FACTORS INFLUENCING ALGAL BIOMASS IN HYDROLOGICALLY DYNAMIC SALT PONDS IN A SUBTROPICAL SALT MARSH

A Thesis

by

CARRIE J. MILLER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2007

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Co-Chairs of Committee,	Daniel L. Roelke
	Stephen E. Davis, III
Committee Members,	Lee A. Fitzgerald
	Russell A. Feagin
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ABSTRACT

Factors Influencing Algal Biomass in Hydrologically Dynamic Salt Ponds in a Subtropical Salt Marsh. (May 2007)

Carrie J. Miller, B.S., Millersville University

Co-Chairs of Advisory Committee: Dr. Daniel Roelke
Dr. Stephen Davis

The interface between land and water is often a dynamic zone that responds to relatively short-term climatic and hydrologic forces. Coastal salt marshes occupy this zone between land and sea and typically are comprised of vegetated marsh intersected by channels and shallow ponds that are subject to flooding by winds, tides, and storm surges. Coastal salt marshes are widely regarded as zones of high macrophyte productivity. However, microalgae may contribute more to salt marsh productivity than previously realized, underscoring the importance of understanding algal dynamics in such systems. Benthic and planktonic chlorophyll-*a* (surrogate for total algal biomass), sediment AFDW, total suspended solids, salinity, and nutrients were examined in marsh ponds in the subtropical Guadalupe Estuary, TX, USA to determine the effects of hydrologic connections on algal biomass in this system. From May 2005 – May 2006 there were several pond connection, disconnection, and desiccation events. During periods of disconnection, algal biomass was higher in both the benthos and the water column than during connection events when supposed flushing occurred. Connection events also flushed out high NH_4 accumulating in pond surface waters, but did not increase NO_x. Therefore, the primary source of DIN seemed to be nutrient cycling within the ponds. There was a temporal effect on surface water salinity, which increased throughout the sampling period as bay water levels and subsequent pond connections decreased, demonstrating interannual variability and the link between seasons (wet vs. dry) and marsh inundation patterns (high water periods vs. low water periods) in this estuary.

I dedicate this to God, who guided my steps throughout this whole process and continues to do so.

ACKNOWLEDGEMENTS

I would like to thank my co-advisors, Dr. Daniel Roelke and Dr. Steve Davis, who exercised great patience with me throughout my masters studies and have continually encouraged me in the accomplishment of my goals. I am deeply indebted to them for the education they have given me at Texas A&M. I must also thank Dr. Lee Fitzgerald and Dr. Russell Feagin, who have given me excellent advice on my thesis research.

I am deeply grateful to the funding agencies that made my research and education a reality. Sea Grant, US Geological Survey, Guadalupe Blanco River Authority, San Antonio River Authority, San Antonio Water System, Regents' Fellowship, and the National Science Foundation via the Information Technology in Science (ITS) Center have all provided monetary and in-kind support towards my education. Thank you also to the staff and volunteers of the Aransas National Wildlife Refuge who provided us with a roof over our heads, a watchful eye on our wellbeing, and a place to launch our boat as this study would have been impossible without them.

I would be remiss if I did not thank my fellow graduate students for their friendship, assistance in the field and lab, and thought-provoking discussions. Special thanks goes to Jose Montoya, Hsiu-Ping (Erin) Li, Rachel Butzler, Matt Driffill, George Gable, and Reagin Errera. Thank you also to all of the other students and technicians who joined me in the field: Leslie Schwierzke, Stephen McDowell, Will Falkner, Chris Llewellyn, Alexis Martinez, and Merissa Ludwig. Thank you also to Amy Snelgrove for her countless hours of GIS support.

I would like to thank my family and friends who may not have understood exactly what I was doing but supported and encouraged me wholeheartedly. I want to especially thank my parents Darrell and Paula Miller who have spent countless hours on the phone with me as well as many visits to Texas and much prayer throughout my time here. My brother Benjamin provided me with much comic relief in his "I was bored…" emails, my thanks goes to him for all of the comics, videos, and funny pictures that were sent my way. Thank you also to Whittington Meyer, my best friend and confidant, who has listened to and encouraged me, especially during the thesis-writing process and who even spent a few late nights helping me get things done in the lab.

Finally, my thanks goes to God who I believe brought me to Texas A&M and helped me on my path to a master's degree. I saw many beautiful and amazing things in the Aransas National Wildlife Refuge and the marsh in the Guadalupe Estuary and for that I am extremely grateful.

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CHAPTER I

INTRODUCTION: RESEARCH AND STUDY SITE OVERVIEW

The interface between land and water is a dynamic zone that responds to relatively short-term climatic and hydrologic forces. Coastal salt marshes are at the land-sea interface that typically are comprised of vegetated marsh intersected by channels and shallow ponds that are subject to flooding by winds, tides, and storm surges. Research indicates that hydrologic connections across these types of water bodies are important for flushing, nutrient exchange, and maintaining high species diversity and primary productivity. (Bornette et al. 1998; Ward et al. 1999; Leibowitz and Vining 2003; Ahearn et al. 2006).

Landscape connectivity is a meaningful concept in ecology that provides explanatory power for understanding species distribution (Moilanen and Nieminen 2002) and exchange of energy and materials (Pringle 2001) between landscape patches. In the case of aquatic systems, connectivity is more complex in that it involves both spatial and temporal components (Ward 1989). Hydrologic connectivity is defined as "water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle" (Pringle 2001; Pringle 2003a, b). This suggests that connectivity and transfer of materials and energy derive from surface water, precipitation, or groundwater—the contributions of which can be difficult to quantify.

Most research on hydrologic connectivity in river-floodplain systems indicates that high residence times in the floodplain following a flood pulse result in higher algal

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This thesis follows the style of *Estuaries and Coasts*.

biomass production which is later transferred to the main river channel during the next flood pulse. This allows for the exchange of both nutrients and labile carbon with the floodplain (Tockner et al. 1999; Schemel et al. 2004; Ahearn, Viers et al. 2006). Although species composition of algae and nature of fresh and saltwater wetlands are different, it is suggested that pulsing hydroperiods result in high productivity in both systems as well as possible organic matter source-sink relationships between the marsh and its associated water body depending on the specific spatial characteristics of the marsh (Odum et al. 1995). Furthermore, understanding the link between hydrology and marsh landscape characteristics may give further insight into the relationship between marsh hydrodynamics, primary productivity, and organic matter distribution (Pinckney et al. 1994; Lathrop et al. 2000; Ahearn et al. 2006).

While organic detritus has long been seen as a major component of salt marsh food webs, recent studies have demonstrated the importance of microalgae in comprising a larger percentage of the food web base than organic detritus from vascular plants (Page 1997; Moens et al. 2002; Fejes et al. 2005). While food webs are traditionally described as being either herbivore- or detritus-based, studies have shown that spatial and temporal changes in food availability result in diet switching (Winemiller 1990; Polis 1996; Akin S. 2006)—i.e. patterns in both microalgal growth and deposition of detritus may be fundamental to food web dynamics and salt marsh productivity. In addition to its importance as a food source (Kneib et al. 1980; Peterson and Howarth 1987; Sullivan and Moncreiff 1990), benthic microalgae is also an important link in nutrient cycling (Hopner and Wonneberger 1985; Rizzo 1990) and serves to stabilize marsh sediments

(Holland et al. 1974). My aim is to understand the driving forces behind patterns in microalgal growth and dispersal in a subtropical coastal marsh in order to determine the potential contribution of benthic microalgae as a labile carbon source in coastal salt marshes.

The Guadalupe Estuary (Fig. 1) is a heterogeneous landscape of tidal creeks, inland bays, and intermittently connected marsh ponds (Fig. 2) surrounded by high and low inter-tidal marsh vegetation. The ponds undergo connection and disconnection at irregular intervals throughout the year. A food web study in an adjacent system (Mad Island Marsh, Matagorda Bay) indicated that detritus and algae were the most important food resources throughout the year (Akin et al. 2006). The potential is therefore high for benthic algal production in the ponds to be a major labile carbon source to the marsh food web.

Stability and productivity of the marsh food web in the Guadalupe Estuary is essential as this system is important habitat for the last naturally migrating population of whooping cranes (Darnell and Smith 2004). This endangered species uses the marsh from mid-October through mid-April as winter feeding grounds, eating primarily Carolina wolfberry (*Lycium carolinianum*) and blue crabs (Hunt and Slack 1989), often found in the marsh ponds where whooping cranes spend much of their time foraging (LaFever 2006; Chavez-Ramirez 1996). In addition to their ecological importance, the ponds can also be used as a sort of natural mesocosym to find evidence of fundamental unpredictability (Huisman and Weissing 2001) on an ecosystem scale.

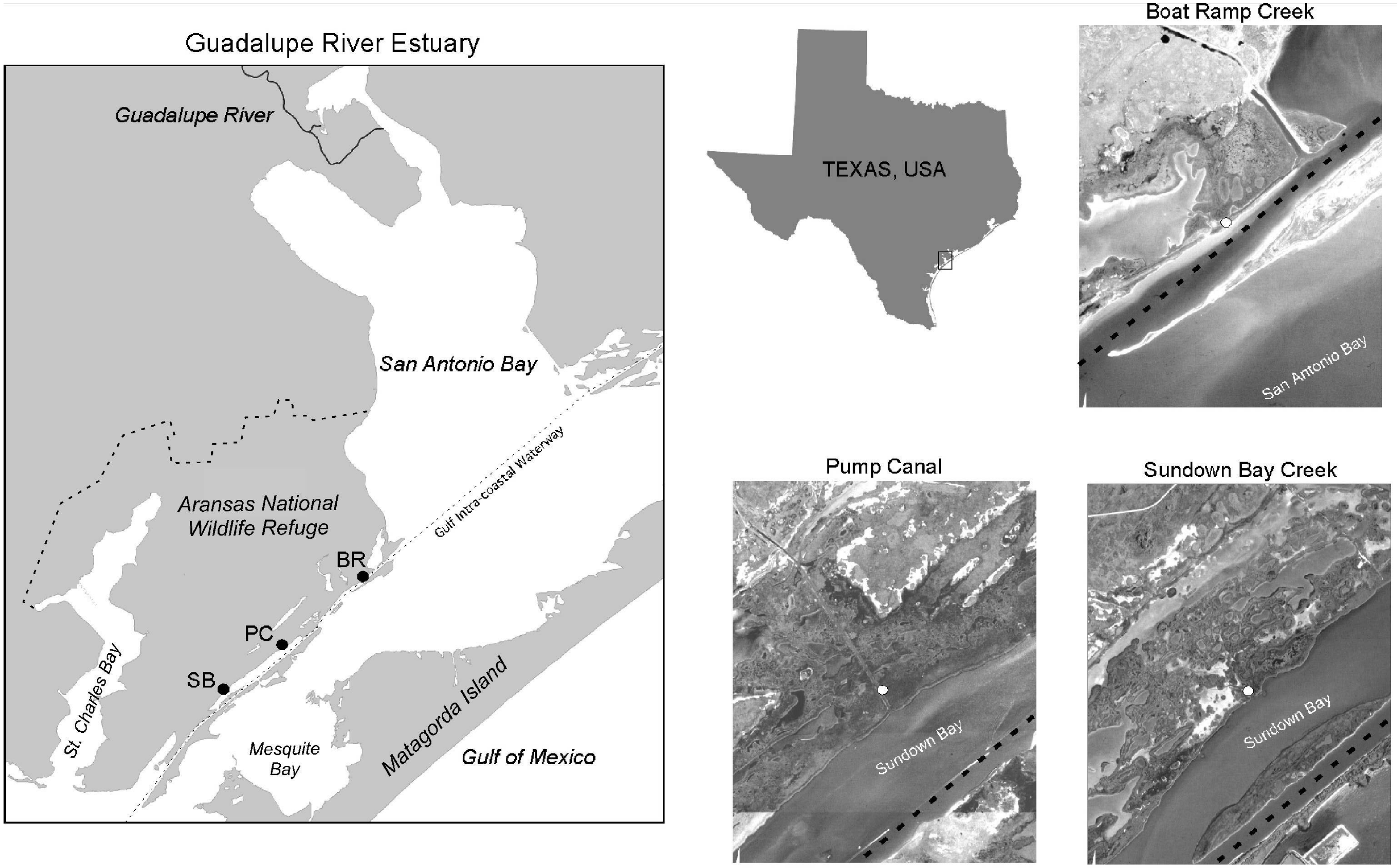

Figure 1. Guadalupe Estuary, TX, USA and three sampling sites: Boat Ramp Creek (BR), Pump Canal (PC), and Sundown Bay Creek (SB).

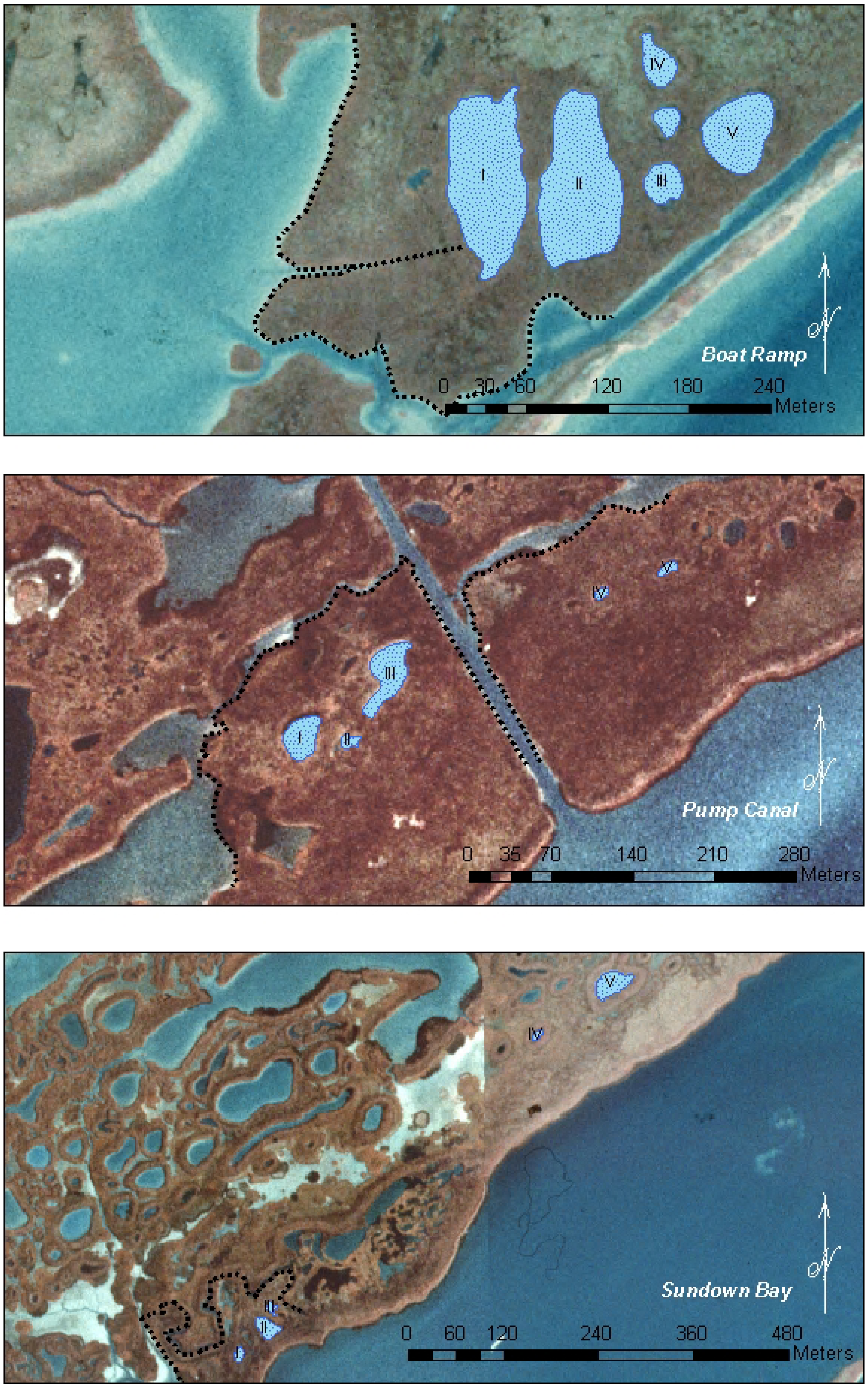

Figure 2. Aerial photographs of Boat Ramp (BR), Pump Canal (PC) and Sundown Bay (SB) sites at site-appropriate scales. Sampled ponds are indicated in blue and labeled, perceived water source is outlined with a black dotted line. Sites are along the same stretch of marsh with BR to the northeast and SB to the southwest and PC in between, approximately 6.5 km from BR and 3.2 km from SB.

OVERARCHING GOAL AND SPECIFIC OBJECTIVES

My overarching goal is to increase understanding of the role of hydrologic connectivity as it influences accumulation of benthic microalgal biomass and organic matter in ponds at ANWR. This is important because both detritus and benthic microalgae can be major sources of labile carbon for the marsh food web. I will achieve this goal by accomplishing the following specific objectives:

1. To quantify benthic and suspended microalgal biomass and organic matter in the ponds, as well as several water quality parameters—salinity, inorganic N and P—and identify any spatial and/or temporal patterns.
2. To determine and measure environmental gradients in order to estimate hydrologic connectivity of the ponds in relation to the surrounding marsh.
3. To examine other factors such as proximity of ponds to the open bay and to each other, precipitation, wind, season and tide that may influence benthic microalgal biomass within the ponds.

CHAPTER II

MICROALGAL DYNAMICS: PEG-MODEL VS. FLOODPULSE CONCEPT

INTRODUCTION

It is well established that coastal salt marshes are highly productive. Crucial to maintaining higher trophic levels that utilize the marsh is a solid food web base made up of macrophytes, detritus, and benthic and planktonic microalgae. While food webs are traditionally described as being either herbivore- or detritus-based, studies have shown that spatial and temporal changes in food availability result in diet switching (Winemiller 1990; Polis 1996; Akin S. 2006)—i.e. patterns in both microalgal growth and deposition of detritus may be fundamental to food web dynamics and salt marsh productivity. Microalgae may contribute more to salt marsh productivity than previously realized (Peterson and Howarth 1987; Sullivan and Moncreiff 1990; Page 1997; Moens et al. 2002; Fejes et al. 2005), underscoring the importance of understanding algal dynamics. Two models commonly employed to describe algal dynamics are the Plankton Ecology Group-model (PEG-model; Sommer 1986) and the flood pulse concept (Junk et al. 1989).

The PEG-model describes the cyclic relationship between resource limitation, grazing, and microalgal growth and succession (Sommer 1986). Developed in temperate lakes, the PEG-model predicts phytoplankton community succession from fast-growing, edible r-selected to slow-growing, less edible k-selected species. On an aggregated level, total phytoplankton biomass increases with stratification and increased nutrient and light availability. This first increase, primarily r-selected species, is quickly grazed by increased herbivore populations to the point of a clear-water phase. During the clear-water phase, nutrients are recycled and accumulate and k-selected species begin to dominate the population. As herbivore populations decrease, phytoplankton biomass increases until water column mixing persists and light becomes limiting, causing a decline in phytoplankton biomass (Sommer 1986). In the PEG-model, each of these stages correspond to season (spring, summer, fall and winter). Although many subtropical systems are not typically characterized by four temperature-based seasons, some subtropical systems have been shown to also follow the PEG-model, including Galveston Bay (Ornolfsdottir et al. 2004) and the Nueces River Estuary (Roelke 1997; Fejes et al. 2005) in Texas, USA.

Unlike the ideal stratifying lakes in which the PEG-model was developed, algal dynamics in floodplain lakes have been conceptualized in a flood pulse model (Junk 1989; Roelke 1997; Junk 2004; Fejes et al. 2005). Floodplain lakes have two basic states: inundated and disconnected. During inundation, the lake may be partially or completely flushed, resulting in low algal biomass. Flooding may add river nutrients to the floodplain lake, however nutrient cycling within the floodplain, as well as terrestrial input is also important. During the disconnection phase algae flourish and biomass increases due to reduction in flushing losses (Tockner et al. 1999; Schemel et al. 2004; Ahearn et al. 2006).

Algal dynamics however, do not have to be dictated by one model or another. Tockner et al. (2000) describe an extension of the flood pulse concept where both temperature effects (season) and floods work in conjunction to dictate changes in the biota. Tockner et al. also describe a third aspect of the flood pulse concept, the “flow pulse” (1999, 2000). The flow pulse is used to describe smaller flooding events that do not inundate the entire floodplain, resulting in the addition of nutrients to the system without high flushing rates.

The Guadalupe Estuary, TX, USA is a heterogeneous landscape of tidal creeks, inland bays, and intermittently connected marsh ponds surrounded by high and low inter-tidal marsh vegetation. Much like a floodplain, the ponds undergo connection, disconnection and desiccation at irregular intervals throughout the year. The primary objective of this study was to examine benthic and planktonic algal biomass in several ponds in a subtropical saltwater marsh and determine the most accurate model of microalgal dynamics in this system. If the system strictly follows the PEG-model—as do two of the Texas bays to the north and south of the Guadalupe Estuary—a spring peak followed by a significant decrease in algal biomass and a summer/fall peak would be expected (Fejes et al. 2005; Ornolfdottir et al. 2004; Roelke et al. 1997; Sommer et al. 1986). If the flood pulse concept dominates however, during times of inundation, algal biomass would be low and begin to increase after disconnection from the main channel (Tockner et al. 1999; Schemel, Sommer et al. 2004; Ahearn et al. 2006). However, it may be that aspects of both describe patterns in this ecosystem, resulting in a modified flood pulse concept where both seasonal and flood pulse effects are present (Tockner et al. 2000).

METHODS

Three sites—Boat Ramp (BR), Pump Canal (PC), and Sundown Bay (SB)—located along Sundown Bay, Guadalupe Estuary, TX were sampled monthly. Sites were located along the NE-SW plane and were approximately 6.5 km (BR-PC) and 3.2 km (PC-SB) apart. Mean site elevation was highest at BR (0.26 m) and lower at SB (0.23 m), with the NE portion of PC (0.22 m) similar to SB and the SW portion of PC similar to BR (0.25 m). Each site included five ponds and an adjacent tidal creek as well as sloughs and larger inland bays. A nested sampling design (Heino et al. 2004) was used, with five ponds at each of the three sites. Each pond was overlaid with a 50-60 square grid depending on the shape of the pond and cells on the grids in each pond were randomly chosen for sampling each month. Cell size was dependent on pond surface area—i.e. the number of cells in each grid remained approximately the same while cell size was variable. Keeping approximately the same number of cells in each pond as well as the randomization of sampling cells achieved balanced sampling of edge and interior grids. Randomizing the sampling cells each month also avoided researcher bias in choosing sampling points. Three replicate Petri-dish sediment cores were taken to an approximate depth of 1 cm to determine benthic chlorophyll-a and ash-free dry weight. Water depth was measured at each sampling location within a pond. 100 and 50 ml water samples from each pond and the associated tidal creek were filtered in triplicate. The filtrant was saved for analysis of water column chlorophyll-*a* concentration and volatile organic matter content, while the filtrate was saved to determine inorganic nutrient concentrations: NO_x, NH_4, and PO_4. Salinity of the pond was determined using a refractometer.

In the laboratory, the sediment cores were divided longitudinally and half of the core was analyzed for chlorophyll-*a*, *b*, and *c* using the acetone-extraction measured with a spectrophotometer (Jeffrey and Humphrey 1975). The other half of the sediment core was dried at 50º C until consecutive weights were within 0.001 g of each other and was then combusted at 500º C for 3 hours and weighed once cool to determine the ash-free dry weight of the sample (Dean 1974; Heiri et al. 2001). Filtrant from the water samples was analyzed for chlorophyll-a using acetone extraction and measured using a fluorometer (APHA 1989). Total suspended solids and volatile organic matter were measured using the same method for the determination of ash-free dry weight of the benthic samples. Data reported herein is total suspended solids only, as three months worth of the ash-free dry weight samples were lost due to a furnace malfunction. The filtrate was analyzed for combined nitrate-nitrite (NO_x; Grasshoff and Koroleff 1999; Pai, Yang et al. 1990) and ammonia (NH_4; Pai, Yang et al. 1990) and soluble reactive phosphorus (Grasshoff and Koroleff 1999).

Paired water level recorders with pressure sensors were located at each site, which provided a continuous record for water level in the tidal creek and nearby pond at each site. Data from a nearby Texas Coastal Ocean Observation Network (TCOON) tide monitoring station at Seadrift, TX (http://lighthouse.tamucc.edu/overview/031) were also compiled for the period of this study as the water level recorders were not always functional. To determine periods of inundation, tidal creek water level was correlated to pond water level using data from existing water level recorders (S. Davis unpublished data; Fig. 3). Times when the ponds exhibited strong correlations with their associated tidal creek indicated that they were physically connected to the tidal creek. Since data from the water level recorders were not always available for the sampling period, water level in the tidal creek was also correlated to data from the Seadrift TCOON monitoring station (Fig. 3). Correlation between the tidal creeks and Seadrift water level was strong, therefore from this point forward, the water level used to determine when ponds were connected or disconnected is according to Seadrift values.

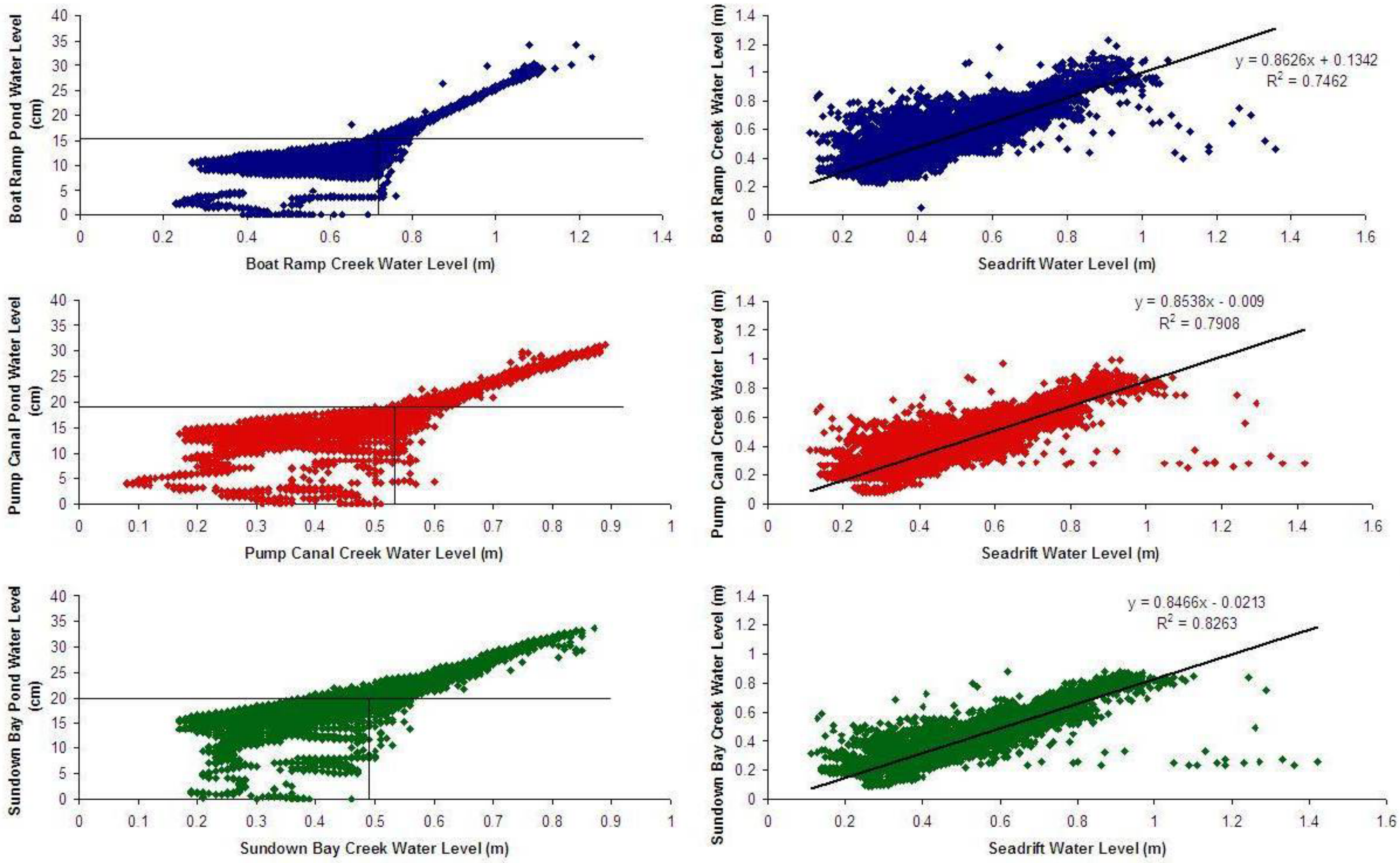

Figure 3. Left-hand column indicates correlation between pond water level and tidal creek water level. Intersection of the two arbitrarily placed lines indicates assumed disconnection point. Right-hand column shows correlation of tidal creek water level to Seadrift water level at fixed monitoring buoy.

Nonmetric multidimensional scaling (NMS) was used to determine statistical significance among hydrologic and geospatial parameters (PCORD). NMS is an ordination technique well suited for large, non-normal data sets, one of the primary reasons it was used for this study. It also allows for the consideration of several parameters and consolidates parameters into only a few dimensions by conducting an iterative search for the solution with the least amount of stress. For this study, benthic data was processed separately from water column data. Benthic data consisted of mean benthic chlorophyll-*a*, mean benthic organic matter, and salinity, with the assumption that salinity of the overlying water column was not significantly different from the pore water salinity. Water column data included mean water column chlorophyll-*a*, mean total suspended solids, combined nitrate/nitrite, ammonia, phosphate, and salinity data. Means were used for chlorophyll-*a*, sediment organic matter, and total suspended solids due to the high volume of samples taken, as well as the need for a filled array (fully determined) to run NMS. Scores were calculated in NMS at least ten times for each data set and the solution with the least amount of stress was chosen for further analysis. NMS scores were imported into a spreadsheet and classified according to site (BR, PC, SB), season (spring, summer, fall and winter), hydrologic season (P1-P7), and connection to tidal creek (connected or disconnected). Graphs were then analyzed for clustering and patterns.

RESULTS

Hydrologic Connectivity (Marsh Inundation)

The most predominant means of hydrologic connectivity was via fluctuations in bay water level. Significant rain events (>5 cm/24 h) were few (Fig. 4). From May through July 2005, there were nine separate connection events over 31 days, the longest lasting 11 days and the shortest 1 day. Most events consisted of Seadrift water levels less than 0.71 m, indicating a connection at Sundown Bay site only. There were four days in late July where water levels allowed all three sites to be connected. Between July 23 and August 30, 2005 there were no connection events and many of the ponds were completely or nearly dry. From late August to mid-October 2005 there were five separate connection events, totaling 29 days. Out of these events, 12 of the days showed water levels over 0.71 m, indicating all three sites were connected to their respective tidal creeks. The longest estimated period of connection lasted 10 days, the shortest 3 days. After October 12, 2005 there were no periods of connection lasting longer than one day, nor reaching a water level of 0.71 m. Of note was the difference in water level between February 2005 and February 2006, where water level was much lower in 2006 than in 2005.

Other hydrologic events during the sampling period included three precipitation events with total daily rainfall exceeding 5 cm and five pond dry events. Rainfall events lasted one day, with cumulative rainfall of 7.42 – 8.53 cm and occurred several months apart in July, October, and November 2005. Of note was the difference between precipitation in March 2005 and March 2006, where more rain fell during 2005 than in 2006. Given the lack of precipitation and the decrease in water level, late winter/early spring of 2006 was dry, leading to an apparently extended dry event in the marsh. Dry pond events were observed in April and August 2005, as well as February, March, and May 2006 (Fig. 4). Dry events entailed smaller ponds becoming completely dry and larger ponds having greatly reduced water levels, some to the point of having only one or two small puddles remaining in the deeper depressions. As these were point observations during sampling trips, the duration and exact timing of dry events is unknown. Some dry events, occurring over several months apart seemed to happen gradually, as water level steadily decreased during the months prior to the dry event. Between the February-March and May 2006 dry events however, water levels were normal to high in April 2006, indicating that the May dry event probably happened very quickly.

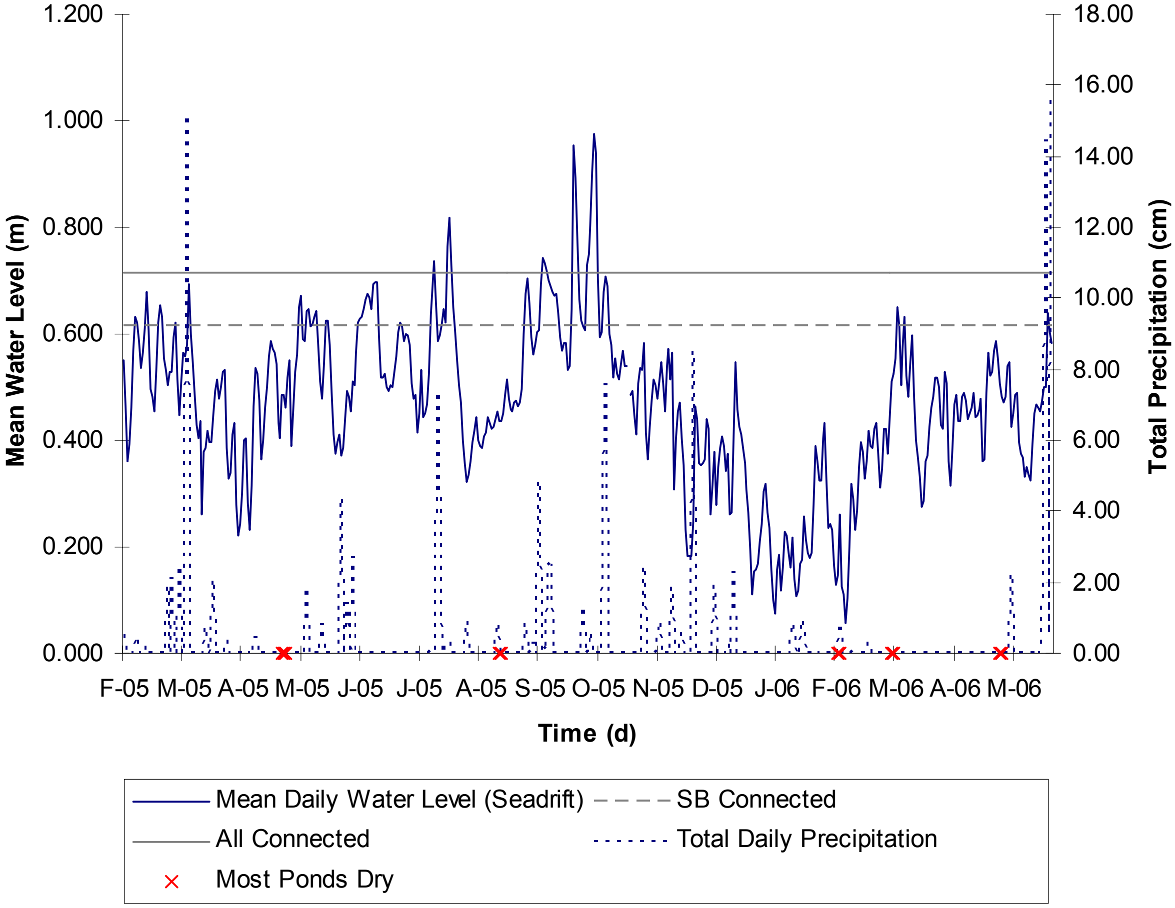

Figure 4. Hydrologic timeline (bay water level and local precipitation) for Guadalupe estuary, February 2005 through May 2006. Sundown Bay (SB) ponds are connected to their respective tidal creek at Seadrift water level 0.616 m and ponds at all sites are connected to their respective tidal creeks at Seadrift water level 0.713 m. A red ‘x’ indicates that most ponds were dry during that sampling period.

Salinity in the ponds increased steadily throughout the sampling period beginning at around 10 ppt in May 2005 and ending at 35-40 ppt in May 2006 (Fig. 5A,B). Salinity was most variable between sites during late spring and summer of 2005 with SB ponds typically having the highest salinities.

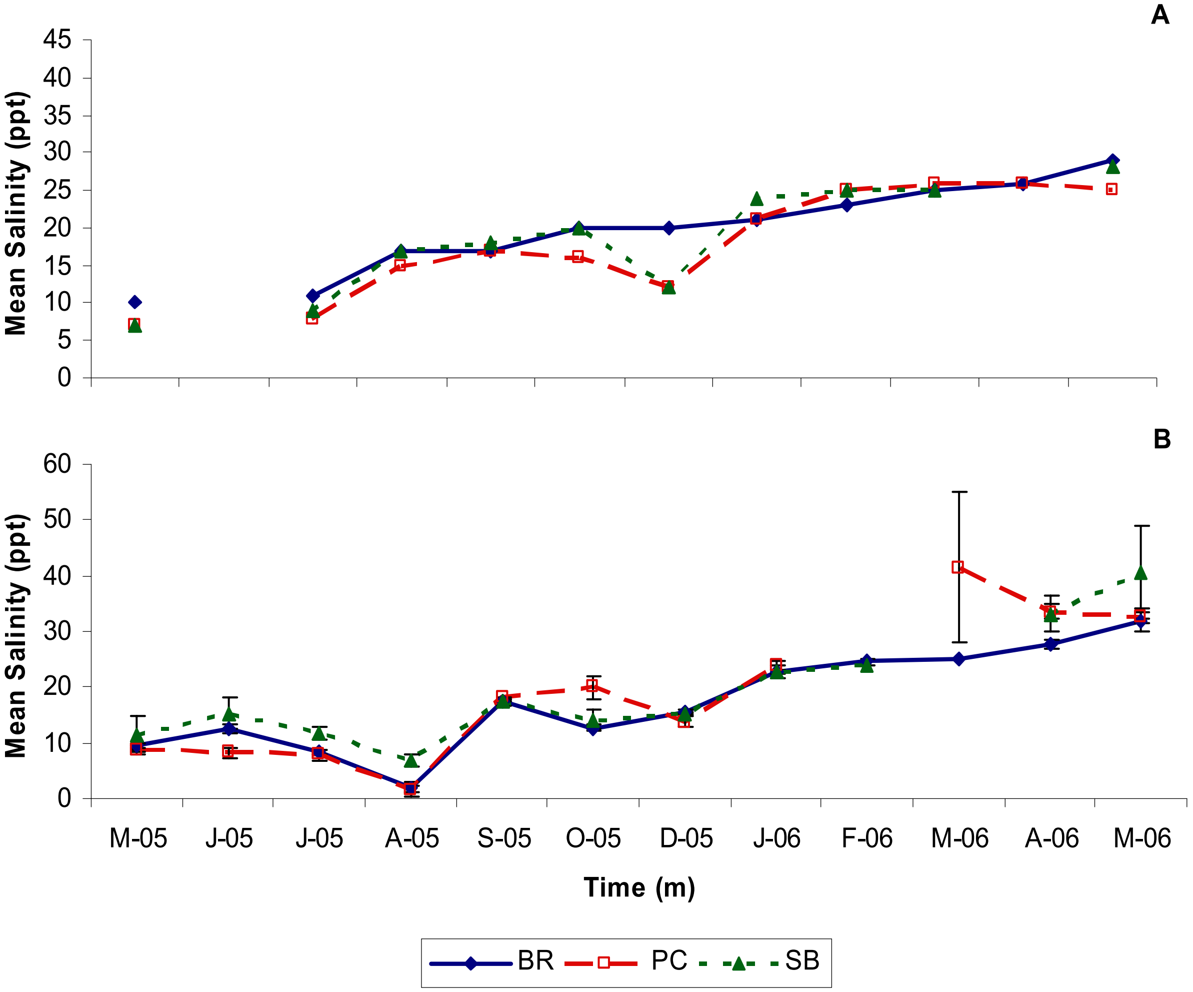

Figure 5. Tidal creek salinity (A) and average salinity by site (B). In both the tidal creek and ponds salinity increased almost linearly throughout the sampling season, note difference in scale between tidal creek and pond salinity. Error bars represent relative error (s/√n).

Algal Biomass and Organic Matter/Suspended Solids

For all parameters, Boat Ramp (BR) and Pump Canal (PC) sites were typically the most similar, while Sundown Bay (SB) tended to differ. In both the benthos and water column, algal biomass usually followed the same trend through time (Fig. 6B,C). In the benthos, SB generally had lowest algal biomass, while Boat Ramp site had the highest. Water column algal biomass, as inferred from chlorophyll-*a*, trends were similar among all three sites. Outliers were removed from August 2005 data, when SB and PC showed a dramatic peak, most likely an inflated value as the contribution of the benthos to the water column during sampling was higher than normal due to shallow water depths in the ponds and was possibly exacerbated by the sampling technique.

Algal biomass in the water column at BR and PC remained relatively low with minor peaks in July/August 2005, January 2006, and April 2006. Water column algal biomass was extremely low in February and March, most likely due to dry conditions. Tidal creek algal biomass was consistently low for all stations, with small peaks in September 2005 and April/May 2006 at BR and PC (Fig. 6A). The peaks in algal biomass at SB occurred in the month before the peaks at BR and PC, indicating lag between the lowermost and uppermost stations. In the benthos, algal biomass was consistently high, with visible algal mats forming in several of the ponds throughout the year. Like the water column, benthic algal biomass showed peaks in August 2005, January/February

2006, and April 2006. Algal biomass was at its lowest in the benthos during March 2006.

Total suspended solids (TSS) followed a similar trend over all three sites with little variability in magnitude between sites except for dry months, where there was high variability in TSS between sites (Fig. 7A,B). In August 2005, TSS peaked and by December 2005 had returned to the lower values seen in late spring/early summer of 2005. TSS data for September and October was lost, barring any analysis during those months. In January 2006, TSS values began to climb almost linearly until it peaked in May 2006, where sampling ended. In the tidal creeks, TSS values were consistently low, regularly 10-50 times less than TSS values in the ponds.

Sediment organic matter showed two different, but similar trends among the three sites (Fig. 8). SB exhibited the highest values for sediment organic content throughout the sampling period, although there was little variability throughout time, with the exception of a small decline in sediment organic content during the winter months and a dramatic peak in May 2006. BR, which had the lowest organic matter, and PC exhibited a slightly different trend throughout time with several small peaks in sediment organic content in June and September 2005 and January and April/May of 2006.

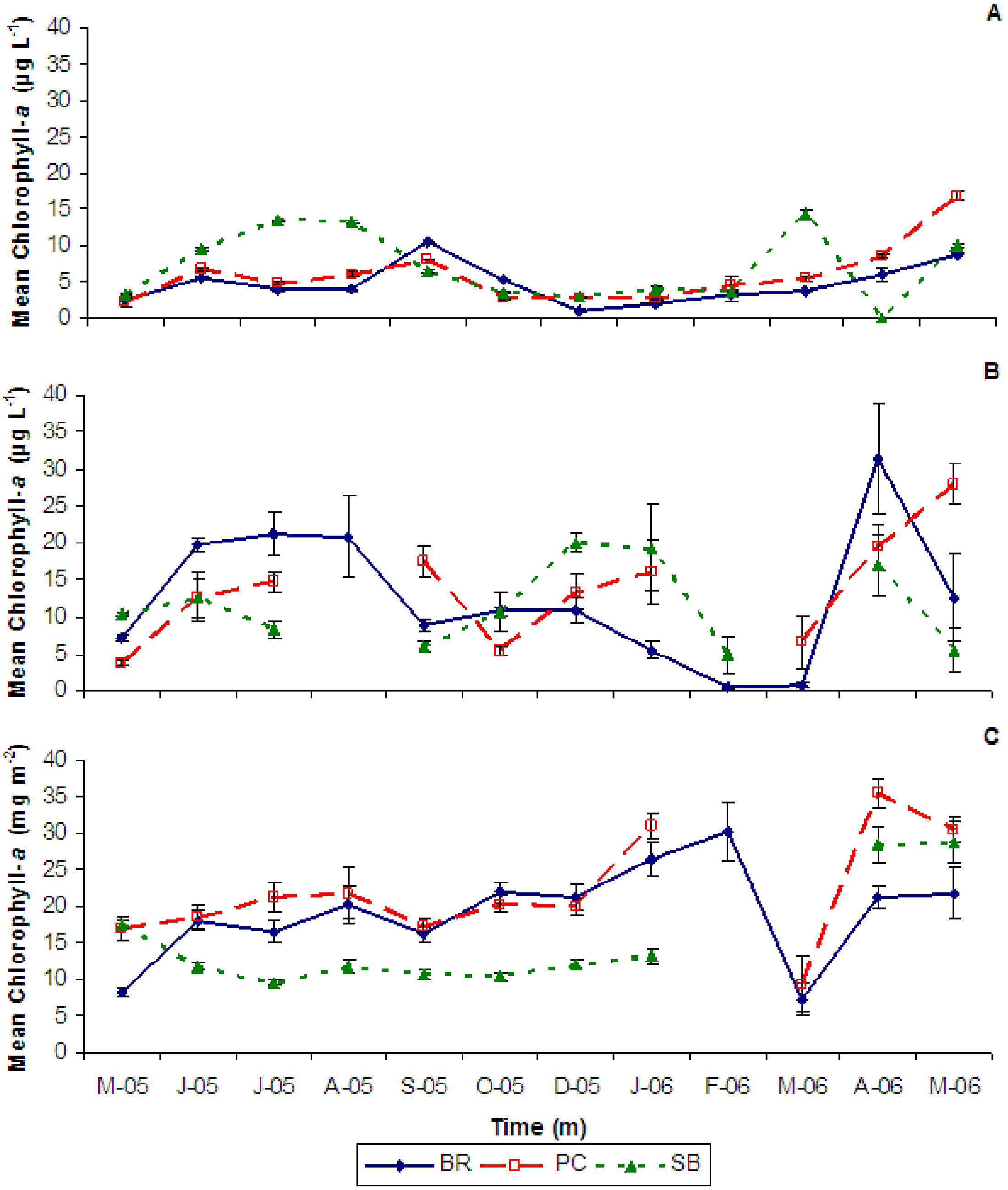

Figure 6. Water column algal biomass in tidal creek measured as chlorophyll-*a* by site (A) and water column algal biomass in ponds measured as chlorophyll-*a* averaged by site (B). C. Benthic algal biomass measured as chlorophyll-*a* averaged by site. Note the difference in units between water column and benthic algal biomass. Error bars represent relative error (s/√n).

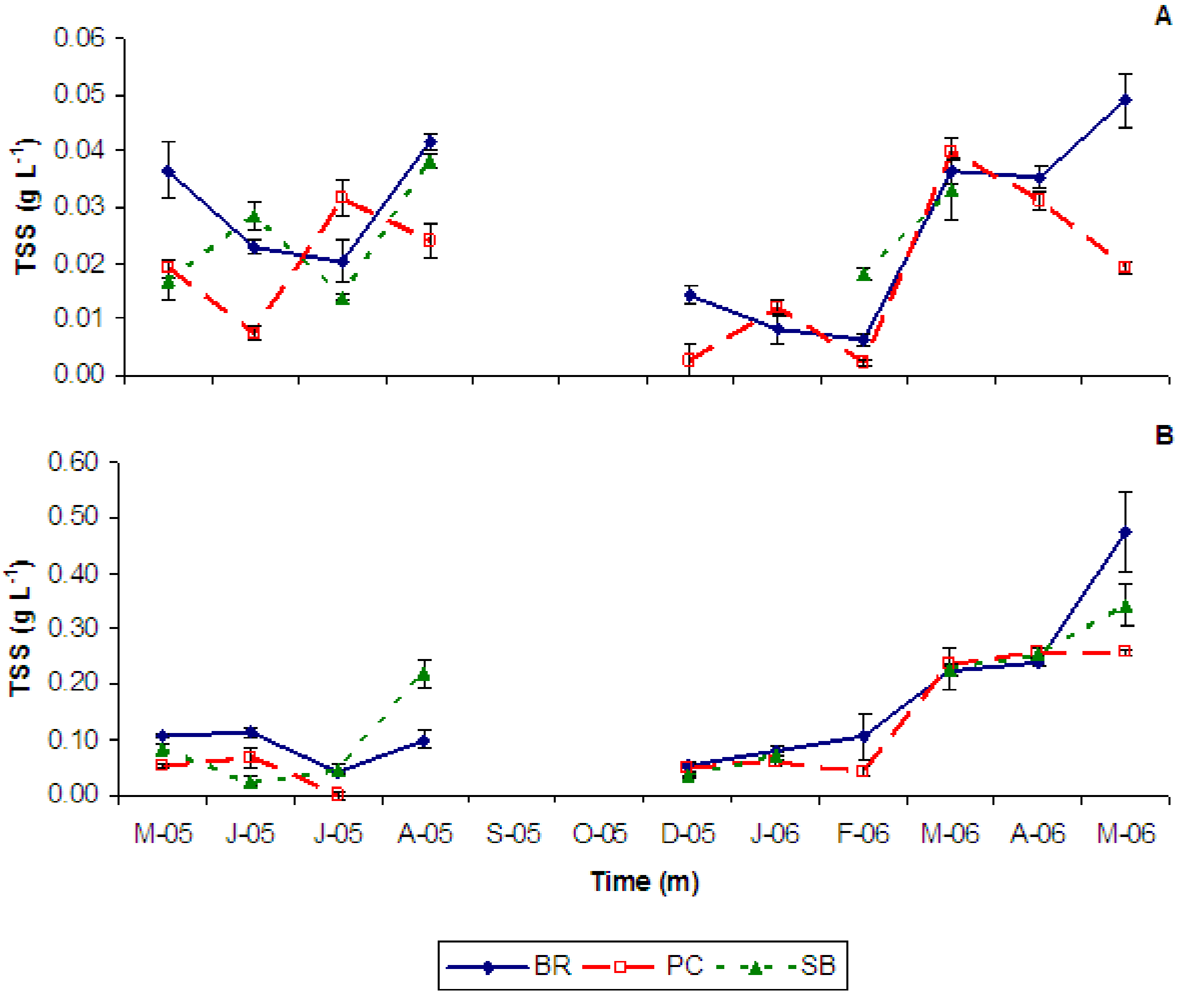

Figure 7. Water column total suspended solids in the tidal creek, by site (A) and water column total suspended solids in the ponds, averaged by site (B). The scale for B is an order of magnitude greater than the scale for A. Error bars represent relative error (s/√n). TSS was in general higher during times of disconnection and low water.

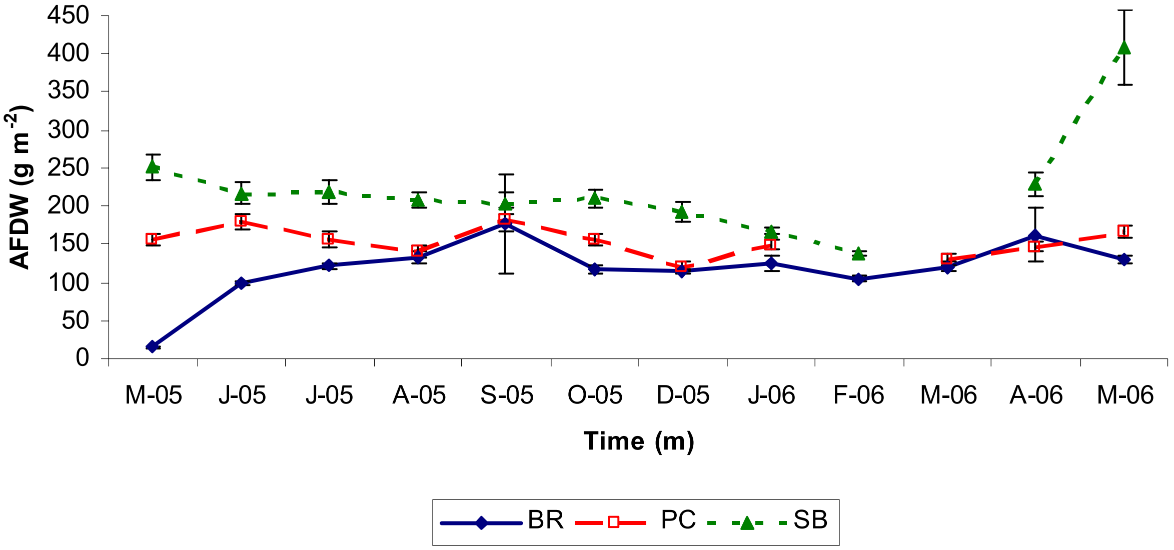

Figure 8. Benthic ash-free dry weight averaged by site. Error bars represent relative error (s/√n). Sediment AFDW remained fairly stable at each site throughout the sampling period.

N and P Nutrients

Combined nitrate/nitrite (NO_x) in the ponds was highly variable between and within ponds across time (Fig. 9). PC and SB followed a similar trend in 2005, with NO_x peaks in June and October. The decline of the July 2005 peak for SB was gradual, reaching the low in August 2005. BR initially showed a lag with a peak in NO_x in August 2005, however it also had a peak in October 2005. In 2006, BR showed three peaks, in January, March, and May. SB also peaked in January/February of 2006, while NO_x values at PC remained consistently low. NO_x values in the tidal creeks were also highly variable, however all three sites seemed to show an increasing trend in values throughout the study period. Values of NO_x in the tidal creek were on average, comparable or higher than values in their associated ponds.

Ammonia (NH_4) values were typically an order of magnitude greater than NO_x values and trends were slightly more consistent among the three sites. Throughout the sampling period, each site showed extreme minimums in May 2005, September 2005, and April 2006. These three months were all months immediately following a dry month. There were also several peaks in ammonia—PC had one peak in August 2005, SB exhibited two major peaks in October 2005 and January 2006, and BR showed frequent peaks in August 2005, October 2005, March 2006, and May 2006. Ammonia was consistently low in the tidal creeks with small peaks occurring in SB and BR the month following high ammonia in the ponds, with some exceptions.

Phosphate values were on the same order of magnitude as NO_x. Phosphorous increased gradually for all three sites from May through October of 2005 with peaks in June and September/October 2005. Phosphate showed a dramatic decrease in December 2005, followed by peaks in the ponds at BR and SB in January and February, respectively. Phosphate continued to show an increasing trend in BR ponds, peaking again in May 2006 at both BR and SB. Phosphate values in ponds at PC remained low throughout the 2006 sampling period. Phosphate values were typically lower in the tidal creeks than in the ponds. There was a peak in phosphate values in all tidal creeks in August 2005, as well as in January 2006 and April 2006.

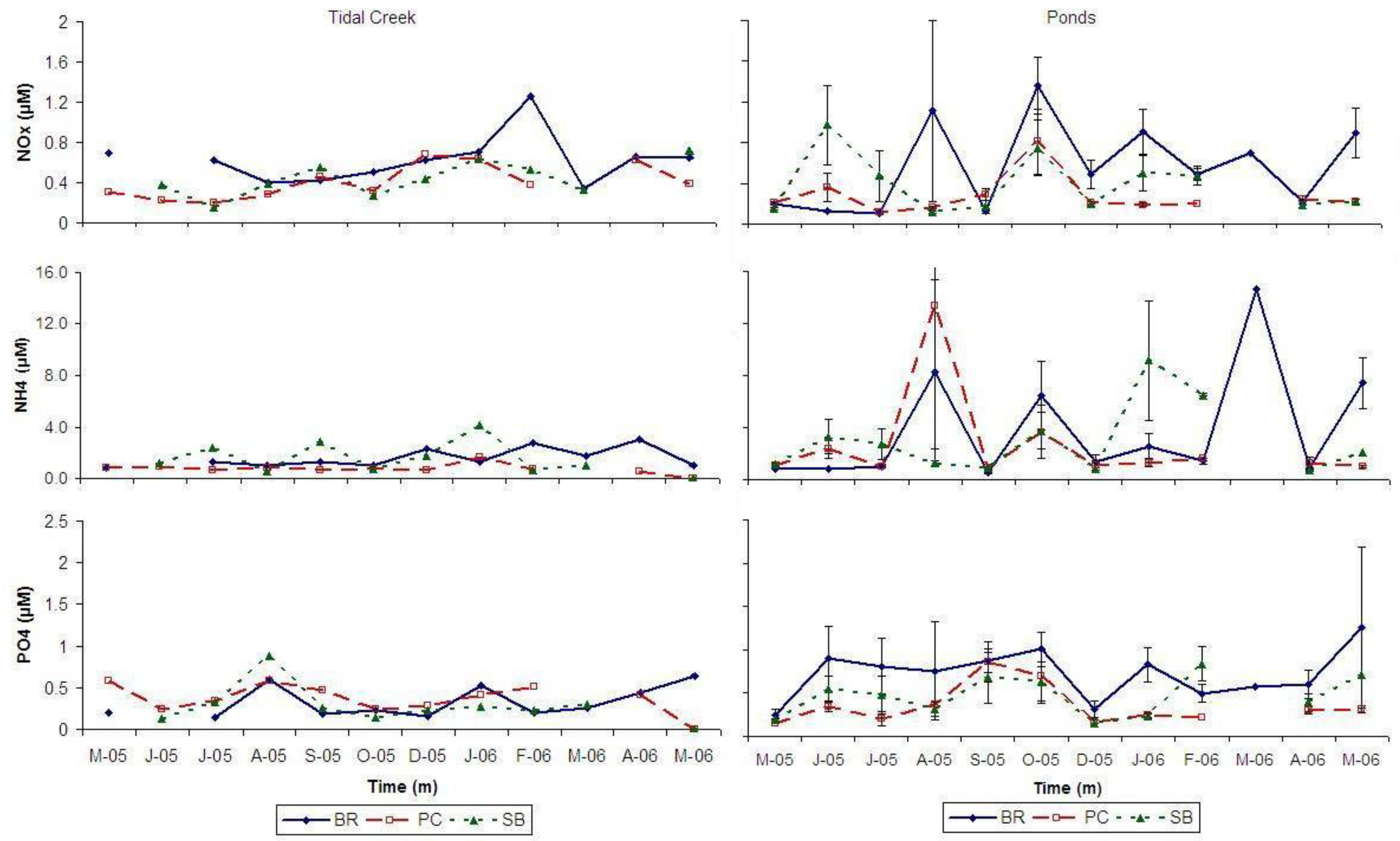

Figure 9. Average nutrients (combined nitrate-nitrite, ammonia, phosphate) by tidal creek and ponds averaged by site. Error bars represent relative error (s/√n). Nutrients were usually lower in the tidal creek than in the ponds. Connection with the tidal creek resulted in a flushing of NO_x and NH_4 which built up in ponds during disconnection periods. PO_4 remained relatively stable, increasing slightly during connection events.

Statistical Results: Benthic Data

Non-metric Multidimensional Scaling (NMS) results confirmed initial observations of a gradient between the three sites. Stress for the benthic NMS results was good, most of the variability in the results was explained by sediment AFDW, chlorophyll-*a*, and salinity. Each parameter correlated well to at least one of the 3 dimensions in the final solution (Table 1). Boat Ramp (BR) and Sundown Bay (SB) sites formed two distinct clusters with little overlap (Fig. 10). Pump Canal (PC) was also fairly clustered but overlapped both BR and SB results. As the separation between BR and SB occurred along NMS dimension 2, sediment ash-free dry weight (AFDW) appears to have been the primary driver of site differences. BR exhibited the lowest AFDW and SB the highest, with PC AFDW values falling in between.

Table 1. Correlations between benthic data and NMS dimensions for single and multiple dimensions. NMS results chosen were from the eighth run with final stress of 6.92318 and zero instability. Dimensions 1, 2, and 3 together account for 97.1% of the variability (47.5, 26.9, and 22.7%, respectively).

	Single Dimension Linear Regression (R^2)			Multiple Regression	
Variable	D1	D2	D3	Adjusted Correlation Coefficient	Regression Equation
Sediment AFDW	0.009	**0.854**	0.220	0.916	164.520 - 16.671(D1) + 125.310(D2) - 38.448(D3)
Chlorophyll-*a*	**0.927**	0.006	0.179	0.927	19.072 + 15.935(D1)
Salinity	0.178	0.000	**0.810**	0.865	18.634 - 4.203(D2) - 14.199(D3)

When benthic points were classified by connection/disconnection to the tidal creek with connection defined as Seadrift water level of 0.71 m for BR and PC and 0.62 m for SB, two clusters were evident (Fig. 11A). While there was some overlap, connected ponds and disconnected ponds separated primarily along NMS dimension 3, although there was some separation along NMS dimension 1 as well. Salinity was strongly correlated with NMS dimension 3 ($R^2 = 0.81$) and algal biomass with dimension 1 ($R^2 = 0.93$). During disconnections from the tidal creek, pond salinity was higher than salinity during connection to the tidal creek (Fig. 11B). The same was true for algal biomass, which was higher during the disconnection period than during the connected period (Fig. 11C).

Using the four temperate seasons as the classification scheme for benthic data, there was separation again, mainly along NMS dimension 3 but again also along dimension 1 (Fig. 12A). This classification is faulty, as there are not four clear seasons in this subtropical region. However as the PEG-model was created in light of four seasons, it seems somewhat appropriate. The summer season clustered fairly well, however the spring season was more scattered, while fall and winter tended to overlap. The primary influence on the NMS ordination again appears to have been salinity, with summer having the lowest salinity and spring the highest, albeit with high variability (Fig. 12B). Algal biomass seems to have been slightly higher in spring and winter (Fig. 12C).

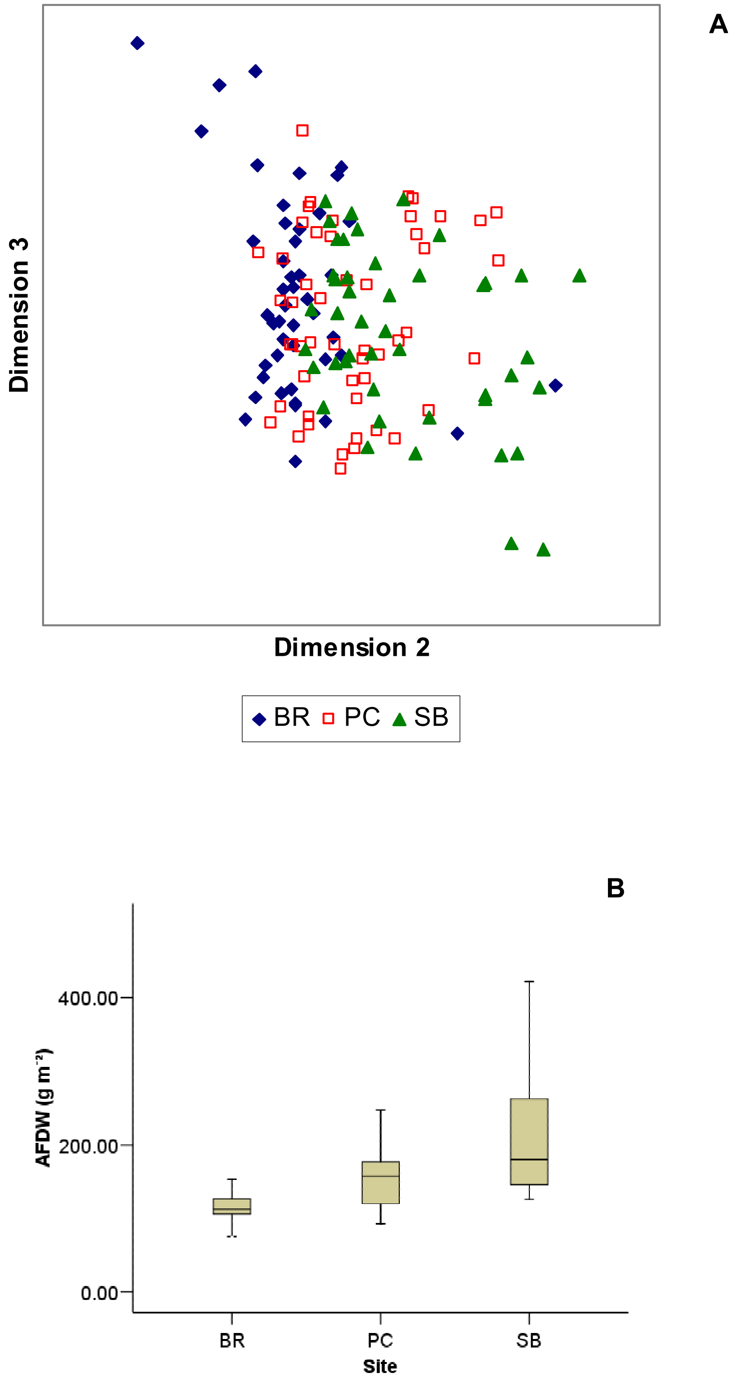

Figure 10. NMS results from 3 benthic variables (chlorophyll-*a*, ash-free dry weight, salinity) categorized by site (A), with associated boxplot of ash-free dry weight corresponding to NMS dimension 2 (B). All sites clustered, with BR and SB having distinct separation. Both sites however were overlapped by PC. Separation was along dimension 2, attributed to differences in AFDW among the three sites.

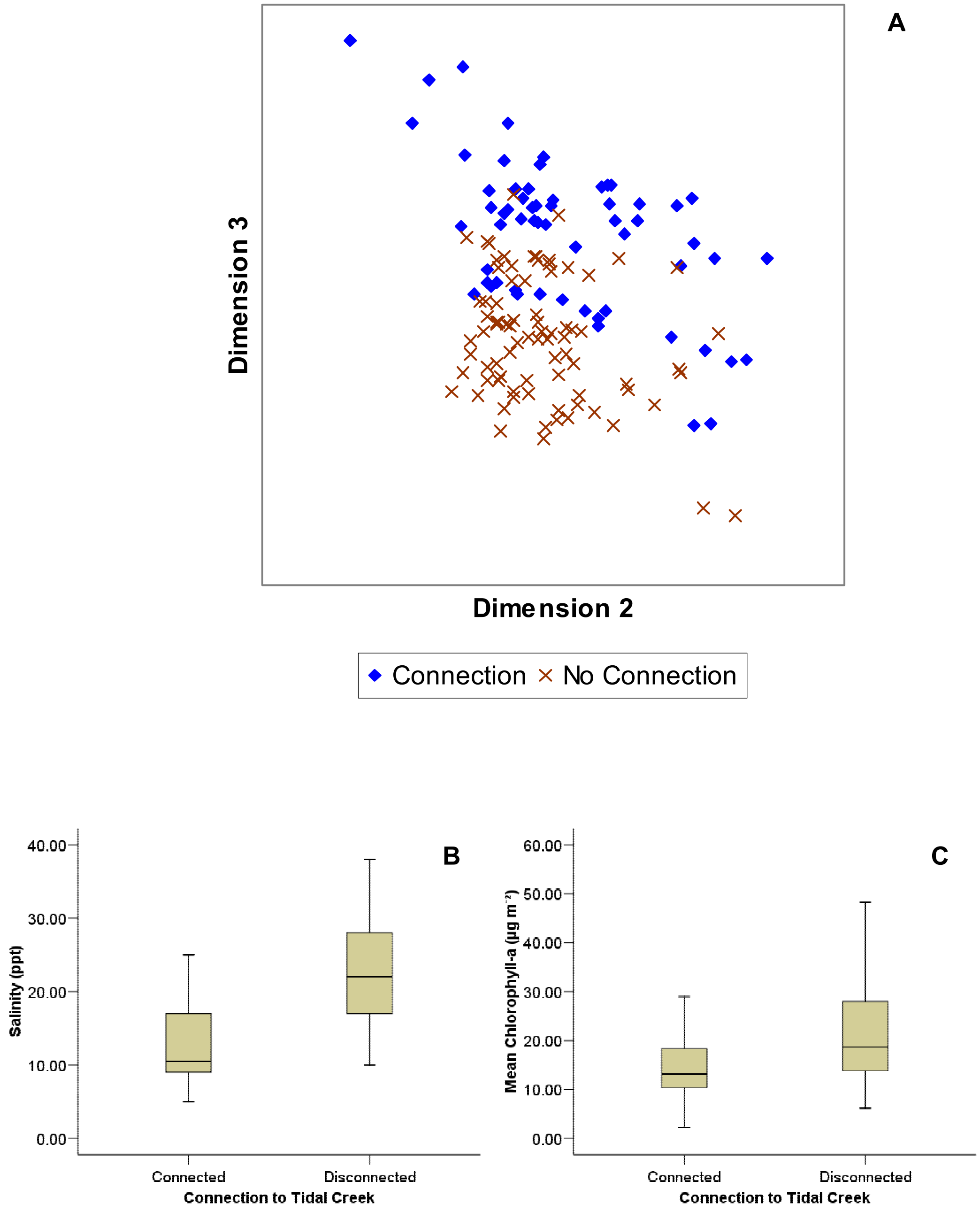

Figure 11. NMS results from benthic data (A) with associated boxplots of salinity (B) and chlorophyll-*a* means (C) categorized by connection to a tidal creek based on water level data. Ponds at BR and PC were connected when Seadrift water level was 0.71 m and ponds at SB were connected when Seadrift water level was 0.61 m. Both salinity and chlorophyll-*a* (representative of algal biomass) were higher during periods of disconnection than during periods of connection when flushing presumably occurred.

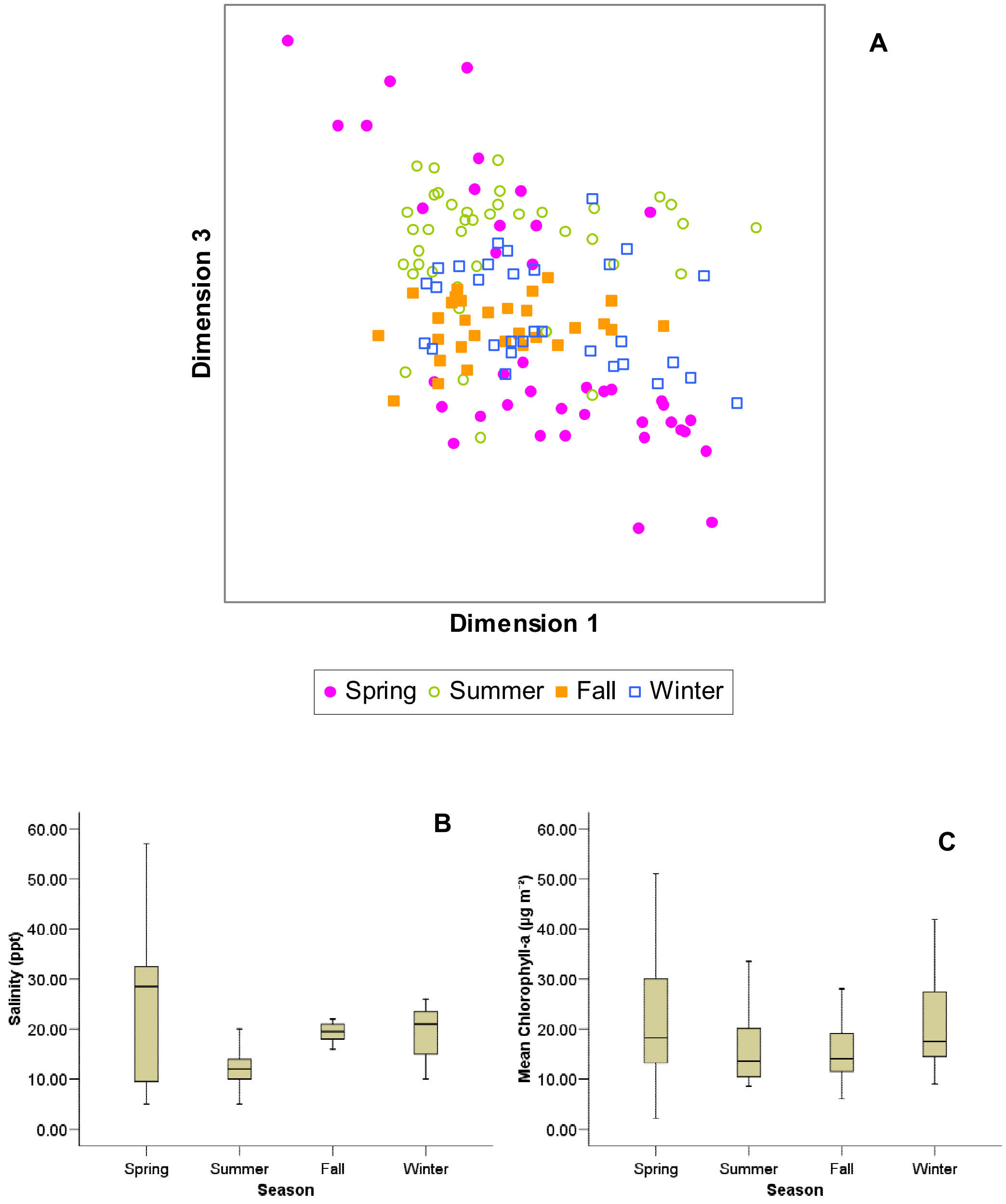

Figure 12. NMS results from benthic data categorized by season (A) with associated boxplot of pond salinities which correspond primarily to NMS dimension 3 (B) and chlorophyll-*a* means corresponding to NMS dimension 1 (C). Season defined as in temperate zones showed weak trends with chlorophyll-*a* (representative of algal biomass) highest in the spring and winter. Salinity was highest and most variable in spring, but also showed an increasing trend from summer to winter.

After analyzing the benthic data according to season or time of year and connectivity to the tidal creek separately, the two aspects were combined into seven successive hydrologic periods to capture interannual variability (Fig. 13). This classification captured changes in the benthos well, with good separation of points along NMS dimension 3 and a movement of clusters from one end of NMS dimension 1 to the other (Fig. 14A). Again, salinity was a primary driver of the separation along dimension 3, however, this classification caused algal biomass to show a stronger influence along dimension 1. Average pond salinity was lowest during period 1 (May – July 2005) and steadily increased throughout the sampling period (Fig. 14B). During period 7 (May 2006), average salinity was at its highest, nearly 3.5 times higher than period 1. Algal biomass in the benthos also showed an increasing trend throughout the sampling period (Fig. 13C), with slight decreases during period 3 (September – December 2005) and period 5 (February – March 2006).

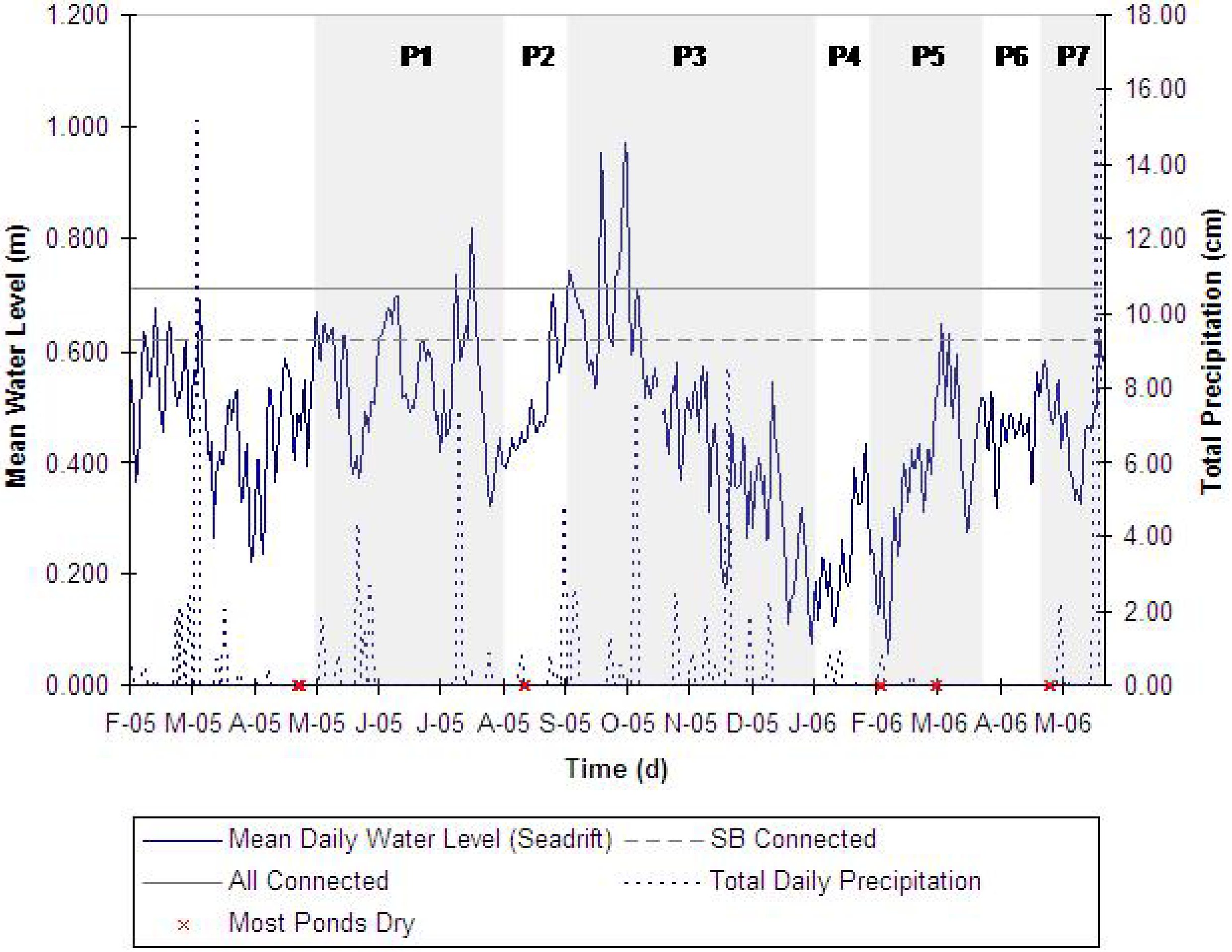

Figure 13. Hydrologic timeline (bay water level and local precipitation) for Guadalupe estuary, February 2005 through May 2006 with grey and white bands indicating seven successive hydrologic periods throughout the sampling period. Periods 2, 5, and 7 had dry pond events, periods 1, 3, and 6 had at least one pond connection/filling events, and period 4 was a pond low-water event.

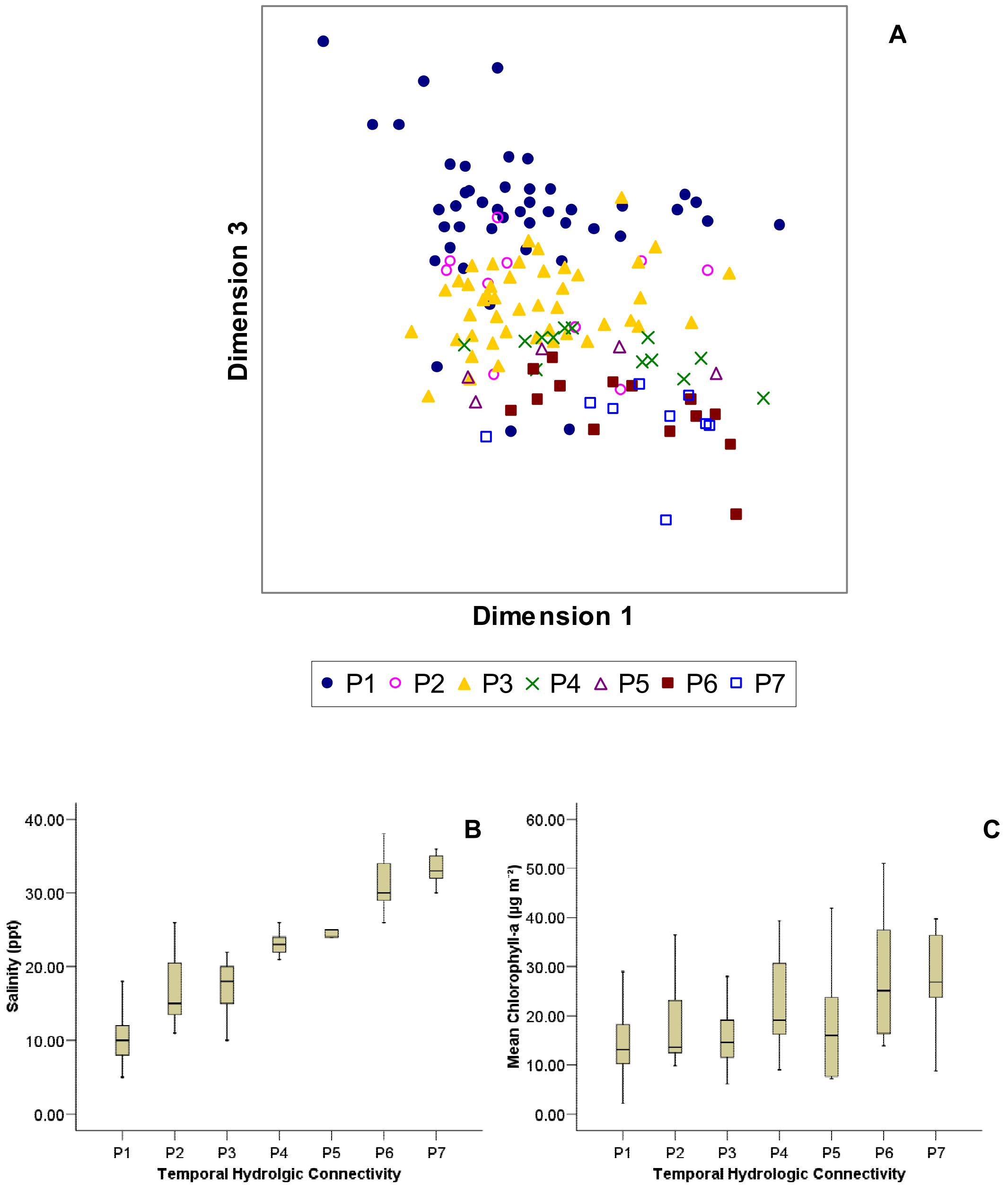

Figure 14. NMS results from benthic data categorized by seven successive periods based on hydrology (A) with associated boxplot of pond salinities which correspond primarily to NMS dimension 3 (B) and chlorophyll-*a* which corresponds to NMS dimension 1 (C). Combining hydrology and time of year showed better separation in NMS than four seasons. Salinity was lowest in P1 and steadily increased throughout the sampling period, as did chlorophyll-*a* (representative of algal biomass).

Statistical Results: Water Column Data

NMS scores were calculated for the water column based on salinity, water column algal biomass, total suspended solids, NO_x, NH_4, and PO_4. Stress for the water column NMS was good, and most of the variability in the results was explained by the water column variables in the matrix. All of the variables correlated well with at least one of the 3-dimensions in the final solution (Table 2). When categorized by site, there was no clear separation of points.

As with the benthic data, there was separation along NMS dimensions 3 and 1 when points were classified according to connection/disconnection to the tidal creek (Fig. 15A). Corresponding to dimension 3, algal biomass was slightly higher and more variable during the disconnection period (Fig. 15B), as was total suspended solids (Fig. 15C). NO_x and NH_4 were correlated to NMS dimension 1 and also showed greater variability during the disconnection period (Fig. 15D,E).

When classified according to four temperate-defined seasons, there was some clustering, but no real trend was visible for the water column data. Combining connectivity to the tidal creek and time of year, clearer trends emerged (Fig. 16A). Separation was more distinct along NMS dimension 1, which was reflected in the NO_x and NH_4 data (Fig. 16D,E). Both N-inorganic nutrients peaked during period 5 (February – March 2006) and showed the most variability during period 4 (January 2006). Variability was also higher during period 7 (May 2006) for both NO_x and NH_4. Along NMS dimension 3, separation was less clear, however there were several points of interest. Period 2 (April 2005) showed high total suspended solids (Fig. 16B) as well as high algal biomass (Fig. 16C), even with higher variability. Periods 5, 6, and 7 (February – March 2006, April 2006, and May 2006, respectively) showed an increasing trend in total suspended solids. Periods 6 and 7 were clustered together on the NMS ordination, however period 5 was offset, most likely due to the extremely low algal biomass during that time.

Table 2. Correlations between water column data and NMS dimensions for single and multiple dimensions. NMS results chosen were from the first run with final stress of 9.36727 and zero instability. Dimensions 1, 2, and 3 together account for 94.0% of the variability (37.3, 29.9, and 26.8%, respectively).

	Single Dimension Linear Regression (R^2)			Multiple Regression	
Variable	D1	D2	D3	Adjusted Correlation Coefficient	Regression Equation
Chlorophyll-*a*	0.028	0.035	**0.382**	0.446	21.302 + 14.844(D1) - 10.247(D2) - 32.925(D3)
TSS	0.036	0.197	**0.521**	0.642	0.128 - 0.077(D2) - 0.152(D3)
Salinity	0.265	0.191	**0.467**	0.728	18.389 - 6.474(D1) - 3.533(D2) - 10.055(D3)
NO_x	**0.535**	0.095	0.106	0.681	0.295 - 0.401(D1) - 0.066(D2) + 0.214(D3)
NH_4	**0.470**	0.002	0.000	0.497	1.996 - 4.500(D1) + 1.124(D2)
PO_4	0.017	**0.691**	0.088	0.870	0.466 + 0.113(D1) - 0.685(D2) + 0.308(D3)

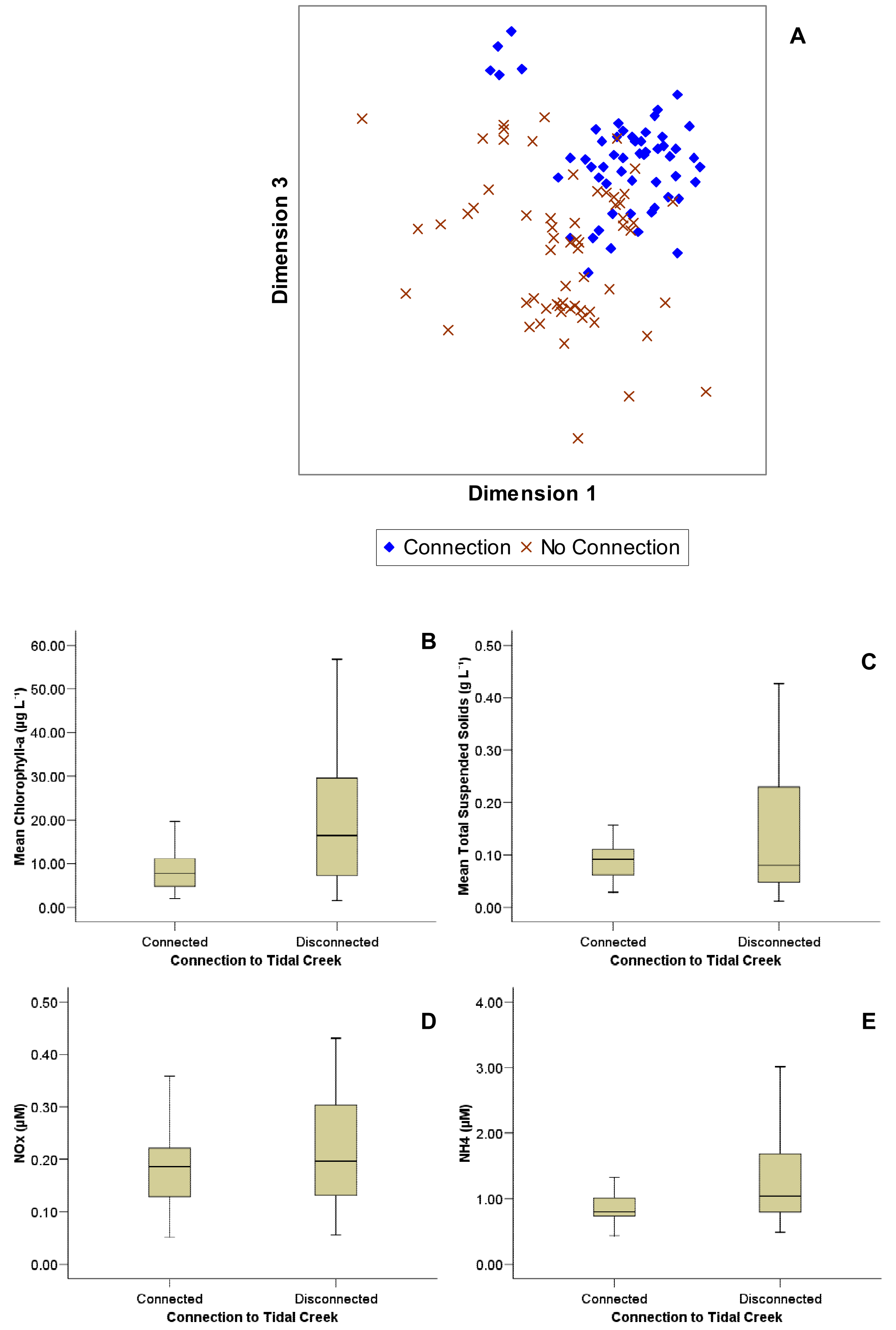

Figure 15. NMS results from water column data categorized by connection to tidal creek based on water level data (A) with associated boxplots of chlorophyll-a means (B), total suspended solids means (C), combined nitrate/nitrite (D), and ammonia (E). Chlorophyll-*a* is well correlated with dimensions 1 and 3 and total suspended solids is well correlated with dimension 3.

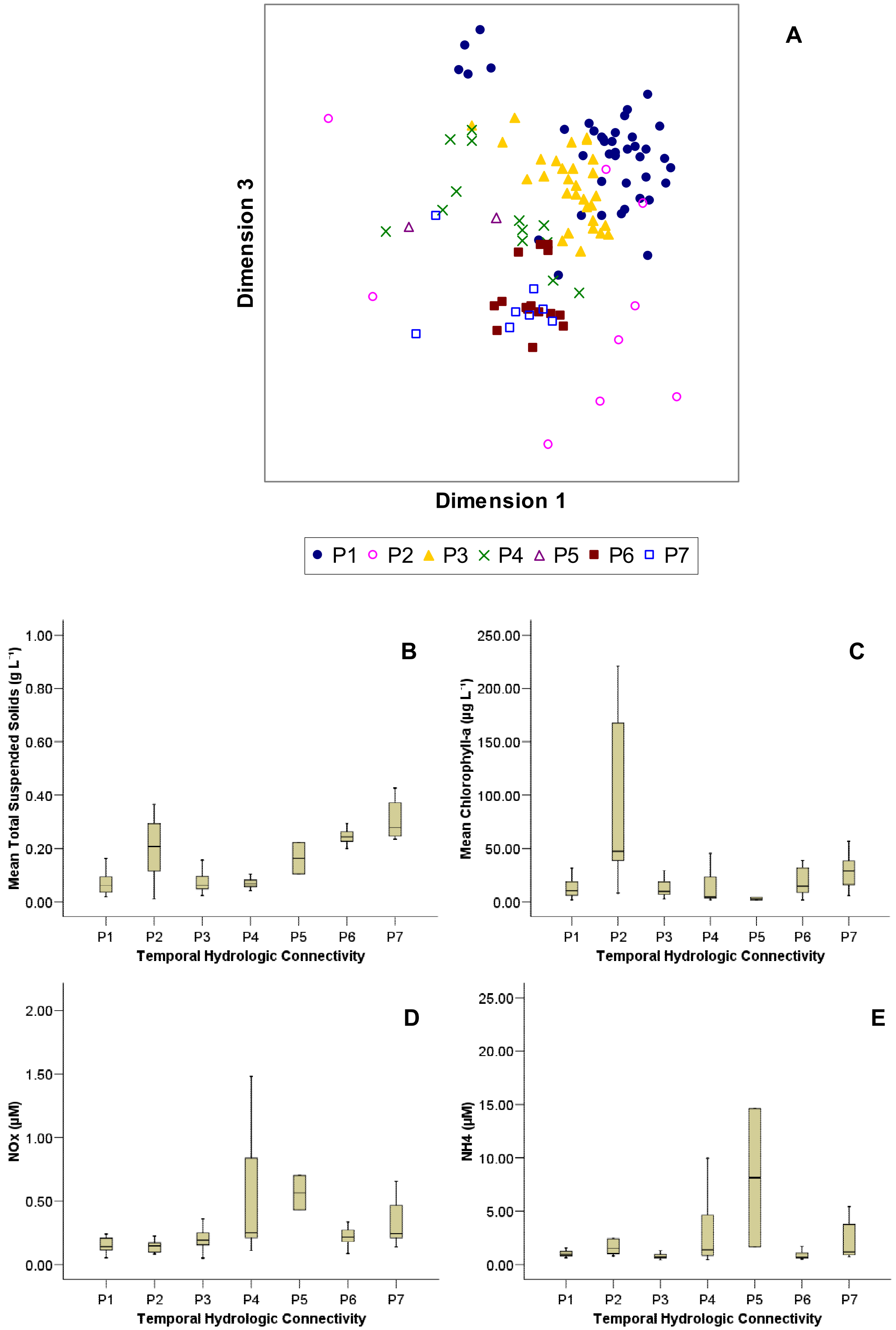

Figure 16. NMS results from water column data categorized by seven successive hydrologic periods (A) with associated boxplots of total suspended solids (B) and chlorophyll-*a* (C) which correspond primarily to NMS dimension 3 and NO_x (D) and NH_4 (E) which correspond to NMS dimension 1.

DISCUSSION

This study examined algal biomass and organic matter in coastal salt marsh ponds in order to determine the most accurate model describing algal dynamics and organic matter deposition in the Guadalupe Estuary. The PEG-model (Sommer et al. 1986) describes a cyclic relationship between resource availability, grazer populations, and algal population growth. The flood pulse concept (Junk et al. 1989) relates algal biomass, nutrients, and organic matter in the floodplain to periods of inundation and disconnection from the river. The possibility of a dynamic combination of these models was also considered.

The algal biomass in both the benthos and the water column did not change significantly enough to point to PEG-model dynamics, although a PEG-model cycle was found in several Texas bay and estuary studies including Galveston Bay and Nueces River Estuary (Fejes et al. 2005; Ornolfsdottir et al. 2004; Roelke et al. 1997). As the Guadalupe Estuary is located in a subtropical region, season as defined in the PEG-model does not necessarily apply to this system, although there is a temporal element present. Instead of being temperature-driven, the Guadalupe Estuary is tidally-driven and related to the hydrodynamics of the San Antonio Bay with high water periods typically occurring in the traditionally defined fall and spring months and low water periods occurring in the traditional summer and winter months. Since the high and low water events are repeated temporally, some seasonality may be present in the data. During the sampling period however, interannual variability resulted in atypical spring (2006) water levels possibly obscuring regular patterns in the pond data. Perhaps if community composition had been assessed along with the aggregate parameter of algal biomass—as had been in the previous Texas studies—PEG-model community succession may have been found, even with interannual variability in the hydrology.

The flood pulse concept better described algal biomass patterns in the Guadalupe Estuary ponds. The importance of floods in the marsh ponds was underscored by the clear grouping of points found in the NMS results when defined by connection or disconnection from the tidal creek. During times of connection, flushing resulted in lower salinity and algal biomass, while lack of flushing during disconnection events algal population growth was increased and algal biomass was higher. Although salinity was also higher during times of disconnection, the relationship between salinity and chlorophyll-*a* was not strong enough to suggest a concentration effect ($R^2 = 0.20$), rather the increase in salinity is an effect of interannual variability. This is similar to the results found in a California freshwater floodplain lake which exhibited higher algal biomass during disconnection from the river and flushing of the system during flooding (Ahearn et al. 2006). Also similar to the flood pulse concept is the lower algal biomass found in the tidal creek, analogous to the river in the freshwater floodplain. The tidal creek experienced higher flushing and has a larger volume that may result in a dilution effect compared to many of the ponds.

Organic matter deposition in the Guadalupe estuary also mirrored the flood pulse concept. Sundown Bay (SB)—the site most frequently inundated—had the highest sediment ash-free dry weight, indicating higher organic content in the sediment, whereas Boat Ramp (BR)—more infrequently inundated—had the lowest. As the sediment at BR was presumably exposed to the air for longer periods of time, decomposition rates of organic matter in the sediment would have been higher than those at SB due to oxygenation, also indicative of a system driven by hydrodynamics, including evaporation and desiccation of the system (Junk et al. 1989).

Nutrients also followed the original flood pulse concept. Subsequent floodplain research (Ahearn et al. 2006; Schemel et al. 2004) seems to indicate that in freshwater floodplains the river flushes out algal biomass and organic matter but brings a fresh supply of nutrients to sustain the new entrained population of microalgae. This would suggest that nutrients are typically higher in the river than on the floodplain. In the tidally-driven system for this study however, nutrients were typically higher in the ponds than in the tidal creek, suggesting that nutrient cycling within the ponds was a more significant source of nutrients than the tidal creek. Detritus that falls or is brought into the ponds along with any waste from megafauna is also more likely to become trapped in the ponds as a nutrient supply as well. This is likely a highly variable and pond-specific process, as indicated by the high variability in NO_x and NH_4 in ponds during the disconnection period. Flooding events however are also important in the nutrient process, not necessarily as a supply, but to flush out waste products such as NH_4. During the connection periods, NO_x was reduced, but not as severely as NH_4, indicating that the tidal creek may be supplying some N-inorganic nutrients to the system. Also possible is that the breakdown of organic matter in the sediment during the oxygen-rich dry events creates a NO_x store that is re-suspended in the water column during flooding (Junk et al. 1989).

While the flood pulse concept is dominant in the Guadalupe Estuary ponds, there was evidence for temporal trends as well. The seven successive time periods based on hydrology gave evidence towards ecosystem movement in the benthos. Throughout the sampling period, salinity increased almost linearly, possibly due to increased evaporation during late spring through fall 2005 as temperatures increased, causing high evaporation in the shallow ponds, followed by infrequent flushing events in winter 2005 and early spring 2006. Algal biomass in the benthos also increased throughout the sampling period, though not as drastically as salinity. Two slight decreases in benthic algal biomass occurred, the first during the fall 2005 connection event when water level across the marsh was high indicating that flow may have been great enough to flush out the ponds, or that large grazers may have been able to access the ponds during this time. Small fish and invertebrates such as shrimp were seen in most ponds throughout the sampling period.

When the same seven periods were applied to the water column data, there were differences, but not according to the same organization throughout time, indicating that the benthos may have a longer biological memory in terms of algal physiology, possibly due to the more attached nature of benthic microalgae. During an extended dry event, algal biomass in the water column was extremely low and total suspended solids were high, which coincided with lower benthic algal biomass during the same period. The reduction of algal biomass in the water column at that time may be attributed to possible increased grazing of filter feeders at this time or to light limitation caused by the increase in total suspended solids.

CONCLUSION

The Guadalupe Estuary is a hydrologically dynamic system that followed the model of Junk’s (1989, 2004) flood pulse concept closer than Sommer’s (1986) PEG-model, at least at the aggregate level of algal biomass. Had algal community composition been included in the study, the PEG-model similarities may have become more apparent. There was evidence towards a mixed model however, as some seasonality to the system existed. Season seemed to have a more indirect effect on the biology of the system via changes in hydrology which acted as a more direct force on the ponds.

CHAPTER III

MICROALGAL DYNAMICS:
CHAOS AND DIVERGENCE OF NEARBY TRAJECTORIES

INTRODUCTION

Although ecosystem models such as the flood pulse concept and the PEG-model can describe general processes accurately within a system, significant variation may be seen at local levels. Indeed, processes that occur within a single pond may differ significantly from processes at a watershed level (Chase 2002).

Competitive interactions at the microalgal level are intricate and the scale at which significant differences between biotic and abiotic factors occur is usually below instrumental and analytical detection. These undetectable differences in the local system cause unpredictability, termed chaos. Even if two ponds appear exactly the same future states of the ponds may be wildly different. Virtually identical systems resulting in different endpoints due to chaos is known as divergence of nearby trajectories (Hilborn 1994).

Chaos solely involving microalgal interactions is typically described in terms of community composition, species diversity, and succession (Roelke et al. 2003; Huisman and Weissing 2001). Because differences in community composition can result in differences in community biomass, it may be possible to look for divergence of nearby trajectories using an aggregate parameter such as algal biomass (Huisman et al. 2006). Many modeling studies (Roelke et al. 2003; Huisman and Weissing, 2001) and laboratory experiments (Buyukates 2005) have been conducted to test divergence of nearby trajectories and the effects of intermediate disturbance, the mesocosym-type nature of the ponds in the Guadalupe Estuary (Fig. 1) seemed well suited to supplement these studies with in-field observation.

Shallow coastal ponds in the Guadalupe Estuary (Fig. 2) of similar size and shape within a site are expected to exhibit similar levels of nutrients and algal biomass during periods of connection to the tidal creek. Once disconnection occurs both nutrient levels and algal biomass are expected to differ significantly.

METHODS

Sample collection and analysis was as previously described. Data from each pond were averaged and graphed to show temporal and spatial patterns. In-field observation was used to determine the most likely direction of flow for marsh flooding. Together with knowledge of direct channel connections to the source body, this allowed for the establishment of a possible connectivity gradient among the ponds—i.e. some ponds may connect faster and stay connected longer than others. Due to the unpredictable and rapid nature of flood events however, the existence of this gradient is theoretical and has not yet been validated. Future studies using more detailed landscape data may unlock the flood sequence that occurs in the Guadalupe Estuary.

Nonmetric multidimensional scaling (NMS) was used to determine statistical significance among hydrologic and geospatial parameters (PCORD). Benthic data was processed separately from water column data. Benthic data consisted of mean benthic chlorophyll-*a*, mean benthic organic matter, and salinity, with the assumption that salinity of the overlying water column was not significantly different from the pore water salinity. Water column data included mean water column chlorophyll-*a*, mean total suspended solids, combined nitrate/nitrite, ammonia, phosphate, and salinity data. Means were used for chlorophyll-*a*, sediment organic matter, and total suspended solids due to the high volume of samples taken, as well as the need for a complete (no spaces) data set to run NMS. NMS was run at least ten times for each data set and the solution with the least amount of stress was chosen for further analysis (Table 3). NMS scores were classified and graphed by connection to tidal creek (connected/disconnected), time since dry (dry, dry previous month, 1-2 months since dry, 3-4 months since dry), direct physical connection to tidal creek (channel/no channel), pond size by surface area ($SA \geq m\ m^2/SA < 630\ m^2$, where $630\ m^2$ was the median surface area), and pond depth ($D \geq 0.17\ m/D < 0.17\ m$). Graphs were analyzed for clustering and patterns.

RESULTS

Boat Ramp

Of the three sites, Boat Ramp (BR) seemed to offer the greatest spatial diversity while maintaining a sense of balance and control as all of the ponds were clustered together and their shapes relatively simple (Fig. 2). The two largest ponds, BI and BII were similar in size and shape, as were the two smallest ponds BIII and BIV. The difference between BI and BII however, seemed primarily to be connectivity. BI had a direct connection to the inland bay to the west via several channels; while BII most likely connects only during flooding events where water from the inland bay floods the marsh. While BIII and BIV lie within the same N-S plane, BIV may be more connected as the area to the north is slightly lower and marshier than the area to the south (personal observation). BV stands alone as a medium-sized pond, farthest from the perceived source of floodwater in the marsh.

In terms of benthic algal biomass (Fig. 17A), BI seemed to consistently exhibit higher values than the other four ponds. Ponds BII, BIII, and BV had similar algal biomass values and trends while values for BIV fell in between those of BV and the other ponds. Water column algal biomass (Fig. 18A) showed a similar trend between all five ponds at BR fairly close in magnitude, especially between ponds BII, BIII, and BV. The same was true for NO_x values, as well as NH_4 values (Fig. 19). In the case of BI however, NH_4 values were extremely high throughout the sampling period. This may be attributed to the use of BI by large fish and wading birds. Whereas BI and BIV typically exhibited higher N-nutrient values, PO_4 values for ponds BII, BV, and BIII were higher and BIV and BV lower, almost an inversion of the N-nutrient graphs, so to speak. AFDW and TSS values for all three ponds were very similar in both trends and values (Fig. 20A, 21A).

Pump Canal

The ponds at PC are in two distinct clusters separated by a tidal creek (Fig. 2). Although the ponds are not as tightly clustered as the ponds at the Boat Ramp site, they all exhibited a moderate to high degree of connectivity due to their proximity to the tidal creek, which is believed to be the primary source of inflow. The three ponds located west of the tidal creek—PI, PII and PIII—were generally larger and had a more complex shape than the two ponds located east of the tidal creek—PIV and PV.

Ponds PI, PII, and PIII showed similar trends in benthic algal biomass with PI having had the highest magnitudes and PIII the lowest (Fig. 17B). Ponds PIV and PV exhibited a slightly different trend than the ponds on the left side of the creek; however throughout the sampling period both the trend and magnitude of algal biomass were extremely similar for those two ponds. In the water column, algal biomass for the ponds at PC continued to have a similar trend although magnitude seemed to be more variable (Fig. 18B). Throughout the sampling period PIV and PV continued to show nearly identical values of algal biomass. Both N- and P- nutrient values were similar for all ponds at PC (Fig 19). All ponds also exhibited similar trends and values for TSS (Fig. 21B). However, AFDW was similar between PI and PIII and higher and more variable for PII, PIV and PV (Fig. 20B).

Sundown Bay

Three of the ponds at Sundown Bay—SI, SII and SIII—were located near the tidal creek, while two of the ponds—SIV and SV—were located a significant distance to the northeast fairly close to an inland bay (Fig. 2). Ponds SI and SII were of similar size and shape. Ponds SIII and SIV were comparable in size, however SIII had a more complex shape. Pond SV was the largest of the SB ponds.

Regardless of size and location, all ponds at SB exhibited a similar trend and magnitude of benthic algal biomass (Fig. 17C). This was true also for algal biomass in the water column (Fig. 18C). Differences between the ponds began to emerge in the N- and P-nutrients (Fig. 19). Ponds SI, SII and SIII showed the same trend in NO_x and PO_4 with SII typically having the highest inorganic nutrient values and SIII the lowest. Trends for SI and SII remained the same for NH_4, but were very low for SIII. SIV and SV always had very low inorganic nutrients throughout the sampling period. TSS trends were similar for all ponds at SB, with some variability in magnitude during August 2005 (Fig. 21C). Trends for AFDW were also similar, however SIV and SIII showed the highest magnitudes, respectively, whereas SV, SI, and SII were more similar in magnitude (Fig. 20C).

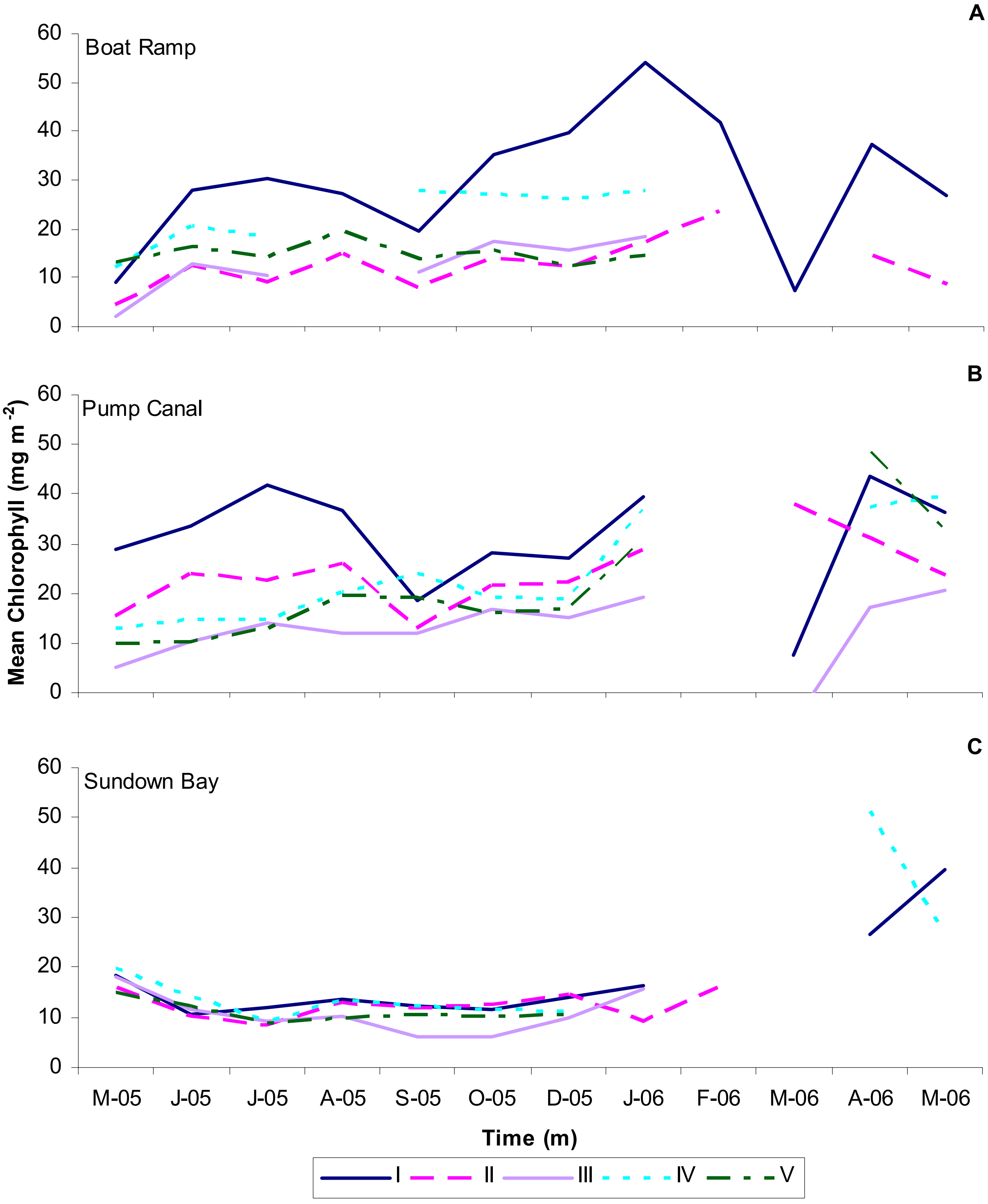

Figure 17. Mean benthic algal biomass as chlorophyll-*a* by pond. A. Boat Ramp B. Pump Canal C. Sundown Bay. Pond I (assumed to be the most connected) at each site typically exhibits the highest chlorophyll-*a*. SB is clearly different from BR and PC as it always has the lowest chlorophyll-*a* values.

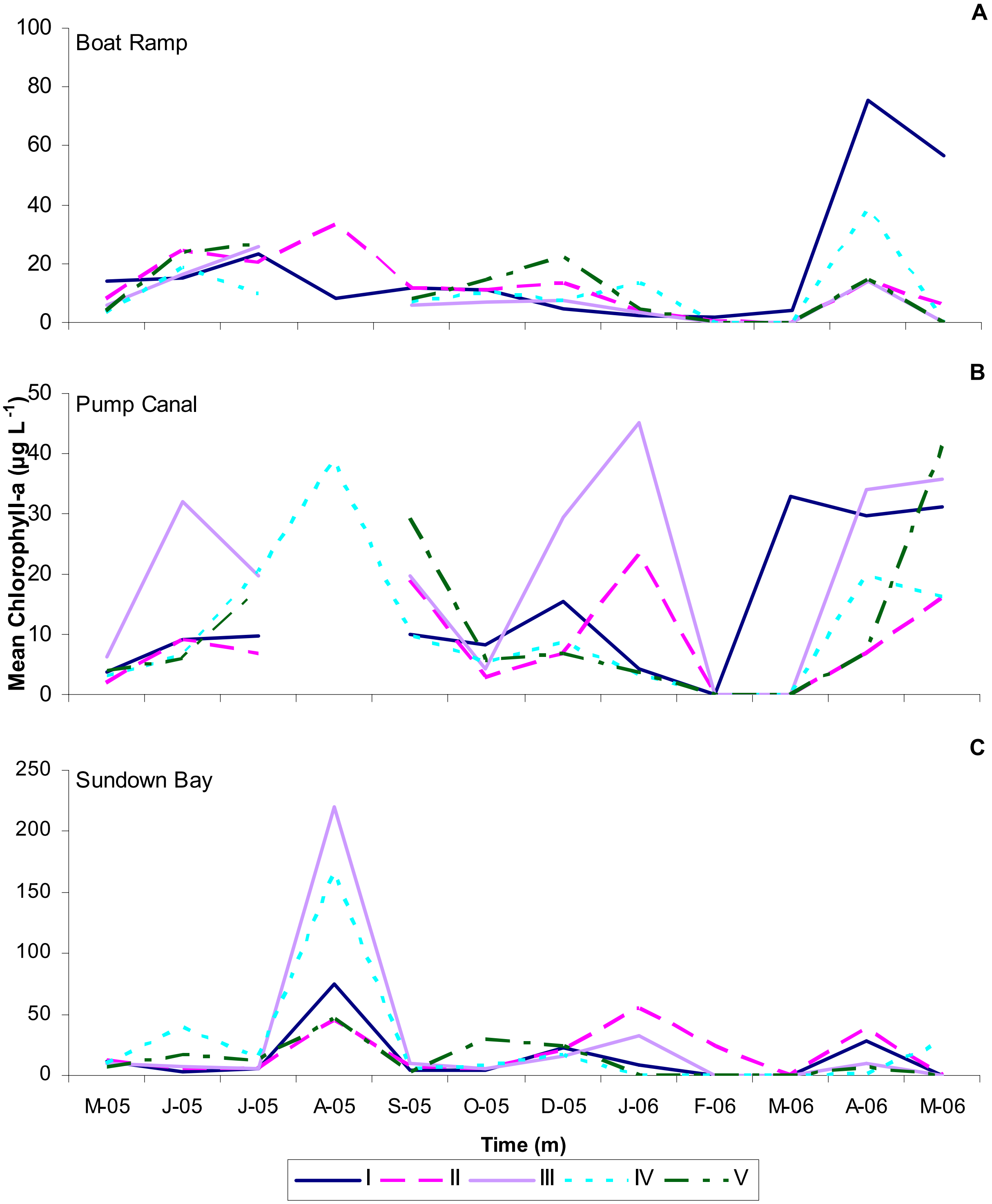

Figure 18. Mean water column algal biomass as chlorophyll-*a* by pond. A. Boat Ramp B. Pump Canal C. Sundown Bay. Please note differences in scale for each site. Chlorophyll-*a* in the water column is highly variable, especially during disconnection periods.

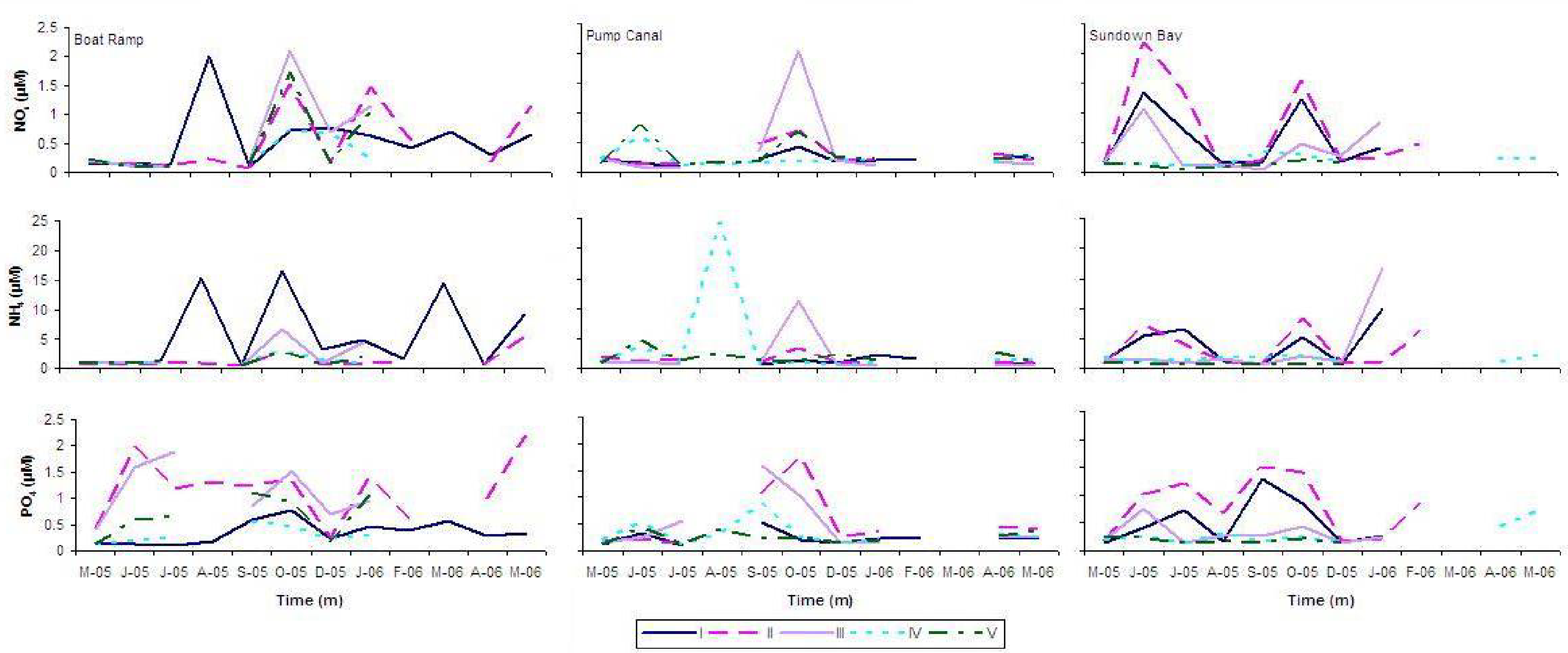

Figure 19. Nutrient (NO$_x$, NH$_4$, PO$_4$) levels of each pond. Nutrients were highly variable throughout the sampling period, but tended to return to a common value during connection events. Ponds with similar connectivity (BR I, IV; PC IV, V; SB IV, V) had consistently similar nutrient values throughout the sampling period.

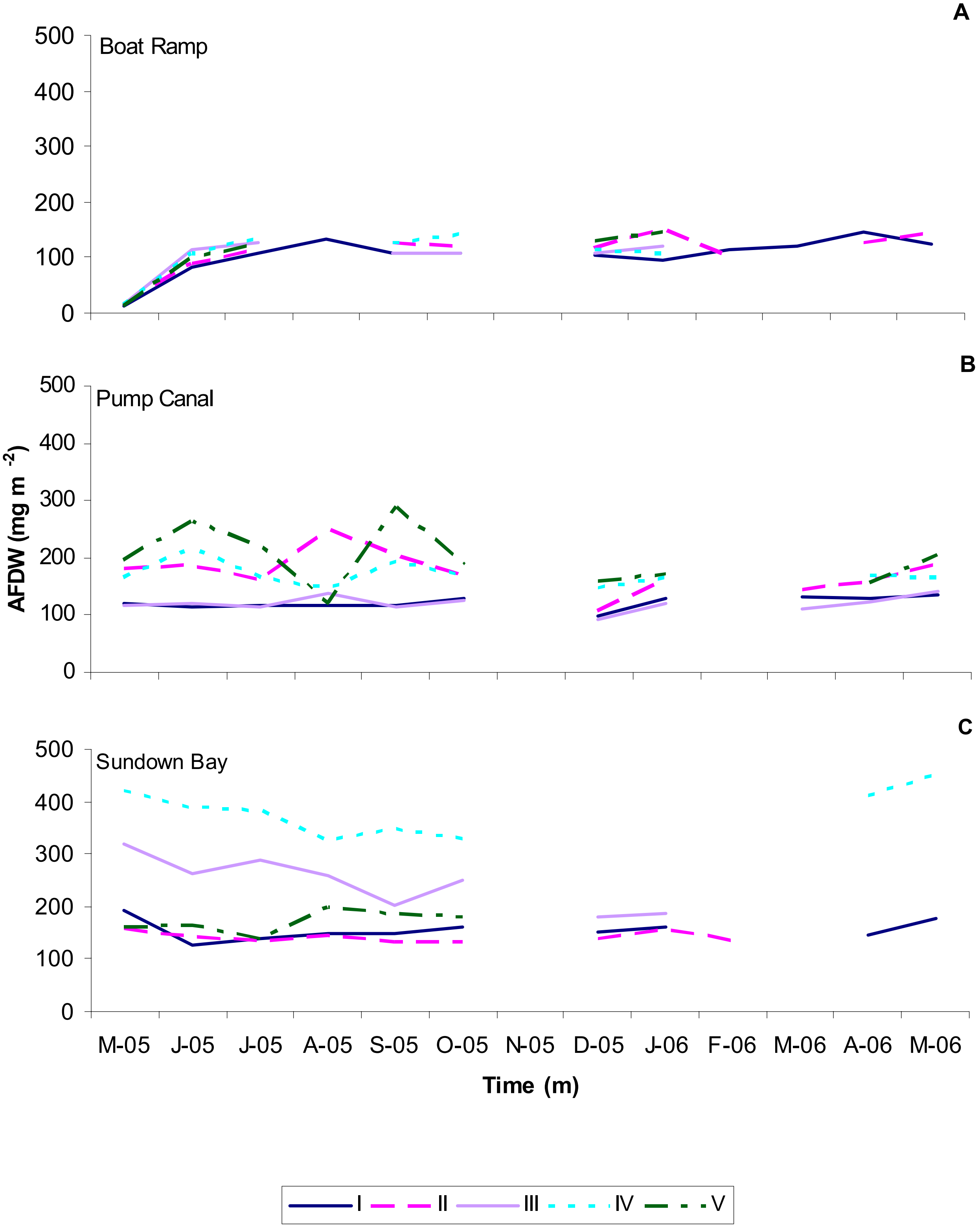

Figure 20. Mean sediment AFDW by pond. A. Boat Ramp B. Pump Canal C. Sundown Bay. Sediment AFDW remained relatively stable in each pond throughout the sampling period.

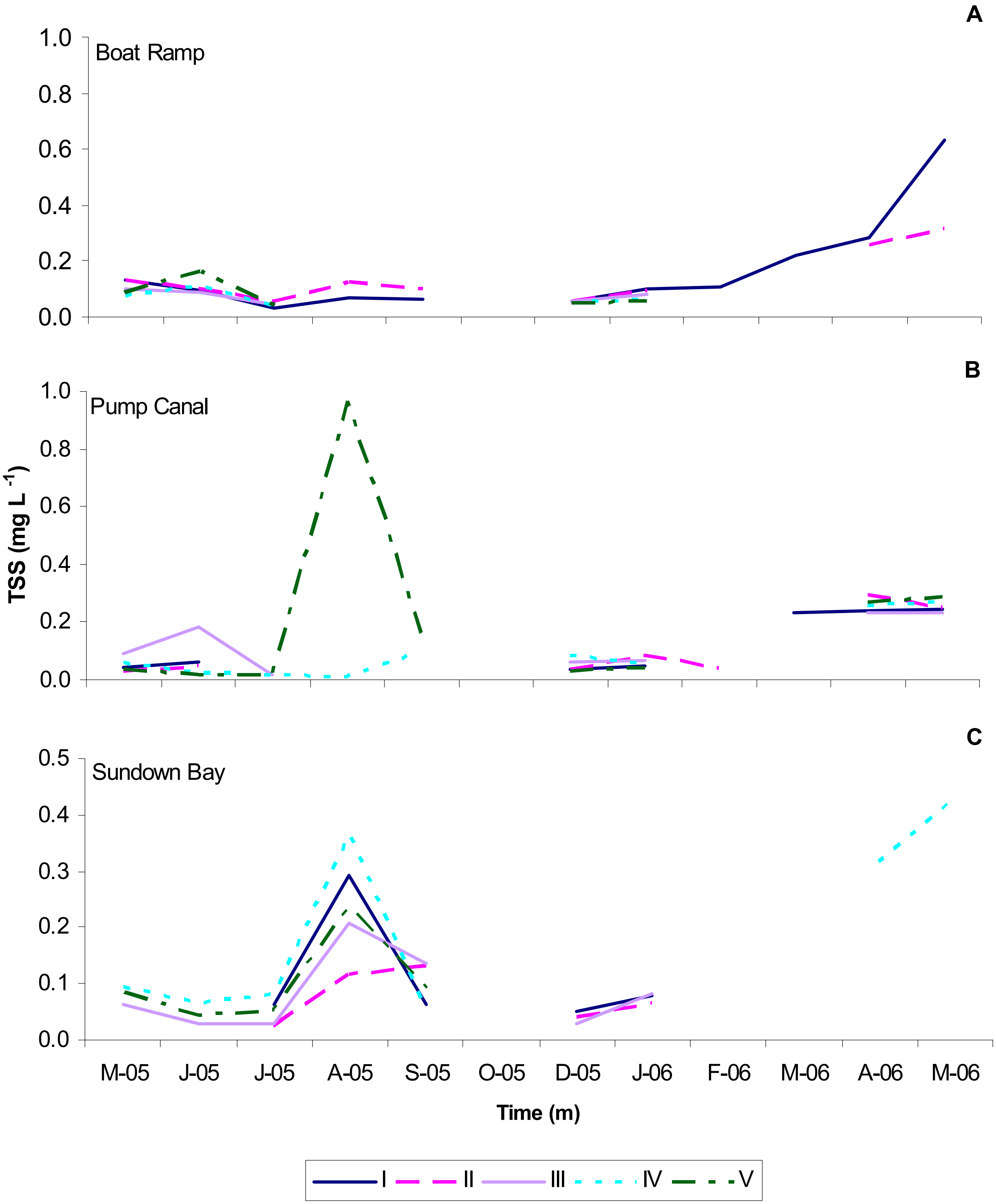

Figure 21. Mean total suspended solids by pond. A. Boat Ramp B. Pump Canal C. Sundown Bay. Please note difference in scale for SB site. TSS was typically low except during times when pond water was extremely low.

Statistical Results: Benthic Data

When NMS scores were classified by size (Table 3) according to median pond size (630 m^2), ponds smaller than the median showed a separate cluster from ponds larger than the median (Fig. 22A). Separation was along dimension 2, which corresponded with AFDW (Fig. 22B). Ponds smaller than the median pond size had higher values of sediment AFDW then larger ponds.

There was no difference between ponds that were deeper or shallower than the mean depth (0.17 m) along any NMS dimension. Neither was there any trend along a gradient of pond succession, except that which could be attributed to changes in salinity throughout the sampling period.

Statistical Results: Water Column Data

Neither size nor depth showed any difference between ponds according to NMS scores. When classified according to a pond hydrologic succession gradient however—marsh flooded, ponds full/disconnecting, ponds disconnected/drying, most ponds dry—a trend did emerge. During times when ponds were connected or recently connected, NMS scores were fairly clustered (Fig. 23A). As ponds began to disconnect and dry however, NMS scores began to spread out, indicating more variability between ponds. Algal biomass, correlated to dimension 1 (Fig. 23B) shows this trend, with variability at its lowest during marsh flooding and at its highest during dry events. NO_x and NH_4

which correspond to dimension 3 (Fig. 23C, D) also show this trend with low variability for the first two phases of hydrologic succession switching to extremely high variability during the last two phases of hydrologic succession.

Table 3. Pond surface areas and depths. Median surface area is 630 m^2 and average pond depth is 0.17 m. Asterisks (*) indicate ponds some distance from the larger group of ponds. At PC, ponds IV and V are on the opposite side of the tidal creek from I, II, and III. Ponds IV and V at SB are approximately 0.5 km NE of ponds I, II, and III.

	Pond Area (m^2)	Pond Depth (m)
Boat Ramp		
I	5956	0.18
II	5941	0.10
III	630	0.08
IV	657	0.07
V	2277	0.08
Pump Canal		
I	859	0.29
II	139	0.12
III	1299	0.28
IV*	82	0.20
V*	116	0.26
Sundown Bay		
I	171	0.28
II	542	0.25
III	138	0.17
IV*	96	0.12
V*	1038	0.13

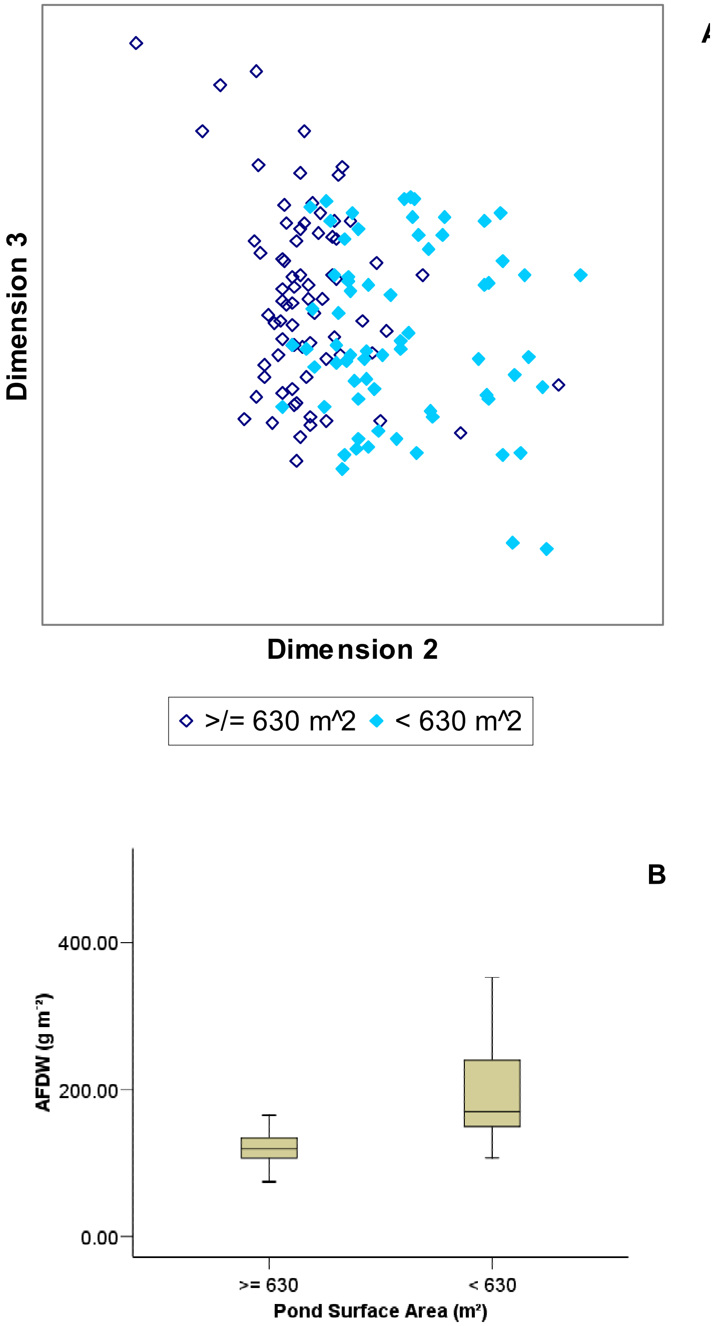

Figure 22. NMS results from 3 benthic variables (chlorophyll-*a*, ash-free dry weight, salinity) categorized by pond size (surface area; A), with associated boxplot of ash-free dry weight corresponding to NMS dimension 2 (B). Larger ponds had lower AFDW values than smaller ponds, possibly due to differences in allocthanous input and pond perimeter.

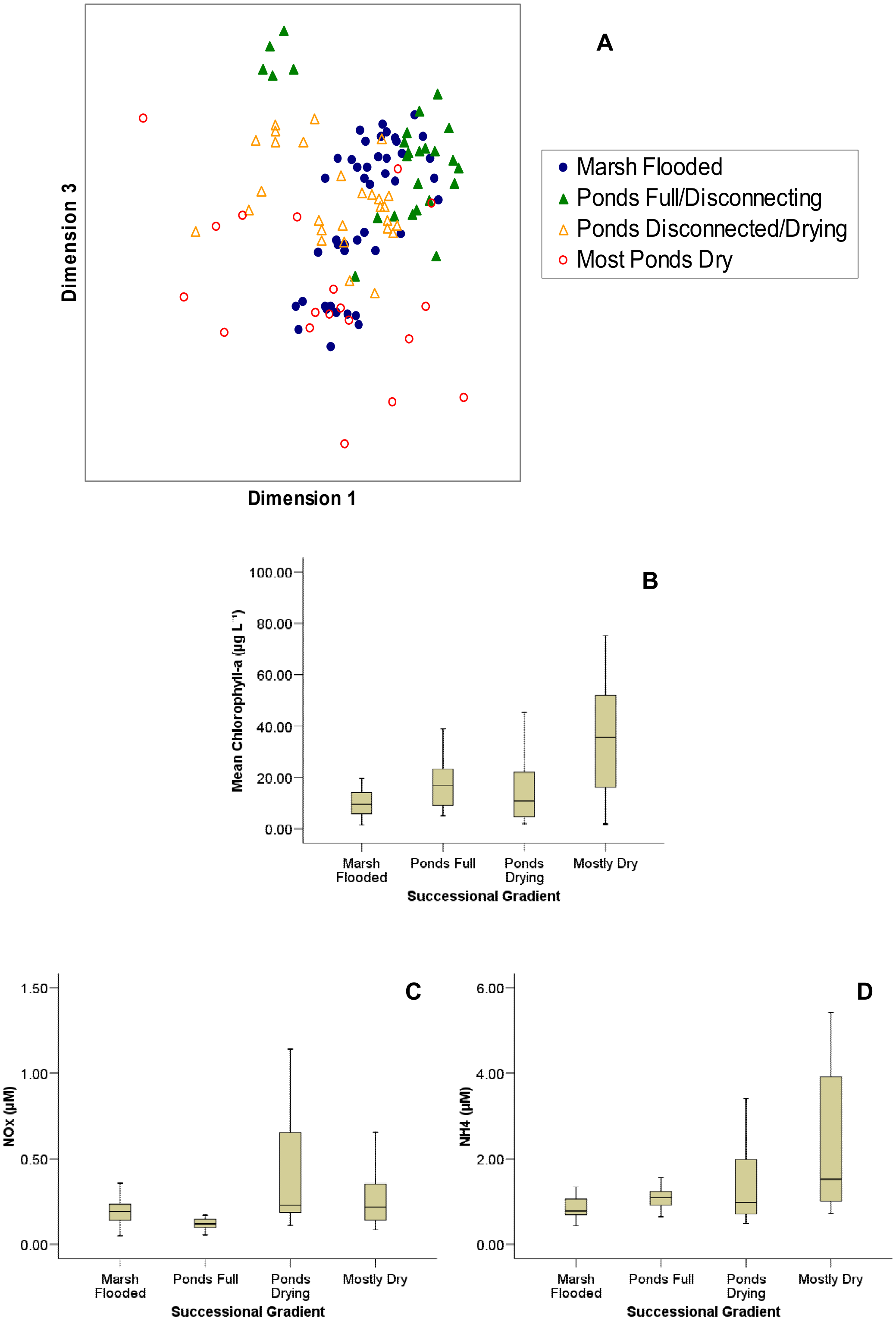

Figure 23. NMS results for water column data categorized by time since dry (A), a measure of succession time/water level gradient between extremely flooded and dry ponds. Ponds that are flooded and remain connected show tight clustering. As ponds begin to dry and disconnect, variability increases and ponds no longer cluster. Associated boxplots of chlorophyll-*a*, correlated to dimension 3 (B), NO_x (C) and NH_4 (D) correlated with dimension 1 also shown. Chlorophyll-*a*, NO_x, and NH_4 all show higher variability after ponds have been disconnected.

DISCUSSION

The purpose of this study was to use aggregate parameters in the salt marsh ponds in the Guadalupe Estuary as a mesocosym-type to find in-field evidence of divergence of nearby trajectories. Such evidence would include ponds returning to common values for algal biomass and inorganic nutrients during flooding and then showing great variability between ponds until the next flood event (Roelke et al. 2003).

Even though the ponds presented a mesocosym-type, differences in size and volume were a possible problem. In the benthos, the only difference between larger and smaller ponds was in terms of AFDW, a parameter that seems to change on a much longer timescale than the algae under consideration. This may be attributed to the larger edge-to-interior ratio that a smaller pond has, in effect concentrating any organic matter that comes into the pond from the surrounding marsh. This leaves room for further research on autochthanous vs. allocthanous carbon sources in these ponds. For the purposes of this research however, neither pond size nor pond depth appeared to have an impact on algal biomass, which changes on a timescale relevant to the theory in question.

When benthic parameters were examined however, there seemed to be little evidence for divergence of nearby trajectories. Flooding events did not "reset" completely the algal biomass of the ponds at any of the sites and NMS results were inconclusive. Considering however, that SB site had the greatest connectivity to the tidal creek and had the lowest algal biomass values with the least amount of variability between ponds at that site, it is possible that connections at SB occur too rapidly for the algae to respond, resulting in low algal biomass. PC and BR had fewer connections to the tidal creek, which may have caused the higher variability between ponds at those sites. If PC is examined more closely, the ponds on the left side of the tidal creek which experienced more of a connectivity gradient were more variable, while PIV and PV on the right side of the tidal creek were along the same plane giving them the same connectivity which may have resulted in the tighter correlation between those two ponds throughout the sampling period. Much of this however, is conjecture without knowing species composition, since changes in diversity do not always result in changes in biomass (Carpenter 1996).

It is also possible that the benthos does not quite "reset" as the water column might during flooding or drying since benthic algae are able to migrate. As long as the pond does not completely dry and flooding did not strip away the top sediments nor deposit sediment faster than the algae could migrate, this would leave a seed bank of sorts allowing benthic interactions to continue after disturbances without much interruption (Pinckney and Zingmark 1993).

Algae in the water column do not have quite the same defense against flooding and drying events and so a "resetting" of conditions would be expected. Neither size nor depth of pond appeared to have any impact on algae nor nutrients in the water column, according to NMS results. Hydrologic succession did show a trend however, with ponds exhibiting the expected similarity of initial conditions during and shortly after marsh flooding. Evidence for divergence of nearby trajectories was present as ponds began to exhibit variability in both algal biomass and N-inorganic nutrients as disconnection and drying occurred. Again however, further research including species composition is necessary to be more conclusive. Variability during disconnection and drying may be attributed to different rates of evaporation in the ponds, which could have concentrated algae more in smaller ponds than in larger ponds. Again however, pond size did not appear to have an impact on algal biomass in the water column, which seems to negate the evaporation rate hypothesis.

CHAPTER IV

CONCLUSION

While neither divergence of nearby trajectories is not clearly evident in this system given the parameters measured, the results are interesting nonetheless and underscore the importance of further research regarding this theory in this and similar systems. Gaining an understanding of the mechanisms of succession and primary production in these ponds may in turn shed light on pond usage and importance up the food chain.

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