The Pennsylvania State University

The Graduate School

School of Forest Resources

SPATIAL AND TEMPORAL VARIATION OF DIATOM PHYSIOLOGICAL CONDITION IN LAKE ERIE BENTHOS: IMPLICATIONS FOR SEASONAL HYPOXIA

A Thesis in

Wildlife and Fisheries Science

by

Aubrey Rain Lashaway

Submitted in Partial Fulfillment
of the Requirements
for the Degree of

Master of Science

May 2009

The thesis of Aubrey Rain Lashaway was reviewed and approved* by the following:

Hunter J. Carrick
Associate Professor of Aquatic Ecology
Thesis Advisor

Katherine H. Freeman
Professor Department of Geosciences
Associate Department Head of Graduate Programs

Lysle S. Sherwin
Director, Center for Watershed Stewardship

Walter M. Tzilkowski
Associate Professor of Wildlife Science

Michael G. Messina
Director, School of Forest Resources

*Signatures are on file in the Graduate School

Abstract

Rapid sedimentation of phytoplankton cells following surface blooms is common in the Great Lakes, yet the fate of these cells is uncertain, particularly in Lake Erie, where hypoxia occurs seasonally. I sampled benthic stations seasonally inside and outside of the hypoxic area for differences in chlorophyll-*a* concentrations, physiological condition (cell viability), and rejuvenation rates (from enclosure experiments). During summer stratification I expected the oxygen rich areas to support lower chlorophyll-*a* concentrations, faster diatom rejuvenation rates, and superior physiological capabilities, compared to hypoxic environments. Hypoxic areas did sustain higher chlorophyll-*a* concentrations, but diatom growth and physiological capability did not differ significantly. Hypoxic areas exhibited exponential growth rates as high as 0.56 d^{-1} (compared to oxic station at 0.53 d^{-1}) and physiological conditions as high as 0.30 µg L^{-1} d^{-1} (compared to oxic station at 0.36 µg L^{-1} d^{-1}). Therefore, sedimentation of phytoplankton cells may not only contribute to the seasonal hypoxia observed in Lake Erie, but sedimentation may also contribute to the seeding of subsequent spring diatom blooms, for those diatoms able to withstand low oxygen concentrations.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

Eternal thanks go out to the following individuals for their help and support. I would like to begin by thanking my Lord and Savior Jesus Christ who gave me strength in the midst of doubt, stress, and overwhelmingly long nights. My parents who have shown endless support and who have been full of hopeful words and to the rest of my loving family. Keith Price, Andrew Scanlan, Rebecca Kolar, Melissa May, Caleb Tzilkowski, and all of my "Pride of the Lions" pep-band and concert band friends for encouragement, help in problem-solving and mostly for friendship. My advisor Dr. Hunter Carrick , as well as my committee members, Dr. Walter Tzilkowski, Dr. Katherine Freeman, and Mr. Lysle Sherwin for indispensable guidance and support. The crew of the NOAA ship *Laurentian,* Tom Nalepa, Dave Fanslow, Nathan Hawley, Jennifer Beals, Andrew Scanlan and Sarah Gustafson for assistance with equipment and collection of Lake Erie samples. Dr. Mike McKay, from Bowling Green State University, for supplying data and collecting Lake Erie samples when I was unable. Funding that was provided by the Watershed Stewardship Option and from the Katherine Mabis McKenna Foundation.

Non tam pares quam superiores: Each successive year must not be equal to, but better than, before. Hail to the Victors! Go Blue.

Chapter 1

Background

Diatoms are unicellular protists that first appeared in the fossil record dating back to the Cretaceous period (144-65 million years ago), and constitute a vital part of the aquatic food webs (Falkowski and Raven 2007). These organisms are found ubiquitously throughout marine and freshwater environments, inhabiting open water and benthic environments (Wehr and Shealth 2005). Diatoms are believed to comprise approximately one quarter of the plant life by weight and produce at least one quarter of the oxygen (Falkowski and Raven 2007). Diatoms are key components of aquatic food webs, because they provide vital food resources for a wide range of animals, from small protozoan to baleen whales (Falkowski and Raven 2007).

Diatoms have established numerous ways to adapt to ecosystem diversity. For instance, diatom blooms, communities of highly successful phytoplankton, occur when the temperature, light conditions, and nutrient surroundings in the water are favorable for growth and life, occurring during periods of overturn in wind-exposed (turbulent) lakes where dissolved silica will be readily available to build their cell wall (Kalff 2002). Blooms are a major source of energy for any aquatic ecosystem, which ultimately can support large predators such as fish, marine mammals and birds (Turner *et al*. 1997). Diatoms have also been known to be harmful, as certain toxins, such as domoic acid, present in diatoms can build up in the tissue of animals that eat them (Turner *et al*. 1997). Survival and reoccurrence of diatom blooms has only been an important part of aquatic biologist research for a brief time. Rapid mass sinking of cells following diatom blooms, observed in lakes and the sea, is argued to be a state

of transition from a growing to a resting stage in the life histories of these microscopic creatures (Smetacek 1985). Mass sinking is of survival value in those diatoms that retain viability over long periods in cold dark water but not in warm, nutrient-depleted surface water (Smetacek 1985, Sicko-Goad *et al.* 1989). Sinking diatoms are important energy sources for deep water environments and for inoculated surface waters (Fig. **1**).

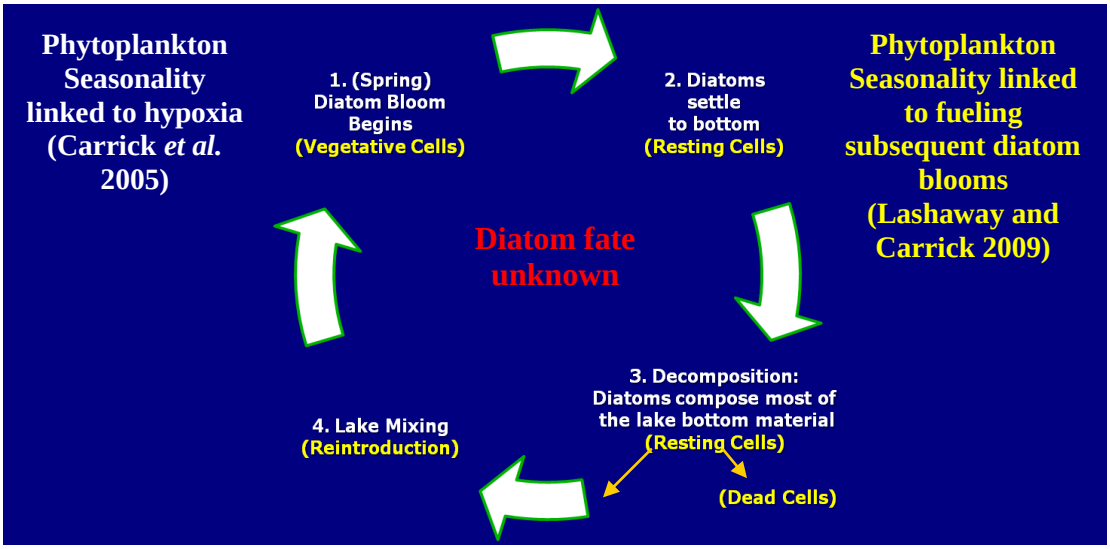


Fig. **1**: Yearly diatom life-cycles explained by two possible scenarios: **1).** Lake Erie phytoplankton seasonality is linked to the seasonal hypoxia problem (white). **2).** Lake Erie phytoplankton seasonality is linked to fueling subsequent diatom blooms (yellow).

After the spring bloom, planktonic as well as meroplanktonic assemblages (organisms that are planktonic for only a part of their life cycle) varied seasonally in abundance and density (Carrick *et al*. 2005). In Lake Erie's eastern basin, typical peaks in biomass of phytoplankton in the spring and fall (April and October) were observed as well as peaks in benthic chlorophyll during the early summer months (May-June) (Carrick 2004). Subsequently, one may infer that this benthic algal layer likely settled out from the water column, as seasonal pulses of plankton have been

observed contributing to the benthos in the Gulf of Mexico (Rowe 2001) as well as in the eastern basin of Lake Erie. Thus, by examining spatio-temporal events along the benthos, as well as, evaluating chlorophyll pigment data, one can observe seasonal trends that may be coupled with the development of viable resting cells.

Chapter 2

Introduction

Events of low oxygen can cause changes in populations of marine and freshwater organisms such as large-scale mortality, changes in species distributions, changes in biodiversity, physiological stress, and other sub-lethal effects, such as reduced growth and reproduction (Service 2004). Hypoxic events are increasing in intensity and frequency worldwide and the sinking and decomposition of diatoms has been attributed with increasing hypoxia (Fig. **1**) in lakes, oceans, and other bodies of water throughout the world, including the Chesapeake Bay, Gulf of Mexico, and Africa's Lake Victoria (Rabalais *et al*. 2002, Chapman *et al*. 1995, Kemp *et al*. 1992). Dortch *et al.* (1994) concluded hypoxia on the Louisiana Shelf, within the Gulf of Mexico, was more widespread when the weather was calmer; thus allowing a more intense water stratification within the system. Electron-transport-system (ETS) measurements were taken to estimate metabolic potential through chemical reactions in living cells of the organisms or communities sampled (Relexans 1996). From these samples, they concluded ETS measurements decreased with depth and distance offshore (Dortch *et al*. 1994). With hypoxia being a world-wide nuisance in all types of aquatic ecosystems, it would be pertinent to know more about what is fueling these hypoxic conditions. However, if diatoms can be rejuvenated into completely operating vegetative cells, perhaps their life-cycle during hypoxic conditions is yet to be fully explained. The physiological modifications that occur within the cell have not been well defined; but from obtaining a better understanding of this "resting

stage" of diatoms, a great deal of knowledge could be obtained pertaining to the diatom blooms that occur throughout the world.

The ability of diatoms to form vegetative resting cells has been known for more than a half a century, although their role in the ecology of coastal waters is poorly understood (Sicko-Goad *et al*. 1989). Research in the early 1950's explains *Aulacoseira italica* (formerly *Melosira italica*) diatom cells taken from surficial lake deposits were illuminated, irrigated with lake water, and transformed into viable plankton cells (Lund 1954). Lund (1954) illustrated that by the seventh day of experimental illumination, cells were capable of division. Sicko-Goad *et al.* (1989) referred to these cells as "vegetative" resting cells. Unlike spores that are readily identifiable by external modifications to their siliceous frustules, resting cells change internally (Sicko-Goad *et al*. 1989). Resting cells have been offered as an explanation for the emergence and rapid growth, a type of "seed bank (Fig. **1**)," for both freshwater and marine diatom species (i.e. diatom blooms) (Sicko-Goad *et al.* 1989). Whipple (as early as 1895) suggested that turnover of the water column was responsible for resuspending diatoms that have been dormant on the bottom. Turnover events that include 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 are commonly observed in the benthos. Previously, Carrick *et al.* (2005) confirmed viable meroplanktonic cells were present in all the samples they analyzed, and that greater than 90% of benthic algal carbon was composed of pelagic diatom species. They concluded the benthic algal layer had

likely settled from the water column. I examined and analyzed viable cell samples taken from Lake Erie's central basin surficial sediments. However, sedimentation of pelagic diatoms may not only contribute to the yearly hypoxia observed in Lake Erie, but sedimentation may also contribute to the seeding of subsequent spring diatom blooms. The specific objectives of this thesis are to: 1) 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), 2) evaluate meroplanktonic diatom physiological condition (via *in vivo* autofluorescence response) following exposure to an illumination of ≈50 µE m^{-2} s^{-1} within stationary growth chambers, 3) and to identify meroplanktonic diatoms retrieved from oxic sites and determine if they are capable of fast rejuvenation rates (indicating vegetative cytology) or slow rates (indicating resting cytology) compared with those collected from hypoxic sites.

Chapter 3

Methods

Study Site

Lake Erie Watershed and Station Characteristics

The Laurentian Great Lakes are among some of the world's largest lakes and comprise 20% of the earth's freshwater (Herdendorf 1984). They have been particularly well-studied and because of human impacts, they are sometimes called large-scale natural biomanipulated experiments (Kalff 2002). However, the term 'well-studied' does not imply complete understanding of all the processes occurring within the lakes. Among the five Great Lakes of the United States, Lake Erie is known for bountiful fish harvests as well as polluted, non-aesthetically pleasing habitats. In the mid-seventeenth century a minimal human population occupied the shores of Lake Erie (Regier and Hartman 1973). At that time, Lake Erie supported a great quantity and quality of fish inhabiting the lake, e.g. small and largemouth bass (*Micropterus dolomieu and Micropterus salmoides*), muskellunge (*Esox masquinongy*), northern and blue pike (*Esox lucius and Sander vitreus glaucus*), lake trout (*Salvelinus namaycush*), channel catfish (*Ictalurus punctatus*), lake herring (*Coregonus artedi*), whitefish (*Coregonus clupeaformis*), lake sturgeon (*Acipenser fulvescens*), and walleye (*Sander vitreus vitreus*). Bordering marshes, savannahs, and large stands of timber helped buffer the lake's periphery (Regier and Hartman 1973). Today, Lake Erie lies in a highly industrialized and heavily populated area (Davis 1964), with more than thirteen million people living in its watershed (Regier and

Hartman 1973). Fish such as the blue pike (*Sander vitreus glaucus)* and lake trout (*Salvelinus namaycush)* have dwindled and nutrient loadings that feed dense blooms of planktonic algae have risen to high levels (Regier and Hartman 1973). The human impact on this Great Lake has been enormous, and water quality reconstruction efforts are of great necessity. Three decades ago, massive U.S. and Canadian programs to reduce nutrient loading from municipal sewage and detergents were implemented (Regier and Hartman 1973), and lake conditions have since improved.

Lake Erie is divided into three basins: the western, central, and eastern basins. Many studies on Lake Erie's aquatic conditions have focused on low hypolimnetic oxygen levels in the central basin (Rosa and Burns 1987). The formation of Lake Erie's hypoxic area has been recognized now for over 30 years (Wilhelm *et al.* 2006). Lake morphology has been thought to influence hypoxia. Rosa and Burns (1987) between 1929 and 1980, established that while there was an increase in oxygen depletion related to eutrophication, the physics and shape of the lake influenced hypoxia. However, when respiration is greater than primary production, lower dissolved oxygen levels result. The primary production in the central basin fuels decomposition and ultimately leads to a swift reduction in dissolved oxygen (Wilhelm *et al.* 2006). A stable thermocline, which occurs during the summer months, puts a limitation on gas exchanges throughout the water column, making Lake Erie an excellent candidate for hypoxic conditions (Wilhelm *et al.* 2006). The design of this study was to establish spatial and temporal variation throughout Lake Erie's central basin. Both hypoxic and oxic stations were sampled including four distinct thermal periods. Spatial and temporal variation within lakes has been

recognized as playing an important role in structuring lake ecosystems at a variety of scales (Soranno 1999). Understanding spatial and temporal patterns within individual lakes has occupied limnologists since the first thermometers were lowered and light gradients, oxygen readings and nutrient levels were observed in deep stratified lakes (Soranno 1999, Birge and Juday 1911). Lake ecologists have recently begun to recognize spatial and temporal patterns among lakes at larger scales attributed to landscape position (Soranno 1999). Lake Erie's western basin receives high nutrient loads from riverine inputs that may be a negative influence on the seasonal hypoxia problem (Dolan and McGunagle 2005). Whereas, the eastern basin, due to its deeper waters (63 m), may be a source of oxygen replenishment for hypoxia burdened areas within the central basin (Lam *et al*. 1983). Neighboring lake areas that share a common climate, geologic setting, and regional species pool may differ in many features such as their hydrologic function and geomorphology (Soranno 1999, Winter 1977). Strong spatial and temporal patterns observed in many lake systems suggest the need to further study these scales.

Field and Laboratory Procedures

Sampling Procedures

To evaluate variation in algal biomass, diatom density and diatom viability, on a seasonal and spatial scale, three stations were sampled throughout Lake Erie's central basin that were representative of its variable limnological conditions. Lake cruises were conducted during four thermal periods, winter, spring, and summer of 2008 and the fall of 2007. 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 completed aboard the NOAA ship *Laurentian (2007)*, the RV *Peter L. Wise 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 (Fig. **2,** Table **1**) and four thermal periods.

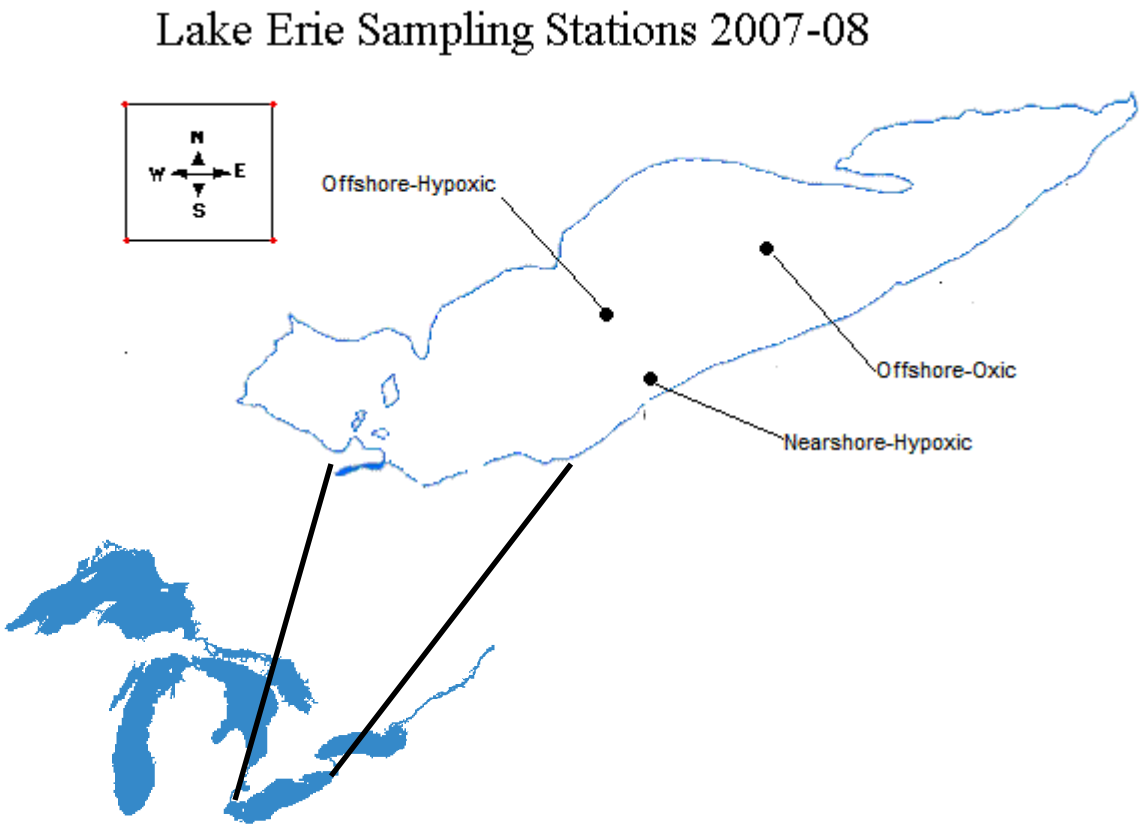


Fig. **2**: Lake Erie central basin sampling station conditions where algae vegetative resting cell patterns were evaluated in 2007-08.

Table **1**: Conditions for vegetative resting cell incubation experiments conducted on surficial Lake Erie central basin sediments spanning three station conditions, four thermal periods, and two experimental temperatures in 2007-08. Light exposure was ≈50 µE m^{-2} s^{-1} on a 12 h light : dark.

Thermal Period (2007-08)	Station	Experimental Temperature	Bottle Type
Winter	Offshore-Hypoxic	4ºC, 10ºC	Illuminated, Dark
Spring-Mixing	Nearshore-Hypoxic	4ºC, 10ºC	Illuminated, Dark
Spring-Mixing	Offshore-Hypoxic	4ºC, 10ºC	Illuminated, Dark
Spring-Mixing	Offshore-Oxic	4ºC, 10ºC	Illuminated, Dark
Summer-Stratification	Offshore-Hypoxic	4ºC, 10ºC	Illuminated, Dark
Summer-Stratification	Offshore-Oxic	4ºC, 10ºC	Illuminated, Dark
Fall-Mixing	Nearshore-Hypoxic	10ºC	Illuminated
Fall-Mixing	Offshore-Hypoxic	10ºC	Illuminated
Fall-Mixing	Offshore-Oxic	10ºC	Illuminated, Dark

At each lake station, a Seabird CTD™ (Conductivity-Temperature-Depth recorder) was used to measure water column profiles for temperature, dissolved oxygen, conductivity, photosynthetically active radiation (PAR), and fluorescence. These measurements depict Lake Erie as a typical dimictic lake including four thermal periods with winter having ice-cover (Table **2**). Benthic samples were collected at each station using a 0.5 m^2 box core sampler (Carrick *et al*. 2005). Upon retrieval of the box core, large amounts of overlaying water were removed through a self-suctioning hose until little to no overlaying water remained. Undisturbed samples were collected by inserting tubes (surface area = 45.6 cm^2) into the surface of each box core. Duplicate box cores (Fig. **3**) were collected from each site and triplicate cores (Fig. **4**) were processed, except in the months of July, August, and September 2007 when duplicate cores were collected. Once retrieved, the top one centimeter of sediment core, average yearly diatom frustules to the surficial sediment (Parker and Edington 1976, Schelske and Stoermer 1972), was extruded from two

cores by pushing sediment through a core tube with a piston. A rod with a rubber stopper was pushed up the tube and samples were dispensed into a beaker and diluted with deionized water to a desired volume.

Table **2**: Seabird CTD™ measurements for temperature, PAR, and dissolved oxygen (where measurements were taken) for the Lake Erie central basin sampling stations and thermal periods in 2007-08.

Thermal Period	Station	Strata	Temperature (ºC)	PAR ($\mu E\ m^{-2}\ s^{-1}$)	Dissolved Oxygen ($mg\ L^{-1}$)
Winter	Offshore-Hypoxic	Epilimnion	0.0	277.2	---
Spring-Mixing	Nearshore-Hypoxic	---	---	---	---
	Offshore-Hypoxic	Epilimnion	4.1	---	---
	Offshore-Oxic	---	---	---	---
Summer-Stratification	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

Fig. **3**: Ship box core sampler (0.5 m^2) collecting surficial Lake Erie central basin sediments 2007-08.

Fig. **4**: Sub-cored surficial Lake Erie central basin sediment collected from the ship box core during 2007-08 These samples were used in the determination of algal pigment concentrations.

Evaluation of Cell Cytology and Rejuvenation Rates

Upon retrieving the triplicate core samples from the duplicate box cores the last core sample was used in the determination of 'vegetative' resting cells on the benthos for each thermal period. When working with the sediment samples, great care was taken ensure minimal light was present, as to not affect the initial results. Sediment cores were sectioned aboard the ship in the shade (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 top, 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-36 L growth chamber was programmed with a desired temperature, light intensity, and photocycle. Hypolimnion lake water that had been collected with Niskin bottles and stored in five liter dark amber bottles was filtered 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 (McQuoid 2002, Sicko Goad *et al.* 1989). Eight grams of sediment core sample was weighed using a Mettler PL-3000 scale and placed into the labeled transparent BOD bottle containing the pre-filtered lake water. Each bottle was then inverted five times (turned bottle

upside down), to simulate lake disturbance, and this was done once every day of the experiment (Sicko-Goad *et al.* 1986).

Analytical Methods

Algal Biomass

In the laboratory, algal biomass was estimated from chlorophyll-*a* concentrations extracted from the sediment samples. 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 (DMSO). Chlorophyll is the green molecule in plant cells that carries out the majority of energy fixation in the process of photosynthesis (Lorenzen 1967). Chlorophyll is probably the most-often used estimator of algal biomass in lakes and streams, at least in North America. When chlorophylls are acidified, the magnesium ion is lost resulting in the production of a phaeophytin. Phaeophytin are the grey photosynthetic pigments also known as detrital chlorophyll (Lorenzen 1967). Chlorophyll-*a* and phaeopigment concentrations were measured fluorometrically using a Turner 10-AU-005 (Carrick *et al*. 1993).

Autofluorescence

Autofluorescence was measured on a Turner 10-AU-005 fluorometer as a proxy for physiological condition. The addition of the inhibitor of non-cyclic electron flow, DCMU (3(3, 4-dichlorophenyl)-1, 1-dimethyl urea), causes an increase in *in vivo* autofluorescence of chlorophyll-a by inhibiting photosynthesis (Vincent, 1980). Each bottle was inverted and 10 mL was placed into a cuvette, in dim light,

and fluorescence was measured. The cuvettes were then placed in the dark for one minute, and 0.1 mL of DCMU stock (at 10^{-3} M) was added to each cuvette. These cuvettes were then tested again for autofluorescence.

Diatom Cell Cytological Determination

Sicko-Goad *et al.* (1989) defined the sequence of cytological events (Fig. **5**). When internally modified resting diatom cells were taken from sediments of a small inland lake, 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 (**1**). Cells that have a condensed cytoplasmic mass usually located in the central cytoplasmic bridge area were classified as true resting cells (**2**). Dead cells were completely devoid of cytoplasm (**3**). 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 (40 X), from each bottle on a Leica DMR research microscope.

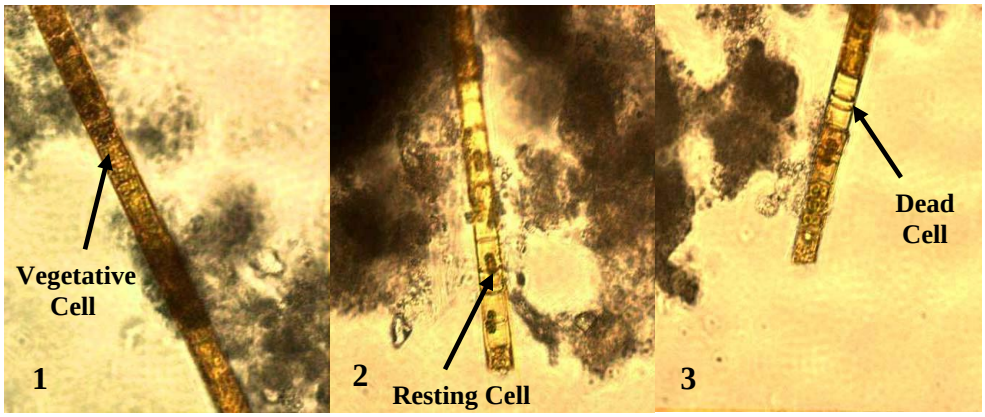


Fig. **5**: Three types of internal cytological modification: **1). vegetative, 2). resting, 3). dead** in *Aulacoseira islandica* diatom rafts.

Data Analysis

For all lake thermal periods, excluding the winter period, a two-way analysis of variance (ANOVA) was performed to compare mean biomass among the thermal periods and lake stations after corrected chlorophyll-*a* concentration was natural log transformed. These tests were followed by Tukey's multiple means comparisons tests to evaluate spatio-temporal differences in chlorophyll mean biomass for each Lake Erie station (Ortega 2007). Mean comparisons and Tukey's multiple means comparisons tests and graphs were performed in Statistical Program for the Social Sciences (SPSS) version 16.0 (© SPSS, Inc., Chicago, IL).

In vivo autofluorescence was 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 paired dark bottles (Bossert and Slobodkin 1983). Due to an unbalanced design, a one-way ANOVA was used to compare the maximum mean physiological efficiency of illuminated bottles spatially; whereas a two-way ANOVA was used to compare the maximum mean physiological efficiency of illuminated bottles temporally and at various incubation temperatures (4ºC and 10ºC). These tests were followed by Tukey's multiple means comparisons tests to evaluate differences in maximum mean physiological efficiency temporally and in different incubation temperatures. A portion of the results displayed an identical mean square error. A fraction of the results were computed for the overall model instead of for individual comparisons. The paired t-test, mean comparisons and Tukey's multiple means comparisons tests and graphs were performed in SPSS

version 16.0 (© SPSS, Inc., Chicago, IL) and Minitab 14.0 (© Minitab, Inc., State College, PA).

Diatom rejuvenation (growth) was used to assess how specific spring bloom dominating species responded to spatio-temporal differences as well as experimental manipulation of light and temperature. Due 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 (4ºC and 10ºC).

Growth rates were used to assess how certain diatom species responded to spatio-temporal variation as well as experimental light and temperature manipulation (Appendix E). The average daily growth rate of increase was calculated in accordance with Mills (2007).

Eq 1: Average daily growth rate of increase = $\ln(N_{t+1}/N_t)/(t_{t+1}-t_1)$

Where: N_{t+1} = the density of cells at time t+1
N_t = the density of cells at time t
t_{t+1} = the time at t+1
t_1 = the initial time

This equation was also applied to the *in vivo* autofluorescence measurements, used to assess the recovery of diatom cell physiological efficiency (Appendix C).

Chapter 4

Results and Discussion

Benthic Chlorophyll

Benthic chlorophyll concentrations in the central basin of Lake Erie exhibited significant spatial and temporal variation; however, the results were complex. Results from a two-way ANOVA indicated a significant interaction between thermal period and lake station (Table **3**). 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. With only limited data for the winter thermal period, conclusions were difficult to formulate.

Table **3**: Two-way analysis of variance explaining spatio-temporal variation in Lake Erie benthic chlorophyll concentrations (mg m^{-2}) from July 2007 through 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

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. **6**). The chlorophyll-a peak during the spring-mixing period can be observed in the benthic water column approximately one month later as a time lag occurs in biomass deposition. Benthic chlorophyll concentrations were generally higher at both hypoxic stations compared

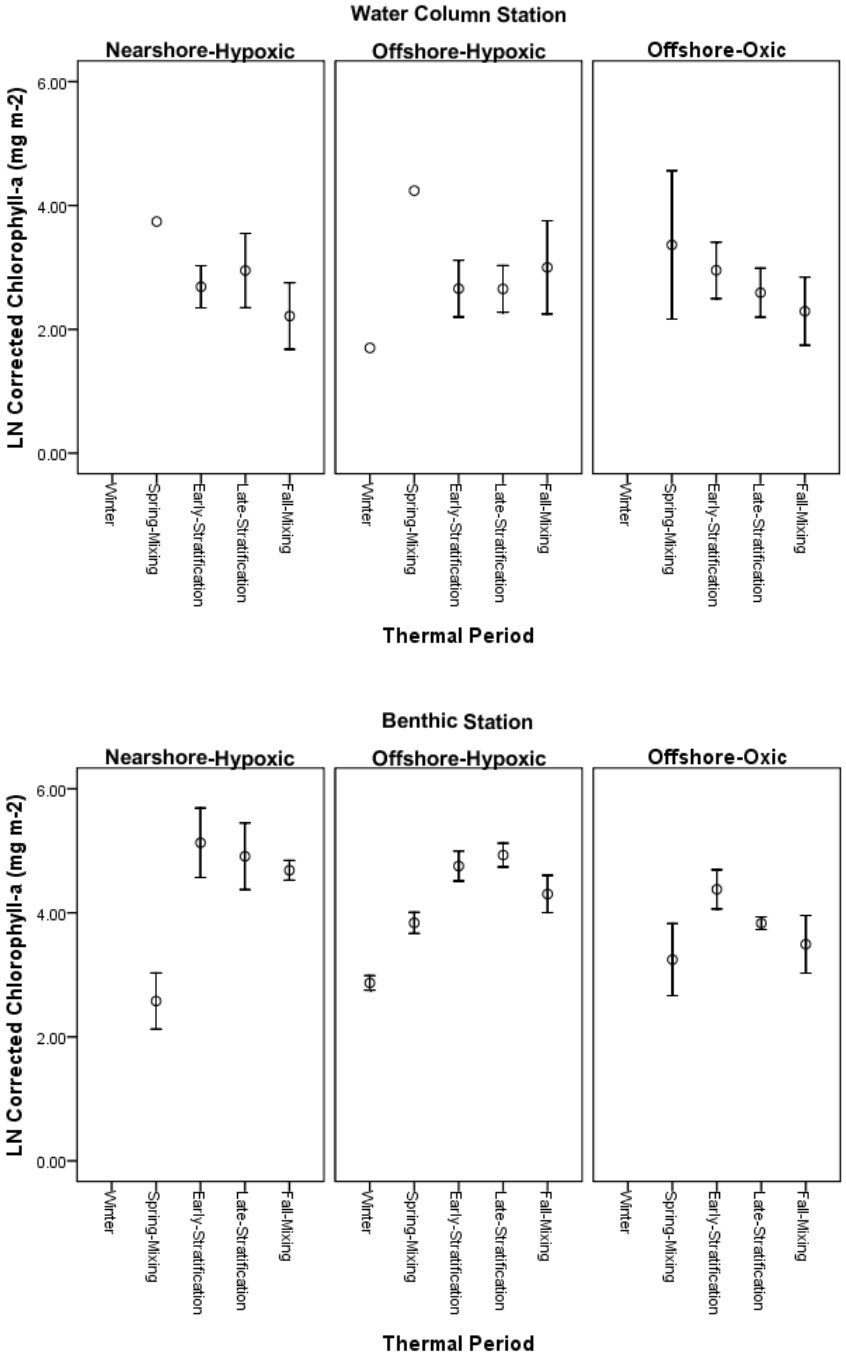


Fig. **6**: Natural log transformations of mean water column and benthic corrected chlorophyll-*a* (mg m^{-2}) collected at three Lake Erie central basin stations over five thermal periods, July 2007 through August 2008.

with the offshore-oxic station (Fig. **6**). Average chlorophyll was approximately double (2.01 times) at the hypoxic stations relative to the oxic station (81.45 mg m^{-2} 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 across lake station from the spring-mixing period to the fall-mixing period (Fig. **6**), revealing an average hypoxic station chlorophyll concentration that was 2.72 times higher compared with that of the oxic station chlorophyll concentration (148.41 mg m^{-2} versus 54.60 mg m^{-2}, respectively). Furthermore, the benthic lake stratification chlorophyll concentrations were more than 2.5 times higher than the mixing periods (101.51 mg m^{-2} versus 40.45 mg m^{-2}, respectively), suggesting that the material is mobile. 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 mg m^{-2} versus 150 mg m^{-2}), chlorophyll-*a* concentrations decline (Carrick *et al.* 2005), suggesting that a large portion of the assemblage may expire over time.

Even a decade after the implementation of the phosphorus removal program in the early seventies, hypoxia remains as a seasonal occurrence in the central basin hypolimnion of Lake Erie (Lam *et al.* 1987). The stations observing hypoxia averaged higher benthic chlorophyll concentrations at the early to mid-stratification periods and declined thereafter (Carrick *et al.* 2005, Rockwell *et al.* 2005), suggesting

that the Lake Erie central basin hypoxia is driven by internal processes that occur due to perfect lake basin structure.

Benthic and water column chlorophyll results corresponded with previous studies suggesting that the assemblage of diatoms inhabiting the benthos is actually a phytoplankton assemblage composed of algae that has settled out of the water column after the onset of unfavorable conditions (Sicko-Goad *et al.* 1989, Nipkow 1950), as seen from similarities in algal composition (Carrick *et al*. 2005). As stratification matures, surface waters become nutrient deficient, temperatures rise, and light intensities increase (Cahill *et al.* 2005, Carrick 2004). A change in water density follows creating a hypolimnion strongly resistant to the mixing power of wave turbulence (Gorham 1989); a characteristic that isolates this area from surface conditions until enough energy to mix the water column from lake storms and changes in water density occur and isothermy results (Schmid 2008). Algal biomass, as well as a variety of other lake fauna, sinks from the surface into the metalimnion and hypolimnion (Carrick *et al.* 2005, Carrick 2004, Catalan *et al.* 2002, Rowe 2001, Nalepa and Quigley 1987, Kingston *et al*. 1983, Stevenson and Stoermer 1981), faster sinking could imply unhealthy lake conditions. A proposed strategy for escaping the deprived surface water conditions was the concept of "algal rain" as discussed by Braidech et al. 1972. This event is observed in the central basin and forms considerable layers atop the sediments that can remain photosynthetically active by forming vegetative resting cells (Sicko-Goad *et al.* 1986, Carrick *et al.* 1993), accounting for the accumulation of chlorophyll later in the year through the months of July to October. This sedimented algal layer has been noted as being meroplanktonic

(Carrick *et al.* 2005), spending a portion of its life throughout the water column and along the benthos, and to seed seasonal algal blooms during the spring-mixing season (Sick-Goad *et al.* 1989).

However, with the increase in water clarity from the invasion of zebra and quagga mussels (*Dreissena polymorpha, Dreissena rostriformis bugensis)*, as well as from decreased nutrient runoff (Effler and Siegfried 1998, Lavrentyev *et al.* 1995, Lowe and Pillsbury 1995, Dolan 1993), temperatures in the meta and hypolimnion during stratification have amplified (Cahill *et al.* 2005). Global warming may currently be affecting cold water species and the lake dynamics, such as algal deposition. In recent years the issue of global climate warming has become a popular subject among environmental scientists and may be influencing the dynamics of Lake Erie more than scientists think. In one case study, water temperature increases were observed to alter the spawning season of the longnose filefish (*oxymonocanthus longirostris*), a species requiring lower temperatures to spawn (Kokita and Nakazona 2000). Increasing water surface temperatures may lead to changes in Lake Erie ice-cover during the winter months while subsequently affecting the lake mixing and stratification events responsible for algal blooms and sedimentation (Cahill *et al*. 2005, Mortsch and Quinn 1996).

These temperature changes may already be influencing the Lake Erie winter waters. While the winter period was not incorporated into the overall results (Table **3**), a rare sample from the central basin described the concentration measured in the winter as being relatively low (< 18.50 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 small. When the lake surface warms and light penetrates through the ice pores, water column density will change creating turbulence (Tilzer 1978). Under these conditions algal blooms are capable of forming, creating conditions similar to that of the popular spring bloom (Jung *et al.* 2008).

If warming happens earlier in the year, this could be a preliminary initiation for the spring-mixing period. Comparable to the winter sample, average chlorophyll concentrations retrieved from the benthos were lower during the mixing periods (40.45 mg m^{-2}). However, the fall was more than 2.72 times higher than the spring chlorophyll concentration (66.69 mg m^{-2} versus 24.53 mg m^{-2}, respectively). Isothermal lake conditions occur as temperatures continue to either increase (spring) or decrease (fall) and the density of the daytime surface and deep waters becomes harder to overcome and turbulent mixing ensues (Lawson 2007). Chlorophyll concentrations from the benthos in mountain lakes were all observed to have lower values during the spring overturn (Catalan *et al.* 2002). With continued mixing and wave action, the chlorophyll concentrations became higher within the water column as benthic algae were resuspended (Catalan *et al*. 2002, Hellstrom 1991, Bengtsson *et al.* 1989). Increases in water column chlorophyll indicate that internal (vertical) loading ultimately drives seasonal productivity during isothermal periods (Catalan *et al*. 2002). With the spring-mixing period showing lower chlorophyll concentrations, I inferred from my results, that the spring overturn disturbs more benthic material; in which case, we would expect a greater algal resuspension event during the spring redistributing, the sometimes viable, population of phytoplankton sedimentation

throughout the water column. Numerous accounts of large spring algal blooms are documented in water columns throughout the world (Depew *et al*. 2006, Carrick *et al*. 2005, Makarewicz 1993), enhancing epilimnion productivity until nutrient depletion commences followed by algal sedimentation.

Lake Erie chlorophyll concentrations as well as hypoxic conditions can be influenced by a number of other possible details. The two hypoxic stations are situated close to the western basin of Lake Erie. This basin is the shallowest with an average depth of 10-11 meters and is biologically the most productive region (Bertram 1993). The western basin is the most productive zone, receiving significant drainage (80%) from the Maumee, Ottawa, and Detroit Rivers (Regier and Hartman 1973). These nutrient rich waters are prime habitat for diatoms and other flora and fauna to survive. Due to its relatively shallow depth, the western basin's deepest waters become warm enough to mix into the epilimnion in the early summer (similar to a polymictic lake), avoiding hypoxia (Bertram 1993). The central basin exhibits an average depth of 24-25 meters. The hypolimnion, because it is cold, tends not to mix with the warmer epilimnion water, and therefore has no opportunity for oxygen replenishment from the atmosphere (Bartish 1984). This oxygen depletion was so severe in the central basin of Lake Erie by the end of the 1960's that large numbers of fish, starved for oxygen, and heavy mats of decaying, floating algae were dying and washing ashore (Bertram 1993). Thus, suggesting that hypoxic areas remain suboptimal for fauna to live and graze (Krieger *et al*. 2007). It is likely that the higher chlorophyll concentrations at the hypoxic stations in the central basin are (in part) driven by material loading from the western basin.

In Lake Erie's eastern basin, hypoxic conditions rarely occur as it is deeper (max depth 63 m) and its hypolimnion is larger and thus resistant to extreme oxygen depletion (Bertram 1993, Lam and Shertzer 1987, Lam *et al*. 1983). The transport of oxygen (via wind transfer, density changes, etc) from the relatively oxygen-rich waters of the eastern basin to the central basin hypolimnion is an important part of the oxygen balance for the central basin (Lam and Shertzer 1987, Boyce *et al.* 1980). Where oxygen is prevalent larger predatory fauna are also present. Castleberry and Cech (1986) explained that hypoxic-exposed fish experienced loss of equilibrium and metabolic failure and even death in some populations. Perch *(Perca flavescens)* and channel catfish (*Ictalurus punctatus*) were once important predators of mayflies (*Ephemeroptera*) until severe hypoxia infected the central basin (Krieger *et al*. 2007, Winter *et al*. 1996, Britt 1955a). Oxygen rich waters are relief regions for organisms to thrive and predate freely on flora inhabiting the water column and benthos (sedimented phytoplankton), creating decreased chlorophyll concentrations, as was observed at the oxic station.

Effects of Illumination on Physiological Condition

The physiological condition of meroplanktonic diatoms collected from the benthos of the central basin was influenced by the addition of modest illumination (Fig. **7**). A significant increase in physiological efficiency (via *in vivo* autofluorescence yield) (Thompson 1997) was observed between illuminated bottles and those bottles which were kept in the dark, mimicking lake bottom conditions. In general, bottles exposed to an illumination of ≈50 μE m^{-2} s^{-1} exhibited higher physiological efficiency compared with bottles that were not exposed to light (Fig. **7**).

Maximum *in vivo* autofluorescence rates, a proxy for physiological efficiency, were observed to be approximately four times higher when exposed to modest illumination (bottles averaged 0.110 µg L^{-1} d^{-1} versus -0.0384 µg L^{-1} d^{-1}, respectively) (Table **4**).

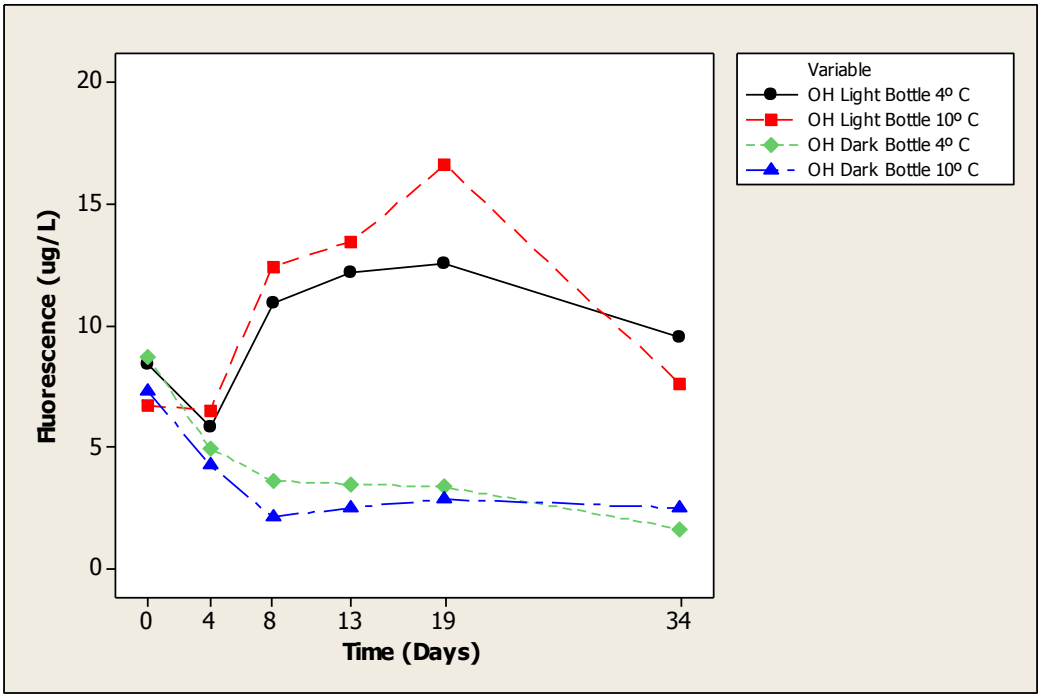


Fig. **7**: Summer-stratification diatom *in vivo* autofluorescence (µg L^{-1}) comparing 4ºC and 10ºC light and dark bottles for the Lake Erie central basin offshore-hypoxic station (Appendix B).

Table **4**: Offshore-hypoxic station light versus dark bottle autofluorescence, expressed as a rate (µg L^{-1} d^{-1}), spanning four lake thermal periods at 10ºC incubation temperature, which did not differ from the 4ºC treatment (Appendix C).

Thermal Period	Light Bottles (µg L^{-1} d^{-1})	Dark Bottles (µg L^{-1} d^{-1})
Winter	0.0568	-0.0182
Spring-Mixing	0.1768	-0.0932
Summer-Stratification	0.0767	-0.1551
Fall-Mixing	0.3061	----------

Within eight days of incubation, a dramatic increase in fluorescence was observed in the experimental bottles exposed to light (≈50 µE m^{-2} s^{-1}) in all four experiments (Fig. **7**). In general, initial fluorescence values were low (≈5-6 units) and increased 3-4 fold. These rejuvenations rates were comparable to that of 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 three days to similar light exposure (Sicko-Goad *et al*. 1989). Also observed were twenty year old sediments containing diatoms (i.e. Aulacoseira *italica*) with the capability of becoming physiologically competent within a one to eight hour period of being exposed to light (Sicko-Goad *et al.* 1986, Lund 1954)

The dark bottle treatment in my experiments mimicked Lake Erie benthic ambient light conditions. The photosynthetically active radiation (PAR) profiles collected from the stations showed that very little light, if any, reached the benthos (Table **5**). Light is attenuated logarithmically with depth revealing that low light alone is capable of inducing a resting phase (Gibson and Fitzsimons 1990). 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 reduced (Smayda and Mitchell-Innes 1974). Darkness rapidly increased the percentage of cells that were in the condensed resting cell formation, from 60% to >90% in 34 days (Fig. **8**), as indicated by the extremely low physiological efficiency of the cells (Sicko-Goad *et al.* 1989). The physiology of diatom cells was drastically affected by the suppressed light levels. Thus, the conditions in my experiments were a reasonable approximation of *in situ* conditions in Lake Erie and appear to be valuable in predicting lake dynamics.

Table **5**: Average photosynthetically active radiation (PAR) (µE m^{-2} s^{-1}) measured at all three lake stations and thermal periods at its maximum depth for the sampling period 2007-08.

Photosynthetically Active Radiation		
Station	Depth (m)	PAR (µE m^{-2} s^{-1})
Nearshore-Hypoxic	18	0.80
Offshore-Hypoxic	23	0.12
Offshore-Oxic	23	0.00

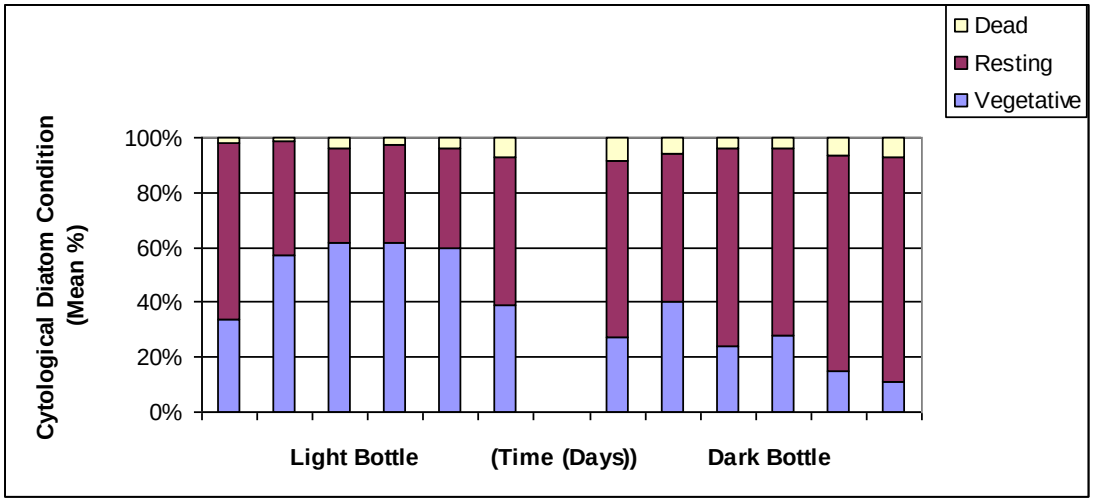


Fig. **8**: Experimental light and dark bottle mean percent of *Aulacoseira islandica* cytological cell condition from the Lake Erie central basin offshore-hypoxic station during the summer-stratification period (2008) for 10°C incubation (Appendix D)

After the onset of unfavorable conditions, a diatom sinking event may be initiated by a number of factors including extreme light causing photoinhibition, nutrient depletion causing lipid stores, and temperature changes (McQuoid 2002, Tiselius and Kuylenstierna 1996, Fitzgerald and Gardner 1993, Sicko-Goad 1989, Smetacek 1985). Sinking may commence the formation of resting cells or resting spores which serve as a survival mechanism and possible 'seed bank' for subsequent populations (McQuoid 2002, Eilerstein *et al*. 1995, Sicko-Goad *et al.* 1989, Sicko-Goad *et al.* 1986, Garrison 1981). In magnitude, resting spores appear to be more frequent in marine species whereas freshwater diatoms are more noted for forming resting cells (Chen et al. 2009). Resting cells also differ in their cellular structure as they are cytologically and physiologically distinguishable from the vegetative cell, containing rounded condensed plastids but show no observable change to the cell wall (Jewson *et al*. 2008, Edlund and Stoermer 1993, Sicko-Goad *et al.* 1986). At collection, an average of 66.15% of cells *(Aulacosiera islandica, Stephanodiscus niagarae, Stephanodiscus binderanus)* on Lake Erie's surficial lake bottom were resting cells. These cells exhibited a low photosynthetic efficiency as their cellular interior is condensed to deal with the low light conditions (Carrick *et al*. 1993, Gibson and Fitzsimmons 1990, Sicko-Goad *et al.* 1986). Resting cells could be described as a dormancy phase. For growth (rejuvenation) to occur, cells must be resuspended, via a lake mixing event, providing them with light, higher temperatures, and nutrients enough to grow (McQuoid 2002), in some cases, causing seasonal algal blooms on Lake Erie. Munawar and Munawar (1986) described that central Lake Erie photosynthetic efficiency of phytoplankton was active during the spring and fall

mixing seasons; thus, resembling a population probably requiring resuspension for growth.

Algal resuspension events are quite common in occurrence. Planktonic species are observed to dominate the surficial sediments of benthos around the world including those off of the Swedish Coast, Switzerland, Africa, Xiamen Bay in Southern China, Hiroshima Bay in Japan, Okoboji Lake in Iowa, East Pike Lake in Minnesota, Lake Michigan, and Lake Erie (Chen *et al.* 2009, McQuoid 2002, Itakura *et al.* 1997, Edlund and Stoermer 1993, Pitcher 1990, Billett *et al.* 1983**,** Stockner and Lund 1970) to name a few. McQuoid (2002) revealed sedimented cells as having no major degradation for most species even after seven months of cold, dark storage. Resting cells are better able to withstand periods of darkness, at cool temperatures, as compared to their vegetative parental cells suggesting that these cells could easily overwinter in the sediments, even at depths up to 1,000 meters (McQuoid and Hobson 1995, Platt *et al*. 1983). This characteristic enables the cell to survive adverse aquatic conditions until resuspension commences.

It is not fully understood what happens to the diatom cellular interior when it is condensed (Sicko-Goad *et al.* 1989). 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). The increase in fluorescence yield could be from stimulated pigments in the diatom's photosynthetic systems, creating higher

chlorophyll concentrations within the cell (Dubinsky *et al*. 1984, Loftus and Seliger 1975).

Illumination appears to be the limiting factor in resting cell populations' ability to rejuvenate in many environments (Harrison and Platt 1986, Hollibaugh *et al*. 1981). Phytoplankton photosynthesis at any depth depends on the quantity and quality of light (Dubinsky *et al*. 1984). Cell culture experiments have shown that significant increases in algae rejuvenation are experienced by the addition of light and turbulence (diel variation) (Falkowski 1984, Vincent 1978, Phillips and Meyers 1954). Hollibaugh *et al*. (1981) recorded that upon exposure to light of 150 µE m^{-2} s^{-1} resting spores began to germinate after 24-36 hours of continuous illumination. Comparatively, surficial sediments from Xiamen Bay in China and Hiroshima Bay in Japan when exposed to light of 50 µE m^{-2} s^{-1} diatom resting cells were able to resume growth within a day of being illuminated (Chen *et al*. 2009, Itakura *et al.* 1997). Thus, the results suggest that the rejuvenation of resting cells is initiated by light.

Spatio-Temporal Effects on Physiological Condition

Based on laboratory enclosure experiments, maximum physiological efficiency in the central basin did not exhibit significant spatial variation (One-Way ANOVA, p-value = 0.964) nor was it altered by different incubating temperatures; however, significant temporal variation was noted (Table **6**). Distinct temporal variation was observed in the fall-mixing period. Maximum physiological efficiency rates averaged 0.384 µg L^{-1} d^{-1} across the three lake stations and incubating temperatures for this thermal period. Whereas, maximum physiological growth

averaged 0.092 µg L^{-1} d^{-1}, approximately 4.17 µg L^{-1} d^{-1} times lower than that of the fall-mixing period.

Table **6**: Two-way analysis of variance explaining maximum physiological efficiency/day (µg L^{-1} d^{-1}), via *in vivo* fluorescence, between Lake Erie thermal period and incubation experimental temperatures (4ºC and 10ºC) from 2007-08.

Factor	df	MS	F-value	p-value
Thermal Period	3	0.010	18.34	0.000
Experimental-Temperature Interaction	1	0.091	2.01	0.170
	2	0.002	0.41	0.667

Phytoplankton cells have been observed to respond so rapidly to their environments that conventional methods of studying their populations tend to fail. Therefore it is extremely difficult to reveal many of the more subtle aspects of their dynamic ecology (Ryther *et al.* 1958). Plants are highly variable in their cellular composition and reactions to their environmental surroundings at different times of the day and year (Ryther *et al.* 1958). Such characteristics create great difficulty in studying such phenomena. It is necessary to make more intensive observations, which may need to be isolated from the entire lake system. Laboratory studies have their difficulties; however, trying to study organisms under completely natural lake conditions should require no further explanation.

After the onset of lake stratification, many planktonic 'bloom' diatoms have the ability to access deeper waters of the lake through sedimentation, until suitable growing conditions return. After stratification and sinking commences, the onset of the diatom resting cell phase is established (Sicko-Goad 1989, Smetacek 1985). Average cell physiological efficiency was low, approximately 0.073 µg L^{-1} d^{-1}. Eadie *et al*. (1984) observed increased light attenuation in the overlying benthic

waters during lake stratification periods. Material deposition and resuspension of sedimentary material composed of nonorganic matter could be the cause. Thus, creating areas of increased darkness on the surficial lake sediments and subsequently generating diatom cells that are not as photosynthetically efficient.

After stratification, isothermal conditions occur after the commencement of lake mixing. Nutrients derived from the sediments are resuspended and introduced back throughout the water column with diatom cells that have been resting on the surficial lake sediments (Cotner *et al*. 2000, Eadie *et al*. 1996). Diatoms are then in position for increased growth rates as warmth and illumination are amplified as well (Stockner and Lund 1970). Increased light from vertical mixing is the final factor needed for diatom rejuvenation; however, severe light intensities have inhibited photosynthesis (Falkowski 1984), so the resuspended particulate matter has been suggested as a form of diatom refuge. Many species, especially those capable of resting cell formation, have adapted to these shaded conditions which actually increases their light utilization efficiencies (Prezelin 1976). Turbulence coupled with increased nutrient availability and light may be enough to trigger an initial response in diatom cell physiological condition (Millie *et al.* 2002, Fahnenstiel *et al.* 2001).

However, average maximum diatom physiological condition was 4.57 times higher during the fall-mixing period compared to the spring-mixing period (0.384 µg L^{-1} d^{-1} versus 0.084 µg L^{-1} d^{-1}, respectively). It is difficult to explain why there would be such a drastic difference between mixing periods. Hollibaugh *et al*. (1981) found that the percentage of resting spores in *Chaetoceros* species that germinated decreased over time, which seems more intuitive. Initial observations illustrated that

80-90% of *Chaetoceros* cells were able to germinate upon exposure to favorable conditions. However, after 167 days an estimated 50% of cells germinated and after 392 days of storage only 20% germinated. This increased lag period of rejuvenation is not uncommon (Sicko-Goad *et al.* 1986). Anderson (1976) reported only some cells of an isolated population of *Amphora coffaeformis* are capable of successfully completing resting cell formation. He observed that growth of fully condensed resting cells, when reintroduced to light, was staggered, as did Sicko-Goad *et al*. (1986) when studying *Aulacoseira granulata* species. Staggered growth resumption could be yet another form of survival mechanism for diatom cells, ensuring that a fraction of viable cells are retained, should unfavorable growth conditions occur close after rejuvenation. The difference I observed in the lake mixing rejuvenation capability may be attributed to this survival mechanism, guaranteeing long term survival of planktonic diatoms in highly fluctuating environments (Itakura *et al.* 1997).

Diatoms in Lake Erie appeared to tolerate both hypoxic and oxic conditions, as well as incubation temperature ranges from 4ºC to 10ºC. Previous laboratory work illustrated that *Aulacoseira* could live in an anoxic environment for up to three years (Stockner and Lund 1970). Diatoms can also survive burial in anoxic water sediments. *Stephanodiscus hantzschii* was capable of rejuvenation after being buried for ten years in a deep Swedish lake (Edlund and Stoermer 1993, Stockner and Lund 1970). Surface sediments from various Swedish Fjords were examined to determine spatial variation in diatom resting stages (McQuoid 2002). Individual species demonstrated distinct patterns of viable cells, some growing faster in nearshore

waters while others preferred the offshore stations (McQuoid 2002). Diatoms have been suggested as being an r-selected species, where large numbers can survive and remain viable even under less than favorable conditions (Itakura *et al.* 1997). For example, areas where low oxygen concentrations are prevalent benthic microfauna are rarely present. Thus, the diatom 'seed bank' can go relatively undisturbed by grazing events. However, in oxygenated sediments predation is more of an important factor controlling the survival and distribution of benthic resting cells (McQuoid 2002). Numerous diatom resting cells have been documented to survive passage through the animal digestive system (Barille and Cognie 2000) increasing the importance of those diatoms that are capable of forming resting stages. Thus, it appears that diatom resting cells have evolved to be spatially unspecific, possessing the ability to survive in various environments (McQuoid 2002).

Variation of incubation temperatures (4ºC and 10ºC) was also ineffective in various diatom resting cell rejuvenation. Temperature has long been suggested to be a major co-factor in diatom growth patterns (Lund 1949); but it is has been difficult to separate the difference between temperature and illumination in the natural environment (which tends to regulate temperature) (Reynolds 1984). Kiefer (1973) reported natural phytoplankton communities in the Gulf of California illustrated no temperature effect on the communities fluorescing capabilities. Physiological stress has also been suggested as a possible reason for variation in physiological efficiency, which is independent of light effects, in environments with fluctuating temperature (Kiefer 1973).

Many diatoms have the ability to adapt to their environment (Goldman and Carpenter 1974). *Skeletoma costatum* was transferred from a 20ºC environment to an 8ºC environment and photosynthetic efficiency initially decreased by one third (Nielson and Jorgensen 1968). However, the cells adapted to the lower temperature and the photosynthetic efficiency became practically the same as previously observed, this response was also observed in *Asterionella glacialis* (Karentz and Smayda 1984, Morris and Farrell 1971, Nielson and Jorgensen 1968). Diatom species were also isolated in different environments, ranging from arctic to temperate, tended to grow within different temperature ranges (Suzuki and Takahashi 1995), reaching maximum growth rates in both. Temperate species tended to require a broader temperature range to cover wider temperature variation within their habitat (Suzuki and Takahashi 1995). Six diatom species were studied, including *Stephanodiscus hantzchii*, which exhibited a temperature range for growth spanning 5ºC to 25ºC, while surviving 2ºC for a month (Suzuki and Takahashi 1995). Ryther (1976) concluded temperature as having little effect on the production of phytoplankton in the sea, observing that meroplanktonic species could germinate anywhere between 7ºC and 20ºC, surviving both summer and winter sediment temperatures in Narragansett Bay. If given the opportunity, diatom species will grow over different temperatures playing an important role in algal competition and in the composition of various specialized niches in the natural environment (Goldman and Carpenter 1974). The considerable variation in apparent optimal temperature for diatom rejuvenation may suggest that other factors are involved and are interacting

with temperature to control species populations, such as nutrients, light, etc (Conley *et al.* 1993, Braarud 1962).

Diatom Rejuvenation and Environmental Niche Space

The meroplanktonic assemblage in Lake Erie is dominated by three centric (radial symmetry in valve view and usually circular, oval, or elliptical) 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 et al. 2005, Carrick 2004). Maximum growth rates among species (Table **7**) and Lake Erie stations and thermal periods differed (Table **8**), suggesting the presence of environmental niches.

Table **7**: Overall maximum experimental growth rates (Vegetative Cells d^{-1}) observed for three Lake Erie diatom species over four thermal periods, three stations, and two experimental temperatures (4ºC and 10ºC) in 2007-2008 (Appendix E).

Diatom Species	Growth Rate (Vegetative Cells d^{-1})
Aulacoseira islandica	0.162
Stephanodiscus niagarae	0.604
Stephanodiscus binderanus	0.589

Large lakes, such as Lake Erie, present the opportunity for spatial or temporal niche space (Table **8**), due to various environmental habitats that may accommodate numerous species. Large lake systems provide opportunity for the separation of phytoplankton populations to occur (Stoermer *et al.* 1981). Many algal populations which normally do not co-occur in smaller systems are found in visible association with each other in the great lakes (Stoermer *et al.* 1981), leading to diatom population characteristic interpretation problems.

Table **8:** One-way analysis of variances comparing Lake Erie central basin maximum diatom species growth rates, vegetative cells d^{-1}, (low to high) among stations and thermal periods (2007-08), non-overlapping lines indicate a significant difference ($p<0.05$).

Station	df	MS	F-value	p-value	Species		
Nearshore-Hypoxic	2	0.280	10.41	0.001	*S. niagarae* 0.017	*A. islandica* 0.019	*S. binderanus* 1.000
Offshore-Hypoxic	2	0.689	3.75	0.033	*A. islandica* 0.049	*S. binderanus* 0.137	*S. niagarae* 0.469
Offshore-Oxic	2	0.171	4.03	0.029	*A. islandica* 0.014	*S. niagarae* 0.190	*S. binderanus* 0.269
Thermal Period	**df**	**MS**	**F-value**	**p-value**	**Species**		
Winter	2	1.072	2.33	0.153	*A. islandica* 0.005	*S. binderanus* 0.013	*S. niagarae* 0.905
Spring-Mixing	2	0.150	2.38	0.180	0.066	0.221	0.283
Summer-Stratification	2	0.650	1.64	0.218	0.010	0.124	0.188
Fall-Mixing	2	0.575	173.06	0.000	*A. islandica* 0.007	*S. niagarae* 0.009	*S. binderanus* 0.545

Observations of advected meroplanktonic diatom populations from surficial nutrient rich lake sediments has documented the ability of diatoms to store nutrients such as phosphorus and to survive transport to considerable distances from the area at which their primary growth niche originated (Stoermer *et al.* 1981). Diatom populations range considerably in polymorphic expression, which can lead to

confusion and problems in identification, as varieties of sub-species have been observed (Theriot *et al.* 2006).

Diatom species, like various other living flora and fauna, have long been observed in special environmental niches. 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 (Stoermer and Sicko-Goad 1985, Theriot and Stoermer 1981). 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). *Stephanodiscus niagarae* has been noted prevalent during the fall and spring-mixing periods in Lake Ontario (Julius *et al.* 1998, Stoermer and Yang 1970), and to be widely distributed in North America as well as throughout interglacial deposits from Asia and Europe (Stoermer *et al*. 1989). An example of diatom evolution comes from Yellowstone Lake in Wyoming. A diatom with *Stephanodiscus niagarae* morphology visibly occupied Yellowstone Lake sometime after glacial recession (Theriot *et al.* 2006). Over time, the secluded diatom species *Stephanodiscus niagarae* evolved, until *Stephanodiscus yellowstonensis* speciated (Theriot *et al*. 2006), demonstrating a rapid diatom speciation event.

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). These great lakes have undergone considerable

anthropogenic eutrophication, which has resulted in substantial variation of several diatom populations (Stoermer *et al.* 1989). Many species of *Aulacoseira* and *Stephanodiscus* are meroplanktonic, and found in the plankton only during periods when the water column is undergoing turbulent mixing (Liukkonen *et al.* 1993, Munawar and Munawar 1986, Willen 1962, Lund 1954, Nipkow 1950). *Aulacoseira islandica* and *Stephanodiscus binderanus* have dominated the diatom peaks thus far, probably due to their generalistic lifestyles (Solovieva *et al.* 2005, Langaste *et al.* 1996). Commonly found in surficial lake sediments forming vegetative resting cell stages, this diatom species has evolved strong environmental adaptations for survival as well as clear thermal tolerances suggested by their distribution throughout the Great Lakes (Langaste *et al.* 1996, Lund 1954, Nipkow 1950). 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 (Solovieva *et al.* 2005, Montagnes and Franklin 2001).

Chapter 5

Conclusions

Benthic surficial biomass, estimated by corrected chlorophyll *a*, showed no spatial difference in biomass, but a temporal difference was observed. A bell-shaped distribution of benthic biomass (Fig. **6**) was present amongst the lake stations with higher values during lake stratification periods and lower values at the lake mixing periods. Sunlight appeared to be the limiting factor in diatom recovery of physiological condition within the central basin of Lake Erie. A significant difference in diatom illuminated bottle physiological condition and those kept in the dark was detected, suggesting the environmental factor, sunlight, was necessary for diatom cell recovery from vegetative resting cells. Maximum diatom physiological condition occurred during the fall-mixing period, when higher autofluorescence values were measured. These high values can be explained by the diatom's ability to preserve their population by turning on and off their rejuvenation capabilities when fully transformed into the vegetative resting state.

Lakes within a related geographic region can exhibit similar year-to-year patterns and fluctuations in limnological variables, an attribute entitled synchrony (Patoine and Leavitt 2006, Kratz *et al*. 1998) or temporal consistency (Magnuson *et al*. 1990). Large-scale synchronous events suggest that environmental factors, such as climate, are involved in the control of lake processes, diatom population abundance, and diatom cytological cell condition (Patoine and Leavitt 2006). Diatom synchrony in abundance and cytological cell condition may occur seasonally. For instance, I observed algal biomass measurements in water column chlorophyll-*a* to be

higher in the spring than in the fall (Carrick *et al.* 2005, George *et al.* 2000), illustrating a recognized synchronous seasonal pattern described by many others. Therefore, algal groups blooming in the spring are synchronous to that thermal period. Patoine and Leavitt (2006) suggested algal synchrony has been examined only as total biomass and that little is known of whether temporal coherence varies among taxonomic groups. Species-specific patterns of synchrony may be useful for a variety of different environmental mechanisms. Certain diatom species (i.e. *Didymosphenia geminata*) can be a nuisance to ecosystem health, affecting sources of food for fish and making recreational activities unpleasant (Bhatt *et al.* 2007). *Didymosphenia geminata,* a diatom once thought to inhabit only northern ecosystems, was introduced to New Zealand in 2004 (Bhatt *et al.* 2007). The distribution of *Didymosphenia geminata* has expanded outside its native range, and excessive growth is becoming hard to control (Bhatt *et al.* 2007). *Didymosphenia geminata* maximum cell growth could be linked to a certain temporal period, and once this period is identified, *Didymosphenia geminata* could be removed from the nonnative ecosystem. Changing land-use patterns and climatic conditions prove to be important factors in lake synchrony events; however, as these factors continue to change, it remains difficult to explain the biological importance of algal synchrony (Patoine and Leavitt 2006).

Diatom species' niches were observed for *Aulacoseira islandica, Stephanodiscus niagarae, and Stephanodiscus binderanus.* Spatio-temporal variation was noted among species, with each diatom favoring different environmental conditions. Previous studies suggest diatoms do favor certain conditions and that

some species, such as *Stephanodiscus niagarae*, are specialists while others are generalistic in their approach (Theriot *et al.* 2006, Stoermer *et al.* 1981), which may explain some of the variation I observed; however, global climate change has also been suggested as influencing aquatic ecosystem functions (Cahill *et al*. 2005).

With global warming and global pollution on the increase our world's freshwater systems are under a great deal of stress. Cahill et al. (2005) suggested the most significant air temperature increase in the Great lakes region will occur in winter with increases ranging 4-9ºC and spring increases ranging 3-8ºC. Phytoplankton dynamics and growth are strongly controlled by temperature, turbulence, and the strength of thermal stratification in the water column (Winder 2004). Reynolds (1984) proposed spring conditions favor fast growing diatoms, with high nutrient, but low light and temperature requirements.

A warming effect has resulted and enhanced evaporation in the Great Lakes (Cahill *et al*. 2005 Sousounis and Bisanz 2000, Magnuson *et al.* 1997, Mortsch and Quinn 1996), subsequently reducing all five of the lakes' water levels. Climate and hydrologic changes affect the quantity and quality of wetland and aquatic habitats, alter the frequency and timing of lake turnover, change dissolved oxygen, and alter flora and fauna community composition and dynamics (Mortsch and Quinn 1996). Sedimentation and rejuvenation of meroplanktonic resting cells may be synchronously linked with yearly climatic and hydrologic lake changes, allowing for diatom survival in hypoxic areas and for diatom seasonal "seed" blooms.

Bibliography

Anderson, O.R. 1976. Respiration and Photosynthesis During Resting Cell Formation in *Amphora coffeaeformis* (Ag.) Kütz. *Limnol. Oceanogr*. 21: pp. 452–6.

Barille, L. and B. Cognie. 2000. Revival Capacity of Diatoms in Bivalve Pseudofaeces and Faeces. Diatom Research. – Biopress Limited.

Bartish, T.M. 1984. Thermal Stratification in the Western Basin of Lake Erie: Its Characteristics, Mechanisms of Formation, and Chemical and Biological Consequences. Technical Report No. 289. Centre for Lake Erie Area Research, Columbus, Ohio.

Bengtsson, L., T. Hellstrom and L. Rakoczi. 1990. Redistribution of Sediments in Three Swedish Lakes. *Hydrobiologia.* 192: pp. 167-181.

Bertram, P.E. 1993. Total Phosphorus and Dissolved Oxygen Trends in the Central Basin of Lake Erie, 1970-1991. *J. Great Lakes Res.* 19: pp. 224-236.

Bhatt, J.P., Bhasker, A., and Pandit, M.K. 2007. Biology, Distribution and Ecology of *Didymosphenia geminate* (Lyngbye) Schmidt an Abundant Diatom from the Indian Himalayan Rivers. *Aquatic Ecology*. 42(3): pp. 347-353.

Billett, D.S.M., R.S. Lampitt, A.L. Rice and R.F. Mantoura. 1983. Seasonal Sedimentation of Phytoplankton to Deep-Sea Benthos. *Nature*. Lond. 302: pp. 520-522.

Birge, E.A. and Juday, C. 1911. The Inland Lakes of Wisconsin: The Dissolved Gases of the Water and Their Biological Significance. *Wisconsin Geol Nat Hist Bull.* 22.

Bossert, P. and Slobodkin, L.B. 1983. The Effect of Fast, and Regeneration in Light vs. Dark, on Regulation in the Hydra-algal Symbiosis. *Biol. Bull.* 164: pp. 396-405.

Braarud, T. 1962. Species Distribution in Marine Phytoplankton. *J. Oceanogr. Soc. Jap.* 20: pp. 628-649.

Braidech, T., P. Gehring and C. Kleveno. 1972. Biological Studies Related to Oxygen Depletion and Nutrient Regeneration Processes in the Lake Erie Central Basin. *In Project HYPO—an intensive study of the Lake Erie central basin hypolimnion and related surface water phenomena*, N.M. Burns and C. Ross,eds. CCIW paper No. 6, U.S. EPA Report No. TS-04-71-208-24.

Britt, N.W. 1955a. Stratification in Western Lake Erie in Summer of 1953: Effects on the *Hexagenia* (Ephemeroptera) Population. *J. of Ecology*. 36: pp. 239-244.

Boyce, F.M., F. Chiocchio, B. Eid, F. Penicka, and F. Rosa. 1980. Hypolimnion Flow Between the Central and Eastern Basins of Lake Erie During 1977 (Interbasin Hypolimnion Flows). *J. Great Lakes Res.* 6(4): pp. 290-306.

Cahill, K.L., J.M. Gunn and M.N. Futter. 2005. Modelling Ice Cover, Timing of Spring Stratification, and End-Of-Season Mixing Depth in Small Precambrian Shield Lakes. *Can. J. Fish. Aquat. Sci.* 62: pp. 2134–2142.

Carrick, H.J. 2004. Algal Distribution Patterns in Lake Erie: Implications For Oxygen Balances in the Eastern Basin. *J. Great Lakes Res.* 30(1): pp. 133-147.

Carrick, H.J., F.J. Aldridge and C.L. Shelske. 1993. Wind Influences Phytoplankton Biomass and Composition in a Shallow, Prodcitve Lake. *Limnol. Oceanogr.* 38(6): pp. 1179-1192.

Carrick, H.J., J.B. Moon and B.F. Gaylord. 2005. Phytoplankton Dynamics and Hypoxia in Lake Erie: A Hypothesis Concerning Benthic-pelagic Coupling in the Central Basin. *J. Great Lakes Res*. Vol. 31 (Suppl. 2): pp. 111-124.

Castleberry, D.T., and J.J. Cech Jr. 1986. Physiological Responses of a Native and an Introduced Desert Fish to Environmental Stressors. *J. of Ecology*. 67(4): pp. 912-918.

Catalan, J., M. Ventura, A. Brancelj, I. Granados, H. Thies, U. Nickus, A. Korhola, A. F. Lotter, A. Barbieri, E. Stuchlík, L. Lien, P. Bitušík, T. Buchaca, L. Camarero, G.H. Goudsmit, J. Kopá‹ek, G. Lemcke, D.M. Livingstone, B. Müller, M. Rautio, M. Šiško, S. Sorvari, F. Šporka, O. Strunecky and M. Toro. 2002. Seasonal Ecosystem Variability in Remote Mountain Lakes: Implications for Detecting Climatic Signals in Sediment Records. *J. of Paleolimnology* 28: pp. 25–46.

Chen, C., L. Sun, Y. Gao, Q. Zhou, M. Zheng, B. Li, Y. Yu, and D. Lu. 2009. Seasonal Changes of Viable Diatom Resting Stages in Bottom Sediments of Xiamen Bay, China. *J. of Sea Research*. Article in Press.

Conley, D.J., Schelske, C.L., and Stoermer, E.F. 1993. Modification of the Biogeochemical Cycle of Silica with Eutrophication. *Mar. Ecol. Prog. Ser.* 101: pp. 179-192.

Cotner, J.B., T.H. Johengen, and B. Biddanda. 2000. Intense Winter Heterotrophic Production Stimulated by Benthic Resuspension. *Limnol. Oceanogr.* 45: 1672–6.

Davis, C.C. 1964. Evidence for the Eutrophication of Lake Erie from Phytoplankton Records. *Limnol. Oceanogr.* 9(3): pp. 275-283.

Depew, D., R. Smith and S. Guildford. 2006. Production and Respiration in Lake Erie Plankton Communities. *J. Great Lakes Res.* 32: pp. 817–831.

Diaz, R.J. 2001. Overview of Hypoxia Around the World. *J. of Env. Qual.* 30: pp. 275-281.

Dolan, D.M. 1993. Point Source Loadings of Phosphorus to Lake Erie: 1986-1990. *J. Great Lakes Res.* 19: pp. 212-223.

Dolan, D.M., and McGunagle, K.P. 2005. Lake Erie Total Phosphorus Loading Analysis and Update: 1996 to 2002. *J. Great Lakes Res.* 31(Supplement 2): pp. 11-22.

Dortch, Q., N.N. Rabalais, R.E. Turner, and G.T. Rowe. 1994. Respiration Rates and Hypoxia on the Louisiana Shelf. *Estuaries*. 17(4): pp. 862-872.

Dubinsky, Z., T. Berman, and F. Schanz. 1984. Field Experiments for *in situ* Measurements of Photosynthetic Efficiency and Quantum Yield. *J. of Plankton Research.* 6(2): pp. 339-349.

Eadie, B.J., R.L. Chambers, W.S. Gardner, and G.L. Bell. 1984. Sediment Trap Studies in Lake Michigan: Resuspension and Chemical Fluxes in the Southern Basin. *J. Great Lakes Res.* 10(3): pp. 307-321.

Eadie, B.,D. Schwab, R. Assel, N. Hawley, B. Lansing, R. Miller, N. Morehead, and J. Robbins. 1996. Development of Recurrent Coastal Plume in Lake Michigan Observed for the First Time. EOS, Trans. Am. Geophys. Un. 77: 337–8.

Edlund, M.B. and E.F. Stoermer. 1993. Resting Spores of the Freshwater Diatoms *Acanthoceras* and *Urosolenia*. *J. of Paleolimnolgy*. 9: pp. 55-61.

Effler, S.W. and C. Siegfried. 1998. Tributary Water Quality Feedback from the Spread of Zebra Mussels: Oswego River, New York. *J. Great Lakes Res.* 24(2): pp. 453-463.

Eilerstein, H.C., S. Sanburg, and H. Tollefsen. 1995. Photoperiodic Control of Diatom Spore Growth: A Theory to Explain the Onset of Phytoplankton Blooms. *Mar. Ecol. Prog. Ser*. 116: pp. 303-307.

Falkowski, P.G. 1984. Physiological Responses of Phytoplankton to Natural Light Regimes. *J. of Plankton Research.* 6(2): pp. 295-307.

Falkowski, P.G. and J.A. Raven. 2007. Aquatic Photosynthesis, 2nd edn, Princeton University Press, Princeton, New Jersey. pp. 484.

Fahnenstiel, G.L. and D. Scavia. 1987. Dynamics of Lake Michigan Phytoplankton: The Deep Chlorophyll Layer. *J. of Great Lakes Res*. 13(3): pp. 285-295.

Fahnenstiel, G.L., R.A. Stone, M.J. McCormick, C.L. Schelske, and S.E. Lohrenz. 2001. Spring Isothermal Mixing in the Great Lakes: Evidence of Nutrient Limitation and Nutrient-Light Interactions in a Suboptimal Light Environment. *Can. J. Fish. Aquat. Sci.* 57: 1901–10.

Fitzgerald, S.A. and W.S. Gardner. 1993. An Algal Carbon Budget for Pelagic-Benthic Coupling in Lake Michigan. *Limnol. Oceanogr.* 38(3): pp. 547-560.

Garrison, D.L. 1981. Monterey Bay Phytoplankton. II. Resting Spore Cycles in Coastal Diatom Populations. *J. of Plankton Research.* 3(1): pp. 137-156.

Gibson, C.E. and A.G. Fitzsimons. 1990. Induction of the Resting Phase in the Planktonic Diatom *Aulacoseira subarctica* in Very Low Light. *Br. Phycol. J.* 25: pp. 329-334.

Goldman, J.C. and E.J. Carpenter. 1974. A Kinetic Approach to the Effect of Temperature on Algal Growth. *Limnol. Oceanogr.* 19(5): pp. 756-766.

Gorham, E. and F.M. Boyce. 1989. Influence of Lake Surface Area and Depth Upon Thermal Stratification and the Depth of the Summer Thermocline. *J. Great Lakes Res.* 15(2): pp. 233-245.

Harrison, W.G. and T. Platt. 1986. Photosynthesis-Irradiance Relationships in Polar and Temperate Phytoplankton Populations. *Polar Biol*. 5: pp. 153-164.

Herdendorf, C. E. 1984. Inventory of the Morphometric and Limnologic Characteristics of the Large Lakes of the World: Ohio State University Sea Grant Program Technical Bulletin OHSU-TB-17.

Hellstrom, T. 1991. The Effect of Resuspension on Algal Production in a Shallow Lake. *Hydrobiologia.* 213: pp. 183-190.

Hollibaugh, J.T., D.R.L. Seibert, and W.H. Thomas. 1981. Observations on the Survival and Germination of Resting Spores of Three *Chaetoceros* (Bacillariophyceae) Species. *J. Phycol*. 17: pp. 1-9.

Itakura, S., I. Imai, and K. Itoh. 1997. "Seed bank" of Coastal Planktonic Diatoms in Bottom Sediments of Hiroshima Bay, Seto Inland Sea, Japan. *Marine Biology*. 128: pp. 497-508.

Jewson, D.H., N.G. Granin, A.A. Zhdanov, L.A. Gorbunova, N.A. Bondarenko, and R.Y. Gnatovsky. 2008. Resting Stages and Ecology of the Planktonic Diatom *Aulacoseira skvortzowii* in Lake Baikal. *Limnol. Oceanogr.* 53(3): pp. 1125-1136.

Julius, M.L., E.F. Stoermer, C.M. Taylor, and C.L. Schelske. 1998. Local Extirpation of *Stephanodiscus niagarae* (Bacillariophyceae) in the Recent Limnological Record of Lake Ontario. *J. Phycol*. 34: pp. 766-771.

Jung, S.W., B.H. Kim, T. Katano, D.S. Kong and M.S. Han. 2008. *Pseudomonas fluorescens* HYK0210-SK09 Offers Species-Specific Biological Control of Winter Algal Blooms Caused by Freshwater Diatom *Stephanodiscus hantzschii*. *Journal of Applied Microbiology.* 105(1): pp. 186-195.

Kalff, Jacob. 2002. Limnology: Inland Water Ecosystems. Prentice-Hall, Inc.

Karentz, D. and T.J. Smayda. 1984. Temperature and Seasonal Occurrence Patterns of 30 Dominant Phytoplankton Species in Narragansett Bay over a 22-Year Period (1959-1980). *Mar. Ecol. Prog. Ser.* 18: pp. 277-293.

Kiefer, D.A. 1973. Fluorescence Properties of Natural Phytoplankton Populations. *Biology*. 22: pp. 263-269.

Kingston, J.C., R.L. Lowe, E.F. Stoermer and T.B. Ladewski. 1983. Spatial and Temporal Distribution of Benthic Diatoms in Northern Lake Michigan. *J. of Ecology.* 64(6): pp. 1566-1580.

Kratz, T. K., Soranno, P.A., Baines, S.B, Benson, B.J., Magnuson, J.J., Frost, T.M., and Lathrop, R. 1998. Interannual Synchronous Dynamics in North Temperate Lakes in Wisconsin, USA. Kluwer Academic, Dordrecht, The Netherlands. pp. 273–287.

Krieger, K.A., M.T. Bur, J.J.H. Ciborowski, D.R Barton and D.W. Schloesser. 2007. Distribution and Abundance of Burrowing Mayflies (*Hexagenia* spp.) in Lake Erie, 1997–2005. *J. Great Lakes Res.* 33 (Supplement 1): pp. 20–33.

Lam D.C.L. and W.M. Shertzer. 1987. Lake Erie Thermocline Model Results: Comparison with 1967-1982 Data and Relation to Anoxic Occurrences. *J. Great Lakes Res*. 13: pp. 757-769.

Lam, D.C.L., W.M. Shertzer, and A.S. Fraser. 1987. Oxygen Depletion in Lake Erie: Modeling the Physical, Chemical, and Biological Interactions, 1972 and 1979. *J. Great Lakes Res.* 13(4): pp. 770-781.

Lam, D.C.L., W.M. Shertzer, and A.S. Fraser. 1983. Simulation of Lake Erie Water Quality Responses to Loading and Weather Variations. IWD Scientific Series No. 134, NWRI, Burlington, Ont.

Langaste, R., V.V Jastremskij, and I. Ott. 1996. Phytoplankton of Lake Peipsi-Pihkva: Species Composition, Biomass and Seasonal Dynamics. *Hydrobiologia.* 338: pp. 49-62.

Lavrentyev, P.J., W.S. Gardner, J.F. Cavaletto, and J.R. Beaver. 1995. Effects of the Zebra Mussel *(Dreissena polymorpha* Pallas) on Protozoa and Phytoplankton from Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21: pp. 545-557.

Lawson, R. and M.A. Anderson. 2007. Stratification and Mixing in Lake Elsinmore, California: An Assessment of Axial Flow Pumps for Improving Water Quality in a Shallow Eutrophic Lake. *Water Research*. 41: pp. 4457-4467.

Liukkonen, M., T. Kairesalo, and J. Keto. 1993. Eutrophication and Recovery of Lake Vesijarvi (South Finland): Diatom Frustules in Varved Sediments over 30-year Period. *Hydrobiologia.* 269/270: pp. 415-426.

Loftus, M.E. and H.H. Seliger. 1975. Some Limitations of the *In Vivo* Fluorescence Tehnique. *Chesapeake Science*. 16(2): pp. 79-92.

Lorenzen, C.J. 1967. Determination of Chlorophyll and Phaeo-pigments: Spectrophotometric Equations. *Limnol. Oceanogr*. 12: pp. 343-346.

Lowe, R.L. and R.W. Pillsbury. 1995. Shifts in Benthic Algal Community Structure and Function Following the Appearance of Zebra Mussels *(Dreissena polymorpha)* in Saginaw Bay, Lake Huron. *J. Great Lakes Res.* 21(4): pp. 558-566.

Lund, J.W.G. 1949. Studies on *Asterionella Formosa*. I. The Origin and Nature of the Cells Producing Seasonal Maxima. *J. of Ecology*. 37: pp. 389-419.

Lund, J.W.G. 1954. The Seasonal Cycle of the Plankton Diatom, Melosira Italica (EHR.) Kutz. Subsp. Subactica O. Mull. *J. of Ecology*. 42(1): pp. 151-179.

Magnuson, J. J., Benson, B.J., and Kratz, T.K. 1990. Temporal Coherence in the Limnology of a Suite of Lakes in Wisconsin, U.S.A. *Freshwater Biology.* 23: pp. 145–159.

Magnuson, J.J., K.E. Webster, R.A. Assel, C.J. Bowser, P.J. Dillon, J.G. Eaton, H.E. Evans, E.J. Fee, R.I. Hall, L.R. Mortsch, D.W. Schindler and F.H. Quinn. 1997. Potential Effects of Climate Changes On Aquatic Systems: Laurentian Great Lakes and Precambrian Shield Region. *Hydrological Processes*. 11: pp. 825-871.

Makarewicz, J.C. 1993. Phytoplankton Biomass and Species Composition in Lake Erie, 1970 to 1987. *J. Great Lakes Res.* 19(2): pp. 258-274.

McQuoid, M.R. 2002. Pelagic and Benthic Environmental Controls on the Spatial Distribution of a Viable Diatom Propagule Bank on the Swedish West Coast. *J. Phycol.* 38: pp. 881-893.

McQuoid, M.R. and L.A. Hobson. 1995. Importance of Resting Stages in Diatom Seasonal Succession. *J. Phycol.* 31: pp. 44-50.

Millie, D.F., G.L. Fahnenstiel, H.J. Carrick, S.E. Lohrenz, and O.M.E. Schofield. 2002. Phytoplankton Pigments in Coastal Lake Michigan: Distribtions During the Spring Isothermal Period and Relation with Episodic Sediment Resuspension. *J. Phycol.* 38: pp. 639-648.

Mills, L.S. 2007. Conservation of Wildlife Populations: Demography, Genetics, and Management. Blackwell Publishing.

Montagnes, D.J.S. and D.J. Franklin. 2001. Effect of Temperature on Diatom Volume, Growth Rate, and Carbon and Nitrogen Content: Reconsidering some Paradigms. *Limnol. Oceanogr.* 46(8): pp. 2008-2018.

Mortsch, L.D. and F.H. Quinn. 1996. Climate Change Scenarios for Great Lakes Basin Ecosystem Studies. *LimnoI. Oceanogr.* 41(5): pp. 903-911.

Morris, I. and K. Farrell. 1971. Photosynthetic Rates, Gross Patterns of Carbon Dioxide Assimilation and Activites of Ribulose Diphosphate Carboxylase in Marine Algae Grown at Different Temperatures. *Physiologia Plantarum.* 25(3): pp. 372-377.

Moyle, P.R. and T.P. Dolley. 2003. With or Without Salt—A Comparison of Marine and Continental-Lacustrine Diatomite Deposits. Chapter D of Contributions to Industrial-Minerals Research. pp. 1-8.

Munawar, M. and I.F. Munawar. 1986. The Seasonality of Phytoplankton in the North American Great Lakes, a Comparative Synthesis. *Hydrobiologia*. 138: pp. 85-115.

Nalepa, T.F. and M.A. Quigley. 1987. Distribution of Photosynthetic Pigments in Nearshore Sediments of lake Michigan. *J. Great Lakes Res.* 13(1): pp. 37-42.

Nielsen, S. and E.G. Jørgensen. 1968. The adaptation of plankton algae. I. General part. *Physiol. Plant.* 21: pp. 401–413.

Nipkow, F. 1950. Ruheformen planktischer Kieselalgen im geschicheten Schlamm des Zurichsees. *Schweiz. Z. Hydrobiologia*. 12: pp. 263-270.

Ortega, H.C. 2007. Trpohic Status of Two Glacial Lakes, West and East Okoboji, in Northwas Iowa. U.S.A. *Idesia*. 25(3): pp. 7-17.

Patoine, A. and Leavitt, P.R. 2006. Century-Long Synchrony of Fossil Algae in a Chain of Canadian Prairie Lakes. *J. of Ecology*. 87(7): pp. 1710-1721.

Parker, J.I. and Edington, D.N. 1976. Concentration of Diatom Frustules in Lake Michigan Sediment Cores. *Limnol. and Oceanogr*. 21(6): pp. 893-900.

Phillips, J.N. and J. Myers. 1954. Growth Rate of Chlorella in Flashing Light. *Plant Physiology.* 29: pp. 152-161.

Pitcher, G.C. 1990. Phytoplankton Seed Populations of the Cape Peninsula Upwelling Plume, with Particular Reference to Resting Spores of C*haetoceros* and Their Role in Seeding Upwelling Waters, *Estuar. Coast. Shelf Sci.* 31: pp. 283–301.

Platt, T., D.V. Subba Rao, J.C. Smith, W.K. Li, B. Irwin, E.P.W. Horne, and D.D. Sameoto. 1983. Photosynthetically-Competent Phytoplankton from the Aphotic Zone of the Deep Ocean. *Mar. Ecol. Prog. Ser*. 10: pp. 105-110.

Prezelin, B.B. 1976. The Role of Peridinin-Chlorophyll-a Proteins in the Photosynthetic Light Adaptation of the Marine Dinoflagellate, *Glenodinium* sp. Planta (Berl.) 130: 225-233.

Rabalais, N., R.E.Turner, W.J. Wiseman Jr. 2002. Gulf of Mexico Hypoxia, A.K.A. "The Dead Zone." *Annu. Rev. Ecol. System.* 33: pp. 235-263.

Regier, H.A. and W.L. Hartman. 1973. Lake Erie's Fish Community: 150 Years of Cultural Stresses. *Science*. New Series. 180(4092): pp. 1248-1255.

Relexans, J.C. 1996. Measurement of the Respiratory Electron Transport System (ETS) activity in Marine Sediments: State-of-the-Art and Interpretation. I. Methodology and Review of Literature Data. *Mar. Ecol. Prog. Ser.* 136: pp. 277-287.

Reynolds, C.S. 1973. The Seasonal Periodicity of Planktonic Diatoms in a Shallow Eutrophic Lake. *Freshwater Biology*. 3: pp. 89-110.

Reynolds, C.S. 1984. The Ecology of Freshwater Plankton. *Cambridge Studies in Ecology*. Cambridge University Press.

Rockwell, D.C., G.J. Warren, P.E. Bertram, D.K. Salisbury, and N.M Burns. 2005. The U.S. EPA Lake Erie Indicators Monitoring Program 1983-2002: Trends in Phosphorus, Silica, and Chlorophyll-a in the Central Basin. *J. Great Lakes Res*. 13: pp. 684-696.

Rosa, F. and N.M. Burns. 1987. Lake Erie Central Basin Oxygen Depletion Changes from 1929-1980. *J. of Great Lakes Res.* 13(4): pp. 684-696.

Rowe. 2001. Seasonal Pulses of Plankton can Contribute to the Benthos of the Gulf of Mexico. *J. Environ. Qual.* 30: 281-290.

Ryther, J.H., C.S. Yentsch, E,M, Hulbert, R.F. Vaccaro. 1958. The Dynamics of a Diatom Bloom. *Biol. Bull.* 115(2): pp. 257-268.

Schelske, C.L. and Stoermer, E.F. 1972. Phosphorus, Silica and Eutrophication of Lake Michigan. Am. Soc. *Limnol. Oceanogr.* Spec. Symp. 1: pp. 157-171.

Schmid, M., and P. Dorji. 2008. Permanent Lake Stratification Caused by a Small Tributary - The Unusual Case of Lej da San Murezzan. *J. Limnol*. 67(1): pp. 35-43.

Service, R. 2004. New Dead Zone Off Oregon Coast Hints at Sea Change in Currents. *Science*. 305: 1099.

Sicko-Goad, L. 1986. Rejuvenation of *Melosira Granulata* (Bacillariophyceae) Resting Cells from the Anoxic Sediments of Douglas Lake, Michigan. II. Elcetron Microscopy. *J. Phycol.* 22: pp. 28-35.

Sicko-Goad, L., E.F. Stoermer and G. Fahnenstiel. 1986. Rejuvenation of Melosira Granulata (Bacillariophyceae) from the Anoxic Sediments of Douglas Lake, Michigan. I. Light Microscopy and ^{14}C uptake. *J. Phycol*. 22: pp. 22-28.

Sicko-Goad, L., E.F. Stoermer and J.P. Kociolek. 1989. Diatom Resting Cell Rejuvenation and Formation: Time Course, Species Records and Distribution. *J. of Plankton Research*. 11(2): pp. 375-389.

Smayda, T.J. and B. Mitchell-Innes. 1974. Dark Survival of Autotrophic, Planktonic Marine Diatoms. *Marine Biology*. 25: pp. 195-202.

Smetacek, V.S. 1995. Role of Sinking in Diatom Life-history Cycles: Ecological, Evolutionary and Geological Significance. *Marine Biology*. 84: pp. 239-251.

Solovieva, N., V.J. Jones, L. Nazarova, S.J. Brooks, H.J.B. Birks, J.A. Grytnes, P.G. Appleby, T. Kauppila, B. Kondratenok, I. Renberg, and V. Ponomarev. 2005. Paleolimnological Evidence for Recent Climatic Change in Lakes from the Northern Urals, Arctic Russia. *J. of Paleolimnology*. 33: pp. 463-482.

Soranno, P.A., Webster, K.E., Riera, J.L., Kratz, T.K., Baron, J.S., Bukaveckas, P.A., Kling, G.W., White, D.S., Caine, N., Lathrop, R.C., and Leavitt, P.R. 1999. Spatial Variation among Lakes within Landscapes: Ecological Organization along Lake Chains. *Ecosystems*. 2: pp. 395-410.

Sousounis, P.J. and J.M. Bisanz. 2000. *Preparing For A Changing Climate. The Potential Consequences Of Climate Variability and Change Great Lakes*. Report of the Great Lakes Regional Assessment Group prepared for the U.S. Global Change Research Program. Michigan: University of Michigan.

Stevenson, R.J. and E.F. Stoermer. 1981. Quantitatve Differences between Benthic Algal Communties along a Depth Gradient in Lake Michigan. *J. Phycol.* 17: pp. 29-36.

Stockner, J.G. and J.W.G. Lund. 1970. Live Algae in Postglacial Lake Deposits. *Limnol. Oceanogr*. 15: pp. 41-58.

Stoermer, E.F., R.G. Kreis, Jr., and L. Sicko-Goad. 1981. A Systematic, Quantitative, and Ecological Comparison of *Melosira islandica* O. Mull. with *M. granulata* (Her.) Ralfs from Laurentian Great Lakes. *J. Great Lakes Res*. 7: pp. 345-356.

Stoermer, E.F., G. Emmert, C.L. Schelske. 1989. Morphological Variation of *Stephanodiscus niagarae* Ehrenb. (Bacillariophyta) in a Lake Ontario Sediment Core. *J. of Paleolimnology*. 2: pp. 227-236.

Stoermer, E.F. and L. Sicko-Goad. 1985. A Comparative Ultrastructural and Morphometric Study of Six Species of the Diatom Genus *Stephanodiscus*. *J. of Plankton Research.* 7(1): pp. 125-135.

Stoermer, E.F. and J.J. Yang. 1970. Distribution and Relative Abundance of Dominant Plankton Diatoms in lake Michigan. Univ. Mich., Great Lakes Res. Div. Publ. 16.

Suzuki, Y. and M. Takahashi. 1995. Growth Responses of Several Diatom Species Isolated from Various Environments to Temperature. *J. Phycol.* 31: pp. 880-888.

Theriot, E.C., S.C. Fritz, C. Whitlock, and D.J. Conley. 2006. Late Quaternary Rapid Morphological Evolution of an Endemic Diatom in Yellowstone Lake, Wyoming. *Paleobiology.* 32(1): pp. 38-54.

Theriot, E. and E.F. Stoermer. 1981. Some Aspects of Morphological Variaiton in *Stephanodiscus Niagarae* (Bacillariophyceae). *J. Phycol.* 17: pp. 64-72.

Thompson, J.A. 1997. Cellular Fluorescence Capacity as an Endpoint in Algal Toxicity Testing. *Chemosphere*. 35(9): pp. 2027-2037.

Tilzer, M.M. and C.R. Goldman. 1978. Importance of Mixing, Thermal Stratificaiton and Light Adaptation for Phytoplankton Productivity in Lake Tahoe (California-Nevada). *J. of Ecology.* 59(4): pp. 810-821.

Tiselius, P. and B. Kuylenstierna. 1996. Growth and Decline of a Diatom Spring Bloom Phytoplankton Species Composition, Formation of Marine Snow and the Role of Heterotrophic Dinoflagellates. *J. of Plankton Research.* 18(2): pp. 133-155.

Turner, Jefferson T., and P.A. Tester. 1997. Toxic Marine Phytoplankton, Zooplankton Grazers, and Pelagic Food Webs. *Limnol. Oceanogr*. 42(5): Part 2: The Ecology and Oceanography of Harmful Algal Blooms. pp. 1203-1214.

Vincent, W.F. 1978. Survival of Aphotic Phytoplankton in Lake Tahoe throughout Prolonged Stratification. *Verh. Internat. Verein. Limnol.* 20: pp. 401-406.

Vincent, W.F. 1980. Mechanisms of Rapid Photosynthetic Adaptations in Natural Phytoplankton Communities. II. Changes in Photochemical Capacity as Measured by DCMU-induced Chlorophyll Fluorescence. *J. Phycol.* 16: pp. 568-577.

Wehr, J.D. and R.G. Sheath. [Eds.] 2003. Freshwater Algae of North America: Ecology and Classification (24 chapters), Academic Press, San Diego, CA.

Wilhelm, S.W., G.S. Bullerjahn, M.L. Eldridge, J.M. Rinta-Kanto, L. Poorvin, and R.A. Bourbonniere. 2006. Seasonal Hypoxia and the Genetic Diversity of Prokaryote Populations in the Central Basin Hypolimnion of Lake Erie: Evidence for Abundant Cyanobacteria and Photosynthesis. *J. of Great Lakes Res*. 32: pp. 657-671.

Willen, T. 1962. Studies on the Phytoplankton of Some Lakes Connected with or Recently Isolated from the Baltic. *Oikes.* 13(2): pp. 169-199.

Winder, M. and D.E.Schindler. 2004. Climate Change Uncouples Trophic Interactions in an Aquatic Ecosystem. *J. of Ecology.* 85(8): pp. 2100–2106.

Winter, A., J.J.H. Ciborowski, and T.B.Reynoldson. 1996. Effects of Chronic Hypoxia and Reduced Temperature on Survival and Growth of Burrowing Mayflies, *Hexagenia limbata* (Ephemeroptera: Ephemeridae). *Can. J. Fish. Aquat. Sci.* 53: pp. 1565-1571.

Winter, T.C. 1977. Classification of the Hydrologic Settings of Lakes in the North Central United States. *Water Resources Res*. 13 (4): pp. 753-767.

Appendix A

Corrected mean benthic Lake Erie central basin chlorophyll-a (mg m^{-2}) comparing lake station versus thermal period (low to high) for 2007-08 (Fig. 6). Non-overlapping lines indicate significant differences ($p<0.05$).

SM: Spring-Mixing
FM: Fall-Mixing
ES: Early-Stratification
LS: Late-Stratification

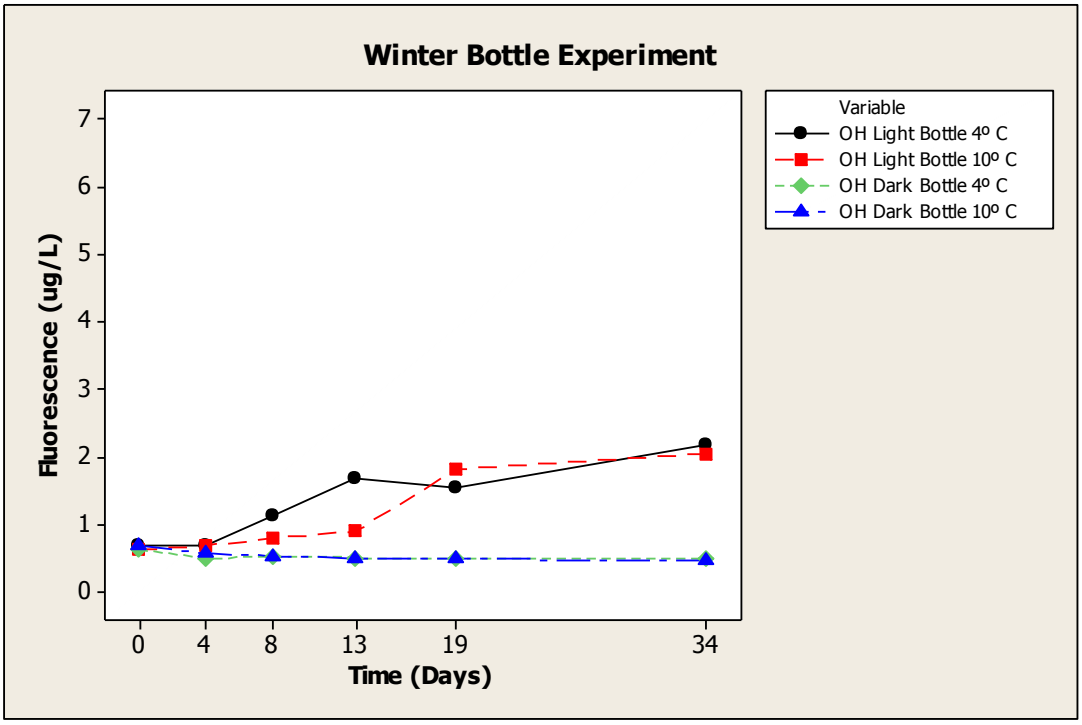
Station	df	MS	F-value	p-value	Thermal Period			
					SM	FM	LS	ES
Nearshore-Hypoxic	3	8.99	15.05	0.000	6.9	108.9	135.6	169.0
Offshore-Hypoxic	3	0.56	8.01	0.003	46.5	73.7	83.9	115.6
Offshore-Oxic	3	1.21	7.01	0.006	25.8	32.8	68.7	79.8

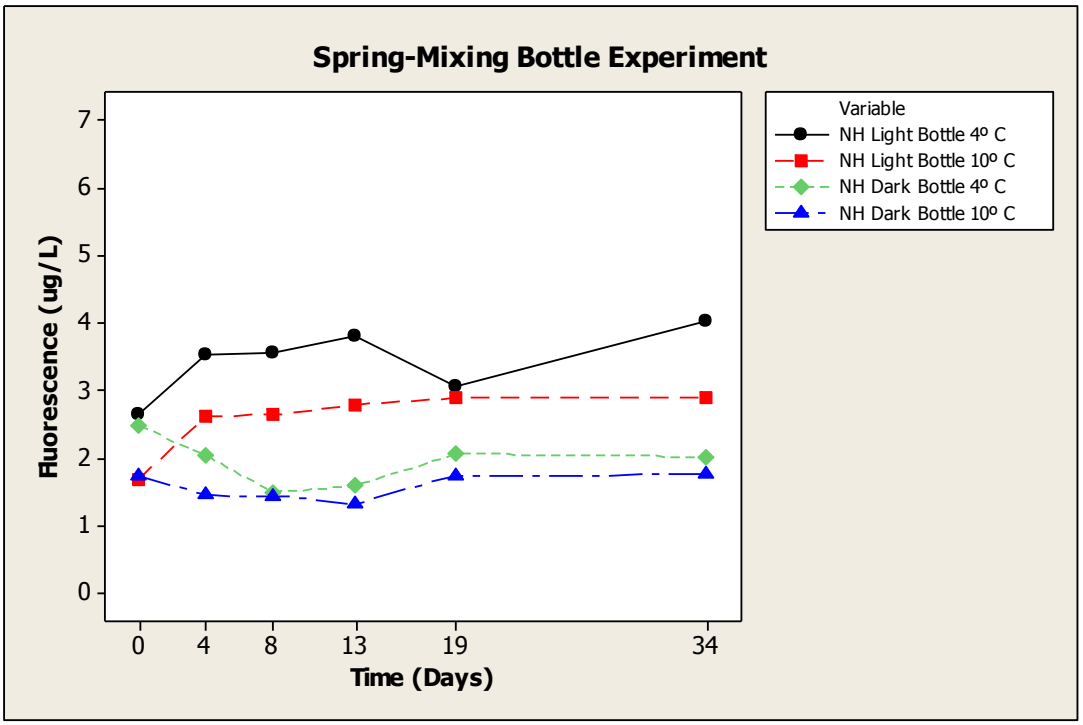
Thermal Period	df	MS	F-value	p-value	Station		
					Nearshore-Hypoxic	Offshore-Oxic	Offshore-Hypoxic
SM	2	3.80	5.36	0.029	6.9	25.8	46.5
					Offshore-Oxic	Offshore-Hypoxic	Nearshore-Hypoxic
ES	2	0.56	3.60	0.071	79.8	115.6	169.0
LS	2	0.53	3.47	0.077	68.7	83.9	135.6
FM	2	1.48	13.39	0.002	32.8	73.7	108.9

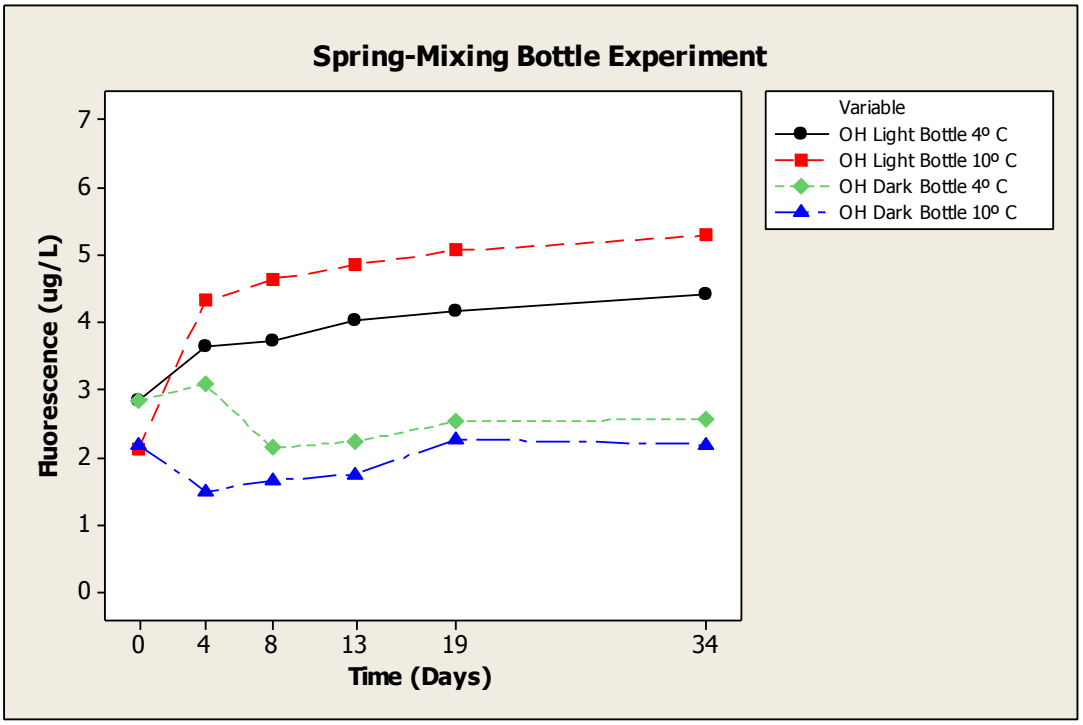
Appendix B

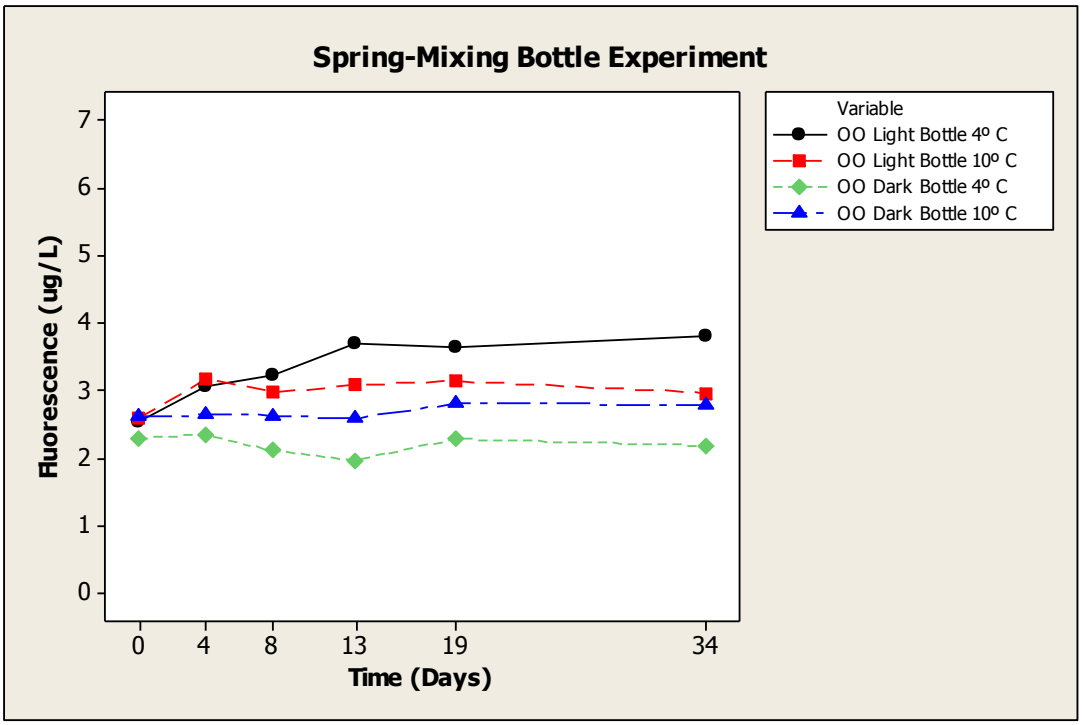
***In vivo* autofluorescence (µg L^{-1}) comparing light versus dark bottles for each Lake Erie central basin thermal period, lake station, and experimental temperature (4ºC and 10ºC) during 2007-08.**

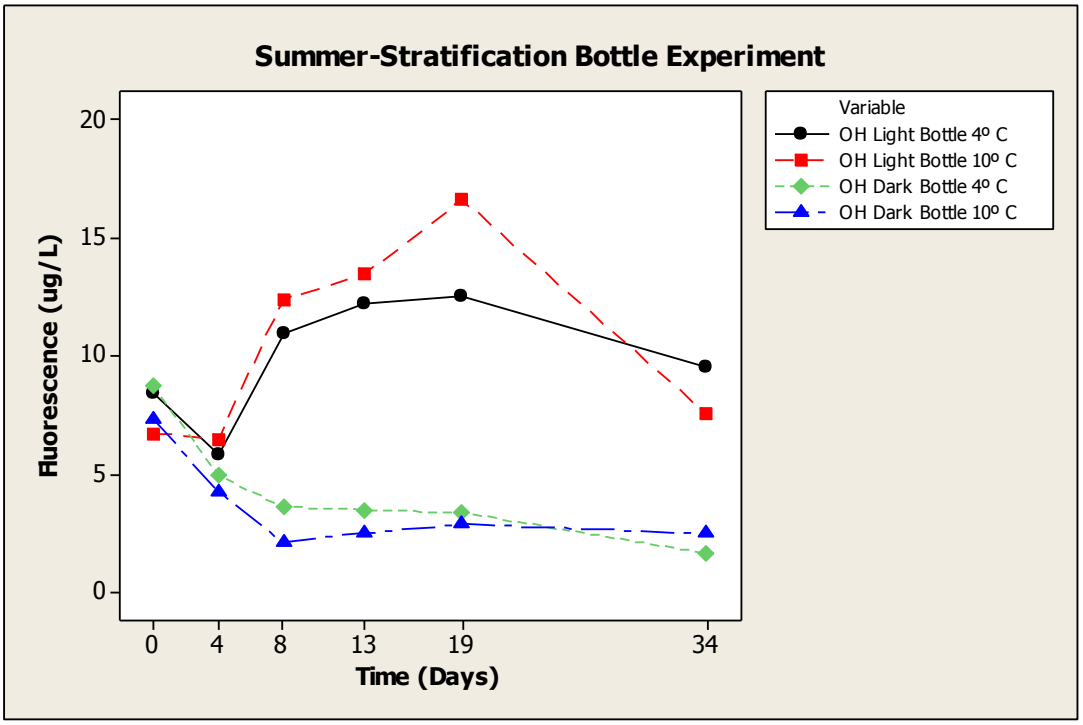
NH: Nearshore-Hypoxic
OH: Offshore-Hypoxic
OO: Offshore-Oxic

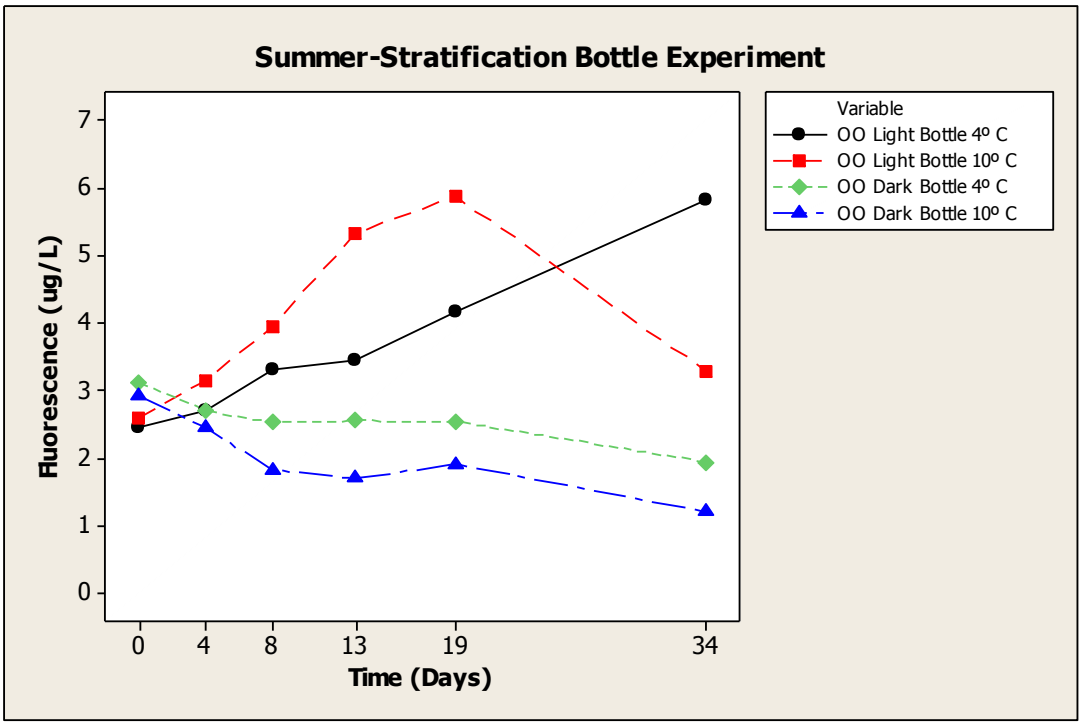


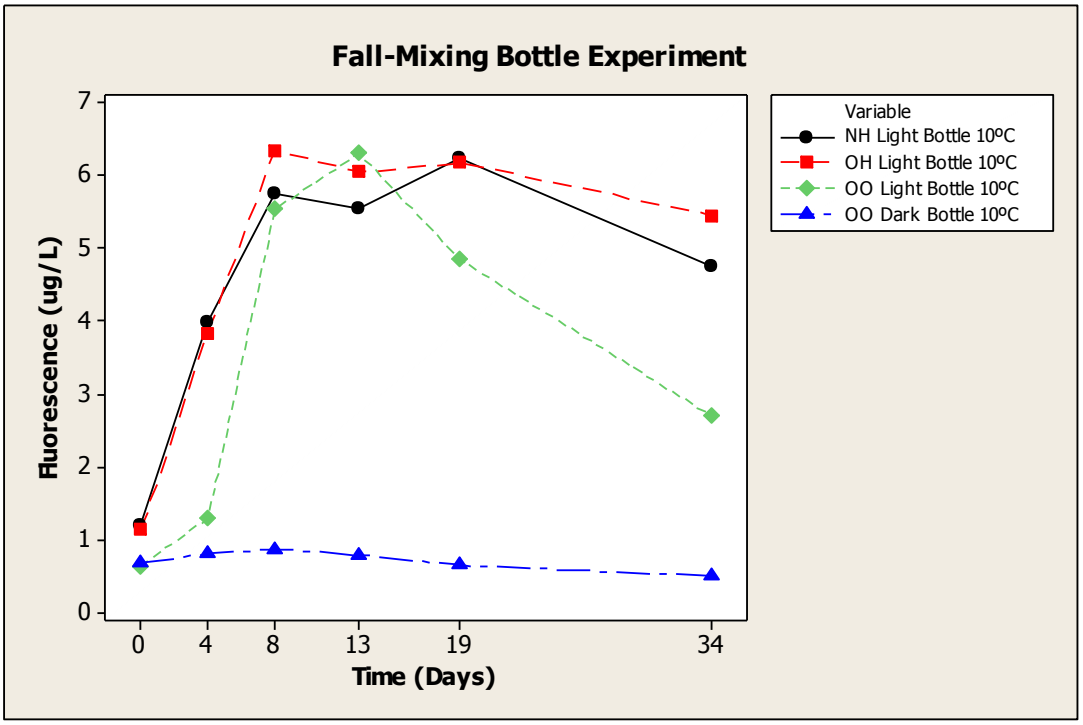

Spring-Mixing Bottle Experiment
Fluorescence (ug/L)
0
1
2
3
4
5
6
7
0
4
8
13
19
34
Time (Days)
Variable
NH Light Bottle 4º C
NH Light Bottle 10º C
NH Dark Bottle 4º C
NH Dark Bottle 10º C


Spring-Mixing Bottle Experiment
Fluorescence (ug/L)
0
1
2
3
4
5
6
7
0
4
8
13
19
34
Time (Days)
Variable
OH Light Bottle 4º C
OH Light Bottle 10º C
OH Dark Bottle 4º C
OH Dark Bottle 10º C


Spring-Mixing Bottle Experiment
Fluorescence (ug/L)
Time (Days)
0
1
2
3
4
5
6
7
0
4
8
13
19
34
Variable
OO Light Bottle 4º C
OO Light Bottle 10º C
OO Dark Bottle 4º C
OO Dark Bottle 10º C


Summer-Stratification Bottle Experiment
Fluorescence (ug/L)
Time (Days)
0
5
10
15
20
0
4
8
13
19
34
Variable
OH Light Bottle 4º C
OH Light Bottle 10º C
OH Dark Bottle 4º C
OH Dark Bottle 10º C


Summer-Stratification Bottle Experiment
Fluorescence (ug/L)
Time (Days)
0
1
2
3
4
5
6
7
0
4
8
13
19
34
Variable
OO Light Bottle 4º C
OO Light Bottle 10º C
OO Dark Bottle 4º C
OO Dark Bottle 10º C


Fall-Mixing Bottle Experiment
Fluorescence (ug/L)
Time (Days)
0
1
2
3
4
5
6
7
0
4
8
13
19
34
Variable
NH Light Bottle 10ºC
OH Light Bottle 10ºC
OO Light Bottle 10ºC
OO Dark Bottle 10ºC

Appendix C

Physiological condition (µg L^{-1} d^{-1}) of incubated light bottles versus dark bottles calculated as growth rates for each Lake Erie central basin thermal period, lake station, and experimental temperature (4ºC and 10ºC) during 2007-08.

Time	Station	Temperature (ºC)	Illuminated Bottle Incubation Period (Days): Maximum Growth Rate (µg L^{-1} d^{-1})					
Fall 2007	Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.3021				
			8	0.1968	0.0914			
			13	0.1185	0.0369	-0.0067		
			19	0.0873	0.0300	0.0077	0.0196	
			34	0.0407	0.0058	-0.0074	-0.0075	-0.0184
Fall 2007	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.3061				
			8	0.2159	0.1256			
			13	0.1291	0.0505	-0.0097		
			19	0.0895	0.0317	-0.0025	0.0035	
			34	0.0463	0.0117	-0.0058	-0.0049	-0.0083
Fall 2007	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1772				
			8	0.2708	0.3643			
			13	0.1766	0.1764	0.0260		
			19	0.1071	0.0884	-0.0120	-0.0437	
			34	0.0426	0.0246	-0.0276	-0.0404	-0.0391

Winter 2008	LE-84	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0048				
			8	0.0624	0.1297			
			13	0.0684	0.1010	0.0780		
			19	0.0424	0.0550	0.0278	-0.0140	
			34	0.0338	0.0389	0.0250	0.0124	0.0229
Winter 2008	LE-84	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0282				
			8	0.0312	0.0342			
			13	0.0287	0.0289	0.0246		
			19	0.0568	0.0644	0.0754	0.1177	
			34	0.0354	0.0363	0.0367	0.0395	0.0083
Spring 2008	Nearshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0705				
			8	0.0367	0.0028			
			13	0.0276	0.0085	0.0130		
			19	0.0075	-0.0093	-0.0138	-0.0361	
			34	0.0122	0.0045	0.0047	0.0027	0.0183

Spring 2008	Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0608				
			8	0.0336	0.0064			
			13	0.0266	0.0113	0.0152		
			19	0.0200	0.0091	0.0100	0.0057	
			34	0.0128	0.0064	0.0064	0.0043	0.0038
Spring 2008	Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0475				
			8	0.0301	0.0127			
			13	0.0289	0.0206	0.0269		
			19	0.0192	0.0116	0.0113	-0.0018	
			34	0.0119	0.0072	0.0064	0.0015	0.0028
Spring 2008	Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1109				
			8	0.0569	0.0029			
			13	0.0394	0.0076	0.0114		
			19	0.0285	0.0066	0.0079	0.0050	
			34	0.0161	0.0035	0.0035	0.0017	0.0003

Spring 2008	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1768				
			8	0.0971	0.0173			
			13	0.0633	0.0129	0.0093		
			19	0.0455	0.0105	0.0081	0.0071	
			34	0.0267	0.0067	0.0051	0.0041	0.0029
Spring 2008	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0500				
			8	0.0171	-0.0159			
			13	0.0131	-0.0034	0.0066		
			19	0.0100	-0.0006	0.0049	0.0035	
			34	0.0039	-0.0023	-0.0002	-0.0018	-0.0039
Summer 2008	Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0918				
			8	0.0325	0.1569			
			13	0.0283	0.0818	0.0216		
			19	0.0209	0.0509	0.0124	0.0047	
			34	0.0036	0.0163	-0.0054	-0.0118	-0.0184

Summer 2008	Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0248				
			8	0.0374	0.0501			
			13	0.0264	0.0272	0.0089		
			19	0.0281	0.0289	0.0212	0.0315	
			34	0.0255	0.0256	0.0218	0.0249	0.0223
Summer 2008	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0089				
			8	0.0767	0.1622			
			13	0.0534	0.0811	0.0163		
			19	0.0476	0.0627	0.0265	0.0351	
			34	0.0035	0.0052	-0.0190	-0.0274	-0.0523
Summer 2008	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0472				
			8	0.0518	0.0564			
			13	0.0553	0.0589	0.0609		
			19	0.0429	0.0417	0.0364	0.0159	
			34	0.0069	0.0016	-0.0069	-0.0230	-0.0386

Time	Station	Temperature (ºC)	Dark Bottle Incubation Period (Days): Maximum Decay Rate (µg L^{-1} d^{-1})					
Fall 2007	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0435				
			8	0.0316	0.0198			
			13	0.0114	-0.0028	-0.0209		
			19	-0.0022	-0.0143	-0.0267	-0.0316	
			34	-0.0093	-0.0164	-0.0219	-0.0222	-0.0184
Winter 2008	LE-84	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0665				
			8	-0.0220	0.0224			
			13	-0.0178	0.0038	-0.0110		
			19	-0.0138	0.0002	-0.0079	-0.0052	
			34	-0.0078	0.0000	-0.0034	-0.0016	-0.0001
Winter 2008	LE-84	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0462				
			8	-0.0319	-0.0177			
			13	-0.0255	-0.0164	-0.0153		
			19	-0.0182	-0.0107	-0.0082	-0.0022	
			34	-0.0117	-0.0071	-0.0055	-0.0032	-0.0035

Spring 2008	Nearshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0494				
			8	-0.0637	-0.0779			
			13	-0.0344	-0.0278	0.0124		
			19	-0.0098	0.0008	0.0294	0.0437	
			34	-0.0061	-0.0003	0.0116	0.0114	-0.0015
Spring 2008	Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0199				
			8	-0.0357	-0.0912			
			13	-0.0186	-0.0357	0.0087		
			19	-0.0063	-0.0133	0.0151	0.0204	
			34	-0.0030	-0.0060	0.0071	0.0067	0.0012
Spring 2008	Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0059				
			8	-0.0102	-0.0264			
			13	-0.0118	-0.0196	-0.0142		
			19	-0.0002	-0.0019	0.0070	0.0248	
			34	-0.0014	-0.0024	0.0013	0.0049	-0.0030

Spring 2008	Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0464				
			8	-0.0237	-0.0009			
			13	-0.0213	-0.0101	-0.0174		
			19	0.0000	0.0124	0.0172	0.0460	
			34	0.0002	0.0064	0.0075	0.0134	0.0004
Spring 2008	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0932				
			8	-0.0335	0.0262			
			13	-0.0168	0.0172	0.0100		
			19	0.0023	0.0277	0.0283	0.0435	
			34	0.0002	0.0126	0.0106	0.0107	-0.0024
Spring 2008	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0024				
			8	0.0010	-0.0005			
			13	-0.0009	-0.0023	-0.0038		
			19	0.0039	0.0043	0.0060	0.0142	
			34	0.0019	0.0018	0.0022	0.0036	-0.0006

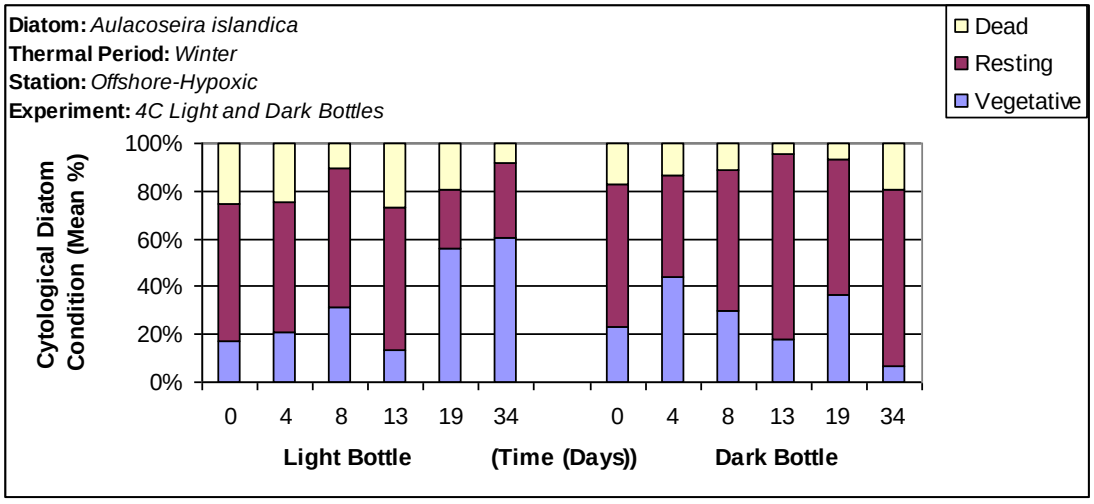
Summer 2008	Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.1421				
			8	-0.1107	-0.0793			
			13	-0.0708	-0.0392	-0.0071		
			19	-0.0502	-0.0257	-0.0063	-0.0056	
			34	-0.0492	-0.0368	-0.0303	-0.0358	-0.0479
Summer 2008	Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0349				
			8	-0.0261	-0.0172			
			13	-0.0151	-0.0064	0.0024		
			19	-0.0106	-0.0041	0.0007	-0.0007	
			34	-0.0138	-0.0110	-0.0101	-0.0130	-0.0180
Summer 2008	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.1345				
			8	-0.1551	-0.1756			
			13	-0.0827	-0.0597	0.0330		
			19	-0.0494	-0.0268	0.0274	0.0227	
			34	-0.0318	-0.0181	0.0062	-0.0002	-0.0094

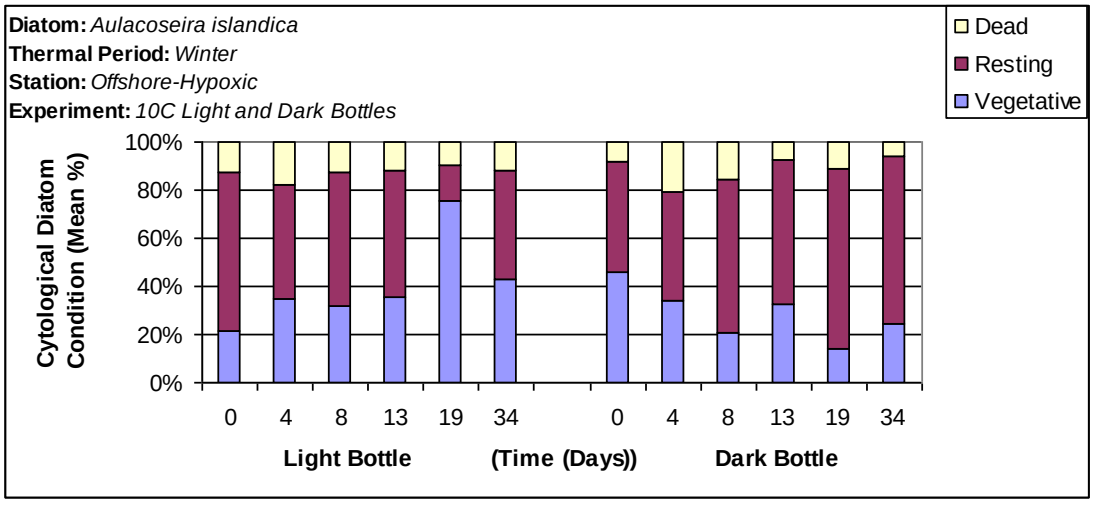
Summer 2008	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0430				
			8	-0.0587	-0.0743			
			13	-0.0416	-0.0409	-0.0142		
			19	-0.0223	-0.0168	0.0041	0.0195	
			34	-0.0261	-0.0238	-0.0160	-0.0165	-0.0308

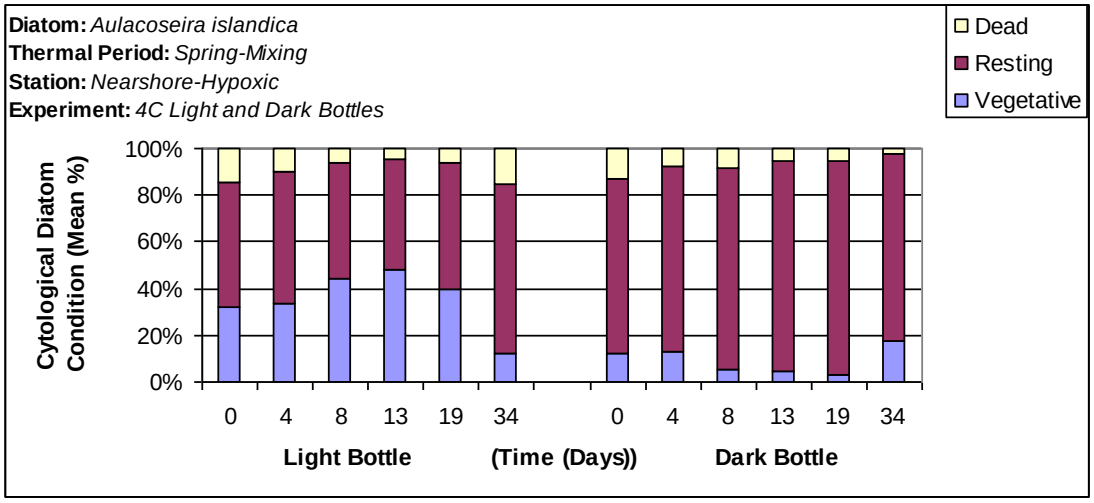
Appendix D

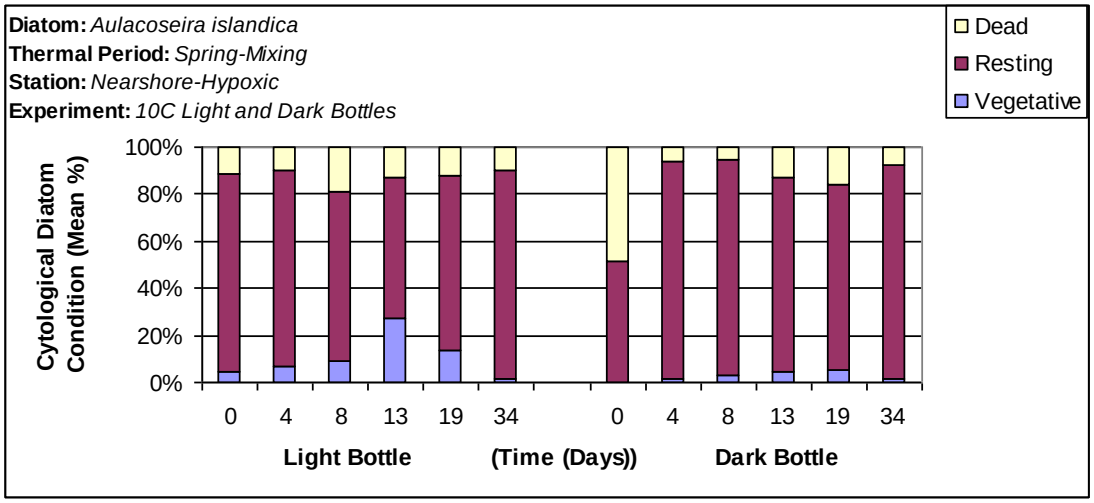
Percent cytological diatom condition (vegetative, resting, dead) for three diatom species *(Aulacoseira islandica, Stephanodiscus niagarae, and Stephanodiscus binderanus)* during each Lake Erie central basin thermal period, lake station, and experimental temperature (4ºC and 10ºC) during 2007-08.

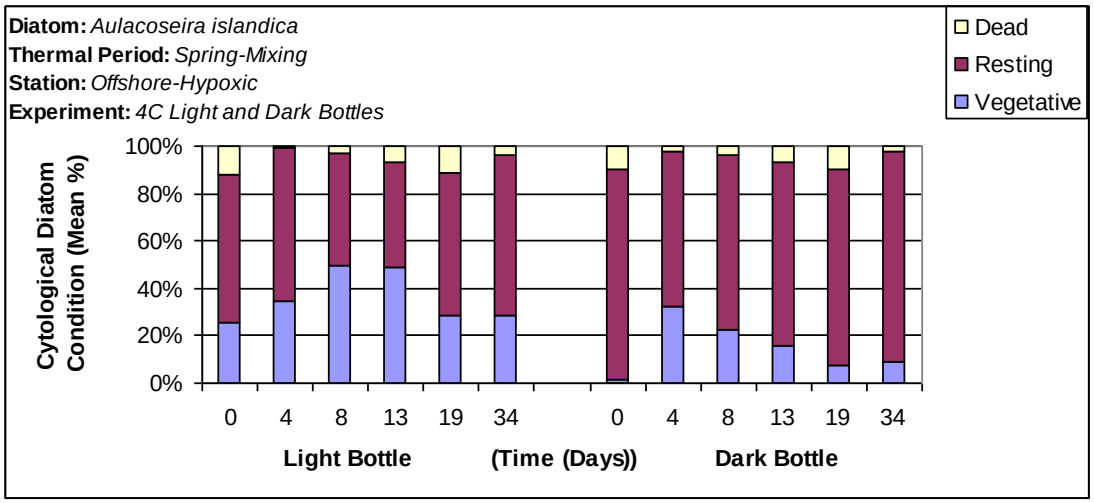
Aulacoseira islandica

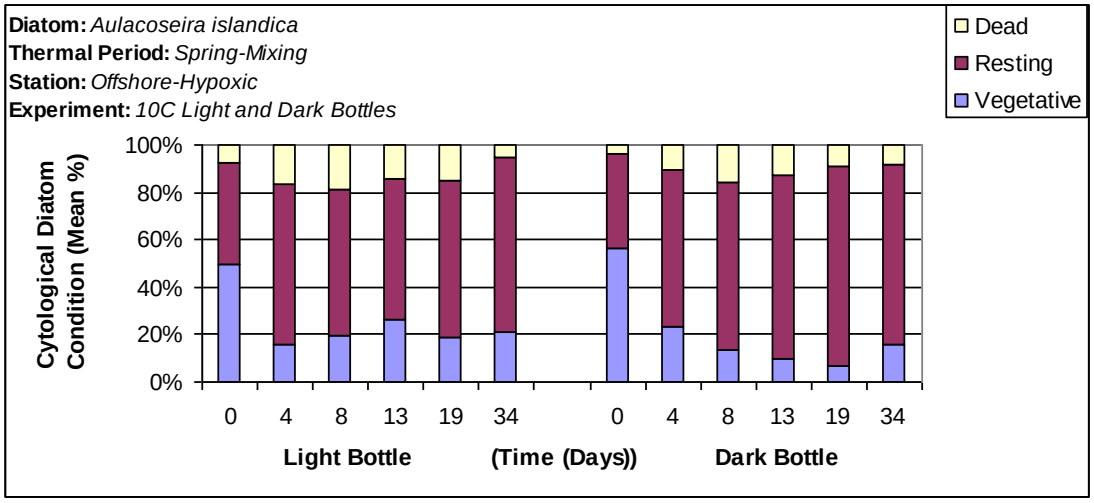


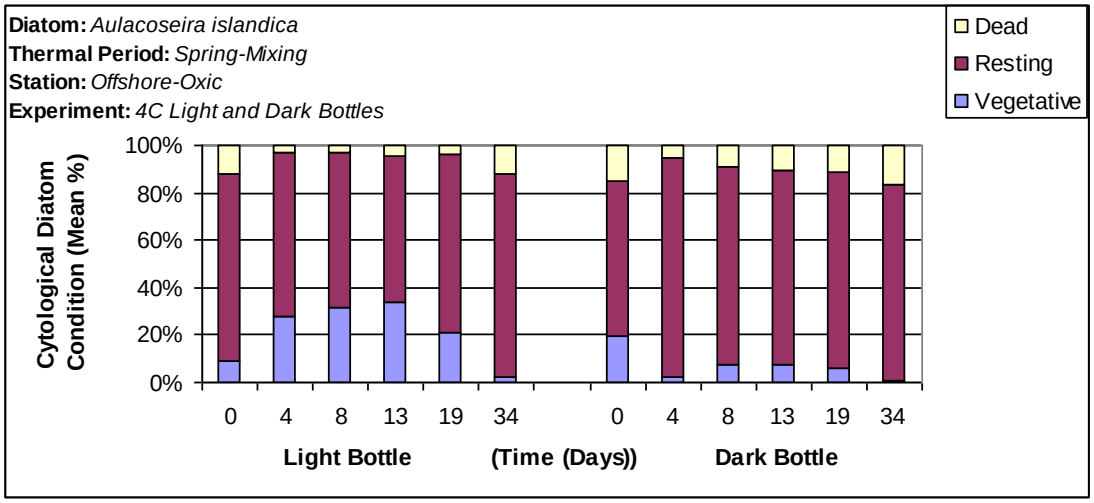


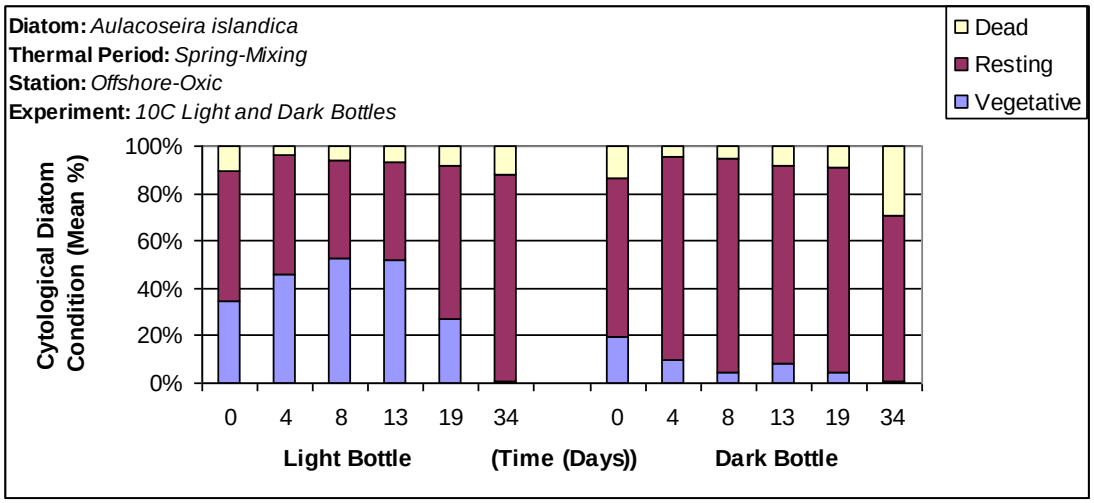

Diatom: Aulacoseira islandica
Thermal Period: Spring-Mixing
Station: Nearshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

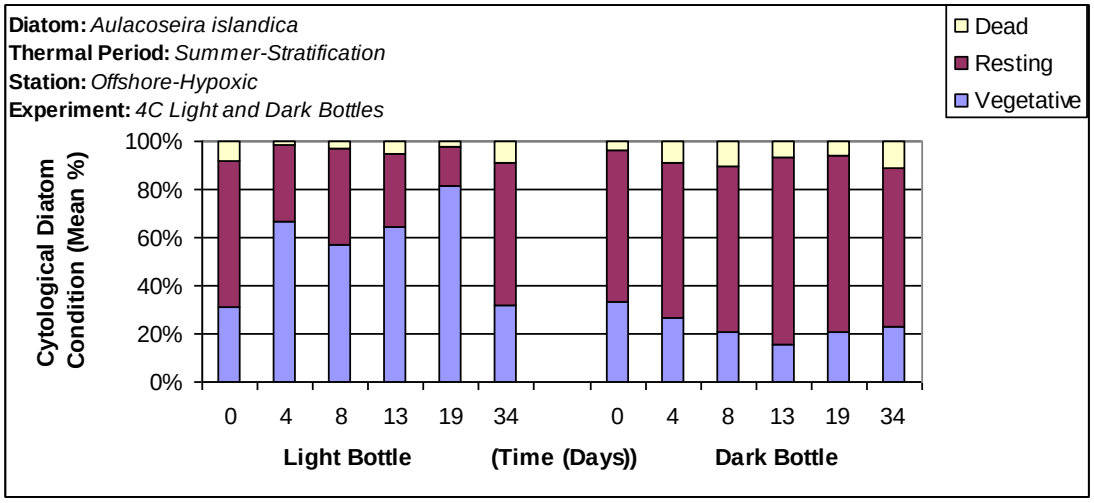

Diatom: Aulacoseira islandica
Thermal Period: Spring-Mixing
Station: Nearshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

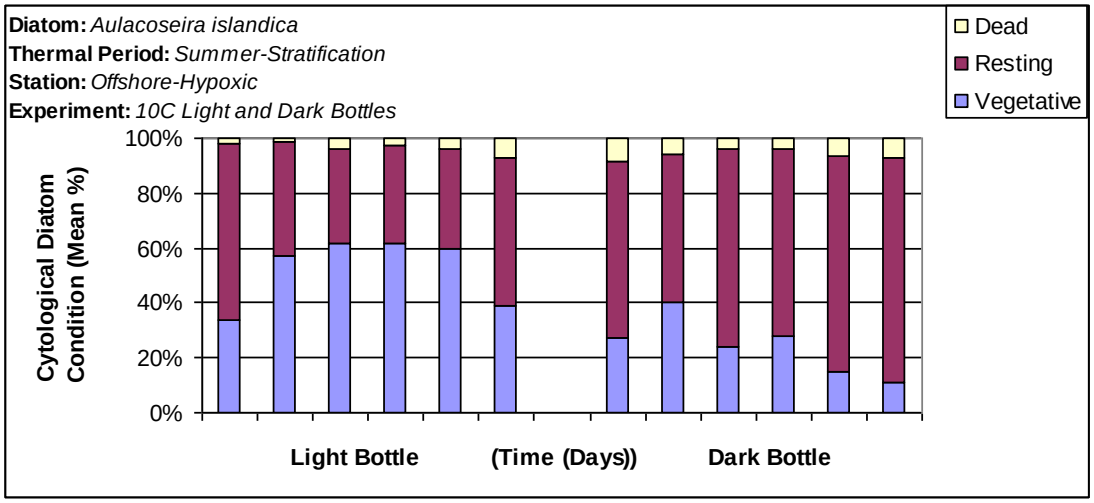

Diatom: Aulacoseira islandica
Thermal Period: Spring-Mixing
Station: Offshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

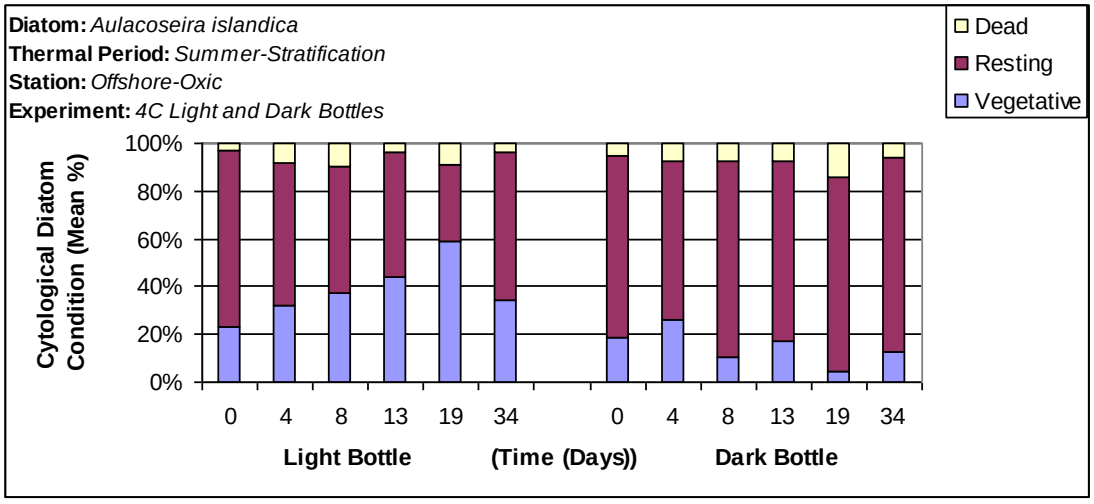

Diatom: Aulacoseira islandica
Thermal Period: Spring-Mixing
Station: Offshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

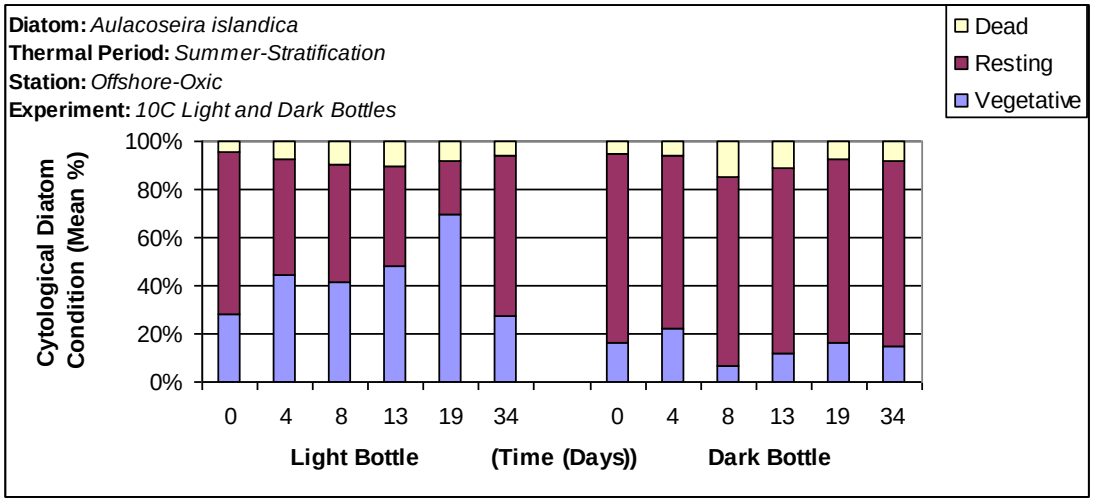

Diatom: Aulacoseira islandica
Thermal Period: Spring-Mixing
Station: Offshore-Oxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

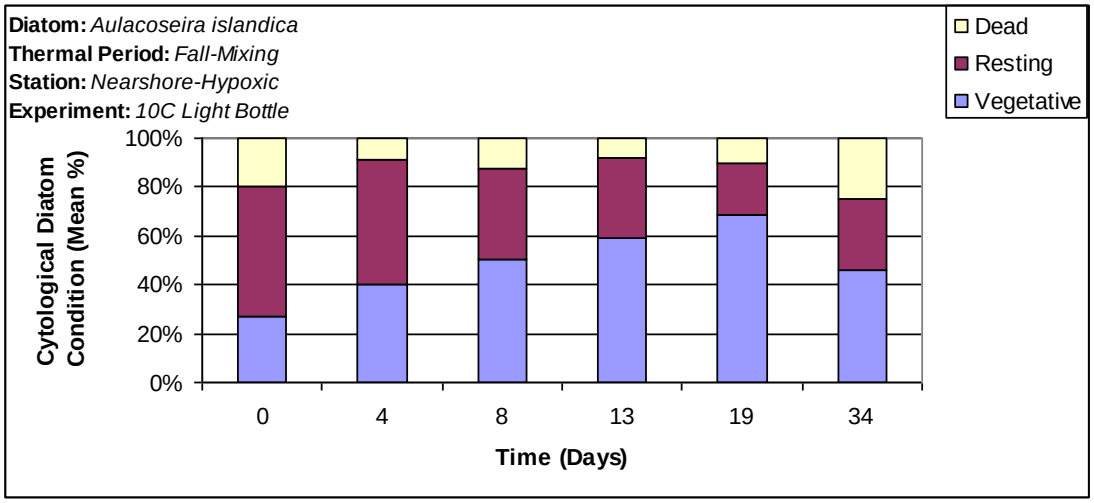

Diatom: Aulacoseira islandica
Thermal Period: Spring-Mixing
Station: Offshore-Oxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

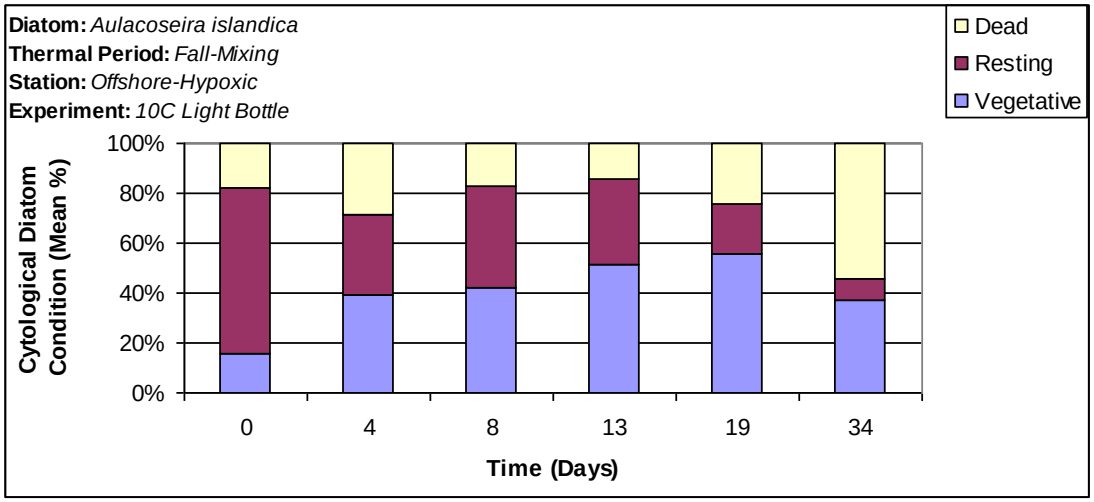

Diatom: Aulacoseira islandica
Thermal Period: Summer-Stratification
Station: Offshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

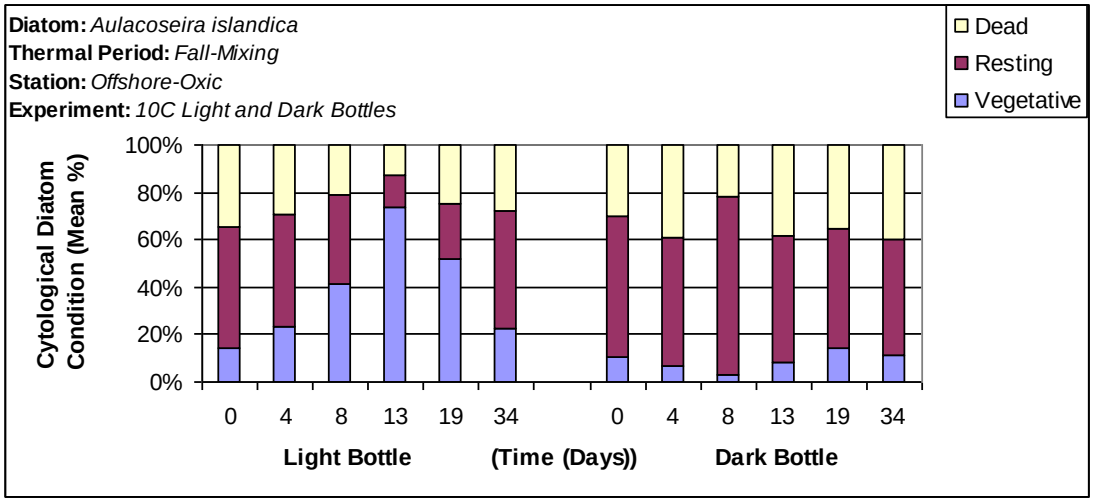

Diatom: Aulacoseira islandica
Thermal Period: Summer-Stratification
Station: Offshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
Light Bottle
(Time (Days))
Dark Bottle


Diatom: Aulacoseira islandica
Thermal Period: Summer-Stratification
Station: Offshore-Oxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

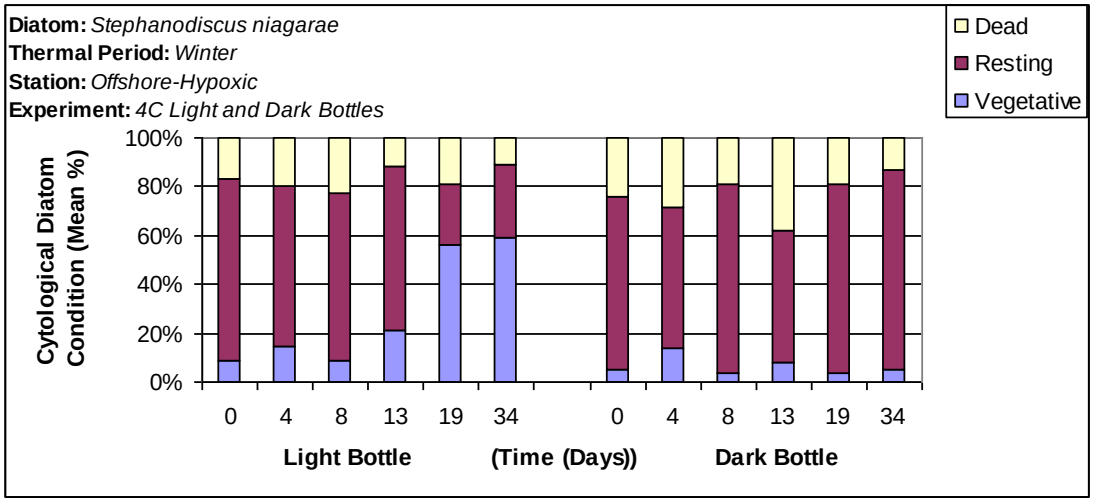

Diatom: Aulacoseira islandica
Thermal Period: Summer-Stratification
Station: Offshore-Oxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

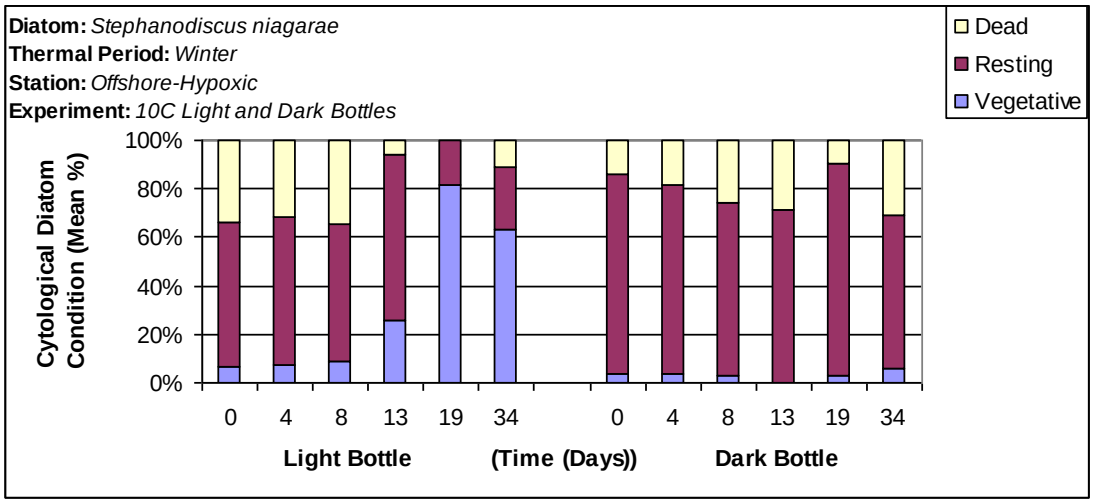

Diatom: Aulacoseira islandica
Thermal Period: Fall-Mixing
Station: Nearshore-Hypoxic
Experiment: 10C Light Bottle
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34
Time (Days)

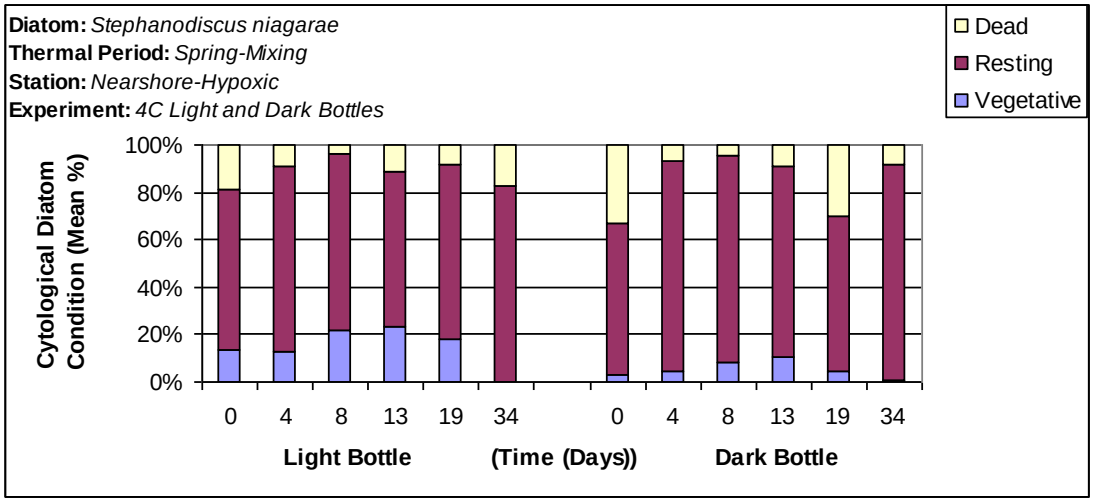

Diatom: Aulacoseira islandica
Thermal Period: Fall-Mixing
Station: Offshore-Hypoxic
Experiment: 10C Light Bottle
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34
Time (Days)

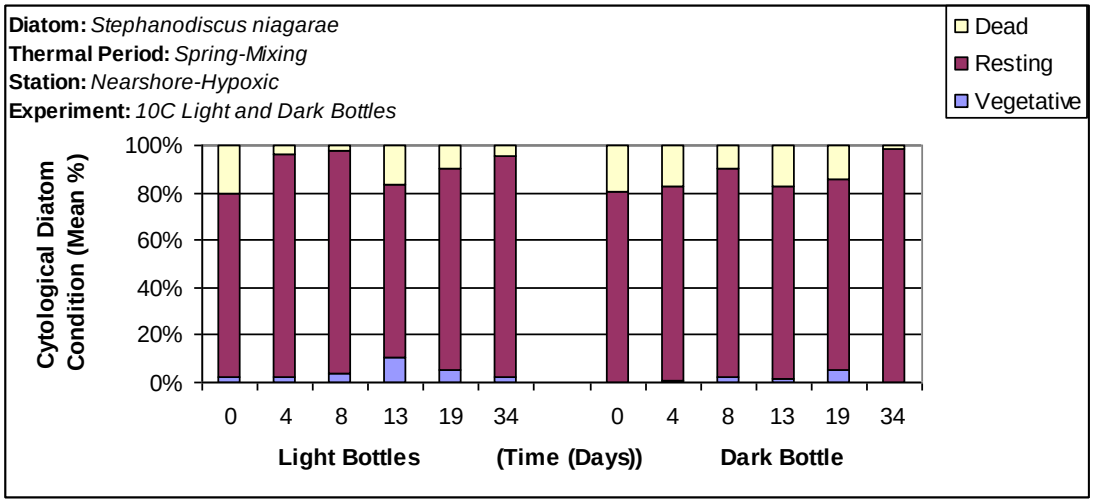


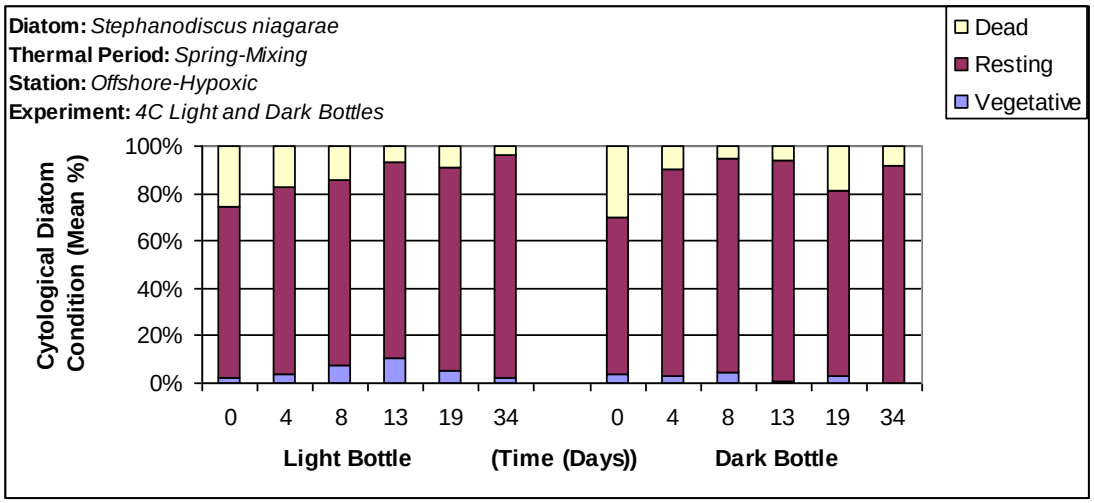
Stephanodiscus niagarae

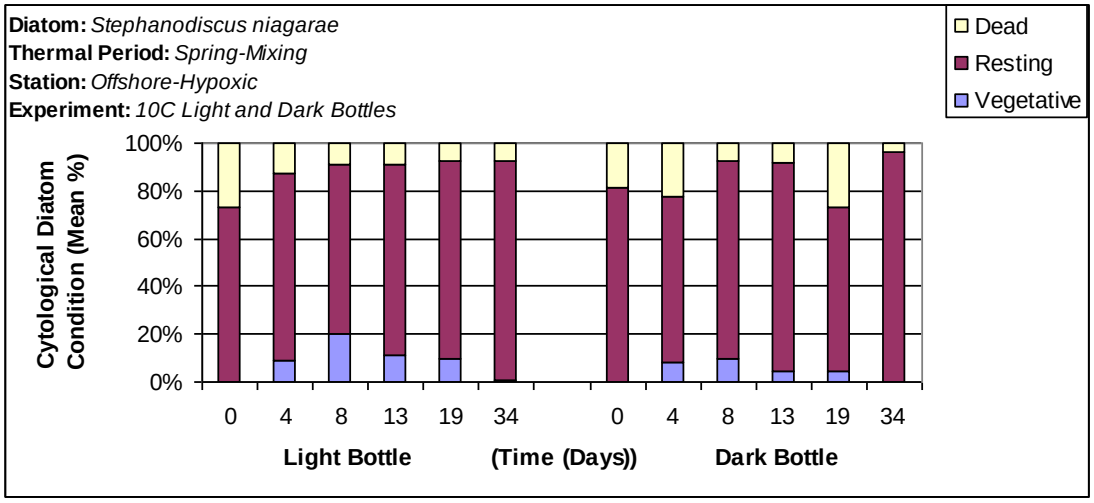


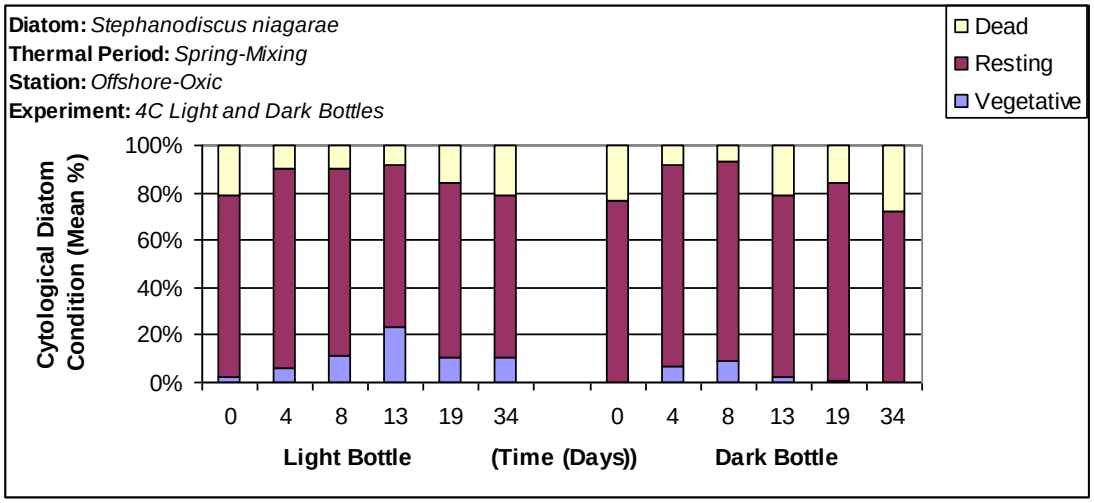


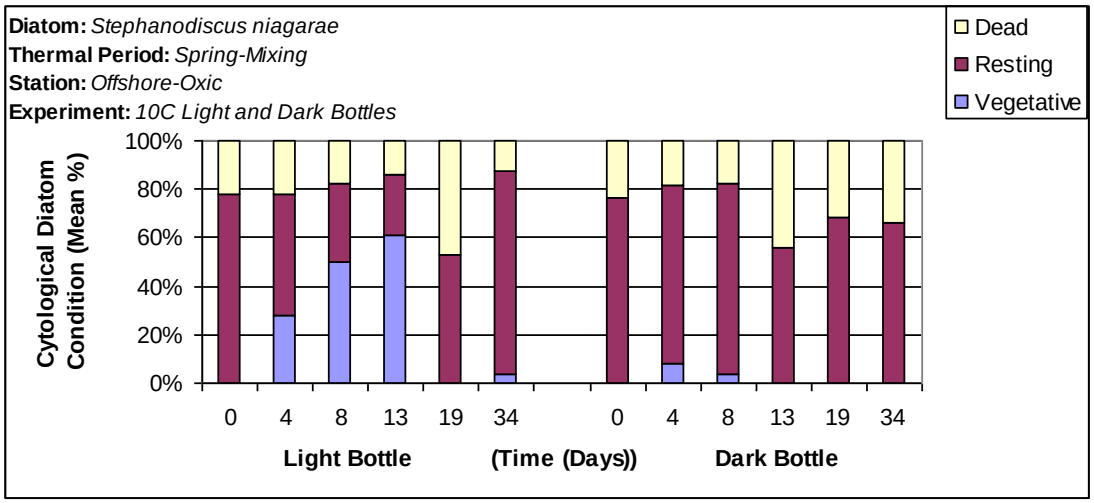

Diatom: Stephanodiscus niagarae
Thermal Period: Spring-Mixing
Station: Nearshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

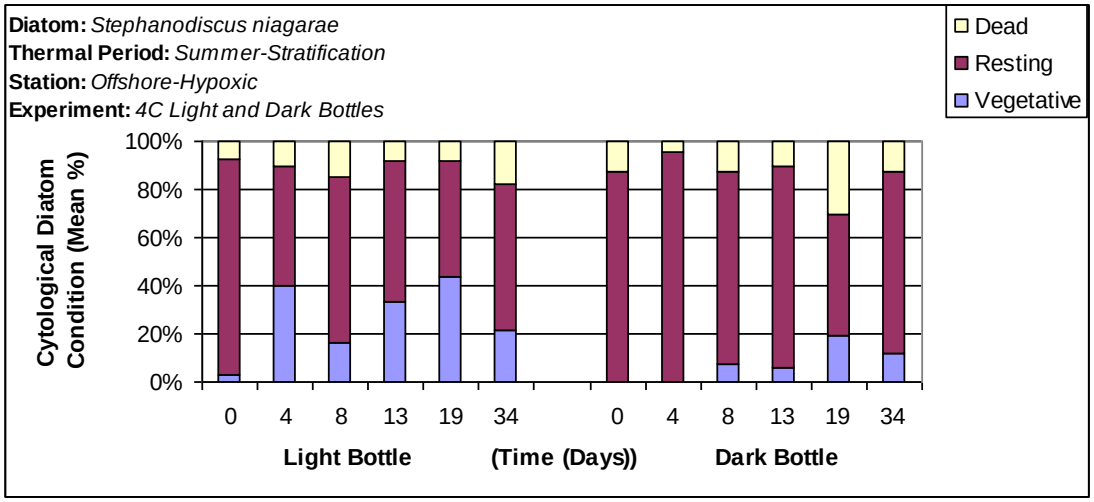

Diatom: Stephanodiscus niagarae
Thermal Period: Spring-Mixing
Station: Nearshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottles
(Time (Days))
Dark Bottle

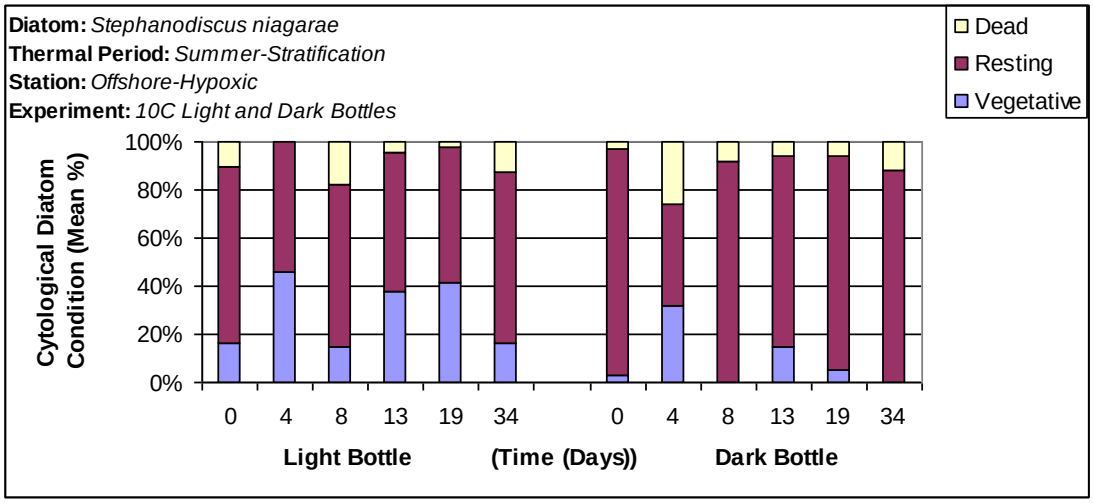

Diatom: Stephanodiscus niagarae
Thermal Period: Spring-Mixing
Station: Offshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

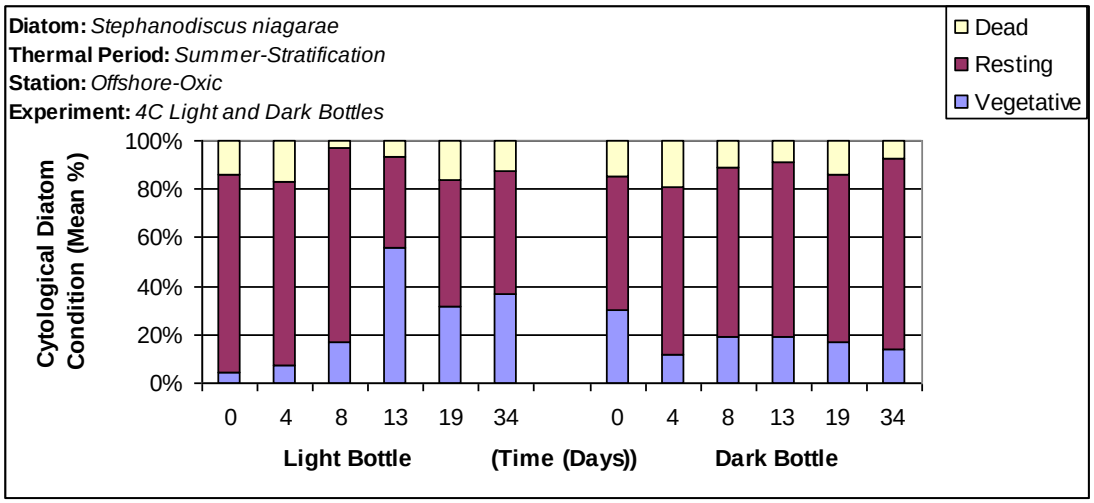

Diatom: Stephanodiscus niagarae
Thermal Period: Spring-Mixing
Station: Offshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

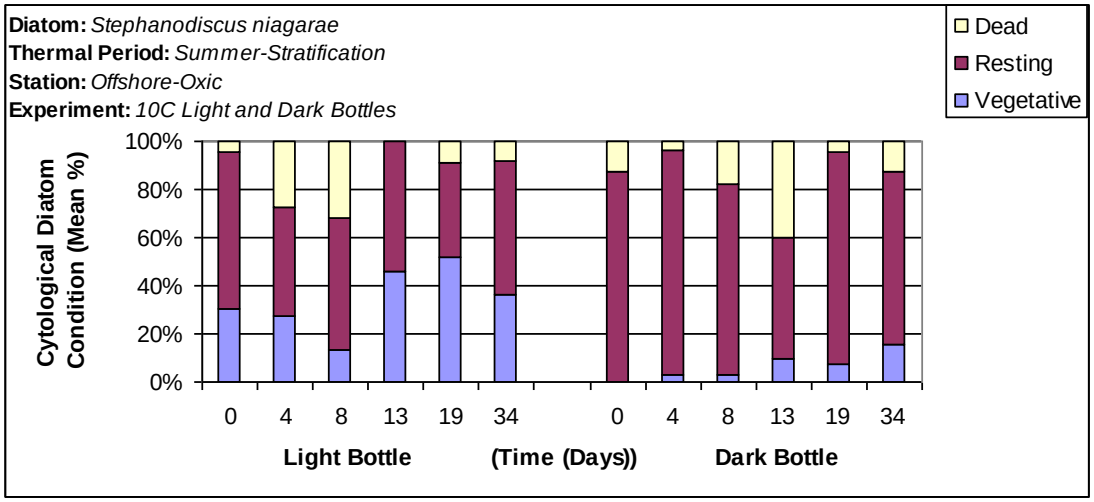

Diatom: Stephanodiscus niagarae
Thermal Period: Spring-Mixing
Station: Offshore-Oxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

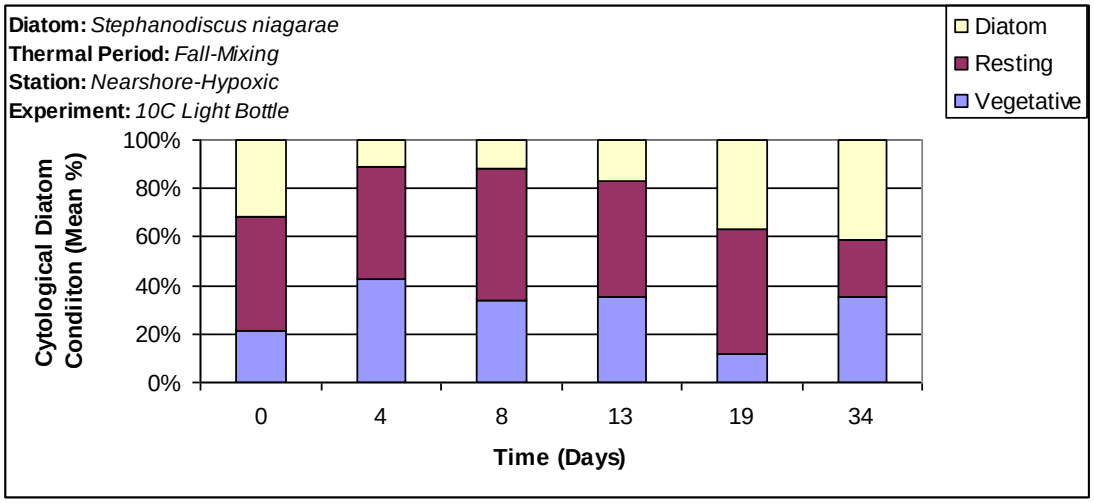

Diatom: Stephanodiscus niagarae
Thermal Period: Spring-Mixing
Station: Offshore-Oxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

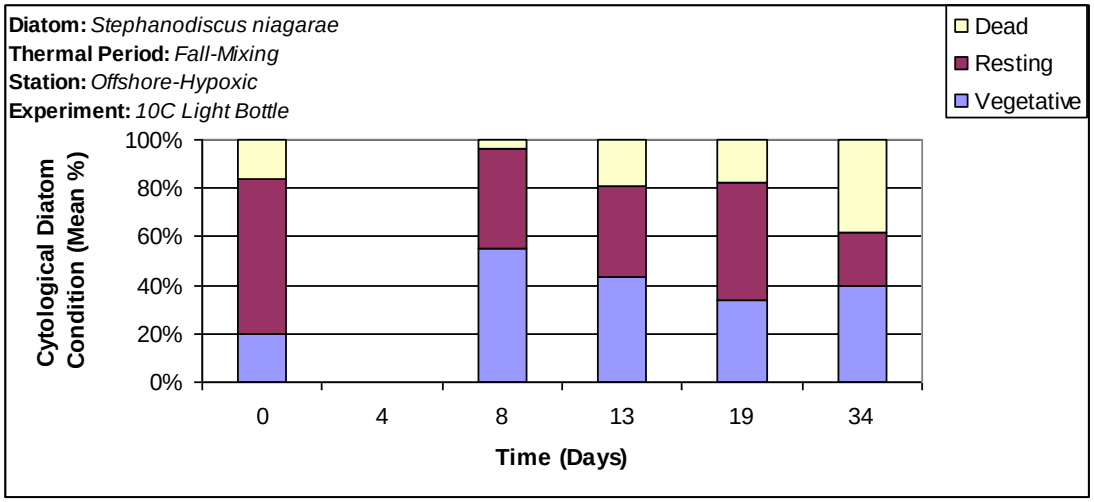

Diatom: Stephanodiscus niagarae
Thermal Period: Summer-Stratification
Station: Offshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

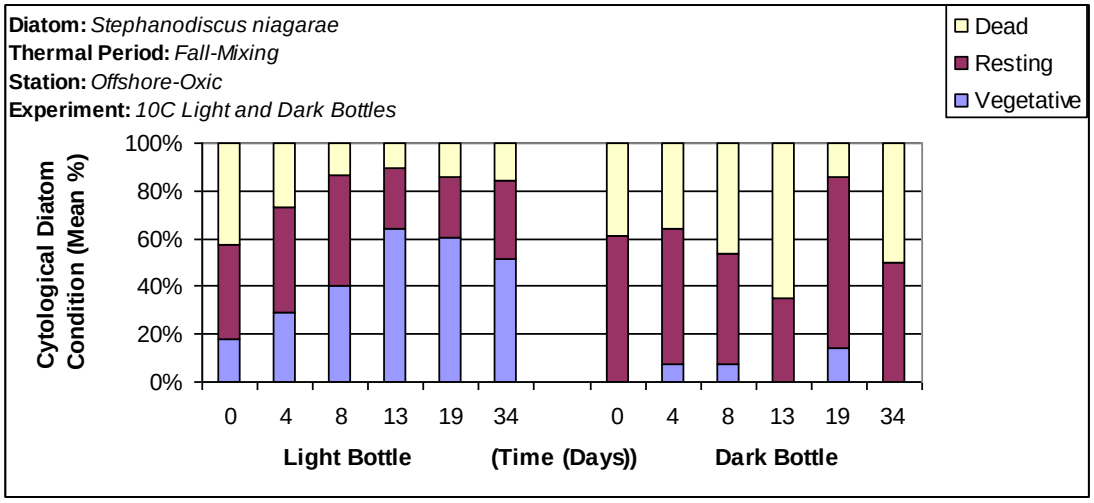

Diatom: Stephanodiscus niagarae
Thermal Period: Summer-Stratification
Station: Offshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle


Diatom: Stephanodiscus niagarae
Thermal Period: Summer-Stratification
Station: Offshore-Oxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

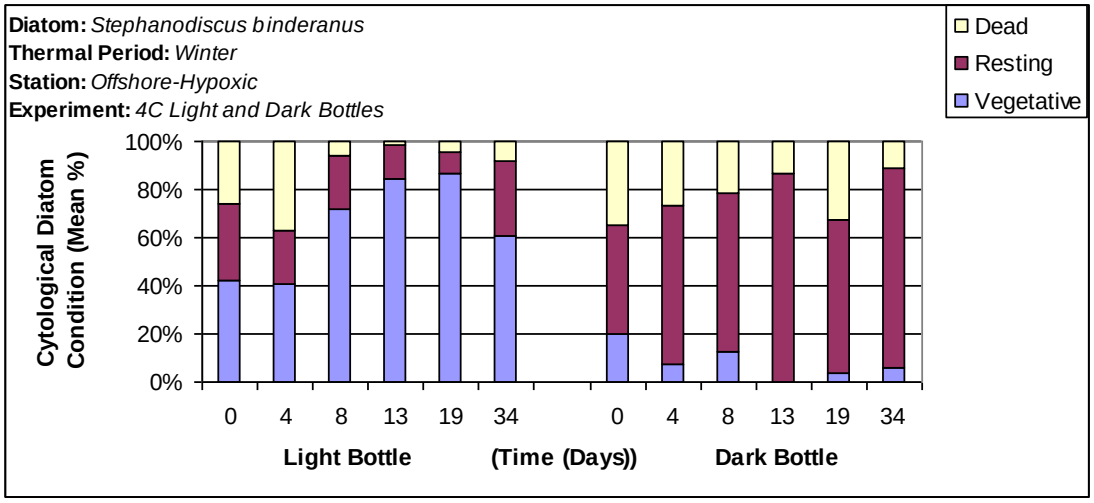

Diatom: Stephanodiscus niagarae
Thermal Period: Summer-Stratification
Station: Offshore-Oxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

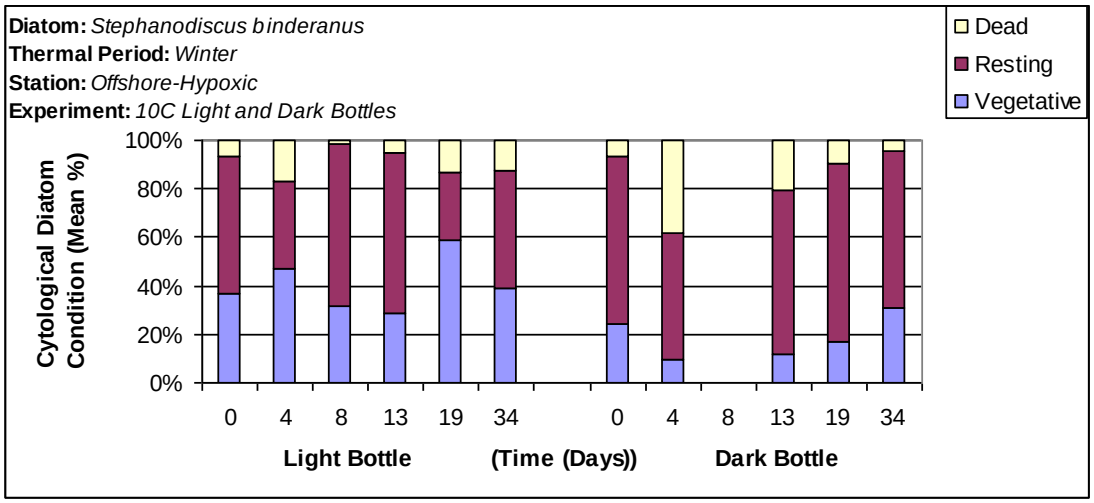

Diatom: Stephanodiscus niagarae
Thermal Period: Fall-Mixing
Station: Nearshore-Hypoxic
Experiment: 10C Light Bottle
Diatom
Resting
Vegetative
Cytological Diatom Condiiton (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34
Time (Days)

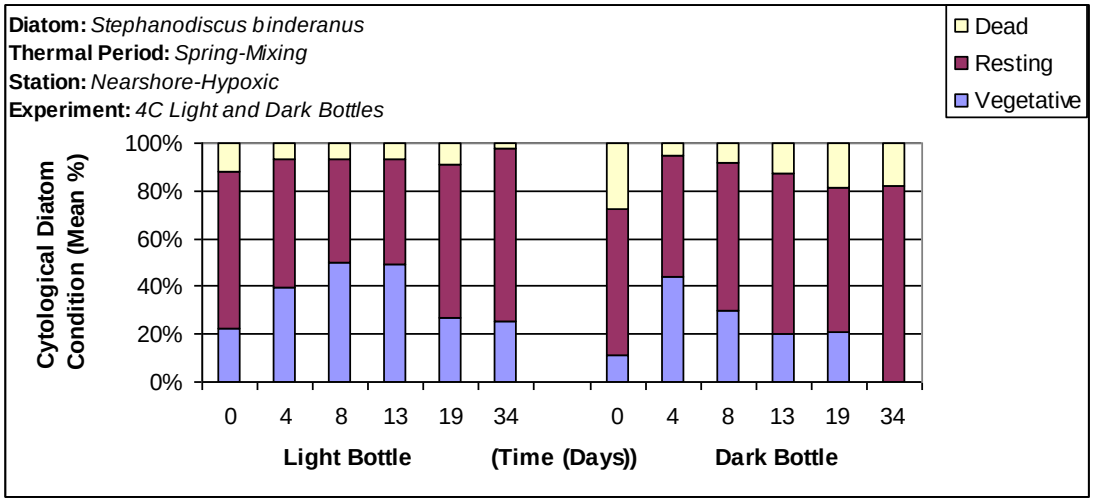

Diatom: Stephanodiscus niagarae
Thermal Period: Fall-Mixing
Station: Offshore-Hypoxic
Experiment: 10C Light Bottle
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34
Time (Days)

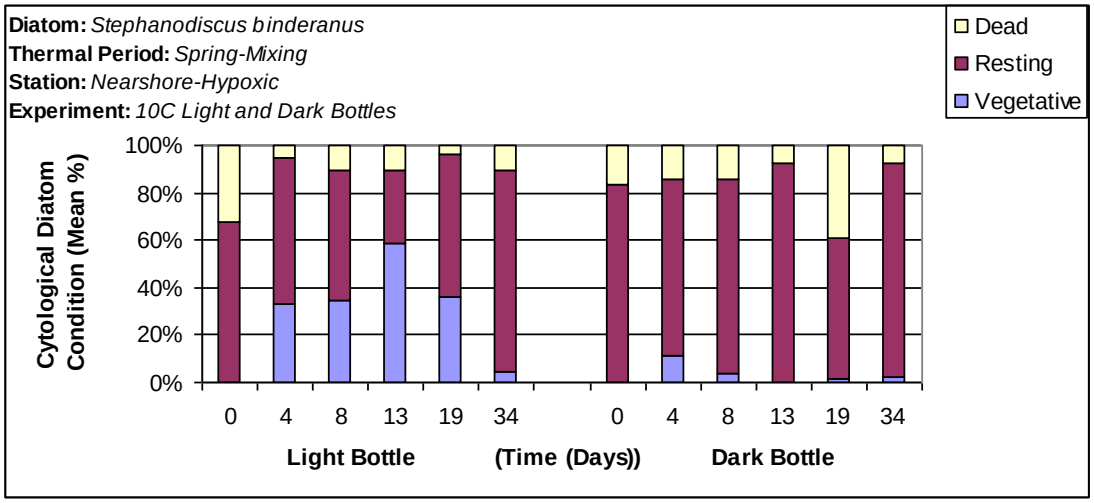


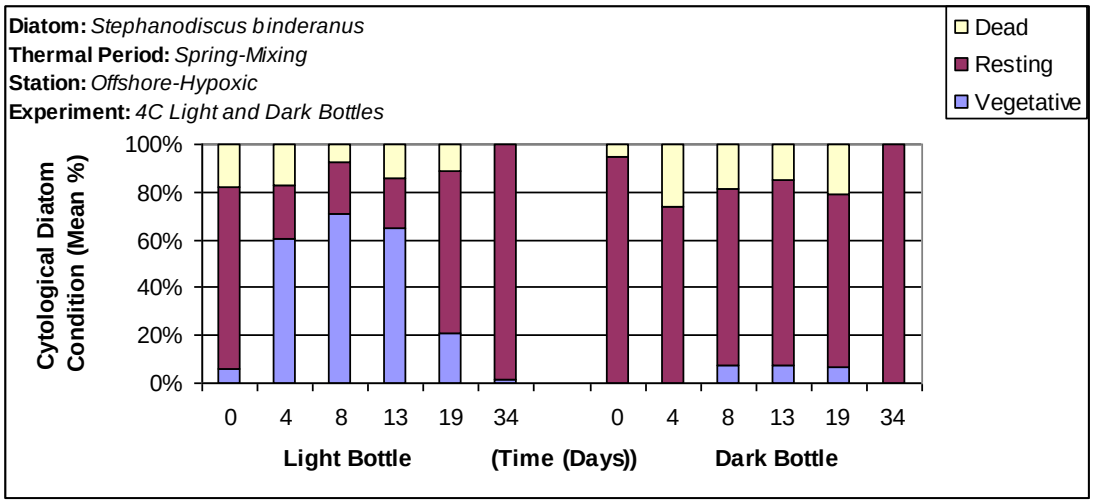
Stephanodiscus binderanus

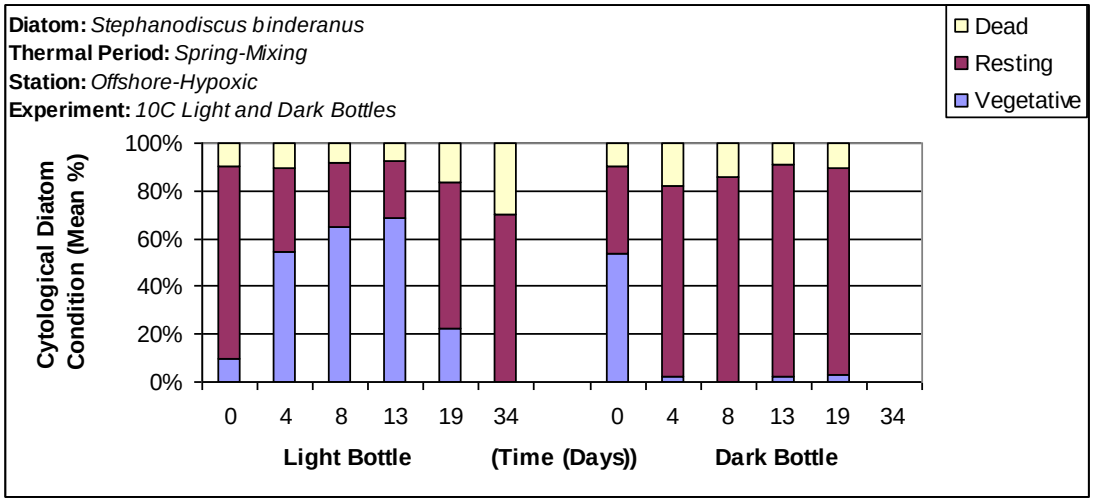


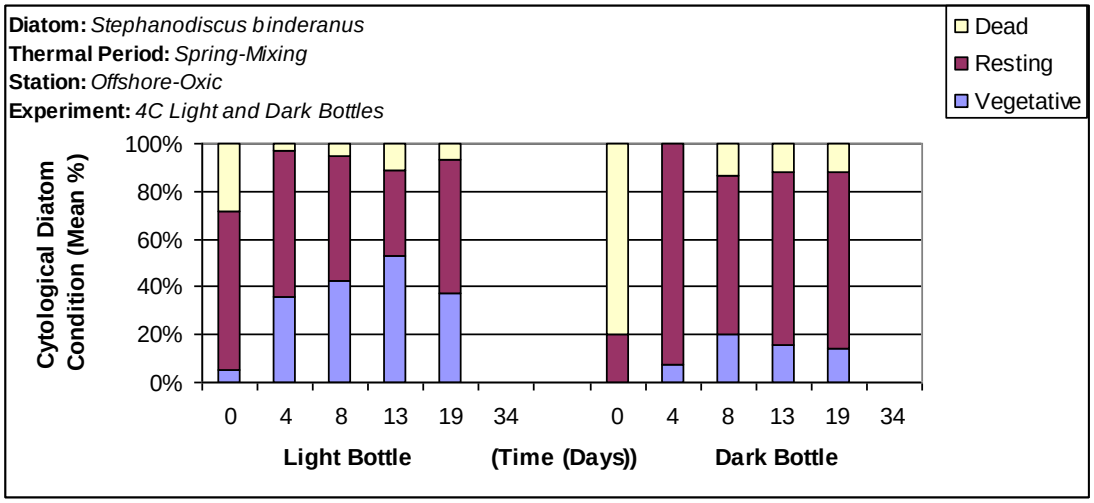


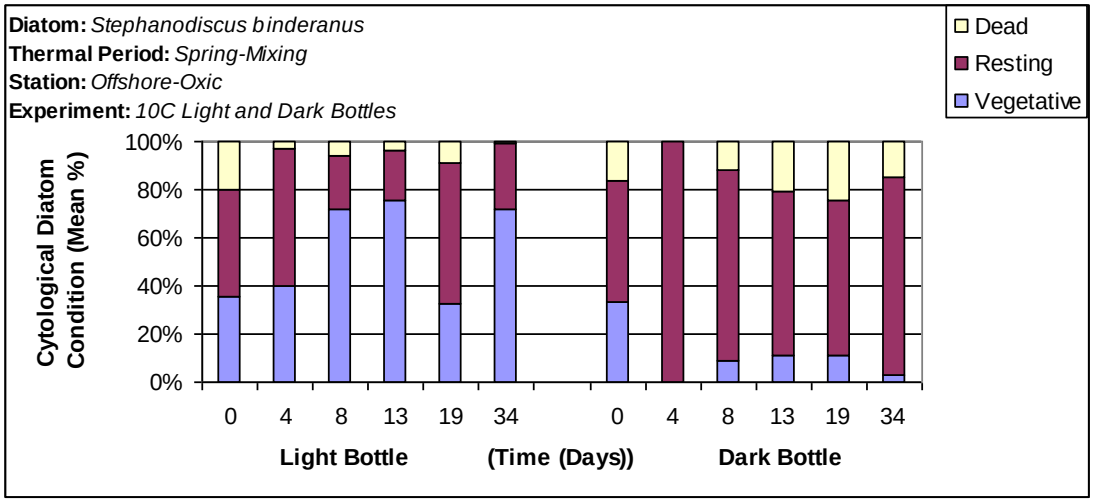

Diatom: Stephanodiscus binderanus
Thermal Period: Spring-Mixing
Station: Nearshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

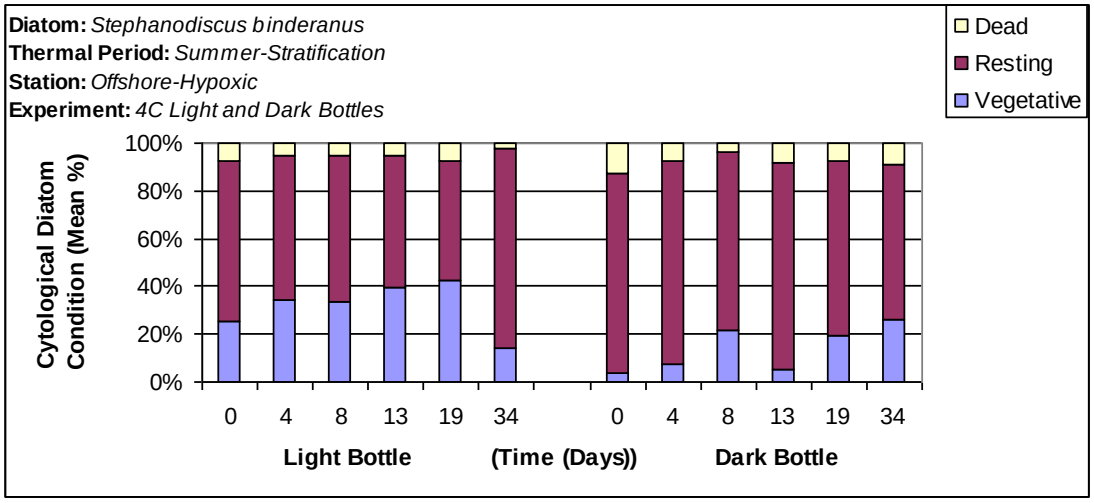

Diatom: Stephanodiscus binderanus
Thermal Period: Spring-Mixing
Station: Nearshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

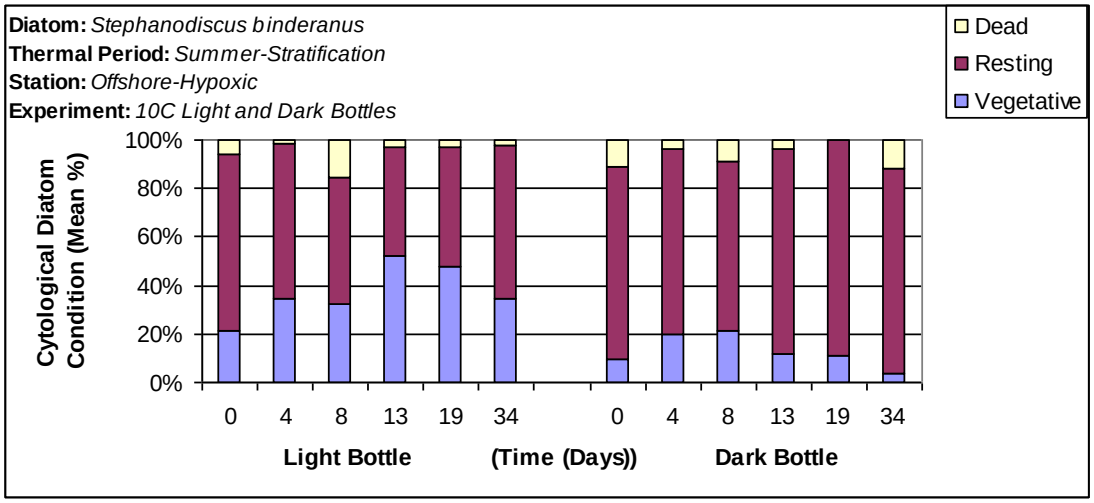

Diatom: Stephanodiscus binderanus
Thermal Period: Spring-Mixing
Station: Offshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

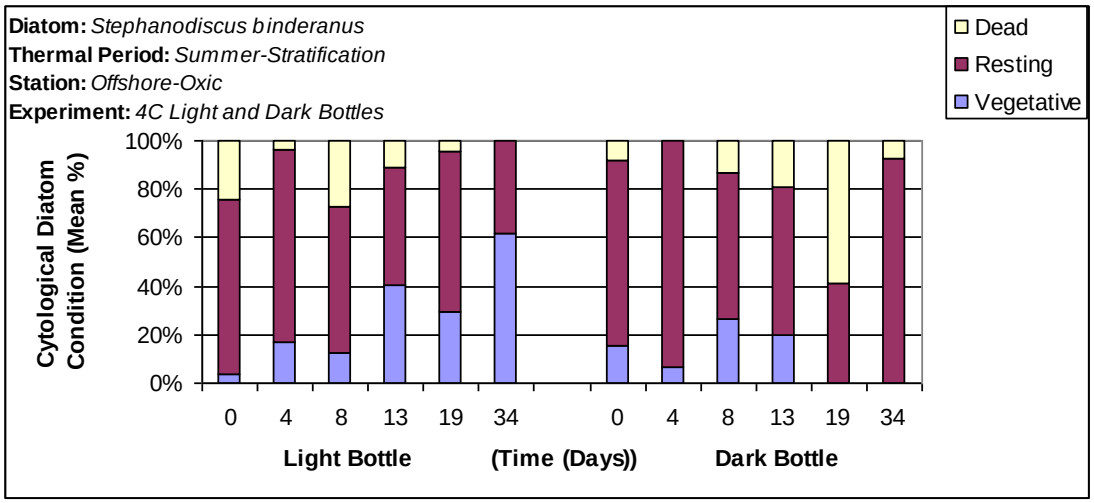

Diatom: Stephanodiscus binderanus
Thermal Period: Spring-Mixing
Station: Offshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

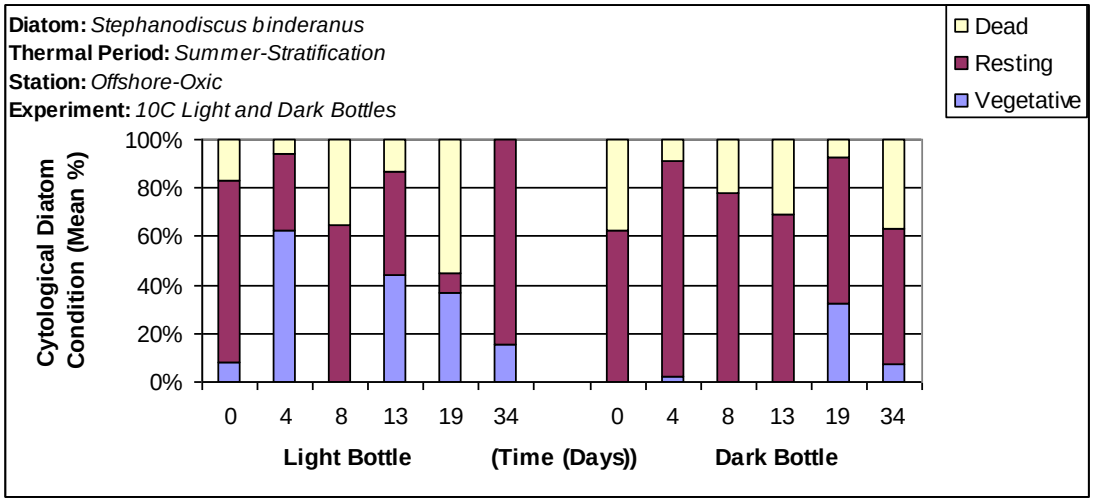

Diatom: Stephanodiscus binderanus
Thermal Period: Spring-Mixing
Station: Offshore-Oxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

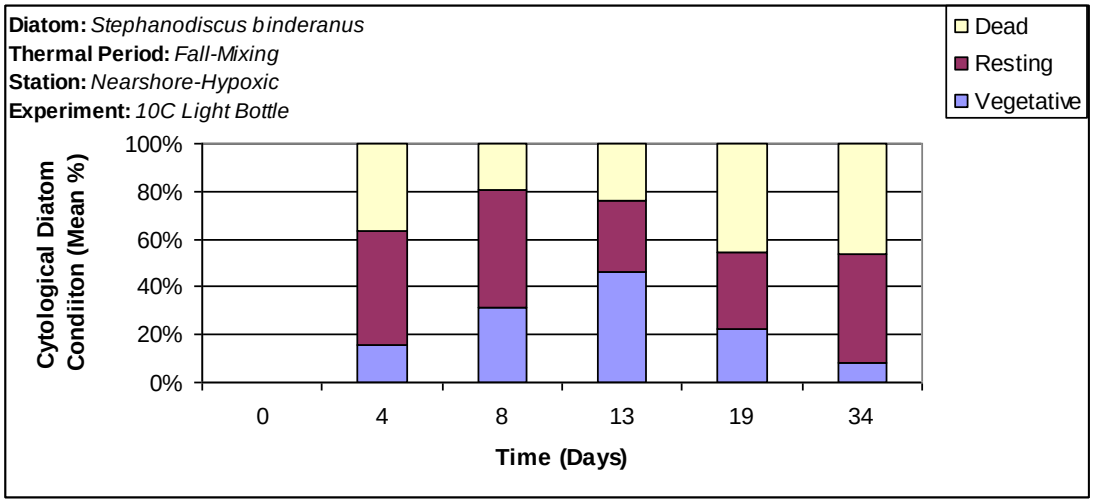

Diatom: Stephanodiscus binderanus
Thermal Period: Spring-Mixing
Station: Offshore-Oxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

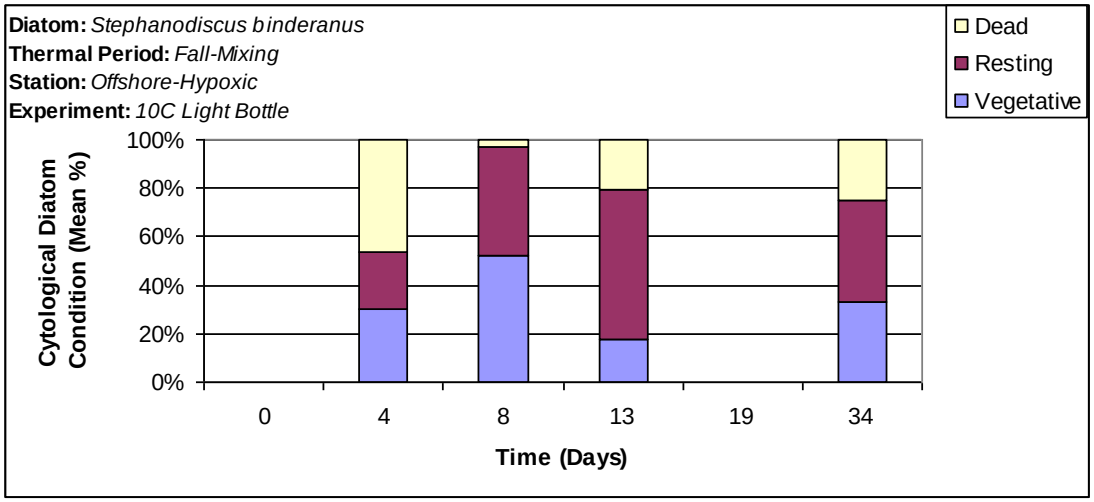

Diatom: Stephanodiscus binderanus
Thermal Period: Summer-Stratification
Station: Offshore-Hypoxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle

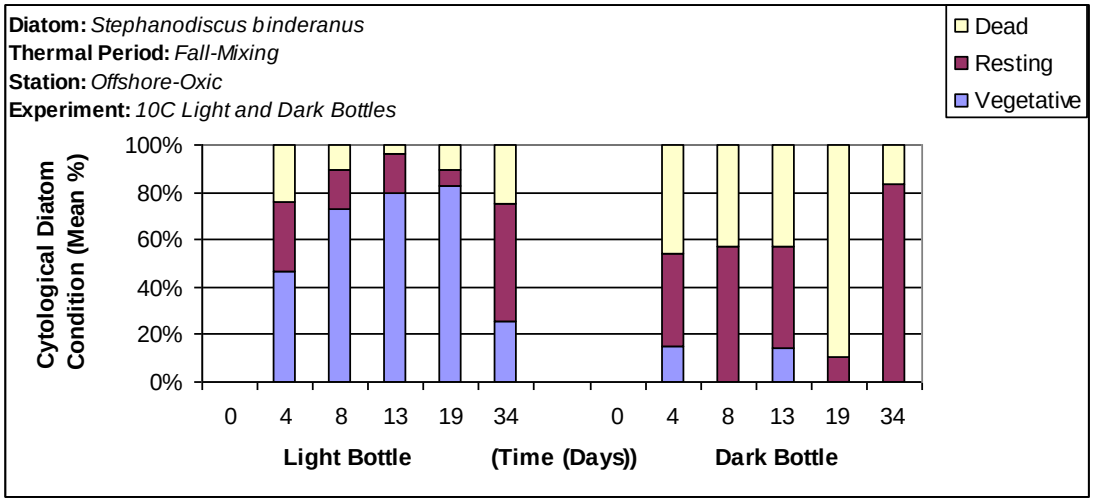

Diatom: Stephanodiscus binderanus
Thermal Period: Summer-Stratification
Station: Offshore-Hypoxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle


Diatom: Stephanodiscus binderanus
Thermal Period: Summer-Stratification
Station: Offshore-Oxic
Experiment: 4C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle


Diatom: Stephanodiscus binderanus
Thermal Period: Summer-Stratification
Station: Offshore-Oxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34 0 4 8 13 19 34
Light Bottle
(Time (Days))
Dark Bottle


Diatom: Stephanodiscus binderanus
Thermal Period: Fall-Mixing
Station: Nearshore-Hypoxic
Experiment: 10C Light Bottle
Dead
Resting
Vegetative
Cytological Diatom Condiiton (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34
Time (Days)


Diatom: Stephanodiscus binderanus
Thermal Period: Fall-Mixing
Station: Offshore-Hypoxic
Experiment: 10C Light Bottle
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0 4 8 13 19 34
Time (Days)


Diatom: Stephanodiscus binderanus
Thermal Period: Fall-Mixing
Station: Offshore-Oxic
Experiment: 10C Light and Dark Bottles
Dead
Resting
Vegetative
Cytological Diatom Condition (Mean %)
100%
80%
60%
40%
20%
0%
0
4
8
13
19
34
0
4
8
13
19
34
Light Bottle
(Time (Days))
Dark Bottle

Appendix E

Rejuvenation rates (Vegetative Cells d^{-1}) for three Lake Erie central basin diatom species *(Aulacoseira islandica, Stephanodiscus niagarae Stephanodiscus binderanus)* over three stations, four thermal periods, and two experimental temperatures (4ºC and 10ºC) during 2007-08.

Time	Station	Temperature (ºC)	*Aulacoseira islandica* Incubation Period (Days): Maximum Growth Rate (Vegetative Cells d^{-1})					
Fall 2007	Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0076				
			8	0.0072	0.0220			
			13	0.0063	0.0125	0.0050		
			19	0.0080	0.0122	0.0086	0.0117	
			34	0.0039	0.0054	0.0029	0.0024	-0.0013
Fall 2007	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0143				
			8	-0.0078	-0.0012			
			13	0.0008	0.0074	0.0144		
			19	0.0039	0.0087	0.0123	0.0106	
			34	0.0022	0.0044	0.0052	0.0031	0.0000
Fall 2007	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0128				
			8	-0.0007	0.0114			
			13	0.0109	0.0215	0.0296		
			19	0.0021	0.0061	0.0042	-0.0170	
			34	0.0036	0.0058	0.0050	-0.0009	0.0056

Winter 2008	84	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0117				
			8	0.0022	0.0162			
			13	-0.0546	-0.0736	-0.1455		
			19	0.0033	0.0073	0.0041	0.1287	
			34	0.0031	0.0051	0.0033	0.0388	0.0028
Winter 2008	84	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0047				
			8	0.0017	-0.0014			
			13	0.0019	0.0006	0.0021		
			19	0.0069	0.0074	0.0106	0.0177	
			34	0.0016	0.0011	0.0015	0.0014	-0.0052
Spring 2008	42 Nearshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0136				
			8	0.0093	0.0051			
			13	0.0062	0.0029	0.0012		
			19	0.0035	0.0008	-0.0008	-0.0024	
			34	-0.0001	-0.0019	-0.0030	-0.0040	-0.0046

Spring 2008	43 Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1622				
			8	0.0851	0.0080			
			13	0.0522	0.0033	-0.0004		
			19	0.0330	-0.0015	-0.0050	-0.0088	
			34	0.0188	-0.0004	-0.0017	-0.0020	0.0008
Spring 2008	78 Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0251				
			8	0.0146	0.0042			
			13	0.0093	0.0023	0.0008		
			19	0.0032	-0.0027	-0.0051	-0.0101	
			34	-0.0027	-0.0064	-0.0080	-0.0101	-0.0101
Spring 2008	42 Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0358				
			8	0.0197	0.0036			
			13	0.0199	0.0129	0.0203		
			19	0.0100	0.0031	0.0029	-0.0116	
			34	-0.0185	-0.0257	-0.0302	-0.0423	-0.0546

Spring 2008	43 Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0173				
			8	-0.0067	0.0039			
			13	-0.0025	0.0041	0.0043		
			19	-0.0045	-0.0011	-0.0029	-0.0089	
			34	-0.0014	0.0007	0.0002	-0.0008	0.0024
Spring 2008	78 Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0117				
			8	0.0058	0.0000			
			13	0.0041	0.0007	0.0013		
			19	-0.0012	-0.0046	-0.0063	-0.0127	
			34	-0.0299	-0.0354	-0.0408	-0.0509	-0.0662
Summer 2008	43 Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0143				
			8	0.0033	-0.0077			
			13	0.0023	-0.0030	0.0008		
			19	0.0010	-0.0026	-0.0007	-0.0019	
			34	-0.0019	-0.0041	-0.0036	-0.0046	-0.0057

Summer 2008	78 Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0128				
			8	0.0021	-0.0086			
			13	0.0029	-0.0015	0.0041		
			19	0.0067	0.0050	0.0099	0.0148	
			34	-0.0007	-0.0025	-0.0015	-0.0028	-0.0099
Summer 2008	43 Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0062				
			8	0.0026	-0.0009			
			13	0.0051	0.0046	0.0090		
			19	0.0011	-0.0002	0.0000	-0.0075	
			34	-0.0004	-0.0013	-0.0013	-0.0038	-0.0023
Summer 2008	78 Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0072				
			8	0.0013	-0.0046			
			13	0.0016	-0.0009	0.0020		
			19	0.0068	0.0067	0.0108	0.0182	
			34	-0.0010	-0.0021	-0.0017	-0.0026	-0.0109

Time	Station	Temperature (°C)	*Stephanodiscus binderanus* Incubation Period (Days): Maximum Growth Rate (Vegetative Cells d^{-1})					
Fall 2007	Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.5461				
			8	0.2855	0.0248			
			13	0.1825	0.0208	0.0176		
			19	0.0933	-0.0274	-0.0464	-0.0999	
			34	0.0474	-0.0190	-0.0258	-0.0361	-0.0107
Fall 2007	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.5595				
			8	0.2938	0.0282			
			13	0.1741	0.0028	-0.0175		
			19	0.0898	-0.0354	-0.0585	-0.0927	
			34	0.0732	0.0084	0.0053	0.0108	0.0521
Fall 2007	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.5314				
			8	0.2879	0.0444			
			13	0.1839	0.0295	0.0177		
			19	0.1193	0.0094	-0.0033	-0.0207	
			34	0.0712	0.0099	0.0046	0.0015	0.0103

Winter 2008	84	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0640				
			8	0.0053	0.0746			
			13	0.0184	0.0551	0.0395		
			19	0.0085	0.0278	0.0108	-0.0132	
			34	0.0036	0.0126	0.0030	-0.0056	-0.0026
Winter 2008	84	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0065				
			8	-0.0717	-0.1500			
			13	-0.0023	-0.0062	0.1088		
			19	0.0031	0.0021	0.0574	0.0146	
			34	0.0029	0.0024	0.0258	0.0060	0.0026
Spring 2008	42 Nearshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0286				
			8	0.0154	0.0021			
			13	0.0102	0.0020	0.0019		
			19	0.0045	-0.0019	-0.0034	-0.0077	
			34	0.0012	-0.0025	-0.0032	-0.0044	-0.0030

Spring 2008	43 Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.2022				
			8	0.1048	0.0074			
			13	0.0640	0.0025	-0.0014		
			19	0.0376	-0.0063	-0.0113	-0.0195	
			34	-0.0055	-0.0332	-0.0395	-0.0486	-0.0602
Spring 2008	78 Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.2318				
			8	0.1227	0.0136			
			13	0.0782	0.0099	0.0068		
			19	0.0513	0.0032	-0.0006	-0.0068	
			34	-0.0397	-0.0759	-0.0897	-0.1127	-0.1550
Spring 2008	42 Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.6037				
			8	0.3033	0.0028			
			13	0.1903	0.0065	0.0094		
			19	0.1288	0.0021	0.0019	-0.0044	
			34	0.0647	-0.0072	-0.0087	-0.0130	-0.0165

Spring 2008	43 Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0523				
			8	0.0251	-0.0020			
			13	0.0153	-0.0011	-0.0004		
			19	0.0048	-0.0079	-0.0101	-0.0181	
			34	-0.0688	-0.0849	-0.0977	-0.1208	-0.1619
Spring 2008	78 Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0290				
			8	-0.0003	0.0285			
			13	0.0055	0.0209	0.0148		
			19	0.0034	0.0120	0.0060	-0.0012	
			34	0.0028	0.0070	0.0037	0.0011	0.0020
Summer 2008	43 Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0012				
			8	-0.0024	-0.0061			
			13	-0.0023	-0.0039	-0.0022		
			19	-0.0014	-0.0021	-0.0007	0.0005	
			34	-0.0051	-0.0059	-0.0059	-0.0067	-0.0097

Summer 2008	78 Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0689				
			8	0.0949	0.1210			
			13	0.0669	0.0660	0.0221		
			19	0.0468	0.0409	0.0118	0.0033	
			34	0.0262	0.0205	0.0050	0.0009	0.0000
Summer 2008	43 Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0065				
			8	-0.0012	0.0041			
			13	0.0002	0.0031	0.0024		
			19	-0.0026	-0.0016	-0.0036	-0.0087	
			34	0.0004	0.0013	0.0009	0.0005	0.0042
Summer 2008	78 Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.2708				
			8	-0.1694	-0.6096			
			13	0.0747	-0.0125	0.4651		
			19	0.0188	-0.0484	0.1557	-0.1022	
			34	0.0039	-0.0317	0.0573	-0.0399	-0.0149

Time	Station	Temperature (ºC)	*Stephanodiscus niagarae* Incubation Period (Days): Maximum Growth Rate (Vegetative Cells d^{-1})					
Fall 2007	Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0087				
			8	0.0121	0.0155			
			13	0.0076	0.0071	0.0003		
			19	-0.0352	-0.0469	-0.0696	-0.1279	
			34	0.0034	0.0027	0.0007	0.0008	0.0523
Fall 2007	Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.2079				
			8	0.0028	0.2135			
			13	-0.0056	0.0842	-0.0192		
			19	-0.0014	0.0537	-0.0044	0.0079	
			34	0.0027	0.0308	0.0027	0.0079	0.0079
Fall 2007	Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0036				
			8	0.0078	0.0120			
			13	0.0143	0.0190	0.0246		
			19	0.0038	0.0038	0.0008	-0.0190	
			34	0.0068	0.0073	0.0065	0.0022	0.0107

Winter 2008	84	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0023				
			8	-0.0181	-0.0385			
			13	-0.0457	-0.0671	-0.0899		
			19	0.0035	0.0039	0.0193	0.1103	
			34	0.0039	0.0041	0.0107	0.0346	0.0044
Winter 2008	84	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0150				
			8	-0.0080	-0.0010			
			13	0.0059	0.0152	0.0281		
			19	0.0106	0.0174	0.0241	0.0208	
			34	0.0073	0.0103	0.0120	0.0082	0.0031
Spring 2008	42 Nearshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0106				
			8	0.0100	0.0094			
			13	0.0062	0.0042	0.0000		
			19	0.0013	-0.0012	-0.0050	-0.0093	
			34	-0.0675	-0.0779	-0.0914	-0.1131	-0.1547

Spring 2008	43 Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1501				
			8	0.0838	0.0174			
			13	0.0533	0.0103	0.0046		
			19	0.0325	0.0011	-0.0048	-0.0127	
			34	0.0169	-0.0009	-0.0037	-0.0057	-0.0029
Spring 2008	78 Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1955				
			8	0.1080	0.0205			
			13	0.0714	0.0162	0.0128		
			19	0.0425	0.0017	-0.0052	-0.0201	
			34	0.0237	0.0008	-0.0022	-0.0058	0.0000
Spring 2008	42 Nearshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0287				
			8	0.0186	0.0084			
			13	0.0187	0.0142	0.0188		
			19	0.0084	0.0030	0.0010	-0.0139	
			34	0.0012	-0.0025	-0.0042	-0.0096	-0.0079

Spring 2008	43 Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.5886				
			8	0.3016	0.0146			
			13	0.1822	0.0016	-0.0088		
			19	0.1234	-0.0006	-0.0062	-0.0040	
			34	0.0430	-0.0298	-0.0366	-0.0432	-0.0589
Spring 2008	78 Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.5289				
			8	0.2781	0.0273			
			13	0.1714	0.0125	0.0007		
			19	0.0000	-0.1410	-0.2023	-0.3714	
			34	0.0390	-0.0264	-0.0346	-0.0430	0.0883
Summer 2008	43 Offshore-Hypoxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1840				
			8	0.0811	-0.0217			
			13	0.0046	-0.0751	-0.1178		
			19	0.0382	-0.0007	0.0069	0.1108	
			34	0.0177	-0.0045	-0.0018	0.0258	-0.0082

Summer 2008	78 Offshore-Oxic	4	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.0404				
			8	0.0894	0.1383			
			13	0.0681	0.0804	0.0340		
			19	0.0460	0.0475	0.0144	-0.0019	
			34	0.0213	0.0187	0.0003	-0.0077	-0.0100
Summer 2008	43 Offshore-Hypoxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	0.1820				
			8	0.0935	0.0050			
			13	0.0598	0.0055	0.0060		
			19	0.0425	0.0053	0.0054	0.0050	
			34	0.0200	-0.0016	-0.0026	-0.0047	-0.0086
Summer 2008	78 Offshore-Oxic	10	**Incubation Period**	**0**	**4**	**8**	**13**	**19**
			4	-0.0051				
			8	-0.0103	-0.0156			
			13	0.0043	0.0084	0.0276		
			19	0.0087	0.0124	0.0226	0.0184	
			34	-0.0005	0.0001	0.0025	-0.0035	-0.0122