

Effects of light, temperature and habitat quality on meroplanktonic diatom rejuvenation in Lake Erie: implications for seasonal hypoxia

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Rapid sedimentation of phytoplankton cells following seasonal blooms is common in lakes and coastal zones throughout the world, yet the fate of these cells is uncertain. Ascertaining the fate of seasonal blooms may be particularly important in ecosystems that experience hypoxia. Benthic stations were sampled seasonally inside and outside of the hypoxic area in Lake Erie to test for differences in chlorophyll *a* concentrations, algal physiological condition (cell viability) and diatom rejuvenation rates (from enclosure experiments). Hypoxic areas did sustain higher chlorophyll *a* concentrations compared with oxic sites; however, diatom growth and physiological capability did not differ significantly. Hypoxic areas exhibited exponential growth rates as high as 0.56 day^{-1} (compared with the oxic station at 0.53 day^{-1} , $P = 0.000$) and chlorophyll rejuvenation rates as high as 0.30 day^{-1} (compared with the oxic station at 0.36 day^{-1} , $P = 0.964$). Therefore, sedimentation of phytoplankton cells may not only contribute to the seasonal hypoxia observed in Lake Erie, but those diatoms able to withstand low oxygen concentrations during the summer, once reintroduced into the water column, may also seed subsequent diatom blooms. Initial estimates indicate that the algal pigment present on the bottom of the central basin, likely sedimented from the overlying water, contributed significantly to hypolimnetic oxygen depletion (11–33%).

KEYWORDS: meroplankton; diatoms; resting cells; Lake Erie; hypoxia

INTRODUCTION

Hypoxic events ($<2 \text{ mg L}^{-1}$ dissolved oxygen) are increasing in intensity and frequency worldwide (Diaz and Rosenberg, 2008). These events can cause changes in species distribution patterns, community biodiversity, and mortality of marine and freshwater organisms (Service, 2004). The deposition and eventual decomposition of diatoms appears to contribute to hypoxia in bodies of water throughout the world, including the

Chesapeake Bay, Gulf of Mexico and Africa's Lake Victoria (Kemp *et al.*, 1992; Rabalais *et al.*, 2002, respectively). That said, some diatoms are capable of forming resting cells, and therefore can resist decomposition such that their contribution to hypoxia is currently unknown.

The capacity of diatoms to form resting cells has been known for more than a half a century, although their role in the aquatic ecology is not fully

understood (Sicko-Goad *et al.*, 1989). Lund (Lund, 1954) showed that cells of the diatom *Aulacoseira italica* (formerly *Melosira italica*) retrieved from surficial aphotic, lake deposits, rejuvenated into viable cells once exposed to moderate illumination; following 7 days of illumination, cells were capable of division and appeared to be fully functional. Unlike spores that are readily identifiable by external modifications to the cell wall, resting cells are formed by internal changes in the cytology of the cell (Sicko-Goad *et al.*, 1989). Resting cells have been offered as an explanation for the emergence and rapid growth of both freshwater and marine diatom species (Hollibaugh *et al.*, 1981; Sicko-Goad *et al.*, 1989). Moreover, the deposition of diatoms into the benthos can be important energy sources for deep-water invertebrates (e.g. Fitzgerald and Gardner, 1993) and resuspended back into the water column these diatoms eventually inoculate surface waters (Eadie *et al.*, 1984). Whipple (Whipple, 1895) suggested that water column mixing was responsible for resuspending diatoms that were dormant amid profundal sediments on the lake bottom. Turbulent mixing and abundance of light, especially in those lakes that are dimictic, have been thought to be circumstances optimal for diatom growth (Reynolds, 1973).

Meroplanktonic diatoms can be commonly observed in the benthos of many lakes and coastal zones. Previously, Carrick (Carrick, 2004) and Carrick *et al.* (Carrick *et al.*, 2005) confirmed viable meroplanktonic cells were present in off-shore, benthic samples analyzed from the eastern and western basins of Lake Erie, respectively; these pelagic diatoms constituted >90% of benthic algal carbon. They concluded the benthic algal layer had likely settled from the water column. Herein, we analyzed surficial sediment samples taken from the central basin of Lake Erie. We hypothesize that sedimentation of pelagic diatoms may not only contribute to the seasonal hypoxia observed in Lake Erie, but these diatoms may also seed subsequent seasonal diatom blooms (see Lashaway, 2009). Thus, the specific objectives of this study are: (i) to evaluate chlorophyll concentrations on the bottom of the central basin in order to determine if they are higher at hypoxic sites (thus providing more organic matter to fuel decomposition), (ii) to evaluate spatio-temporal variation in diatom physiological condition (via *in vivo* fluorescence response) following exposure to relevant illumination and temperature regimes and (iii) to compare variation in species-specific diatom rejuvenation rates and relate these changes to seasonal dynamics in the water column.

METHOD

Lake erie ecosystem and field sampling

The Laurentian Great Lakes are among some of the world’s largest lakes and comprise 20% of the earth’s freshwater (Herdendorf, 1984). Among the five Great Lakes, Lake Erie supports the most productive fishery. Lake Erie is divided into three basins: the western, central and eastern basins. Lake Erie receives high nutrient loads from riverine inputs, particularly in the western basin; these inputs appear to have promoted seasonal hypoxia in the lake (Rosa and Burns, 1987; Dolan and McGunagle, 2005).

We evaluated variation in algal biomass and diatom physiological condition in time and space by sampling three stations situated throughout Lake Erie’s central basin; these sites reflect the broad range of limnological conditions in the basin (e.g. Carrick *et al.*, 2005). Lake cruises were conducted during four thermal periods, namely fall (2007), winter, spring and summer (all in 2008). These periods have been observed in other studies to characterize the bulk of seasonal variation in the Great Lakes (Fahnenstiel and Scavia, 1987). Lake cruises were carried out aboard the *R/V Laurentian* (2007), the *R/V Lake Guardian* (2008) and the Canadian Coast Guard Ice-Breaker *Griffon* (2008). Variation in algal biomass, algal viability and algal rejuvenation capabilities were examined to compare results among the three stations and four thermal periods (Table I).

At each station, water column profiles for temperature, dissolved oxygen, conductivity, photosynthetically active radiation (PAR) and fluorescence were made using a Seabird CTDTM. Benthic samples were collected at each station using a 0.5 m² box core sampler

Table I: Conditions used in incubation experiments conducted on surficial Lake Erie central basin sediments

Thermal period (2007–2008)	Station	Experimental temperature	Bottle type
Winter-strat	Offshore-hypoxic	4°C, 10°C	Light, dark
	Spring-mixing	Nearshore-hypoxic	4°C, 10°C
Summer-strat	Offshore-hypoxic	4°C, 10°C	Light, dark
	Offshore-oxic	4°C, 10°C	Light, dark
	Offshore-hypoxic	4°C, 10°C	Light, dark
	Offshore-oxic	4°C, 10°C	Light, dark
Fall-mixing	Nearshore-hypoxic	10°C	Light
	Offshore-hypoxic	10°C	Light
	Offshore-oxic	10°C	Light, dark

Experiments were done at four thermal periods, and two experimental temperatures in 2007–2008. Light exposure was 50 μE m⁻² s⁻¹ on a 12 h light:dark cycle.

(Carrick *et al.*, 2005). Duplicate box cores were collected from each site and triplicate subcores were processed, except in the months of July, August and September (2007) when duplicate subcores were collected. Intact sediments were collected from each box core by inserting coring tubes (surface area = 45.6 cm²). The top centimeter of sediments captured in the coring tube was then retained for further analysis; this material represents an annual integration of material on the surficial sediment (Parker and Edgington, 1976; Schelske and Hodell, 1998).

Biochemical analyses

Algal pigments

Duplicate lake water or sediment subsamples (except in July when a single subsample was taken from the sediments) were concentrated onto Whatmann EPM-2000 membrane filters and chlorophyll *a* was extracted in a 50:50 mixture of 90% acetone and dimethyl sulfoxide. Chlorophyll *a* and phaeopigment concentrations were measured fluorometrically using a Turner 10-AU-005 (Carrick *et al.*, 1993).

In vivo fluorescence

In vivo fluorescence was measured as a proxy for algal physiological condition using a Turner 10-AU-005 fluorometer (Vincent, 1980). Briefly, samples were mixed and placed in the dark for 20 min, following which the fluorescence was measured. A second reading was made following the addition of the inhibitor of non-cyclic electron flow, 3 (3, 4-dichlorophenyl)-1,1-dimethyl urea. The ratio of these readings can be used as a simple estimate of algal physiological condition (Vincent, 1980).

Experimental protocol/cell stage

Sediment cores were sectioned aboard the ship in subdued light so as not to compromise the samples (placed in a dark cooler to minimize light exposure and mimic surficial lake sediment conditions). One centimeter of the core sample was sectioned from the surficial sediments, giving two samples from each station for a total of six samples. Each core sample was placed into a whirl-pack, labeled, wrapped in foil to minimize light exposure, and placed in a cooler to keep chilled (Sicko-Goad *et al.*, 1989). In the laboratory, a Percival model E-36L growth chamber was programmed for ambient temperature, light intensity and photoperiod. Hypolimnion lake water was collected with Niskin bottles and transferred into 5 L bottles to avoid excess agitation. The water was then passed through

Whatmann EPM-2000 filters, to provide the least nutrient-rich conditions as possible (Sicko-Goad *et al.*, 1989).

After filtering, 250 mL of each water sample was placed into a labeled transparent 300 mL sterile culture flask (two flasks for each water depth). Two dark bottles were prepared as well for each depth, to serve as controls (Sicko-Goad *et al.*, 1989; McQuoid, 2002). Eight grams of sediment core sample was weighed using a Mettler PL-3000 balance and placed into the labeled transparent biochemical oxygen demand (BOD) bottle containing the pre-filtered lake water. Each bottle was then inverted five times, to simulate lake disturbance, and this was done once every day of the experiment (Sicko-Goad *et al.*, 1986).

Sicko-Goad *et al.* (Sicko-Goad *et al.*, 1989) defined the sequence of cytological events. Internally modified resting diatom cells were taken from a small inland lake; they were exposed to light and allowed to resume rapid vegetative growth. Fully expanded cells are fully differentiated vegetative cells with cytoplasmic components at the periphery of the cell, a central cytoplasmic bridge and well-defined vacuolar areas on either side of the central cytoplasmic bridge. Cells that have a condensed cytoplasmic mass usually located in the central cytoplasmic bridge area were classified as true resting cells. Dead cells were completely devoid of visible cytoplasm. The number of diatom rafts was tallied and the variety of cells (vegetative, resting or dead) was tallied. Transects were used to count >100 cells (400× magnification), from each bottle on a Leica DMR research microscope. Oxygen concentrations were not measured in the experimental BOD bottles during or at the end of our experiments. However, oxygen concentrations were determined prior to our experiments. That said, the samples and experimental containers were handled and prepared using clean techniques, and it is understood that oxygen concentrations may have deviated from ambient conditions (Table II).

Statistical analysis

Variation in benthic algal biomass (as chlorophyll *a* concentration) was evaluated using two-way analysis of variance (ANOVA), where thermal periods and lake stations were considered fixed factors. Pair-wise differences among stations and thermal periods were identified using Tukey's multiple means comparisons tests (Ortega, 2007). Moreover, species specific changes in the physiology of key diatoms were used to assess how illumination affected diatom physiological efficiency. A paired *t*-test was used to compare the maximum mean physiological efficiency of illuminated bottles versus the

Table II: A summary of water column profiles for temperature, PAR and dissolved oxygen (Seabird CTD measurements) in the central basin of Lake Erie 2007–2008

Thermal period	Station	Strata	Temperature (°C)	PAR ($\mu\text{E m}^{-2} \text{s}^{-1}$)	Dissolved oxygen (mg L^{-1})	
Winter	Offshore-hypoxic	Epilimnion	0.0	277.2	—	
	Spring-mixing	Nearshore-hypoxic	—	—	—	
Summer-stratification	Offshore-hypoxic	Epilimnion	4.1	—	—	
		—	—	—		
		Offshore-oxic	—	—	—	
		—	—	—		
	Nearshore-hypoxic	Epilimnion	22.7	60.34	6.79	
		Metalimnion	22.6	18.11	6.67	
		Hypolimnion	18.1	4.88	2.74	
		Bottom	17.9	3.09	2.51	
		Offshore-hypoxic	Epilimnion	22.6	18.65	7.09
			Metalimnion	18.7	11.56	6.02
			Hypolimnion	11.4	2.15	2.57
			Bottom	11.4	0.71	2.35
		Offshore-oxic	Epilimnion	21.4	0.00	7.12
			Metalimnion	16.4	0.00	6.37
			Hypolimnion	12.4	0.00	6.31
Bottom	12.4		0.00	5.58		
Fall-mixing	Nearshore-hypoxic	Epilimnion	18.4	27.80	6.96	
		Metalimnion	18.3	3.15	6.96	
		Hypolimnion	18.3	0.36	6.94	
		Bottom	18.3	0.12	6.93	
	Offshore-hypoxic	Epilimnion	18.2	0.00	6.98	
		Metalimnion	18.2	0.00	7.02	
		Hypolimnion	18.1	0.00	6.95	
		Bottom	18.1	0.00	6.93	
	Offshore-oxic	Epilimnion	17.8	0.18	7.12	
		Metalimnion	17.8	0.00	7.23	
		Hypolimnion	17.8	0.00	7.29	
		Bottom	17.8	0.00	7.31	

paired dark bottles (Bossert and Slobodkin, 1983). Owing to an unbalanced design, a one-way ANOVA was used to compare the maximum growth rate of illuminated bottles spatially, whereas a two-way ANOVA was used to compare the maximum growth rate of illuminated bottles temporally and at various incubation temperatures (4°C and 10°C). Tukey’s multiple means comparisons tests evaluated differences in maximum growth rates temporally and in different incubation temperatures.

Rejuvenation (as cell growth) was measured to assess if diatom species that commonly occur in Lake Erie exhibited spatio-temporal differences in their response to experimental manipulations with light and temperature in the laboratory. Owing to an unbalanced design, a one-way ANOVA was used to compare the maximum mean rejuvenation of the three diatom species spatially; whereas a two-way ANOVA was used to compare the maximum mean rejuvenation of the three diatom species temporally and at different incubation temperatures (4°C and 10°C).

Growth rates were used to assess how certain diatom species responded to experimental light and temperature manipulations. The average daily growth rate was

calculated in accordance with Mills (Mills, 2007). This equation was also applied to the *in vivo* fluorescence measurements, used to assess the recovery of diatom cell physiological efficiency. All data analyses were performed using SPSS (version 16.0, Chicago, IL, USA) and Minitab (version 14.0, State College, PA, USA).

RESULTS AND DISCUSSION

Variation in benthic chlorophyll

Benthic chlorophyll concentrations in the central basin of Lake Erie exhibited significant spatial and temporal variation. Benthic and water column chlorophyll results suggest the assemblage of diatoms inhabiting the benthos is phytoplankton that has settled out of the water column (Nipkow, 1950; Sicko-Goad *et al.*, 1989), as seen from similarities in algal composition (Carrick *et al.*, 2005). The sedimented algal layer is meroplanktonic (Carrick *et al.*, 2005), spending a portion of its life throughout the water column and along the benthos. The benthic algal layer, through natural decomposition, affects seasonal hypoxia; however, this layer is composed

of resting diatoms that are also capable of seeding algal blooms during the spring-mixing season (Sicko-Goad *et al.*, 1989). Results from a two-way ANOVA indicated a significant interaction between thermal period and lake station ($P = 0.000$) (Table III). These results encompass four lake thermal periods (spring-mixing, early-stratification, late-stratification and fall-mixing) over lake stations that have hypolimnia resulting in hypoxic conditions as well as hypolimnia that do not.

The rare winter sample from the lake benthos supported unique results. Although the winter period was not incorporated into the overall results, a single sample from the central basin showed that the concentration in the winter was relatively low ($< 20 \text{ mg m}^{-2}$). There are limited inferences that can be made from this single value; however, in previous winter lake studies, benthic chlorophyll concentrations were low. When the lake surface warms and light penetrates through the ice pores, water column density will change creating turbulence (Tilzer and Goldman 1978). Under these conditions, algal blooms are capable of forming, creating conditions similar to that of the spring bloom (Jung *et al.*, 2008).

Water column chlorophyll *a* concentrations decreased after the spring-mixing period for all stations implying material sedimentation from the water column into deeper waters, especially after lake stratification (Fig. 1). Algal biomass, as well as a variety of other lake fauna, sinks from the surface into the metalimnion and hypolimnion (Stevenson and Stoermer, 1981; Kingston *et al.*, 1983; Fahnenstiel and Scavia, 1987; Rowe, 2001; Catalan *et al.*, 2002; Carrick, 2004; Carrick *et al.*, 2005). The chlorophyll *a* peak during the spring-mixing period can be observed in the benthic water column approximately 1 month later as a time lag occurs in biomass deposition. A proposed strategy for escaping the deprived surface water conditions is the concept of “algal rain” (Braidech *et al.*, 1972). This event is observed in the central basin and forms considerable layers atop sediments that can remain photosynthetically active by forming vegetative resting cells (Carrick *et al.*, 1993) accounting for the accumulation of

chlorophyll later in the year through the months of July to October.

Benthic chlorophyll concentrations were generally higher at both hypoxic stations compared with the offshore-oxic station (Fig. 1). Average chlorophyll was approximately 2-fold greater at the hypoxic stations relative to the oxic station (81.45 versus 40.45 mg m^{-2} , respectively). A more pronounced station difference was apparent following thermal stratification, when peaks in benthic chlorophyll concentrations showed a bell-shaped distribution of biomass (Quigley and Robbins, 1984) across lake station from the spring-mixing period to the fall-mixing period (Fig. 1), revealing an average hypoxic station chlorophyll concentration that was nearly 3-fold greater compared with chlorophyll at the oxic station (148.41 versus 54.60 mg m^{-2} , respectively). Furthermore, the benthic lake stratification chlorophyll concentrations were more than 2.5-fold higher than the mixing periods (101.51 versus 40.45 mg m^{-2} , respectively), again suggesting that either benthic material is resuspended or it is oxidized. Seasonal pulses of plankton have also been observed contributing to the benthos in numerous parts of the world (e.g. the Gulf of Mexico, Chesapeake Bay, Swedish West Coast, Africa’s Lake Victoria and many more) (Dortch *et al.*, 1994; Rowe, 2001; McQuoid, 2002; Rabalais *et al.*, 2002).

After the peak in benthic chlorophyll, during lake stratification, a decline in biomass follows. Seasonal change in benthic chlorophyll *a* may be explained by the degradation of the assemblage (Carrick *et al.*, 2005). With an increase in phaeopigments (common results of degraded chlorophyll) from July to September (20 versus 150 mg m^{-2}), chlorophyll *a* concentrations decline (Carrick *et al.*, 2005), suggesting that a large portion of the assemblage may be decomposed over time. This observation is in agreement with the seasonal decline of hypolimnetic oxygen in the basin (see Carrick *et al.*, 2005 and Table V).

Light versus temperature effects on diatom rejuvenation

The physiological condition of meroplanktonic diatoms collected from the benthos of the central basin was influenced by modest illumination (Fig. 2). A significant increase in *in vivo* fluorescence yield was observed between illuminated bottles and those kept in the dark, mimicking lake bottom conditions. In general, bottles exposed to an illumination of $\approx 50 \mu\text{E m}^{-2} \text{ s}^{-1}$ exhibited higher growth rates compared with bottles that were not exposed to light (Fig. 2). Maximum growth rates were observed to be approximately four times higher when exposed to modest illumination (bottles

Table III: Two-way ANOVA assessing spatio-temporal variation in benthic chlorophyll concentrations (mg m^{-2}) in Lake Erie (July 2007–August 2008)

Factor	df	MS	F-value	P-value
Thermal period	3	7.22	25.732	0.000
Station	2	1.03	3.655	0.036
Interaction	6	1.78	6.332	0.000

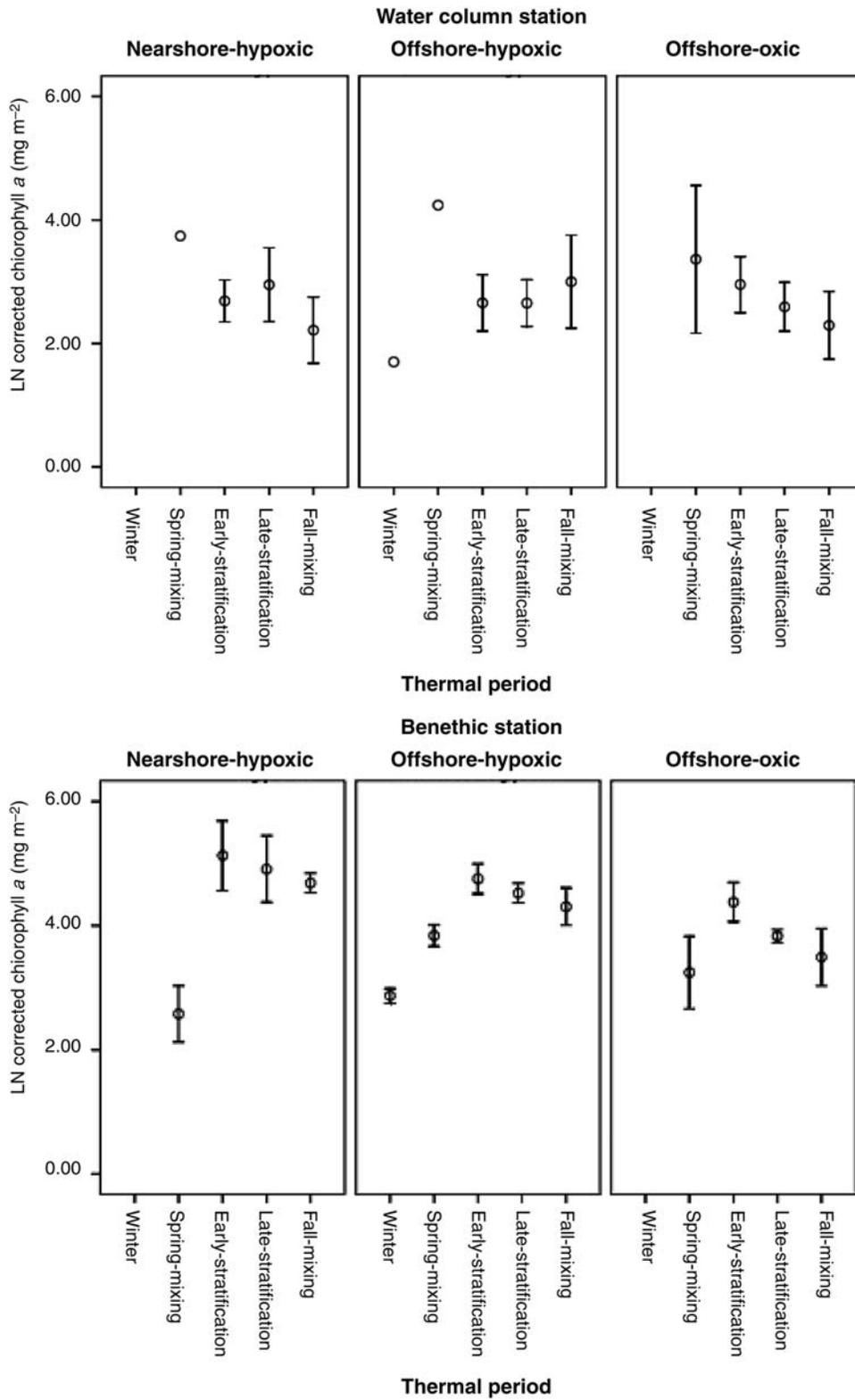


Fig. 1. Water column and benthic chlorophyll *a* concentrations (average ± 1 standard error, mg m⁻²) collected at three Lake Erie central basin stations over five thermal periods during 2007–2008.

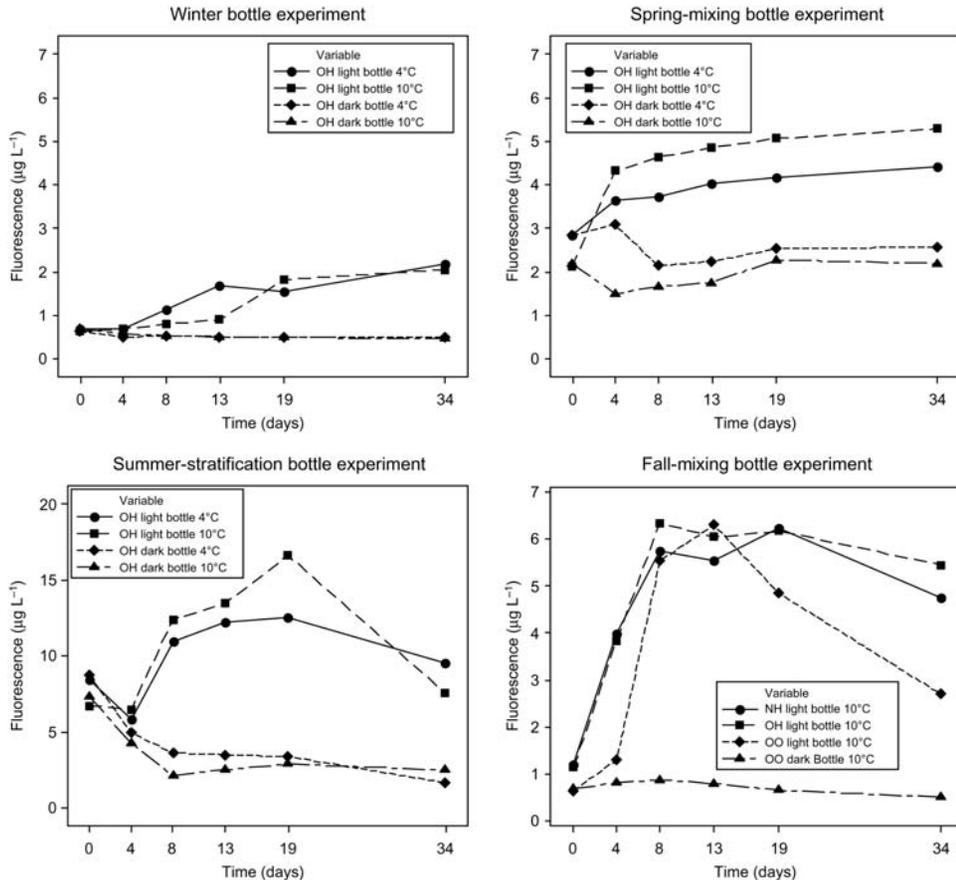


Fig. 2. Thermal period diatom *in vivo* fluorescence ($\mu\text{g L}^{-1}$) comparing 4°C and 10°C light and dark bottles for the Lake Erie central basin experimental stations.

averaged 0.110 versus -0.0384 day^{-1} , respectively). However, maximum growth rates in the central basin did not exhibit significant spatial variation (one-way ANOVA, $P = 0.964$) nor was it altered by different incubation temperatures, but significant temporal variation was noted ($P = 0.000$). Distinct temporal variation was observed in the fall-mixing period. Maximum growth rates averaged 0.384 day^{-1} across the three lake stations and incubation temperatures for this thermal period, whereas maximum growth averaged 0.092 day^{-1} , which is approximately 4-fold less than that of the fall-mixing period.

Within 8 days of incubation, a dramatic increase in fluorescence was observed in the experimental bottles exposed to light ($\approx 50 \mu\text{E m}^{-2} \text{ s}^{-1}$) in all four experiments (Fig. 2). In general, initial fluorescence values were low (≈ 5 – 6 units) and increased 3–4-fold. These rejuvenation rates were comparable to that of Sicko-Goad (Sicko-Goad, 1986), who observed rapid physiological efficiency increase in *Fragilaria construens* populations in Green Bay, Lake Michigan. These

diatom populations from the Great Lakes exhibited up to 65% rejuvenation within 3 days exposure to similar light exposure (Sicko-Goad *et al.*, 1989). Also observed were 20-year-old sediments containing diatoms (i.e. *A. italica*) with the capability of becoming physiologically competent within a 1–8 h period after exposure to light (Lund, 1954; Sicko-Goad *et al.*, 1986; Carrick *et al.*, 1993).

The dark bottle treatment mimicked Lake Erie ambient benthic light conditions. The PAR profiles at each station showed that very little light, if any, reached the benthos (averaged $0.31 \mu\text{E m}^{-2} \text{ s}^{-1}$) (Table II). Aphotic conditions may not be an absolute requirement for resting cells (as some cells remained in the resting stage when provided light), but rather may act simultaneously with other factors such as temperature reduction to promote resting cell formation (Anderson, 1976; Sicko-Goad *et al.*, 1989). Drastic changes in photosynthetic capacity of the incubated cells came with prolonged exposure to darkness. Loss in viability was followed by a fluorescence yield that was greatly

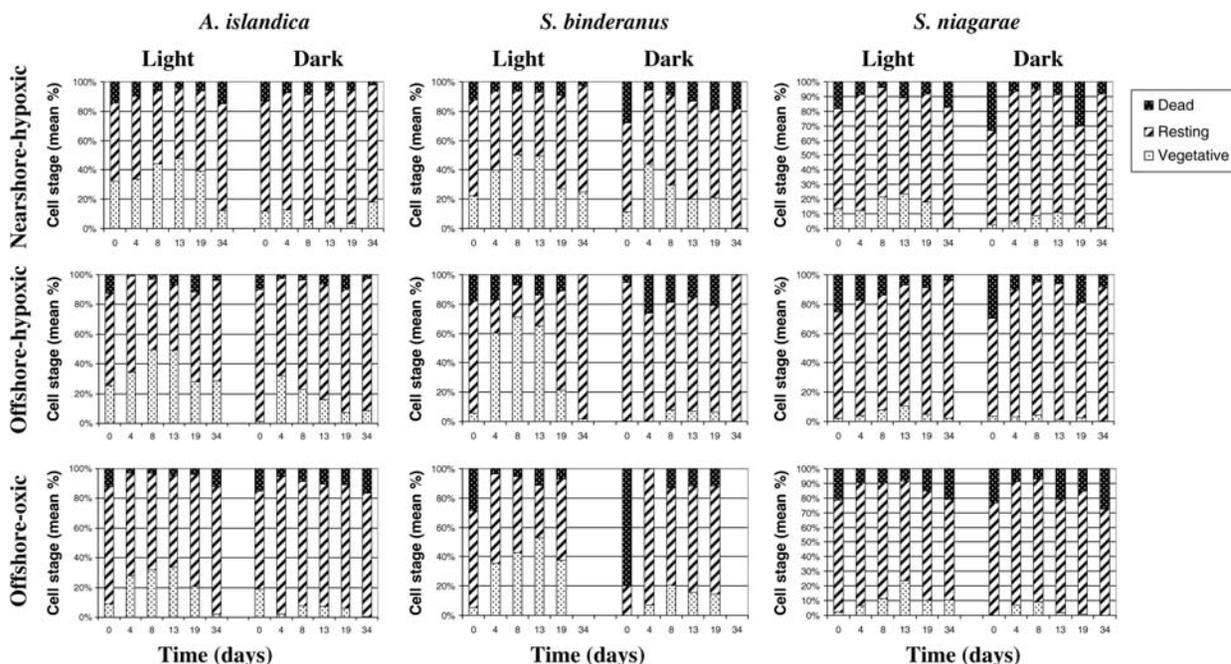


Fig. 3. The 4°C experimental light and dark bottle mean percents of *A. islandica*, *S. niagarae* and *S. binderanus* cell stage from the Lake Erie central basin offshore-oxic, offshore-hypoxic and nearshore-hypoxic stations during the spring-mixing period (2008).

reduced (Smayda and Mitchell-Innes, 1974; Gibson and Fitzsimons, 1990). Darkness rapidly increased the percentage of cells that were in the condensed resting cell formation, from 60% to >90% in 34 days (Fig. 3), as indicated by the extremely low physiological efficiency of the cells (Sicko-Goad *et al.*, 1989; Gibson and Fitzsimons, 1990). This pattern was observed in >70% of the experiments.

Based on laboratory enclosure experiments, variation of incubation temperatures (4°C and 10°C) exhibited no significant difference in maximum growth rates (one-way ANOVA, $P = 0.964$). Sicko-Goad *et al.* (Sicko-Goad *et al.*, 1989) recorded that temperature increase/reduction could alter cell physiological state. Results indicated that at 20°C the greatest vegetative growth in *Melosira granulata* was observed; however, the greatest proportion of vegetative cells was observed at 10°C (Sicko-Goad *et al.*, 1989). The Lake Erie rejuvenation experiment did not test 20°C, as this temperature is a summer surface water temperature (Lam and Schertzer, 1999). During a lake-mixing event, where Lake Erie experiences average temperatures of 10°C (Lam and Schertzer, 1999), diatom cells may experience resuspension and rejuvenation, initiating a bloom of vegetative diatom cells. Temperature has long been suggested to be a major co-factor in diatom growth patterns (Lund, 1949), but it has been difficult to separate

the difference between temperature and illumination in the natural environment (Reynolds, 1984). Kiefer (Kiefer, 1973) reported that natural phytoplankton communities in the Gulf of California showed no temperature effect on the communities fluorescing capabilities. Physiological stress has also been suggested as a possible reason for variation in growth rates which is independent of light effects, in environments with fluctuating temperature (Kiefer, 1973).

Diatom rejuvenation and seasonal phytoplankton dynamics

The meroplanktonic assemblage in Lake Erie is dominated by three centric diatom species studied here (*Aulacoseira islandica*, *Stephanodiscus niagarae* and *Stephanodiscus binderanus*); interestingly, these species are also prevalent in the seasonal diatom blooms in the lake (Carrick, 2004; Carrick *et al.*, 2005). Maximum growth rates among species and Lake Erie stations and thermal periods differed, suggesting the presence of environmental niches. Large lakes, such as Lake Erie, present the opportunity for spatial or temporal niche space, due to various environmental habitats that may accommodate numerous species.

Large lake systems provide opportunities for the separation of phytoplankton populations to occur

Table IV: One-way ANOVAs comparing diatom rejuvenation rates (day^{-1} , ranked low to high) in Lake Erie benthos, where lake stations and thermal periods (2007–2008) were treated as fixed factors

Species	df	MS	F-value	P-value	
					Station
<i>A. islandica</i>	2	0.0005	0.14	0.867	<u>OO</u> NH OH
<i>S. binderanus</i>	2	0.1619	2.34	0.115	OH <u>OO</u> NH
<i>S. niagarae</i>	2	0.0857	1.41	0.261	NH <u>OO</u> OH
					Period
<i>A. islandica</i>	3	0.0024	0.73	0.545	WS FM <u>SS</u> SM
<i>S. binderanus</i>	3	0.2712	5.12	0.006	<u>WS</u> <u>SS</u> SM FM
<i>S. niagarae</i>	3	0.1391	2.60	0.074	FM <u>SS</u> SM WS

Non-overlapping lines indicate a significant difference ($P < 0.05$). NH, nearshore-hypoxic; OH, offshore-hypoxic; OO, offshore-oxic; WS, winter-stratification; SM, spring-mixing; SS, summer-stratification; FM, fall-mixing.

(Stoermer *et al.*, 1981). Many algal populations which normally do not co-occur in smaller systems are found in association with each other in the great lakes (Stoermer *et al.*, 1981), leading to interpretation problems (Table IV). The diatom genus *Stephanodiscus* is widely distributed. It has been observed and noted to be ecologically important in many freshwater lakes, reservoirs and large rivers as well as oligotrophic and extremely eutrophic systems (Theriot and Stoermer, 1981; Stoermer and Sicko-Goad, 1985). Many variations in the *Stephanodiscus* species are difficult to identify due to incomplete understanding in their numerous cell variations (Theriot and Stoermer, 1981). Variations can occur due to changing environmental conditions and possibly isolation of a portion of *Stephanodiscus* cells (Theriot and Stoermer, 1981).

Aulacoseira islandica has also experienced modifications in cell morphology, which correlated well with the beginning of European settlement in Lake Erie and Ontario (Stoermer *et al.*, 1989). Many species of *Aulacoseira* and *Stephanodiscus* are meroplanktonic and found in the plankton only during periods when the water column undergoes turbulent mixing (Nipkow, 1950; Lund, 1954; Willen, 1962; Munawar and Munawar, 1986; Liukkonen *et al.*, 1993). Commonly found in surficial lake sediments forming vegetative resting cell stages, these diatom species have evolved strong environmental adaptations for survival as well as clear thermal tolerances, which is suggested by their distribution throughout the Great Lakes (Nipkow, 1950; Lund, 1954).

At collection, an average of 66.2% of cells in the benthos (*A. islandica*, *S. niagarae*, *S. binderanus*) were vegetative resting cells. These cells exhibited a low photosynthetic efficiency as their cellular interior is condensed to

deal with the low light conditions (Sicko-Goad *et al.*, 1986; Gibson and Fitzsimons, 1990; Carrick *et al.*, 1993). Decreases in fluorescence have been observed coincidentally with the shrinkage of diatom chloroplasts (Loftus and Seliger, 1975); however, samples gathered from below a 1% light depth, which had been in near darkness for an extended time, showed a marked increase in fluorescence once exposed to light (Loftus and Seliger, 1975). Phytoplankton photosynthesis at any depth depends on the quantity and quality of light (Dubinsky *et al.*, 1984). For growth (rejuvenation) to occur, cells must be resuspended, via a lake-mixing event, providing them with light, higher temperatures and sufficient nutrients to grow (McQuoid, 2002), in some cases, causing seasonal algal blooms on Lake Erie. The last 100 years have marked a century of global warming and global pollution. Spring diatom peaks are now beginning earlier, under the ice, which may be the beginning of another diatom speciation event (Montagnes and Franklin, 2001; Solovieva *et al.*, 2005).

Algal resuspension of meroplanktonic species is experienced around the globe: Gulf of Mexico, Great Lakes, Chesapeake Bay, Gullmar Fjord (Sweden), Lake Okeechobee, Switzerland Coast, African Coast, Xiamen Bay in Southern China, Hiroshima Bay in Japan, Okoboji Lake in Iowa, East Pike Lake in Minnesota (Stockner and Lund, 1970; Billett *et al.*, 1983; Pitcher, 1990; Carrick *et al.*, 1993; Edlund and Stoermer, 1993; Dortch *et al.*, 1994; Itakura *et al.*, 1997; Rowe, 2001; McQuoid, 2002; Rabalais *et al.*, 2002; Chen *et al.*, in press). McQuoid (McQuoid, 2002) revealed sedimented cells as having no major degradation for most species even after seven months of cold, dark storage suggesting that these cells could easily overwinter in the sediments or lower water column, even at depths up to 1000 m (Reynolds, 1973; Platt *et al.*, 1983; McQuoid and Hobson, 1995). This characteristic enables the cell to survive adverse conditions (aphotic, low temperature, nutrient depletion and even anoxic conditions) until resuspension commences (Lund, 1954; Sicko-Goad *et al.*, 1986; Sicko-Goad *et al.*, 1989). Garrison (Garrison, 1981) suggests a similar role for marine diatom resting spores stating that his study “demonstrated the potential for resting spores to function as survival stages in Monterey Bay and act as potential seed populations for diatom blooms.” The observations in this study imply a similar conclusion to that of Garrison (Garrison, 1981). Lake Erie benthic diatoms may not simply be decomposing and contributing to the seasonal anoxia; they may possess an important competitive mechanism. The sedimentation of diatoms occurring in Lake Erie may also contribute to the seeding of

Table V: Mass-balance calculations estimating the oxidation of algal matter and its contribution to oxygen depletion in the hypolimnion at three areas in Lake Erie

Station/region	Total oxidation (oxygen, g m ⁻²)	Algal oxidation (chl. pigment, g m ⁻²)	Contribution (%)
Offshore-oxic	8.45	0.95	11.25
Nearshore-hypoxic	8.63	0.97	11.24
Offshore-hypoxic	15.58	5.17	33.17

All calculations were based upon empirical data collected during thermal stratification in 2008. Total oxidation was derived from changes in hypolimnetic oxygen concentrations during the stratified period. Algal oxidation was estimated from changes in chlorophyll pigment concentrations in the profundal zone during the stratified period. Chlorophyll concentrations were converted to carbon (assuming a chlorophyll to carbon ratio of 100; H.J. Carrick, unpublished results).

subsequent spring diatom blooms, consequently enabling the success of subsequent diatom species and their populations.

Algal contribution to seasonal hypoxia

We calculated first-order estimates for the contribution of algal organic matter oxidation made toward hypolimnetic oxygen depletion at three sites in Lake Erie using a mass-balance approach during the stratified period (August-September). Quantitative estimates such as these have not been made in Lake Erie, although this mechanism has been identified as a major contributor to hypoxia in other coastal ecosystems (Diaz and Rosenberg, 2008). Total oxidation was inferred from changes in oxygen concentrations in the hypolimnion (measured from CTD casts), while algal oxidation was estimated from changes in chlorophyll pigment concentrations in the benthos. The largest contribution of algal oxidation was measured at the offshore-hypoxic station (Table V and Fig. 1). We believe these estimates are reasonable, given that they agree well with those previously determined for Lake Erie (Charlton *et al.*, 1993), and fall within the range of estimates determined elsewhere (see Kemp *et al.*, 1992). Interestingly, lesser oxygen depletion was observed both at the offshore-oxic and nearshore-hypoxic stations, which was predictable based on the measured chlorophyll concentrations. Thus, our data suggest that a substantial proportion of oxygen depletion at these stations can be attributed to the oxidation of algal matter present in the sediments. Previous work along with our observations here indicated that most of the algal material present in the surficial sediments was composed of planktonic diatoms (Carrick, 2004; Carrick *et al.*, 2005) The high fraction of oxidation at the nearshore station seems to suggest that

the nearshore zone is likely to contribute to “seed” populations during mixing events. However, it should be noted that chlorophyll estimates represent fully vegetative cells and do not include cells in the resting phase. Therefore, a potentially large portion of sedimented chlorophyll, in the diatom resting phase, may in fact be available as “seed” during mixing events (Sicko-Goad, 1986).

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