A Final Report for Lake Erie Protection Fund project SG 336-08

PI: Robert Michael L. McKay
Department of Biological Sciences
Bowling Green State University

Meeting the Objectives Outlined in SG 336-08

Goal: *We proposed to conduct a six (6) day research cruise on a Canadian Coast Guard icebreaker on Lake Erie in February 2008 to follow up on our initial 2007 survey.*

LEPF support helped fund our participation on three (3) separate cruises on the CCGS *Griffon* (14 days total). This was made possible through additional *in kind* support from our collaborators at Environment Canada as well support through Ohio Sea Grant (permission to re-allocate some funds associated with a separate grant related to phosphorus quotas of Lake Erie phytoplankton).

Additional in kind support from US-EPA and the US Coast Guard enabled us to expand our sampling regimen into late winter and spring in order to follow the decline of the winter diatom bloom.

Activities and Timeline

1. *February 2008: Confirm location of CACHEs by aerial survey.*
   Not completed; rather, ship personnel made observations from the bridge of the *Griffon* leading up to our cruises

2. *February 2008: Finalize cruise track and provide to CCGS Griffon for approval.*
   Completed

3. *Late February 2008: Board icebreaker for 6-day expedition across Lake Erie.*
   Feb. 2008 cruise was of 5 day duration. We lost a day at the start of the cruise due to the vessel being called away for icebreaking duties

   a. Conduct winter assessment of microbial biomass and metabolism at 10 hydrographic stations
   Six (6) stations were occupied along with two (2) CACHE sites

   b. Quantify CACHE density by standard ship-borne surveying methods.
   Completed

   c. Measure physical, chemical and biological properties of several CACHES by working from ice-surface and processing samples onboard ship.
   Completed

4. *April 2008: Complete sample and data analysis and prepare manuscript.*
Sample analysis by BGSU participants largely completed by this time. A large number of collaborators participated in this interdisciplinary study (10 scientists from six different institutions) which resulted in some delays processing samples and sharing data. Remaining data for the Feb 2008 cruise was circulated in Feb 2009. A manuscript is in preparation stage and will be submitted in summer 2009.

5. *summer 2008: Present findings at scientific meeting (IAGLR, ASLO).*
Accomplished:

Twiss, M.R., R.A. Bourbonniere, G.S. Bullerjahn, H.J. Carrick, N. D'Souza, P.C. Furey, R.M.L McKay, N.E. Ostrom, M. Saxton, R.E.H. Smith, and S.W. Wilhelm. Winter assessment of microbial biomass and metabolism: February 2007 & 2008. The Fifth Biennial Conference of the Lake Erie Millennium Network. University of Windsor, Windsor, ON, Canada (29-30 April, 2008).

Twiss, M.R., S.W. Wilhelm, R.M.L. McKay, G.S. Bullerjahn, J.P. Dempsey, H.J. Carrick and R.E.H. Smith. The CACHE: A unique limnological feature in ice covered Lake Erie. International Association for Great Lakes Research 51st Annual Conference on Great Lakes Research. Trent University, Peterborough, ON, Canada (19-23 May, 2008).

Wilhelm, S.W., R.M.L. McKay, M.R. Twiss, G.S. Bullerjahn, R.A. Bourbonniere, H.J. Carrick, N.E. Ostrom, M.M.D. Al-Rshaidat, G.R. LeCleir, R.W. Sterner, C.J.H. Marvin and R.E.H. Smith. Winter assessment of microbial biomass and metabolism (WAMBAM): A first look at winter pelagic biology in Lake Erie and the implications of climate change. International Association for Great Lakes Research 51st Annual Conference on Great Lakes Research. Trent University, Peterborough, ON, Canada (19-23 May, 2008).

Wilhelm, S.W., R.A. Bourbonniere , G.S. Bullerjahn, , H.J. Carrick, N.E. Ostrom, C.J.H. Marvin, R.M.L. McKay, M.R. Twiss and R.E.H. Smith. Winter assessment of microbial biomass and metabolism (WAMBAM): The implications for climate change on winter biological activity in a Laurentian Great Lake. American Society of Limnology and Oceanography (ASLO) Conference, St. John's, NL, Canada (9-13 June, 2008).

D'souza, N., S.W. Wilhelm, M.R. Twiss, H.J. Carrick, R.A. Bourbonniere, G.S. Bullerjahn and R.M.L. McKay. Primary Production in Ice-Covered Lake Erie. International Association for Great Lakes Research 52nd Annual Conference on Great Lakes Research. University of Toledo, Toledo, OH (18-22 May, 2009).

6. *September 2008: Submit final report to LEPF.*
When award was granted, due date of 12/31/2008 was listed. Request for extension was made in Nov. 2008 and granted by Ohio Lake Erie Commission with revised final report due date of 4/30/2009.

Work Products

1. *We expect to produce at least one peer-reviewed manuscript from this work.*
   A manuscript is planned for submission in summer 2009.

2. *We expect to isolate microbes (phytoplankton, bacteria and fungi) from water samples and submit them for public access at a national culture collection.*
   While pure phytoplankton isolates have thus far eluded us, we have been successful in maintaining mixed cultures at 4 °C that are dominated by *A. islandica*.

3. *We expect to present several presentations at scientific conferences based on this work and that completed in 2007.*
   Accomplished – see response to Activities and Timeline # 5 above.

4. *We anticipate that the funding provided by this small grant will allow us to successfully compete for a grant (e.g. USEPA, NSF) allowing establishment of a long-term winter monitoring program of Lake Erie.*
   A grant proposal to NSF was not successful. However, dedicated grant support from Ohio Sea Grant was awarded and is anticipated to start spring/summer 2009 (award was made late fall 2007 but award was deferred by Sea Grant for 1 year). Our collaborator at Clarkson University (Dr. Michael Twiss) has used his participation in this project as leverage for a successful NY Sea Grant award that commenced in 2009.

5. *Establish binational participation through collaboration with Canadian researchers (funded by NSERC or Environment Canada).*
   Accomplished with participation of personnel from Environment Canada (Drs. R. Bourbonniere and C. Marvin) and from the University of Waterloo (Dr. R. Smith). Project was also highlighted in the newsletter "AuCanada" (Fall 2008, Vol. 15, Issue 2) published by the Canadian Studies Center at Bowling Green State University.

Dissemination

We will publish our results in a peer-reviewed journal (e.g., Journal of Great Lakes Research, Limnology & Oceanography) and we will release updates to popular press outlets such as Ohio Sea Grant TwineLine. We have an extensive track record for publication on Lake Erie microbiology and limnology (see http://www.bio.utk.edu/wilhelm/melee.htm).
In addition, we will present these results at appropriate scientific meetings (e.g. International Association for Great Lakes annual meeting or Lake Erie at the Millennium meeting.)

Plans are to submit an article for consideration this summer by the journal Limnology & Oceanography, the premiere journal in the discipline. We are also considering submission of an article detailing our hypothesis on the link between winter production and formation of the "dead zone" to Eos, the newsletter of the American Geophysical Union.

The project was highlighted in the newsletter AuCanada (Fall 2008, Vol. 15, Issue 2) published by the Canadian Studies Center at Bowling Green State University and in Bio:Life (Spring 2008), a semi-annual alumni magazine published by the Department of Biological Sciences at BGSU.

LAKE ERIE PROTECTION FUND

SMALL GRANT - FINAL ACCOUNTING

Grant Number: SG 336-08 v2008

Budget Categories	Orignal Budget	Funds Spent	Current Balance	Matching Funds
A. Salaries & Wages				
				7379.00
B. Fringe Benefits				
				2214.00
C. Total Salaries & Benefits (A+B)	$0.00	$0.00	$0.00	$9,593.00
D. Non-expendable Equipment				
E. Expendable Materials & Supplies				
	1000.00	702.57	297.43	
F. Travel				
	500.00	458.49	41.51	
G. Services or Consultants				
	1000.00	1000.00	0.00	
H. Computer Costs				
I. Publications/Presentations				
J. All other direct costs				
	10500.00	10838.94	-338.94	
K. Total Direct Costs (C thru J)	$13,000.00	$13,000.00	$0.00	$9,593.00
L. Indirect Costs				
	1300.00	1300.00	0.00	3740.00
Total Costs (K + L)	$14,300.00	$14,300.00	$0.00	$13,333.00

Ohio Lake Erie Commission
One Maritime Plaza, 4th Floor
Toledo, OH 43604
p 419-245-2514
f. 419-245-2519
www.epa.state.oh.us/oleo

I certify that the grant expenitures listed and descriptions of the charges are true and accurate to the best of my knowledge. These expenditures represent approved grant costs that have been previously paid for and for which complete documentation is on file.

		Date
Project Director	[signature]	4/14/09
Authorizing Agent	Cynthia A. Price	4/16/09
Fiscal Agent	Christy McCartney	4/7/09

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Winter assessment of microbial biomass in an ice-covered large lake

Abstract

Winter limnological surveys of Lake Erie were undertaken between 2007 - 2009 during periods when the lake was ~90% ice covered and continuing through to the period of vernal mixis. During winter, the lake supported high phytoplankton biomass dominated by nutrient sufficient, low-light adapted, filamentous, centric diatoms of the species *Aulacoseira islandica*. April surveys conducted in 2008-09 demonstrated that high *Aulacoseira* spp. biomass persisted into spring. During each cruise, samples were analyzed for dissolved nutrients and elemental stoichiometry (C, N, P) of seston. Rates of primary production were measured using dual proxies including [^{14}C]-$NaHCO_3$ uptake and photosynthetic oxygen evolution. Total light-saturated winter primary production estimated using [^{14}C]-uptake ranged from 1–7 g C g Chl*a*$^{-1}$ h^{-1}, whereas net photosynthetic oxygen evolution of net plankton ranged from 0.05–2.5 mol O_2 g Chl*a*$^{-1}$ h^{-1}. Photosynthesis vs. irradiance (PE) curves obtained using both approaches yielded median E_k values of 29 ([^{14}C]-uptake) and 44 (O_2 evolution) µmol photons m^{-2} s^{-1} respectively, suggestive of a low light-adapted community. Our findings support the existence of a physiologically robust assemblage of nutrient sufficient, psychrophilic diatoms in Lake Erie, the contributions to carbon cycling of which must be considered when deriving whole lake carbon budgets.

Introduction

The majority of our knowledge about the biological limnology of the Laurentian Great Lakes is based on studies completed in early spring to late summer. The void in our knowledge of winter processes is in part due to the difficulties associated with collecting relevant samples during the winter season and may also stem from the belief that much of the "activity" in these lakes occurs during the warmer summer months. Very few studies have been carried out in other seasons, particularly winter. One question that arises from this uneven data collection is how models of ecosystem system function and thus, our predictive capabilities are biased.

Historically research into winter limnology has been episodic. The most comprehensive study of winter limnology (including the period of ice cover) in Lake Erie to date is the 4-year (1938-1942) western basin study by Chandler (Chandler 1940; 1942a; b; Chandler and Weeks 1945). During these studies Chandler observed pulses (blooms) of diatoms in mid-winter (mid February to late March) under the ice, low zooplankton populations, and a variable light environment.

Amongst the other Laurentian Great Lakes, studies during the period of ice cover are rare. Wallen (1977, 1979, 1990) and Wallen and Tuppling (1977) conducted research on ice-covered Lake St. Clair, the smallest lake in the Laurentian Great Lakes system. During ice cover in January, diatoms (mainly *Fragilaria* spp.) were the dominant phytoplankton taxon in Lake St. Clair (60-80%), accumulating moderate chl-*a* biomass (1-2 µg L^{-1}) and with rates of primary

production comparable to open-water winter production in Lakes Ontario and Erie (Glooschenko et al. 1974). A late-winter decline in the diatom component at one site coincided with a decline in reactive silicate to <100 μg L^{-1} (Wallen and Tuppling, 1977), a threshold level below which diatoms are reported to be Si-limiting (Schelske and Stoermer, 1971). Subsequent microcosm studies supported limitation of the phytoplankton at this site by silicic acid (Wallen, 1979).

To our knowledge, the only additional concerted effort to conduct studies of under-ice limnology of the Great Lakes was made by a team from GLERL in the mid-1980s who established 3 stations in the east arm of Grand Traverse Bay, Lake Michigan (Bolsenga et al. 1988; Bolsenga and Vanderploeg, 1992; Vanderploeg et al. 1992). A guiding motivation behind this research was to examine the effect of ice cover on reproductive output of calanoid copepods, which affects the recruitment success of larval whitefish, a species of commercial importance to Lake Michigan. During their study period, wind activity kept the ice relatively free of snow, thus ensuring high transmittance of photosynthetically active radiation (PAR) through the ice (Bolsenga and Vanderploeg, 1992). This, in turn stimulated an under-ice bloom of phytoplankton dominated by diatoms (*Fragilaria crotonensis* and *Tabellaria* spp.) that augmented reproductive output of the copepods (Vanderploeg et al. 1992).

Work during this time also provided some of the earliest estimates of bacterial carbon production for the Laurentian Great Lakes (Scavia and Laird 1987; Scavia et al. 1986) which estimated that carbon production and demand were in disequilibrium based on bacterial production rates measured in open waters from Lake Michigan. High rates of summer carbon demand by heterotrophic bacteria exceeded supply rates by primary production in the summer months, implying that either allochthonous carbon or materials fixed photosynthetically in the winter months were meeting this demand. While similar summer rates of bacterial production have been measured in other Laurentian Great Lakes (e.g., DeBruyn et al. 2004), winter measurements remain scarce.

Constraining wintertime rates of primary and secondary production will be important for future modelling efforts as well as for examining possible links between winter algal production and formation later in the summer of the so-called "*dead zone*". Loss of oxygen in the hypolimnion of the central basin of Lake Erie in late summer is well documented (Burns and Ross, 1972; Bertram 1993; Charlton et al. 1993) and of binational concern due to internal loading of nutrients (phosphorus) into the lake during the summer that can lead to proliferation of algal blooms including harmful and noxious varities. Hypoxia can also result in loss of habitat to benthic macrofauna (Krieger et al. 1996) and fish. This area of hypoxia associated with Lake Erie's central basin can exceed 10,000 km^2 (Hawley et al. 2006), and thus comparable in surface area to the low oxygen "*dead zone*" in the Gulf of Mexico.

The integrative NOAA-GLERL funded International Field Years on Lake Erie (IFYLE) 2005 program (Hawley et al. 2006) assessed the extent and impact of hypoxia in Lake Erie. However, beyond the known constraints to maintaining adequate oxygen in the hypolimnion of Lake Erie's central basin (*viz.*, hypolimnion depth, temperature, organic carbon loading) the cause of summer hypoxia remains unresolved.

Through support of the LEPF, we have begun to address the paucity of winter limnological data for Lake Erie. Winter limnological surveys coordinated with the assistance of three governmental agencies (Canadian Coast Guard, US Environemntal Protection Agency and US Coast Guard) were undertaken between 2007 - 2009 during periods when the lake was ~90% ice covered through the period of spring break-up. Collaboration with an interdisciplinary team of scientists from US and Canadian institutions ensured the comprehensive collection and analysis of physical, chemical and biological data.

METHODS

Stations and locations – Hydrographic stations in Lake Erie were sampled during Feb 21-23 2007, Feb 12-16 2008, Jan 12-16 2009 and Feb 17-20 2009 on the icebreaker CCGS *Griffon*. Additional stations were occupied in 21-23 April 2008 on the US EPA research vessel RV *Peter Wise Lake Guardian*. Finally, late winter and spring samples were collected on 4 dates in 2009 (Feb 24, Feb 27, March 19, April 24) by personnel stationed on the USCGC *Neah Bay*. Stations (Table 1; Fig. 1) occupied were distributed in each of the three basins of the lake. Water column samples collected on the CCGS *Griffon* were taken using a 10-L Niskin bottle on a metered deck winch and by use of a submersible pump deployed 1 m below the surface. On board the RV *Peter Wise Lake Guardian*, 10-L Niskin bottles arranged in a CTD-rosette were used for sample collection whereas on the USCGC *Neah Bay*, a 2-L VanDorn bottle was used to sample water. Collection of filamentous diatom biomass was facilitated by vertical net tow (154 μm pore-size mesh) deployed to 10-15 m depth.

In February 2008, whilst underway, visible accumulations of algae were enumerated in the 13 m wide wake of the ship by manual observation during daylight hours along a track recorded using navigational software. Thirteen transects (9 in central basin, 4 in western basin) were surveyed for a total of 1.33 km^2.

Water Chemistry – Samples for nutrients (total dissolved P [TDP], soluble reactive P [SRP], total dissolved N [TDN], NH_4^+, NO_3^- + NO_2^- and SiO_2) were collected from 1 m at each station, passed through a 0.45 μm filter and stored at 4 °C in darkness. On board the CCGS Griffon, additional samples were collected at near the bottom of the water column (bottom – 2 m). Nutrient analysis was conducted by respective agencies for CCGS *Griffon* (National Laboratory for Environmental Testing [NLET]; Environment Canada) and RV *Peter Wise Lake Guardian* (US EPA – Great Lakes National Program Office) using standardized techniques (NLET 1994). Samples collected by the USCGC *Neah Bay* were analyzed at the National Center for Water Quality Research, Heidelberg University.

Samples for dissolved inorganic carbon (DIC) were clarified through 0.4 μm glass fibre filters (Macherey-Nagel GF5) and stored in sealed serum bottles prior to measurement by manual injection using a Dohrmann DC-190 Carbon analyzer. Determination of dissolved organic carbon (DOC) was made by high temperature combustion and infrared detection using an Apollo 9000 Carbon Analyzer.

Particulate organic carbon (POC) and nitrogen (PON) was determined on seston collected on pre-combusted GF/F filters using facilities at the University of Minnesota with a Perkin Elmer series II CHN analyzer using acetanilide as a standard. In 2008, POC and PON were determined also by NLET (NLET 1994). Particulate phosphorus (PP) was measured as described previously (Hood *et al.* 2006). Briefly, samples collected on GF/F filters were digested by adding 5% potassium persulfate and autoclaving for 30 min. Liberated SRP was analyzed colorimetrically with the molybdate ascorbic acid method (Strickland and Parsons, 1968) using a 10-cm cell and Shimadzu UV 160U spectrophotometer.

Chlorophyll (chl)-*a* was measured by fluorometry after Welschmeyer (1994) following extraction of polycarbonate membrane filters containing seston in 90% acetone in the dark at 4 °C. Size-fractionated estimates of chl *a* concentrations were determined on duplicate samples using polycarbonate membranes of 20-, 2- and 0.2- μm nominal pore size. The fluorometer (Turner Designs model TD-700) was calibrated using a solid standard prior to each measurement.

Alkaline phosphatase activity (APase; E.C. 3.1.3.1) was measured as an index of phytoplankton P status using fluorescent substrate methylumbelliferyl phosphate (MUB-P) as described previously (Sterner *et al.* 2004). Samples of water collected from 1 m depth were incubated with MUB-P at ambient lab temperature for 2-3 h prior to measuring APase-catalyzed fluorescence using a TD-700 fluorometer equipped with a near-UV lamp and a methylumbelliferyl filter set (ex_{λ} 300-400 nm; em_{λ} 410-610 nm).

Underwater spectral irradiance - A Satlantic OCI 200 system together with a Biospherical BIC radiometer provided estimates of downwelling irradiance in 2 nm (Satlantic) or 5 nm (Biospherical) wavebands centered at 305, 320, 340, 380, 400, 440, 480, 510, 540 and 665 nm. The BIC also measured PAR.

Phytoplankton production rates – In winter 2007, uptake of [^{14}C]-$NaHCO_3$ was used to measure phytoplankton primary production using a photosynthetron as described previously (McKay *et al.* 1997) whereas in winters 2008-09, multiple proxies as described below were extended to evaluate primary production (Ostrom *et al.* 2005).

[^{14}C]-$NaHCO_3$ uptake - Photosynthetic carbon incorporation rates were estimated using a photosynthetron (CHPT Mfg. Inc.) where [^{14}C]-$NaHCO_3$ (22 μCi; MP Biomedicals) was added to 30 mL of lakewater following a 30 min dark adaptation at 4 °C. The cell suspension was distributed as 1 mL aliquots into 7 mL glass scintillation vials that were incubated simultaneously in the photosynthetron under 24 different light intensities for 1-3 h at 3-4 °C. The reaction was terminated by the addition of 50 μL of formaldehyde to each sample. Acid-stable ^{14}C assimilation was measured by liquid scintillation counting following the addition of 4.5 mL of Ecolite (+) cocktail (MP Biomedicals) to each vial. Total activity of the added ^{14}C was determined by adding 20 μL of the sample at t=0 to scintillation cocktail containing 200 μL of ß-phenylethylamine (Sigma). Background activity was determined at t=0 by dispensing a sample aliquot directly into formaldehyde prior to adding scintillation cocktail. Experiments were performed on unfiltered water collected at 1 m depth and on samples collected by vertical

net tow. Dissolved inorganic carbon was measured by gas chromatography and was used for calculating carbon uptake and assimilation. Rates of photosynthesis were determined by using a non-linear regression curve fitting function (SigmaPlot 9.0, Systat Software, Inc.) based on the equation of Platt *et al.* (1980).

Uptake of [^{14}C]-$NaHCO_3$ was also evaluated amongst phytoplankton size fractions following Wetzel and Likens (2000). To water collected by Niskin bottle from 1 m depth and distributed to triplicate 300 mL clear borosilicate BOD bottles was added 7.5 µCi of [^{14}C]-$NaHCO_3$. Bottles were incubated in an illuminated (15-25 µmol photons m^{-2} s^{-1}) and temperature-controlled (1-2 °C) incubator (Percival) for up to 10 h following which samples were filtered for size fractionated ^{14}C content onto polycarbonate membranes (47 mm dia., Millipore) of 20-, 2- and 0.2-µm pore size. Filters were rinsed with 2 × 10 mL of filter-sterilized lakewater and stored frozen prior to counting by liquid scintillation. Sub-samples (0.5 mL × 2) from each bottle were fixed with 40 µL β-phenethylamine for measurement of total ^{14}C.

Oxygen evolution and respiration: Modified Winkler procedure - From a common reservoir, triplicate initial, clear (light), and black (dark) 300 mL BOD bottles were filled with sample water. The [O_2] in water samples was determined using a modified Winkler technique (Fahnenstiel and Carrick 1988; Carrick 2004). Bottles were incubated for 4-6 hours at ambient light and temperature in a temperature-controlled incubator (Percival). At the end of the incubation period or immediately after collection for the initial sample, BOD bottles were fixed with 2 mL of 3 M $MnCl_2$ followed by 2 mL of alkali-iodide consisting of a mixture of 8 N NaOH and 4M NaI. Bottles were shaken, allowed to settle, and then placed in a cooler until titration. Just prior to titration (20-30 min), 2 mL of 10 N H_2SO_4 was added to each BOD bottle. Whole bottles were then titrated with 0.02 N sodium thiosulfate using a Brinkman Metrohom potentiometric end-point detection system (Carrick 2004). Standardization of the thiosulfate solution and blank determinations were performed. Coefficients of variation among triplicate samples were typically < 0.2%.

At three stations, an additional set of dark bottles were incubated at higher temperature (8-10 °C) to evaluate the activity of the winter assemblage under summertime hypolimnetic temperature conditions.

Dissolved oxygen electrode - A temperature controlled Qubit Systems Dissolved Oxygen sensor was used to measure photosynthetic oxygen evolution of plankton acquired from net tows. Following the net tow, material was transferred to a plastic, amber bottle and maintained at 4 °C prior to measurement. Surface water from the same station was filtered (0.2 µm Polycap AS; Whatman), sparged with N_2 gas (~ 10 min) and used to dilute the net tow sample 2:1 prior to measurement of O_2 evolution. This ensured that the sample would not be O_2-saturated prior to measurement. Measurements were initiated by placing a black cloth over the water-jacketed cuvette containing the sample until a steady trace was obtained. The cloth was removed and the cuvette was illuminated using fiber-optic halogen light sources. At intervals of 3 min, the light intensity was increased through 10 steps between 10-450 µmol photons m^{-2} s^{-1} with duplicate curves measured for most samples. Following each experiment, a 2.5 mL sample from the cuvette was withdrawn to measure chl *a* in order to normalize photosynthetic rates. Rates of

oxygen evolution were determined from regressions through dissolved oxygen profiles using Logger Pro 3.5.0 data acquisition software (Vernier Software and Technology) via a LabPro interface (Vernier).

Fluorescence kinetics of photosynthesis - Variable fluorescence of chl *a* was measured by Pulse Amplitude Modulated (PAM) fluorometry using a WATER-PAM chl fluorometer (Heinz Walz GmbH). The dark-adapted variable fluorescence ratio of chl *a* (F_v/F_m) is a measure of the maximum quantum yield of PSII and an index of photosynthetic integrity.

Photochemical energy conversion efficiency was also measured as F_v/F_m on dark-acclimated (30-90 min), unfiltered samples using a FASTtracka fast repetition rate fluorometer (FRRF; Chelsea Technologies Group). Samples of net seston were diluted using filtered (< 0.2 μm) lake water and similarly dark-adapted. Repeated measurements were made at 11 second intervals over a 10-18 min period.

Plankton diversity

Algal biomass and taxonomic composition - Water sampled at each station from a depth of 1 m was preserved with glutaraldehyde (1% v/v final concentration), acid Lugol's solution (1% v/v final concentration) or with sodium borate-buffered formalin (4% v/v final concentration). All samples were refrigerated and stored in darkness prior to processing. Microscope slides for enumeration of pico- and nanoplankton were prepared within 1-2 days of sampling (Carrick and Schelske 1997). For microplankton analysis, samples were concentrated by use of sedimentation chambers, transferred to a Palmer-Maloney cell and enumerated by microscopy.

For identification of diatoms, samples obtained from net tows were cleaned in nitric acid to remove organic materials and air dried onto coverslips for light microscope and scanning electron microscope (SEM) analysis. Strewn diatom slides were made using Naphrax mounting medium and the diatoms analyzed using an Olympus BX51 Photomicroscope with high resolution Nomarski DIC optics. Taxa were identified using taxonomic keys (Krammer and Lange-Bertalot, 1991). Samples, mounted on aluminum stubs and sputter coated with 10 nm of AuPd, were examined under a high resolution Hitachi S2700 SEM.

Mesozooplankton biomass and taxonomic composition - Mesozooplankton abundance and biomass was estimated from water column collections made using a Wisconsin type plankton net (mesh size 153-μm). Vertical net hauls were made between 10-15 m depth, the contents dispensed into sample jars, and subsequently preserved with formaldehyde (20% v/v final concentration).

RESULTS AND DISCUSSION

Prelude: Whereas funds from the LEPF provided support for field seasons in 2008-09, data from the 2009 efforts has not yet been analyzed. As a result, our comments are restricted mainly to data collected in 2007 (initial unfunded survey) and 2008 (LEPF-sponsored survey). Restricting discussion to data collected in 2007-08 also precludes speculation regarding the possible link between winter production and summer hypoxia. While we began to address this link in 2008, the majority of our efforts to do so (sediment trap deployment and measures of bacterial

productivity) commenced in earnest only in 2009. We await analysis of samples collected in 2009, however, our preliminary data supports benthic export as the primary fate of winter diatoms in Lake Erie. Reduced zooplankton grazing on these large cells coupled with low measured rates of bacterial decomposition during winter means that most of the biomass is likely exported to the bottom as resources required for their growth become depleted. As summer progresses and bottom temperatures warm, bacteria accelerate the decomposition of the accumulated diatom biomass, a process that eventually depletes the now stratified bottom waters of oxygen.

Moderate Resolution Imaging Spectroradiometer (MODIS) images indicate Lake Erie was 80-90% ice-covered during the cruises in 2007 and 2008 (Fig. 2), an observation supported by Daily Ice Analysis Charts from the Canadian Ice Service (http://www.ice-glaces.ec.gc.ca/), which are derived from microwave-based RADARSAT data with additional input from MODIS. These charts document that during the cruise period in February 2007, the western basin and the far reaches of the eastern basin were covered with fast ice whereas total ice concentration in the central and southern reaches of the central basin as well as much of the eastern basin reached 9+ (International Egg Code; Canadian Ice Service, 2005), indicating > nine-tenths ice coverage for this area with 90% of this ice characterized as medium lake ice of 15-30 cm thickness present in big floes of 500-2000 m width. Ice coverage was more variable along the north shore of the lake, in Long Point Bay and at the junction between western and central basins with total ice concentration of 2 (i.e. two-tenths coverage) and the ice being comprised of either new ice (< 5 cm thickness) or thin lake ice (5-15 cm thickness).

Ice coverage during the February 2008 cruise presented a similar picture although Fast Ice was limited in scope with most of the western basin ice characterized rather as 9+ total concentration and with ice thickness varying between medium (15-30 cm) and thin (5-15 cm) present as medium floes of 100-500 m width. The southern half of the central basin and the eastern reaches of the eastern basin were characterized similarly whereas much of the northern portion of the central basin, while predominantly ice-covered (9+), was characterized by new ice (< 5 cm) or thin ice present in small floes (20-100 m width). Similar to 2007, ice coverage was sporadic along the north shore of Lake Erie and along the junction between western and central basins with total ice concentration ranging between 4 (14 Feb) and 3 (18 Feb) and varying between thin lake ice and new ice.

Progression of ice cover appeared to be similar in 2007 and 2008 with warmer than normal temperatures (-1 to +6 °C) recorded during the first half of January 2008 limiting ice to mainly shoreline regions. In 2007, normal average temperatures during the remainder of January (~ -4 °C) followed by below normal temperatures during the first 3 weeks of February (-9 to -11 °C) resulted in rapid ice cover progression such that by 12 February, total ice coverage across the entire lake was 9+ with Fast Ice developing in the western and extreme eastern basins by the following week (Weekly Ice Analysis Charts, Canadian Ice Service). During 2008, slightly warmer than normal temperatures (0 to -1.5 °C) were consistent with large open patches of water in the eastern half of the central basin and the absence of Fast Ice in the western basin. In both

2007 and 2008, ice persisted in the eastern extremes of the lake near to the entrance of the Welland Canal until the third week of April.

Dissolved nutrient levels were high through the entire lake, yet a concentration gradient existed in terms of nitrate (nitrate + nitrite) and silica (dissolved reactive SiO_2) with levels in the western basin (Sta. 357) exceeding those measured in the central (Sta. 84) and eastern basins (Sta. 23) by 2-3 times (Table 2). Interannual differences were also apparent, especially in the western basin (Sta. 357) and at Sta. 340 located at the junction between west and central basins with elevated levels of all nutrients measured in February 2008 compared to 2007 (Table 2). The largest interannual difference was associated with SRP with a 2007 lakewide mean of 138 nmol L^{-1} compared to a 2008 mean of 403 nmol L^{-1}. Such variability in annual basin-wide averages has been demonstrated previously for Lake Erie and is possibly related to wind resuspension (Barbiero et al. 2006).

Nutrient levels measured as part of our study were comparable to average post-*Dreissena* spring levels reported previously by Makarewicz et al. (2000). Considering all nutrients, differences in levels of silicic acid are perhaps most notable between pre- and post-*Dreissena* eras with present-day levels > 2 × higher than historical winter/spring maxima (Barbiero et al. 2006). Since the *Dreissena* invasion, average April silicic acid levels in the eastern basin of Lake Erie are 0.76 mg L^{-1} compared to maxima < 0.32 mg L-1 measured during limited winter sampling lead by EPA-GLNPO in 1984-85. This increase in Si, in turn, is thought to be an important factor in shaping diatom communities in modern day Lake Erie.

Seston stoichiometric ratios indicated a P-sufficient assemblage during both years of the study. N:P ratios were generally <16 whereas C:P ratios were at or below Redfield stoichiometry in 2008 and only modestly higher than Redfield in 2007 (Table 3). Community alkaline phosphatase activity was negligible in both years (data not shown) further supporting the existence of a P sufficient assemblage. Whereas seston C:N ratios were uniformly higher than the Redfield ratio of 6.6 (Table 3), they are within range of values reported for N-sufficient phytoplankton in lakes (Sterner et al. 2008). Median dissolved nitrate was ~15 µmol L^{-1} during each year of the study, which further argues against the likelihood of N deficiency.

Biomass, as gauged by total POC, was ~ 2-fold lower at the eastern basin site (Sta. 23) in 2007 compared to western and central basin sites (one-way ANOVA; $P< 0.0001$), a trend that was paralleled by changes in chl *a* (Table 3). In 2008, the two proxies offered differing results with total chl again suggestive of lower biomass at Sta. 23 whereas changes in POC did not support the existence of a lakewide gradient in biomass (one-way ANOVA followed by Tukey HSD Test). Limited depth-resolved sampling was conducted in 2008 with a sample collected near the bottom of the water column at each station. At most sites, depth-resolved variability associated with either biomass proxy was < 20% between 1 m and the sample collected at depth (data not shown).

Size-fractionated analysis of chl *a* conducted in 2008 demonstrated that phytoplankton in the central basin of the lake were dominated by the microplankton (> 20 µm) size class (data not shown). At the three central basin stations analyzed (Sta. 84, 949, 1026), microplankton

accounted for ~60% of the total assemblage whereas the picoplankton (0.2-2 μm) fraction did not exceed 20% (mean: 13%). Picoplankton was also present in low abundance in the eastern basin (11%); however, they were co-dominant (40%) along with nanoplankton (2-20 μm) at western basin Sta. 357. Assessment of size-fractionated chl in this instance was supported by direct enumeration of picophytoplankton abundance by epifluorescence microscopy which demonstrated picoplankton abundance at Sta. 357 of 3.9×10^5 cells mL^{-1}, ~ two orders of magnitude higher than the mean abundance of 5.8×10^3 cells mL^{-1} enumerated at central and eastern basin stations. The picophytoplankton were composed mainly of cyanobacteria that appeared to be similar in morphology to types observed in other periods during the year, namely single-celled cocci (e.g., *Synechococcus*), or small colonies of coccoid cells. A coccoid picoeukaryote component of this fraction was also identified, although typically occurring at low densities of ~10^2 cells mL^{-1}.

In both years of the study, microplankton were routinely observed in aggregates located under the ice which we identified as CACHE (Concentrated Algal Communities and Heterotrophic Ecosystems) formations. Algal densities within CACHEs were high and conferred a brown coloration to these formations. CACHEs were present throughout the western and central basins of the lake ranging from ~10 - 2000 m^2 in size and interspersed approximately every 200 - 300 m in the central basin as observed while breaking through ice at 12 knots.

In CACHEs and elsewhere, the microplankton was dominated by the filamentous diatom *Aulacoseira islandica* (O. Müller) Simonsen (Fig. 3) which accounted for > 60% of the microplankton assemblage at all locations (Fig. 4). At Sta. 84 and at a CACHE site located nearby in Feb. 2007, *A. islandica* accounted for > 80% of the microplankton component. At the CACHE site, abundance of *A. islandica* was ~2.7×10^7 cells L^{-1}, nearly an order of magnitude higher than measured in surface waters at other sites (Fig. 4). *A. islandica* was also present in an ice melt sample from Sta. 340 at a density similar to that of the sample collected at 1 m depth. Other notable genera included members of *Stephanodiscus* spp., particulary *S. binderanus*, which accounted for ~20% of the microplankton at western and central basin station. *Fragilaria* spp., *Asterionella* spp. and *Cyclotella* spp. were also routinely observed.

Whereas *A. islandica* has long been identified a component of the spring diatom assemblage in Lake Erie, particularly in the western basin (Munawar and Munawar 1976; Barbiero et al. 2006), it has emerged as a spring dominant species only since the early 1990's, a shift coinciding with the introduction of dreissenid mussels to the lake (Barbiero et al. 2006). The changes to Lake Erie following the introduction of *Dreissena* spp. are widespread and well-documented and include shifts in nutrient cycling as well as changes in biomass and composition of the phytoplankton community (Holland et al. 1995; Makarewicz et al. 2000; Barbiero et al. 2006). Particularly relevant to the emergence of *A. islandica* as a dominant species during vernal mixis has been the dramatic increase in silica levels measured during spring with averages 2-4 × higher than pre-*Dreissena* concentrations (Makarewicz et al. 2000; Barbiero et al. 2006). Pennate diatoms such as *Asterionella formosa*, *Fragillaria crotonensis* and *Tabellaria flocculosa* that dominated the pre-*Dreissena* spring assemblage possess relatively low calculated Si optima of < 0.2 mg SiO_2 L^{-1} (Barbiero et al. 2006). By contrast, *A. islandica* along with *Stephanodiscus parvus* and *S. hantszchii*, centrics reported to co-dominate the spring assemblage in the eastern

403 basin of Lake Erie, are characterized as high silica species with calculated Si optima exceeding
404 0.6 mg SiO_2 L^{-1} (Barbiero et al. 2006).
405
406 Whereas our observations document robust communities dominated by *A. islandica* in
407 winter and persisting into the period of vernal mixis, we have yet to characterize the temperature
408 optimum for growth of this species. Based on analogies with *Aulacoseira* congeners isolated
409 from Lake Baikal (Richardson et al. 2000; Jewson et al. 2008), we expect the Lake Erie *A.*
410 *islandica* to be a true psychrophile whose growth is no longer supported once surface
411 temperatures increase beyond 8-10 °C. This would be consistent with the previous observations
412 documenting domination by *Stephanodiscus* hantzschii, during 1998 and 2000, years that
413 experienced unusually high spring temperatures. *S. hantzschii* shares ecological characteristics
414 with *A. islandica* but possesses a higher growth temperature optimum (Stoermer 1993).
415
416 Total (> 0.2 µm) primary production ranged from 0.7 to 1.7 g C g Chl-*a*$^{-1}$ h^{-1}, values that are
417 similar to those measured at comparable light intensities using the ^{14}C technique
418 (photosynthetron) and a light:dark DO technique. These primary production values are
419 approximately 20-60% of values measured using the same technique during summer 2003 and
420 incubated at 150-300 µmol photons·m-2·s-1 (Ostrom et al. 2005).
421
422 Levels of primary production in Lake Erie measured using a modified Winkler approach
423 ranged from 0.4 to 11.6 µg C L^{-1} h^{-1} (Table 4). These values correspond well with those
424 measured on summer assemblages incubated at moderate irradiance (< 80 µmol quanta m^{-2} s^{-1}).
425 Respiration rates were relatively uniform between stations with the exception of extremely high
426 rates measured at Sta. 357 (Table 4). At each station tested, higher respiration rates were
427 achieved in bottles incubated at higher than ambient temperature (10 °C versus 2 °C).
428
429 Total light-saturated winter primary production estimated using [^{14}C]-uptake ranged from 1–
430 7 g C g Chl*a*$^{-1}$ h^{-1} (Figs. 5a,b) whereas net photosynthetic oxygen evolution of net plankton
431 ranged from 0.05–2.5 mol O_2 g Chl*a*$^{-1}$ h^{-1} (Fig. 6a,b). Photosynthesis vs. irradiance (PE) curves
432 obtained using both approaches yielded median E_k values of 29 ([^{14}C]-uptake) and 44 (O_2
433 evolution) µmol photons m^{-2} s^{-1} respectively, suggestive of a low light-adapted community, and
434 consistent with attributes previously associated with *A. islandica*, the dominant member of the
435 winter diatom assemblage (Stoermer 1993).
436
437 Measures of F_v/F_m indicated that the maximum quantum efficiency of PSII was high
438 (median: 0.55) in surface water samples collected from western and central basin stations in
439 February 2008 (Table 5). Likewise, samples collected directly from CACHE formations in the
440 vicinity of Sta. 84, from a vertical net tow at this same station and from ice-melt samples from
441 central basin Sta. 949 demonstrated high F_v/F_m (Table 5). Only the sample from eastern basin
442 Sta. 23 and an ice-melt sample from near Sta. 84 in the central basin had relatively low F_v/F_m (≤
443 0.4) indicating sub-optimal physiological condition and suggesting that these samples were
444 stressed or contained senescent algal cells.
445

Taken together, our findings support the existence of a physiologically robust assemblage of nutrient sufficient, psychrophilic diatoms in Lake Erie, the contributions to carbon cycling of which must be considered when deriving whole lake carbon budgets.

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585
586
587

Table 1. Environment Canada Station hydrographic and meteorological parameters.

Station	Latitude	Longitude	Z_m (m)	Air Temp. (°C)		Wind Speed (kt)		Water Temp. (°C)	
				2007	2008	2007	2008	2007	2008
357	41 49.30	82 58.30	11.9	-3.8	-7.0	6	23	1	1
340	41 45.25	82 24.08	11.2	-0.5	-6.3	8	15	1	1
1026	41 58.26	82 16.18	21	-	-7.0	-	4	-	1
84	41 56.07	81 39.11	22.3	-10.4	-5.5	20	8	1	1
949	42 14.59	81 06.23	20.1	-	-5.7	-	7	-	1
452	42 30.24	79 54.00	64	0.3	-1.0	20	16	1	1

Table 2. Dissolved nutrients at 1 m depth (2007/2008).

Station	SRP µg P L^{-1}	TP µg P L^{-1}	[a] NO_3^- mg N L^{-1}	NH_3 µg N L^{-1}	TN mg N L^{-1}	Silica[b] mg L^{-1}
357	1.6/17	9.9/18.9	0.68/1.3	BD[c]/64	0.87/1.71	2.29/2.85
340	1.6/18.7	9.9/21.2	0.18/0.63	BD/27	0.40/0.86	0.46/2.04
1026	nd/5.4	nd/8.3	nd/0.11	nd/BD	nd/0.28	nd/0.25
84[d]	7.9/15.3	16/16.7	0.25/0.22	BD/BD	0.56/0.41	0.89/1.7
949	nd[e]/10.8	nd/12.2	nd/0.19	nd/BD	nd/0.37	nd/0.99
452	6.5/10.3	15.4/12.2	0.29/0.24	BD/5	0.50/0.42	0.98/0.89

[a] reported as $NO_3^- + NO_2^-$

[b] reactive SiO_2

[c] below detection

[d] 2008 values represent the mean of 3 independent samples taken over 2 consecutive days

[e] not determined

Table 3. Chemical and biological properties of seston at 1 m depth (2007/2008).

Station	POC µmol L^{-1}	PON µmol L^{-1}	PP µmol L^{-1}	C:P mol:mol	C:N mol:mol	N:P mol:mol	Chl a µg L^{-1}
357	18.9/31.1	1.5/3	0.17/nd[a]	115/nd	13/10.4	8.8/nd	1.2/0.6
340	33.7/30.3	3.3/3.7	0.27/0.29	125/100	10.2/7.1	12.3/14.1	8.4/2.4
1026	nd/24.1	nd/3.2	nd/0.16	nd/109	nd/9	nd/12.2	nd/3.3
84	18.7/32.7	1.4/3.9	0.19/0.27	97.6/85.5	13.5/7.6	7.2/11.2	2.4/1.7
CACHE	nd	nd	nd	nd	nd	nd	20.5/5.8[b]
949	nd/43.1	nd/3.3	nd/0.35	nd/86.3	nd/7.9	nd/10.9	nd/1.5
452	9.9/27.3	1.2/1.8	0.07/0.20	151/85.2	8/10.5	18.9/8.2	0.6/0.6

[a] not determined

[b] mean of two separate CACHE sites. The two sites differed by < 5%

Table 4. Primary production and respiration at 1 m depth using a modified Winkler method.

Station	Net Production µg C L^{-1} h^{-1}	Respiration µg C L^{-1} h^{-1}	Respiration: 10°C µg C L^{-1} h^{-1}	Gross Production µg C L^{-1} h^{-1}
357	3.66	-74.76	n.d.	78.42
340	3.48	-1.90	n.d.	5.38
1026	1.20	-1.71	-5.74	2.90
84	11.60	-1.01	-14.86	12.61
452	0.41	-5.89	-6.65	6.30

Table 5. Variable fluorescence of seston at 1 m depth.

Station	F_v/F_m	P_m	A	E_k µmol quanta m^{-2} s^{-1}
340	0.56	68.1	.220	310
1026	0.51	39.3	.274	143
84[a]	0.56	55.8	.242	231
ice	0.33	29.4	.106	277
Cache	0.59	66.2	.228	290
Cache	0.62	68.9	.246	280
net	0.56	n.d.	n.d.	n.d.
949	0.55	59.4	.227	261
ice	0.57	40.6	.215	189
ice	0.51	19.6	.181	108
23	0.40	30.5	.152	201

[a] mean of independent samples taken over 2 consecutive days

FIGURE LEGENDS

Fig. 1. Map of Lake Erie sampling stations occupied during Feb 2008 CCGS *Griffon* survey.

Fig. 2. MODIS images of a) Feb 23, 2007 and b) Feb 16, 2008 (credit: NOAA CoastWatch – Great Lakes Region).

Fig. 3. Scanning electron micrographs of *Aulacoseira islandica* collected from plankton tows in Feb 2008. Scale bars shown in each panel (credit: Dr. P. Furey, BGSU).

Fig. 4. Pie charts showing percent composition of microplankton collected during 2007 survey. Values reported as cells $\times 10^5$ L^{-1}.

Fig. 5. PE curves showing chlorophyll normalized $^{14}C\text{-}HCO_3^-$ uptake in response to light fluence rate. a) sample of net plankton collected at central basin Station 949 in Feb 2008. b) water sample collected from a central basin CACHE site in Feb 2007.

Fig. 6. PE curves showing chlorophyll normalized rates of photosynthetic oxygen evolution of net plankton in response to light fluence rate. a) sample collected from central basin Station 949 in Feb 2008, corresponding with sample shown in Fig. 5a. b) sample collected from Station 340 located near the junction between west and central basins in Feb 2008.

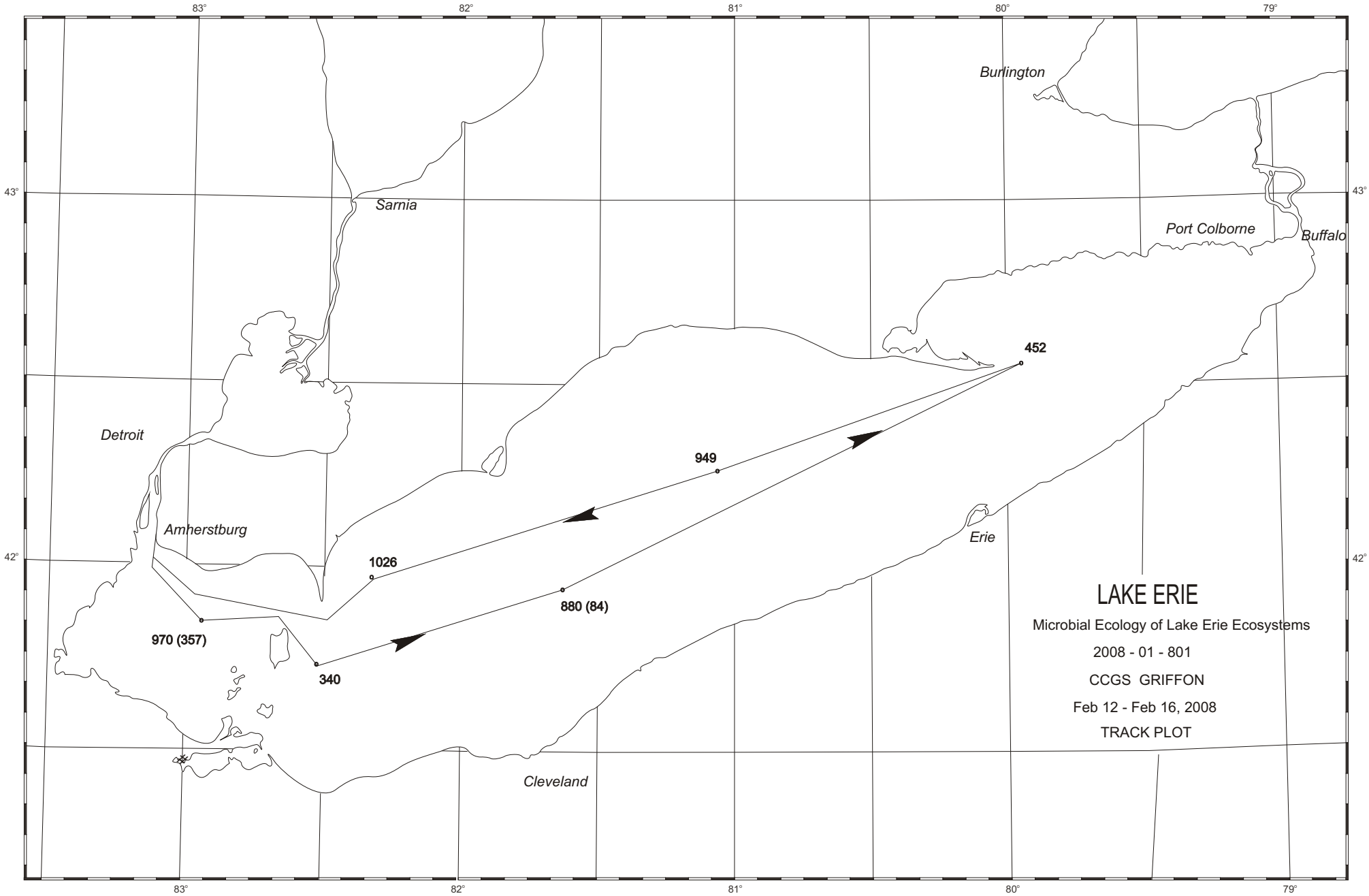
83°
82°
81°
80°
79°
43°
42°
Burlington
Sarnia
Port Colborne
Buffalo
Detroit
Amherstburg
Erie
Cleveland
452
949
1026
880 (84)
970 (357)
340
LAKE ERIE
Microbial Ecology of Lake Erie Ecosystems
2008 - 01 - 801
CCGS GRIFFON
Feb 12 - Feb 16, 2008
TRACK PLOT

Fig. 1

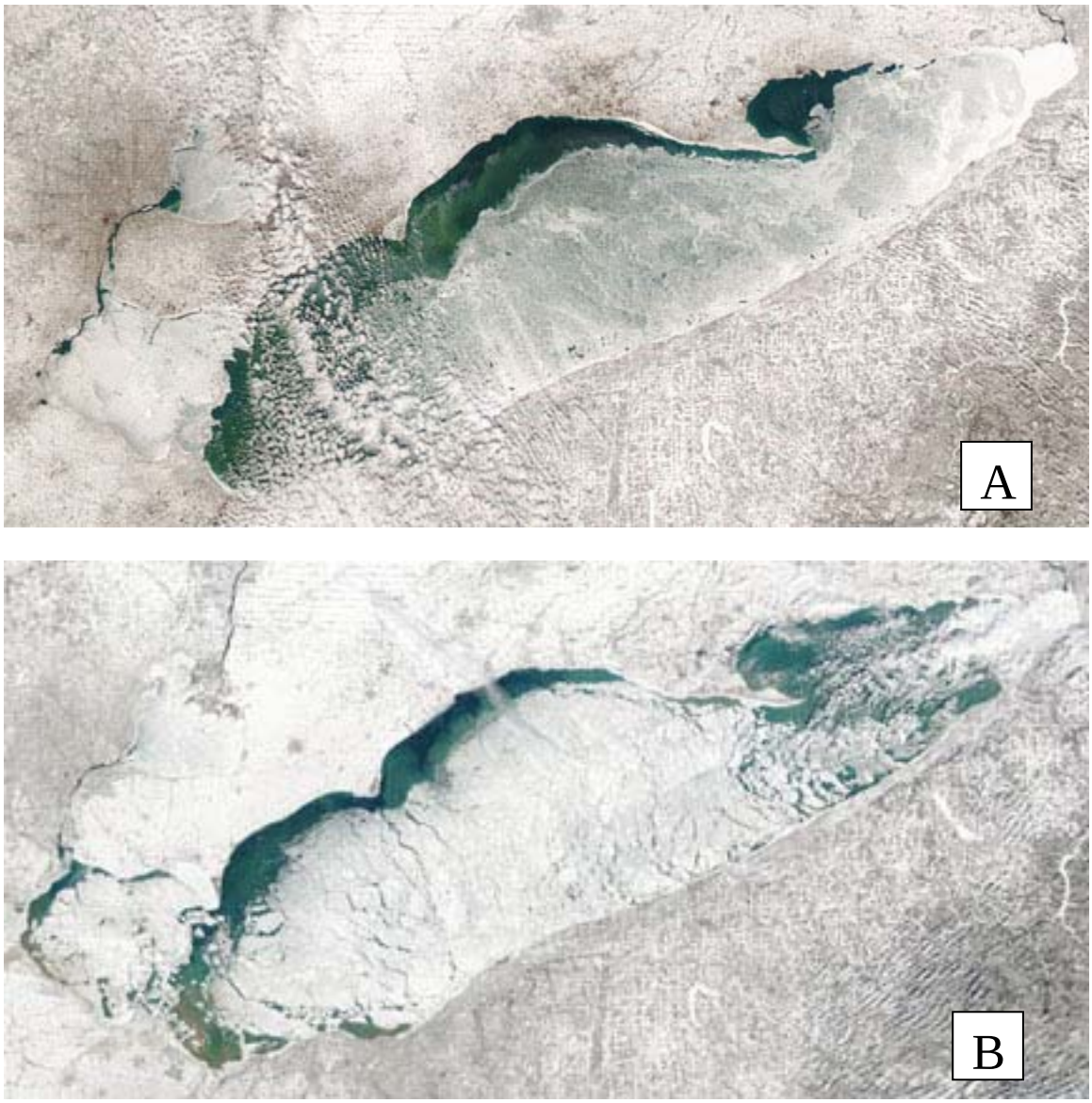

Fig. 2

Aulacoseira islandica (O. Müller) Simonsen

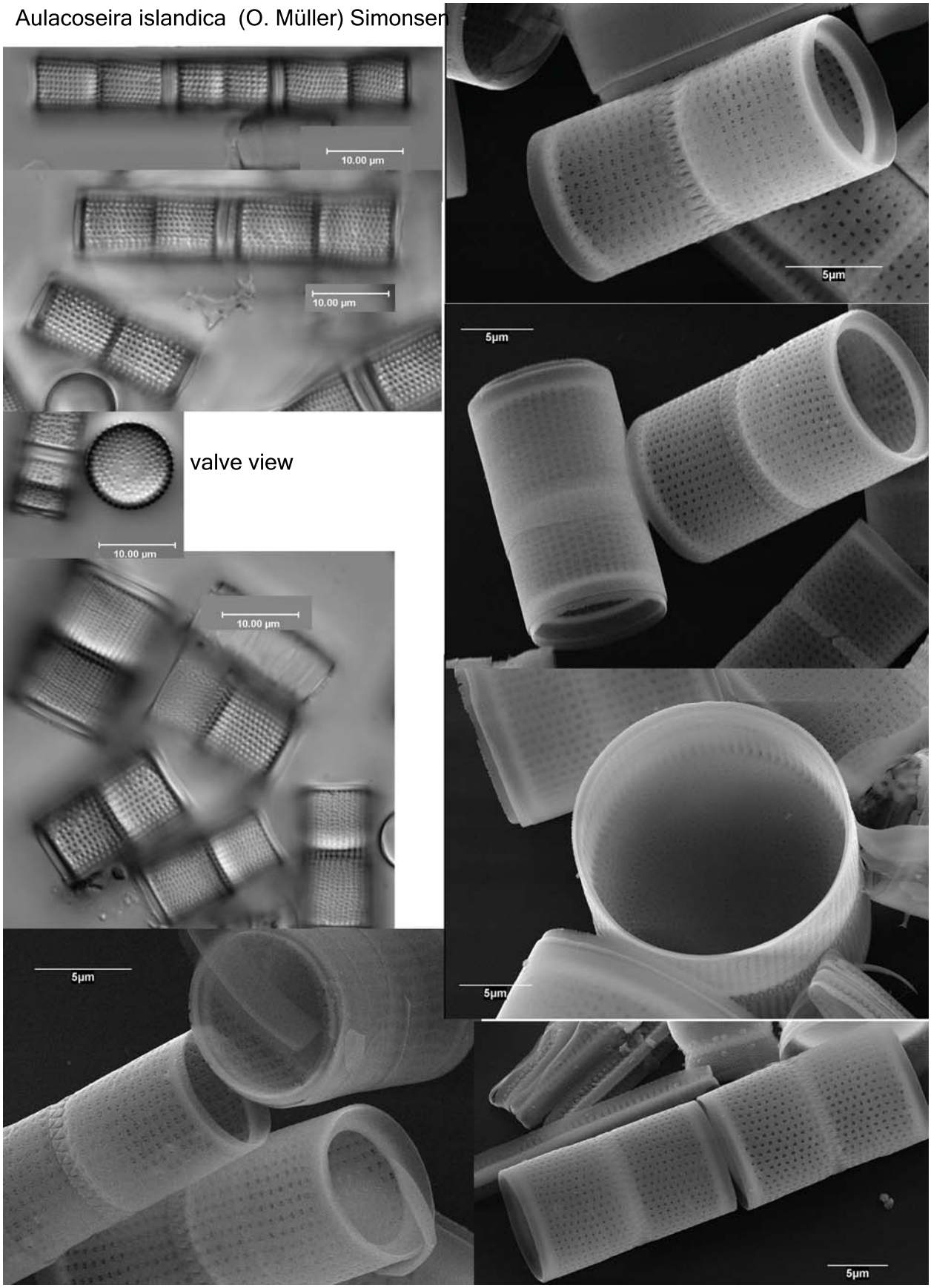

Fig. 3

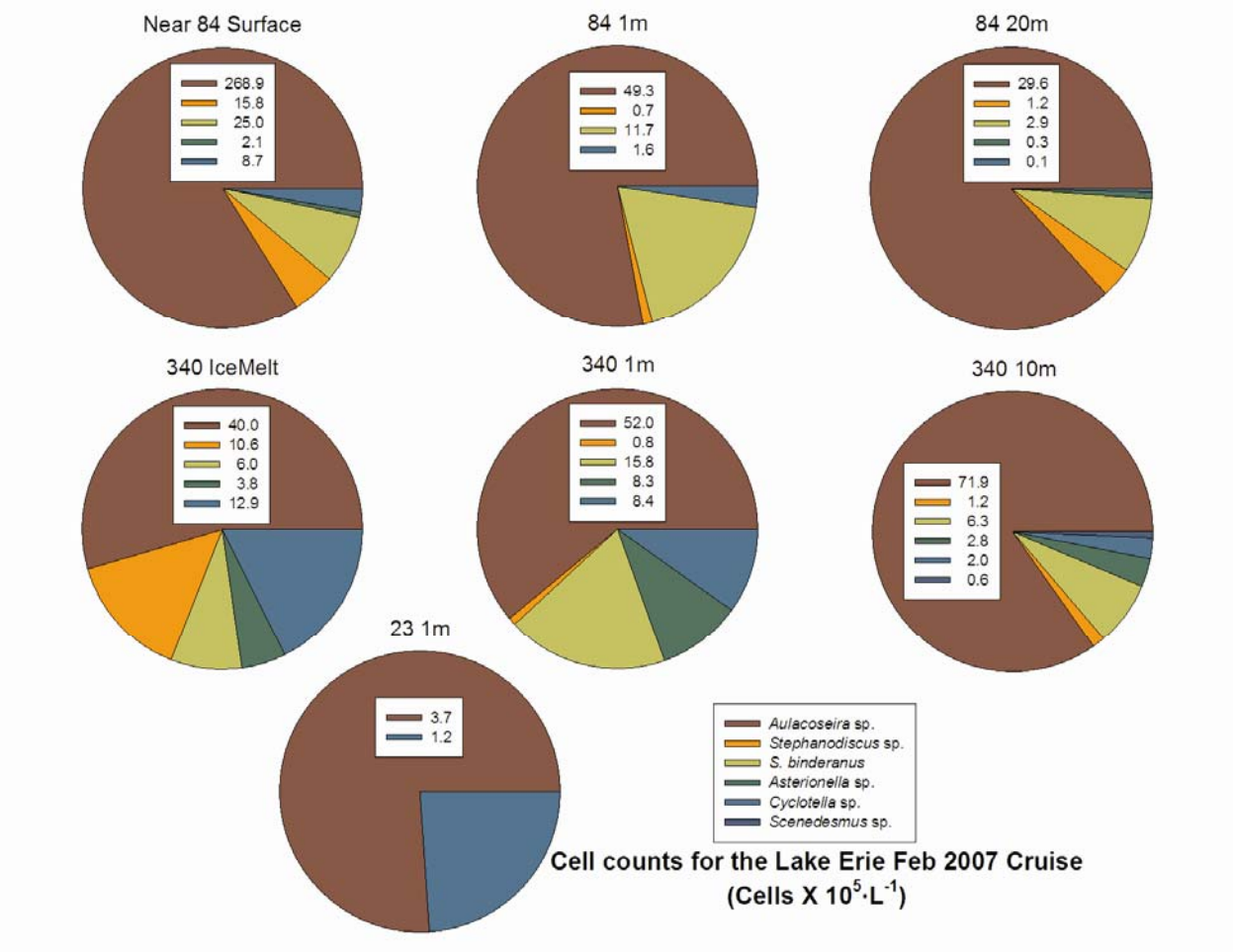
Near 84 Surface
268.9
15.8
25.0
2.1
8.7
84 1m
49.3
0.7
11.7
1.6
84 20m
29.6
1.2
2.9
0.3
0.1
340 IceMelt
40.0
10.6
6.0
3.8
12.9
340 1m
52.0
0.8
15.8
8.3
8.4
340 10m
71.9
1.2
6.3
2.8
2.0
0.6
23 1m
3.7
1.2
Aulacoseira sp.
Stephanodiscus sp.
S. binderanus
Asterionella sp.
Cyclotella sp.
Scenedesmus sp.
Cell counts for the Lake Erie Feb 2007 Cruise
(Cells X 10^5·L^{-1})

Fig. 4

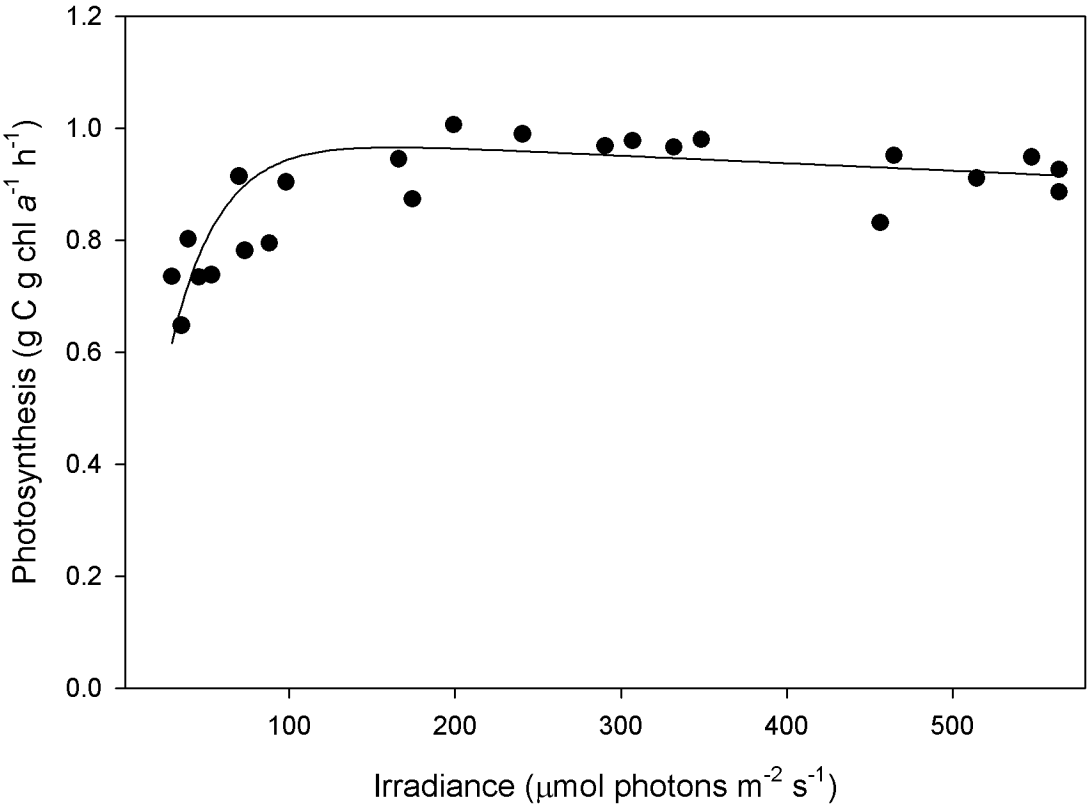
Sta. 949 (net plankton)
2/15/2008
Photosynthesis (g C g chl a^{-1} h^{-1})
1.2
1.0
0.8
0.6
0.4
0.2
0.0
100
200
300
400
500
Irradiance (μmol photons m^{-2} s^{-1})

Fig. 5a

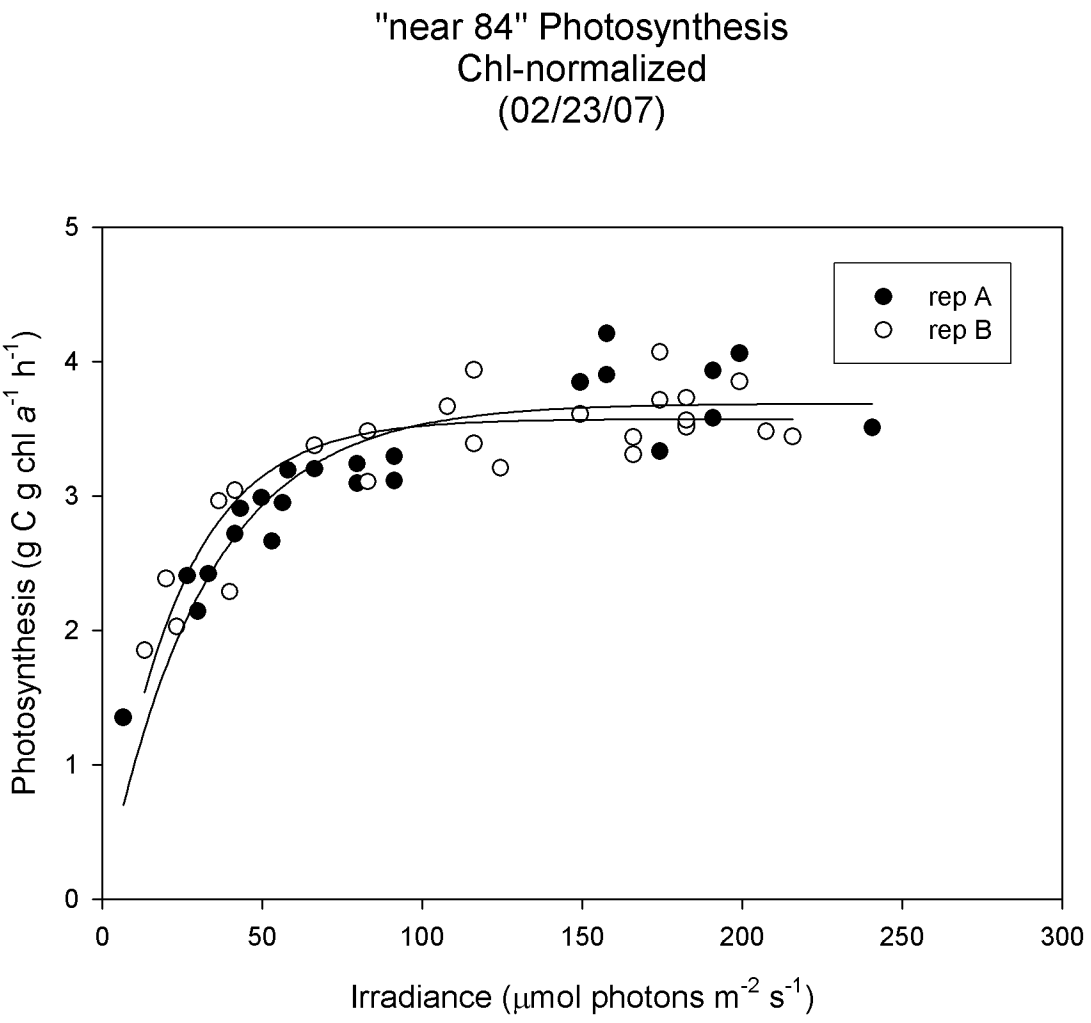
"near 84" Photosynthesis
Chl-normalized
(02/23/07)
rep A
rep B
Photosynthesis (g C g chl a-1 h-1)
Irradiance (µmol photons m-2 s-1)
0
1
2
3
4
5
0
50
100
150
200
250
300

Fig. 5b

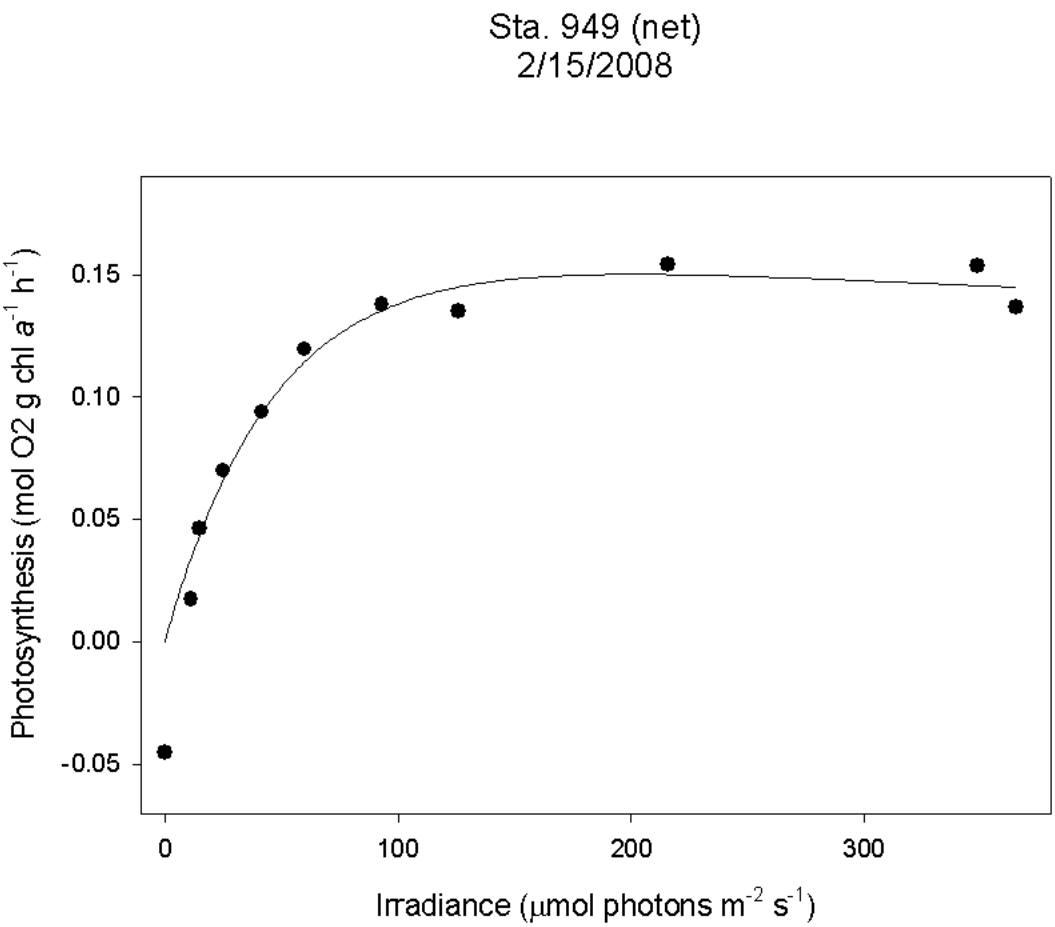
Sta. 949 (net)
2/15/2008
Photosynthesis (mol O2 g chl a-1 h-1)
0.15
0.10
0.05
0.00
-0.05
0
100
200
300
Irradiance (μmol photons m-2 s-1)

Fig. 6a

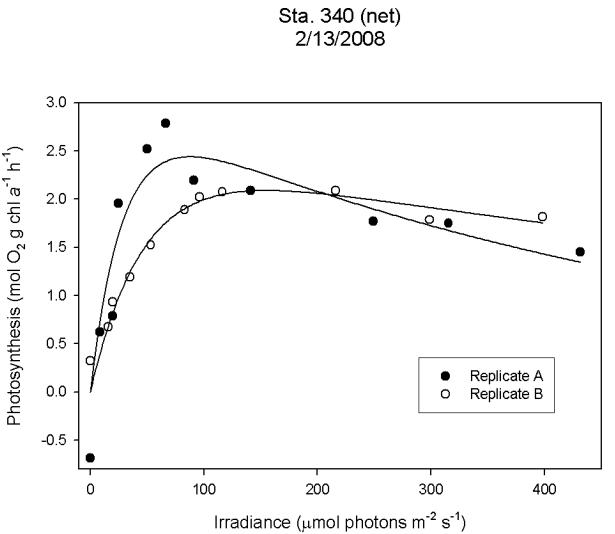
Sta. 340 (net)
2/13/2008
Photosynthesis (mol O_2 g chl a^{-1} h^{-1})
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
0
100
200
300
400
Irradiance (μmol photons m^{-2} s^{-1})
Replicate A
Replicate B

Fig. 6b