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PREFACE

Dreissena polymorpha in the Saginaw Bay, Lake Huron Ecosystem: Overview and Perspective

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After the zebra mussel, *Dreissena polymorpha*, was first discovered in Lake St. Clair in 1988 and rapidly spread throughout the Great Lakes, broad ecological changes became apparent in regions where this species was most abundant. Previous investigations documented dramatic increases in water clarity (Hebert *et al.* 1991, Marsden *et al.* 1993, Leach 1993), declines in chlorophyll and phytoplankton abundances (Leach 1993, Nicholls and Hopkins 1993, Holland 1993), and changes in benthic invertebrate communities (Griffiths 1993, Dermott *et al.* 1993, Stewart and Haynes 1994). These studies were conducted in various regions and defined impacts on a specific ecosystem component. Taken together, results indicate a major shift in energy flow patterns from the pelagic to the benthic region. Such a shift is so fundamental that every component of the food web from bacteria to fish would likely be affected either directly or indirectly. Thus, to truly understand the significance of shifts in energy flow patterns, impact assessments should be as holistic as possible within a given ecosystem. Despite the magnitude of observed impacts, however, establishing cause-effect relationships at the ecosystem-level is not an easy task. Not all changes occur at the same rate, and natural variation, along with man-induced influences such as nutrient abatement programs, confound interpretations of any mussel-induced impacts. For this reason, ecosystem-level impacts can best be examined, interpreted, and certainly modeled, by integrating studies of both ecosystem structure and function within a specific, well-defined region.

Soon after *Dreissena* was first discovered in the Great Lakes, we identified Saginaw Bay as an ideal location to assess ecosystem impacts. The bay had all the general characteristics defined by Officer *et al.* (1982) as potentially important in delineating impacts of a benthic filter-feeding population. First, the inner bay is shallow (mean depth = 5 m) and well-mixed, maximizing the ratio of bottom area to water volume and minimizing vertical gradients. Second, the inner bay is a partially enclosed region of substantial size with a hydraulic retention time of about 120 days (entire bay 60 days; Bratzel *et al.* 1977); this minimizes the significance of hydraulic exchange as a confounding variable. Third, nutrient supplies are adequate to support a high phytoplankton population; values of primary production and phytoplankton biomass were among the highest recorded in the Great Lakes (Vollenweider *et al.* 1974).

In addition, other, more specific considerations led to the decision to focus our efforts in Saginaw Bay: 1) at the time, *Dreissena* was not yet established in the bay, thus baseline conditions immediately prior to the mussels' invasion could be documented; further, previous surveys of water

quality parameters in 1974-80 (Smith *et al.* 1977, Bierman *et al.* 1984) could provide a longer-term perspective to assess potential changes; 2) the bay had extensive areas of hard bottom, along with ideal temperature and food regimes, and thus large populations of mussels were expected to develop; 3) there existed an important commerical and sport fishery that could be affected; 4) with a natural gradient between the eutrophic inner bay and the more oligotrophic outer bay, the bay provided an opportunity to assess impacts over a wide range of trophic conditions; and 5) the bay is an Area of Concern as designated by the International Joint Commission and the subject of remedial action by the State of Michigan. After a decade of little or no monitoring in the bay, initial surveys would provide information on the bay's response to continued efforts to improve water quality.

In 1990, we initiated a small study in Saginaw Bay in which a limited number of variables (chlorophyll, primary production, phytoplankton, zooplankton, and benthos) were measured three times a year at 13 sites. The study was greatly expanded beginning in 1991 when funds were appropriated by Congress as part of the Nonindigenous Aquatic Nuisance Prevention and Control Act. Because of the great interest in Saginaw Bay, other agencies (U.S. Environmental Protection Agency, Michigan Department of Natural Resources, Sea Grant) became participants as the study expanded to examine more variables over larger temporal and spatial scales.

Papers in this Special Section present results of studies conducted mainly during the early years of *Dreissena*'s invasion into Saginaw Bay (1990–93). The papers summarize data collected in the bay over the long term (months, years), and also data derived from experimental manipulations over the short term (hours, days). The former document broad temporal and spatial changes in water quality parameters (Fahnenstiel *et al.* 1995a), primary production (Fahnenstiel *et al.* 1995b), nutrients (Johengen *et al.* 1995), and submersed macrophytes/benthic algae (Skubinna *et al.* 1995, Lowe and Pillsbury 1995), while the latter determine impacts of *Dreissena* on planktonic bacteria (Cotner *et al.* 1995), protozoa (Lavrentyev *et al.* 1995), and nutrient dynamics (Gardner *et al.* 1995, Heath *et al.* 1995). Other papers examine rate processes to assess the relative importance of mussel filtration (Fanslow *et al.* 1995) and zooplankton grazing (Bridgeman *et al.* 1995) in effecting changes ob-

served over the study period. Interpretations of mussel impacts are dependent upon estimates of population standing stocks, which were provided by Nalepa *et al.* (1995).

The papers contained herein illustrate the dramatic and immediate impact *Dreissena* can have on a given ecosystem. Changes in water quality parameters were apparent in Saginaw Bay soon after the inital population explosion of *Dreissena* in summer 1991. By fall 1991 and through 1992 and 1993, chlorophyll concentrations in the inner bay declined by 59%, total phosphorus declined by 42%, and water transparency increased by 60% (Fahnenstiel *et al.* 1995a). Similar declines were observed in particulate nutrients such as particulate organic carbon, particulate phosphorus, and particulate silica (Johengen *et al.* 1995). To put these changes into a long-term perspective, declines in chlorophyll immediately after the *Dreissena* infestation were similar to, or greater than, declines noted immediately after phosphorus control measures were implemented in the mid-1970s (Fahnenstiel *et al.* 1995a). Thus, measures of water quality in Saginaw Bay show three distinct phases over the past 20 years: pre-phosphorus control (1974–75), post-phosphorus control (1979–90), and post-*Dreissena* (1992–93). Trends in phosphorus loading into the bay between 1979 and 1992 were not evident and were, therefore, not a factor in the observed water quality changes.

Because of a decline in phytoplankton standing stocks (as measured by chlorophyll), phytoplankton production decreased by 38% in the inner bay after mussel colonization (Fahnenstiel *et al.* 1995b). On the other hand, primary production in the benthic region increased, as evidenced by an increase in the areal extent of submersed macrophytes (Skubinna *et al.* 1995), and an increase in benthic algal biomass and productivity (Lowe and Pillsbury 1995). Increased benthic productivity was most likely a result of increased light penetration to the bottom (Fahnenstiel *et al.* 1995b). When existing standing stocks and measures of phytoplankton growth rates, *Dreissena* filtration rates, and zooplankton grazing are compared, observed shifts in productivity can only be attributed to the filtering activities of the mussel population (Fahnenstiel *et al.* 1995b). Overall, it does not appear *Dreissena* altered the trophic state of the Saginaw Bay system, but rather altered the spatial partitioning of resources and productivity (Fahnenstiel *et al.* 1995a, b)

Because rate processes of most components of

the planktonic food web (nutrients, bacteria, protozoa, phytoplankton) occur over very short time scales, studies to examine changes in these rates are useful in interpreting trends in standing stocks and composition of the plankton community over the long term. Also, interactions between lower food web components are potentially complex (see Fig. 1 in Gardner *et al.* 1995) and often best examined under controlled conditions. Results of short-term bottle and mesocosm experiments showed that *Dreissena* can not only affect food web components directly by selective removal, but also indirectly by nutrient excretion (Cotner *et al.* 1995, Gardner *et al.* 1995, Heath *et al.* 1995). For example, in mesocosm experiments, *Dreissena* decreased standing stocks of phytoplankton, but increased growth rates of phytoplankton that remained (Heath *et al.* 1995). Excretion of remineralized nutrients (phosphorus) by *Dreissena* stimulated phytoplankton growth in a phosphorus-limited system. Similar changes were observed in the inner bay over the long term; chlorophyll concentrations were lower in 1992 and 1993 compared to 1991, but growth rates of phytoplankton increased (Fahnenstiel *et al.* 1995a; Fahnenstiel unpublished data). In the mesocosm experiments, soluble reactive phosphorus initially increased because of mussel excretion, but then declined with increased phytoplankton growth. Similarly, values of soluble reactive phosphorus in the inner bay declined after *Dreissena* became established (Johengen *et al.* 1995). Short-term experiments further indicated that *Dreissena* filtration and/or nutrient excretion can alter phytoplankton composition. Despite declines in other phytoplankton groups in treatments with *Dreissena*, biovolumes and abundances of cyanophytes were unchanged over the experimental period (Heath *et al.* 1995, Lavrentyev *et al.* 1995). Thus, *Dreissena* may increase the relative abundance of cyanophytes and even contribute to blooms. These results are provocative and contrast to the findings of others. For example, in a study of the effect of *Dreissena* on phytoplankton in Lake Erie, Nicholls and Hopkins (1993) reported *Dreissena* affected all phytoplankton groups equally, including cyanophytes. Certainly more research is needed on the possible role of *Dreissena* in causing changes in phytoplankton composition.

There are few studies in fresh water that document ecosystem-level changes resulting from the introduction of a benthic suspension feeder. In the tidal freshwater Potomac, the establishment of the

asiatic clam, *Corbicula fluminata*, led to a 3-fold increase in water clarity, a 40–65 % decline in chlorophyll, and an increase in submersed aquatic macrophytes in a section of the river where clams were most abundant (Cohen *et al.* 1984, Phelps 1994). Clams theoretically filtered the river section in 3-4 days compared to 33 days for zooplankton. In 2 years of study in Saginaw Bay, *Dreissena* filtered the inner bay in 0.8 and 4 days (Fanslow *et al.* 1995) compared to a maximum of 17 and 37 days for zooplankton (Bridgeman *et al.* 1995). Thus, our findings in Saginaw Bay are remarkably similar to those in the Potomac. In the Potomac, the clam population declined dramatically 8 years after reaching a peak. Subsequently, water clarity declined, submersed aquatic vegetation declined, and cyanophyte blooms once again became evident (Phelps 1994).

Given findings in Saginaw Bay, the establishment of *Dreissena* has long-term implications when defining ecosystem response to management actions. For one, eutrophication models that link nutrient loadings and pelagic measures of water quality are no longer valid in areas with large populations of *Dreissena*. The Saginaw Bay ecosystem has been fundamentally altered, shifting from a system where productivity is focused in the pelagic region to a system where benthic productivity is also important. Previous eutrophication and water quality models were strictly based on a pelagic system, with phytoplankton the dominant primary producers and crustacean zooplankton the dominant herbivores (DiToro and Matystik 1980, Bierman *et al.* 1984). Simple re-paramaterization of existing mathematical models may not be adequate to describe the response of this altered system to management actions. For example, changes in nutrient loadings may now be more reflected in corresponding changes in metaphytonic and benthic algae, and not phytoplankton. Many metaphytonic and benthic algae belong to the order Zgynematales, an algal group that is extremely diverse and for which little information exists in the Great Lakes. Moreover, increases in primary production due to increased nutrient loadings may now be more reflected in first-order shifts in populations of benthic-dwelling decapods rather than crustacean zooplankton. The internal cycling of nutrient inputs also needs to be reconsidered. In Saginaw Bay, a phosphorus budget indicated standing stocks of *Dreissena* were a significant sink for phosphorus, accounting for 13–200% of the annual phosphorus pool in the water

column in the inner bay, and a maximum of 56% of the total phosphorus load (Johengen *et al.* 1995). The long-term fate of phosphorus sedimented via feces and pseudofeces is still an unknown.

Future eutrophication and ecosystem models will likely be very different from past models, with new relationships and energy pathways identified. Assumptions will need to be validated with experimental data, and predictions will need to be calibrated and verified against long-term data sets. In addition, other management tools to understand and assess the state of water quality, fisheries, toxic contaminants, etc. will also need to be re-evaluated. For example, the abundance and diversity of benthic invertebrates have often been used as an indicator of water quality in the Great Lakes. With the establishment of large populations of *Dreissena*, we can no longer assume that changes in abundance and composition of the benthic community reflect changes in water quality. *Dreissena* has altered the abundance and composition of benthic invertebrates in Saginaw Bay (Nalepa unpublished data), but has not altered the bay's trophic state (Fahnenstiel *et al.* 1995b). Not only are shallow regions with large *Dreissena* populations impacted, but any system which receives a large supply of its chemical loading (nutrients, toxic contaminants, etc.) from a *Dreissena*-impacted region (such as tributaries, bays, nearshore zone) will likely also be impacted.

One of the key issues that needs to be resolved is the extent by which *Dreissena* changes the stability and predictability of the ecosystem. In the past, most changes in ecosystem components have permeated through the top (fisheries) or bottom (nutrients, toxic contaminants) of the food web. The introduction of a non-discriminate, benthic filter-feeder in the "middle" of the food web in the Great Lakes adds another controlling variable. In addition, not only does the mussel population create instability by altering normal energy pathways, but populations in turn readily respond to induced changes (Nalepa *et al.* 1995). Models of estuarine systems have clearly established suspension-feeders that form pseudofeces as the most important determinant of stability in the lower food web (Cloern 1982, Officer *et al.* 1982, Herman and Scholten 1990, Rodhouse and Roden 1987). In one carbon-flow model, suspension feeders contributed to functional stability of the ecosystem by exerting continuous pressure on phytoplankton populations, but in so doing, greatly increased the vulnerability of the system to nutrient loadings (Herman and

Scholten 1990). When biomass of suspension feeders was at equilibrium, an increase in nutrient loading had little impact on phytoplankton biomass; however, with the same nutrient increase, a small decrease in suspension-feeder biomass led to drastic increases in phytoplankton biomass. In Saginaw Bay, a 10-fold decline in *Dreissena* biomass between 1992 and 1993 had little impact on water quality parameters (Fahnenstiel *et al.* 1995a). Yet even with this biomass decline in 1993, the population could still theoretically filter the entire volume of the inner bay in 4 days (Fanslow *et al.* 1995). Given *Dreissena* standing stocks in Saginaw Bay have fluctuated and may not yet be at equilibrium (Nalepa *et al.* 1995), relationships between *Dreissena* populations and water quality parameters may not be fully understood until more yearly data are available.

Hopefully, results from this Special Section will be useful for assessing the Great Lakes system in the post-*Dreissena* era. Monitoring of water quality parameters, *Dreissena* standing stocks, and food web components in Saginaw Bay has continued through 1995. In future papers, we will focus on trends in the abundance and composition of phytoplankton, zooplankton, and benthos. Other important topics being examined are the role of *Dreissena* in sediment resuspension, and interactions between *Dreissena* filtration/rejection activities and cyanophyte blooms.

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REFERENCES

Bierman, V. J., Dolan, D. M., and Kasprzyk, R. 1984. Retrospective analysis of the response of Saginaw Bay, Lake Huron, to reductions in phosphorus loadings. *Environ. Sci. Technol.* 18:23–31.

Bratzel, M. P., Thompson, M. E., and Bowden, R. J. (eds.) . 1977. *The Water of Lake Huron and Lake*

Superior, Vol. II (Part A). Lake Huron, Georgian Bay, and the North Channel. Report to the International Joint Commission by the Upper Great Lakes Reference Group, Windsor, Ontario.

Bridgeman, T. B., Fahnenstiel, G. L., Lang, G. A., and Nalepa, T. F. 1995. The relative importance of zooplankton grazing during the zebra mussel (*Dreissena polymorpha*) colonization of Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21:567–573.

Cloern, J.E. 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.* 9:191–202.

Cohen, R.R.H., Dresler, P.V., Philips, E.J.P., and Cory, R.L. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol. Oceanogr.* 29: 170–180.

Cotner, J. B., Gardner, W. S., Johnson, J. R., Sada, R. H., Cavaletto, J. F. , and Heath, R. T. 1995. Effects of zebra mussels (*Dreissena polymorpha*) on bacterioplankton: evidence for both size-selective consumption and growth stimulation. *J. Great Lakes Res.* 21:517–528.

Dermott, R., Mitchell, J., Murray, I., and Fear, E. 1993. Biomass and production of zebra mussels (*Dreissena polymorpha*) in shallow waters of Northeastern Lake Erie. In *Zebra Mussels: Biology, Impacts, and Control*, eds. T. F. Nalepa and D. W. Schloesser, pp. 399–413. Boca Raton, FL: Lewis Publishers/CRC Press.

DiToro, D. M., and W. F. Matystik. 1980. *Mathematical models of water quality in large lakes. Part 1: Lake Huron and Saginaw Bay.* EPA–600/3-80-056.

Fahnenstiel, G. L., Lang, G. A., Nalepa, T. F., and Johengen, T. H. 1995a. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21:435–448.

_____, Bridgeman, T. B., Lang, G. A., McCormick, M. J., and Nalepa, T. F. 1995b. Phytoplankton productivity in Saginaw Bay, Lake Huron: effects of zebra mussel (*Dreissena polymorpha*) colonization. *J. Great Lakes Res.* 21:465–475.

Fanslow, D. L., Nalepa, T. F., and Lang, G. A. 1995. Filtration rates of zebra mussels (*Dreissena polymorpha*) on natural seston from Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21:489–500.

Gardner, W. S., Cavaletto, J. F., Johengen, T. H., Johnson, J. R., Heath, R. T., and Cotner, J. B. 1995. Effects of the zebra mussel (*Dreissena polymorpha*) on nitrogen dynamics in Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21:529–544.

Griffiths, R.W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair. In *Zebra Mussels: Biology, Impacts, and Control*, eds. T. F. Nalepa and D. W. Schloesser, pp. 415–437. Boca Raton, FL: Lewis Publishers/CRC Press.

Heath, R. T., Fahnenstiel, G. L., Gardner, W. S., Cavaletto, J. F., and Hwang, S. J. 1995. Ecosystem-level effects of zebra mussels (*Dreissena polymorpha*): an enclosure experiment in Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21:501–516.

Hebert, P. D. N., Wilson, C. C., Murdoch, M. H., and Lazar, R. 1991. Demography and ecological impacts of the invading mollusc, *Dreissena polymorpha. Can. J. Zool.* 69:405–409.

Herman, P.M.J., and Scholten, H. 1990. Can suspension-feeders stabilise estuarine ecosystems? In *Trophic Relationships in the Marine Environment*, eds. M. Barnes and R.N. Gibson, pp. 104–116. Aberdeen, UK: Aberdeen University Press.

Holland, R. E. 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, Western Lake Erie since the establishment of the zebra mussel. *J. Great Lakes Res.* 19:617–624.

Johengen, T. H., Nalepa, T. F., Fahnenstiel, G. L., and Goudy, G. 1995. Nutrient changes in Saginaw Bay, Lake Huron, after the establishment of the zebra mussel (*Dreissena polymorpha*). *J. Great Lakes Res.* 21:449–464.

Lavrentyev, P.J., Gardner, W.S., Cavaletto, J.F., and Beaver, J.R. 1995. Effects of the zebra mussel (*Dreissena polymorpha* Pallas) on protozoa and phytoplankton from Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21:545–557.

Leach, J. H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In *Zebra Mussels: Biology, Impacts, and Control*, eds. T. F. Nalepa and D. W. Schloesser, pp. 381–397. Boca Raton, FL : Lewis Publishers/CRC Press.

Lowe, R.L., and Pillsbury, R.W. 1995. Shifts in benthic algal community structure and function following the appearance of zebra mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. *J.Great Lakes Res.* 21:558–566.

Marsden, J. E., Trudeau, N., and Keniry, T. 1993. *Zebra mussel study of Lake Michigan.* Aquatic Ecology Technical Report 93/14, Illinois Natural History Survey.

Nalepa, T. F., Wojcik, J. A., Fanslow, D. L., and Lang, G. A. 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: population recruitment, density and size structure. *J. Great Lakes Res.* 21:417–434.

Nicholls, K. H., and Hopkins, G. J. 1993. Recent changes in Lake Erie (north shore) phytoplankton: cumulative impacts of phosphorus loading reduction and the zebra mussel introduction. *J. Great Lakes Res.* 19:637–647.

Officer, C. B., Smayda, T. J., and Mann, R. 1982. Benthic filter feeding: a natural eutrophication control. *Mar. Ecol. Prog. Ser.* 9:203–210.

Phelps, H.L. 1994. The Asiatic clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River Estuary near Washington, D.C. *Estuaries* 17:614–621.

Rodhouse, P.G., and Roden, C.M. 1987. Carbon budget for a coastal inlet in relation to intensive cultivation of suspension-feeding bivalve molluscs. *Mar. Ecol. Prog. Ser.* 36:225–236.

Skubinna, J. P., Coon, T. G., and Batterson, T. R. 1995. Increased abundance and depth of submersed macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21: 476–488.

Smith, V.E., Lee, K.W., Filkins, J.C., Hartwell, K.W., Rygwelski, K.R., and Townsend, J.M. 1977. *Survey of chemical factors in Saginaw Bay* (*Lake Huron*). EPA-600/3-77-125, U.S. Environmental Protection Agency, Duluth, Minnesota.

Stewart, T.W., and Haynes, J.M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena. J. Great Lakes Res.* 20:479–493.

Vollenweider, R. A., Munawar, M., and Stadelman, P. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. *J. Fish. Res. Board Can.* 31:739–762.