Watershed Connections to Lake Erie Water Quality: the Algal Loading Hypothesis

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Abstract. Intensive work to reduce the phosphorus load from its watershed improved Lake Erie's water quality through 1995, but water quality has since declined, resulting in recurring harmful algal blooms throughout the lake and summer hypolimnetic hypoxia in the central basin. We hypothesized that input of live, biological material (especially algae) from large tributaries directly contributed to the offshore processes causing algal blooms and hypoxia. To test this hypothesis, we proposed three objectives: to determine the amounts and types of algal loading from a large Lake Erie watershed; to determine the growth and "bloom formation capacity" of various algal communities; and to identify management strategies to remediate tributary algal loading effects. Working in the Sandusky River, Bay, and subbasin, we found extremely high phytoplankton biomasses in the river and bay, with phytoplankton growth only limited by light availability because nutrient concentrations were extremely high. These nutrient-replete phytoplankton were "primed" for growth once transported offshore, thereby supporting our hypothesis. Thus the watershed's biological loads are important components of offshore Lake Erie beneficial use impairments, namely, eutrophication due to excessive nutrient loading, degradation of biological communities and aesthetics by harmful algal blooms, and loss of fish or other wildlife habitat due to hypoxia.

Activities and timelines. Activities associated with testing the Algal Loading Hypothesis were subdivided into three main parts: (1) determining the abundance of river, bay, and offshore plankton communities throughout the growing season; (2) determining whether nutrients or light limited the growth of phytoplankton moving from the river, into the bay, and offshore into Lake Erie; and, (3) determining how important phytoplankton load was in affecting offshore hypolimnetic hypoxia and harmful algal blooms. These three parts are addressed in succession in Chapters 2-4 in Conroy (2007). Here, we briefly summarize the major findings.

The classic view of tributary-lake interactions solely considers tributaries as sources of nutrients for phytoplankton growing offshore. We tested how river phytoplankton affected phytoplankton dynamics in a lacustrine estuary (Sandusky Bay) and how these phytoplankters could, upon discharge, affect offshore (Sandusky subbasin) phytoplankton dynamics. In addition, we sought to determine whether phytoplankton biomass was controlled by bottom-up abiotic factors (stream flow, temperature, light attenuation, and nitrogen and phosphorus concentrations) or top-down biotic factors (zooplankton herbivory) and the role the lacustrine estuary played in modifying the quality of the water discharged into the lake. We tested these possibilities using field sampling over two years in the Sandusky River, Bay, and subbasin of Lake Erie in conjunction with river flow and nutrient monitoring and multivariate statistical analysis of the relationships among the various data. We found that nutrient loading to the estuary corresponded with watershed input and that nutrients were used within the estuary, decreasing nutrient loads to the lake. However, phytoplankton biomass was extremely high in the estuary and was much higher at the bay/subbasin junction than offshore indicating that the estuary discharges phytoplankton at least to the nearshore area of the subbasin. An information-theoretic analysis of 15 candidate models predicting phytoplankton biomass showed that biomass was best predicted by the ratio of total inorganic nitrogen to total phosphorus, indicating bottom-up control of phytoplankton biomass. Consequently, the lacustrine estuary functions as a chemostat, using incoming nutrients to grow large amounts of phytoplankton. Our results indicate that the classic model of tributary-bay interactions needs revision to include phytoplankton load and its subsequent effects offshore and that the Sandusky River is important in supplying phytoplankton to the Sandusky Bay which, in turn, is important in supplying phytoplankton to the Sandusky subbasin potentially perturbing offshore harmful algal blooms and supplying excess organic matter to the hypolimnion.

Tributary phytoplankton, replete with nutrients, loaded into freshwater offshore ecosystems may contribute to offshore harmful algal blooms and hypolimnetic hypoxia, given their high growth when exposed to higher offshore light. In tributaries, we investigated the hypothesis that light limits phytoplankton productivity due to high nutrients and sediments, whereas nutrients, particularly phosphorus, limit offshore phytoplankton productivity. By measuring light and nutrient abundance and phytoplankton biomass, phosphorus deficiency, and productivity in the Sandusky River, Bay, and subbasin of Lake Erie, we determined which factors (light availability, phytoplankton biomass, or photosynthetic parameters) most influenced integrated phytoplankton productivity. At river and bay sites, nutrients were not limiting; increased light, however, led to greater integrated phytoplankton productivity; offshore, nutrients were limiting and productivity increased when phytoplankton physiology changed. Consequently, when river and bay phytoplankton are transported offshore, they may grow rapidly and bloom, adding to the effect of tributary nutrient load in affecting offshore algal blooms.

To better understand whether organic matter supplied from the watershed or the surface waters offshore or the thickness of the hypolimnion was most important in affecting hypolimnetic oxygen depletion rate (HOD) and hypoxic zone formation, we evaluated the relative importance of (1) tributary organic matter load, (2) epilimnetic organic matter load, and (3) basin morphometry in affecting HOD in the Sandusky subbasin of Lake Erie. Previous studies of the factors controlling HOD focused on the relative contributions of epilimnetic organic matter production from excessive tributary nutrient load due to human activities and basin morphometry while tributary organic matter load is largely untested due to the historical significance attributed to, and the ability to manage for, nutrient load. We tested the relative importance of these factors by determining HOD and associated limnological (temperature, chlorophyll *a* concentrations, hypolimnetic thickness, water level, and streamflow) and meteorological (wind speed and wave height) parameters during 2005 and 2006 with synoptic surveys and moored multiparameter instruments. We measured carbon stable isotope ratios ($\delta^{13}C$) to determine the hypolimnetic organic matter source. The Sandusky subbasin HOD ranged 1.91-3.75 mg L^{-1} mo^{-1} depending on site, and was most influenced by basin morphometry, followed by large-scale hydrodynamic and meteorological events, and then tributary load. Hypolimnetic seston $\delta^{13}C$ values (mean = -23.3‰) were similar to epilimnetic (mean = -23.6‰) and river (mean = -23.4‰) seston $\delta^{13}C$ values, but distinct from bay seston $\delta^{13}C$ (mean = -26.9‰), revealing an epilimnetic source for hypolimnetic organic matter and a complex connection between river, bay, and subbasin organic matter. Consequently, we conclude that managing HOD through one-lever approaches (e.g., reducing nutrient input) are unlikely to be successful due to the primary importance of basin morphometry and the non-linear connection between river input and lake processes.

In testing the Algal Loading Hypothesis, we also found and reported the first documented observation of the potentially toxic cyanobacterium *Cylindrospermopsis* in Lake Erie and Sandusky Bay in 2005 (0.043 – 1.326 mg L^{-1} wet weight, 16 – 1942 trichomes mL^{-1}). As we also had many concurrently collected data, we quantified the physical and chemical parameters and the cyanobacterial community composition contemporaneous to its occurrence. We hypothesized that the high temperature, low light intensity, and high nutrient content of Sandusky Bay provided an ideal habitat for *Cylindrospermopsis*. Our predictions were consistent with published laboratory and field studies that showed these physical and chemical conditions facilitate *Cylindrospermopsis* growth. Using multivariate statistics, we found that *Cylindrospermopsis* biomass correlated with high temperatures and shallow depths, conditions often found in Sandusky Bay. Light climate and nutrient concentrations were not associated with *Cylindrospermopsis* biomass, most likely because the light climate did not systematically change during the season and because nutrients exceeded demand. Consequently, we proposed that *Cylindrospermopsis* will increase in importance in Lake Erie, as previous research on climate change in the Great Lakes region predicted future higher water temperatures and lower water levels.

Testing the Algal Loading Hypothesis was originally planned to include activities during two months of the year (April and August) in two of Lake Erie's large tributaries (Maumee and Sandusky Rivers). Additionally, one of the specific methods we planned on using to test phytoplankton productivity variations was the low-tech light/dark bottle method. However, as we began our Sandusky River sampling in April 2005, we found that there were many unanswered variables (such as seasonal dynamics) that needed to be more fully addressed.

Sampling the Maumee River also was much more difficult logistically. The Maumee River lacked an adjacent potentially-hypoxic zone similar to the Sandusky subbasin limiting the amount we could learn about the importance of phytoplankton load on hypolimnetic hypoxia zones. As a result of discussions with Dr. Robert T. Heath (Kent State University), we also switched from the less sensitive light/dark-bottle primary productivity techniques to more sensitive radiotracer techniques. These changes necessitated excluding the Maumee watershed from further examination. While this exclusion is unfortunate due to the importance of the Maumee system, we feel that the finer detail afforded the Sandusky system compensates for the lack of sampling in the Maumee system.

This project was originally scheduled to conclude at the end of calendar year 2006, however, as field collection did not cease until mid-September 2006, we requested and received an extension running through the end of calendar year 2007. With this extended time, we were able to complete nutrient determinations, plankton abundance enumerations, and phytoplankton physiology experiments.

Work products. In completing our testing of the Algal Loading Hypothesis, we involved two graduate students, seven undergraduate students working on independent projects, and numerous other technicians, collaborators at other institutions (namely, Drs. Erin Quinlan, United States Environmental Protection Agency; Douglas Kane, Defiance University; William Edwards, Niagara University; and Jeffrey Reutter, Ohio Sea Grant and F.T. Stone Laboratory). We developed one dissertation (Joseph D. Conroy), one peer reviewed publication (with another under review and several additional manuscripts in preparation), two peer reviewed abstracts (one of which was by an undergraduate working on one aspect of the project with two additional abstracts submitted), 19 presentations (2007: 10, 2006: 7, 2005: 2) at local, national, and international meetings, two undergraduate and graduate course laboratory and field experiments, and three popular press articles. We have appended copies of all of the publications, peer reviewed abstracts, and popular press articles.

<u>Doctoral Dissertation</u>

Conroy, J. D. 2007. Testing the algal loading hypothesis: The importance of Sandusky River phytoplankton inputs to offshore Lake Erie processes. The Ohio State University, 219 pp. 3 printed copies plus electronic copy attached.

<u>Peer reviewed publications</u>

Conroy, J.D., E.L. Quinlan, D.D. Kane, and D.A. Culver. 2007. *Cylindrospermopsis* in Lake Erie: testing its association with other cyanobacterial genera and major limnological parameters. *Journal of Great Lakes Research* 33: 519-535.

Conroy, J.D., D.A. Culver, and R.T. Heath. 2007. Gloom and blooms: simulating phytoplankton growth moving out of a tributary into a large lake. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* (*Proceedings of the International Society of Theoretical and Applied Limnology*). In review.

Conroy, J.D., D.D. Kane, E.L. Quinlan, W.J. Edwards, and D.A. Culver. 2008. Abiotic and biotic controls of phytoplankton biomass dynamics in a freshwater tributary, estuary, and large lake ecosystem: the Sandusky Bay chemostat. Target: *Freshwater Biology*. In prep.

Conroy, J.D., D.A. Culver, C.C. Clevinger, and R.T. Heath. 2008. Tributary, bay, and offshore phytoplankton productivity in Lake Erie – simple switching from light- to nutrient-limitation along the loading gradient? Target: *Limnology & Oceanography*. In prep.

Conroy, J.D., D.D. Kane, E.L. Quinlan, M.A. Thomas, W.J. Edwards, and D.A. Culver. 2008. Relative importance of allochthonous and autochthonous particulate organic matter and basin morphometry on hypolimnetic hypoxia in Lake Erie. Target: *Ecological Applications*. In prep.

Conroy, J.D., H. Zhang, L. Boegman, W.J. Edwards, and D.A. Culver. 2008. Dead zone dynamics: shaped by weather, disrupting ecosystems. Target: *Journal of Experimental Marine Biology and Ecology*. In prep.

Peer reviewed abstracts

Marasco, M.C., J.D. Conroy, D.D. Kane, L.E. Hitchcock, and D.A. Culver. 2007. Does tributary-derived phytoplankton biomass influence hypolimnetic hypoxia in the Sandusky subbasin of Lake Erie? *Ohio Journal of Science* 107: A-27.

Conroy, J.D., C.C. Clevinger, R.T. Heath, and D.A. Culver. 2007. Phosphorus limitation of phytoplankton growth along a transect from the Sandusky River to Lake Erie. *Ohio Journal of Science* 107: A-28.

Conroy, J.D. 2008. Comparing annual trends of dissolved oxygen depletion in Lake Erie: the importance of weather. *Ohio Journal of Science*. In review.

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Popular press articles

Conroy, J.D. 2006. What about the REU experience? *Twine Line* 28(1): 9.

Conroy, J.D. 2006. Dead zone expands. *North American Fisherman*. April: 27.

Conroy, J.D. 2005. The mini dead zone – an old problem in a new area in Lake Erie. *Twine Line* 27(3): 4-5.

Course laboratory and field exercises

Watersheds, Rivers, and Estuaries – Connecting People with Lakes. An all-day field trip developed for the course EEOB 125 – Introductory Aquatic Biology. The learning outcome for this exercise was to connect watershed processes with river water quality by studying changes in watershed land use moving from head waters to downstream areas.

Specifying the Phytoplankton Community Niche. A field and laboratory exercise developed primarily for the course EEOB 647 – Plankton taught on the main campus of The Ohio State University but adapted for use at OSU's field station on Lake Erie at F.T. Stone Laboratory in the course EEOB 125 – Introductory Aquatic Biology. The learning outcome for this exercise was to better understand temporal and spatial variability in the major parameters that determine phytoplankton growth.

Presentations

2007

Conroy, J.D. 2007. *Recent changes in the lower trophic levels of Lake Erie: the roles of external phosphorus load, exotic mussels, and algal loading*. Department of Zoology Seminar Series, Miami University. Oxford, Ohio, 1 October. Invited.

Conroy, J.D. 2007. *Connecting watersheds and large lakes: algal loading affects primary productivity in Lake Erie*. International Society of Theoretical and Applied Limnology, 30th Congress. Montreal, Canada, 13 August.

Conroy, J.D. 2007. *Phosphorus, cyanobacteria, and hypoxia, oh my! Continued impairments in Lake Erie.* F.T. Stone Laboratory Research Brief. Put-in-Bay, Ohio, 26 July.

Conroy, J.D., R.T. Heath, and D.A. Culver. 2007. *The importance of a large tributary (Sandusky River) as a source of cyanobacteria to a large lake (Lake Erie)*. International Association of Great Lakes Research, Annual Meeting. State College, Pennsylvania, 31 May.

Conroy, J.D., C.C. Clevinger, R.T. Heath, and D.A. Culver. 2007. *Phosphorus loading from a large tributary (Sandusky River) of Lake Erie: expansion of the classic model*. International Association of Great Lakes Research, Annual Meeting. State College, Pennsylvania, 29 May.

Clevinger, C.C., J.D. Conroy, and R.T. Heath. 2007. *Analysis of microbial community structure and ecosystem functions in Sandusky Bay*. International Association of Great Lakes Research, Annual Meeting. State College, Pennsylvania, 29 May.

Conroy, J.D., C.C. Clevinger, R.T. Heath, and D.A. Culver. 2007. *Phosphorus limitation of phytoplankton growth along a transect from the Sandusky River to Lake Erie*. Ohio Academy of Science, Annual Meeting. Highland Hills, Ohio, 21 April.

Marasco, M.C., J.D. Conroy, D.D. Kane, L.E. Hitchcock, and D.A. Culver. 2007. *Does tributary-derived organic phytoplankton biomass influence hypolimnetic hypoxia in the Sandusky subbasin of Lake Erie?* Ohio Academy of Science, Annual Meeting. Highland Hills, Ohio, 21 April.

Conroy, J. and D.A. Culver. 2007. *Cyanobacteria loading to Lake Erie: what is it good for?* Ohio Department of Natural Resources, Division of Wildlife Annual Research Review. Columbus, Ohio, 25 January.

2006

Conroy, J., D. Kane, E. Quinlan, M. Thomas, M. Beam, M. Dufour, and S. Percival. 2006. *The influence of algal loading on hypolimnetic hypoxia: the Sandusky Subbasin 'Dead Zone'*. Ohio Lake Erie Conference: Lake Erie Protection and Restoration – Our Achievements, Our Challenges. Elyria, Ohio, 7 September. Poster.

Kane, D.D., J.D. Conroy, E.L. Quinlan, W.J. Edwards, M.A. Thomas, and D.A. Culver. 2006. *Cyanobacterial loading to Lake Erie: nutrient and light effects in the Sandusky System*. International Association of Great Lakes Research, Annual Meeting. Windsor, Ontario, Canada, 26 May.

Quinlan, E.L., J.D. Conroy, D.D. Kane, and D.A. Culver. 2006. *A corridor to invasion:* Cylindrospermopsis *in Lake Erie*. International Association of Great Lakes Research, Annual Meeting. Windsor, Ontario, Canada, 25 May.

Conroy, J.D., E.L. Quinlan, M.A. Thomas, D.D. Kane, W.J. Edwards, and D.A. Culver. 2006. *Sandusky subbasin (Lake Erie) hypoxia – causes, development, and consequences*. International Association of Great Lakes Research, Annual Meeting. Windsor, Ontario, Canada, 23 May.

Conroy, J.D. 2006. *From streams to reservoirs and rivers to lakes: the effect of people on water resources*. Earth Day Environmental Justice Conference, Kent State University – East Liverpool. East Liverpool, Ohio, 22 April. Invited.

Stanford, K.M. and J.D. Conroy. 2006. *Are you experienced? Research experience for undergraduates program at F.T. Stone Laboratory*. Friends of Stone Laboratory and Ohio Sea Grant College Program Winter Program. Columbus, Ohio, 22 February. Invited.

Conroy, J.D., V.C. Crane, D.D. Kane, E.L. Quinlan, and D.A. Culver. 2006. *Cyanobacteria, zooplankton, and young-of-year percids: re-eutrophication and re-cruitment in Lake Erie*. Ohio Department of Natural Resources, Division of Wildlife Annual Research Review. Columbus, Ohio, 24 January.

2005

Conroy, J., D. Kane, E. Quinlan, M. Thomas, M. Beam, M. Dufour, and S. Percival. 2005. *The influence of algal loading on hypolimnetic hypoxia: the Sandusky Subbasin 'Dead Zone'*. Ohio Sea Grant Program Assessment. Columbus, Ohio, 21 August. Poster.

Conroy, J.D. 2005. *Watershed connections to Lake Erie: the Algal Loading Hypothesis*. F.T. Stone Laboratory Research Brief. Put-in-Bay, Ohio, 11 August.

The Lake Erie Protection Fund is supported by Ohioans who voluntarily purchase the "Erie... Our Great Lake" license plate, featuring the Marblehead Lighthouse as drawn by Ohio artist, Ben Richmond. The Lake Erie Protection Fund provided funding to this project. For more information, visit http://www.epa.state.oh.us/oleo/Grant/grants.htm

"In the waters of the Great Lakes are found species which. . .born in the semi-warmed pools and tepid swamp waters, and poured by nature's vicissitudes into the great preserving reservoir, where, removed from the sudden and violent changes of their native habitat, they soon adapt themselves to the equable conditions of the great body of water, and, with probably some constitutional changes, flourish amain."

- C.M. Vorce, 1881. Proc. Am. Soc. Microsc. 4: 51-52.

TESTING THE ALGAL LOADING HYPOTHESIS: THE IMPORTANCE OF SANDUSKY RIVER PHYTOPLANKTON INPUTS TO OFFSHORE LAKE ERIE PROCESSES

DISSERTATION

Presented in Partial Fulfillment of the Requirements for

the Degree Doctor of Philosophy in the Graduate

School of The Ohio State University

By

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* * * * *

The Ohio State University
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ABSTRACT

Studies of tributary-lake interactions most often consider only tributary nutrient stimulation of offshore phytoplankton growth. However, in freshwater ecosystems, input of tributary phytoplankton may directly affect offshore processes, such as nutrient cycling, phytoplankton-bloom formation, and hypolimnetic hypoxia. To explore these interactions, we propose the Algal Loading Hypothesis which predicts (1) tributaries contain phytoplankton; (2) tributary phytoplankton are light-limited due to high nutrient concentrations and high light attenuation; (3) offshore phytoplankton are nutrient-limited due to low nutrient concentrations and low light attenuation; and, (4) as tributary phytoplankton move offshore, productivity increases in response to greater light availability, using tributary-stored nutrients to drive offshore productivity. We used field sampling during April-September 2005 and 2006, phytoplankton physiological measures, and computer simulations to test these predictions and to determine the effect of loaded phytoplankton on offshore phytoplankton dynamics and hypolimnetic oxygen depletion in the Sandusky system (Sandusky River, Bay, and subbasin) of Lake Erie.

We found extremely high phytoplankton biomasses in the Sandusky River and Bay (Chapter 2) including an invasive cyanobacterial phytoplankter, *Cylindrospermopsis* (Chapter 5). Phytoplankton biomass was best predicted by the ratio of total inorganic nitrogen to total phosphorus (Chapter 2) whereas *Cylindrospermopsis* biomass correlated

with increased temperatures and shallow depths (Chapter 5). River and bay phytoplankton communities were not phosphorus limited but the offshore phytoplankton community was (Chapter 3). Phytoplankton communities at all sites were not strictly light limited; however, simulated phytoplankton productivity was most sensitive to light availability. For example, when we simulated increased light for the bay phytoplankton community, productivity increased > 200% (Chapter 3). Hypolimnetic oxygen depletion rates, however, were not affected by bay input of particulate organic matter but were most strongly influenced by basin morphometry (Chapter 4).

Overall, we found support for the predictions of the Algal Loading Hypothesis with the exception of light limitation for tributary phytoplankton. Input of tributary phytoplankton "primed" for growth offshore must be considered when attempting to manage offshore water quality, especially in a system extensively modified by human activity, such as Lake Erie.

Dedicated to Jennifer Anne, Elliott Marie, and Julianne Lynn Conroy

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A familiar African proverb says "it takes a village to raise a child." Similarly, it takes a village to train a scientist. I feel lucky to have been that scientist child surrounded by a very active, interesting, and dedicated group of villagers. While I wrote the ensuing dissertation, its completion would have been impossible without a great deal of help.

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PUBLICATIONS

Research Publications

1. Conroy, J.D. and D.A. Culver. 2005. Do dreissenids affect Lake Erie ecosystem stability processes? Am. Midl. Nat. 153: 20-32.

2. 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. Freshw. Biol. 50: 1146-1162.

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5. Conroy, J.D., D.D. Kane, and D.A. Culver. 2005. Declining Lake Erie ecosystem health – Evidence from a multi-year, lake-wide plankton study. *In* M. Munawar and R. Heath [eds.], Checking the Pulse of Lake Erie. Ecovision World Monograph Series, Aquatic Ecosystem Health and Management Society, Canada. In press.

6. Tew, K.S., J.D. Conroy, and D.A. Culver. 2006. Effect of lowered phosphorus fertilization rates on pond production of percid fingerlings. Aquaculture 255: 436-446.

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1. Conroy, J.D. and D.A. Culver. 2005. Lake Erie ecosystem change: phytoplankton communities. Ohio J. Sci. 105: A-32.

2. Marasco, M.C., J.D. Conroy, D.D. Kane, L.E. Hitchcock, and D.A. Culver. 2007. Does tributary-derived phytoplankton biomass influence hypolimnetic hypoxia in the Sandusky subbasin of Lake Erie? Ohio J. Sci. 107: A-27.

3. Conroy, J.D., C.C. Clevinger, R.T. Heath, and D.A. Culver. 2007. Phosphorus limitation of phytoplankton growth along a transect from the Sandusky River to Lake Erie. Ohio J. Sci. 107: A-28.

Popular Press Publications

1. Conroy, J.D. 2003. OSU's class sizes necessary, worthwhile. To the editor. Columbus Dispatch, January 29; Section A: 14.

2. Conroy, J.D. 2004. Regents' decision to cut lab funds short-sighted. To the editor. Columbus Dispatch, November 8; Section A: 6.

3. Conroy, J.D. 2005. The mini dead zone – an old problem in a new area in Lake Erie. Twine Line 27(3): 4-5.

4. Conroy, J.D. 2006. Dead zone expands. North Am. Fisherman April: 27.

5. Conroy, J.D. 2006. What about the REU experience? Twine Line 28(1): 9.

FIELDS OF STUDY

Major Field: Evolution, Ecology, and Organismal Biology

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5.7 Canonical correspondence analysis results showing the correlations between cyanobacterial genera (circles) and physical and chemical parameters (arrows) and the canonical axes. Panel (a) shows the relationship for the entire dataset and panel (b) shows the relationship when we excluded the data for 18 April 2005 at sites SBM and Soff. All physical and chemical parameters and cyanobacterial genera remained in the same quadrants in moving from (a) to (b) except *Cylindrospermopsis* sp. We included all important cyanobacterial genera (comprising > 94% of the total cyanobacterial biomass on all dates) in the analysis but only included the parameters with factor loading absolute deviations > 0.50 (from factor analysis, see Table 3). Abbreviations are given in Table 5.3 and the legend of Fig. 5.6.....199

CHAPTER 1

INTRODUCTION

Understanding energy and nutrient flow through human-impacted ecosystems remains a challenge for ecosystem ecology. While arguably no ecosystem extends beyond the reach of humans (Vitousek et al. 1997), people greatly affect large lake ecosystems for four main reasons. First, large lakes provide a consistent, readily accessible source of fresh drinking water that supports large human populations (Postel et al. 1996). Second, large lakes serve as important centers of commerce, providing a method of transport, an opportunity for commercial fishing, a source of cooling water for power-generating plant use, and a sink for the wastes of humans and manufacturing and agricultural industries. Third, large lakes serve as vast playgrounds, with humans crowding lakeshores for sunbathing, and the lake itself for fishing and boating (Carpenter et al. 1998). Fourth, large lakes have large watersheds, meaning that distant processes still affect lake function. Future understanding of how humans affect large lake ecosystems and for better forecasting of how large lakes will respond to disturbances requires identifying current energy and nutrient flow through these systems.

Lake Erie, the world's 11th largest lake by surface area and 17th by volume (Herdendorf 1990), has been greatly affected by people in its watershed. The greatest effect of the human population has been the accelerated eutrophication of Lake Erie by

increased nutrient loading (Beeton 1965, 2002). Two negative results of this loading are cyanobacteria blooms (Munawar and Munawar 1976, Makarewicz 1993, Conroy et al. 2005c), which often release toxic chemicals (Brittain et al. 2000, Rinta-Kanto et al. 2005), and the potential for increased extent and duration of hypolimnetic oxygen depletion (Charlton et al. 1993, Burns et al. 2005). After implementation of the Great Lakes Water Quality Agreement in 1978, phosphorus loading to Lake Erie decreased (Dolan 1993), total phytoplankton and total crustacean zooplankton biomass decreased (Makarewicz 1993a, 1993b), and cyanobacteria blooms became less frequent (Makarewicz 1993a). These observations were cited as evidence that the phosphorus control program was successful in remediating Lake Erie ecosystem problems (Bertram 1993). However, recent data reveal that cyanobacteria biomass increased during the last decade (Conroy and Culver 2005, Conroy et al. 2005c) and that hypolimnetic hypoxia continues to occur during summer (Charlton and Milne 2004, Burns et al. 2005) without a concomitant increase in external phosphorus loading (Dolan and McGunagle 2005). The recurrence of ecological problems in Lake Erie without associated changes in the forcing functions believed to control nutrient and energy flow demonstrates that further investigation into lower trophic level nutrient dynamics is warranted.

Most previous studies of large lake trophic dynamics simply consider within-lake processes. For example, the classic eutrophication models modeled lower trophic level (*e.g.*, chlorophyll *a* concentration) relationships to nutrient dynamics (*e.g.*, total phosphorus concentrations) as direct linear regressions or as linear regressions with time lags (OECD 1982). If tributaries were considered at all, they were modeled only as nutrient sources (OECD 1982, Carpenter et al. 1998) and lacked a biological load factor.

Treating tributaries solely as nutrient sources is not restricted to studies performed decades ago. Rather, even recent, well-cited studies restrict tributaries to serving as aseptic nutrient inputs to a lacustrine chemostat (see Fig. 1 in Carpenter et al. 1998), even though tributaries contain particulate matter including phytoplankton (Malmaeus and Håkanson 2003). Coastal marine studies recognize the important role of tributaries as particle loaders and emphasize their study to better understand offshore processes (Rabalais et al. 1996, Paerl et al. 1998).

Recognizing that Lake Erie system health has declined in recent years as evidenced by increases in total phytoplankton biomass, cyanobacteria biomass, and recurrent areas of hypolimnetic hypoxia and anoxia (Conroy et al. 2005b), I formulated three complementary, non-exclusive hypotheses to explain the recent recurrence of ecological problems in Lake Erie. These include (1) external phosphorus loading increased; (2) invasive dreissenid mussels altered Lake Erie's nutrient budget by increasing internal nutrient remineralization (recycling); and, (3) tributary-discharged phytoplankton formed a critical inoculum that increased the offshore phytoplankton growth rate, increasing total organic matter burden to the offshore. These hypotheses do not necessarily operate independently, nor are they an exhaustive list. Rather, they approach the problem of recent changes in Lake Erie water quality from a lower trophic level point-of-view and integrate lake function with watershed processes. I examined the first two hypotheses previously and present results below. The remainder of this dissertation tests the postulates and predictions of the third hypothesis.

Combining external phosphorus loading data (Dolan 1993, Dolan and McGunagle 2005) with published phytoplankton biomass data (Munawar and Munawar 1976,

Makarewicz 1993, Makarewicz et al. 1999) and recent data from the Lake Erie Plankton Abundance Study, and working with several coauthors, I found little correlation between external total phosphorus load and the total phytoplankton or cyanobacteria biomass in Lake Erie (Conroy et al. 2005c). In a related study, breakpoint analysis revealed that annual mean phytoplankton biomass increased from 1996, without a concurrent change in external phosphorus loading (Kane 2004). Because external phosphorus has not increased in recent years and does not correlate with either total phytoplankton or cyanobacteria biomass, I conclude that external phosphorus loading was not responsible for the increased phytoplankton and anoxia.

To test the role of invasive dreissenid mussels on internal nutrient cycling, I again worked with several coauthors to measure size-specific ammonium-nitrogen (N) and phosphate-phosphorus (P) excretion rates in mussels of various sizes in the laboratory (Conroy et al. 2005a). I merged the resultant excretion rate measures with mussel length and weight data to form linear regressions of excretion rate as a function of size. I then used these regressions in addition to field measures of mussel density and size distribution to compare the calculated dreissenid community N and P excretion rates with those of the crustacean zooplankton community. I found that dreissenids added about 50 mg m^{-2} day^{-1} of N (twice that of the crustacean zooplankton community) and 3 mg m^{-2} day^{-1} of P (one-quarter that of the crustacean zooplankton community). While I calculated these estimates from laboratory excretion measurements and field abundance surveys from only a few sites, they emphasize the importance of dreissenids in converting particulate nutrients to soluble nutrients as emphasized by other scientists (Hecky et al. 2004). Furthermore, dreissenid mussel excreta are of sufficiently low nitrogen to

phosphorus ratio to favor cyanobacteria blooms (Conroy et al. 2005a), especially in lakes with total phosphorus concentrations less than 25 μg L^{-1} (Raikow et al. 2004), but greater than 9 μg L^{-1} (Sarnelle et al. 2005).

The Algal Loading Hypothesis (ALH) applies decades of research on marine estuaries to large lake ecosystems. Many marine studies have shown that tributary phytoplankton and nutrients affect offshore processes such as hypolimnetic hypoxia (Rabalais et al. 1996, Paerl et al. 1998) and harmful algal blooms (Paerl 1988) in large estuaries, including the Mississippi River delta, Chesapeake Bay, and the Neuse River estuary. In contrast to marine estuaries, tributary phytoplankton entering freshwater estuaries (drowned river mouths) eventually flow into freshwater offshore areas without experiencing the salinity shock that kills phytoplankton in marine systems as they move from freshwater to marine water. So, freshwater tributary phytoplankton may well continue to grow in the lake. Furthermore, these tributaries have higher nutrient concentrations and turbidity than do the offshore areas, phytoplankton entering freshwater estuaries and offshore areas may be "primed" for growth. That is, tributary phytoplankton is presumed to be nutrient replete but light limited and, once loaded into the offshore areas, light limitation decreases and phytoplankton can use stored nutrients to grow rapidly, increasing the total organic matter burden to the offshore area. Growth of phytoplankton from tributaries can increase absolute organic matter load to the hypolimnion in thermally stratified regions of the lake, increasing hypolimnetic respiration and sediment oxygen demand (Edwards et al. 2005). Phytoplankton loaded from the tributaries also may be composed primarily of cyanobacteria because nutrients are abundant there, thereby initiating and/or contributing to offshore cyanobacteria

blooms. My dissertation focuses on deriving a better understanding of the relationships between watershed-derived nutrients, phytoplankton growth, and offshore ecological problems.

Postulates and Predictions of the Algal Loading Hypothesis

The above discussion implicitly details the postulates (statements of facts) and predictions (statements of expected results) that form the Algal Loading Hypothesis (ALH). Here, I make those implicit postulates and predictions explicit:

Postulate 1: Lake Erie's tributaries contain phytoplankton.

Postulate 2: Nutrient concentrations and suspended sediments are high in Lake Erie's tributaries.

Prediction i: Light limits tributary phytoplankton growth.

Postulate 3: Nutrient concentrations and suspended sediments in offshore Lake Erie are low relative to the tributaries.

Prediction ii: Nutrients limit offshore phytoplankton growth.

Postulate 4: Tributary phytoplankton, sediment, and nutrients flow from the tributary into the offshore region forming loading gradients.

Prediction iii: Tributary phytoplankton are nutrient replete and respond to decreased light-limitation as they flow from the river to the offshore area where they grow and increase offshore hypolimnetic oxygen depletion.

Testing these postulates and predictions of the ALH comprises the dissertation that follows. In the remainder of this Introduction, I will first describe the tributary system used to evaluate the ALH; next, I will describe historical studies on Sandusky Bay to put

my current study in an historical context; then, I will briefly describe which aspects of the ALH will be tested in each dissertation chapter; and, finally I will summarize the major research findings I found working with several coauthors as they relate to each chapter and the postulates and predictions of the ALH.

Study Site

Lake Erie has 20 significant inlet streams and rivers (inflows of > 5 m^3 s^{-1}, Bolsenga and Herdendorf 1993). Of these, the Detroit River provides most of the water (Bolsenga and Herdendorf 1993), while other tributaries, especially the Maumee and the Sandusky rivers, provide most of the nutrients and sediments due to the prevalence of agriculture in their watersheds (Richards et al. 2002).

A rigorous study of the effects of tributary phytoplankton on offshore processes and on the growth-limiting factors of tributary and offshore phytoplankton requires an appropriate study site. I chose the Sandusky system for several reasons. First, several types of water bodies compose the Sandusky system, with water flowing from a river source, into a shallow bay, and then to an offshore subbasin, allowing me to determine how phytoplankton communities and nutrient concentrations change as water flows from one component to the next. Second, other scientists have previously studied phytoplankton dynamics in this system allowing me to place the current research in an historical context. Third, logistically, the Sandusky system provides easy access from F.T. Stone Laboratory (on South Bass Island, Ohio) and from laboratories in Columbus, Ohio. Fourth, and most importantly, the structure of the Sandusky system, with a tributary (the Sandusky River) supplying nutrients and presumably phytoplankton to a

shallow, productive basin (Sandusky Bay) which in turn empties into a less productive basin that often becomes hypoxic or anoxic in the hypolimnion (Sandusky subbasin) simulates the structure of Lake Erie's Maumee River, western basin, and central basin. Consequently, by studying the Sandusky system, I may also gain insights into the function of a larger portion of Lake Erie without having the logistical difficulties of studying the entire western and central basins.

The Sandusky River begins 90 km south of its confluence with the bay and has a watershed area of about 3,700 km^2 (Fig. 1.1). Sandusky Bay has an area of 162 km^2 (CLEAR 1975), an average depth of 2.6 m (Richards and Baker 1985), and a total volume of 0.423 km^3. A natural constriction in conjunction with railroad and highway bridges at the mid-point separates the bay into western and eastern portions (Fig. 1.1). Sandusky Bay then flows into the Sandusky subbasin through a narrow connecting channel between the Marblehead and Cedar Point peninsulas. The Sandusky subbasin, an approximately 900 km^2 diamond-shaped area with a mean depth of 13.3 m and a total volume of 11.7 km^3, lies between the western and central basins of Lake Erie. Its boundaries are the Pelee-Lorain ridge, the shoreline from Lorain to the Marblehead peninsula, and a line back to the northern terminus of the Pelee-Lorain ridge (Fig. 1.1).

Previous Studies on Sandusky System Plankton Ecology

Research on the relations of the flora and fauna of Sandusky Bay with time of year, weather, Sandusky River discharge, and nutrient loading has a long history. Vorce (1881) comments that the abundance of *Aphanizomenon* in Sandusky Bay was of such a quantity to "line the shores with a film of yellowish green scum for miles." Kellicott

(1896, 1897) published the first studies of investigations on the rotifers of Sandusky Bay. Kellerman (1901) briefly mentioned that the study of algae of this area would provide a sufficient "harvest" for "enthusiastic students" but did not give a description of the organisms present. Such a description was provided by the species list of Riddle (1902). Of particular note in this list is the presence of a still common cyanobacterial species, *Aphanizomenon flos-aquae*, and the dominance of desmids (Chlorophyta: Chlorophyceae: Zygnematales: Desmidiaceae). Riddle did not report the relative abundances, biomasses, or dates of collection. Scientists conducted these natural history studies from The Ohio State University's Lake Erie laboratory in Sandusky, Ohio, the precursor to F.T. Stone Laboratory.

Chandler and Bodenlos (1938) published the first limnological study of Sandusky Bay. Working from F.T. Stone Laboratory, the authors conducted a 3-week investigation of the physical, chemical, and biological dynamics of the upper bay (west of the mid-point constriction) at 10 stations during August. They found a predominantly eutrophic system (mean Secchi disk transparency = 17.1 cm, total phytoplankton density = 1.20 x 10^6 phytoplankters L^{-1} versus the western basin average of 0.19 x 10^6 phytoplankters L^{-1} [Wright and Tidd 1933], prevalence of Cyanophyta = 0.97 x 10^6 cyanophytes L^{-1} in Sandusky Bay versus 0.06 x 10^6 L^{-1} in the western basin of Lake Erie, [Wright and Tidd 1933], especially the nitrogen fixers, *Aphanizomenon* spp. and *Anabaena* spp. [averaged 71% of the total density]). Chandler and Bodenlos (1938) also reported a high density of zooplankters (809 L^{-1} excluding Protozoa) with the density of cyclopoid copepodites (54 L^{-1}) three times greater than, the density of nauplii (105 L^{-1}) six times greater than, and daphnids (3 L^{-1}) approximately equal to the densities found in the island region of Lake

Erie. Chandler and Bodenlos (1938) concluded that the upper region of Sandusky Bay was highly productive, that physical and chemical parameters were similar between all 10 stations, that *Aphanizomenon* spp. were the most important phytoplankton taxa at this time of year, and that sufficient numbers of zooplankton made this region an important area for larval fish growth.

During February through June 1954, McQuate (1954) studied light penetration (by calculating the decimal reduction distance [DRD] or 10% light penetration [~ Secchi disk transparency depth] from photronic cell measurements), phytoplankton standing crop (in volumetric units of $\mu m^3\ L^{-1}$), rates of photosynthesis and respiration (using pH changes standardized by Winkler methods), and other limnological data (*i.e.*, pH, alkalinity, temperature, weather conditions, etc.) in the western part of Sandusky Bay near the confluence of the Sandusky River and the bay. He found that DRD varied from 0.03 to 0.92 m (mean of 0.36 m), that phytoplankton standing crop varied from approximately 0.01 to 4.1 x $10^{10}\ \mu m^3\ L^{-1}$ (or 0.1 to 41 mg L^{-1} assuming a specific density of 1 g cm^{-3}), and that the rate of photosynthesis (mean rate of 74.0 μmol CO_2 $10^{10}\ \mu m^{-3}\ h^{-1}$) varied inversely with standing crop and DRD and showed the typical pattern with increasing light (initial linear increase that reaches an asymptote with photoinhibition at high light). The Bacillariophyceae (Chrysophyta) dominated the phytoplankton community (96.7% of the total density with *Cyclotella* spp. early in the season and *Melosira* [*Aulacosira*] spp. later in the season), with lesser contributions by the Chlorophyceae (Chlorophyta; < 1%) and *Oscillatoria*, *Microcystis*, and *Aphanizomenon* of the Cyanophyta. His study represented the first attempt to make process-based measures of plankton ecology in Sandusky Bay.

The Center for Lake Erie Area Research (CLEAR) conducted the most extensive study on Sandusky Bay in terms of number of parameters measured and sampling throughout nearly the entire year (CLEAR 1975). The study provided comprehensive baseline data for a feasibility study of situating a nuclear power plant on the southern shore of the far western basin of Sandusky Bay. During November 1972 through November 1974, CLEAR examined multiple physical, chemical, and biological parameters at 38 stations throughout Sandusky Bay. Thirty-two stations were located adjacent to the potential site of the plant, two were at the river mouth, two others were farther east in the western portion of the bay, and the final two were in the eastern basin of Sandusky Bay. CLEAR (1975) found extremely high concentrations of phosphate (range = 10 – 3600 $\mu g\ L^{-1}$ as orthophosphate, mean = 510) and nitrate (range = 10 – 37000 $\mu g\ L^{-1}$ as nitrogen, mean = 8150). The use of Hach analytical kits may have overestimated these concentrations, but other investigators using other methods also found high concentrations in the Sandusky River (orthophosphate mean = 76 $\mu g\ L^{-1}$ and nitrate-N mean = 5150 $\mu g\ L^{-1}$, D.B. Baker, Heidelberg University, *personal communication* in CLEAR 1975). For the phytoplankton community, the CLEAR study found August values lower (mean = 0.03×10^6 phytoplankters L^{-1}) than those reported by Chandler and Bodenlos (1938) but a continued dominance by *Aphanizomenon flos-aquae*. For the zooplankton community, CLEAR found higher August densities of copepods (215 L^{-1} combined for copepodites and nauplii with the latter being "dominant") and cladocerans (56 L^{-1}). Additionally, they found calanoid copepods (both copepodites and nauplii) to be present. The differences between the CLEAR (1975) study and the Chandler and Bodenlos (1938) study may be real or could be an artifact of

differing sampling and analytical methods between studies and/or multiple years of study and the inclusion of the lower bay east of the mid-point constriction in the CLEAR study. Importantly, the CLEAR study concluded that the Sandusky Bay ecosystem was highly productive and that it would continue to become more eutrophic unless conservation practices were implemented in the watershed, thereby making the connection between causes in the watershed and effects in the water body for the first time.

Building upon the concept of the watershed affecting Sandusky Bay ecology and recognizing that sporadic high precipitation events govern the discharge from the bay into Lake Erie, Richards and Baker (1985) examined the interaction between the magnitude of river flow and the amount of nutrients (primarily dissolved and total phosphorus, nitrate- and nitrite-nitrogen, and silica) and phytoplankton (as chlorophyll *a*) found in the bay. Specifically, they hypothesized that during low-flow conditions, the bay processes nutrients (*i.e.*, they would either be taken up by the biota or would settle out to the sediments) and any effect on Lake Erie would be restricted to the nearshore. Conversely, under high-flow conditions (*i.e.*, at some time after a storm), the momentum of the river discharge breaks the long-shore transport in Lake Erie, and nutrients, sediment, *and* biological load flow freely out to the offshore region of the lake. The authors did not study the ultimate fates of these loaded materials but conjectured that a storm "pulse" could load sufficient organic matter (including phytoplankton) to create a substantial oxygen sink for the offshore hypolimnion. Sampling successively before, during, and after high-load events at river, bay, and lake sites, they plotted the advance of a plume of nutrients, sediments, and/or phytoplankton through the bay and out into the lake stations. They estimated that during storms, nutrient concentrations decreased between 66-90% for

total phosphorus, 67-95% for soluble reactive phosphorus, and 31-97% for nitrate-nitrogen from the confluence of the river and bay to the confluence of the bay and lake. Storm characteristics (*e.g.*, resultant river flow velocity) defined the range in nutrient amounts processed. Under low-flow conditions, the authors found higher chlorophyll *a* concentrations and lower nutrient concentrations in the bay indicating that phytoplankton may have a better opportunity to grow during low-flow conditions. Richards and Baker found general support for their conceptual models for differences in bay function and influence on Lake Erie under different flow regimes. Most importantly, even during high-flow events, the bay and its associated physical, chemical, and biological features remove a large portion of the nutrients loaded by the Sandusky River (Richards and Baker 1985). Also, they found that a large amount of chlorophyll (> 100 $\mu g\ L^{-1}$; *e.g.*, phytoplankton) moved from the bay to the lake under low-flow conditions. Consequently, Sandusky Bay removes nutrients while growing phytoplankton, potentially serving as a "priming point" for growth where nutrients, temperature, and phytoplankton interact before transport to the lake and a biological filter that removes nutrients from the watershed before they influence within-lake processes.

Expanding on the Sandusky Bay phytoplankton growth and nutrient supply hypotheses, Garono (1993) undertook extensive studies of phosphorus supply, forms, and use by both bacterioplankton and phytoplankton along a transect from the confluence of the Sandusky River and Bay out to the offshore waters of Lake Erie during the summers of 1990 and 1991. Garono found that phosphorus did not simply decrease along the transect as expected from a simple mixing of river and lake water model. Rather, total (TP) and particulate phosphorus (PP; both bacterial and phytoplankton particulate

phosphorus) decreased along the transect while soluble reactive phosphorus (SRP) was lower at bay sites than at river or lake sites and total soluble phosphorus (TSP) increased at bay sites. These patterns indicated that some component of TSP was created in the bay. Garono (1993) hypothesized that this component was dissolved organic phosphorus (DOP), implying that DOP is an important phosphorus source for the bacterio- and/or phytoplankton communities in Sandusky Bay and that the biota of Sandusky Bay serve to transform phosphorus from SRP into DOP. Using nutrient-uptake assays and other methods of assessing nutrient limitation, he found that Sandusky Bay phytoplankton communities were generally not phosphorus-limited. Interestingly, however, he found that phosphorus turnover times were shortest at bay sites (both west and east of the mid-point constriction) and that some evidence exists for nutrient limitation (turnover times < 20 min, Lean et al. 1983) at an eastern bay site during June through August and at a western bay site in August of 1990 with no limitation at a river site or in Lake Erie. In 1991, the river site had a short phosphorus turnover time indicating phosphorus limitation in May, the western bay site was limited in July, the eastern bay site in May, July, and August, and the offshore site in May. Recognizing that phosphorus is not homogenously distributed in the water column or throughout time, Garono concluded that phytoplankton in Sandusky Bay acclimated to varying phosphorus supply by varying the uptake and storage mechanisms throughout the season. Furthermore, due to relatively high phosphorus concentrations without a corresponding high phytoplankton density, Garono conjectured that light limitation may have been important in restricting phytoplankton growth at river sites. Garono et al. (1996) analyzed phytoplankton community composition data to determine whether Sandusky Bay communities were merely mixtures

of river and lake communities or were distinct. Using detrended correspondence analysis, Garono et al. (1996) determined that presence-absence data alone did not resolve the phytoplankton data into groups, but inclusion of abundance data classified the data into bay, lake, and river communities along an axis that included the variables, total phosphorus, soluble reactive phosphorus, and phytoplankton phosphatase activity (among others) indicating that phosphorus dynamics separated the phytoplankton communities (Garono et al. 1996). Taken together, the results of their study indicate that phosphorus, light, and the various phytoplankton taxa interact along the river to lake transect in a non-linear manner (*i.e.*, phosphorus concentration does not necessarily predict the phytoplankton community composition), making understanding of the lower trophic level dynamics in the Sandusky system more complex.

Previous studies of Sandusky Bay focusing on natural history descriptions of taxa present (Vorce 1881, Kellicott 1896, 1897, Kellerman 1901, Riddle 1902) showed the prevalence of Cyanophyta during the late 19th and early 20th centuries and indicated that Sandusky Bay was already a productive system at this time. Later limnological studies (Chandler and Bodenlos 1938, McQuate 1954) further quantified high phytoplankton densities during both the spring (primarily consisting of the Bacillariophyceae; McQuate 1954) and summer (primarily consisting of Cyanophyta, especially *Aphanizomenon flos-aquae*; Chandler and Bodenlos 1938). These studies presented the first data on physical (*i.e.*, temperature and light penetration) and chemical (*i.e.*, pH and dissolved oxygen) parameters. Later studies began with physical, chemical, and biological surveys to determine the trophic relationships of the biota and limitations to growth (CLEAR 1975, Garono 1993) or the importance of sporadic precipitation in the watershed in affecting

bay influence on Lake Erie (Richards and Baker 1985). Taken together, these studies emphasize the importance of the watershed in shaping the physical, chemical, and biological composition and interrelations of the Sandusky Bay ecosystem. Also, these studies emphasize the importance of Bacillariophyceae in spring and Cyanophyta in summer and light and nutrients in limiting growth of the phytoplankton community. Understanding how concurrent changes in environmental parameters affect phytoplankton growth in the bay and subbasin and how phytoplankton discharge from Sandusky Bay into the Sandusky subbasin affects subbasin lower trophic levels and hypolimnetic dissolved oxygen dynamics remains to be studied. Testing the Algal Loading Hypothesis in this dissertation will fill in these knowledge gaps.

Overview of Chapters

To test the postulates and predictions of the Algal Loading Hypothesis, I used a combination of field, laboratory, and modeling approaches. Here, I describe how I organized the chapters to test ALH and briefly describe the major findings. I emphasize whether my study supported or contradicted the postulates and predictions of the ALH. A conceptual diagram of the organization among chapters follows (Fig. 1.2).

Chapter 2 tests Postulate 1 of the ALH using regular field sampling of the plankton community, chemical concentrations, and physical parameters. I found high phytoplankton biomass in the Sandusky River at times during the growing season (April – September) and extremely high biomass in the Sandusky Bay during the entire growing season. These findings support Postulate 1 of the ALH. Phytoplankton biomass was lower in the Sandusky subbasin. The community composition in Sandusky Bay was

generally distinct from the river and subbasin, but at times there was evidence for similar community composition and biomasses at a Sandusky Bay station and a station at the junction of the bay and subbasin. Using an information-theoretic approach, I found that phytoplankton biomass in the Sandusky system was predicted by bottom-up, abiotic factors (most support was for the ratio of total inorganic nitrogen and total phosphorus); little support existed for top-down, biotic control by herbivorous zooplankton. Analyses in this chapter reveal that Sandusky Bay mediates water quality from the Sandusky River before it enters the Sandusky subbasin by using nutrients flowing into the bay to grow large amounts of phytoplankton. Export of this phytoplankton to the subbasin seems restricted to the nearshore areas but additional research is needed to determine the ultimate fate of loaded phytoplankton.

Chapter 3 tests Postulates 2 and 3 and Predictions i and ii of the ALH using laboratory determinations of phytoplankton growth rates, phosphorus uptake rates, and phosphorus debt and simulations of phytoplankton primary production as affected by varying light climate at sites in the river, bay, and subbasin. I found that nutrients decreased from the river into the bay and offshore into the subbasin and phosphorus concentration and phytoplankton physiological indices revealed periods of phosphorus limitation occurred more often for the subbasin phytoplankton community than either the river or bay communities. These findings support Postulates 2 and 3 and Prediction ii of the ALH. Although light increased moving from the river, into the bay, and offshore, I did not find clear evidence of light limitation in the river and bay, most likely due to the shallow depths in these areas. This finding does not support Prediction i of the ALH. Sensitivity analyses of a phytoplankton productivity simulation model revealed that with

increased light, river and bay phytoplankton communities could greatly increase their productivity, supporting the ALH prediction for loaded phytoplankton affecting offshore processes by growing rapidly upon entering the offshore lake system. Rapid phytoplankton growth following input may synergistically interact with the effect of tributary nutrient load, making the resultant effect of tributaries on offshore processes greater than the effect of nutrients or phytoplankton load individually.

Chapter 4 tests Postulate 4 and Prediction iii of the ALH using determinations of hypolimnetic dissolved oxygen depletion rates and the correlation between dissolved oxygen depletion rates and morphometric and environmental variables. I also used carbon stable isotope analyses to determine whether tributary-derived or epilimnion-derived organic matter was the source of hypolimnetic organic matter in the Sandusky subbasin. I found that hypolimnetic oxygen depletion rates were most affected by hypolimnion thickness such that shallow sites had higher volumetric depletion rates (mg O_2 L^{-1} mo^{-1}) than deeper sites. Large-scale water movement caused by seiches or tributary load also affected dissolved oxygen dynamics. Stable isotope analyses revealed that hypolimnetic seston most likely originated in the epilimnion, indicating the importance of epilimnion production in supplying organic matter to the hypolimnion. These findings show a connection between tributary and offshore systems, supporting Postulate 4, and give some indication of the importance of tributary phytoplankton in affecting dissolved oxygen depletion rates as proposed by Prediction iii of the ALH. However, much work remains to clearly identify this connection and to quantify how tributary-loaded phytoplankton affect hypolimnetic dissolved oxygen depletion rates.

Finally, Chapter 5 presents a case study of how physical, chemical, and biological parameter dynamics along the loading gradient from river, to the bay, and into the subbasin contribute to the success of the invasive phytoplankter *Cylindrospermopsis*. I found that *Cylindrospermopsis* occurred in the Sandusky system throughout 2005 and that its biomass correlated with high temperatures and shallow depths. Biomass of *Cylindrospermopsis* also correlated with that of *Oscillatoria* spp. and *Microcystis* spp. It did not correlate with light availability or nutrient concentrations, most likely because light conditions were similar at the stations throughout the sampling season and because nutrients were always in high concentrations in the river and bay. These results suggest that *Cylindrospermopsis* could become more prevalent in the Lake Erie and Laurentian Great Lakes ecosystems as regional climate change models suggest that Lake Erie will become warmer and shallower with continued climate change.

In this project, I sought to identify how phytoplankton loaded from a tributary of Lake Erie affected offshore processes by proposing and testing the Algal Loading Hypothesis. I found (1) large phytoplankton amounts in the tributary; (2) that tributary phytoplankters were phosphorus-replete and increased productivity in simulations of increased light availability (lower attenuation coefficients); and, (3) that offshore phytoplankton were phosphorus-limited. Loaded phytoplankton did not directly perturb offshore hypolimnetic oxygen depletion; I found that basin morphometry was more important. Accordingly, the classic tributary-lake model which considers only nutrient load from tributaries to offshore areas may need to be exchanged for one that includes the effect of loaded phytoplankton.

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Fig. 1.1. Map of the Sandusky system (lower panel) including the Sandusky River, Bay, and subbasin and its location (small heavy rectangle) in context of the other Laurentian Great Lakes (upper panel). The Sandusky subbasin is delineated by the Lorain-Pelee ridge on the northeast, and imaginary lines running from Lorain, Ohio, to Huron, Ohio on the southeast, from Huron to the eastern tip of the Marblehead Peninsula on the southwest, and from the tip of the Marblehead Peninsula to the northern tip of the Lorain-Pelee ridge on the northwest. Open squares show major cities in the region and depths (m) are indicated by bathymetric lines. Note that the width of the river is exaggerated to aid in illustration.

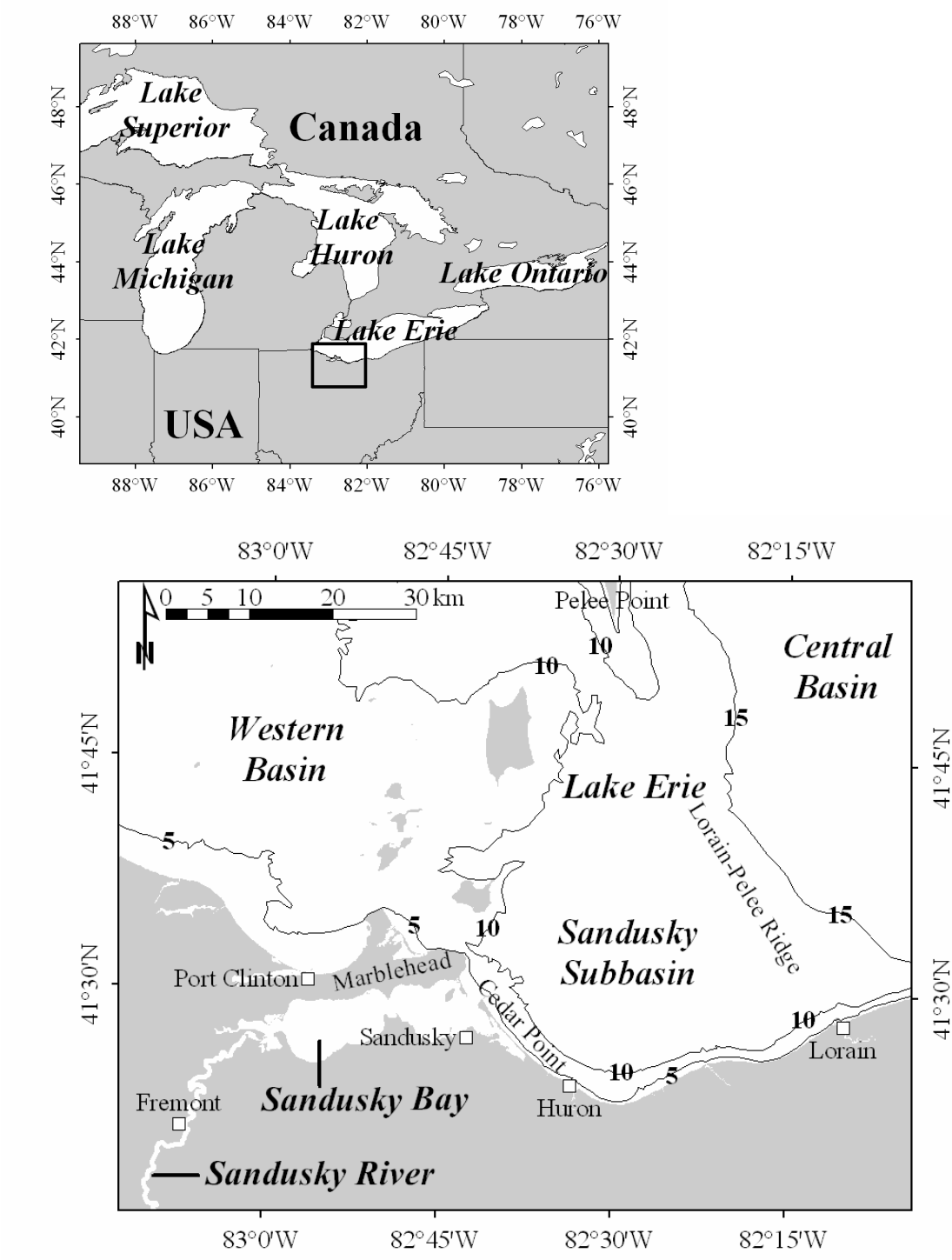
88°W
86°W
84°W
82°W
80°W
78°W
76°W
48°N
46°N
44°N
42°N
40°N
Lake Superior
Canada
Lake Michigan
Lake Huron
Lake Ontario
Lake Erie
USA
83°0'W
82°45'W
82°30'W
82°15'W
41°45'N
41°30'N
0 5 10 20 30 km
N
Pelee Point
Central Basin
Western Basin
Lake Erie
Lorain-Pelee Ridge
Sandusky Subbasin
Port Clinton
Marblehead
Cedar Point
Sandusky
Lorain
Fremont
Sandusky Bay
Huron
Sandusky River
5
10
15

Fig. 1.1.

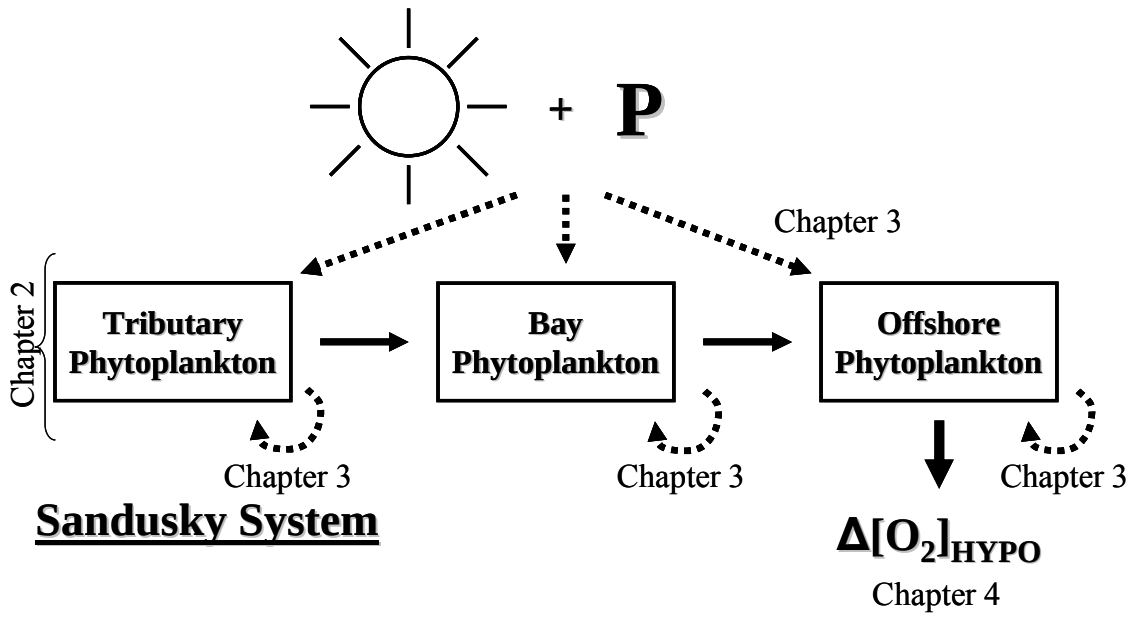

Fig. 1.2. Conceptual diagram outlining the connections between the dissertation chapters. Chapter 2 identifies and describes tributary, bay, and offshore phytoplankton communities and the physical, chemical, and biological parameters along the loading gradient from river to subbasin. This chapter tests Postulate 1 of the Algal Loading Hypothesis (ALH) and is represented by the boxes and solid arrows in the center of the figure. Chapter 3 measures the growth rates of the phytoplankton from various regions and tests whether light limits tributary phytoplankton growth and whether nutrients limit offshore phytoplankton growth (Postulates 2 and 3 and Predictions i and ii of the ALH); the dotted arrows connecting symbols for light and phosphorus at the top of the figure with phytoplankton from the various regions represent this chapter; the semi-circular dotted arrows represent phytoplankton growth rates. Chapter 4 tests whether offshore phytoplankton that originates in productive basins affects hypolimnetic oxygen dynamics (Postulate 4 and Prediction iii); the bolded arrow and symbol for dissolved oxygen dynamics represent this section. Finally, Chapter 5 applies the ALH to the invasion of the exotic phytoplankter *Cylindrospermopsis* sp. by testing what physical, chemical, and biological parameters facilitate this invasion.

CHAPTER 2

ABIOTIC AND BIOTIC CONTROLS OF PHYTOPLANKTON BIOMASS DYNAMICS IN A FRESHWATER TRIBUTARY, ESTUARY, AND LARGE LAKE ECOSYSTEM: THE SANDUSKY BAY CHEMOSTAT

Introduction

Tributaries serve as the connection between watershed processes and lakes, conducting agricultural (*e.g.*, suspended sediments (SS), nitrogen (N), and phosphorus (P)), municipal (*e.g.*, N and P from waste water treatment plants), and industrial (*e.g.*, polychlorinated biphenyls and heavy metals) wastes, among others, to distant receiving waters. When considering cultural eutrophication of estuaries in freshwater and marine ecosystems, scientists usually consider only the delivery of growth-limiting nutrients from tributaries (Carpenter et al. 1998, Burkholder et al. 2006, Paerl et al. 2006), focusing on the balance of point sources (*i.e.*, waste water treatment plants, manufacturing effluents) and non-point or diffuse sources (*i.e.*, row-crop agriculture, concentrated animal feeding operations) of nutrient to phytoplankton growing offshore. In marine estuaries, reduced riverine phytoplankton biomass (Muylaert and Sabbe 1999, Lionard et al. 2005) with increased salinity due to osmotic stress (Kirst 1990) justifies viewing tributaries solely as nutrient sources, although the load of decaying particulate organic matter may be important (Paerl 1988, Paerl et al. 1998). In freshwater estuaries, however, phytoplankton can increase their growth rates upon entering the estuary due to

increased light penetration once suspended sediments in the river settle out (Muylaert et al. 1997, Conroy 2007b), and in many freshwater systems, the load of healthy phytoplankton may serve as an inoculum and affect offshore phytoplankton growth.

If freshwater tributaries link watersheds with lakes, then estuaries are the zones of primary interaction between these two systems. An estuary, classically defined, consists of a semi-enclosed water body connected to open waters with saline water that is diluted with fresh, tributary-delivered water (Schubel and Pritchard 1971). Herdendorf (1990) modified this classical definition to include Great Lakes' estuaries, by changing the last aspect to include the "mixing of two kinds of water." Although Schubel and Pritchard (1990) rejected this modification of the classical definition on several grounds, other scientists recognized its applicability to all lakes (generalizing the term to a lacustrine estuary; Dyer 1990, Odum 1990) and subsequent reviews have identified similarities between marine estuaries and their lacustrine equivalents (Bedford 1992). In large lake systems, lacustrine estuaries may be especially important in mediating tributary water quality before it enters the offshore waters (Moll et al. 1980, Klarer and Millie 1989, Garono et al. 1996).

The Laurentian Great Lakes in general, and Lake Erie in particular, have been extensively modified by European settlers living in the watershed (Sly 1976). Most of the original wetlands in Lake Erie's watershed have been drained for agriculture (Richards et al. 2002b), removing much of the natural capacity of the watershed to buffer human influence on the Lake Erie ecosystem while modifying the land in ways that increase human impact. Further, continued development in the Great Lakes basin has focused on coastal areas (Wolter et al. 2006).

Conspicuous blooms of cyanobacteria and fish kills due to hypolimnetic hypoxia in the late 1960's and early 1970's caused public outcry throughout the Great Lakes and focused scientists of the region on determining the ultimate cause of these impairments (McGucken 2000). Although excessive watershed nutrient load (especially P from detergents) was mitigated through the Great Lakes Water Quality Agreement (Dolan 1993), and cyanobacterial blooms decreased in the mid-1980's (Makarewicz 1993), hypolimnetic hypoxia continued to be a problem (Charlton et al. 1993). Recent data reveals that increased total phytoplankton and cyanobacteria biomasses (Conroy et al. 2005c) and prevalent hypolimnetic hypoxia (Charlton and Milne 2004, Burns et al. 2005) still occur in Lake Erie. Several hypotheses have been proposed to explain recent increased phytoplankton biomass and continued hypolimnetic hypoxia including (1) increased external P load (Conroy et al. 2005c); (2) increased internal P remineralization due to the invasion of dreissenid mussels (Conroy et al. 2005a); and/or, (3) the Algal Loading Hypothesis (ALH; Conroy et al. 2005b, Conroy 2007a). Other studies have shown that external total P load was similar in recent years to the low values during the 1980's (Dolan and McGunagle 2005, Conroy et al. 2005c) and that dreissenid mussels' contributions may be important (Conroy et al. 2005a, 2005c); in this study, we test predictions of the ALH.

The ALH proposes that phytoplankton in the tributaries of lakes are nutrient replete, but light limited, due to the high nutrient and sediment concentrations in rivers, and that once this phytoplankton is loaded offshore, available light increases and phytoplankters use nutrients stored while in the river to form blooms in the lake. Tributary-derived phytoplankton, therefore, would directly affect the offshore lake

ecosystem in addition to any tributary-derived nutrients reaching the lake and facilitate the growth of within-lake phytoplankton. However, lacustrine estuaries also may mediate the effect of tributary-derived phytoplankton and nutrients on offshore processes by providing suitable habitat to facilitate phytoplankton growth and/or sedimentation in the estuary. Depending on the amount of nutrients and phytoplankton loaded to the estuary and the prevailing hydrodynamic conditions, the lacustrine estuary thus (1) may serve solely as a nutrient source for the lake (*i.e.*, little nutrient remediation when estuarine phytoplankton growth is low or flow is high); (2) may remediate the effect of tributary-derived products for the lake (*i.e.*, tributary nutrients are taken up by growing estuarine phytoplankton, with subsequent consumption of phytoplankton by estuarine zooplankton or phytoplankton death with burial in estuarine sediments); or, (3) may be a phytoplankton source while depleting nutrients (*i.e.*, estuarine phytoplankton grow in the estuary taking up nutrients, but these phytoplankton are subsequently transported offshore). In this manner, the lacustrine estuary may serve as a chemostat (*sensu* Moll et al. 1980), growing either tributary-derived or estuary-derived phytoplankton using tributary-derived nutrients. Under various flushing rates, estuarine phytoplankton or nutrients can be exported to the offshore area of an adjacent large lake.

In this study, we sought to assess the relative importance of these three potential roles of a lacustrine estuary through two study objectives. First, we sought to determine the connection among nutrient, light, and phytoplankton community dynamics in a river, its lacustrine estuary, and the offshore area of a large lake. We hypothesized that if the riverine nutrient input is unaffected by the estuary and is the primary influence on the lake, then nutrient concentrations should be similar in all three regions. On the other

hand, if the estuary removes nutrients and suspended solids through phytoplankton uptake, growth, and eventual sedimentation, then bay sites should show higher phytoplankton abundance than either tributary or lake sites, although a strict mass balance may not be expected since sedimentation, zooplankton consumption of phytoplankton, and/or dilution of estuary input by offshore waters could also be important. Finally, if the tributary is an important phytoplankton source for the estuary and if the estuary is an important source for the lake, these three areas should have similar phytoplankton community compositions and biomasses. Therefore, under varying conditions (*e.g.*, high versus low tributary discharge), the estuary could either remediate or degrade tributary water quality before it enters the offshore.

Second, we sought to determine the abiotic (stream flow, temperature, light, and nutrients) and biotic (zooplankton community functional structure; Barnett et al. 2007) factors that most influence phytoplankton biomass dynamics in the linked tributary, estuary, and lake system. We hypothesized that abiotic control of phytoplankton biomass by light and nutrients would be most important, whereas biotic control (*e.g.*, presence of herbivorous zooplankton) would be less important.

We tested these hypotheses using multivariate statistical methods with physical, chemical, and biological field data collected over two phytoplankton growing seasons (April to September in 2005 and 2006) for a Lake Erie tributary, lacustrine estuary, and offshore lake system. Distinct streamflow and nutrient load patterns in 2005 (high flow and nutrient load early in the season) and 2006 (high flow and nutrient load later in the season) permitted examination of lacustrine estuary function under different discharge conditions relative to phytoplankton dynamics and community composition.

Materials and methods

Study site–The Sandusky system is a coupled watershed-aquatic system in the Laurentian Great Lakes (Fig. 2.1a) and is composed of three water bodies: (1) the Sandusky River, (2) the Sandusky Bay, and (3) the Sandusky subbasin of Lake Erie. The Sandusky River travels > 90 km through a primarily (> 85%; Richards and Baker 1985, Richards et al. 2002b) agricultural watershed (Fig. 2.1b) draining about 3,700 km^2 (Richards and Baker 1985). During 1975-1995, most of the highly erodable agricultural land was put into the Conservation Reserve Program (97% of highly erodable land) or tillage conservation programs (3% of all farmland) and phosphorus fertilizer use declined considerably (25% decrease from the maximum recorded value) whereas nitrogen fertilizer use increased (+ 46%; Richards et al. 2002a) with corresponding decreases in suspended sediment (27%), total phosphorus (46%), and soluble reactive phosphorus (85%) loading, but increased nitrate-nitrogen loading (+ 12%; Richards and Baker 2002). However, over the same time, total land farmed decreased (< 8%; Richards et al. 2002a). Consequently, suspended sediment and phosphorus loading into Sandusky Bay currently should be lower than its historical maximum and nitrate loading higher. Discharge of Sandusky River water to Sandusky Bay is regulated by precipitation events in the watershed as they are modified by the Ballville Dam just upstream of Fremont, Ohio (Fig. 2.1c). Further, below the dam, river and bay water levels are regulated by the height of Lake Erie (Richards and Baker 1985), and Sandusky Bay, therefore, functions as a lacustrine estuary.

Sandusky Bay receives > 80% of its input from the Sandusky River, with Muddy Creek and several smaller tributaries along the south shore contributing the remainder (CLEAR 1975). The bay is split into western and eastern portions (Fig. 2.1c) by a natural constriction and highway and railroad bridges near the mid-point and has a surface area of 162 km^2, a mean depth of 2.6 m, and is extremely productive (May-September 2006 mean primary productivity = 2.2 g C m^{-2} d^{-1}, Conroy 2007b). The bay discharges into the Sandusky subbasin, a shallower (compared to the rest of the central basin; mean depth = 13.3 m), diamond-shaped (~ 1,000 km^2), seasonally stratifying area (Conroy 2007c) in the south-western portion of the central basin of Lake Erie. The subbasin also receives input from the productive western basin of Lake Erie, and the combination of its thin hypolimnion and the inflow from adjacent productive basins frequently causes it to become the first part of Lake Erie to show summer hypoxia or anoxia (Conroy 2007c, Conroy 2005, Bolsenga and Herdendorf 1993). Using a connected system that included a river, lacustrine estuary, and offshore portion of a large lake allowed us to test our hypotheses relating the influence of a large river on a lacustrine estuary, the factors that affected phytoplankton dynamics in the lacustrine estuary, and the ability of the estuary to ameliorate the quality of water entering from the river.

Field sampling and laboratory analyses–We established a set of six stations in the Sandusky system to capture the full gradient of abiotic and biotic parameters as water moved from the watershed into the river, bay, and offshore in Lake Erie (Fig. 2.1c). Field sampling commenced 18 April and concluded 24 August in 2005, and commenced 8 May and concluded 15 September in 2006. Our six stations in the Sandusky system (Fig. 2.1c) included: (1) a site on the Sandusky River at Wolf Creek County Park

(Sandusky upstream, Sup) located about 32 km upstream of Sandusky Bay and 4 km upstream of the United States Geological Survey (USGS) flow gauge (#04198000, Fig. 2.1c); (2) a second site (Sandusky River Mouth, SRM) at the junction of the Sandusky River and Sandusky Bay; two sites in Sandusky Bay, (3) one west (Sandusky west bay, SWB), and (4) one east (Sandusky east bay, SEB) of the mid-point constriction; (5) a site at the point where Sandusky Bay meets Lake Erie (Sandusky Bay mouth, SBM); and, (6) a final site offshore in Lake Erie (Sandusky offshore, Soff), in the approximate middle of the Sandusky subbasin. The upstream site (Sup) was sampled on only three dates in 2005, whereas the remaining sites were sampled seven times. During 2006, all sites were sampled eight times. At each site except Sup, on all dates, routine data such as latitude and longitude, time sampled, site depth, and Secchi disk (20 cm black and white disk) transparency were also collected. At Sup, sampling restrictions precluded station depth and Secchi disk transparency measurements. Site depth at Sup was estimated from USGS gauge height measurements at the time of sampling and Secchi disk transparency at SRM was used as the most likely proxy of Sup transparency.

We measured temperature (°C) using a multiparameter instrument sonde (Model 6600, YSI, Inc., Yellow Springs, Ohio) and photosynthetically active radiation (PAR, μmol photons m^{-2} s^{-1}) using an underwater spherical sensor (Model LI-193, Li-Cor, Inc., Lincoln, Nebraska) corrected to surface irradiance using a cosine-corrected deck sensor (Model LI-190). We logged temperature continuously with depth, but PAR was recorded at discrete 0.5-m intervals at each station (except the shallow station Sup). We calculated water column mean light attenuation coefficients (k, m^{-1}) at each site by estimating

attenuation coefficients for successive 0.5-m strata using Lambert-Beer's Law and taking the arithmetic mean over all strata at a particular site (Bledsoe and Phlips 2000).

We took whole-water samples at each site to determine total and soluble macronutrient concentration and phytoplankton community composition dynamics. At the upstream site (Sup), we collected surface water with a rinsed 10-L bucket. At all other sites we collected water with an integrated tube sampler deployed to twice the Secchi disk transparency depth (~ compensation depth) or to 3 m (if the Secchi transparency was ≥ 1.5 m). Integrated tube samples were dispensed into a rinsed 10-L bucket. A 500-mL subsample from the bucket was preserved with Lugol's iodine solution in a glass jar for phytoplankton enumeration. A 250-mL (during 2005 or 60-mL during 2006) whole water sample was dispensed into a translucent polyethylene bottle, held on ice in the field, and frozen upon return to the laboratory for subsequent total nutrient concentration determinations. De-ionized, glass-distilled water was taken into the field for use as a macronutrient blank.

Lugol's-preserved phytoplankton samples were condensed by pouring 250 mL into a graduated cylinder, sealing the top with plastic wrap, and settling the contents for a minimum of 3 d in a dark box. After settling, we removed the top 220 mL by gentle suction and the remaining 30 mL was stirred and poured into a labeled sample vial. Phytoplankton sample enumeration generally followed Utermöhl (1958) and is more fully described in Conroy et al. (2005c). We identified taxa to genus following Prescott (1978), Taft and Taft (1971), Tiffany (1934), and Wehr and Sheath (2003). We enumerated known subsample volumes of each concentrated sample at 400x with an inverted microscope. All phytoplankton genera in sequential random transects were

enumerated until at least 100 algal units (cells, colonies, or filaments/trichomes) of a single genus were encountered and recorded. For each subsample, at least two random transects were made, even if 100 algal units of a single taxon were recorded before the completion of two transects. The dimensions of the first 20 algal units of each genus encountered were measured with calibrated ocular micrometers. For filamentous taxa, however, all encountered filaments (or trichomes) were measured and total filament length (mm) for a particular taxon was calculated as the sum of the measured lengths. Taking this total taxon length and average width allowed us to calculate total taxon biovolume by assuming the trichome was a cylinder. For the remaining taxa, average algal unit dimensions for each taxon were combined with appropriate geometric equations to calculate taxon cell volume (mm^3) according to Kane (2004). Cell volume was converted to biomass (wet g m^{-3}) by assuming a cellular density of 1.0 g cm^{-3} (Conroy et al. 2005c). We next combined related taxa into higher taxonomic groups focusing our analysis on five major groups: (1) Chlorophyta; (2) Chrysophyta, including diatoms; (3) Cryptophyta; (4) Cyanobacteria; and, (5) Pyrrhophyta.

Zooplankton was sampled by vertically towing a metered (Model 2030R, General Oceanics, Inc., Miami, Florida), front-weighted (2-kg weight attached to the bridle by a 1-m line), 0.5-m diameter, 64-µm mesh net fitted with a 1-L bottle on the cod-end. The net was lowered with the open end down, until the weight hit the bottom, and immediately retrieved, thereby sampling nearly the entire water column on the way down and up while avoiding sample contamination with mud. At shallow bay sites, repeated up and down deployments were used to collect sufficient numbers of organisms for subsequent enumeration. Unfortunately, zooplankton samples could not be taken at Sup

due to shallow water. Net samples were concentrated with a sieve (32- or 64-µm mesh) and preserved to a final concentration of 4% sugar formalin (Haney and Hall 1973). The volume of the water column sampled by the net was calculated by multiplying the cross-sectional area of the net (0.196 m^2) by the distance traveled (m) calculated from flow meter readings. An average of 0.81 m^3 was sampled over all zooplankton samples taken, with an accordingly higher average volume offshore (1.74 m^3) than at the river/bay junction (0.48 m^3). Zooplankton enumeration followed Conroy et al. (2005c). Briefly, each concentrated sample was diluted to a known volume (~ 500-3000 mL), subsamples (two or more with a total volume between 5 and 50 mL) were withdrawn from the diluted volume and dispensed into a counting wheel, and all zooplankton taxa (rotifers, cladocerans, cyclopoid and calanoid copepods, and dreissenid veliger larvae) were identified according to Balcer et al. (1984), Brooks (1959), and Wilson and Yeatman (1959) and enumerated using a Wild dissecting microscope at 50x. Cladocerans and copepods were identified to species and sex whereas rotifers and dreissenid veligers were identified to genus. Successive subsamples were analyzed until at least 100 individuals of the most common taxa were recorded. We also used the average of the lengths of the first 20 individuals in each taxon to calculate taxon-specific average individual biomass from length-weight regressions (Culver et al. 1985). Species-specific total biomasses were summed over all taxa to provide a total crustacean zooplankton biomass (dry g m^{-3}) for a given sampling site, for a given date.

As we were more interested in the functional aspects of different zooplankton taxa, especially the potential for top-down control of phytoplankton biomass through zooplankton herbivory, we used Barnett et al.'s (2007) recently proposed functional

classification scheme to aggregate our taxonomic groupings into five main functional groups. These consisted of (1) littoral and pelagic small, herbivorous cladocerans and calanoid and cyclopoid copepods; (2) the remaining omnivorous and carnivorous copepods; (3) large, pelagic cladocerans; (4) large, littoral cladocerans; and, (5) *Diaphanosoma* (Barnett et al. 2007). The crustacean zooplankton taxa that we identified that were not functionally categorized were assigned to the most likely functional group based upon the criteria given in Barnett et al. (2007) and the sparse functional ecology descriptions given in Balcer et al. (1984). Taxa we identified and enumerated not functionally categorized by Barnett et al. (2007) (*i.e.*, rotifers and dreissenid veliger larvae) were assigned new functional groups, (1) omnivorous rotifers and (2) predacious rotifers, and (3) dreissenid veligers. Biomasses of zooplankton eggs and unidentifiable organisms were not included in any subsequent analyses.

Total phosphorus ([TP]) and total inorganic nitrogen ([TN]) concentrations were determined using an auto-analyzer (QuikChem 8500, Lachat Instruments, Loveland, Colorado) according to validated Lachat methods and/or Standard Methods (APHA et al. 1998). Whole-water samples were first oxidized using alkaline persulfate digestion (APHA et al. 1998) with subsequent determination of orthophosphate or nitrate. Total carbon ([TC]), total organic carbon ([TOC]), and total inorganic carbon ([TIC]) were determined on a TOC analyzer (Model DC-190, Rosemount Dohrmann, Santa Clara, California). Total carbon and total inorganic carbon were determined separately; total organic carbon was determined by difference.

Other data sources–We obtained Sandusky River flow data (USGS site #04198000) during April through September during 2005 and 2006 and historical

minimum (fifth percentile of observations on a particular date), median, and maximum (95th percentile) flows by downloading approved daily mean flows and the summary of historical flows from the USGS's National Water Information System (http://waterdata.usgs.gov/nwis; accessed 23 April 2007). Additionally, we calculated contemporaneous measures of suspended sediment (SS), total phosphorus (TP), soluble reactive phosphorus (SRP), and nitrate plus nitrite (NO_3+NO_2) flux (Mg d^{-1}) and SRP:TP (mass ratio) from water quality data from the Heidelberg College National Water Quality Laboratory's (NWQL) concentration and flow data (http://www.heidelberg.edu/wql/; accessed 18 May 2007). Heidelberg's sampling location was located at the USGS flow gauge (Fig. 2.1c) and all of their analyses were performed according to United States Environmental Protection Agency standard methods (USEPA 1979) on either a balance (suspended sediments; Mettler-Toledo Inc., Columbus, Ohio), auto-analyzers (TP: model AAII; SRP: model TRAACS, Technicon Corp., Tarrytown, New York) or an ion exchange column (NO_3+NO_2: Dionex Corporation, Sunnyvale, California). Further details on methods can be found on the NWQL web site.

Assessing between-site similarity in phytoplankton community structure–To test whether the river was a source of phytoplankton to the bay and the offshore subbasin, we graphically compared the relative biomasses of the five main taxonomic groups and performed a hierarchical clustering analysis of sites using average linkage clustering of annual site-specific mean total phytoplankton biomass using PROC CLUSTER (SAS version 9.1, SAS Institute Inc., Cary, North Carolina). We used a z-score standardization before performing the cluster analysis to minimize bias due to different variable values having unequal numerical ranges (Hair and Black 2000). We then inferred relatedness

from the resultant total phytoplankton dendrogram, recognizing that more closely related sites in the output merely had similar total phytoplankton biomasses throughout the season which could be caused by factors other than being downstream from other sites in the analysis. However, we expected clear differences between sites (*i.e.*, river and lake sites should group separately) and also that sites would form nested groups due to the movement of water from the river into the estuary and from the estuary to the lake (*e.g.*, SRM would group with SWB and SEB would group with the combined group).

Abiotic versus biotic control of phytoplankton biomass–Once we established correspondence between sites, we sought to determine whether site-specific biomass was controlled by bottom-up, abiotic factors, or by top-down, biotic factors to better understand what controlled phytoplankton growth. To test a suite of possibilities, we used an information-theoretic approach (Burnham and Anderson 2002) to evaluate which factors best predicted total phytoplankton biomass. We proposed 15 potential models, 10 of which were composed of only individual factors (three physical: flow, k, T; three chemical: [TN], [TP], [TN]:[TP]; four biological: biomasses of (1) small, pelagic cladocerans and copepods, (2) omnivorous and carnivorous copepods, (3) large cladocerans, and (4) omnivorous rotifers), four combined-factor models (physical, chemical, zooplankton, and abiotic = physical and chemical), and the global model which contained all physical, chemical, and biological factors (Table 1). We fit the models using PROC REG (SAS version 9.1) and calculated the Akaike Information Criterion corrected for a small sample size relative to the number of fitted parameters (AIC_c, Burnham and Anderson 2002). We then assessed how well each model fit our data by calculating the difference in AIC_c for each model and the model with the minimum AIC_c

(Δ_i) and the Akaike weight (w_i) for each model. Data reveal high support for models with $\Delta_i < 2.0$ and little support for models with $\Delta_i > 10.0$; the w_i allow an additional way to evaluate our proposed models relative to the entire set (Burnham and Anderson 2002).

Results

Correspondence among Sandusky system site biotic community dynamics–Total phytoplankton biomass was extremely high (Fig. 2.2) with river (Sup; Figs. 2.2a, 2.2.b), river/bay junction (SRM; Figs. 2.2c, 2.2d) and bay (SWB and SEB; Figs. 2.2e, 2.2f and 2.2g, 2.2h, respectively) biomasses greater than at the bay/lake junction (SBM; Figs. 2.2i, 2.2j), or offshore (Soff; Figs. 2.2k, 2.2l). Phytoplankton biomasses during 2005 were greater earlier in the season (Fig. 2.2, left panels) than those in 2006 (Fig. 2.2, right panels). More taxonomic groups comprised the phytoplankton community early in the season than later in 2005 with the community composed primarily of cyanobacteria by early June in the bay (Figs. 2.2e, Fig. 2.2g) and by mid-July at SRM (Fig. 2.2c) and SBM (Fig. 2.2i). At Soff during 2005, cyanobacteria became a small portion of the community by mid-July although a sizable fraction existed in mid-April (Fig. 2.2k). Chlorophytes, chrysophytes (including diatoms), and cryptophytes were important components of the phytoplankton communities in the river (Fig. 2.2a) and near the bay (Figs. 2.2c, 2.2e, 2.2g, 2.2i) early in the season and continued to be important offshore into the summer (Fig. 2.2k). During 2006, phytoplankton biomass increased by mid- to late July at river (Fig. 2.2b) and bay (Figs. 2.2d, 2.2.f, 2.2h) sites with the community composed primarily of cyanobacteria; at the bay/lake junction and in the lake (Figs. 2.2j, 2.2l) chrysophytes (including diatoms) were relatively more important.

Zooplankton community functional group composition and biomass also differed between sites and years (Fig. 2.3). Biomasses were greatest at the river/bay junction (Fig. 2.3a, 2.3b) and in the western part of the bay (Fig. 2.3c, 2.3d). At SRM, early season biomasses during 2005 were extremely low (Fig. 2.3a), but in 2006 omnivorous rotifers were extremely abundant (Fig. 2.3b). Biomasses during the remainder of the season at SRM were similar between years (Figs. 2.3a, 2.3b). At SWB, low biomasses early in 2005 were followed by increasing biomasses of large cladocerans and omnivorous and carnivorous copepods in early- to mid-June (Fig. 2.3c) showing evidence for seasonal succession. During 2006, omnivorous rotifers were much more abundant, coupled with less of a seasonal pattern (Fig. 2.3d). In eastern Sandusky Bay (SEB), seasonal patterns were observed during both years (Figs. 2.3e, 2.3f), but the peak biomass in 2005 was composed of all four functional groups in relatively similar amounts, whereas in 2006, the peak was extended and was composed of increasing amounts of small, pelagic herbivorous cladocerans and copepods and omnivorous rotifers, especially later in the season (Fig. 2.3f). At the bay/subbasin junction (SBM) omnivorous and carnivorous copepods were important in 2005 (Fig. 2.3g) whereas omnivorous rotifers and small, pelagic herbivorous cladocerans and copepods were important in 2006 (Fig. 2.3h). Offshore (Soff), biomass was lower than at the other sites and rotifers played much less of a role (Figs. 2.3i, 2.3j). Again, seasonal patterns were observed with a peak in early-June in 2005 (Fig. 2.3i) and mid- to late-June in 2006 (Fig. 2.3j) with a second peak later in the season in 2006. The discrepancies between the total zooplankton biomass lines and the bars in 2005 (Fig. 2.3g, i) and 2006 (Fig. 2.3h, j) were caused by the inclusion of dreissenid veliger larvae and *Diaphanosoma* in the total zooplankton biomass.

Correspondence among Sandusky system site abiotic parameters–Physical and chemical conditions varied from the river to the lake and between years. In 2005, streamflow had two major flow events (peaks on 3 April and 27 April 2005; flows ≥ 95% of the historical [1924-2005] flows for that date) during spring (Fig. 2.4a), one of which was during our chemical and biological sampling (18 April-11 July). Most other 2005 flows were at or below historical median flows (Fig. 2.4a). During 2006, four major flow events occurred (16 May, 27 May, 23 June, and 17 July) during our sampling (8 May-15 September) with two additional minor events (peaks on 4 and 10 June) with flows well above median flows (Fig. 2b). The timing of the high flows thus differed between years; consequently, input of sediments and nutrients to the bay differed (Figs. 2.4c-2.4l).

During 2005, there were two main sediment (Fig. 2.4c) and nutrient (Figs. 2.4e, 2.4g, 2.4k) influx events that corresponded with high streamflow events. Suspended sediment (SS) flux (Fig. 2.4c) peaked early during both high flow events and more SS was loaded during the first high flow event although the second event had greater flows (Fig. 2.4a). Total phosphorus (TP; Fig. 2.4e), soluble reactive phosphorus (SRP; Fig. 2.4g), and nitrate plus nitrite (NO_3+NO_2; Fig. 2.4k) fluxes all reached maximal values during the high flows. Peak TP fluxes were similar between events (Fig. 2.4e) although SRP and NO_3+NO_2 fluxes were greater during the second event than the first (Figs. 2.4g, 2.4k). Similar, but smaller, patterns of nutrient flux with minor precipitation events occurred during the remainder of the season (Figs. 2.4a, 2.4c, 2.4g, 2.4k). The SRP:TP ratio increased just after the first high flow event, peaked during the second high flow event, and oscillated during the remainder of the season with generally increased ratios during increased flow events and ratios near zero during low flow (Fig. 2.4g). During

2006, SS flux was low during April but was higher during May-July (Fig. 2.4d). Nutrient input was correspondingly low during April but was elevated in May-July 2006 (Figs. 2.4f, 2.4h, 2.4l) compared to 2005. Patterns of TP (Fig. 2.4f), SRP (Fig. 2.4h), and NO_3+NO_2 (Fig. 2.4l) inputs closely followed high flow events. The minor flow events influenced sediment and nutrient influx to correspondingly lower levels. Due to the different pattern of nutrient influx, the SRP:TP ratio stayed consistently elevated in 2006 (Fig. 2.4j) compared to 2005, except during low flows in August 2006. The relative abundance of nutrients available for phytoplankton, therefore, differed between years.

Physical measurements made at our sampling sites also differed between years and often corresponded to changes induced by streamflow changes (Figs. 2.4m-2.4p). Temperature (T) decreased from the river and bay junction (SRM) moving offshore (Soff) and progressively increased throughout the season until mid- to late July when T decreased (Figs. 2.4m, 2.4n). May T was slightly warmer in 2006 although June through mid-July T was warmer in 2005 (Figs. 2.4m, 2.4n). Light attenuation (k; Figs. 2.4o, 2.4p) followed SS flux. Peak k (low light in the water column) at river and bay sites during 2005 (Fig. 2.4o) occurred just at the end of peak SS flux (Fig. 2.4c); during the remainder of 2005, k decreased (increased light) at all sites except SRM (Fig. 2.4o). During 2006, the first (16 May), second (27 May), and fourth (17 July) high flow events had less effect on k in the river and bay (sites SRM, SWB, and SEB) although the third event (23 June) greatly increased k, especially at in the bay (SWB and SEB; Fig. 2.4p). Our lack of an observed effect of the other three flow events could have been due to sample timing although the first two high flow events had lower flows (Fig. 2.4b) and less SS flux (Fig. 2.4d). Comparing sites, k decreased from river to offshore with offshore k consistently

distinct from river and bay values indicating greater light penetration offshore (Figs. 2.4o, 2.4p). Variability and no marked seasonal pattern characterized Soff k dynamics (Figs. 2.4o, 2.4p). These results reveal that SS input affected the downstream light climate at river (Sup), river/bay junction (SRM), and bay (SWB and SEB) sites, with less effect at the bay/lake junction (SBM) and offshore (Soff) whereas T was controlled by weather.

Carbon, nitrogen, and phosphorus concentration dynamics in the river and bay generally followed the patterns of watershed input, river flow (Figs. 2.4a, 2.4b), and nutrient flux (Figs. 2.4c-2.4l). Total carbon ([TC]) and total inorganic carbon ([TIC]) concentrations decreased from upstream (Sup) through the bay, and offshore in Lake Erie (Figs. 2.4q, 2.4r). Total organic carbon concentration ([TOC]), however, was often greater in the bay (especially in the eastern part) than at the other sites (Figs. 2.4u, 2.4v). During 2005, TOC was greater during April but lower during the remainder of the season (Fig. 2.4u). During 2006, TOC peaked at all sites in late June (Fig. 2.4v).

Total inorganic nitrogen concentrations ([TN]; Figs. 2.4w, 2.4x) measured at our sampling sites showed patterns similar to flux patterns in 2005 but not in 2006 (Figs. 2.4k, 2.4l). During 2005, [TN] increased at river and bay stations (Fig. 2.4w) similar to that of NO_3+NO_2 flux (Fig. 2.4k). During 2006, however, a peak in [TN] occurred (Fig. 2.4x) upstream (Sup), at the river/bay junction (SRM), and in the western part of the bay (SWB) contemporaneous only with the second NO_3+NO_2 peak (Fig. 2.4l). Eastern bay (SEB) [TN] was lower and peaked after the upstream sites (Fig. 2.4x) but at the same time as bay/subbasin junction (SBM) and offshore sites (Soff), although SBM and Soff peaks had lower concentrations. During the remainder of the season, [TN] decreased (Fig. 2.4x), although high NO_3+NO_2 fluxes occurred in late June and mid-July (Fig. 2.4l).

Total phosphorus concentrations ([TP]; Figs. 2.4y, 2.4z) at our sampling sites during 2005 followed TP flux (Fig. 2.4e) early in the season. Late in the season, however, [TP] greatly increased at SRM and SWB with moderate increases at Sup and SEB (Fig. 2.4y). During 2006, [TP] was higher throughout the season in the river and bay with peaks at Sup (Fig. 2.4z) contemporaneous to those in the flux measurements (Fig. 2.4f). Whereas [TP] during May and June decreased in 2005 (Fig. 2.4y), [TP] increased during the same time period in 2006 (Fig. 2.4z). Further, concentrations remained elevated throughout the growing season (Fig. 2.4z). Similar to [TN], [TP] was consistently lower at Soff than at the other sites during both years (Figs. 2.4y, 2.4z). The ratio [TN]:[TP] decreased at SRM, SWB, SEB, and SBM during 2005 with a small peak at SWB, SEB, and SBM in early-June (Fig. 2.4aa). At Soff, however, [TN]:[TP] increased during 2005 (Fig. 2.4aa). Patterns in the [TN]:[TP] ratio in 2006 decreased through the season at all stations with ratios at Soff greater than those at the other stations (Fig. 2.4ab). Consequently, nutrient availability varied according to watershed nutrient flux with clear differences in nutrient availability between 2005 and 2006, primarily with more available phosphorus (higher measured concentrations and longer elevated concentrations) in 2006.

Similarity of total phytoplankton biomass among sites–We expected hierarchical cluster analysis of total phytoplankton biomass to group sites moving from the river, into the bay, and out into the offshore Sandusky subbasin if transport of phytoplankton communities was an important factor structuring downstream communities. Our cluster analysis (Fig. 2.5) revealed little evidence for strict hierarchical grouping (*e.g.*, Sup biomasses clustering with SRM biomasses, with this combined group clustering with SWB). West bay (SWB) 2005 biomass was distinct from the rest of the sites (Fig. 2.5)

due to the extremely high cyanobacteria biomass in late-May (256 g m^{-3}; Fig. 2.2e). Considering the remaining dendrogram, we found that offshore (Soff) sites were distinct (Fig. 2.5) as this site had lower biomasses (Figs. 2.2k, 2.2l). All of the remaining river and bay sites formed one group (Fig. 2.5), although this group resolved poorly. Potentially two years' data is insufficient to fully resolve within-river and bay differences, or river/bay biomasses did not greatly differ (Fig. 2.2).

Predicting total phytoplankton biomass–We found that our data supported only one multiple regression model predicting total phytoplankton biomass, namely, lower [TN]:[TP] gave greater total phytoplankton biomasses (Table 2.1). Other individual physical (flow, k, and T) and chemical ([TP] and [TN]) factors and the combined Chemical and Physical factors were better ($\Delta_i < 10.0$) at predicting total phytoplankton biomass than were the individual zooplankton factors, the combined Zooplankton and Abiotic factors, and the global model ($\Delta_i > 10.0$; Table 2.1). There was a distinct drop-off in weight of evidence (w_i) from the best to the remaining models (Table 2.1).

Discussion

The lacustrine estuary as a chemostat–We originally hypothesized three potential pathways for lacustrine estuary processing of river nutrients and phytoplankton and its subsequent effect offshore. These included: (1) acting as a flow-through system, loading river nutrients directly offshore with little transformation of nutrient form or amounts; (2) remediating river nutrient input effects on the offshore by facilitating either tributary or estuary phytoplankton use of river nutrients with the subsequent loss of phytoplankton to estuarine zooplankton or the estuarine sediments; or, (3) detrimentally affecting the

offshore by facilitating the growth of high amounts of phytoplankton using river-derived nutrients with little loss to estuarine zooplankton or sediments. The first hypothesized effect described the classic concept of tributary influence on the offshore areas of lakes (Carpenter et al. 1998). This conceptual model considered tributaries as nutrient sources to growing offshore phytoplankton communities. The second and third hypothesized effects modified the traditional conceptual model by considering the lacustrine estuary to function similar to a chemostat. In this way, the lacustrine estuary may use tributary-supplied nutrients and biota and, depending on the physical (*i.e.*, hydrodynamics, temperature, light), chemical (*i.e.*, nutrients), and biological (*i.e.*, food web structure) characteristics within the estuary, either remove significant amounts of nutrients and phytoplankton with little offshore export or remove significant amounts of nutrients while exporting large amounts of phytoplankton.

We found evidence for the Sandusky Bay lacustrine estuary removing large amounts of nutrients while growing extremely high amounts of phytoplankton. Nutrient concentrations at the bay/subbasin junction (SBM) were always lower than those at the river/bay junction (SRM) and phytoplankton biomass was extremely high in the bay (SWB and SEB). Nitrogen and phosphorus concentrations were consistently lower in the eastern portion of the bay (SEB) than the western portion (SWB) indicating nutrient use by phytoplankton largely occurred before water moved into the eastern bay. At times, the estuarine phytoplankton was not exported, at other times it was, as revealed by phytoplankton community composition and biomass similarities at SEB and SBM.

Is the river the source of estuary suspended sediments, nutrients, phytoplankton, and zooplankton?–A primary focus of this study was to determine whether the tributary

(Sandusky River) functioned as sterile culture medium, devoid of biota but rich in nutrients, or as a chemical/biological conduit, contributing nutrients and phytoplankton and zooplankton communities, to the receiving lacustrine estuary (Sandusky Bay). We found that changes in suspended sediment concentrations (SS; inferred from light attenuation, k) at the river/bay junction (SRM) and in the bay (SWB and SEB) closely corresponded to high flow events and river SS inputs, indicating simple material transport downstream. Klarer and Millie (1994) found a similar pattern moving downstream in the Old Woman Creek estuary, Lake Erie. Our data revealed that the river transported sediments from the watershed into the lacustrine estuary, decreasing light penetration in the estuary and favoring phytoplankton adapted to low-light conditions such as cyanobacteria (Reynolds et al. 2002, Reynolds 2006).

Estuarine nutrient concentrations also closely followed upstream river influx. In particular, total phosphorus TP flux peaks observed early in 2005 and throughout 2006 upstream (Sup) and in the bay (SRM, SWB, and SEB) occurred contemporaneously with or just following high flow events. Later in 2005 (mid-June through mid-July), however, TP concentrations increased at SRM, SWB, and SEB without a concurrent upstream TP flux. This late-season release could be the result of wetland P release due to increased temperatures (Koerselman et al. 1993), decomposition (Reddy et al. 1995), and sediment drying (Qiu and McComb 1994), as the far western end of Sandusky Bay has extensive wetlands (Richards and Baker 1985) and 2005 flow was low from mid-May through mid-July. Additionally, P release from some watershed source downstream of the monitoring site may contributed “unmonitored” P.

Nitrogen input also followed peak flow events during 2005 and early 2006. As most of the total inorganic nitrogen (TN) measured in the bay was nitrate (Conroy et al. 2007), the lack of correspondence between river nitrate plus nitrate (NO_3+NO_2) flux and bay TN concentrations during 2006 was interesting. Other than missing the flux due to the timing of our sampling, we cannot propose an explanation for why TN concentrations did not increase when NO_3+NO_2 flux increased in the river.

Given that most of the nutrients entered the lacustrine estuary from the watershed early in 2005, we expected that phytoplankton biomass would be greater in early 2005 than late 2005. We found, instead, that biomasses were greatest after June at river and bay sites, but were higher in April and May at bay/lake junction and offshore sites. In 2006, conversely, nutrients entered the estuary later in the season with P more available relative to N (as indicated by [TN]:[TP] ratios) throughout summer, setting the potential for higher cyanobacterial biomass later in 2006 than in 2005. We found greater cyanobacterial biomass in late 2006 than 2005 though sampling ended in mid-July 2005.

The river affects lacustrine estuary (bay) phytoplankton dynamics potentially through both loaded nutrients and loaded phytoplankton. There were taxonomic similarities between upstream (Sup) and the junction of the river/bay (SRM) stations at times (*e.g.*, early June 2005 with similar contributions by chlorophytes, chrysophytes (including diatoms), cryptophytes, and cyanobacteria to total biomass) but downstream stations (SWB and SEB) had higher cyanobacterial biomasses during 2005 and early 2006 indicating that either the downstream stations had distinct phytoplankton communities that did not originate from upstream or that the particular conditions at these sites facilitated growth by the smaller cyanobacterial portion of the upstream community.

In a related, more taxonomically detailed study of the 2005 cyanobacterial community at these sites, Conroy et al. (2007) found that the predominant cyanobacterial genera at SWB and SEB was *Planktothrix* and/or *Chroococcus*; at SRM, the cyanobacterial community was more often composed of *Microcystis*. On some dates, *Aphanizomenon* or *Anabaena* comprised nearly the entire community at SRM whereas these taxa made up a smaller portion of the SWB and SEB communities (Conroy et al. 2007). We propose that these findings support selective growth of phytoplankton taxa moving downstream due to changes in growth-limiting factors (*e.g.*, light availability, nutrient concentrations).

Determining the effect of the river on the downstream zooplankton community was complicated by the lack of zooplankton samples from our upstream sampling site (Sup). However, as water moves downstream clear shifts in zooplankton community biomass and composition occurred. At bay sites (SWB and SEB), the relative biomass of omnivorous rotifers increased, especially at SEB. In the bay, other functional groups were important at various sites and times (*e.g.*, large, pelagic herbivorous cladocerans at SWB in 2005) indicating that the community gradually changed as environmental parameters and the phytoplankton community changed.

Phytoplankton and zooplankton results suggest the river/lacustrine estuary (bay) continuum is an ecocline similar to that of the Suwannee River estuary, Florida (Quinlan and Phlips 2007), and emphasize the similarity between the functions of lacustrine and marine estuaries. That is, the river functions as a conduit, transporting sediments, nutrients, and biota from the watershed into the lacustrine estuary. The particular environmental conditions select for those species best able to exploit the site-specific conditions, whereas simple downstream transport appears less important.

Is the estuary the source of lake suspended sediments, nutrients, phytoplankton, and zooplankton?–We tested whether transport of estuarine materials into the offshore subbasin played an important role in subbasin dynamics. A simple comparison of suspended sediments (SS) does not allow us to estimate sediment transfer from the estuary to offshore subbasin. However, light attenuation (k) at the bay/subbasin junction (SBM) generally followed the pattern that occurred in the rest of the bay (SWB and SEB) which, in turn, followed measured SS flux from the river. Because k offshore (Soff) varied little, we conclude that either SS transfer did not occur from the lacustrine estuary to that lake sampling site or that any sediment loaded from the estuary quickly settled out of the water column. Certainly sediment plumes do flow from the Maumee Bay and the Detroit River into western Lake Erie (CLEAR 1976). Recent satellite images reveal substantial suspended material input (measured as turbidity; Vincent et al. 2004) coming from the Maumee River and Bay, indicating that these systems may function in a similar manner. Further, other satellite images (Landsat 5 and 7, http://landsat.ohiolink.edu/GEO/LS7/) show visible sediment plumes entering the subbasin from the estuary. The Sandusky Bay-subbasin hydrologic link needs to be better quantified (Conroy 2007c) as does the ultimate fate of sediment after entering the subbasin. Sediment input from the estuary may reduce light availability and limit primary productivity in nearshore and estuarine systems (Cloern 1987, Conroy 2007b).

Nutrient dynamics at SBM and Soff were generally similar, although SBM concentrations were greater than at Soff. Concentrations at both sites, however, were lower than in the estuary or river as were phytoplankton biomasses. Phytoplankton taxonomic composition differed between sites with cyanobacteria dominant at SBM and

chrysophytes and cryptophytes dominant at Soff. The distinct composition of the offshore phytoplankton community indicates that the bay was an unlikely source of the phytoplankton community offshore in the subbasin. However, on some dates, phytoplankton community structure at SBM and Soff were similar but distinct from the estuary (*i.e.*, late-August 2006) indicating a likely connection between sites. Regarding zooplankton biomass and functional composition, Soff again was distinct from the other sites, including SBM. Biomass at SBM was lower than in the estuary, and Soff biomass was lower yet. Functional zooplankton community composition at Soff differed from the other sites due to the lack of omnivorous rotifers.

These results indicate only temporary connections between physical, chemical, and biological dynamics in the lacustrine estuary and offshore in the subbasin. Estuary inputs flowed either directly north or east along shore after they exit Sandusky Bay (Richards and Baker 1985), making Soff unlikely to receive direct estuarine input. However, other subbasin sites showed potential effects due to proximity to estuarine loading such as higher hypolimnetic oxygen depletion rates at sites in the western and south-western subbasin (Conroy 2007c). Consequently, the estuary may serve as a source for parts of the Sandusky subbasin, emphasizing the potential importance of this area in affecting offshore processes (Conroy 2007a) although the particular transport mechanisms and the ultimate fate of input materials needs additional research.

Abiotic or biotic control of phytoplankton biomass–Determining whether the Sandusky system phytoplankton community was under abiotic or biotic control is important from a management perspective. If we found that nutrients (an abiotic, bottom-up factor) were most important in predicting phytoplankton biomass, managers

should continue or increase nutrient regulations to decrease phytoplankton biomass. On the other hand, if we found that the presence of herbivores was most important, little could be done to affect zooplankton except through indirect food web management through regulation of commercial and sport collection of top predators (*e.g.*, walleye and yellow perch in Lake Erie). Most abiotic and biotic factors tested influenced total phytoplankton biomass in the direction (*e.g.*, either positive or negative effects) we would have predicted, although some did not. For example, we predicted *a priori* that sites with lower light penetration (higher k) would have lower total phytoplankton biomass. We did not find this pattern, however, because of the high phytoplankton in the shallow bay relative to the subbasin. Only abiotic factors controlled total phytoplankton biomass with [TN]:[TP] dominant; further, no support existed for top-down control.

Our results agreed with those of Garono et al. (1996), who found correlations between measures of phosphorus availability (total phosphorus, total soluble phosphorus, and soluble reactive phosphorus concentrations and total and algal phosphatase activity) and phytoplankton abundance at sites in Sandusky Bay and subbasin in 1990. Interestingly, they found that phytoplankton communities at the river/bay junction and subbasin were similar to one another whereas those in Sandusky Bay were distinct; we found here and in a related study (Conroy et al. 2007) that river/bay junction (SRM) phytoplankton communities were more similar to those in the bay, with lake communities more distinct. Either conditions have changed in the Sandusky River since Garono et al.'s (1996) study or annual phytoplankton community composition variation was sufficiently great for phytoplankton exiting the river to be similar to that in the subbasin one year and similar to that in the bay in another. Garono et al.'s (1996) 1990 fieldwork

was conducted during a period of decreased nutrient load from the Sandusky River (Richards and Baker 2002); evidence exists that nutrient loads have increased since 1995 (P. Richards and D. Baker, Heidelberg College, *personal communication*) which could lead to cyanobacteria becoming more abundant in the river. From this and previous studies, we know that nutrient load from the watershed supports phytoplankton biomass in this lacustrine estuary and Lake Erie.

Managing total phytoplankton biomass in a coupled tributary, lacustrine estuary, and lake system–Reducing excessive total phytoplankton biomass may be possible by continuing to reduce nutrient input, especially the timing of external nutrient loading, which has been relatively neglected in previous nutrient management strategies. For example, the Great Lakes Water Quality Agreement (GLWQA) mandates that total phosphorus loading to Lake Erie not exceed 11,000 metric tonnes per annum (DePinto et al. 1986). GLWQA limited phosphorus load through source reduction strategies including discharge limits for wastewater treatment plants, phosphate-based detergent elimination, and implementation of conservation tillage practices (DePinto et al. 1986). These strategies limited integrated loading over the entire year and have been effective in reducing phosphorus load to Lake Erie to the mandated level (Dolan and McGunagle 2005). However, offshore phytoplankton biomass remains at high levels (Conroy et al. 2005c). Further, areas of hypoxia and anoxia continue to occur throughout large parts of the Sandusky subbasin (Conroy 2007c) and the larger central basin (Burns et al. 2005) and large populations of macroinvertebrates continue to be killed due to periods of hypoxia in the shallower western basin (Bridgeman et al. 2006). In general, system health is declining (Conroy et al. 2005b). Further nutrient input remediation, therefore,

may be needed. This remediation could include additional limitation of the total amount of phosphorus load (*e.g.*, decrease the annual limit to < 11,000 metric tonnes), could limit loading during particularly important times such as late-winter and spring by targeting watershed practices that occur during this period (*e.g.*, fertilizer application), and/or could include additional watershed intervention techniques (*e.g.*, increased use of buffer strips).

The Sandusky Bay estuary, therefore, was important in remediating nutrient concentrations before water entered the subbasin but may perturb organic matter load to the nearshore area of the subbasin by serving as a source of physiologically healthy phytoplankton (Conroy 2007b). Exported phytoplankton may potentially affect subbasin nutrient dynamics, phytoplankton bloom formation, and hypolimnetic oxygen depletion rates (Conroy 2007c). Consequently, revision of the classic model of lake-tributary interactions (*e.g.*, Carpenter et al. 1998) to include the effects of tributary phytoplankton load may need to be included to ameliorate continuing offshore impairments.

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Model	Dir.	k	Δ_i	w_i	R^2
[TN]:[TP]	–	3	0.00	0.827	0.24
Flow	–	3	5.24	0.060	0.12
[TP]	+	3	5.84	0.045	0.11
k	+	3	7.24	0.022	0.07
Chemical		5	7.91	0.016	0.25
T	+	3	8.25	0.013	0.05
Physical		5	8.93	0.010	0.23
[TN]	–	3	9.80	0.006	0.01
Omn. rotifers	+	3	15.45	0.000	0.06
Abiotic		7	15.69	0.000	0.31
Omn., carn. copepods	+	3	16.53	0.000	0.02
Lg., pelagic herb. cladocerans	+	3	16.89	0.000	0.01
Sm., pelagic herb. clad. & cope.	+	3	16.92	0.000	0.01
Zooplankton		6	28.08	0.000	0.07
Global		12	44.31	0.000	0.37

Table 2.1. Rankings of models used to predict total phytoplankton wet biomass at all Sandusky system, Lake Erie, sites during 2005 and 2006. The model, direction of the relationship between individual model factors and total phytoplankton biomass (+ = positive relationship, – = negative relationship), number of modeled parameters (K = # of model regression coefficients + intercept + residual variance) the difference between the "best" model and the other models (Δ_i), the probability that each model is the "best" model given all the proposed models (w_i = Akaike weight), and the traditional measure of fit (R^2 = proportion of variance explained). Abbreviations are: [TN] = total nitrogen concentration, [TP] = total phosphorus concentration, k = attenuation coefficient, T = temperature, omn. = omnivorous, carn. = carnivorous, lg. = large, and sm. = small. Note that flow and [TN]:[TP] were log-transformed and zooplankton variables were square root-transformed prior to performing regressions.

Fig. 2.1. Maps showing the (a) relative position of the study area (enclosed by heavy black square) relative to that of the Laurentian Great Lakes and the Sandusky Bay watershed; (b) an enlarged depiction of the Sandusky River (white line) and its watershed (central area bounded by heavy black lines) in addition to the remainder of the Sandusky Bay watershed (two additional areas bounded by heavy black lines north and west and south of Sandusky Bay); and, (c) map of the Sandusky system, Lake Erie sampling sites (filled dots) including locations upstream on the Sandusky River (Sup), at the junction of the river and bay (SRM), in the west (SWB) and east (SEB) parts of the Sandusky Bay, at the junction of the bay and the subbasin (SBM), and offshore in the subbasin (Soff). Empty squares in (b) and (c) show cities in the watershed and region, a filled square in (c) shows the location of the Ballville Dam upstream from Fremont, Ohio, and a filled cross in (c) shows the location of the river flow gage. Note that in (b) and (c) the width of the river is exaggerated to aid in illustration.

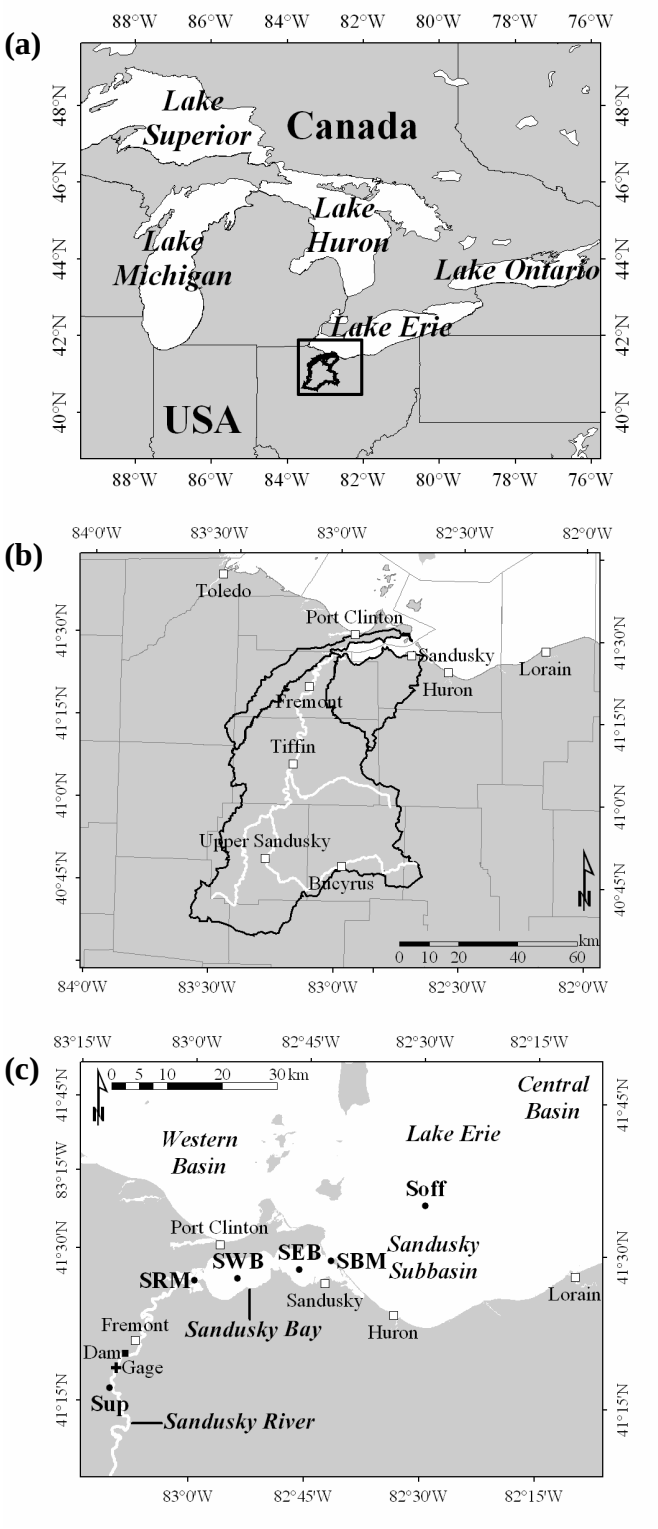
(a)
Lake Superior
Canada
Lake Huron
Lake Michigan
Lake Ontario
Lake Erie
USA
(b)
Toledo
Port Clinton
Sandusky
Lorain
Huron
Fremont
Tiffin
Upper Sandusky
Bucyrus
km
0 10 20 40 60
(c)
0 5 10 20 30 km
Central Basin
Western Basin
Lake Erie
Soff
Port Clinton
SWB
SEB
SBM
Sandusky Subbasin
SRM
Sandusky
Lorain
Fremont
Sandusky Bay
Huron
Dam
Gage
Sup
Sandusky River

Fig. 2.1.

Fig. 2.2. Phytoplankton community taxonomic group biomass (wet g m^{-3}) dynamics during 2005 (left panels) and 2006 (right panels) upstream in the Sandusky River (Sup; a and b), at the junction of the river and bay (SRM; c and d), in the western (SWB; e and f) and eastern (SEB; g and h) portions of the Sandusky Bay, at the junction of the bay and Lake Erie (SBM; i and j), and offshore in the Sandusky subbasin (Soff; k and l) in the Sandusky system, Lake Erie. Groups include Chlorophyta (open bars), Chrysophyta including diatoms (light grey bars), Cryptophyta (filled bars), Cyanobacteria (hatched bars), and Pyrrhophyta (dark grey bars). Biomasses of bars terminating off of the figure are indicated by the values next to the bar. Note that ordinate ranges differ among sites.

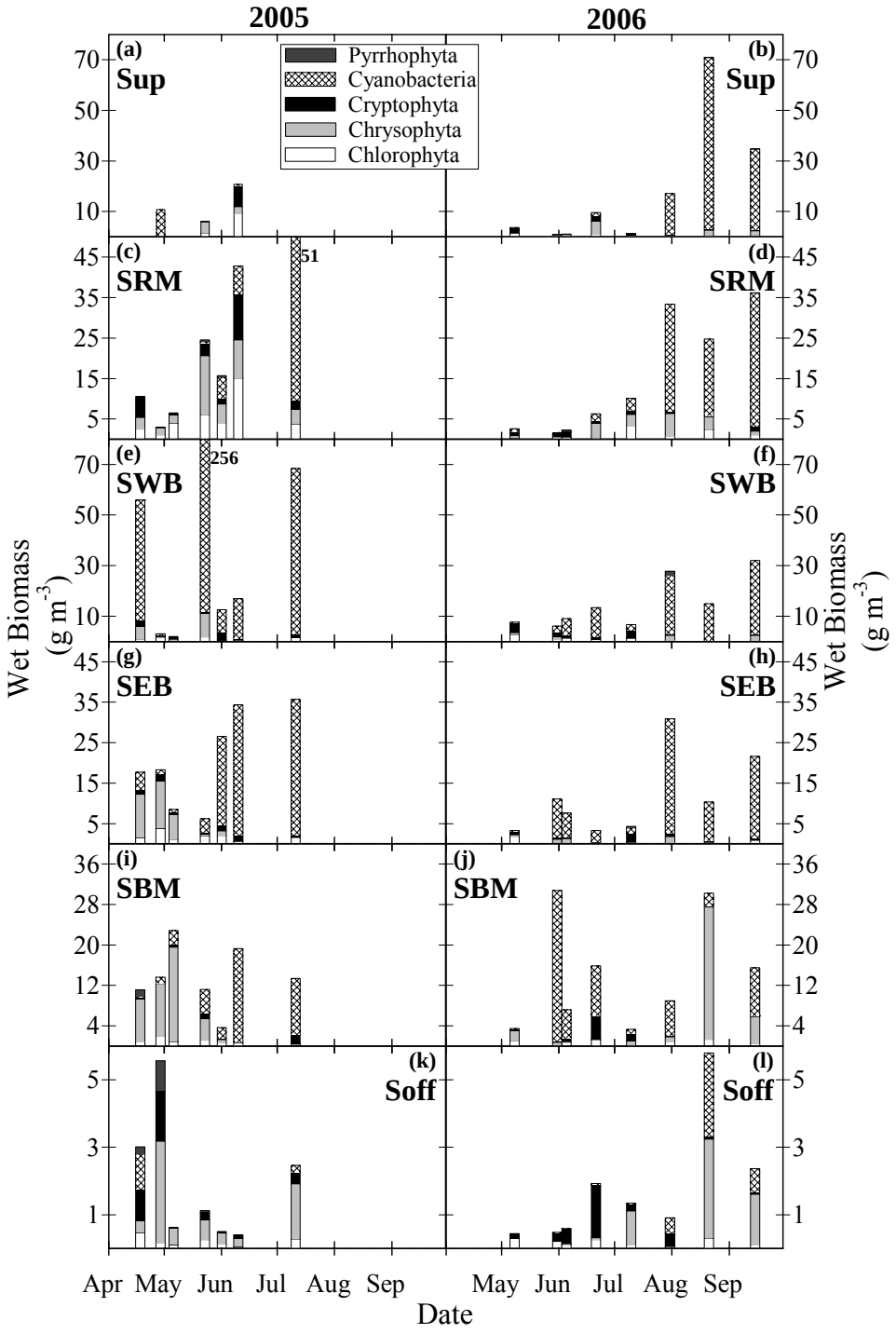
2005
2006
(a)
Sup
(b)
Sup
Pyrrhophyta
Cyanobacteria
Cryptophyta
Chrysophyta
Chlorophyta
(c)
SRM
51
(d)
SRM
(e)
SWB
256
(f)
SWB
(g)
SEB
(h)
SEB
(i)
SBM
(j)
SBM
(k)
Soff
(l)
Soff
Wet Biomass
(g m-3)
Apr May Jun Jul Aug Sep
May Jun Jul Aug Sep
Date

Fig. 2.2.

Fig. 2.3. Zooplankton community functional group biomass (dry g m^{-3}) dynamics during 2005 (left panels) and 2006 (right panels) in the Sandusky system, Lake Erie at the junction of the river and bay (SRM; a and b), in the western (SWB; c and d) and eastern (SEB; e and f) portions of Sandusky Bay, at the junction of the bay and Lake Erie (SBM; g and h), and offshore (i and j) in the Sandusky subbasin (Soff). The bars give the dry biomasses of small, pelagic, primarily herbivorous cladocerans and copepods (*e.g.*, *Bosmina* and *Tropocyclops*; filled bars), omnivorous and carnivorous, larger copepods (*e.g.*, *Leptodiapotomus* and *Diacyclops*; grey bars), large, pelagic cladocerans (*e.g.*, *Daphnia*; open bars), and omnivorous rotifers (*e.g.*, *Keratella*; cross-hatched bars) and were used to predict total phytoplankton biomass (Table 2.1). The lines and symbols give total zooplankton community functional group biomass at each site on a particular sampling date; differences between the line and the bars were due to the presence of dreissenid mussel veligers which were not assigned to functional groups, or other minor functional groups (*e.g.*, large, littoral cladocerans) in the zooplankton sample. Functional group assignments were based primarily on Barnett et al. (2007). Note that ordinate ranges differ among sites.

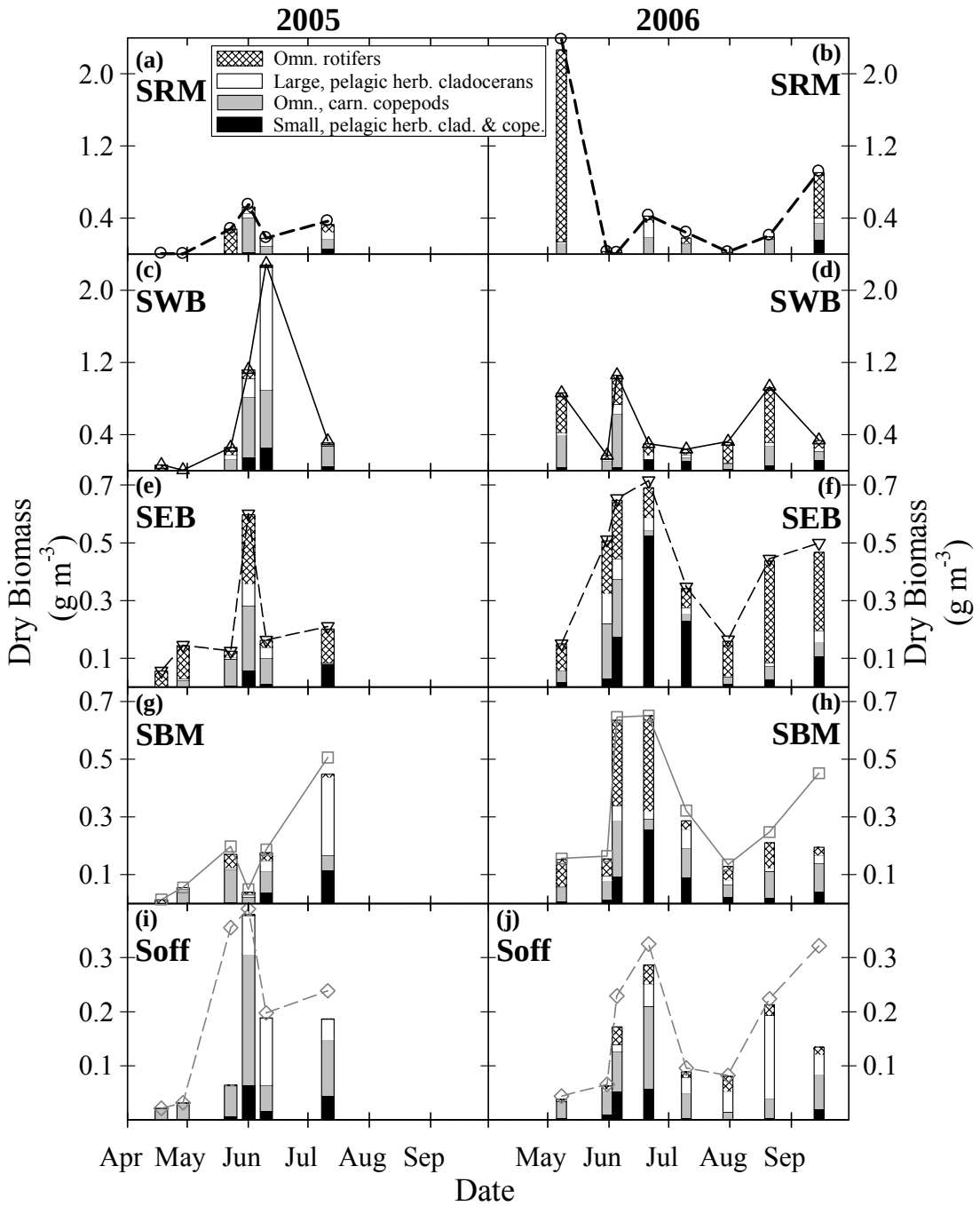
2005
2006
(a)
SRM
(b)
SRM
Omn. rotifers
Large, pelagic herb. cladocerans
Omn., carn. copepods
Small, pelagic herb. clad. & cope.
(c)
SWB
(d)
SWB
(e)
SEB
(f)
SEB
(g)
SBM
(h)
SBM
(i)
Soff
(j)
Soff
Dry Biomass
(g m-3)
Apr May Jun Jul Aug Sep
May Jun Jul Aug Sep
Date

Fig. 2.3.

Fig. 2.4. Seasonal variation in physical and chemical parameter dynamics during 2005 (left panels) and 2006 (right panels) including streamflow (a and b) measured by the United States Geological Survey (USGS; http://waterdata.usgs.gov) at the Sandusky River stream gauge (Fig. 2.1) and fluxes of suspended sediment (SS, c and d), total phosphorus (TP, e and f), soluble reactive phosphorus (SRP, g and h), the ratio of SRP:TP (i and j), and the sum of nitrate and nitrite (NO_3+NO_2, k and l) measured by the Heidelberg National Water Quality Laboratory at the USGS stream gauge and temperature (T, m and n), attenuation coefficient (k, o and p), concentrations of total carbon ([TC], q and r), total inorganic carbon ([TIC], s and t), total organic carbon ([TOC], u and v), total nitrogen ([TN], w and x), and total phosphorus ([TP], y and z), and the ratio of [TP]:[TN] (aa and ab) measured at our six Sandusky system stations (legend applies to panels (m) through (ab)). In (a) and (b), maximum (95th percentile, open down triangles) and median (filled black squares) stream flow values for the period 1924-2005 are shown. Note that the arrows and values shown in panels (aa) and (ab) indicate [TN]:[TP] ratios for site Soff on 10 June 2005 and site SWB on 31 May 2006, respectively.

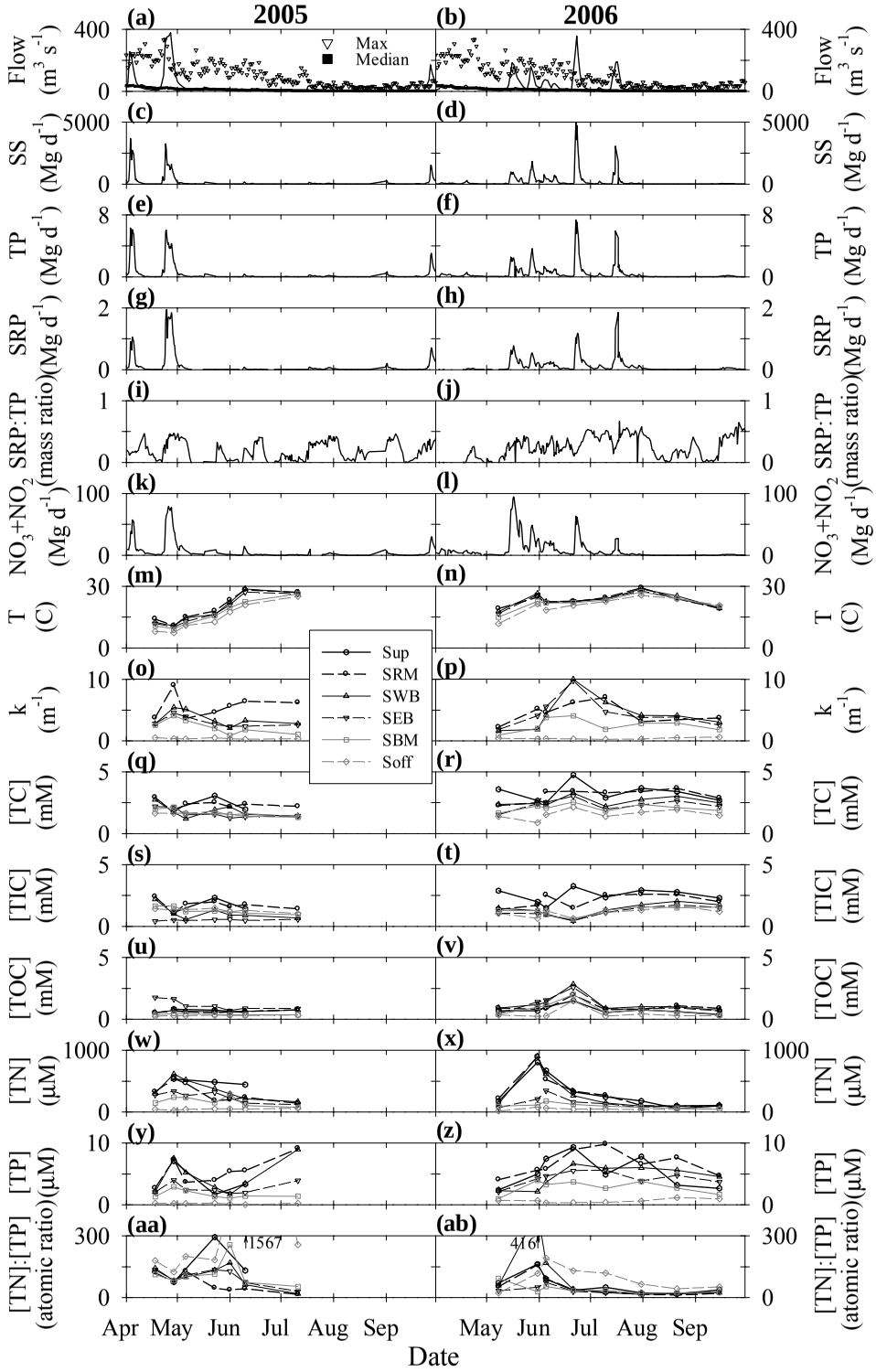
2005
2006
Max
Median
Flow (m3 s-1)
SS (Mg d-1)
TP (Mg d-1)
SRP (Mg d-1)
SRP:TP (mass ratio)
NO3+NO2 (Mg d-1)
T (C)
k (m-1)
[TC] (mM)
[TIC] (mM)
[TOC] (mM)
[TN] (µM)
[TP] (µM)
[TN]:[TP] (atomic ratio)
Sup
SRM
SWB
SEB
SBM
Soff
!1567
416!
Apr May Jun Jul Aug Sep
May Jun Jul Aug Sep
Date

Fig. 2.4.

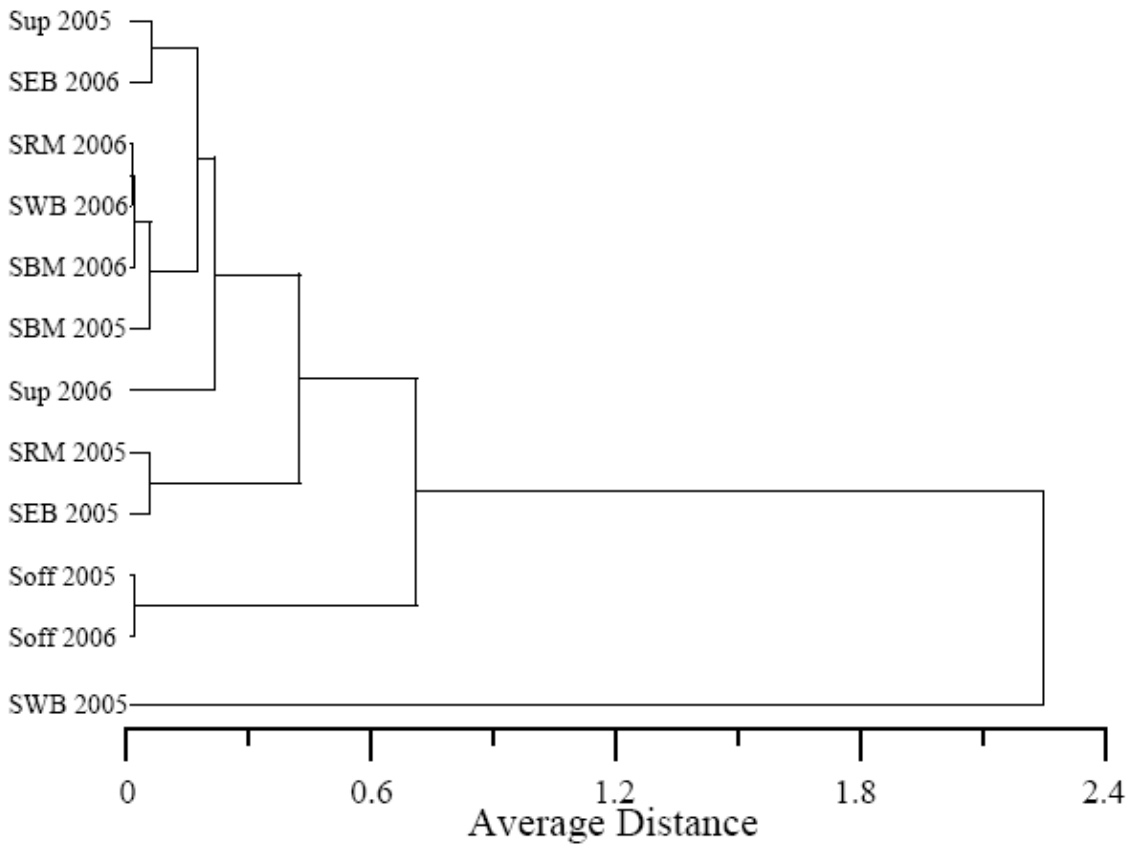

Fig. 2.5. Hierarchical clustering distance dendrogram of annual, site-specific average total phytoplankton biomass (wet g m^{-3}) measures at river, bay, and lake sites in the Sandusky system, Lake Erie during 2005 and 2006. Site locations and abbreviations are given in Fig. 2.1.

CHAPTER 3

TRIBUTARY, BAY, AND OFFSHORE PHYTOPLANKTON PRODUCTIVITY IN LAKE ERIE – SIMPLE SWITCHING FROM LIGHT- TO NUTRIENT-LIMITATION ALONG THE LOADING GRADIENT?

Introduction

Macronutrients and light commonly limit phytoplankton primary productivity from ponds to large lakes and oceans and on temporal scales ranging from seconds to decades (Reynolds 1988, 2006). In large-lake phytoplankton research, the seasonal outcomes of primary productivity limitation have been commonly considered (*e.g.*, seasonal succession; Sommer et al. 1986), with intra-system spatial variation studied less frequently. Even when spatial considerations have been considered, studies often focused on differences between offshore sites in separate basins (Millard et al. 1996, Fahnenstiel et al. 2000, Smith et al. 2005), whereas more recent large lake studies have focused on nearshore/offshore coupling (Millie et al. 2003, Lohrenz et al. 2004, Depew et al. 2006). Nearshore/offshore coupling has been studied in marine systems focusing on how tributaries influence coastal estuary and offshore phytoplankton community biomass (Cloern 1987, Salisbury et al. 2001), seasonal dynamics (Cloern et al. 1983), primary productivity (O'Donohue and Dennison 1997, Burford and Rothlisberg 1999), and bloom-formation capacity (Carstensen et al. 2007), and net ecosystem production (Ram et al. 2003). Clearly, offshore large lake phytoplankton productivity is likely similarly

influenced by tributary inflow (Moll et al. 1993); as tributaries connect people in the watershed with lake ecosystem function, understanding how human activities in the watershed affect offshore processes requires knowledge of how tributary input affects coastal and offshore areas (Eyre 1998).

Most work with lake tributary influences on offshore processes has focused on nutrient loading (Carpenter et al. 1998) with secondary foci on sediment (Richards et al. 2001, Malmaeus and Håkanson 2003) and toxin loading (Kelly et al. 1991, Hurley et al. 1998). However, tributaries, due to high nutrients and well-mixed waters, may provide sufficient, but not ideal, habitat for phytoplankton. Indeed, they may contribute phytoplankton to coastal and offshore ecosystems, a function that has been overlooked in freshwater systems. Tributary-loaded phytoplankton may affect coastal and offshore processes more in freshwater systems than marine systems because freshwater phytoplankton could continue growing or even grow faster (due to increased light penetration) as they move from turbid tributaries to clear offshore areas; in marine systems, strong salinity gradients generally select against freshwater phytoplankton growth (Lionard et al. 2005) due to osmotic stress (Kirst 1990). To our knowledge, phytoplankton growth rates from tributary to coastal to offshore parts of a large lake have not previously been investigated, although loaded phytoplankton have the potential to negatively affect offshore areas by forming harmful algal blooms and increasing hypolimnetic oxygen depletion rates (Edwards et al. 2005).

Watershed anthropogenic activities have greatly modified the Lake Erie ecosystem. From its post-glacial natural state with extensive wetlands, the watershed has been modified for agricultural, urban, suburban, industrial, and manufacturing uses (Sly

1976). These modifications increased nutrient load that in turn led to cultural eutrophication and its consequent recurrent cyanobacterial blooms, hypolimnetic hypoxia, benthic macroinvertebrate and fish kills, and toxic chemical loadings (Beeton 2002). Through public and legislative action, phosphorus control programs were implemented (DePinto et al. 1986), nutrient loads decreased (Dolan 1993), and offshore phytoplankton biomass decreased into the mid-1980's (Makarewicz 1993). However, since phytoplankton biomass minima in the mid-1990's, recent biomass increased (Conroy et al. 2005b), cyanobacterial blooms resumed (Vincent et al. 2004, Conroy and Culver 2005), and hypolimnetic hypoxia continues to form (Burns et al. 2005) with no concurrent increase in total phosphorus load (Dolan and McGunagle 2005). These studies indicate that external phosphorus loading may no longer control within-lake phytoplankton biomass. Among the alternative factors that have been proposed are nutrient recycling (Conroy et al. 2005a), selective phytoplankton rejection by invasive dreissenid mussels (Vanderploeg et al. 2001), and micronutrient control of phytoplankton growth (North et al. 2007). Here we investigate the potential importance of tributary-derived phytoplankton.

The goal of our study was to examine the Algal Loading Hypothesis of phytoplankton bloom development as a means of understanding processes by which tributaries contribute to offshore phytoplankton community dynamics in large lakes (Conroy 2007). We hypothesized that tributary phytoplankton were phosphorus-replete but light-limited whereas lake phytoplankton were phosphorus-limited but light-replete. We examined this hypothesis by quantifying limitations to, and rates of, phytoplankton primary productivity along the loading gradient from a tributary, into a coastal lacustrine

estuary, and out into the offshore zone of a large lake to better understand how tributaries contribute to offshore phytoplankton growth, harmful algal blooms, and hypolimnetic hypoxia. We used a combination of chemical, physiological, and modeling methods to test these hypotheses in a large, north temperate lake ecosystem, the Sandusky system of Lake Erie.

Materials and methods

Study location–We chose to use the Sandusky system (consisting of the Sandusky River, Bay, and subbasin) as our study site because of its (1) primarily agriculture-based watershed (> 85%, Richards et al. 2002) similar to other watersheds in Lake Erie and the Laurentian Great Lakes; (2) its importance in loading nutrient and suspended sediments to Lake Erie (Richards and Baker 1985); and, (3) its large tributary (Sandusky River, watershed area = 4600 km^2, CLEAR 1975), coastal lacustrine estuary (Sandusky Bay, 162 km^2 area, mean depth = 2.6 m; Richards and Baker 1985), and deep offshore area (Sandusky subbasin, 900 km^2 area, mean depth = 13.3 m; Conroy et al. 2007). The Sandusky River receives high nutrient loads from its watershed (Richards and Baker 2002), Sandusky Bay is hypereutrophic with phytoplankton wet biomass often > 25 g m^{-3} (Conroy et al. 2007), and the Sandusky subbasin receives outflow from Sandusky Bay and is often the first area to become hypoxic during the summer in Lake Erie (Richards and Baker 1985).

To quantify limitations to the rates of phytoplankton productivity (PPr), we established six sites in the Sandusky River (Sup), Bay (SRM, SWB, SEB, SBM), and subbasin (Soff; Fig. 3.1) and measured light limitation, as well as chemical and

physiological indicators of nutrient limitation, and PPr. Light and chemical limitation was usually assessed at all sites on all sampling dates but physiological limitation indicators and PPr were assessed only on a subset of dates and sites. For physiological indicators and PPr, we initially used sites SRM, SEB, and Soff as representatives of river, bay, and offshore phytoplankton communities, respectively, but changed our river site to Sup as initial results revealed that SRM phytoplankton community response was similar to that of the SEB phytoplankton community.

Field sampling and laboratory methods–At each site except Sup, we measured Secchi disk transparency (SD) and vertical profiles (0.5 m intervals) of temperature, fluorescence, and photosynthetically active radiation (PAR) with a multiparameter instrument package (YSI, Inc., Yellow Springs, Ohio and Li-Cor, Inc., Lincoln, Nebraska). Whole-water samples were taken at all sites either from just below the surface (Sup), to twice the Secchi disk transparency depth (SRM, SWB, SEB, and SBM), or to 3 m (Soff) with an integrating sampler and dispensed into amber polyethylene bottles for subsequent determination of nutrient concentrations, chlorophyll *a* concentrations (Chl *a*), physiological nutrient limitation metrics, and PPr. Nutrient concentration samples were held on ice in the field and frozen until later analysis; Chl *a* samples were filtered (0.7 μm nominal pore size; GF/F Whatman plc, Middlesex, United Kingdom) aboard the sampling vessel and frozen; and, samples for metabolic determinations were held in amber polyethylene bottles for later analysis (within 24 h).

Total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP) were determined on unfiltered whole water samples according to standard methods (APHA et al. 1998) on a TOC analyzer (high-temperature catalytic combustion method; Rosemount

Dohrmann, Santa Clara, California) and an autoanalyzer (persulfate digestion followed by nitrate and orthophosphate determination, respectively; Lachat Instruments, Loveland, Colorado). Chl *a* was determined spectrophotometrically after manual extraction with 90% aqueous acetone (Lorenzen 1967, USEPA 1997).

Light and nutrient indicators of limitation–We tested for light limitation using indicators based on site-specific light attenuation and phytoplankton physiology. To describe the light climate at all sites, we calculated the light attenuation coefficient (k) according to Bledsoe and Phlips (2000) and mean PAR in the water column (I_a) according to Smith et al. (2005). To test for light limitation using phytoplankton physiological response at river (Sup), bay (SEB), and offshore (Soff) sites, we determined the onset of light saturation ($I_k = P^B_{max}/\alpha^B$; see below for definitions of P^B_{max} and α^B). We calculated the photic depth as twice the Secchi disk transparency depth ($z_{p,SD}$) for all sites and the mean of $z_{p,SD}$ and the depth of the onset of light limitation ($z_{p,k}$) for the subset of sites (Sup, SEB, and Soff). At all sites, we calculated the ratio of the photic and mixed depths ($z_{p,SD}$:z_m) to determine the light-limited proportion of the water column and additionally calculated $z_{p,k}$:z_m and I_a/I_k for the subset of sites. We considered phytoplankton communities light-limited when z_p:z_m < 0.16 (Alpine and Cloern 1988) and/or $I_a/I_k < 1$ (Knoll et al. 2003).

We tested the nutrient limitation status of the phytoplankton community chemically using the ratios TOC:TN, TOC:TP, and TOC:Chl *a*. Guildford et al. (2005) previously used ratios of particulate C, N, and P to chemically assess nutrient limitation of Lake Erie phytoplankton communities during May – October 1997. Because we did not specifically measure particulate C (see *Field sampling and laboratory methods*

above), we used TOC for our limitation metrics as this fraction represented most of the particulate matter (but also included dissolved organic C) while excluding inorganic C. Measuring particulate C in our study would have biased our results due to the large amount of suspended matter (including clays, detritus, minerals) in the river and bay (Richards and Baker 1985) that was unavailable for phytoplankton growth.

We assessed light and chemical nutrient limitation at all six sites from the river through the bay and out into the lake. Because we could not deploy light profiling equipment at Sup, we used PAR profiles from SRM as the most likely surrogate when calculating light limitation metrics. Nutrient concentrations were determined from 18 April – 11 July 2005 and 12 April – 15 September 2006.

Phosphorus physiology determinations–To assess how phosphorus limitation changed along the loading transect, we performed phosphorus debt and phosphorus uptake rate determinations at river, bay, and offshore sites. We determined P-debt from SRM, SEB, and Soff twice in 2005 (11 July and 24 August) and from Sup, SEB, and Soff six times in 2006 (5 June, 10 and 31 July, 21 August, and 15 September). We determined P-uptake rates at all of the above dates except we substituted 26 June 2006 for 5 June 2006.

P-debt observations followed the techniques of Healey and Hendzel (1979) but were modified to use radiometric techniques, making the test more sensitive. To triplicate 10-mL whole-water samples from each site (plus one formalin-fixed control for adsorption of phosphate to inorganic sediment particles, detritus, cells, and other material in the water), we added 50 μmol of KH_2PO_4 and 1 MBq of carrier-free radiotracer ($^{32}PO_4$). Experimental tubes were incubated in the dark at room temperature for 24 h,

after which 1 mL was dispensed into scintillation vials for counts of total radioactivity and the remaining volume was filtered through 1.0-µm filters. Filters were rinsed with water, dried, and counted by liquid scintillation (Model LS6800, Beckman Coulter, Inc., Fullerton, California). Uptake of P was determined by multiplying the ratio of the amount of radioactivity taken up to that available by the amount of non-radioactive P supplied. The P taken up was scaled by Chl *a* giving the P-debt as µmol P µg Chl a^{-1}. Phosphorus-deficient phytoplankton communities have P-debt > 0.075 µmol P µg Chl a^{-1} (Guildford et al. 2005).

Phosphorus uptake rate was determined according to Heath (1986). To triplicate 10-mL whole-water samples from each site (plus one formalin-fixed control), 1 MBq carrier-free radiotracer ($^{32}PO_4$) was added. At 2, 4, and 6 min after radiotracer addition, 1.0-mL was removed and filtered through a 1.0-µm filter. At the end of the experiment, 1.0-mL was dispensed into a scintillation vial for determination of total radioactivity added. Filters were rinsed with water, dried, and samples were counted by liquid scintillation. The P-uptake rate (K, min^{-1}) was calculated from the slope of the regression of ln Q versus time since addition (minutes) where

$$\ln Q = \ln\left(\frac{DPM_{total}}{DPM_{total} - DPM_{filter}}\right),$$

DPM_{total} was the total amount of radioactivity added, and DPM_{filter} was the amount of radioactivity taken up in the experimental containers. Turnover time (TT, min) was calculated as the inverse of the uptake rate. Phytoplankton communities show extreme P-deficiency with TT < 10 min, moderate deficiency with TT < 60 min, and no deficiency with TT > 60 min (Guildford et al. 2005).

Productivity versus irradiance determinations–We assessed PPr from river (SRM or Sup), bay (SEB), and offshore (Soff) sites once during 2005 (24 August) and seven times in 2006 (8 May, 5 and 26 June, 10 and 31 July, 21 August, and 15 September) using the small volume, short incubation method of Lewis and Smith (1983). To 60 mL whole water, 0.74 MBq of $NaH^{14}CO_3$ was added and 3-mL subsamples were then dispensed into 18 scintillation vials. These vials were incubated for 60 min in a temperature-controlled photosynthetron with PAR levels ranging from 0 – ~9.0 mol photons m^{-2} h^{-1} (measured with a Li-Cor LI-190 sensor). Irradiance levels varied approximately logarithmically, with 16 of the wells receiving irradiance at levels less than ~1.5 mol photons m^{-2} h^{-1}. Use of two light levels higher than this allowed detection of photoinhibition. For PPr measurements on 24 August 2005 and 8 May 2006, we were unable to simulate light levels greater than 1.0 and 3.5 mol photons m^{-2} h^{-1}, respectively, due to photosynthetron limitations and could not properly assess photoinhibition. After 60 min of incubation, the vials were removed from the photosynthetron and 10 μL of concentrated HCl was added to sparge the samples of unfixed bicarbonate overnight. Samples were counted the following day by liquid scintillation.

We calculated the amount of ^{12}C fixed in each subsample (mg C h^{-1}) using the proportionality relationship:

$$\frac{^{12}C_{fixed}}{^{12}C_{available}} \propto \frac{^{14}C_{fixed}}{^{14}C_{available}},$$

where $^{12}C_{available}$ was determined by potentiometric titration with 0.02 N H_2SO_4 (APHA et al. 1998), $^{14}C_{fixed}$ was determined from scintillation counts, and $^{14}C_{available}$ was the amount of $NaH^{14}CO_3$ added. This value was scaled to sample Chl *a* giving PPr (mg C

mg chl^{-1} h^{-1}). We then plotted these productivity values against measured irradiance in the photosynthetron (hereafter referred to as PPr-I). Results from 24 August 2005 were not used in any of the following analysis due our inability to simulate higher irradiance levels leading to extreme values for photosynthetic parameters.

Determining photosynthetic parameters–We used two methods to fit photosynthetic parameters to the non-linear relationship describing PPr-I. In the first method, Fee's (1998) software (PSPARMS) was used to fit α^B (mg C mg Chl a^{-1} [mol photons m^{-2}]$^{-1}$), the biomass-corrected (Chl *a*) parameter of photosynthetic efficiency at low irradiances, and P^B_{max} (mg C mg chl a^{-1} h^{-1}), the biomass-corrected maximum productivity. This routine minimizes the sum of squared deviations to determine the best fit. As this method does not take into account photoinhibition, we developed an iterative search algorithm (herein after referred to as the Beta method, J.D. Conroy, manuscript in preparation) that is essentially similar to the method of Fee except it includes the biomass-corrected photoinhibition parameter β^B (mg C mg Chl a^{-1} [mol photons m^{-2}]$^{-1}$). The Beta method is nested in the Microsoft Excel environment (Microsoft Corporation, Redmond, Washington) with a search algorithm based on the examples of Hilborn and Mangel (1997) which is used to fit the productivity versus irradiance model of Platt et al. (1980). The Beta method began with a user-defined search range for the parameters to be fit and then minimized the sum of squared deviations between observed data (PPr-I) and modeled data (calculated using the Platt et al. [1980] model), similar to Fee's (1998) method. In the Beta method, we used three implementations of the search algorithm moving from broad parameter ranges with large step values to narrower ranges with smaller step values (Table 3.1).

Calculating integral productivity–When assessing depth-integrated phytoplankton community productivity at sites with varying depths, light conditions, and nutrient concentrations, we compared areal productivities (sum over depths) not volumetric productivities, because areal measures better integrate the effects of these variables, removing potential bias. To do so, we combined field measures of k and vertical profiles of Chl *a* (calculated from fluorescence profiles) at SRM, SEB, and Soff with laboratory measures of PPr-I at Sup, SEB, and Soff and simulated solar PAR to calculate daily areal productivity (P_{int}) using novel methods (J.D. Conroy, unpublished algorithms) similar to Fee's (1998). Due to sampling limitations, we could not deploy our *in situ* profiling equipment at Sup (see above); therefore, we used k and Chl *a* from SRM as the most comparable surrogate.

Fee's (1998) method (DPHOTO) combines 70% cloud-free simulated solar PAR, its attenuation with depth, and Chl *a* vertical profiles with the photosynthetic parameters determined in PSPARMS to calculate volumetric productivities (mg C m^{-3} h^{-1}) at successive depths. Volumetric productivities are then integrated over the water column depth at 30-min intervals for an entire day giving P_{int} (g C m^{-2} d^{-1}). Our method (J.D. Conroy, manuscript in preparation) follows the same steps, but includes the effects of photoinhibition (by including β^B) and integrates volumetric productivity at 1-h intervals. In our method, we estimated variability in P_{int} estimates by also using 100% and 40% cloud-free simulated solar PAR and recalculating P_{int}.

Testing the importance of light, phytoplankton biomass, and photosynthetic parameters on productivity–To determine how light and nutrients affect phytoplankton productivity along the loading gradient, we conducted a sensitivity analysis of those

parameters used to calculate P_{int} at river (Sup), bay (SEB), and offshore (Soff) sites. We could directly test the effect of light by varying k, but could assess the importance of nutrients only through their effects on phytoplankton community biomass (Chl *a*) and physiology (α^B, P^B_{max}, or β^B). Therefore, we conducted a sensitivity analysis in which we systematically varied one of the parameters (either Chl *a*, α^B, P^B_{max}, or β^B) while holding the remaining parameters constant and calculated the percent differences between the resulting P_{int} value and the initial values (those for each site with their original parameters) on all dates with the appropriate data. We could have arbitrarily chosen to vary the parameter values by some percentage of the original values, but instead we used the other two sites' parameter values to simulate the range of possible parameters as these represented a wide range of field-measured values. Similar methods have been used to investigate dreissenid mussel effects on P_{int} (Fahnenstiel et al. 1995) and differences in P_{int} between Lake Erie's western and eastern basins (Smith et al. 2005).

When varying k, α^B, P^B_{max}, and β^B, we used the actual parameter values from the other sites directly. For Chl *a*, we first determined areal integrated Chl *a* (mg m^{-2}, by multiplying the mean concentration [mg m^{-3}] by mean depth [m]) and then dividing by the other site's mean depth. This procedure simulated Chl *a* changes by accounting for the total Chl *a* at one site and equally distributing it over the entire water column at the other site. Using only site averages of Chl *a* would have greatly over- or underestimated the effect by adding or removing much more phytoplankton biomass than was realistic. For example, on 26 June 2006, mean volumetric concentrations were 33.0 and 7.1 mg Chl *a* m^{-3} and areal integrated concentrations were 85.4 and 95.9 mg Chl *a* m^{-2} at SEB and Soff, respectively. Distributing these areal concentrations over the water column at

the reciprocal sites gave volumetric Chl *a* of 37.8 and 6.3 mg Chl *a* m^{-3} at SEB and Soff respectively, showing the effects of simulating slightly higher Chl *a* at SEB and slightly lower Chl *a* at Soff. If instead, we took the mean volumetric Chl *a* and assumed these were the average concentrations at the reciprocal sites, areal concentrations would have been 18.0 and 445.5 mg Chl *a* m^{-2} at SEB and Soff, respectively, underestimating Chl *a* at SEB and overestimating it at Soff. For our sensitivity analysis, we expected that river and bay P_{int} was most sensitive to light (represented by k) whereas subbasin P_{int} was most sensitive to phytoplankton biomass (as Chl *a*) and phytoplankton physiology (as photosynthetic parameter values).

Statistical analyses–To test for differences in light and nutrient limitation indicators, photosynthetic parameters, and P_{int} among sites from the river to offshore, we used one-way ANOVA followed by Tukey's HSD test for all pairwise comparisons. To compare the Beta algorithm to the established Fee method, we iterated the Beta method without inclusion of the photoinhibition parameter (by setting the search range for $\beta^B = 0$) and determined the best fit of α^B and P^B_{max} (fits of the beta method with $\beta^B = 0$ herein referred to as the JDC method, J.D. Conroy, manuscript in preparation). The resulting parameter values and sum of squares were then compared to those of Fee's (1998) routine with ANOVA combined with Tukey's HSD test. We considered the JDC and Beta algorithms adequate if they found photosynthetic parameter values similar to Fee's (1998) method without increasing the sum of squares; we considered them better if they found similar values while decreasing the sum of squares. For all tests, we Bonferroni-corrected α-levels for each set of tests, so that the light limitation α-level = 0.008 (six tests), the chemical nutrient limitation, photosynthesis parameter fitting methods, and

photosynthetic parameters α-levels = 0.017 (three tests per set), the physiological nutrient limitation α-level = 0.025 (two tests), and P_{int} α-level = 0.050 (one test). All ratios were log_{10}-transformed before testing and all tests were conducted using JMP (SAS Institute Inc., Cary, North Carolina).

Results

Water clarity increased moving from the river to the offshore. Secchi transparency (SD) was greatest ($F_{5,128} = 110.1$, $P < 0.001$; Fig. 3.2a) and light attenuation coefficients (k) smallest ($F_{5,128} = 42.1$, $P < 0.001$; Fig. 3.2b) at the offshore station. This resulted in increased ($F_{5,128} = 8.5$, $P < 0.001$) mean light in the water column (I_a) at sites directly adjacent to the bay (SBM) and offshore (Soff; Fig. 3.2c). Comparisons of photic depths based on the ratio of 2 x SD to mixing depths ($z_{p,SD}$:z_m, Fig. 3.2e) revealed no light limitation, although there were differences between sites ($F_{5,128} = 12.8$, $P < 0.001$). At phytoplankton productivity (PPr) measurement sites during 2006, neither $z_{p,k}$:z_m ($F_{2,17} = 2.7$, $P = 0.09$; Fig. 3.2f) nor I_a/I_k ($F_{2,17} = 3.1$, $P = 0.07$; Fig. 3.2d) indicated light limitation and ratios were similar among sites.

Chemical indicators revealed some nutrient limitation in the Sandusky system (Fig. 3.3). Ratios of total organic carbon concentrations to total nitrogen concentrations (TOC:TN) increased ($F_{5,88} = 3.6$, $P < 0.006$) with distance from the river to offshore, but TOC:TN rarely indicated N-limited phytoplankton communities, with only Soff showing moderate limitation (Fig. 3.3a). Ratios of TOC to total phosphorus concentrations (TOC:TP) also increased ($F_{5,88} = 23.9$, $P < 0.001$) with distance from the river to offshore, and TOC:TP for all sites revealed either moderate or extreme P-limitation (Fig.

3.3b). All ratios of TOC to chlorophyll *a* concentrations (TOC:Chl *a*) indicated extreme limitation, with TOC:Chl *a* ratios at Sup and Soff greater than those ($F_{5,84} = 17.8$, $P < 0.001$) in and near the bay (SWB, SEB, SBM; Fig. 3.3c).

Phytoplankton physiological phosphorus limitation indicators generally supported the chemical indicators (Fig. 3.4), with P-debts differing among sites ($F_{2,19} = 7.7$, $P = 0.004$) and values at Sup and Soff indicating P-limitation (Fig. 3.4a). P-debt at Soff clearly indicated P-limitation but the Sup P-debt on 5 June 2006 (mean of triplicate measures = 0.61 μmol μg Chl a^{-1}; each of the triplicate values had z-scores > 2.5) greatly influenced the remaining data (mean Sup P-debt excluding this date = 0.03). P-turnover times were similar among sites and all indicated P-sufficiency (Fig. 3.4b).

We found that our novel beta method provided a good fit to the Platt et al. (1980) model and included photoinhibition. The best-fit values of α^B and P^B_{max} from the Fee, JDC, and Beta methods did not differ among models (α^B: $F_{2,57} = 0.5$, $P = 0.636$, P^B_{max}: $F_{2,57} = 0.8$, $P = 0.470$). However, the Beta method reduced the sum of squares ($F_{2,57} = 5.2$, $P = 0.009$), indicating a better fit. Comparing model fits from one date (26 June 2006, Fig. 3.5) at SEB illustrates that PPr was inhibited at high irradiances, so including β^B better represented the data (SS = 4.80, 3.79, and 0.77 for the Fee, JDC, and Beta methods, respectively). On this date, α^B was similar among methods (42.5, 54.8, and 47.5 mg C mg Chl a^{-1} (mol photons $m^{-2})^{-1}$) for the Fee, JDC, and Beta methods, respectively) as was P^B_{max} for the Fee and JDC methods (4.92 and 5.00 mg C mg Chl a^{-1} h^{-1}, respectively), but P^B_{max} for the Beta method was greater than the other methods (5.65 mg C mg Chl a^{-1} h^{-1}). Although this difference was not significant over the year, a higher P^B_{max} on any particular date may increase P_{int}.

Photosynthetic parameters varied seasonally among sites (Fig. 3.6). At Sup, α^B decreased from early June through August and increased in September (Fig. 3.6a). Bay (SEB) α^B was greatest early in the season, decreased from mid-June through August, and increased in September (Fig. 3.6a). At Soff, α^B decreased from May to early June, increased through late July, decreased in August, and increased to its highest level in September (Fig. 3.6a). Comparing mean values among sites, α^B was greater ($F_{2,17} = 13.2$, $P < 0.001$) at SEB than at Sup and Soff (Fig. 3.6b). At Sup, P^B_{max} was high in early June, lower from late June through August, and increased in September (Fig. 3.6c). At SEB, P^B_{max} varied little from May through mid-July, decreased in late July and mid-August, and increased on the last sampling date (Fig. 3.6c). At Soff, values were lower than the other sites from May through August but similar to them in September (Fig. 3.6c). Values of P^B_{max} were greater ($F_{2,17} = 5.2$, $P = 0.006$) at SEB than at Soff with Sup intermediate (Fig. 3.6d). At all sites, β^B was either greatest in September (SEB and Soff) or was high at this time (Sup; Fig. 3.6e) and either fluctuated (at Sup and SEB) or was consistently lower (Soff) prior to this. Although Soff seasonally-averaged values appeared less than those at the other sites, the difference was not significant ($F_{2,17} = 3.1$, $P = 0.07$; Fig. 3.6f). Seasonal variations in photosynthetic parameters integrated site-specific differences in phytoplankton community structure, phytoplankton community photoadaptation to the *in situ* light climate, and seasonal variations of temperature and nutrients.

Integrated productivity (P_{int}) showed various patterns through time at all three sites: a unimodal peak with a maximum in August at Sup, a nearly monotonic decrease throughout the season at SEB, and successive high and low values on consecutive dates

at Soff (Fig. 3.7a). Simulating P_{int} with increased light (100% cloud-free) changed values less than simulations using decreased light (40% cloud-free; Fig. 3.7a). Mean P_{int} values were greater ($F_{2,17} = 3.7$, $P = 0.045$) at SEB than Soff with Sup intermediate to the other sites (Fig. 3.7b).

Sensitivity analyses showed that light, phytoplankton biomass (as Chl *a*), and phytoplankton physiology affected P_{int} in the Sandusky system (Fig. 3.8). At Sup, increased light penetration (by decreasing k to Soff values) increased P_{int} 88%, on average (Fig. 3.8a). Increasing phytoplankton biomass (Chl *a*) at Sup to SEB and Soff values increased P_{int} more than 40%, although mean values were influenced by large differences in early June (Fig. 3.8a). At SEB, P_{int} increased over 150% when light attenuation was decreased (k to Soff values; Fig. 3.8b). Varying phytoplankton biomass (Chl *a*) at SEB led to small P_{int} changes (< 10%; Fig. 3.8c). At Soff, decreasing light penetration (k to Sup or SEB values) decreased P_{int} more than 85% and increasing phytoplankton biomass (Chl *a*) increased P_{int} over 50% (Fig. 3.8c), although the biomass effect was influenced by large differences in July. Increasing the Sup phytoplankton community's ability to use light at low irradiances (by increasing α^B to SEB values) or its maximum photosynthesis at light saturation (by increasing P^B_{max} to SEB values) increased P_{int} > 40% (Fig. 3.8d). Changing α^B or P^B_{max} to Soff values had little effect (Fig. 3.8d). Changing the photoinhibition of Sup's phytoplankton community (by changing β^B) also had little effect (Fig. 3.8d). At SEB, decreasing the phytoplankton community's light utilization efficiency or maximum photosynthesis (α^B or P^B_{max}, respectively) decreased P_{int} more than 30% but lessening photoinhibition (by decreasing β^B) only increased P_{int} by at most 5% (Fig. 3.8e). At Soff, increasing the phytoplankton

community's light utilization efficiency (by increasing α^B to SEB levels) or maximal photosynthesis at light saturation (by increasing P^B_{max} to Sup or SEB values) increased P_{int} over 100% but increasing photoinhibition (by increasing β^B) decreased P_{int} only 3% (Fig. 3.8f).

Discussion

Light and nutrient limitation of phytoplankton productivity–Tributaries to large lakes may serve as important phytoplankton sources due to their high nutrients and the potential for phytoplankton luxury nutrient uptake under light-limiting conditions. We hypothesized that in tributaries, light would limit phytoplankton primary productivity, whereas offshore, nutrients would limit productivity. Our findings supported those expectations only in part: nutrients limited productivity offshore and not in Sandusky Bay or River, but we never observed light limitation of productivity. We found quick light attenuation and consequently low light levels in Sandusky River and Bay, and increased light levels offshore, as hypothesized. However, light did not limit phytoplankton productivity, most likely due to the shallow depths in the river (~ 1-2 m) and bay (max depth ≈ 3 m). Even with the high attenuation coefficients found in the river and bay (Sup, SRM, SWB, and SEB), over 40% of the water column had irradiances high enough for photosynthesis. Additionally, N was rarely limiting either in the river, bay, or offshore, but the extent of P limitation increased from river to offshore sites. Ratios of TOC to Chl *a* indicated extreme nutrient deficiency at all sites with greatest deficiency offshore and in the river. However, spatial patterns in TOC ratios were complicated by the covariance of C and either N, P, or Chl *a*. Concentrations of TOC, N, P, and Chl *a* all

decreased moving offshore (data not shown), but the relative magnitude of the decrease in each caused the observed ratio changes. For example, Sup TOC (740 μM) and TN (353 μM) were greatest among the sites, but the faster N reduction with distance from the tributary (*e.g.*, Soff's TOC and TN concentrations were 370 and 52 μM, respectively) increased TOC:TN. Likewise, Chl *a* was greater at Sup than Soff (21.0 and 3.8 μg L^{-1}, respectively), but TOC:Chl *a* was similar at these sites because TOC was also greater at Sup (see above).

Where other studies (*e.g.*, Guildford et al. 2005) used TOC:Chl *a* as an index of nutrient limitation, we propose that it also could feasibly be used to indicate light limitation under nutrient-sufficient conditions. Viewed in this manner, chemical limitation indicators supported some light deficiency at Sup and nutrient limitation at Soff (*i.e.*, similar high TOC:Chl *a* at Sup and Soff) with decreased limitation at SEB and SBM (*i.e.*, TOC:Chl *a* approaching moderately limiting values) due to sufficient nutrients and increased light levels. Taken together, light and chemical nutrient indicators, *sensu stricto*, provided support for our hypothesis that nutrient limitation increased, but did not support our hypothesis that light limitation decreased moving from the river to the offshore. However, light was less available, and nutrients more abundant in the river and bay than offshore, supporting our hypothesis, *sensu lato*.

Phytoplankton physiological metrics showed partial evidence for increased P limitation moving from the river to the offshore. P-debt, a measure of the amount of P taken up by the phytoplankton community over a 24-h period under light-deficient conditions, revealed P-limitation at Soff and P-sufficiency at SEB. The majority of our P-debt observations at Sup indicated that the phytoplankton community was not P-

limited; only observations on 5 June 2006 indicated the contrary (see Results above), and these values were significantly different from all the others ($F_{1,22} = 1477$, $P < 0.001$). P-turnover times, however, indicated P-sufficiency of the phytoplankton communities at all sites. Why would P-debt but no P-uptake indicate P-limitation? P-debt involves longer incubations (time) than P-uptake (< 10 min) and could allow time for phytoplankton from all sites to deplete internal P stores before starting to take up additional P. The Sandusky system has high P concentrations relative to other parts of Lake Erie and other inland systems in Ohio (Makarewicz et al. 2000, Gao and Heath 2005, J.D. Conroy unpublished data) and it may take longer than 10 min for phytoplankton from these sites to deplete internal P stores and begin taking up more. If so, we would expect that P-debt better describes P-limitation on a time scale similar to that of phytoplankton doubling times during the summer (approximately daily, Reynolds 2006) because it allows time for depletion of internal P stores. Overall, chemical and phytoplankton physiological nutrient limitation metrics indicate phytoplankton were P-limited, but apparently not strongly so, in offshore areas of Lake Erie. Our findings are similar to those of other authors (Guildford et al. 2005).

If light constrains phytoplankton productivity in the river and bay but P limits offshore phytoplankton, we would expect greater α^B, P^B_{max}, and β^B at river (Sup) and bay (SEB) sites than offshore (Soff), because of increased light-use efficiency with adaptation to low light and greater nutrient concentrations (Knoll et al. 2003). Overall, we found equivocal support of these expectations. We found that α^B was greatest at SEB, a site of relatively low light penetration and quick light attenuation, supporting our hypothesis. However, α^B was similar at Sup and Soff indicating that phytoplankton at these sites had

comparable abilities to use light at low irradiances, whereas we predicted that Sup α^B would be greater than that at Soff and SEB. Despite an apparent pattern of increased β^B at river and bay sites and decreased β^B offshore, this pattern was not statistically supported. Patterns in P^B_{max} generally supported our hypothesis with greatest photosynthesis at light saturation at SEB, lowest rates at Soff, and intermediate rates at Sup. In summary then, photosynthetic physiological parameter results (except α^B) suggested that river and bay phytoplankton communities were more light-deficient and nutrient-replete than offshore communities.

Our measurements of photosynthetic physiological parameters were generally similar to those found by Smith et al. (2005) for phytoplankton communities in the west-central basin of Lake Erie (just east of the Sandusky subbasin) and Depew et al. (2006) for nearshore phytoplankton communities in the eastern basin of Lake Erie, yet also varied in systematic ways based on the light and nutrient conditions in the Sandusky system. Our α^B values were greater than those found by Smith et al. (2005) and Depew et al. (2006), especially at SEB (Table 3.2), suggesting Sandusky system phytoplankton communities were more efficient using light at these sites with high light attenuation coefficients (Table 3.2). Values of P^B_{max} were also greater at SEB than in the west-central or nearshore eastern basins, but Sup and Soff values were lower (Table 3.2). Sandusky system sites had higher phosphorus concentrations than west central or the nearshore eastern basins of Lake Erie (Table 3.2) which suggests that some other variable may be restricting P^B_{max} at Sup and Soff. We found greater P_{int} at Sup and SEB than in the west-central or nearshore eastern basins and Soff P_{int} was intermediate to the west-central basin and the nearshore eastern basin (Table 3.2). These differences among Lake

Erie sites emphasize the heterogeneity of the phytoplankton community along river to offshore, nearshore to offshore, and basin to basin gradients (Conroy 2007, Conroy et al. 2005b). Further, comparable parameter values and P_{int} at Soff and the west central basin (Smith et al. 2005) provides support for our novel Beta and JDC methods as Smith et al. (2005) used Fee's (1998) fitting method.

Phytoplankton productivity along a loading gradient–Phytoplankton community productivity was greatest at SEB, especially early in the season. Fitted photosynthetic parameters revealed that the SEB phytoplankton community was highly efficient at using even small amounts of light to fix large amounts of carbon. Sandusky Bay appeared to be an ideal habitat for phytoplankton growth during May through June with optimal combinations of nutrients and light. By September, P_{int} at river, bay, and offshore sites converged, due to increased photosynthetic parameters caused by decreased light and increased fertilization from autumnal overturn.

At Sup, sensitivity analysis indicated that light affected P_{int} the most. Similarly, SEB P_{int} increased with increased light. Light was also important at Soff, with decreased P_{int} with increased light attenuation. Soff P_{int} was most sensitive to changes in photosynthetic parameters, with increased α^B and P^B_{max} causing increased P_{int}. Both Sup and SEB were less sensitive to changes in α^B and P^B_{max}. Across sites, modifying β^B resulted in very little P_{int} change. The lack of contribution of photoinhibition to P_{int} was not surprising as the irradiance levels causing photoinhibition (> 2.0 mol photons m^{-2} d^{-1}) were found only in the uppermost 0.3, 0.5, or 3.0 m at Sup, SEB, and Soff, respectively. These findings again implicate the direct importance of light in affecting phytoplankton

productivity in the river and bay and the indirect importance of nutrients in affecting offshore productivity through modifications of photosynthetic parameters.

Understanding how various parameters interact to cause changes in phytoplankton productivity along the loading gradient can be important in determining how tributary-loaded phytoplankton affect offshore dynamics. If bay phytoplankton increase their productivity once loaded into the offshore due to increased light penetration, they may contribute substantially to harmful algal blooms and exacerbate hypolimnetic oxygen depletion rates. We found that bay phytoplankton increased their productivity > 150% when light attenuation decreased in our sensitivity analysis, supporting the potential importance of phytoplankton load on offshore dynamics.

Tributaries are not the sole sources of phytoplankton loading to offshore phytoplankton communities. Phytoplankton communities resuspended during basin-scale mixing events (Lohrenz et al. 2004), nearshore communities (Depew et al. 2006), communities from upstream lakes in a chain of lakes (Patoine et al. 2006), and communities entrained by a thermal bar caused either by differential heating of the nearshore or by the discharge of river water (Holland and Kay 2003), all can affect offshore dynamics. Determining the resultant effects of these other "loaded" phytoplankton remains an area where significant contributions can be made.

Contribution of respiration to net primary productivity–P_{int} rates were high at all sites and showed important seasonal dynamics. Because ^{14}C-incubated PPr experiments estimate a quantity between gross and net phytoplankton productivity (Peterson 1980) and P_{int} calculations performed in this experiment integrate over only the light portions of the day (*e.g.*, dark $P_{int} = 0$; Fee 1998), understanding carbon cycling in this system

requires consideration of the role of respiration. Previous authors have illustrated the importance of night respiration in calculations of net productivity (Cole et al. 1992); we used a similar approach here. Assuming 10 h of darkness each day, we estimated daily respiration (R; g C m^{-2} d^{-1}) as a function of P^B_{max} (5, 25, and 50%, Cole et al. 1992) then subtracted it from P_{int} giving an estimate of daily areal integrated net PPr (Net PPr). Note that this calculation neglected respiration of that part of the phytoplankton community outside of the photic zone and therefore underestimated R, overestimating Net PPr. Results of these calculations reveal that night respiration consumes a fair proportion of the fixed carbon (Fig. 3.9), even indicating the possibility of net heterotrophy late in the summer at the highly productive SEB site. Mean R:P_{int} averaged 0.02-0.24, 0.05-0.53, and 0.05-0.50 for Sup, SEB, and Soff, respectively, indicating that up to 50% of C fixed by photosynthesis each day could be consumed by the phytoplankton community that same day. Further, these calculations do not include bacterial respiration, which likely is an important component, especially offshore (Heath et al. 2003); consequently, Net PPr may be even lower. Determining the balance of autotrophy and heterotrophy in tributary, coastal lacustrine estuary, and offshore areas of large lake ecosystems is important when considering how tributaries and nearshore systems may affect offshore function, especially as these pertain to offshore problems such as harmful algal blooms and hypolimnetic hypoxia.

Determining and assessing the importance of tributary phytoplankton on offshore processes relies on understanding the limits to phytoplankton growth and rates of phytoplankton productivity in both areas and the temporal dynamics of phytoplankton transport from the tributary offshore. In this study, we quantified light and nutrient

limitation at river, bay, and offshore sites in a large lake ecosystem to better understand how phytoplankton growth-limiting factors varied along this loading transect. We found that light attenuation in the water column was considerable faster at river and bay sites than offshore, but due to the shallowness of these habitats and the turbulence of the water, we did not observe light limitation at these sites. We found that the phytoplankton community became progressively P-limited along this transect. However, phytoplankton productivity was high in the river, coastal lacustrine estuary, and offshore, indicating that the phytoplankton communities at these sites effectively used available resources to grow. Sensitivity analysis revealed that river and bay phytoplankton responded to increased light by increasing productivity, indicating that these phytoplankters may increase their growth rates as they are transported offshore. Consequently, loaded phytoplankton may contribute to the development of harmful algal blooms and hypolimnetic hypoxia and in order to ameliorate these effects, stricter watershed management practices will be needed.

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(a) β^B Fit						**(b)** $\beta^B = 0$	
Parameter	Min	Max	Step	Iter	T	Iter	T
α^B	0	200	10				
P^B_{max}	0	25	1				
β^B	0.001	50	1				
				25000	10.9	1000	1.1
α^B	-15	+15	1				
P^B_{max}	-1.5	+1.5	0.1				
β^B	-7.5	+7.5	0.5				
				13113	5.6	674	0.9
α^B	-1.5	+1.5	0.1				
P^B_{max}	-0.10	+0.10	0.005				
β^B	-0.75	+0.75	0.05				
				36000	14.4	900	1.0

Table 3.1. Minimum (Min) and maximum (Max) search range bounds, step values, and mean number of search iterations (Iter) and run times (T; in s) for the Beta algorithm used to estimate photosynthetic parameters for PPr-I. In (a), we fit the full Beta model, including α^B, P^B_{max}, and β^B but in (b) we set $\beta^B = 0$ and fit only α^B and P^B_{max} to compare the Beta method parameter values to Fee's (1998) method (see Statistical analyses section). Three successive implementations of the model used wide search ranges with large step values (top panels) followed by narrower search ranges and small step values (middle and bottom panels). Ranges in the second and third implementations were defined by subtracting and adding the amounts shown from/to the best-fit parameter of the previous model run. Search range bounds and step values were identical for implementations with and without β^B and are only shown in (a).

Site	k	k *s*	TP	TP *s*	Chl *a*	Chl *a s*	α^B	α^B *s*	P^B_{max}	P^B_{max} *s*	P_{int}	P_{int} *s*
Sup	4.70	1.61	6.08	1.61	18.50	19.53	12.6	4.4	3.28	1.56	1.45	0.31
SEB	4.22	2.29	4.03	2.29	88.48	33.79	41.6	17.8	5.39	1.16	2.22	0.49
Soff	0.37	0.10	0.68	0.10	3.75	2.51	14.0	7.4	2.22	2.03	0.91	0.16
WC	0.26	0.19	0.26	0.19	4.44	5.06	8.64	3.31	4.51	1.74	1.20	0.37
NS E	0.29	0.09	0.29	0.09	1.53	0.66	9.19	4.35	4.05	2.27	0.56	0.35

Table 3.2. Comparison of recent measures (mean and standard deviation, *s*) of Lake Erie light attenuation k (m^{-1}), total phosphorus concentration (TP; µM), chlorophyll *a* concentration (Chl *a*; mg m^{-3}), and phytoplankton photosynthetic parameters α^B (mg C mg chl^{-1} [mol photons m^{-2}]$^{-1}$), the biomass-corrected (Chl *a*) parameter of photosynthetic efficiency at low irradiances, P^B_{max} (mg C mg chl^{-1} h^{-1}), the biomass-corrected maximum rate of photosynthesis, and P_{int}, the areal integrated productivity rate (g C m^{-2} d^{-1}) from the Sandusky River (Sup), Sandusky Bay (SEB), Sandusky subbasin (Soff), the western part of the central basin (WC), and the nearshore area of the eastern basin (NS E) in 2006 (Sup, SEB, and Soff), 1997 (WC), and 2001-2002 (NS E). Data for the Sandusky system came from this study (Figs. 3.6b, d, f, 3.7b), for the WC came directly from Smith et al. (2005, Table 1), and for the NS E came from averaging over the spring through late summer data from Depew et al. (2006, Table 2).

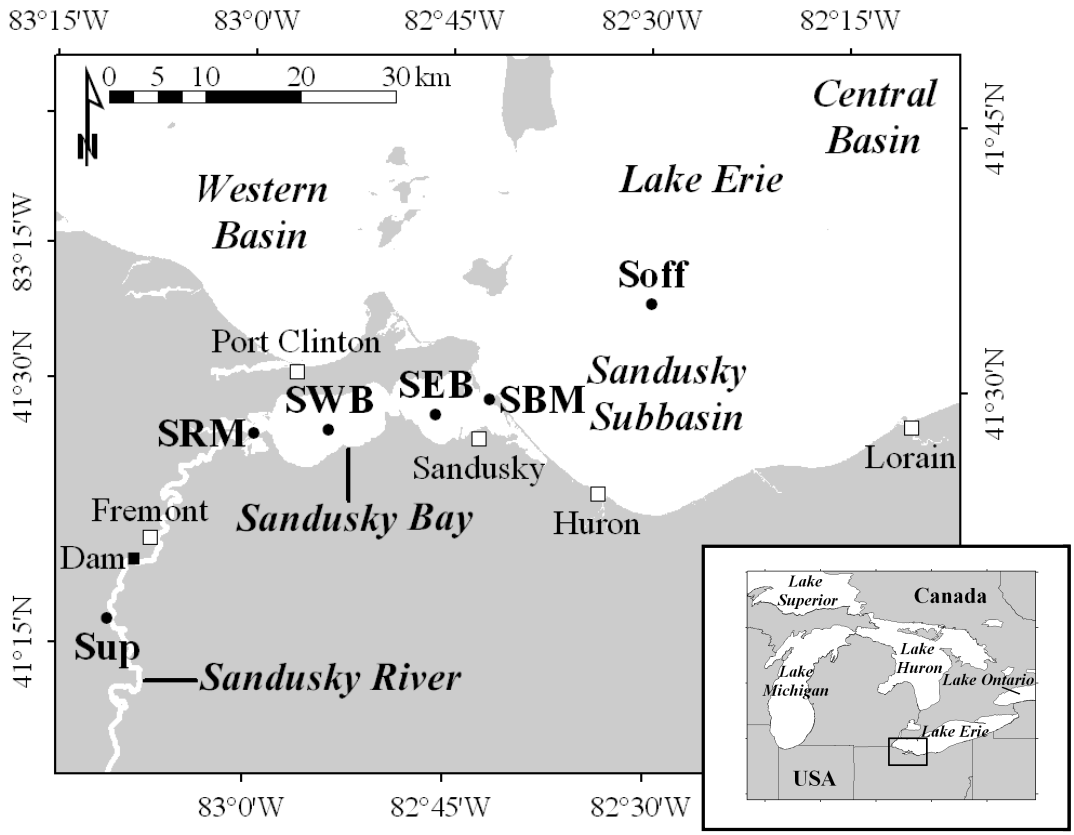

Fig. 3.1. Portion of western Lake Erie depicting the Sandusky system sampling sites. Sites include: upstream (Sup) in the Sandusky River; at the river mouth (SRM); in the western (SWB) and eastern (SEB) portions of Sandusky Bay; at the bay mouth (SBM); and, offshore (Soff) in the Sandusky subbasin.

Fig. 3.2. Mean (plus one standard error) 2005-2006 field data describing the light climate (open bars) and metrics of light limitation (filled bars) at river (Sup), bay (SRM, SWB, SEB, and SBM), and offshore (Soff) sites of the Sandusky system, Lake Erie. Secchi disk transparencies (a), attenuation coefficients (b), mean light in the water column (I_a, c), and the ratio of photic zone depth versus mixed depth $z_{p,SD}$:z_m (e) for all sites indicate increasing transparency, attenuation, and mean light in the water column moving from the river to the offshore. However, the ratio of mean light in the water column to the onset of light limitation I_a/I_k (d) and $z_{p,k}$:z_m (f) gave no indication that phytoplankton communities were light limited with all means above limitation thresholds (dashed lines) from Knoll et al. (2003; I_a/I_k) and Alpine and Cloern (1988; z_p:z_m). Note that different letters above bars indicate significant differences among sites (one-way ANOVA with Tukey's HSD test, α-level = 0.008), numbers following letters are sample sizes, and ND = no data.

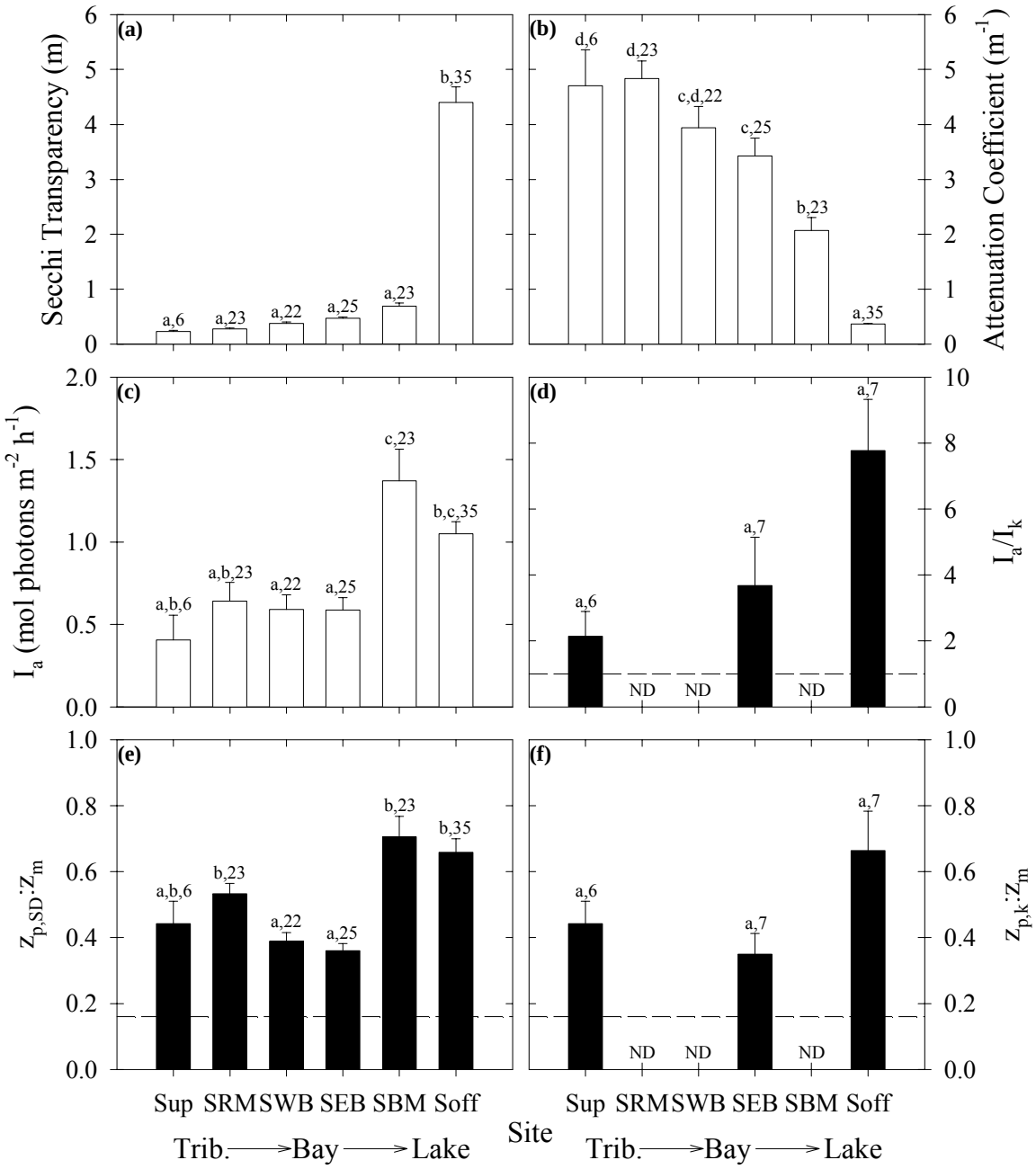
(a)
(b)
(c)
(d)
(e)
(f)
Secchi Transparency (m)
Attenuation Coefficient (m-1)
Ia (mol photons m-2 h-1)
Ia/Ik
zp,SD:Zm
zp,k:Zm
a,6
a,23
a,22
a,25
a,23
b,35
d,6
d,23
c,d,22
c,25
b,23
a,35
a,b,6
a,b,23
a,22
a,25
c,23
b,c,35
a,6
ND
ND
a,7
ND
a,7
a,b,6
b,23
a,22
a,25
b,23
b,35
a,6
ND
ND
a,7
ND
a,7
Sup SRM SWB SEB SBM Soff
Trib. → Bay → Lake
Site
Sup SRM SWB SEB SBM Soff
Trib. → Bay → Lake

Fig. 3.2.

Fig. 3.3. Mean (plus one standard error) of the ratios of total organic carbon concentration (TOC) to total nitrogen concentration (TN) (a), TOC:total phosphorus concentration (TP) (b), and TOC:Chlorophyll *a* concentration (Chl *a*) (c) at river (Sup), bay (SRM, SWB, SEB, SBM), and offshore (Soff) sites. All graphs are trisected into areas of extreme nutrient deficiency (above dashed line), moderate nutrient deficiency (between dashed and dotted lines), and no nutrient deficiency (below dotted line) based upon values in Guildford et al. (2005). Note that different letters above bars indicate significant differences among sites (one-way ANOVA with Tukey's HSD test, α-level = 0.017) and numbers following letters are sample sizes.

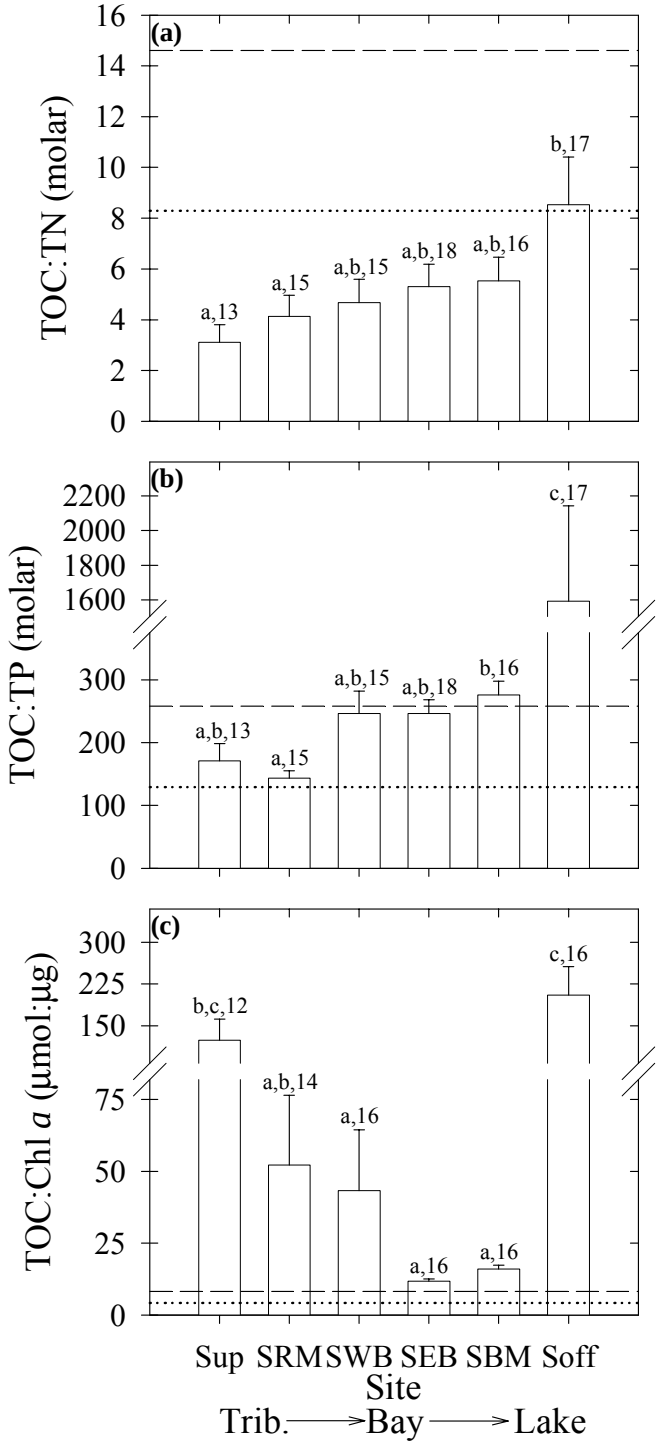
(a)
TOC:TN (molar)
16
14
12
10
8
6
4
2
0
a,13
a,15
a,b,15
a,b,18
a,b,16
b,17
(b)
TOC:TP (molar)
2200
2000
1800
1600
300
200
100
0
a,b,13
a,15
a,b,15
a,b,18
b,16
c,17
(c)
TOC:Chl a (µmol:µg)
300
225
150
75
50
25
0
b,c,12
a,b,14
a,16
a,16
a,16
c,16
Sup
SRM
SWB
SEB
SBM
Soff
Site
Trib.
Bay
Lake

Fig. 3.3.

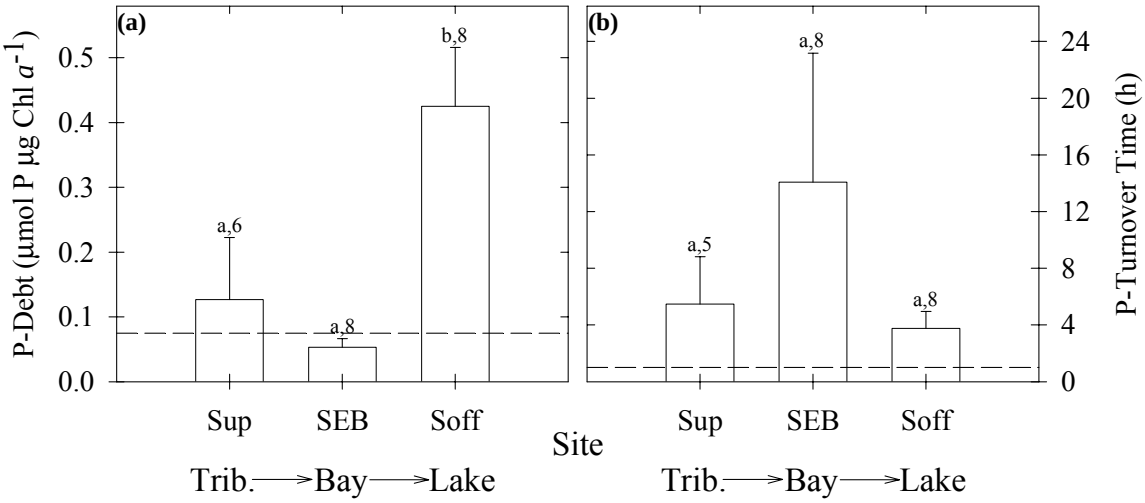

Fig. 3.4. Mean (plus one standard error) P-debts (a) and P-turnover times (b) at river (Sup), bay (SEB), and offshore (Soff) sites during 2006 in the Sandusky system, Lake Erie. Phytoplankton communities with mean values above the dashed limitation thresholds (Guildford et al. 2005) were considered P-limited. Note that different letters above bars indicate significant differences (one-way ANOVA with Tukey's HSD test, α-level = 0.025) among sites and numbers following letters are sample sizes.

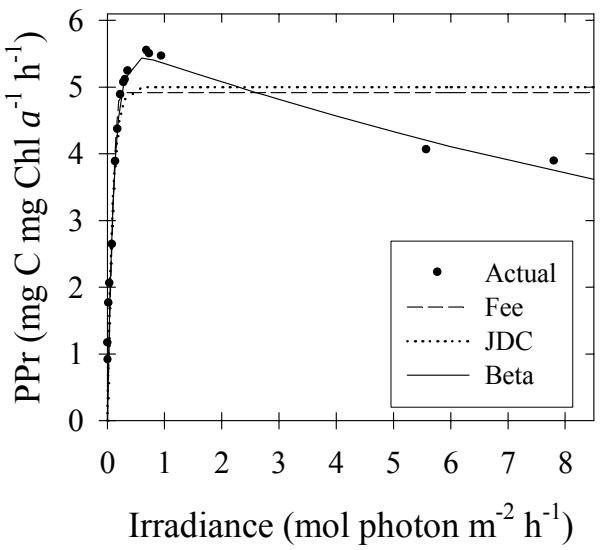

Fig. 3.5. Comparison of the three methods used to fit photosynthetic parameters to actual (filled circles) productivity (PPr) versus irradiance measurements on 26 June 2006 in the Sandusky system, Lake Erie. The Fee (dashed line) and JDC (dotted lines) routines fit α^B (the initial linear increase in productivity versus depth) and P^B_{max} (the maximum productivity at saturating light) using different equations whereas the Beta (solid line) routine includes both of the above parameters but includes β^B to allow for photoinhibition at high irradiances.

Fig. 3.6. Seasonal variation (left panels, a, c, e) and mean values (right panels, b, d, f) of the photosynthetic parameters α^B (the initial linear increase in photosynthesis with light, a and b), P^B_{max} (the maximum photosynthesis at light saturation, c and d), and β^B (the photoinhibition parameter leading to decreased photosynthesis at high values of light, e and f) at river (Sup), bay (SEB), and offshore (Soff) sites during 2006 in the Sandusky system, Lake Erie. The large difference in α^B and P^B_{max} means is mainly caused by much greater α^B at SEB early in the season. Note that β^B is zero for SEB and Soff on 8 May because photoinhibitory light intensities could not be simulated in the laboratory on this date; different letters above the bars indicate significant differences (one-way ANOVA with Tukey's HSD test, α-level = 0.017) and numbers following letters are sample sizes.

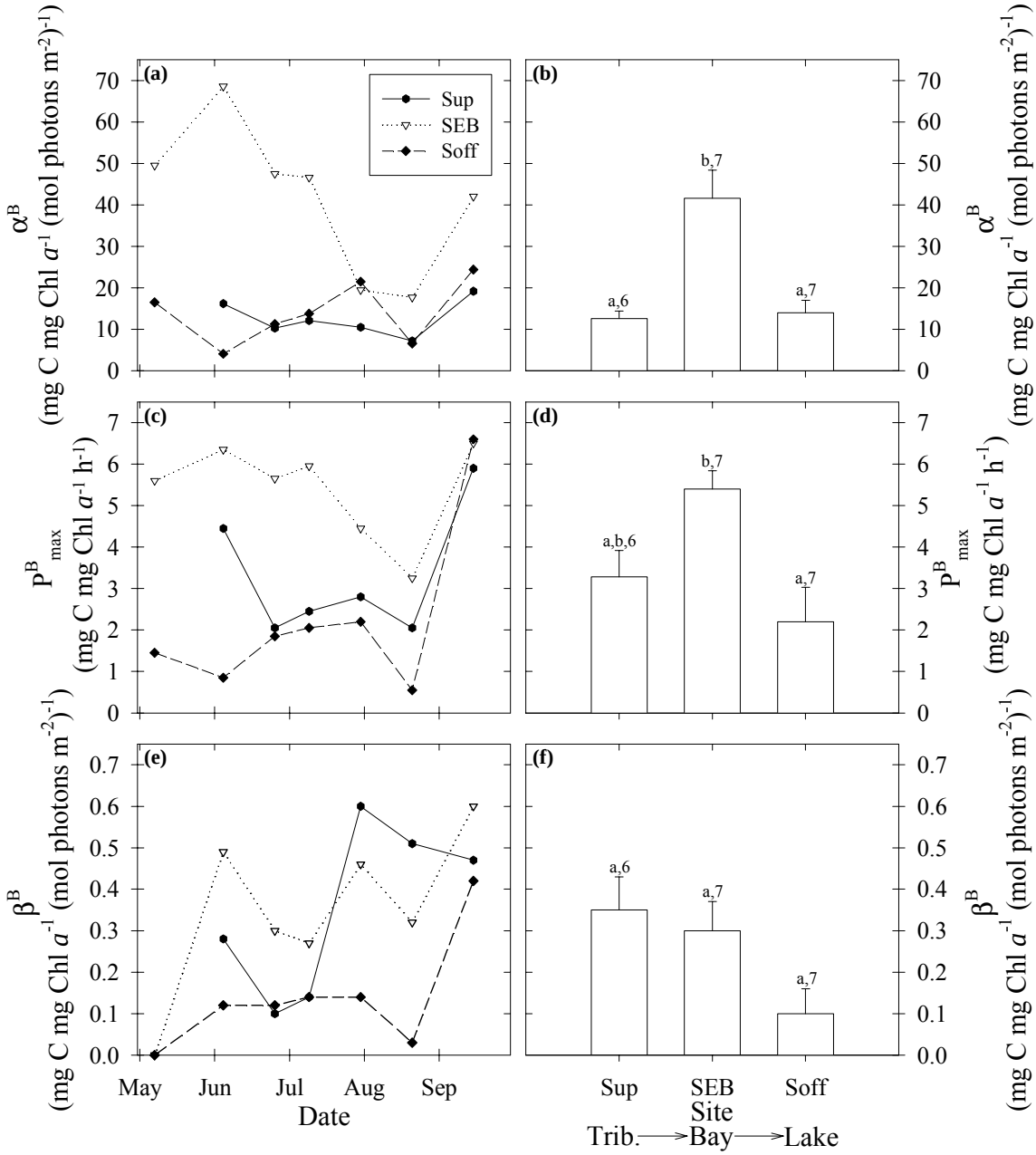
(a)
(b)
(c)
(d)
(e)
(f)
Sup
SEB
Soff
α^B (mg C mg Chl a^{-1} (mol photons m^{-2})$^{-1}$)
P^B_{max} (mg C mg Chl a^{-1} h^{-1})
β^B (mg C mg Chl a^{-1} (mol photons m^{-2})$^{-1}$)
a,6
b,7
a,7
a,b,6
May
Jun
Jul
Aug
Sep
Date
Site
Trib.→Bay→Lake

Fig. 3.6.

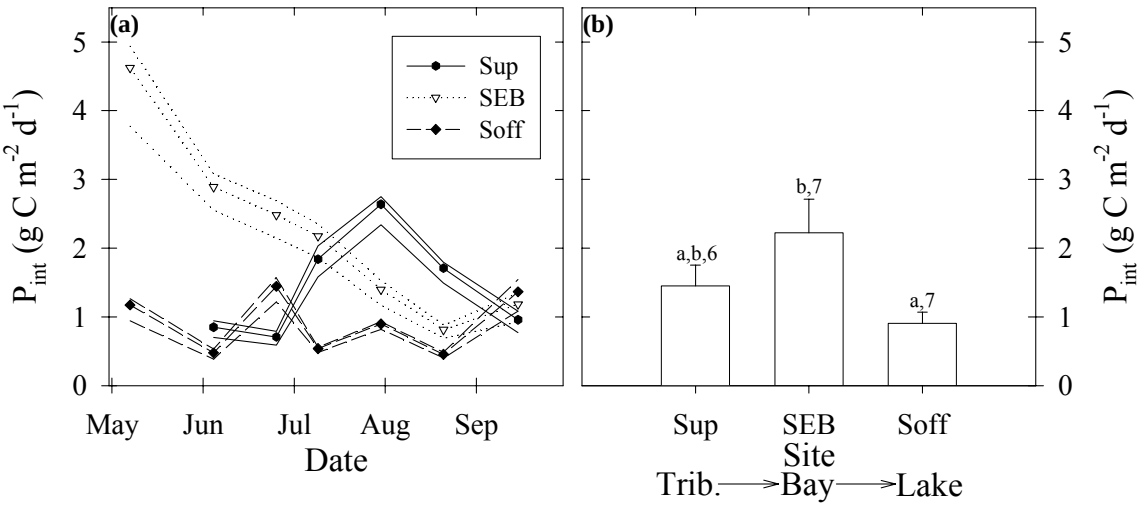

Fig. 3.7. Seasonal variation (a) and mean (plus one standard error) values (b) of integrated productivity (P_{int}) at river (Sup), bay (SEB), and offshore (Soff) sites during 2006 in the Sandusky system, Lake Erie. Integrated productivity values were calculated based upon simulated 70% cloud-free light values but the upper and lower lines bracketing P_{int} values in (a) show simulations using 100% and 40% cloud-free light values, respectively. Note that different letters above the bars indicate significant differences (one-way ANOVA with Tukey's HSD test, α-level = 0.050) and numbers following letters are sample sizes.

Fig. 3.8. Seasonal sensitivity analysis of the importance of changes in light (k) and Chl *a* (upper panels) and photosynthetic parameters α^B, P^B_{max} (P^B_m), and β^B (lower panels) for river (Sup, a and d), bay (SEB, b and e), and offshore (Soff, c and f) sites during 2006 in the Sandusky system, Lake Erie. For each site (*e.g.*, Sup), parameters (*e.g.*, k) were changed to the one of the other two sites (*e.g.*, SEB) on a particular date (*e.g.*, 8 May) and the percent difference between the modified (*e.g.*, k_{SEB} in a) and initial (data shown in Fig. 3.7a) integrated productivities is depicted (*e.g.*, filled bar showing a 19% decrease in Sup P_{int} in a). Parameter changes yielding the largest percent differences were considered the parameters most essential for P_{int} for that site. Note that numbers on the graphs indicate the percent difference of cut-off bars, ND indicates no data available because PPr was not determined at Sup on 8 May, and asterisks show comparisons that were not made.

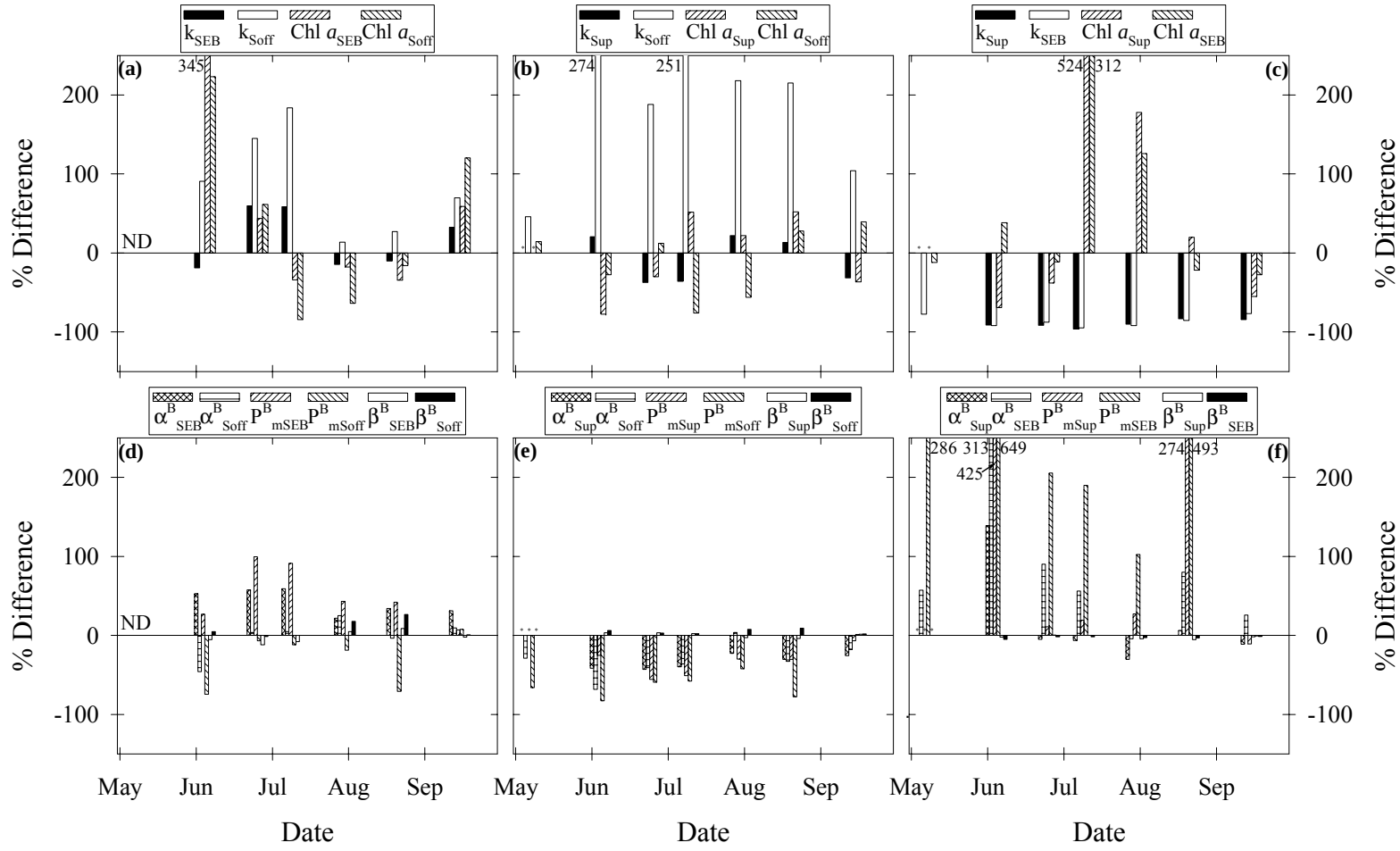
(a)
(b)
(c)
(d)
(e)
(f)
% Difference
Date
May
Jun
Jul
Aug
Sep
ND
345
274
251
524
312
286
313
649
425
274
493

Fig. 3.8.

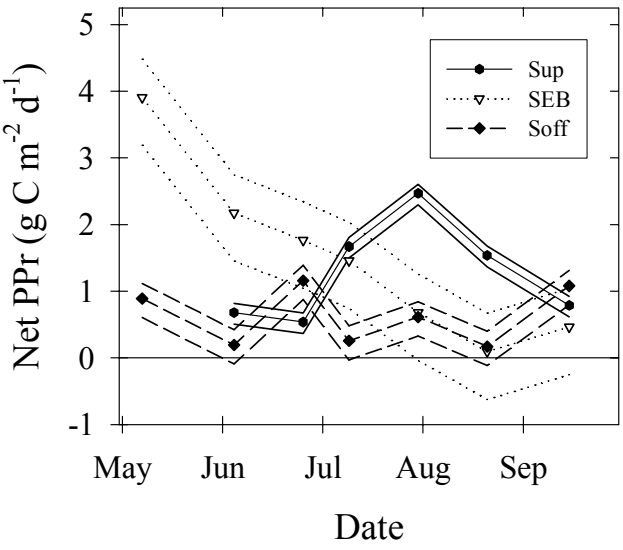

Fig. 3.9. Net phytoplankton productivity (PPr = P_{int} – R) at river (Sup), bay (SEB), and offshore (Soff) sites during 2006 in the Sandusky system, Lake Erie, calculated assuming respiration was 5% (upper line within each site-set of three lines), 25% (center line with symbols within each site-set of three lines), and 50% (lower line within each site-set of three lines) of P^B_{max} (Cole et al. 1992). Net PPr > 0 indicates periods of net autotrophy while Net PPr < 0 indicates periods of net heterotrophy. Note that these calculations do not take into account respiration of the fraction of the phytoplankton community below the photic zone or the microbial community.

CHAPTER 4

RELATIVE IMPORTANCE OF ALLOCHTHONOUS AND AUTOCHTHONOUS PARTICULATE ORGANIC MATTER AND BASIN MORPHOMETRY ON HYPOLIMNETIC HYPOXIA IN LAKE ERIE

Introduction

Understanding the relative contributions of natural variability, natural processes, and anthropogenic activities in forcing global (> 10^6 km^2), regional (10^2-10^6 km^2), and local (10^0-10^2 km^2; Dearing 2006) ecosystem function remains an essential goal of ecological research (Fukami and Wardle 2005). For example, global climate change research extensively studies the effects of human-derived greenhouse gases on recent changes in air temperature within the bounds of natural variability (Stouffer et al. 1994, Petit et al. 1999). Whereas little debate exists that human activities drive most of recent global temperature change (Hansen et al. 2006), the balance between human actions and natural processes in affecting other global phenomena such as El Niño-Southern Oscillation events (Gergis et al. 2006) and regional- and local- processes such as species extinction (Roberts et al. 2001, Cupper and Duncan 2006), precipitation patterns and water availability (Rasmussen and Arkin 1993, Pederson et al. 2006), desertification (Kim et al. 2006), wildfire regimens (Veblen et al. 2000), plant pathogen outbreaks (Burdon et al. 2006), and eutrophication of coastal and offshore lacustrine and marine systems (Beeton 2002, Paerl et al. 2006) remains under investigation. Most studies of

eutrophication have focused on the effects attributable to human activities for good reason – cultural eutrophication caused by discharge of untreated raw sewage, the increasing use of fertilizers in agriculture, high concentrations of phosphates in detergents, excessive nitrogen emissions from automobiles, and industrial pollution increased sharply during the 20th century (Schindler 2006). However, cultural eutrophication accelerates otherwise natural processes in aquatic systems (*e.g.*, excessive nutrients generate harmful algal blooms which in turn increase hypolimnetic oxygen depletion rates). Disentangling the human contribution to eutrophication would allow ecosystem managers to anticipate the extent of possible ecosystem remediation, but assessing how humans influence eutrophication is difficult. Long-term datasets of ecological processes and their associated causative human effects are required, yet identifying the signal amongst the natural noise is difficult.

Increased occurrence, duration, and spatial extent of hypoxic and anoxic hypolimnetic waters (so-called "Dead Zones") in marine and large lake ecosystems have become some of the greatest regional cultural eutrophication-associated problems of the 21st century (Diaz 2001, Beeton 2002), although in Lake Erie, hypolimnetic oxygen depletion has long been recognized as a water quality impairment (Carr 1962). Distinguishing the relative contributions of cultural eutrophication and basin morphometry to hypolimnetic oxygen depletion in Lake Erie has been extensively debated (Dobson and Gilbertson 1971, Burns 1976, Charlton 1980a, 1987, Barica 1982, Rosa and Burns 1987, Charlton et al. 1993, Charlton and Milne 2004, Burns et al. 2005) leading to different conclusions depending on the data used and methods for calculating depletion rates. Cultural eutrophication was often indicated as the most important factor

affecting hypolimnetic oxygen depletion rates in Lake Erie (Rosa and Burns 1987) although paleolimnological evidence suggests areas of anoxia prior to European settlement (Delorme 1982, Reynoldson and Hamilton 1993). Unfortunately, dissolved oxygen concentrations reported for the earliest years (Fish 1960) were subject to methodological errors making trend identification subjective (Charlton 1987). Conversely, given its basin morphometry, low oxygen concentrations (< 4 mg L^{-1}) are possible in Lake Erie's central basin hypolimnion even with low chlorophyll *a* concentrations (< 3 μg L^{-1}) in years when the hypolimnion is very thin (< 4 m; Charlton 1980b). Further, Charlton et al. (1993) highlighted system resilience processes in mediating the effects of human perturbations. As such, legislative restrictions on nutrient (primarily phosphorus) loading may not decrease hypolimnetic oxygen depletion rates in the short-term (< 10 y, Charlton 1987) or even over longer periods (> 20 y, Charlton and Milne 2004) owing to system resilience or because of the predominant importance of morphometry, rather than nutrient stimulation of offshore epilimnetic phytoplankton production.

Classical models considered tributaries solely as nutrient sources to offshore lake areas (*e.g.*, Carpenter et al. 1998). However, excessive nutrients in tributaries may also stimulate phytoplankton growth within the tributary and/or allow luxury nutrient uptake there. The balance between growth stimulation and luxury uptake depends on light limitation manifested through suspended sediment load (Conroy 2007b). Once tributary phytoplankton is transported offshore, light limitation declines, phytoplankton growth increases, and the remaining tributary-derived nutrients further stimulate offshore phytoplankton growth (the Algal Loading Hypothesis, Conroy 2007a). Tributaries then

can increase hypolimnetic oxygen depletion by loading excess particulate organic matter (either actively growing phytoplankton, phytoplankton "primed" for growth, and/or detritus) in addition to the traditional nutrient stimulation of offshore phytoplankton.

Here we assess the relative importance of epilimnetic offshore particulate organic matter, morphometry, and tributary-derived particulate organic matter on offshore hypolimnetic oxygen depletion rates. In the Sandusky system in west-central Lake Erie, we hypothesize that tributary-derived organic matter directly affects hypolimnetic oxygen depletion. We test this hypothesis at several sites with varying morphometry and perceived influence of tributary-derived versus epilimnion-derived particulate organic matter. Through regular synoptic surveys and moored multiparameter instruments, we determined rates of hypolimnetic oxygen depletion in relation to differences in morphometry and changes in temperature, chlorophyll *a* concentration, storm events, and large-scale hydrodynamic processes (such as seiches). We used carbon stable isotope analyses to determine whether hypolimnetic particulate organic matter originated from terrestrial or epilimnetic sources allowing us to infer the relative importance of tributary-derived allochthonous and epilimnion-derived autochthonous particulate organic matter in affecting hypolimnetic hypoxia.

Materials and methods

Using stable isotopes to determine organic matter source–Assigning organic matter to tributary-derived versus epilimnion-derived sources requires: (1) an understanding of carbon isotope fractionation due to biological processes; (2) an ability to detect source signal even after the signal has been diluted through mixing; and, (3) an

ability to distinguish tributary-derived organic matter isotope signals from epilimnion-derived organic matter isotope signals. Before collecting any field data we searched the literature to evaluate these requirements (Fig. 4.1).

Allochthonous carbon input to tributaries originates with terrestrial plants. Carbon isotope signals ($\delta^{13}C$) from C_3 plants can be distinguished from those of C_4 plants (Fry and Sherr 1984; Fig. 4.1), and Munson and Carey (2004) found that river particulate matter $\delta^{13}C$ switched from a C_3 signal (MCs, Fig. 4.1) during low-flow, late-summer sampling, to a C_4 or autochthonously produced phytoplankton source (MCa, Fig. 4.1) during high-flow, late-autumn sampling. Fry and Sherr (1984), reviewing previous studies, indicated that river-estuarine phytoplankton have $\delta^{13}C$ ranging -24‰ – -30‰ (FSr-est, Fig. 4.1). This wide range of values was supported by several additional studies. Cifuentes et al. (1988) found upper Delaware River estuary (~ 120 km upstream of the mouth of the estuary; Cup, Fig. 4.1) $\delta^{13}C$ depleted (more negative) compared to lower estuary $\delta^{13}C$ (~ 40 km; Clow, Fig. 4.1). In a tropical river-reservoir system in Venezuela, Bellanger et al. (2004) found river particulate $\delta^{13}C$ signatures near the mean C_3 values (BeR; Fig. 4.1). In their high-flushing-rate reservoir basin that received the river inflow, hypolimnetic particulate $\delta^{13}C$ clearly matched those of the river (BeB, Fig. 4.1), whereas hypolimnetic particulate matter $\delta^{13}C$ in an adjacent, low-flushing-rate reservoir basin were more depleted (Bellanger et al. 2004; BebT, Fig. 4.1). Barnard et al. (2006) found St. Lawrence River algae in the estuarine transition zone to have $\delta^{13}C$ between -19‰ and -21‰ (BaETZ, Fig. 4.1), whereas algae from an upstream freshwater river site had more depleted $\delta^{13}C$ between -24‰ and -29‰ (BaFW, Fig. 4.1) due to the use of terrestrial-derived detrital carbon as a C source. Offshore, $\delta^{13}C$ increases (Fry and

Sherr 1984, Garton et al. 2005) due to the increasing use of dissolved carbon of atmospheric origin (Hoefs 2004). Fry and Sherr (1984; FSmar, Fig. 4.1) indicated temperate marine phytoplankton has a $\delta^{13}C$ between -18‰ and -24‰ and Garton et al.'s (2005) seston $\delta^{13}C$ measurements in western Lake Erie fall at the depleted end of this range (-23.9‰, LE, Fig. 4.1). Marine studies demonstrate enriched sediment $\delta^{13}C$ moving away from inputs from the Orinoco, Nile, and Changjiang (Yangtze) rivers (Kennicutt et al. 1987), the Mississippi River (Sackett and Thompson 1963, Goñi et al. 1997), and the Oder River (Voss and Struck 1997), revealing a switch from terrestrial carbon to atmospheric carbon moving from estuarine to marine systems. Although the ranges of river, areas adjacent to the river, and offshore particulate matter $\delta^{13}C$ potentially overlap, we propose, based upon gradients evident in previous studies, that $\delta^{13}C$ can be used to distinguish tributary-derived organic matter from offshore epilimnion-derived organic matter.

Previous documentation of $\delta^{13}C$ moving from river to offshore areas neglected the potential effect of organismal discrimination against ^{13}C. However, consideration of several processes, including higher photosynthetic productivity, decomposition, and chemoautotrophic/methanotrophic bacterial production needs to be included when comparing $\delta^{13}C$ dynamics, especially in Lake Erie, which is highly productive (Smith et al. 2005) and has large hypoxic areas (Burns et al. 2005). As phytoplankton productivity increases and carbon availability decreases, producers discriminate less against ^{13}C-uptake or take up heavy isotope rich bicarbonate leading to enriched $\delta^{13}C$ (O'Leary 1988, Fogel and Cifuentes 1993, McKenzie 1985). For example, Gu et al. (1996) found that planktonic $\delta^{13}C$ significantly increased with increasing standing crop for a wide range of

chlorophyll *a* concentrations (1 – > 100 μg L^{-1}) in Florida lakes and attributed this enrichment to reduced isotopic discrimination at high rates of primary productivity. Annual temporal variations in $\delta^{13}C$ signature of particulate matter in epilimnetic waters in the same system often show enriched values during either spring (Cifuentes et al. 1988) or summer (Lehmann et al. 2004) phytoplankton blooms. Further, paleolimnological studies of sediment cores use enriched $\delta^{13}C$ to document periods of eutrophication (McKenzie 1985, Schelske and Hodell 1995). Based on these findings, we expect Sandusky Bay carbon to be $\delta^{13}C$-enriched relative to other sites based upon the high primary productivity by the bay phytoplankton community (Conroy 2007b).

Hypolimnetic particulate matter is often depleted in ^{13}C relative to that found in epilimnetic waters (McKenzie 1985) due the contribution of organic matter decomposition (Lehmann et al. 2002, Harvey and Macko 1997), chemoautotrophic/ methanotrophic bacterial mineralization during anoxia (Bellanger et al. 2004, Lehmann et al. 2004), greater discrimination between ^{13}C and ^{12}C under low rates of primary productivity with abundant carbon (Lehmann et al. 2004), and/or a greater contribution of epilimnion-derived, highly discriminating phytoplankton to hypolimnetic particulate matter (Bellanger et al. 2004, Matthews and Mazumder 2006). Bellanger et al. (2004) proposed that in the hypolimnion of a reservoir basin adjacent to river input, increased suspended sediment concentration with depth and a particulate-matter $\delta^{13}C$ similar to the river (BeB, Fig. 4.1) revealed riverine particulate matter as the most important factor affecting $\delta^{13}C$. In a hypoxic reservoir basin not adjacent to the river, the depleted $\delta^{13}C$ of hypolimnetic particulate matter (BeT, Fig. 4.1) was attributed to selective decomposition of ^{13}C-enriched carbohydrate and amino-acid portions and the greater contribution of

actively discriminating phytoplankton (Bellanger et al. 2004). Matthews and Mazumder (2006) found more depleted $\delta^{13}C$ of deep-water-particulate matter during stratification (MMstrat, Fig. 4.1) than during mixing (MMmix, Fig. 4.1) and attribute this finding to an increased proportion of highly selective phytoplankton carbon (versus terrestrial carbon) to particulate matter in deeper waters. Miyajima et al. (1997) modeled particulate organic matter $\delta^{13}C$ at three stations of varying depth (A = 90 m, B = 73 m, and C = 40 m) in Lake Biwa (Fig. 5.1) and found more ^{13}C depleted particulate organic matter deeper in the hypolimnion at sites A (MaL and MaU, lower and upper hypolimnion, respectively; Fig. 4.1) and B (MbL and MbU, Fig. 4.1). They then compared their modeled $\delta^{13}C$ with $\delta^{13}C$ of different particulate organic matter size fractions (representing phytoplankton, a cyanobacteria/detritus mixture, and detritus) and found that most hypolimnetic organic matter was phytoplankton or a mixture of cyanobacteria and detritus revealing an epilimnetic origin of the hypolimnetic organic matter (Miyajima et al. 1997). Thus, biological discrimination can modify source $\delta^{13}C$ signals, complicating source detection; however, these modifications inform source recognition when considered in context with other environmental processes.

Detecting source signal after dilution is the least known aspect of using stable isotopes in this study. Whereas in carbon stable isotope analyses of food web structure, the upper trophic levels approximate their food source allowing inference of energy flow (Fry 2006), source detection studies are severely complicated by mixing (Bellanger et al. 2004). Ideally, other source-derived physical, chemical, or biological measures (*e.g.*, nutrient concentration) would serve as tracers by co-varying with stable isotope measurements (Fry 2006).

As much of Lake Erie's watershed is agricultural and predominantly planted with a mixture of C_3 soybeans and C_4 corn (Richards et al. 2002a), river particulate organic matter $\delta^{13}C$ could be between the C_3 and C_4 extremes; we expect river seston $\delta^{13}C$ to have a C_3-plant signal due to the predominance of depleted river values found in our literature review (Fig. 4.1). Moving downstream, we hypothesize that surface water seston will become ^{13}C enriched in the bay due to decreasing biological fractionation under high rates of primary productivity (Conroy 2007b). Moving offshore, surface water (epilimnetic) seston will be less ^{13}C enriched than bay seston and deep water (hypolimnion) seston will be depleted in ^{13}C relative to surface water (Fig. 4.1). We hypothesize that if tributary-derived organic matter is important in affecting offshore hypolimnetic oxygen depletion, then hypolimnion particulate $\delta^{13}C$ will more closely resemble tributary than epilimnion $\delta^{13}C$. Conversely, if epilimnion-derived organic matter is more important, hypolimnion $\delta^{13}C$ should closely approximate epilimnion $\delta^{13}C$. However, modification of hypolimnion $\delta^{13}C$ obscuring the source through biological discrimination and mixing is possible.

Study area–We quantified how tributary load is connected with hypolimnetic hypoxia in Lake Erie, the 11th largest lake in the world by surface area (Herdendorf 1990) and the shallowest, warmest, and most productive of the Laurentian Great Lakes. Lake Erie's watershed has been extensively modified since European settlement, with much of its historical wetlands drained for agricultural use (Sly 1976). The Sandusky system, composed of the Sandusky River, Sandusky Bay, and Sandusky subbasin (Fig. 4.2), drains about 3700 km^2 (Richards and Baker 1985) of primarily agricultural land (> 85%, Richards et al. 2002b). The Sandusky River travels over 90 km and drains > 80% of the

Sandusky Bay watershed (CLEAR 1975). The river is dammed at Fremont, Ohio, with water levels of the downstream section controlled by water level oscillations in the bay (Richards and Baker 1985). Sandusky Bay is a shallow (mean depth = 2.6 m), productive (~ 2.0 g C fixed m^{-2} d^{-1}, Conroy 2007b) drowned river mouth setoff from the Sandusky River and the Sandusky subbasin by natural geological constrictions. The Sandusky subbasin lies between the western and central basins of Lake Erie and often is the first part of the lake to become hypoxic during the summer (Bolsenga and Herdendorf 1993).

Synoptic surveys–We conducted monthly or more frequent synoptic surveys, 18 April to 24 August 2005 and 12 April to 15 September 2006, at an upstream river station (Sup), at the river and bay junction (SRM), in the eastern part of the bay (SEB), and offshore (Soff) in the subbasin (Fig. 4.2). Additionally, from 10 June to 12 August 2005 and 31 May to 28 August 2006 we sampled six offshore subbasin sites (NW, NE, W, E, SW, SE, Fig. 4.2) weekly. We selected offshore sites for their depth and proximity to organic matter loading sources (*e.g.*, western sites were closer to organic matter sources from the western basin and Sandusky Bay) using existing river to lake gradients as treatments (Fukami and Wardle 2005). At each station we measured vertical profiles of temperature (°C), dissolved oxygen concentration (DO, mg L^{-1}), and chlorophyll *a* concentration (Chl *a*, μg L^{-1}; from *in situ* fluorescence converted to Chl *a* using a Sandusky system-specific relationship: log [Chl *a*] = 0.079 + 1.193 log [fluorescence], $F_{1,198} = 510.6$, $P < 0.0001$, $r = 0.85$) with a multiparameter instrument (Model 6600, YSI Inc., Yellow Springs, Ohio). See Conroy et al. (2007) for additional details.

We calculated annual site-specific hypolimnetic oxygen depletion rates (HOD) for 2005 and 2006 using DO from the earliest sampling date at each site in each year until

water column turnover. We plotted mean hypolimnetic DO as a function of date with the resultant least-squares linear regression slope giving daily HOD (mg L^{-1} d^{-1}; Charlton 1980a). As most Lake Erie HOD studies give monthly HOD, we converted daily HOD to monthly HOD by multiplying by 30 (Charlton 1980a). To minimize bias we used HOD calculated with DO concentrations from 10 June 2005 and 31 May 2006 until turnover at all sites in all subsequent analyses. Due to weather, NW and NE sites were not sampled on 21 June 2006. Some previous studies in Lake Erie have corrected HOD for changes in temperature, vertical mixing, hypolimnetic thickness, and seasonal variation in HOD when comparing annual depletion rates (Rosa and Burns 1987, Burns et al. 2005). We did not correct our HOD in these ways because we were interested in differences among sites due to some of these very parameters.

We tested for differences among (1) HOD between years; (2) site-specific HOD; (3) HOD at western (NW, W, and SW) and eastern (NE, E, and SE) sites; and, (4) HOD at sites near organic matter load from outside the subbasin (NW, W, SW, and SE) and sites away from organic matter load (Soff, NE, and E). We first tested for differences between years; if we found differences, all subsequent tests would require year-specific tests. We tested for site-specific differences to broadly examine the importance of proximity to loading sources and morphometry as the seven offshore sites have different depths (Fig. 4.2) and some are located closer (*i.e.*, W and SW) and others farther (*i.e.*, Soff and E) from organic matter and nutrient sources. We hypothesized that western subbasin sites (NW, W, and SW) would have higher HOD than eastern sites (NE, E, SE) or that sites closer to shore (NW, W, SW, and SE) would have higher HOD than those farther away (Soff, NE, and E). All tests comparing site-specific HOD were performed

in SAS (Version 9.1, SAS Institute Inc., Cary, North Carolina) using either one-way analysis of variance (PROC ANOVA; test of site-specific differences) or Student's t-test (PROC TTEST; all other tests). We used a Bonferroni-corrected α-level of 0.0125 (four HOD comparisons) to guard against Type I errors due to multiple HOD comparison tests.

To test for the importance of basin morphometry, we used the natural gradient of site depth (Fig. 4.2) as a proxy for hypolimnion thickness. We assumed that in the Sandusky subbasin, the thermocline forms at the same depth relative to the surface at each site so that deeper sites have thicker hypolimnia. Sandusky subbasin sites vary by depth where eastern sites (mean depth measured during synoptic sampling = 14.3, 13.8, 13.5, and 13.3 m for E, SE, Soff, and NE, respectively; Fig. 4.2) were deeper than western sites (mean depth = 12.7, 12.5, and 12.2 m for W, SW, and NW, respectively; Fig. 4.2). We then conducted a simple linear regression (PROC REG, SAS Version 9.1) to determine the amount of variation in annual site-specific HOD explained by site depth.

Multiparameter instrument deployment–To investigate fine-scale temporal differences (~ hourly or daily) of DO dynamics we moored a multiparameter sonde instrument (Model 6600, YSI, Inc., Yellow Springs, Ohio) 1 m above bottom and a thermistor chain (HOBO pendant, Onset Corporation, Bourne, Massachusetts) at a depth of 13 m in the Sandusky subbasin (site MPS in Fig. 4.2) during 10 July through 3 October 2005. The sonde measured temperature, DO, and Chl *a* (calculated from *in situ* fluorescence) at 1-h intervals. Thermistors, also recording at 1-h intervals, were deployed from the bottom to 10 m above bottom.

Deploying the multiparameter sonde allowed fine-scale temporal quantification of DO dynamics and associated limnological parameters (*e.g.*, temperature, Chl *a*). Sonde

deployment unfortunately occurred after the Sandusky subbasin hypolimnion had become anoxic (DO < 0.25 mg L^{-1}); consequently, we could not compare sonde HOD to HOD calculated from synoptic survey DO measurements. However, we could explore parameters associated with brief (days-week) re-oxygenation/de-oxygenation events using sonde measurements and hypolimnion thickness ($Hypo_z$) from the thermistor chain. Additional limnological (surface water temperature, water level, and streamflow) and meteorological parameters (wind speed and wave height) were added to the analysis using measurements from National Oceanic and Atmospheric Administration (NOAA) weather buoy # 45005 (surface water temperature, wind speed, and wave height: http://www.ndbc.noaa.gov/station_page.php?station=45005; accessed 23 April 2007), NOAA/National Ocean Service (NOS) weather station # 9063079 (water level: http://tidesandcurrents.noaa.gov/data_menu.shtml?stn=9063079; accessed 14 May 2007), and United States Geological Survey (USGS) streamflow gauge # 04198000 (http://waterdata.usgs.gov/nwis/uv?04198000; accessed 18 May 2007) located near our sampling sites (Fig. 4.2). We used sonde deployment data for the anoxic period (10 July to 31 August 2005) to qualitatively test for correlations between re-/de-oxygenation events and other processes including: (1) storm-induced mixing (inferred from wind speed and wave height); large-scale hydrodynamic processes including (2) tributary influx (inferred from temperature and Chl *a* after high flow) and (3) seiches (inferred from temperature and water level oscillations); and, (4) coupled weather/biological or hydrodynamic/biological processes (*e.g.*, storm-induced mixing of epilimnion-derived organic matter into the hypolimnion and its subsequent decomposition). Specifically, we contrasted two events of re-oxygenation of hypolimnetic DO and the subsequent de-

oxygenation to infer the importance of several processes on DO. We compared these two events because the first (July event: 24 July to 3 August 2005) had concurrent reduced hypolimnetic temperatures whereas the second (August event: 23 to 28 August 2005) had concurrent increased hypolimnetic temperatures indicating the likeliness of different water sources between events.

Stable isotope analysis–To assess the relative contributions of tributary-derived and epilimnetic-derived organic matter to hypolimnetic oxygen depletion, whole water samples were collected monthly during 2006 from just below the surface (~ 0.5-1.0 m) using an 8-L Niskin bottle at river (Sup), bay (SRM and SEB), and offshore (Soff) sites and in deeper waters (12 m) at Soff. Additionally, we collected surface (epilimnetic) and bottom (hypolimnetic) water at the seven offshore sites (Soff, NW, NE, W, E, SW, and SE; Fig. 2) during hypolimnetic hypoxia (24 July 2006; mean [DO] = 1.94 mg L^{-1}) and normoxia (28 August 2006; mean [DO] = 6.80 mg L^{-1}) to determine: (1) whether sites closer to Sandusky Bay were more affected by terrestrial organic matter load, (2) whether there were systematic differences in epilimnetic and hypolimnetic seston $\delta^{13}C$, and (3) whether bottom-water seston $\delta^{13}C$ differed between periods of hypoxia and normoxia. Whole water was dispensed into pre-rinsed amber polyethylene bottles and held on ice in the field. Once back in the laboratory, a known volume of water was filtered through pre-combusted (4 h at 450 °C) GF/F (0.7 µm-nominal pore size; Whatman plc, Middlesex, United Kingdom) filters until the build-up of a visible residue. Filters were subsequently dried at 60 °C for 24 h and frozen (-20 °C) for later $\delta^{13}C$ determinations. Isotopic analysis was carried out with elemental analyzer isotope ratio mass spectroscopy on an ECS 4010 elemental analyzer (Costech Analytical Technologies, Inc., Valencia,

California) and DELTA Plus Advantage isotope ratio mass spectrophotometer (Thermo Fisher Scientific, Inc., Waltham, Massachusetts) under continuous flow (CONFLO III, Thermo Fisher Scientific, Inc.). Stable isotope ratios were expressed in standard delta (δ) notation in units of per mille (‰) relative to the Vienna Pee Dee Belemnite limestone standard using a reference standard (USGS24 graphite) according to the equation,

$$\delta^{13}C = \left[\frac{R_{Sam}}{R_{Std}} - 1\right] \cdot 1000,$$

where R_{Sam} is the sample ^{13}C:^{12}C and R_{Std} is the ratio of a standard reference sample (Fry 2006). We tested for site-specific differences in $\delta^{13}C$ using one-way ANOVA and used t-tests to test for differences in $\delta^{13}C$ (1) between western (NW, W, and SW) and eastern (NE, E, and SW) sites, (2) between sites nearer to (NW, W, SW, and SE) and farther from (Soff, NE, and E) organic matter and nutrient loads, (3) between epilimnetic and hypolimnetic organic matter $\delta^{13}C$, and (4) between hypolimnetic seston $\delta^{13}C$ during anoxia and normoxia. All tests were performed in SAS with a Bonferroni-corrected α-level of 0.01 (five stable isotope tests).

Results

Synoptic surveys and the importance of morphometry and allochthonous input– Hypolimnetic dissolved oxygen depletion rates (HOD) ranged 1.93 – 3.14 mg L^{-1} mo^{-1} during 2005 and 1.91 to 3.75 mg L^{-1} mo^{-1} during 2006, varying by site (Fig. 4.3). Hypolimnia at Sandusky subbasin sites began to lose oxygen by early May (Fig. 4.3g, h) with faster HOD between May and late June than between late June and July (Fig. 4.3). Turnover occurred at all Sandusky subbasin sites by mid-August in both years (Fig. 4.3).

We found that 2005 HOD were similar to those in 2006 ($t_{12} = 0.58$, $P = 0.57$) with identical depletion rate estimates at site NW (Fig. 4.3a, b) and maximal annual differences at site W (29% difference, Fig. 4.3e, f). Similarity of HOD between years allowed us to use 2005 and 2006 data as site-specific replicates of HOD in our remaining tests. We found marginally significant differences (relative to our HOD corrected α-level of 0.0125) in HOD between sites ($F_{6,7} = 5.37$, $P = 0.022$) with western subbasin sites (NW, W, and SW; mean = 3.17 mg O_2 L^{-1} mo^{-1}) having faster HOD ($t_{10} = 2.85$, $P = 0.017$) than eastern sites (NE, E, and SE; mean = 2.51 mg O_2 L^{-1} mo^{-1}). Sites nearer to Sandusky Bay and western basin loading sources (NW, W, SW, and SE; mean = 3.07 mg O_2 L^{-1} mo^{-1}) had marginally faster depletion rates ($t_{12} = 2.55$, $P = 0.026$) than those away from loading sources (NE, E, and Soff; mean = 2.51 mg O_2 L^{-1} mo^{-1}). Mean depth (a proxy for basin morphometry), however, alone explained > 55% of the variation in HOD differences among sites (HOD = 9.36 – 0.50 mean depth, $F_{1,12} = 14.73$, $P < 0.01$, $r = 0.74$).

Multiparameter instrument deployment and the importance of hydrodynamics and tributary input–At a 13-m Sandusky subbasin site monitored from 10 July through 31 August 2005, hypolimnetic dissolved oxygen concentration (DO) was near zero with the exception of two conspicuous re-oxygenation events (Fig. 4.4a). The July event (from 24 July to 3 August 2005) had a maximum DO of 4.79 mg L^{-1} on 26 July 2005 (Fig. 4.4a) from a concentration < 0.10 mg L^{-1} on 22 July 2005. Concurrent with the DO increase, hypolimnetic temperature decreased 2.6 °C (Fig. 4.4b), Chl *a* increased approximately 5 μg L^{-1} (Fig. 4.4c), and hypolimnetic thickness decreased 1 m (Fig. 4.4d). Prior to the July re-oxygenation event, wind speeds were between 0.2 and 8.7 m s^{-1} (Fig. 4.4e) and wave

heights were between 0 and 0.33 m (Fig. 4.4f). During the July re-oxygenation event, wind speeds increased to a maximum of 13.5 m s^{-1} with several days with mean speeds > 6 m s^{-1} (Fig. 4.4e). Concurrently, wave heights increased to > 1 m (Fig. 4.4f) and water levels oscillated > 0.5 m (Fig. 4.4g) indicating the likelihood of a seiche. Streamflow increased just prior to (35 m^3 s^{-1}) and during (26 m^3 s^{-1}) the re-oxygenation event with the second and third greatest flows over the entire time period (peak flow = 46 m^3 s^{-1} on 1 September 2005; Fig. 4.4h). Surface temperatures at the NOAA weather buoy, at a nearby offshore subbasin site (Soff), and in Sandusky Bay (SEB) were all greater than 26 °C (Figs. 4.4i, j). Surface Chl *a* at Soff was 29.9 µg L^{-1} and at SEB was 30.0 µg L^{-1} (Fig. 4.4k). Peak DO was followed by decreased DO (0.54 mg L^{-1}) by 28 July 2005 with an additional DO peak on 29 July 2005 (2.72 mg L^{-1}). As wind speeds decreased (Fig. 4.4e), the lake calmed (Figs. 4.4f,g). Following the 29 July 2005 DO peak, DO decreased at an extremely high rate of 16.78 mg L^{-1} mo^{-1} (Fig. 4.4a), much greater than the mean site-specific HOD at the nearby site Soff (Fig. 4.3), such that DO reached concentrations < 0.3 mg L^{-1} by 3 August 2005.

The August hypolimnetic re-oxygenation event occurred from 23 to 28 August 2005 when DO increased from < 0.3 to 8.04 mg O_2 L^{-1} and to 8.22 mg O_2 L^{-1} on 25 and 26 August 2005, respectively (Fig. 4.4a). During the August event, DO increased more rapidly than the July event (Fig. 4.4a) and hypolimnetic temperatures increased (+ 5.4 °C from 23 to 25 August 2005) rather than decreasing. Chlorophyll *a* concentrations were much greater (to > 50 µg L^{-1}), but variable, during the August event (Fig. 4.4c) than during the July event and the hypolimnion was briefly lost (Fig. 4.4d). Wind speeds and wave heights just prior to the August event were comparable to those during it (Figs.

4.4e, f). Neither surface water level (Fig. 4.4g) nor streamflow (Fig. 4.4h) changed. Surface water temperatures at the NOAA buoy (Fig. 4.4i), at a nearby offshore station (Soff; Fig. 4.4j), and in Sandusky Bay (SEB; Fig. 4.4j) were all > 23 °C prior to, and during, the August event. Soff Chl *a* was 9.7 μg L^{-1} during the event and 4.1 μg L^{-1} 12 days prior to the event (Fig. 4.4k) whereas SEB chla was 48.8 μg L^{-1} and 145.3 μg L^{-1} during and 12 days prior to the event (Fig. 4.4k), respectively. Dissolved oxygen concentrations quickly decreased after the event and remained < 0.10 mg L^{-1} until turnover on 31 August 2005 (Fig. 4.4a) following a large storm (Figs. 4.4e, f, g).

All comparisons of DO dynamics with co-occurring limnological or meteorological parameters were qualitative due to (1) the potentially non-direct relationship between DO and processes affecting DO, (2) the importance of time lags of unknown duration between precipitation input to the river, water transport offshore, and biological decomposition processes, (3) the inherent ambiguity in identifying the source of incoming water from remotely collected data, and (4) the difficulty in testing specific hypotheses with unreplicated data. Nevertheless, we propose that our present qualitative tests can inform future targeted research.

Stable isotope analysis and organic matter source–Mean carbon isotope ratios ($\delta^{13}C$) ranged -27.5‰ to -21.8‰ with the most depleted ^{13}C values at the river and bay junction (SRM) and in the bay (SEB), with most enriched values in the western part of the subbasin at site W (Fig. 4.5a). Sites differed significantly ($F_{9,75} = 17.14$, $P < 0.001$) due to the depleted ratios in the bay (Fig. 4.5). River (Sup) $\delta^{13}C$ were similar to those offshore (Fig. 4.5b). There was no significant difference ($t_{24} = 0.82$, $P = 0.42$; Fig. 4.5b) between $\delta^{13}C$ at western (mean = -23.2‰) and eastern subbasin sites (mean = -23.6‰)

nor between sites near to (mean = -23.2‰) and away from (mean = -23.7‰) organic matter load (t_{40} = 1.31, P = 0.20). Epilimnetic seston $\delta^{13}C$ (mean = -23.6‰) were not significantly different (t_{40} = 0.84, P = 0.41; Fig. 4.5) from hypolimnetic seston $\delta^{13}C$ (mean = -23.3‰) and we found no significant difference (t_{19} = 0.50, P = 0.62) between hypolimnetic seston $\delta^{13}C$ during hypoxia (-23.7‰) and normoxia (-24.3‰).

River (Sup) $\delta^{13}C$ were between -24‰ and -25‰ during May through early July and increased to > -23‰ later in July and through September (Fig. 4.6). Values at the river and bay junction (SRM) steadily decreased through the season from about -25‰ to -31‰ (Fig. 4.6), whereas values in the bay (SEB) were generally more depleted than the other sites at values around -28‰ except for one date in late June (Fig. 4.6). Offshore (Soff), $\delta^{13}C$ were between -25.5‰ and -21.4‰ (Fig. 4.6). Epilimnetic (Soff Epi) $\delta^{13}C$ were greater than hypolimnetic (Soff Hypo) values on all dates except 24 July 2006. The most enriched offshore $\delta^{13}C$ occurred in late summer (15 September 2006; Fig. 4.6).

Discussion

The importance of basin morphometry on hypolimnetic oxygen depletion rates (HOD)–We chose seven offshore sites in the Sandusky subbasin with varying distance from organic matter sources and of varying depths to test for the relative importance of particulate organic matter load and basin morphometry. We used two different gradients (west/east and nearshore/offshore) in sites to test for proximity to organic matter loading because Sandusky Bay input often flows along the southern shore of the subbasin lake or north into the subbasin (Herdendorf and Braidech 1972). Neither of these tests showed

statistically that sites nearer organic matter loading had faster depletion rates than those distant from loading, although sites closer to loading had qualitatively greater HOD.

However, we found more support for the importance of basin morphometry in affecting site-specific HOD through its influence on the hypolimnion volume. Sandusky subbasin HOD decreased with increased site depth (site depth served as a proxy for mean hypolimnetic thickness during summer). Charlton (1980b), using data for many large lakes from Thienemann (1928), demonstrated that deeper lakes lost less oxygen during summer. Further, Charlton (1980b) showed that calculated HOD decreased with increasing hypolimnion thickness; variation in the relationship was caused by differences in organic matter input. Our findings, together with the analyses of Charlton (1980a, 1980b, 1987, Charlton and Milne 2004) support the primacy of basin morphometry (and the related hypolimnetic thickness) in affecting HOD and the secondary effect of organic matter supply. However, basin morphometry is difficult, if not impossible to change in large lakes. Basin morphometric and hypolimnion thickness effects on HOD are mediated through sediment oxygen demand (Charlton 1980b) so that decreased organic matter supply may decrease sediment oxygen demand through longer time periods. In Lake Erie, there has been little change in HOD through time (Charlton and Milne 2004, Burns et al. 2005) indicating that either the current regulations on phosphorus supply have not greatly decreased sediment oxygen demand (Schloesser et al. 2005) or that hypolimnion thickness has decreased.

The importance of hydrodynamics on HOD–We studied differences between two re-oxygenation events (one beginning in July, another beginning in August) and associated limnological and meteorological parameters in the Sandusky subbasin to

qualitatively infer the relative importance of tributary load of organic matter and large-scale hydrodynamics on HOD during 2005. During late July, re-oxygenation was primarily driven by a weather-induced seiche moving central basin hypolimnetic water into the Sandusky subbasin as indicated by increased dissolved oxygen concentrations (DO) concurrent with lower temperatures (T), increased wind speeds and wave heights, and surface water oscillations. In the central basin hypolimnion during late July, DO are normally ≥ 4 mg L^{-1} (Charlton and Milne 2004) and T are < 14 °C (Herdendorf 1967), making the central basin more oxygen-rich and cooler compared to the Sandusky subbasin. At this time, epilimnetic water in the Sandusky subbasin or central basin and Sandusky Bay water also would be more oxygen-rich, but much warmer. Consequently, a storm-induced mixing or tributary load signal would have greater DO and higher T. Further evidence for a seiche comes from oscillations in water levels and the DO peak. Internal seiches result in water movement back and forth in the hypolimnion, and we observed this "sloshing" signal (mean oscillation period ≈ 18 h). Consequently, we conclude that a weather-induced seiche led to the horizontal advection of cool, relatively oxygen-rich water from the central basin hypolimnion into the Sandusky subbasin hypolimnion providing evidence that large-scale hydrodynamic processes affect HOD.

During the August event, we observed that DO increased rapidly accompanied by higher T. Concurrently, Chl *a* increased in the hypolimnion with Sandusky Bay Chl *a* extremely high (> 100 μg L^{-1}) 12 days previous to the August re-oxygenation event. Because subbasin epilimnetic Chl *a* was much lower than bay Chl *a*, we assert that the bay was the source of the large Chl *a* input into the subbasin hypolimnion. Whereas we do not know the processes responsible, or the timescale, for transporting bay water into

the subbasin, heavy rains or a seiche can cause bulk loading of bay material to the subbasin (Richards and Baker 1985). Potentially, water that entered the Sandusky River during the July re-oxygenation event may have displaced the Sandusky Bay water just prior to or during the August event. The speed of this event – a sharp increase followed by a sharp decrease – resembled tributary water flowing past a stationary measuring device; further, without repeated oscillatory behavior or significant changes in water levels, seiche transport likely did not occur. Contrasting the DO dynamics of the July and August events, we found that following central basin water influx during the July event, the water remained in the subbasin with subsequent DO depletion. Simple mixing down of epilimnetic water did not occur during the August re-oxygenation event because such an event would be permanent as occurred at the end of August 2005 when a large storm completely mixed the water column with no subsequent hypolimnetic DO loss.

These findings emphasize that multiple origins were possible for rapid changes in DO over a short time period. Depletion events are primarily thought of as continuous decomposition of organic matter over a seasonal time period as affected by biological communities and their physiological processes (Edwards et al. 2005), but our data support the inclusion of several hydrodynamic influences such as bulk lake water transport and influx of tributary or nearshore water with the static view proposed by other researchers (Burns et al. 2005, Edwards et al. 2005).

The importance of terrestrial-derived particulate organic matter on HOD–We found that offshore particulate organic matter did not originate in Sandusky Bay based on comparisons of Sandusky subbasin and Bay $\delta^{13}C$ values. Further, seston $\delta^{13}C$ at sites nearer to and distant from organic matter load, epilimnetic and hypolimnetic seston $\delta^{13}C$

values, and hypolimnetic $\delta^{13}C$ during normoxia and hypoxia were similar throughout our study. These results indicate that Sandusky Bay organic matter contributed little to Sandusky subbasin hypolimnetic organic matter. Consequently, terrestrial-derived particulate organic matter did not affect HOD, nor was terrestrial carbon detectable in the offshore waters of a large lake like Lake Erie as has been found in other smaller systems (*e.g.*, Bellanger et al. 2004). We conclude, therefore, that the lack of a terrestrial signal in the offshore $\delta^{13}C$ values and the similarity of epilimnetic and hypolimnetic $\delta^{13}C$ values are consistent with an autochthonous origin for hypolimnetic organic matter.

With more frequent sampling (*e.g.*, may need particulate matter from earlier in the spring) or by sampling in a Lagrangian framework (*e.g.*, following the plume of materials from Sandusky Bay rather than a set of static stations) we may have detected some terrestrial signal. Further, additional sampling would help clarify the general applicability of carbon stable isotope measurements to the problem of organic matter source identification and biotic fractionation especially in light of systematically depleted $\delta^{13}C$ value in the bay $\delta^{13}C$ relative to river and offshore values and several other patterns we found that contrast with those in the literature. For example, we found that hypolimnetic seston $\delta^{13}C$ values were similar to those for epilimnetic seston although previous research showed that hypolimnetic seston carbon is are typically more ^{13}C depleted than that of epilimnetic seston (McKenzie 1985) because (1) higher epilimnetic productivity promotes less biological fractionation (Fogel and Cifuentes 1993), (2) decomposition leaves isotopically light organic matter (Lehmann et al. 2002), or (3) low rates of highly discriminating hypolimnetic phytoplankton productivity under low light and high carbon concentrations leaves isotopically light organic matter (Lehmann et al.

2004). Further, Sandusky Bay is extremely productive (Conroy 2007b) and we therefore expected bay $\delta^{13}C$ to be enriched in ^{13}C (*sensu* Cifuentes et al. 1988). However, we found bay sites (SRM and SEB) had the most depleted values and that temporal patterns were distinct between these two indicating the potential for different origins for this pattern including: (1) highly selective phytoplankton uptake of ^{12}C as opposed to ^{13}C at these sites; (2) substantial input of C_3-plant carbon downstream from the river site (Sup); and/or, (3) a shift in particulate organic carbon $\delta^{13}C$ caused by the extensive wetland complex at the western end of Sandusky Bay. Identifying the causes of the different carbon signals between the river (Sup) and bay (SRM and SEB) would help explain the fate of terrestrial-derived carbon as much of it apparently did not reach the offshore subbasin.

Using the Sandusky subbasin to test which factors most affect HOD in Lake Erie– Management of HOD in Lake Erie has historically focused on reducing total phosphorus load to the lake from the watershed (Bertram 1993) yet HOD continues to be a problem (Charlton and Milne 2004, Burns et al. 2005, this study). To assess the effectiveness of total phosphorus load reductions, surveys conducted by the United States Environmental Protection Agency during summer measure DO at 10 sites in the central basin either monthly or more frequently (Burns et al. 2005, Bertram 1993). These surveys are time, personnel, and monetarily expensive and focus primarily on documenting hypolimnetic hypoxia in the large central basin. The identification of cultural eutrophication as a problem in Lake Erie has focused solely on phosphorus loading while determining the relative importance of other causative factors has been neglected (Bertram 1993). As Charlton (1980b) and we have shown, however, other factors (*e.g.*, basin morphometry)

may be as important or of greater importance in controlling HOD. The varying effects of organic matter load and basin morphometry have not been explicitly tested, most likely due to the sheer size, complexity, and lack of a suitable replicate of the central basin. We propose the Sandusky subbasin as such a model for the central basin of Lake Erie, and propose that using it would allow targeted, intensive studies for a fraction of the time, personnel, and money investment required for comparable central basin studies.

Before the Sandusky subbasin can be rigorously used as an appropriate central basin model, we must determine that HOD rates are comparable. Charlton (1980a), Bertram (1993), Charlton and Milne (2004), and Burns et al. (2005) all describe past HOD in the central basin. Bertram (1993) and Burns et al. (2005) correct their calculated depletion rates for temperature increases, vertical mixing, hypolimnion thickness, and seasonal effects (Rosa and Burns 1987) whereas Charlton (1980a) and Charlton and Milne (2004) use either minimal corrections (for hypolimnion thickness, Charlton 1980) or no corrections (Charlton and Milne 2004).

Corrected central basin oxygen depletion rates for 1929 to 2003 ranged 2.0 – 4.7 mg L^{-1} mo^{-1} with a mean of 3.1 mg L^{-1} mo^{-1}, with most rates falling between 2.5 and 4.0 mg L^{-1} mo^{-1} (Fig. 4.7). HOD appeared to increase from the late 1920's through the mid-1960's (Rosa and Burns 1987), with reduced HOD during 1970 through 1990 (Burns et al. 2005, Bertram 1993); since 1990, depletion rates remain unchanged (Charlton and Milne 2004, Burns et al. 2005; Fig. 4.7). Charlton (1980a, 1987) questioned the early data, asserting that HOD had not changed or had changed less dramatically. Comparing our HOD with the literature, Sandusky subbasin rates were similar to central basin rates

(Fig. 4.7). Consequently, Sandusky subbasin HOD appears generally comparable to central basin HOD, allowing it to be used as a model of central basin processes.

Future Lake Erie studies should emphasize the importance of non-traditional controls of HOD in addition to simply monitoring dissolved oxygen concentrations each summer. For example, Donner and Scavia (2007) found that the annual extent of the Gulf of Mexico hypoxic zone depended on the combined effects of nutrient loading and climatic forcing (*e.g.*, areal extent correlated with the May-June nitrate flux which in turn correlated with March-May and November-December precipitation patterns) indicating that the timing of precipitation and nutrient flux may be more important than the absolute total amount of nutrient loaded from the watershed. Similar analyses of the timing of phosphorus load and organic matter load to the lake and the time lag between tributary load and subsequent offshore hypolimnetic oxygen depletion would be extremely useful in Lake Erie.

The relative importance of various factors: how should HOD be managed for in Lake Erie?–We used multiple approaches to determine the relative influences of tributary-derived organic matter, epilimnion-derived organic matter, and basin morphometry on hypolimnetic oxygen depletion rates (HOD) in a subbasin of Lake Erie. Calculated HOD from synoptic surveys during 2005 identified basin morphometry (inferred from the proxy mean site depth) as the most important factor with secondary evidence that proximity to organic matter loading was relevant. Contrasting dynamics of limnological (temperatures, chlorophyll *a* concentrations, hypolimnion thickness, water level) and meteorological (wind speed, wave height) parameters during two re-oxygenation events measured with a multiparameter sonde instrument during 2005

demonstrated the potential for large-scale hydrodynamic (*e.g.*, a seiche) and coupled biological/hydrodynamic (*e.g.*, riverine input of organic matter) processes to affect hypolimnetic oxygen dynamics differently. Stable carbon isotope analyses of particulate organic matter from the Sandusky River, Bay, and subbasin epilimnion and hypolimnion showed that offshore hypolimnetic organic matter was most similar to epilimnetic material, implying that most of the material decomposed in the hypolimnion was derived from autochthonous carbon. These findings are consistent with those of Edwards et al. (2005) who, using a 1-dimensional oxygen budget model found that hypolimnetic oxygen depletion was most sensitive to hypolimnetic mixing, hypolimnetic respiration, and sediment oxygen demand, but contrast with those of Burns et al. (2005) who found evidence for the importance of the previous year's phosphorus load.

We conclude, then, that the inherent complexity of hypolimnetic oxygen depletion suggests that successful ecosystem management through only one policy lever (*e.g.*, controlling phosphorus load) is unlikely, especially when processes beyond direct human control (*e.g.*, weather and climate effects on thermocline setup and mixing) are equally or more important than human effects. We do not conclude that controlling nutrient input to Lake Erie and other human-impacted ecosystems is unimportant; rather, we emphasize the need to manage the ecosystem as just that, a system, and to consider that "silver bullets," such as phosphorus control, may not exist. Reducing phosphorus input to Lake Erie had demonstrable effects on lower trophic level abundance (Conroy et al. 2005) but keeping phosphorus at mandated levels may never cease the occurrence of central basin hypolimnetic hypoxia (Charlton and Milne 2004) or even result in aerobic conditions during 90% of the year as mandated by the Great Lakes Water Quality Agreement

(Bertram 1993). Consequently, implementation of other policy levers (*e.g.*, taking steps to control climate change and the invasion of more non-indigenous species, regulating non-point source and combined sewer overflow phosphorus input) may need to be enacted to force further beneficial changes or to prevent detrimental ones.

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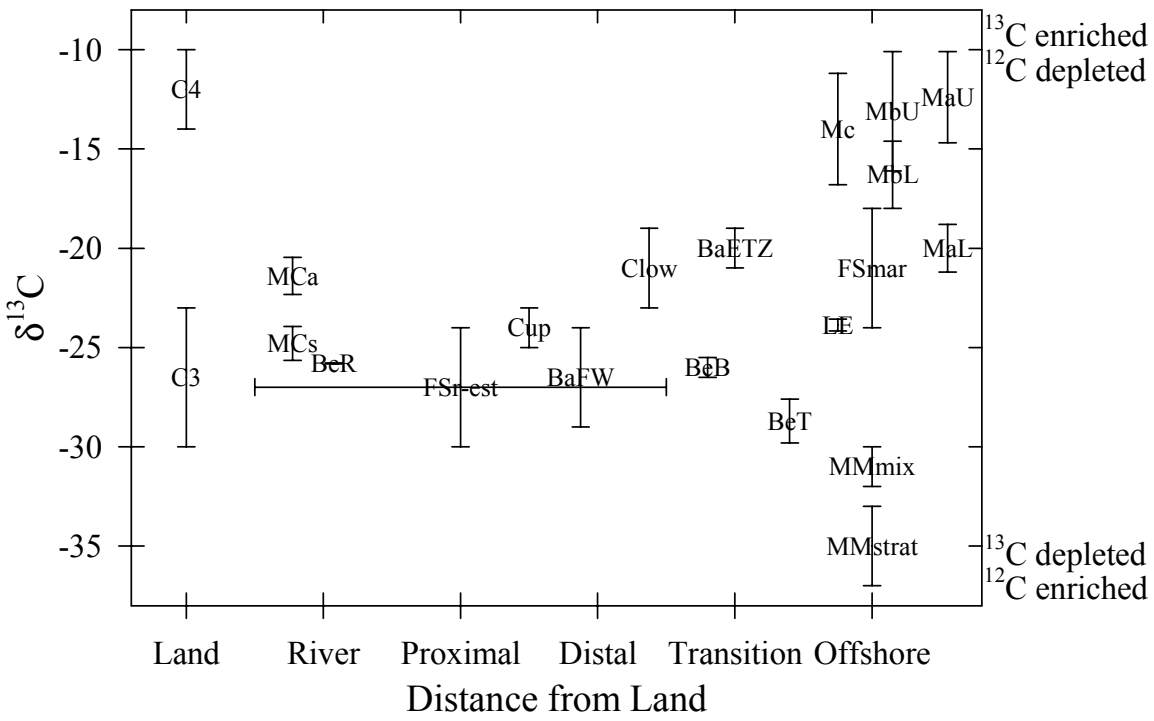

Fig. 4.1. Literature-derived estimates in the ranges of variation in $\delta^{13}C$ of particulate matter at sites moving from land, to river, to sites proximal (upper estuary or reservoir basins receiving river input) and distal (lower estuary or reservoir basins not receiving river input) to the river, in transition zones, and offshore in lacustrine and marine systems (left to right). The text symbol and error bars give either the reported mean and the reported variation (*e.g.*, standard deviation) taken directly from a particular study or a estimates of the mean and variation (from a table or figure). Less negative values indicate ^{13}C enrichment (^{12}C depletion) of organic matter whereas more negative values indicate organic matter enriched with ^{12}C (depletion of ^{13}C). Different symbols indicate the data source: C4, C3, FSr-est, and FSmar: Fry and Sherr 1984; BaFW and BaETZ: Barnard et al. 2006; BeR, BeB, and BeT: Bellanger et al. 2004; Cup and Clow: Cifuentes et al. 1988; LE: Garton et al. 2005; MMmix and MMstrat: Mathews and Mazumder 2006; Mc, MbU, MbL, MaU, and MaL: Miyajima et al. 1997; and, MCa and MCs: Munson and Carey 2004. See the text for further details.

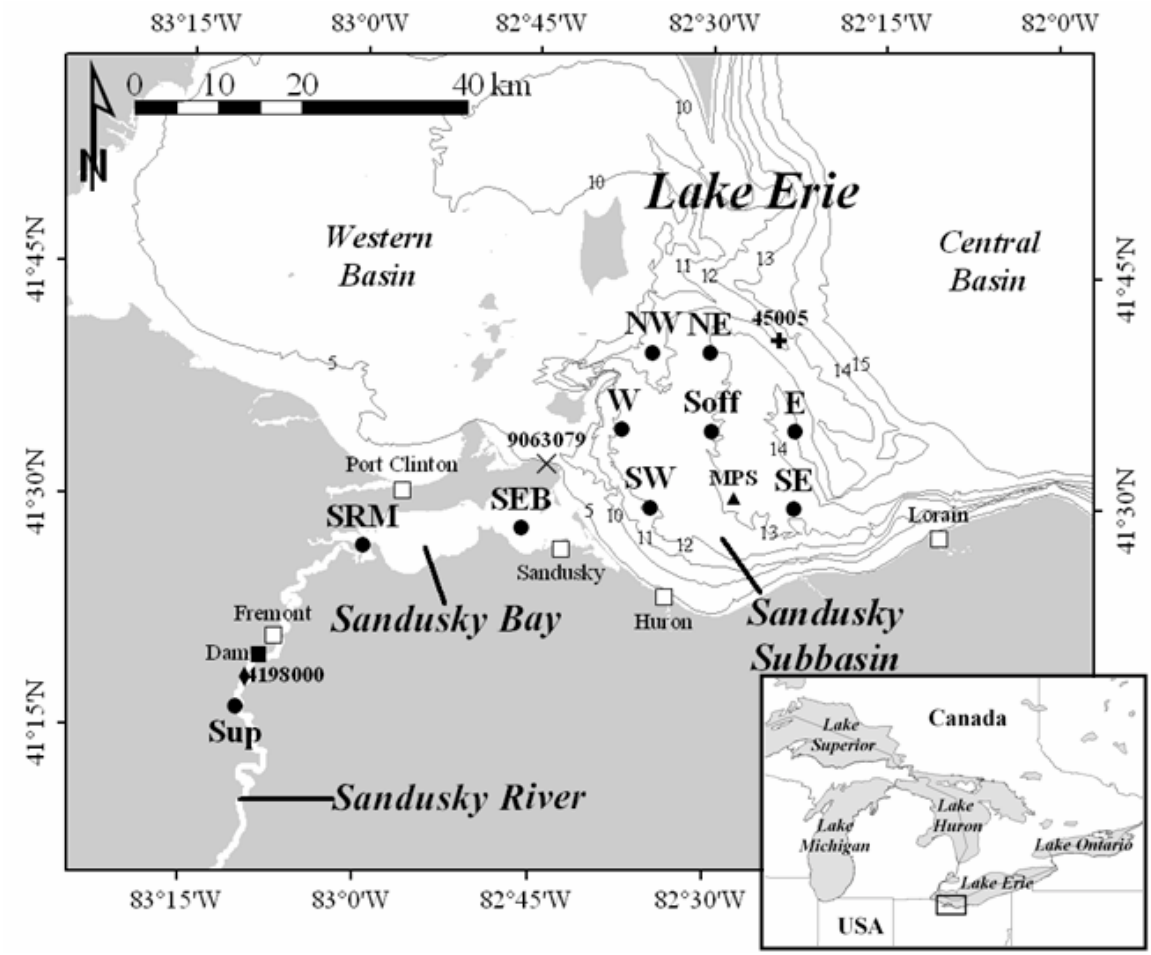

Fig. 4.2. Sandusky system, Lake Erie, map (with gray land, white water) indicating synoptic survey and stable isotope sampling sites (filled dots) upstream on the Sandusky River (Sup), at the junction of the river and bay (SRM), in the eastern portion of Sandusky Bay (SEB), and offshore in the subbasin (Soff, NW, NE, W, E, SW, and SE) and the location of the multiparameter instrument sonde and thermistor chain (filled triangle, MPS); the inset shows the relative position (small rectangle) of the Sandusky system relative to the other Laurentian Great Lakes. Light grey lines show the 5 and 10 – 15 m depth contours. NOAA buoy 45005 is shown with a cross, NOAA/NOS weather station 9063079 is shown with an x-mark, USGS streamflow gauge 04198000 is shown with a filled diamond, the dam upstream of Fremont, Ohio is shown with a filled square, and distance is shown with the scale bar. Note that river width is exaggerated to aid in illustration.

Fig. 4.3. Dissolved oxygen concentrations (filled dots) and simple linear regression models (lines) of dissolved oxygen depletion rates (mg L^{-1} mo^{-1}; slopes) for 2005 (left panels) and 2006 (right panels) at Sandusky subbasin, Lake Erie, sites NW (a and b), NE (c and d), W (e and f), Soff (g and h), E (i and j), SW (k and l), and SE (m and n). Dissolved oxygen depletion rates were calculated for the period from 10 June 2005 and 31 May 2006 through turnover (solid lines, larger fonts) for all sites. Rates were also calculated at Soff for the period from the earliest sampling date (18 April 2005 and 12 April 2006) to turnover (dotted line, smaller font). All dissolved oxygen depletion rate regressions were significant at an α-level < 0.10 (no asterisk after the given depletion rate); most were significant at an α-level < 0.05 (one asterisk), 0.01 (two asterisks), or 0.001 (three asterisks).

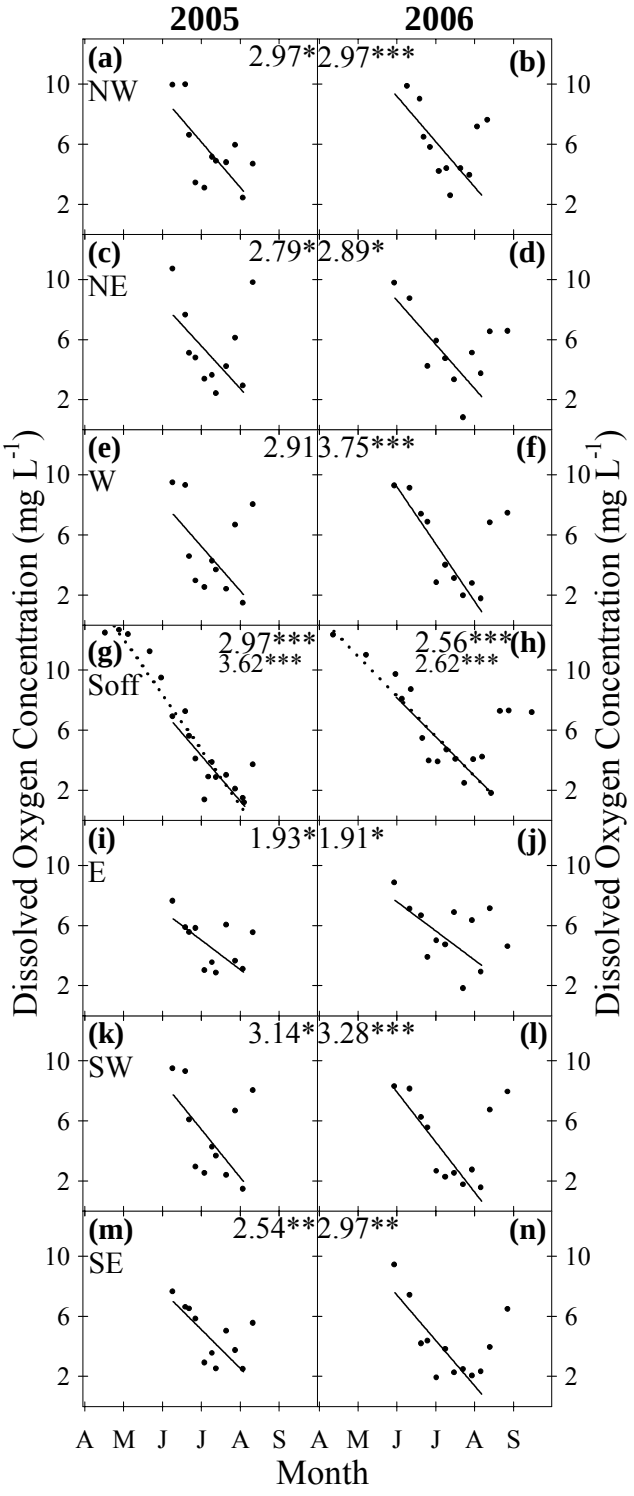
2005
2006
(a)
NW
2.97*
2.97***
(b)
(c)
NE
2.79*
2.89*
(d)
(e)
W
2.91
3.75***
(f)
(g)
Soff
2.97***
3.62***
2.56***
2.62***
(h)
(i)
E
1.93*
1.91*
(j)
(k)
SW
3.14*
3.28***
(l)
(m)
SE
2.54**
2.97**
(n)
Dissolved Oxygen Concentration (mg L-1)
Dissolved Oxygen Concentration (mg L-1)
10
6
2
A M J J A S A M J J A S
Month

Fig. 4.3.

Fig. 4.4. Limnological (dissolved oxygen concentration, DO; temperature, Temp; chlorophyll *a* concentration, Chl *a*; hypolimnion thickness, $Hypo_z$; water level, and streamflow, Flow) and meteorological (windspeed, WSPD; wave height, WVHT) parameters measured with an *in situ* deployment of a sonde multiparameter instrument and thermistor chain (a-d), from a NOAA buoy (e-f, i), from a NOAA/NOS weather station (g), from a USGS stream gauge (h), or during synoptic surveys at sites Soff and SEB in the Sandusky subbasin and Sandusky Bay (j-k), respectively, during July through mid-September during 2005. The sonde instrument, NOAA buoy, NOAA/NOS weather station, and USGS streamflow gauge measurements were made hourly and are shown as continuous lines. Soff (filled squares, solid line) and SEB (empty circle, dotted line) temperature measurements are for the surface waters. Chlorophyll *a* concentrations at Soff are in the epilimnion (filled squares, solid line) and hypolimnion (open square, heavy line) and at SEB are at the surface (empty circle, dotted line). Vertical dashed lines indicate two periods of increased dissolved oxygen in the hypolimnion: during 24 July through 3 August 2005 when increased dissolved oxygen corresponded with decreased temperature and during 23 through 28 August 2005 when increased dissolved oxygen corresponded with increased temperature.

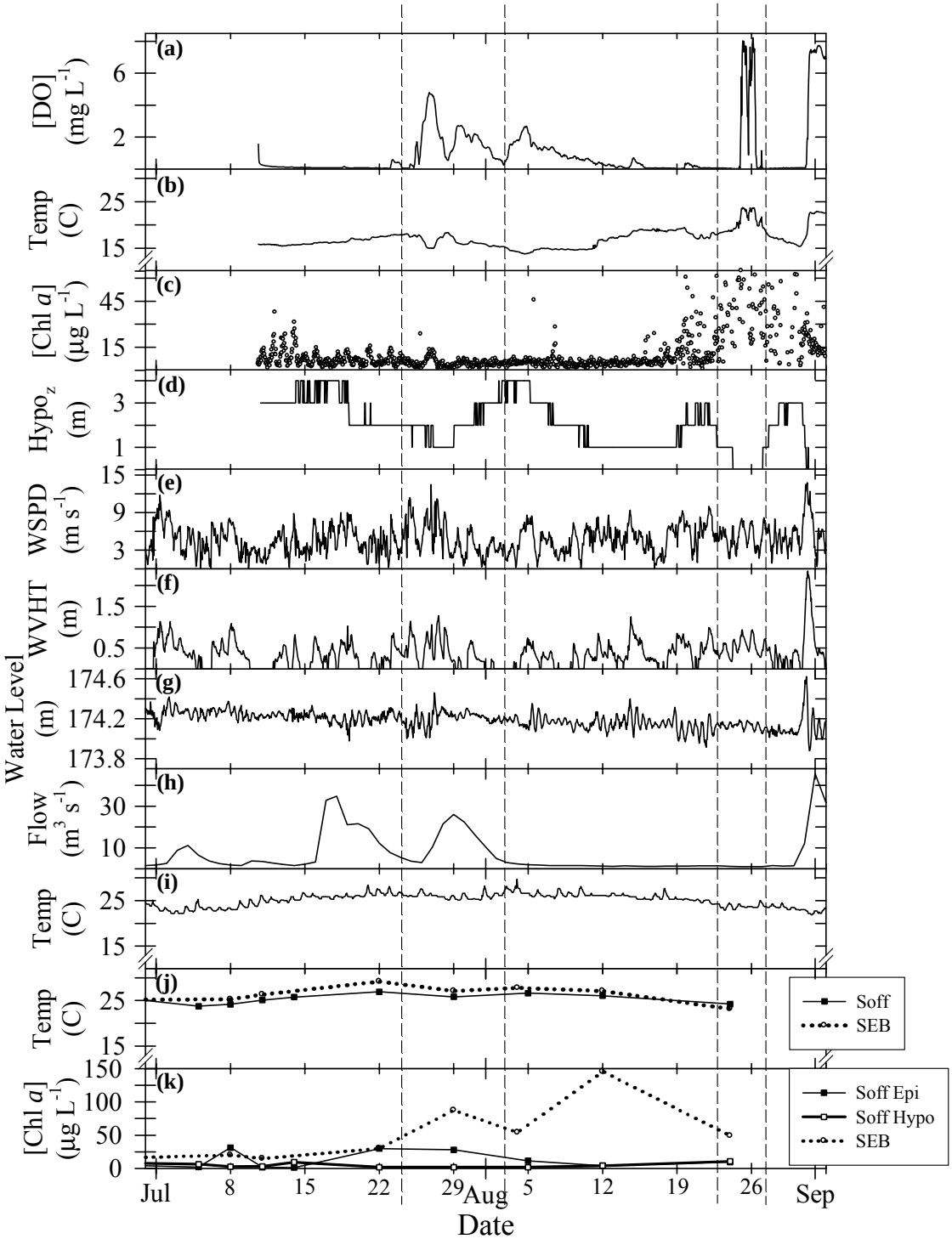
(a)
[DO] (mg L-1)
6
2
(b)
Temp (C)
25
15
(c)
[Chl a] (µg L-1)
45
15
(d)
Hypoz (m)
3
1
(e)
WSPD (m s-1)
15
9
3
(f)
WVHT (m)
1.5
0.5
(g)
Water Level (m)
174.6
174.2
173.8
(h)
Flow (m3 s-1)
30
10
(i)
Temp (C)
25
15
(j)
Temp (C)
25
15
Soff
SEB
(k)
[Chl a] (µg L-1)
150
100
50
0
Soff Epi
Soff Hypo
SEB
Jul
8
15
22
29
Aug
5
12
19
26
Sep
Date

Fig. 4.4.

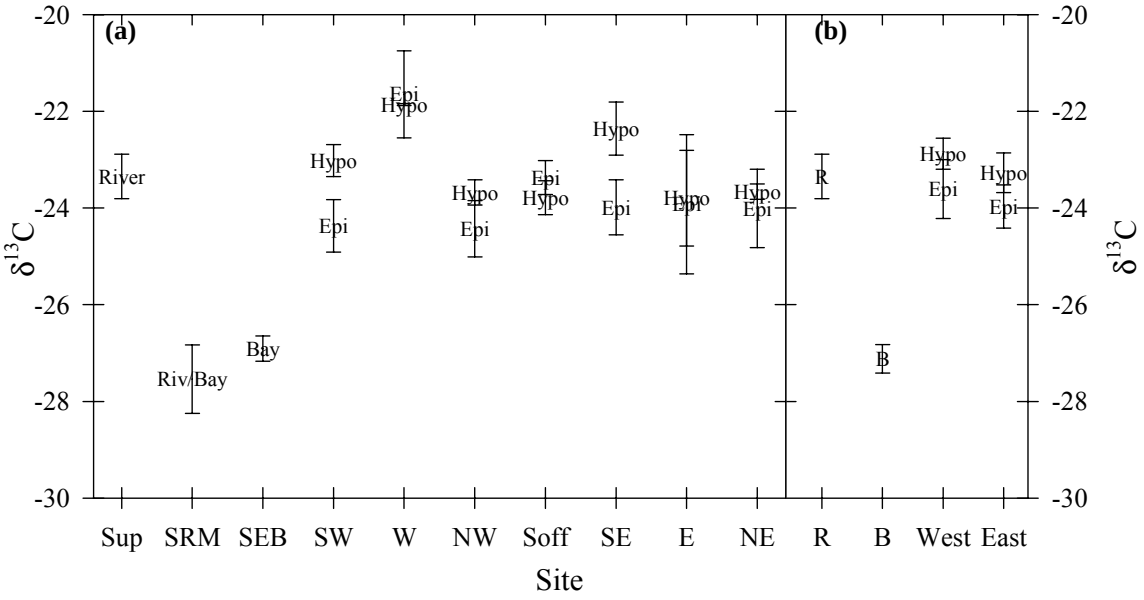

Fig. 4.5. Mean (+/- one standard error) site-specific seston (particulate matter > 0.7 µm) carbon stable isotope ratios ($\delta^{13}C$, ‰) at an upstream Sandusky River site (Sup, n = 10), at the river and bay junction (SRM, n = 11), in Sandusky Bay (SEB, n = 22), and in the epilimnion (Epi, n = 8 for Soff, n = 3 for SW, and n = 2 for all other sites) and hypolimnion (Hypo, n = 8 for Soff, n = 3 for SW, and n = 2 for all other sites) offshore in the Sandusky subbasin, Lake Erie during 2006 (a). In (b), site-specific $\delta^{13}C$ were averaged over river (R: Sup), bay (B: SRM and SEB), and western (West: sites NW, W, SW) and eastern (East: sites NE, E, and SE) epilimnion and hypolimnion.

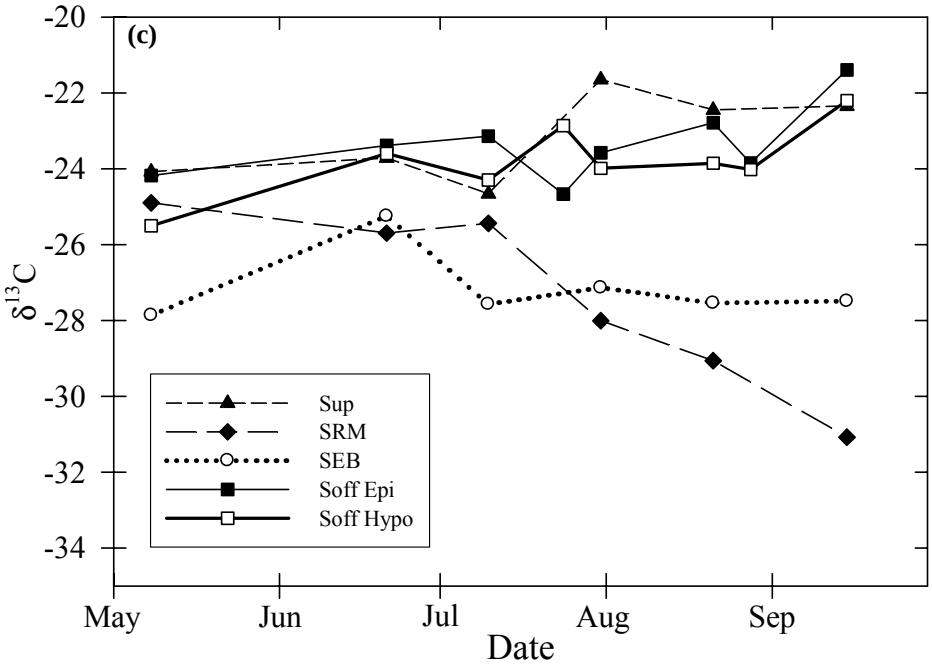

Fig. 4.6. Temporal variation in $\delta^{13}C$ values during 2006 at river (Sup), bay (SRM and SEB), and in the offshore epilimnion (Soff Epi) and hypolimnion (Soff Hypo) sites in the Sandusky system, Lake Erie.

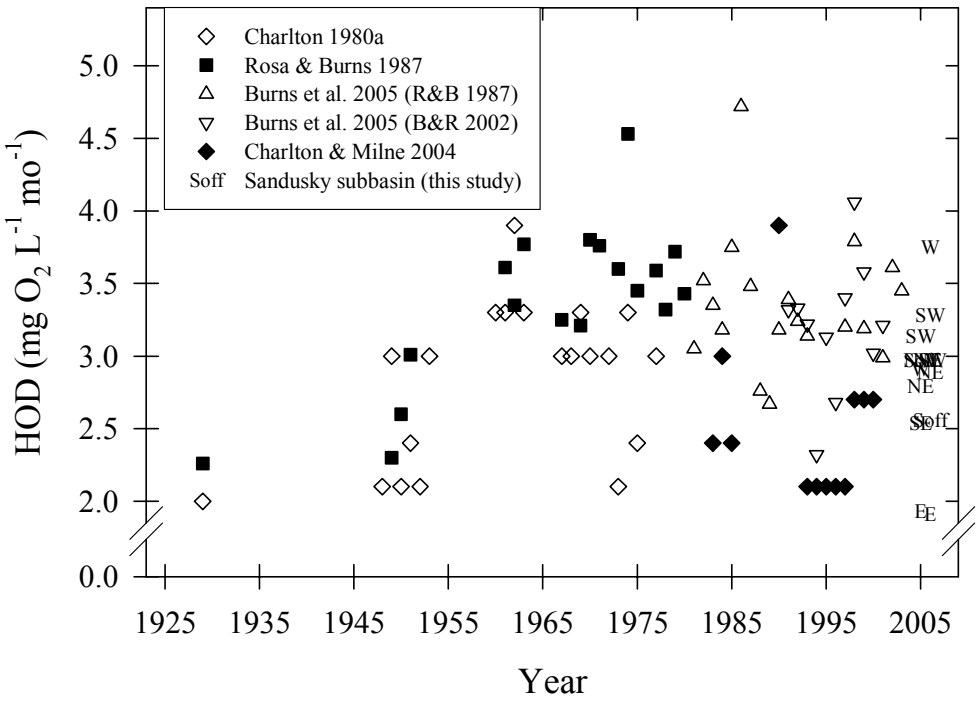

Fig. 4.7. Hypolimnetic oxygen depletion rates (HOD; mg L^{-1} mo^{-1}) for the central basin (Charlton 1980a, Rosa and Burns 1987, Charlton and Milne 2004, Burns et al. 2005) and Sandusky subbasin (this study) of Lake Erie from 1929 through 2006. The data from Charlton (1980a) and Charlton and Milne (2004) are uncorrected whereas those from Rosa and Burns (1987) and Burns et al. (2005) are corrected for temperature, vertical mixing, hypolimnetic thickness, and seasonal adjustments according to Rosa and Burns (1987; R&B 1987) or Burns and Ross (2002; B&R 2002). See the original reports for data sources and calculation methods. Note that the mean HOD for the literature data is 3.1 mg L^{-1} mo^{-1}.

CHAPTER 5

CYLINDROSPERMOPSIS IN LAKE ERIE: TESTING ITS ASSOCIATION WITH OTHER CYANOBACTERIAL GENERA AND MAJOR LIMNOLOGICAL PARAMETERS[1]

Introduction

The spread of invasive species and the occurrence of harmful algal blooms are two of the greatest threats to freshwater ecosystems throughout the world. The Laurentian Great Lakes have received numerous invasive species resulting in the modifications of nutrient cycling (Conroy et al. 2005a), food web dynamics (Laxson et al. 2003, Kane et al. 2003, Garton et al. 2005), and potentially, ecosystem stability processes (Conroy and Culver 2005). Further, the recurrence of potentially-toxic cyanobacterial blooms in Lake Erie (Budd et al. 2001, Vincent et al. 2004) threatens ecosystem "health" in terms of limiting energy transfer to higher trophic levels and causing beneficial use impairments for people (Conroy et al. 2005b).

The cyanobacterial genus *Cylindrospermopsis* Seenayya and Subba Raju, first identified from Java, Indonesia, has successfully invaded many lakes throughout the world (Padisák 1997). In the western hemisphere, this genus has been found in Brazil (Branco and Senna 1994), Mexico (Gugger et al. 2005), Ontario, Canada (Hamilton et al. 2005), and within the freshwater lakes of Florida (Chapman and Schelske 1997), Kansas

[1] – In press *in* J. Great Lakes Res. 33: 519-535 2007. Author list: Conroy, J.D., E.L. Quinlan, D.D. Kane, and D.A. Culver.

(Prescott and Andrews 1955), Minnesota (Hill 1969-1970), and most recently in Michigan in drowned river mouths adjacent to Lake Michigan (Hong et al. 2006) in the United States of America. The successful invasion of *Cylindrospermopsis* into various areas in the western hemisphere and the world is attributable to its tolerance of a wide temperature range (Dokulil and Mayer 1996, Saker et al. 1999, Saker and Griffiths 2000, Briand et al. 2004), competitive dominance with respect to nitrogen and phosphorus acquisition and storage (Présing et al. 1996, Isvánovics et al. 2000), adaptability to low light conditions (Saker et al. 1999, Briand et al. 2004), resistance to zooplankton grazing (Hawkins and Lampert 1989, Leonard and Paerl 2005), and its production of resting cells (akinetes) (Moore et al. 2005).

Cylindrospermopsis has been previously documented in water bodies connected to the Laurentian Great Lakes (Hong et al. 2006) but has not been previously reported within the lakes, although it has been found in other smaller, shallower lakes throughout North America (St. Amand 2002) and non peer-reviewed literature references exist citing its occurrence in the Laurentian Great Lakes (Hong et al. 2006). Because previous research indicated increasing cyanobacterial abundance in Lake Erie since 1996 (Conroy et al. 2005b, 2005c) and the presence of toxic Cyanobacteria other than *Microcystis* spp. Kützing *ex* Lemmermann in Sandusky Bay (Rinta-Kanto et al. 2005, Rinta-Kanto and Wilhelm 2006), we took advantage of an ongoing research project studying the importance of algal loading from tributaries to Lake Erie (Conroy et al. 2005b) to initiate a field survey during 2005 to determine whether or not this cyanobacterium was present in the Sandusky system. We hypothesized that conditions favorable for its invasion were present in Sandusky Bay, especially high temperatures, excessive nutrients, and low light

conditions. Here, we document the second observation of *Cylindrospermopsis* in the Laurentian Great Lakes' basin cyanobacterial community, characterize the physical (irradiance and temperature) and chemical (nitrogen, phosphorus, and carbon concentrations) conditions contemporaneous with its occurrence using multivariate statistics, and discuss the expected ecological outcomes of *Cylindrospermopsis* blooms for lower trophic levels and human users of the Sandusky system.

Methods

Study site–Three water bodies compose the Sandusky system – the Sandusky River plus its watershed, the Sandusky Bay and its watershed, and the Sandusky subbasin, a portion of Lake Erie's central basin (Fig. 5.1). The Sandusky River begins 90 km south of the river-bay junction, flowing primarily through an agricultural area (Richards et al. 2002). The reach of the Sandusky River below the Ballville dam near Fremont, Ohio, U.S.A. functions as a freshwater estuary, with water levels controlled by processes in Sandusky Bay and Lake Erie (Richards and Baker 1985).

Sandusky Bay, a 162 km^2 shallow (average depth = 2.6 m; Richards and Baker 1985) drowned river mouth (CLEAR 1975) between the Sandusky River and Lake Erie, is divided into two portions by a natural constriction and the Thomas A. Edison Memorial Bridge (Fig. 5.1). The western portion has a greater area but the two parts have nearly equal volumes (CLEAR 1975) because the eastern basin is deeper. Sandusky Bay empties into the Sandusky subbasin through a narrow constriction between the Marblehead peninsula to the northwest and the Cedar Point peninsula to the southeast. A

dredged navigation channel between these two peninsulas also facilitates water exchange between Sandusky Bay and the Sandusky subbasin (Richards and Baker 1985).

The Sandusky subbasin is a diamond-shaped area (~ 900 km^2, average depth = 13.3 m) between the western and central basins of Lake Erie (Fig. 5.1). Deeper portions of the subbasin often show the first signs of hypoxia in the lake during the summer (Richards and Baker 1985, Bolsenga and Herdendorf 1993, Conroy 2005) due to organic matter outwash from the hypereutrophic Sandusky Bay and the eutrophic western basin of Lake Erie.

Field sampling–We monitored for the presence of *Cylindrospermopsis* and the abiotic and biotic factors that contributed to its presence in the Sandusky system as part of regular field sampling of temperature, light, macronutrients, and phytoplankton during the spring and summer of 2005. While the site of collection was not necessarily the site of growth due to the potential for transport from one site to the next, we assumed that the phytoplankton community at the site of collection had experienced the conditions measured at that site long enough to influence community structure. Sampling commenced 18 April and concluded 24 August and included six stations in the Sandusky system (Fig. 5.1). The first (shown on Fig. 5.1 as "Sup"), upstream on the Sandusky River at Wolf Creek County Park, is approximately 32 km upstream of Sandusky Bay. The second site (SRM) is located where the Sandusky River meets Sandusky Bay. Two sites are located in Sandusky Bay, one west of the mid-point constriction (SWB) and one east (SEB). A fifth site is at the point where Sandusky Bay meets Lake Erie (SBM) outside of the maintained navigation channel. The final site is offshore in Lake Erie (Soff), in the approximate middle of the Sandusky subbasin. Sup was sampled on only

three dates in 2005, whereas SRM and SEB were sampled 15 times, SWB and SBM were sampled 14 times, and Soff was sampled 18 times. At each site, on all dates, routine data such as latitude and longitude, time sampled, site depth, and Secchi disk (20 cm black and white disk) transparency were collected. Due to changing personnel and the coordination of our sampling trips with other research groups during the sampling season, not all parameters were sampled on each trip (Table 5.1).

Physical parameters, including temperature and photosynthetically active radiation (PAR), were sampled at depth using electronic sensors. Temperature (°C) was measured as part of a multiparameter instrument array (Model 6600, YSI, Inc., Yellow Springs, Ohio). PAR (µmol photons m^{-2} s^{-1}) was measured with an underwater spherical sensor (Model LI-193, Li-Cor, Inc., Lincoln, Nebraska) corrected to surface irradiance using a cosine-corrected deck sensor (Model LI-190). Temperature was logged continuously with depth while PAR was logged at discrete 0.5-m intervals from the surface to the bottom at each station. To assess differences in light climate amongst the sites, we calculated mean light attenuation coefficients (k_z, m^{-1}) for each site and determined mean irradiance at 1 m over all sampling dates. To calculate the mean attenuation coefficient (k_z) for each site on a particular date we estimated attenuation coefficients for successive 0.5 m strata using Lambert-Beer's Law and took the arithmetic mean over all strata at a particular site (Bledsoe and Phlips 2000). We calculated the site-specific mean attenuation coefficient over all sampling dates for each site by averaging all measured attenuation coefficients for a particular site. We determined mean irradiance at 1 m for each site by calculating the arithmetic mean of

measured irradiance at 1 m over all sampling dates to estimate the average light climate for phytoplankton growth during our sampling period.

Whole water samples were taken for phytoplankton enumeration and total and soluble macronutrient concentration determination. At the upstream site, surface water was collected with a 10-L bucket. At river mouth, bay, bay mouth, and offshore sites, water was collected using integrated tube samplers to twice the Secchi disk transparency depth (approximately the compensation depth) or to 3 m (if the Secchi transparency was ≥ 1.5 m). Integrated tube samples were dispensed into a pre-rinsed 10-L bucket. A 500-mL subsample from the bucket was preserved with Lugol's iodine solution in a glass jar for phytoplankton enumeration. Both a 250-mL whole water sample and a 250-mL filtered (Whatman GF/F, 0.7-µm nominal pore size; Whatman, Inc., Florham Park, New Jersey) sample were dispensed into translucent polyethylene bottles, held on ice in the field, and frozen upon return to the laboratory for subsequent total and soluble nutrient concentration determinations, respectively. De-ionized, glass-distilled water was filtered through an identical filter in the field for use as blanks, with unfiltered water used as a total macronutrient blank and filtered water as a soluble macronutrient blank.

Laboratory techniques–Lugol's-preserved phytoplankton samples were condensed by pouring 250 mL into a graduated cylinder, covering the top with plastic wrap, and allowing the contents to settle for a minimum of 3 d in a dark box. After settling, the top 220 mL was removed by gentle suction and the remaining 30 mL was stirred and poured into a labeled sample vial. Phytoplankton sample enumeration generally followed Utermöhl (1958) and is more fully described in Conroy et al. (2005c). In order to maximize the number of samples enumerated, we identified taxa only to genus

following Prescott (1978), Taft and Taft (1971), Tiffany (1934), and Wehr and Sheath (2003). Identification of *Cylindrospermopsis* followed Komárek and Kling (1991), Hindák (1988), Komárek and Komárková (2003), and Komárková et al. (1999). Due to its small size, variable morphology (Singh 1962, Komárek and Komárková 2003), and co-occurring similar-looking species (Dokulil and Mayer 1996), only trichomes with terminal tear drop-shaped heterocytes could be positively identified visually as *Cylindrospermopsis*. No intercalary, consecutive heterocytes were observed in narrow trichomes that would suggest that we were actually observing *Anabaenopsis* (Woloszynska) Miller, a genus found once in Sandusky Bay (CLEAR 1975) and reported from Lake Erie (Tiffany 1934, Taft and Taft 1971). Note that plates in both Tiffany (1934) and Taft and Taft (1971) depict *Anabaenopsis* as a circinate trichome with spherical terminal heterocytes inconsistent with the *Cylindrospermopsis* that we identified as having straight trichomes and tear drop-shaped heterocytes. No circinate *Cylindrospermopsis* trichomes were observed. Genetic analysis using rRNA coding sequences or other structural genes was not performed. Due to the high variability among morphotypes of *Cylindrospermopsis*, the variation in assigning trichomes to particular species in the literature, and the absence of genetic analysis in this study, we conservatively refer to the organisms we identified simply as *Cylindrospermopsis* sp. The organisms we observed and enumerated were most likely *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya and Subba Raju, as this species has been identified in North America (Chapman and Schelske 1997, Hamilton et al. 2005, Hong et al.2006), but we prefer to assign only genus presently and will perform genetic analysis in the future to ascertain the species present.

For enumeration, subsamples of each concentrated sample were examined at 400x using an inverted microscope. All phytoplankton genera in sequential random transects were enumerated until at least 100 algal units (cells, colonies, or filaments/trichomes) of a single genus were encountered and recorded. For each subsample, at least two random transects were made, even if 100 algal units of a single taxon were recorded before the completion of two transects. The dimensions of the first 20 algal units of each genus encountered were measured with calibrated ocular micrometers. For filamentous taxa, however, all filaments (or trichomes) encountered were measured and total filament length (mm) for a particular taxon was calculated as the sum of the measured lengths. Taking this total taxon length and average width allowed us to calculate total taxon biovolume by assuming the trichome was a cylinder. For the remaining taxa, average algal unit dimensions for each taxon were combined with appropriate geometric equations to calculate taxon cell volume according to Kane (2004). Cell volume was converted to wet biomass (mg L^{-1}) assuming a cellular density of 1.0 mg mm^{-3} (Munawar and Munawar 1976, Makarewicz 1993).

Total phosphorus and total inorganic nitrogen and soluble nitrate-, nitrite-, and ammonium-nitrogen and orthophosphate-phosphorus were determined using an auto-analyzer (QuikChem 8500, Lachat Instruments, Loveland, Colorado) according to validated Lachat methods and/or Standard Methods (APHA et al. 1998). Total phosphorus and total inorganic nitrogen were analyzed by first oxidizing all phosphorus forms to orthophosphate and all nitrogen forms to nitrate using alkaline persulfate digestion (APHA et al. 1998) with subsequent determination of orthophosphate or nitrate. Nitrate was determined by subtraction after reducing nitrate to nitrite using a cadmium

column and subsequently determining nitrite. Total dissolved carbon, organic carbon, and inorganic carbon were determined on a TOC analyzer (Model DC-190, Rosemount Dohrmann, Santa Clara, California). Total carbon and total inorganic carbon were determined separately and total organic carbon was determined by difference.

Ecological conditions favorable to Cylindrospermopsis–We tested whether temperature, light, and nutrient conditions favorable to *Cylindrospermopsis* occurrence were present in Sandusky Bay using a series of multivariate tests in SAS (version 9.1.3, SAS, Inc., Cary, North Carolina). We conducted factor analysis to determine which of the physical and chemical parameters were most important in distinguishing river, bay, and offshore stations. Factors with eigenvalues greater than 1.0 were retained in subsequent factor loading determination of individual physical and chemical parameters, whereas individual parameters were considered important to a specific factor if their factor loading was greater than 0.50 for that factor (Zeng and Rasmussen 2005). We then performed canonical correspondence analysis (CCA) to assess relationships between biomasses of different cyanobacterial genera and those physical and chemical parameters found to be important from factor analysis. As discussed more fully in the Results, we were concerned that the dominance of *Cylindrospermopsis* early in mid-April at stations SBM and Soff may have skewed relationships in the CCA. Therefore, we subsequently removed the data from SBM and Soff on 18 April 2005 and re-ran the CCA. Canonical correspondence analysis allowed us to compare the hypotheses that warm temperatures, low light, and high nutrient concentrations facilitated the invasion of *Cylindrospermopsis*, with the temporal and spatial distributions that we actually measured. Further, using

CCA we assessed the relationship between *Cylindrospermopsis* and other cyanobacterial genera, and between other cyanobacterial genera and physical and chemical parameters.

Results

We found *Cylindrospermopsis* (Fig. 5.2) in relatively low abundance (0.043 – 1.326 mg L^{-1}, 16 – 1942 trichomes mL^{-1}) sporadically throughout the growing season at all sites except at the upstream Sandusky River site (Sup), where it was never observed (Table 5.2). Occurrences showed little obvious, systematic correlation with hypothesized predictors. Consequently, we used further planned analyses to assess the importance of physical (temperature, light), chemical (nitrogen, phosphorus, carbon), and community (other cyanobacterial genera) parameters that might contribute to *Cylindrospermopsis* abundance.

Temperature and light contributions to Cylindrospermopsis *dynamics*–First seasonal occurrence should be expected at akinete germination temperatures (22-23.5°C, Gorzó 1987 in Padisák 1997), which were not reached until the beginning of June 2005 at river (SRM) and bay (SWB and SEB) sites (Fig. 5.3a), mid-June at a Lake Erie nearshore (SBM) site (Fig. 5.3b), and late June or late July at Lake Erie offshore (Soff) surface and bottom depths (Fig. 5.3b), respectively. Surface temperatures conducive to positive growth (20-35°C, Briand et al. 2004) were reached contemporaneously to germination temperatures at SRM, SWB, SEB, and SBM (Fig. 5.3) as these sites are less than 2.5 m deep. Surface temperatures reached 20-25°C by mid-June at Soff, but bottom temperatures lagged two months behind (Fig. 5.3b). Maximal growth temperatures (25-

30°C) were first attained at river and bay sites on 10 June, dipped below 25°C on 20 June, and were then above 25°C until late August (Fig. 5.3a). At SBM and Soff, temperatures did not remain above 25°C until 11 July; temperatures dropped below 25°C in late August.

Light attenuation coefficients increased from Soff to SRM (Figs. 5.4a and b) due to the large sediment load entering the Sandusky system from its watershed. Seasonal variation in k_z at river and bay sites exceeded that at Soff (Fig. 5.4a). Similarly, mean photosynthetically active radiation (PAR) at 1 m increased dramatically from SRM (13 μmol m^{-2} s^{-1}) to Soff (1156 μmol m^{-2} s^{-1}; Fig. 5.4c), but only SRM mean irradiance values at 1 m (Fig. 5.4c) were below the onset of light limitation for *Cylindrospermopsis* (18 μmol m^{-2} s^{-1}, Briand et al. 2004). Mean irradiance at 1 m at SWB (47 μmol m^{-2} s^{-1}) was half of the value of maximal *Cylindrospermopsis* growth (approximately 100 μmol m^{-2} s^{-1}, Briand et al. 2004), while irradiance at SEB (101 μmol m^{-2} s^{-1}) was at the value of maximal growth. Site SBM (399 μmol m^{-2} s^{-1}) again was intermediate to bay and offshore sites.

Macronutrient contributions to Cylindrospermopsis *dynamics*–Macronutrients most likely do not limit *Cylindrospermopsis* or other phytoplankton growth in the Sandusky River or Bay due to their extremely high concentrations (Fig. 5.5). Total inorganic nitrogen (TIN) concentrations were greater than 100 μM at SRM, SWB, and SEB from April to August 2005 (Fig. 5.5a). TIN concentrations were also high at SBM (> 75 μM, Fig. 5.5a). At Soff, TIN concentrations were lower but still sufficient for phytoplankton growth (Fig. 5.5a). Nitrate-N dominated the N pool (Fig. 5.5b), potentially favoring those phytoplankters better able to utilize nitrate-N for growth or to

those capable of N-fixation (*e.g.*, *Cylindrospermopsis*). Total phosphorus (TP) concentrations were extremely low at Soff, potentially limiting phytoplankton growth while they were much higher at the remaining sites (Figs. 5.5c and d). Soluble orthophosphate was found in appreciable amounts only in the Sandusky River or at SWB (Fig. 5.5d, inset), suggesting that phytoplankton and bacteria utilized all of this readily accessible macronutrient before it reached the eastern portion of Sandusky Bay. We found that the ratio of total inorganic nitrogen:total phosphorus (N:P) was at or above the Redfield ratio (16 N:1 P; Redfield 1958) at the beginning of our sampling and subsequently decreased (with a moderate increase in late May to early June) at river, bay, and bay mouth sites, but increased at Soff (Fig. 5.5e).

These patterns indicate that phosphorus became more abundant relative to nitrogen in the river, bay, and at the bay mouth, and less abundant relative to nitrogen at the offshore site during our sampling. We found no indication that carbon concentrations ever dropped low enough to induce carbon deficiency for the phytoplankton (Fig. 5.5f). From these results, we infer that conditions favoring *Cylindrospermopsis* growth were generally present in the Sandusky River and Bay and may have become more favorable as the N:P ratio dropped as the season progressed.

Cylindrospermopsis *and cyanobacterial community dynamics*– *Cylindrospermopsis* was found at all sites except Sup at some point during the sampling season but was rarely a large component of the total cyanobacterial biomass (Fig. 5.6). *Cylindrospermopsis*, however, was surprisingly a dominant component of the cyanobacterial biomass early in the growing season (18 April 2005) at SBM (0.261 mg L^{-1}, 143 trichomes mL^{-1}, Fig. 5.6d) and Soff (1.050 mg L^{-1}, 16 trichomes mL^{-1}, Fig. 5.6e),

although the total cyanobacterial biomass at these stations on this date were greater than two orders of magnitude lower than those at the other sites (Figs. 5.6a-e). We found *Cylindrospermopsis* sporadically throughout the season at SRM, SWB, and SEB with maximum biomasses of 0.250, 1.326, and 0.151 mg L^{-1} and maximum trichome densities of 754, 1942, and 253 trichomes mL^{-1} for the three sites, respectively.

Seasonal dynamics of other cyanobacterial genera varied by site (Fig. 5.6). At SRM, *Microcystis* spp., *Oscillatoria* spp. Vaucher *ex* Gomont, and to a lesser extent *Aphanizomenon* spp. Morren *ex* Bornet and Flahault dominated the Cyanobacteria present (Fig. 5.6a). At SWB, *Chroococcus* spp. Nägeli were the most abundant with additional dominance at various times by *Oscillatoria* spp. and *Aphanizomenon* spp. (Fig. 5.6b). The cyanobacterial community at SEB was dominated by *Oscillatoria* spp. at all times except for 24 August when *Microcystis* spp. were most important (Fig. 5.6c). At SBM, *Oscillatoria* spp. were again important, followed by *Aphanizomenon* spp. and *Microcystis* spp. (Fig. 5.6d). Finally, at Soff, cyanobacteria were often not present (Fig. 5.6e), but when they were, *Microcystis* spp. and *Oscillatoria* spp. were most abundant.

Correlations among physical, chemical, and biological parameters–We determined the importance of physical, chemical, and biological parameters to *Cylindrospermopsis* occurrence using multivariate factor analysis. We found two important factors (eigenvalues > 1.0) that together explained 86% of the variance in our measured parameters (Table 5.3a). The greatest parameter loadings for the first factor were station depth, the light parameters PAR at 1 m and k_z, TIN concentrations, TP concentrations, N:P, and total phytoplankton biomass, whereas only temperature was important to the second factor (Table 5.3b).

When all of the data were included in the canonical correspondence analysis (CCA), *Oscillatoria* and *Microcystis* spp. generally correlated with high temperature, greater k_z (quicker light attenuation), and shallow depth (Fig. 5.7a), whereas *Aphanizomenon* and *Anabaena* spp. correlated with high total phosphorus and low N:P (Fig. 5.7a). When we included all data *Cylindrospermopsis* did not correlate strongly with any predictor variable, showing some correlation with increased depth (Fig. 5.7a). *Chroococcus* spp. showed some correlation with PAR at 1 m (Fig. 5.7a). Suspecting that the early-season *Cylindrospermopsis* abundances at SBM and especially Soff were unduly biasing the CCA results, we re-ran the analysis without these data (Fig. 5.7b). Little changed with one important exception: *Cylindrospermopsis* biomass switched to being most closely associated with increased temperature, shallower depths, and *Oscillatoria* and *Microcystis* spp. biomass (Fig. 5.7b).

Discussion

Cylindrospermopsis *in Lake Erie–Cylindrospermopsis* rarely constituted a dominant portion of the total phytoplankton biomass in the Sandusky system, comprising less than 2% of the biomass on all occasions except 18 April 2005 at SBM and Soff. However, we conclusively identified *Cylindrospermopsis* in our visual enumeration only when it bore terminal, tear drop-shaped heterocytes (see Methods). As TIN concentrations rarely dropped below 200 μM at river and bay stations, it is unlikely that N limited growth and therefore *Cylindrospermopsis* would be less likely to bear heterocytes. *Cylindrospermopsis* without terminal heterocytes often have pointed terminal cells (Komárek and Kling 1991, Komárek and Komárková 2003) leading to

difficulty in their identification from mixed phytoplankton assemblages (Dokulil and Mayer 1996). Citing this difficulty, Dokulil and Mayer (1996) presented phytoplankton community dynamics and the other results of their study by amalgamating *Cylindrospermopsis raciborskii* and *Limnothrix redekei* (Van Goor) Meffert. Similarly, it is likely that some of the trichomes identified as *Oscillatoria* spp. found at our stations were actually *Cylindrospermopsis* without heterocytes. We chose to be conservative in our identifications and analyses and did not amalgamate these groups as *Planktothrix* spp. Anagnostidis and Komárek are known components of the Sandusky Bay cyanobacterial community (Rinta-Kanto and Wilhelm 2006). However, the close correlation between *Cylindrospermopsis* and *Oscillatoria* spp. with temperature and depth in the CCA (with the mid-April data points removed) supports our contention that at least a portion of the trichomes identified as *Oscillatoria* spp. were *Cylindrospermopsis*. The remaining non-*Cylindrospermopsis* trichomes that we identified as *Oscillatoria* spp. are most likely *Planktothrix* spp. (S.W. Wilhelm, University of Tennessee, personal communication). Future genetic analyses will properly separate *Cylindrospermopsis* from *Oscillatoria* spp. and identify the remaining *Oscillatoria* spp.

Densities of *Cylindrospermopsis* in Lake Erie were lower than in published reports from small lakes in Florida but greater than those reported from drowned river mouths adjacent to Lake Michigan (*cf.* Hong et al. 2006 Table 3). Our observation of *Cylindrospermopsis* at Soff on 18 April 2005 was one of the most interesting findings in our study and the first documentation of *Cylindrospermopsis* offshore in a Laurentian Great Lake. On this date at Soff, surface water temperature was 8.8 °C. Dokulil and Mayer (1996) reported positive growth rates of the *Cylindrospermopsis*/*Limnothrix*

association at temperatures below 5 °C in an Austrian lake during January of 1993 and 1994. The occurrence of *Cylindrospermopsis* at SBM and Soff on 18 April 2005 (Fig. 5.6) suggests that the trichomes found at the offshore station may have originated in Sandusky Bay. We did not sample before this date and therefore cannot determine whether the *Cylindrospermopsis* found at these two sites originated in the river or in the bay.

If *Cylindrospermopsis* became established in the Sandusky system in 2005 only through akinete germination, it most likely originated in the shallow waters of the Sandusky River and/or Bay where it experienced high enough temperatures to germinate and attain positive growth by April. *Cylindrospermopsis* is unlikely to germinate from akinetes deposited in the Sandusky subbasin because the sediment temperatures (based upon bottom temperatures) did not reach akinete germination temperatures until late July, and the *Cylindrospermopsis* growing season only lasted until late August offshore. Site SBM is shallow, like the river and bay sites, but its temperature regime more closely resembled that of Soff, indicating that it, too, is less likely to be an area of significant *Cylindrospermopsis* growth until later in the summer.

Temperature, light, and nutrient effects on Cylindrospermopsis *abundance*–Based upon previous laboratory and field studies of *Cylindrospermopsis* physiology and growth, we hypothesized that *Cylindrospermopsis* abundance in Sandusky Bay would depend on high temperatures, low light intensities, and high nutrient concentrations. The Sandusky River had insufficient irradiance for maximal *Cylindrospermopsis* growth and the bay mouth and Sandusky subbasin epilimnion had too high irradiances, but Sandusky Bay (SWB, SEB) appeared to have an ideal light climate for *Cylindrospermopsis* growth (Fig.

5.4). Multivariate analyses showed that *Cylindrospermopsis* biomass correlated with high temperatures and shallow depths when two early season data points were removed from the analysis (Fig. 5.7b). Consequently, we conclude that in the Sandusky system the river mouth and bay (areas of highest temperatures and shallowest depth) were the most important for *Cylindrospermopsis* germination and growth.

Although we found little correlation between *Cylindrospermopsis* biomass and light metrics or nutrient concentrations in the multivariate analysis, we do not suggest that light and nutrients were unimportant for *Cylindrospermopsis* occurrence in the Sandusky system. Rather, we propose that the light climate did not change enough throughout our sampling (even though there was variation) to substantially affect cyanobacterial community dynamics and that nutrient concentrations rarely limited phytoplankton growth in the Sandusky River or Bay. Seasonal dynamics of k_z showed little evidence for a positive (less light penetration) or negative (more light penetration) trend at any site except SBM indicating that light was attenuated quickly in the river and bay regardless of the time of year. Evidence for nutrient sufficiency comes from the extremely high phytoplankton biomasses found at these stations and slow phosphate uptake rates found in other experiments (J.D. Conroy, unpublished data). We found nutrient concentrations and ratios correlated with the biomass of other cyanobacterial taxa (*i.e.*, *Aphanizomenon* and *Anabaena* spp. biomasses increased with increased total phosphorus concentrations and decreased N:P). The Sandusky subbasin, conversely, had much lower nutrient concentrations and correspondingly lower total phytoplankton biomasses. The phytoplankton community at Soff also differed from those found at river and bay sites, especially later in the season. Offshore, extremely high N:P ratios coupled

with low phosphorus concentrations likely favored the best phosphorus competitors of the cyanobacterial genera, which may include *Cylindrospermopsis* (Isvánovics et al. 2000). The bay mouth functioned as a gateway to the offshore, showing characteristics of both river and bay sites (*i.e.*, higher total phytoplankton biomasses, increased cyanobacterial biomass later in the season) and also some characteristics of the offshore site (higher PAR at 1 m).

Importance of Sandusky Bay for Cylindrospermopsis growth–We propose that Sandusky Bay provides an ideal habitat for *Cylindrospermopsis* germination and growth in the Sandusky system and Lake Erie. Water temperatures rise quickly, warming the sediments, in turn allowing sediment akinete germination earlier in the season. In the relatively shallow Sandusky subbasin (compared to the central basin of Lake Erie), sediments may not reach germination temperatures until late July, but in Sandusky Bay germination temperatures may be attained nearly two months earlier. Quick warming of the water column to ideal growth temperatures (Fig. 5.3a) may facilitate rapid *Cylindrospermopsis* growth in the bay at times when offshore temperatures are less than ideal (*e.g.*, temperatures reach optimal growth temperatures in the bay by early June but do not reach this level until late June or mid-July offshore; Fig. 5.3b). Low PAR irradiance at 1 m in Sandusky Bay also facilitates *Cylindrospermopsis* growth in the Sandusky system. Even at SBM, PAR at 1 m is four times greater than in the bay (Fig. 5.4c) and may possibly cause photoinhibition of growth (Briand et al. 2004) in this shade-tolerant genus (Padisák and Reynolds 1998). Nutrient concentrations are excessive in Sandusky Bay compared to the subbasin, facilitating the growth of this superior competitor for nitrogen (Présing et al. 1996) and phosphorus (Isvánovics et al. 2000).

Potential for Cylindrospermopsis *growth in Lake Erie*–Future increases in the growth of *Cylindrospermopsis* in Lake Erie depend on future expansion of appropriate habitats. Most importantly, increased temperatures and shallower depths, in conjunction with increased nutrients and less light penetration could make Lake Erie more hospitable for *Cylindrospermopsis*. Recent research into the consequences of climate change in the Great Lakes region indicates that such conditions are occurring or are expected. Working with data sets from throughout the Great Lakes, McCormick and Fahnenstiel (1999) found increased surface water temperature and potential duration of summer stratification at Put-in-Bay in the western basin of Lake Erie in a data set spanning from 1918 to 1993. However, they found no evidence for increased water temperature for a shorter Sandusky Bay water temperature data set (1961-1993). Jones et al. (2006), extending the Put-in-Bay surface water temperature data set from McCormick and Fahnenstiel (1999), found increased monthly average temperatures in all months except autumn months. They also found evidence that summer water temperatures as a whole increased (Jones et al. 2006). Magnuson et al. (1997), using longer data sets (1895-1993 for temperature, 1911-1993 for precipitation), found increased annual air temperature and annual precipitation. Reviewing future climate predictions derived from several global climate models (Sousounis and Grover 2002, Lofgren et al. 2002, Mortsch and Quinn 1996), Jones et al. (2006) concluded that the Laurentian Great Lakes will experience decreased ice cover (an observation supported by Assel et al. 2003), lower annual runoff due to increased evapotranspiration, and decreased lake levels. Integrating these findings and predictions, it is likely that Lake Erie will become warmer and shallower, the two scenarios most associated with increased *Cylindrospermopsis* biomass in our analysis (Fig. 5.7b).

Earlier ice out or decreased ice cover coupled with decreased lake levels could lead to more mixing throughout the year, increased resuspension of bottom materials, and decreased light penetration. All future climate change indicators for the Great Lakes region and for Lake Erie in particular predict a more habitable environment for *Cylindrospermopsis* although other invasive species (*e.g.*, dreissenid mussels) may also affect the realized outcome.

Increased future *Cylindrospermopsis* biomass in the Great Lakes may detrimentally affect people who use these ecosystems for fresh drinking water, commercial activities (*e.g.*, shipping and cooling water withdrawals), and tourist activities such as sunbathing, recreational fishing, and swimming. *Cylindrospermopsis* is a known toxic cyanobacterial genus that can produce a hepatotoxin and two neurotoxins (Carmichael 2001). The hepatotoxin accumulated in tissue of fish and crayfish in aquaculture ponds (Saker and Eaglesham 1999), and caused severe hepatoenteritis in a human population in Australia (Hawkins et al. 1985). Further outbreaks of human poisonings are unlikely due to increased sophistication of water treatment operations. However, toxicity to zooplankton or excessive growth above World Health Organization limits (*i.e.*, low probability of conditions adverse to human health: < 2,000 cyanobacterial cells mL^{-1} or 0.2 mg cyanobacteria L^{-1}; moderate to high probability: < 100,000 cells mL^{-1} or < 10 mg L^{-1}; very high probability: > 100,000 cells mL^{-1} or > 10 mg L^{-1}; Chorus and Bartram 1999) may cause *Cylindrospermopsis* to directly affect beneficial uses of Lake Erie.

In summary, we investigated the physical, chemical, and biological parameters co-occurring with *Cylindrospermopsis* in the Sandusky system, a portion of Lake Erie.

Multivariate analysis identified increased water temperature and shallower depths as most important to the success of this genus provided nutrient concentrations are adequate. Further, global climate models predict future increases in water temperature and lower water levels, potentially increasing the future success of *Cylindrospermopsis* sp. in Lake Erie.

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Date	Sup	SRM	SWB	SEB	SBM	Soff
4/18		n p l t	n p l t	n p l t	n p l t	n p l t
4/29	n p	n p l t	n p l t	n p l t	n p l t	n p l t
5/6		n p l t	n p l t	n p l t	n p l t	n p l t
5/23	n p	n p l t	n p l t	n p l t	n p l t	n p l t
6/1		n p l t	n p l t	n p l t	n p l t	n p l t
6/10	n p	n p l t	n p l t	n p l t	n p l t	n p l t
6/20		p l t	p l t	p l t	p l t	p l t
6/23		p l t	p l t	p l t	p l t	p l t
6/28						p l t
7/5						l t
7/8		p l t	p l t	p l t	p l t	l t
7/11		n p l t	n p l t	n p l t	n p l t	n p l t
7/14						p l t
7/22		p l t	p l t	p l t	p l t	p l t
7/29		p l t	p l t	p l t	p l t	p l t
8/4-5		l t	l t	l t	l t	l t
8/12		l t	l t	l t	l t	l t
8/24		p t		p t		p t

Letters in each cell correspond to a particular sample taken: n = macronutrients; p = phytoplankton; l = light; and t = temperature.

Table 5.1. Site- and date-specific description of samples taken. Station locations are upstream on the Sandusky River (Sup), at the junction of the river and Sandusky Bay (SRM), in the western (SWB) and eastern (SEB) portions of the bay, at the junction of the bay and the subbasin (SBM), and offshore in the Sandusky subbasin (Soff). Locations are shown in Fig. 5.1.

Date	Sup	SRM	SWB	SEB	SBM	Soff
4/18		○	○	○	●	●
4/29	○	○	○	○	○	○
5/6		○	○	○	○	○
5/23	○	○	○	○	○	○
6/1		●	○	○	○	○
6/10	○	○	○	○	●	○
6/20		○	○	⊙	○	○
6/23		○	○	○	○	
6/28						○
7/5						○
7/8		○	○	●	○	○
7/11		○	○	⊙	○	○
7/14						○
7/22		○	○	●	○	○
7/29		○	●	⊙	○	○
8/4-5						
8/12						
8/24		●		○		○

Table 5.2. Matrix of *Cylindrospermopsis* presence and absence from phytoplankton samples taken during 2005. Empty circles indicate no *Cylindrospermopsis* enumerated, circles with a dot indicate *Cylindrospermopsis* was enumerated and calculated biomass was less than 0.1 mg L^{-1}, and filled circles indicate *Cylindrospermopsis* was enumerated and calculated biomass was greater than 0.1 mg L^{-1}. Spaces in the matrix with no circle indicate that no phytoplankton sample was taken at that station on that sampling date. Note that the greatest *Cylindrospermopsis* biomass was 1.326 mg L^{-1} at SWB on 29 July 2005.

(a)

Factor	Eigenvalue	Individual	Cumulative
1	5.26	71.3	71.3
2	1.08	14.7	86.0
3	0.55	7.4	93.4
4	0.48	6.5	99.9

(b)

	Factor	
Description	1	2
Station depth (m)	**-0.932**	0.037
Surface temperature (C)	0.303	**-0.692**
PAR at 1 m (μmol m^{-2} s^{-1})	**-0.890**	-0.222
Attenuation coefficient (m^{-1})	**0.951**	0.203
Total carbon concentration (mM)	0.331	0.309
Total inorganic nitrogen concentration (μM)	**0.788**	0.378
Total phosphorus concentration (μm)	**0.960**	-0.042
TIN:TP ratio (by atoms)	**-0.763**	0.396
Total phytoplankton biomass (wet mg L^{-1})	**0.606**	-0.337

Table 5.3. Results of factor analysis performed to determine the most important physical, chemical, and biological parameters in separating the river mouth, bay, and offshore sites. Factors with eigenvalues greater than 1.0 (a) were considered most important and loadings for these factors are presented (b). Parameters with factor loading absolute values > 0.50 were considered most important (bolded). Factors whose contribution to total variance were less than 0.1% were not included.

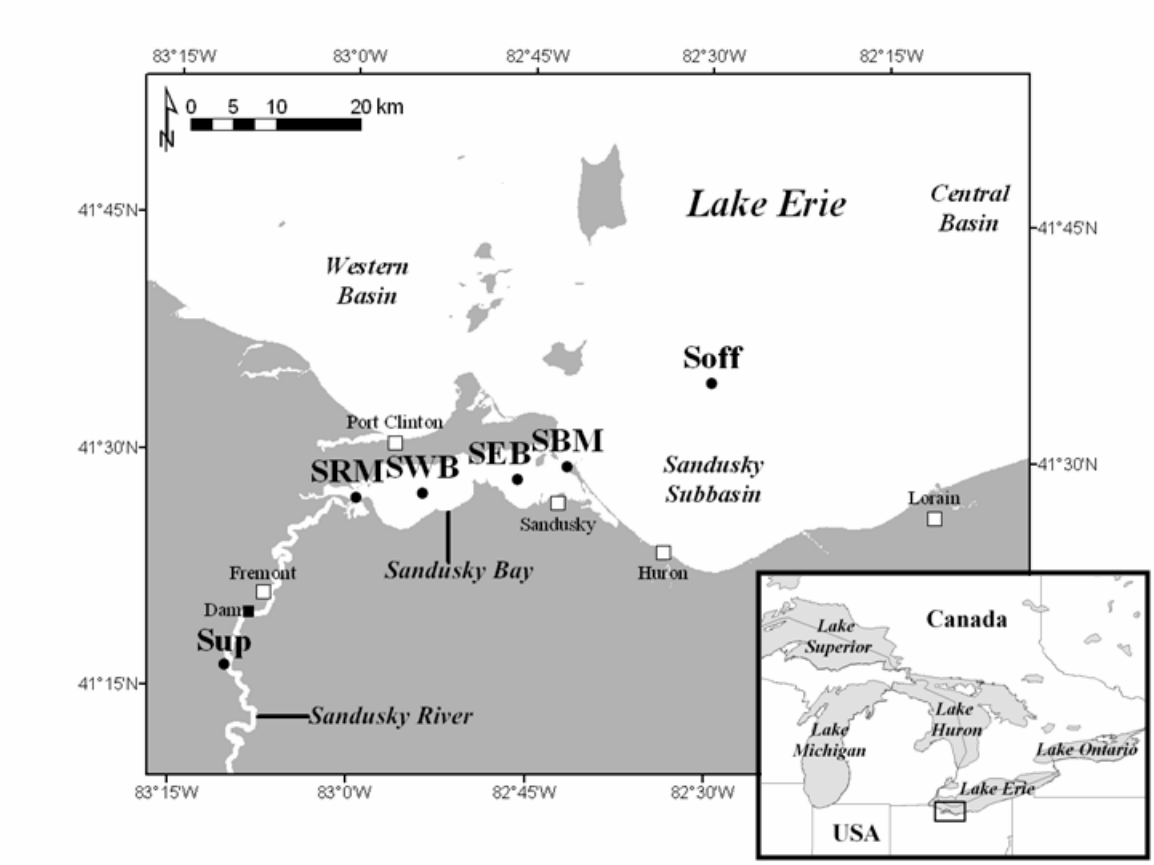

Fig. 5.1. Map of the Sandusky system sampling sites (filled dots) including the Sandusky River (Sup = Sandusky upstream, SRM = Sandusky river mouth), Bay (SWB = Sandusky west bay, SEB = Sandusky east bay), and subbasin (SBM = Sandusky bay mouth, Soff = Sandusky offshore); inset shows the relative position (small rectangle) of the larger map in context of the other Laurentian Great Lakes. Empty squares show cities in the region, a filled square shows the location of the Ballville dam, and the scale bar indicates distance. Note that the width of the river is exaggerated to aid in illustration.

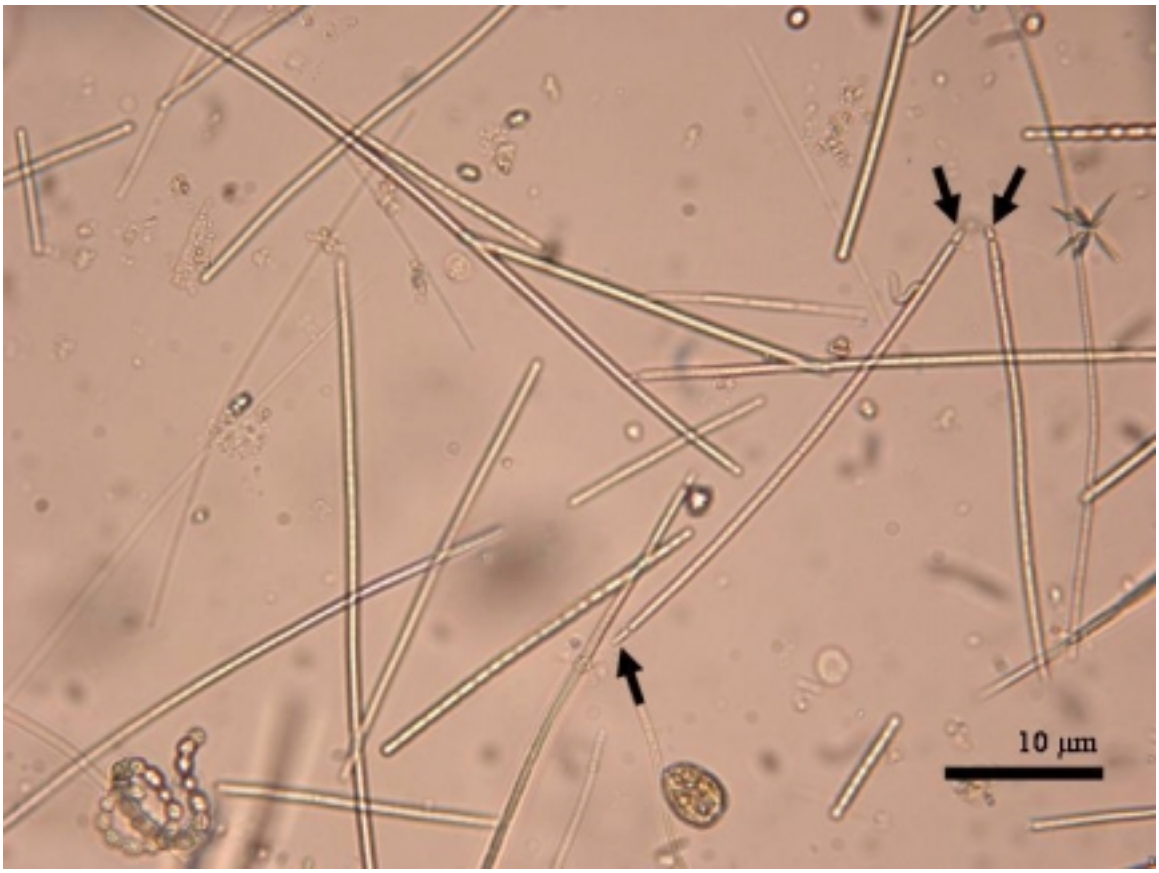

Fig. 5.2. Photomicrograph (400x magnification) of a field of view of a phytoplankton sample from SWB on 29 July 2005 showing the mixed phytoplankton community including *Cylindrospermopsis* (terminal, tear drop-shaped heterocytes are indicated with arrows).

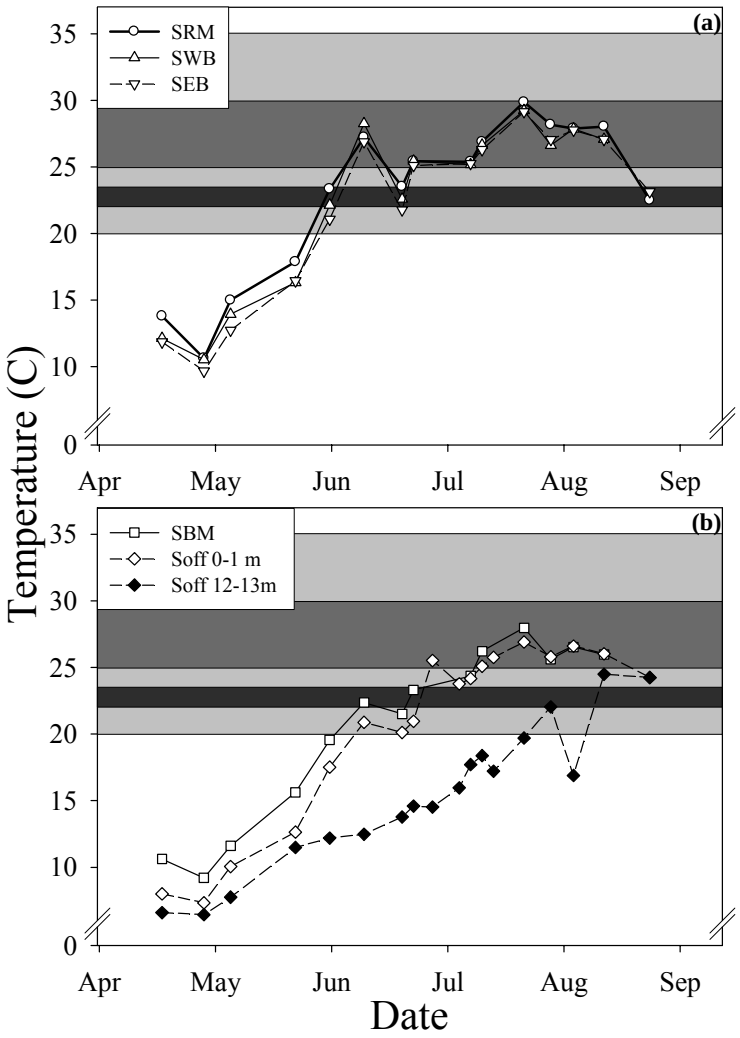

Fig. 5.3. Site-specific temperature (°C) seasonal dynamics at (a) upstream (SRM, SWB, and SEB) and (b) downstream (SBM and Soff surface and near bottom) sites. The shaded areas depict the range of temperatures (20-35°C) at which *Cylindrospermopsis raciborskii* shows positive growth (light grey-shaded area; Briand et al. 2004, Saker et al. 1999), the temperature range (25-30°C) of *Cylindrospermopsis raciborskii* maximal growth (medium grey-shaded area; Briand et al. 2004, Saker et al. 1999), and the sediment temperature (22-23.5°C) at which *Cylindrospermopsis raciborskii* akinetes germinate (dark grey-shaded area; Gorzó 1987 in Padisák 1997).

Fig. 5.4. Seasonal dynamics of (a) light attenuation coefficient (k_z, m^{-1}), (b) site-specific attenuation coefficients (m^{-1}; mean plus one standard error), and (c) site-specific irradiance (μmol m^{-2} s^{-1}) at 1 m (mean plus one standard error). The long-dash line shows the irradiance of maximal *Cylindrospermopsis raciborskii* growth (approximately 100 μmol m^{-2} s^{-1}; Briand et al. 2004) whereas the solid line shows the irradiance of the onset of light limitation of *Cylindrospermopsis* (18 μmol m^{-2} s^{-1}; Briand et al. 2004).

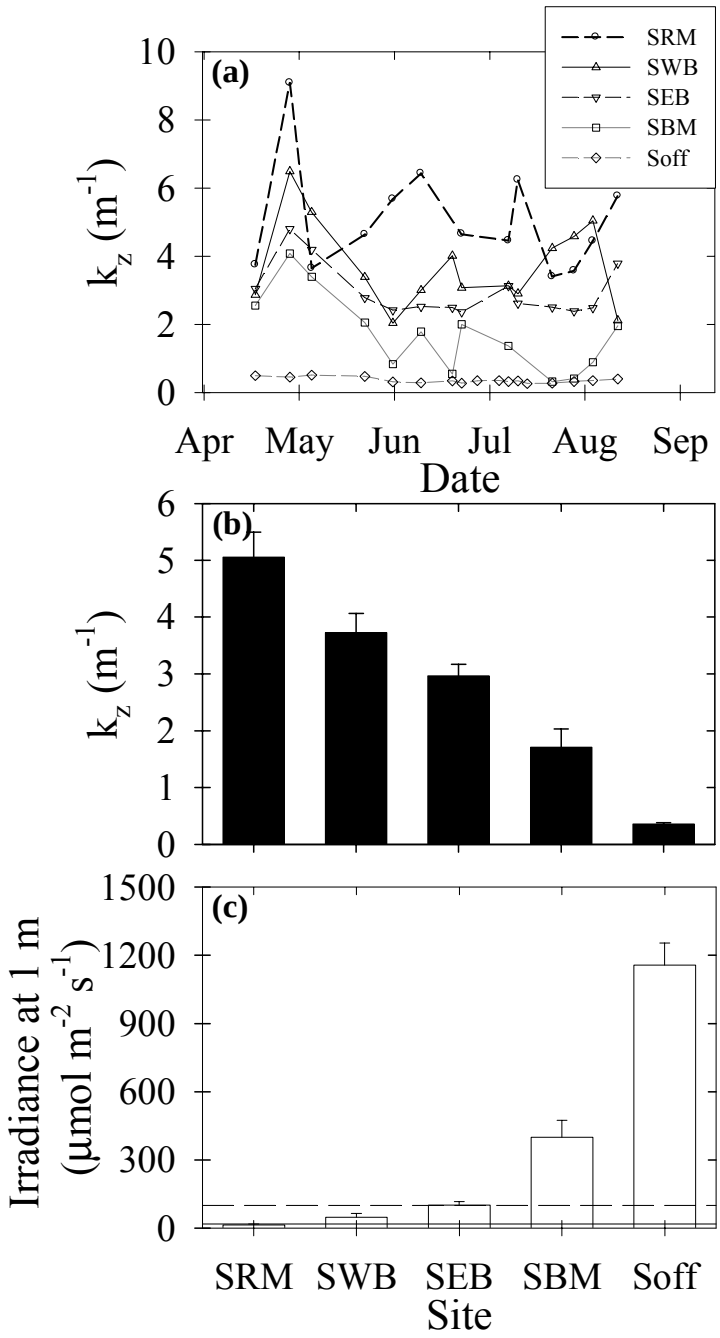
(a)
SRM
SWB
SEB
SBM
Soff
k_z (m^{-1})
10
8
6
4
2
0
Apr
May
Jun
Jul
Aug
Sep
Date
(b)
k_z (m^{-1})
6
5
4
3
2
1
0
(c)
Irradiance at 1 m
(μmol m^{-2} s^{-1})
1500
1200
900
600
300
0
SRM
SWB
SEB
SBM
Soff
Site

Fig. 5.4.

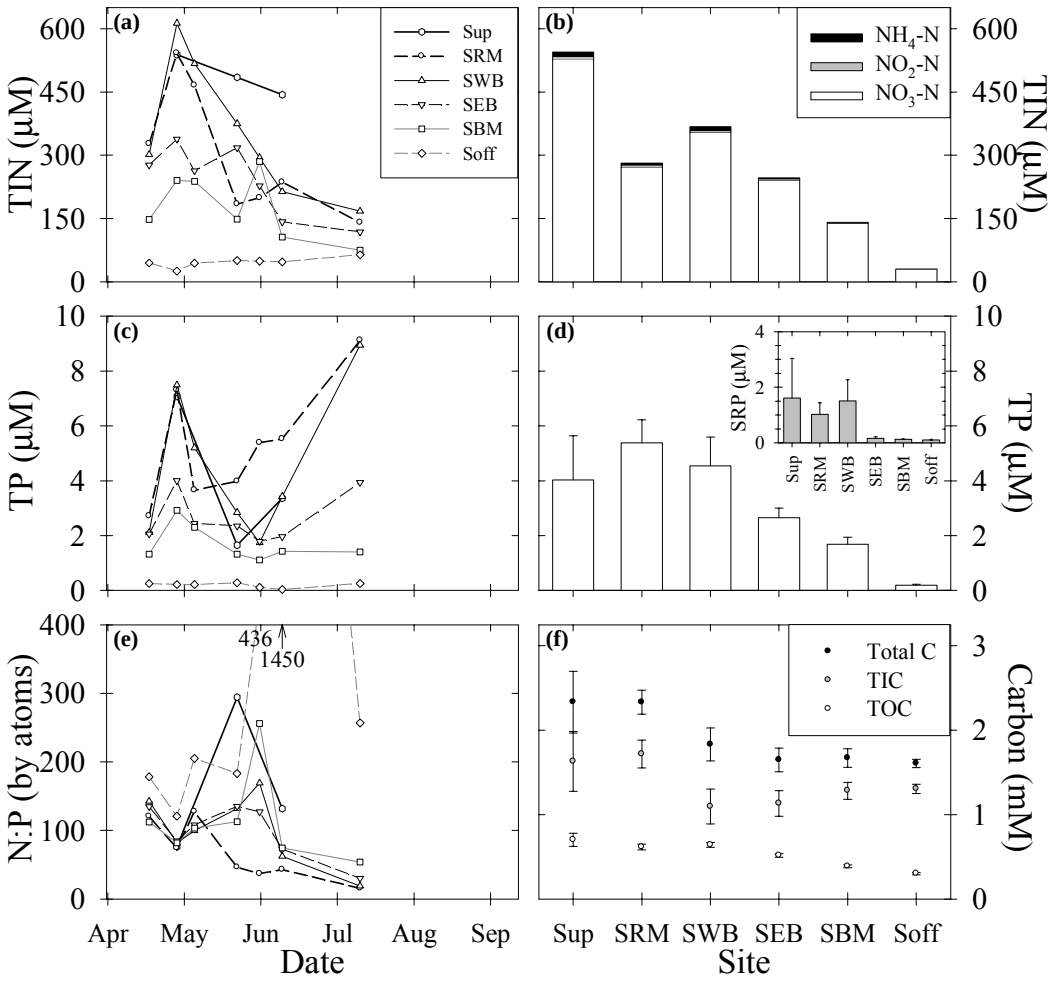

Fig. 5.5. Temporal and spatial dynamics of Sandusky system nitrogen, phosphorus, and carbon concentrations during 2005. The top panels show total inorganic nitrogen seasonal (a) and nitrate-, nitrite-, and ammonium-nitrate mean site (b) concentrations, the middle panels show total phosphorus seasonal (c) and site-specific total phosphorus (d) and soluble reactive phosphate-phosphorus (d, inset) concentrations, and the lower panels show total inorganic nitrogen:total phosphorus seasonal ratio (e) and total, inorganic, and organic carbon site-specific dynamics (f). In (b), nitrite- and ammonium-nitrogen are very small components of the total inorganic nitrogen concentration, especially at SEB, SBM, and Soff stations where concentrations of these components were < 3 µM. Error bars in (d) and (f) show one standard error of the mean. Standard errors of the mean for nitrogen components ranged from 12-38% of the mean value for nitrate-nitrogen, 12-31% for nitrite-nitrogen, and 63-93% for ammonium-nitrogen. Note that all panels on the left use the legend in (a) and that the units in (f) are 1000 times those in panels (a-d).

Fig. 5.6. Cyanobacteria percent composition (bars) and total cyanobacterial biomass (mg L^{-1}; line) seasonal dynamics for SRM (a), SWB (b), SEB (c), SBM (d), and Soff (e). Zeros indicate that Cyanobacteria were not present on those dates. Abbreviations for cyanobacterial genera are: *Cyl.* = *Cylindrospermopsis*, *Osc.* = *Oscillatoria* spp., *Mic.* = *Microcystis* spp., *Aph.* = *Aphanizomenon* spp., *Ana.* = *Anabaena* spp., and *Chr.* = *Chroococcus* spp. Note that the biomass axis for Soff (e) is 0.8% that of the other sites. These six cyanobacterial genera comprised > 99.3% of the total cyanobacterial biomass at river, bay, and bay mouth sites and > 94.3% of the total cyanobacterial biomass at the offshore site on all dates.

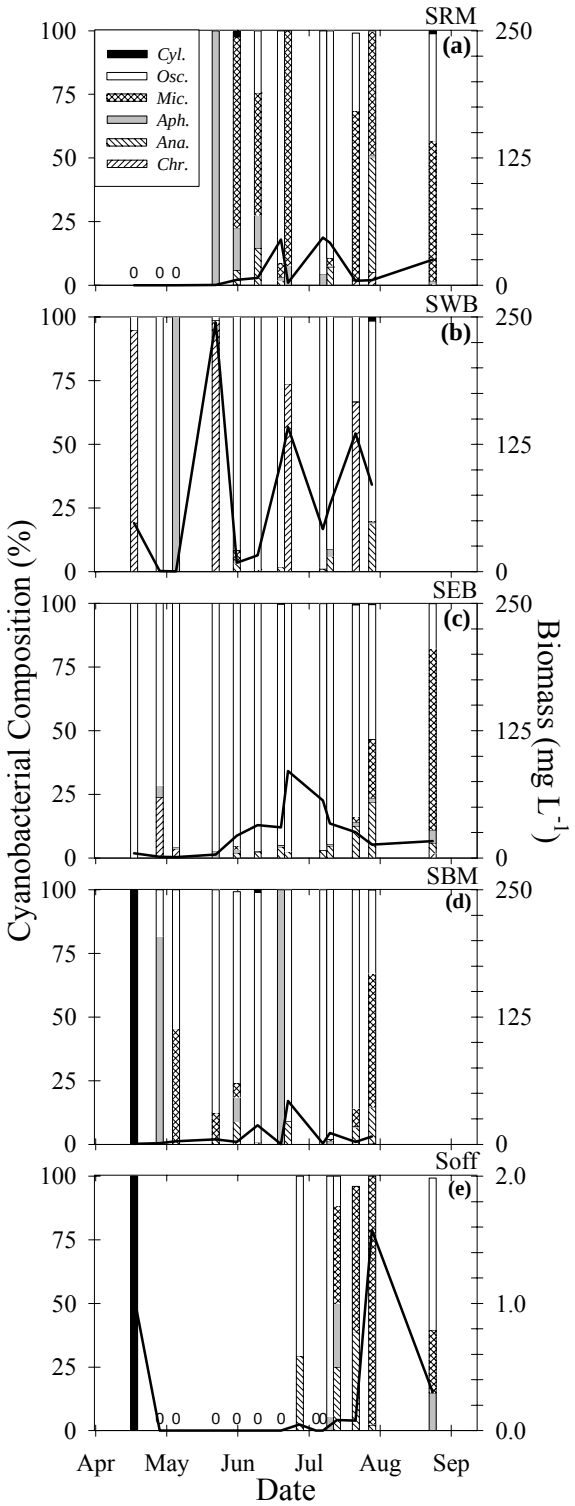
SRM
(a)
SWB
(b)
SEB
(c)
SBM
(d)
Soff
(e)
Cyl.
Osc.
Mic.
Aph.
Ana.
Chr.
Cyanobacterial Composition (%)
Biomass (mg L-1)
Apr
May
Jun
Jul
Aug
Sep
Date

Fig. 5.6.

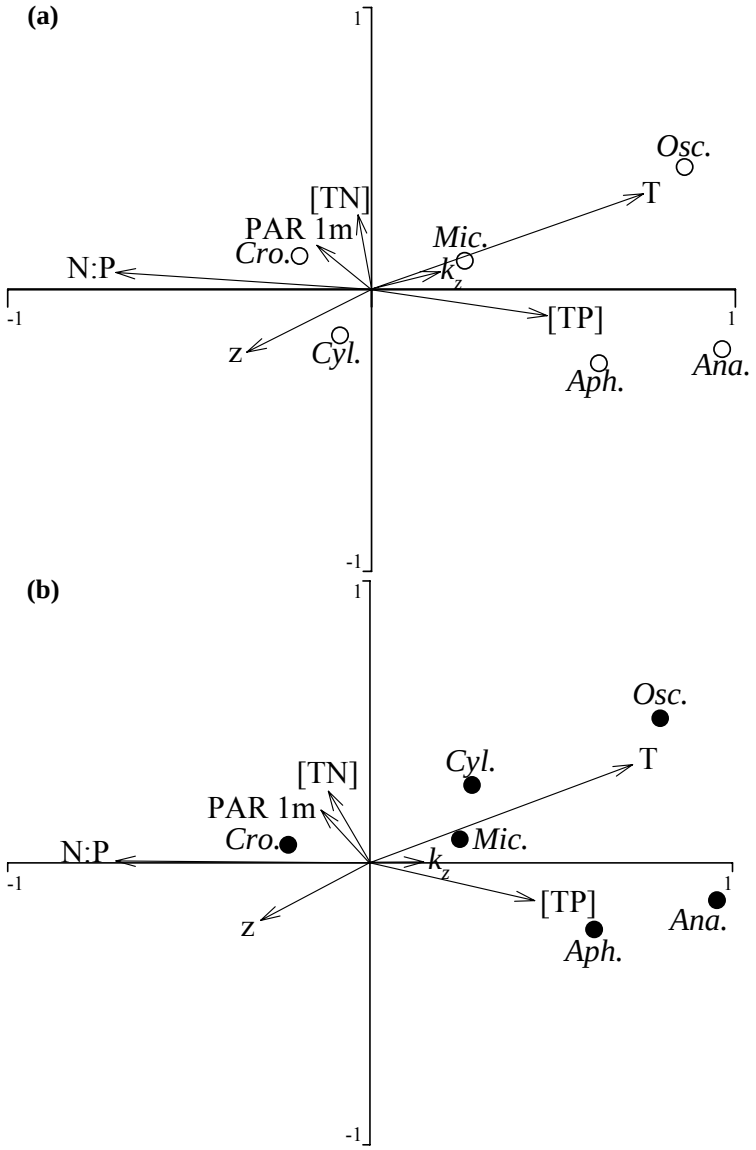

Fig. 5.7. Canonical correspondence analysis results showing the correlations between cyanobacterial genera (circles) and physical and chemical parameters (arrows) and the canonical axes. Panel (a) shows the relationship for the entire dataset and panel (b) shows the relationship when we excluded the data for 18 April 2005 at sites SBM and Soff. All physical and chemical parameters and cyanobacterial genera remained in the same quadrants in moving from (a) to (b) except *Cylindrospermopsis* sp. We included all important cyanobacterial genera (comprising > 94% of the total cyanobacterial biomass on all dates) in the analysis but only included the parameters with factor loading absolute deviations > 0.50 (from factor analysis, see Table 5.3). Abbreviations are given in Table 5.3 and the legend of Fig. 5.6.

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