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 $3.0 \times 10^9$ and $8.7 \times 10^{12}$ 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 g Cy 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. 1992; 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

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**FIG. 1.** Locations in Lake Ontario of estimates of Dreissenidae mussel density in 1991 to 1994.
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 Lake Ontario Ecosystem

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).
Effect of variation in depth-specific secondary production of Dreissenidae on their consumption efficiency in Lake Ontario as estimated by the food demand model. Contour lines show equal consumption efficiency with different combinations of production of dreissenid mussels in shallow (0–15 m) and deep (> 15 m) water.

Food Demand Model

For Lake Ontario dreissenids at the same densities as those used in the Filtration Model (1–5 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 the 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 means 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...
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/yr 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 substrate, 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
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 dreissenid samples 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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REFERENCES


May, B., and Marsden, J.E. 1992. Genetic identification and implications of another invasive species of dreis-
Dreissenidae in Lake Ontario


Reynoldson, T.B., Bailey, R.C., Day, K.E., and Norris, R.H. 1995. Biological guidelines for freshwater sedi-


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