

PHYTOPLANKTON PRODUCTIVITY AND DYNAMICS IN THE CALOOSAHATCHEE
ESTUARY, FLORIDA, USA

By

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To Fisher

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LIST OF ABBREVIATIONS

<i>B</i>	phytoplankton biomass as chlorophyll <i>a</i> (CHL <i>A</i>) concentration
<i>BV</i>	total phytoplankton biovolume concentration
BY	San Carlos Bay
C	carbon
\bar{C}	long-term CHL <i>A</i> mean
°C	degrees celsius
C-43	Caloosahatchee River portion of trans-state canal
CAL	Caloosahatchee Estuary Program
CCHM	Coastal Charlotte Harbor Monitoring Program
CDOM	color dissolved organic matter
CERP	Comprehensive Everglades Restoration Plan
CES	Center for Environmental Studies program
CESWQ	Caloosahatchee Estuary Water Quality Monitoring Program
CF.	confer or compare
CHL <i>A</i>	chlorophyll <i>a</i> , a measure of phytoplankton abundance
C_{ij}	CHL <i>A</i> concentration in year <i>i</i> and month <i>j</i>
CWA	Clean Water Act
D	day
DIN	dissolved inorganic nitrogen
DIP	dissolved inorganic phosphorous
DO	dissolved oxygen
ε	residual component of phytoplankton biomass variability
E^{-1}	e-folding time or water residence time, representing the time needed for a total water mass to reach 37% of its initial water mass
ECP	Everglades Construction Project

E.G.	for example
ENSO	El Niño/Southern Oscillation
ERD	Environmental Research and Design Program
ET AL.	and others
FDEP	Florida Department of Environmental Protection
FEFA	Florida Everglades Forever Act
G	gram
GPP	gross primary productivity
GPP_D	daily gross primary productivity
GPP_Y	annual gross primary productivity
HB	Harbor Branch Project
I.E.	that is
I_0	total daytime surface irradiance or the level of solar radiation just above the surface of the water column
KM	kilometer
K_T	light attenuation coefficient
L	liter
LBOD	luminescent biological oxygen demand
LE	Lower Estuary
M	meter
M	seasonal (monthly) component of phytoplankton biomass variability
ME	Middle Estuary
MEI	Multivariate ENSO Index
MFL	minimum flow and level
MG	milligram
ML	milliliter

MOL	mole
N	total number of observations
NCP	net community productivity
NELAP	National Environmental Laboratory Accreditation program
NH_3	ammonia
NO_2	nitrite
NO_3	nitrate
NPP	net primary productivity
NPP_D	net daily primary productivity
NPP_Y	net annual primary productivity
NTU	nephelometric turbidity units
P	level of significance for statistical hypothesis testing
ρ	Spearman correlation coefficient adjusted for tied ranks
PAR	photosynthetically active radiation
PCU	platinum colbalt units
PSU	practical salinity unit
PSU	photosynthetic unit
PUR	photosynthetically usable radiation
R^2	coefficient of determination
S	second
S	similarity coefficient
S-77	Moore Haven Lock and Dam
S-78	Ortona Lock and Dam
S-79	Franklin Lock and Dam
SAL	salinity

SAV	submerged aquatic vegetation
SD	standard deviation
SI	silica
SRP	soluble reactive phosphorous
SFWMD	South Florida Water Management District
TEMP_W	water temperature
TKN	total Kjeldahl nitrogen
TMDL	total maximum daily load
TN	total nitrogen
TP	total phosphorous
TSN	total soluble nitrogen
TSP	total soluble phosphorous
TSS	total suspended solids
TURB	turbidity
UE	Upper Estuary
USA	United States of America
USACE	United States Army Corps of Engineers
VEC	valuable ecosystem component
W	watt
Y	year
Y	annual component of phytoplankton biomass variability
Z_p	photic depth or the depth where 1% of the incident irradiance is available
Z_w	water depth
Z_s	secchi disk depth

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By

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Urban and agricultural development in and around the Caloosahatchee Estuary on the southwest coast of Florida in the USA has altered the flow and quality of water in the system since the late 1800s. Increasing algal blooms have brought attention to water quality and processes affecting phytoplankton production and biomass accumulation there. The primary objectives of this project were to (1) measure phytoplankton productivity to test a previously developed empirical model that is based on simple measures of phytoplankton biomass and light availability in the photic zone, (2) define the abundance and composition of the phytoplankton community to identify patterns of succession, (3) assess changes in water quality for its direct and indirect effect on the phytoplankton community, primary production, and the model relationship, and (4) apply the phytoplankton productivity model to analyze long-term changes in the estuary's trophic status. Experiments and analyses were conducted using integrated water samples collected monthly between February 2009 and February 2010 at four sites (one in each region of the estuary and bay). Primary production rates, in terms of oxygen evolution, were measured using simulated *in situ* light:dark bottle incubations in a flow-through raceway. Measurements of daily gross primary productivity (GPP_d)

ranged from 90 to 3121 $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ with the overall annual mean estimated at 346 $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. When the estimates from all four sites were pooled there was a strong linear relationship between GPP_d and the 'light•biomass' model predictor ($r^2 = 0.84$, $p < 0.001$). The model tended to overestimate productivity during the dry period when dinoflagellates were dominant and underestimate productivity during the wet period when diatoms were dominant. These deviations in the model were examined as indicators of secondary controls on phytoplankton production in the Caloosahatchee Estuary. The model relationship was then applied over a twenty-five year period using a water quality data set compiled there between January 1986 and December 2010. Estimates of annual gross primary productivity (GPP_y) varied spatially and temporally from oligotrophic (less than 100 $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) to hypertrophic levels (greater than 500 $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), given the influence of both natural and anthropogenic drivers on the productivity potential of the phytoplankton community.

CHAPTER 1 INTRODUCTION

Anthropogenic Influences in Estuaries and Coastal Ecosystems

Estuaries and coastal ecosystems are both historical and modern hotspots for human development due to their provision of food, energy, transportation, recreation, aesthetics, and other valuable resources. The great civilizations of our time have been centered along the seas, and even now, over half of the world's population live and work within two hundred kilometers of a coast, representing a mere 10% of the earth's land surface (Hinrichsen 1999). Despite the constraints on space, coastal population growth is expected to continue in this century. In the United States alone, an increase from 153 million people in 2003 to 165 million people in 2015 is expected within the limits of 673 contiguous coastal counties, constituting only 17% of the total land area of the United States, excluding Alaska (Crossett et al. 2004).

This attraction to, and dependency on, our coastlines does not come without consequences, and these impacts stem from human activities occurring both within and beyond the traditional, political boundaries of these areas. Increases in coastal population densities give rise to human domination and alteration of these ecosystems and their watersheds, making them susceptible to habitat degradation and loss, hydrological modification, pollution, overfishing, invasive species, and a number of other issues (Vitousek et al. 1997a, Crossett et al. 2004). Eutrophication of estuaries and coastal ecosystems has also emerged as one of the most pressing and increasingly studied problems of the late 20th and early 21st centuries (Nixon 1995, Cloern 2001, Schindler 2006). The formation and accumulation of toxic, harmful, and/or nuisance

algal blooms that are commonly associated with anthropogenic nutrient enrichment have been linked to a suite of ecological and economic impacts.

Primary Production in Estuaries and Coastal Ecosystems

The dominant influences of humanity, with eutrophication being a prime example, ultimately affect the structure and function of estuaries and coastal ecosystems (Day et al. 1989, Vitousek et al. 1997a, Zingone et al. 2010). A better understanding of the structure and function of estuaries and coastal ecosystems is desired so that cross-comparisons and sound management decisions can be made (Odum 1968, Boyer et al. 1993, Sand-Jensen 1997). One of the fundamental ways that scientists define and compare the structure and function of ecosystems is by their rates of production. The production of organic matter through the assimilation and transformation of solar energy serves as the basis for natural food webs and plays a major role in the global carbon cycle (MacFadyen 1948, Odum 1968, Sand-Jensen 1997). Measures of production are therefore characterizations of the trophic status of ecosystems, indicating their ability to support the metabolic demands of organisms and the related processes going on within them relative to other places in the world (Nixon 1995). For example, estuaries and coastal ecosystems having a supply of organic carbon greater than 300 but less than $500 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ are said to be eutrophic (Nixon 1995). Measurements of primary production have thus become an important part of characterizing both aquatic and terrestrial ecosystems, as well as defining the impacts of anthropogenic influences on their health (Barbour et al. 1987, Sorokin 1999).

Phytoplankton are major contributors to primary production in estuaries and coastal ecosystems, making them a key component of the overall structure and function of these environments (Zingone et al. 2010). They are a ubiquitous and diverse

assemblage of free-floating, microscopic algae that produce food-energy via photosynthesis (Day et al. 1989, Paerl et al. 2010). Phytoplankton production typically varies spatially and temporally within and across different estuaries (Boynton et al. 1982, Day et al. 1989). This variability is due to morphological, physical, chemical, and biological factors that are unique to each ecosystem (Brylinsky and Mann 1973, Boynton et al. 1982, Day et al. 1989). These regulatory factors can influence phytoplankton production on various scales from the individual cell, through ecophysiological responses to environmental changes, to entire ecosystems by forcing species selection and succession (Day et al. 1989, Falkowski 1994).

Phytoplankton are thus sensitive and important indicators for detecting ecological change in estuaries due to their fast growth rates and rapid responses to a wide range of environmental disturbances (Paerl et al. 2010). Efforts to directly measure rates of phytoplankton production are therefore of great importance, but the methods used often encounter major logistical barriers to their application (Ryther 1956b, Tilzer 1989, Sand-Jensen 1997). Attempts to model production using easily and broadly measured parameters have become popular for bridging gaps in methodology (Odum 1968, Vollenwider 1969, Brylinsky and Mann 1973, Boyer et al. 1993, Scardi 1996). The development of phytoplankton productivity models has been based on the assumptions that (1) primary productivity is proportional to primary producer biomass, (2) phytoplankton biomass is closely correlated with chlorophyll *a* concentrations, and 3) photosynthesis is proportional to light availability (Ryther 1956a, Ryther 1956b, Ryther and Yentsch 1957, Brylinsky and Mann 1973, Geider and Osborne 1992). Cole and Cloern (1987) combined these principles in the form of a simple empirical model that

predicts daily phytoplankton productivity from the composite parameter $BZ_p I_0$, which is the product of phytoplankton biomass (B) in terms of chlorophyll a , the photic depth (Z_p), and the total amount of solar radiation (I_0). The relationship was initially developed from field measurements taken in San Francisco Bay, California (Cole and Cloern 1984), but Cole and Cloern (1987) and other researchers have since tested and applied this 'light•biomass' approach to reasonably predict phytoplankton productivity in a number of estuaries, varying in location and classification (Keller 1988, Mallin et al. 1991, Boyer et al. 1993, Kelly and Doering 1997, Murrell et al. 2007, Bouman et al. 2010).

Using easily and commonly measured variables from routine oceanographic investigations, the $BZ_p I_0$ or 'light•biomass' model has provided an opportunity to eliminate burdensome, expensive, time consuming, and often unreliable primary production studies and acquire more robust productivity estimates over larger spatial and temporal scales than the traditional approaches allow (Ryther and Yentsch 1957, Cole and Cloern 1987, Boyer et al. 1993, Kelly and Doering 1997). These productivity estimates can expand the usefulness of long time series by extracting the necessary biomass and light availability data to create ecosystem baselines and track the effects of natural and anthropogenic changes (Zingone et al. 2010). The collection and interpretation of time series data is useful in the study of estuarine and coastal ecosystem structure and function since these environments limit the use of whole-ecosystem experiments (Cloern 2001).

Study Overview and Objectives

The overall goal of this study was to describe the primary production of phytoplankton in the Caloosahatchee Estuary, Florida as a means of assessing its current conditions and long-term changes in trophic status. The Caloosahatchee

Estuary is a shallow, microtidal, subtropical system and one that has been extensively modified and managed by humans since the late 1800s, creating a combination of features that has altered the system's response to both natural and anthropogenic influences. Due to its relatively shallow morphology, the photic zone of the Caloosahatchee Estuary often extends to the bottom, expanding the capacity for phytoplankton production throughout the water column. The microtidal range keeps the delivery and resuspension of sediments relatively low in the Caloosahatchee Estuary, allowing phytoplankton to respond positively to nutrient inputs without being inhibited by turbidity. As a subtropical system, the Caloosahatchee Estuary experiences relatively high temperatures and solar radiation levels year-round, supporting phytoplankton growth through all seasons, including the winter. The subtropical climate also contributes significant rainfall, particularly during the summer to fall wet season, increasing the supply of nutrients to support the productivity potential of the phytoplankton community.

This study was implemented in the context of the following objectives and corresponding hypotheses:

- **Objective 1.** The applicability of the $BZ_p I_0$ or 'light•biomass' model in the Caloosahatchee Estuary was tested using measurements of phytoplankton biomass, photic depth, surface irradiance, and primary productivity. The hypothesis was that the model relationship would not hold due to the system's complex and dynamic changes in water quality that either magnify or truncate the underlying natural, seasonal patterns.
- **Objective 2.** The phytoplankton community of the Caloosahatchee Estuary was defined in terms of species abundance and composition to identify patterns of succession that could influence the predictive power of the model. The hypothesis was that any shifts in the phytoplankton community would correspond to shifts in water quality (i.e., salinity, nutrient availability, light availability, etc.) and reflect the species-specific preferences for and adaptations to variable environmental conditions, thereby, altering the productivity potential of the

phytoplankton community given the quantity of biomass and light that is present in the water column.

- **Objective 3.** Changes in water quality (i.e., salinity, nutrient availability, light availability, etc.) were assessed in the Caloosahatchee Estuary for their direct or indirect effect on the phytoplankton community, primary production, and the model relationship. The hypothesis was that water quality would vary with respect to natural and anthropogenic inputs of freshwater into the estuary, creating a combination of factors that could support or suppress phytoplankton productivity at different spatial and temporal scales, which may not be accounted for by the simple 'light•biomass' model.
- **Objective 4.** The adapted primary productivity model was applied to an existing twenty-five year discontinuous water quality data set from the Caloosahatchee Estuary as a means of examining the responses of the phytoplankton community to both natural and anthropogenic changes in the system. The hypothesis was that phytoplankton productivity would fluctuate between extremes in response to anthropogenically enhanced seasonal patterns, El Niño/Southern Oscillation (ENSO) cycles, and episodic storm events, thereby creating spatial and temporal variations in the estuary's trophic status that challenge current management practices and plans.

CHAPTER 2 SYSTEM BACKGROUND AND LITERATURE REVIEW

History of the Caloosahatchee Estuary

Prior to the movement of settlers to and the development of the area, the Caloosahatchee Estuary and its watershed was an expansive mixture of sloughs, sawgrass marshes, and pine flatwoods (Flaig and Capece 1998, Knight and Steele 2005, Perry 2008). Like the rest of the Florida Everglades, the system was completely dependent on and susceptible to the natural flow of water that moved freely between Lake Okeechobee, the surrounding floodplains, the Caloosahatchee River, and out to the Gulf of Mexico. A small canoe trail used by Native Americans connected Lake Okeechobee to Lake Flirt (located just east of La Belle), which served as the headwaters to the small, meandering Caloosahatchee River that flowed to Beautiful Island and into the estuary (Flaig and Capece 1998, Knight and Steele 2005).

Following the Civil War in the 1860's, many southerners and squatters were eager to settle in South Florida with the promise of cheap land that could be drained and used for farming (Foster and Wessel 2007, Perry 2008). By 1881, the governor of Florida had encouraged Hamilton Disston, a Philadelphia toolmaker and developer, to purchase and drain the land around Lake Okeechobee, the heart of the Everglades, to allow farmers to work its surrounding rich, dark soils (Foster and Wessel 2007). Disston began by dredging an approximately fifteen meter wide canal along the existing Native American canoe trail between Lake Okeechobee and Lake Flirt to provide a navigable steamboat channel for the movement of people and goods throughout the area (Flaig and Capece 1998, Foster and Wessel 2007). These development efforts were tested in the 1920s when two major hurricanes hit the area causing extensive flooding,

devastation, and death. Despite the hard economic times of the Great Depression, President Hoover responded in 1930 with money appropriated by Congress to construct the Herbert Hoover Dike around Lake Okeechobee to prevent future flooding (Foster and Wessel 2007). In the years to follow, southern Florida oscillated between too little and too much water due to periods of drought and hurricane flooding, respectively. The state and federal government responded again in 1948 to the water demands and devastation by authorizing the U.S. Army Corps of Engineers (USACE) to start a \$208 million dollar flood control project that would eventually include over 2,800 kilometers of canals and levees and some 200 water control structures throughout central and southern Florida (Guest 2001, Perry 2008). The Central and Southern Florida Flood Control District, now known as the South Florida Water Management District (SFWMD), was subsequently created to serve as the local sponsor and manager of this federal project, which was referred to by the same name (Guest 2001, Kranzer 2003, Perry 2008).

As part of the Central and Southern Florida Flood Control Project, the Caloosahatchee River was further dredged, straightened, deepened, widened, and connected to the St. Lucie River on the opposite side of Lake Okeechobee to create a trans-state shipping channel (named the C-43 Canal) that linked the Gulf of Mexico to the Atlantic Ocean. The dredging resulted in the construction of a series of other canals, locks, and pumping stations that were designed to remove excess water from the surrounding lands (Foster and Wessel 2007). Two lock and dam structures were completed in the 1930s at the towns of Moore Haven (referred to as S-77) and Ortona (referred to as S-78) to control the river flow and discharge from Lake Okeechobee

(Doering and Chamberlain 1999). The final structure, the W.P. Franklin Lock and Dam (referred to as S-79), was built in the 1960s approximately forty-two kilometers upstream from the Gulf of Mexico near Olga in east Lee County (Flaig and Capece 1998, Foster and Wessel 2007). This structure was designed to assure a fresh water supply for the lower region of the watershed and to prevent salt water intrusion from the Caloosahatchee Estuary into the upstream aquifers (Flaig and Capece 1998, Foster and Wessel 2007, Doering and Chamberlain 1999). Moreover, S-79 created two distinct river systems within the Caloosahatchee. Upstream and east of S-79, the river is characterized as a pooled freshwater system that is isolated from the tidal influences of the Gulf of Mexico, while the downstream and western part of the river remains an estuary where seawater from the Gulf of Mexico mixes with freshwater inflows from the surrounding watershed and eastern stretch of the river (Wessel and Capece 2007).

Today, the Caloosahatchee River, Estuary and Watershed represent a system that was originally used, subsequently altered, and currently maintained to meet the immediate needs and priorities of Florida residents. What started as an effort to make the lands more inhabitable and cultivatable has resulted in historic changes to the natural water flow patterns in the Everglades and across central and southern Florida. These historical changes and current demands have created a great challenge to understand and manage the balance between natural and anthropogenic processes going on in the entire Caloosahatchee River Watershed.

Critical Issues in the Caloosahatchee Estuary

The modifications to the physical shape and hydrology of the Caloosahatchee River, Estuary, and Watershed have subsequently altered the flow of water into and throughout the entire system. These changes have caused large fluctuations in the

quantity, quality, timing, and distribution of freshwater inflow from the river to the estuary, impacting the ecology and economy of the system (Chamberlain and Doering 1998a, Barnes 2005, SFWMD et al. 2009). Anthropogenic control over the delivery of freshwater into the Caloosahatchee Estuary has been associated with unnatural variations in salinity and nutrient loads, which together are considered the major issues affecting downstream organisms and the overall health and value of the system (SFWMD et al. 2009).

The delivery of freshwater into the Caloosahatchee Estuary varies naturally between periods of heightened and reduced rainfall and corresponding runoff, occurring in the summer/fall wet season (May through October) and winter/spring dry season (November through April), respectively. However, the development of the area has caused rainfall runoff that was once retained within the watershed to reach the estuary more quickly and in higher volumes (Barnes 2005). In addition, these seasonal patterns are exacerbated by regulatory releases of freshwater from Lake Okeechobee (through S-77) and the Upper Caloosahatchee River and Watershed (through S-78) into the Caloosahatchee Estuary (through S-79). Upstream discharges occur in order to maintain prescribed water levels in Lake Okeechobee, prevent flooding, and flush algal blooms, salt water, and other contaminants out of the Caloosahatchee River (Flaig and Capece 1998, Doering and Chamberlain 1999, Rand and Bachman 2008). Freshwater releases are withheld to meet the urban and agricultural demands on the public water supply. The combined effects of rainfall, runoff, and regulatory releases cause the estuary to receive excessive freshwater inflows during the wet season, while flow is reduced or stopped completely during the dry season (SFWMD et al. 2009).

Salinity in the Caloosahatchee Estuary varies widely in time and space in response to both natural and anthropogenic inputs of freshwater. However, the volume of freshwater entering the Caloosahatchee Estuary through S-79 overwhelms any other source (Chamberlain and Doering 1998a, Flaig and Capece 1998), so inflows from the Caloosahatchee River have the greatest implications for monitoring and control and, therefore, receive the highest attention with respect to their influence on the physiological tolerances of downstream organisms (Chamberlain and Doering 1998b). Oysters and submerged aquatic vegetation (SAV), including *Vallisneria americana* (tape grass) and the seagrasses *Halodule wrightii* (shoal grass) and *Thalassia testudinum* (turtle grass) are considered key species or valuable ecosystem components (VECs) in the Caloosahatchee Estuary (SFWMD et al. 2009), so the limits of freshwater inflows that protect and enhance oyster and SAV productivity should lead to a healthy and diverse estuarine ecosystem (Chamberlain and Doering 1998a). A gradient of freshwater to euhaline conditions is present in the Caloosahatchee Estuary when monthly inflow averages between 14.2 and 28.3 m³•s⁻¹ (Bierman 1993), providing desirable salinities for all organisms somewhere in the system (Chamberlain and Doering 1998a, Knight and Steele 2005). Flows below this range limit the distribution of tape grass and increase the susceptibility of oysters to disease and predation, while flows above this range reduce salinities below the preferred tolerances of the seagrasses and oysters (Chamberlain and Doering 1998a, Chamberlain and Doering 1998b, SFWMD et al. 2009). Excessive mean monthly inflows greater than about 79.3 m³•s⁻¹ are detrimental to other estuarine biota and cause stress to the estuary (Chamberlain and Doering 1998b, SFWMD et al. 2009). A minimum mean monthly

inflow of $8.5 \text{ m}^3 \cdot \text{s}^{-1}$ from S-79 was established in 2001 as the specific minimum flow and level (MFL) required to maintain sufficient salinities at the Ft. Myers monitoring station, although a minimum monthly mean target of $12.7 \text{ m}^3 \cdot \text{s}^{-1}$ is necessary to avoid MFL violations during dry periods (Knight and Steele 2005, SFWMD 2008, SFWMD et al. 2009).

Nutrient concentrations across the Caloosahatchee Estuary are the product of point and non-point sources of natural and anthropogenic inputs, including those derived from river flow, rainfall runoff, wastewater disposal, sewage overflow, atmospheric deposition, and elemental recycling (Knight and Steele 2005). However, the loading of new nutrients into the Caloosahatchee Estuary is primarily dependent on both the quantity and quality of freshwater entering the system through S-79. Annual flows through S-79 are large enough, on average, to fill the entire volume of the estuary over eight times per year (Doering and Chamberlain 1999). The majority of this freshwater comes in the form of rainfall runoff from the Caloosahatchee River Basin as opposed to direct discharges from Lake Okeechobee (Chamberlain and Doering 1998a, Doering and Chamberlain 1999), so its composition is a function of land use and anthropogenic activities in the upper watershed. Current land use in the upper (freshwater) portion of the river basin is dominated by agriculture and ranching (Knight and Steele 2005). Runoff from these areas carries excess concentrations of nitrogen and phosphorous from over fertilization and animal defecation. Concentrations of phosphorous are already naturally high in the waters of the Caloosahatchee Estuary due to the leaching of phosphate-rich rock formations underlying the watershed (Odum et al. 1998). As a result, the loading of nitrogen to the Caloosahatchee Estuary is

perceived to be more critical with respect to limiting primary productivity and managing eutrophication (McPherson and Miller 1990, McPherson et al. 1990, Montgomery et al. 1991, Doering et al. 2006, Heil et al. 2007, Bailey et al. 2009). Multiple studies in the Caloosahatchee Estuary have confirmed that increases in nitrogen loads are associated with increases in phytoplankton productivity, which in turn, are associated with peak concentrations of phytoplankton biomass (McPherson and Miller 1990, McPherson et al. 1990, Montgomery et al. 1991, Doering et al. 2006). The resulting algal blooms reduce water quality by decreasing light availability for SAV and depleting oxygen in the water column needed by fish and other aquatic organisms (Day et al. 1989). Additionally, certain species of algae produce toxins that can directly or indirectly harm invertebrates, fish, birds, mammals, and humans (Cloern 2001, Brand and Compton 2007, SFWMD et al. 2009). Total maximum daily loads (TMDLs) of total nitrogen (TN) into the Caloosahatchee Estuary were recently implemented by the Florida Department of Environmental Protection in order to reach target concentrations of chlorophyll *a* (annual average of 11 mg·m⁻³) in these impaired waters (Bailey et al. 2009). A maximum load of 4,121 metric tons of TN per year, representing a 23% load reduction, should restore the Caloosahatchee Estuary to pre-development concentrations and provide suitable conditions for a healthy SAV community, and by default, the entire estuarine ecosystem (Bailey et al. 2009).

Management and Restoration Efforts in the Caloosahatchee Estuary

The extensive changes to freshwater inflows along with the associated salinity fluxes and nutrient loads have negatively impacted water quality in the Caloosahatchee Estuary for more than 130 years. These impacts have been most notably documented as declines in SAV beds and oyster reefs and increases in algal blooms in the area

(Chamberlain and Doering 1998a, Volety 2008, Barnes 2005, Brand and Compton 2007, Lapointe and Bedford 2007, Perry 2008, SFWMD et al. 2009). These outcomes have been taken as indicators of poor estuarine health and eutrophication in the Caloosahatchee Estuary and have become the primary focus of management plans and restoration efforts in the system (SFWMD et al. 2009).

Efforts to manage and restore the Caloosahatchee Estuary and the Florida Everglades have increased since the 1970s, starting with the passing of the Clean Water Act (CWA) in 1972 as an amendment to the Federal Water Pollution Control Act of 1948. The CWA established regulations for discharging pollutants and setting water quality standards for the Nation's waters (Adler et al. 1993). In the same year, the Florida Water Resources Act updated the state's water policies from traditional riparian landowner rights into a form of administrative water law that brought all waters of the state under regulatory control through the establishment of five water management districts (Rand and Bachman 2008, Carriker and Borisova 2009). Around this time, the last of the major works of the 1948 Central and Southern Flood Control Project was completed, and the Florida Legislature began to recognize the harm that the project had caused to South Florida (Guest 2001). The final report from the project concluded that "nutrient pollution from agriculture and drainage had begun to eutrophy Lake Okeechobee" and recommended "hydrologic restoration toward natural hydric conditions to the maximum extent possible" (Guest 2001). In response, the newly named SFWMD shifted its focus from strictly flood mitigation to more general water control in 1975, but it continued to ignore state mandates to regulate nutrient pollution from agricultural runoff and back-pumping into the lake (Guest 2001). Just downstream,

a waste-load allocation study in the early 1980s confirmed that the Caloosahatchee Estuary had already reached its nutrient loading limits as indicated by elevated chlorophyll *a* and depressed dissolved oxygen concentrations, suggesting that increased nutrient inputs would cause chlorophyll *a* concentrations to reach dangerous levels (Degrove 1981, Doering et al. 2006).

Water quality in these South Florida ecosystems received national attention in 1988 when the United States Federal Government filed a lawsuit against the SFWMD and the Florida Department of Environmental Protection (FDEP) alleging that agricultural runoff and water discharges in the Everglades were in violation of state water quality standards (Guest 2001, Perry 2008). The resulting settlement essentially sparked the state of Florida to take action to improve water quality, starting with the passing of the Florida Everglades Forever Act (FEFA) in 1994 (Guest 2001). Under the FEFA, the SFWMD initiated the Everglades Construction Project (ECP), whereby they were to purchase land, construct stormwater treatment areas, and improve the quality of waters coming from the Everglades agricultural area (Guest 2001, Perry 2008).

By the mid 1990s, it was more and more evident that the 1948 project that was intended to make the Everglades more conducive to development and agriculture was damaging Lake Okeechobee and the connected ecosystems (Guest 2001). A task force was formed under the direction of the USACE to review the original project and come up with a corrective plan, which became known as the 'Restudy' (Guest 2001, Kranzer 2003, Rand and Bachman 2008). The ultimate goal of the 'Restudy' was to modify the works of the Central and Southern Florida Flood Control Project of 1948 to restore natural hydrological patterns, while maintaining flood control and improving

urban and agricultural water supplies (Guest 2001, Rand and Bachman 2008). The resultant plan was adopted by the State of Florida in 1999 and the United States Congress in 2000 as the Comprehensive Everglades Restoration Plan (CERP), which was to be implemented over a period of 40 years at an estimated cost of eight billion dollars (Guest 2001, Kranzer 2003, Rand and Bachman 2008). CERP has been described as the largest ecosystem restoration effort in history, encompassing an area of approximately 47,000 square kilometers that covers 16 counties (Kranzer 2003, Perry 2008).

In conjunction with CERP, the Florida Legislature has passed a number of additional acts and adopted more programs to underscore the State's commitment to ecosystem restoration in the greater Everglades. Much of these were focused on improving water quality in Lake Okeechobee, such as the 2000 Lake Okeechobee Protection Act and its subsequent program. It was not until 2007 that the state of Florida expanded this effort into the Northern Everglades and Estuaries Protection Program to recognize the connectivity of the watersheds surrounding Lake Okeechobee (SFWMD et al. 2008). This latest program guided the development of new comprehensive, systematic, and multi-agency plans that specifically addressed the objectives and benefits of CERP and other projects in the rivers and estuaries connected to Lake Okeechobee. The Caloosahatchee River Watershed Protection Plan was adopted in 2009 and is still used today as the preferred plan that consolidates and outlines the best combination of construction projects, pollutant control programs, research, and water quality monitoring programs needed to improve the quantity, quality, timing, and distribution of water in the system (SFWMD et al. 2009).

CHAPTER 3
MODELING PHYTOPLANKTON PRODUCTIVITY IN A SHALLOW, MICROTIDAL,
EXTENSIVELY MODIFIED, SUBTROPICAL ESTUARY IN SOUTHWEST FLORIDA

Concepts and Applications

In many estuaries, phytoplankton are the largest contributors to primary production and therefore play a central role in estuarine ecosystem structure and function (Boynton et al. 1982, Day et al. 1989). The ability to measure primary productivity, or rates of primary production, is therefore of great importance, but the methods used to make such determinations can be complicated, expensive, and inconsistent (Ryther 1956b, Ryther and Yentsch 1957, Tilzer 1989, Sand-Jensen 1997). These challenges have led to the development of model relationships that estimate primary productivity using more easily determined and broadly measured parameters, such as light flux, photic depth, and phytoplankton biomass (most often in terms of chlorophyll *a*). The utility of light availability and chlorophyll *a* in modeling phytoplankton productivity was recognized by the mid-twentieth century (Ryther 1956b, Ryther and Yentsch 1957). These early developments provided researchers a tool to estimate primary productivity using data routinely collected during oceanographic investigations (Ryther and Yentsch 1957). More recently, Cole and Cloern (1987) combined these principles in the form of a simple empirically-based model for predicting daily phytoplankton productivity, i.e., $BZ_p I_0$, where *B* is phytoplankton biomass in terms of chlorophyll *a*, Z_p is photic depth, and I_0 is daily incident irradiance. The $BZ_p I_0$ model is commonly referred to as the 'light•biomass' approach because the formulation is essentially a measure of phytoplankton biomass multiplied by a term representing light availability in the water column (Boyer et al. 1993, Brush and Brawley 2009). The model was derived from its original form $B I_0 K_T^{-1}$ (Cole and Cloern 1984), where K_T is the

light attenuation coefficient and equated to $4.61Z_p^{-1}$. The more commonly used BZ_p/I_0 relationship was compared to field measurements of phytoplankton productivity for several estuaries, including San Francisco Bay in California, Puget Sound in Washington, Hudson River plume in New York, Delaware Bay in Delaware, and the Neuse and South Rivers in North Carolina (Cole and Cloern 1987). A strong linear relationship ($r^2 = 0.82$) was obtained between the observed and modeled values ($N = 211$) of primary productivity (Cole and Cloern 1987). The model has been applied to a number of other estuaries, including Narragansett Bay in Rhode Island (Keller 1988), Neuse River Estuary in North Carolina (Mallin et al. 1991, Boyer et al. 1993), Massachusetts Bay and Boston Harbor in Massachusetts (Kelly and Doering 1997), Escambia Bay in Florida (Murrell et al. 2007), and Tokyo Bay in Japan (Bouman et al. 2010), reaffirming the adaptability of the model to a range of ecosystem types.

Like other significant oceanographic investigations and advances made throughout history, little effort has been put forth to extend this concept to regions beyond the temperate zone. Except for the study done in Escambia Bay, which lies at 30°N latitude in a warm-temperate/subtropical region of northwest Florida, all other previous model applications have been conducted in temperate estuaries located at latitudes between 35 and 50°N. This paper describes the first field test of the Cole and Cloern (1987) model in a low latitude subtropical system, the Caloosahatchee Estuary, located at 26°N latitude on the southwest coast of Florida. Despite being categorized into similar geographic and climatic regions, the Caloosahatchee Estuary differs from Escambia Bay by having water temperatures that typically do not fall below 20°C in comparison to lows of 10°C in the winter in Escambia Bay (Murrell et al. 2007).

Furthermore, the seasonal pattern of rainfall and river flow in Escambia Bay is more common to temperate systems with peaks occurring in the winter and spring (February to April) and valleys occurring in the summer and fall (June to November) (Murrell et al. 2007). The Caloosahatchee Estuary has the opposite freshwater inflow pattern, which is more characteristic of tropical systems, and one that is accentuated by anthropogenic flushing events. As a result, the Caloosahatchee Estuary experiences a 'perfect storm' scenario during the wet season (May through October) when freshwater inputs from the watershed are coupled with high light levels and warm water temperatures, creating a combination of presumably ideal conditions for phytoplankton blooms. This high potential for phytoplankton production in the Caloosahatchee Estuary is further attributed to the system's shallow bathymetry and microtidal range, which are shared characteristics of most river-dominated Gulf of Mexico estuaries, including Escambia Bay (Murrell et al. 2007).

Further distinguishing itself from the previously tested systems, the Caloosahatchee Estuary has been significantly altered by human development since the late 1800s when it was artificially connected to Lake Okeechobee (Doering et al. 2006). The system has been further modified from its original state by the addition of three water control structures along the Caloosahatchee River and years of dredging to maintain a trans-state waterway. These and other changes to the physical shape and hydrology of the system have caused unnatural salinity fluctuations, excess nutrient loading, elevated dissolved color concentrations, increased sediment deposition, and the formation and accumulation of both autochthonous and allochthonous harmful algal blooms (Chamberlain and Doering 1998a, Barnes 2005, Knight and Steele 2005,

SFWMD et al. 2009, RECOVER 2011). The responses of the phytoplankton community to changes in water quality, in particular the formation and accumulation of harmful algal blooms, have become a growing management concern (McPherson and Miller 1990, Doering et al. 2006, Brand and Compton 2007, Perry 2008).

Considering the characteristics and issues that are unique to this shallow, microtidal, extensively modified, subtropical system, the usefulness of a simple model for estimating phytoplankton productivity in the Caloosahatchee Estuary was questioned. The purpose of this study was primarily to test the applicability of the $BZ_p I_0$ model in the Caloosahatchee Estuary using field measurements of phytoplankton productivity collected in a manner similar to those described by Cole and Cloern (1987). Modifications to the study methods (using O_2 evolution instead of ^{14}C uptake productivity measurements) and model parameters, particularly the biomass (B) and photic depth (Z_p) terms, were done to investigate their influence on the overall relationship. Model deviations and productivity patterns were described in terms of spatial and temporal variations in freshwater inflow (i.e., rainfall and river flow), water quality (i.e., salinity, light, nutrients, etc.), and phytoplankton community structure (i.e., abundance and composition). The 'fitted' (in terms of its statistical significance and strength) and 'best suited' (in terms of its appropriateness and usefulness) $BZ_p I_0$ model adapted to the Caloosahatchee Estuary was used to determine annual estimates of phytoplankton productivity for the Caloosahatchee Estuary so that system-wide comparisons to other systems could be made.

Methods

Study Area

The Caloosahatchee Estuary covers an area of 62 km² in Lee County on the southwest coast of Florida. It is considered to be part of the larger, neighboring Charlotte Harbor National Estuary (SFWMD et al. 2009) (Figure 3-1). The Caloosahatchee Estuary empties into and exchanges water tidally with the Gulf of Mexico through San Carlos Bay and Charlotte Harbor at Shell Point (Figure 3-2). Approximately 42 km upstream, the estuary is fed primarily by the Caloosahatchee River through the Franklin Lock and Dam (S-79) (Figure 3-2). The width of the estuary is irregular, ranging from 160 m near S-79 to 2,500 m in San Carlos Bay (Scarlatos 1988). The narrow section extending from S-79 to Beautiful Island has an average depth of 6 m, but the area downstream of Beautiful Island has an average depth of 1.5 m (Scarlatos 1988). A narrow navigation channel (part of the Intracoastal Waterway) is maintained at a depth of approximately 3.5 m (Scarlatos 1988). The area experiences a combination of diurnal and mixed semi-diurnal tides with a mean tidal range of 0.30 m in the middle of the estuary near downtown Fort Myers (Scarlatos 1988, NOAA 2010).

Freshwater is released into the estuary through S-79 in order to maintain prescribed water levels in Lake Okeechobee, control flooding, and flush algal blooms and salt water out of the river (Flaig and Capece 1998, Doering and Chamberlain 1999). In an average year, enough freshwater flows from S-79 to fill the entire volume of the estuary over eight times (Doering and Chamberlain 1999). The flow through S-79 is composed of 75% rainfall runoff and 25% regulatory discharges from Lake Okeechobee (Chamberlain and Doering 1998a). Runoff comes from the 3,625 km² sized watershed

(Knight and Steele 2005), which is made up of agricultural areas in the east and urban areas in the west. Additional sources of freshwater entering the estuary downstream of S-79, including the Orange River near Beautiful Island (Figure 3-2), are considered to be minor in comparison to S-79 (Scarlatos 1988, Flaig and Capece 1998, Knight and Steele 2005).

Water Sampling

Four sampling sites were included in this study (Figure 3-2). Site UE was located in the Upper Estuary near Beautiful Island, which is northeast of downtown Ft. Myers. Site ME was located in the Middle Estuary near downtown Fort Myers. Site LE was located in the Lower Estuary near Iona Shores. Site BY was located in San Carlos Bay near Picnic Island. The four sites were located just outside the main navigation channel. Depths at the sampling sites were between 2 and 3 m.

The sites were sampled once a month from February 2009 to February 2010 (excluding March 2009). For the first six monthly sampling events, water was collected from each site on four different, but consecutive days, within one hour before sunrise to provide water for the primary productivity experiments. Water was also collected from each site during the afternoon prior and afternoon following the pre-dawn collections so that adjustments for differing water quality conditions during the primary productivity experiments could be made. In the later sampling months, water was collected from each site in the morning on the same day so that the productivity model could be applied to the remainder of the year. All water samples were collected with a 3 m vertically integrating pole sampler to collect a mixed sample of water from the entire water column (Wetzel and Likens 1991). From each collection, sample water was retained, stored, and preserved for chemical and phytoplankton analyses.

Field Measurements

Temperature (TEMP_W), salinity (SAL), and dissolved oxygen (DO) profiles were measured during each sampling event at 0.5 m intervals from the surface to the bottom of the water column using a HACH (Loveland, Colorado) HQ40D meter. Light readings were taken simultaneously with paired LI-190 reference (deck) and LI-192 downwelling (2π) LI-COR (Lincoln, Nebraska) quantum cosine corrected photosynthetically active radiation (PAR) sensors above the surface (incident irradiance) and at 0.5 meter intervals to the bottom, respectively. For the pre-dawn sampling events, light attenuation was estimated from measurements taken during the afternoon before and after the primary productivity experiments.

Light attenuation coefficients (K_T) were calculated with the Beer-Lambert relationship and taken as an average of the two coefficients obtained from inputting the downwelling irradiances at the 0.5 to 1.5 m depth and the 1.0 to 2.0 m depth, respectively. In cases where an average light attenuation coefficient could not be determined in this manner, K_T was calculated with the same relationship using the incident irradiance corrected for 5% surface reflection (Ryther 1956a) and the downwelling irradiance at 1.0 m depth. For the pre-dawn samples, light attenuation coefficients were then estimated by selecting the afternoon coefficient that most closely represented the water conditions in the morning based on chlorophyll *a* (CHL A), color dissolved organic matter (CDOM), and turbidity (TURB) values. The final K_T (Table 3-1), representing light availability in the water column during the primary productivity experiments, was then derived by applying correction factors for differences in CHL A (0.03; Wolfson 1983), CDOM (0.015; McPherson and Miller 1987), and TURB (0.1152; determined from the relationship between turbidity and tripton during the study period).

Photic depth (Z_p) one of the three main variables in the Cole and Cloern (1987) model, was defined as the depth of 1% incident irradiance and calculated as $4.61K_T^{-1}$ (Table 3-1).

Meteorological and Hydrological Data

A separate LI-COR (Lincoln, Nebraska) LI-190 reference (deck) cosine corrected quantum sensor, with LI-1000 data logger, was used to determine the total PAR light flux over the incubation period of the primary productivity experiments (February through August 2009, excluding March). To test the Cole and Cloern (1987) model, total daytime surface irradiance (I_0) was estimated by multiplying the total PAR light flux during the six-hour incubations (sunrise to mid-day) by 2 to represent a typical twelve-hour light day (Table 3-1). To obtain productivity estimates from the $BZ_p I_0$ model adapted to the Caloosahatchee Estuary for the entire annual study period (February 2009 through February 2010, excluding March 2009), PAR values recorded at three stations in Lee, Collier, and Hendry Counties (Figure 3-1) were compiled from the South Florida Water Management District's online environmental database (SFWMD 2010). Instantaneous readings at fifteen minute intervals were converted into $\text{mol}\cdot\text{photons}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and summed across the daylight period to provide estimates of daily PAR flux. The maximum values of daily PAR flux across the tri-county area were used to estimate monthly maximum I_0 (Table 3-1).

Daily rainfall and flow values recorded at S-79 (Figure 3-2) were obtained from the South Florida Water Management District's online environmental database (SFWMD 2010). Values were converted into metric equivalents, cm and $\text{m}^3\cdot\text{s}^{-1}$, respectively. These records were used to identify wet and dry periods during the study since they represent the main sources of freshwater into the estuary, which in turn were

used to investigate seasonal changes in water quality, phytoplankton abundance and composition, and primary productivity.

Chemical Analyses

Chemical analyses were conducted by the Dr. Edward J. Philips Laboratory at the University of Florida using methods certified by the National Environmental Laboratory Accreditation Program (NELAP). Aliquots of whole (unfiltered) and filtered sample water were retained, transported on ice, and stored frozen until subsequent chemical analysis. Whole water was used in the determination of chlorophyll *a* (CHL *A*), total nitrogen (TN), total phosphorous (TP), silica (SI), and turbidity (TURB). To analyze samples for concentrations of ammonia (NH₃), nitrite (NO₂), nitrate (NO₃), total soluble nitrogen (TSN), total soluble phosphorous (TSP), soluble reactive phosphorous (SRP), and color dissolved organic matter (CDOM), triplicate samples of whole water were first filtered in the field using 0.7 μm glass-fiber filters.

Filters were stored frozen and in the dark until spectrophotometrically analyzed using a Hitachi U2810 (Tokyo, Japan) for CHL *A* following hot ethanol extraction of pigments (Sartory and Grobbelaar 1984, APHA 2005). Both uncorrected and pheophytin-corrected concentrations were determined. Average CHL *A* concentrations, based on triplicate samples, were used in the phytoplankton productivity model (Cole and Cloern 1987) as the phytoplankton biomass parameter (*B*) (Table 3-1).

Whole water samples for TN and TP analysis were digested using the persulfate oxidation method (APHA 2005) and measured colorimetrically on a Bran-Luebbe AA3 auto-analyzer (Norderstedt, Germany) and a Hitachi U2810 dual-beam spectrophotometer (Tokyo, Japan), respectively. Measurements of TSN and TSP were obtained in the same manner, except that filtered water was used. SI concentrations

were determined spectrophotometrically by the molybdosilicate method with a correction for turbidity (APHA 2005). NH_3 and NO_3 were first converted into NO_2 using an oxidation reaction with hypochlorite in an alkaline medium and a copperized cadmium reductor, respectively, and the three forms were then measured colorimetrically on the auto-analyzer (Strickland and Parsons 1972, APHA 2005). Dissolved inorganic nitrogen (DIN) was defined as the sum of NH_3 , NO_2 , and NO_3 . SRP concentrations were determined spectrophotometrically with the ascorbic acid method (APHA 2005). CDOM values were measured against platinum-cobalt color standards on the spectrophotometer (APHA 2005). TURB was measured immediately from whole water that had not been frozen with a LaMotte (Chestertown, Maryland) 2020 turbidity meter against two (1 and 10 ntu) reference standards (APHA 2005).

Phytoplankton Analyses

Whole (unfiltered) water samples were preserved on-site with Lugol's solution (APHA 2005) and analyzed microscopically for phytoplankton abundance and species composition (Susan Badylak, Dr. Edward J. Philips Laboratory, University of Florida). For general phytoplankton abundance and composition, preserved samples were settled in 19 mm diameter chambers according to the Utermohl method (Utermohl 1958). Cells were identified and counted at 400x and 100x with a Leica (Wetzler, Germany) DMIL phase contrast inverted microscope. At 400x, a minimum of 100 cells of a single taxon and at least 30 grids were counted. If 100 cells were not counted within 30 grids, up to a maximum of 100 grids were counted until 100 cells of a single taxon was reached. At 100x, a total bottom count was completed for taxa greater than 30 μm in size.

Picoplankton abundances were determined using fluorescence microscopy (Fahnenstiel and Carrick 1992). Whole, unpreserved samples were filtered onto 0.2 μm Nucleopore filters and mounted between a microscope slide and cover slip with immersion oil. Slides were stored frozen and analyzed using a Nikon (Tokyo, Japan) labophot 219146 research microscope equipped with a mercury short arc photo optic lamp (Hg 100 W).

Counts for individual taxa were converted to total phytoplankton biovolume concentrations (*BV*) (Table 3-1), using the closest geometric shape method (Smayda 1978). Biovolume was calculated for each species from specific phytoplankton dimensions measured for a minimum of 30 individuals. The designation 'cf.' for the Latin word 'confer' was used to identify species that were comparable but not identical to known taxa.

Primary Productivity Experiments

Primary productivity experiments were conducted monthly during the first half of the study period (February to August 2009, excluding March). Primary productivity was indirectly determined from changes in DO concentrations over half-day (approximately six-hour) incubations using a simulated *in situ* light:dark bottle method (Wetzel and Likens 1991, Cole and Cloern 1987). The O₂ evolution method was selected over the ¹⁴C uptake method used by Cole and Cloern (1987) so that estimates of both gross and net primary productivity (GPP and NPP, respectively) could be obtained. The O₂ evolution method has been more commonly used in shallow systems (Brawley et al. 2003), and it provided a safer, less complicated, less expensive, and more portable field approach than the ¹⁴C uptake method (Wetzel and Likens 1991, Köhler 1998).

Incubations were conducted in a black, gel-coated (polyester resin) fiberglass raceway (2.44 m long by 0.61 m wide by 0.1 m deep) that was placed on shore near each respective site. Clear polystyrene flasks were filled with approximately 300 mL of the morning water sample and incubated (in triplicate) at a minimum of six and a maximum of eight light levels of varying percent transmittance under natural sunlight. Samples were not pre-screened for bacteria or zooplankton due to the potential for altering the phytoplankton community in the process (Stickland 1960, Wetzel and Likens 1991). One group was the dark treatment in which the triplicate flasks were wrapped in black tape and aluminum foil prior to filling. A second group of triplicate flasks received full sunlight, representing light conditions at the surface of the water column. The remaining groups of triplicate flasks received different light treatments to emulate the specific light transmittance-depth profile for the water column at each site (Figure 3-3; parts A and B). Light levels were created using neutral density Plexiglas panels that were tinted to allow approximately 75, 50, 35, 30, 20, 15, and 5% light transmittance (Custom Glass Tinting, Gainesville, Florida). Twenty-eight additional light levels were created by stacking two panels together.

Flasks were surrounded by a constant flow of water from the estuary that was pumped through the raceway in order to maintain temperatures at *in situ* levels. The morning water samples collected for the primary productivity experiments were approximately 1 to 2°C cooler than their respective water column temperatures by the time they were used to fill the light and dark flasks. Temperatures of the samples contained in the flasks increased 1 to 5°C over the course of the incubation period.

DO concentrations in the flasks were measured at the beginning and end of the incubation period using a HACH (Loveland, Colorado) HQ40D meter with a luminescent biological oxygen demand (LBOD) electrode. GPP for each treatment group was calculated from the oxygen fluxes in the dark and light flasks. GPP obtained from the half-day incubation periods were multiplied by 2 to represent full light-day rates. A molar mass ratio of 0.375 (grams per mole of carbon to grams per mole of oxygen) and the standard photosynthetic quotient (moles of oxygen liberated to moles of carbon dioxide assimilated during photosynthesis) of 1.2 were applied to convert rates into units of carbon fixation (Wetzel and Likens 1991).

GPP from each triplicate group were averaged to represent the total amount of carbon fixed at each corresponding light treatment level. The percent light transmittance received by each treatment group was then related back to a depth in the water column at each site using the Beer-Lambert relationship. The averaged GPP values were plotted against the calculated incubation depths to produce a curve of photosynthetic activity per unit volume of water at each site (Figure 3-3; part C). The curves were integrated over the water column (down to water depth, Z_w) to yield daily gross primary productivity (GPP_d) in $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for each site and experimental month (Table 3-1).

NPP from each site and experimental month was also calculated for model comparison purposes by adjusting daily gross primary productivity for respiratory activity. Average respiratory activity in the triplicate dark flasks during the half-day incubation periods was converted into full light-day rates as was done for GPP except the standard respiratory quotient (ratio of moles of carbon dioxide liberated to moles of

oxygen consumed during respiration) of 1.0 was used (Wetzel and Likens 1991). The resulting respiratory rates were integrated over the respective water column depths and subtracted from the corresponding GPP_d values to yield daily net primary productivity (NPP_d) in $mg \cdot C \cdot m^{-2} \cdot d^{-1}$ for each site and experimental month (Table 3-1). The NPP_d estimates obtained from this approach could be argued as more representative of net community productivity (NCP) since the respiratory activity of both bacteria and zooplankton was incorporated in the oxygen fluxes observed in the dark flasks. However, net productivity was still defined as NPP_d with the assumption that respiratory activity was less than 10% of total productivity in the flasks and due to the fact that there was no ideal method for isolating phytoplankton separately from the other commonly associated non-photosynthetic plankton (Ryther 1956a, Howarth and Michaels 2000). Furthermore, the term NCP could be perceived as taking into account the respiratory activity of the entire water column 'community' even though benthic plants and animals, fish, and other large nekton were obviously and purposefully excluded from the samples and incubation flasks.

Primary Productivity Model Test

A model of daily integrated primary productivity for the Caloosahatchee Estuary was tested using the approach described by Cole and Cloern (1987). The more commonly applied model that uses $BZ_p I_0$ as the composite parameter (Cole and Cloern 1987) was related to the original model form $BI_0 K_T^{-1}$ (Cole and Cloern 1984) using the relationship $K_T = 4.61 Z_p^{-1}$. Applications of the 1984 and 1987 models were compared by dividing the slopes of the 1984 model applications by 4.61 or vice versa (Table 3-2).

In this study, GPP_d obtained from the simulated *in situ* incubations ($N = 24$) were regressed against the modeled values using the formula $BZ_p I_0$; where B is CHL A

concentration (an indicator of phytoplankton biomass), Z_p is the photic depth, and I_0 is the total daytime surface irradiance (Table 3-1). The model was also tested using NPP_d obtained for each site and experimental month to determine if methodology (using gross vs. net rates) affected the overall relationship. The February 2009 data point from Site BY was removed from the net productivity model test ($N = 23$) because it yielded an unexplainable negative NPP_d value. Both the GPP_d and NPP_d models were tested with and without a correction for photic depth based on corresponding water column depths to determine if this relationship affected the potential for phytoplankton productivity and, thus, the strength of the model. In cases where the photic depth (Z_p) exceeded the water column depth (Z_w), the value of Z_p was cut-off and made equal to Z_w so that the model estimated phytoplankton productivity based on the actual volume of water present and the quantity of light truly available. Lastly, each of these four model scenarios (i.e., combination of two different productivity methods and two different photic depth approaches) were tested using CHL A concentrations that were either uncorrected or corrected for pheophytin to determine if pigment degradation products affected the overall relationship.

Model parameters were determined with least-squares regression analysis in SAS Version 9.2 (SAS Institute Inc. 2009). A p -value of 0.05 was used to determine the significance of model parameters. Model strengths were evaluated using r^2 correlation coefficients of determination with values closer to ± 1 indicating a 'stronger' fit. The 'fitted' (in terms of its statistical significance and strength) and 'best suited' (in terms of its appropriateness and usefulness) model for the Caloosahatchee Estuary was selected so that the resulting adapted relationship provided the simplest, most practical

approach to predicting phytoplankton productivity using measurements of biomass and light availability that are routinely collected (Cole and Cloern 1987). The residuals (difference in measured and predicted productivity values) of the 'fitted' and 'best suited' $BZ_p I_0$ model adapted to the Caloosahatchee Estuary were analyzed to identify factors contributing to the deviations from the model (Cole and Cloern 1987).

Primary Productivity Model Application

The 'fitted' and 'best suited' $BZ_p I_0$ model adapted to the Caloosahatchee Estuary was used to estimate phytoplankton productivity for the year-long study period (February 2009 to February 2010, excluding March 2009). The independent composite parameter ($BZ_p I_0$) was calculated for each month using *in situ* field measurements of phytoplankton biomass as CHL A (B) and photic depth (Z_p) from monthly sampling events and monthly maximum values of I_0 for the area (see previous method explanations). Average estimates of annual gross and net phytoplankton productivity, GPP_y and NPP_y ($g \cdot C \cdot m^{-2} \cdot y^{-1}$), respectively, were determined from modeled daily rates for each site and across all sites for system comparison purposes.

Results

Physical – Chemical Conditions

Daily rainfall and flow at the Franklin Lock and Dam (S-79) exhibited similar seasonal patterns during the study period (Figure 3-4). Rainfall and flow were low between February and the middle of May 2009, creating a dry period. Both rainfall and flow increased from the second half of May through the beginning of October 2009, corresponding to the normal wet period for this area (Scarlatos 1988, Chen and Gerber 1990, Stoker 1992, Chamberlain and Doering 1998a). From the middle of October

2009 to the following February 2010, rainfall and flow declined. The second dry period had somewhat higher rainfall and flow levels than the first dry period.

Salinity (SAL) ranged from near 0 to approximately 35 psu across the four sites over the study period (Figure 3-5). San Carlos Bay (BY) had the highest and least variable salinities. SAL levels decreased with distance from the mouth of the estuary. SAL was greatest at all sites during the dry period and lowest at all sites during the wet period, reflecting the influence of seasonal freshwater inputs throughout the estuary. The largest differences between surface and bottom SAL were observed at the Upper (UE) and Middle (ME) Estuary sites in June 2009 and at the Lower Estuary (LE) site in September and October 2009.

Water temperature (TEMP_W) showed little spatial variation and was uniform throughout the water column. However, TEMP_W gradually increased throughout the study period from a low of 18°C in February 2009 to a high of 32°C in August 2009 (Figure 3-6). Following the summer peak, TEMP_W decreased in the fall and early winter to levels that resembled those observed in the previous spring and late winter, respectively. TEMP_W in January and February 2010 dropped to a low of 14°C, well below what was seen one year prior, corresponding to record cold air temperatures from January to March 2010 (NCDC 2010).

Total daytime surface irradiance (I_0) (i.e., PAR light flux) measured on the days of the primary productivity experiments, were higher in February, April, and May than in June, July, and August 2009 (Figures 3-7, 3-8, 3-9, and 3-10; part A). The decrease in PAR light flux during the summer months coincided with greater cloud cover observed during the primary productivity experiments, even though monthly maximum I_0 for the

region ranged from 30 to 40 mol•m⁻²•d⁻¹ in the winter to 50 to 60 mol•m⁻²•d⁻¹ in the summer (i.e., in the absence of cloud cover) (Figure 3-11; part A).

Light penetration through the water column, expressed as vertical light attenuation coefficients (K_T) varied by site and season during the study period (Figure 3-12; part A). In general, light transmission through the water column was greater during the dry period than the wet period. Light attenuation increased as freshwater inflow increased, particularly at the sites in the inner estuary (UE, ME, and LE). Variability in K_T was linked to changes in the concentrations of CDOM, TURB, and CHL A at each of the four sites (Figure 3-12). Light attenuation at site UE was primarily coupled with CDOM, particularly in July, August, and December 2009, while CHL A and TURB played a role in February 2009 and 2010, respectively. The increase in K_T at site ME in the wet summer months corresponded to an increase in TURB and CHL A in June 2009, CDOM in July 2009, CHL A in August 2009, and TURB in October 2009. At site LE, changes in K_T closely matched changes in TURB and CHL A (July 2009) with CDOM having a lesser influence in August and December 2009. The less pronounced increase in K_T at site BY in August 2009 was primarily attributable to minor increases in CDOM and CHL A.

Photic depth (Z_p ; depth at 1% PAR light flux) varied by date and site (Figures 3-7, 3-8, 3-9, 3-10, and 3-11; part B), while water depth (Z_w) was consistently between 2 and 3 m at all four sites throughout the study period. Z_p was shallower than Z_w at site UE throughout much of the study period and at sites ME and LE during the wet summer months. At site BY, Z_p exceeded Z_w throughout the study period with the greatest difference observed during the dry months.

Concentrations of TSP, TP, TSN, TN, SRP, DIN, and SI were generally higher in the wet period than the dry period (Figures 3-13, 3-14, and 3-15), coinciding with increased freshwater inflows from the watershed. Spatially, the peaks in nutrient concentrations appeared first and most prominently at sites UE and ME in the inner estuary. Substantial increases in concentrations were also observed at site LE, and to a lesser extent at site BY, but a month or more later. Seasonal patterns were less apparent at site BY, which is furthest from the headwaters of the estuary and most strongly influenced by tidal water exchange.

Ratios of TN to TP concentrations fluctuated around the Redfield molecular mass ratio of 7 (mostly in the range of 5 to 9) throughout the study period at all four sites (calculated ratios not shown). By comparison, ratios of DIN to SRP concentrations were consistently below the Redfield molecular mass ratio of 7 (Figure 3-14). SRP concentrations from each site and month were greater than $0.015 \text{ mg}\cdot\text{L}^{-1}$, which is five times the minimum phosphorous requirement suggested for phytoplankton growth (Reynolds 2006). DIN concentrations were comparatively less than expected based on Redfield stoichiometry. Levels of DIN below $0.03 \text{ mg}\cdot\text{L}^{-1}$, the nitrogen concentration needed for sufficient phytoplankton growth in coastal waters (Reynolds 2006), were observed in February 2009 (site LE), April 2009 (site BY), May 2009 (sites UE, LE, and BY), June 2009 (site ME), and February 2010 (site BY). SI concentrations from each site and month were never below $0.5 \text{ mg}\cdot\text{L}^{-1}$, the minimum requirement suggested for phytoplankton growth, including diatoms (Reynolds 2006). However, relatively low levels of SI were observed at site BY in June 2009, site ME in November 2009, and site BY in January 2010 when they fell within the range of 0.6 to $0.9 \text{ mg}\cdot\text{L}^{-1}$ (Figure 3-15).

The phytoplankton biomass potential (amount of expected CHL *A*) based on observed concentrations of SRP, DIN, and SI (according to Redfield stoichiometry) also showed that SRP and SI are relatively more abundant than DIN in terms of the needs of phytoplankton growth at all four sites (Table 3-3). During most dry months (February 2009 to May 2009 and November 2009 to February 2010), the potential for additional biomass represented by the amount of available DIN was low. In some of the wet months (July to October 2009), the biomass potential was high based on DIN levels in the water column, however, the observed CHL *A* remained low.

Phytoplankton Abundance and Composition

Phytoplankton biomass (*B*) in terms of uncorrected CHL *A*, and total phytoplankton biovolume (*BV*) concentrations were both considered as measurements of phytoplankton abundance in this study. All four sites experienced their largest *B* peaks in the summer (June, July, and August 2009) (Figures 3-7, 3-8, 3-9, 3-10, and 3-11; part C). Additional peaks in *B* occurred at site UE in the winter (February 2009, January 2010, and February 2010) and spring (May 2009) and at site ME in the winter (January 2010). *BV* followed similar trends as *B* (Figure 3-16), although the relative peak heights differed somewhat. Overall, approximately 68% of the variability in *BV* was explained by the variability in *B*, regardless if CHL *A* concentrations were corrected or not for pheophytin pigments (relationship not shown).

The major peaks in *BV* were associated with dinoflagellates at sites UE and ME but with diatoms at sites LE and BY (Figures 3-16). At site UE, the dinoflagellate *Akashiwo sanguinea* contributed between 65 and 95% of the total phytoplankton biovolume during the five main peaks in *BV* (Figures 3-16 and 3-17). *A. sanguinea* contributed 95% of *BV* during the major peak at site ME in June 2009. Another

dinoflagellate, *Polykrikos schwartzi*, was responsible for the January 2010 peak at that site (Figures 3-16 and 3-17). At site LE, the diatom *Skeletonema cf. costatum* was the dominant phytoplankton species during the *BV* peak in July 2009, contributing up to 86% of the total phytoplankton biovolume (Figures 3-16 and 3-17). *S. cf. costatum* was also present at site BY, but the relatively small *BV* peaks in August and September 2009 were attributed to relatively large centric diatoms (60 to 140 μm), i.e., *Coscinodiscus cf.* and *Rhizosolenia setigera*, respectively.

Cyanobacteria (blue-green algae) and 'other' phytoplankton, including chlorophytes, euglenoids, cryptophytes, Chattonella (raphidophytes), and small flagellates, played a significant but lesser role in terms of phytoplankton biovolume in the Caloosahatchee Estuary (Figures 3-16 and 3-17). Cyanobacteria (blue-green algae) were more abundant at sites LE and BY than at sites UE and ME, while the opposite pattern was observed for taxa in the 'other' group (Figure 3-17). The increased prevalence of 'other' phytoplankton at sites UE and ME during the wet summer months was attributable to small flagellates in July 2009 and to both chlorophytes and euglenoids in August 2009 (Figure 3-17).

Measured Primary Productivity

Measured daily gross primary productivity (GPP_d) followed the patterns seen in phytoplankton biomass (B) in terms of uncorrected CHL A concentrations (Figures 3-7, 3-8, 3-9, and 3-10; part D). B alone explained approximately 80% of the variability in GPP_d regardless of whether or not the CHL A concentrations were corrected for pheophytin pigments (relationship not shown). Gross productivity estimates from the simulated *in situ* experiments ranged from 90 to 3121 $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table 3-4). The median measured productivity values increased from site BY to the inner estuary.

Despite the substantial range of productivity estimates observed during the six-month experimental period, all sites exhibited one or more dates when measured GPP_d exceeded $1500 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table 3-4).

Primary Productivity Model Fit

The linear regression relationships between measured productivity (using the simulated *in situ* incubation experiments) and predicted productivity (using the $BZ_p I_0$ model parameter) were significant for all possible model scenarios (using either GPP_d or NPP_d values, calculated or corrected Z_p values, and uncorrected or corrected CHL A concentrations for B) (Table 3-5). Between 78 and 85% of the variability in daily productivity was explained by the variability in the composite parameter $BZ_p I_0$ depending on which productivity method was used, whether or not the photic depth values were corrected for water depths, and whether or not the CHL A concentrations were corrected for pheophytin, as indicated by the strength of the coefficients of determination (r^2).

In general, the model relationships were 'strongest' (i.e., having the largest r^2 values) when (1) GPP_d values were used instead of NPP_d values and (2) uncorrected CHL A was used instead of corrected CHL A as an indicator of biomass (B). Between the remaining two model scenarios (GPP_d values for the productivity term and uncorrected CHL A concentrations for the biomass term), the r^2 values were almost equal (0.85 and 0.84) and the slopes were very similar (0.70 to 0.73) whether photic depths were corrected for water column depths or not, respectively. However, the use of corrected Z_p values greatly increased (by a factor of 3.4) the model intercept, shifting the line further from the origin. Without the Z_p correction, which was the approach presumably taken by Cole and Cloern (1987), the model relationship based on

measured GPP_d and uncorrected CHL A concentrations yielded an intercept not significantly different from zero (p -value = 0.4849) (Figure 3-18).

Based on this 'fitted' and 'best suited' model relationship, $GPP_d = 75 + 0.73BZ_pI_0$, differences between measured and predicted primary productivity values varied by site and season (Figure 3-19). In general, the residuals were positive from February through May 2009 and negative in July and August 2009, which indicated that the model over- and underestimated primary productivity during these respective time periods. June 2009 represented a transition month in which the model produced significant over- and underestimates of primary productivity at different sites in the estuary. There was only one case (July 2009, site ME) when the difference between the measured and predicted productivity values was less than detection limit of the method, which was estimated at $45 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}$ (HACH 2006). Most of the residuals were within $\pm 350 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, except for five cases (April 2009, site LE; May 2009, site BY; June 2009, site UE; July 2009, site LE; July 2009, site BY) in which the absolute values of the differences in the measured and predicted values were between 523 and $724 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Figure 3-19). The measurements of primary productivity obtained in these five experiments were well outside the range (higher or lower) of average estimates bounded by the 95% confidence interval of the mean (Figure 3-18).

Modeled Primary Productivity

After applying the 'fitted' and 'best suited' model ($GPP_d = 75 + 0.73BZ_pI_0$) adapted to the Caloosahatchee Estuary to the year-long data set of B , Z_p , and I_0 , modeled productivity was between 163 and $4405 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, which is a higher and wider range of values in comparison to those obtained in the simulated *in situ* experiments (Table 3-4). Under modeled conditions, GPP_d exceeded

1800 $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at each site at least once over the course of the year, which is a higher mark of the system's productivity potential than was portrayed in the six monthly simulated *in situ* experiments. The largest peaks in modeled GPP_d occurred at all four sites during the summer (June, July, and August 2009) with additional peaks appearing in the winter (February 2009, January 2010, and February 2010) at sites UE and ME (Figure 3-11; part D), which is the same pattern set forth in the six-month experimental period. Over the course of the year, peaks in modeled GPP_d corresponded to periods of increased water temperatures, PAR influx, freshwater inflow, and/or nutrient loading.

Annualized rates of modeled GPP_d yielded an average annual gross phytoplankton productivity estimate (GPP_y) of $346 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ across all four sites in the Caloosahatchee Estuary for the year-long study period. Since estuarine and other ecosystem comparisons are commonly based on net productivity estimates in literature, the alternative model relationship $NPP_d = 102 + 0.63 BZ_{\rho l_0}$ was also applied and yielded an average annual net phytoplankton productivity estimate (NPP_y) of $312 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ for the Caloosahatchee Estuary. Spatially, annualized mean GPP_y increased from $268 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ ($245 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ NPP_y) at site BY to $424 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ ($379 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ NPP_y) at site UE (Table 3-6), which followed the spatial trend in bioavailable and total nutrient concentrations in the Caloosahatchee Estuary.

Discussion

Modeling Phytoplankton Productivity

The $BZ_{\rho l_0}$ or 'light-biomass' model developed by Cole and Cloern (1987) for estimating daily phytoplankton productivity yielded a strong linear relationship with simulated *in situ* measures of productivity in the Caloosahatchee Estuary, explaining most of the variability (84%) in daily gross productivity. This relationship is one of the

strongest outcomes among the various efforts to apply the model to estuaries in North America and across the globe (Table 3-2). The model has been applied in a variety of estuarine types, including lagoons (South San Francisco Bay), fjords (Puget Sound), and river-dominated systems (North San Francisco Bay, Narragansett Bay, Neuse River Estuary, Escambia Bay, and Tokyo Bay) (Table 3-2). While most of the applications of the model have been in temperate estuaries, the results of this study and an earlier study in Escambia Bay, Florida (Murrell et al. 2007) indicate that the model also fits some warmer water systems. The Caloosahatchee Estuary application extends the usefulness of the BZ_{pI_0} model to distinct low latitude subtropical systems, particularly those having higher annual water temperatures, higher rainfall and river flow in the summer and fall, and greater anthropogenic influence in the system.

The current application of the model to the Caloosahatchee Estuary was also unique in using the O_2 evolution method to estimate both gross and net productivity, instead of the ^{14}C uptake method, which generally yields net productivity values, particularly in the case of extended incubation periods (Peterson 1980, Wetzel and Likens 1991). In addition to providing more information (both gross and net productivity), the O_2 evolution method was both easier and cheaper to perform than the more commonly used ^{14}C method, avoiding the need for hazardous chemicals and expensive equipment (Wetzel and Likens 1991, Köhler 1998). To validate the comparability between this and the other model applications, the Caloosahatchee Estuary model relationships were also examined using NPP_d , and the overall significance of the models did not change. The NPP- and GPP-based model relationships were similar in strength, but the NPP_d models had somewhat lower slopes

than the GPP_d models, while the intercepts were not affected in terms of their significance. Keller (1988) conducted a similar analysis using pooled data ($N=1010$) to compare NPP- and GPP-based models for Narragansett Bay, Rhode Island. The slopes of the NPP and GPP models were 0.63 and 0.70, respectively (Keller 1988), similar to the slopes observed in this study. The strength and comparability of the GPP_d and NPP_d Caloosahatchee Estuary models suggest that either GPP or NPP data can yield reasonable estimates of phytoplankton productivity.

This study was also the first to examine some previously unaddressed complexities involved in defining the variables in the model predictor, $BZ_p I_0$ (Cole and Cloern 1987). In the development and original application of the 'light•biomass' model (Cole and Cloern 1984, 1987), data from different sources used both uncorrected and corrected CHL A concentrations as a proxy for phytoplankton biomass (B). In later model applications, only one study specified that corrected CHL A concentrations were used (Boyer et al. 1993), while the remaining studies gave no indication either way (Keller 1988, Murrell et al. 2007, Bouman et al. 2010). To determine if the $BZ_p I_0$ model was affected by the type of CHL A values used, relationships were tested for both uncorrected CHL A concentrations and values corrected for pheophytin. Although the significance of the models did not change, the coefficients of determination (r^2) decreased slightly. Using corrected CHL A concentrations for B increased the slopes and intercepts slightly, but the increase was likely not enough to change the interpretation of the model. Since system monitoring projects often analyze and report one of the two forms of CHL A (uncorrected or corrected for pheophytin), it is helpful

knowing that either could be used as an indicator of phytoplankton biomass in the Cole and Cloern (1987) model without changing the overall viability of the model.

Another issue examined in this study was the definition of photic depth (Z_p) used in the model. The $BZ_p I_0$ model assumes that Z_p is completely contained within the total water column depth (Z_w) because the relationship was derived and tested in relatively deep estuarine systems, which is probably why Cole and Cloern (1984, 1987) did not provide instructions on how to handle situations when this is not the case. The relative shallowness of the Caloosahatchee Estuary and typically low light attenuation (K_T) during the dry months could explain why Z_p was greater than Z_w at site BY in San Carlos Bay throughout the experimental period and at sites UE, ME, and LE in the inner estuary between February and May 2009. As a result, predicted productivity (using the $BZ_p I_0$ composite parameter) was generally higher than measured productivity (using the simulated *in situ* incubation experiments) during these cases. Brush et al. (2002) and Boyer et al. (1993) note that the $BZ_p I_0$ model may overestimate productivity when Z_p exceeds Z_w because the model assumes that the phytoplankton have access to all of the available light and, thus, that all of the photic depth was used in carbon fixation. To investigate the effect on the Caloosahatchee Estuary primary productivity relationships, models were run separately with Z_p values cut off at Z_w . The resulting relationships had slightly lower, yet, comparable slopes and substantially higher intercepts that became significantly different from zero. By shifting the intercept approximately 2 to 3 times further from the origin, productivity estimates based on the new model predictor would be higher than those obtained using the uncorrected model predictor, assuming B and I_0 are held constant. Since the natural and more logical productivity model centers closer

to the origin (i.e., zero phytoplankton biomass and/or zero light availability theoretically yields zero primary productivity), as Cole and Cloern's 1984 and 1987 models do, the Z_p correction was not used for the BZ_p/I_0 model application in the Caloosahatchee Estuary, but alternative approaches should be considered in future model tests. For example, Brush and Brawley (2009) suggested that simply substituting Z_w for Z_p when Z_p is greater than Z_w is not a valid approach because the relationships between water column depth and irradiance and between irradiance and photosynthesis are non-linear. Brawley et al. (2003) proposed a correction factor to adapt the BZ_p/I_0 model to shallow systems which took into account these non-linear relationships, however, it did not improve the estimates of productivity in the system in which it was tested (Waquoit Bay, Massachusetts). The authors attributed the difficulties in validating the correction factors to the limited availability of ^{14}C uptake data, variable productivity estimates, problematic estimation of light attenuation, and complex bathymetry in shallow systems (Brawley et al. 2003). An approach that ultimately provided good agreement between measured and predicted productivity involved the use of ten different depth correction polynomials that were developed for varying irradiance levels (Brush and Brawley 2009). The use of these polynomials went beyond the level of analysis and interpretation desired for a simple empirical model for robust productivity estimation in the Caloosahatchee Estuary, but it should be explored in other systems as deemed necessary.

Interpretation of Model Residuals

Residual outputs from model applications provide opportunities to examine factors that may be important in defining the causes of variability in the relationship between independent and dependent model variables. In this application of the

'light•biomass' model, the residuals represent differences between measured (using the simulated *in situ* incubation experiments) and predicted (using the $BZ_p I_0$ composite parameter) productivity values. The model residuals can therefore help identify factors other than CHL A and PAR availability that may affect phytoplankton productivity, aside from the inherent variance associated with experimental or analytical error.

Cole and Cloern (1987) suggest that deviations of measured productivity from model-predicted productivity are related to variability in eco-physiological factors that affect photosynthetic capacity, such as nutrient availability, the quality of the underwater light field, and the presence of toxic compounds in the water column. In addition, such deviations can reflect changes in phytoplankton community structure, since genotypic differences in photosynthetic mechanisms and growth strategies impact the responses of phytoplankton to changes in light availability. In more general terms, deviations from model predictions can be viewed as a reflection of differences in photosynthetic efficiency (Welschmeyer and Lorenzen 1981, Geider and Osborne 1992, Geider and MacIntyre 2002). Since photosynthetic efficiency essentially represents the productivity potential of a given phytoplankton standing stock, with respect to the available light in the water column, processes contributing to phytoplankton biomass gains and losses, such as growth, allochthonous inputs, flushing, and grazing, have also been considered for their indirect influence on model deviations (Brush et al. 2002).

The 'light•biomass' model assumes that all phytoplankton biomass (B) expressed as CHL A concentration, is equally capable and efficient at capturing and using PAR for photosynthesis. The model also assumes that photic depth (Z_p) and total PAR light flux (I_0) accurately depict the availability of photosynthetically usable radiation (PUR) in the

water column (Kirk 1994, Falkowski 1994). However, CHL A does not necessarily provide an exact assessment of photosynthetic potential (Welschmeyer and Lorenzen 1981), and all PAR is not equally efficient in driving photosynthesis (Kirk 1994). To summarize, phytoplankton may be more or less photosynthetically efficient due to (1) environmental changes that enhance or diminish their ability to use light for photosynthesis (e.g., changes in nutrient availability), (2) genotypic differences in community structure and function that alter the efficiency with which available light is used for photosynthesis (e.g., species engaging in alternative nutritional strategies), and (3) variability in underwater light quality that alter the level of PUR. An understanding of these factors is important in interpreting the output of primary productivity models (Geider and MacIntyre 2002).

Residual GPP_d model values followed a seasonal pattern in which measured productivity values were typically lower than predicted in the winter and spring (February, April, and May 2009) but higher than predicted in the summer (July and August 2009). This shift between model over- and underestimates of productivity roughly aligned with the transition from the dry period to the wet period, with the exception of June 2009. June 2009 was an anomalous month due to strong salinity stratification in the water column. The mixing of near freshwater with saline water could account for the over-estimation of productivity by the model at site UE, relative to the *in situ* experiment, due to osmotic stress.

The seasonal switch between the model over- and underestimating primary productivity may be viewed from two main perspectives; (1) changes in environmental conditions, most notably increased nutrient levels, altered underwater light quality, and

shifting salinity regimes associated with the onset of elevated rainfall and river flow in June 2009 and (2) a shift in phytoplankton composition from biomass peaks dominated by dinoflagellates, mainly *A. sanguinea*, at site UE and ME during the dry period and in the month of June, to peaks dominated by diatoms, such as *S. cf. costatum* and other centric diatoms, at sites LE and BY in July and August 2009. These spatial and temporal trends are, of course, inter-dependent since environmental changes are primary driving factors in species succession.

Model overestimation

Two potential reasons for model overestimates in the dry period are the presence of relatively low levels of dissolved inorganic nitrogen (DIN) in the water column and the dominance of biomass peaks by *A. sanguinea*. Nitrogen limitation, as indicated in this study by ratios of DIN:SRP below 7, can directly impact photosynthetic capacity by limiting important cell functions, such as protein synthesis (Falkowski 1994, Bergmann et al. 2002, Geider and MacIntyre 2002). Low levels of DIN also influence photosynthetic efficiency indirectly by favoring species capable of acquiring nitrogen nutrition using alternative strategies, such as mixotrophy or behavioral approaches to acquiring nitrogen, e.g., vertical migration (Smayda 1997). The dinoflagellate *A. sanguinea* exhibits both of these capabilities (Gaines and Elbrachter 1987, Levandowsky and Kaneta 1987, Taylor 1987, Smayda 1997, Burkholder et al. 2008).

Mixotrophy has been observed in many dinoflagellates, which are capable of growth based on photo-autotrophic and heterotrophic modes of nutrition (Gaines and Elbrachter 1987, Smayda 1997, Burkholder et al. 2008). *A. sanguinea* can incorporate dissolved organic substances, such as lysine, alanine, leucine, and phenylalanine, which are building blocks of proteins, through osmotrophy (Gaines and Elbrachter

1987). *A. sanguinea* can also ingest cyanobacteria and microfaunal prey through phagotrophy (Burkholder et al. 2008). In addition, a vertical nutrient-retrieval strategy is commonly used by dinoflagellates to access nutrient enriched layers in the water column (Smayda 1997). Populations of nutrient-deficient *A. sanguinea* have been found to accumulate near the depth at which irradiance saturates photosynthesis during the daytime and then migrate below the nitracline at night, allowing for dark uptake of nitrate (Smayda 1997). Due to the relatively shallow and generally polymictic character of the Caloosahatchee Estuary, *A. sanguinea* may migrate to the bottom where it could access DIN diffusing from the sediment surface (Day et al. 1989).

The prominence of *A. sanguinea* during the dry period may also have been aided by relatively low light attenuation and long water residence times compared to the wet period. Light availability in the water column was greatest at all sites between February and May 2009, as indicated by lower values of K_T and estimates of Z_p being approximately equal to or greater than Z_w . Increased light availability during this time period coincided with reduced freshwater inflow and CDOM input, supporting phytoplankton productivity through the water column across the four sites. Water residence times, defined here as the time it takes for a total mass of water to be reduced to e^{-1} or 37% of the initial mass, in the upper and middle regions of the Caloosahatchee Estuary estimated at 6 to 11 days during the dry period compared to 1 to 4 days during the wet period due to changes in flow from S-79 (Qiu et al. 2007). Since dinoflagellates typically have relatively low maximum growth rates, i.e., near or below one doubling per day (Stolte and Garcés 2008) (1.13 d^{-1} for *A. sanguinea*; Matsubara et al. 2007), water residence time is an important factor in their bloom

dynamics. Decreased flushing rates would allow a slower growing species such as *A. sanguinea* to maintain its population and make use of the increased light availability for photosynthesis or focus on other nutritional strategies if nutrients are limited, as they were in this case.

Although not directly related to photosynthetic efficiency, model overestimation during the dry period could also be linked to the effect of zooplankton grazing in the productivity experiment flasks. One of the greatest challenges associated with the use of incubation techniques is the difference between the natural ecosystem and the portion of the system that is contained in the flasks (Howarth and Michaels 2000). Since the morning water samples used in the productivity experiments were not pre-screened for zooplankton, to avoid damaging or altering the phytoplankton community, there was possibly a predator-prey situation created in the flasks that differed from that in the water column. Zooplankton densities in the Caloosahatchee Estuary have been found to be highest at distances further from S-79, particularly in regions having salinities above 20 psu (Chamberlain et al. 2003). In this study, salinities were close to or greater than 20 psu at sites ME and LE during the dry months and at site BY throughout the experimental period. Whole (unfiltered) water samples taken from these sites during these times and enclosed in the productivity flasks could have had more intense zooplankton grazing of phytoplankton due to the confined space and potentially unbalanced predator to prey ratio than in the water column. Since the model predictions were based on CHL A samples retained prior to the start of the incubation period, any decreases in phytoplankton biomass in the flasks due to zooplankton grazing would likely yield lower rates of productivity than the model expected. This

same 'bottle effect' (Howarth and Michaels 2000) did not likely affect the model in the wet period due to the decline and 'wash-out' of the zooplankton community following high freshwater inflows and drops in salinity (Chamberlain et al. 2003).

Model underestimation

In the wet period, the model most likely underestimated productivity due to an increase in macronutrient concentrations (i.e., N, P, and SI) and the shift in phytoplankton community composition towards dominance by the diatom *S. cf. costatum*, both of which may have contributed to an increase in photosynthetic efficiency. During the wet summer months (June to August 2009), concentrations of total and inorganic nutrients increased throughout the estuary, following increased freshwater inflows from the watershed. Concentrations of DIN, which typically limit productivity in the Caloosahatchee Estuary (McPherson and Miller 1990, Doering et al. 2006, Heil et al. 2007), were introduced at levels well above the minimum requirement needed for sufficient nitrogen uptake (Reynolds 2006). SI concentrations, which were potentially limiting to diatoms at the end of the dry period, were also added to the system at levels in excess of the suggested requirement for phytoplankton growth (Reynolds 2006). *S. cf. costatum* and other diatoms likely exhibited enhanced productivity following this nutrient stimulation, which is the classic response in nutrient limitation 'bioassay' experiments (Day et al. 1989).

The trade-off to nutrient loading during the wet period was the decrease in light availability in the water column, which was linked to increased CDOM input. Phytoplankton can adapt to changing light availability at the cellular level by altering their pigment content, photosynthetic capacity, chemical composition, cell volume, and other photosynthetic responses (Falkowski and Owens 1980, Mallin and Pearl 1992).

These adaptations allow phytoplankton to modify their photosynthetic processes and efficiencies, given light levels that range from limiting to inhibitory (Gallagher et al. 1984, Bergmann et al. 2002). Light-harvesting pigments in the photosynthetic apparatus capture and transfer light energy to the photo-chemical reaction centers where it is coupled to an electrochemical gradient (Falkowski and Owens 1980, Gallagher et al. 1984). Chlorophyll *a*, which is most effective at absorbing blue and red light, is the major light-harvesting pigment in photosynthesis and is therefore used as both a measure of phytoplankton abundance and light absorption capability. In the ocean, red light is attenuated more rapidly than blue and green light (Kirk 1994, Falkowski 1994), accentuating the importance of blue light with depth in terms of absorption in the water column. In inland and coastal waters, the presence of CDOM, which absorbs strongly in the blue range, further restricts light availability for chlorophyll *a* (Kirk 1994).

To fill the gaps between the total intensity of photosynthetically active radiation (PAR) and the portion of that which is photosynthetically usable radiation (PUR), phytoplankton may alter their pigment content to optimize the ability of the cell to harvest the available light (Falkowski and Owens 1980). Diatoms have been found to increase the concentration of chlorophyll *a* and fucoxanthin, an accessory carotenoid pigment, as a photoadaptive response to low light intensities (Falkowski and Owens 1980, Perry et al. 1981, Gallagher et al. 1984). Fucoxanthin allows increased absorption of green light, which fills the chlorophyll absorption 'window' and makes use of the available PAR in colored coastal waters (Yentsch 1980, Falkowski 1994, Kirk 1994). To accommodate these pigment changes, diatoms, including *S. cf. costatum*, have shown to increase the size and not the number of its photosynthetic units (PSUs)

in order to maximize its photosynthetic efficiency in response to low light (Falkowski and Owens 1980, Perry et al. 1981, Gallagher et al. 1984, Smayda 1997, Reynolds 2006).

The success of *S. cf. costatum* and other diatoms during the wet period is further enhanced by their resistance to increased freshwater inflows and decreased water residence times, which likely dropped to less than 4 days based on S-79 flow rates (Qiu et al. 2007). Shortened residence times could indirectly affect the production potential, or photosynthetic efficiency, of phytoplankton by transporting biomass downstream and out of the estuary (Day et al. 1989). The ability of *S. cf. costatum* and other diatoms to maintain their populations in these conditions is related to their superior growth rates. Unlike dinoflagellates, diatoms such as *S. cf. costatum* are able to replenish their populations more quickly at rates that are often greater than two doublings per day (Stolte and Garcés 2008), allowing them to sustain relatively high levels of biomass and productivity during a time of increased flushing and in an area of the estuary prone to tidal mixing. It should be noted that the observed peaks in biomass and productivity could also be attributed to populations of diatoms that are not purely autochthonous in their origin, possibly emanating from adjoining waters of the Gulf of Mexico or Charlotte Harbor. The dominant species of phytoplankton constituting the peaks during this time, *S. cf. costatum*, is a common bloom-forming diatom in the coastal waters of southwest Florida (Saunders et al. 1967).

Other considerations

The explanation for the seasonal pattern identified in the model residuals from this study has alluded to the role that nutrient availability can play in controlling phytoplankton productivity, despite the absence of a nutrient term in the regression relationships (Brush et al. 2002). The original development and success of the BZ_{p/l_0}

model was based on the fact that most estuaries are turbid and nutrient rich, making light availability the most important factor in controlling biomass-specific productivity (Cole and Cloern 1987). In systems where this is not the case, one would need to adjust the potential production predicted by the model from measurements of biomass and light availability to a level of production that there are nutrients to support (Brush et al. 2002). Since no such adjustments were considered, it could be argued that one of the primary assumptions of the $BZ_{p}I_0$ model was violated in this study due to the potential for nutrient limitation in the Caloosahatchee Estuary, particularly during the dry period when nitrogen concentrations are proportionally less than phosphorous concentrations. Ultimately, the overall model selected for the Caloosahatchee Estuary was still a 'strong' fit compared to previous model applications despite being based on experimental data collected across two periods (dry and wet) having distinct freshwater and nutrient inputs. Had the model been tested using just the wet period data ($N = 12$), when nutrients were likely not limiting, the resulting model relationship $GPP_d = 280 + 0.70 BZ_{p}I_0$ ($r^2 = 0.88$) would have yielded even higher overestimates of productivity during the dry period in comparison to deviations derived from the overall model, reaffirming the influence of nutrient availability on the accuracy of the $BZ_{p}I_0$ model.

Comparative Rates of Production

The combined range of daily gross productivity (0.09 to 4.41 $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) obtained from the six-month experimental period and the twelve-month application of the 'fitted' and 'best' suited $BZ_{p}I_0$ model is similar to the ranges of productivity that have been observed in other river dominated estuaries in North America, such as the Hudson River in New York and Narragansett Bay in Rhode Island (Boynton et al. 1982). These measurements and predictions validate the appropriateness of the methodological

techniques used in this study and the usefulness of the $BZ_{p/o}$ model in providing reasonable estimates of estuarine phytoplankton productivity in the Caloosahatchee Estuary. The peak rates of modeled GPP_d exceeding $1.8 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at all four sites demonstrate the productivity potential of the phytoplankton community in a given year. These levels of productivity compare to temperate coastal waters on the low end of the range (Ryther 1963, Boynton et al. 1982) and sea grass and mangrove communities on the high end of the range (Day et al. 1989, Valiela 1995).

The average annual phytoplankton productivity estimate across all four sites in the Caloosahatchee Estuary ($346 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ GPP_y or $312 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ NPP_y) is greater than the $300 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ mean value for upwelling areas reported by Ryther (1963), reflecting the high overall productivity of the Caloosahatchee Estuary. The estimated annual rate of phytoplankton productivity in the Caloosahatchee Estuary is comparable to a number of highly productive river-dominated estuaries in the southeastern United States, including those connected to the Gulf of Mexico (Table 3-6). The Caloosahatchee Estuary, and the majority of the river-dominated estuaries of the Gulf of Mexico, lie between 26° and 31°N latitudes, and are therefore subject to relatively high annual light flux and water temperatures (Kirk 1994, Odum et al. 1998, Pennock et al. 1999, Murrell et al. 2007), helping to support high annual productivity levels year-round (Day et al. 1989). The Gulf of Mexico estuaries, including the Caloosahatchee, are also characteristically microtidal and shallow, in which photic depths are frequently deeper than bottom depths, further enhancing production potential.

The Caloosahatchee Estuary, like other river-dominated systems, is characterized by considerable spatial and temporal variability in phytoplankton biomass

and productivity. The variability is in part attributable to fluctuations in salinity regimes, nutrient distributions, light availability, and water residence times, which are driven by seasonal variability in rainfall and freshwater flow from the watershed (Boynton et al. 1982, Day et al. 1989, Pennock et al. 1999). The shallow nature of the Caloosahatchee Estuary accentuates this variability, resulting in short water residence times and sharp drops in salinity during periods of high freshwater discharge, restricting the potential for the accumulation of phytoplankton biomass (Monbet 1992, Pennock et al. 1999), despite the associated increase in nutrient loads from the watershed.

In this study, phytoplankton biomass and productivity followed a spatial gradient and seasonal pattern that primarily corresponded to the loading and distribution of bioavailable and total nutrient concentrations. However, peaks in phytoplankton biomass and productivity were not always observed when the potential for added growth was high with respect to concentrations of DIN, SRP, and SI in the water column. Spatially, nutrient concentrations were typically higher at the upper and middle estuary sites (UE and ME) than in the lower estuary and bay sites (LE and BY), reflecting the impact of nutrient inputs from the upstream watershed and the role of tidal mixing. Nitrogen was identified as the most likely limiting nutrient for phytoplankton growth, confirming the hypothesis of previous studies in the Caloosahatchee Estuary (McPherson and Miller 1990, Doering et al. 2006, Heil et al. 2007), because of the low Redfield ratios of DIN to SRP throughout the study period and the low biomass potential represented by low concentrations of DIN, particularly in the dry months. In comparison, proportionately higher concentrations of phosphorous were likely supported throughout the study across the four sites by the natural geologic and

hydrologic processes occurring in the nearby and connected Charlotte Harbor watershed, which is rich in phosphate deposits and home to an extensive mining operation (McPherson and Miller 1990). Peaks in phytoplankton biomass and productivity during the dry period and the beginning of the wet period, including the winter, at the upper and middle estuary sites (UE and ME) were likely supported by small pulses of nutrient-enriched water from the watershed and the presence of flocculent muddy sediments, which could serve as an internal source of nutrients for phytoplankton growth (Day et al. 1989). With the onset of the wet period, elevated freshwater flow from the watershed and the corresponding increase in nutrient concentrations would have supported primary productivity throughout the estuary and the bay. However, elevated nutrient concentrations at sites UE and ME in July, August, September, and October 2009 did not correspond with high phytoplankton biomass or productivity, most likely due to strong declines in salinity, light availability, and/or water residence times. With salinities at or below 5 psu, the cells of *A. sanguinea*, the dominant species at these sites, would have likely burst and been incapable of photosynthesizing (Matsubara et al. 2007). Elevated levels of CDOM increased light attenuation and would have reduced the amount of usable PAR, likely affecting the productivity potential of the phytoplankton. Shortened water residence times likely hindered the formation and accumulation of relatively slow growing phytoplankton, such as dinoflagellates. High flushing rates and drops in salinity also likely reduced zooplankton grazing, allowing relatively fast growing phytoplankton like diatoms the opportunity to thrive in the lower estuary and bay during this time.

Summary

This study demonstrated that the BZ_p/I_0 or 'light•biomass' model (Cole and Cloern 1987) can provide reasonable estimates of phytoplankton primary productivity in the Caloosahatchee Estuary, Florida, even given the features of the estuary that distinguish it from previously described systems, including its low latitude subtropical location, individual physical features, unique watershed characteristics, and distinctive phytoplankton community structure and dynamics. The strength of the relationship supports the primary importance of biomass and light in the control of phytoplankton productivity, while the model deviations point to the secondary influence of nutrients, species composition, and light quality on the productivity potential or photosynthetic efficiency of the phytoplankton community. Water residence times, zooplankton grazing, and additional physical-chemical properties were also identified for their indirect impact on the predictive power of the model.

The results also confirmed that the model can give robust estimates of estuarine phytoplankton productivity despite differences in methodologies (using O_2 evolution versus ^{14}C uptake techniques, gross versus net productivity estimates, uncorrected or corrected chlorophyll *a* concentrations, and calculated or corrected photic depths). Thus, model applications from this and a variety of estuaries can be used as a tool to assess productivity on larger spatial and temporal scales to make system-wide comparisons of productivity from data that is routinely collected in monitoring projects, saving ecologists the time and money that is required when conducting traditional field measurements. The level of uncertainty associated with the model, as well as, the tendency of the model to deviate with seasonal shifts in water quality and phytoplankton

community structure, brings caution to the use of the model to accurately predict primary productivity on finer scales.

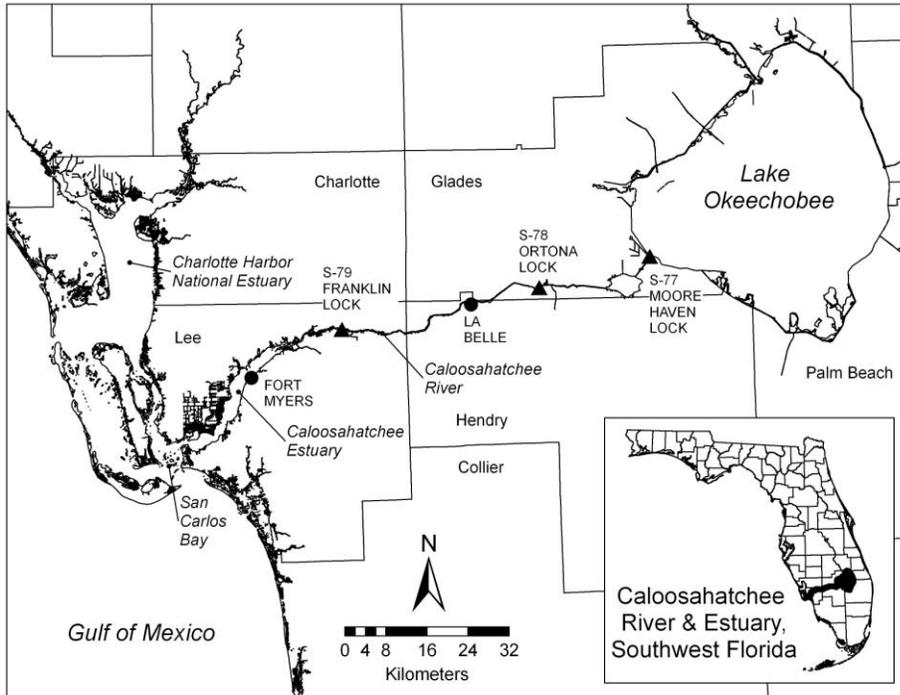


Figure 3-1. Location of the Caloosahatchee Estuary, FL. The Caloosahatchee Estuary is connected to Lake Okeechobee via the Caloosahatchee River (C-43 Canal) and to the Gulf of Mexico and Charlotte Harbor via San Carlos Bay.

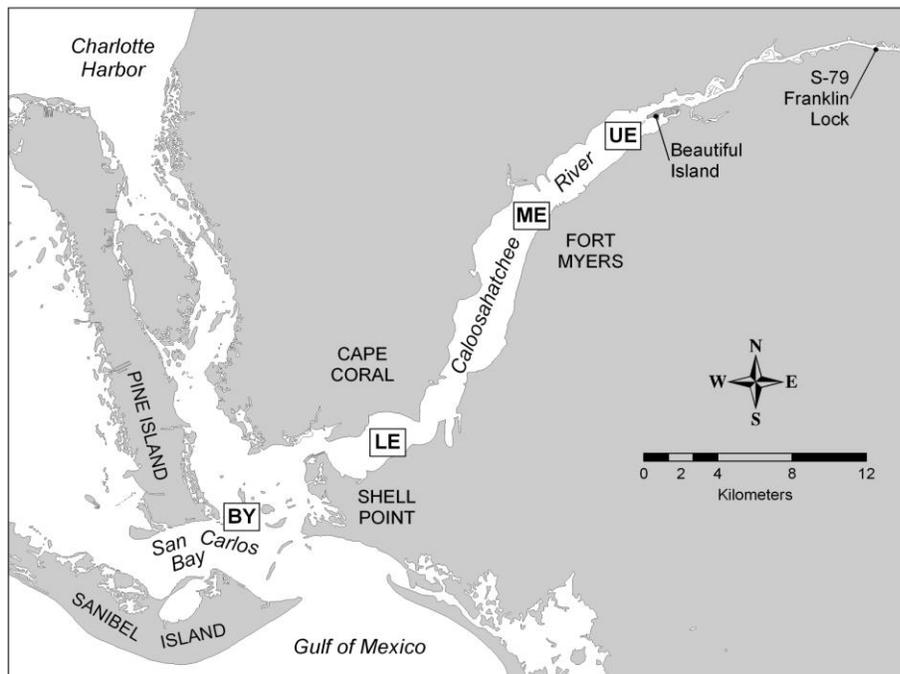


Figure 3-2. Location of the four sampling sites in the Upper Estuary (UE), Middle Estuary (ME), Lower Estuary (LE), and San Carlos Bay (BY).

Table 3-1. Definitions of variables and their units of measure.

variable	definition	units
B	phytoplankton biomass as chlorophyll <i>a</i> concentration	$\text{mg}\cdot\text{CHL}\cdot\text{A}\cdot\text{m}^{-3}$
BV	total phytoplankton biovolume concentration	$10^6\cdot\mu\text{m}^3\cdot\text{mL}^{-1}$
K_T	light attenuation coefficient	m^{-1}
I_0	total daytime surface irradiance (PAR light flux)	$\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$
GPP_d	daily gross primary productivity	$\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$
NPP_d	daily net primary productivity	$\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$
Z_p	photic depth	M
Z_w	water depth	M

Table 3-2. Summary of significant applications of ‘light•biomass’ estuarine productivity models. Year corresponds to date of the reference and not the date of the experiments.

reference	location	N	$BZ_p I_0$ model	r^2
Cole & Cloern (1984)	San Francisco Bay, CA	77	$P_d = 3.8(BI_0K_T^{-1}) + 58$ $= 0.82(BZ_p I_0) + 58$	0.82
Cole & Cloern (1987)	San Francisco Bay, CA Puget Sound, WA Hudson River Plume, NY	211	$P_d = 0.73(BZ_p I_0) + 150$	0.82
Keller (1988)	Narragansett Bay, RI	1010	$P_d = 0.70(BZ_p I_0) + 220$	0.82
Boyer et al. (1993)	Neuse River Estuary, NC	335	$\ln [(P_d) = 0.96(BZ_p I_0) - 0.08]$	0.66
Kelly & Doering (1997)	Massachusetts Bay, MA Boston Harbor, MA	12	$P_d = 0.79(BZ_p I_0) + 285$	0.66
Murrell et al. (2007)	Escambia Bay, FL	22	$P_d = 0.59(BZ_p I_0) + 124$	0.77
Bouman et al. (2010)	Tokyo Bay, Japan	72	$P_d = 1.87(BI_0K_T^{-1}) + 72.7$ $= 0.41(BZ_p I_0) + 72.7$	0.52
this study	Caloosahatchee Estuary, FL	24	$P_d = 0.73(BZ_p I_0) + 75$	0.84

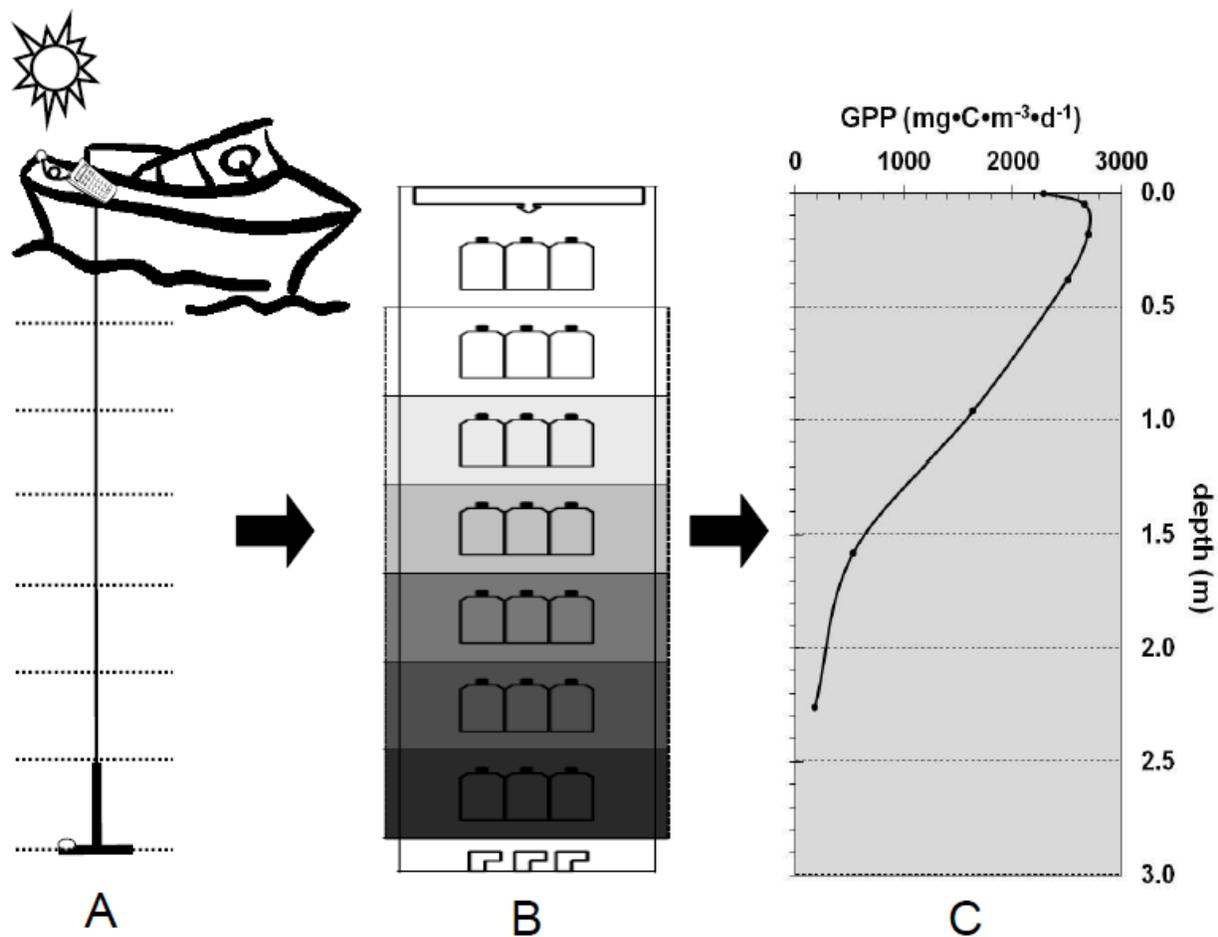


Figure 3-3. Schematic showing how the specific light transmittance-depth profile in the water column at each site (A) was emulated with various light treatment levels in the incubation raceway (B). Primary productivity rates were then plotted for each treatment group, which corresponded back to a water depth (C).

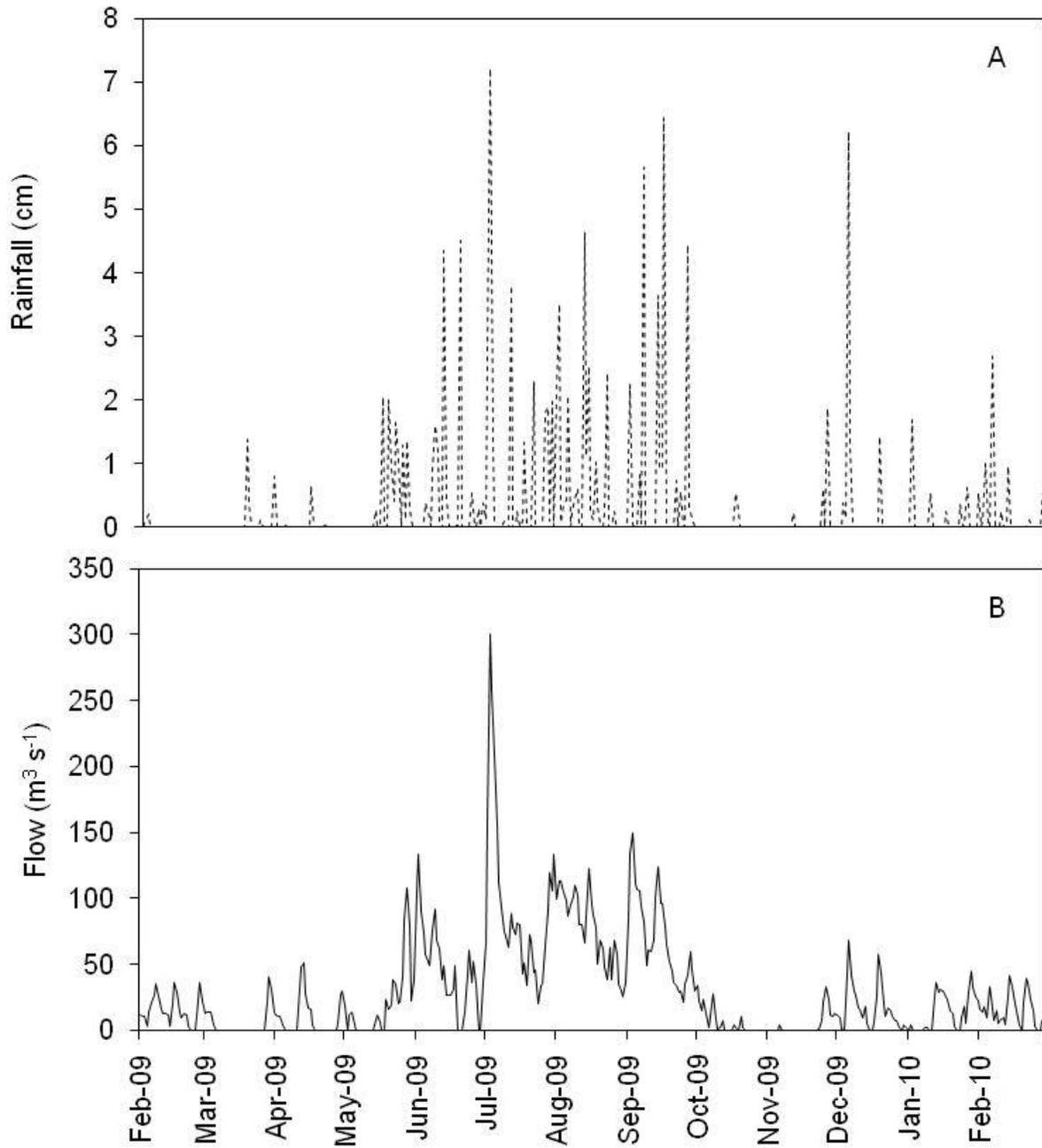


Figure 3-4. Daily rainfall (cm) (A) and flow (m³·s⁻¹) (B) from February 2009 to February 2010 at the Franklin Lock and Dam (S-79), FL, which serves as the head of the Caloosahatchee Estuary and the predominant source of freshwater.

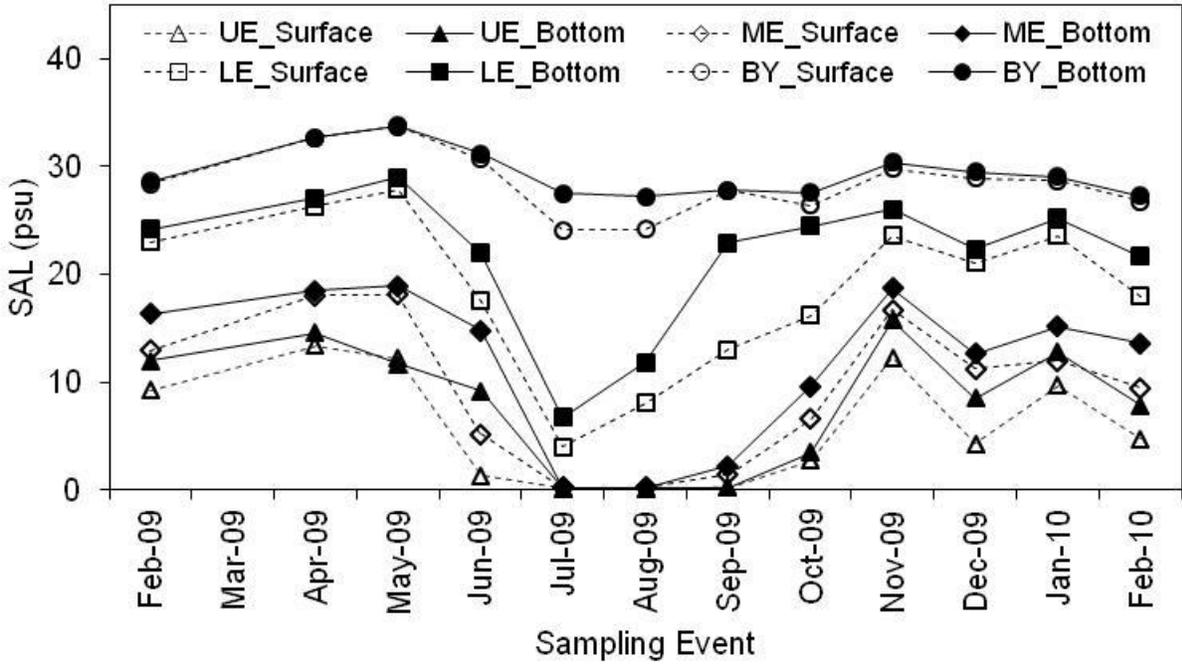


Figure 3-5. Surface and bottom salinities (SAL in psu) at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

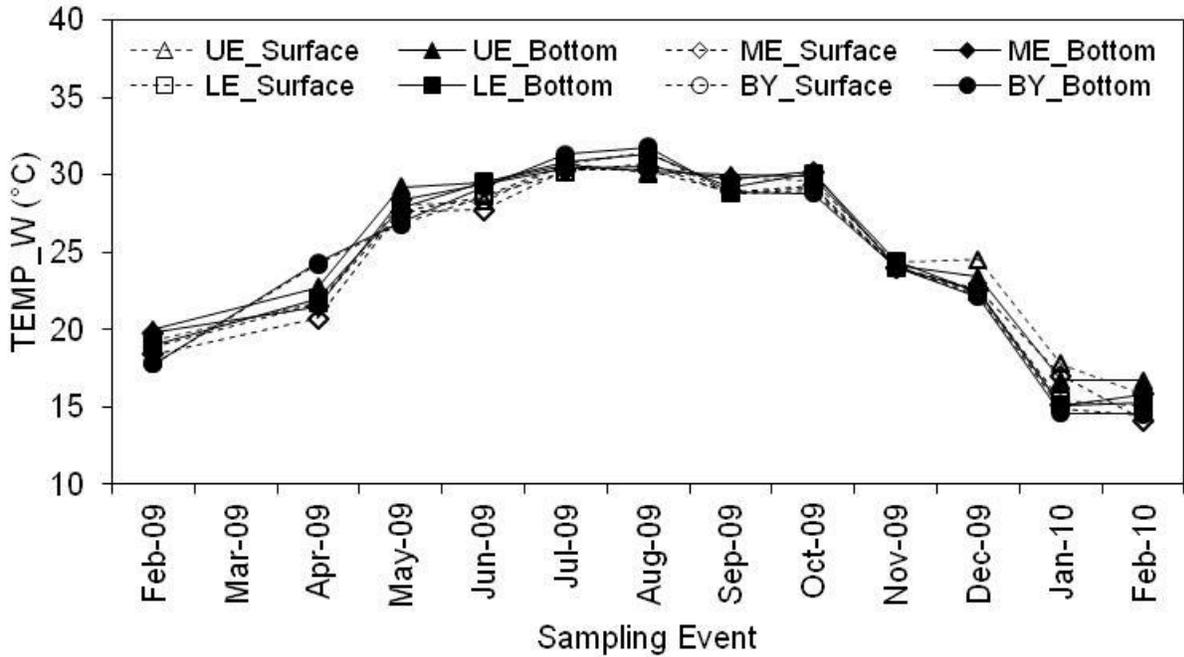


Figure 3-6. Surface and bottom water temperature (TEMP_W in °C) at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

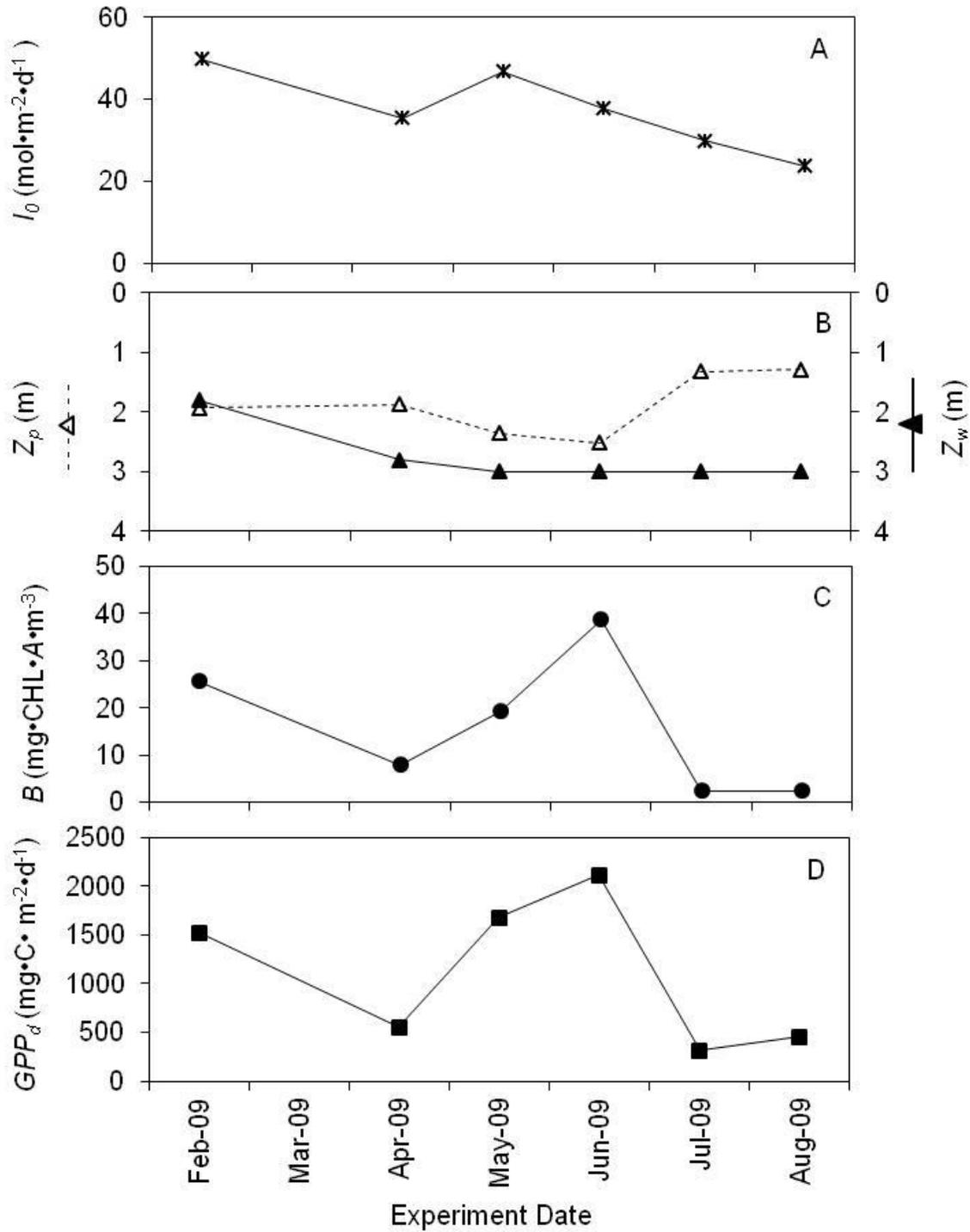


Figure 3-7. Model parameters for site UE in the Caloosahatchee Estuary, FL. Monthly variation of (A) total daytime surface irradiance (I_0 in $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), (B) photic depth (Z_p in m), and water depth (Z_w in m), (C) phytoplankton biomass (B in $\text{mg}\cdot\text{CHL}\cdot\text{A}\cdot\text{m}^{-3}$) as uncorrected chlorophyll a , and (D) measured daily gross primary productivity (GPP_d in $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), during the six-month model test.

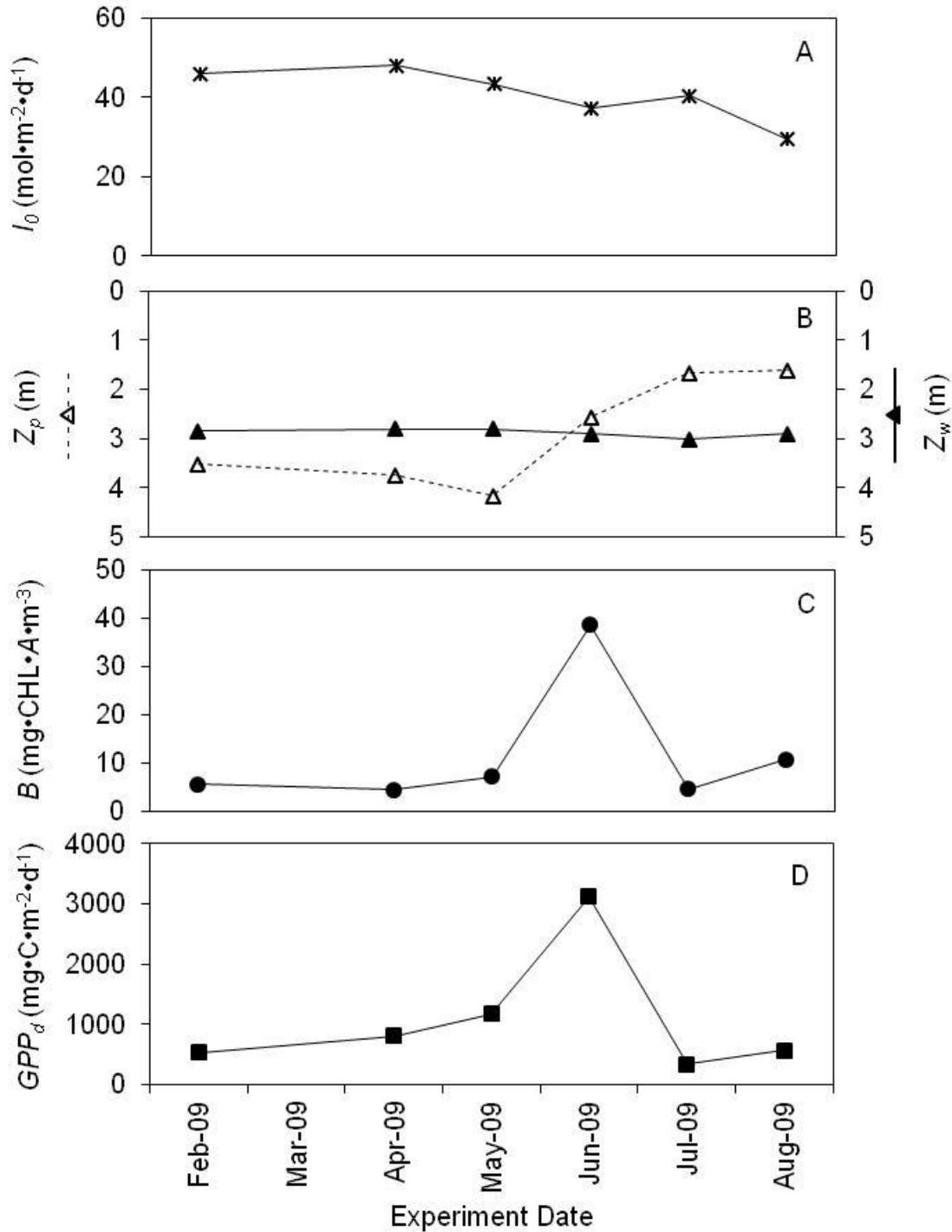


Figure 3-8. Model parameters for site ME in the Caloosahatchee Estuary, FL. Monthly variation of (A) total daytime surface irradiance (I_0 in $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), (B) photic depth (Z_p in m), and water depth (Z_w in m), (C) phytoplankton biomass (B in $\text{mg}\cdot\text{CHL}\cdot\text{A}\cdot\text{m}^{-3}$) as uncorrected chlorophyll *a*, and (D) measured daily gross primary productivity (GPP_d in $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), during the six-month model test.

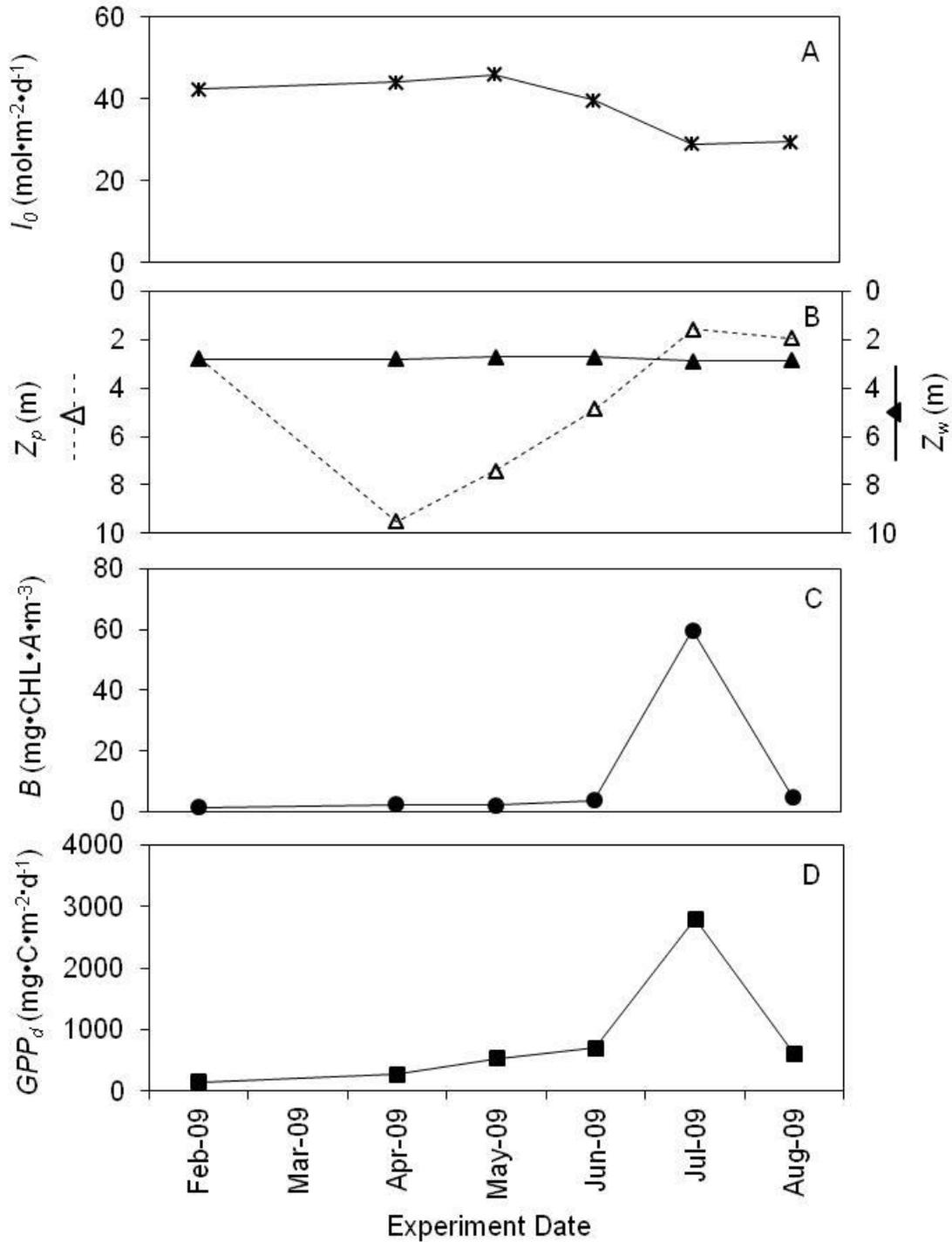


Figure 3-9. Model parameters for site LE in the Caloosahatchee Estuary, FL. Monthly variation of (A) total daytime surface irradiance (I_0 in $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), (B) photic depth (Z_p in m), and water depth (Z_w in m), (C) phytoplankton biomass (B in $\text{mg}\cdot\text{CHL}\cdot\text{A}\cdot\text{m}^{-3}$) as uncorrected chlorophyll *a*, and (D) measured daily gross primary productivity (GPP_d in $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), during the six-month model test.

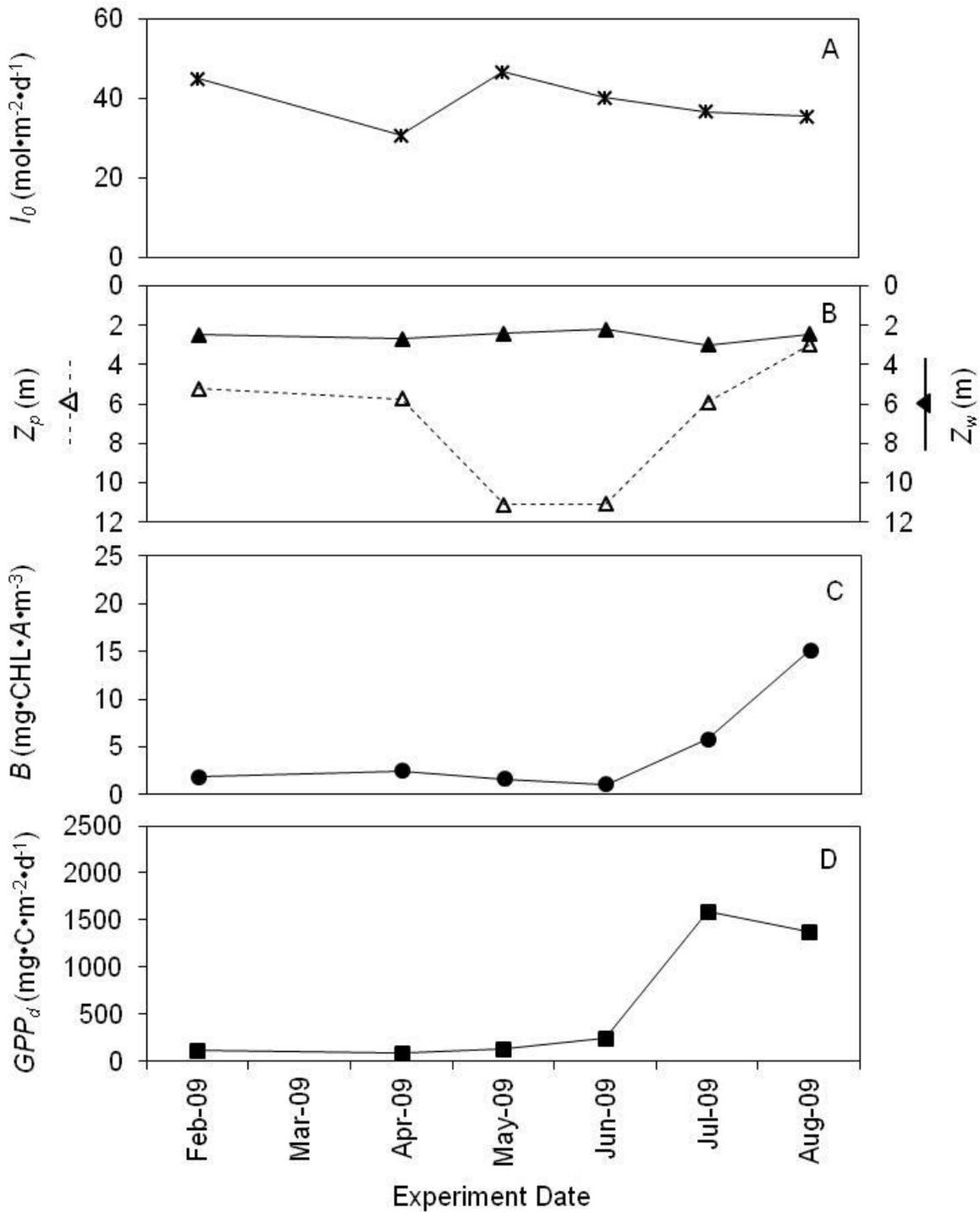


Figure 3-10. Model parameters of site BY in the Caloosahatchee Estuary, FL. Monthly variation of (A) total daytime surface irradiance (I_0 in $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), (B) photic depth (Z_p in m), and water depth (Z_w in m), (C) phytoplankton biomass (B in $\text{mg}\cdot\text{CHL}\cdot\text{A}\cdot\text{m}^{-3}$) as uncorrected chlorophyll a, and (D) measured daily gross primary productivity (GPP_d in $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), during the six-month model test.

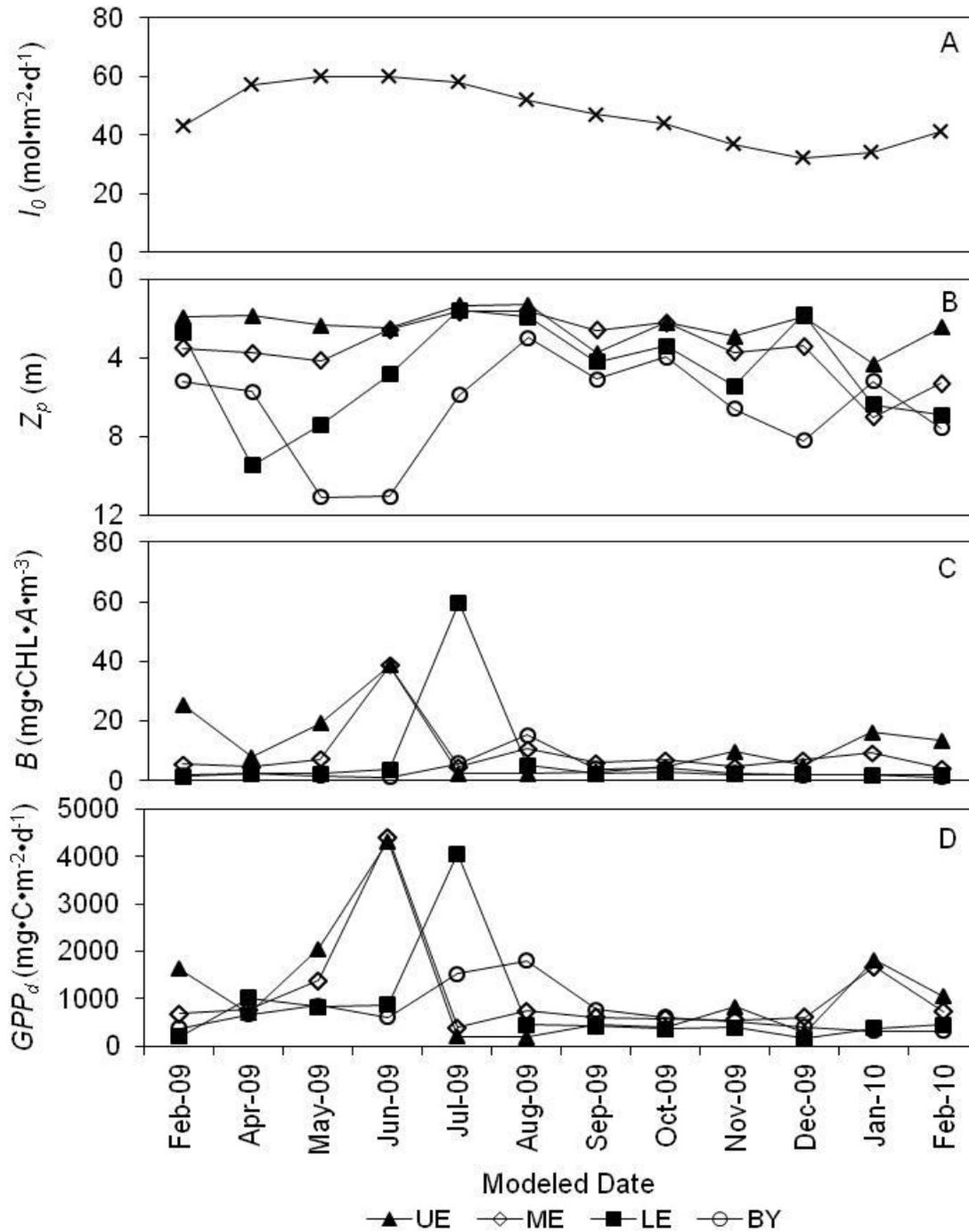


Figure 3-11. Model application for the Caloosahatchee Estuary, FL based on annual variation in (A) total daytime surface irradiance (I_0 in mol·m⁻²·d⁻¹), (B) photic depth (Z_p in m), (C) phytoplankton biomass (B in mg·CHL·A·m⁻³) as uncorrected chlorophyll a, yielding (D) modeled daily gross primary productivity (GPP_d in mg·C·m⁻²·d⁻¹), at each of the four sites from February 2009 to February 2010 (excluding March 2009).

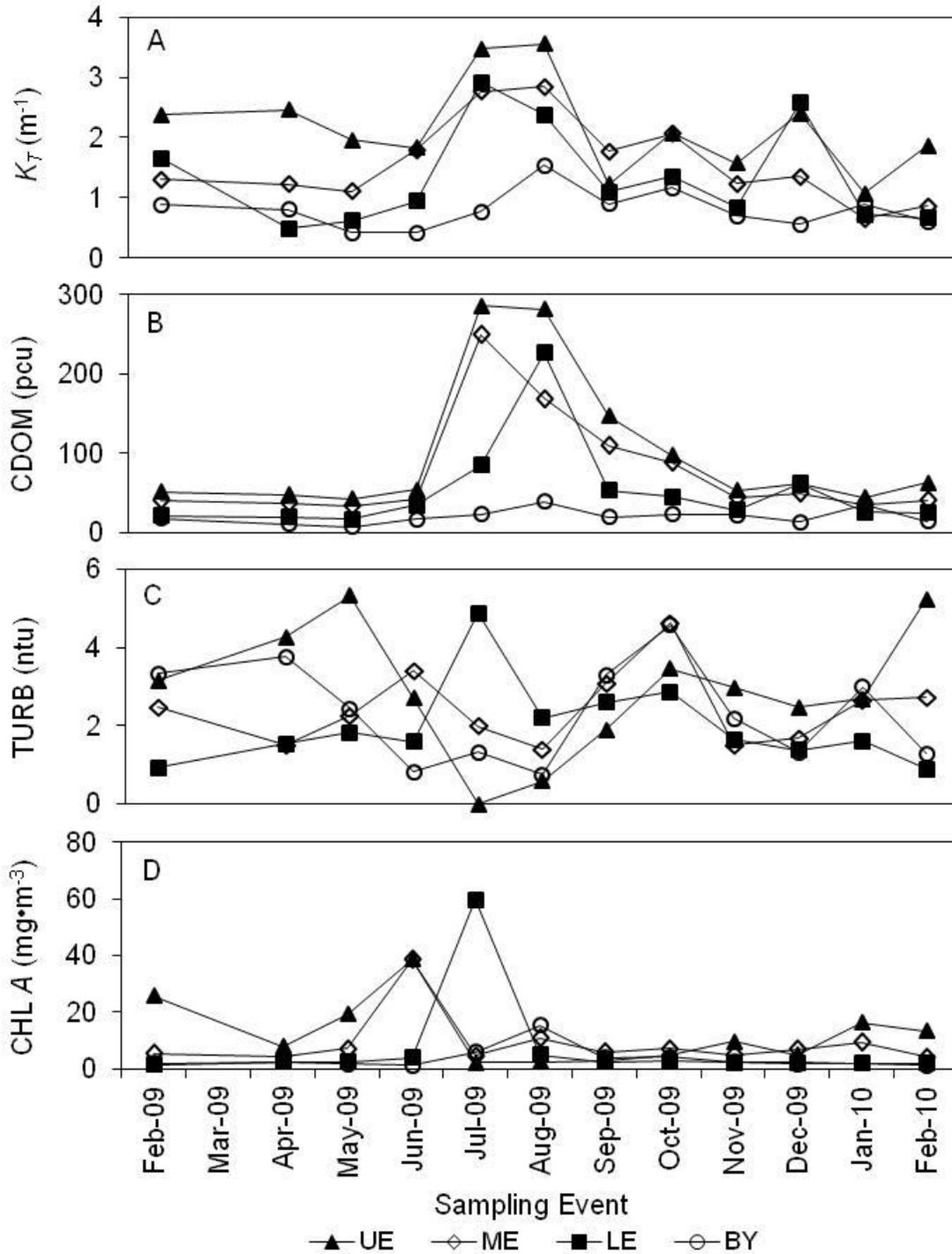


Figure 3-12. Estimates of light attenuation coefficients (K_T in m^{-1}) and corresponding concentrations of (A) color dissolved organic matter (CDOM in pcu), (B) turbidity (TURB in ntu), (C) and uncorrected chlorophyll a (CHL A in $mg \cdot m^{-3}$) at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

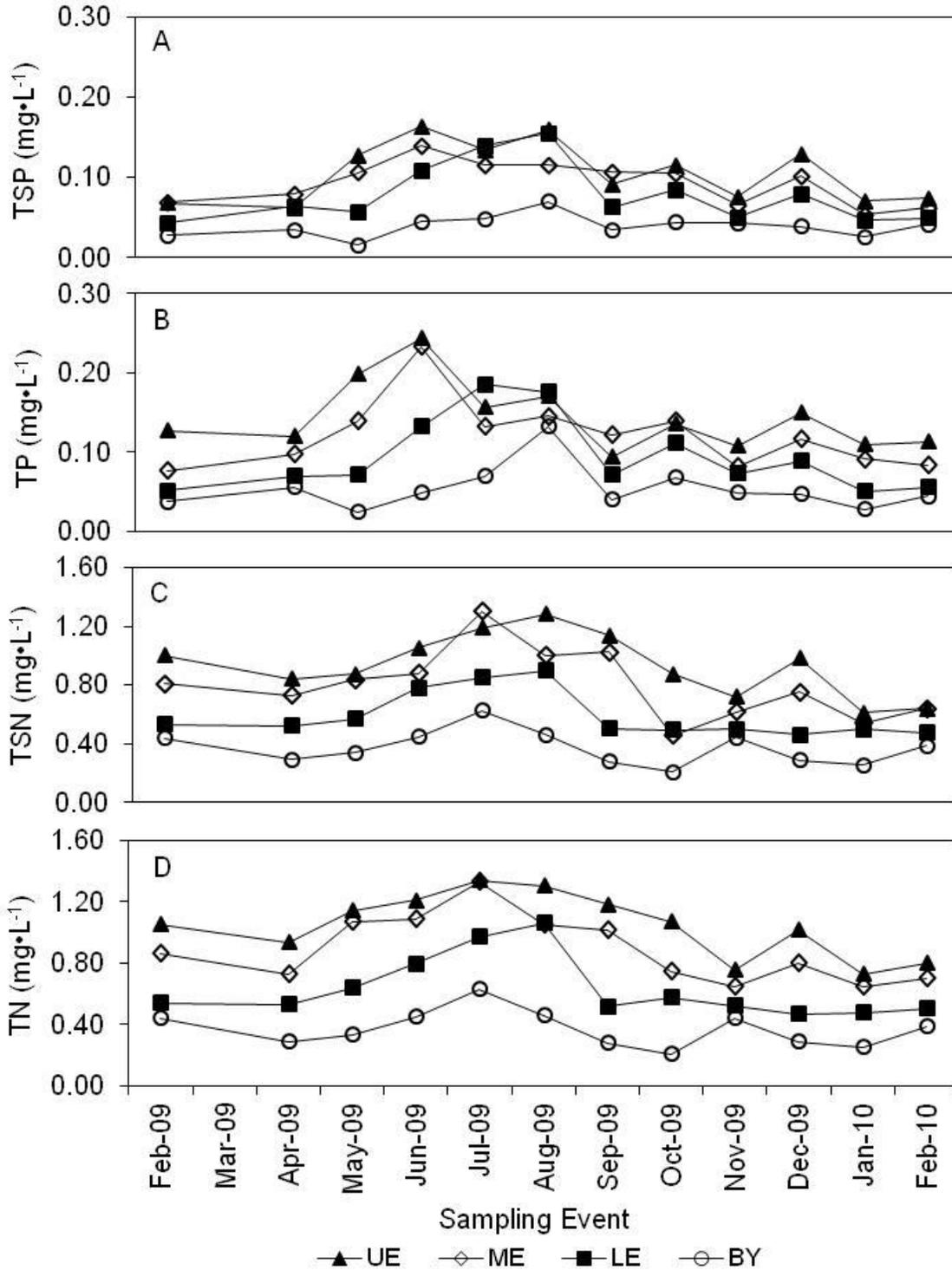


Figure 3-13. Concentrations ($\text{mg}\cdot\text{L}^{-1}$) of (A) total soluble phosphorous (TSP), (B) total phosphorous (TP), (C) total soluble nitrogen (TSN), and (D) total nitrogen (TN) at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

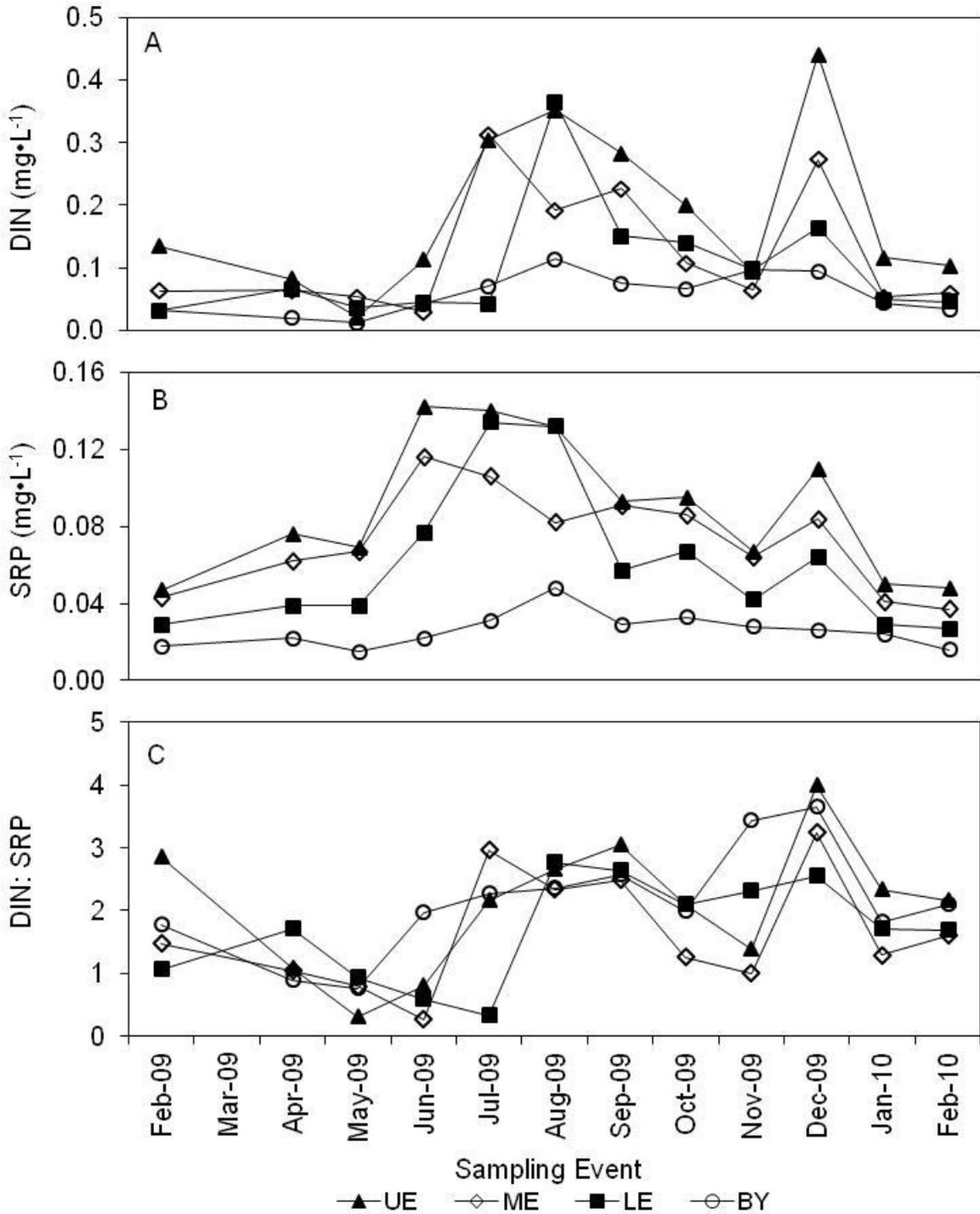


Figure 3-14. Concentrations (mg·L⁻¹) of (A) dissolved inorganic nitrogen (DIN) and (B) soluble reactive phosphorous (SRP) and (C) mass ratios of DIN to SRP at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

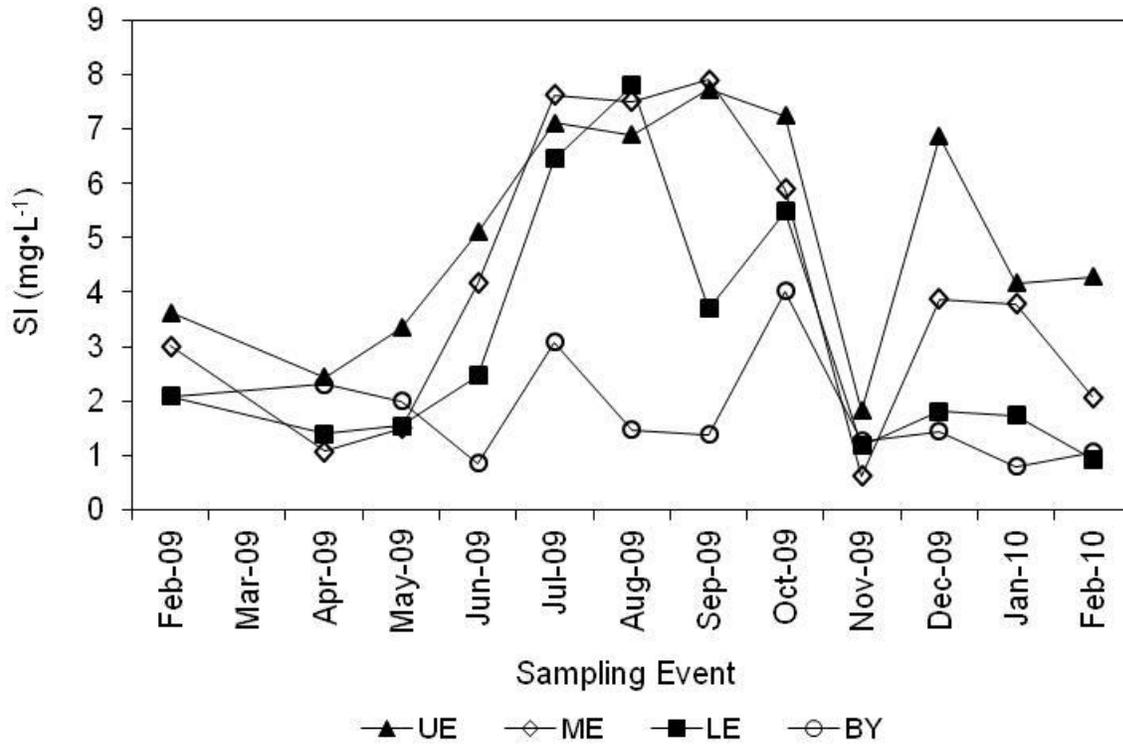


Figure 3-15. Concentrations ($\text{mg}\cdot\text{L}^{-1}$) of silica (SI) at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

Table 3-3. Phytoplankton biomass potential based on Redfield stoichiometric proportions of SRP, DIN, and SI with respect to observed phytoplankton biomass measured as CHL A.

month	site	biomass potential based on SRP	biomass potential based on DIN	biomass potential based on SI	observed biomass as CHL A
Feb-09	UE	47	19	91	26
Apr-09	UE	76	12	61	8
May-09	UE	69	3	83	19
Jun-09	UE	142	16	128	39
Jul-09	UE	140	43	178	2
Aug-09	UE	132	50	172	2
Sep-09	UE	93	40	193	3
Oct-09	UE	95	29	181	5
Nov-09	UE	67	13	46	10
Dec-09	UE	110	63	171	5
Jan-10	UE	50	17	104	16
Feb-10	UE	48	15	107	13
Feb-09	ME	43	9	75	6
Apr-09	ME	62	9	27	4
May-09	ME	67	8	38	7
Jun-09	ME	116	4	104	39
Jul-09	ME	106	45	190	5
Aug-09	ME	82	27	187	11
Sep-09	ME	91	32	197	6
Oct-09	ME	86	15	147	7
Nov-09	ME	64	9	16	5
Dec-09	ME	84	39	97	7
Jan-10	ME	41	8	95	9
Feb-10	ME	37	8	52	4
Feb-09	LE	29	4	52	2
Apr-09	LE	39	9	35	2
May-09	LE	39	5	39	2
Jun-09	LE	77	6	62	4
Jul-09	LE	134	6	161	60
Aug-09	LE	132	52	195	5
Sep-09	LE	57	22	92	2

Table 3-3. Continued.

month	site	biomass potential based on SRP	biomass potential based on DIN	biomass potential based on SI	observed biomass as CHL A
Oct-09	LE	67	20	137	3
Nov-09	LE	42	14	29	2
Dec-09	LE	64	23	45	2
Jan-10	LE	29	7	43	2
Feb-10	LE	27	7	23	2
Feb-09	BY	18	5	52	2
Apr-09	BY	22	3	58	3
May-09	BY	15	2	50	2
Jun-09	BY	22	6	22	1
Jul-09	BY	31	10	77	6
Aug-09	BY	48	16	37	15
Sep-09	BY	29	11	34	4
Oct-09	BY	33	9	100	4
Nov-09	BY	28	14	32	2
Dec-09	BY	26	14	36	2
Jan-10	BY	24	6	20	2
Feb-10	BY	16	5	26	1

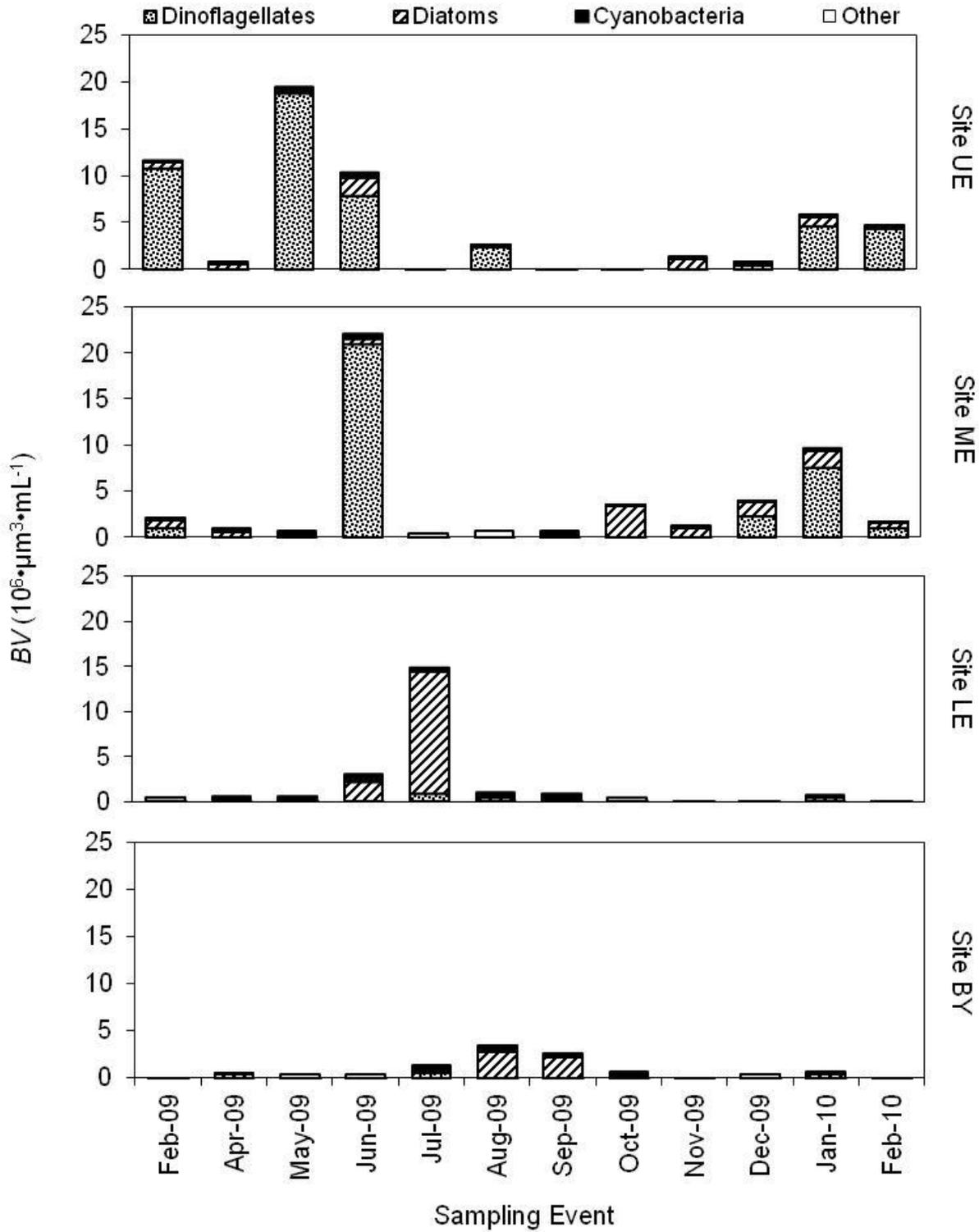


Figure 3-16. Total phytoplankton biovolume concentration (BV in $10^6 \cdot \mu\text{m}^3 \cdot \text{L}^{-1}$) of dinoflagellates, diatoms, cyanobacteria, and other phytoplankton taxa at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

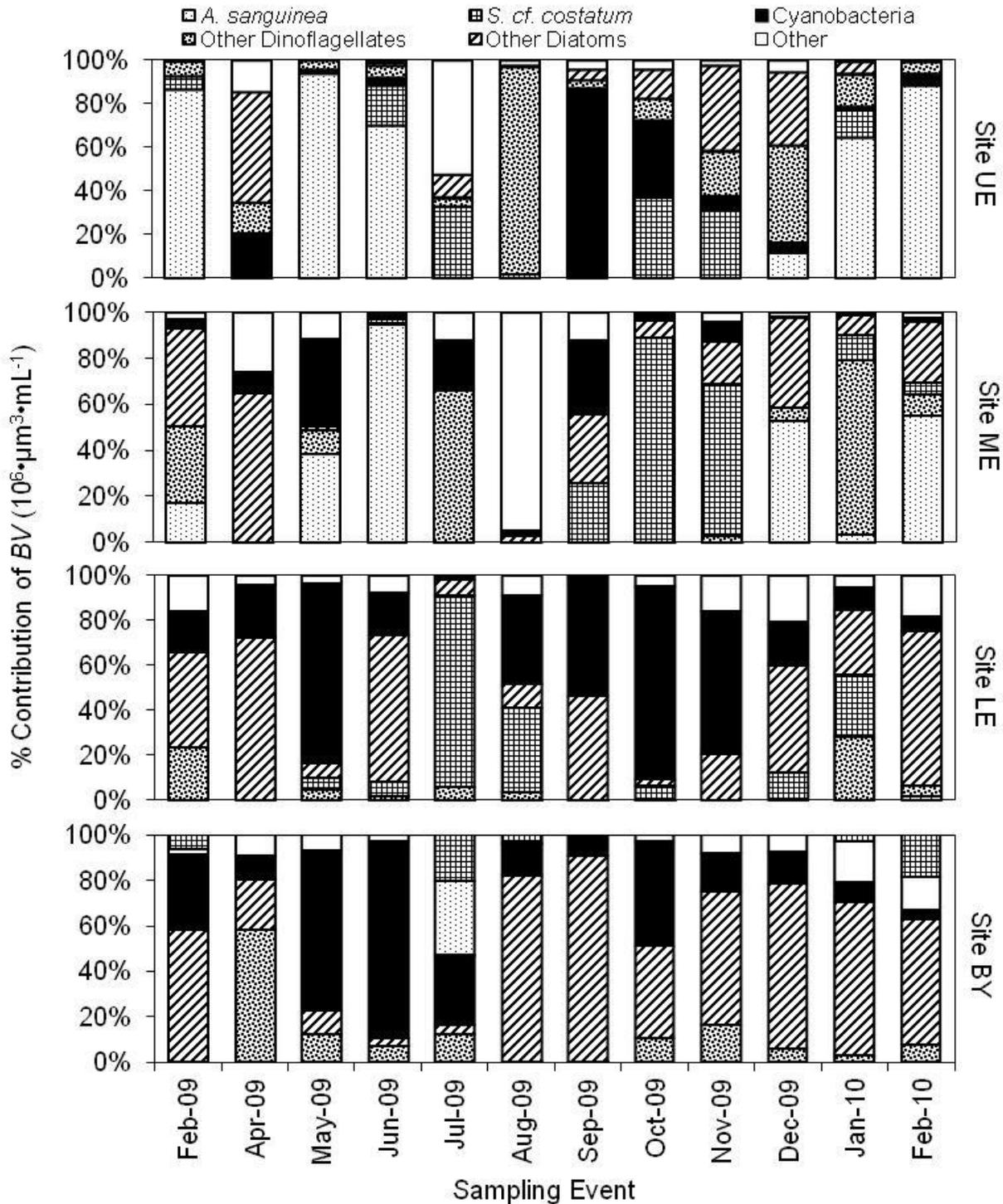


Figure 3-17. Percent contribution of *A. sanguinea* and other dinoflagellates, *S. cf. costatum* and other diatoms, cyanobacteria, and other phytoplankton taxa to total phytoplankton biovolume concentration (BV in $10^6 \cdot \mu\text{m}^3 \cdot \text{mL}^{-1}$) at each of the four sites in the Caloosahatchee Estuary, FL from February 2009 to February 2010 (excluding March 2009).

Table 3-4. Summary of measured and modeled daily primary productivity (GPP_d in $mg \cdot C \cdot m^{-2} \cdot d^{-1}$) from each of the four sites in the Caloosahatchee Estuary, FL. Measured values were obtained from six monthly simulated *in situ* incubation experiments between February and August 2009 (excluding March). Modeled values were obtained from twelve monthly applications of the ‘fitted’ and ‘best suited’ BZ_{p/l_0} model between February 2009 and February 2010 (excluding March 2009).

	Upper Estuary (UE)	Middle Estuary (ME)	Lower Estuary (LE)	San Carlos Bay (BY)
<i>measured GPP_d</i>				
minimum	322	328	153	90
median	1040	679	576	188
maximum	2120	3121	2797	1587
mean	1108	1083	847	590
<i>modeled GPP_d</i>				
minimum	189	398	163	324
median	763	711	433	612
maximum	4318	4405	4061	1799
mean	1161	1096	800	735

Table 3-5. Summary of tested model relationships based on phytoplankton biomass (B) in terms of CHL A concentrations (uncorrected or corrected for pheophytin), photic depth (Z_p) calculated or corrected for water depth (Z_w), and productivity (measured gross or net daily rates). The NPP_d models included one less data point ($N = 23$) than the GPP_d models ($N = 24$) due to the negative net productivity value observed in February 2009 at site BY, which was removed from the dataset since no explanation could be given. Intercepts that were significantly different from zero at a 0.05 significance level are marked with an asterisk (*).

B	Z_p	productivity	slope	intercept	r^2	p -value
unc CHL A	calculated	GPP_d	0.73	75	0.84	<0.0001
unc CHL A	calculated	NPP_d	0.63	102	0.82	<0.0001
unc CHL A	corrected	GPP_d	0.70	256 *	0.85	<0.0001
unc CHL A	corrected	NPP_d	0.59	262 *	0.81	<0.0001
corr CHL A	calculated	GPP_d	0.76	111	0.80	<0.0001
corr CHL A	calculated	NPP_d	0.65	132	0.78	<0.0001
corr CHL A	corrected	GPP_d	0.75	277 *	0.83	<0.0001
corr CHL A	corrected	NPP_d	0.63	281 *	0.80	<0.0001

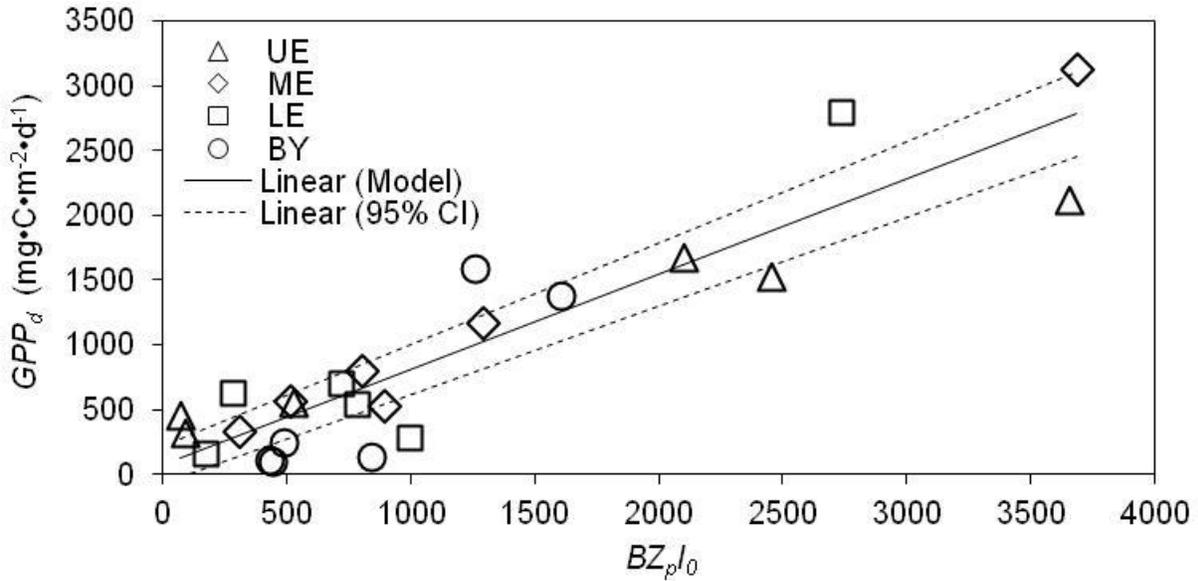


Figure 3-18. Regression of daily gross primary productivity (GPP_d in $mg \cdot C \cdot m^{-2} \cdot d^{-1}$), against the composite parameter $BZ_{\rho} I_0$ for 24 incubation experiments. Uncorrected CHL A was used for B and calculated Z_{ρ} values were not corrected for water column depths. $GPP_d = 75 + 0.73BZ_{\rho} I_0$ (solid line); 95% confidence interval of mean (dashed lines); $r^2 = 0.84$; overall model and slope were significant ($p < 0.0001$); intercept was not significant ($p = 0.4849$).

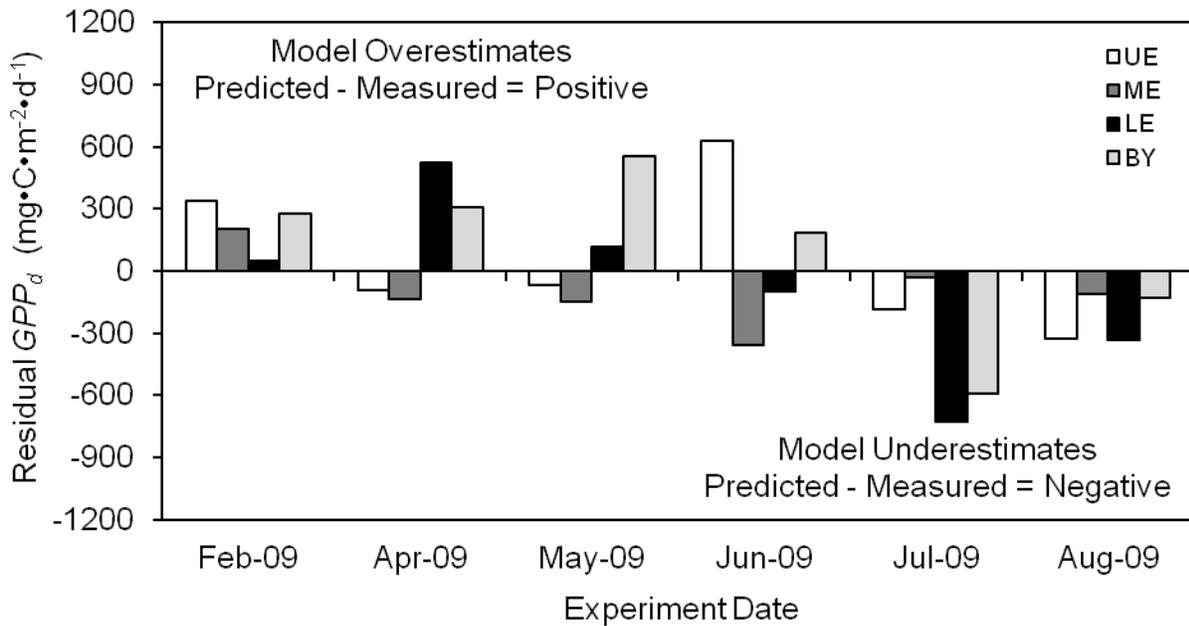


Figure 3-19. Estimated differences between predicted and measured primary productivity values for all four sites across six monthly incubation experiments.

Table 3-6. Annual phytoplankton productivity estimates (system-wide ranges or site-specific means) of various river-dominated estuaries. All estimates are assumed to be net primary productivity although not all investigators specified the methodology used. Year corresponds to date of the reference and not the date of the experiments.

system	productivity $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$	sampling location	reference
North San Francisco Bay, CA	95 110-130	Suisun Bay San Pablo Bay	Cole & Cloern (1984)
Fourleague Bay, LA	120 317	Upper Bay Lower Bay	Randall and Day (1987)
Narragansett Bay, RI	189 308	dock Mid-Bay	Keller (1988) Furnas et al. (1976)
Hudson River Estuary, NY	200 370	Lower Bay Bight	Malone (1977) Malone (1976)
Mobile Bay, AL	242		Pennock et al. (1999)
Apalachicola Bay, FL	240 255		Pennock et al. (1999) Mortazavi et al. (2000)
Escambia Bay, FL	291		Murrell et a. (2007)
Caloosahatchee Estuary, FL	245 266 359 379	San Carlos Bay Lower Estuary Middle Estuary Upper Estuary	this study
Neuse River Estuary, NC	343 456		Mallin et al. (1991) Boyer et al. (1993)
Nueces River Estuary, TX	370		Pennock et al. (1999)
Delaware Bay, DE	190-400		Pennock & Sharp (1986)
Charlotte Harbor, FL	83-438		McPherson et al. (1990)
Tokyo Bay, Japan	370-580		Bouman et al. (2010)
Mid-Chesapeake Bay, MD	337-782		Boynton et al. (1982)

CHAPTER 4
NATURAL AND ANTHROPOGENIC INFLUENCES ON THE SPATIAL AND
TEMPORAL PATTERNS OF PHYTOPLANKTON PRODUCTIVITY IN THE
CALOOSAHATCHEE ESTUARY, FLORIDA

Concepts and Applications

With coastal eutrophication emerging as one of the most pressing and widespread problems of the late 20th and early 21st centuries (Nixon 1995, Cloern 2001, Schindler 2006, Bricker et al. 2008), tracing and understanding major shifts in the trophic status of estuaries and coastal ecosystems have become the primary focus of many research and management efforts (Zingone et al. 2010). The trophic status of an ecosystem is best defined by its supply of organic matter as rates of primary production (Nixon 1995, Schindler 2006), but the associated terminology is more commonly used to characterize the level of anthropogenic influence on a system, primarily in the form of nutrient enrichment (Nixon 1995, Cloern 2001). Inputs of nutrients, namely nitrogen and phosphorous, have accelerated in coastal waters due to human activities in the surrounding watershed, such as land clearing, fertilizer production and application, animal consumption, sewage emission, and fossil fuel combustion (Nixon 1995, Vitousek et al. 1997b, Cloern 2001). Nutrient levels in coastal ecosystems are also affected by natural processes like geochemical weathering and internal recycling, which are largely regulated by climate and weather (Schindler 2006). A major consequence of coastal eutrophication is the over-production and accumulation of plant biomass, which can come in the form of toxic, harmful, and/or nuisance algal blooms that have been associated with hypoxic conditions, fish kills, community shifts, human health risks, and a suite of other responses (Nixon 1995, Cloern 2001, Bricker et al. 2008).

Because the trophic status of an ecosystem can change as a result of both natural and anthropogenic influences, it should be treated more as a dynamic process rather than a static description of the conditions of an ecosystem (Nixon 1995). The ability to fairly assess and manage changes in the trophic status of an ecosystem thus requires long time series that encompass seasonal, interannual, and decadal variations in primary production (Zingone et al. 2010). Long time series of primary productivity data from estuaries and coastal ecosystems are rare due to the historical focus of aquatic research in freshwater ecosystems (Boynton et al. 1982, Cloern 2001), as well as the logistical limitations of the traditional methods used to measure photosynthetic rates (Ryther 1956b, Ryther and Yentsch 1957, Tilzer 1989, Sand-Jensen 1997). Attempts to determine and compare the trophic status of aquatic ecosystems have primarily relied on a suite of biological and physical-chemical parameters and/or symptoms that serve as proxies for primary production rates and indicators of water quality including concentrations of chlorophyll *a*, levels of dissolved oxygen, concentrations of limiting nutrients, measures of water transparency, and appearances of key plant and animal species (Ryding and Rast 1989, Schindler 2006, Bricker et al. 2008, Boyer et al., 2009). Chlorophyll *a* has been the more widely used and accepted index of productivity and trophic status in estuaries and coastal ecosystems because it is easily and routinely measured in oceanographic investigations, and it provides a generally good assessment of the structure and function of both lower and higher order trophic levels and the associated biogeochemical processes (Cloern 2001, Boyer et al. 2009, Cloern and Jassby 2010, Zingone et al. 2010). However, very few time series clearly document trends of increasing chlorophyll *a* in concert with trends of increasing

nutrients associated with coastal eutrophication and, in some cases, the opposite relationship is observed (Boynton et al. 1982, Cloern 2001). Inconsistencies in the responses of estuaries and coastal ecosystems to natural and anthropogenic stressors are due to a number of morphological, physical, chemical, and biological factors that are unique to each ecosystem and have the potential to regulate photosynthetic biomass and production (Brylinsky and Mann 1973, Boynton et al. 1982, Day et al. 1989, Cloern 2001). As an indicator of phytoplankton biomass, chlorophyll *a* represents the net result of both growth and loss processes, so using it alone to characterize trophic status may not accurately portray the productivity potential of an ecosystem.

To overcome the challenges encountered when using traditional methods for measuring primary productivity and assessing trophic status on the basis of more descriptive indices, investigators have turned to ecosystem modeling to identify factors that govern production and obtain accurate production estimates (Odum 1968, Vollenwider 1969, Brylinsky and Mann 1973, Boyer et al. 1993, Scardi 1996). The $BZ_p I_0$ or 'light•biomass' model developed by Cole and Cloern (1987) is an example of a simple, empirical relationship founded on long-standing paradigms that emerged in the mid-twentieth century that address the primary factors controlling phytoplankton productivity in aquatic ecosystems (Ryther 1956b, Ryther and Yentsch 1957). This approach has provided robust estimates of phytoplankton productivity in estuaries and coastal ecosystems around the world (Cole and Cloern 1987, Keller 1988, Mallin et al. 1991, Boyer et al. 1993, Kelly and Doering 1997, Murrell et al. 2007, Bouman et al. 2010). Most of the model applications were in temperate systems, except for Escambia Bay, Florida, which was classified as being subtropical despite its annual temperature,

rainfall, and river flow patterns that are more characteristic of temperate environments (Murrell et al. 2007). The recent adaptation of the BZ_{p/l_0} or 'light•biomass' model to the Caloosahatchee Estuary, Florida extended its applicability to a truly subtropical system and one with additional distinct features (Chapter 3).

The Caloosahatchee Estuary is a shallow, microtidal subtropical system that has been extensively modified from its natural state since the late 1800s. It is one of many ecosystems making up the Florida Everglades that have been originally used, subsequently altered, and currently maintained in order to accommodate agriculture and urban development in an otherwise uninhabitable area prone to prolonged flooding. The Caloosahatchee Estuary was once fed by a small, sinuous river that originated from a small lake that was “scarcely more than a swamp” amid an extensive sawgrass marsh (Teeter 1980, Flaig and Capece 1998, Knight and Steele 2005). The estuary is now artificially connected to Lake Okeechobee, the headwaters of the Florida Everglades and the heart of a major agriculture, cattle, and dairy industry, via a trans-state canal that is deeper, wider, and straighter than the original Caloosahatchee River. Three lock and dam structures control the flow of water between Lake Okeechobee, the Caloosahatchee Estuary, and ultimately the Gulf of Mexico. The trophic status of the Caloosahatchee Estuary has become a growing concern over the last few decades due to the contribution of hypertrophic waters, released from Lake Okeechobee and flushed downstream, to coastal eutrophication and the prevalence of harmful algal blooms (Perry 2008).

The purpose of this study was to use the BZ_{p/l_0} or 'light•biomass' model (Cole and Cloern 1987) previously adapted to the Caloosahatchee Estuary, Florida (Chapter 3) to

obtain long-term estimates of daily gross primary productivity (GPP_d) for the system. Model parameters were extracted from an existing discontinuous twenty-five year water quality data set, thereby extending the usefulness of the associated monitoring programs/research projects to trace and understand changes in the system's trophic status. Multivariate statistical methods were employed to build a complete subset of data in order to identify potential environmental drivers of phytoplankton productivity in the Caloosahatchee Estuary. Variability in chlorophyll *a* associated with seasonal cycles, annual disturbances (i.e., human actions, climatic shifts), and residual events (i.e., phytoplankton blooms), was also explored using the methods of Cloern and Jassby (2010), since phytoplankton biomass was previously identified as the main explanatory variable of GPP_d (Chapter 3). Long-term changes in GPP_d and the estuary's trophic status were examined for their connection to both natural and anthropogenic influences in the surrounding watershed on the structure and function of the entire ecosystem.

Methods

Study Area

The Caloosahatchee Estuary is an extensively modified, shallow, microtidal, subtropical system located on the southwest coast of Florida in Lee County (Figure 4-1). The upper reach of the Caloosahatchee Estuary is connected to Lake Okeechobee via the Caloosahatchee River (C-43 Canal), and the lower reach of the estuary is connected to the Gulf of Mexico and Charlotte Harbor via San Carlos Bay. The physical shape and hydrology of the system has been modified from its natural state since the late 1800s. In addition to a series of canals and pumping stations, three lock and dam structures now control the flow of water between Lake Okeechobee and the Caloosahatchee Estuary along the C-43 Canal. The Franklin Lock and Dam (S-79)

artificially serves as the head of the estuary and main source of freshwater approximately 42 km upstream of Shell Point (Figure 4-2). The width of the estuary is irregular, ranging from 160 m near S-79 to 2,500 m in San Carlos Bay (Scarlatos 1988). The narrow section extending from S-79 to Beautiful Island has an average depth of 6 m, but the area downstream of Beautiful Island has an average depth of 1.5 m (Scarlatos 1988). A narrow navigation channel (part of the Intracoastal Waterway) is maintained at a depth of approximately 3.5 m (Scarlatos 1988). The area experiences a combination of diurnal and mixed semi-diurnal tides with a mean tidal range of 0.30 m in the middle of the estuary near downtown Fort Myers (Scarlatos 1988, NOAA 2010).

Freshwater flows through S-79 at a rate great enough to fill the entire volume of the estuary over eight times in an average year (Doering and Chamberlain 1999). Flow rates are set by the South Florida Water Management District (SFWMD) and the United States Army Corps of Engineers (USACE) to maintain prescribed water levels in Lake Okeechobee, control flooding, and flush algal blooms, salt water, and other contaminants out of the Caloosahatchee River (Stoker 1992, Flaig and Capece 1998, Doering and Chamberlain 1999, Rand and Bachman 2008). The estuary also receives an average of 137 cm of rainfall per year (NCDC 2011), of which the majority (75%) arrives during the months of May through October, defining a typical wet season (Stoker 1992). Surface water runoff accompanying this rainfall passes through agricultural areas in the east and urban areas in the west. The combination of rainfall, runoff, and releases from the watershed and canals causes large fluctuations in the quantity, quality, timing, and distribution of freshwater inflow to the estuary, which has affected

the structure, function, and overall health of the ecosystem (Chamberlain and Doering 1998a, Barnes 2005, Knight and Steele 2005, SFWMD et. al 2009).

Water Quality Data Sources and Manipulations

A twenty-five year data set (January 1986 through December 2010) was compiled using water quality data collected in the vicinity of the Caloosahatchee Estuary during five monitoring programs/research projects either conducted or supported by the South Florida Water Management District, West Palm Beach, Florida (SFWMD 2011). No water quality data were available for the periods of June 1989 through September 1994 and July 1997 through March 1999. Additional months in the twenty-five year period were also missing water quality data, although they occurred at random times and do not represent significant gaps in the data set. Water quality data collected at sites outside the bounds of the defined study area (i.e., the Caloosahatchee Estuary between S-79 and Shell Point) and San Carlos Bay, were not included in the combined data set, unless otherwise noted.

The five monitoring programs/research projects that contributed water quality data include:

1. The Caloosahatchee Estuary (CAL) program sampled eighteen stations (1 through 18) in the Caloosahatchee Estuary (S-79 to Shell Point), San Carlos Bay, Matlacha Pass, and Pine Island Sound. The two stations in Pine Island Sound (15 and 16) were excluded from the data set due to their distance from S-79 and physical separation from the other stations in the study area by Pine Island. The station described as being in Matlacha Pass (14) was still included in the data set due to its close vicinity and connectivity to San Carlos Bay. Stations were sampled monthly from December 1985 to May 1989, although the December 1985 measurements were not included in the data set. Sampling continued at a subset of stations from October 1994 to August 1996. Additional samples were collected at a select few sites in April 1997 and April 1999.
2. The Coastal Charlotte Harbor Monitoring (CCHM) project was created for the Charlotte Harbor National Estuary Program. The Caloosahatchee Estuary (S-79 to Shell Point) was divided into fifty grid squares (3.4 km² each) according to the

Florida Fish and Wildlife Conservation Commission – Florida Marine Research Institute Fisheries Independent Monitoring Program Grid System (Corbett 2004), and sampling occurred at a random location within the grid squares. Stations were registered according to the GPS location of the bottom right-hand corner of the grid in which the sample was collected. Samples were collected monthly within five randomly selected grids from September 2006 to September 2009.

3. The Center for Environmental Studies (CES) program was initially developed as an on-going water quality monitoring program, but it was later redesigned and renamed the Caloosahatchee Estuary Water Quality Monitoring Program (CESWQ). A total of eleven stations (1 through 11) in the Caloosahatchee River (upstream of S-79), Caloosahatchee Estuary (S-79 to Shell Point), and San Carlos Bay have been sampled since the program's start. The station located upstream of S-79 (1) was excluded from the data set for being outside the boundaries of the defined study area. Stations were sampled monthly between April 1999 and March 2002. Monthly sampling resumed in May 2002 and continues today at a smaller subset of stations. Only measurements through December 2010 were included in the data set. Additional sampling occurred at selected times and at specific sites to capture event-driven effects of freshwater releases from Lake Okeechobee to the Caloosahatchee Estuary.
4. The Environmental Research and Design (ERD) program sampled fifteen (1 through 15) sites in the Caloosahatchee Estuary (S-79 to Shell Point), San Carlos Bay, and Gulf of Mexico. The two stations in the Gulf of Mexico on the south side of the Sanibel Causeway (1 and 2) were excluded from the data set for being beyond the boundaries of the defined study area. Stations were sampled four times (approximately ten days apart) during the wet and dry seasons over a three-year period from 2000 to 2002.
5. The Harbor Branch (HB) project included seven (1 through 7) stations in the Caloosahatchee Estuary (S-79 to Shell Point), San Carlos Bay, and Pine Island Sound. The station in Pine Island Sound (7) was excluded from the data set due to its distance from S-79 and physical separation from the other stations by Pine Island. Stations were visited between May 1996 and March 1997. The frequency of sampling was not consistent; samples were collected on a weekly or bi-weekly schedule for some months, while other months had only one collection or none at all.

The resulting twenty-five year data set, hereafter referred to as 'data set', was a compilation of all discontinuous sampling efforts from the five monitoring programs/research projects. All monthly, bi-weekly, weekly, and event-driven sample collections were included in the data set so that the most comprehensive span of water quality, phytoplankton biomass, and primary productivity data could be obtained. To

address the issue of inconsistent sampling frequencies, monthly means were taken across the measurements obtained from multiple collections at the same site and used to represent conditions there for a given month. When sites were only sampled once in a given month, then the measurements from the single collection were used to represent average conditions there for the entire month. Measurements from individual collections were also considered separately (and noted when done so) to identify the timing of bloom events. The data set was further manipulated to prevent errors with mathematical computations and statistical analyses. Any reported negative values were replaced with zero. Values recorded in conjunction with a 'less than' symbol (e.g., $\text{NH}_3 < 5$) were taken as the value alone (e.g., $\text{NH}_3 = 5$).

The compiled data set encompassed the sampling efforts at a total of eighty different sites, having unique GPS (latitude and longitude) coordinates, not counting multiple locations that were used in more than one project. Because sampling efforts were not continuous at each of the sites over the extent of the data set, sites were classified using two systems (geographic and physical-chemical) so that spatial, in addition to temporal, variation in water quality, phytoplankton biomass, and primary productivity in the estuary could be addressed. The validity of using a site classification scheme to pool data was tested with a hierarchical agglomerative clustering analysis and corresponding similarities profile analysis (further details provided in the **Statistical Analyses for Identification of Environmental Drivers** section).

Sites were grouped into four geographic regions according to their distance from S-79 (Doering and Chamberlain 1999, Doering et al. 2006), The four regions were classified as the Upper Estuary (UE), Middle Estuary (ME), Lower Estuary (LE), and

San Carlos Bay (BY) (Figure 4-2), and sites lying between 0 to 14, 14 to 28, 28 to 40, and 40 to 48 km from S-79 were assigned to each region accordingly (Table 4-1). The division of the Caloosahatchee Estuary into segments of varying distance from S-79 has been the traditionally used approach in system monitoring and modeling efforts there because it accounts for spatial differences in geology, bathymetry, and hydrology (Scarlatos 1988, Bierman 1993, Doering and Chamberlain 1999, Doering et al. 2006).

Sites were also assigned to one of five salinity zones using the Venice System (Anonymous 1959) based on water column conditions at the time of sample collection. Sites having measured salinities between 0 to 0.5, 0.5 to 5, 5 to 18, 18 to 30, and 30 to 40 psu were categorized in salinity zones freshwater, oligohaline, mesohaline, polyhaline, and euhaline, respectively (Table 4-2). This approach essentially divided the Caloosahatchee Estuary into ecoclines governed by gradual and progressive gradients of salinity (Quinlan and Philips 2007). Here, salinity was assumed to be the dominant environmental factor defining a water mass and regulating the phytoplankton community structure and function in the Caloosahatchee Estuary since it corresponds directly to changes in freshwater inflow and tidal exchange.

The five salinity zones roughly encompassed the previously described median salinity values for each of the four geographic regions (Table 4-2). Although the four geographic regions (UE, ME, LE, and BY) represented a fixed spatial classification system based on sampling location, sites were expected to shift between the five salinity zones (freshwater, oligohaline, mesohaline, polyhaline, and euhaline) due to variation in freshwater inflow and tidal influence in the estuary. For example, the location of the freshwater-saltwater interface (the point at which the salinity is 0.5 psu)

moves upstream and downstream daily with the tide and seasonally with the volume of freshwater inflow (Stoker 1992).

Water Sampling and Analyses

For each of these monitoring programs/research projects, water samples were collected at a depth of 0.5 m using a van Dorn or similar horizontal sampling device (Doering and Chamberlain 1999, Corbett 2004, Doering et al. 2006). Any measurements on water collected at depths other than 0.5 m were excluded from the data set to maintain consistency in methodology across the twenty-five year time period. Depending on the scope of the respective monitoring programs/research projects, a number of physical and chemical measurements were taken directly in the field or from laboratory analyses.

At each site, vertical profiles of temperature (TEMP_W), salinity (SAL), and dissolved oxygen (DO) were recorded using a Hydrolab or YSI. Only the readings taken at a depth of 0.5 m were included in the data set to correspond to the collected water sample since bottom measurements were not consistently provided. Estimates of photic depth (Z_p ; depth of 1% incident irradiance) were derived from secchi disk depths (Z_s) using the relationship $Z_p = 2 * Z_s$ (Wetzel 1983). For the ERD project, Z_s measurements were not available, so Z_p estimates were calculated as $4.61/K_T$. Light attenuation coefficients (K_T) were calculated using the Beer-Lambert relationship $\ln(I_z/I_0) = -K_T * Z$ based on simultaneous photosynthetic active radiation (PAR) readings taken at the surface (I_0) and a depth of 1.0 m (I_z) with deck (reference) and downwelling cosine-corrected quantum sensors (Li-Cor or equivalent). Surface (incident) irradiance readings (I_0) were corrected for 5% reflection prior to calculating K_T .

Samples for the determination of color (CDOM) were passed through a 0.45 μm filter using a syringe in the field. Unfiltered water samples were retained for total phosphorous (TP), total Kjeldahl nitrogen (TKN), silica (SI), turbidity (TURB), total suspended solids (TSS), and chlorophyll a (CHL A). All samples were stored on ice until their return to the laboratory. CHL A samples were filtered in the laboratory within 24 hours of collection. Water quality parameters were analyzed by standard methods (APHA 2005) using a spectrophotometer or auto-analyzer. Concentrations of CHL A not corrected for pheophytin degradation pigments (if the distinction was noted by the respective monitoring programs/research projects) were used as a proxy for phytoplankton biomass (B), a measure of phytoplankton abundance. The term 'bloom' was defined to indicate the top 10% of CHL A concentrations observed during the twenty-five year period (Phlips et al. 2010). All laboratory analyses were conducted in accordance to the specifications of the South Florida Water Management District Quality Assurance Plan and in compliance with the National Environmental Laboratory Accreditation Program (Doering and Chamberlain 1999, Corbett 2004, Doering et al. 2006).

Meteorological and Hydrological Data Sources

Measurements of PAR light flux recorded at three stations in Lee, Collier, and Hendry Counties (Figure 4-1) were compiled from the South Florida Water Management District's online environmental database (SFWMD 2011). Instantaneous readings at fifteen minute intervals were converted into $\text{mol}\cdot\text{photons}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and summed across the daylight period to provide estimates of total daytime surface irradiance (I_0). The maximum values of I_0 across the tri-county area were plotted and used to extrapolate monthly maxima I_0 . Monthly maximum I_0 values from February 2009 to January 2010,

which were verified with field measurements and observations (Chapter 3), were applied across the long-term data set to predict phytoplankton productivity using the BZ_p/I_0 approach.

Daily measurements of flow recorded at S-77, S-78, and S-79 (Figures 4-1 and 4-2) were obtained from the South Florida Water Management District's online environmental database (SFWMD 2011). Flow values were converted into metric equivalents ($\text{m}^3 \cdot \text{s}^{-1}$) and then averaged across each collection month (January 1986 through December 2010). Monthly means, opposed to daily rates, took into consideration the travel time of freshwater from S-79 through the estuary and the effect of preceding flow conditions (Stoker 1992). Mean monthly flow has been previously determined as an acceptable approach to analyzing freshwater inflow effects on water quality because it adequately represents the approximate expected residence time for a variety of flow regimes observed in the system (Chamberlain and Doering 1998a). The mean monthly flows were used to identify intra- and interannual discharge patterns and unusual water release or withdrawal events in the long-term data set. Daily inflows from the three water control structures were also used to identify the timing and sources of freshwater into the estuary.

Monthly rainfall totals and average air temperatures recorded in Fort Myers and Punta Gorda (Figure 4-1) were obtained from the National Climatic Data Center (NCDC 2011). Punta Gorda values were only used when Fort Myers readings were unavailable, mainly between October 1995 and February 1998. Values were converted into metric equivalents, cm and $^{\circ}\text{C}$, respectively. Departures from normal were taken as the average value of the meteorological element over a recent thirty-year time period

(NCDC 2011). Monthly rainfall totals and departures from normal were used to identify intra- and interannual precipitation patterns and potential flood and drought conditions in the long-term data set. Monthly average air temperatures and departures from normal were used to identify intra- and interannual temperature patterns and unusual warm and cold periods in the long-term data set. Daily sums of rainfall at S-79 were also obtained from the South Florida Water Management District's online environmental database (SFWMD 2011), converted into metric equivalents as before, and used to identify the timing and sources of freshwater into the estuary.

Bi-monthly values of the Multivariate ENSO (El Niño/Southern Oscillation) Index (MEI) were obtained from the Earth System Research Laboratory (ESRL 2011). MEI values were used to identify periods of ENSO based on six main observed variables over the tropical Pacific, including (1) sea-level pressure, (2) zonal and (3) meridional components of the surface wind, (4) sea surface temperature, (5) surface air temperature, and (6) total cloudiness fraction of the sky (ESRL 2011). Monthly indices were taken as the bi-monthly value (i.e., December/January, January/February, February/March, etc.) of the listed second month (i.e., January, February, March, etc.) since there is an understood time lag required for the global atmosphere to respond to tropical sea surface temperature anomalies (ESRL 2011). Positive MEI values represented the warm ENSO phase (El Niño), while negative values represented the cold ENSO phase (La Niña) (ESRL 2011). The severity of ENSO events were compared using MEI ranks, a number between 1 and 62, which were based on the MEI values of similar bimonthly seasons since the beginning of record in December 1949/January 1950 (ESRL 2011). Monthly ranks were taken from the bi-monthly values

using the same approach as the indices. Months having ranks 1 through 6 were classified as strong La Niña events, while months having ranks 56 through 62 were classified as strong El Niño events, representing the top ten percent of each (ESRL 2011). Weak La Niña periods corresponded to ranks 7 through 19, and weak El Niño periods corresponded to ranks 44 through 55 (ESRL 2011). Months having ranks in the middle (20 through 43) were classified as near-normal periods (ESRL 2011).

Primary Productivity Estimates

Estimates of daily gross primary productivity (GPP_d) of the phytoplankton community in the water column were obtained using the model relationship $GPP_d = 75 + 0.73BZ_pI_0$, which was previously derived for the Caloosahatchee Estuary (Chapter 3). Model predicted GPP_d was calculated across the twenty-five year data set for each given site and month as long as there were corresponding values for B , Z_p , and I_0 available. Estimates of GPP_d were averaged across years and converted into estimates of annual gross primary productivity (GPP_y) so that the estuary's trophic status could be evaluated and system-wide comparisons could be made. The trophic scheme proposed by Nixon (1995) for estuaries and coastal ecosystems was used to classify annual production rates as oligotrophic (less than $100 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), mesotrophic (between 100 and $300 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), eutrophic (between 301 and $500 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), or hypertrophic (greater than $500 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$). Seasonal contributions to GPP_y were obtained by averaging GPP_d across wet and dry months and multiplying by the number of days in each season in an average year (181 days in the dry season between November 1 and April 30; 184 days in the wet season between May 1 and October 31).

Decomposition of Phytoplankton Biomass Variability

The methods of Cloern and Jassby (2010) were followed to examine the long-term time series of monthly mean CHL *A* concentrations and isolate the underlying mechanisms controlling phytoplankton biomass and, thus, phytoplankton productivity by inference, at different timescales in the four regions of the Caloosahatchee Estuary. Phytoplankton biomass, in terms of CHL *A* was previously identified as the primary model parameter explaining most of the variability in GPP_d (Chapter 3). The analysis required that each region have at least 8 years of data with at least 10 months of data for each year (Cloern and Jassby 2010). This latter criterion was relaxed to 9 months of data for each year as long as the three missing months were not from the same season (winter, spring, summer, or fall) so that the minimum number of years could be met. It was further required that each month be represented by at least 6 years of data from each region (Cloern and Jassby 2010). These criteria were selected to obtain the longest time series of CHL *A* for each region of the estuary while reducing bias associated with missing data. The multiplicative model expressed as $c_{ij} = Cy_i m_j \epsilon_{ij}$, was used to partition each CHL *A* time series into a long-term mean and three other components: an annual effect, a seasonal pattern, and residual 'events' (Cloern and Jassby 2010). Here, c_{ij} was defined as the CHL *A* concentration in year i and month j ; C was the long-term CHL *A* mean of the time series; y_i was the annual effect in year i defined as the annual mean Y_i divided by C ; m_j was the seasonal (monthly) effect in month j taken as the mean CHL *A* concentration for each calendar month j over all years of the CHL *A* concentrations from each month j and year i divided by the Y_i ; and ϵ_{ij} was the residual term (Cloern and Jassby 2010). Values of $y_i > 1$, $m_j > 1$, and $\epsilon_{ij} > 1$ were used to identify years with above-average mean CHL *A* from the long-term mean,

months with above-average mean CHL A from the annual mean, and individual observations greater than the expected value for a given month and year, respectively (Cloern and Jassby 2010). The standard deviations of y_i , m_j , and ϵ_{ij} were used as coefficients of variation, allowing comparisons of phytoplankton biomass variability to be made within and across different ecosystems (Cloern and Jassby 2010).

Statistical Analyses for Identification of Environmental Drivers

Multivariate statistical analyses were performed using PERMANOVA+ for PRIMER software (Plymouth, United Kingdom) and were focused on two objectives: addressing discontinuities in the data, and ultimately, identifying key environmental drivers of phytoplankton productivity in the Caloosahatchee Estuary. Because the parameters of interest were not sampled each month across the 80 unique sites over the twenty-five year time period, steps were taken to select closely matched data that would fill in gaps to create a useable matrix of measurements across a consistent spatial extent and temporal duration. The results of this approach were suitable for further investigation to identify correlations among potential environmental drivers and estimates of GPP_d .

An initial hierarchical agglomerative clustering (Anderson et al. 2008) grouped sites according to similarities calculated across 9 physical-chemical variables (i.e., SAL, TEMP_W, DO, TP, TKN, SI, CDOM, TURB, and Z_p). The target data set for this analysis was the largest possible block of data for all 9 parameters gathered in consecutive months at 80 sites spanning the Caloosahatchee Estuary. Where necessary, missing values were replaced by shifting multiple samples collected early or late in one month to the previous or following month, interpolating one to three month gaps linearly, inserting a value from a neighboring month or site, or using means for

multiple samples in a given month. Values in the resulting square matrix were range standardized, which converted measurements from multiple scales to a more comparable, dimensionless scale ranging from 0 to 1 (Anderson et al. 2008). Bray-Curtis similarity coefficients (Bray and Curtis 1957) were calculated between pairs of sites, with a similarity coefficient, S , of 1 representing 100% or total similarity, and a value of 0 representing total dissimilarity (Anderson et al. 2008). Hierarchical agglomerative clustering based on a group-average algorithm was performed, and statistically significant clusters were identified by a similarity profile permutation test (Anderson et al. 2008). Within the selected site clusters, discontinuous strings of data from the relevant sites could be combined (i.e., by calculating mean values) to improve the spatial-temporal continuity of the data set documenting potential environmental drivers and GPP_d .

The continuity of the resulting data set was further improved by clustering sampling events according to Bray-Curtis similarities calculated on range standardized values. For each site group, the data comprised of 9 physical-chemical parameters (i.e., SAL, TEMP_W, DO, TP, TKN, CDOM, TURB, TSS, and Z_p) and 3 meteorological and hydrological forcing factors that operated across all sites (i.e., MEI, total monthly rainfall, and mean monthly flow). Measures of SI were excluded from this analysis because they were too sparse. The inclusion of TSS in this step was done to decouple its possible influence on water quality from that of TURB. A matrix of site groups and year and month combinations between January 1986 and December 2010 was created from the means of values across sites within groups and linear interpolation across 1 to 2 month gaps. As before, hierarchical agglomerative clustering and similarities profile

analysis were used to identify groups of sampling events having similar spatial patterns in water quality and meteorological and hydrological conditions (Anderson et al. 2008). Selected groups of sampling events augmented site groups as a basis for replacing missing values with values from a sampling period deemed similar or means of values from multiple, similar sampling periods. In conjunction with pooling across sites, combining data from sampling events generated a more robust data set for investigation of correlations with GPP_d .

Ultimately, two new data sets were generated for combinations of site and time groups. One data set contained 14 water quality, meteorological, and hydrological parameters (i.e., SAL, TEMP_W, DO, TP, TKN, SI, CDOM, TURB, TSS, Z_p , I_0 , MEI, total monthly rainfall, and mean monthly flow) and the other one contained the potential biological response variable, GPP_d . The variables Z_p and I_0 were excluded from correlation analyses involving GPP_d because they were parameters used in conjunction with CHL A to estimate gross primary productivity. These data sets maximized the spatial and temporal coverage of the original twenty-five year data set for the Caloosahatchee Estuary. Values within the data sets were range standardized across combinations of site and parameter for all relevant time periods. Resemblance matrices were calculated for response variables using Bray-Curtis similarity coefficients (Bray-Curtis 1957), and a stepwise permutation procedure (BVSTEP; Anderson et al. 2008) was used to find the 'best' combination of environmental drivers. 'Best' was classified as the minimum number of drivers that yielded the highest Spearman correlation coefficient (ρ) adjusted for tied ranks (Kendall 1970) when the resemblance matrices were compared. The search for the 'best' combination of environmental

drivers to explain the biological response was terminated when $\rho > 0.95$ or when the change in ρ between successive comparisons was less than 0.001. Values of ρ for 99 random permutations provided a distribution for evaluating statistical significance, with a statistically significant result being a ρ value greater than those generated from the randomized data.

Results

Spatial and Temporal Similarity Groupings of Data

Only 12 out of 80 sites were sampled relatively consistently by the five monitoring programs/research projects that were active during the twenty-five year time period. After missing values were addressed, data from these sites provided continuous time series for 9 parameters across 40 months that were used to calculate resemblances and evaluate clusters of sites. All of the 9 physical-chemical parameters (i.e., SAL, TEMP_W, DO, TP, TKN, SI, CDOM, TURB, and Z_{ρ}) used to identify spatial groups in the data contributed to similarity among sites within groups, without a dominant contribution from any parameter. The results of the similarities profile test indicated six clusters of paired sites lying along a spatial gradient characterized by distances from S-79. Two pairs of sites at distances of 6 and 14 km, respectively, clustered at a similarity of 76%. Additionally, two pairs of sites at 21 and 26 km, respectively, clustered at a similarity of 80%. Given the degree of similarity among data from these sites and the fact that they fell within the existing geographic boundaries of the Upper Estuary (UE) and Middle Estuary (ME) regions, respectively, the pairs of sites were combined in further analyses. The remaining pairs of sites that clustered at 83 and 67% similarity aligned with the geographic boundaries of the Lower Estuary (LE) and San

Carlos Bay (BY), respectively. These results confirmed a previously documented gradient in water quality in the Caloosahatchee Estuary based on distances from S-79 (Doering and Chamberlain 1999, Doering et al. 2006); therefore, further analyses treated sites within the four regions (UE, ME, LE, and BY) as replicates.

Between January 1986 and December 2010, samples were collected in at least one region of the Caloosahatchee Estuary in 197 of the possible 300 months covered by the twenty-five year time period. A smaller number of months (76) yielded nearly complete data for 12 parameters across each of the four regions, and these data were used to calculate resemblances for use in hierarchical agglomerative clustering. None of the 9 physical-chemical (i.e., SAL, TEMP_W, DO, TP, TKN, CDOM, TURB, TSS, and Z_p) and 3 meteorological or hydrological parameters (i.e., MEI, total monthly rainfall, and mean monthly flow) represented a dominant cause of similarity among monthly sampling events. A similarities profile analysis indicated 33 clusters comprising one to seven sampling events, with clusters separating at similarities of 76.5% or greater. Because the 76 months of data used in this analysis included a wide range of meteorological and hydrological conditions, the corresponding patterns in water quality across the four regions of the Caloosahatchee Estuary were considered representative of the potential natural and anthropogenic drivers of primary productivity during the entire twenty-five year time period. Thus, samples from the same site group and time period were treated as replicates in order to build a complete subset of data needed to test for correlations between the environmental and biological response variables.

Meteorological and Hydrological Observations

Between January 1986 and December 2010, there were approximately 15 alternating El Niño/Southern Oscillation (ENSO) phases based on switches between

positive (El Niño) and negative (La Niña) Multivariate ENSO Index (MEI) values (Figure 4-3; part A). There was a greater occurrence of El Niño conditions, but not all of these events were considered to be significant. In comparison to past ENSO events occurring in the same month since January 1950 (ESRL 2011), conditions were considered to be near-normal during 111 of the 300 months (37%) of the twenty-five year period (Figure 4-3; part B). An additional 26% and 19% of months experienced weak El Niño and La Niña conditions, respectively. Strong El Niño and La Niña events occurred during 14% and 4% of the 300 months, respectively. The summer and fall of 1997 was ranked the strongest El Niño event, while the summer and fall of 2010 was ranked the strongest La Niña event during the twenty-five year period.

Average monthly air temperatures typically ranged from 18 to 28°C on an annual basis between January 1986 and December 2010, reflecting the subtropical climate of the Caloosahatchee Estuary (Figure 4-4; part A). Summer air temperature averages were maintained around 28°C with smaller departures from normal, while winter air temperature averages showed greater variability (Figure 4-4). Unusually low winter air temperature averages below 16°C were observed in December 1989, January 2001, January 2003, December 2003, January 2010, February 2010, and December 2010, corresponding to 2 to 5°C departures below normal, respectively. During the January 2003 and December 2010 cold spells, water temperatures (TEMP_W) in the Caloosahatchee Estuary fell to a twenty-five year low of 14°C (Figure 4-5). These cooler than normal winter temperatures were typically observed during El Niño or near-normal conditions (Figures 4-3, 4-4, and 4-5). Unusually high winter air temperatures with monthly averages reported at 3 to 5°C above normal were observed

in November and December 1986, January 1989, January and February 1990, January 1991, January 1993, February 1994, February 1997, and February 2001 (Figure 4-4). During the unusually warm late fall/early winter of 1986, water temperatures between 25 and 29°C were observed in the Caloosahatchee Estuary when they typically do not exceed 24°C during that time of year (Figure 4-5). The January 1989, February 1997, and February 2001 warmer than normal winter temperatures occurred under La Niña conditions (Figures 4-3 and 4-4).

Monthly rainfall totals ranged from 0 to 48 cm and averaged 12 cm over the twenty-five year study period (Figure 4-6; part A). Rainfall was typically higher from May through October (the defined wet season) than November through April (the defined dry season). Wet season months showed the greatest variability in rainfall, ranging from flood to drought conditions with respect to normal (Figure 4-6). The months of September 1988, September 1992, June 1994, August 1996, August 1997, June 2001, July 2003, June 2009 and July 2009 showed well below normal levels of rainfall (Figure 4-6; part B). These drier than normal months typically occurred during La Niña, near-normal, or weak El Niño periods (Figures 4-3 and 4-6). Flooding conditions were more common during the positive (El Niño) phases, including the summer of 1986 to the fall of 1987, the summer of 1990 to the summer of 1992, the late spring and summer of 1995, the fall and winter of 1997, the late summer of 2001, the late summer of 2003 to the early fall of 2005, the summer of 2006, and the spring of 2010 (Figures 4-3 and 4-6). Unusually high rainfall totals in the wet season months often, though not always, corresponded to the occurrence of nearby episodic storm events, including an unnamed storm in late October 1987, Tropical Storm Ana in July

1991, Hurricane Gabrielle in September 2001, Hurricane Erika in August 2003, and Hurricanes Charley and Frances in August 2004 (NOAA 2012). Other episodic storm events, such as the Category 5 Hurricane Andrew in August 1992, did not bring above average levels of rainfall to the Caloosahatchee Estuary, although it may have to other parts of south Florida.

Mean monthly flow from S-79 into the Caloosahatchee Estuary was typically greater in the summer and fall months of each year between January 1986 and December 2010, providing drainage for the upper Caloosahatchee River watershed and Lake Okeechobee when rainfall totals were at their highest (Figure 4-7). The major peaks in mean monthly flow from S-79 occurred immediately prior to or following an episodic storm event, including Hurricane Erin and Tropical Storm Jerry (July and August 1995), Hurricane Erika (August 2003), Hurricanes Charley, Frances, Ivan, and Jeanne (August and September 2004), and Hurricanes Katrina and Wilma (August and October 2005) (NOAA 2012). Although it occurred outside of the usual wet/storm season, the January to March 1998 peak in mean monthly flow into the Caloosahatchee Estuary from S-79 was traced upstream to large releases of freshwater from Lake Okeechobee at S-77 and the upper Caloosahatchee River at S-78, during a strong El Niño period with higher than normal rainfall levels (Figures 4-3, 4-6, 4-7, and 4-8). Other periods of high rainfall did not always correspond to high mean monthly flows even though there were extreme single day freshwater releases contributing to the monthly mean, which was the case in June 1992 (Figures 4-6, 4-7, and 4-8). In general, the daily flow rates at S-77 and S-78 were almost identical, while the volume released at S-79 was often three to four times greater than that upstream around the

same time periods (Figure 4-8). In comparison to the distribution of mean monthly inflows recommended for the Caloosahatchee Estuary by the South Florida Water Management District (SFWMD), more than 50% of the mean monthly inflows observed between January 1986 and December 2010 were at levels recommended less than one percent of the time (Table 4-3). The closest agreement among the distributions of observed and recommended mean monthly inflows during the twenty-five year period was for moderate rates between 22.7 to 42.5 m³•s⁻¹.

Water Quality Variations

Salinities (SAL) ranged from 0 to 38 psu in the Caloosahatchee Estuary over all observations from the twenty-five year period. In general, salinities increased with distance from S-79 towards San Carlos Bay. Each region (UE, ME, LE, BY) encountered the entire range of salinities from freshwater to euhaline, except for region BY, which did not fall into the freshwater zone (Figures 4-9 and 4-10). Oligohaline salinities were observed at the mouth of the estuary in region BY in June 2003, September 2003, July 2005, and November 2005, corresponding to mean monthly inflows at S-79 greater than 167 m³•s⁻¹. Euhaline salinities were observed in region UE in July 2007 when the average inflow was approximately 7 m³•s⁻¹ or less for that month and the six months prior. These extremely low and high regional salinities occurred in months having positive (El Niño) and negative (La Niña) ENSO phase conditions with above and below normal rainfall events, respectively (Figures 4-3, 4-6, and 4-9). At other times, these non-recommended high and low flow levels corresponded to salinities within the expected range for each region (Table 4-3; Figures 4-10 and 4-11).

Total phosphorous (TP) concentrations averaged 0.11 mg•L⁻¹ over the twenty-five year period, and monthly means rarely exceeded 0.3 mg•L⁻¹ across the five

salinity zones or four regions of the Caloosahatchee Estuary (Figure 4-12).

Concentrations were generally lower and less variable in the higher salinity zones (polyhaline and euhaline), particularly when these zones were contained within region BY (Figure 4-12; Tables 4-4 and 4-5). The highest monthly means were generally observed during the wet seasons of 2000, 2001, and 2007 corresponding to periods of above average rainfall and/or inflow from S-79 in otherwise dry La Niña phases (Figures 4-3, 4-6, 4-7, 4-8, and 4-12). The isolated TP peak in oligohaline waters of region UE in November 1996 occurred during a relatively dry month with respect to rainfall and inflow levels, but it lagged a couple of weeks behind a period of heightened rainfall and freshwater releases at S-78 and S-79 (Figures 4-3, 4-6, 4-7, 4-8, and 4-12).

Total Kjeldahl nitrogen concentrations (TKN) averaged $0.9643 \text{ mg}\cdot\text{L}^{-1}$ overall, and monthly means typically fell between 0.5 and $1.5 \text{ mg}\cdot\text{L}^{-1}$ during the twenty-five year period in the Caloosahatchee Estuary (Figure 4-13). Concentrations below this range generally occurred in the LE and BY regions when salinities exceeded 18 psu (Figure 4-13; Tables 4-4 and 4-5). Concentrations above this range were more common in the UE and ME regions under freshwater and oligohaline conditions. Similar to the pattern observed with TP, the highest TKN monthly means (greater than $2 \text{ mg}\cdot\text{L}^{-1}$) were associated with the wet seasons of 2000 and 2001. TKN concentrations also peaked in the UE and ME regions during the springs and early summers of 1987 and 1988, following several weeks of unusually high freshwater discharge that originated from S-77 during an otherwise dry period with below average rainfall (Figures 4-3, 4-6, 4-8, and 4-13).

Silica (SI) concentrations averaged $4.662 \text{ mg}\cdot\text{L}^{-1}$ over the twenty-five year period, while monthly means ranged from 0 to $18 \text{ mg}\cdot\text{L}^{-1}$ across the different regions and salinity zones (Figure 4-14). The largest variability was associated with the mesohaline salinity zone, which spanned all four regions of the estuary at some point between January 1986 and December 2010. In general, the highest SI concentrations (greater than $5 \text{ mg}\cdot\text{L}^{-1}$) were consistently found in the UE and ME regions of the estuary, respectively, when salinities were less than 5 psu (Figure 4-14; Tables 4-4 and 4-5). The major SI peaks were observed in the late summer/early fall of 1986 and the summer of 2000 in all three inner regions of the estuary (UE, ME, and LE) when salinities ranged from 0 to 18 psu. The 1986 SI peaks followed a period of above average rainfall in June and several large pulses of freshwater released from S-79 in August, which both corresponded to the onset of a strong El Niño event (Figures 4-3, 4-6, 4-7, 4-8, and 4-14).

Photic depth (Z_p) fluctuated both spatially and temporally with respect to salinity in the Caloosahatchee Estuary during the twenty-five year time period (Figure 4-15). Light availability in the water column was typically greater, as indicated by larger Z_p values, at higher salinities (polyhaline and euhaline zones) and at distances farther from S-79 (regions LE and BY) (Figure 4-15; Tables 4-4 and 4-5). However, light conditions in these regions were also more variable between seasons and across years with values ranging from near 0 to approximately 6 m given a range of salinities created at the interface of freshwater outflow and tidal inflow. The monthly mean Z_p values of 0.02 m^{-1} observed in the polyhaline and euhaline zones of regions BY and LE, respectively, were suspicious in that they corresponded to secchi disk depths (Z_s) of

0.01 m, which is the approximate thickness of a standard disk. Photic depths were consistently shallow with respect to average water column depths and less variable across seasons and years in regions UE and ME, particularly under freshwater conditions. Mean concentrations of TSS over the twenty-five year period showed the same pattern as Z_p with the highest, long-term averages associated with euhaline waters and regions LE and BY. Mean concentrations of CDOM followed an opposite pattern with the highest, twenty-five year averages found in freshwater and region UE (Tables 4-4 and 4-5). The long-term averages of TURB decreased with distance from S-79 until region BY, while the highest mean concentrations were observed in both oligohaline and euhaline waters (Table 4-4 and 4-5).

Phytoplankton Biomass and Productivity Patterns

Phytoplankton biomass (B) in terms of chlorophyll a (CHL A) concentration averaged $9 \text{ mg}\cdot\text{m}^{-3}$ overall and was less than $20 \text{ mg}\cdot\text{m}^{-3}$ in 90% of individual collections from the twenty-five year period. Blooms with mean CHL A concentrations greater than $20 \text{ mg}\cdot\text{m}^{-3}$ occurred in all four regions of the Caloosahatchee Estuary and under all salinity conditions below 30 psu, excluding the euhaline zone (Figure 4-16). Freshwater blooms were primarily confined to region UE, although they were often flushed downstream into region ME where they were exposed to salinities up to 18 psu, which was the case in May and June 2000. Blooms with the highest CHL A concentrations were most often associated with oligohaline salinities, particularly in region ME in the early 2000s, and this pattern was reflected in the spatial gradient of the mean CHL A concentrations over the twenty-five year period with respect to salinity and distance from S-79 (Figure 4-16; Tables 4-4 and 4-5). The high summer and early fall peaks in CHL A from the early 2000s occurred after rainfall and/or freshwater inflow increased in

conjunction with the sporadic changes from dry La Niña to wet El Niño conditions (Figures 4-3, 4-6, 4-7, 4-8, and 4-16). Under polyhaline and euhaline salinity conditions, there appeared to be limited potential for phytoplankton blooms in the Caloosahatchee Estuary during the twenty-five year period (Figure 4-16). However, an unusual peak in *B* was detected in the polyhaline zone of region UE and nowhere else in the estuary at that magnitude in November 2007, which was a very dry La Niña month with essentially no rainfall and no freshwater inflow from S-79 (Figures 4-3, 4-6, 4-7, 4-8, and 4-16). Similarly, the maximum monthly mean CHL *A* concentration observed in salinities greater than 30 psu was $16 \text{ mg}\cdot\text{m}^{-3}$ in region LE in June 2008, corresponding to the end of an extended dry La Niña period with nearly no rainfall or freshwater inflow from S-79 (Figures 4-3, 4-6, 4-7, 4-8, and 4-16).

Daily estimates of gross phytoplankton productivity (GPP_d) averaged $694 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ overall but exceeded $2000 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in 5% of the samples collected during the twenty-five year period (Figure 4-17). Monthly mean GPP_d estimates greater than $2000 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ were observed in all four regions and associated with all salinities, except in the euhaline zone. The maximum monthly mean GPP_d estimate that occurred in salinities greater than 30 psu was $1200 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ from region LE in August 2001. The UE region exhibited most of the highest mean estimates of GPP_d , and these outlying peaks were predominately found in the mesohaline zone (Figure 4-17). The excessive GPP_d peak in April 1989 under mesohaline conditions of region UE did not correspond to any unusually high inputs of freshwater from rainfall or S-79, but the one detected in June 2002 followed a dramatic increase in rainfall and inflow relative to the dry La Niña period preceding it (Figures 4-3,

4-6, 4-7, 4-8, and 4-17). The oligohaline zone had the highest average GPP_d estimates overall, and the peaks associated with those salinities were observed in all three regions of the inner estuary (UE, ME, and LE) at various times between January 1986 and December 2010 (Figure 4-17; Tables 4-4 and 4-5). The spikes in GPP_d in 1986, 1988, 1995, 1996, 2000, 2001, 2009, and 2010 all occurred within a month or two of a notable switch in the ENSO cycle (Figure 4-3 and 4-17). The BY region only exhibited mean GPP_d estimates in excess of $2000 \text{ mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ under polyhaline conditions, and these peaks also occurred concurrently with El Niño and La Niña cycle changes.

A close-up view of the actual (as opposed to monthly mean) observations of CHL *A* and corresponding estimates of GPP_d in two contrasting periods were compared to identify phytoplankton community responses to shifting salinity zones and associated water quality conditions given both natural and anthropogenic variations in freshwater inputs (Figures 4-18, 4-19, 4-20, and 4-21). The late spring and early summer of 2000 coincided with an abrupt shift in the ENSO cycle from extended dry La Niña to temporary wet El Niño conditions (Figures 4-3, 4-6, 4-7, and 4-8). Starting in April 2000, below average rainfall and low inflows from S-79 restricted phytoplankton biomass and primary productivity in the predominantly mesohaline to euhaline salinities across the four regions of the Caloosahatchee Estuary (Figures 4-18 and 4-19). With small inputs of rainfall and gradual increases in river inflows, salinities began to decline to freshwater and oligohaline levels in region UE and to mesohaline levels in region LE. Phytoplankton biomass and productivity showed an initial increase in oligohaline waters with the first blooms appearing at distances closest to S-79. By the end of May/beginning of June, both CHL *A* and GPP_d had reached their seasonal peaks, which

were most pronounced in regions UE and ME in fresh and oligohaline waters, respectively. The return of La Niña conditions caused rainfall, river flow, salinity, CHL A, and GPP_d to return to dry season levels despite it being the month of June. The summer and fall of 1995, in contrast, was the final wet season in a five and half year long El Niño phase with well above average rainfall and excessive inflows from S-79 (Figures 4-3, 4-6, 4-7, and 4-8). At the beginning of June 1995, daily pulses of freshwater in the form of rainfall and river flow were promoting high levels of phytoplankton biomass and productivity in the oligohaline and mesohaline waters of the UE and ME regions, respectively (Figures 4-20 and 4-21). By early August, excessive inflows in conjunction with additional rainfall reduced salinities throughout the estuary from freshwater in region UE to polyhaline conditions in region BY. Blooms were flushed downstream and out to San Carlos Bay, where they reached peak GPP_d levels CHL A concentrations for that region (BY). Continued freshwater inputs suppressed salinities below 18 psu, even in region BY, which restricted phytoplankton productivity and biomass accumulation through the end of the wet season.

Spatial and Temporal Changes in Trophic Status

The average, overall trophic status of the Caloosahatchee Estuary was mesotrophic ($253 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) across space and time when all model estimates of GPP_d from the twenty-five year period were considered together and converted into average estimates of annual gross primary productivity (GPP_y). When the estuary was divided into regions, the overall GPP_y averages for regions UE and ME were higher (295 and $282 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$, respectively), while the overall GPP_y averages for regions LE and BY were lower (220 and $183 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), than that for the entire system, creating a general decreasing spatial gradient of mesotrophic productivity levels with distance from S-79

(Figure 4-22; Table 4-4). When overall GPP_y averages were determined for each salinity zone, the average trophic status of the freshwater, polyhaline, and euhaline zones of the Caloosahatchee Estuary was mesotrophic (194, 218, and 155 $g \cdot C \cdot m^{-2} \cdot y^{-1}$, respectively), while the average trophic status of the oligohaline and mesohaline zones of the system was eutrophic (350 and 322 $g \cdot C \cdot m^{-2} \cdot y^{-1}$, respectively) across the twenty five year period (Figure 4-23; Table 4-5). From both spatial perspectives, GPP_y ranged from oligotrophic to hypertrophic levels across the four regions or the five salinity zones within the Caloosahatchee Estuary between 1986 and 2010 (Figures 4-22 and 4-23).

These average, minimum, and maximum estimates of GPP_y were taken as measures of the spatial and temporal changes in the trophic status of the Caloosahatchee Estuary despite the bias associated with missing data. Out of the twenty-five year period, GPP_y could not be determined in any region or zone of the Caloosahatchee Estuary for at least six of those years due to the discontinuation of all sampling efforts (1990, 1991, 1992, 1993, and 1998) or the lack of sufficient measurements (2003) of CHL A and/or Z_p required by the 'light•biomass' model (Figures 4-22 and 4-23). An additional number of annual estimates were missing for some or all of the regions (UE, ME, LE, and BY) or salinity zones (freshwater, oligohaline, mesohaline, polyhaline, and euhaline). Furthermore, the values of GPP_y for each year in each location were dependent on the number and seasonality of the monthly mean estimates of GPP_d used to calculate the annual means. For example, the minimum annual rates across the regions or zones were based on single, dry season month estimates of GPP_d , (i.e., November 1994 from region UE; April 1999 from the euhaline zone), while the maximum annual rates across the regions or zones were

heavily weighted by wet season month estimates of GPP_d (i.e., June, July, and August 1996 from region LE; June and July 2002 from the mesohaline zone).

Considering the 13 years (12 for region BY) out of the twenty-five year period that had seasonally diverse (both wet and dry season) estimates of primary productivity contributing to GPP_y in the four regions of the Caloosahatchee Estuary, the system still fluctuated between states of oligotrophy (region UE in 2005) and hypertrophy (region LE in 1996) (Figure 4-24). Regions UE and BY dropped to minimum GPP_y levels of oligotrophy (in 2005 and 2009, respectively), while regions ME and LE maintained mesotrophic levels of GPP_y at a minimum over time. Maximum GPP_y levels from each region corresponded to periods of hypertrophy in regions UE and LE (in 2000 and 1996, respectively), eutrophy in region ME (in 1996), and mesotrophy in region BY (in 2001). The years 1988, 1995, 1996, and 2000 produced eutrophic and/or hypertrophic levels of GPP_y in at least two of the three regions of the inner estuary (UE, ME, or LE). Eutrophic levels of GPP_y were also detected in 2008 and 2009 in region UE and in 1986 in region ME. A smaller number of years had both wet and dry season estimates of primary productivity contributing to GPP_y in each salinity zone (Figure 4-25) due to insufficient sampling and/or shifting water quality conditions given interannual variations in rainfall and flow (i.e., certain salinity zones may have not existed in the estuary in a given year). Regardless, the Caloosahatchee Estuary showed the same range of GPP_y (oligotrophy to hypertrophy) across the range of salinities (freshwater to euhaline). Minimum oligotrophic levels of GPP_y produced in the freshwater and euhaline zones were comparable to those observed in regions UE and BY, while minimum mesotrophic levels of GPP_y maintained in the oligohaline, mesohaline, and polyhaline zones were

similar to those observed in regions ME and LE. The years having eutrophic and/or hypertrophic levels of GPP_y in the inner regions of the Caloosahatchee Estuary were associated with salinities between 0.5 and 30 psu. The oligohaline zone produced the highest maximum GPP_y across both seasons in the year 2000. Overall, the breakdown of GPP_y into seasonal averages for each year and region or zone revealed that wet season productivity was generally higher and more variable than dry season productivity across the Caloosahatchee Estuary during the twenty-five year time period (Figures 4-24 and 4-25).

The productivity potential of the Caloosahatchee Estuary was also examined given CHL A concentrations at the threshold for a violation of the Florida Department of Environmental Protection (FDEP) Impaired Water Rule (Bailey et al. 2009, SFWMD et al. 2009). At an annual average CHL A concentration of $11 \text{ mg}\cdot\text{m}^{-3}$, the overall trophic status of the Caloosahatchee Estuary was expected to be mesotrophic given average values of Z_p (given the corresponding levels of phytoplankton biomass) and I_0 observed during the twenty-five year period (Figure 4-26). When spatial differences in photic depth were taken into consideration, the productivity potential of region UE and the mesohaline zone increased to eutrophic levels overall. When predicted GPP_y values from each region and zone were broken down into the seasonal contributions to productivity across the wet and dry months given spatial and seasonal differences in Z_p and I_0 , the trophic status of the Caloosahatchee Estuary was maintained at mesotrophic levels or lower. Across the spatial and seasonal differences, wet season productivity was consistently higher than dry season productivity.

Phytoplankton Biomass Variability at Different Scales

Patterns of phytoplankton biomass variability were examined according to the approach of Cloern and Jassby (2010) using a subset of regional monthly mean CHL A concentrations selected from the original Caloosahatchee Estuary data set according to the three data criteria. Only 8 out of 25 years of data for each region had at least 9 monthly CHL A values (taken as means when there were multiple collections in the same month) with each season (i.e., winter, spring, summer, and fall) represented and each of these months sampled in at least 6 of those years. Regional monthly mean CHL A concentrations from the years 1986, 1987, 1988, 1995, 2004, 2005, 2006, and 2010 showed notable similarities and distinctions with respect to the annual, seasonal, and residual components of phytoplankton biomass variability in the Caloosahatchee Estuary (Figures 4-27, 4-28, 4-29, and 4-30). Each of these years had at least one prominent peak in the monthly mean CHL A time series that stood out against the long-term averages taken over the eight years of data in at least one region of the estuary. Several of these peaks were shared between regions, occurring simultaneously or within a span of one or two months of being first observed.

Over the eight years of data included in this analysis, region ME had the highest long-term mean CHL A concentration at $12.6 \text{ mg}\cdot\text{m}^{-3}$ (Figures 4-27, 4-28, 4-29, and 4-30; part A). Region UE had the next highest long-term CHL A average at $9.5 \text{ mg}\cdot\text{m}^{-3}$, followed by region LE at $6.9 \text{ mg}\cdot\text{m}^{-3}$ and region BY at $4.7 \text{ mg}\cdot\text{m}^{-3}$, respectively. These long-term CHL A means taken across the eight-year subset of data were comparable in magnitude and spatial distribution to the average CHL A concentrations calculated over all individual samples collected in each region of the Caloosahatchee Estuary during the twenty-five year period (Table 4-4). Thus, the patterns in phytoplankton biomass

variability observed in the eight-year subset of data were considered representative of the general responses of the phytoplankton community to the variety of meteorological and hydrological conditions observed in the original twenty-five year Caloosahatchee Estuary data set.

The annual (y) component of phytoplankton biomass variability showed a relatively narrow range across four regions of the Caloosahatchee Estuary (Figures 4-27, 4-28, 4-29, and 4-30; part C). Annual variability in CHL A in the Caloosahatchee Estuary was small (y did not deviate much from 1) except for several years that stood out in the eight-year data subset. The highest ($y \gg 1$) mean CHL A concentrations in the eight-year subset were observed in 2004 in region ME. Above average CHL A concentrations (relative to the long-term mean over the eight years) were also observed at a lesser magnitude in 2004 in regions LE and UE, respectively, while the same year brought below average CHL A concentrations to region BY. Concentrations of CHL A were relatively high in 1995 in all regions of the Caloosahatchee Estuary, particularly in regions BY and UE, respectively. The lowest ($y < 1$) mean CHL A concentrations in the eight-year subset were observed in region UE and ME in 2005, although this year brought above average CHL A concentrations to region BY. Below average mean CHL A was observed at similar levels in all four regions of the Caloosahatchee Estuary in the year 2006.

From a seasonal perspective, the monthly (m) component of phytoplankton biomass variability was fairly uniform across the four regions of the Caloosahatchee Estuary with the wet season months having mean CHL A concentrations above the annual average (Figures 4-27, 4-28, 4-29, and 4-30; part D). Throughout the estuary,

there were one to three consecutive wet season months that maintained above average CHL A concentrations ($m > 1$), and the timing of these peaks moved downstream with the flow of freshwater. The highest CHL A averages occurred first in May, June, and July in region UE and were followed by above average CHL A concentrations in June, July, and August in region ME. Region LE had its seasonal increase in phytoplankton biomass in July and August, and region BY had the latest rise in CHL A concentrations in August and September. The regions differed seasonally with respect to the timing of below average CHL A concentrations. Regions LE and BY had the lowest mean CHL A concentrations in the winter months (December, January, February), but regions UE and ME had their lowest mean CHL A concentrations in the fall (September, October, November).

The residual (ϵ) component of phytoplankton biomass variability identified that 40 to 45% of the monthly mean CHL A concentrations in the eight-year subset were higher than expected for the given month and year ($\epsilon > 1$) within each of the four regions of the Caloosahatchee Estuary (Figures 4-27, 4-28, 4-29, and 4-30; part B). Region ME had two months with unusually high CHL A monthly means ($\epsilon > 3$), but only one of these months (June 1995) corresponded to a prominent peak in the CHL A time series. The unusually high CHL A concentration detected in region ME in January 2005 was overshadowed by the magnitude of other monthly mean spikes in the phytoplankton biomass time series of that and other regions. The residual component confirmed that several of the other noticeable monthly mean peaks (August 1988 in regions ME and BY, December 1988 in region UE, June 1995 in regions UE, June/July/August 2004 in regions ME and LE, and April 2006 in region ME) were also high ($\epsilon > 2$) for the given

month and year. A number of other deviations from the annual and seasonal patterns of phytoplankton biomass variability did not correspond to recognizable bloom events (i.e., monthly mean CHL A concentrations greater than $20 \text{ mg}\cdot\text{m}^{-3}$), and most of these cases occurred in the cooler and drier months of the year (November through April) when concentrations were typically lower in comparison.

The standard deviations of y (SD_y) and m (SD_m) were taken as measures of annual and seasonal variability, respectively (Cloern and Jassby 2010). Values of SD_y showed a broader range (0.32 to 0.51) than the values of SD_m , which were more uniform (0.36 to 0.43) across the four regions of the Caloosahatchee Estuary (Table 4-6). Seasonal variability had a larger influence on phytoplankton biomass patterns than annual variability overall and in all regions of the Caloosahatchee Estuary except for region ME. The residual component ϵ was more variable than the annual component y and seasonal component m with a standard deviation (SD_ϵ) range of 0.45 to 0.71, and the consistently larger values of SD_ϵ indicate there were sources of CHL A variability beyond the average seasonal patterns and annual mean fluctuations (Cloern and Jassby 2010). In comparison to the patterns of phytoplankton biomass variability analyzed by Cloern and Jassby (2010) across 84 sites sampled within 51 estuarine-coastal ecosystems, the four regions of the Caloosahatchee Estuary had moderate (regions UE, LE, and BY) to high (region ME) levels of annual variability, moderate levels of seasonal variability (regions UE, ME, LE, and BY), and low (region BY), moderate (regions UE and LE), and high (region ME) levels of residual variability (Table 4-6). The values of SD_y and SD_m position the four regions of the Caloosahatchee Estuary in the middle of the pool of 84 other sites sampled within 51

other estuarine-coastal ecosystems, in terms of the degree of natural and/or human disturbance and the influence of annual climate cycles, respectively, on CHL A variability (Figure 4-31). The circle sizes representing the median SD_{ε} value for the four regions of the Caloosahatchee Estuary were also moderate in comparison to levels of nutrient enrichment in other systems around the world (Figure 4-31).

Environmental Drivers of Phytoplankton Productivity

Data sets created for combinations of 4 regions and 14 parameters across 33 time periods were used in analyses designed to identify environmental drivers correlated with patterns in GPP_d . Correlations with patterns in phytoplankton productivity were explained using a pool of 48 environmental driver combinations representing the possible influences of 12 of the 14 different environmental variables (i.e., SAL, TEMP_W, DO, TP, TKN, SI, CDOM, TURB, TSS, MEI, total monthly rainfall, and mean monthly flow) in the 4 different regions of the Caloosahatchee Estuary. The parameters Z_p and I_0 were not considered because they were used along with CHL A to estimate GPP_d .

A combination of 11 variables across the four regions yielded the highest correlation ($\rho = 0.525$) with the spatial-temporal pattern in GPP_d (Table 4-7). In region UE, the variables MEI, total monthly rainfall, CDOM, TSS, TEMP_W, and TURB were correlated with estimates of GPP_d . Concentrations of SI and TEMP_W were correlated with estimates of GPP_d in region ME. Values of MEI and SAL correlated with primary productivity in region LE. In region BY, MEI values were most strongly correlated with primary productivity.

Discussion

Relationships between Phytoplankton Productivity and Environmental Variables

Correlations between GPP_d and selected environmental parameters, encompassing a variety of meteorological, hydrological, and physical-chemical conditions that have been traditionally considered in similar analyses (Boynton et al. 1982), were examined to gain insights into possible driving factors of phytoplankton productivity in the Caloosahatchee Estuary. Out of 48 possible driver combinations, representing the potential influence of 12 environmental parameters on GPP_d in each of the 4 regions, 11 provided the best overall correlation to the spatial-temporal patterns in phytoplankton productivity in the Caloosahatchee Estuary. Some regional differences were observed in the nature of these relationships. Climate and weather had a broad influence in the Caloosahatchee Estuary on monthly mean GPP_d estimates. ENSO patterns (with respect to MEI values) were correlated to primary productivity throughout the Caloosahatchee Estuary, except in region ME, while rainfall played an important role in region UE only. Water temperature, in combination with other variables, was correlated to monthly mean GPP_d estimates in regions UE and ME. Salinity influenced the pattern in primary productivity in region LE only. Monthly mean estimates of GPP_d were partially correlated to light availability (with respect to CDOM, TSS, and TURB) in region UE only. Lastly, SI was the only nutrient correlated to the patterns in primary productivity, and this relationship was significant in region ME only.

Climate and weather

Climate and weather are naturally interrelated due to the impact of alternating phases of the ENSO cycle on the displacement of atmospheric heat overlaying warm ocean waters, which change global atmospheric circulation and, thus, regional weather

conditions (TAO 2011). Because ENSO cycles are characterized by changes in wind, temperature, and rainfall, it is difficult to dissect the correlations found between MEI values and patterns in phytoplankton productivity in the Caloosahatchee Estuary. However, the impacts of alternating ENSO cycles and their respective strengths on the climate and weather in regions outside the equatorial Pacific are evident in shifting seasonal temperatures and precipitation patterns (IRI 2007). Rainfall and temperature were unique variables in this correlation analysis as they were considered to be inherent components of the MEI metric of ENSO and independent environmental drivers of phytoplankton productivity; they were therefore examined separately. Wind was not considered as a separate variable in the correlation analysis since the Caloosahatchee Estuary is shallow and presumably well-mixed under normal conditions with the help of tidal exchange (McPherson et al. 1990). In addition, variations in wind fields operate at very short time scales, making comparisons with other variables in the data set tenuous.

Temperature

The effect of temperature on phytoplankton productivity is largely due to the role of enzymes in photosynthesis. Photosynthetic activity increases with temperature until an optimum level is reached. Optimum temperature levels vary among species in different environments, but a range of 20 to 25°C is widely accepted for phytoplankton (Day et al. 1989). As a subtropical system, seasonal variations in water temperatures in the Caloosahatchee Estuary are less dramatic than in temperate estuaries, providing greater year-round photosynthetic potential. The highest productivity rates and biomass concentrations were observed in the warmest months of the year as expected (Boynton et al. 1982), however, blooms with CHL A concentrations greater than 20 mg•m⁻³ were

also detected in cooler months, confirming year-round potential for high rates of productivity.

The impacts of El Niño and La Niña on temperatures in the Caloosahatchee Estuary were more apparent in the winter, as is the case in other systems at latitudes above the tropics (TAO 2011). Cooler than normal winters were more common in El Niño periods, and warmer than normal winters were more common in La Niña periods, following the expected outcomes of alternating ENSO phases in Florida (Jones et al. 1999) and in temperate areas (IRI 2007, TAO 2011). Variations in air temperatures are quickly matched in the water column of a system as shallow as the Caloosahatchee Estuary, potentially augmenting or hindering primary productivity. Strong terrestrial watershed inflows and small tidal exchanges in regions UE and ME make these areas even more susceptible to shifts in water temperatures.

Rainfall

Rainfall plays an important and widely recognized role in the regulation of phytoplankton biomass and primary productivity in estuaries around the world (Mallin et al. 1993, Zingone et al. 2010). The delivery of freshwater to estuaries via rainfall naturally replenishes nutrient supplies, increases turbidity, and aids in the transport of phytoplankton biomass (Zingone et al. 2010). However, the degree to which rainfall impacts estuarine water quality and corresponding responses of the phytoplankton community is dependent on anthropogenic manipulations of freshwater inflow (Alber 2002). In estuaries with relatively few upstream modifications, rainfall is directly coupled with flow, with inputs following a natural, seasonal, and relatively consistent pattern with respect to the timing, quantity, quality, and distribution of the delivery. The situation in the Caloosahatchee Estuary, and the one commonly associated with many estuaries,

involves dams, diversions, and withdrawals, which result in unnatural freshwater inflow delays, shortages, and/or purges, depending on the needs of the surrounding human population (Alber 2002).

The Caloosahatchee Estuary is a classic example of an extensively modified system with obstructed and managed inflows that either hinder or exacerbate the natural patterns of rainfall. Patterns in rainfall and flow were relatively consistent and well coupled on a seasonal basis, with both peaking during the wet season months of May through October. However, unusually high rainfall events associated with strengthening El Niño phases and episodic storms did not always translate to high mean monthly inflows. In these cases, rainfall was likely retained in the Caloosahatchee Watershed and used for agriculture and public consumption. Conversely, mean monthly inflows were sometimes high when rainfall was at or below average. High volume releases done outside of the normal seasonal and annual cycles are typically used to flush algal blooms, salt water, and other contaminants out of the Caloosahatchee River, which was likely the case in the spring of 1998.

As an independent variable in the examination of environmental drivers of phytoplankton productivity, total rainfall was only correlated to GPP_d in region UE of the Caloosahatchee Estuary. This region encompasses a 14 km stretch of the narrowest and deepest portion of the estuary closest to S-79 (Scarlatos 1988). The upper estuary also has the least amount of industrial, commercial, and residential development in comparison to the downstream regions, and it is home to a national wildlife refuge (SFWMD et al. 2009). The delivery of freshwater via runoff from the northern and southern shores of this region is likely synchronized with minimal time delays of actual

rainfall, providing 'real-time' responses of the phytoplankton community to the corresponding changes in water quality. This correlation was less evident in the downstream regions of the Caloosahatchee Estuary possibly due to the extensive urban channelization network in Cape Coral and Fort Myers (Stoker 1992), which causes rainfall runoff that would have been historically retained by an undeveloped watershed to reach the estuary in higher volumes and in less time (Barnes 2005).

The fact that mean monthly inflows were not correlated to patterns in phytoplankton productivity, while measures of ENSO and rainfall were, is most likely related to the timing discrepancies between weather events, regulated flow schedules, and sample collections. In this study, mean monthly inflows were used to represent the hydrological conditions in the Caloosahatchee Estuary for an entire month, while the collection of samples occurred erratically between the beginning, middle, and end of each month over the twenty-five year time period. Depending on the variability of flow and the corresponding changes in water residence times and water column characteristics (i.e., salinity, nutrient levels, light attenuation), GPP_d estimates may have occurred under flow conditions not accurately depicted by a monthly mean. For example, samples collected within the first few days of a month may have been better correlated to average flow rates from one month prior. Similarly, samples collected at the end of a month under flow conditions that were vastly different than the rest of the month would have been tested for correlations against higher/lower mean rates than the true conditions at the time of collection.

Salinity

Fluctuating salinity is a major variable in the Caloosahatchee Estuary in terms of the structure and function of phytoplankton, as well as other key biota (SFWMD et al.

2009). Salinities that exceed or fall short of the physiological requirements of organisms can cause stress and/or mortality. For example, oysters and submerged aquatic vegetation (tapegrass and seagrasses) have been identified as key species and extensively studied for their adaptability to altered salinity in the Caloosahatchee Estuary (Chamberlain and Doering 1998a). High salinities increase the susceptibility of oysters to predation and parasites and decrease the distribution of tapegrass (*Vallisneria americana*). On the other hand, prolonged low salinities can kill oysters, shoal grass (*Halodule wrightii*), and turtle grass (*Thalassia testudinum*). These key species are valuable ecosystem components (VECs) that provide important habitats, nursery grounds, and food sources for many fish, invertebrates, birds, and other organisms in the Caloosahatchee Estuary, making it a recreationally and commercially valued system worth studying and monitoring.

Phytoplankton are also sensitive to changes in salinity, although many estuarine species are euryhaline and capable of adapting to natural variations in salinity (Brand 1984). Two of the dominant cosmopolitan species observed in the Caloosahatchee Estuary (Chapter 3), *Akashiwo sanguinea* and *Skeletonema cf. costatum*, are able to grow in salinity ranges of 10 to 40 psu and 15 to 45 psu, respectively, although their growth rates peak at salinities of 20 and 25 psu, respectively (Brand 1984, Matsubara et al. 2007). With these salinity preferences, it is not surprising that these two species are common features of the Caloosahatchee Estuary (Chapter 3, Saunders et al. 1967, McPherson et al. 1990, Montgomery et al. 1991).

Phytoplankton assemblages in the Caloosahatchee Estuary often follow a salinity gradient, from more fresh to more marine dominated communities, which is the case in

other river-dominated estuaries in Florida (Quinlan and Philips 2007). The spatial and temporal extent of phytoplankton assemblages are altered by seasonal patterns and episodic events that change freshwater inflow and the associated physical-chemical properties of the water column (Quinlan and Philips 2007). Spatial and temporal variation in salinity in the Caloosahatchee Estuary is primarily related to the quantity, quality, timing, and distribution of freshwater via rainfall and river flow. Tidal exchange is believed to play a secondary role in the determination of salinity in the estuary (Bierman 1993, Chamberlain and Doering 1998b), particularly in the Bay and the lower regions of the system. During the twenty-five year period, the Caloosahatchee Estuary shifted between fresh and euhaline conditions, with the size and position of the different salinity zones changing in response to rainfall, freshwater inflows, and tidal exchanges. Lower salinities and the associated higher nutrient concentrations and shallower photic depths were generally observed closer to S-79 but spread throughout the estuary during flood periods, while higher salinities and the associated lower nutrient concentrations and deeper photic depths were observed closer to the Gulf of Mexico and throughout the estuary during drought periods.

Patterns in primary productivity were partially explained by salinity in region LE only. The relationship between GPP_d and salinity in this region was negative, so that higher phytoplankton productivity was associated with lower salinities. The highest peaks in GPP_d in region LE were more commonly observed under mesohaline conditions. A wide range of moderate to excessive S-79 flows (14.2 to $127.4 \text{ m}^3 \cdot \text{s}^{-1}$) produce mesohaline salinities in region LE (Bierman 1993) due to the larger, and more variable influence of tidal mixing in the lower extent of the Caloosahatchee Estuary.

Phytoplankton productivity in this region responds to shifts in nutrient and light availability and the corresponding changes in water residence times given the balance between freshwater inflows and tidal exchanges. Lower (or higher) flow rates in the given range would increase (or decrease) the extent of tidal mixing in the lower estuary, decreasing (or increasing) nutrient availability while increasing (decreasing) light availability through the dilution of the nutrient-rich, highly colored freshwater inputs. Residence times under this range of flows would fluctuate between 1 and 3 days (Qiu et al. 2007) in region LE, accommodating the growth of both faster (diatoms) and slower (dinoflagellates) species under varying conditions.

Light

Both the quantity and quality of light penetrating the water column is important to phytoplankton productivity. The quantity of light reaching the surface waters of a system varies naturally on a daily and seasonal basis. Because of the subtropical location of the Caloosahatchee Estuary, this system receives relatively high levels of incident solar radiation year-round. The transmission of light through the water column depends on the levels of light-absorbing constituents. The water itself, color dissolved organic matter (CDOM), algae, and tripton (i.e., non-algae suspended solids) create a disparity between the total intensity of photosynthetically active radiation (PAR) and the portion that is photosynthetically usable radiation (PUR) depending on the absorption spectrum of the phytoplankton (Kirk 1994), driving phytoplankton adaptations at the cellular level and/or species succession at the community level.

Light availability in the water column varied spatially and temporally with respect to Z_p values, representing the depth of 1% surface irradiance where gross production and algal respiration rates are equal (Day et al. 1989). Photic depths were deeper in

the water column in higher salinity zones of the Caloosahatchee Estuary, particularly in regions LE and BY. Tripton was the major component of light attenuation in these regions, as reflected in the relatively high values of TSS and TURB relative to CHL *A* and CDOM. In the freshwater and upper portions of the Caloosahatchee estuary, photic depths were shallower and less variable given the large fluctuation in rainfall and freshwater inflows via S-79 during the twenty-five year period. Smaller values of Z_p at distances closer to S-79 and in lower salinities corresponded to high average concentrations of CDOM, confirming the influence of highly-colored humic waters on light attenuation under these conditions in the Caloosahatchee Estuary (Doering and Chamberlain 1999, Doering et al. 2006).

Parameters affecting light availability provided important correlations to GPP_d throughout the Caloosahatchee Estuary, except in region BY. Photic depths in San Carlos Bay were typically deep enough to preclude significant periods of light limitation of photosynthesis due to the dilution of humics via tidal mixing. As a result, phytoplankton productivity was likely limited by factors other than light in region BY, such as nutrient availability or water residence times. In contrast, patterns in GPP_d were negatively correlated with patterns in CDOM in region UE, highlighting the influence of humics on the attenuation of PAR, as observed in other highly colored aquatic environments (Kirk 1994, Falkowski 1994).

Nutrients

Nitrogen is the most important nutrient limiting factor for phytoplankton production in the Caloosahatchee Estuary (McPherson and Miller 1990, Doering et al. 2006, Heil et al. 2007), as in many other estuaries and coastal ecosystems worldwide (Boynton et al 1982, Cloern 2001). Being a subtropical system, the Caloosahatchee

Estuary is acutely vulnerable to nitrogen pollution via agricultural runoff since lower latitude systems are exceeding global consumption trends in fertilizer use (Beman et al. 2005). The potential for nitrogen limitation is accentuated by excess phosphorous loads from natural weathering and anthropogenic mining of local phosphate-rich limestone rock (Odum et al. 1998). Silica has been considered for its secondary role in shaping the structure of the phytoplankton community given its use in the growth and maintenance of diatom cells.

Previous researchers in the Caloosahatchee Estuary have found that the distribution of nutrients in this system is linked to riverine inputs, freshwater runoff, tidal exchange, and nutrient recycling (McPherson and Miller 1990). The Caloosahatchee River via S-79 plays the dominant role in nutrient distribution by contributing substantial nutrient loads and flushing nutrients downstream and out of the system (McPherson and Miller 1990). Rainfall works in conjunction with river flow to control the supply of new nutrients to the Caloosahatchee Estuary given the urban, agricultural, and environmental demands on water in the system and surrounding watershed. Six wastewater treatment facilities also discharge directly in the Caloosahatchee Estuary, but their combined average daily nutrient loads are less than those of S-79 by an order of magnitude in both the wet and dry seasons (Doering et al. 2006, Bailey et al. 2009).

Higher concentrations of TKN, TP, and SI were associated with lower salinities and at distances closer to S-79, reflecting the influence of freshwater inflow on nutrient loading and spatial distribution in the Caloosahatchee Estuary between January 1985 and December 2010. Similar results have been previously reported for shorter timescales (McPherson and Miller 1990, Doering and Chamberlain 1998, Doering and

Chamberlain 1999, Doering et al. 2006). Long-term trends in the concentrations of these macronutrients were not statistically tested in this study due to the discontinuity of the pooled data set, but no visual patterns were evident in the twenty-five year time series of monthly means. Previous efforts to identify changes in nutrient levels in the Caloosahatchee Estuary over time was accomplished by comparing three hydrologically different periods of discontinuous data, including a relatively dry period from 1986 to 1989, a relatively wet period from 1994 to 1996, and an intermediate period from 1999 to 2003 (Doering et al. 2006). Across the four regions of the Caloosahatchee Estuary, salinity was lowest during the wet period, while concentrations of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorous (DIP) were lowest and highest, respectively, during the dry period (Doering et al. 2006). These changes in water quality were not reflected in concentrations of CHL A (Doering et al. 2006), possibly indicating the role of other factors in the regulation of phytoplankton biomass and, thus, primary productivity in the Caloosahatchee Estuary.

In this study, silica was the only nutrient correlated with the patterns in phytoplankton productivity in the Caloosahatchee Estuary. Higher average estimates of GPP_d were generally observed in conjunction with higher average concentrations of SI, but the relationship in region ME was less clear. A slight negative correlation between monthly mean concentrations of SI and monthly mean estimates of GPP_d in this part of the estuary may point to cases of model over simplification caused by differences in photosynthetic efficiency among the species present in the Caloosahatchee Estuary (Chapter 3). It is possible to hypothesize that diatoms, which typically dominate in regions LE and BY (Chapter 3), are less productive in region ME in comparison to other

phytoplankton groups, regardless of the availability of silica, if some other factor, such as salinity stress or light quality affects their growth potential.

Patterns of Phytoplankton Biomass Variability

As one of the major variables used in the adapted $BZ_{p/o}$ model to estimate GPP_d in this study, it was important to consider trends in CHL *A* levels in the Caloosahatchee Estuary. Phytoplankton biomass, in terms of CHL *A* concentrations, explained 80% of the variability in GPP_d during the model development period (Chapter 3), so variations in this parameter alone may partially explain variations in GPP_d over the twenty-five year period. The partitioning of the variability associated with the eight-year subset of regional monthly mean CHL *A* concentrations revealed that phytoplankton biomass in the Caloosahatchee Estuary fluctuated both temporally and spatially in response to seasonal cycles, annual disturbances, and residual events. The greatest contribution to phytoplankton biomass variability in the Caloosahatchee Estuary was the residual component, with the seasonal and annual components explaining approximately one-third to one-half of the CHL *A* pattern observed during the eight years selected from the original twenty-five year data set, respectively. In comparison to the median values obtained from Cloern and Jassby's (2010) analysis of 84 sites sampled within 51 estuarine-coastal ecosystems worldwide, the Caloosahatchee Estuary as a whole had relatively moderate influences of annual, seasonal, and residual variability on the patterns in phytoplankton biomass.

Annual variability

In general, the annual component explained the smallest portion of the phytoplankton biomass variability in the Caloosahatchee Estuary during the eight-year subset. However, in region ME, annual variability had a greater influence than the

seasonal component. The findings of Cloern and Jassby (2010) suggest that sites having large annual variability have been disturbed by climatic shifts or human actions. Large-scale changes in climatic conditions (i.e., temperature, winds, pressure, etc.) caused by oscillating phases of global climate patterns have altered pelagic and benthic grazing pressures on phytoplankton biomass and, consequently, the long-term patterns in CHL A, in places such as Gulf of Naples (Italy), Narragansett Bay (Rhode Island), Massachusetts Bay (Massachusetts), and South San Francisco Bay (California) (Cloern and Jassby 2010). Anthropogenic disturbances (e.g., habitat modifications, invasive species, etc.) that also altered trophic interactions (e.g., bivalve grazing) or nutrient availability have been linked to deviations from long-term CHL A trends in Florida Bay (Florida), North San Francisco Bay (California), Ringkøbing Fjord (Denmark), and Tampa Bay (Florida) (Cloern and Jassby 2010).

In the Caloosahatchee Estuary, the year 2004 produced unusually high CHL A concentrations in region ME and, to a lesser extent, in regions LE and UE. Elevated CHL A concentrations above the annual mean were observed in the inner regions of the Caloosahatchee Estuary just prior to the passing of Hurricanes Charley, Frances, Ivan, and Jeanne. In conjunction with the start of the wet season and a strengthening El Niño, the estuary went from a very dry state in the month of May with almost no rainfall (total of 1.2 cm at 7.5 cm below normal) and river flow (monthly mean of $7.5 \text{ m}^3 \cdot \text{s}^{-1}$) to a very wet state in the month of June with well above average rainfall (total of 38.3 cm at 13.5 cm above normal) and steady, moderate-level releases of freshwater (monthly mean of $19.8 \text{ m}^3 \cdot \text{s}^{-1}$). The corresponding delivery of nutrients to the estuary likely caused the initial increase in CHL A concentrations observed in regions UE and ME in

June. By mid-July and into the beginning of August, average flow rates were maintained between 20 and 80 $\text{m}^3\cdot\text{s}^{-1}$ in preparation for the arrival of the first storm. The resulting higher volume inflows would have reduced water residence times in the upper estuary to one or two days (Qiu et al. 2007) and flushed the nutrients and the phytoplankton downstream where light conditions would have been more favorable after dilution by tidal exchange, helping to explain the large CHL *A* peaks in the latter months in regions ME and LE. The annual decline in CHL *A* that was detected further downstream in region BY that same year could be explained by a subsequent crash of the phytoplankton bloom since the water mass would have been depleted of its nutrients and unable to sustain production once it reached San Carlos Bay. Additionally, the high concentrations of phytoplankton biomass may have been grazed down by zooplankton, which are typically more densely concentrated in the higher salinity zones of the lower and outer regions of the Caloosahatchee Estuary (Chamberlain et al. 2003, Tolley et al. 2010). However, the zooplankton (and the phytoplankton themselves) would have been flushed out to the Gulf of Mexico under flows greater than 80 $\text{m}^3\cdot\text{s}^{-1}$ (Chamberlain et al. 2003, Tolley et al. 2010), which started in mid-August and continued through the end of the storm season.

A similar series of events occurred in 1995 when above average CHL *A* concentrations were observed in all four regions of the Caloosahatchee Estuary, although the largest annual deviation from the long-term mean occurred in region BY. High monthly CHL *A* means were observed throughout the estuary as early as April 1995, which corresponded to an early start to the wet season with above average rainfall (total of 13.6 cm at 10.9 cm above normal) during an El Niño period.

Phytoplankton blooms were likely triggered by the supply of nutrients delivered through rainfall runoff, which was again replenished in June and sustained through August with the arrival of Hurricane Erin and Tropical Storm Jerry. The above average rainfall levels were coupled with subsequent increases in freshwater releases from Lake Okeechobee (via S-77) and the upper watershed (via S 78) into the Caloosahatchee Estuary (via S-79), which would have carried the phytoplankton biomass to the lower regions of the system and Bay. Because the high CHL A concentrations were first observed in the freshwater and oligohaline zones, it is likely that the bloom originally formed upstream of S-79 and was subsequently flushed out to the Gulf of Mexico through the estuary. This latter hypothesis is supported by reports of the presence of blooms of the toxic blue green *Microcystis* during that summer in Lake Okeechobee and the Caloosahatchee River, which ultimately impacted the estuary (Burns 2008). At the same time, a major red tide *Karenia brevis* bloom was reported off the west coast of Florida between Tampa Bay and Charlotte Harbor (FDEP 2005, Walsh et al. 2006), which may have infiltrated region BY on incoming tides, explaining the presence of high CHL A concentrations in that region in 1995.

Seasonal variability

A general underlying seasonal pattern was detected in the CHL A time series of the four regions of the Caloosahatchee Estuary, but its contribution to the overall variability in phytoplankton biomass was relatively small and influence on the magnitude of mean CHL A concentrations changed over time. Such is the case in many estuaries and coastal ecosystems worldwide, where regular seasonal patterns are commonly absent, less pronounced, or increasingly found to shift over time periods longer than a decade (Cloern and Jassby 2010). Irregularity in the timing and amplitude of

phytoplankton biomass seasonal variability has been attributed to the shallowness and connectivity of estuarine-coastal ecosystems to land and sea, allowing unique and complex processes (e.g., upwelling, tidal mixing, wind-driven re-suspension, river flow, hydraulic manipulations, nutrient inputs, benthic grazing, species introductions, etc.) to interject the annual climatologically-driven cycles of biomass growth and senescence that function in the open ocean and on land (Cloern and Jassby 2008).

In the Caloosahatchee Estuary, regional monthly mean CHL *A* concentrations were typically higher in the wet summer and early fall months, and the timing of these peaks followed the downstream flow of freshwater from the upper estuary (region UE) to San Carlos Bay (region BY). The recurrence of this pattern was attributed to the seasonal increase in rainfall during the months of May through October and the subsequent need for more frequent and higher volume freshwater discharges through S-79 as a way to maintain prescribed water levels in Lake Okeechobee and control flooding in the upper watershed. Rainfall runoff and regulatory releases provide a seasonal supply of new nutrients to the Caloosahatchee Estuary and the resident phytoplankton communities, stimulating primary productivity there (Doering et al. 2006). Here, the wet season also coincides with annual peaks in temperature, solar radiation, and photoperiod, providing a combination of ideal phytoplankton bloom conditions. Phytoplankton biomass and productivity tend to be highest during the warmer months of the year (i.e., May through October) in a broad spectrum of estuarine-coastal ecosystem types (e.g., river-dominated, embayments, lagoons, and fjords) (Boynton et al. 1982), but these annual climatology cycles have been more commonly associated with regular and high-amplitude seasonal patterns in temperate estuaries worldwide,

including South San Francisco Bay (California), North Inlet (South Carolina), and Oosterschelde (Netherlands) (Cloern and Jassby 2010). At 26°N latitude, the influence of these climatologically driven forces on phytoplankton seasonal patterns in the Caloosahatchee Estuary is weakened (i.e., levels are relatively high throughout the year), and, therefore, cannot be solely responsible for the observed trends.

Regional differences in the timing of the seasonal declines in mean CHL A concentrations further suggest the role of both natural and anthropogenic processes in the regulation of phytoplankton biomass in the Caloosahatchee Estuary. Low mean CHL A concentrations in the lower estuary (region LE) and San Carlos Bay (region BY) during the winter were likely tied to natural declines in temperature, solar radiation, and nutrient supplies due to decreased rainfall and river inflow. However, the seasonally low mean CHL A concentrations in the upper and middle estuary (regions UE and ME) during the fall were likely the result of a downstream 'wash-out' effect (Doering et al. 2006) caused by excessive anthropogenic flushing of rainfall reserves at the end of the wet season with the biggest events occurring in the months of August, September, and October. Alternatively, the inflow of nutrient-rich, colored water may have first aided the accumulation of phytoplankton biomass at the beginning of the season but later hindered the maintenance of blooms due to depleted nutrient supplies and/or decreased light availability from elevated CDOM concentrations and shading by the phytoplankton themselves. Phytoplankton biomass and productivity declines in the late wet season have also been observed in neighboring Charlotte Harbor and have been attributed to reduced light availability from increased river inflow color (McPherson et al. 1990). Zooplankton were likely not responsible for the decline of phytoplankton biomass in the

late wet season months in regions UE and ME since their densities typically reach reported lows during this time and in these areas in response to increased freshwater inflow and reduced salinity (Chamberlain et al. 2003, Tolley et al. 2010).

Residual variability

The major contribution of CHL A variability from the residual component indicated that there was a high occurrence of deviations from average seasonal patterns of, and annual shifts in, productivity in the Caloosahatchee Estuary (Cloern and Jassby 2010). This outcome can be considered the norm based on the findings of Cloern and Jassby (2010) in their analysis of 84 different CHL A time series from within 51 estuarine-coastal ecosystems worldwide. Variability of this type can be great when the seasonal pattern changes strongly from year-to-year (Cloern and Jassby 2010). This explanation did not seem to apply in the Caloosahatchee Estuary since CHL A concentrations were consistently highest in the wet season months (May through October), creating a relatively uniform seasonal pattern across the twenty-five year time period. Therefore, the residual 'events' were likely associated with temporally irregular phytoplankton blooms, appearing as spikes in the CHL A time series (Cloern and Jassby 2010). The larger values of $SD\epsilon$ in regions UE, ME, and LE confirm that the frequency and magnitude of these bloom events were greater in the inner regions of the Caloosahatchee Estuary than in San Carlos Bay (region BY). This pattern was likely explained by the fact that region BY had very low CHL A concentrations throughout the study period due to its relatively low concentrations of nutrients (i.e., TP, TKN, and SI). The few phytoplankton blooms that did occur in region BY were likely allochthonous in nature since they were previously or simultaneously observed in upstream regions of the Caloosahatchee Estuary under natural and/or anthropogenic flushing events. In

general, the formation and accumulation of phytoplankton biomass blooms throughout the Caloosahatchee Estuary were most commonly associated with periods of above average rainfall and/or freshwater inflow that stemmed from changes in ENSO conditions and/or episodic storm events. The major effect of weather and/or management action was the creation of high-nutrient habitats, which facilitated the development of phytoplankton biomass blooms in this and other estuaries worldwide (Cloern and Jassby 2010).

In all four regions of the Caloosahatchee Estuary, the residual component of phytoplankton biomass variability identified unusually high mean CHL *A* concentrations for a given month and year that did not correspond to spikes in the time series. The occurrence of residual events outside of these prescribed bloom conditions was most likely the result of sampling errors that can be large when single measurements are used as estimators of monthly mean CHL *A* concentrations (Cloern and Jassby 2010), which was the approach used in this analysis. Infrequent and inconsistent sampling efforts miss phytoplankton community responses to changes in water quality that occur on timescales shorter than a month, causing discrepancies in the scales at which variability can be explained (Cloern and Jassby 2010).

Variations in Trophic Status

The trophic status of the Caloosahatchee Estuary varied spatially and temporally between 1986 and 2010 given a wide range of meteorological, hydrological, physical, chemical, and biological factors likely influencing phytoplankton productivity. Taking into account all model estimates of phytoplankton productivity observed during the twenty-five year period, average long-term conditions in the Caloosahatchee Estuary were mesotrophic ($253 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$). This overall trophic status classification is lower

than the eutrophic estimate ($346 \text{ g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) derived during the model development study (February 2009 to February 2010, excluding March 2009) (Chapter 3), reflecting the added influence of interannual and decadal changes in water quality, beyond the previously detected seasonal/intraannual influence, on patterns of productivity in the Caloosahatchee Estuary. The previous annual estimate of phytoplankton productivity in the Caloosahatchee Estuary was based on field tested measurements taken across a phase shift between a relatively weak La Niña period to a relatively strong El Niño period corresponding to seasonally low and high inputs of freshwater into the system, respectively. In comparison, the long-term overall estimate of GPP_y derived from this study encompassed the effect of fifteen alternating ENSO phases, as well as the passing of more than twenty named storms, suggesting the importance of natural and anthropogenic inputs of freshwater on the regulation of phytoplankton productivity in the Caloosahatchee Estuary.

When temporal and spatial differences in phytoplankton biomass and light availability (the primary variables used to estimate GPP_y) were considered, the trophic status of the Caloosahatchee Estuary varied between oligotrophic and hypertrophic years between 1986 and 2010. Years producing eutrophic and/or hypertrophic levels of GPP_y were associated with average annual CHL *A* concentrations greater than $11 \text{ mg}\cdot\text{m}^{-3}$, the threshold set by the Florida Department of Environmental Protection (FDEP) for defining impaired estuaries and coastal waters (Bailey et al. 2009, SFWMD et al. 2009). These high annual levels of productivity primarily occurred in years experiencing climatic shifts with respect to alternating ENSO phases, which is a

recognized source of annual variability in phytoplankton biomass and, thus, primary productivity (Cloern and Jassby 2010).

Under the current total maximum daily loads (TMDLs) set by FDEP, the annual average CHL A threshold of $11 \text{ mg}\cdot\text{m}^{-3}$ has been linked to elevated nutrient levels (primarily TN) and reduced DO concentrations that are above and below, respectively, the state of Florida's water quality standards (Bailey et al. 2009). These dense accumulations of phytoplankton biomass, and the high levels of phytoplankton productivity that support them, threaten the "recreation, propagation, and maintenance of a healthy, well-balanced population of fish and wildlife in marine waters" (Bailey et al. 2009). If CHL A levels are maintained below this water quality standard, the trophic status of the Caloosahatchee Estuary should not exceed mesotrophic levels given the spatial and temporal variations in light availability expected in the system. This target conforms to the Comprehensive Everglades Restoration Program (CERP) goal of avoiding transformations of oligotrophic systems into eutrophic ones (Boyer et al. 2009).

These variations in trophic status observed during the twenty-five year period may not fairly represent the range of productivity potential in the Caloosahatchee Estuary due to the bias associated with missing data across both space and time. A better representation of the actual temporal and spatial variations in GPP_y and the corresponding trophic status of the Caloosahatchee Estuary would have been depicted had the annual rates for each region or zone incorporated monthly estimates of productivity across each of the calendar seasons (i.e., winter = December through February, spring = March through May, summer = June through August, fall = September through November), or at the very least, from each of the more inclusive wet

and dry seasons (i.e., wet = May through October, dry = November through April). The limitation of the available data is a (potentially large) source of error in the analysis of seasonal, interannual, and decadal trends in phytoplankton productivity (Winder and Cloern 2010).

Summary

This study extended the usefulness of a long-term water quality data set encompassing the monitoring and research efforts of five programs/projects occurring discontinuously between January 1986 and December 2010 in the Caloosahatchee Estuary, Florida, for tracing and understanding changes in the system's trophic status. Field measurements of phytoplankton biomass, in terms of chlorophyll *a* concentrations, and light availability, with respect to incident PAR flux and photic depths, were compiled and used to estimate phytoplankton productivity using the BZ_{p/l_0} or 'light•biomass' approach (Cole and Cloern 1987) over the twenty-five year period. The GPP_d model previously adapted to the Caloosahatchee Estuary depicted variations in the seasonal, interannual, and decadal responses of the phytoplankton community to natural and anthropogenic influences in the surrounding watershed.

Correlations between GPP_d and selected environmental parameters were used to identify possible drivers of phytoplankton productivity in the Caloosahatchee Estuary. Climate and weather, with respect to ENSO cycles, rainfall, and water temperatures, largely influenced the patterns in phytoplankton productivity throughout the system. Salinity, nutrients, and light availability also partially explained the patterns in GPP_d , although their influence varied spatially. Flow through the main water control structure was not correlated to GPP_d , likely due to the time lag between natural freshwater inputs,

anthropogenic manipulations, and sampling events, although changes in productivity in response to river releases were observed on shorter time scales.

Variations in CHL *A* with respect to seasonal patterns, annual disturbances, and residual events, were considered as likely explanations for variations in GPP_d . Spatial and temporal deviations in phytoplankton biomass and, thus, primary productivity, were primarily linked to temporally irregular, excessive phytoplankton blooms that followed natural and anthropogenic inputs of new nutrients. Seasonal peaks in CHL *A*, coupled with peaks in GPP_d , occurred during the warmer, wetter months, given elevated temperatures, light levels, and freshwater inputs. Years having the greatest concentrations of CHL *A*, matched by high estimates of GPP_d , had been disturbed by climatic shifts in the ENSO cycle.

These patterns in phytoplankton biomass and primary productivity corresponded to spatial and temporal shifts in the trophic status of the Caloosahatchee Estuary from oligotrophic to hypertrophic levels. Allochthonous blooms, originating from the upper watershed and coastal waters likely contributed to the high levels of productivity through flushing events and tidal exchanges. Mesotrophic levels of productivity are theoretically achievable when CHL *A* concentrations are maintained at or below the state of Florida's standard for water quality, protecting the ecological and economic value of the system. However, a more complete time series of water quality data and in-depth analysis of these and additional factors controlling phytoplankton productivity in the Caloosahatchee Estuary is needed to confirm the appropriateness of current management and restoration efforts.

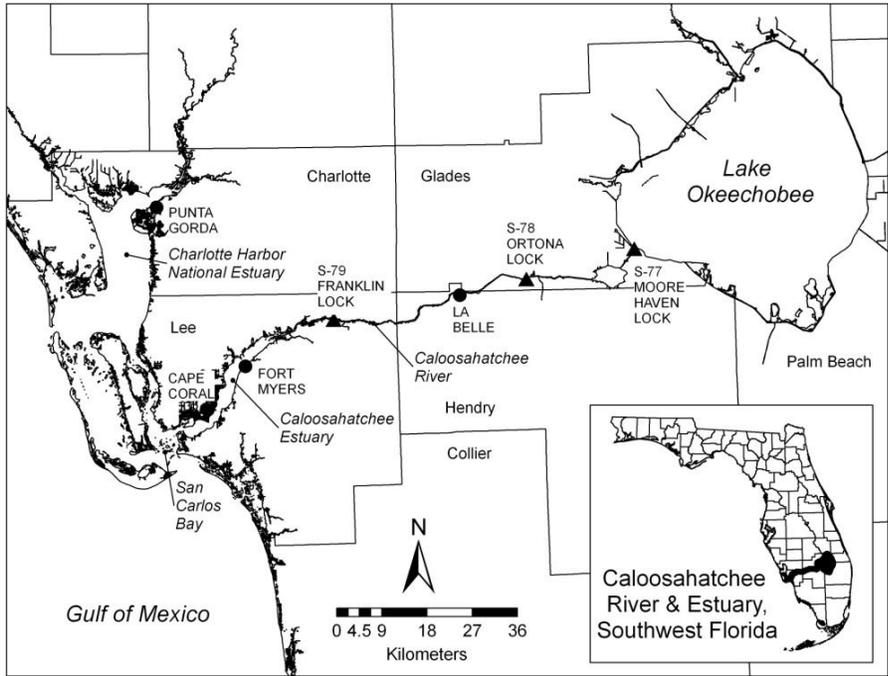


Figure 4-1. Location and connection of the Caloosahatchee Estuary, FL with respect to Lake Okeechobee via the Caloosahatchee River (C-43 Canal) and the Gulf of Mexico and Charlotte Harbor via San Carlos Bay.

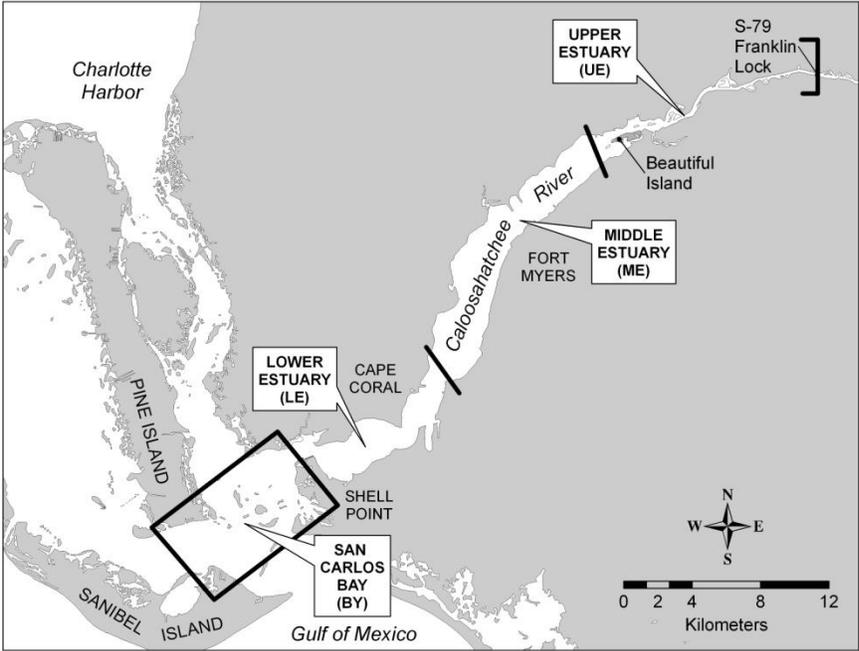


Figure 4-2. Four regions of the Caloosahatchee Estuary sampled in long-term water quality monitoring programs/research projects.

Table 4-1. Sampling sites used in water quality monitoring programs/research projects in the four regions of the Caloosahatchee Estuary, defined by their distance in kilometers from S-79, the Franklin Lock and Dam. For the CCHM project, site numbers represent reference points for the location of sampling grids. Samples for this project were taken randomly within a particular grid. For all other projects, site numbers represent specific and consistent locations (based on registered GPS points) where samples were collected.

project	Upper Estuary (UE)	Middle Estuary (ME)	Lower Estuary (LE)	San Carlos Bay (BY)
CAL	1, 2, 3, 4	5, 6, 7, 8	9, 10, 17	11, 12, 13, 14, 18
CES	2, 3, 4	5, 6	7, 8	9, 10, 11
CCHM	450, 451, 453, 454, 455, 456, 457, 461, 462, 463, 467, 468, 469, 470, 471, 472	413, 414, 417, 418, 419, 422, 423, 427, 428, 429, 430, 434, 436, 437, 441, 442, 443, 444, 447, 448, 449, 452	386, 387, 388, 389, 391, 392, 393, 394, 395, 396, 404, 411, 412, 464	---
ERD	12, 13, 14, 15	9, 10, 11	6, 7, 8	3, 4, 5
HB	1	2, 3	4, 5	6
km from S-79	0 – 14	14 – 28	28 – 40	40 – 48

Table 4-2. Median salinity values observed in the four regions of the Caloosahatchee Estuary from December 1985 to May 1989, November 1994 to August 1996, and April 1999 to June 2003 (Doering et al. 2006) and the corresponding salinity zone classification.

	Upper Estuary (UE)	Middle Estuary (ME)	Lower Estuary (LE)	San Carlos Bay (BY)
salinity (psu) ---	4.1	10.1	22.6	29.4
salinity zone 0 – 0.5 (A) freshwater	0.5 – 5 (B) oligohaline	5 – 18 (C) mesohaline	18 – 30 (D) polyhaline	30 – 40 (E) euhaline

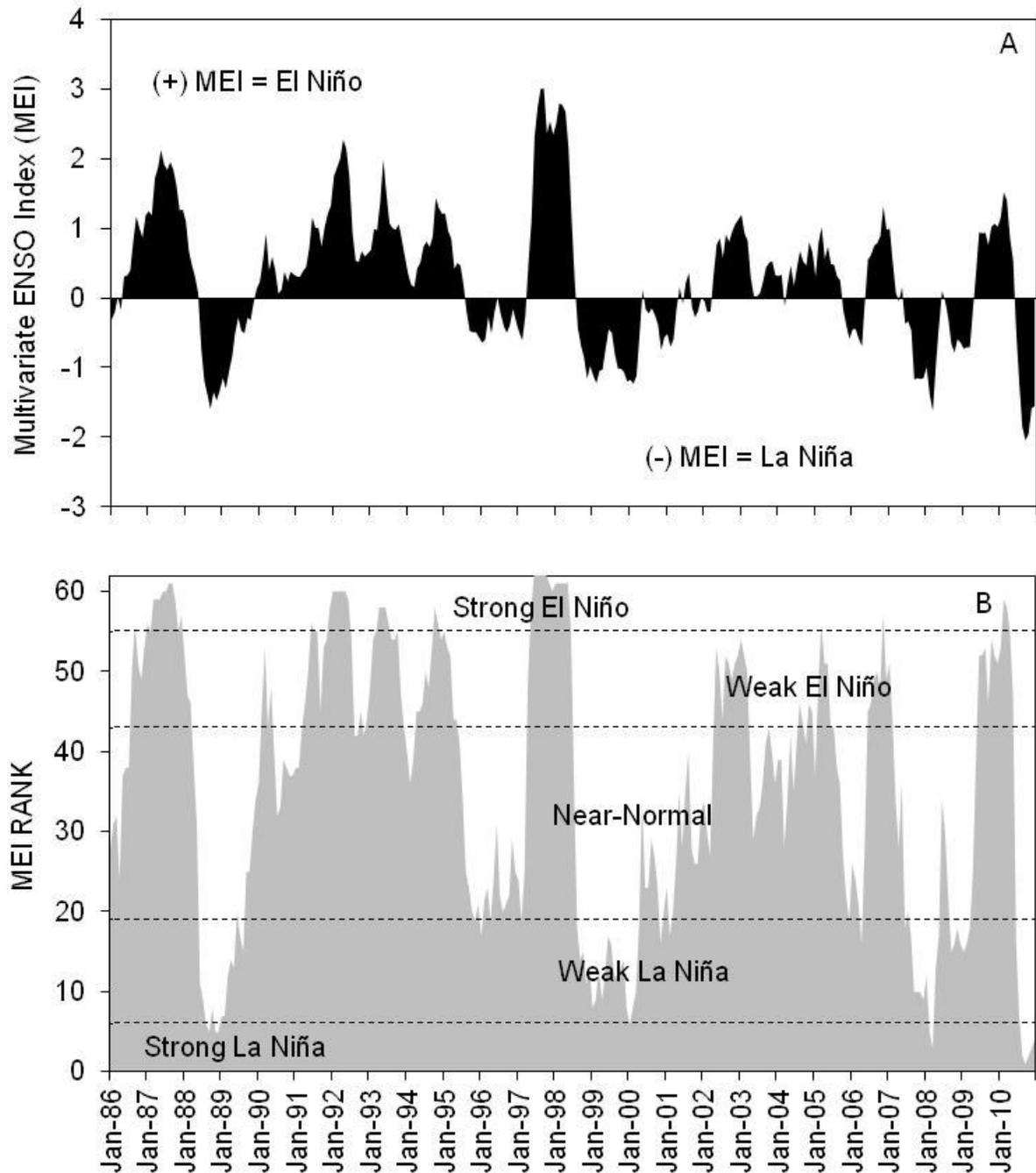


Figure 4-3. (A) Multivariate ENSO (El Niño/Southern Oscillation) Index (MEI) between January 1986 and December 2010. Positive MEI values represent the warm ENSO phase (El Niño), while negative MEI values represent the cold ENSO phase (La Niña). (B) Corresponding MEI ranks based on MEI values across the same bimonthly seasons since the beginning of record in December 1949/January 1950.

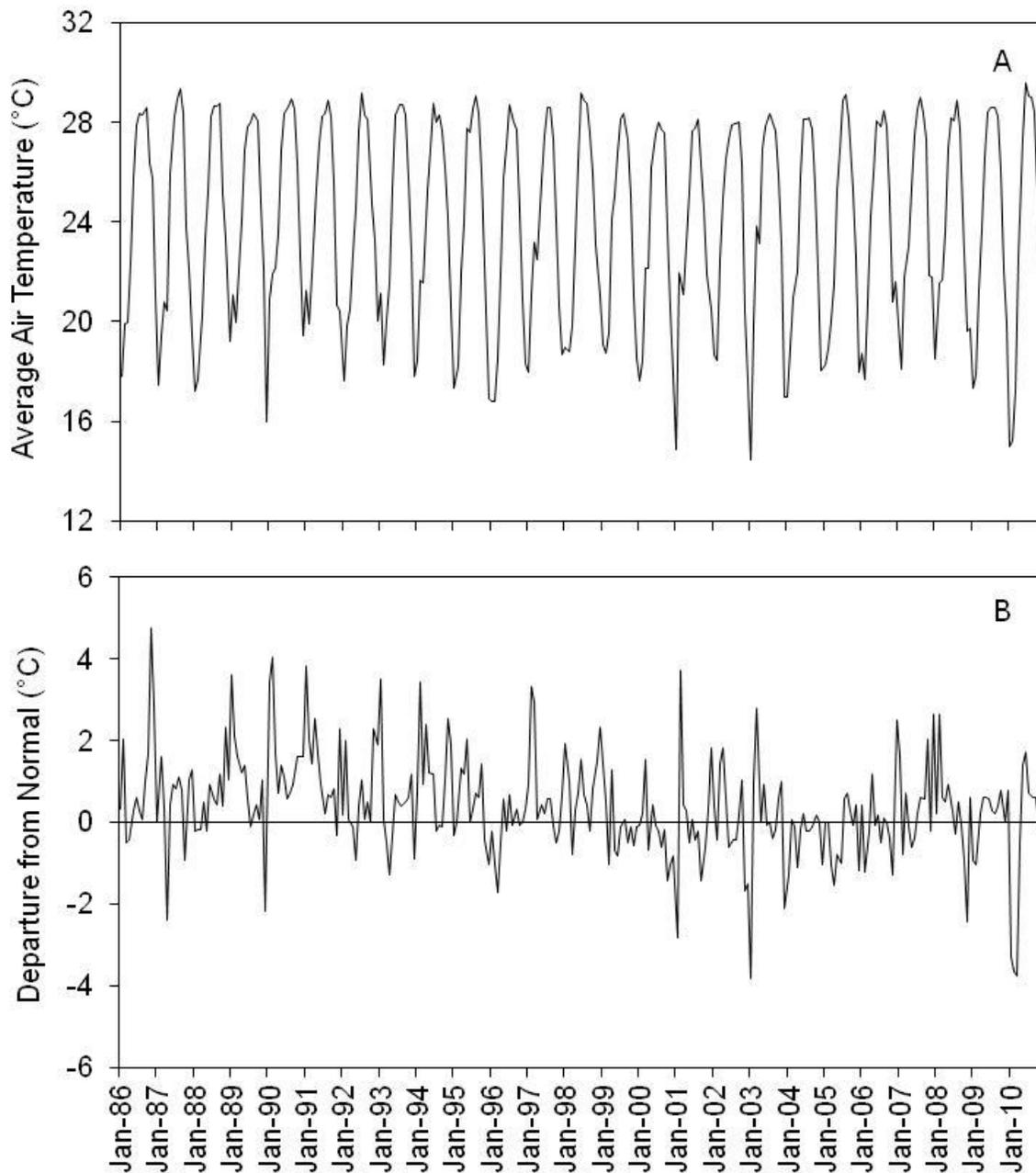


Figure 4-4. Average monthly air temperatures (°C) (A) and departures from normal (°C) (B) recorded at the meteorological station in Fort Myers, FL (from January 1986 to December 2010 (after U.S. National Climatic Data Center, Florida Climatological Data Annual Summaries).

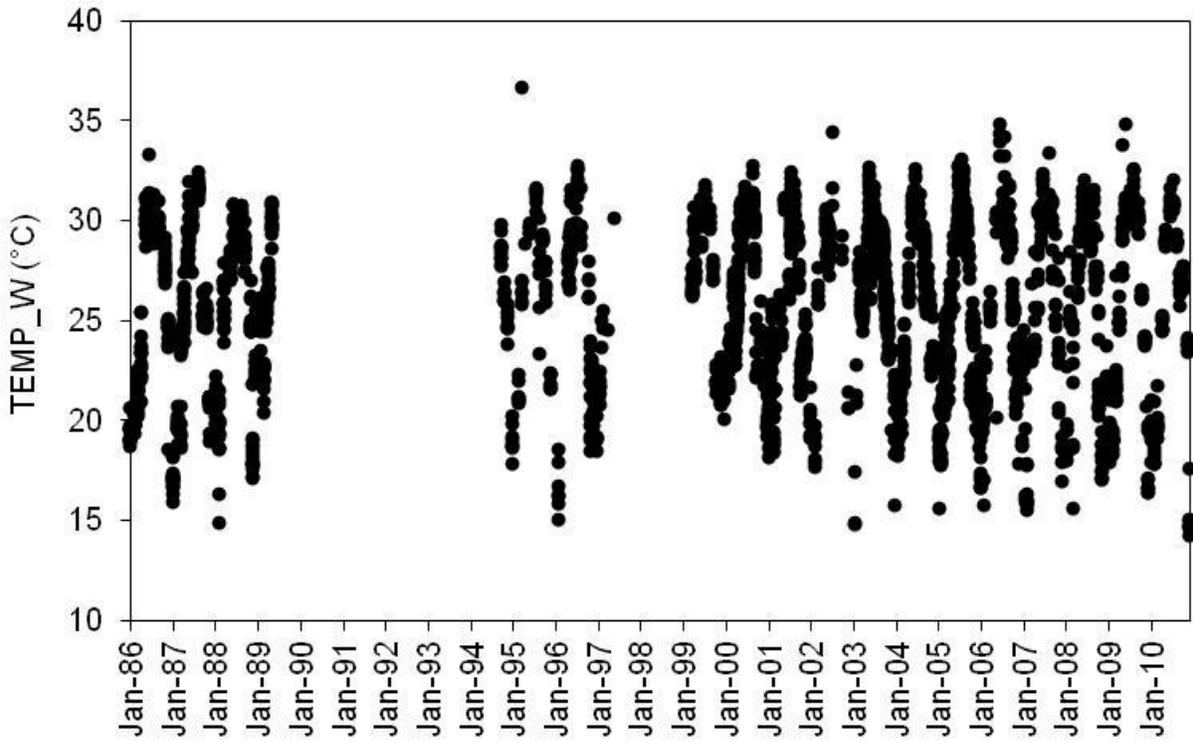


Figure 4-5. Actual water temperatures (TEMP_W in °C), observed in the Caloosahatchee Estuary, FL between January 1986 and December 2010.

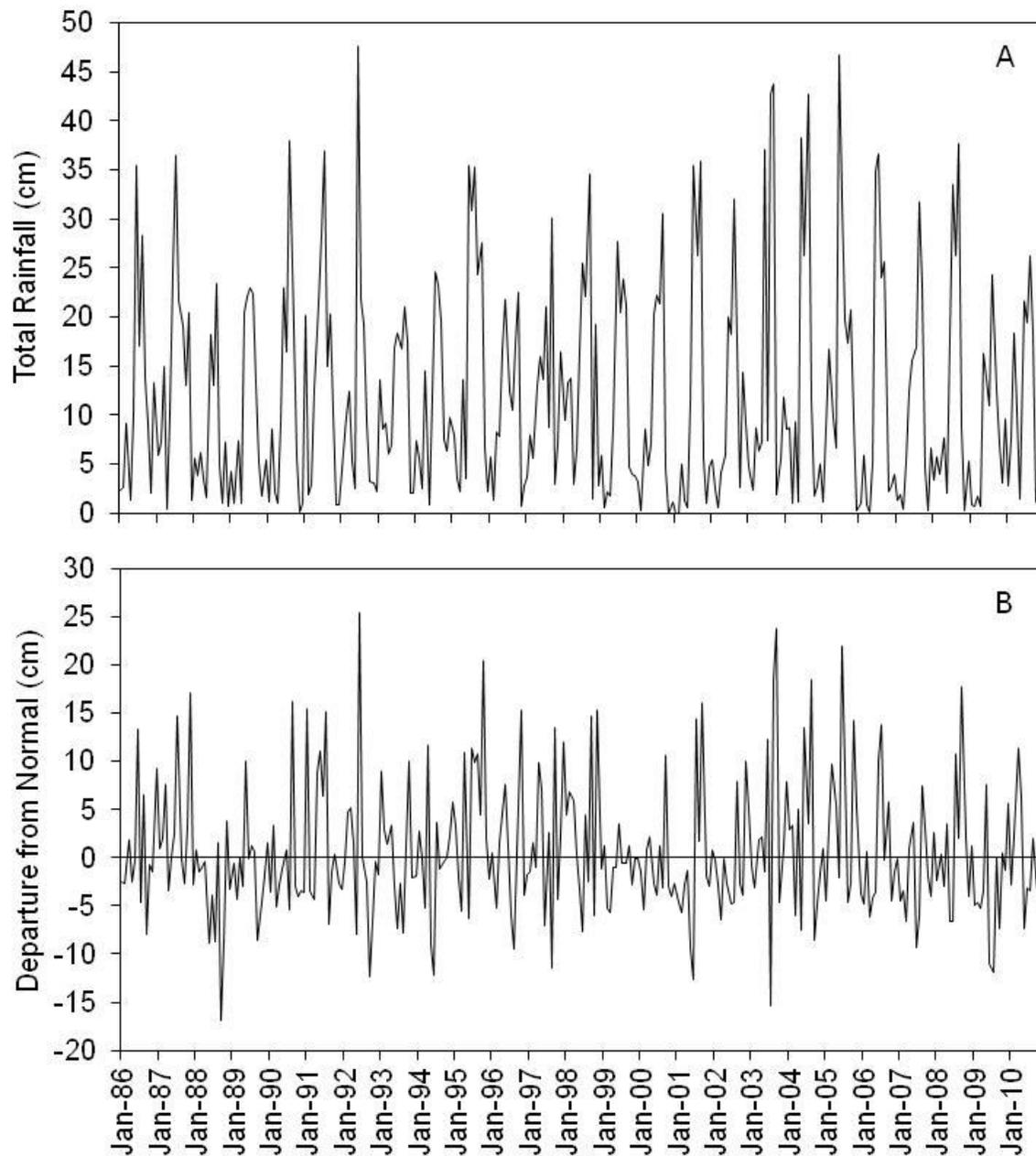


Figure 4-6. Monthly rainfall totals (cm) (A) and departures from normal (cm) (B) recorded at the meteorological station in Fort Myers, FL from January 1986 to December 2010 (after U.S. National Climatic Data Center, Florida Climatological Data Annual Summaries).

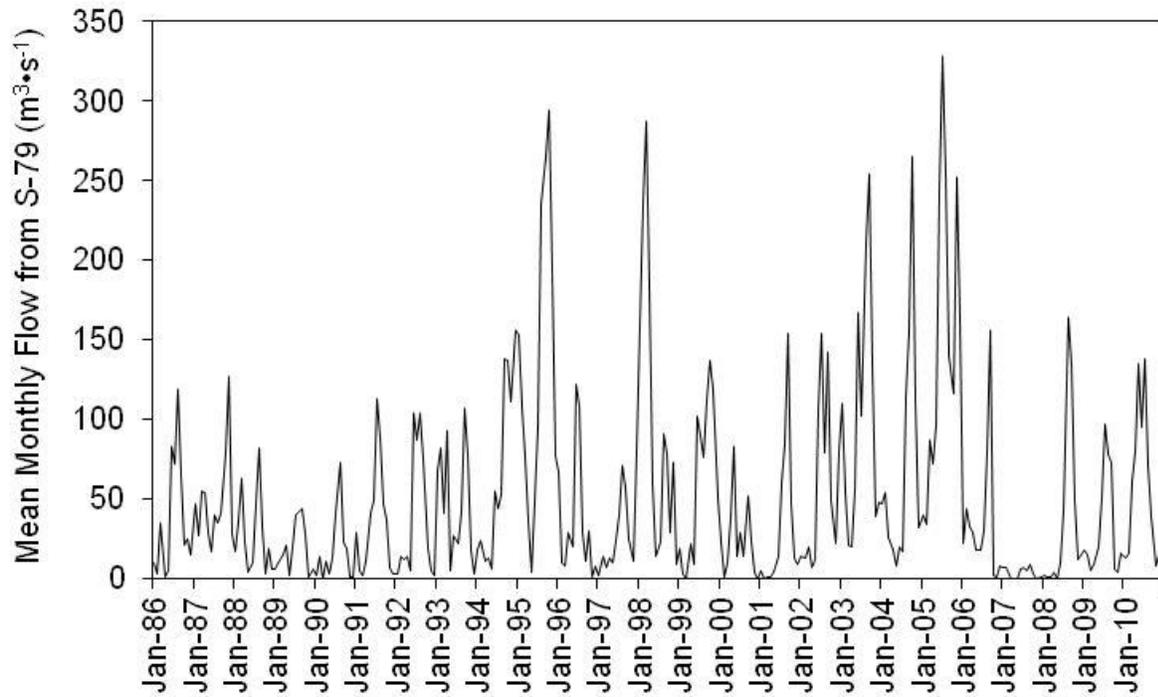


Figure 4-7. Mean monthly flow ($\text{m}^3 \cdot \text{s}^{-1}$) from S-79 into the Caloosahatchee Estuary, FL between January 1986 and December 2010.

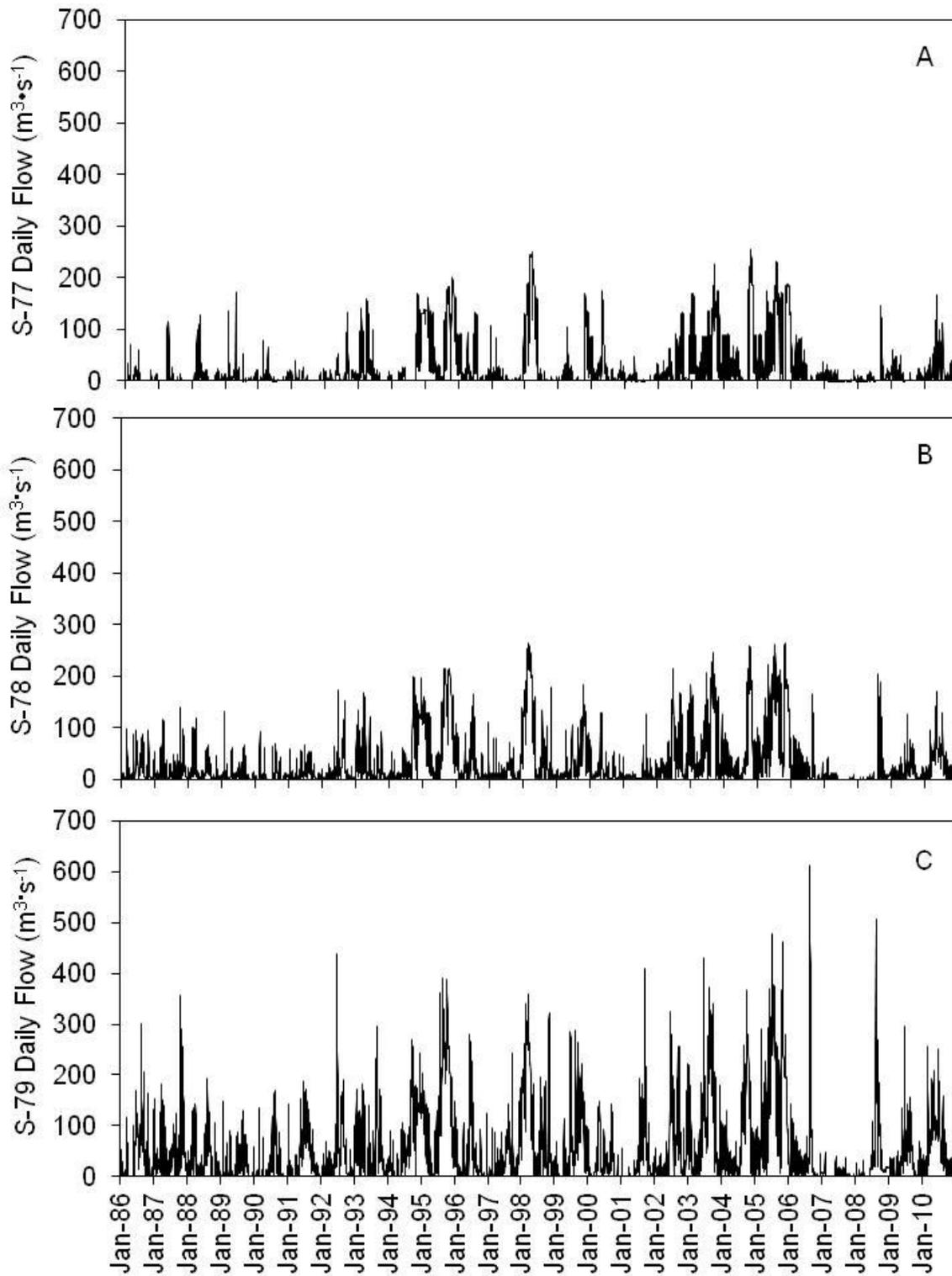


Figure 4-8. Daily flows ($\text{m}^3 \cdot \text{s}^{-1}$) along the Caloosahatchee River between Lake Okeechobee and the Caloosahatchee Estuary at water control structures S-77 (A), S-78 (B), and S-79 (C).

Table 4-3. Recommended (SFWMD et al. 2009) and observed (January 1986 to December 2010) frequency distribution of mean monthly inflows to the Caloosahatchee Estuary, FL from S-79.

flow level	flow range ($\text{m}^3 \cdot \text{s}^{-1}$) from S-79	recommended percent distribution of flows from S-79	observed percent distribution of flows from S-79
1	0 to 12.7	0%	30%
2	12.7 to 14.2	42.8%	4%
3	14.2 to 22.7	31.7%	12%
4	22.7 to 42.5	19.2%	14%
5	42.5 to 79.3	5.6%	16%
6	79.3 to 127.4	0.7%	13%
7	>127.4	0%	11%

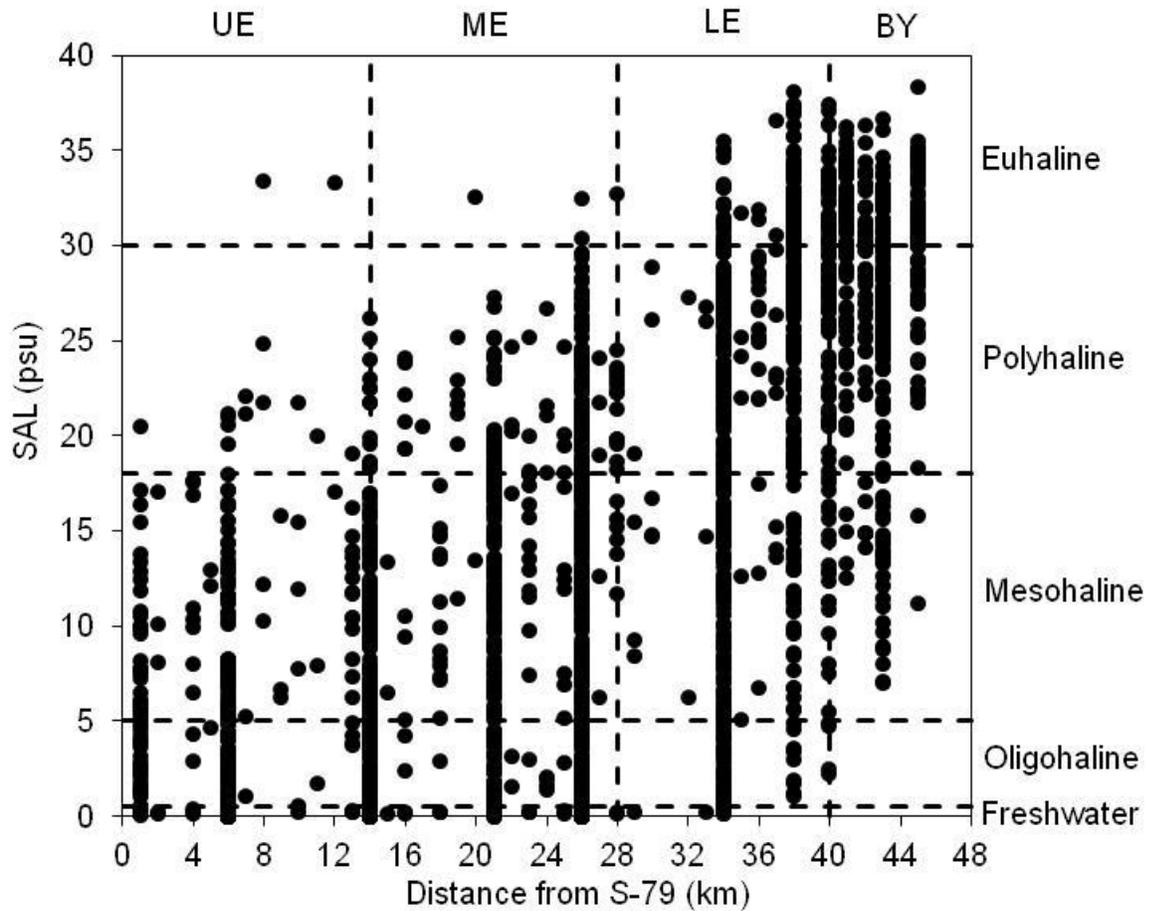


Figure 4-9. Salinity (SAL in psu) ranges divided into five zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) observed in the four regions (UE, ME, LE, BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010.

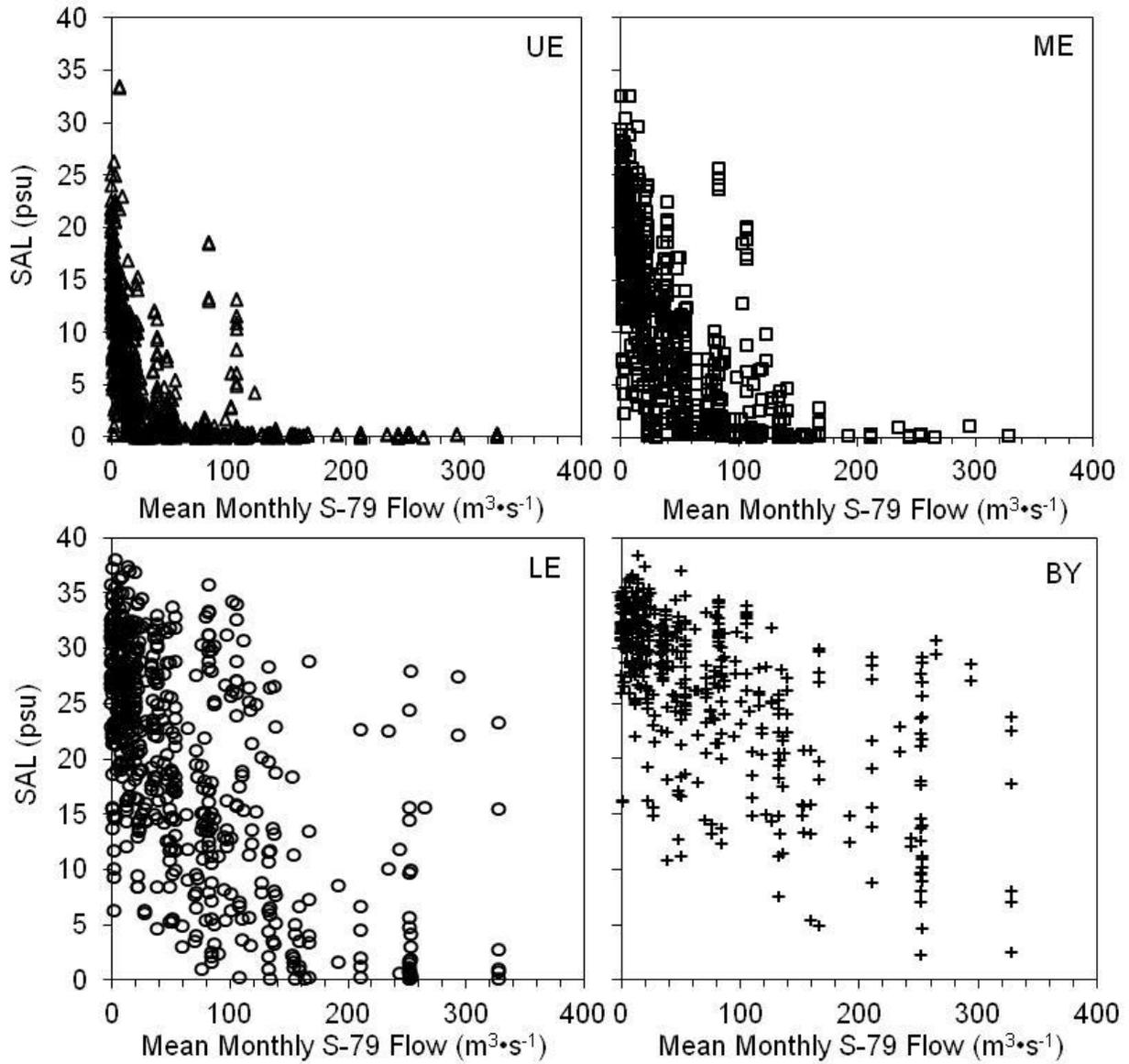


Figure 4-10. Salinity (SAL in psu) observed in each of the four regions of the Caloosahatchee Estuary, FL between January 1986 and December 2010 with respect to mean monthly inflow ($m^3 \cdot s^{-1}$) of freshwater at S-79.

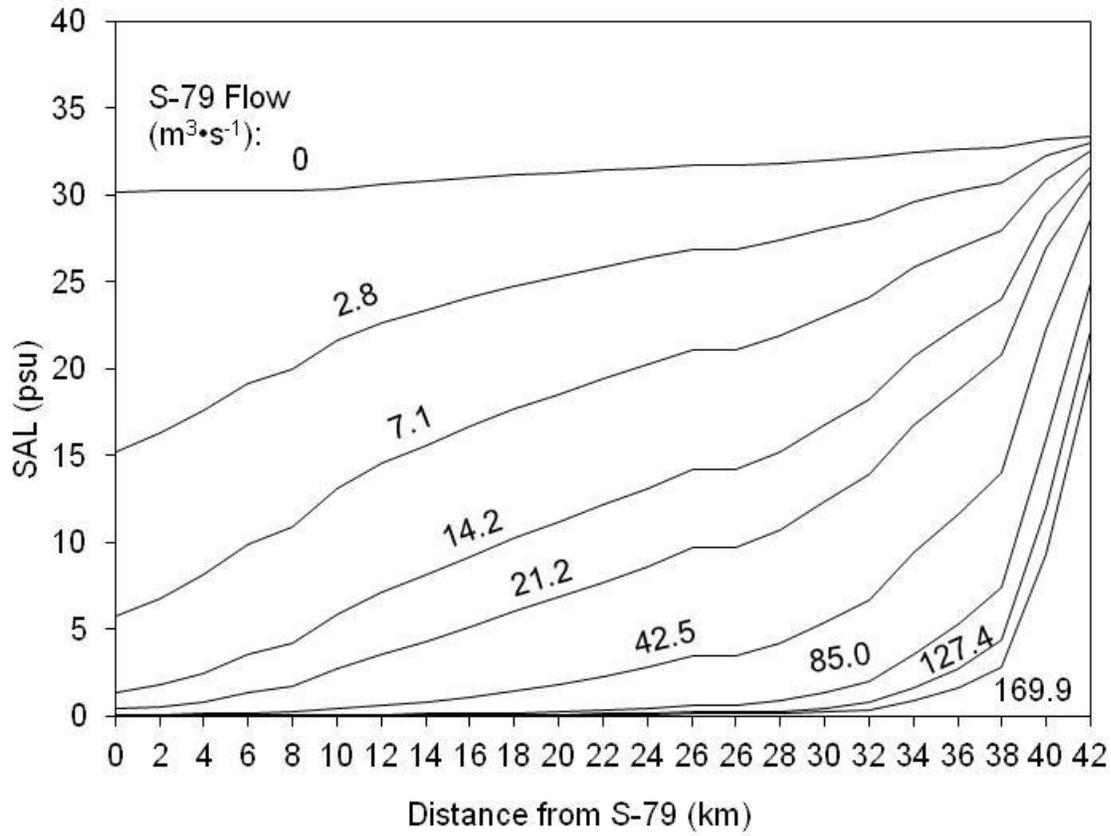


Figure 4-11. Predicted steady-state salinity (SAL in psu) distribution along a spatial gradient in the Caloosahatchee Estuary, FL for a range of freshwater inflows ($\text{m}^3 \cdot \text{s}^{-1}$) from S-79 (Bierman 1993).

Table 4-4. Mean (with standard deviations) physical-chemical, biomass, and productivity values associated with the four regions (UE, ME, LE, and BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010. Standard deviations are provided in parentheses.

	Upper Estuary (UE)	Middle Estuary (ME)	Lower Estuary (LE)	San Carlos Bay (BY)
SAL (psu)	4.14 (5.78)	10.0 (8.49)	20.1 (9.91)	26.7 (7.05)
DO (mg•L ⁻¹)	6.36 (2.00)	7.45 (1.74)	7.06 (1.47)	7.52 (1.63)
TEMP_W (°C)	26.0 (3.97)	25.6 (4.12)	25.8 (4.23)	25.9 (4.25)
CDOM (pcu)	88.0 (58.2)	63.2 (52.1)	37.8 (40.4)	17.8 (17.8)
TURB (ntu)	4.35 (4.22)	4.20 (3.28)	4.18 (3.15)	5.12 (3.26)
TSS (mg•L ⁻¹)	8.55 (11.6)	11.8 (11.0)	18.4 (19.5)	18.2 (13.0)
Z _p (m ⁻¹)	1.77 (1.04)	2.05 (0.91)	2.57 (1.04)	2.55 (1.40)
TP (mg•L ⁻¹)	0.14 (0.08)	0.12 (0.06)	0.09 (0.07)	0.05 (0.02)
TKN (mg•L ⁻¹)	1.16 (0.45)	1.03 (0.47)	0.75 (0.49)	0.71 (0.44)
SI (mg•L ⁻¹)	6.34 (3.24)	4.64 (3.23)	3.18 (2.41)	1.53 (1.47)
CHL A (mg•m ⁻³)	11.4 (13.4)	12.3 (22.8)	7.27 (11.1)	4.91 (5.05)
GPP _d (mg•C•m ⁻² •d ⁻¹)	809 (1057)	774 (727)	602 (576)	500 (392)

Table 4-5. Mean (with standard deviations) physical-chemical, biomass, and productivity values associated with the five salinity zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) of the Caloosahatchee Estuary, FL between January 1986 and December 2010. Standard deviations are provided in parentheses.

	freshwater	oligohaline	mesohaline	polyhaline	euhaline
SAL (psu)	0.22 (0.10)	2.42 (1.30)	11.4 (3.77)	24.1 (3.48)	32.6 (1.79)
DO (mg•L ⁻¹)	5.57 (1.88)	7.24 (1.83)	7.49 (1.66)	7.40 (1.36)	7.53 (1.57)
TEMP_W (°C)	27.0 (3.65)	26.2 (4.07)	25.3 (4.07)	25.1 (4.28)	25.1 (4.30)
CDOM (pcu)	135 (61)	88.2 (45.3)	50.4 (23.4)	25.0 (22.8)	11.0 (10.0)
TURB (ntu)	4.10 (3.37)	5.00 (5.04)	4.59 (3.75)	3.95 (2.79)	4.74 (3.40)
TSS (mg•L ⁻¹)	5.25 (5.45)	8.09 (10.5)	12.7 (11.3)	17.1 (15.5)	24.0 (21.2)
Z _p (m ⁻¹)	1.38 (0.54)	1.74 (0.70)	2.13 (1.10)	2.64 (1.07)	3.07 (1.43)
TP (mg•L ⁻¹)	0.14 (0.08)	0.15 (0.10)	0.12 (0.06)	0.08 (0.05)	0.05 (0.04)
TKN (mg•L ⁻¹)	1.20 (0.41)	1.24 (0.42)	1.04 (0.46)	0.74 (0.42)	0.55 (0.42)
SI (mg•L ⁻¹)	8.20 (2.42)	7.45 (2.87)	4.50 (2.60)	2.11 (1.62)	1.45 (1.15)
CHL A (mg•m ⁻³)	8.94 (13.70)	15.0 (16.6)	11.4 (11.0)	5.90 (6.08)	3.29 (2.26)
GPP _d (mg•C•m ⁻² •d ⁻¹)	531 (772)	958 (897)	882 (999)	598 (468)	424 (252)

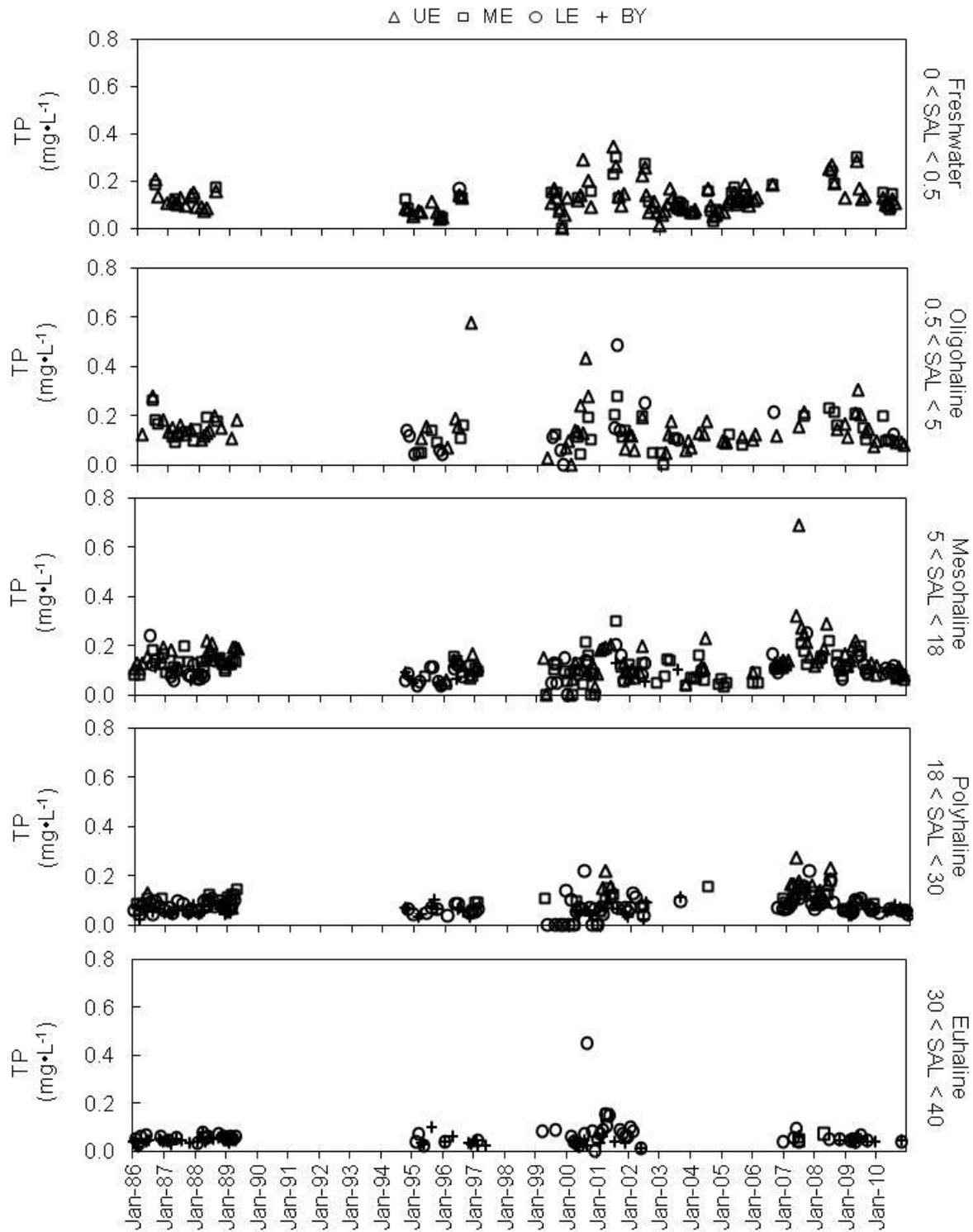


Figure 4-12. Monthly mean total phosphorous (TP in mg·L⁻¹) across five salinity (SAL) zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) in each of the four regions (UE, ME, LE, BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010.

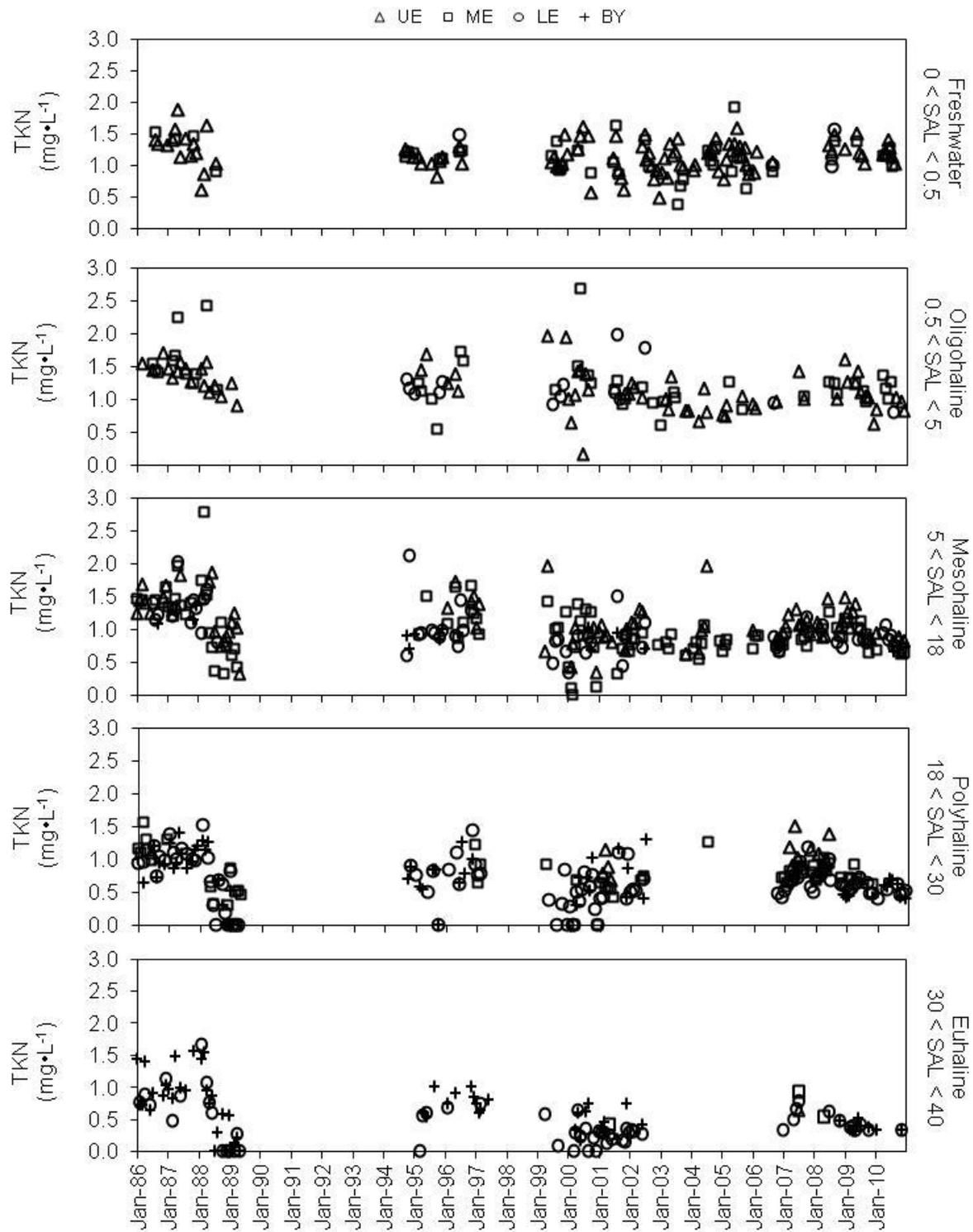


Figure 4-13. Monthly mean total Kjeldahl nitrogen (TKN in $\text{mg}\cdot\text{L}^{-1}$) across five salinity (SAL) zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) in each of the four regions (UE, ME, LE, BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010.

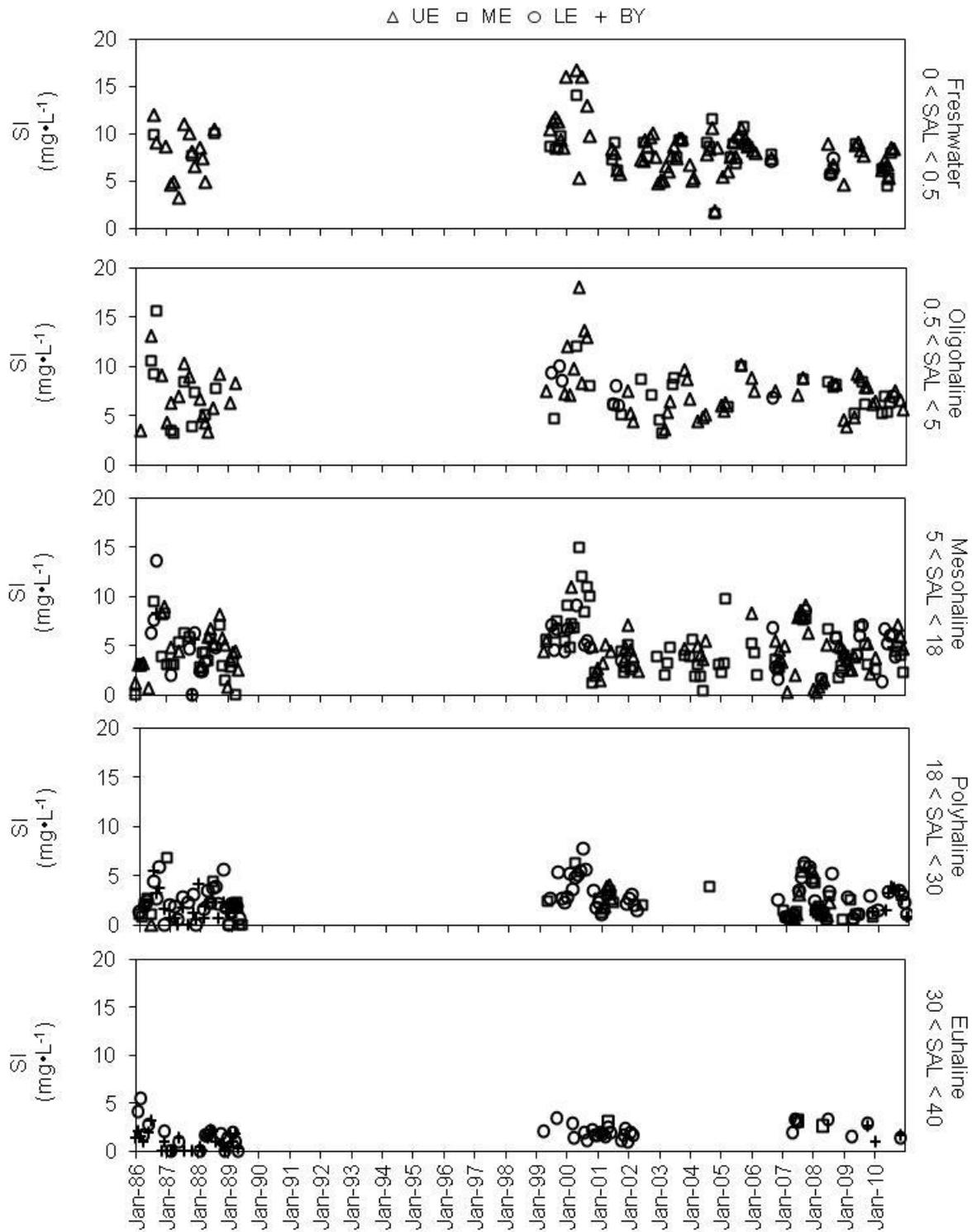


Figure 4-14. Monthly mean silica (SI in $\text{mg}\cdot\text{L}^{-1}$) across five salinity (SAL) zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) in each of the four regions (UE, ME, LE, BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010.

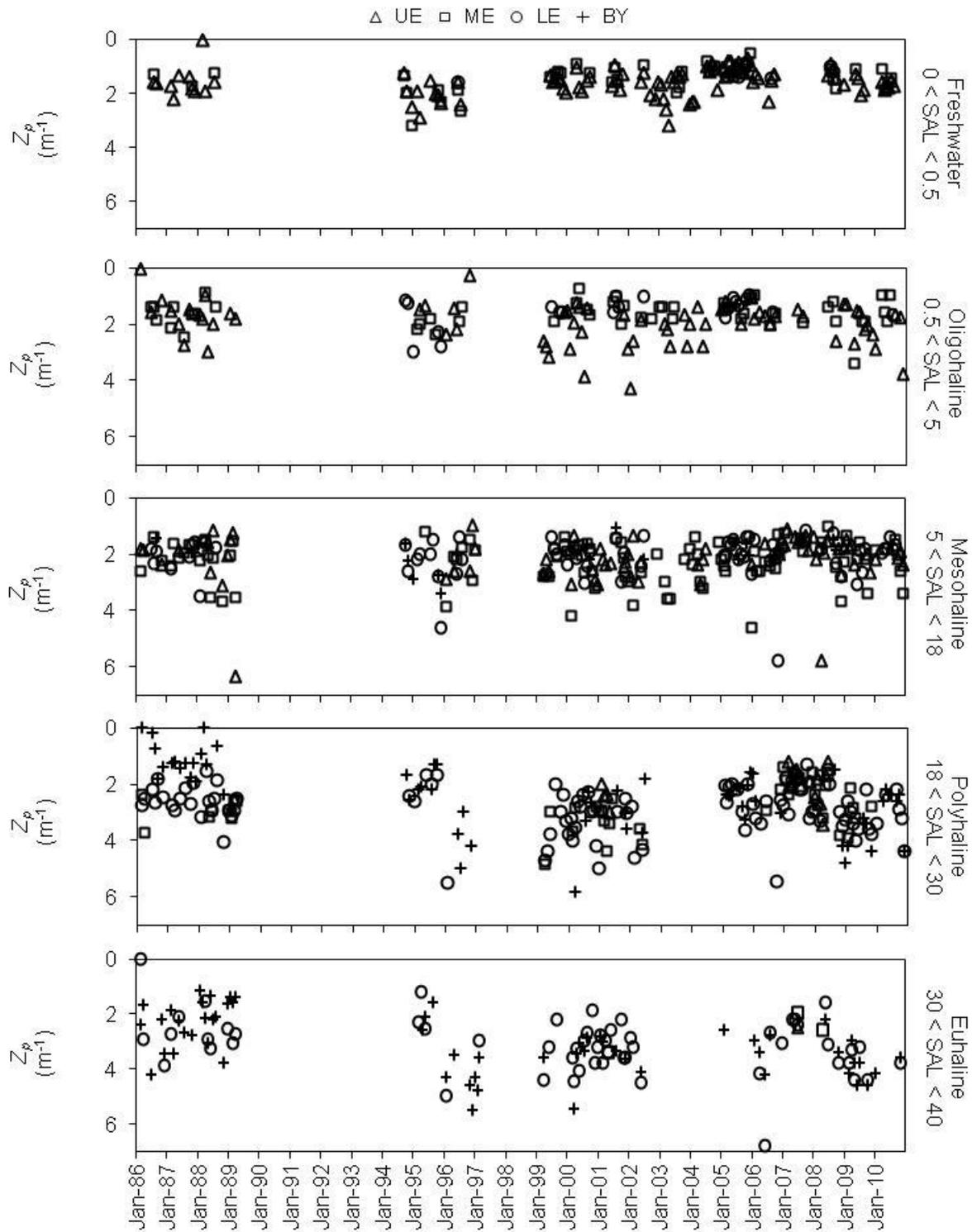


Figure 4-15. Monthly mean photic depth (Z_p in m^{-1}) across five salinity (SAL) zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) in each of the four regions (UE, ME, LE, BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010

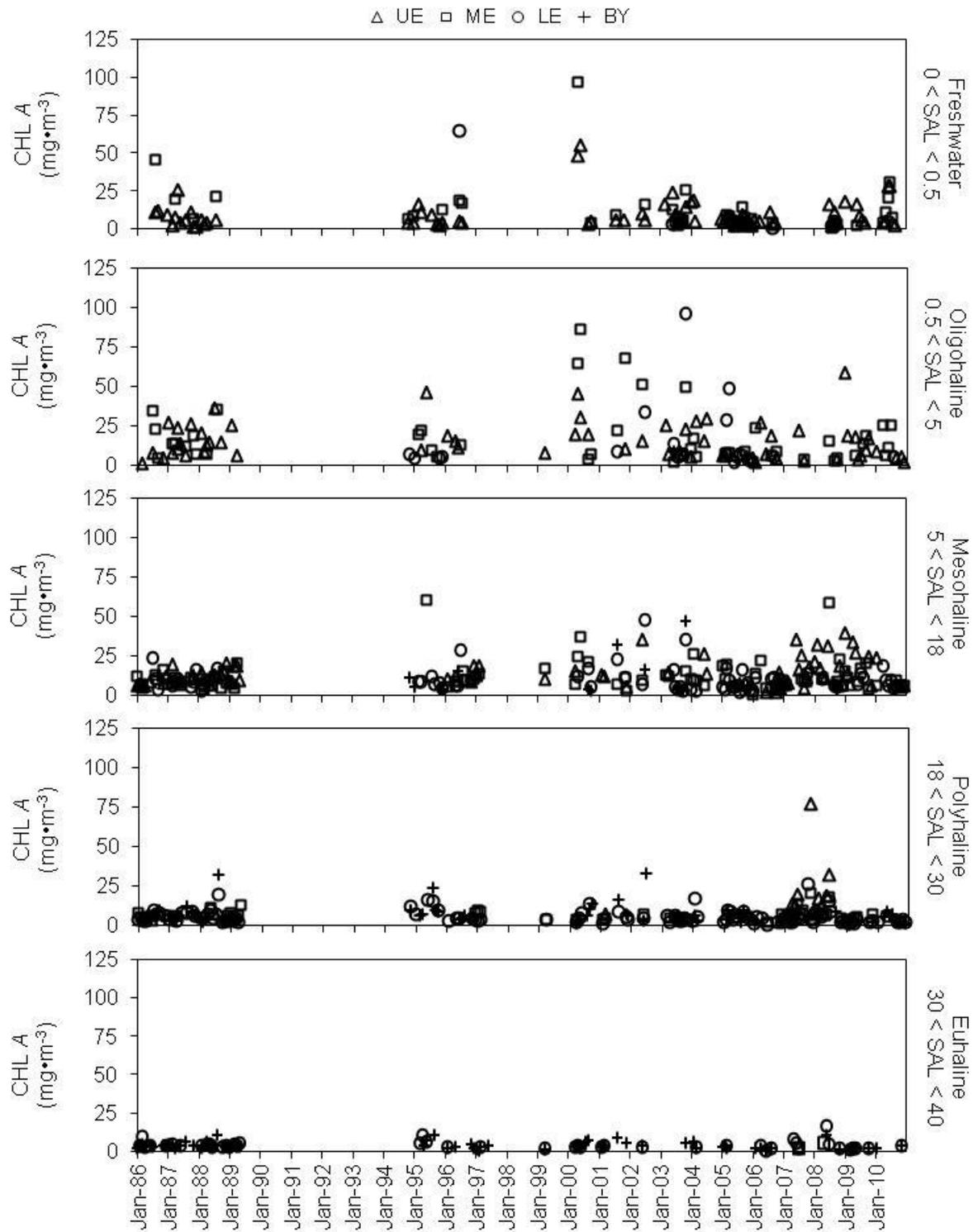


Figure 4-16. Monthly mean chlorophyll a (CHL A in $\text{mg}\cdot\text{m}^{-3}$) across five salinity (SAL) zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) in each of the four regions (UE, ME, LE, BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010

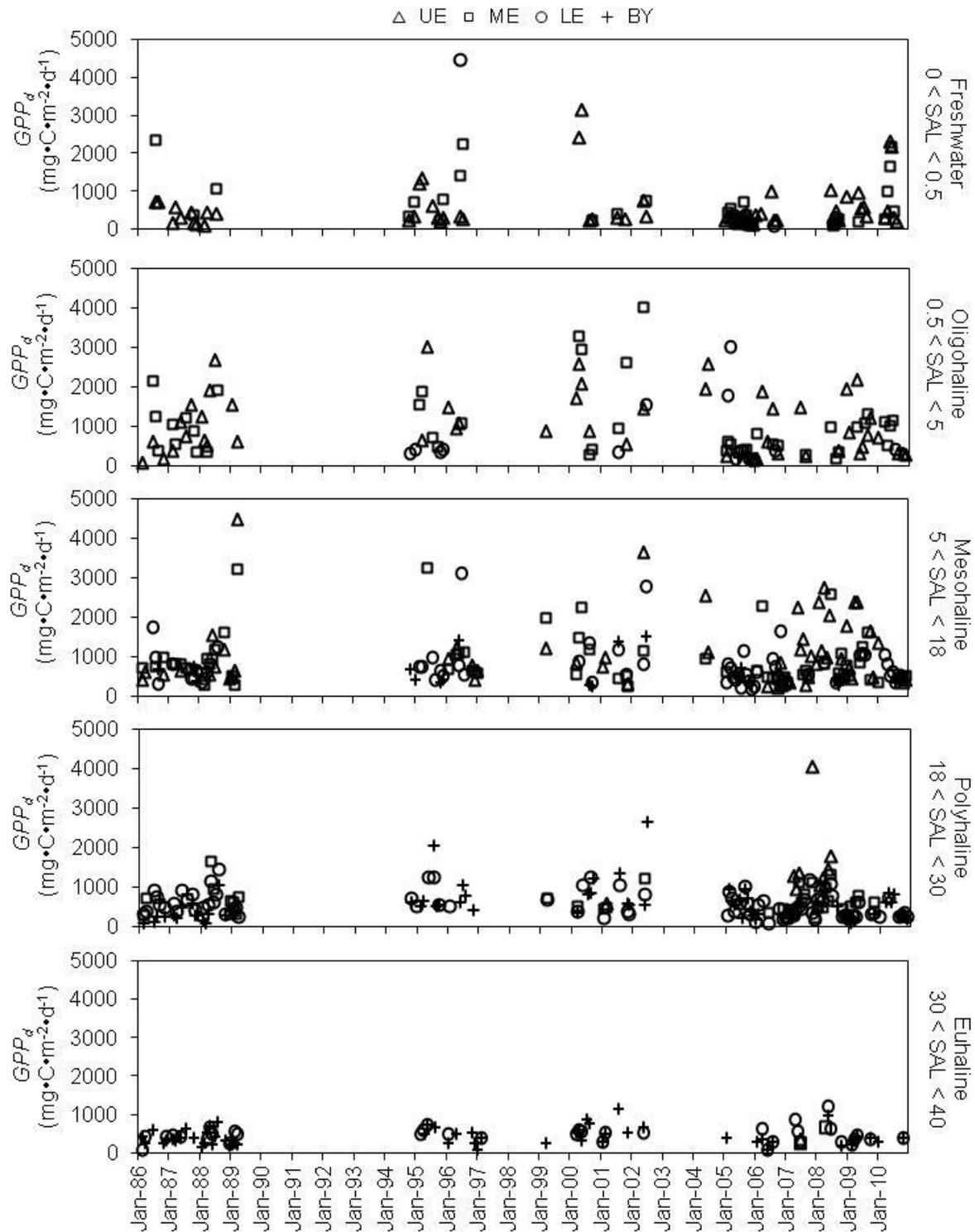


Figure 4-17. Monthly mean daily gross primary productivity (GPP_d in $\text{mg}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) across five salinity (SAL) zones (freshwater, oligohaline, mesohaline, polyhaline, euhaline) in each of the four regions (UE, ME, LE, BY) of the Caloosahatchee Estuary, FL between January 1986 and December 2010.

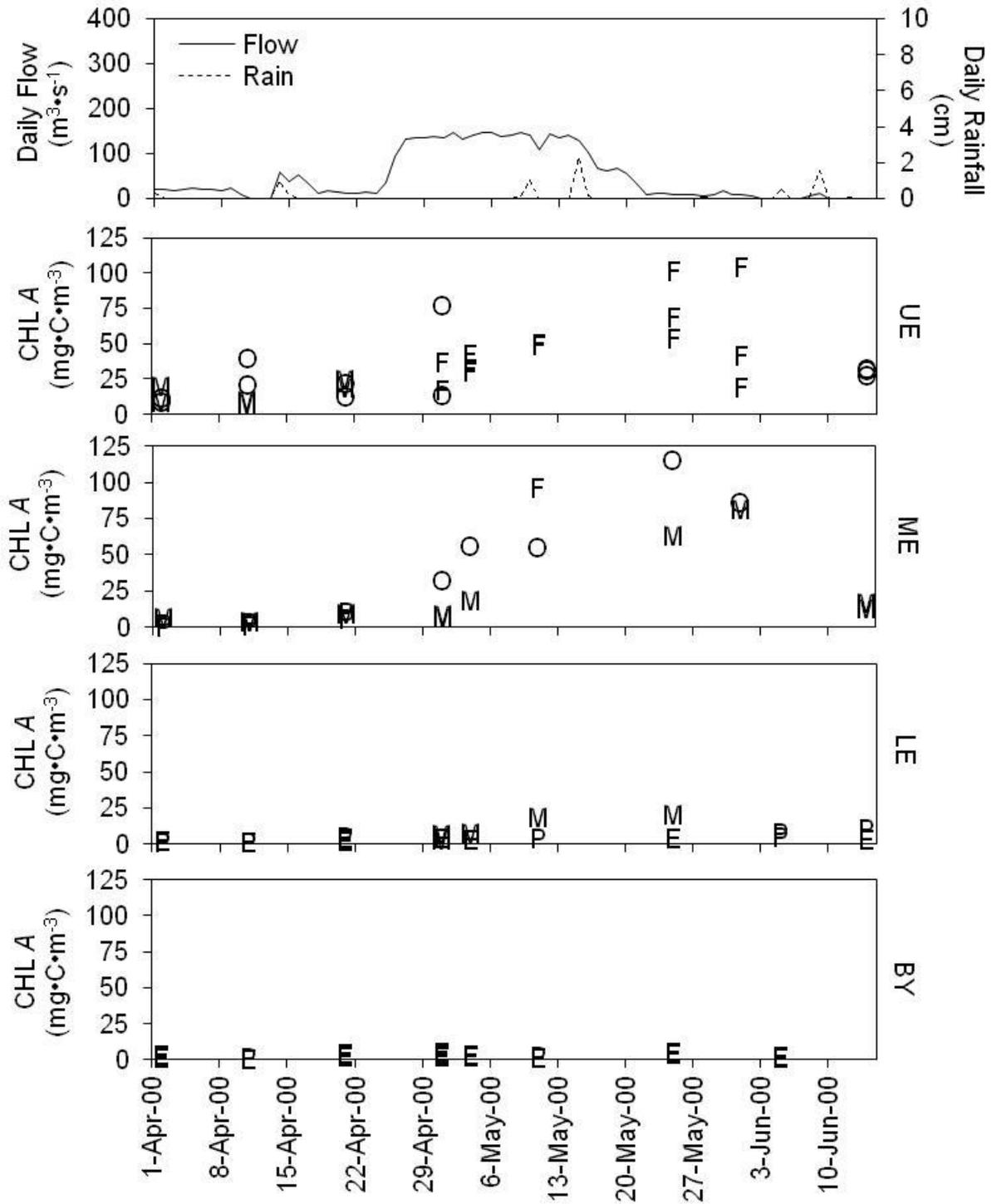


Figure 4-18. Close-up view of phytoplankton biomass responses (in terms of CHL A concentrations in $mg \cdot C \cdot m^{-3}$) in variable salinities (F = freshwater, O = oligohaline, M = mesohaline, P = polyhaline, E = euhaline) from April to June 2000 given daily S-79 inflows and rainfall inputs in the four regions (UE, ME, LE, and BY) of the Caloosahatchee Estuary, FL.

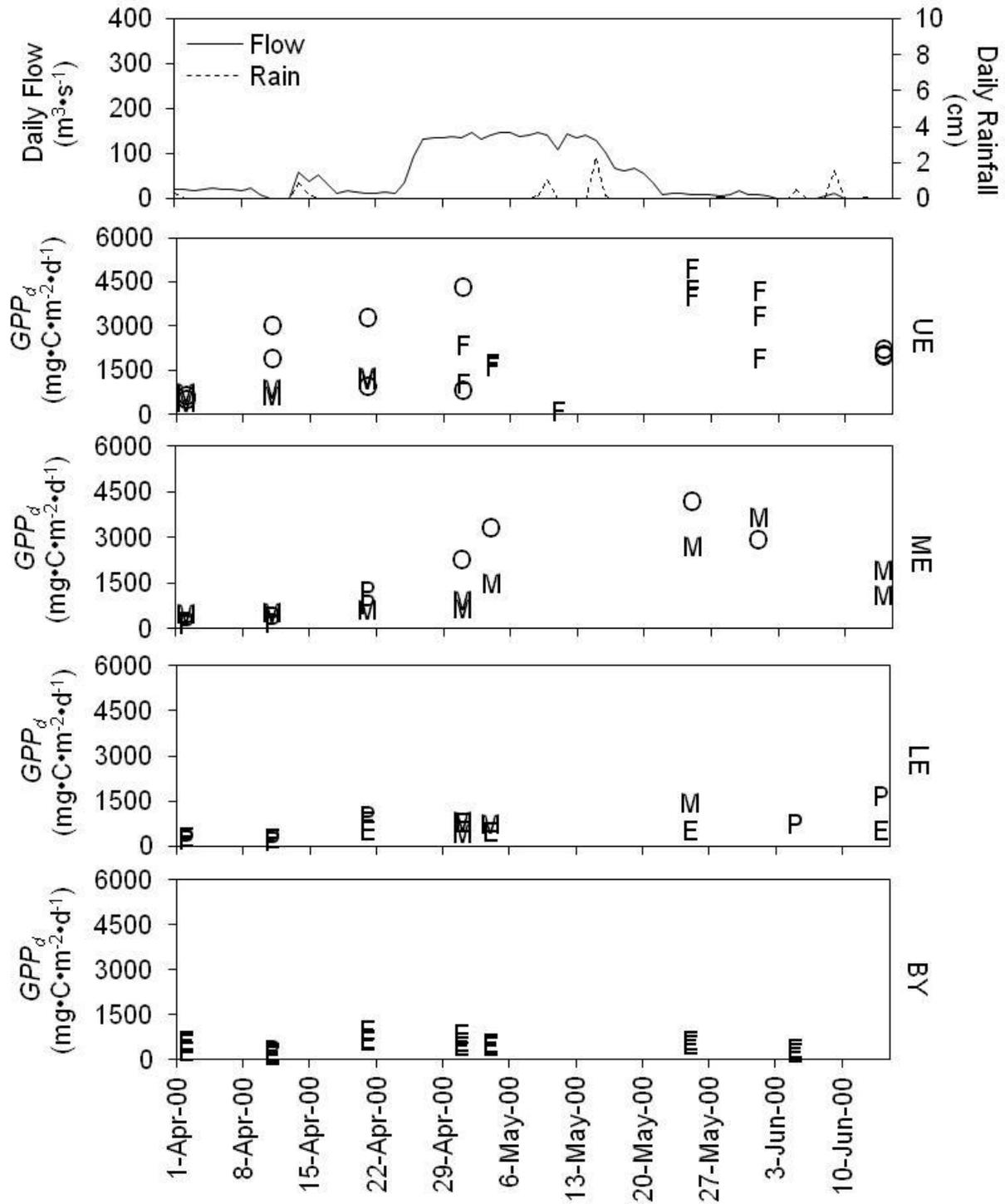


Figure 4-19. Close-up view of phytoplankton productivity responses (as GPP_d estimates in $mg \cdot C \cdot m^{-2} \cdot d^{-1}$) in variable salinities (F = freshwater, O = oligohaline, M = mesohaline, P = polyhaline, E = euhaline) from April to June 2000 given daily S-79 inflows and rainfall inputs in the four regions (UE, ME, LE, and BY) of the Caloosahatchee Estuary, FL.

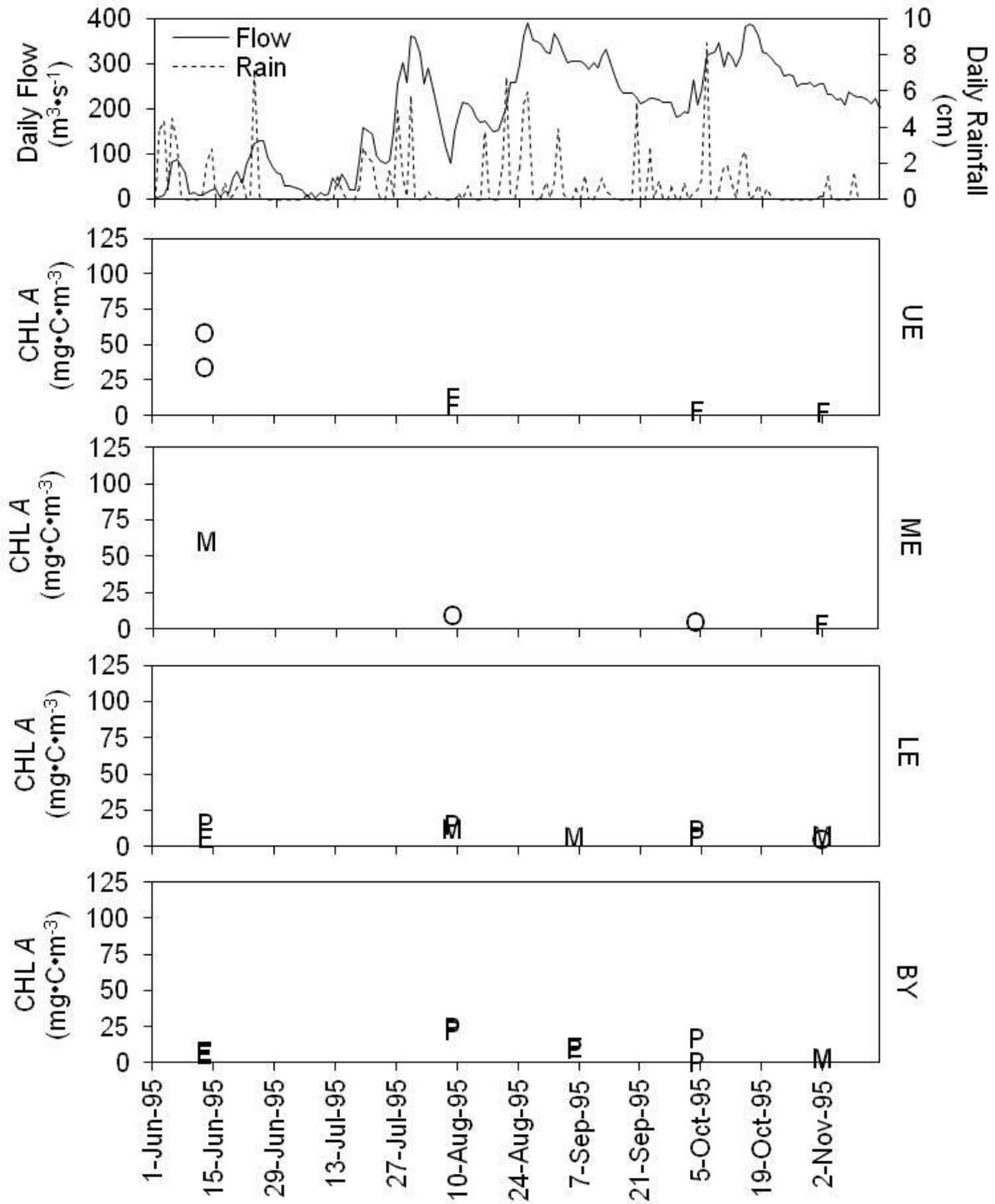


Figure 4-20. Close-up view of phytoplankton biomass responses (in terms of CHL A concentrations in $\text{mg}\cdot\text{C}\cdot\text{m}^{-3}$) in variable salinities (F = freshwater, O = oligohaline, M = mesohaline, P = polyhaline, E = euhaline) from June to November 1995 given daily S-79 inflows and rainfall inputs in the four regions (UE, ME, LE, and BY) of the Caloosahatchee Estuary, FL.

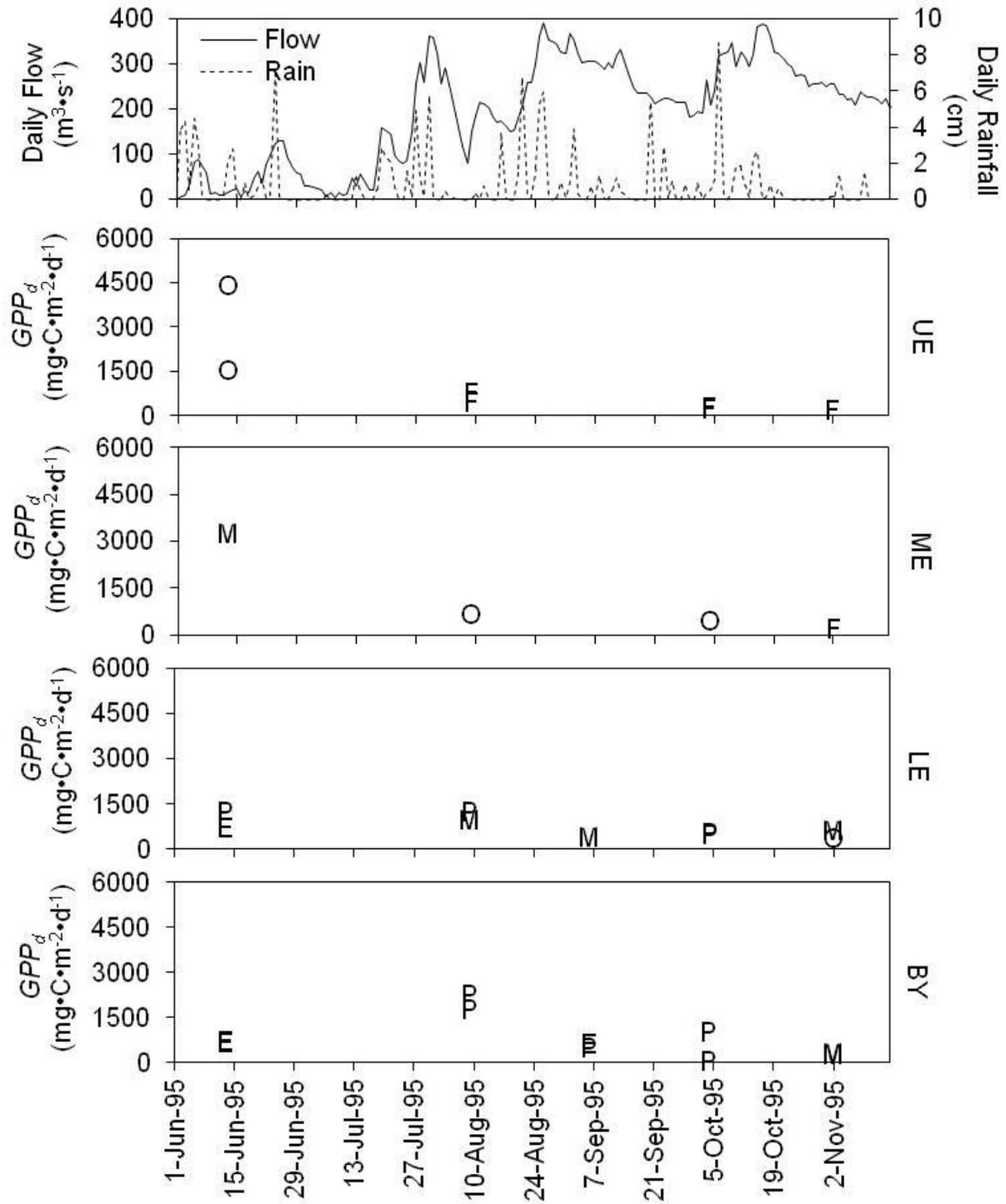


Figure 4-21. Close-up view of phytoplankton productivity responses (as GPP_d estimates in $mg \cdot C \cdot m^{-2} \cdot d^{-1}$) in variable salinities (F = freshwater, O = oligohaline, M = mesohaline, P = polyhaline, E = euhaline) from June to November 1995 given daily S-79 inflows and rainfall inputs in the four regions (UE, ME, LE, and BY) of the Caloosahatchee Estuary, FL.

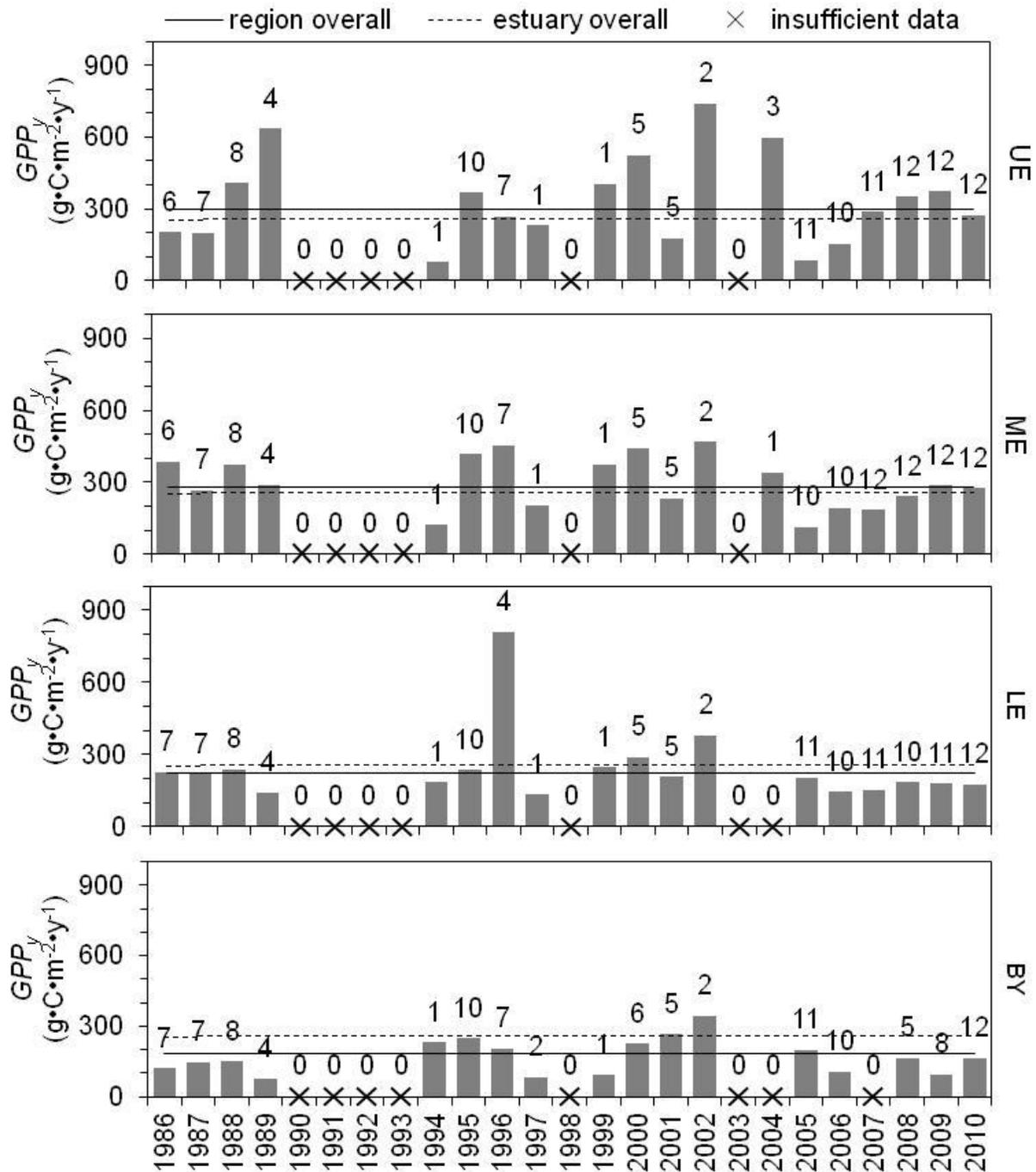


Figure 4-22. Modeled average annual gross primary productivity (GPP_y in $g \cdot C \cdot m^{-2} \cdot y^{-1}$) in the four regions (UE, ME, LE, and BY) of the Caloosahatchee Estuary, FL between 1986 and 2010. The numbers above the bars indicate the number of months used to calculate the annual average. Estimates of GPP_y could not be obtained using the $BZ_p I_o$ model for years with insufficient measurements of phytoplankton biomass (B) as CHL A concentration and/or photic depth (Z_p). The solid and dashed lines represent the overall, long-term averages for the specific regions and the entire estuary, respectively.

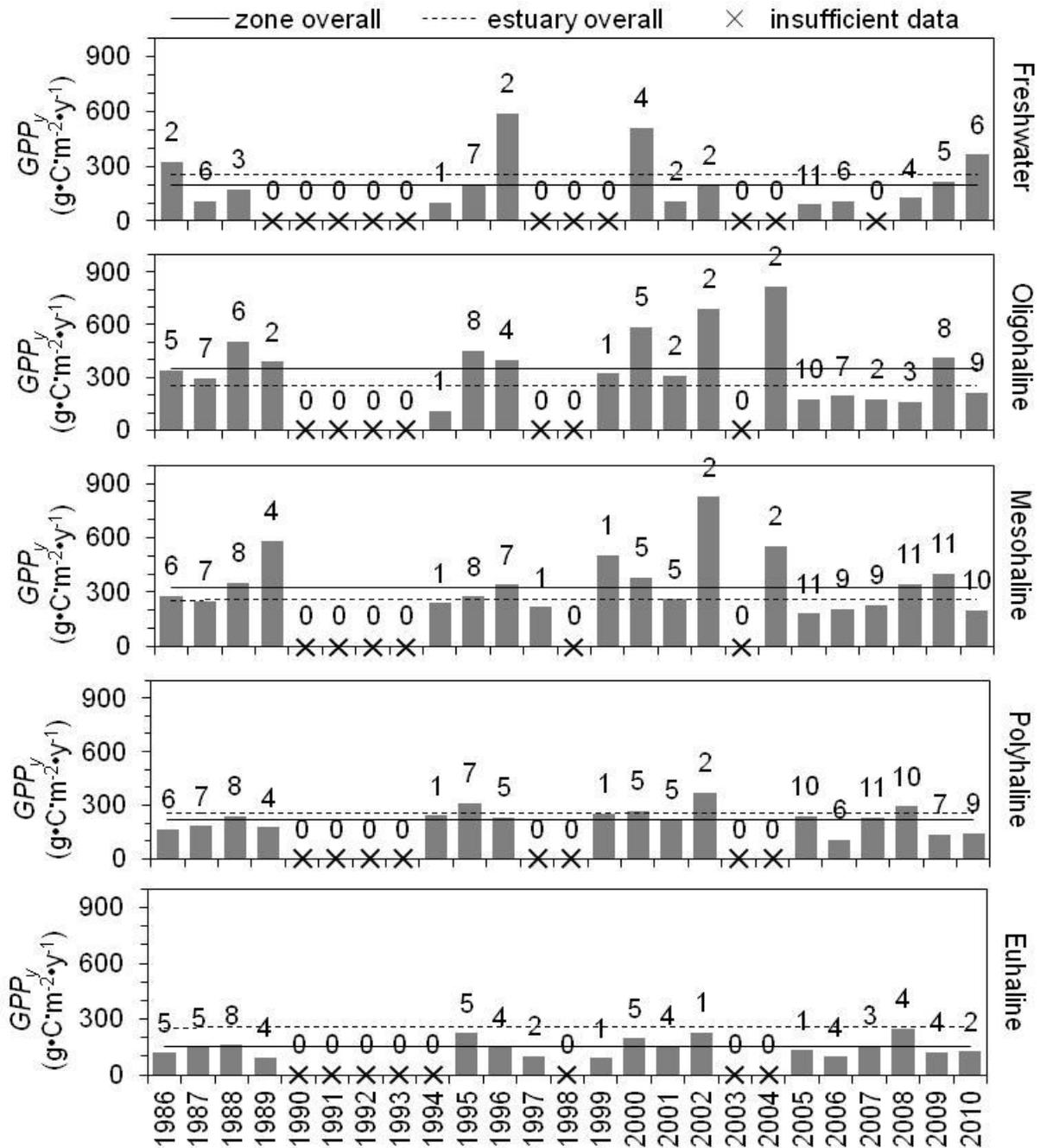


Figure 4-23. Modeled average annual gross primary productivity (GPP_y in $g \cdot C \cdot m^{-2} \cdot y^{-1}$) by salinity zone (freshwater, oligohaline, mesohaline, polyhaline, and euhaline) in the Caloosahatchee Estuary, FL between 1986 and 2010. The numbers above the bars indicate the number of months used to calculate the annual average. Estimates of GPP_y could not be obtained using the BZ_{p/l_0} model for years with insufficient measurements of phytoplankton biomass (B) as CHL A concentration and/or photic depth (Z_p). The solid and dashed lines represent the overall, long-term averages for the specific zones and the entire estuary, respectively.

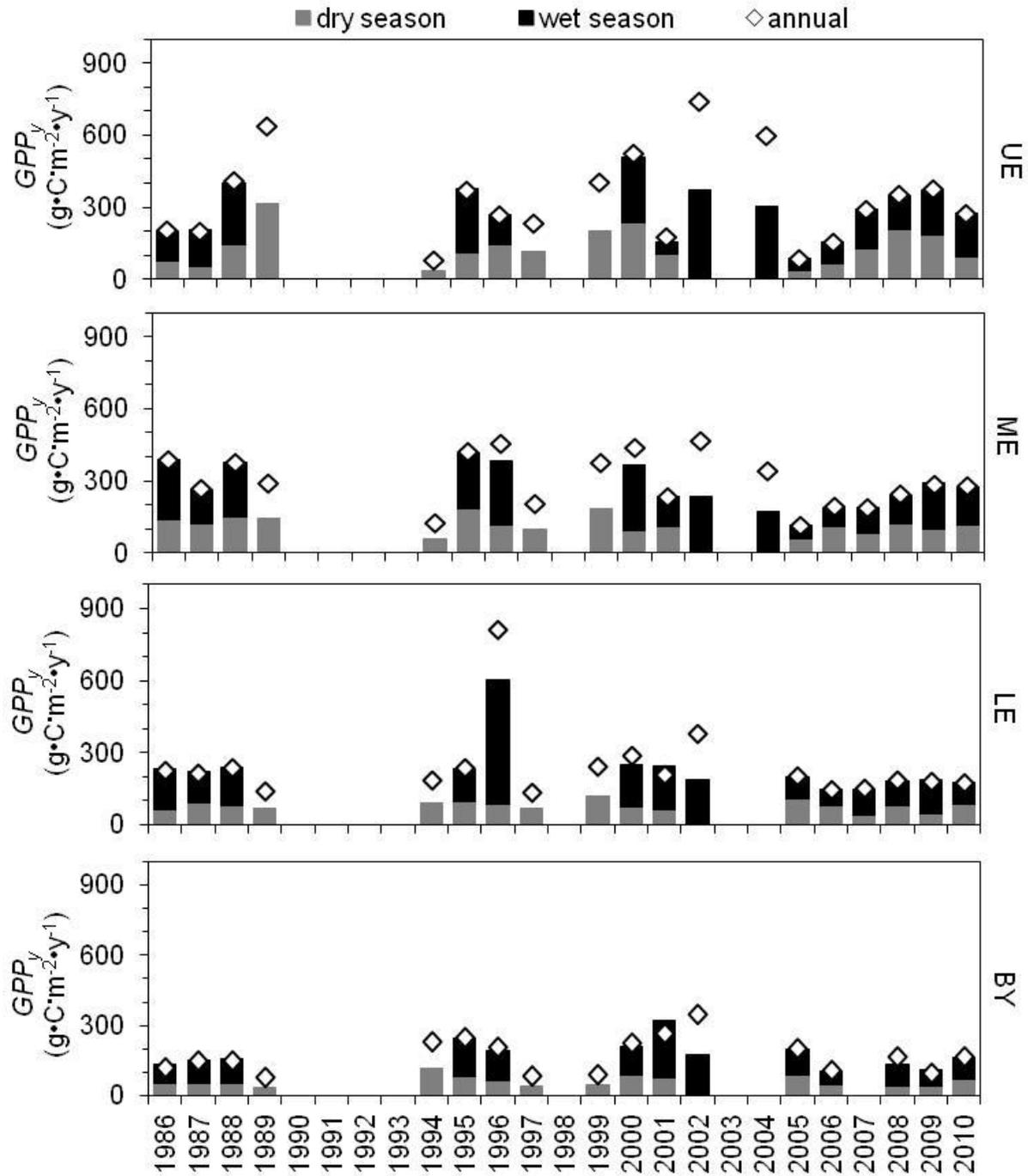


Figure 4-24. Modeled average annual gross primary productivity (GPP_y in $g \cdot C \cdot m^{-2} \cdot y^{-1}$) in the four regions (UE, ME, LE, and BY) of the Caloosahatchee Estuary, FL between 1986 and 2010 with respect to season (DRY = November through April, WET = May through October). The diamonds represent the overall annual GPP_y averages for the individual regions.

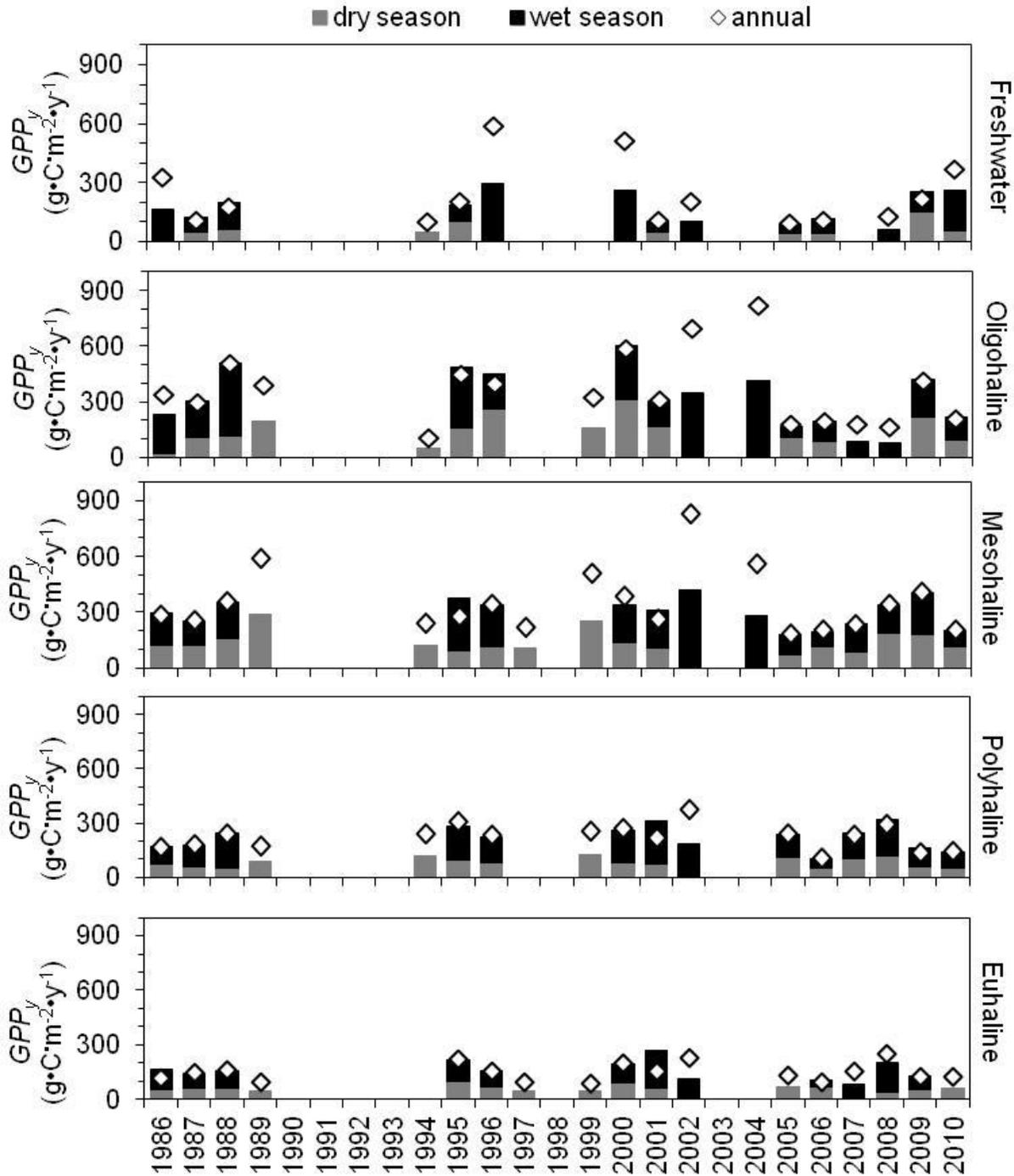


Figure 4-25. Modeled average annual gross primary productivity (GPP_y in $g \cdot C \cdot m^{-2} \cdot y^{-1}$) by salinity zones (freshwater, oligohaline, mesohaline, polyhaline, and euhaline) of the Caloosahatchee Estuary, FL between 1986 and 2010 with respect to season (DRY = November through April, WET = May through October). The diamonds represent the overall annual GPP_y averages for the individual zones.

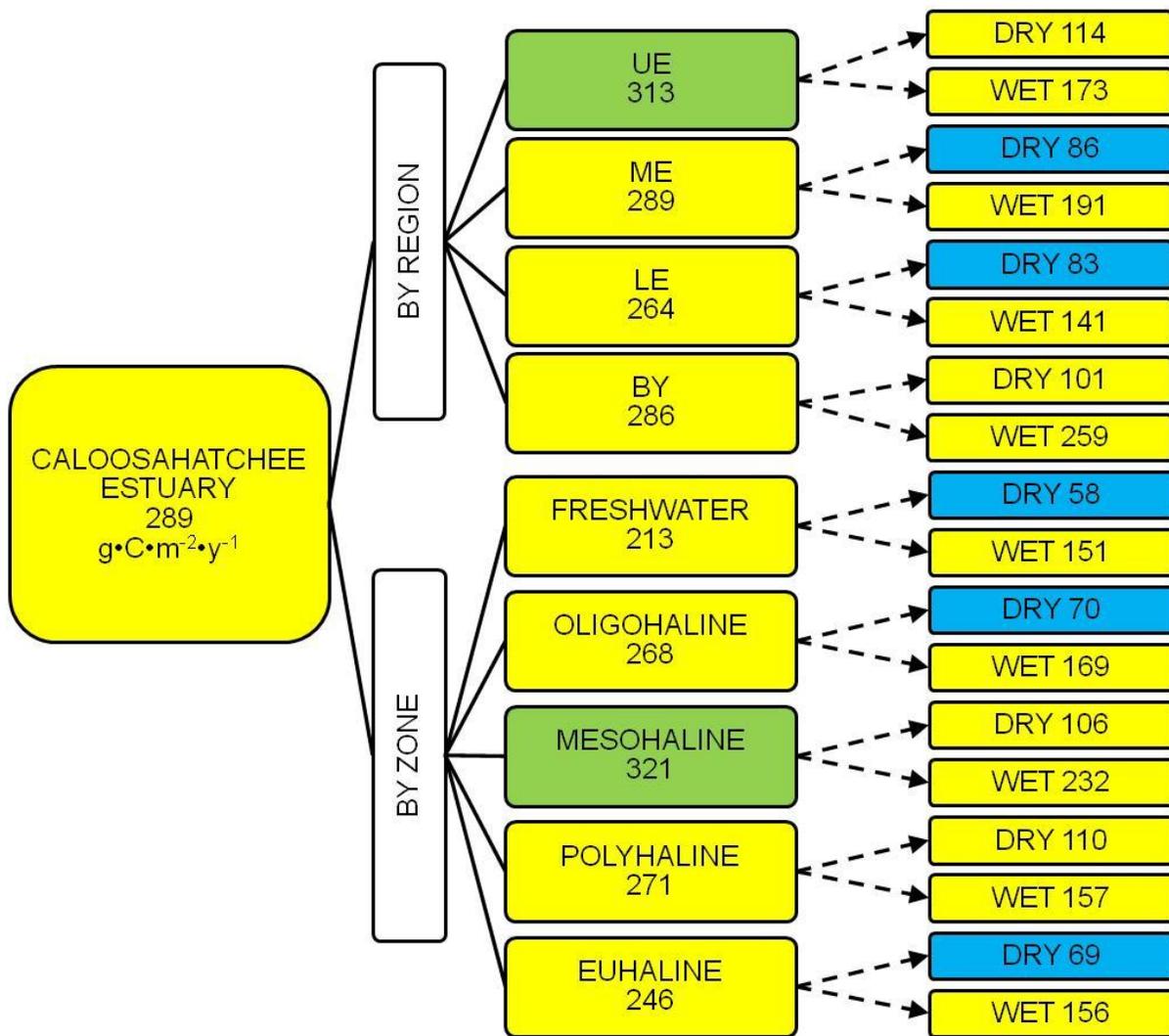


Figure 4-26. Average expected annual gross primary productivity (GPP_y in $\text{g}\cdot\text{C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$) for the Caloosahatchee Estuary, FL overall and for each region (UE, ME, LE, and BY) and salinity zone (freshwater, oligohaline, mesohaline, polyhaline, and euhaline). Estimated contributions to the annual averages from each season (dry or wet) were based on 181 or 184 days per season, respectively. Model estimates were calculated using the Florida Department of Environmental Regulation (FDEP) annual threshold for CHL A (SFWMD et al. 2009) and mean photic depths and light flux levels observed in the given region, zone, and/or season. Colors identify the corresponding trophic status (blue = oligotrophic; yellow = mesotrophic; green = eutrophic) using Nixon's (1995) classification scheme.

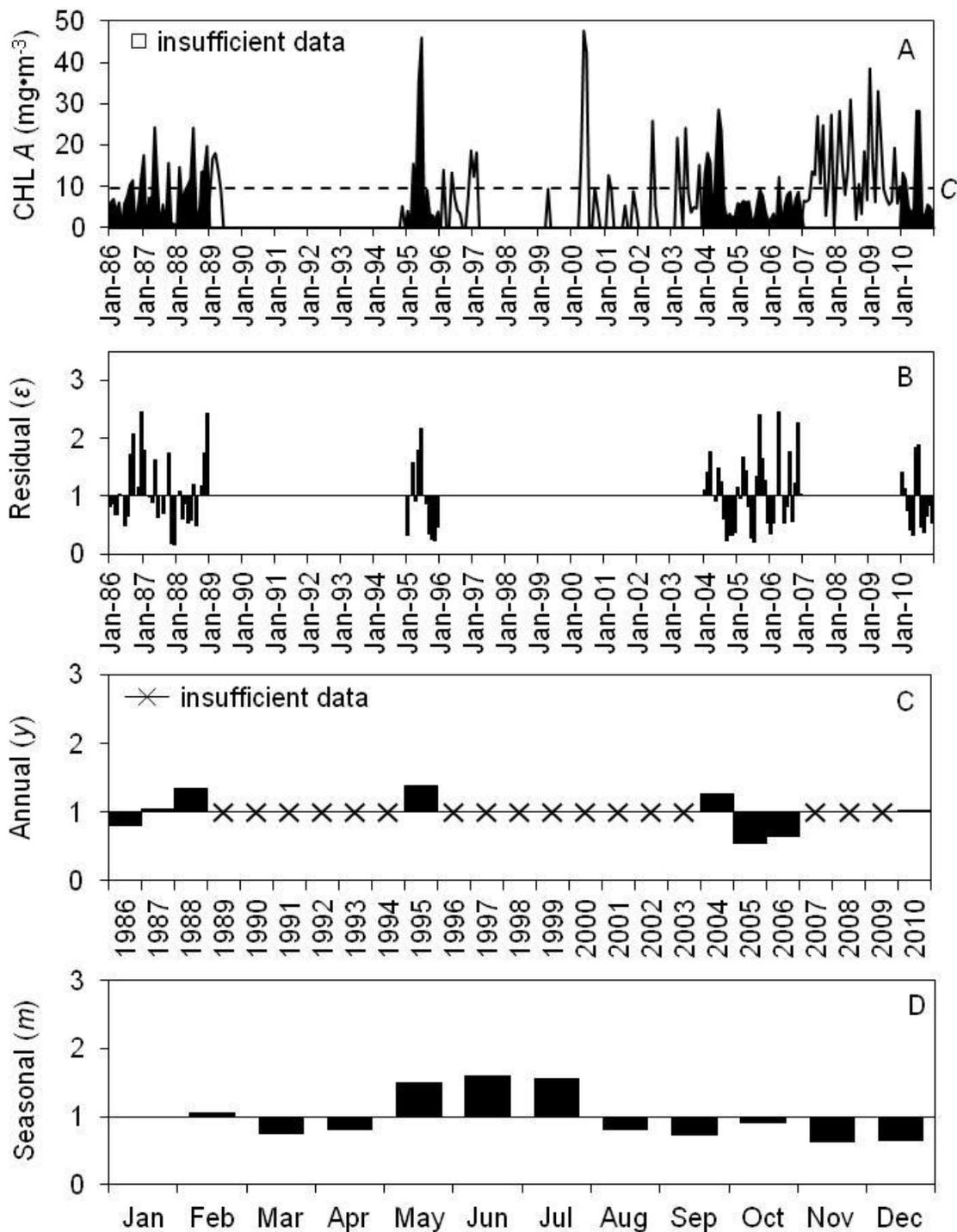


Figure 4-27. Region UE monthly mean chlorophyll a concentrations (CHL A in $\text{mg}\cdot\text{m}^{-3}$) and the long-term mean (C) (A) with the residual (ϵ) (B), annual (y) (C), and seasonal, (m) (D) components of phytoplankton biomass variability in the Caloosahatchee Estuary, FL across the years 1986, 1987, 1988, 1995, 2004, 2005, 2006, and 2010.

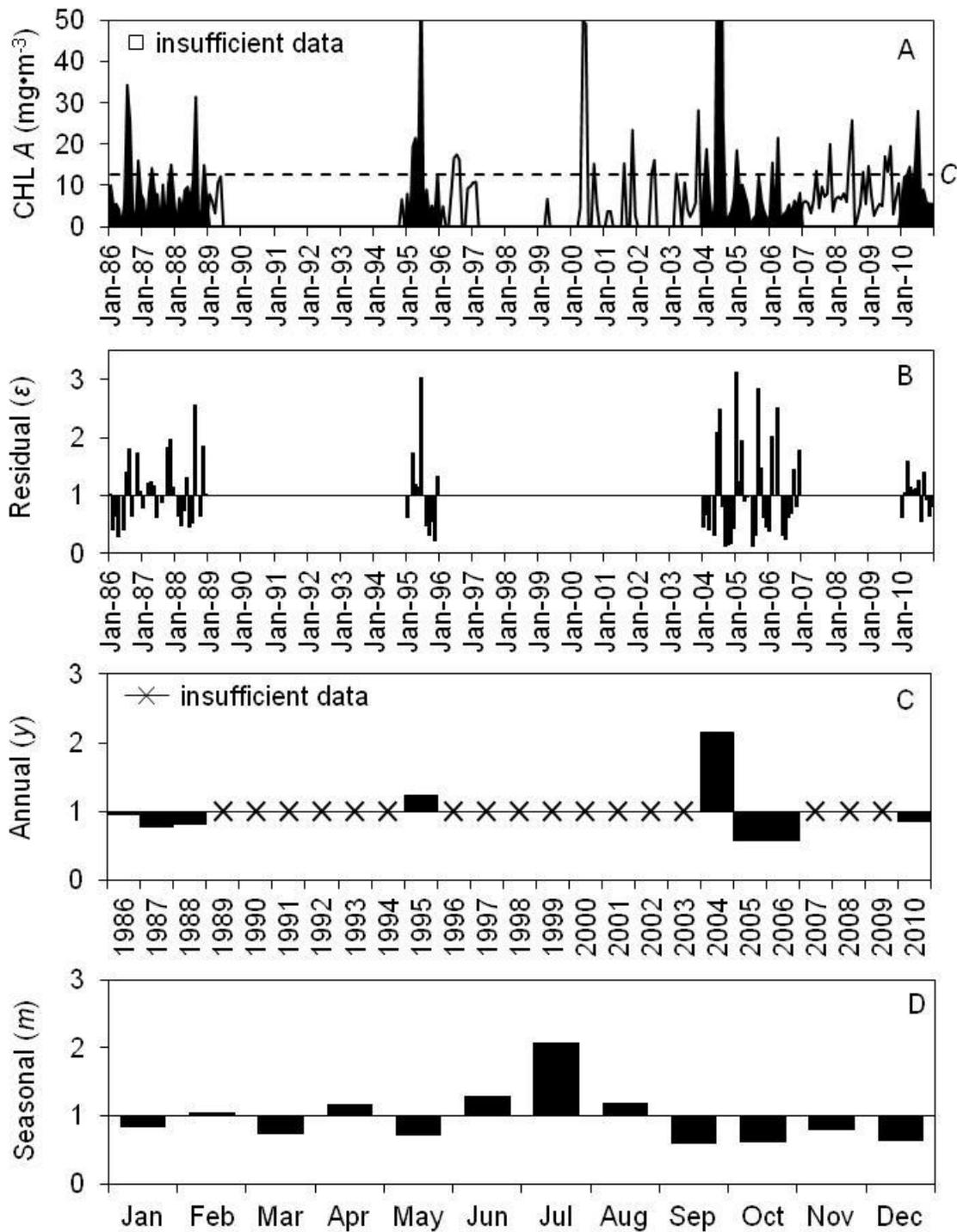


Figure 4-28. Region ME monthly mean chlorophyll *a* concentrations (CHL A in $\text{mg}\cdot\text{m}^{-3}$) and the long-term mean (C) (A) with the residual (ϵ) (B), annual (y) (C), and seasonal, (m) (D) components of phytoplankton biomass variability in the Caloosahatchee Estuary, FL across the years 1986, 1987, 1988, 1995, 2004, 2005, 2006, and 2010.

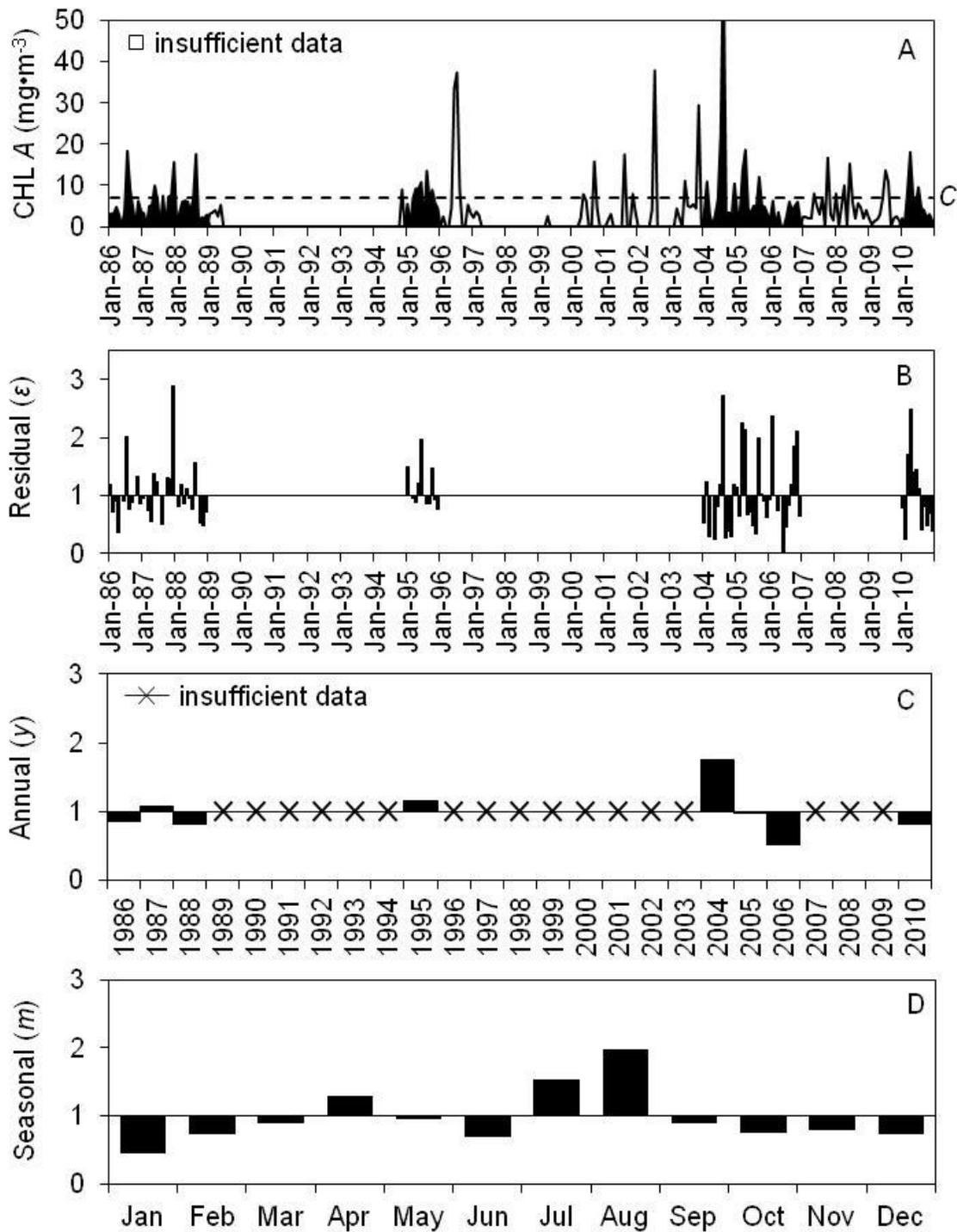


Figure 4-29. Region LE monthly mean chlorophyll a concentrations (CHL A in $\text{mg}\cdot\text{m}^{-3}$) and the long-term mean (C) (A) with the residual (ϵ) (B), annual (y) (C), and seasonal, (m) (D) components of phytoplankton biomass variability in the Caloosahatchee Estuary, FL across the years 1986, 1987, 1988, 1995, 2004, 2005, 2006, and 2010.

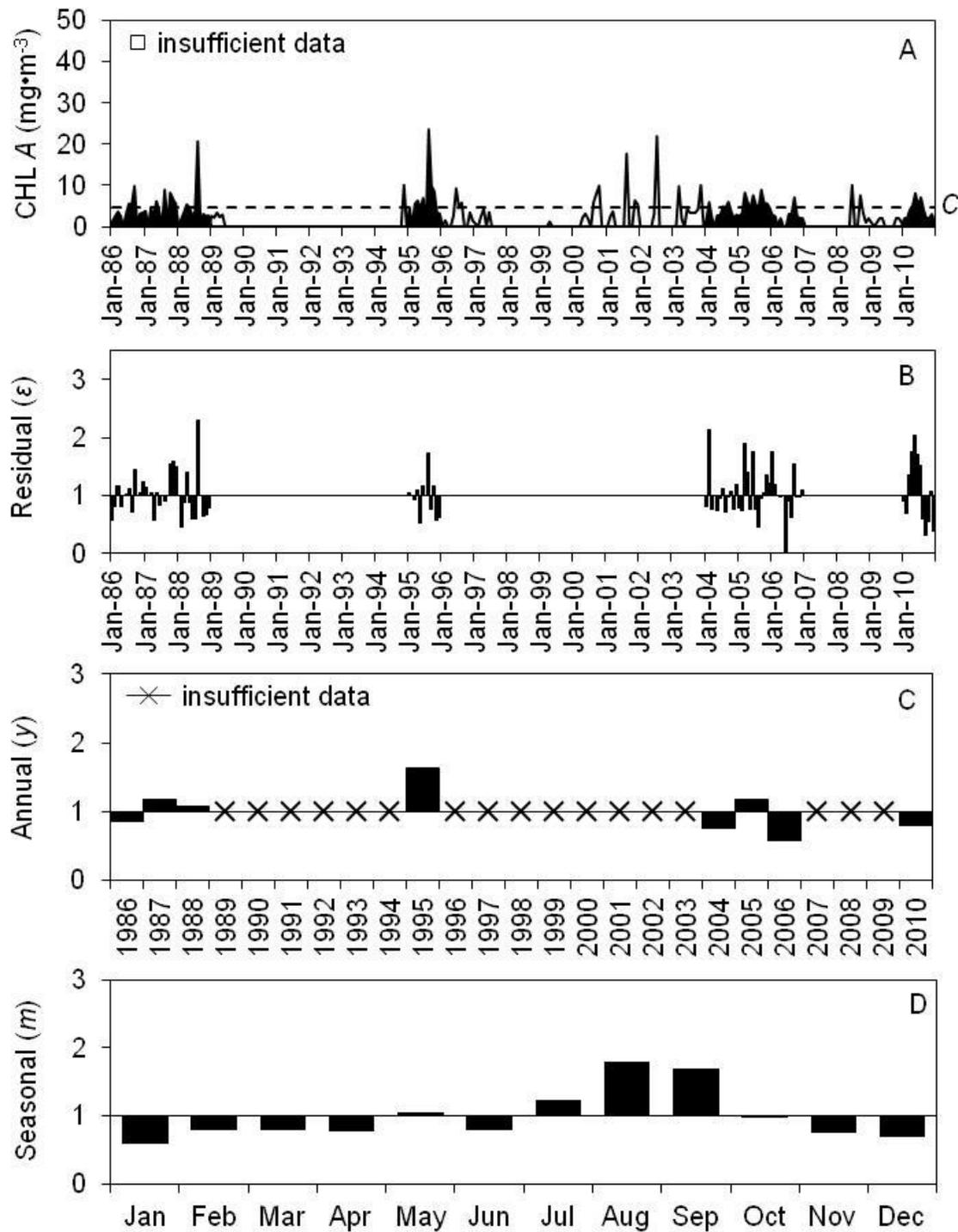


Figure 4-30. Region BY monthly mean chlorophyll a concentrations (CHL A in $\text{mg}\cdot\text{m}^{-3}$) and the long-term mean (C) (A) with the residual (ϵ) (B), annual (y) (C), and seasonal, (m) (D) components of phytoplankton biomass variability in the Caloosahatchee Estuary, FL across the years 1986, 1987, 1988, 1995, 2004, 2005, 2006, and 2010.

Table 4-6. Standard deviations of the annual (SD_y), seasonal (SD_m), and residual (SD_ϵ) components of phytoplankton biomass variability in the Caloosahatchee Estuary, FL in comparison to the median values of SD_y , SD_m , and SD_ϵ obtained from the analysis of chlorophyll *a* variability in 84 sites sampled within 51 estuarine-coastal ecosystems (Cloern and Jassby 2010).

	Upper Estuary (UE)	Middle Estuary (ME)	Lower Estuary (LE)	San Carlos Bay (BY)	median (Caloosahatchee Estuary)	median (Cloern and Jassby 2010)
SD_y	0.32	0.51	0.36	0.33	0.35	0.30
SD_m	0.36	0.43	0.43	0.39	0.41	0.39
SD_ϵ	0.64	0.71	0.61	0.45	0.63	0.59

Table 4-7. Best combinations of environmental drivers that explained patterns in daily gross primary productivity (GPP_d) in the four regions of the Caloosahatchee Estuary, FL.

	Upper Estuary (UE)	Middle Estuary (ME)	Lower Estuary (LE)	San Carlos Bay (BY)
GPP_d $\rho = 0.525$	MEI RAINFALL TEMP_W TURB CDOM TSS	TEMP_W SI	MEI SAL	MEI

CHAPTER 5 CONCLUSION

The structure, function, and overall health of the Caloosahatchee Estuary, located on the southwest coast of Florida in the USA, have been jeopardized by human activities going on in its watershed since the expansion of urban and agricultural development began there in the late 1800s. Modifications to the physical shape and hydrology of the system, including the impoundment of Lake Okeechobee, the creation of a trans-state navigable canal, and the installation of three water control structures along the Caloosahatchee River, have subsequently altered the quantity, quality, timing, and distribution of freshwater flow into and through the estuary. Natural underlying seasonal and annual variations in salinity and nutrient loads, in particular, have been amplified or truncated by anthropogenic control over the delivery of freshwater into the Caloosahatchee Estuary, affecting the ecological balance among and economic value of downstream organisms and the ecosystem overall. One associated impact of these changes is the increase in the frequency and distribution of algal blooms, which has brought attention to water quality and processes affecting phytoplankton production and biomass accumulation there. While phytoplankton production and biomass support natural food webs and the global carbon cycle, harmful, toxic, and/or nuisance algal blooms have been found to directly and indirectly harm aquatic plants, invertebrates, fish, birds, mammals, and humans, raising concerns and stimulating action amongst the scientific community, managing authorities, and general public.

Because of the potentially widespread impact of phytoplankton dynamics on the health of an entire ecosystem, measurements of phytoplankton productivity in the Caloosahatchee Estuary, and other coastal ecosystems, are thus desired so that the

structure and function of these ecosystems can be defined, better understood, and compared. However, the methods traditionally employed to gain such knowledge have been limited in their spatial and temporal extent due to the amount of money, labor, and time required to assess productivity at the scale of entire ecosystems over an extended period of time. Approaches that instead estimate production using easily obtained and readily available parameters have become popular tools for building long time series of productivity data across large areas, which, in turn, can be used to establish ecosystem baselines and track natural and anthropogenic shifts in the system's trophic status.

The $BZ_p I_0$ or 'light•biomass' model (Cole and Cloern 1987) is one such approach that predicts daily rates of phytoplankton production from measurements of chlorophyll *a*, photic depth, and PAR light flux, which are routinely collected in oceanographic investigations and system-wide monitoring efforts. The model was founded on long-standing principles that underline the major role of plant biomass and light availability in the control of primary production. The original development and subsequent uses of the model to provide reasonable estimates of phytoplankton productivity (i.e., with fitted relationships having r^2 values greater than 0.50) have involved a variety of estuary types having a wide range of conditions. Previous model tests demonstrated the applicability of the $BZ_p I_0$ relationship to estuaries having temperate to warm-temperate/subtropical climates, shallow to deep water depths, and low to high tidal ranges.

This study was unique in that the Caloosahatchee Estuary has a combination of features that distinguish it from other estuaries and coastal ecosystems in which the $BZ_p I_0$ or 'light•biomass' approach (Cole and Cloern 1987) had been previously adapted.

Being a low latitude subtropical estuary, the Caloosahatchee has warmer water temperatures, stronger light levels, and higher inputs of rainfall and river flow in the summer and fall. In addition, the estuary's shallow morphology, low tidal energy, and altered hydrology create a presumably ideal recipe for phytoplankton blooms. Together, the climate/weather, bathymetry, and hydrology of the system were expected to hinder the model's predictive power of phytoplankton productivity, although the resulting relationship yielded a stronger fit than that of other model applications. The adaptability of the model to the Caloosahatchee Estuary extended the utility of the BZ_p/I_0 parameter for predicting phytoplankton productivity to systems having features commonly associated with tropical systems, including those that have been extensively modified and are currently maintained to meet the immediate needs and priorities of nearby residents and businesses.

The methods employed during the model adaptation in the Caloosahatchee Estuary also provided clarity regarding the effect of methodological differences and variable confusion on the model's usefulness and appropriateness. Estimates of both gross and net primary productivity provided statistically comparable models in terms of their strengths (coefficients of determination), intercepts, and slopes. The use of either uncorrected or corrected (for pheophytin degradation pigments) chlorophyll *a* concentrations as a proxy for phytoplankton biomass was also accommodated by the model's flexibility. On the other hand, adjusting the photic depths to account for shallow water column depths resulted in a significantly different model relationship having an intercept that did not support the natural and logical expected outcome in productivity when there is zero biomass or light available. By allowing the use of O_2 evolution or ^{14}C

fixation techniques to measure productivity, uncorrected or corrected chlorophyll *a* to represent biomass, and photic depths not requiring any *post hoc* correction, the $BZ_{\rho l_0}$ or 'light•biomass' model proved to be a simple and flexible tool that provided reasonable estimates of phytoplankton productivity that were comparable across different studies despite these frequently encountered differences in methodology.

The relationship ultimately selected as the 'fitted' (in terms of its statistical significance and strength) and 'best suited' (in terms of its appropriateness and usefulness) model for the Caloosahatchee Estuary confirmed the primary importance of biomass and light in the control of phytoplankton productivity. Model deviations, or differences in measured and predicted productivity, indicated the secondary influence of nutrients, light quality, and species composition on the productivity potential or photosynthetic efficiency of the phytoplankton community. Seasonal variations in freshwater inflow (i.e., rainfall and river flow) created distinct dry and wet periods with lower and higher nutrient loads and wider and narrower underwater light fields, which when coupled with longer and shorter water residence times, supported dominating communities of dinoflagellates and diatoms, respectively.

The dynamics of phytoplankton community responses to these and other natural and anthropogenic influences in the Caloosahatchee Estuary were further explored by applying the adapted model over a discontinuous twenty-five year period using data collected during routine monitoring programs and other research projects. The estimates of phytoplankton productivity obtained from this model application identified spatial, as well as, seasonal, interannual, and decadal sources of variation in the rates of production and, thus, the trophic status of the Caloosahatchee Estuary.

Phytoplankton productivity was consistently highest in the upper and middle regions of the estuary closest to S-79, the Franklin Lock and Dam, primarily due to the influx of new nutrients that accompany freshwater releases from the Caloosahatchee River and access to nutrient reserves in the flocculent muddy sediments there. Blooms of phytoplankton having chlorophyll *a* concentrations greater than $20 \text{ mg}\cdot\text{m}^{-3}$, representing the top 10% of observations from the twenty-five year period, were also more frequently observed in oligohaline and mesohaline salinities. On a seasonal basis, productivity and biomass were typically highest in the summer and fall wet season, given the high water temperatures, PAR flux levels, and nutrient inputs. However, years that had wetter than normal wet seasons due to above average rainfall and/or excessive flushing events reduced salinities, water residence times, and the quantity and quality of light needed for photosynthesis throughout the estuary, restricting phytoplankton productivity and biomass accumulation. Cyclical El Niño phases and episodic storm events contributed to the interannual and decadal variability in the estuary's trophic status from oligotrophic to hypertrophic levels due to their direct effect on rainfall and temperatures and their indirect effect on any corresponding dependent factors.

Ultimately, this study confirmed the importance of long-term data sets in tracing, understanding, and predicting shifts in the structure and function of phytoplankton communities and, thus, entire ecosystems in response to natural and anthropogenic changes occurring at multiple time scales. The morphology and hydrology of the Caloosahatchee Estuary were linked to variations in tidal mixing, water residence times, and light availability, which act as filters that enhance or mask the responses of the phytoplankton community to nutrient enrichment and other stressors (e.g., climate

change, hydrologic manipulations, etc.). These interactions have profound impacts on the economic and social utility of the Caloosahatchee Estuary and other coastal ecosystems and, ultimately, the vitality of humanity due to the dependency on these ecosystems (Cloern 2001). These and other concepts addressed in this study are central to the development of a broader conceptual model of coastal eutrophication that is needed to guide the development of strategies and tools to be used in the management and restoration of damaged estuaries and coastal ecosystems worldwide (Cloern 2001).

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BIOGRAPHICAL SKETCH

Loren Mathews grew up in Peachtree City, Georgia, a suburb of Atlanta. She attended the University of Miami where she received a Bachelor of Science degree in marine science and biology in 2005 and a Master of Arts degree in marine affairs and policy in 2007. During her time in Miami, Loren worked full time at Miami Seaquarium, the oldest, privately owned marine life park in the United States. She worked first as an Education Programs Lead and was later promoted to the Park Operations Supervisor, where she oversaw day-to-day park activities and helped plan the functioning of a new swim-with-the-dolphins facility. Her master's thesis was based on her experiences there and focused on the role of aquariums in public education and conservation efforts. In 2007, Loren moved to Gainesville, Florida with her husband, so he could attend law school at the University of Florida. Loren obtained a part-time position as a laboratory assistant for Edward Philips in the Fisheries and Aquatic Sciences Program. She soon became the full-time Quality Assurance/Quality Control Officer, for which she maintained the laboratory's quality program required for state certification in water sampling and chemical analyses. Interested in staying current in her field, Loren became a graduate student in the Fisheries and Aquatic Sciences Program in 2008 under the guidance of Edward Philips. A grant from the South Florida Water Management District of West Palm Beach, Florida provided her the opportunity to lead a phytoplankton productivity study in the Caloosahatchee Estuary, Florida. The results of that project were the basis of her Doctor of Philosophy degree research and this dissertation. Loren moved to Savannah, Georgia in 2012 with her husband, who is a practicing attorney, and their one-year old son.