such small-scale impacts may aggregate to greater effects on the whole-lake ecosystem than the sum of their parts. Lake Ontario as a whole may change in unpredictable ways because of the presence of Dreissenidae in the food web and its marked impact at the spatial scale of areas like the Bay of Quinte. Feedbacks at this scale to energy flow and nutrient cycling in the lake as a whole are impossible to quantify with simple models like those presented here.

Finally, more data needs to be collected in three areas, so that the longer-term dynamics of the Lake Ontario ecosystem can be better predicted. First, abundance of Dreissenidae, particularly in deeper water, needs to be more precisely estimated. If, as in the western basin of Lake Erie (H. MacIsaac, pers. comm.), clumps of mussels form on soft substrata, this could substantially alter the assessment of the lake-wide impact of dreissenids in Lake Ontario. Second, the food demand of both dreissenid mussels and other, potentially competing organisms (daphniid crustaceans) needs to be more precisely estimated so that the relative importance of dreissenids and other Lake Ontario fauna can be assessed. Finally, spatially explicit estimates of net primary production, to augment the work done by Millard et al. (1996), would better characterize the
lower end of the Lake Ontario food web and allow a better prediction of the long-term effects of dreissenid colonization and other changes in the lake.

**Modeling Limitations**

There is considerable danger in using these small-scale, point samples and parameter estimates to inform a larger scale problem (Schneider 1994). Lake Ontario has a bottom area of about 19,000 km², and the model of density and secondary production variation in dreissenids is largely built on data from a total of 100 to 500 m² of that bottom, collected over a 4-year period. It is risky to base a whole-lake model on a sampling coverage of about 0.000002%, since larger scale processes including, but not limited to, veliger transport and distribution, intra-specific competition, and vertical and horizontal water movement will no doubt influence large-scale effects of the mussels.

With respect to individual mussel processes, the filtering rates were derived from laboratory studies of individuals or small groups of mussels (Kryger and Riisgård 1988). Extrapolation of these processes to real, three-dimensional populations of 1,000s of mussels is also risky. It is expected that this extrapolation would provide a liberal estimate of lakewide process rates (i.e., mussels in a real patch at the bottom of Lake Ontario don’t filter as fast as they do in a laboratory aquarium). Millard et al. (1996) are also clear about the limitations of their primary production estimates for Lake Ontario. Here this simple extrapolation and assessment of dreissenid effects on the Lake Ontario ecosystem is presented as a point of departure for more refined and precise models rather than presuming it to be a finished product.

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