

Nutrient Regeneration by Veliger and Adult Dreissenids

FINAL REPORT

LAKE ERIE PROTECTION FUND SMALL GRANT SG 189-02

Joseph D. Conroy, M.S.
Department of Evolution, Ecology, and Organismal Biology
The Ohio State University, Columbus, Ohio 43210

David A. Culver, Ph. D.
Department of Evolution, Ecology, and Organismal Biology
The Ohio State University, Columbus, Ohio 43210

Submitted to:
Edwin J. Hammett, Executive Director
Ohio Lake Erie Commission
One Maritime Plaza, Fourth Floor
Toledo, Ohio 43604-1866

July 2006

EXECUTIVE SUMMARY

Recent large, collaborative research projects emphasize that Lake Erie is a changing ecosystem and that modifications in terms of the invasion of non-indigenous species, urbanization in the watershed, and changes in nutrient loading are mainly responsible for these changes. In this Lake Erie Protection Fund-supported project, we tested the hypothesis that dreissenid mussel remineralization of nitrogen and phosphorus from particulate to soluble forms was in part responsible for increased total phytoplankton biomass throughout Lake Erie, recurrence of cyanobacterial blooms in the western basin and nearshore regions of the central and eastern basins, and the persistence of hypolimnetic zones of hypoxia and anoxia in the central basin.

To test this hypothesis we proposed three objectives: (1) to measure horizontal heterogeneity in nutrients, chlorophyll, phytoplankton biomass, and zooplankton biomass at up to 30 stations sampled monthly in the western, central, and eastern basins of Lake Erie; (2) to measure size-specific excretion rates of dreissenid adults and veligers from Lake Erie; and, (3) to measure vertical profiles of temperature-gradient microstructure to quantify vertical mixing rates throughout the water column. We used a combination of field sample collection, laboratory experiments, and computer modeling to evaluate these three objectives.

In evaluating these objectives to test our hypothesis, we found that nutrient concentrations and phytoplankton biomass decreased from the western basin to the central basin. We found that adult dreissenid mussels quickened nitrogen and phosphorus turnover times whereas larval dreissenids appeared to take up soluble phosphate. Simulations of oxygen depletion rates in the central basin indicated that rates were most sensitive to vertical mixing in the hypolimnion, respiration by the hypolimnetic biological community, and sediment oxygen demand. Stimulation of phytoplankton growth rates by dreissenid mussel excretion would add to the hypolimnetic biological community respiration term and thereby increase oxygen depletion rates.

These results indicate that dreissenid mussels are important to the function of Lake Erie and that they may be essential in considering some of the most relevant problems in Lake Erie. Further research is needed to more completely elucidate the role of dreissenids in shaping these problems especially in the areas of directly connecting benthic dreissenid excretion to pelagic phytoplankton and in truly understanding the role of veliger larvae in the phosphorus budget.

Results from this project were widely distributed with the data being published in three scientific, peer-reviewed articles in regional and international journals and presented in 14 presentations at regional and international conferences.

INTRODUCTION

Lake Erie is a changing ecosystem. Due to the invasion of non-indigenous species, urbanization in the watershed, changes in nutrient loading, and many other impacts, the function of Lake Erie is substantially different than it was even 25 years ago. These changes are obvious in terms of increasing nutrient concentrations (Makarewicz et al. 2000), the resurgence of cyanobacterial blooms (Vincent et al. 2004, Conroy and Culver 2005, Conroy et al. 2005b, c), and modifications in Lake Erie's food web (Kane et al. 2003, Laxson et al. 2003, Garton et al. 2005).

Among the most detrimental of these recent changes was the invasion of dreissenid mussels, the zebra mussel (*Dreissena polymorpha*, Hebert et al. 1989) and the quagga mussel (*D. bugensis*, May and Marsden 1992). These mussels, natives to the Ponto-Caspian region of Eastern Europe, quickly spread throughout the Laurentian Great Lakes after introduction (Griffiths et al. 1991) and reached extremely high densities ($> 100,000$ individuals m^{-2} , Leach 1993) causing some scientists to hypothesize that they could overwhelm phytoplankton standing stocks due to their voracious filter-feeding (MacIsaac 1996). However, phytoplankton standing stocks increased throughout Lake Erie from the mid-1990's to the present (Conroy et al. 2005b, c) and, as mentioned above, nuisance cyanobacterial blooms (especially of the potentially-toxic cyanobacterium *Microcystis* spp., Conroy et al. 2005a) began to recur during the same time period. These changes were unexpected, especially because of the controls on nutrient loading (especially phosphorus) implemented by the Great Lakes Water Quality Agreement and the subsequent decrease in total phosphorus load to Lake Erie (Dolan 1993, Dolan and McGunagle 2005).

In this project, we hypothesized that dreissenid mussels, both the benthic adult form and the larval veliger form, contributed significantly to the remineralization of nutrients from particulate form to soluble form by consuming particulate nutrients (i.e., phytoplankton and detritus) and in turn excreting soluble nutrients (i.e., ammonium-nitrogen and phosphate-phosphorus). If this were the case, dreissenid mussels could facilitate the increase in phytoplankton biomass and cyanobacterial blooms by essentially fertilizing the lake from within – that is, by transforming nutrients that would otherwise have settled out of the water column and remained in the sediments into soluble nutrients available for use by growing phytoplankton. Investigating the capacity for adults and larvae to affect remineralization rates separately is important because adults are limited to the benthos while veliger larvae are becoming an increasingly important part of the pelagic zooplankton community. Whereas our project focused on the effects on the phytoplankton community, other scientists have hypothesized a similar role for dreissenid mussels in fertilizing benthic algae (Hecky et al. 2004).

To investigate the hypothesis that dreissenid mussels affect remineralization rates in Lake Erie, we proposed three objectives. These were to (1) measure horizontal heterogeneity in nutrients, chlorophyll, phytoplankton biomass, and zooplankton biomass at up to 30 stations sampled monthly in the western, central, and eastern basins of Lake Erie; (2) measure size-specific excretion rates of dreissenid adults and veligers from Lake Erie; and, (3) measure vertical profiles of temperature-gradient microstructure to quantify vertical mixing rates throughout the water column.

METHODS

We tested these three objectives to assess our hypothesis using a combination of field, laboratory, and computer methods. We collected samples to test the first objective aboard the United States Environmental Protection Agency's (USEPA) *R/V Lake Guardian* during the summer of 2002 as part of the USEPA-supported Lake Erie Trophic Status Collaborative Study (Matisoff and Ciborowski 2005). On four, week-long cruises during June, July, August, and September, we measured the nutrient, chlorophyll, phytoplankton, and zooplankton concentrations and abundances at 25 stations (Fig. 1).

Whole water samples from mid-depth (at unstratified stations) or mid-epilimnion depth (at stratified stations) were collected for determination of nutrient and chlorophyll *a* concentrations and phytoplankton biomass. For nutrient samples we dispensed 250 mL of whole or filtered (Whatman GF/C, 1.2 μm nominal pore size) water into pre-labeled and pre-rinsed polyethylene bottles and froze the samples for later transport to the Heidelberg College Water Quality Laboratory. Fluoride, chloride, sulfate, silicon, total Kjeldahl nitrogen, ammonia, nitrate, nitrite, total phosphorus, total soluble phosphorus, and soluble reactive phosphate were determined by the WQL according to standard methods (APHA et al. 1998). For chlorophyll *a* concentration determinations, we filtered a known amount of whole water through Whatman GF/C filters, put the filter in an opaque canister, and froze the filter for subsequent analysis. In the laboratory, we used aqueous-acetone extraction followed by spectrophotometric analysis (Lorenzen 1967, USEPA 1997) to determine chlorophyll *a* concentrations. Total phytoplankton samples were dispensed into a 500-mL canning jar and preserved with Lugol's iodine solution. Phytoplankton biomass was determined according to Utermöhl (1958) through the use of inverted light microscopy at 400x. For zooplankton, we lowered a front-weighted, 0.5-m diameter, 64- μm mesh net to within 1 m of the bottom and then retrieved it. Zooplankton samples were preserved with sugar formalin (Haney and Hall 1973) and later counted under a dissecting light microscope. Further details on phytoplankton and zooplankton methods can be found in Conroy et al. (2005c).

To test the second objective, we determined the ammonium-nitrogen and phosphate-phosphorus excretion rates of adult dreissenids (both zebra and quagga mussels; Conroy et al. 2005a) and of dreissenid veligers. The methods for the adult dreissenid methods are extensively described in Conroy et al. (2005a). Briefly, mussels were collected from Peach Point Reef, South Bass Island, Ohio during late-July 2002. Mussels were removed from the substrate using a scalpel and transported to laboratories at The Ohio State University, Columbus, Ohio where they were later sorted by species and into five size classes (<10, 10-15, 15-20, 20-25, and 25-30 mm). Mussels were added to containers filled with filtered lake water and allowed to filter and excrete for six hours. After the six hour experimental period, mussels were removed from the containers and frozen for later biomass determination and the water was filtered (Whatman GF/C) and frozen for subsequent ammonium and phosphate concentration determination. Mussel biomass determinations followed Pontius and Culver (2000). Nutrient concentration determinations followed standard methods (APHA et al. 1998). Filtered lake water was used as a control to determine nutrients added from extraneous sources over the six-hour incubation period. Once mussel biomass and nutrient concentrations were determined, excretion rates (μg

nutrient mg dry weight⁻¹ d⁻¹) were determined. Excretion rates were plotted versus mussel biomass and linear mussel excretion models were determined by linear regression. For veligers excretion experiments, we collected organisms from the western basin by carefully sedimenting and resuspending a zooplankton sample collected as described above. We found that veligers quickly sedimented due to their heavy shell and therefore concentrated in the bottom layer of a large sample jar. Veligers were held in aerated, filtered lake water overnight and brought to a concentration of 5,000 veligers mL⁻¹. We used this preparation to inoculate 90 mL of aerated filtered (Whatman GF/C) lake water to obtain final veliger concentrations of 100, 33, 10, 3.3, and 1 veligers mL⁻¹. Four replicates of each concentration along with one filtered lake water control were prepared. Immediately after inoculation, one replicate was harvested by passing the sample through a 64 µm filter. The veligers were put into a glass vial and preserved with sugar-formalin. The filtrate was dispensed into beakers and frozen for subsequent soluble reactive phosphate analysis according to standard methods (APHA et al. 1998). Harvesting was repeated at 2, 4, and 12 h after inoculation.

To test the third objective, we deployed a self-contained autonomous temperature gradient microprofiler (SCAMP) at several sites throughout Lake Erie to measure eddy diffusivity. We then used the data collected to parameterize and implement a 1-D oxygen dynamics model for the central basin of Lake Erie. We performed sensitivity analyses with the parameterized 1-D model to determine the importance of vertical mixing, oxygen flux across the air-water interface, oxygen production through phytoplankton photosynthesis, oxygen consumption through organismal community respiration, and sediment oxygen demand on rates of oxygen consumption. More detailed methods are described in Edwards et al. (2005).

RESULTS AND DISCUSSION

The results of our experiments generally supported our hypothesis that dreissenid mussels are important in promoting internal fertilization of Lake Erie. The tests of our first objective show several marked patterns. First, nutrient concentrations decrease from the western to eastern basins (Table 1). Mean concentrations over all dates from the western basin were moderately high in the western basin (271, 43, 301, 15, and 2 µg N or P L⁻¹ for TKN, NH₃, NO₃, TP, and SRP, respectively). Mean TKN concentrations were similar among basins (267 and 223 µg N L⁻¹ in the central and eastern basins, respectively) whereas the mean NH₃ concentration was lower in the central basin (35 µg N L⁻¹) than the western basin but higher in the eastern basin (69 µg N L⁻¹). Mean NO₃ concentrations were similar in the central (146 µg N L⁻¹) and eastern (160 µg N L⁻¹) but much lower than in the western basin. Mean TP concentrations were lower in the central (8 µg P L⁻¹) and eastern (6 µg P L⁻¹) basins than in the western basin. Mean SRP concentrations were similar between the western and central (3 µg P L⁻¹) basins but the eastern (0.8 µg P L⁻¹) basin had a lower mean concentration. Nutrient concentrations in all basins were often greater nearshore (Table 1) with some exceptionally high concentrations (e.g., Cleveland on 7/17/2002 and Port Dover on 8/17/2002). Temporally, concentrations for some nutrients (e.g., SRP) were greater earlier in the season with concentrations falling below detection limits by August and September (Table 1).

Mean chlorophyll *a* concentrations were greatest in the western basin (mean concentration of 4.3 µg L⁻¹) and declined in the central (2.1 µg L⁻¹) and eastern (1.7 µg L⁻¹)

basins (Table 1). Similarly, mean total phytoplankton wet biomass declined from the western ($2271 \mu\text{g L}^{-1}$) to the central ($906 \mu\text{g L}^{-1}$) and eastern ($841 \mu\text{g L}^{-1}$) basins (Table 1). Mean cyanobacteria biomass decreased from the western ($645 \mu\text{g L}^{-1}$) to the central ($147 \mu\text{g L}^{-1}$) but increased in the eastern ($337 \mu\text{g L}^{-1}$) basin (Table 1). The mean cyanobacteria biomass was particularly influenced by the inclusion of the biomass observations from Barcelona on 8/17/2002 and Port Dover on 9/17/2002 (Table 1). When these two data points were removed, the mean cyanobacteria biomass decreased to $106 \mu\text{g L}^{-1}$, somewhat lower than the central basin mean. Total zooplankton dry weight biomass was similar between the western ($212 \mu\text{g L}^{-1}$) and central ($202 \mu\text{g L}^{-1}$) basins but decreased in the eastern ($85 \mu\text{g L}^{-1}$) basin (Table 1). There do not seem to be systematic temporal changes in the dataset for chlorophyll *a* concentration, total phytoplankton biomass, or total zooplankton biomass (Table 1), but cyanobacteria biomass was virtually nil in June and July but was much greater in August and September.

Tests of the second objective emphasize the importance of dreissenid mussels in the remineralization of nitrogen and phosphorus in Lake Erie. In the adult dreissenid excretion experiments, we found that with dreissenid mussels present ammonium-nitrogen turned over much faster (calculated turnover time decreased from 13.9 d with only crustacean zooplankton present to 4.2 d with dreissenids and crustacean zooplankton) and that phosphate-phosphorus turned over slightly faster (calculated turnover time decreased from 14.5 to 11.3 d). These results indicate that adult dreissenids may be more important in quickening the turnover rates of nitrogen rather than phosphorus in Lake Erie. Conroy et al. (2005a) report related results.

Results of the veliger excretion experiment showed patterns contrary to those of the adult mussel experiments (Fig. 2). In this experiment, soluble reactive phosphate concentrations decreased through time converse to the expectations of an excretion rate determination experiment. These results indicate that phosphate was taken up during the course of the experiment, either by the veligers themselves or by bacteria in the water. Although the water that the veligers were added had been filtered (see Methods), the filter pore size was large enough ($1.2 \mu\text{m}$) that bacteria could pass through the filter. It is interesting to note that the phosphate uptake rate increased with increasing veliger densities (Fig. 2) lending some support to the contention that veligers were taking up at least some of the soluble phosphate.

As part of the test of the third objective, we determined eddy diffusivity rates throughout Lake Erie. We then used these diffusivity rates to parameterize a 1-D oxygen model of Lake Erie's central basin with subsequent sensitivity analysis to determine what parameters were important in contributing toward oxygen consumption in the central basin. We found that hypolimnetic oxygen depletion was most sensitive to hypolimnetic mixing, hypolimnetic respiration, and sediment oxygen demand (Edwards et al. 2005). Mussel-induced nutrient recycling can increase phytoplankton biomass and potentially cause cyanobacteria blooms increasing hypolimnetic respiration as this biomass is decomposed. Further, Edwards et al.'s (2005) results demonstrate the importance of linking benthic and pelagic processes when investigating the importance of dreissenid mussels on current Lake Erie function. A nitrogen and phosphorus budget modeling analysis similar to the one Edwards et al. performed for oxygen would help to clarify the role of adult and larval dreissenids in the turnover of these nutrients in Lake Erie. Further, it would clarify the importance of internal fertilization from dreissenids on phytoplankton growth and the formation of cyanobacteria blooms.

CONCLUSIONS

In our project, we sought to evaluate the role of nutrient remineralization by dreissenids in fertilizing Lake Erie from within and in turn contributing to increased phytoplankton biomass, cyanobacteria blooms, and central basin hypoxia. Through a combination of field and laboratory methods, we found that adult dreissenid mussels could significantly contribute to nitrogen and phosphorus turnover that in turn could facilitate phytoplankton growth. Field observations during the summer of 2002 show that cyanobacteria biomass increased during the later summer months supporting other studies' observations of returning cyanobacteria blooms in Lake Erie. Explicitly connecting dreissenid mussels' physiological activities to increases in cyanobacteria biomass remains to be done. However, since there have not been measured increases in external phosphorus loading to Lake Erie in recent years (Dolan and McGunagle 2005), an internal fertilization source seems likely. Further, directly connecting dreissenid mussels to hypolimnetic oxygen depletion remains an active area of research. Our published research (Conroy et al. 2005a, c) supports an indirect connection where dreissenid nutrient excretion supports excess phytoplankton growth which later sinks and is decomposed in the central basin hypolimnion, using up oxygen. Results from this project were widely distributed in the peer-reviewed literature (Appendix A) and at scientific meetings (Appendix B).

REFERENCES

- APHA (American Public Health Association), American Water Works Association and Water Pollution Control Federation. 1998. *Standard methods for the examination of water and wastewater*. American Public Health Association, New York. 1220 pp.
- Conroy, J.D. and D.A. Culver. 2005. Do dreissenids affect Lake Erie ecosystem stability processes? *Am. Midl. Nat.* 153: 20-32.
- Conroy, J.D., W.J. Edwards, R.A. Pontius, D.D. Kane, H. Zhang, J.F. Shea, J.N. Richey, and D.A. Culver. 2005a. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. *Freshw. Biol.* 50: 1146-1162.
- Conroy, J.D., D.D. Kane, and D.A. Culver. 2005b. Declining Lake Erie ecosystem health – Evidence from a multi-year, lake-wide plankton study. In: M. Munawar, R. Heath (Eds.), *Checking the Pulse of Lake Erie*. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Canada. In press.
- Conroy, J.D., D.D. Kane, D.M. Dolan, W.J. Edwards, M.N. Charlton, and D.A. Culver. 2005c. Temporal trends in Lake Erie plankton biomass: roles of external phosphorus loading and dreissenid mussels. *J. Great Lakes Res.* 31(Suppl. 2): 89-110.
- Dolan, D. 1993. Point source loading of phosphorus to Lake Erie: 1986-1990. *J. Great Lakes Res.* 19: 212-223.
- Dolan, D. and K.P. McGunagle. 2005. Lake Erie total phosphorus loading analysis and update: 1996-2002. *J. Great Lakes Res.* 31(Suppl. 2): 11-22.
- Edwards, W.J., J.D. Conroy, and D.A. Culver. 2005. Hypolimnetic oxygen depletion dynamics in the central basin of Lake Erie. *J. Great Lakes Res.* 31(Suppl. 2): 262-271.
- Garton, D.W., C.D. Payne, and J.P. Montoya. 2005. Flexible diet and trophic position of dreissenid mussels as inferred from stable isotopes of carbon and nitrogen. *Can. J. Fish. Aquat. Sci.* 62: 1119-1129.
- Haney, J.F. and D.J. Hall. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. *Limnol. Oceanogr.* 18:331-333.
- Hebert, P.D.N., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusk in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 46: 1587-1591.
- Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61: 1285-1293.
- Kane, D.D., E.M. Haas, and D.A. Culver. 2003. The characteristics and potential ecological effects of the exotic crustacean zooplankter *Cercopagis pengoi* (Cladocera: Cercopagidae), a recent invader of Lake Erie. *Ohio J. Sci.* 103: 79-83.
- Laxson C.L., K.N., McPhedran, J.C. Makarewicz, I.V. Telesh, and H.J. MacIsaac. 2003. Effects of the non-indigenous cladoceran *Cercopagis pengoi* on the lower food web of Lake Ontario. *Freshw. Biol.* 48: 2094-2106.
- Leach, J.H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In: T.F. Nalepa, D.W. Schloesser (Eds.), *Zebra Mussels: Biology, Impacts, and Control*. Lewis Publishers, Boca Raton, Florida. pp. 381-397.

- Lorenzen, C.J. 1967. Determination of chlorophyll and phaeo-pigments: spectrophotometric equations. *Limnol. Oceanogr.* 12:343-346.
- MacIsaac, H.J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *Amer. Zool.* 36: 287-299.
- Makarewicz, J.C., P. Bertram, and T.W. Lewis. 2000. Chemistry of the offshore surface waters of Lake Erie: pre- and post-*Dreissena* introduction (1983-1993). *J. Great Lakes Res.* 26: 82-93.
- Matisoff, G. and J.J.H. Ciborowski. 2005. Lake Erie Trophic Status collaborative study. *J. Great Lakes Res.* 31(Suppl. 2): 1-10.
- May, B. and J.E. Marsden. 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. *Can. J. Fish. Aquat. Sci.* 49: 1501-1506.
- Pontius, R.A. and D.A. Culver. 2000. Estimating zebra mussel impact on pelagic food webs: the role of size-specific grazing rates. *Verh. Internat. Verein. Limnol.* 27:3025-3028.
- USEPA (United States Environmental Protection Agency). 1997. *Methods for the determination of chemical substances in marine and estuarine environmental matrices.* 2nd Edition. EPA/600/R-97/072.
- Utermöhl, H. 1958. Zur Vervollkommung der quantitativen phytoplankton-methodik. *M. H. Ver. Limnol.* 9:1-38.
- Vincent, R.K., X. Qin, R.M.L. McKay, J. Miner, K. Czajkowski, J. Savino, and T. Bridgeman. 2004. Phycocyanin detection from LANDSAT TM data for mapping cyanobacterial blooms in Lake Erie. *Remote Sens. Environ.* 89: 381-392.

Table 1. Nutrient concentrations (mg L⁻¹: Cl = chloride, SO₄ = sulfate, SiO₂ = silicon; µg L⁻¹: F = fluoride, TKN = total Kjeldahl nitrogen as N, NH₃ = ammonia as N, NO₃ = nitrate as N, NO₂ = nitrite as N, TP = total phosphorus as P, TSP = total soluble phosphorus as P, and SRP = soluble reactive phosphate as P), chlorophyll *a* concentrations (µg L⁻¹; Chla), total phytoplankton biomass (µg wet weight L⁻¹; Total PP), cyanobacteria biomass (µg wet weight L⁻¹; Cyano), and total zooplankton biomass (µg dry weight L⁻¹; Total ZP) from the western **(a)**, central **(b)**, and eastern **(c)** basins taken during the summer of 2002 as part of the Lake Erie Trophic Status Collaborative Study. Note 1: cells with zeros indicate concentrations below detectable limits. Note 2: empty cells indicate no samples taken for a particular parameter on a particular date. Note 3: nutrient concentration data from several sites on a few dates are erroneous – Sandusky 7/21/2002, 37 7/18/2002, and Port Alma 7/17/2002.

(a)

SITE	Date	Cl	SO ₄	SiO ₂	F	TKN	NH ₃	NO ₃	NO ₂	TP	TSP	SRP	Chla	Total PP	Cyano	Total ZP
971	6/24/2002	9.4	17.3	1.91	90.0	219.3	83.0	0.0	0.0	11.7	1.3	4.3	3.5	985.6	0.0	247.4
972	6/24/2002	9.0	17.9	2.06	10.0	169.3	27.0	353.3	0.0	8.7	2.3	4.3	3.6	736.9	10.4	53.6
973	6/24/2002	20.3	30.7	2.18	10.0	508.3	9.0	1703.3	0.0	29.7	7.3	6.3	11.9	3901.7	0.0	292.1
Sandusky	6/28/2002	13.7	20.3	2.26	10.0	224.3	11.0	343.3	0.0	10.7	0.3	4.3	1.9	11.2	0.0	171.3
91	7/21/2002	12.9	22.0	2.71	10.0	424.3	21.0	323.3	0.0	19.7	4.3	4.3		2995.9	1590.5	322.2
Sandusky	7/21/2002	0.0	0.0	0.00	0.0	237.3	0.0	0.0	0.0	3.7	0.0	4.3		658.3	1.0	243.1
55	8/21/2002	11.0	17.2	1.33	0.0	283.3	40.0	113.3	0.0	18.1	4.3	0.0	6.5	8888.5	4227.8	576.6
91	8/21/2002	6.2	10.8	0.81	0.0	273.3	44.0	153.3	0.0	19.1	4.3	0.0	3.9	4240.3	1085.3	149.2
Sandusky	8/21/2002	15.8	22.5	1.76	0.0	263.3	52.0	213.3	0.0	7.0	2.3	0.0	3.1	1741.3	535.0	215.8
55	9/18/2002	7.5	14.5	1.97	0.0	309.3	114.0	43.3	0.0	24.6	8.3	1.3	1.5	445.8	12.5	94.8
61	9/18/2002	7.1	16.1	1.93	0.0	150.3	71.0	223.3	0.0	8.6	0.3	0.0	1.9	590.6	121.4	19.0
91	9/18/2002	7.6	16.1	1.84	0.0	188.3	47.0	143.3	0.0	15.7	1.3	0.0	4.6	2041.7	70.2	143.5
Sandusky	9/18/2002												5.2	2288.1	726.8	226.4

Continued

(b)

SITE	Date	Cl	SO ₄	SiO ₂	F	TKN	NH ₃	NO ₃	NO ₂	TP	TSP	SRP	Chla	Total PP	Cyano	Total ZP
30	6/26/2002	15.6	22.5	2.06	10.0	233.3	0.0	43.3	0.0	6.7	2.3	4.3	1.3	8.8	0.5	31.2
31	6/26/2002	16.7	24.3	2.27	10.0	235.3	41.0	173.3	0.0	6.7	0.3	6.3	3.7	0.6	0.0	112.4
32	6/26/2002	16.2	22.9	2.24	10.0	227.3	41.0	113.3	0.0	5.7	3.3	4.3	1.0	605.7	0.0	110.6
36	6/25/2002	15.8	22.8	2.64	10.0	238.3	85.0	283.3	0.0	7.7	0.3	4.3	0.0	781.1	0.0	306.2
37	6/25/2002	16.2	22.8	2.11	10.0	238.3	4.0	33.3	0.0	7.7	0.3	4.3	2.4	1023.0	0.0	222.2
38	6/26/2002	16.1	22.7	2.94	10.0	253.3	44.0	163.3	0.0	13.7	5.3	4.3	1.9	797.5	2.5	110.6
42	6/25/2002	15.9	22.4	1.60	10.0	209.3	23.0	0.0	0.0	6.7	0.3	3.3	0.6	212.9	0.0	246.5
43	6/25/2002	16.3	22.7	1.68	10.0	200.3	0.0	193.3	0.0	5.7	0.3	4.3	2.1	297.4	0.0	261.5
78	6/26/2002	15.7	22.4	2.43	10.0	272.3	23.0	193.3	0.0	7.7	2.3	4.3	3.7	1480.4	60.3	57.7
30	7/18/2002	14.2	21.2	1.56	10.0	223.3	0.0	193.3	0.0	3.7	3.3	4.3	1.6	951.1	1.4	328.2
31	7/18/2002	15.6	22.6	1.59	10.0	258.3	0.0	73.3	0.0	3.7	3.3	3.3		372.1	0.0	189.1
32	7/18/2002	15.2	22.0	1.82	10.0	224.3	19.0	43.3	0.0	2.7	3.3	3.3		296.5	0.0	116.8
36	7/18/2002	15.7	22.6	1.81	10.0	245.3	5.0	143.3	0.0	7.7	1.3	5.3	1.6	394.1	0.0	126.0
37	7/18/2002	15.8	22.5	1.91	10.0	256.3	0.0	3.3	0.0	6.7	2.3	5.3	1.5	904.6	12.6	182.0
38	7/18/2002	14.6	21.5	1.88	10.0	257.3	10.0	233.3	0.0	6.7	2.3	5.3		723.9	0.0	207.6
42	7/17/2002	15.7	22.2	1.70	10.0	311.3	0.0	253.3	0.0	5.7	1.3	4.3		415.0	49.6	143.4
43	7/17/2002	15.9	22.8	2.14	10.0	295.3	0.0	283.3	0.0	5.7	1.3	5.3	1.2	322.4	0.0	189.0
73	7/18/2002	15.7	22.3	1.92	10.0	274.3	0.0	203.3	0.0	7.7	1.3	4.3		314.9	0.0	187.1
78	7/18/2002	17.6	25.7	1.92	40.0	225.3	0.0	40.0	3.3	4.7	4.3	3.3	1.7	527.4	0.0	138.6
Cleveland	7/17/2002	18.5	24.1	2.18	10.0	897.3	133.0	453.3	0.0	14.7	10.3	5.3	1.0	161.5	0.0	116.3
Port Alma	7/17/2002	15.7	22.1	2.58	10.0	331.3	0.0	0.0	0.0	11.7	3.3	4.3	2.5	1730.0	0.0	370.1
Port Stanley	7/18/2002	15.7	22.8	2.31	10.0	262.3	8.0	123.3	0.0	8.7	4.3	7.3	0.1	430.3	0.0	163.6
30	8/18/2002	11.2	15.1	1.28	0.0	228.3	61.0	133.3	0.0	6.9	1.3	0.0	1.8	935.3	347.6	269.3
31	8/18/2002	13.6	20.5	0.93	0.0	232.3	43.0	223.3	0.0	8.5	1.3	0.0	1.9	540.2	113.7	15.4
32	8/18/2002	12.7	17.5	1.23	0.0	244.3	35.0	143.3	0.0	7.1	1.3	0.0	1.1	1043.5	443.7	167.6
36	8/20/2002	9.1	13.5	0.97	0.0	336.3	60.0	113.3	0.0	7.1	1.3	0.0	2.2	653.1	312.4	276.1
38	8/20/2002	9.2	13.6	1.63	0.0	298.3	56.0	153.3	0.0	11.0	3.3	5.3	4.4	5353.8	662.2	352.4
42	8/20/2002	9.6	12.7	2.39	0.0	236.3	38.0	123.3	0.0	5.6	1.3	0.0	1.4	1027.3	722.2	119.5
43	8/20/2002	15.1	21.9	0.58	0.0	269.3	56.0	203.3	0.0	7.4	1.3	0.0	1.9	3004.3	1444.5	173.3
78	8/18/2002	14.2	20.8	0.96	0.0	260.3	51.0	213.3	0.0	6.7	1.3	0.0	2.0	524.8	86.1	225.9
Cleveland	8/20/2002	16.0	22.7	1.10	0.0	239.3	47.0	203.3	0.0	8.2	1.3	0.0	1.5	1263.4	427.0	54.1
Port Alma	8/20/2002	11.6	18.3	1.05	0.0	292.3	80.0	133.3	0.0	11.3	2.3	0.0	5.2	2572.4	22.4	695.0
Port Stanley	8/18/2002	13.8	19.4	0.89	0.0	294.3	72.0	193.3	0.0	8.3	2.3	0.0	1.3	281.9	0.0	242.1
30	9/15/2002	8.9	11.5	0.98	0.0	262.3	69.0	63.3	0.0	10.7	1.3	0.0	3.5	709.8	80.3	383.3
31	9/15/2002	12.2	16.3	0.83	0.0	157.3	60.0	143.3	0.0	7.4	1.3	3.3	1.9	927.1	351.9	261.7
37	9/15/2002	15.2	21.7	0.98	0.0	291.0	16.0	120.0	0.0	9.2	1.0	0.0	3.0	696.6	103.5	146.1
38	9/15/2002	9.5	13.1	1.14	0.0	184.3	52.0	53.3	0.0	12.2	1.3	0.0	2.8	1351.8	267.4	191.8
78	9/15/2002	13.1	17.8	0.87	0.0	236.3	62.0	123.3	0.0	7.0	1.3	0.3	3.2	727.4	105.1	165.4
Port Stanley	9/15/2002	13.5	19.2	1.45	0.0	175.3	54.0	113.3	0.0	7.5	1.3	0.0	4.2	983.3	127.3	216.7

(c)

SITE	Date	Cl	SO ₄	SiO ₂	F	TKN	NH ₃	NO ₃	NO ₂	TP	TSP	SRP	Chla	Total PP	Cyano	Total ZP
15	7/20/2002	16.6	23.3	1.89	10.0	246.3	62.0	123.3	0.0	5.7	17.3	4.3	1.9	309.0	0.0	162.5
15	8/17/2002	11.3	15.1	1.70	0.0	219.3	68.0	123.3	0.0	5.6	1.3	0.3	1.3	365.7	64.4	62.2
63	8/17/2002												2.0	1523.1	52.2	86.7
Barcelona	8/17/2002												1.8	1904.4	1662.7	39.9
Port Dover	8/17/2002	22.1	22.3	1.51	0.0	287.3	112.0	213.3	0.0	8.0	7.3	0.0	1.2	411.8	109.2	77.1
15	9/17/2002	13.5	18.1	0.96	0.0	234.3	49.0	133.3	0.0	4.4	0.3	0.0	1.9	530.8	135.4	113.5
63	9/17/2002	15.2	21.2	0.79	0.0	185.3	60.0	193.3	0.0	5.4	0.3	0.0	1.4	872.5	357.8	63.0
93	9/17/2002	12.0	16.1	0.9	0.0	167.8	62.5	173.3	0.0	5.6	0.3	0.2	1.2	903.7	61.9	93.1
Barcelona	9/17/2002												1.2	339.7	65.7	13.7
Port Dover	9/17/2002												2.7	1253.8	856.2	138.1

Figure 1. Station map showing nutrient concentration, chlorophyll a concentration, phytoplankton biomass, and zooplankton biomass sampling locations. Note: collections were not made at all sites on all sampling visits and three sites in the western basin (971, 972, 973) are not shown.

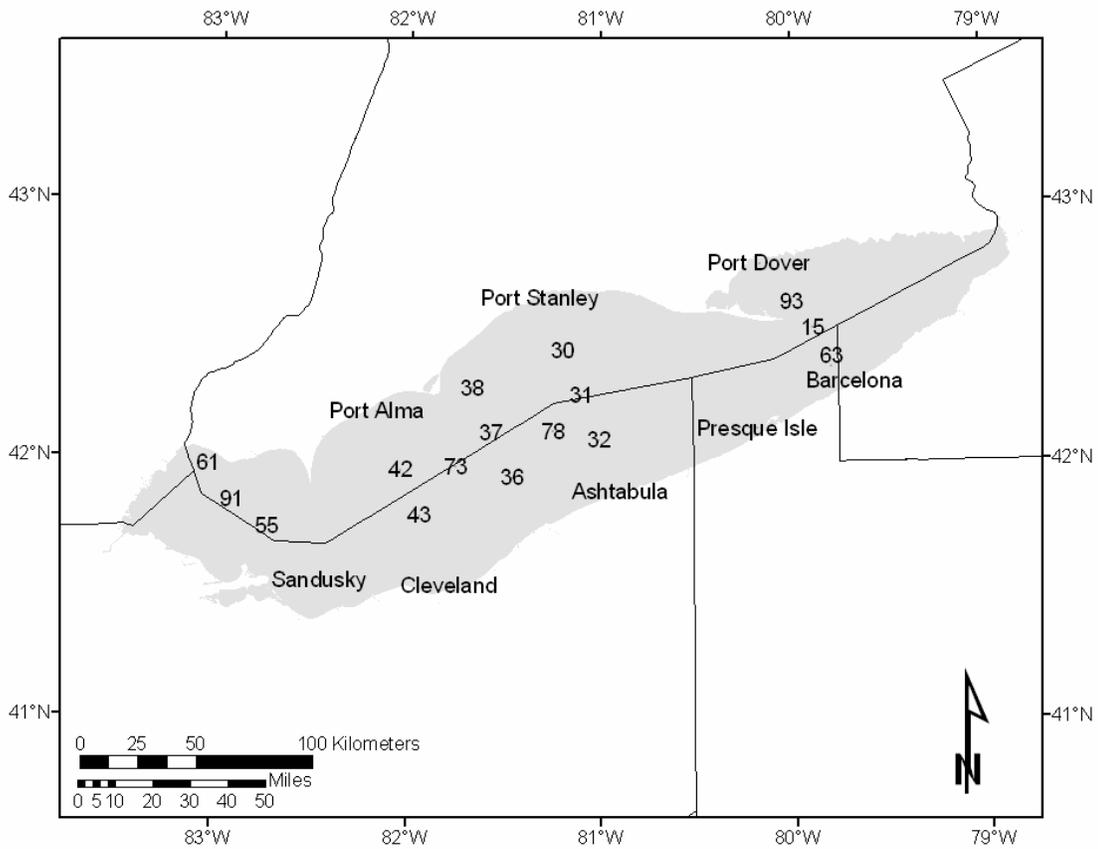
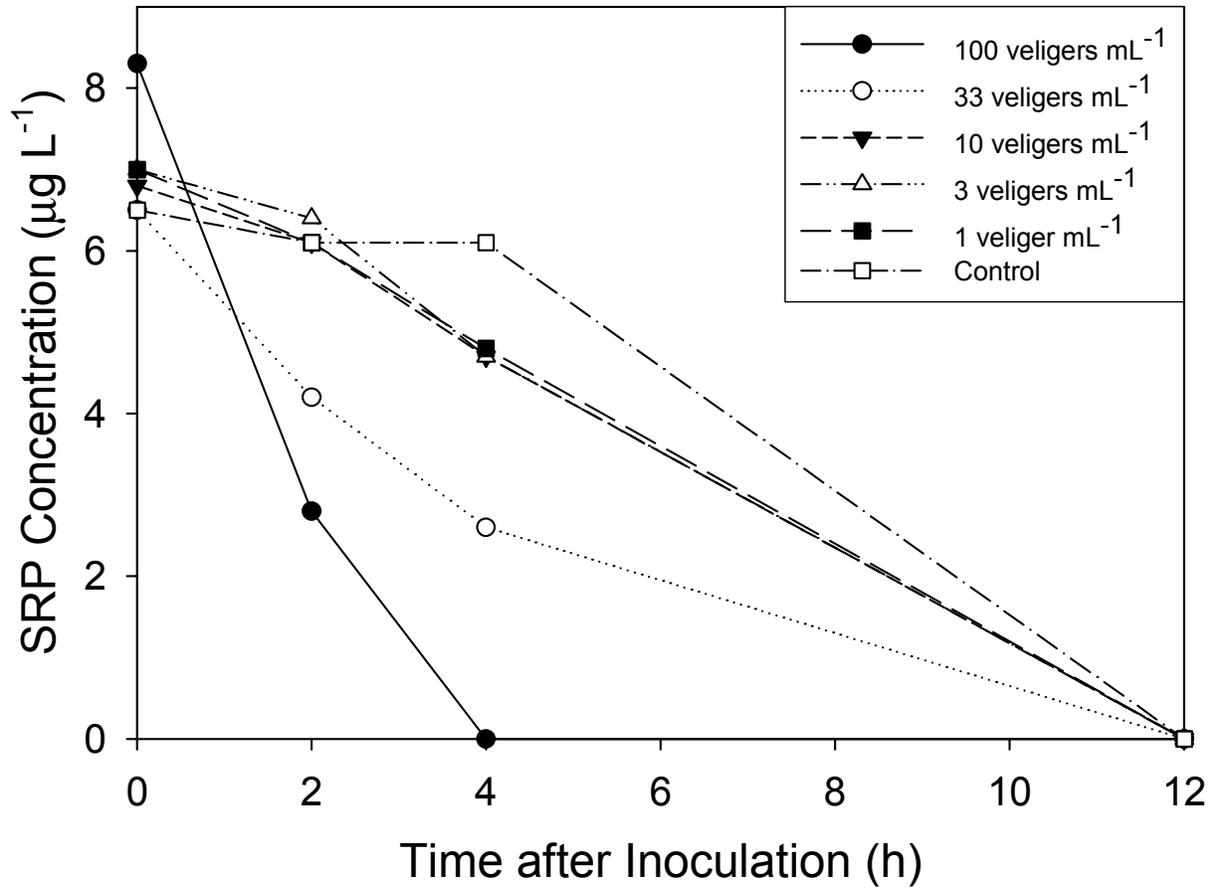


Figure 2. Time course of soluble reactive phosphate concentrations (SRP; $\mu\text{g P L}^{-1}$) in treatments of various dreissenid veliger larvae densities. If veligers' excretion added phosphate to the water, we would expect concentrations to increase through time. However, the pattern observed shows decreases through time indicating phosphate uptake. Further, treatments with higher densities appear to have quicker uptake rates (lower concentrations at similar time intervals).



APPENDIX A – Manuscripts published using data from LEPF Project SG 189-02

(See attached copies.)

- Conroy, J.D. and D.A. Culver. 2005. Do dreissenids affect Lake Erie ecosystem stability processes? *American Midland Naturalist* 153: 20-32.
- Conroy, J.D., W.J. Edwards, R.A. Pontius, D.D. Kane, H. Zhang, J.F. Shea, J.N. Richey, and D.A. Culver. 2005. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. *Freshwater Biology* 50: 1146-1162.
- Edwards, W.J., J.D. Conroy, and D.A. Culver. 2005. Hypolimnetic oxygen depletion dynamics in the central basin of Lake Erie. *Journal of Great Lakes Research* 31(Suppl. 2): 262-271.

APPENDIX B – Presentations given using data from LEPF Project SG 189-02

- Conroy, J.D., R.A. Pontius, W.J. Edwards, and D.A. Culver. 2005. *Excretion by invasive dreissenid mussels: evidence for changes in Lake Erie*. American Society of Limnology and Oceanography Aquatic Sciences Meeting. Salt Lake City, Utah, 22 February.
- Culver, D.A., J.D. Conroy, W.J. Edwards, and R.A. Pontius. 2004. *The impact of dreissenid ammonia and phosphate excretion on Lake Erie*. The 13th International Conference on Aquatic Invasive Species. Ennis, County Clare, Ireland, 24 September.
- Culver, D.A. and J.D. Conroy. 2004. *Differential excretion of ammonia and phosphate by three dreissenid taxa*. The 13th International Conference on Aquatic Invasive Species. Ennis, County Clare, Ireland, 24 September.
- Edwards, W.J., J.D. Conroy, D.D. Kane, D.M. Dolan, M.N. Charlton, and D.A. Culver. 2004. *Recent increases in Lake Erie phytoplankton biomass: roles of external phosphorus loading and exotic dreissenid mussels*. International Association of Great Lakes Research, Annual Meeting. Waterloo, Ontario, Canada, 27 May.
- Conroy, J.D. and D.A. Culver. 2004. *The role of invasive mussels, Dreissena spp., on Lake Erie ecosystem processes*. Midwest Ecology and Evolution Conference. South Bend, Indiana, 7 March.
- Culver, D.A., J.D. Conroy, H. Zhang, D.M. Dolan, and M.N. Charlton. 2004. *Eutrophication of coastal waters: a large lake perspective*. American Society of Limnology and Oceanography Ocean Research Conference. Honolulu, Hawai'i, 17 February.
- Conroy, J.D., D.A. Culver, W.J. Edwards, D.D. Kane, R.A. Pontius, J.N. Richey, J.F. Shea, and H. Zhang. 2003. *Differences in excretion by dreissenid congeners: implications for the nearshore ecosystem*. International Association of Great Lakes Research, Annual Meeting. Chicago, Illinois, 25 June.
- Culver, D.A., J.D. Conroy, W.J. Edwards, D.D. Kane, R.A. Pontius, J.N. Richey, J.F. Shea, and H. Zhang. 2003. *Do dreissenid mussels cause the Lake Erie "Dead Zone"?* International Association of Great Lakes Research, Annual Meeting. Chicago, Illinois, 24 June.
- Edwards, W.J., J.D. Conroy, G. Matisoff, H. Carrick, and D.A. Culver. 2003. *Sensitivity of hypolimnetic oxygen concentrations to recent changes in the Lake Erie ecosystem*. International Association of Great Lakes Research, Annual Meeting. Chicago, Illinois, 24 June.

- Edwards, W.J., J.D. Conroy, and D.A. Culver. 2003. *Interaction of large scale physical processes on the Lake Erie Central Basin hypoxia*. International Association of Great Lakes Research, Annual Meeting. Chicago, Illinois, 24 June.
- Conroy, J.D., D.A. Culver, W.J. Edwards, D.D. Kane, R.A. Pontius, J.N. Richey, J.F. Shea, and H. Zhang. 2003. *Excretion in two dreissenid congeners: implications for the Lake Erie ecosystem*. Midwest Ecology and Evolution Conference. Akron, Ohio, 29 March.
- Conroy, J.D., W.J. Edwards, and D.A. Culver. 2003. *Contributions of lower trophic level dynamics, dreissenid mussels, and physical processes to Lake Erie changes*. The Third Biennial Conference of the Lake Erie Millennium Network. Windsor, Ontario, Canada, 6 May. **Invited**.
- Culver, D.A., J.D. Conroy, W.J. Edwards, D.D. Kane, R.A. Pontius, J.N. Richey, J.F. Shea, and H. Zhang. 2003. *Do dreissenid mussels cause the Lake Erie "Dead Zone"?* American Society of Limnology and Oceanography, Aquatic Sciences Meeting. Salt Lake City, Utah, 10 February.
- Culver, D.A. and J.D. Conroy. 2003. *Lake Erie update: phosphorus loading, zebra mussels, fish recruitment, and the "Dead Zone"*. 43rd Ohio Fish and Wildlife Conference. Columbus, Ohio, 7 February. **Invited**.