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Primary Productivity Distributions Along the River-Dominated Shoreline of the Bay of St. Louis, MS Estuary

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The University of Southern Mississippi

PRIMARY PRODUCTIVITY DISTRIBUTIONS ALONG THE RIVER-DOMINATED SHORELINE OF THE BAY OF SAINT LOUIS, MS ESTUARY

by

Adam Douglas Boyette

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ABSTRACT

PRIMARY PRODUCTIVITY DISTRIBUTIONS ALONG THE RIVER-DOMINATED SHORELINE OF THE BAY OF SAINT LOUIS, MS ESTUARY

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May 2013

Potential primary production was measured for six consecutive months (July 2010 to December 2010) at selected stations along the shoreline of the Bay of Saint Louis (BSL) estuary. Monthly surface and a series of subsurface (0.5 m) samples were taken to observe the temporal (monthly and short-term) and spatial variability in production relative to environmental variables that potentially could influence phytoplankton photosynthesis. Daily areal primary production, PP was modeled using photosynthesis-irradiance (P-E) parameters in conjunction with *in situ* irradiance measurements and biomass data collected during sampling. Although spatial variability was not observed, PP varied seasonally and ranged from 1.90 g C m^{-2} d^{-1} in July to 0.06 g C m^{-2} d^{-1} in December. Short-term variability also was observed. Production ranged from 0.25 to 0.84 g C m^{-2} d^{-1}over the course of a week and within-day values ranged from 0.36 to 0.72 g C m^{-2} d^{-1} with peak production occurring at midday. Temporal variability was attributed primarily to changes in temperature (seasonal), river discharge (week-long), and incident irradiance (diurnal). Annual production for the BSL estuary was estimated at 197.3 g C m^{-2} y^{-1} and is comparable to other temperate, mesotrophic estuaries. The results from this study provide the first modeled estimates of primary production within the BSL system and will facilitate ecological research and monitoring efforts within this locally important estuary.

DEDICATION

This work is dedicated to Alma.

ACKNOWLEDGMENTS

I want to thank my academic advisor Dr. Donald G. Redalje for his advice, humor, and encouragement during this study: without it, this work would not have been possible. I also want to thank my committee members, Drs. Stephen Howden and Kjell Gundersen for their guidance and input, and to Dr. Xiaogang Chen for his expert advice and technical assistance. I want to thank Allison K. Mojzis for her help with nutrient analysis and to Matthew Stone and Amy Glover for their help with field work, technical assistance, and editing. Finally, I want to thank my loving family for their support.

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Ammonium	NH_4^+
Bay of Saint Louis	BSL
Bayou Portage	BP
Bay-Waveland Yacht Club	BWYC
Chlorophyll *a*	Chl *a*
Daily Areal Primary Production	PP
Daily Integrated Photosynthetically Available Irradiance	PAR
Disintegrations per Minute	DPM
Dissolved Inorganic Carbon	DIC
Dissolved Inorganic Nitrogen	DIN
Dissolved Oxygen	DO
Light Saturation Parameter	E_k
Hydrochloric Acid	HCl
Instantaneous Tidal Level	ITL
Irradiance	E
Jourdan River	JR
Light Attenuation Coefficient	K_d
Kolmogorov-Smirnov	KS
Kruskal-Wallis	KW
Mann-Whitney	MW
Maximum Photosynthetic Rate	P^B_{max}
Mean Lower Low Water	MLLW

Mean Tidal Level	MTL
Mississippi Department of Environmental Quality	MDEQ
Mississippi Sound	MS
National Oceanic and Atmospheric Administration	NOAA
Nitrate	NO_3^-
Nitrite	NO_2^-
Orthophosphate	PO_4^{3-}
Particulate Matter	PM
Photoinhibition	β^B
Photosynthesis-Irradiance	P-E
Photosynthetic Efficiency	α^B
Principal Component Analysis	PCA
River Mouth	RM
Salinity	S
Sewage Outfalls	SO
Silicate	$Si(OH)_4$
Standard Error	SE
Temperature	T
Total Dissolved Inorganic Carbon Dioxide	$\sum CO_2$
United States Geological Survey	USGS
Volumetric Production	P_{ZT}
Water Depth	z
Wolf River	WR

CHAPTER I

INTRODUCTION

The Bay of Saint Louis (BSL) is a shallow, coastal estuary (mean depth < 2 m) situated at the western end of the Mississippi Sound (MS) on the northern Gulf of Mexico coast. It is a vital economic resource for local communities and is an essential coastal habitat for indigenous wetland flora and fauna (MDEQ 2007, Liu 2008). This small, microtidal estuary of the Jourdan River (JR) and Wolf River (WR) is also a critical feeding, spawning, and nursery habitat for many species of fish and shellfish (MDEQ 2007). The BSL watershed is subject to flooding during episodic storm events, and this can introduce a significant amount of freshwater, organic matter, and nutrients into the bay. This has the potential to support dense populations of microalgae and enhance primary production. The BSL is shallow and well-mixed, and episodic changes in physical forcing variables (*e.g.* freshwater input, wind) are regarded as the primary regulators of environmental quality within the BSL estuary (Phelps 1999; Sawant 2009). These variables have also been shown to regulate primary production in other estuaries (Cloern 1987; Mallin *et al.* 1991; MacIntyre and Cullen 1996; Azevedo *et al.* 2010). It is well known that aquatic photosynthesis by phytoplankton is the primary driver of complex food webs within temperate, coastal ecosystems (Mann and Lazier 1991; Mortazavi 2000; Livingston 2001). Therefore, it is useful to quantify autotrophic production and identify some of the environmental parameters potentially responsible for the observed variability.

For this study, potential primary production was estimated along a salinity gradient extending from the JR and WR mouths to the Mississippi Sound (MS).

Photosynthesis-irradiance (P-E) parameters, *in situ* irradiance measurements, and biomass data collected during sampling were used to model daily areal primary production, PP for the BSL estuary. Monthly shoreline samples were taken to observe the temporal (monthly and short-term) and spatial variability in production relative to environmental variables that potentially could influence phytoplankton photosynthesis.

Background

Phytoplankton production varies considerably over different timescales and often is related to variations in environmental conditions. These environmental variables frequently act in concert to regulate phytoplankton physiology and the overall photosynthetic performance of the resident phytoplankton community (Lohrenz *et al.* 1994; Azevedo *et al.* 2010). Seasonal variability in phytoplankton production usually is linked to seasonal changes in temperature and photosynthetically available raditation (PAR), while day to day variability is regulated primarily by short-term changes in the physical structure of the water column (e.g. temperature, salinity, PAR) (Cloern 1987; Kirk 1996; MacIntyre and Cullen 1996; Falkowski and Raven 2007; Azevedo *et al.* 2010). Phytoplankton respond to some of these parameters either by photoacclimation or by inhibitory effects due to high light (*i.e.* photoinhibition).

Numerous studies (Eppley 1972; Pennock and Sharp 1986; Randall and Day 1987; Mallin *et al.*. 1991; Mann and Lazier 1991; Lohrenz *et al.* 1994; Cole 1998; Mortazavi *et al.* 2000; Azevedo *et al.* 2010) have shown that much of the seasonal variability in phytoplankton production can be attributed to shifts in temperature. Temperature regulates the rate of photosynthesis through intermolecular collisions (e.g. diffusion of electron carriers plastoquinone and plastocyanin) and membrane fluidity, through which some electron transfer processes rely (Eppley 1972; Falkowski and Raven 2007). This rate reaction is described by the Arrhenius equation:

$$k = Ae^{-Ea/RT} \qquad \textit{Equation 1}$$

where k is the rate constant, *A* is the concentration of the substrate, and *Ea* is the minimum amount of energy required for activation of the reaction, *R* is the Boltzmann gas constant, *T* is the temperature (Kelvin) (Falkowski and Raven 2007).

Estuaries are typically shallow, turbid environments, and light, rather than nutrients, often becomes the limiting resource for primary production (Cloern 1987). Changes in water clarity can occur on the order of a few minutes to several hours, such that turbidity may increase either through sediment resuspension (e.g. wind-induced vertical mixing) or through convergence of water masses (e.g. riverine input of suspended particulate matter or tidal advection) (Cloern 1987; Kirk 1996; Falkowski and Raven 2007). Such increases in particulate matter (PM) act to greatly enhance light attenuation and confine the euphotic zone to a relatively shallow depth (Cloern 1987). Thus, the rate of mixing out of the euphotic zone can have pronounced effects on photosynthesis. For example, if the rate of mixing is faster than the rate of acclimation, then the representative population will be homogenous throughout the water column (Lewis *et al.* 1984a; Lewis *et al.* 1984b; Bailey 1997). However, if the rate is slower and the phytoplankton population becomes photoacclimated to low light levels at depth and high light levels near the surface, there will be a pronounced vertical structure with respect to the photosynthetic parameters (Lewis *et al.* 1984a; Lewis *et al.* 1984b; Bailey 1997). Since phytoplankton production is coupled to the movement of carbon through marine food webs (Lohrenz *et al.* 1994; Chen 2000; Livingston 2001), the photosynthetic response to light is a useful parameter to describe the environmental quality of coastal and marine ecosystems and processes that contribute ultimately to eutrophication (Lohrenz *et al.* 1994). The photosynthetic response to changing environmental conditions reflects the physiological condition of the representative phytoplankton population and is used to calculate primary production. This response can be quantified by a simple empirical relationship between the photosynthetic fixation of carbon and light.

The photosynthesis-irradiance (P-E) curve is an empirical function relating photosynthesis to light. Moreover, it correlates potential primary production to environmental variables such as irradiance, temperature, and nutrients (Jassby and Platt 1976; Lohrenz *et al.* 1994; Chen 2000; Johnson 2007) at a given time. The mathematical relationship between photosynthesis and irradiance is expressed by the initial slope of the P-E curve normalized to biomass (i.e. chlorophyll *a*), α^B, and the chlorophyll *a*-specific maximum rate of photosynthesis P^B_{max} (Chen 2000). While α^B is a measure of the photosynthetic efficiency, P^B_{max} provides a measure of the photosynthetic capacity (Chen 2000). The light intensity at the onset of photosynthetic saturation, E_k, is proportional to P^B_{max} and α^B (i.e. $E_k = P^B_{max} / \alpha^B$) and is commonly used as an index of photoacclimation (Chen 2000). Because high light intensity alters phytoplankton physiology significantly, the rate of photoinhibition, β^B is often included in P-E models to accurately quantify the phytoplankton response (Platt *et al.* 1980; Chen 2000). Together, these parameters provide insight into the photophysiology of the representative phytoplankton community and can be useful to further describe the ecology of aquatic ecosystems (Platt *et al.* 1980; Cullen and Lewis 1988; Chen 2000).

The entire BSL watershed complex, combined with nearly 30 bayous and small tributaries, encompasses some 2,117 km^2 (Mojzis 2010). Average daily discharge rates for the JR and WR are 117.3 and 17.3 m^3 s^{-1}, respectively (Sawant 2009). The JR enters at the western margin and flows along the western shore to the estuary mouth. The WR enters in at the northeastern quadrant and flows along the eastern margin of the estuary where it mixes with Bayou Portage (BP) and continues out of the bay. While modeled circulations studies of the BSL have shown that wave- and tidally-induced currents can influence mixing in the bay (Cobb and Blain 2002), wind-driven circulation tends to act as the primary episodic forcing agent responsible for the movement of water into and out of the estuary (Sawant 2009).

Climatological data indicates that this system is characterized by long, hot and humid summers and short, temperate winters. The average annual air temperature for this area is 19 °C and range from an average of 30 °C in summer to an average of 9 °C in winter. The region is subjected to episodic thunderstorms and tropical storms during the summer months and is followed by dry periods in autumn. Precipitation averages more than 150 cm annually and distributed quite evenly throughout the year (Waveland Weather Center).

Significance of Study

Although numerous biological (Phelps 1999; Holtermann 2001; Pluhar 2007; Rowe 2008; Sawant 2009), geochemical (Cai *et al.* 2009; Wang 2009), and physical modeling (Cobb and Blain 2002) studies have been conducted within BSL, no recent efforts have been made to estimate primary productivity in this local system. A comprehensive environmental assessment of the bay that included the only known primary productivity estimates of BSL, was conducted by Woodmansee *et al.* (1980). However, that study was conducted prior to trace-metal clean techniques, which are now standard procedure, and utilized an archaic method for productivity incubations. One of the primary goals of this project was to estimate primary production in the BSL by utilizing modern techniques and compare the resulting production rates to those of other temperate estuaries (see Table 1). Further, this research will facilitate future ecological studies within the BSL by providing baseline productivity measurements. This data will be useful in observing long-term changes within this dynamic ecosystem.

Table 1

Estimates of Water Column Primary Productivity for Some North American Estuaries.

Region	Daily PP ($gC\ m^{-2}\ d^{-1}$)	Annual PP ($gC\ m^{-2}\ y^{-1}$)	Author
Neuse River Estuary NC	0.9	N/A	Mallin et al. 1991
Neuse River Estuary NC	N/A	202-320	Mallin et al. 1993
Apalacicola Bay, FL	0.8 ± 0.1	N/A	Mortazavi et al. 2000
Apalacicola Bay, FL	1.0	N/A	Caffrey 2004
Escambia Bay, FL	0.02 - 2.2	290	Murrell et al. 2007
Delaware Estuary, DE	0.1-1.1	70-392	Pennock and Sharp 1986
San Antonio Bay, TX	0.1 - 2.5	N/A	MacIntyre and Cullen 1996
Tomales Bay, CA	0.2 - 2.2	400	Cole 1989
Chesapeake Bay	0.1 - 2.6	N/A	Harding et al. 1986
Mobile Bay, AL	0.8	N/A	Kiene et al. 2004
Weeks Bay, AL	1.8	N/A	Mortazavi et al. 2012
Fourleague Bay, LA	N/A	120 - 317	Randall and Day 1987
MS River Plume	0.9	N/A	Lohrenz et al. 1990
LA Continental Shelf	0.4	159	Chen 2000
LA Continental Shelf	0.1 - 8.7	N/A	Redalje et al. 1994
MS Sound	1.2	N/A	Vandermeulen 2012
MS Bight	1.6	N/A	Vandermeulen 2012
Bay of Saint Louis, MS	0.3*	97*	Woodmansee et al. 1980

* Daily and annual production rate values reported in $gC\ m^{-3}$.

Objectives

The objective for the proposed study was to provide an estimate of primary productivity and identify some of the fundamental physical and chemical processes that help regulate phytoplankton photosynthesis, physiology, and growth along the river-dominated coastlines of BSL. The proposed study will address two important questions regarding phytoplankton photosynthetic responses to environmental forcing along the BSL shoreline: what are the rates of primary production and what environmental variables are responsible for regulating photosynthesis-irradiance (P-E) responses?

Hypotheses

1. Variations in P-E parameters will correlate with observed environmental variables along the river-dominated coastal margin of BSL such that:

1a. Productivity estimates will correlate negatively with river discharge, wind and turbidity, while irradiance, temperature, and chlorophyll correlate positively with production estimates, and

1b. Tidal forcing will contribute little to phytoplankton productivity relative to the effects of freshwater influences.

2. Lowest productivity rates will be observed near sewage outfalls and river mouth and highest at stations near the Mississippi Sound;

3. Because the BSL shore waters are well-mixed, P-E parameters will be uniform with depth; $P^B{}_{max}$ and α^B will vary throughout the day as a function of incident PAR, but not with depth, at selected stations along the eastern and western shores of BSL;

3a. Although $P^{B}{}_{max}$ and α^{B} are expected to be uniform throughout the water column at selected stations, surface β^{B} will be pronounced at stations proximal to the Mississippi Sound than at stations near the river-bayou mouths.

CHAPTER II

MATERIALS AND METHODS

In order to test the three primary hypotheses for this study, six stations were selected along the BSL shoreline that would reflect the influence of the JR, WR and Bayou Portage (BP) outflows (Figure 1). The stations were chosen with respect to their accessibility from shore, reflected river outflow along the shoreline of BSL, and provided additional information not addressed in previous studies in the bay. Station 1 (S1) was positioned at the mouth of the JR near the Hollywood Casino, a sewage outfall, and a boat launch. Station 2 (S2) and Station 3 (S3) represented the outflow of the JR along the western coast of the bay with increasing distance toward the Mississippi Sound (MS). On the eastern margin of the BSL, Station 4 (S4) was positioned in Delisle Bayou near the mouth of the WR in BSL, Station 5 (S5) was positioned at the mouth of Mallini Bayou and represented the WR and BP outflow, and Station 6 (S6) was positioned in close proximity to the MS. Samples for S1 and S5 were obtained alongside a retaining wall, S2 and S3 were located at the end of a pier, S4 was off the side of a bridge, and S6 was sampled by wading into the water. Station 7 (S7) was an alternate station and was positioned at a boat launch near the mouth of the WR. However, due to dredging and constant work on the pier during sampling, S7 was sampled only twice during the study. Thus, results from S7 were not evaluated as part of this study and are reported in Appendix B.

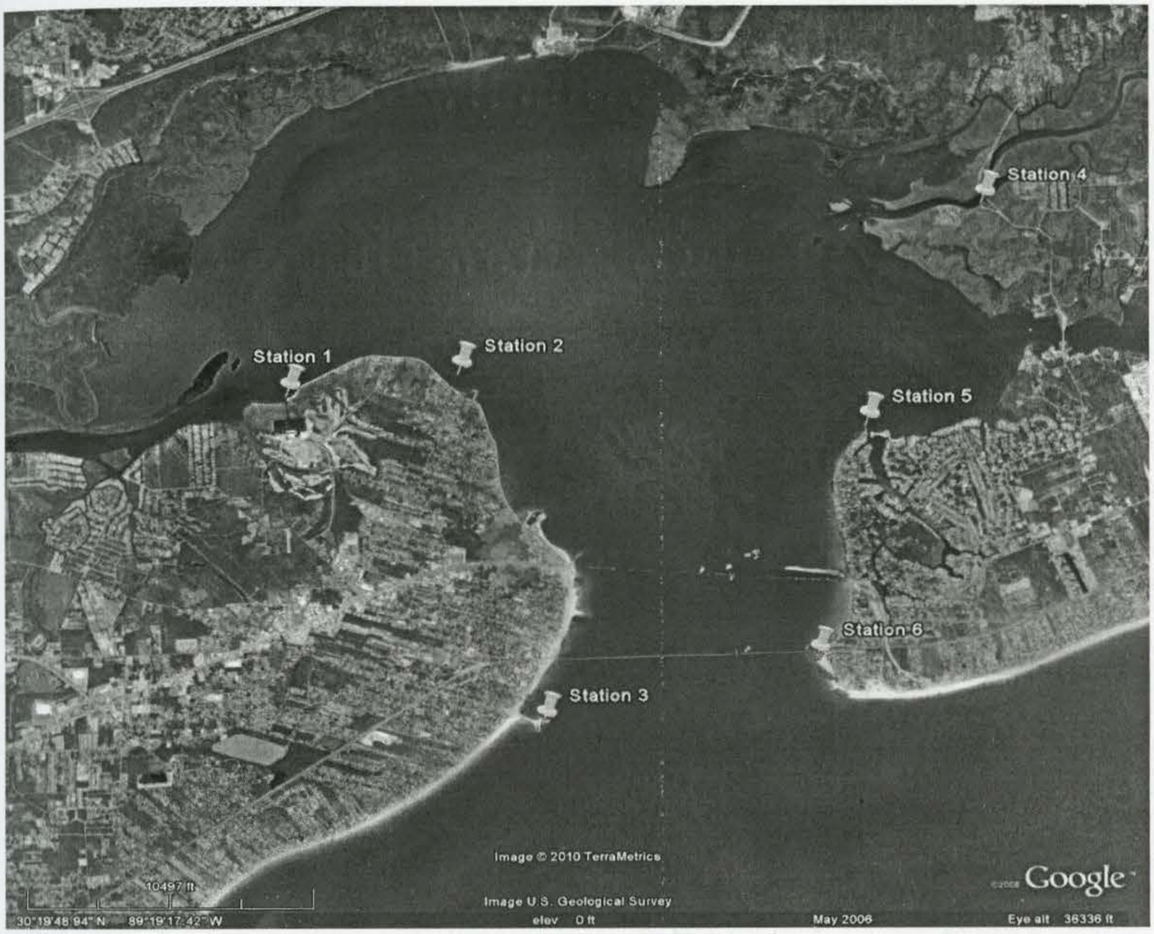


Figure 1. Sampling stations (S1-S6) along the shoreline of the BSL estuary (courtesy of Google Earth). List of Stations (S): mouth of the Jourdan River (S1); Dunbar Street pier (S2); Washington Street Pier (S3); Wolf River near BSL (S4); Sweet Bay Drive (S5); Henderson Point (Baptist Convention Center) (S6); and Bayou Portage boat launch (S7) (not shown).

Sampling Scheme

Surface and subsurface samples were obtained monthly to observe the spatial and temporal variability in environmental characteristics and for the determination of primary production. All stations were sampled on two consecutive days each month for six months from July to December 2010 during both incoming and outgoing tides (Table 2). Due to time constraints and sensitivity of the samples, field sampling was split so that the western shore and eastern shore were sampled on consecutive days. Over the course of the seasonal study, two short-term experiments were conducted to examine day to day variability (week-long), tidal phase and daily irradiance effects (diurnal) on primary production.

For the week-long study, S2 and S3 were visited once per day at the same time during an outgoing tide in order to assess variability in phytoplankton productivity over the course of a week (Table 2.1). These stations were also sampled three times from 09:00 to 15:00 hours on Day 6 during the week-long study to assess the photosynthetic response to changes in irradiance over the course of the photoperiod. These two studies were conducted in mid-October and were in addition to the monthly samples taken in October.

Table 2

Experimental Design and Sampling Scheme for Determining Spatio-Temporal Variability in Phytoplankton Photosynthetic Performance.

Experiment	Seasonal	Week-long	Diurnal
Frequency	once per month	once	once
Start date	7/16/2010	10/11/2010	10/16/2010
End date	12/16/2010	10/17/2010	10/16/2010
Sampling time	09:00-11:00	09:00-11:00	09:00, 12:00, 15:00
Stations	all	S2, S3	S2, S3
Sampling depth(s)*	s	s, b	s, b
Temporal scale variability	long-term	mid-term	short-term
Spatial scale variability	horizontal	horizontal	vertical

*Sample depths are represented by those taken at the surface (s) and those taken from 0.5 m (b).

Field Methods and Data Collection

Prior to sampling, meteorological and hydrological observations were retrieved via the internet from the Bay Waveland Yacht Club (BWYC) National Oceanic and Atmospheric Administration (NOAA) Tides and Currents data station (Station ID:

8747437), the Waveland Weather Center in Waveland, MS, and from the United States Geological Survey (USGS) Real-Time Water data station for the JR (station id: 02481660) and WR (station ID: 02481510) near Bay Saint Louis, MS.

Field observations of atmospheric (e.g. wind direction, percent cloud cover, air temperature) and water conditions (e.g. wave action, water color, Langmuir lines, and anthropogenic activities) were recorded at each station. Sky conditions and percent cloud were quantified by observer estimations using the system implemented by Pluhar (2007) (Table 3).

Table 3

Estimations of Sky Conditions and Percent Cloud Cover During Sampling.

Sky Condition	% Cloud Cover
sunny	0
mostly sunny	17
partly sunny	33
partly cloudy	50
mostly cloudy	66
cloudy	83
overcast	100
no sun	NA

In situ measurements of water temperature (*in situ* T, °C), salinity, turbidity (NTU), pH, and dissolved oxygen (mg L^{-1}) were determined using an In-Situ^{TM} multi-parameter TROLL 9500 WQP-100. Incident (E_0) and subsurface ($E_0(z_1)$) irradiance, quantified as photosynthetically available radiation (PAR) (μmol quanta m^{-2} s^{-1}), was determined using a LI-COR^{TM} LI-192 underwater quantum sensor and LI-250A light meter at the desired depths for respective experiments. Subsurface irradiance ($E_0(z_1)$)

was taken at just below the water surface and at 0.5 m ($E_0(z_2)$) depth intervals for the monthly samples and at 0.1 m depth intervals to 0.5 m for the week long and diurnal studies. The attenuation coefficient for downwelling irradiance (K_d) was calculated using the relationship:

$$K_d = 1/(z_2 - z_1)\ \ln(E_0(z_1) / E_0(z_2))$$ *Equation 2*

where $E_0(z_1)$ and $E_0(z_2)$ are subsurface scalar irradiance at respective sampling depths z_1 and z_2. On sampling days where $E_0(z_2)$ was unattainable, whether due to shallow depths or human error, $E_0(z_2)^*$ was computed as follows:

$$E_0(z_2)^* = E_0 \bullet \exp(-K_d^* \bullet \Delta z)$$ *Equation 3*

where K_d^* is the average vertical attenuation coefficient (3.59 m^{-1}) calculated over the course of the study and Δz is the change in depth z_1 to z_2. Sampling dates when this was applied include all stations in October and December and at S5 and S6 in July and November, respectively.

Surface and subsurface water samples were collected at the sample sites along the BSL shoreline using a 2 L horizontal polycarbonate Niskin-style water sampler with a silicone tubing closure mechanism. To ensure that each subsurface sample was collected at the proper depth, a marker was placed at 10 cm increments along the line. Samples for photosynthesis-irradiance (P-E) incubations, biomass (Chl *a*), nutrients, and total dissolved inorganic carbon dioxide (ΣCO_2) were placed into a single opaque acid clean 2 L polypropylene carboy (Fitzwater *et al.* 1982), then put immediately into a cooler filled with ambient bay water to preserve the integrity of the water samples until laboratory analysis. All water samples were transported back to the lab for analysis.

Photosynthesis-Irradiance (P-E) and Water Sample Analysis

The methods for estimating the photosynthetic rates using small volume, short incubation period P-E saturation curves closely followed that of Lewis and Smith (1983). This experiment utilized three standard 20-well photosynthetrons to serve as the incubators. The light source was a 300 watt Eiko GY5.3 projector bulb situated beneath the PVC/aluminum sample holder block for each photosynthetron. In order to accurately simulate the spectral quality for these artificial incubations, an acrylic heat filter positioned between the light source and the vial holder block was filled with a solution of copper sulfate (40 g L^{-1}) as described by Jitts *et al.* (1964). A combination of neutral density filters was used to create a light gradient for P-E saturation curves. Prior to each P-E incubation, this light gradient was quantified by discrete light measurements using a Biospherical Instruments QSL-2101 radiometer.

One 70 mL sample from each station was inoculated with 70 μL of a 1 mCi mL^{-1} $NaH^{14}CO_3$ stock solution. Aliquots of 3 mL of ^{14}C-labeled samples were incubated for 0.5 hour in 7 mL glass scintillation (LS) vials. A baseline timestamp, T_0 was made at the exact moment that incubation began by dispensing 3 mL of sample into a prepared 7 mL LS vial filled with 500 μL of 10% HCl and placed immediately into a dark box. The ^{14}C spike activity (S) was determined by dispensing two 50 μL aliquots of ^{14}C-labeled sample into 50 μL 1:1 (v/v) ethanol/ethanolamine mixture in a 7.0 mL LS vial, followed by fixing with 5.0 liquid scintillation cocktail. After 0.5 h samples were acidified with 10% HCl to terminate any further carbon fixation. Samples were shaken overnight on a VWR counting using a Wallac WinSpectral α/β 1414 Liquid Scintillation Counter. Photosynthesis (P, mgC h^{-1} m^{-3}) was calculated using the relationship in Equation 4 (Parsons *et al.* 1984):

$$P = [(DPM_{cell} - DPM_{t0}) * 1.05 * 12011.2 * \Sigma CO_2]/S * t \qquad \textit{Equation 4}$$

where DPM_{cell} is the volume-normalized disintegrations per minute of each sample in the photosynthetron, DPM_{t0} is the volume-normalized disintegrations per minute at time zero, 1.05 is the carbon discrimination factor, 12011.2 is the conversion factor for total inorganic carbon (ΣCO_2) from meq L^{-1} to mg C m^{-3}, *S* is the ^{14}C spike added to the sample, and *t* is the length of incubation, in hours. At the same time that the subsample was taken for the P-E incubations, subsamples for ΣCO_2 and Chl *a* extraction were also taken. Total alkalinity was determined by Gran titration and converted to ΣCO_2. Chlorophyll *a* concentrations (mg m^{-3}) were determined fluorometrically following methanol extraction (Welschmeyer 1994).

Photosynthetic rates normalized to biomass, P^B (g C (g Chl *a*)$^{-1}$ h^{-1}), were calculated from the resulting counts using a conventional photosynthesis-light saturation relationship normalized to biomass (Platt *et al.* 1980) presented in Equation 5. Parameters were fit simultaneously using MATLAB (The Mathworks, Inc. 7.8.0, 2009):

$$P^B \equiv P^B_s \cdot (1 - exp(-\alpha^B E/P^B_s)) \cdot (exp(-\beta^B E/P^B_s)) \qquad \textit{Equation 5}$$

where, P^B (g C (g Chl *a*)$^{-1}$ h^{-1}) is the specific photosynthetic rate normalized to Chl *a* at irradiance *E* (μmol photon m^{-2} s^{-1}), $P_s{}^B$ (g C (g Chl *a*)$^{-1}$ h^{-1})is the saturated rate of photosynthesis in the absence of photoinhibiton, α^B (g C (g Chl *a*)$^{-1}$ h^{-1})(μmol photon m^{-2} s^{-1})$^{-1}$ is the initial slope of the P-E curve and is a measure of photosynthetic efficiency, and β^B is the photoinhibition parameter (g C (g Chl *a*)$^{-1}$ h^{-1}) (μmol photon m^{-2} s^{-1})$^{-1}$.

The photosynthetic capacity, or maximum rate of photosynthesis, $P^{B}_{\max}$ was determined using Equation 6.

$$P^{B}{}_{max} \equiv P^{B}{}_{s}\,(\alpha^{B}/\,(\alpha^{B}+\beta^{B}))(\,\beta^{B}\,/(\alpha^{B}+\beta^{B}))^{\beta/\alpha} \qquad \textit{Equation 6}$$

Water column daily areal primary production, PP was calculated by integrating daily photosynthetic rates over depth. Using the equation by Platt *et al.* (1980), the specific photosynthetic rate normalized to biomass, P^{B} was multiplied by biomass concentrations to yield the volumetric production, $P_{z,t}$ (gC m^{-3} h^{-1}) as described by Fee (1973). Two profiles of $P_{z,t}$ were constructed for each set of samples, one using the P-E parameters, Chl *a*, and $E_0(z_1)$ obtained at the surface and the other using the set of P-E parameters, Chl *a*, and $E_0(z_2)$ obtained at the bottom of the water column (0.5 m). For stations where bottom samples were not obtained, $P_{z,t}$ was estimated by assuming that the P-E parameters and Chl *a* concentrations did not vary with depth. Integration of these values over depth, z, and daylight hours, *t* resulted in an estimate of daily areal production, PP (gC m^{-2} d^{-1}) (Equation 7).

$$PP = \sum_{z}\sum_{t} P_{z,t} \qquad \textit{Equation 7}$$

Nutrients ($NO_2^{-} + NO_3^{-}$, NH_4^{+}, $Si(OH)_4$, and PO_4^{3-}) were analyzed using fluorometric (NO_2^{-}, NO_3^{-}, and NH_4^{+}) and spectrophotometric ($Si(OH)_4$, and PO_4^{3-}) techniques using an Astoria-Pacific A2+2 Nutrient Autoanalyzer (Method # A179, A027, A205, and A221 Astoria-Pacific International, OR USA). Prior to analysis, all samples were filtered using 0.45 μm, 25 mm nylon syringe filters.

Data Analysis

Statistical analyses were performed using SPSS (SPSS, Version 14.0, 2005) to evaluate the relationships between observed environmental parameters and estimated rates of primary production derived from the P-E curves. All variables were initially tested for normality using a Kolomogorov-Smirinov (KS) test. Non-parametric statistics were implemented since most of the environmental data were not distributed normally ($p \leq 0.05$). Temporal and spatial variability was evaluated using the Kruskal-Wallace (KW) analysis of variance test for two or more groups of data (*e.g.* months or stations) or the Mann-Whitney (MW) analysis of variance test between exactly two groups (*e.g.* seasons). Bonferroni adjustments of alpha values were implemented to prevent a Type I error (Mojzis 2010). Spearman's rank correlation analysis was used to highlight significant relationships between productivity and environmental parameters over the course of the study. Finally, a principal component analysis (PCA) was run to determine whether any significant relationships occurred between the other measured variables.

CHAPTER III

RESULTS

The objective of this study was to determine primary productivity at selected stations along the shoreline of the Saint Louis Bay (BSL) estuary in Mississippi with a focus on three temporal scales: a seasonal scale consisting of 6 months (July 2010 to December 2010), a weekly scale consisting of 7 consecutive days, and a diurnal scale, which involved sampling at morning (09:00), midday (12:00), and afternoon (15:00). In addition, spatial distributions in phytoplankton productivity were addressed to determine whether significant differences in production occurred among the sample stations (see Figure 1). Results from the tests show that phytoplankton productivity varied both temporally and spatially and that variability was correlated significantly (Spearman's rank, $p \leq 0.05$) with observed environmental parameters.

Temporal Variability

Seasonal Primary Production, Environmental Conditions, and P-E Parameters

Patterns in the data suggested that seasonal differences may have existed in production, P-E parameters, and environmental variables over the course of the six-month study. The results of a Mann-Whitney (MW) test suggested that the data could be grouped into two seasons: summer, which included July, August, and September, and autumn, which included October, November, and December (Table 3.1). Daily areal primary production (PP), the P-E parameters P^{B}_{max} and E_k, and Chl *a*, as well as some physical properties of the water column (*in situ* temperature (T), salinity(S), dissolved oxygen (DO), incident irradiance (E_0)), were different significantly (MW test, $p \leq 0.05$)

between seasons (Table 4). Values for seasonal environmental, hydrological and meteorological, and P-E parameters are listed in the Appendixes A-D.

Table 4.

MW Test for Differences Between Seasons: Summer and Fall.

Parameter	U	Significance
PP (g C m^{-2} d^{-1})	21	**0.000**
P^B_{max} (g C (g Chl a)$^{-1}$ h^{-1})	66	**0.001**
α^B (g C (g Chl a^{-1})h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$)	173	-
E_k (μmol photon m^{-2} s^{-1})	38	**0.000**
NH_4^+ (μM)	125	-
NO_2^- + NO_3^- (μM)	140	-
PO_4^{3-} (μM)	174	-
N:P	163	-
$Si(OH)_4$ (μM)	70	**0.001**
Chl a (mg m^{-3})	70	**0.001**
In situ T(°C)	0	**0.000**
Salinity (S)	51	**0.000**
DO(mg L^{-1})	15	**0.004**
pH	48	-
Turbidity (NTU)	108	0.035
E_0 (μmol photon m^{-2} s^{-1})	25	**0.000**
Air T (°C)	9	**0.000**
Wind Speed (m s^{-1})	154	-
Precipitation (cm)	159	-
WR Gauge Ht (m)	156	-
WR Discharge ($m^3 s^{-1}$)	130	-
JR Gauge Ht (m)	174	-
MTL (m)	0	**0.000**

The MW statistic (U) with confidence intervals set at $p \leq 0.01$ for values in bold, $p \leq 0.05$ for values in standard type, and dashed lines for values that were not significant. N = 38.

Primary Production

The median (range) for daily areal primary production, PP was g C m^{-2} d^{-1} and was greatest in August and was lowest in December (Figure 2). There was a significant difference (MW test, $p < 0.01$) in summer relative to autumn for the seasonal study, with rates greater in summer than in autumn (Table 4).

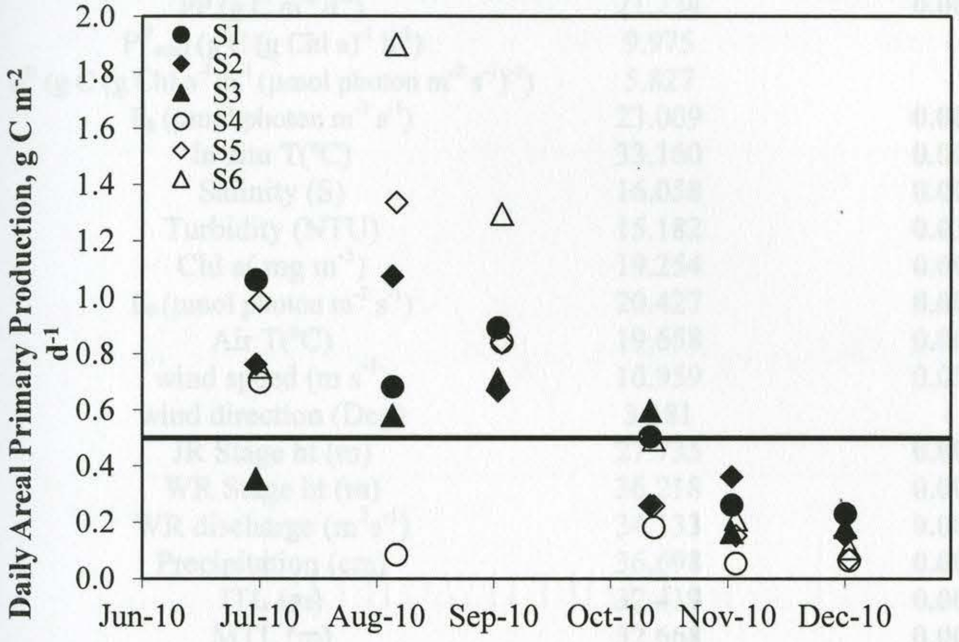


Figure 2. Seasonal distribution of daily areal productivity, PP (g C m^{-2} d^{-1}) for the seasonal study. Points represent monthly PP values at each station over the sample period and the horizontal black line represents the study median for PP (0.50 g C m^{-2} d^{-1}) for the BSL study area.

Environmental Conditions

Freshwater input into the BSL estuary, indicated by WR discharge, JR and WR stage height, and precipitation, varied greatly during the study period (Figure 3). The WR discharge rate and WR and JR stage heights decreased between summer and autumn (Figure 3). The median (range) daily stage heights for the WR and JR were 1.57 (1.45-2.23) m and 0.27 (0.06-0.40) m, respectively. Precipitation, quantified as rainfall, also was greater in summer than in autumn, and was negligible (< 1.0 cm) up to five days prior to sampling at all stations over the course of the study. Total precipitation was 60.7 cm during the study period.

Table 5.

Kruskal-Wallis Analysis of Temporal Variability for the Seasonal Scale.

Parameter	χ^2	Significance
PP (g C m^{-2} d^{-1})	21.234	**0.001**
P^B_{max} (g C (g Chl a)$^{-1}$ h^{-1})	9.975	-
α^B (g C (g Chl a^{-1})h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$)	5.827	-
E_k (μmol photon m^{-2} s^{-1})	23.009	**0.000**
In situ T(ºC)	33.160	**0.000**
Salinity (S)	16.058	**0.007**
Turbidity (NTU)	15.182	**0.010**
Chl a(mg m^{-3})	19.254	**0.002**
E_0 (μmol photon m^{-2} s^{-1})	20.427	**0.001**
Air T(ºC)	19.658	**0.003**
wind speed (m s^{-1})	10.959	0.052
wind direction (Deg)	3.181	-
JR Stage ht (m)	27.735	**0.000**
WR Stage ht (m)	36.218	**0.000**
WR discharge ($m^3 s^{-1}$)	34.133	**0.000**
Precipitation (cm)	36.698	**0.000**
ITL (m)	32.419	**0.000**
MTL (m)	32.668	**0.000**

Significance between stations is given by the KW statistic (χ^2) with a significance level $p \leq 0.01$ indicated in bold and $p \leq 0.05$ values in standard type. Values without any statistical significance are indicated by a dashed line. N = 38, df = 5 for all parameters except DO and pH where N = 25, df = 3.

Because the instantaneous tidal level, ITL was correlated significantly (Spearman's rank, $p \leq 0.001$, N = 38) to MTL, only MTL was used to address tidal flow for the seasonal study. Mean lower-low water (MLLW) decreased from summer to autumn (Figures 4 A-B).

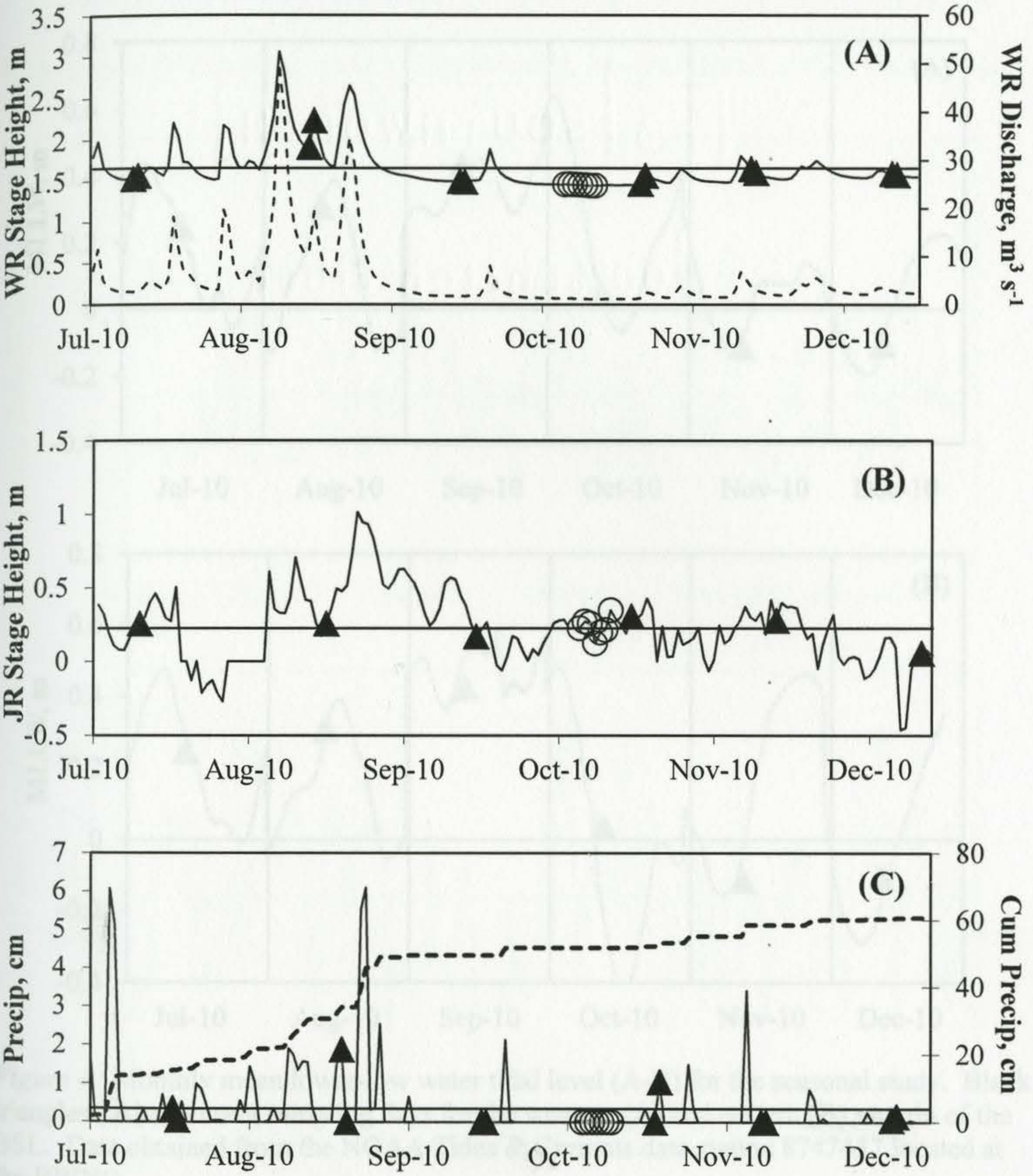


Figure 3. Stage heights and discharge rates for the WR (A) and JR (B), and daily precipitaion (C) for the seasonal study. Daily average stage heights (A-B) and daily precipitaion (C) are indicated by a solid blue line (–). Mean stage heights for the study are indicated by the horizontal solid black line (–) for the two rivers. Daily average discharge rates for the WR are indicated by the black dotted line (--) in panel (A). Cumulative precipitation is indicted by the bold dashed blue line (--) in panel (C). Sampling days are indicated by solid black triangles (▲) and open circles (○) for the monthly and week-long studies, respectively in panels (A-C).

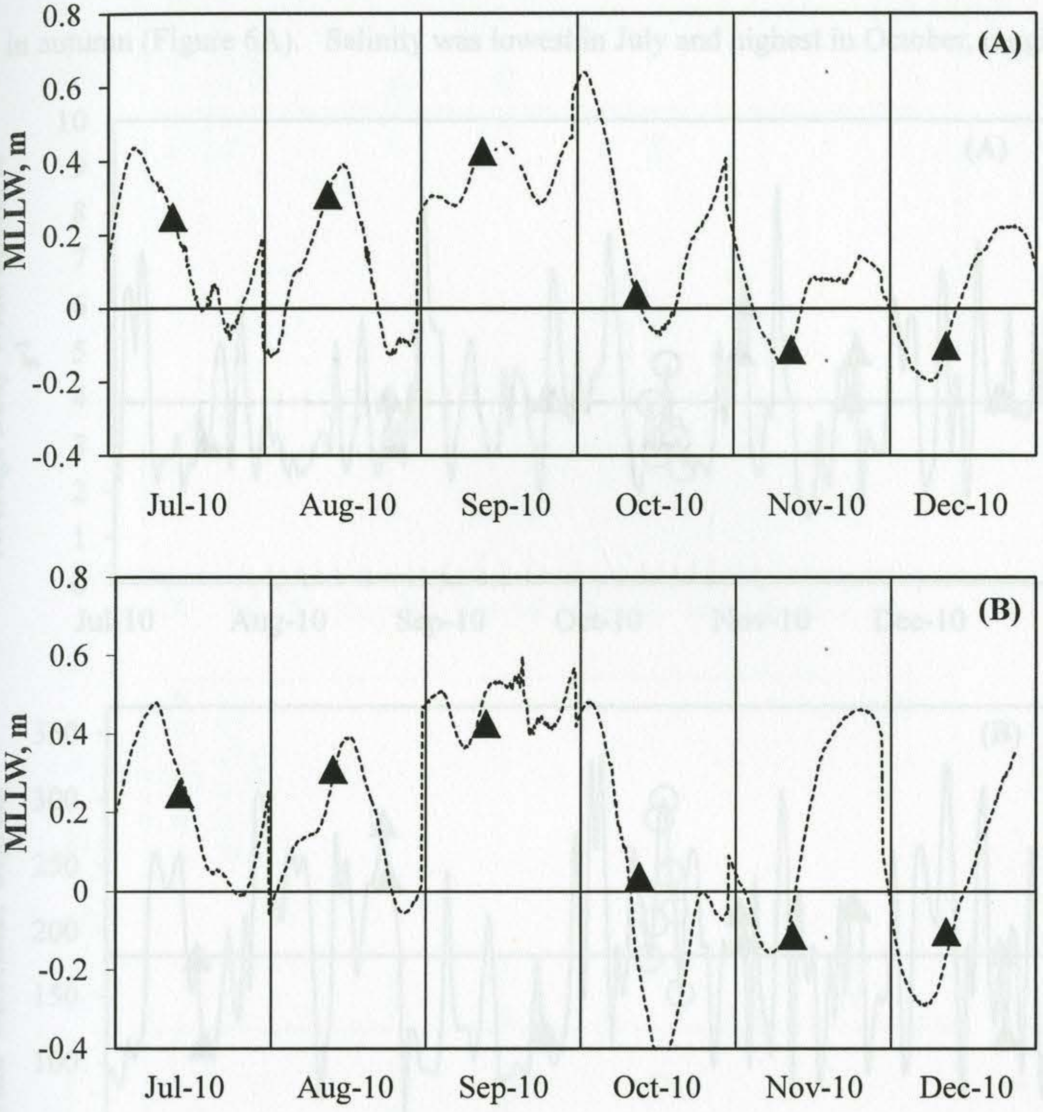


Figure 4. Monthly mean lower-low water tidal level (A-B) for the seasonal study. Black triangles (▲) represent sampling days for the western (A) and eastern (B) margin of the BSL. Data obtained from the NOAA Tides & Currents data station 8747437 located at the BWYC.

Wind speed and direction fluctuated episodically throughout the study period and were highly variable prior to and during sampling days. Neither wind speed nor wind direction was different significantly (MW test, $p < 0.05$) between seasons during the study (Table 4). The median (range) for daily wind speed was 4.2 (2.2 to 9.0) m s^{-1} and was predominately out of the southwest for the seasonal study (Figure 5 A-B).

Median *in situ* T varied seasonally, decreasing from 29.2 °C in summer to 17.6 °C in autumn (Figure 6A). Salinity was lowest in July and highest in October, ranging

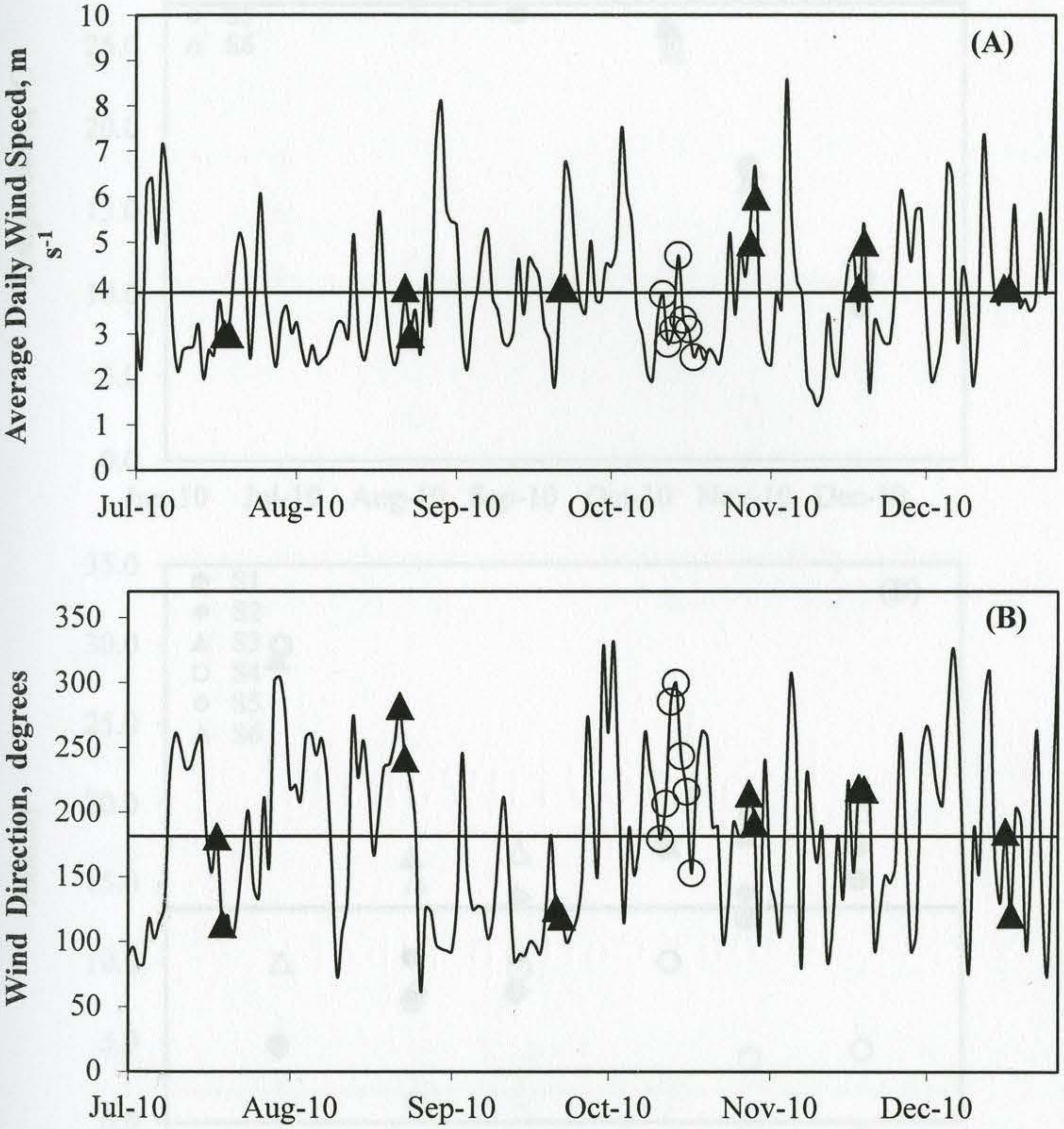


Figure 5. Average daily wind speed (m s^{-1}) (A) and wind direction (B) for the seasonal study. Black trainagles (▲) and open circles (○) represent sampling days for the seasonal study and week-long study, respectively. The median for the average daily wind speed and wind direction is indicated by the solid horizontal black line (–). Wind direction given in degrees (*e.g.* north, N = 360; east, E = 90; south, S = 180; west, W = 270). Data obtained from the NOAA Tides & Currents data station 8747437 located at the BWYC.

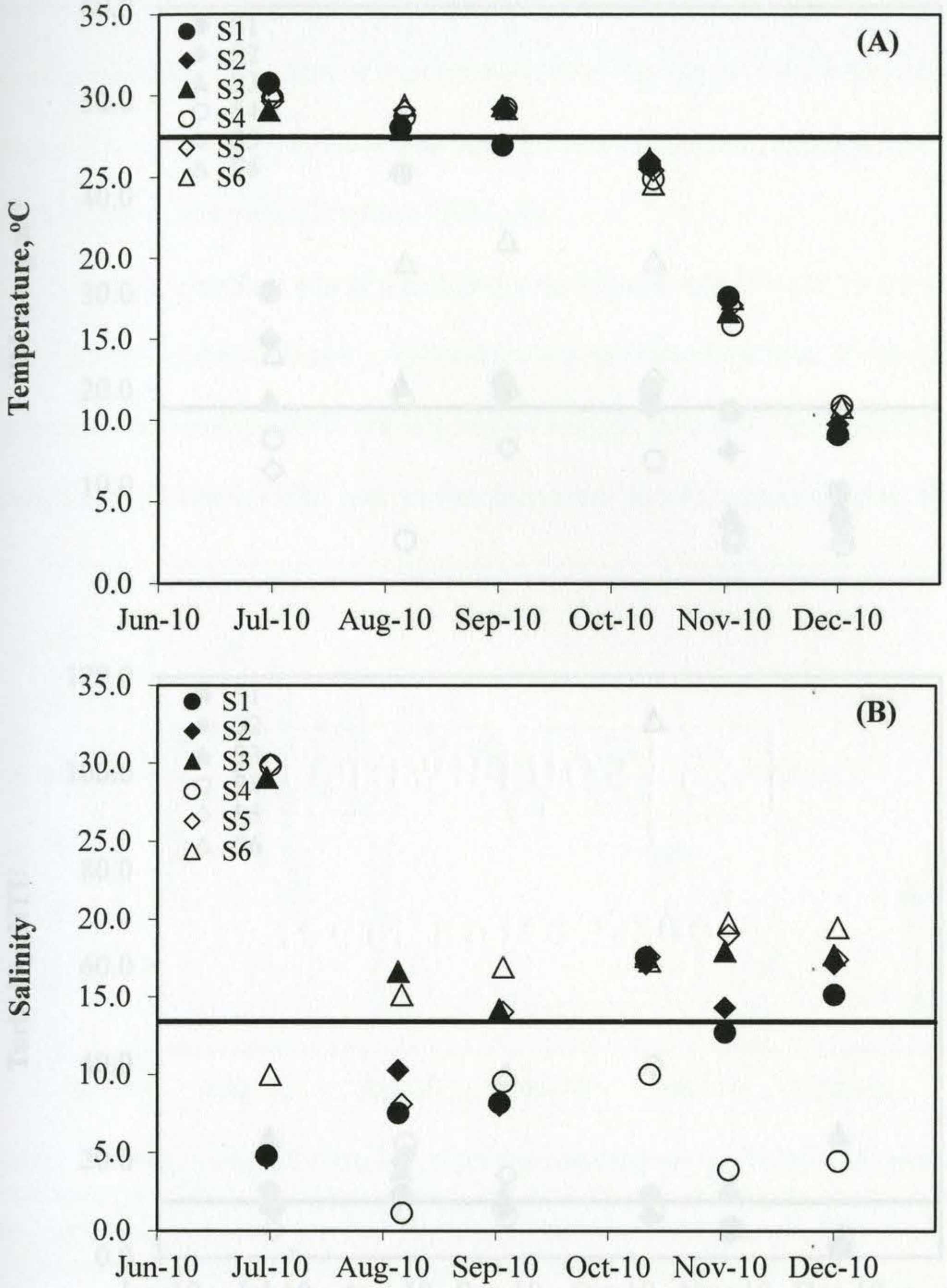


Figure 6. Seasonal range of values for *in situ* T (A) and salinity (B) for the seasonal study. The study median for each parameter is indicated by a solid black line (–).

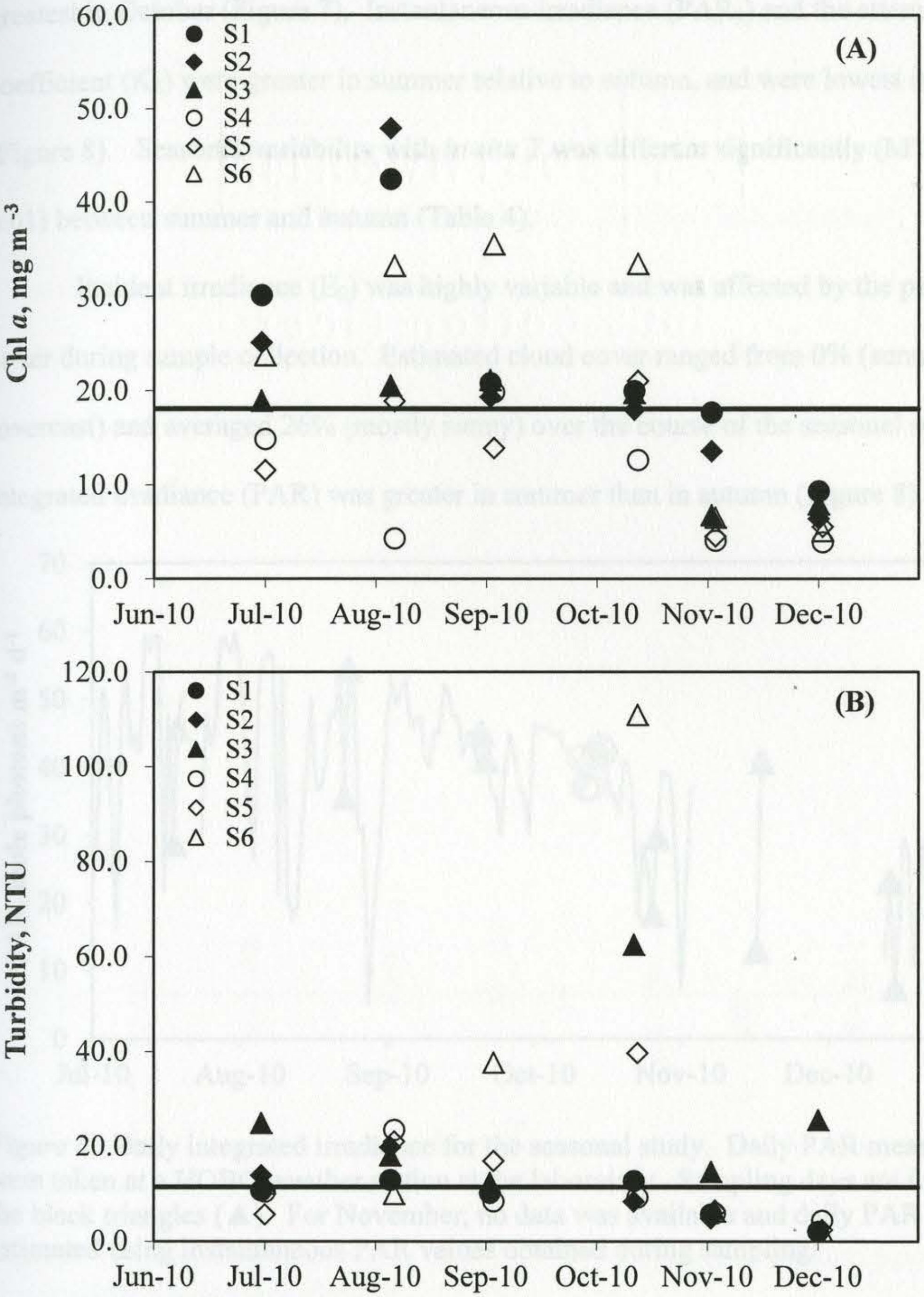


Figure 7. Seasonal range of values for Chl *a* (A) and turbidity (B) for the seasonal study. The study median for each parameter is indicated by a solid black line (–).

from 1.04 to 19.8 (Figure 6). Median chlorophyll *a* concentration, Chl *a* ranged from 3.9 to 47.9 mg m^{-3} over the course of the study and varied in concert with turbidity (Figure 7). Turbidity varied throughout the study, ranging from 2.05 to 110.95 NTU, and was greatest in October (Figure 7). Instantaneous irradiance (PAR_0) and the attenuation coefficient (K_d) were greater in summer relative to autumn, and were lowest in October, (Figure 8). Seasonal variability with *in situ* T was different significantly (MW test, $p < 0.01$) between summer and autumn (Table 4).

Incident irradiance (E_0) was highly variable and was affected by the percent cloud cover during sample collection. Estimated cloud cover ranged from 0% (sunny) to 100% (overcast) and averaged 26% (mostly sunny) over the course of the seasonal scale. Daily integrated irradiance (PAR) was greater in summer than in autumn (Figure 8).

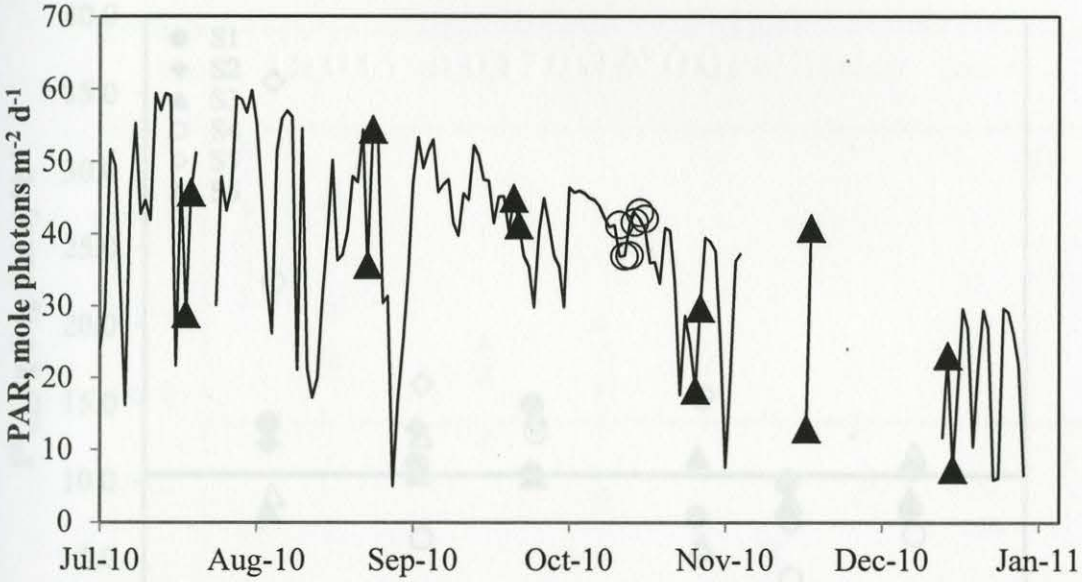


Figure 8. Daily integrated irradiance for the seasonal study. Daily PAR measurements were taken at a HOBO weather station at the laboratory. Sampling days are indicated by the black triangles (▲). For November, no data was available and daily PAR was estimated using instantaneous PAR values obtained during sampling.

Seasonal Phytoplankton Photosynthetic Response to Environmental Variables

Seasonal values varied markedly for the light saturated rates of photosynthesis (P^B_{max}), photosynthetic efficiency (α^B), and the light saturation parameter (E_k) (Figures 9-10).

Light saturated rates of photosynthesis varied seasonally and were greatest in summer and lowest in autumn (Figure 10). Median P^B_{max} (g C (g Chl*a* h)$^{-1}$) decreased from 12.71 in summer to 8.86 in autumn. Although no clear temporal patterns (MW test, $p < 0.05$, $N = 38$) emerged for the seasonal study, photosynthetic efficiency, α^B (g C (g Chl*a* h)$^{-1}$(μmol photon m^{-2} s^{-1})$^{-1}$) was greatest in October (0.081) and lowest in November (0.013). The study median for the light saturation parameter, E_k (μmol photon m^{-2} s^{-1}) varied seasonally during the study and also was greatest in summer (441.28) and lowest in autumn (157.40).

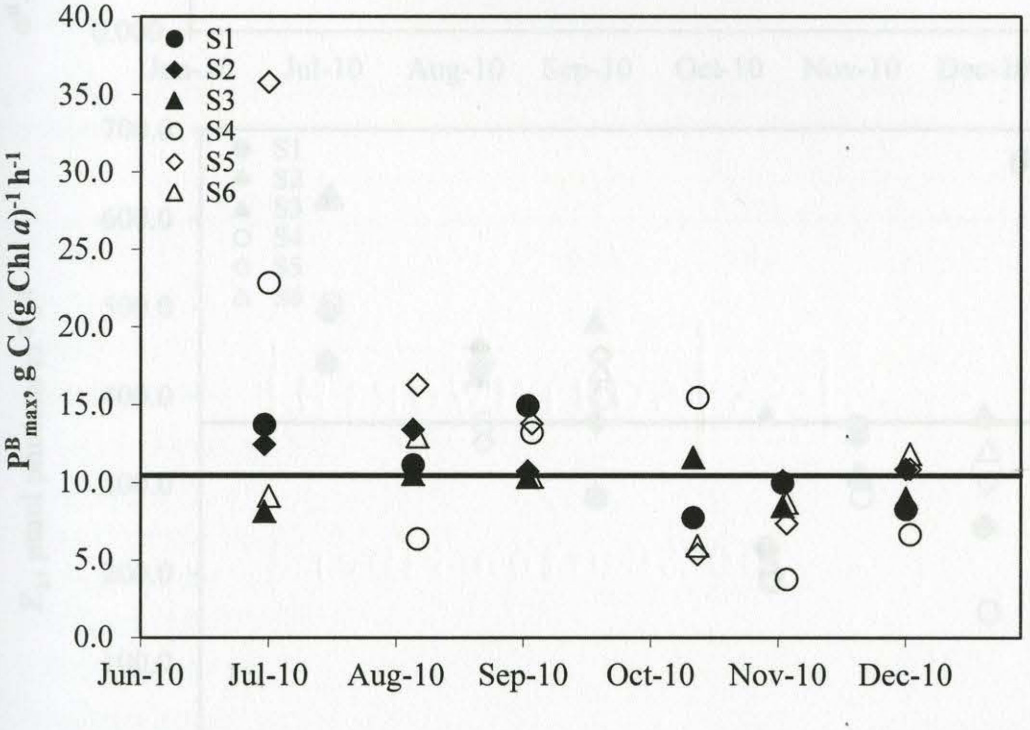


Figure 9. Seasonal range of values for P^B_{max}. The study median for each parameter is indicated by a solid black line (–).

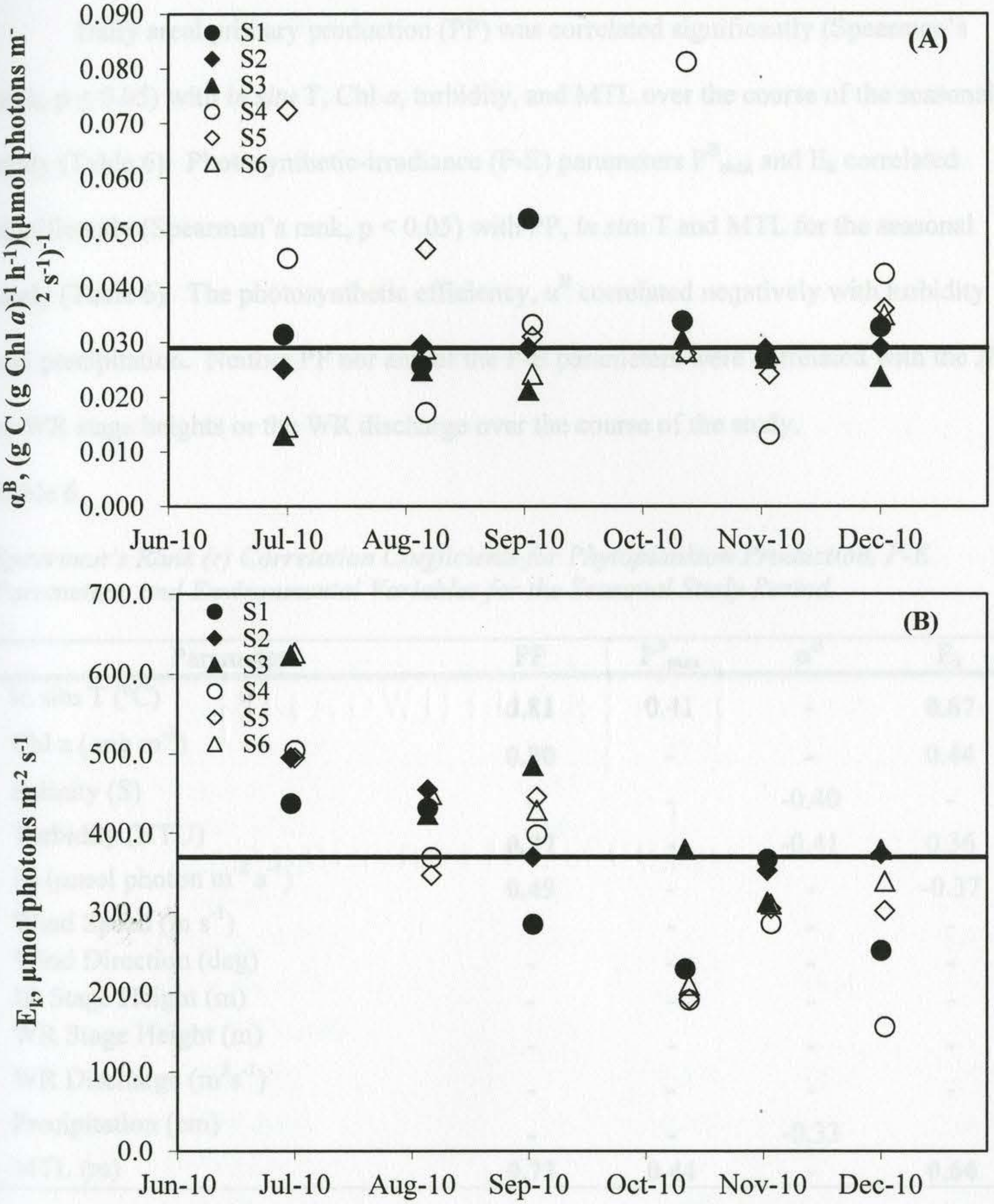


Figure 10. Seasonal range of values for α^B (A) and E_k (B) for the seasonal study. The study median for each parameter is indicated by a solid black line (–).

Seasonal Correlations

Daily areal primary production (PP) was correlated significantly (Spearman's rank, $p \leq 0.05$) with *in situ* T, Chl *a*, turbidity, and MTL over the course of the seasonal study (Table 6). Photosynthetic-irradiance (P-E) parameters P^B_{max} and E_k correlated significantly (Spearman's rank, $p < 0.05$) with PP, *in situ* T and MTL for the seasonal study (Table 6). The photosynthetic efficiency, α^B correlated negatively with turbidity and precipitation. Neither PP nor any of the P-E parameters were correlated with the JR or WR stage heights or the WR discharge over the course of the study.

Table 6

Spearman's Rank (r) Correlation Coefficients for Phytoplankton Production, P-E Parameters, and Environmental Variables for the Seasonal Study Period.

Parameter	PP	P^B_{max}	α^B	E_k
in situ T (°C)	**0.81**	0.41	-	**0.67**
Chl a (mg m^{-3})	**0.80**	-	-	0.44
Salinity (S)	-	-	-0.40	-
Turbidity (NTU)	**0.37**	-	-0.41	0.36
E_0 (µmol photon $m^{-2} s^{-1}$)	**0.49**	-	-	-0.37
Wind Speed (m s^{-1})	-	-	-	-
Wind Direction (deg)	-	-	-	-
JR Stage Height (m)	-	-	-	-
WR Stage Height (m)	-	-	-	-
WR Discharge ($m^3 s^{-1}$)	-	-	-	-
Precipitation (cm)	-	-	-0.33	
MTL (m)	**0.73**	**0.44**	-	**0.64**

Only significant correlations were presented ($p \leq 0.05$, $\mathbf{p \leq 0.01}$) for daily areal productivity, $P_{t,n}$ (gC $m^{-3}d^{-1}$), daily areal primary production, P (gC $m^{-2}d^{-1}$), P^B_{max} (gC g $Chla^{-1}$ h^{-1}), α^B (gC[g Chla h]$^{-1}$[µmol photon $m^{-2} s^{-1}$]$^{-1}$), and E_k (µmol photon $m^{-1} s^{-1}$). Values without any statistical significance are indicated by a dashed line.

Principal Component Analysis

The results of the PCA identified four components representing 17 measured environmental quality variables (Table 7). These four components described 76.1% of the variability within the total data set. The first component (PC 1, 25.7% variability explained) described tidal influences. Components two (PC II, 20.5% variability explained) and three (PC III, 15.8% variability explained) were associated with inputs from the Mississippi Sound (MS) and wind speed, respectively. The last component (PC IV, 14.1% variability explained) was regarded as variables influencing water clarity.

Table 7

Rotated Principal Component Loadings for the 17 Variables Evaluated for the Seasonal Sudy.

Variable	PC I	PC II	PC III	PC IV
Eigenvalue	34.178	21.317	14.560	8.274
% of Variance	25.7	20.5	15.8	14.1
PP (g C m^{-2} d^{-1})	0.937	-	-	-
In situ T(°C)	0.860	-	-	-
Salinity (S)	-	0.937	-	-
turbidity	-	-	-	0.812
Turbidity (NTU)	0.688	-	-	0.646
Chl a(mg m^{-3})			0.910	
$NO2^{-} + NO3^{-}$(μM)	-	-	-	-
PO_4^{3-}(μM)	-	0.638	0.631	-
$Si(OH)_4$(μM)	-	-0.883	-	-
DO (mg L^{-1})	-0.711	-	-	-
pH	-	0.836	-	-
K_d (m^{-1})	-	-	-	0.735
wind speed (m s^{-1})			0.771	-
WR discharge (m^{3}s^{-1})	-0.492	-	-	-0.441
MTL (m)	0.929	-	-	-

Table values represent loading values ($r \geq 0.400$).

Between-day Distribution, Variation, and Environmental Control of Primary Production and Phytoplankton Photosynthesis

Between-Day Primary Production

The median (range) for PP was 0.42 (0.25-0.84) gC m^{-2} d^{-1} and varied over the course of a week. Production was lowest on Day 2 and Day 7, and was greatest on Day 4 (Figure 11).

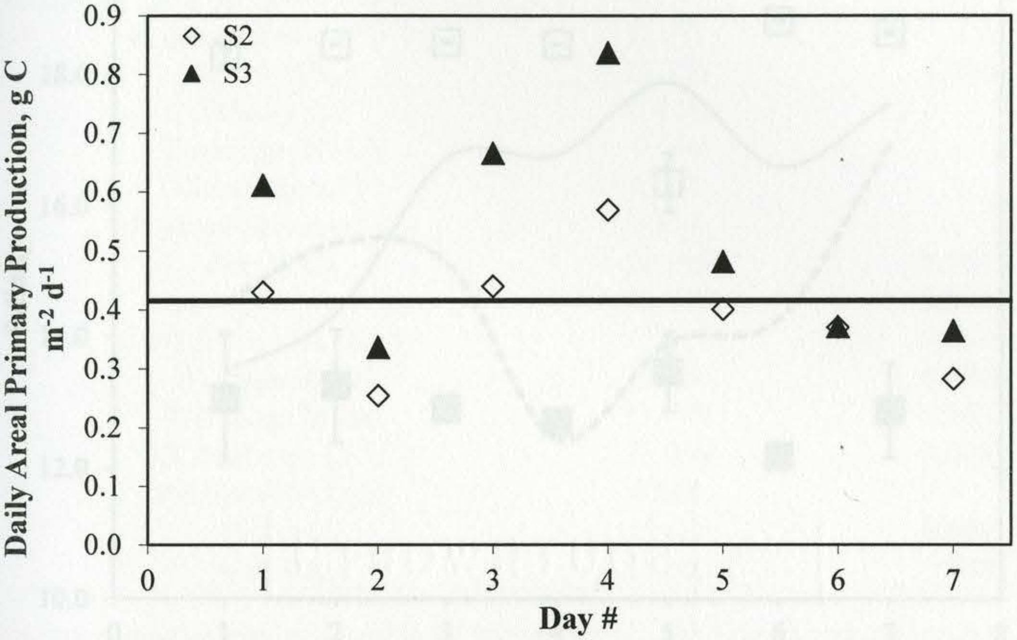


Figure 11. Daily areal production, PP (gC m^{-2} d^{-1}) for the week-long study. The study period ranged from 10/11/2010 to 10/17/2010. The median for the week-long study is indicated by the solid black line (–).

Between-Day Environmental Conditions

The JR stage height was variable over the course of the week, though precipitation was not observed or recorded in the JR watershed for the 7-day sampling period. Stage height was lowest on Day 4 (0.12 m) and highest on Day 7 (0.35 m) (Figure 12). Freshwater input via the WR did not vary greatly and ranged from 1.4 to 1.5 m (Figure 12).

MTL ranged from 0.14 m to 0.37 m and ITL ranged from 0.16 m to 0.40 m over the course of a week. Instantaneous tidal levels were lowest on Day 1 and were highest on Day 5. Salinity did not vary significantly (KW test, $p < 0.05$) over the course of the week at either station and ranged from 12.1 to 18.8 (Figure 12). However, S was lower significantly (MW test, $p < 0.05$) on Day 5 at S3 (Figure 12).

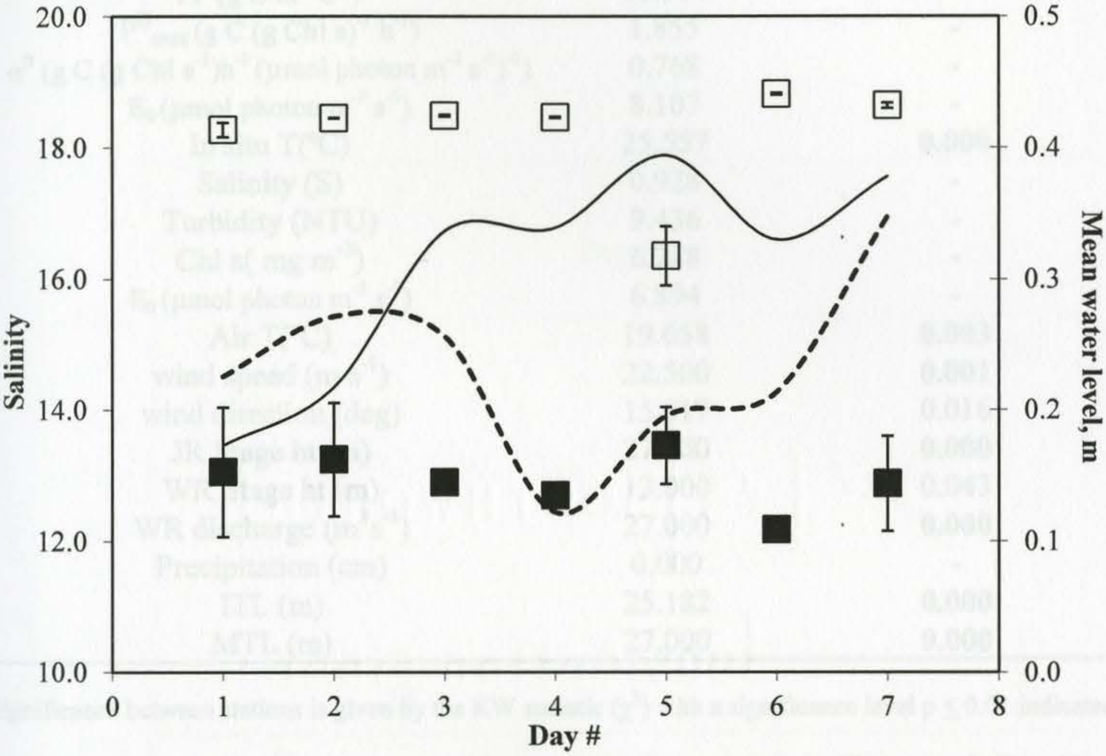


Figure 12. Salinity and mean water level along the western shoreline of the BSL estuary for the week-long study. The study period ranged from 10/11/2010 to 10/17/2010. Mean (± SE) values for salinity are indicated by the black boxes (■) and open boxes (□) for station 2 and station 3, respectively. Instantaneous tidal level, ITL is represented by the solid black line (—) and JR stage height is indicated by the dashed line (--).

The median air T was 19.8 ºC for the week and was lowest on day 4. *In situ* T was 22.6 ºC and ranged from a maximum of 23.8 ºC to a minimum of 15.9 ºC during the week-long study, with lowest temperatures recorded on day 7.

Incident irradiance ranged from 908.3 μmol photon m^{-2} s^{-1} to 169.4 μmol photon m^{-2} s^{-1}. Lowest E_0 was recorded on Day 2 and corresponded to overcast skies observed during sampling on that day (Appendix C). Skies were clear and sunny for all other sample days, with median PAR values greater than 700 μmol photon m^{-2} s^{-1}.

Table 8

Kruskal-Wallis Analysis of Temporal Variability for the Week-Long Scale.

Parameter	χ^2	Significance
PP (g C m^{-2} d^{-1})	11.314	-
P^B_{max} (g C (g Chl a)$^{-1}$ h^{-1})	1.855	-
α^B (g C (g Chl a^{-1})h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$)	0.768	-
E_k (μmol photon m^{-2} s^{-1})	8.107	-
In situ T(°C)	25.557	**0.000**
Salinity (S)	0.928	-
Turbidity (NTU)	9.436	-
Chl a(mg m^{-3})	6.288	-
E_0 (μmol photon m^{-2} s^{-1})	6.894	-
Air T(°C)	19.658	**0.003**
wind speed (m s^{-1})	22.500	**0.001**
wind direction (deg)	15.617	0.016
JR Stage ht (m)	27.000	**0.000**
WR Stage ht (m)	13.000	0.043
WR discharge (m^3s^{-1})	27.000	**0.000**
Precipitation (cm)	0.000	-
ITL (m)	25.182	**0.000**
MTL (m)	27.000	**0.000**

Significance between stations is given by the KW statistic (χ^2) with a significance level $p \leq 0.01$ indicated in bold and $p \leq 0.05$ values in standard type. Values without any statistical significance are indicated by a dashed line. N = 38, df = 5 for all parameters except DO and pH where N = 25, df = 3

Wind speed was highly variable prior to and during sampling and was greatest on Day 4. Chlorophyll *a* concentrations were greatest on Day 4 and were lowest on Day 7 for the study (Figure 13). Turbidity ranged from 6.4 to 44.6 NTU and was greatest also on Day 4 (Figure 13). Day-to-day variations in average Chl *a* concentration ranged from 12.2 mg m^{-3} to 27.6 mg m^{-3}.

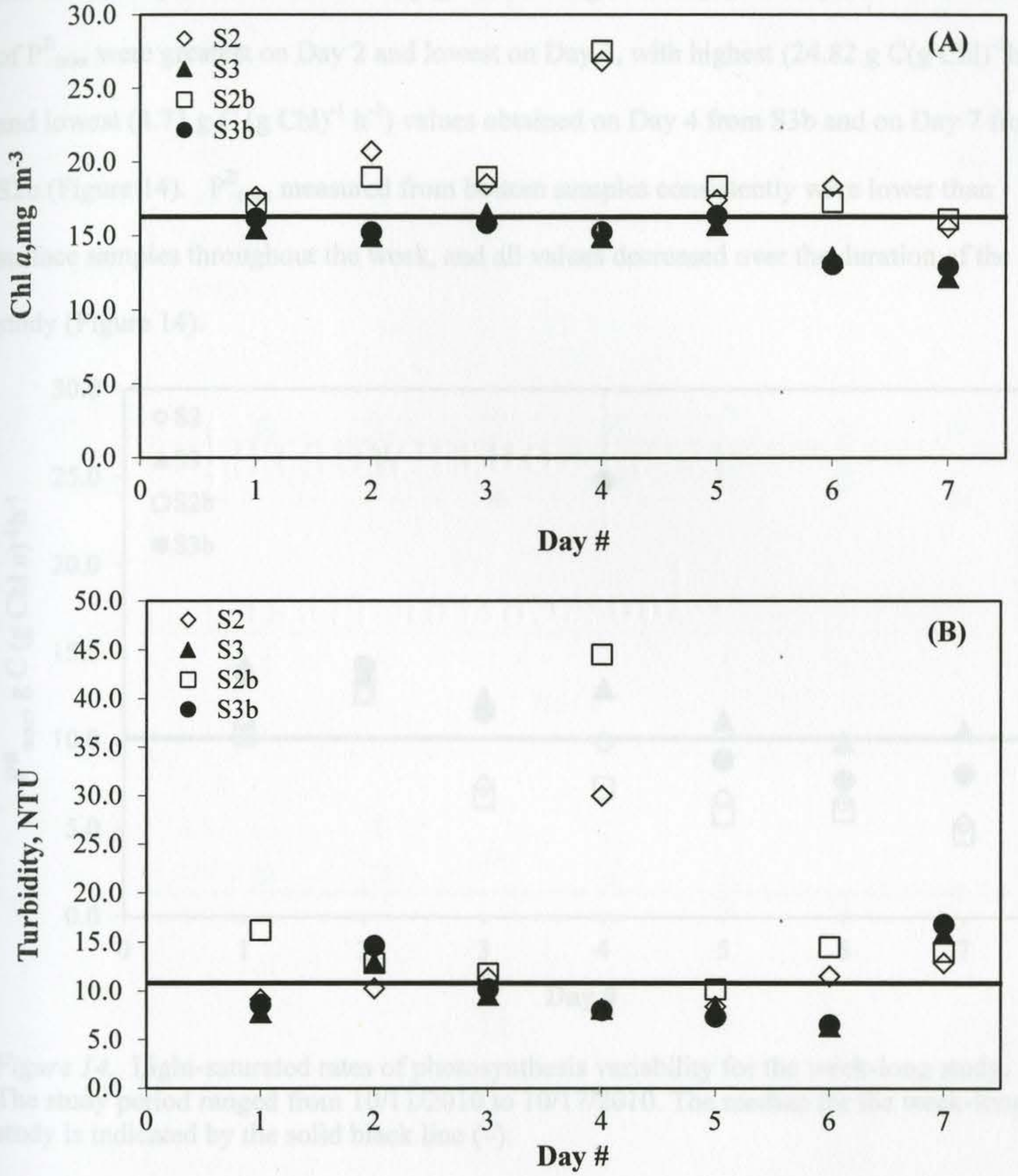


Figure 13. Chl a (A) and turbidity (B) variability over the course of the week-long study. The study period ranged from 10/11/2010 to 10/17/2010. The median for the week-long study is indicated by the solid black line (–).

Between-Day Variability in Phytoplankton Photosynthetic Response

Although light saturated rates of photosynthesis, $P^B{}_{max}$ ranged from 4.73 g C (g Chl)$^{-1}$ h^{-1} to 24.82 g C (g Chl)$^{-1}$ h^{-1} over the course of the week, between-day values were not statistically different (KW test, $p \leq 0.05$) during the study (Table 8). Median values of P^B_{max} were greatest on Day 2 and lowest on Day 3, with highest (24.82 g C(g Chl)$^{-1}$h^{-1}) and lowest (4.73 g C (g Chl)$^{-1}$ h^{-1}) values obtained on Day 4 from S3b and on Day 7 from S2b (Figure 14). P^B_{max} measured from bottom samples consistently were lower than surface samples throughout the week, and all values decreased over the duration of the study (Figure 14).

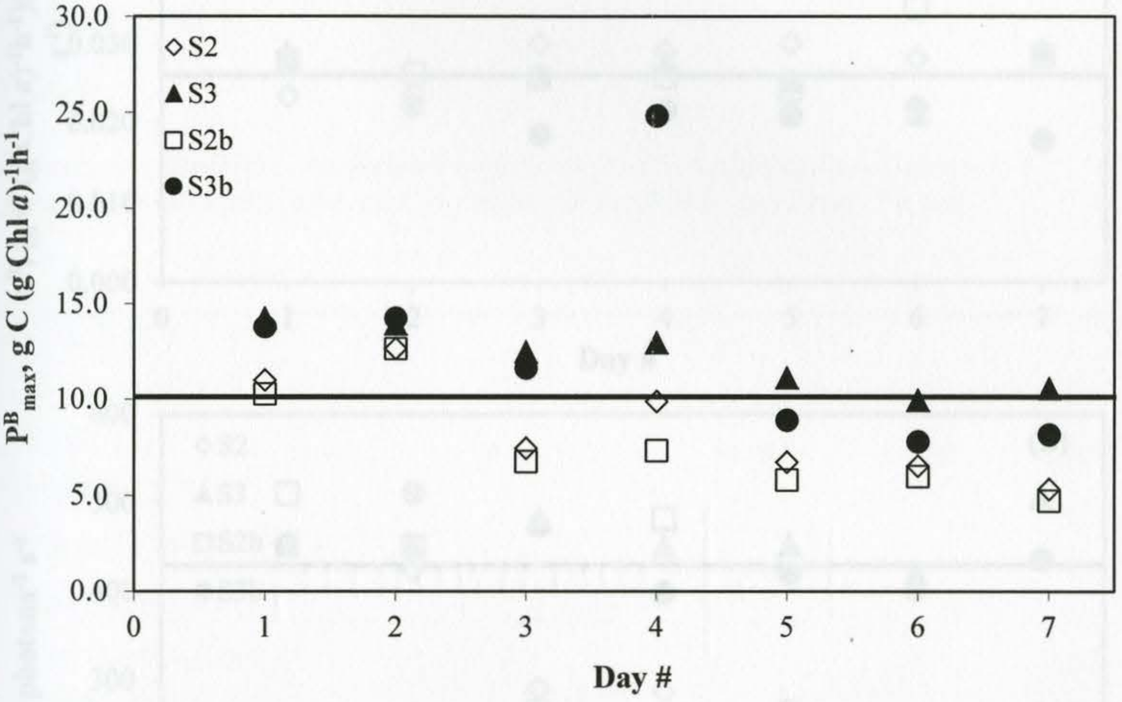


Figure 14. Light-saturated rates of photosynthesis variability for the week-long study. The study period ranged from 10/11/2010 to 10/17/2010. The median for the week-long study is indicated by the solid black line (–).

The week-long study median (range) for α^B was 0.026 (0.018-0.060) g C ((g Chl)$^{-1}$ h^{-1})(µmol photon m^{-2} s^{-1})$^{-1}$, although variability was not statistically significant (KW test, $p \geq 0.05$) during the study (Figure 15; Table 8). The light saturation parameter, E_k ranged from 212.01 to 510.70 µmol photon m^{-2} s^{-1} over the course of the week, and was greatest on Day 1 and lowest on Day 6 (Figure 15). However, test results indicated that between-day values of E_k were not significantly different (MW test, $p \leq 0.05$) from one another (Table 8).

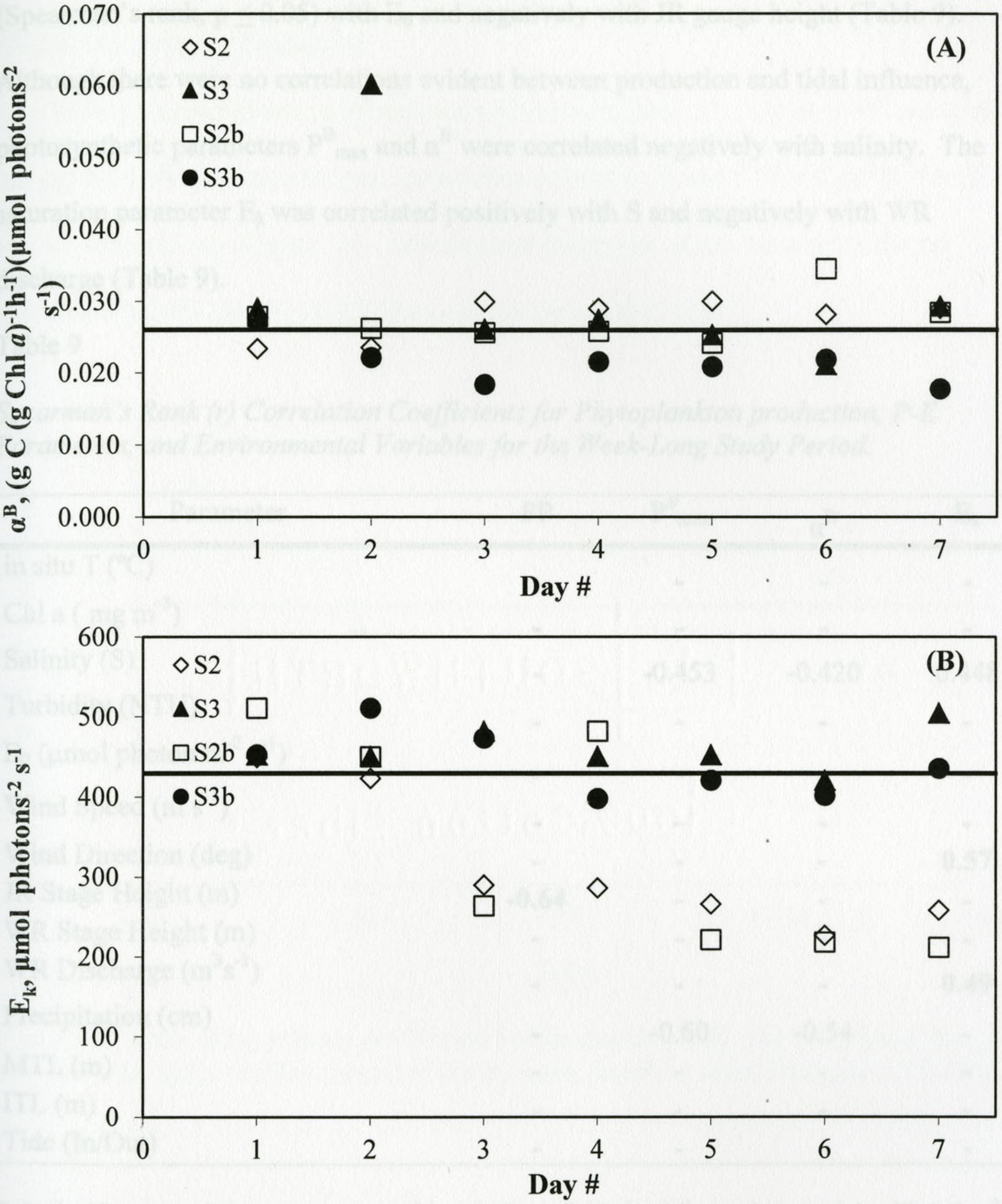


Figure 15. Photosynthetic efficiency (A) and the light saturation parameter (B) variability for the week-long study. The study period ranged from 10/11/2010 to 10/17/2010. The median for the week-long study is indicated by the solid black line (–).

Between-Day Correlations

Between day variability in daily areal production was correlated positively (Spearman's rank, $p \leq 0.05$) with E_0 and negatively with JR gauge height (Table 9). Although there were no correlations evident between production and tidal influence, photosynthetic parameters P^B_{max} and α^B were correlated negatively with salinity. The saturation parameter E_k was correlated positively with S and negatively with WR discharge (Table 9).

Table 9

Spearman's Rank (r) Correlation Coefficients for Phytoplankton production, P-E Parameters, and Environmental Variables for the Week-Long Study Period.

Parameter	PP	P^B_{max}	α^B	E_k
in situ T (ºC)	-	-	-	-
Chl a (mg m^{-3})	-	-	-	-
Salinity (S)	-	-0.453	-0.420	0.448
Turbidity (NTU)	-	-	-	-
E_0 (μmol photon m^{-2} s^{-1})	-	-	-	-
Wind Speed (m s^{-1})	-	-	-	-
Wind Direction (deg)	-	-	-	**0.57**
JR Stage Height (m)	**-0.64**	-	-	-
WR Stage Height (m)	-	-	-	-
WR Discharge (m^3s^{-1})	-	-	-	**0.49**
Precipitation (cm)	-	-0.60	-0.54	-
MTL (m)	-	-	-	-
ITL (m)	-	-	-	-
Tide (In/Out)	-	-	-	-

Only significant correlations were presented ($p \leq 0.05$, **$p \leq 0.01$**) for daily areal productivity, PP (gC $m^{-2}d^{-1}$), daily areal primary production, P (gC $m^{-2}d^{-1}$), P^B_{max} (gC g $Chla^{-1}$ h^{-1}), α^B (gC[g Chla h]$^{-1}$[μmol photon $m^{-2}s^{-1}$]$^{-1}$), and E_k (μmol photon m^{-1} s^{-1}). Values without any statistical significance are indicated by a dashed line. N = 28 for all parameters except DO and pH (N = 24), and P (N = 14).

Within-Day Distribution, Variation, and Environmental Control of Primary Production and Phytoplankton Photosynthesis

Within-Day Primary Production

Within-day variations in PP also were observed (Table 10). Greatest PP occurred at midday for both stations with peak production rates of 0.72 and 0.50 g C $m^{-2}d^{-1}$ for S2 and S3, respectively (Figure 16). Morning and afternoon values were not different significantly (MW test, $p \leq 0.05$) from one another (Table 11).

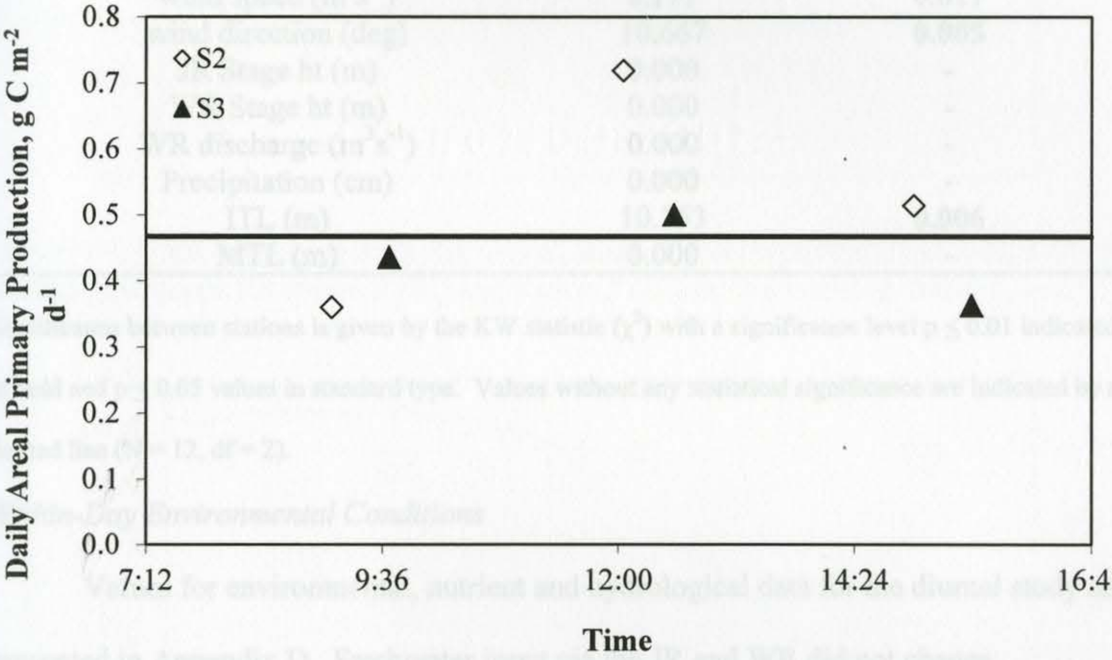


Figure 16. Daily areal primary production for the diurnal study. The solid black line (–) represents the study median measured during three sampling times throughout the day.

Table 10

Kruskal-Wallis Analysis of Temporal Variability for the Diurnal Time Scale.

Parameter	χ^2	Significance
PP (g C m^{-2} d^{-1})	2.571	-
P^B_{max} (g C (g Chl a)$^{-1}$ h^{-1})	5.538	-
α^B (g C (g Chl a^{-1})h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$)	2.808	-
E_k (μmol photon m^{-2} s^{-1})	4.885	-
In situ T(°C)	8.79	0.012
Salinity (S)	0.808	-
Turbidity (NTU)	3.231	-
Chl a(mg m^{-3})	0.500	-
E_0 (μmol photon m^{-2} s^{-1})	8.171	0.017
Air T(°C)	10.667	**0.005**
wind speed (m s^{-1})	8.171	0.017
wind direction (deg)	10.667	**0.005**
JR Stage ht (m)	0.000	-
WR Stage ht (m)	0.000	-
WR discharge (m^3s^{-1})	0.000	-
Precipitation (cm)	0.000	-
ITL (m)	10.353	**0.006**
MTL (m)	0.000	-

Significance between stations is given by the KW statistic (χ^2) with a significance level $p \leq 0.01$ indicated in bold and $p \leq 0.05$ values in standard type. Values without any statistical significance are indicated by a dashed line (N = 12, df = 2).

Within-Day Environmental Conditions

Values for environmental, nutrient and hydrological data for the diurnal study are presented in Appendix D. Freshwater input via the JR and WR did not change throughout the day. Stage height was 0.2 m for the JR and 1.4 m for the WR during the sample period. No precipitation occurred. PAR varied throughout the day and peaked at 1262.5μmol photon m^{-2} s^{-1} at midday, while lowest values (542.5 μmol photon m^{-2} s^{-1}) were obtained in the morning. Skies were sunny and cloudless. Light attenuation was greater at S2 than at S3 throughout the day. K_d was 2.5 (± 0.1) m^{-1} at S2 and was 1.3 (± 0.2) m^{-1} at S3 (Figure 17).

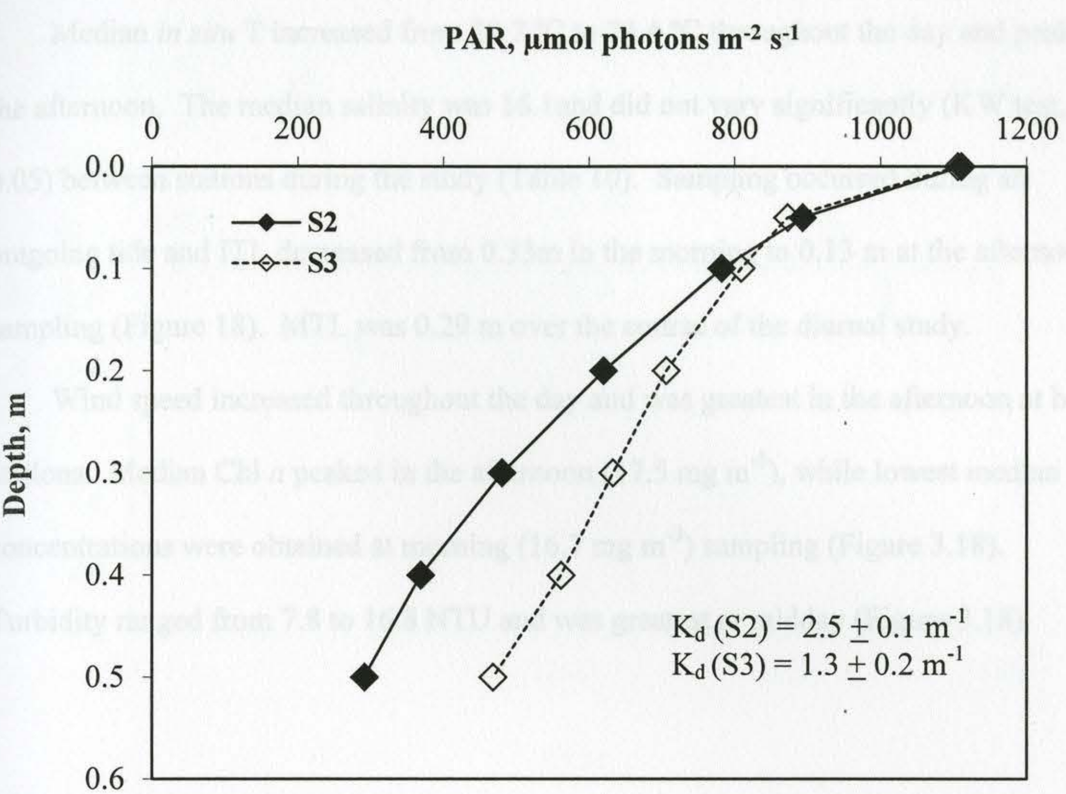


Figure 17. PAR versus depth for the diurnal study. Points represent mean values of PAR measured at depth for station 2 (S2) and station 3 (S3) during morning, midday, and afternoon sampling.

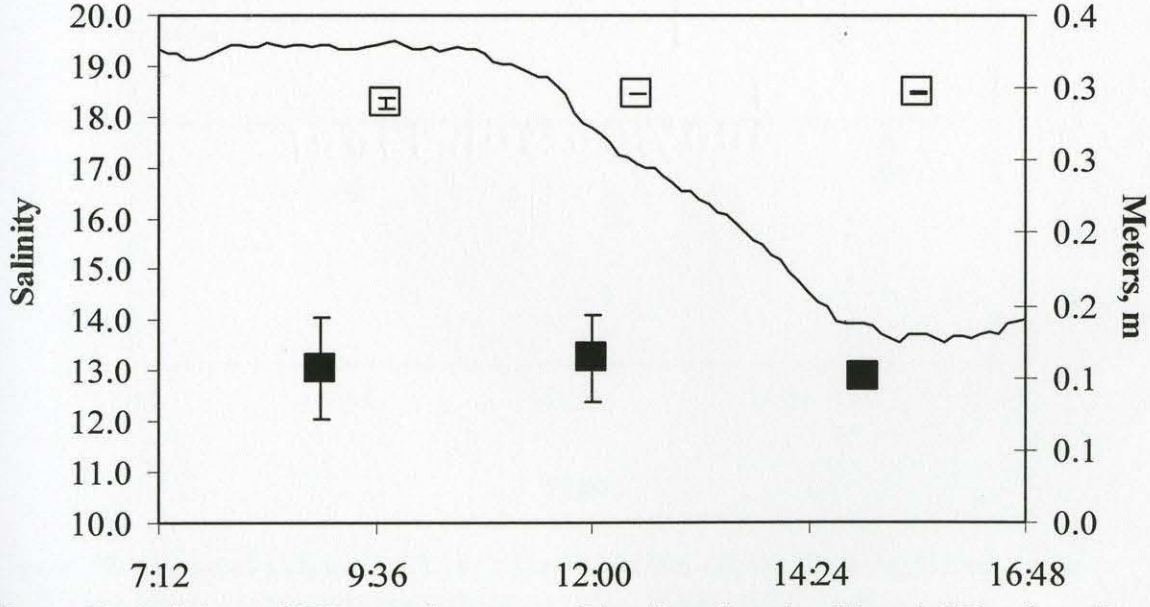


Figure 18. Salinity and ITL over the course of the diurnal study. Mean (+SE) values for salinity are indicated by the black boxes (■) and and open boxes (□) for station 2 and station 3, respectively. Mean (SE) values represent the average of surface and bottom samples at each respective station. The solid black line (□) represents ITL.

Median *in situ* T increased from 20.7 ºC to 23.4 ºC throughout the day and peaked in the afternoon. The median salinity was 16.1and did not vary significantly (KW test, $p \leq 0.05$) between stations during the study (Table 10). Sampling occurred during an outgoing tide and ITL decreased from 0.33m in the morning to 0.13 m at the afternoon sampling (Figure 18). MTL was 0.29 m over the course of the diurnal study.

Wind speed increased throughout the day and was greatest in the afternoon at both stations. Median Chl *a* peaked in the afternoon (17.5 mg m^{-3}), while lowest median concentrations were obtained at morning (16.7 mg m^{-3}) sampling (Figure 3.18). Turbidity ranged from 7.8 to 16.8 NTU and was greatest at midday (Figure 3.18).

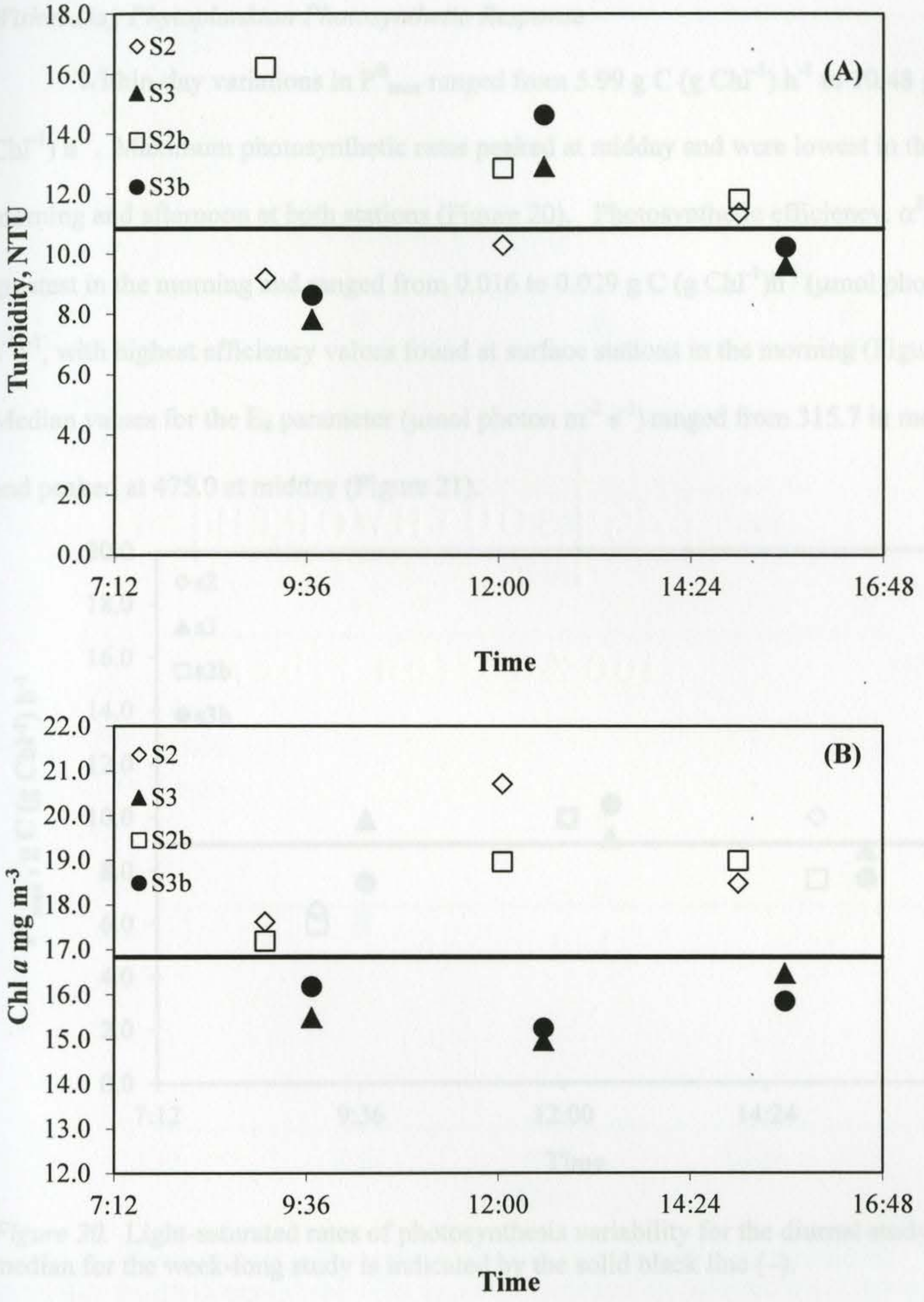


Figure 19. Range of values for Chl *a* (A) and turbidity (B) for the diurnal study. The solid black line (–) represents the median over the course of the study.

Within-Day Phytoplankton Photosynthetic Response

Within-day variations in P^{B}_{max} ranged from 5.99 g C (g Chl^{-1}) h^{-1} to 10.48 g C (g Chl^{-1}) h^{-1}. Maximum photosynthetic rates peaked at midday and were lowest in the morning and afternoon at both stations (Figure 20). Photosynthetic efficiency, α^{B} was greatest in the morning and ranged from 0.016 to 0.029 g C (g Chl^{-1})h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$, with highest efficiency values found at surface stations in the morning (Figure 21). Median values for the E_k parameter (μmol photon m^{-2} s^{-1}) ranged from 315.7 in morning and peaked at 475.0 at midday (Figure 21).

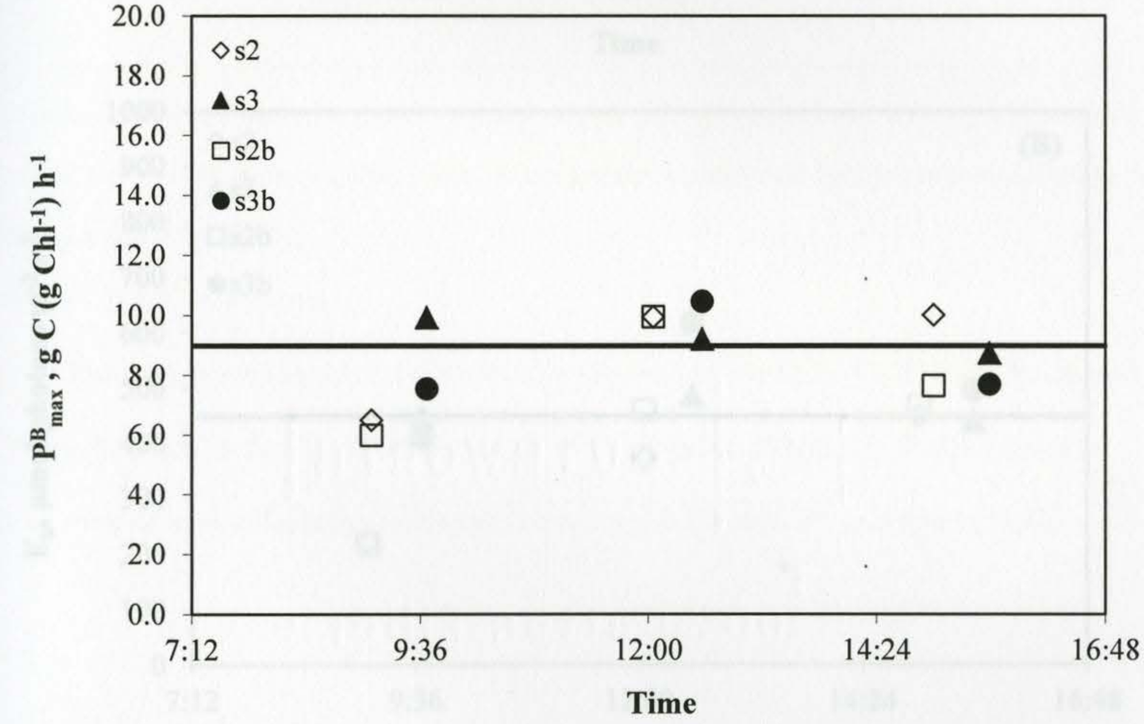


Figure 20. Light-saturated rates of photosynthesis variability for the diurnal study. The median for the week-long study is indicated by the solid black line (–).

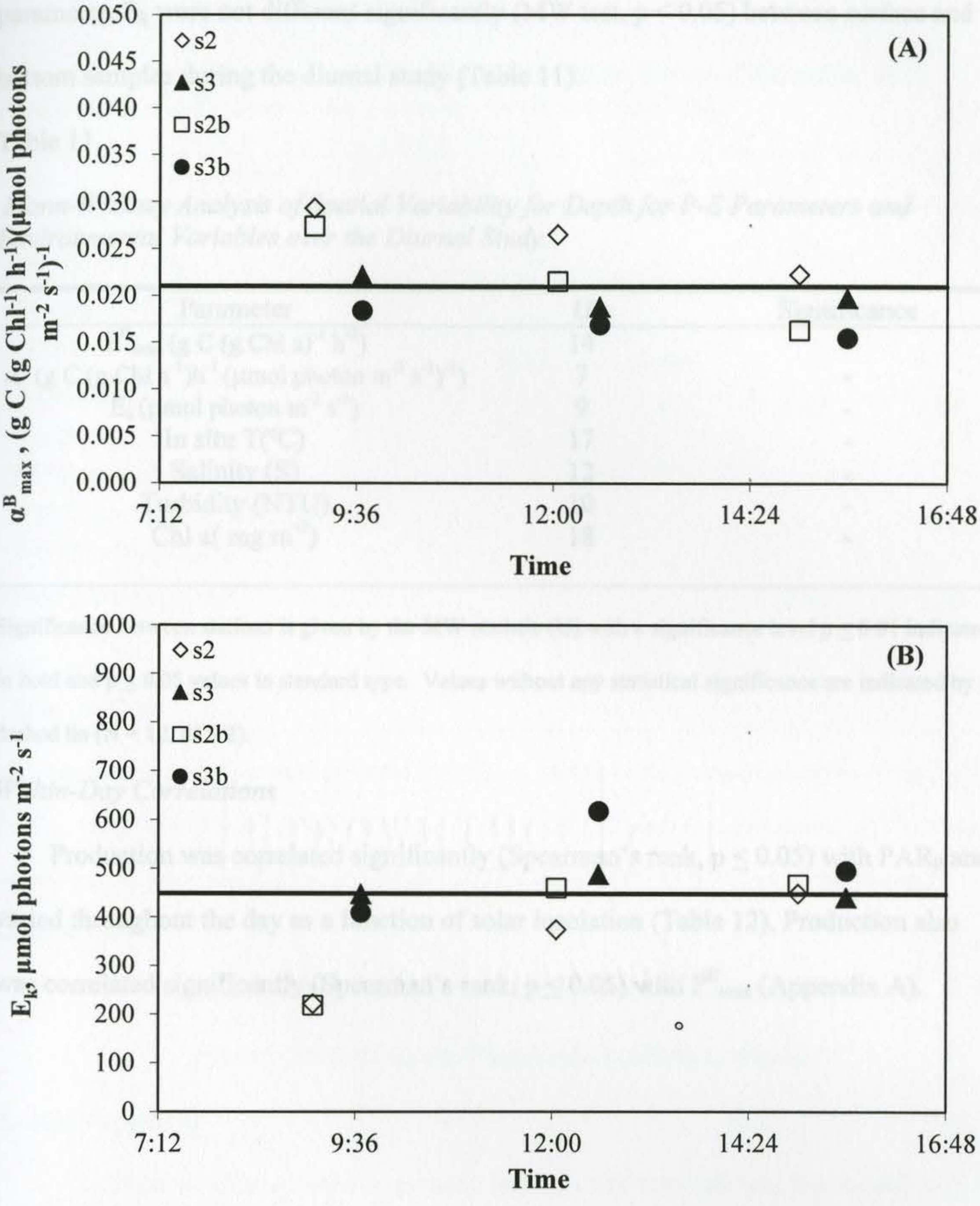


Figure 21. Photosynthetic efficiency (A) and the light saturation parameter (B) variability for the diurnal study. The median is indicated by the solid black line (–).

A MW test was conducted to determine if differences existed between surface values P^{B}_{max} and α^{B} (surface) and values for samples taken at a depth of 0.5 m (bottom). The MW test showed that the P-E parameters P^{B}_{max} and α^{B}, and the light saturation parameter, E_k were not different significantly (MW test, $p < 0.05$) between surface and bottom samples during the diurnal study (Table 11).

Table 11.

Mann-Whitney Analysis of Spatial Variability for Depth for P-E Parameters and Environmental Variables over the Diurnal Study.

Parameter	*U*	Significance
P^B_{max} (g C (g Chl a)$^{-1}$ h^{-1})	14	-
α^B (g C (g Chl a^{-1})h^{-1} (µmol photon m^{-2} s^{-1})$^{-1}$)	7	-
E_k (µmol photon m^{-2} s^{-1})	9	-
In situ T(°C)	17	-
Salinity (S)	12	-
Turbidity (NTU)	10	-
Chl a(mg m^{-3})	18	-

Significance between stations is given by the MW statistic (U) with a significance level $p \leq 0.01$ indicated in bold and $p \leq 0.05$ values in standard type. Values without any statistical significance are indicated by a dashed lin ($N = 12$, $df = 2$).

Within-Day Correlations

Production was correlated significantly (Spearman's rank, $p \leq 0.05$) with PAR_0 and varied throughout the day as a function of solar insolation (Table 12). Production also was correlated significantly (Spearman's rank, $p \leq 0.05$) with P^B_{max} (Appendix A).

Table 12.

Spearman's Rank (r) Correlation Coefficients for Phytoplankton Production, P-E Parameters, and Environmental Variables for the Diurnal Study.

Parameter	PP	P^{B}_{max}	α^B	E_k
in situ T (°C)	-	-	-	0.66
Chl a (mg m^{-3})	-	-	-	
Turbidity (NTU)	-	-	-	
E_0 (µmol photon m^{-2} s^{-1})	**0.83**	**0.76**	-	0.61
Wind Speed (m s^{-1})	-	-	-0.66	0.65
Wind Direction (deg)	-	-	-	-
JR Stage Height (m)	-	-	-	-
WR Stage Height (m)	-	-	-	-
WR Discharge (m^3s^{-1})	-	-	-	-
Precipitation (cm)	-	-	-0.65	0.58
MTL (m)	-	-	-	-
ITL (m)	-	-	0.58	-0.62
Tide (In/Out)	-	-	-	-

Only significant correlations were presented ($p \leq 0.05$, $\mathbf{p \leq 0.01}$) for daily areal productivity, PP (gC $m^{-2}d^{-1}$), P^{B}_{max} (gC g $Chla^{-1}$ h^{-1}), α^B (gC[g Chla h]$^{-1}$[µmol photon m^{-2} s^{-1}]$^{-1}$), and E_k (µmol photon m^{-1} s^{-1}). Values without any statistical significance are indicated by a dashed line (N = 12 for all parameters except P, where N = 6).

Distribution, Variation, and Environmental Control of Primary Production and Phytoplankton Photosynthesis

Spatial Variability

In order to address whether primary productivity was different at selected stations along the BSL shoreline, spatial variability in PP was evaluated based on seasonal (July through December) values. Further, when evaluating the differences in PP between river mouths (RM), sewage outfalls (SO), or stations near the Mississippi Sound (MS), station parameters were averaged based on their location such that S1 and S4 reflected RM, S1 and S5 represented SO, and S3 and S6 represented MS. In addition, six environmental quality parameters were examined that characterized the quality of the water: measurements of water clarity (turbidity); algal biomass (Chl *a*); total dissolved inorganic nitrogen, DIN concentrations (NO_3+NO_2+NH_4); orthophosphate concentrations (PO_4^{3-}); nutrient molar ratios (N:P); dissolved oxygen (DO); and pH (Table 13). The results from a KW analysis of variance test for spatial variability proved that daily areal productivity, P-E parameters (P^B_{max}, α^B, and E_k) and most of the environmental quality parameters were not different significantly (KW test, $p \geq 0.05$) between stations (Table 10). Thus, only DIN, PO_4^{3-}, N:P, and pH were different significantly KW test, $p \leq 0.05$) between stations or between the two shorelines over the course of the study (Table 10).

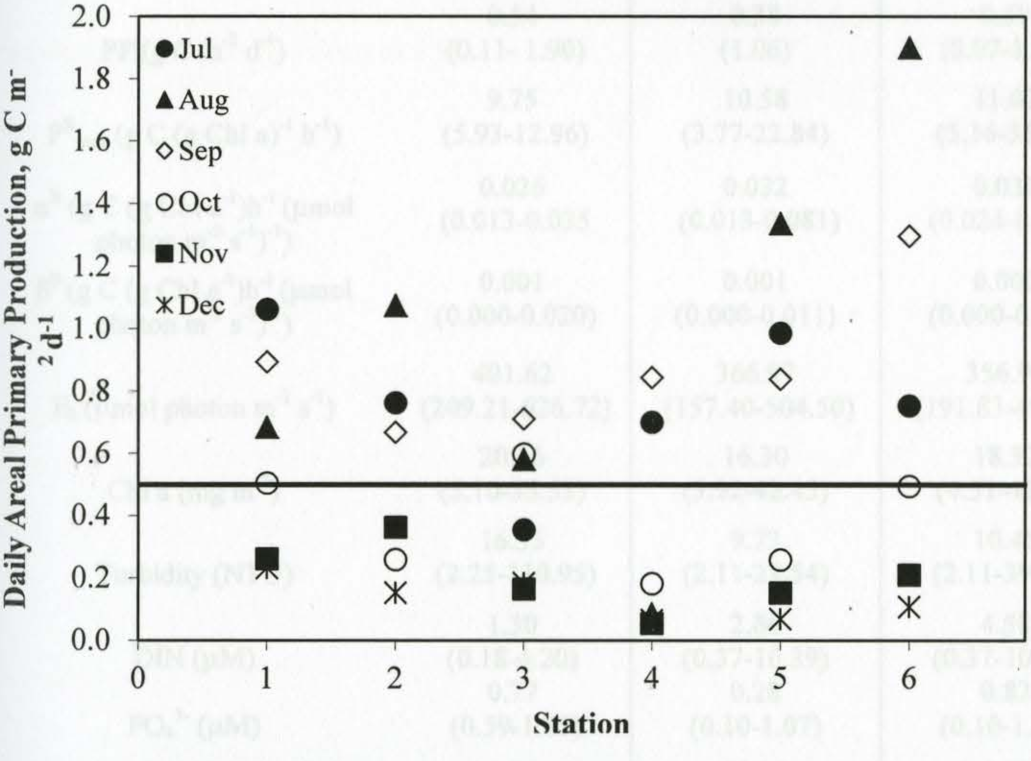


Figure 22. Spatial distributions of daily areal productivity, PP (gC m^{-2} d^{-1}) for the seasonal study. The median is indicated by the solid black line (–).

Spatial variability was observed, with PP decreasing from the JR mouth to the MS along the western margin of the BSL, while the inverse was observed along the eastern shoreline (Figure 22). PP values ranged from a minimum of 0.065 g C m^{-2} d^{-1} at S4 to a maximum of 1.90 g C m^{-2} d^{-1} at S6 (Figure 3.21). Median values for station groups were 0.54 g C m^{-2} d^{-1} at MS, 0.38 g C $m^{-2}d^{-1}$ at RM, and 0.59 g C m^{-2} d^{-1} at SO (Table 13).

Table 13

Median (range) Values for Daily Areal Productivity, P-E Parameters and Environmental Quality Parameters for Stations Located at River Mouths (RM), Sewage Outfalls (SO), and Near the Mississippi Sound (MS).

Parameter	MS median (range)	RM median (range)	SO median (range)
PP (g C m^{-2} d^{-1})	0.54 (0.11- 1.90)	0.38 (1.06)	0.59 (0.07-1.34)
P^B_{max} (g C (g Chl a)$^{-1}$ h^{-1})	9.75 (5.93-12.96)	10.58 (3.77-22.84)	11.02 (5.36-35.80)
α^B (g C (g Chl a^{-1})h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$)	0.026 (0.013-0.035	0.032 (0.013-0.081)	0.031 (0.024-0.031)
β^B (g C (g Chl a^{-1})h^{-1} (μmol photon m^{-2} s^{-1})$^{-1}$)	0.001 (0.000-0.020)	0.001 (0.000-0.011)	0.002 (0.000-0.011)
E_k (μmol photon m^{-2} s^{-1})	401.62 (209.21-626.72)	366.97 (157.40-504.50)	356.91 (191.83-494.88)
Chl a (mg m^{-3})	20.16 (5.10-35.53)	16.30 (3.92-42.45)	18.32 (4.51-42.45)
Turbidity (NTU)	16.35 (2.25-110.95)	9.73 (2.11-23.54)	10.46 (2.11-39.71)
DIN (μM)	1.30 (0.18-4.20)	2.86 (0.37-10.39)	4.58 (0.37-10.40)
PO_4^{3-} (μM)	0.77 (0.59-1.85)	0.28 (0.10-1.07)	0.82 (0.10-1.67)
N:P	1.86 (0.17-5.24)	13.15 (0.34-25.50)	5.39 (0.34-15.79)
DO (mg L^{-1})	8.28 (6.97-10.36)	7.01 (4.73-10.17)	7.17 (4.35-10.17)
pH	7.97 (7.78-8.03)	7.40 (7.07-7.78)	7.62 (7.44-7.96)

Conversely, P^B_{max} and α^B were greatest at SO and were lowest at MS, but maximum E_k values were measured at MS. Photoinhibition, β^B was negligible and was not different between RM, SO, and MS (Appendix B).

Concentrations of Chl *a* ranged from 3.9 to 47.9 mg m^{-3} at MS. Turbidity varied spatially and ranged from 2.0 to 110.9 NTU. Nutrient concentrations were significantly different (KW test, $p \leq 0.01$) between RM, SO, and MS stations. Dissolved inorganic nitrogen ranged from 0.2 to 10.4 µM and concentrations were greatest at SO, while PO_4^{3-} concentrations ranged from 0.4 to 1.8 µM and were greatest at MS. The N:P ratios (mol:mol) ranged from 0.2 to 117.1 and were greatest at RM and lowest near MS. Dissolved oxygen concentrations and pH ranged from 4.4 to 9.3 mg L^{-1} and 6.8 to 8.0, respectively, and were lowest at RM.

CHAPTER IV

DISCUSSION

The objective of this study was to provide a clear estimate of primary productivity (PP) by phytoplankton along the shallow shoreline waters of the Saint Louis Bay (BSL) estuary and identify the environmental variables that contribute to the observed spatial and temporal variability. Phytoplankton production varied temporally and was correlated primarily with temperature (i.e. seasonal changes), while freshwater discharge and irradiance accounted for much of the variability observed over the course of a week and over the course of a day, respectively. Spatial variability was observed and a gradient increasing from the river mouth to the estuary mouth was evident on the eastern shoreline, while the opposite trend was observed on the western shoreline. However, because there was a lack of significant statistical variability between stations near the Mississippi Sound (MS), sewage outfalls (SO), and near river mouths (RM), it was concluded that these results do not support the hypothesis that PP would be greatest at MS and lowest at RM and SO. However, the results do support previous studies (Phelps 1999, Rowe 2010, Mojzis 2010), which suggest that while variability between stations does exist, the response to environmental forcing occurs simultaneously across the entire bay, thus defining the BSL estuary as a system.

Evaluation of Hypotheses

Temporal Variability

Environmental parameters were assessed over the course of a month to examine seasonal variability, over the course of a week to evaluate weather and tidal forcing, and diurnally to observe phytoplankton photosynthesis relative to irradiance effects. The data supports this hypothesis. Monthly variability in PP was correlated primarily with variations in *in situ* T, PAR, Chl *a*, and turbidity. On a day-to-day basis, river discharge accounted for much of the variability (Spearman's rank, $p \leq 0.05$) in PP, while PAR was correlated significantly with PP over the course of a day (Table 6). Further, a Spearman's correlation analysis indicated that PP was affected primarily by river discharge rather than tidal influences over the course of a week (Table 6).

Seasonal Variability

Daily areal primary production varied seasonally from July to December and was greatest in summer and lowest in autumn. Production rates were similar to other studies (Pennock and Sharp 1986; Randall and Day 1987; Mallin *et al.*. 1991; Mann and Lazier 1991; Lohrenz *et al.*; 1994; Cole 1998; Mortazavi *et al.*. 2000; Azevedo *et al.* 2010) and fell within the range of other temperate to sub-topical mesotrophic estuaries (see Table 1). Monthly variability in primary production was correlated significantly (Spearman's rank, $p < 0.05$) with *in situ* T, Chl *a*, turbidity and incident irradiance in the BSL as was observed commonly in the studies cited above (Table 6, Appendix A). However, correlation analysis found no statistical correlations evident with respect to wind speed, wind direction, or river discharge relative to variability in productivity at this time scale (Table 6, Appendix A). This was not surprising since these environmental conditions occur on much shorter time scales.

There was a distinct seasonal trend with respect to PP over the course of the study (see Figure 2), and variability correlated significantly ($p < 0.01$) with *in situ* T. This was expected since many coastal and estuarine studies have demonstrated that phytoplankton photosynthesis is coupled tightly with *in situ* T and that primary production varies seasonally in response to seasonal changes in temperature (Eppley 1972; Pennock and Sharp 1986; Randall and Day 1987; Mallin *et al.*. 1991; Mann and Lazier 1991; Lohrenz *et al.* 1994; Cole 1998; Mortazavi *et al.*; 2000, Azevedo *et al.* 2010). Eppley (1972) emphasized the importance of temperature effects on growth rates by suggesting that carbon assimilation by phytoplankton is a temperature-dependent, enzyme-controlled process. In the BSL estuary, Woodmansee *et al.* (1980) observed similar patterns and correlations with respect to *in situ* T and potential primary production. The present body of data supports the initial hypothesis that variability in PP was associated with variability in bay surface water temperature.

In addition to *in situ* T, seasonal variability of PP in the BSL was associated with variations in irradiance, E_0. Variations in insolation regulate the amount of photosynthetically available radiation (PAR) utilized in phytoplankton photosynthesis. Cole (1998) observed that irradiance, in addition to phytoplankton biomass and euphotic depth, were responsible for limiting production in many estuaries. Studies in the Delaware estuary (Pennock and Sharp, 1986), Chesapeake Bay (Harding *et al.* 1986), Neuse River Estuary (Mallin *et al.* 1993), San Antonio Bay (McIntyre and Cullen 1996), and San Joaquin River Delta complex (Jassby *et al.* 2002) have all attributed light availability as the predominate variable regulating seasonal primary production. It was expected that seasonal variations in E_0 would account for much of the seasonal variability in PP within the BSL system as well. The results support this assertion (Table 6, Appendix A). Woodmansee *et al.* (1980) also found that strong correlations existed between surface irradiance and volumetric production in the BSL estuary. Light harvesting capabilities must therefore be correlated to light availability. The studies cited above have shown that the amount of light available for photosynthesis is inversely correlated to the amount of light harvesting pigments, especially Chl *a*, in algae and higher plants (Kirk 1996). That relationship was not observed in this study. Rather, Chl *a* was correlated positively with E_0 (see Appendix A). Further, studies have also demonstrated that algal biomass concentrations in aquatic environments are proportional to primary production (Kirk 1996; Falkowski and Raven 2007; Cole and Cloern 1987; Lohrenz *et al.* 1994). Because the BSL shoreline waters were shallow and turbid and instantaneous irradiance values were used in correlation analysis, it is suggested that variability in PP was associated with the ambient light conditions available for photosynthesis.

Biomass (i.e. Chl *a*) concentrations were correlated significantly ($p \leq 0.01$) to PP in the BSL over the seasonal scale (Table 6, Appendix A). Biomass was greater in summer than in autumn and was associated most likely with changes in *in situ* T. Previous studies in the BSL also have established that biomass is tightly coupled with *in situ* T (Pluhar 2007; Rowe 2008; Sawant 2009; Mojzis 2010). Mallin *et al.* (1991) and Randall and Day (1989) also found that biomass varied seasonally in the Neuse River Estuary (NRE) due to changes in *in situ* T and was common among other temperate estuaries. Correlations between PP and Chl *a* were documented in other studies as well. Chen (2000) and Lohrenz *et al.* (1994) found that significant positive correlations existed between primary production and Chl *a* in the coastal waters of the northern Gulf of Mexico. Production studies conducted by Woodmansee *et al.* (1980) also found that rates of surface volumetric production was correlated significantly with surface concentrations of Chl *a*. The results in the current study were expected, as Chl *a* is a direct measure of the light harvesting capability and photosynthetic potential used for carbon-fixation by phytoplankton; thus, Chl *a* is also an expression of biomass and is used extensively as an indicator for primary production.

Turbidity also was correlated positively with PP. However, this was not expected, as turbidity is a primary source of light attenuation in shallow estuarine and coastal waters (Cloern 1987; Cole and Cloern 1987; Kirk 1996). Because the sampling stations were located in shallow water (< 1.0 m) and were in close proximity to the mouths of two rivers, input of particulate matter (PM) and resuspension of sediments due to wind contributed greatly to the turbidity of these waters. As mentioned previously, numerous studies have attributed limitations in phytoplankton productivity in coastal and estuarine waters to light availability for photosynthesis within the water column. However, some studies found that production rates were enhanced as a result of resuspension of microalgal cells from the sediment surface. For example, Cloern (1987) observed a negative correlation between turbidity and primary production, but MacIntyre and Cullen (1996) found that PP was highly correlated with turbidity in the San Antonio Bay. They found significant positive correlations between PP, turbidity and Chl *a*. It was shown in that study that resuspension of photosynthetically competent cells settled on the seafloor and benthic phytoplankton were responsible for a significant portion of water column primary production in the shallow bay. Like the San Antonio Bay, the present study was conducted along the shoreline of the BSL in water that averaged less than 1.0 m throughout the study. Mojzis (2010) also found significant ($p < 0.05$) positive correlations between turbidity and Chl *a* in the BSL and that turbidity was highest at stations of shallower depth. Thus, the significant relationships ($p < 0.01$) between turbidity, PP, and Chl *a* suggest that much of the primary production along the shoreline may have been due to a combination of resuspension of microalgal cells from the benthos and phytoplankton already suspended in the water column.

Monthly variability in PP was not correlated to wind speed or wind direction during the study. It was hypothesized that wind speed would affect PP negatively based on the assumption that wind stress on the surface would cause complete vertical mixing, thereby resuspending sediments into the water column and enhance light attenuation. Sawant (2009) identified wind forcing as a primary regulator of water quality (e.g. water clarity, biological oxygen demand (BOD), and nutrient concentrations) in the BSL. Further, there may be a lag phase in which the cells respond and decrease production rates. At this time scale, however, wind speed and direction were not correlated with PP or turbidity, although it was observed that the water was choppier and more turbid on days when wind speed was greatest. Because variations in wind speed and direction occur on much shorter time scales, these changes would not translate into helping explain PP variability over much longer time scales.

It was expected that freshwater input via the two rivers and precipitation would impact phytoplankton production negatively in the BSL. While river stage heights and precipitation rates varied seasonally, there were no correlations evident with PP. This is not unreasonable since studies in the bay have shown that environmental quality is comprised mainly from a 3-5 day lag response from episodic storm events (Pluhar 2007; Rowe 2008; Sawant 2009). No significant storm events occurred on or up to 5 days prior to sampling during course of this study. However, long- term changes in precipitation delivered to the watershed and changes to the hydrology of the rivers may affect production in the BSL over a decadal scale. Mallin *et al.* (1993) found significant correlations with phytoplankton production and river discharge in the Neuse River Estuary during heavy flow years, where it was noted that under normal flow conditions, the estuary acts as filter, thereby removing nutrients. However, during years of higher precipitation like those found in decadal climate oscillations, heavy river flow increased nutrient input into the Neuse River Estuary that enhanced primary production (Mallin *et al.* 1993). Similar responses to river flow and nutrient input that stimulate algal blooms have been documented in other estuaries as well. Sawant (2009) noted that the environmental quality in the BSL changes in response to El Niño Southern Oscillation (ENSO) phases, and that change in land use practices in the river watersheds may alter the hydrology of the JR and WR and the delivery of nutrients to the estuary. These changes potentially could affect primary production in the BSL. For the current study, a moderate-to-strong La Niña event developed in July and intensified throughout the remainder of the study (NOAA Climate). This climate pattern was reflected in the low river flow and negligible precipitation amounts observed in autumn (Figure 3). Thus, climate phase may have regulated the amount of freshwater input and nutrients via the JR and WR and potentially influenced the seasonal variability in primary production in the BSL.

Short-term Variability

Daily areal primary production varied over the course of a week and was correlated negatively with JR stage height. This was expected since river discharge has been characterized as the primary forcing mechanism within the BSL system (Phelps 1999; Rowe 2008; Sawant 2009). Studies within the BSL estuary have all shown that environmental quality changes in response to episodic freshwater input occurring at scales from 3 to 5 days (Phelps 1999; Pluhar 2007; Rowe 2008; Sawant 2009). Sawant (2009) reported that the JR discharge rate is greater than WR and that the total river discharge into the bay varies in response to precipitation within the respective watersheds. In the current study, river stage height varied 0.1 m over the course of the week and varied possibly in response to changes in wind speed and direction, evidence that wind stress can drive short-term variability in primary production. Sawant (2009) also found that heavy offshore winds contribute to the flushing of the BSL significantly by pushing estuarine waters into and out of the bay. For the current study, mean stage height for the JR was lowest on Day 4, which possibly resulted from a sustained northerly wind > 5.0 m s^{-1} throughout the day (Figure 12, Appendix C). In estuaries like the BSL, tidal reach and the residence time of nutrients depend on river flow and can also affect the advection and potential transport of varied phytoplankton communities (MacIntyre and Cullen 1996). A study by Thronson (2008) found that primary production was enhanced after increased river discharge from episodic storms in the Galveston Bay, though the response time was up to one month after the event. However, Kiene *et al.* (2010) found that PP in the Mobile Bay was enhanced with reduced river discharge. That study suggested that productivity in the Mobile Bay system was driven mainly by heterotrophic nutrient regeneration and that increased river discharge and subsequent reduced residence times decreased PP in the Mobile Bay over the course of a week to ten days (Kiene *et al*. 2004). For the BSL estuary, results suggest that PP variability can be accounted for by variations in flushing time out of the bay via river discharge, especially along the shoreline.

Within-day variations in PP were evident as well. Production peaked at midday and was not different significantly ($p < 0.05$) between the morning and afternoon samples (Table 11). A significant correlation ($p \leq 0.05$) was evident between PP and E_0 (Table 12). This was expected since studies have shown that short-term response in phytoplankton photosynthesis often varies with ambient light intensity, water clarity (i.e. turbidity) and stratification (Pennock and Sharp 1986).

Another factor to consider is the rate of mixing, which can subject phytoplankton cells to a wide range of light intensity. This is contingent upon turbidity and the mixing depth due to wind stress. Cloern (1987) also found that algal photosystems are affected by increased time in low light in highly turbid waters. These fluctuations in light intensity give rise to a 'flashing light' effect, which can greatly affect phytoplankton photosynthesis (Bailey 1997; Falkowski and Raven 2007; Stone 2012). Figure 17 clearly illustrates that irradiance at depth ($E_0(z_2)$) was much less than at surface waters. This suggests that the phytoplankton were subjected to varying light intensities during mixing. However, results from a Mann-Whitney statistical analysis indicated that surface and bottom measurements of photosynthetic-irradiance (P-E) parameters (i.e. P^B_{max}, α^B, E_k) and Chl *a* were not different significantly ($p < 0.05$) (Table 11). Thus, it is assumed that the phytoplankton experienced variable irradiance throughout the water column during mixing, but the vertical profile of the photosynthetic parameters was homogenous. This suggests that phytoplankton cells may have been adapted to high irradiance at the surface and that vertical mixing rates were faster than the adaptive responses by the cells to variable irradiance within the water column.

Superimposed on phytoplankton photosynthesis over the diurnal cycle are variations in light intensity, which can enhance or suppress photosynthetic performance, and diel periodicity (Falkowski and Raven 2007). Studies have demonstrated that natural populations of phytoplankton exhibit diel periodicity with respect to light-saturated rates of photosynthesis and photosynthetic efficiency (i.e. Harding *et al.* 1982), and these effects also were observed in the present study. Diel cycles and circadian rhythms can account for much of the variability when calculating daily production rates in oceanic systems (Harding *et al.* 1982; Lohrenz *et al.* 1994; Cerveny and Nedbal 2009). Further, fluctuating light effects also should be considered as a short-term process potentially affecting PP along the shallow shoreline. In summary, PP along the shoreline is reflective of the resident phytoplankton community and the moderate to high rates of photosynthesis maintained over the course of the day.

Tidal Influence

As a corollary to the negative influence of river discharge on PP, it was hypothesized that tidal forcing would have little, if any effect on PP. Studies in the BSL have shown that freshwater input via the two rivers and terrestrial runoff during episodic storms is the primary physical forcing agent driving seasonal and short-term variability in viral and bacterial abundances (Rowe 2008; Mojzis 2010) and environmental quality (Phelps 1999; Pluhar 2007; Sawant 2009). Moreover, the BSL system is a microtidal estuary with a tidal amplitude of less than 1.0 m. Production did not vary with either river discharge or precipitation, but rather significant correlations ($p \leq 0.01$) were evident with MTL and ITL over the course of the seasonal study (Table 6, Appendix A). This may just be an artifact of decreased river discharge over time. At shorter time-scales (*e.g.*

over the course of a week), however, PP was correlated inversely with JR discharge while there were no significant correlations between PP and MTL, ITL, or the tidal cycle (e.g. ebbing versus flooding). Further, PP did not vary with respect to ITL or the tidal cycle during the diurnal study either. Figure 12 illustrates that sampling over the course of the week occurred at near low tide, and diurnal sampling occurred during the outflow of a low neap tide. It was not expected that the tidal stage would have much effect on PP through enhanced light attenuation (i.e. resuspension). Rather, it was hypothesized that FW discharge would increase turbidity primarily through the input of nutrients that would stimulate biomass growth. Studies have shown also that tidal advection of different phytoplankton cells can account for much of the short-term variability observed in estuarine PP (Malone and Neale 1981; Cote and Platt 1983; Geider *et al.* 1998; Lohrenz *et al.* 1994; MacIntyre and Cullen 1996). However, this was not quantified for this study. Results from the present study indicated that PP was correlated primarily with FW discharge over the course of a week while tidal effects were not (Table 6, Appendix A). This also supports previous research in the BSL, which suggests that water quality is affected primarily by freshwater input via the JR and WR, and that tidal flushing has a minimal effect (Eleuterius 1978; Cobb and Blaine 2002; Phelps 1999; Sawant 2009; Mojzis 2010).

Spatial Variability

Another component of this study was to determine whether PP varied spatially. It was hypothesized that PP would be greater at stations near the MS (i.e. away from nutrient sources) and rates would be lower near SO and RM. (i.e. near nutrient sources). While PP was not statistically different over the course of the monthly study, patterns do illustrate that PP varied between stations (see Figure 22, Table 8). Phelps (1999) established that the BSL can be viewed as an entire system based on the co-occurrence of variability of measurements of water clarity, algal biomass, sediment C:N ratios and low trophic diversity. Because the BSL has many point and non-point sources of nutrients, the current study incorporated DIN, PO_4^{3-}, DO, pH, and nutrient molar (N:P) ratios to serve as indicators assessing whether PP was different at stations MS, RM, and SO. The results indicated that while these parameters spatially were different statistically (KW test, $p < 0.05$), PP and the P-E parameters were not. Furthermore, neither PP nor the P-E parameters P^B_{max} and α^B were correlated with any of the water quality parameters cited above (Appendix A). However, other studies found that estuarine primary production is coupled tightly with nutrient input. Research by Mallin *et al.* (1993) found that PP in the Neuse River Estuary was related primarily to the fluvial input of nutrients. However, the current BSL study found no significant correlations with respect to nutrient concentrations and PP. This does not suggest that resident phytoplankton communities were nutrient replete or nutrient limited, but implies simply that nutrients were abundant enough to sustain moderate to high rates of primary production along the shoreline. Patterns from the current study illustrate that PP decreased from the RM to MS along the western shoreline while the inverse was observed along the eastern shoreline (Figure 22, Appendix B). One reasonable explanation for this is that nutrients were more abundant at S1 near the JR mouth, at S5 near the confluence of Mallini Bayou, and at S6 near the estuary mouth along the eastern shoreline (see Appendix E). However, statistical analysis suggested that PP was not different significantly (KW test, $p < 0.05$) between stations over the duration of the seasonal study (see Table 5). From these observations, it is proposed that PP is regulated by a combination of biological, chemical and physical variables acting in concert and where no single variable is easily discernible. This pattern of variability is common in dynamic estuarine ecosystems like the BSL system.

Photosynthetic Response

Lastly, it was hypothesized that phytoplankton photosynthesis would vary diurnally as a function of irradiance in the shallow waters along the BSL shoreline and that photoinhibition would be greater at MS relative to SO and RM. Results from a MW test indicated that surface and bottom values of PP and the P-E parameters were not different significantly (MW test, $p < 0.05$) throughout the diurnal study (Table 11). Thus, it was assumed that surface samples were sufficient enough to represent accurately the entire water column at selected shoreline stations.

Short-Term Variability

Light-saturated rates of photosynthesis, P^B_{max}, were within the range expected and similar in magnitude and variability to what has been observed for other temperate estuaries (Harding *et al.* 1987; Mallin *et al.* 1991; Lohrenz *et al.* 1994, MacIntyre and Cullen 1996; Chen 2000; Azevedo *et al.* 2010; Vandermuelen 2012). In general, P^B_{max} was lowest in the morning and afternoon, and peaked at midday. Similar patterns were observed in the San Antonio Bay (MacIntyre and Cullen 1996), the Chesapeake Bay (Harding *et al.* 1987), the Neuse River Estuary (Mallin *et al.* 1991), the Douro Estuary (Azevedo *et al.* 2010), and the coastal waters of the northern Gulf of Mexico (Lohrenz *et al.* 1994; Chen 2000). MacIntyre and Cullen (1996) found that although much of the variability in P^B_{max} could be attributed to changes in irradiance, shifts in the phytoplankton community can account for some short term variability observed through tidal advection. It has been observed in natural waters that increased values of P^B_{max} can be attributed also to smaller phytoplankton species (Malone and Neale 1981; Cote and Platt 1983; Lohrenz *et al.* 1994; MacIntyre and Cullen 1996; Geider *et al.* 1998). Cote and Platt (1983) documented higher P^B_{max} values in smaller cells such as cryptophytes and dinoflagellates, whereas larger phytoplankton species like diatoms tended to have lower P^B_{max} values. This was not assessed as part of this study. However, previous studies (Holtermann 1999; Molina 2011) in the BSL estuary indicated that shifts in the phytoplankton community do not occur over the course of a day and the phytoplankton population is comprised primarily of diatoms. Thus, it is suggested that variability was due mainly to physiological changes responding to variable light conditions. Physiological adaptations occur on the order of minutes to hours and vary with different phytoplankton communities (Falkowski and Raven 2007). While shifts in the phytoplankton community cannot be ruled out, the present body of data suggests that diurnal variability in P^B_{max} was most likely due to the daily irradiance cycle.

Conversely, α^B was greatest in the morning and was not correlated with PAR. Short-term changes in the P-E parameters are generally associated with changes in the physiological state of the phytoplankton (Harding *et al.* 1987; Pennock and Sharp 1986; Falkowski and Raven 2007). Adaptations to low irradiance levels are usually manifested as improvements in the photosynthetic efficiency, either through increased numbers of light harvesting pigments or enhanced physiological adaptations (Pennock and Sharp 1986; Falkowski and Raven 2007). This could explain why α^B was greatest in the morning, although no correlations were evident between Chl *a* concentrations, PAR, and α^B (Appendix A).

Photoinhibition was not observed at any point during the study. Reasons for this may be due to the phytoplankton maintaining high maximum rates of photosynthesis. Studies in the San Antonio Bay made similar observations and suggest that high rates of P^{B}_{max} can be an adaptive strategy in phytoplankton to reduce the potential for photoinhibition (MacIntyre and Cullen 1996). Helbling *et al.* (2010) attributed this to the possibility that this is a photoprotective strategy in which the cells are acclimated to high light intensities. Although the rate of mixing was not quantified in the current study, it is proposed that photoinhibition was not observed due to the algal cells maintaining high P^{B}_{max} in response to exposure variable irradiance throughout the water column. Turbulent mixing by wind increases the frequency into and out of light saturation and light limited irradiance levels (Walsh and Legendre 1983; Laws *et al.* 1986; Terry 1986; Lohrenz *et al.* 1994). Studies by Marra (1978) and Phillips and Myers (1954) demonstrated that photosynthesis increased in a fluctuating light regime and found that the oxygen yield via carbon fixation increased in response to variable irradiance frequencies. Similar studies by Walsh and Legendre (1983) found considerable changes in the photosynthetic parameters when cells were subjected to a flashing light condition, such as those found during mixing. Physiological adaptations to fluctuating light are not well known but are thought to be related to either a reduced respiration rate during the dark reaction or efficient utilization of photochemically-produced substrates during the Calvin-Benson cycle (Falkowski and Raven 2007). Either adaptation results in a hysteresis in the short-term photosynthetic-irradiance response during algal growth (MacIntyre *et al.* 2000; Raven and Kübler 2002; Falkowski and Raven 2007).

The results of this study indicate that primary production by phytoplankton varied temporally and spatially. Estimates of daily areal primary production in the BSL were similar to those reported in other estuaries and temperate coastal ecosystems and variability was attributed primarily to changes in T (seasonal), river discharge (week-long), and irradiance (diurnal). The daily production rate for the BSL determined in this study were a factor of two greater than the rates presented by Woodmansee *et al.* (1980) and are more consistent with other contemporary estuarine studies (Table 1.1). The annual production rate for the BSL estuary was estimated at 197 g C m^{-2} y^{-1}, which is comparable to other temperate and subtropical mesotrophic estuaries (Pennock and Sharp 1986; Randall and Day 1987; Mallin *et al.*1991; Mann and Lazier 1991; Lohrenz *et al.*. 1994; Cole 1998; Mortazavi *et al.*. 2000; Azevedo 2010). This study provides the first modeled estimates of primary production in the BSL and will add to the growing body of literature characterizing this important estuary in Mississippi. Moreover, this study supports previous studies indicating that the BSL estuary varies in response to environmental forcing as a single system. These results can serve as a baseline for long term and future short term monitoring studies in the bay. Moreover, as climate change and shifting weather patterns alter the amount of rainfall in the JR and WR watersheds, nutrient supply to the BSL will also change. This change invariably will affect primary production and subsequent trophic levels in the estuary.

Summary

In conclusion, this study provided a reasonable estimate of primary productivity for the shoreline waters of the BSL estuary. It identified some of the physical factors responsible for the observed temporal and spatial variability and was comparable to other mesotrophic estuarine studies. Seasonal variability in phytoplankton production was strongly influenced by temperature, while freshwater discharge and irradiance accounted for much of the variability observed over shorter time scales. In addition, freshwater discharge affected phytoplankton variability more than tides in this study. Although spatial variability was not observed statistically results from this study support previous research, which suggests that the BSL estuary may be viewed as a single system that can vary in a coherent manner over time. Previous studies have also shown that this system varies in response (up to 5 days) to periods of increased freshwater input from episodic rain events. Thus, future research should explore primary production relative to the effects of increased river discharge. As weather patterns shift in response to climate change, alterations in the hydrologic cycle within coastal watersheds may affect nutrient concentrations and phytoplankton biomass, and potentially alter food webs in these dynamic ecosystems. Results from this study illustrate the need to continuously monitor the BSL over the long-term since production in the system has been shown to vary in relation to variability in environmental forcing.

APPENDIX A

CORRELATIONS

Spearman's Rank Correlation for environmental parameters and nutrient data for the seasonal study (total dataset). Significance between values are given by a significance level **$p \leq 0.01$** *in bold and $p \leq 0.05$ in standard type, values without any statistical significance are indicated by a dashed line, ($N = 38$) for all data except DO and pH, where ($N = 25$).*

	P^B_{max}	α^B	E_k	*In situ* T	S	Turb	Chl *a*	NH_4	NO_2 $+NO_3$	DIN	PO_4^{3-}	N:P	$Si(OH)_3$	DO	pH
PP	**0.640**	-	**0.611**	**0.813**	-	**0.371**	**0.789**	-	-	-	-	-	-	**0.703**	-
P^B_{max}		**0.66**	**0.473**	0.411	-	-	-	-	-	-	-	-	0.368	-	-
α^B			-	-	-	-0.402	-	-	-	-	-	-	-	-	-
E_k				**0.671**	-	-	**0.436**	-	-0.351	-0.397	-	-0.38	-	-	-
In situ T					**-0.57**	0.366	**0.583**	-	-	-	-	-	**0.458**	**-0.863**	-0.348
S						-	-	-	-	-	**0.462**	**-0.486**	**-0.789**	0.425	**0.656**
Turb							**0.525**	-	-	-	-	-	-	**-0.615**	-
Chl *a*								-	-0.391	-	-	-	-	**-0.662**	-
NH_4									**0.611**	**0.879**	-	**0.53**	-	-	-
NO_2+NO_3										**0.865**	-	**0.774**	-	-	-
DIN												**0.695**	-	-	-
PO_4^{3-}												**-0.648**	-0.346	-	0.437

Spearman's Rank Correlation for environmental parameters and nutrient data for the seasonal study (total dataset) (continued). Significance between values are given by a significance level ***p ≤ 0.01*** *in bold and p ≤ 0.05 in standard type, values without any statistical significance are indicated by a dashed line, (N = 38) for all data except DO and pH, where (N = 25).*

	P^B_{max}	α^B	E_k	*In situ* T	S	Turb	Chl *a*	NH_4	NO_2 $+NO_3$	DIN	PO_4^{3-}	N:P	$Si(OH)_3$	DO	pH
N:P													0.392	-	**-0.639**
$Si(OH)_3$														**-0.584**	**-0.696**
DO															**0.548**

Spearman's Rank Correlation for meteorological and hydrological parameters for the seasonal study. Significance between values are given by a significance level ***p ≤ 0.01*** *in bold and p ≤ 0.05 in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, (N = 38) for all data except DO and pH, where (N = 25).*

	PAR	PAR_0	Air T	Wind Speed	Wind Direction	JR	WR	WR Dischg	Precip	ITL	MTL	Tide In/Out
PP	**0.487**	**0.360**	**0.787**	-	-	-	-	-	-	**0.725**	**0.734**	-
P^B_{max}	-	-	0.359	-	-	-	-	-	-	**0.417**	**0.441**	-
α^B	**-0.479**	-	-	-	-	-	-	-	-0.332	-	-	-
E_k	**0.533**	0.359	**0.675**	-0.368	-	-	-	-	-	**0.574**	**0.641**	-
In situ T	**0.645**	**0.441**	**0.884**	-	-	-	-	-	-	**0.769**	**0.739**	-
S	-0.371	-	-0.386	-	-	-	-	-	-	**-0.440**	**-0.417**	-
Turb	**0.463**	-	**0.466**	-	-	-	-	-	-	-	-	-
Chl *a*	0.328	-	**0.625**	-	-	-	-	-	-	0.382	**0.470**	-
NH_4	-0.345	-0.403	-0.341	-	-	0.355	-	-	-	-0.335	-0.344	-
NO_2+NO_3	-	-	-	-	-	-	-	-	-	-	-	-
DIN	-0.361	-0.382	-0.395	-						-0.347	-0.389	-
PO_4^{3-}	-	-	-	-	-0.325	-	-	-	-	-	-	-
N:P	-	-	-	-	-	-	-	-	-	-	-	-
$Si(OH)_3$	-	-	0.330	-	-	-	-	-	-	**0.482**	**0.479**	-
DO	-		**-0.718**	-0.474	-	-	**0.659**	**0.667**	**0.698**	**-0.546**	**-0.522**	-
pH	-	-	-	-	-	-	-	-	-	-	-	-
PAR	-	**0.822**	**0.719**	-	-	-	-	-	-	**0.741**	**0.663**	-
PAR_0	-	-	**0.538**	-	-0.321	-	-	-	-	**0.735**	**0.658**	-

*Spearman's Rank Correlation for meteorological and hydrological parameters for the seasonal study (continued). Significance between values are given by a significance level **p ≤ 0.01** in bold and p ≤ 0.05 in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, (N = 38) for all data except DO and pH, where (N = 25).*

	PAR	PAR_0	Air T	Wind Speed	Wind Direction	JR	WR	WR Dischg	Precip	ITL	MTL	Tide In/Out
Air T	-	-	-	-	-	-	-	-	-0.378	**0.776**	**0.745**	-
Wind Speed	-	-	-	-	-0.401	-	-0.399	**-0.464**	-0.389	-	-	-
Wind Direction	-	-	-	-	-	-	-	-	-	-	-	-
JR Gauge ht	-	-	-	-	-	-	-	-	**0.516**	-	-	-
WR Gauge ht	-	-	-	-	-	-	-	**0.963**	**0.818**	-	-	**-0.590**
WR Discharge	-	-	-	-	-	-	-	-	**0.815**	-	-	**-0.445**
Precipitation	-	-	-	-	-	-	-	-	-	-	-	-
Inst TL	-	-	-	-	-	-	-	-	-	-	**0.957**	-
MTL	-	-	-	-	-	-	-	-	-	-	-	-
Tide	-	-	-	-	-	-	-	-	-	-	-	-

Spearman's Rank Correlation for environmental parameters and nutrient data for the week long study. Significance between values are given by a significance level ***$p \leq 0.01$*** *in bold and $p \leq 0.05$ in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, ($N = 28$) for all data except DO and pH, where ($N = 25$).*

	In situ T	S	Turb	Chl *a*	NH_4	$NO_2 + NO_3$	DIN	PO_4^{3-}	N:P	$Si(OH)_3$	DO	pH
PP	-	-	-	-	-	-	-	-	-	-	-	-
P^B_{max}	-	-0.453	-	-	-	-	-	-	**0.527**	0.449	-	**-0.529**
α^B	-	-0.420	-	-	-	**0.503**	0.386		**0.608**	0.403	-	**-0.547**
E_k	-	0.448	-	-	-	-	-	**0.608**	-0.399	-0.377	-	-
In situ T		-	-	0.401	-	0.377	-	-	-	-	**-0.663**	-0.472
Salinity			-	**-0.763**	-	-	-	**0.849**	**-0.848**	**-0.799**	-	**0.576**
Turbidity				-	-	-	-	-0.412	0.462	0.436	-	-0.496
Chl *a*					-	-	-	**-0.677**	**0.732**	**0.698**	-	**-0.613**
NH_4						**0.676**	**0.976**	-	0.408	-	**-0.505**	-0.505
$NO_2 + NO_3$							**0.785**	-	**0.514**	-	-0.419	-0.482
DIN									0.473	-	**-0.499**	**-0.538**
PO_4^{3-}									**-0.829**	**-0.674**	-	-
N:P										**0.697**		**-0.658**
$Si(OH)_3$											-	**-0.665**
DO												**0.627**

Spearman's Rank Correlation for meteorological and hydrological data for the week long study (continued). Significance between values are given by a significance level ***$p \leq 0.01$*** *in bold and $p \leq 0.05$ in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, (N = 28) for all data except DO and pH, where (N = 25).*

	PAR	PAR_0	Air T	Wind Speed	Wind Dir	JR	WR	WR Dischg	Precip	ITL	MTL	Tide In/Out
PP	**0.678**	-	-	-	-	**-0.638**	-	-	-	-	-	-
P^B_{max}	-0.404	-	-	-	-	-	-	-	**-0.598**	-	-	-
α^B	-	-	-	-	-	-	-	-	**-0.537**	-	-	-
E_k	-	-	0.412	-	**0.566**	-	-	**0.492**	-	-0.396	-0.467	-
In situ T	-	**0.483**	-	-	-	**0.920**	**0.837**	-	-0.470	**-0.642**	-	-
Salinity	**0.595**	-	-	-	0.418	-	-	-	**0.878**	-	-	-
Turbidity	-	-0.426	-	-	-	-	-	-	-	-	-	-
Chl *a*	-0.428	-0.417	-	-	-	-	-	-	**-0.724**	-	-	-
NH_4	-	-	-	-	-	-	**0.812**	**0.532**	-	-0.430	**-0.564**	-
NO_2+NO_3	-	-	-	-	-	-	-	**0.588**	-	**-0.521**	**-0.521**	-
DIN	-	-	-	-	-	-	**0.767**	**0.559**	-	-0.478	**-0.586**	-
PO_4^{3-}	**0.583**	-	**0.479**	-	**0.640**	-	-	-	**0.697**	-	-	-
N:P	**-0.660**	-	-	-	-0.435	-	-	-	**-0.802**	-	-	-
$Si(OH)_3$	**-0.540**	-	-	-	-	-	-	-	**-0.832**	-	-	-
DO	-	0.456	-	-	-	-	**-0.758**	**-0.727**	-	0.437	**0.650**	-
pH	**0.659**	0.417	-	-	-	-	-	-0.515	**0.721**	-	**0.525**	-
PAR	-	**0.561**	-	-	-	-	-	-	**0.481**	-	-	-
PAR_0	**0.561**	-	-	-	-	-	-	-	-	-	-	-

Spearman's Rank Correlation for meteorological and hydrological data for the week long study (continued). Significance between values are given by a significance level ***$p \leq 0.01$*** *in bold and $p \leq 0.05$ in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, (N = 28) for all data except DO and pH, where (N = 25).*

	PAR	PAR_0	Air T	Wind Speed	Wind Dir	JR	WR	WR Dischg	Precip	ITL	MTL	Tide In/Out
Air T	-	-	-	-	**0.608**	-	0.629	**0.669**	-	**-0.791**	**-0.726**	-
Wind Speed	-	-	-	-	-	-	-	-	-	-	-	-
Wind Dir	-	-	**0.608**	-	-	-	-	0.432	-	**-0.617**	-0.455	-
JR	-	-	-	-	-	-	-	-	-	-	-	-
WR	-	-	0.629	-	-	-	-	**0.963**	-	-0.604	**-0.764**	-
WR Dis	-	-	**0.669**	-	0.432	-	**0.963**	-	-	**-0.721**	**-0.847**	-
Precip	**0.481**	-	-	-	-	-	-	-	-	-	-	-
Inst TL	-	-	**-0.791**	-	**-0.617**	-	-0.604	**-0.721**	-	-	**0.901**	-
MTL	-	-	**-0.726**	-	-0.455	-	**-0.764**	**-0.847**	-	**0.901**	-	-

Spearman's Rank Correlation for environmental parameters and nutrient data for the diurnal study. Significance between values are given by a significance level ***$p \leq 0.01$*** *in bold and $p \leq 0.05$ in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, (N = 12).*

	P^B_{max}	α^B	E_k	*In situ* T	S	Turb	Chl *a*	NH_4	NO_2 $+NO_3$	DIN	PO_4^{3-}	N:P	$Si(OH)_3$	DO
PP	0.886	-	-	-	-	-	-	-	-	-	-	-	-	-
P^B_{max}		-	-	-	-	-	-	-	-	-	-	-	-	-
α^B			- **0.797**	-	**-0.713**		-	-	-	-			-	-
E_k				0.664				-	-	-			-	-
In situ T					-	-	-	-	-	-	-	-	-	-
Salinity						-	**-0.734**	-	-	-	-	-	-	-
Turb							-	-	-	0.587	-	0.650	-	- 0.678
Chl *a*								-	-	-	-	-	-	-
NH_4									-	**0.944**	-	0.706	-	-
NO_2 $+NO_3$											-0.636	**0.713**	**0.797**	-
DIN												**0.804**	-	-
PO_4^{3-}												**-0.804**	-0.699	-
N:P													0.685	-
$Si(OH)_3$														-
DO														

Spearman's Rank Correlation for meteorological and hydrological data for the diurnal study (continued). Significance between values are given by a significance level **$p \leq 0.01$** *in bold and $p \leq 0.05$ in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, (N = 12).*

	PAR	PAR_0	Air T	Wind Speed	Wind Dir	JR	WR	WR Dischg	Precip	ITL	MTL	Tide In/Out
PP	-	0.829	-	-	-	-	-	-	-	-	-	-
P^B_{max}	0.65	**0.763**	-	-	-	-	-	-	-	-	-	-
α^B	-	-	-	-0.664	-	-	-	-	-0.651	0.581	-	-
E_k	-	0.608	0.604	0.65	-	-	-	-	0.579	-0.624	-	-
In situ T	-	-	**0.903**	**0.848**	**0.844**	-	-	-	**0.858**	**-0.918**	-	-
Salinity	-	-	-	-	-	-	-	-	-	-	-	-
Turbidity	-	-	-	-	-	-	-	-	-	-	-	-
Chl *a*	-	-	-	-	-	-	-	-	-	-	-	-
NH_4	-	-	-	-	-	-	-	-	-	-	-	-
$NO_2 + NO_3$	-	-	-	-	-	-	-	-	-	-	-	-
DIN	-	-	-	-	-	-	-	-	-	-	-	-
PO_4^{3-}	-	-	-	-	-	-	-	-	-	-	-	-
N:P	-	-	-	-	-	-	-	-	-	-	-	-
$Si(OH)_3$	-	-	-	-	-	-	-	-	-	-	-	-
DO	-	-	-	-	-	-	-	-	-	-	-	-
pH	**-0.878**	**-0.878**	**0.873**	-	**0.873**	-	-	-	**0.951**	**-0.878**	-	-
PAR	-	**0.943**	-	-	-	-	-	-	-	-	-	-
PAR_0	-	-	-	-	-	-	-	-	-	-	-	-

Spearman's Rank Correlation for meteorological and hydrological data for the diurnal study (continued). Significance between values are given by a significance level ***p ≤ 0.01*** *in bold and p ≤ 0.05 in standard type. Values without any statistical significance are indicated by a dashed line (-). Only significant correlations were presented, (N = 12).*

	PAR	PAR_0	Air T	Wind Speed	Wind Dir	JR	WR	WR Dischg	Precip	ITL	MTL	Tide In/Out
Air T	-	-	-	**0.883**	**0.939**	-	-	-	**0.889**	**-0.955**	-	-
Wind Speed	-	-	-	-	**0.765**	-	-	-	**0.875**	**-0.841**	-	-
Wind Direction	-	-	-	-	-	-	-	-	**0.834**	**-0.955**	-	-
JR Gauge ht	-	-	-	-	-	-	-	-	-	-	-	-
WR Gauge ht	-	-	-	-	-	-	-	-	-	-	-	-
WR Discharge	-	-	-	-	-	-	-	-	-	-	-	-
Precipitation	-	-	-	-	-	-	-	-	-	**-0.891**	-	-
Inst TL	-	-	-	-	-	-	-	-	-	-	-	-
MTL	-	-	-	-	-	-	-	-	-	-	-	-

APPENDIX B

SEASONAL PARAMETERS

Photosynthesis-irradiance parameters measured during the seasonal study. Photosynthetic parameters with standard error (SE) are given. Units are as follows: P^B_{max} *(g C (g Chl)*$^{-1}$ *h*$^{-1}$*),* α^B *and* β^B *(g C (g Chl)*$^{-1}$ *h*$^{-1}$ *(μmol photon m*$^{-2}$ *s*$^{-1}$*)*$^{-1}$*), and* E_k *(μmol photon m*$^{-2}$ *s*$^{-1}$*). Missing data is indicated by a dash (-).*

Tide	Date	Local Time	Station	P^B_{max}	SE	α^B	SE	β^B	SE	E_k	SE
Outgoing	7/18/2010	9:41	1	13.752	5.579	0.031	0.003	0.004	0.006	437.350	181.428
		10:05	2	12.466	2.268	0.025	0.001	0.003	0.002	495.496	93.592
		10:27	3	8.141	0.535	0.013	0.001	-	-	623.529	0.001
	7/19/2010	9:29	4	22.837	11.124	0.045	0.003	0.011	0.013	504.496	247.641
		10:05	5	35.796	6.361	0.072	0.004	0.008	0.005	494.882	91.472
		10:23	6	9.140	0.599	0.015	0.001	-	-	626.721	0.001
			7	-	-	-	-	-	-	-	-
Incoming	8/23/2010	8:58	1	11.148	2.662	0.026	0.002	0.001	0.002	431.674	110.987
		9:19	2	13.410	5.145	0.029	0.002	0.004	0.005	454.760	177.393
		9:37	3	10.538	2.742	0.025	0.002	0.003	0.002	423.615	115.640
	8/24/2010	9:55	4	6.373	2.424	0.017	0.002	0.003	0.003	369.491	145.328
		10:40	5	16.277	13.127	0.047	0.013	0.002	0.011	346.844	296.553
		10:06	6	12.957	21.604	0.029	0.002	0.020	0.052	448.980	749.103
		11:35	7	0.366	0.049	0.001	0.000	0.000	0.000	286.029	43.967

Photosynthesis-irradiance parameters measured during the seasonal study (continued). Photosynthetic parameters with standard error (SE) are given. Units are as follows: P^{B}_{max} (g C (g Chl)$^{-1}$ h^{-1}), α^{B} and β^{B} (g C (g Chl)$^{-1}$h^{-1} (µmol photon m^{-2} s^{-1})$^{-1}$), and E_k (µmol photon m^{-2} s^{-1}). Missing data is indicated by a dash (-).

Tide	Date	Local Time	Station	P^{B}_{max}	SE	α^{B}	SE	β^{B}	SE	E_k	SE
Incoming	9/21/2010	10:06	1	14.964	1.656	0.052	0.005	0.000	0.001	285.103	40.847
		10:28	2	10.735	1.671	0.029	0.002	0.001	0.001	369.559	60.860
		10:40	3	10.351	2.107	0.021	0.001	0.001	0.001	485.159	104.168
	9/22/2010	9:15	4	13.222	1.519	0.033	0.002	0.001	0.001	397.902	52.018
		10:12	5	13.807	14.378	0.031	0.002	0.011	0.024	445.200	464.362
		10:27	6	10.376	1.939	0.024	0.002	0.001	0.001	428.771	84.788
		9:32	7	15.335	2.452	0.036	0.002	0.004	0.002	431.826	72.230
Outgoing	10/27/2010	8:53	1	9.350	2.500	0.025	0.004	0.000	0.002	366.973	116.093
		9:20	2	7.755	0.649	0.034	0.008	-	-	229.322	0.008
		9:38	3	11.625	1.571	0.031	0.002	0.002	0.001	379.627	56.721
	10/28/2010	9:45	4	15.480	3.418	0.081	0.017	0.003	0.004	190.637	57.915
		10:10	5	5.361	1.171	0.028	0.003	0.004	0.002	191.825	46.590
		10:45	6	5.927	0.934	0.028	0.003	0.001	0.001	209.206	38.982
			7	-	-	-	-	-	-	-	-
Incoming	11/18/2010	9:35	1	10.004	0.676	0.027	0.005	-	-	366.975	0.005
		10:00	2	10.132	1.104	0.029	0.002	0.000	0.001	352.478	44.209
		10:15	3	8.478	0.627	0.027	0.002	0.000	0.000	312.914	29.240
	11/19/2010	9:45	4	3.770	0.777	0.013	0.003	0.000	0.000	285.670	81.634
		10:15	5	7.364	1.421	0.024	0.002	0.001	0.001	304.486	61.717
		10:45	6	8.704	0.240	0.028	0.002	-	-	310.204	0.002
			7	-	-	-	-	-	-	-	-

Photosynthesis-irradiance parameters measured during the seasonal study (continued). Photosynthetic parameters with standard error (SE) are given. Units are as follows: P^B_{max} (g C (g Chl)$^{-1}$ h^{-1}), α^B and β^B (g C (g Chl)$^{-1}$h^{-1} (µmol photon m^{-2} s^{-1})$^{-1}$), and E_k (µmol photon m^{-2} s^{-1}). Missing data is indicated by a dash (-).

Tide	Date	Local Time	Station	P^B_{max}	SE	α^B	SE	β^B	SE	E_k	SE
Incoming	12/16/2010	9:15	1	8.285	0.949	0.033	0.011	-	-	252.473	0.011
		9:25	2	10.865	1.933	0.029	0.002	0.001	0.001	373.562	71.096
		10:00	3	9.020	0.932	0.024	0.001	0.001	0.001	379.266	44.711
	12/17/2010	9:00	4	6.675	0.682	0.042	0.016	-	-	157.396	0.016
		9:25	5	10.893	1.965	0.036	0.002	0.002	0.002	301.894	57.085
		9:50	6	11.858	0.342	0.035	0.002	-	-	339.169	0.002
			7	-	-	-	-	-	-	-	-

Values for nutrients for the seasonal study. Units are given in µM except for N:P, which is unitless. Missing data is indicated by a dash (-).

Date	Station	NH_4^+	NO_2^-	NO_3^-	$NO_2^- + NO_3^-$	DIN	PO_4^{3-}	N:P	$Si(OH)_4$
7/18/2010	1	0.20	0.01	0.16	0.17	0.36	1.07	0.34	88.96
	2	2.92	0.08	1.32	1.41	4.32	0.15	29.61	91.02
	3	0.14	0.04	0.06	0.10	0.24	0.83	0.29	64.46
7/19/2010	4	1.48	0.07	0.78	0.85	2.33	0.24	9.71	106.97
	5	3.41	0.11	1.30	1.41	4.81	0.86	5.58	90.25
	6	0.16	0.04	-0.02	0.02	0.18	1.07	0.17	75.57
	7	-	-	-	-	-	-	-	-
8/23/2010	1	3.24	0.08	0.25	0.33	3.57	0.28	12.80	95.12
	2	1.27	0.09	0.00	0.09	1.36	0.63	2.15	86.73
	3	0.93	0.10	0.20	0.30	1.22	1.85	0.66	69.78
8/24/2010	4	1.17	0.07	1.64	1.71	2.88	0.11	25.50	107.96
	5	3.62	0.00	0.72	0.73	4.34	1.30	3.33	96.17
	6	2.69	0.02	0.55	0.56	3.25	1.33	2.44	73.32
	7	1.75	0.08	3.09	3.17	4.92	0.04	117.06	59.12
9/21/2010	1	0.51	0.02	0.50	0.52	1.03	0.10	9.90	92.76
	2	0.50	0.02	0.43	0.45	0.95	0.08	11.74	95.76
	3	0.05	0.04	0.32	0.37	0.42	1.39	0.30	88.65
9/22/2010	4	0.52	0.06	0.72	0.78	1.30	0.36	3.65	101.10
	5	6.24	0.22	2.24	2.46	8.70	1.67	5.20	93.42
	6	0.57	0.02	-0.05	-0.02	0.55	0.59	0.92	70.83
	7	0.71	0.02	0.19	0.21	0.92	0.10	9.46	92.18
10/27/2010	1	1.16	0.07	0.34	0.41	1.57	0.63	2.51	70.85

Values for nutrients for the seasonal study (continued). Units are given in μM except for N:P, which is unitless. Missing data are indicated by a dash (-).

Date	Station	NH_4^+	NO_2^-	NO_3^-	$NO_2^- + NO_3^-$	DIN	PO_4^{3-}	N:P	$Si(OH)_4$
	2	1.18	0.03	0.17	0.20	1.37	0.77	1.78	63.91
	3	2.41	0.05	0.22	0.27	2.68	0.75	3.59	50.07
10/28/2010	4	3.17	0.03	1.16	1.19	4.35	0.20	21.98	114.58
	5	8.97	0.15	1.28	1.43	10.40	1.31	7.92	69.25
	6	3.44	0.07	0.69	0.76	4.20	0.80	5.24	31.54
	7	-	-	-	-	-	-	-	-
11/18/2010	1	2.77	0.15	6.26	6.40	9.17	0.58	15.79	68.11
	2	0.95	0.11	4.05	4.16	5.11	0.49	10.39	62.87
	3	0.90	0.04	0.44	0.48	1.39	0.66	2.11	54.19
11/19/2010	4	2.79	0.02	1.26	1.28	4.06	0.28	14.56	145.01
	5	3.68	0.11	1.09	1.20	4.88	1.10	4.45	46.03
	6	0.85	0.05	0.21	0.26	1.11	0.69	1.61	36.81
	7	-	-	-	-	-	-	-	-
12/16/2010	1	1.92	0.14	8.34	8.48	10.39	0.77	13.50	54.44
	2	0.62	0.06	0.24	0.29	0.91	0.72	1.27	48.21
	3	1.19	0.09	0.40	0.49	1.67	0.71	2.34	48.05
12/17/2010	4	1.71	0.09	1.04	1.14	2.84	0.20	14.58	156.14
	5	1.17	0.04	0.30	0.33	1.50	0.56	2.70	45.21
	6	1.49	0.09	0.44	0.53	2.02	0.69	2.92	40.11
	7	-	-	-	-	-	-	-	-

Environmental data for the seasonal study. Values (units) for chlorophyll a (mg m^{-3}), turbidity (NTU), salinity (unitless), DO (mg L^{-1}), and pH (unitless) are presented. Missing data is indicated by a dash (-).

Tide	Date	Station	Chl *a*	Turbidity	*in situ* T	S	DO	pH
Outgoing	7/18/2010	1	30.12	10.72	30.75	4.81	-	-
		2	25.12	13.87	30.63	4.71	-	-
		3	18.94	24.93	29.09	9.45	-	-
	7/19/2010	4	14.87	10.47	29.86	2.27	-	-
		5	11.57	5.67	29.90	8.04	-	-
		6	23.76	12.14	30.27	10.01	-	-
		7	-	-	-	-	-	-
Incoming	8/23/2010	1	42.45	12.93	28.05	7.56	-	-
		2	47.89	19.87	28.06	10.29	-	-
		3	20.53	18.06	27.93	16.64	-	-
	8/24/2010	4	4.29	23.54	28.68	1.17	-	-
		5	18.91	21.05	29.07	8.12	-	-
		6	33.21	9.98	29.41	15.14	-	-
		7	15.55	19.92	30.49	1.04	-	-
Incoming	9/21/2010	1	20.83	10.20	26.96	8.20	5.93	7.49
		2	19.35	10.06	29.16	8.03	7.66	6.87
		3	21.16	12.30	29.37	14.21	7.06	8.02
	9/22/2010	4	19.87	8.42	29.23	9.55	4.73	7.11
		5	13.91	16.94	29.18	14.05	4.35	7.44
		6	35.53	37.71	29.18	16.93	7.74	8.03
		7	18.18	12.35	29.48	10.15	4.82	7.23

Environmental data for the seasonal study (continued). Values (units) for chlorophyll a (mg m^{-3}), turbidity (NTU), salinity (unitless), DO (mg L^{-1}), and pH (unitless) are presented. Missing data is indicated by a dash (-).

Tide	Date	Station	Chl *a*	Turbidity	*in situ* T	S	DO	pH
Outgoing	10/27/2010	1	20.00	12.75	25.77	17.56	6.21	7.60
		2	18.02	8.35	26.00	17.14	7.81	6.83
		3	19.79	62.50	26.13	17.60	6.97	7.94
	10/28/2010	4	12.68	9.27	24.90	10.03	5.33	7.07
		5	21.06	39.71	25.41	17.60	6.33	7.62
		6	33.45	110.94	24.58	17.33	7.14	7.78
		7	-	-	-	-	-	-
Incoming	11/18/2010	1	17.73	5.72	17.62	12.76	8.01	7.62
		2	13.59	4.81	17.40	14.32	8.17	7.74
		3	6.78	14.63	16.71	17.99	8.82	7.91
	11/19/2010	4	4.09	5.92	15.88	3.93	7.81	7.13
		5	4.51	6.49	17.12	19.02	8.44	7.79
		6	6.54	6.28	17.51	19.80	9.32	7.98
		7	-	-	-	-	-	-
Incoming	12/16/2010	1	9.34	2.11	9.12	15.17	10.17	7.78
		2	6.41	2.05	9.76	17.15	10.57	8.07
		3	7.94	25.60	9.51	17.72	10.01	7.96
	12/17/2010	4	3.92	4.39	10.91	4.49	9.74	7.30
		5	5.53	2.42	10.77	17.44	9.96	7.96
		6	5.10	2.25	10.81	19.49	10.36	8.02
		7	-	-	-	-	-	-

Irradiance and meteorlogical data for the seasonal study. Values (units) for E_0, $E_0(z_1)$ and $E_0(z_2)$ (μmol photons m^{-2} s^{-1}), air T (^oC), wind speed (m s^{-1}), wind direction (degrees). Calculated $E_0(z_2)$ values are indicted by an asterisk (*). Missing data is indicated by a dash (-).

Tide	Date	Station	% Sky Cond	E_0	$E_0(z_1)$	$E_0(z_2)$	Air T	Wind Speed	Wind Direction
Outgoing	7/18/2010	1	15	1496.83	600.23	34.41	28.78	2.92	161.54
		2	10	1628.80	611.13	40.37	29.13	3.11	161.58
		3	10	1701.73	701.90	72.50	29.19	4.15	151.13
	7/19/2010	4	55	834.60	325.20	69.20	26.63	2.84	356.48
		5	65	544.83	449.90	89.32*	27.49	3.61	40.99
		6	75	1740.43	792.23	396.20	29.49	4.26	76.66
		7		-	-	-	-	-	-
Incoming	8/23/2010	1	40	874.13	248.40	16.74	25.03	4.02	358.79
		2	30	676.77	305.53	13.23	25.39	2.99	304.67
		3	10	1519.53	583.17	62.04	27.32	4.62	6.03
	8/24/2010	4	0	1909.03	826.77	47.43	26.39	5.65	15.64
		5	0	1615.67	734.43	297.97	27.21	4.04	13.21
		6	0	1424.20	773.03	373.17	28.78	4.30	3.96
		7	0	1835.13	694.23	24.89	28.78	4.14	9.06

Irradiance and meteorlogical data for the seasonal study (continued). Values (units) for E_0, $E_0(z_1)$ and $E_0(z_2)$ (µmol photons m^{-2} s^{-1}), air T (°C), wind speed (m s^{-1}), wind direction (degrees). Calculated $E_0(z_2)$ values are indicted by an asterisk (*). Missing data is indicated by a dash (-).

Tide	Date	Station	% Sky Cond	E_0	$E_0(z_1)$	$E_0(z_2)$	Air T	Wind Speed	Wind Direction
Incoming	9/21/2010	1	0	1345.00	930.03	27.39	27.30	4.19	61.88
		2	0	1549.67	1149.10	83.12	28.76	3.59	53.65
		3	5	1595.00	1058.33	157.88	28.90	4.90	115.00
	9/22/2010	4	30	1212.30	796.80	134.49	28.76	5.44	114.42
		5	35	1439.53	896.60	326.00	28.83	6.91	111.22
		6	30	1669.63	1112.33	179.95	28.96	5.06	128.70
		7	25	1303.43	1038.53	116.05	29.21	6.03	120.13
Outgoing	10/27/2010	1	45	611.97	550.80	109.35*	25.80	3.70	188.00
		2	45	324.70	192.48	38.21*	26.60	4.60	165.00
		3	45	880.97	525.50	104.33*	26.80	4.50	167.00
	10/28/2010	4	10	93.44	64.57	12.82*	23.84	9.04	348.28
		5	10	324.70	192.48	38.21*	21.40	8.40	3.00
		6	10	481.30	271.30	53.86*	20.42	7.94	0.17
		7	-	-	-	-	-	-	-

Irradiance and meteorlogical data for the seasonal study (continued). Values (units) for E_0, $E_0(z_1)$ and $E_0(z_2)$ (µmol photons m^{-2} s^{-1}), air T (^oC), wind speed (m s^{-1}), wind direction (degrees). Calculated $E_0(z_2)$ values are indicted by an asterisk (*). Missing data is indicated by a dash (-).

Tide	Date	Station	% Sky Cond	E_0	$E_0(z_1)$	$E_0(z_2)$	Air T	Wind Speed	Wind Direction
Incoming	11/18/2010	1	100	289.47	158.36	97.58	14.30	2.50	332.00
		2	100	376.34	368.33	182.23	14.80	3.60	336.00
		3	100	409.97	318.70	207.93	15.50	2.20	339.00
	11/19/2010	4	0	809.30	626.57	223.03	11.51	6.04	345.91
		5	0	1182.60	1029.07	494.57	12.59	5.66	7.24
		6	0	1404.73	1123.60	223.07*	14.00	4.10	9.00
		7	-	-	-	-	-	-	-
Incoming	12/16/2010	1	25	742.17	535.83	106.38*	16.25	4.30	180.00
		2	25	668.48	432.88	85.94*	17.57	4.13	201.81
		3	25	990.53	581.47	115.44*	18.68	3.07	184.17
	12/17/2010	4	10	307.83	235.20	46.69*	12.20	5.00	50.00
		5	10	223.93	138.06	27.41*	12.20	5.50	18.00
		6	10	368.68	297.77	59.12*	11.60	4.10	38.00
		7	-	-	-	-	-	-	-

Hydrological data for the seasonal study. Values (units) JR and WR stage height, and MTL (m), WR discharge ($m^{-3}\ s^{-1}$), and precipitation (cm) are given. Missing data is indicated by a dash (-).

Tide	Date	Station	JR Stage ht	WR Stage ht	WR Dischg	Precip	MTL
Outgoing	7/18/2010	1	0.26	1.53	90	0.19	0.52
		2	0.26	1.53	90	0.19	0.52
		3	0.26	1.53	90	0.19	0.52
	7/19/2010	4	0.30	1.56	110	0.19	0.57
		5	0.30	1.56	110	0.19	0.57
		6	0.30	1.56	110	0.19	0.57
		7	-	-	-	-	-
Incoming	8/23/2010	1	0.26	2.23	681	0.49	0.58
		2	0.26	2.23	681	0.49	0.58
		3	0.26	2.23	681	0.49	0.58
	8/24/2010	4	0.36	1.99	438	0.49	0.56
		5	0.36	1.99	438	0.49	0.56
		6	0.36	1.99	438	0.49	0.56
		7	0.36	1.99	438	0.49	0.56
Incoming	9/21/2010	1	0.17	1.50	61	0.00	0.68
		2	0.17	1.50	61	0.00	0.68
		3	0.17	1.50	61	0.00	0.68
	9/22/2010	4	0.21	1.49	58	0.00	0.78
		5	0.21	1.49	58	0.00	0.78
		6	0.21	1.49	58	0.00	0.78

Hydrological data for the seasonal study (continued). Values (units) JR and WR stage height, and MTL (m), WR discharge (m^{-3} s^{-1}), and precipitation (cm) are given. Missing data is indicated by a dash (-).

Tide	Date	Station	JR Stage height	WR Stage height	WR Discharge	Precipitation	MTL
		7	0.21	1.49	40	0.00	0.78
Outgoing	10/27/2010	1	0.31	1.45	40	0.07	0.31
		2	0.31	1.45	40	0.07	0.31
		3	0.31	1.45	39	0.07	0.31
	10/28/2010	4	0.29	1.45	39	0.07	0.09
		5	0.29	1.45	39	0.07	0.09
		6	0.29	1.45	39	0.07	0.09
		7	-	-	-	-	-
Incoming	11/18/2010	1	0.28	1.65	133	0.68	0.17
		2	0.28	1.65	133	0.68	0.17
		3	0.28	1.65	133	0.68	0.17
	11/19/2010	4	0.40	1.60	106	0.68	0.23
		5	0.40	1.60	106	0.68	0.23
		6	0.40	1.60	106	0.68	0.23
		7	-	-	-	-	-
Incoming	12/16/2010	1	0.05	1.59	101	0.03	0.16
		2	0.05	1.59	101	0.03	0.16
		3	0.05	1.59	101	0.03	0.16
	12/17/2010	4	0.08	1.57	93	0.03	0.09
		5	0.08	1.57	93	0.03	0.09
		6	0.08	1.57	93	0.03	0.09
		7	-	-	-	-	-

APPENDIX C

WEEK PARAMETERS

Photosynthesis-irradiance parameters measured during week-long study (10/11/2010 through 10/17/2010). Photosynthetic parameters with standard error (SE) are given. Units are as follows: P^{B}_{max} *(g C (g Chl)$^{-1}$ h^{-1}),* α^{B} *and* β^{B} *(g C (g Chl)$^{-1}$h^{-1})(μmol photon m^{-2} s^{-1})$^{-1}$), and* E_k *(μmol photon m^{-2} s^{-1}). Missing data is indicated by dashes (-).*

Date	Local Time	Station	Depth	P^{B}_{max}	SE	α^{B}	SE	β^{B}	SE	E_k	SE
10/11/2010	9:00	2	Surface	10.892	1.584	0.023	0.002	0.001	0.001	465.918	76.837
			0.5	9.928	3.469	0.024	0.002	0.002	0.003	422.230	150.664
	9:30	3	Surface	14.112	2.144	0.030	0.002	0.001	0.001	470.792	80.572
			0.5	13.672	2.077	0.029	0.002	0.001	0.001	470.793	80.572
10/12/2010	9:12	2	Surface	12.709	1.613	0.030	0.003	0.000	0.001	422.964	68.588
			0.5	12.717	2.861	0.028	0.002	0.000	0.002	451.744	108.213
	9:44	3	Surface	13.733	2.496	0.029	0.003	0.001	0.002	474.187	95.544
			0.5	14.234	0.691	0.028	0.001	-	-	578.901	44.607
10/13/2010	9:00	2	Surface	7.433	0.922	0.026	0.004	0.000	0.000	283.443	55.665
			0.5	6.776	0.763	0.026	0.002	0.000	0.001	264.324	37.172
	9:38	3	Surface	12.465	0.415	0.026	0.002	-	-	454.132	42.861
			0.5	11.313	3.335	0.024	0.002	0.000	0.002	467.068	143.405
10/14/2010	9:15	2	Surface	9.890	0.865	0.035	0.004	0.000	0.000	286.290	38.318
			0.5	7.280	0.765	0.028	0.002	0.000	0.001	255.929	33.580
	9:38	3	Surface	13.046	1.868	0.029	0.003	0.000	0.001	449.169	80.843
			0.5	24.093	5.698	0.060	0.004	0.002	0.004	400.274	99.268
10/15/2010	9:00	2	Surface	6.655	0.627	0.026	0.003	0.000	0.000	254.500	40.331
			0.5	5.752	0.510	0.027	0.003	0.000	0.000	209.208	27.445

Photosynthesis-irradiance parameters measured during week-long study (10/11/2010 through 10/17/2010) (continued). Photosynthetic parameters with standard error (SE) are given. Units are as follows: P^{B}_{max} *(g C (g Chl)*$^{-1}$ *h*$^{-1}$*),* α^{B} *and* β^{B} *(g C (g Chl)*$^{-1}$*h*$^{-1}$*)(μmol photon m*$^{-2}$ *s*$^{-1}$*)*$^{-1}$*), and* E_k *(μmol photon m*$^{-2}$ *s*$^{-1}$*). Missing data is indicated by dashes (-).*

Date	Local Time	Station	Depth	P^{B}_{max}	SE	α^{B}	SE	β^{B}	SE	E_k	SE
	9:35	3	Surface	11.134	1.216	0.025	0.002	0.000	0.001	438.567	62.668
			0.5	8.903	0.322	0.021	0.001	-	-	379.044	30.648
10/16/2010	9:05	2	Surface	6.500	0.469	0.029	0.003	0.000	0.000	221.848	27.857
			0.5	5.991	0.500	0.027	0.002	0.000	0.000	218.527	24.948
	9:40	3	Surface	9.930	1.440	0.022	0.003	0.000	0.001	447.877	84.914
			0.5	7.547	2.412	0.018	0.002	0.001	0.002	409.511	135.217
10/17/2010	9:10	2	Surface	5.213	0.489	0.022	0.003	0.000	0.000	241.506	39.666
			0.5	4.750	0.593	0.021	0.002	0.001	0.001	227.339	34.952
	9:35	3	Surface	10.532	1.581	0.022	0.003	0.000	0.001	480.232	91.756
			0.5	7.845	3.710	0.018	0.002	0.002	0.003	441.775	213.500

Values for nutrients for the seasonal study. Units for all values are measured in µM except for depth (m) and N:P, which is unit less.

Date	Station	Depth	NH_4^+	NO_2^-	NO_3^-	$NO_2^- + NO_3^-$	DIN	PO_4^{3-}	N:P	$Si(OH)_4$
10/11/2010	2	Surface	2.35	0.04	0.22	0.25	2.60	0.20	1.05	95.88
		0.5	0.95	-0.01	0.21	0.20	1.15	0.46	0.46	90.60
	3	Surface	0.98	0.00	0.35	0.35	1.33	0.70	0.50	89.35
		0.5	1.42	0.00	0.26	0.26	1.69	0.53	0.49	92.37
10/12/2010	2	Surface	0.83	-0.01	0.40	0.39	1.21	1.00	0.40	87.87
		0.5	0.76	0.01	0.32	0.34	1.10	0.88	0.37	90.61
	3	Surface	0.79	0.01	0.16	0.16	0.95	0.67	0.23	86.63
		0.5	1.73	0.03	0.28	0.31	2.04	0.40	0.71	102.06
10/13/2010	2	Surface	0.69	-0.01	0.21	0.20	0.89	0.40	0.52	92.28
		0.5	0.87	0.00	0.21	0.21	1.09	0.43	0.49	90.92
	3	Surface	1.76	0.01	0.25	0.25	2.01	0.49	0.50	86.24
		0.5	0.72	-0.01	0.12	0.11	0.83	0.25	0.50	82.43
10/14/2010	2	Surface	1.24	0.01	0.32	0.33	1.57	0.90	0.36	87.59
		0.5	1.12	0.01	0.11	0.12	1.23	0.30	0.38	89.28
	3	Surface	0.76	0.02	0.27	0.29	1.06	0.18	1.49	77.07
		0.5	2.43	0.04	0.45	0.49	2.92	0.31	1.46	77.09
10/15/2010	2	Surface	1.31	0.02	0.28	0.29	1.60	0.20	1.38	63.51
		0.5	0.95	0.02	0.20	0.22	1.17	0.15	1.36	70.74
	3	Surface	0.76	0.02	0.16	0.19	0.95	0.19	0.86	72.98
		0.5	0.39	0.02	0.13	0.15	0.54	0.08	1.65	72.30

Values for nutrients for the seasonal study (continued). Units for all values are measured in µM except for depth (m) and N:P, which is unit less.

Date	Station	Depth	NH_4^+	NO_2^-	NO_3^-	NO_2^- + NO_3^-	DIN	PO_4^{3-}	N:P	$Si(OH)_4$
10/16/2010	2	Surface	0.57	0.02	0.14	0.17	0.74	0.09	1.59	73.99
		0.5	2.65	0.03	0.35	0.38	3.03	0.24	1.47	73.32
	3	Surface	2.36	0.03	0.38	0.41	2.77	0.27	1.42	70.28
		0.5	0.79	0.01	0.20	0.22	1.01	0.14	1.43	69.49
10/17/2010	2	Surface	0.72	0.02	0.16	0.19	0.91	0.12	1.40	72.09
		0.5	0.72	0.03	0.15	0.18	0.90	0.16	0.94	76.56
	3	Surface	0.80	0.02	0.13	0.15	0.95	0.08	1.59	68.41
		0.5	0.67	0.01	0.13	0.14	0.82	0.10	1.29	75.34

Environmental data for the week-long study (10/11/2010 through 10/17/2010). Values (units) for depth (m), chlorophyll a (mg m^{-3}), turbidity (NTU), salinity (unitless), DO (mg L^{-1}), and pH (unitless) are presented. Missing data is indicated by a dash (-).

Date	Station	Depth	Chl *a*	Turbidity	*in situ* T	S	DO	pH
10/11/2010	2	Surface	17.62	9.18	22.90	12.07	7.34	-
		0.5	20.71	10.30	23.76	12.38	7.35	7.94
	3	Surface	18.49	11.35	23.53	12.88	7.16	7.94
		0.5	26.81	29.97	22.75	12.72	7.13	7.89
10/12/2010	2	Surface	17.41	8.43	20.90	12.87	7.53	7.97
		0.5	18.35	11.50	20.41	12.11	7.68	8.07
	3	Surface	15.56	12.87	17.62	12.15	7.93	8.07
		0.5	17.20	16.23	22.44	14.04	6.56	-
10/13/2010	2	Surface	18.97	12.87	23.60	14.11	6.81	7.93
		0.5	18.99	11.81	23.55	12.91	7.12	7.96
	3	Surface	27.56	44.56	22.84	12.67	7.06	7.94
		0.5	18.36	10.21	21.42	14.04	6.90	8.03
10/14/2010	2	Surface	17.27	14.53	20.49	12.24	7.55	8.09
		0.5	16.11	14.04	17.40	13.60	7.39	8.06
	3	Surface	15.49	7.83	22.68	18.16	7.20	-
		0.5	14.97	12.92	23.06	18.44	5.05	7.85
10/15/2010	2	Surface	16.48	9.62	22.93	18.47	7.34	8.13
		0.5	14.91	8.19	22.89	18.45	7.19	8.12
	3	Surface	15.72	8.38	21.14	15.90	7.64	8.13
		0.5	13.54	6.42	21.00	18.80	7.63	8.10

Environmental data for the week-long study (10/11/2010 through 10/17/2010) (continued). Values (units) for depth (m), chlorophyll a (mg m^{-3}), turbidity (NTU), salinity (unitless), DO (mg L^{-1}), and pH (unitless) are presented. Missing data is indicated by a dash (-).

Date	Station	Depth	Chl *a*	Turbidity	*in situ* T	S	DO	pH
10/16/2010	2	Surface	12.21	15.90	16.70	18.60	7.48	8.10
		0.5	16.18	8.63	22.56	18.38	7.04	-
	3	Surface	15.25	14.64	23.05	18.45	5.34	7.94
		0.5	15.86	10.22	22.95	18.50	7.34	8.16
10/17/2010	2	Surface	15.26	8.04	22.93	18.47	7.17	8.16
		0.5	16.35	7.36	21.24	16.80	7.61	8.17
	3	Surface	13.07	6.57	20.97	18.83	7.60	8.17
		0.5	12.90	16.80	15.88	18.68	7.56	8.24

Irradiance and meteorological data for the week-long study. Values (units) for depth (m), E_0 and $E_0(z)$ (µmol photons m^{-2} s^{-1}), air T (^oC), wind speed (m s^{-1}), wind direction (degrees).JR and WR stage height, and MTL (m), WR discharge (m^{-3} s^{-1}), and precipitation (cm) are given. Missing data is indicated by a dash (-).. Missing data is indicated by a dash (-).

Date	Station	Depth	E_0	$E_0(z)$	% Sky Cond	Air T	Wind Speed	Wind Dir	JR Gauge ht	WR Gauge ht	WR Dischg	Precip	MTL
10/11/2010	2	Surf	926.80	572.30	0	21.00	1.30	360.00	0.23	1.45	44.00	0.00	0.14
		0.5	-	202.3	100	22.00	2.90	202.50					
	3	Surf	960.0	742.9	0	19.00	1.60	22.50	0.23	1.45	44.00	0.00	0.14
		0.5	-	338.5	0	16.00	5.80	22.50					
10/12/2010	2	Surf	261.87	169.4	0	18.00	0.60	22.50	0.27	1.46	44.00	0.00	0.18
		0.5	-	53.7	0	18.00	3.10	112.50					
	3	Surf	439.8	316.4	0	19.50	0.10	0.00	0.27	1.46	44.00	0.00	0.18
		0.5	-	160.0	0	21.00	1.30	360.00					
10/13/2010	2	Surf	943.2	639.5	100	22.00	2.90	202.50	0.26	1.45	43.00	0.00	0.31
		0.5	-	216.9	0	19.00	1.60	22.50					
	3	Surf	1132.5	908.3	0	16.00	5.80	22.50	0.26	1.45	43.00	0.00	0.31
		0.5	-	412.4	0	18.00	0.60	22.50					
10/14/2010	2	Surf	925.1	447.1	0	18.00	3.10	112.50	0.12	1.45	42.00	0.00	0.24
		0.5	-	65.5	0	19.50	0.10	0.00					
	3	Surf	1036.9	798.6	0	22.00	1.70	337.50	0.12	1.45	42.00	0.00	0.24
		0.5	-	365.6	100	21.00	2.50	202.50					

Irradiance and meteorological data for the week-long study (continued). Values (units) for depth (m), E_0 and $E_0(z)$ (μmol photons m^{-2} s^{-1}), air T (^oC), wind speed (m s^{-1}), wind direction (degrees).JR and WR stage height, and MTL (m), WR discharge (m^{-3} s^{-1}), and precipitation (cm) are given. Missing data is indicated by a dash (-).. Missing data is indicated by a dash (-).

Date	Station	Depth	E_0	$E_0(z)$	% Sky Cond	Air T	Wind Speed	Wind Dir	JR Gauge ht	WR Gauge ht	WR Dischg	Precip	MTL
10/15/2010	2	Surf	766.6	600.1	0	20.00	1.70	360.00	0.20	1.45	41.00	0.00	0.37
		0.5	-	235.4	0	20.00	3.20	22.50					
	3	Surf	897.0	746.5	0	18.00	1.80	45.00	0.20	1.45	41.00	0.00	0.37
		0.5	-	270.4	0	20.00	2.10	360.00					
10/16/2010	2	Surf	822.5	542.5	0	18.50	1.60	157.50	0.21	1.44	39.00	0.00	0.32
		0.5	-	168.8	0	22.00	1.70	337.50					
	3	Surf	985.4	755.7	100	21.00	2.50	202.50	0.21	1.44	39.00	0.00	0.32
		0.5	-	349.1	0	20.00	1.70	360.00					
10/17/2010	2	Surface	822.5	632.2	0	20.00	3.20	22.50	0.23	1.45	38.00	0.00	0.35
		0.5	-	243.7	0	18.00	1.80	45.00					
	3	Surface	981.0	861.7	0	20.00	2.10	360.00	0.23	1.45	38.00	0.00	0.35
		0.5	-	352.4	0	18.50	1.60	157.50					

APPENDIX D

DIURNAL PARAMETERS

Photosynthesis-irradiance parameters measured during diurnal study on 10/16/2010. Photosynthetic parameters with standard error (SE) are given. Units are as follows: depth (m), P^B_{max} *(g C (g Chl)*$^{-1}$ *h*$^{-1}$*),* α^B *and* β^B *(g C (g Chl)*$^{-1}$*h*$^{-1}$ *)(µmol photon m*$^{-2}$ *s*$^{-1}$*)*$^{-1}$*), and* E_k *(µmol photon m*$^{-2}$ *s*$^{-1}$*). Missing data is indicated by dashes (-).*

Local Time	Station	Depth	P^B_{max}	SE	α^B	SE	β^B	SE	E_k	SE
9:05	2	Surface	6.500	0.469	0.029	0.003	0.000	0.000	221.848	27.857
		0.5	5.991	0.500	0.027	0.002	0.000	0.000	218.527	24.948
9:40	3	Surface	9.930	1.440	0.022	0.003	0.000	0.001	447.877	84.914
		0.5	7.547	2.412	0.018	0.002	0.001	0.002	409.511	135.217
12:03	2	Surface	9.951	0.914	0.027	0.002	0.000	0.000	374.885	49.055
		0.5	9.961	0.280	0.022	0.001			461.128	24.732
12:34	3	Surface	9.216	2.035	0.019	0.002	0.001	0.001	488.797	119.694
		0.5	10.476	6.634	0.017	0.002	0.000	0.004	617.998	397.569
15:00	2	Surface	10.014	1.384	0.022	0.003	0.000	0.001	449.398	80.284
		0.5	7.654	0.194	0.016	0.001			468.315	22.449
15:35	3	Surface	8.750	1.251	0.020	0.002	0.000	0.001	442.006	76.812
		0.5	7.700	1.375	0.016	0.001	0.000	0.001	496.291	95.307

Nutrient data for the diurnal study. Units are given in μM except for depth (m) and N:P, which is unit less.

Time	Station	Depth	NH_4^+	NO_2^-	NO_3^-	$NO_2^- + NO_3^-$	DIN	PO_4^{3-}	N:P	$Si(OH)_4$
9:05	2	Surface	0.20	0.01	0.16	0.17	0.36	1.07	0.34	88.96
		0.5	2.92	0.08	1.32	1.41	4.32	0.15	29.61	91.02
9:40	3	Surface	0.14	0.04	0.06	0.10	0.24	0.83	0.29	64.46
		0.5	1.48	0.07	0.78	0.85	2.33	0.24	9.71	106.97
12:03	2	Surface	3.24	0.08	0.25	0.33	3.57	0.28	12.80	95.12
		0.5	1.27	0.09	0.00	0.09	1.36	0.63	2.15	86.73
12:34	3	Surface	0.93	0.10	0.20	0.30	1.22	1.85	0.66	69.78
		0.5	1.17	0.07	1.64	1.71	2.88	0.11	25.50	107.96
15:00	2	Surface	0.51	0.02	0.50	0.52	1.03	0.10	9.90	92.76
		0.5	0.50	0.02	0.43	0.45	0.95	0.08	11.74	95.76
15:35	3	Surface	0.05	0.04	0.32	0.37	0.42	1.39	0.30	88.65
		0.5	0.52	0.06	0.72	0.78	1.30	0.36	3.65	101.10

Environmental data for the diurnal study (10/16/2010). Values (units) for depth (m), chlorophyll a (mg m^{-3}*), turbidity (NTU), salinity (unitless), DO (mg* L^{-1}*), and pH (unitless) are presented. Missing data is indicated by a dash (-).*

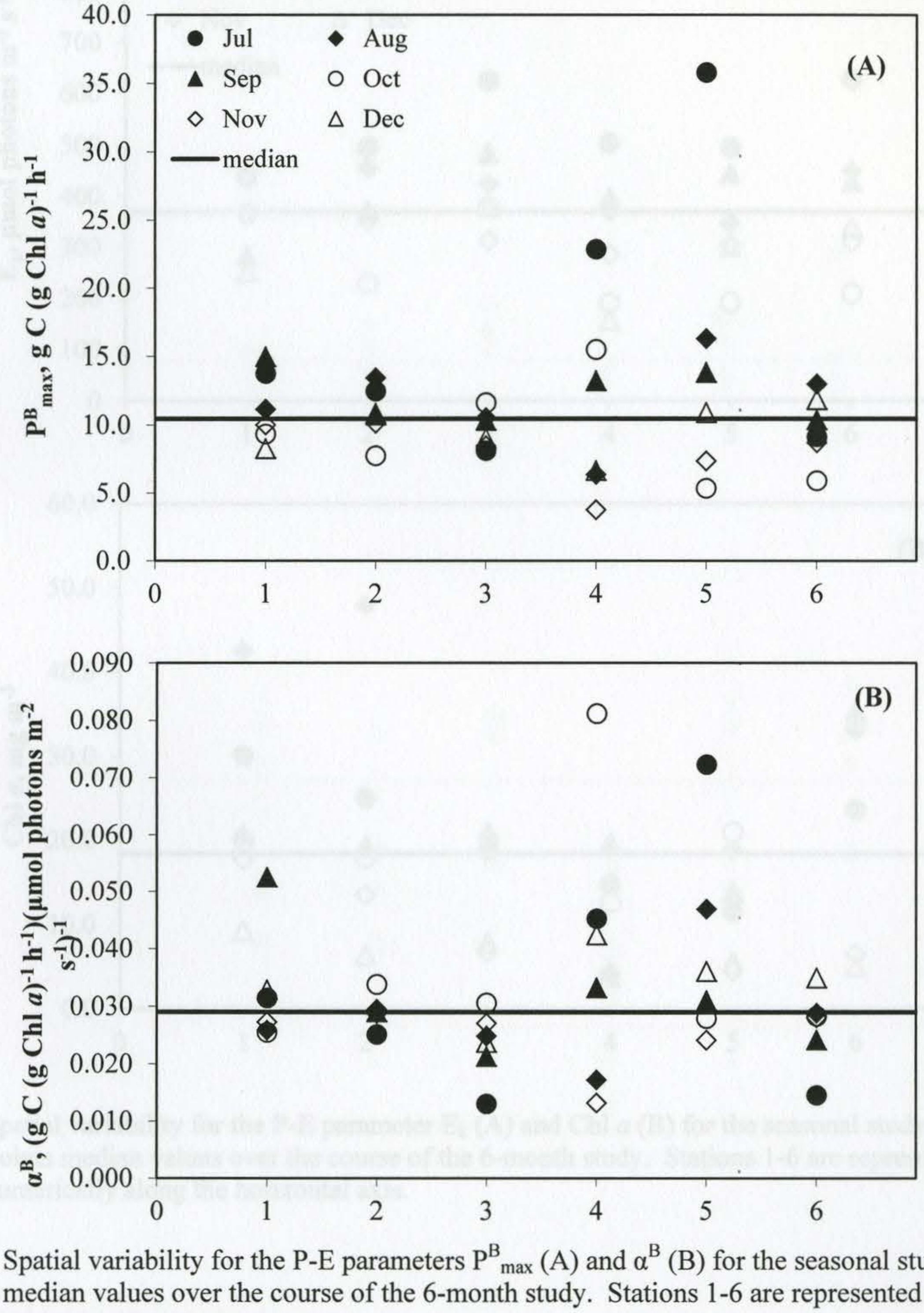
Time	Station	Depth	Chl *a*	Turbidity	*in situ* T	S	DO	pH
9:05	2	Surface	17.62	9.18	20.40	12.07	7.34	-
		0.5	17.20	16.23	20.47	14.04	6.56	-
9:40	3	Surface	15.49	7.83	20.97	18.16	7.20	-
		0.5	16.18	8.63	20.97	18.38	7.04	-
12:03	2	Surface	20.71	10.30	22.09	12.38	7.35	7.94
		0.5	18.97	12.87	21.77	14.11	6.81	7.93
12:34	3	Surface	14.97	12.92	22.68	18.44	5.05	7.85
		0.5	15.25	14.64	22.70	18.45	5.34	7.94
15:00	2	Surface	18.49	11.35	23.70	12.88	7.16	7.94
		0.5	18.99	11.81	22.52	12.91	7.12	7.96
15:35	3	Surface	16.48	9.62	23.31	18.47	7.34	8.13
		0.5	15.86	10.22	23.43	18.50	7.34	8.16

Irradiance and meteorological data for the diurnal study. Values (units) for depth (m), E_0 and $E_0(z)$ (µmol photons m^{-2} s^{-1}), air T (^{o}C), wind speed (m s^{-1}), wind direction (degrees).JR and WR stage height, and MTL (m), WR discharge (m^{-3} s^{-1}), and precipitation (cm) are given. Missing data is indicated by a dash (-). Missing data is indicated by a dash (-).

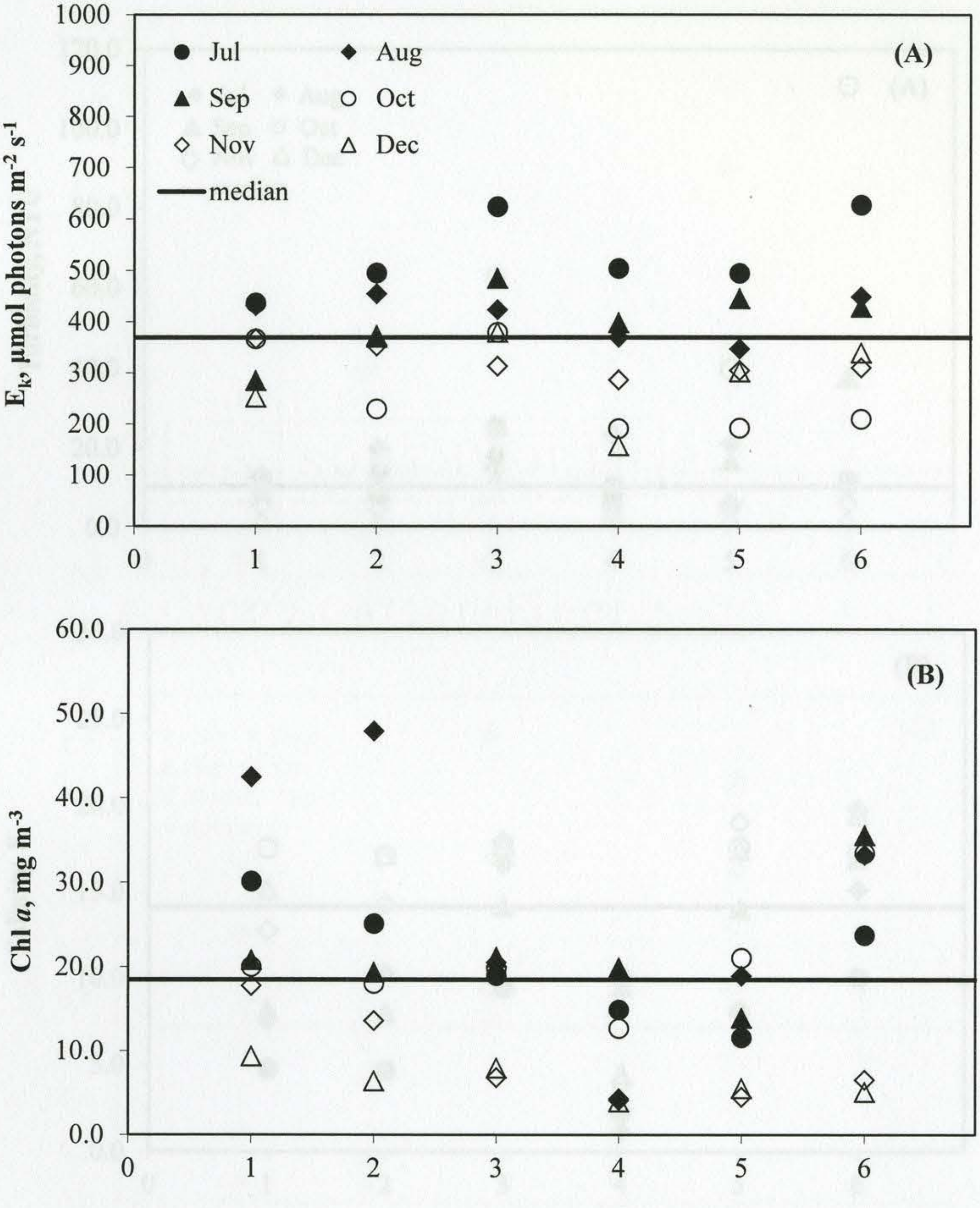
Time	Station	Depth	E_0	$E_0(z)$	%sky Cond	Air T	Wind Speed	Wind Dir	JR Gauge ht	WR Gauge ht	WR Dischg	Precip	ITL
9:05	2	Surf	822.5	542.5	0	17.9	1.5	29	0.21	1.44	1.11	0.00	0.329
		0.5	822.5	168.7	0	17.9	1.5	29	0.21	1.44	1.11	0.00	0.329
9:40	3	Surf	985.4	755.7	0	19.6	2.1	27	0.21	1.44	1.11	0.00	0.329
		0.5	985.4	349.1	0	19.6	2.1	27	0.21	1.44	1.11	0.00	0.329
12:03	2	Surf	1267.3	1234.7	0	21.7	1.8	134	0.21	1.44	1.11	0.00	0.273
		0.5	1267.3	425.4	0	21.7	1.8	134	0.21	1.44	1.11	0.00	0.273
12:34	3	Surf	1550.2	1290.5	0	21.7	3.2	134	0.21	1.44	1.11	0.00	0.245
		0.5	1550.2	738.5	0	21.7	3.2	134	0.21	1.44	1.11	0.00	0.245
15:00	2	Surf	1242.9	903.7	0	23	4.7	154	0.21	1.44	1.11	0.00	0.137
		0.5	1242.9	280.3	0	23	4.7	154	0.21	1.44	1.11	0.00	0.137
15:35	3	Surf	782.4	572.6	0	23	3.5	154	0.21	1.44	1.11	0.00	0.131
		0.5	782.4	316.8	0	23	3.5	154	0.21	1.44	1.11	0.00	0.131

APPENDIX E

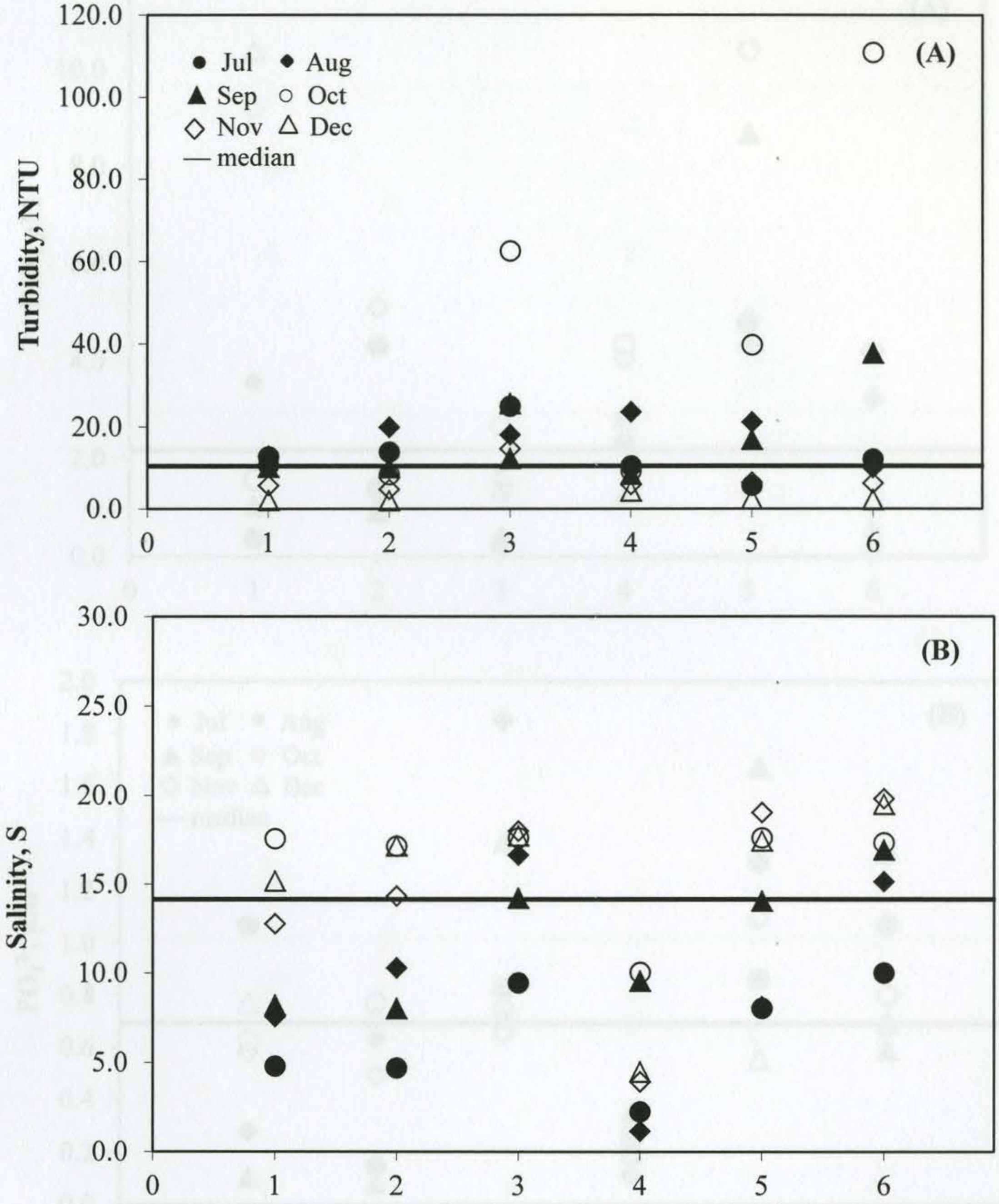
SPATIAL VARIABILITY



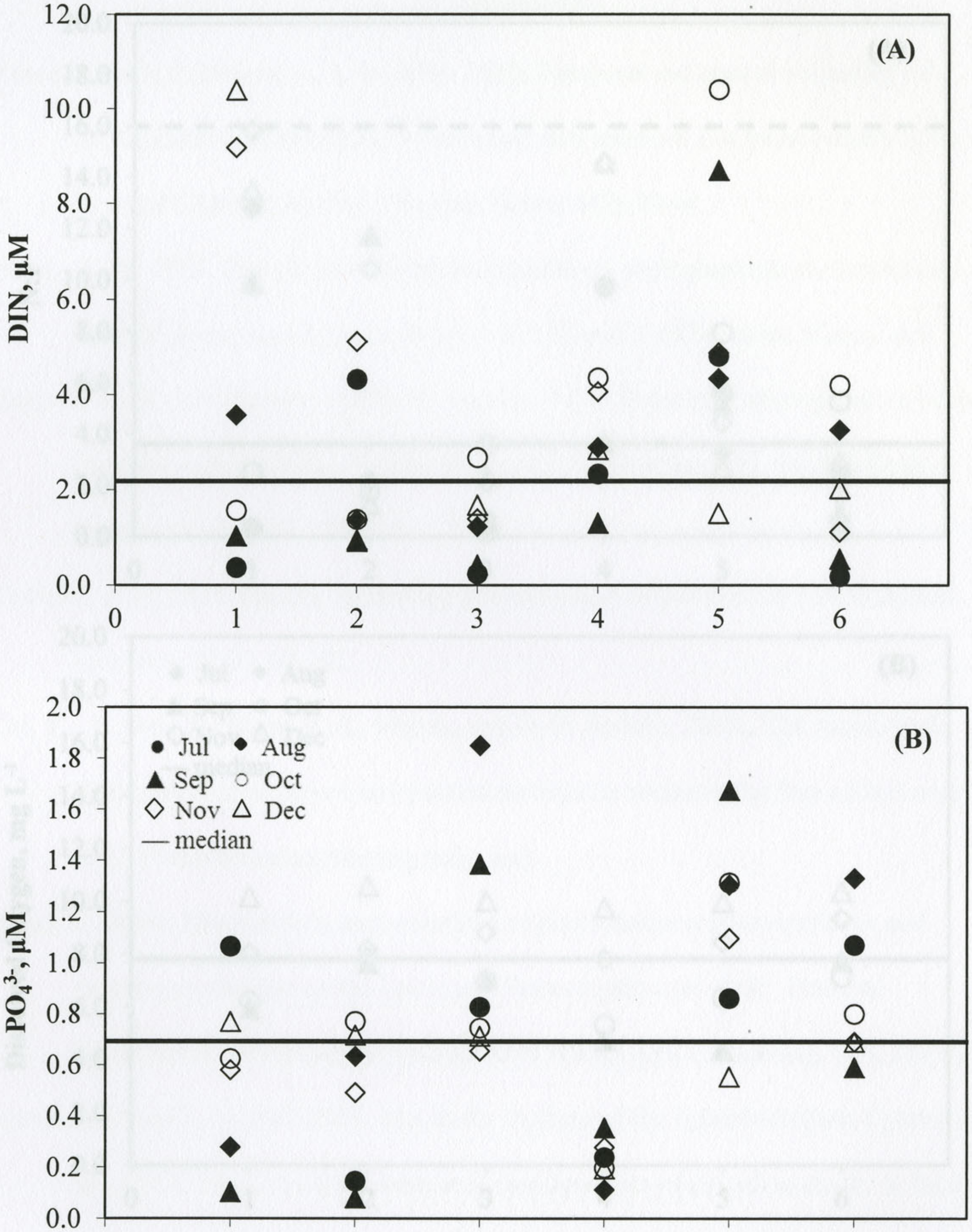
Spatial variability for the P-E parameters P^B_{max} (A) and α^B (B) for the seasonal study. Points median values over the course of the 6-month study. Stations 1-6 are represented numerically along the horizontal axis.



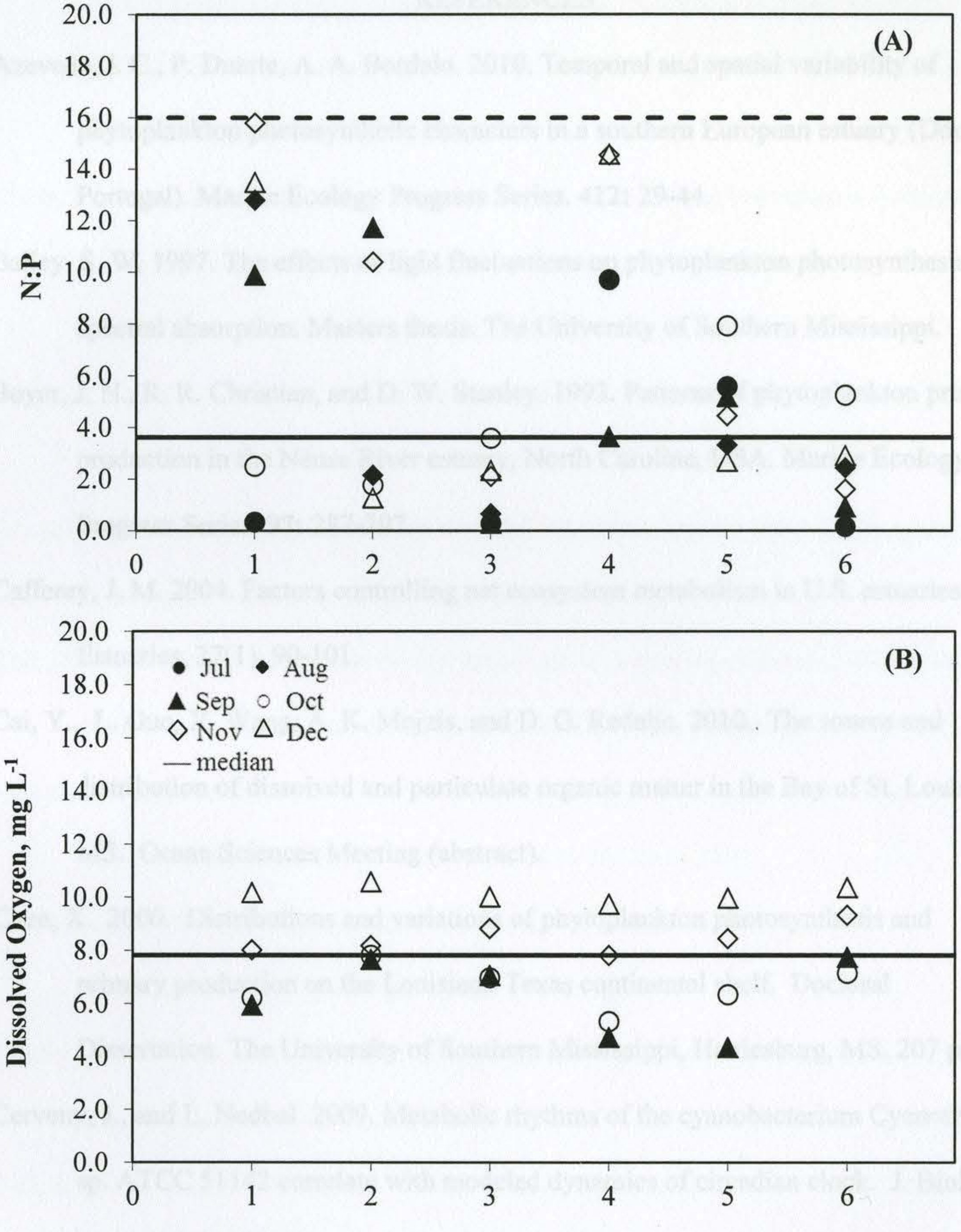
Spatial variability for the P-E parameter E_k (A) and Chl *a* (B) for the seasonal study. Points median values over the course of the 6-month study. Stations 1-6 are represented numerically along the horizontal axis.



Spatial variability for turbidity (A) and salinity (B) for the seasonal study. Points median values over the course of the 6-month study. Stations 1-6 are represented numerically along the horizontal axis.



Spatial variability of DIN (A) and PO$_4^{3-}$ (B) for the seasonal study. Points median values over the course of the 6-month study. Stations 1-6 are represented numerically along the horizontal axis.



Spatial variability of N:P (A) and DO (B) for the seasonal study. Points median values over the course of the 6-month study. Stations 1-6 are represented numerically along the horizontal axis.

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Links

Gulf Coast Research Laboratory tide tables

http://www.usm.edu/gcrl/MStide/StLouisBay_10.pdf

National Oceanic and Atmospheric Administration

http://tidesandcurrents.noaa.gov/data_menu.shtml?stn=8747437%20Bay%20Waveland%20Yacht%20Club,%20MSandtype=Meteorological+Observations

United States Geological Survey

http://waterdata.usgs.gov/nwis/monthly/?search_site_no=02481510andamp;agency_cd=USGSandamp;referred_module=swandamp;format=sites_selection_links

Waveland Weather Center

http://waveland-weather.org