2010-05-08

The Effect of Salinity Variability on the Mesozooplankton Community of Florida Bay

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Recommended Citation

Kelble, Christopher Richard, "The Effect of Salinity Variability on the Mesozooplankton Community of Florida Bay" (2010). *Open Access Dissertations*. 392.
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UNIVERSITY OF MIAMI

THE EFFECT OF SALINITY VARIABILITY ON THE MESOZOOPLANKTON COMMUNITY OF FLORIDA BAY

By

Christopher R. Kelble

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

May 2010

UNIVERSITY OF MIAMI

A dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

THE EFFECT OF SALINITY VARIABILITY ON THE MESOZOOPLANKTON COMMUNITY OF FLORIDA BAY

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KELBLE, CHRISTOPHER R. (Ph.D., Marine Biology & Fisheries)
The Effect of Salinity Variability on the (May 2010)
Mesozooplankton Community of Florida Bay.

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professors Gary L. Hitchcock and Peter B. Ortner.
No. of pages in text. (174)

The greater Everglades ecosystem, including Florida Bay, has undergone significant anthropogenic manipulation over the past century. These actions resulted in a series of ecologically undesirable events in the Everglades ecosystem, prompting passage of the Comprehensive Everglades Restoration Plan (CERP). It is necessary to understand the variability in, and relationship between, salinity and ecology to fully evaluate the potential effects of CERP on Florida Bay. A seven-year dataset on surface salinity along with eleven-year and eight-year datasets on mesozooplankton and planktivorous fish were analyzed. Overall, mean Bay-wide salinity varied from a low of 24.2 just after the passing of Hurricane Irene in October 1999 to a high of 41.8 near the end of a drought period in July 2001. Bay-wide mean salinity exhibited dramatic decreases, up to 0.5 per day, whereas increases in bay-wide salinity were slower, with a maximum rate of 0.1 per day. Meteorological phenomena, such as tropical cyclones and ENSO, dramatically altered the salinity patterns of Florida Bay on interannual time scales. There was a large degree of spatial heterogeneity in salinity between sub-regions of Florida Bay due to differing freshwater sources and geomorphology. Mesozooplankton abundance displayed interannual variability and a positive correlation with salinity. Both of these features were also closely correlated with abundance of the dominant planktivorous fish, *Anchoa* *mitchilli*, indicating the importance of top-down control. The hypersaline periods appear to provide a refuge from predators, allowing mesozooplankton to increase in abundance during periods of increased physiological stress. The interaction between mesozooplankton and *A. mitchilli*, along with its correlation to salinity, was further investigated through the development of a mechanistic model of the populations in Florida Bay. The model indicated predation alone was insufficient to control mesozooplankton populations; rather, it was necessary to incorporate density-dependence utilizing a logistic prey population. With both mechanisms the model was able to replicate the observed interannual variability pattern and positive correlation between mesozooplankton and salinity. A preliminary management scenario evaluation suggests a two to six-fold difference in *A. mitchilli* and mesozooplankton populations between targeted and general salinity reductions. This suggests alternative freshwater management scenarios could produce drastically different ecological consequences.

ACKNOWLEDGEMENTS

This dissertation was by no means a singular work and was only possible through the help of my family, advisors and colleagues. My wife, Amy Kelble, supported me through the many long hours required to produce this dissertation while still maintaining my position at the Cooperative Institute for Marine and Atmospheric Studies. She was always patient and loving, while providing unwavering support and encouragement. My daughter, Calla Naomi was born halfway through my degree and in many respects provided the greatest motivation for me to finish this degree. Calla allowed me to escape from the rigors of school and work for a few hours each day.

This dissertation and my scientific career would not have been possible without my co-advisors, Drs. Gary L. Hitchcock and Peter B. Ortner. Gary gave me the opportunity to work in his lab as an undergraduate developing instrumentation. Then, Gary convinced Peter to give an inexperienced and, at that time, young scientist a job running nutrient analyses. Peter provided the professional support and guidance to allow me to evolve from a technician conducting nutrient analyses to the field supervisor of the South Florida Ecosystem Research Program and finally into a Principal Investigator supervising several projects. Peter and Gary were always willing to impart wisdom and knowledge whenever it was needed and provided the strong scientific guidance necessary for me to successfully earn both my M.S. and Ph.D. degrees. I consider both to be great mentors and great friends.

I am indebted to my other committee members, Drs. Joseph N. Boyer, Donald L. DeAngelis and Michael J. Dagg. Joe was always unwavering in his support and captivating in our discussions regarding the ecology of Florida Bay. He along with Gary and Peter provided a support system I could call on at any time to discuss a scientific challenge or problem. Don was unbelievably helpful in the development of the bay anchovy-mesozooplankton model and provided the knowledge to place my research in the context of larger ecological theories. Mike taught me a great deal regarding zooplankton dynamics and always provided thought-provoking comments and questions that improved this dissertation significantly.

Last but by no means least; I am thankful for the support of my parents, Richard and Elizabeth Kelble. I first told them I was going to be a marine biologist when I was 10-years old and did not waver from this desire over the next 22-years. They remained ever supportive even when this goal was the daydream of a child and the mere hope of a teenager. I can only hope to be as good of a parent to my children as they have been to me.

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CHAPTER 1

INTRODUCTION

Motivation

The Greater Everglades ecosystem, which includes Florida Bay has been significantly altered over the past century as the human population in adjacent areas has exponentially increased. Florida Bay forms a vital link in the hydrology of south Florida. The Bay receives water from the Everglades and exchanges with the Florida Keys coastal waters (Smith 1998). The first anthropogenic activity believed to have significantly affected Florida Bay was the construction of the overseas railway in 1912. Numerous fill islands were created during the construction process along the southeast edge of Florida Bay. These islands restrict exchange between Florida Bay and Atlantic coastal waters, an result in increased residence times within the Bay; this change is hypothesized to have resulted in increased occurrence and intensity of hypersalinity (Swart et al. 1996). However, the dominant anthropogenic activity was likely Everglades land reclamation, which drained large portions of the Everglades to create land suitable for human habitation and agriculture. This process was accomplished by the construction of an extensive system of canals throughout South Florida that diverts the historic sheet-flow to canals that discharge into the adjacent coastal ocean. The diversion of freshwater has lowered water level 2 to 4-fold in the Everglades, and resulted in a 2.5 to 4-fold decrease in the amount of freshwater runoff reaching Florida Bay from the Everglades ecosystem (Marshall et al. 2009).

These changes to the hydrology of South Florida began a cascade of negative environmental events throughout the Everglades ecosystem. The first that garnered significant attention in Florida Bay was a mass seagrass die-off which began in 1987 (Zieman et al. 1988). The seagrass die-off was succeeded by several other events that indicated a decline in environmental health, including a persistent (six year) cyanobacterial bloom and sponge die-off (Butler et al. 1995). The ecological degradation in Florida Bay, along with numerous other detrimental changes throughout the Everglades ecosystem, motivated the State of Florida legislature and U.S. Congress to pass the Comprehensive Everglades Restoration Plan (CERP) (WRDA 2000, FFA 2000). The primary goal of CERP is to restore the quality, quantity, timing, and distribution of freshwater flow through the Everglades in order to recreate a sustainable ecosystem. Concurrently, CERP must permit continued human development within the presently-utilized areas. If CERP is successful at restoring freshwater flow, it will alter the distribution of salinity in Florida Bay.

This likelihood of significant future changes in the salinity field of Florida Bay underscores the importance of understanding the dynamics of salinity variability prior to the implementation of CERP. Moreover, as in most estuarine systems, salinity variability is among the most significant environmental parameters that affect Bay organisms through either direct (e.g. physiological tolerances) or indirect (e.g. by affecting prey or competitor populations) effects. This dissertation (1) investigates salinity variability in Florida Bay and identifies its underlying causes, (2) determines the relationship between observed mesozooplankton community composition and observed salinity distribution, and (3) uses a model to investigate how the key trophic interaction between mesozooplankton and *Anchoa mitchilli* could vary under different salinity conditions.

Study Site

Florida Bay is a shallow marine embayment located at the southern tip of the Florida Peninsula. It is triangular in shape and borders the Florida Keys on the southeast, the Everglades to the north and, along its western border, is an open boundary that freely exchanges with the southwest Florida shelf (Fig. 1.1). Florida Bay is a seasonally hypersaline estuary, in that the net freshwater supply per annum (calculated as precipitation plus runoff minus evaporation) is near zero. It is located in a sub-tropical area with a typical wet/dry seasonal cycle (Nuttle et al. 2000). This seasonal cycle, combined with the complex geomorphology of the Bay and near zero net freshwater supply, produces wide temporal and spatial salinity fluctuations in the Bay (Kelble et al. 2007).

The extensive system of shallow mud-banks in Florida Bay (Fig. 1.1) restrict flow and isolates sub-regions, some of which have residence times on the order of 6-months (Lee et al. 2006). This isolation creates a large degree of spatial heterogeneity in Florida Bay for many variables, including freshwater supply (Nuttle et al. 2000), light attenuation (Kelble et al. 2005), phytoplankton (Phlips & Badylak 1996), small fish (Thayer et al. 1999), and water quality (Boyer et al. 1997). It is possible to utilize the isolation of sub-regions in Florida Bay to conduct comparative studies to better understand the factors that influence the different sub-regions of Florida Bay.

Rationale

A positive result of the detrimental ecological events that began in 1987 was the initiation of monitoring programs and intensive ecological studies of Florida Bay. These studies have quantified the dynamics and distribution of many individual components of the Bay ecosystem, including nutrients (Boyer et al. 1999), phytoplankton (Phlips & Badylak 1996), seagrass (Zieman et al. 1999), shrimp (Browder et al. 2002), and fish (Thayer et al. 1999). Many of these studies have examined how the distribution and dynamics of different variables change throughout the year, often in parallel with salinity. Salinity is often selected as the primary independent abiotic variable since fluctuations in salinity are greater than temperature. In fact, hyper- and hyposalinity conditions are often observed simultaneously in different regions of the Bay and salinity fluctuates by more than 10 per annum (Fig. 1.2). This dissertation presents the first study of observed high-resolution spatial salinity fields in Florida Bay in order to evaluate the effects of freshwater sources in each of the four sub-regions. Different freshwater sources likely have different characteristic water quality attributes (e.g. nutrient distributions, Dissolved Organic Matter (DOM), total suspended solids, etc.), which further complicate relationships between organisms or processes and salinity.

Despite these monitoring studies, a significant gap has remained in our understanding of zooplankton dynamics in Florida Bay. These organisms form a vital trophic link that transfers energy from pelagic primary producers and microzooplankton to higher trophic levels, including the larvae of many commercial or recreational fishery species (Wiebe et al. 2000). Thus, zooplankton have the potential to significantly affect the extent and duration of phytoplankton blooms via grazing (Dagg 1995) and possibly the distribution and abundance of their predators that include larval, juvenile, and small adult fish (Dagg & Govoni 1996). It has been hypothesized, based on the changes in the abundance and distribution of larval, juvenile, and small adult fish species, that there has been a regime shift in Florida Bay associated with the mass seagrass die-off. The die-off resulted in a shift in the trophic web from benthic to pelagic dominance (Thayer et al. 1999). More recent investigations have not clearly confirmed that this shift actually occurred (Chasar et al. 2005). However, none of the studies have investigated all of the trophic components and energy pathways in the Bay.

Objectives

This dissertation focuses on understanding salinity, mesozooplankton and *A. mitchilli* dynamics in Florida Bay. In chapter 2 “Salinity patterns of Florida Bay”, a seven-year dataset of high-resolution salinity surveys is analyzed with a box-model to determine the mechanisms that drive salinity variability in Florida Bay. The relative contribution of runoff, precipitation and evaporation to net freshwater supply was quantified. The effect of meteorological events, such as El Niño and tropical cyclones, on salinity patterns in Florida Bay was investigated. Distinctions between sub-regional salinity patterns were investigated due to the known spatial differences in runoff to Florida Bay. The observational data were further examined in conjunction with a box model to quantify the effect of these phenomena and identify the underlying causes and mechanisms of atypical salinity distributions.

Chapter 3 “Temporal and spatial variability of mesozooplankton in a shallow sub-tropical bay: Influence of top-down control” analyzes an 11-year dataset of mesozooplankton in Florida Bay. This chapter describes the typical abundances and distributions of mesozooplankton in the Bay and examines spatial differences as well as commonalities. The temporal distribution was examined to determine if external meteorological phenomena, which alter salinity patterns (chapter 2), also alter mesozooplankton distributions. The mesozooplankton dataset was analyzed with a complementary dataset of environmental variables to determine which of the environmental parameters are closely correlated with mesozooplankton. The specific correlations between mesozooplankton and salinity were further examined to gain insight as to how CERP may alter mesozooplankton distributions in Florida Bay. In addition to environmental variables, a contemporaneous dataset for *A. mitchilli* is considered to investigate the potential effects of top-down control on mesozooplankton populations.

Chapter 4 “Modeling bay anchovy, *Anchoa mitchilli*, predation on mesozooplankton communities in sub-tropical embayments” develops a mechanistic model that examines the impact of top-down controls on mesozooplankton in Florida Bay. The model was first run without density-dependence to determine if predation alone is sufficient to control mesozooplankton populations. The model was then run without predation to evaluate the contribution of predation to the observed pattern of mesozooplankton interannual variability. Last, the model was run without salinity variability (and with the salinity index removed from the mesozooplankton module) to gain insight into the mechanism(s) governing the correlation between mesozooplankton and salinity.

Chapter 5 synthesizes these results and evaluates the potential impact of two freshwater management alternatives for CERP. The two alternatives are (1) an increase in freshwater runoff at the end of the dry-season to specifically mitigate hypersalinity and (2) an increase in freshwater discharge throughout the year. The results of the model scenarios are then compared to determine the relative influence of each of the alternatives on *A. mitchilli* and mesozooplankton populations in Florida Bay. Finally, the possible linkages between mesozooplankton and *A. mitchilli*, and their impact on the Florida Bay ecosystem are considered.

Significance

CERP aims to restore the quantity, quality, timing, and distribution of freshwater flow in the greater Everglades Ecosystem. If it is successful, it will likely alter the salinity distribution in Florida Bay and possibly the water quality regimes. These changes will differ significantly in the distinct sub-regions of the Bay. Furthermore, the combination of the analysis in this dissertation with analysis of the inner-basin circulation within Florida Bay has resulted in a recommendation to mitigate hypersalinity in north-central Florida Bay (Lee et al. 2008).

The long-term study of mesozooplankton in Florida Bay is a significant contribution to our understanding of mesozooplankton communities in coastal ecosystems. There are relatively few long-term studies of mesozooplankton assemblages in coastal regions with simultaneous measurements of the parameters affecting their abundance and distribution. Long-term open ocean studies have observed significant fluctuations in zooplankton assemblages on inter-annual time scales that are related to climate-scale phenomena (Beaugrand & Reid 2003, Piontkovski et al. 2006). Conversely, the few extant long-term studies in coastal embayments tend to focus directly on the effects of water quality variables, or water source, on zooplankton community composition. Few have examined the role of larger scale phenomena (Kimmel & Roman 2004, David et al. 2005). This study has not only investigated the influence of climactic forcing and freshwater runoff, but also the influence of trophic forcing through an analysis of the mesozooplankton data with a contemporaneous study of planktivorous fish. This study further compared coastal embayment mesozooplankton assemblages to an extensive suite of synoptically measured environmental variables over time and space scales that are sufficient to investigate the effects of salinity, water quality, predation and climactic phenomena on these assemblages.

Quantification of salinity effects on the pre-CERP mesozooplankton and *A. mitchilli* communities provides a baseline against which it is possible to detect changes and make predictions on the potential effects of CERP (if any) upon this key trophic interaction in Florida Bay. Mesozooplankton and *A. mitchilli* both have been shown to be vital links in the structure and function of the trophic web in other coastal marine ecosystems (Baird & Ulanowicz 1989, Wiebe et al. 2000). Changes in mesozooplankton can equate to changes in grazing pressure on phytoplankton and microzooplankton. If mesozooplankton grazing is a significant fraction of total phytoplankton senescence, changes in mesozooplankton could equate to changes in phytoplankton bloom dynamics. Phytoplankton blooms are an undesirable phenomenon in Florida Bay that must be monitored and understood to ensure they are not exacerbated by CERP activities (Butler et al. 1995, Phlips et al. 1999, Boyer et al. 2009). *A. mitchilli* may occupy a key trophic niche and function as wasp-waist species in Florida Bay, as variability in their population propagates up the trophic chain to alter populations of commercially- and recreationallyimportant fishery species (Bakun 1996, Verity & Smetacek 1996). Therefore, improved understanding of the factors that control mesozooplankton and *A. mitchilli* populations and the development of a mechanistic model of these populations, not only provide insight into the mechanisms that govern their interaction, but also provide an important assessment tool for CERP. CERP management requires that the ecological benefit of a proposed project be quantified prior to approving the project for implementation (USACoE 1999) and predictive ecological models are the only means to accomplish this goal.

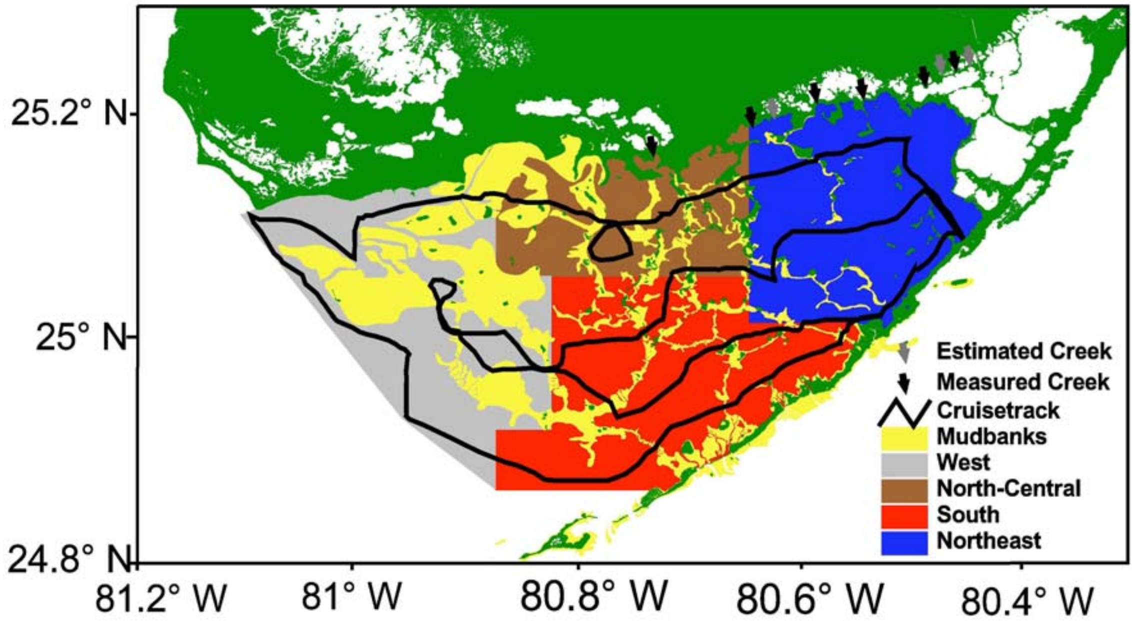

Figure 1.1 Map of Florida Bay displaying the breakdown of the four sub-regions, shallow mud-banks, locations of direct freshwater runoff, and the typical cruise track that is sampled by the flow-through system.

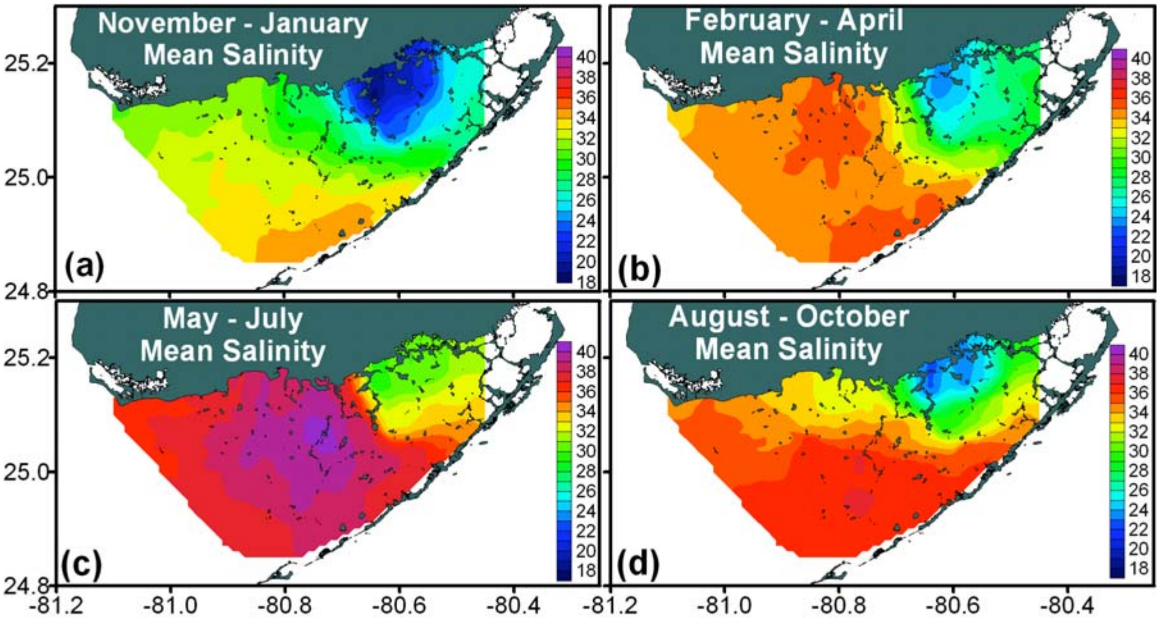

Figure 1.2 Contour maps of the mean seasonal salinity distributions in Florida Bay depict the wide variability both temporally and spatially in salinity.

CHAPTER 2

SALINITY PATTERNS OF FLORIDA BAY

Summary

The salinity of Florida Bay has undergone dramatic changes over the past century. Salinity values reached their most extreme, up to 70, in the late 1980's, concurrent with ecological changes in Florida Bay including a mass seagrass die-off. In this study, surface salinity was measured at approximately monthly intervals between 1998 and 2004. The seven-year data set was analyzed to quantify the effects of precipitation, runoff, evaporation, and climatic variability on salinity in Florida Bay. Overall mean Bay-wide salinity varied from a low of 24.2 just after the passing of Hurricane Irene in October 1999 to a high of 41.8 near the end of a drought period in July 2001. Bay-wide mean salinity exhibited dramatic decreases, up to 0.5 per day, whereas increases were slower, with a maximum rate of -0.1 per day. The freshwater budget for Florida Bay was slightly negative on an annual basis with significant positive monthly values observed during the peak of the rainy season (August through October) and significant negative monthly values observed during the peak of the dry season (March through May). This resulted in a minimum mean monthly Bay-wide salinity in January and a maximum monthly mean in July. Mean salinity for the overall Bay and for each of its four sub-regions could be predicted with reasonable accuracy utilizing a mass balance box model. There was no monotonic trend in salinity over this seven-year study; however, meteorological phenomena, such as tropical cyclones and El Niño-Southern Oscillation, dramatically altered the salinity patterns of Florida Bay on interannual time scales.

Background

Florida Bay is a triangular shaped shallow marine embayment located in a subtropical region. Morphologically, the Bay is dominated by an extensive system of shallow mud-banks and adjacent basins of relatively shallow depths (Fig. 2.1). This mud-bank/shallow basin system results in a mean water depth of 1.4 meters with long residence times for the basins (over 6 months in the north-central Bay) (Lee et al. 2006). Florida Bay is bound to the north by the Everglades and receives freshwater input via several streams, nearly all located in the northeastern corner of Florida Bay (McIvor et al. 1994). To the west is a relatively open connection with the southwest Florida shelf, through which a large amount of physical forcing (e.g. wind and tidal) exchanges into Florida Bay (Wang et al. 1994). To the south, Florida Bay is bound by the Florida Keys; however, there is a limited exchange with the coastal Atlantic Ocean through tidal channels between the Keys (Smith 1998).

Florida Bay is a unique ecosystem that has undergone numerous changes over the past century due to upstream water management and land use changes. The first such activity that may have had an influence on circulation and therefore salinity in Florida Bay was the building of spoil islands along the Florida Keys tract for the construction of the Florida Overseas Railway, 1907-1912 (Swart et al. 1996). The likely more significant activities were the upstream drainage and water management projects associated with Everglades land reclamation that began in 1952. These water management projects included the construction of a south Florida canal system, which diverted freshwater from its natural pathway directly into either the Gulf of Mexico or the Atlantic Ocean (Light & Dineen 1994). As a result, freshwater delivery was greatly reduced to downstream ecosystems including Florida Bay and the southwest Florida shelf. The exact magnitude of this reduction is not known, but it has been estimated that canal construction and subsequent water management practices, intended to control flooding and make more of the land useful for habitation or agriculture, may have resulted in a nearly 60% decrease in freshwater reaching Florida Bay (Smith et al. 1989). The shallow bathymetry of Florida Bay amplifies the effects of water management, resulting in highly variable temporal and spatial salinity distributions (Nuttle et al. 2000). In fact, it is not uncommon to simultaneously observe hypersaline and estuarine salinities within different sub-regions of Florida Bay (Nuttle et al. 2000).

The three primary sources of salinity variation in Florida Bay are precipitation and freshwater runoff (which decrease salinity) and evaporation (which increases salinity). The sum of these three components, runoff plus precipitation minus evaporation, is referred to as the net freshwater supply. There are three classifications of estuaries based upon the net freshwater supply. “Classical estuaries” have lower salinity than the adjacent coastal ocean, because the net freshwater supply is overwhelmingly positive, most often due to large quantities of runoff. “Inverse estuaries” have higher salinity than the adjacent coastal ocean as a result of overwhelmingly negative net freshwater supply. i.e. evaporation is dominant. The third type of estuary is a “seasonally hypersaline estuary” where episodic hypersalinity and estuarine conditions occur at different times of the year. In “seasonally hypersaline estuaries” the net freshwater supply fluctuates widely throughout the year, but is near zero on an annual basis. This pattern is typical of Florida Bay, where hypersaline conditions prevail during early summer at the end of the dry season and estuarine conditions prevail in early winter at the end of the wet season.

Scientific and public interest in Florida Bay accelerated in 1987, when a multi-year drought resulted in observed mid-Bay salinities as high as 70 (all salinities reported herein were measured using the Practical Salinity Scale) that were followed by deleterious changes in the ecosystem (Fourqurean & Robblee 1999, Hunt & Nuttle 2007). Beginning in 1987, Florida Bay experienced a massive seagrass die-off in the central and western sub-regions, the proximate cause of which has yet to be indisputably determined (Zieman et al. 1988, Robblee et al. 1991). The high salinity and reduced seagrass coverage coincided with a historic decline in the pink shrimp (*Farfantepenaeus duorarum*) fishery in the Dry Tortugas which use Florida Bay as a nursery (Nance 1994), and preceded a decline in water quality and a series of algal blooms (Boyer et al. 1999). Federal public trust responsibilities were implicated due to the Bay's importance as a nursery for many of the adjacent commercial and recreational fisheries (Tilmant 1989), as a primary habitat for several endangered species including the American crocodile (*Crocodylus acutus*) and Florida manatee (*Trichechus manatus latirostris*), and because the majority of the Bay is within Everglades National Park boundaries (McIvor et al. 1994). Threats to Florida Bay's ecosystem, along with growing recognition that the overall Everglades ecosystem was endangered, lead to the passage of Federal and State legislation (FFA 2000, WRDA 2000) aimed at implementing the Comprehensive Everglades Restoration Plan (CERP). CERP's primary goal is to restore the quantity, quality, timing, and distribution of freshwater flow to the Everglades and adjacent ecosystems, including Florida Bay. This will, by design, influence salinity patterns in

Florida Bay; as such, it is vital to understand the variability of salinity in Florida Bay prior to the implementation of CERP.

In this study we examine a seven-year record of salinity in Florida Bay, collected via approximately monthly survey cruises. We also analyze ancillary data related to components of the freshwater budget to quantify the effects of runoff, precipitation, and evaporation on Florida Bay salinity. Further, we examine the influence of specific large scale phenomena, such as the passage of tropical cyclones and the El Nino Southern Oscillation (ENSO). This analysis describes the principal salinity characteristics of the sub-regions in Florida Bay and the role of regional hydrology in maintaining these characteristics.

Methods

To monitor Florida Bay water quality, the National Oceanic and Atmospheric Administration's (NOAA) South Florida Program conducted a total of 76 survey cruises between January 1998 and December 2004. The surveys were nominally conducted at monthly intervals; however, the exact timing varied slightly. Surveys were carried out using the *R/V Virginia K*, a special purpose shallow draft power catamaran. The vessel's underway flow-through system incorporates a Seabird Model 21 thermosalinograph with a global positioning system (GPS) receiver (initially a JRC model DGPS200, upgraded in June 2003 to a Wide Area Augmentation System (WAAS) Garmin model 2010C GPS) to record temperature, salinity, and position at seven second intervals along the cruise track, resulting in approximately 6000 data points per survey.

For data comparison between surveys, the raw data were normalized by estimating salinity every hundredth of a decimal degree in latitude and longitude using a kriging gridding procedure (Delhomme 1978). This interpolation procedure produces a grid of equally distributed data points throughout Florida Bay (although the estimations are of course more accurate near the actual data points), minimizing biases that may occur as a result of over-sampling any one area during a particular survey.

Mean monthly precipitation values were obtained from NOAA's National Climatic Data Center (NCDC) for the three domains of Florida south of Lake Okeechobee (5, 6, and 7), from January 1997 through December 2004. These data are available via the climate visualization project (Climvis) (*http://www.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmgrg3.html*). NCDC's Division 7 consists of Flamingo and the Florida Keys; thus, mean monthly precipitation values recorded for Division 7 were used as the measurements of direct precipitation, and were assumed for our purposes to be randomly distributed with respect to Florida Bay.

The runoff data for six estuarine creeks (McCormick Creek, Taylor River, Mud Creek, Trout Creek, Stillwater Creek, and West Highway Creek) that discharge freshwater directly into Florida Bay were obtained from the United States Geological Survey (USGS). The discharge values at these creeks were calculated at fifteen-minute intervals using an Acoustic Doppler Velocity Meter (ADVM), which measures velocity at a single point in the creeks. These velocity measurements were calibrated to produce discharge measurements for each creek using 24 hour shipboard acoustic Doppler current profiler (ADCP) transects along the mouth of the creek following the methodology of Lee and Smith (2002). The data from West Highway Creek were also used to estimate freshwater discharge from three other creeks in the area (East Creek, East Highway Creek, and Oregon Creek), according to a relationship previously reported (Hittle and Zucker 2004). The sum of these nine creeks is thought to approximate total freshwater runoff into Florida Bay, except during exceptional precipitation events when runoff may occur through the Buttonwood Embankment, located along the northern shore to the west of the creeks. Runoff values in m^3 s^{-1} were transformed to cm per month to bring runoff into agreement with the precipitation and evaporation data units. Specifically, mean monthly runoff was multiplied by the length of the month in seconds to convert runoff to m^3 per month, which was then divided by the area of Florida Bay (2000 km^2) resulting in runoff units of cm per month.

Evaporation was also assumed to be uniform over the Bay, and was estimated from a bulk aerodynamic flux equation previously used to estimate evaporation over Florida Bay (Pond et al. 1974, Smith 2000).

$$E = \rho_a C_E V_{10} \Delta q \qquad (2.1)$$

In this equation, ρ_a is the density of air in kg m^{-3}, C_E is the non-dimensional evaporation coefficient for bulk aerodynamic fluxes which varies with wind speed and the difference between the measured and potential temperature (Smith 1988), V_{10} is the wind speed at 10 m above sea-level, and Δq is the specific humidity difference between 10 m above sea-level and the water's surface. The density of air was calculated from the pressure and virtual temperature (List 1963). The wind speed was adjusted to a 10 m height from the 7 m collection height assuming a power law profile with an exponent of 0.1 (Kourafalou et al. 1996). All of the observational data used for this calculation were collected by a National Data Buoy Center (NDBC) Coastal-Meteorological Automated Network (C-

MAN) station located in southern Florida Bay just north of Long Key (*http://www.ndbc.noaa.gov/station_page.php?station=lonf1*), except for specific humidity which was calculated from measurements collected by the National Weather Service (NWS) Marathon Airport station (*http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwDI~StnSrch~StnID~20004208*), located approximately 35 km southwest of Florida Bay.

A dynamic mass balance model was implemented for Florida Bay following an approach previously applied to other embayments (Hornberger & Spear 1980). This is an extension of the steady-state four-box model previously applied to Florida Bay by Nuttle et al. (2000). The model calculates salinity values for each of the four connected sub-regions (Fig. 2.1) at the beginning of each month, utilizing weekly time steps to reduce the possibility of numerical instabilities. The salinity values are simulated for each sub-region from the salinity at the beginning of the previous month along with precipitation, runoff, salinity at the Bay's western boundary, and evaporation in the preceding month, the area, and average depth of the sub-region, and parameters that characterize the magnitude of exchange between adjacent sub-regions and the western boundary, X1-X7 (Fig. 2.2). The model incorporates exchange with the southwest Florida shelf (X6 in Fig. 2.2). However, exchange with the Atlantic Ocean via tidal passages in the Florida Keys is ignored, because the net long term transport is out of Florida Bay and tidal exchanges affect only local salinities very near the tidal passages (Lee & Rooth 1972, Smith 1998). Salinity time series data along the western boundary with the southwest Florida shelf are from the data set described in detail elsewhere (Boyer et al. 1997, 1999). The model does not use directly measured evaporation, and instead calculates monthly evaporation based on an assumed sinusoidal seasonal distribution derived by Nuttle et al. (2000). We estimate sub-region depths from bathymetric data collected in a recent high resolution bathymetric survey (Hansen & Dewitt 2000), which covered about 80 percent of Florida Bay, and fill the gaps with older bathymetric data compiled by Nuttle et al. (2000).

The model calculates the volume-averaged salinity for each sub-region at the beginning of a month from the salinity at the beginning of the previous month and the effect of advection and dispersive exchange with adjacent sub-regions during the course of the previous month, Equation 2.

$$S^i_{j+1} = S^i_j + \frac{1}{V^i}\sum_{k(\neq i)}\left[S^k_j - S^i_j\right]X^{i,k}\Delta t - \frac{1}{V^i}\sum_{k(\neq i)} S_\Delta Q^{i,k}_j \Delta t \tag{2.2}$$

where S^k_j is the average salinity in sub-region i at the beginning of month j; V^i is the volume (assumed constant) of sub-region i; and Δt is the length of the time step, one month. The second term on the right-hand-side of Equation 2.2 calculates the effect of dispersive exchange with adjacent sub-regions and the coastal ocean, where refers to one of the calibrated exchange parameters X1-X7 (units of volume per month) that describes the exchange flux between sub-regions i and k (Fig. 2.2). The third term on the right-hand-side of Equation 2.2 calculates the effect of advection by the net flow for the month between sub-regions, where $Q^{i,k}_j$ refers to the net flow between sub-regions i and k calculated for month j. In the calculation of the advective flux, S_Δ is the salinity of the "upstream" sub-region. If $Q^{i,k}_j$ is directed out of sub-region i and into sub-region k, then $S_\Delta = S^i_j$ otherwise $S_\Delta = S^k_j$.

Net freshwater supply, i.e. the balance of precipitation plus runoff minus evaporation, influences salinity through the net flows, $Q^{i,k}_j$. The flows $Q^{i,k}_j$ are calculated at each time step by solving simultaneous equations that describe the mass balance for water in the network of sub-regions for the month (Fig. 2.2). In this implementation of the model, the volumes of the sub-regions are assumed to be constant; therefore the net flows into and out of each sub-region, including the net supply of freshwater to the sub-region, must sum to zero for each time step. If precipitation plus runoff exceed evaporation in a month, then the values of $Q_j^{i,k}$ will be positive, and their effect will be to decrease salinity, Equation 2.2. And conversely, if evaporation exceeds precipitation plus runoff, then the values of $Q_j^{i,k}$ will be negative, and their effect will be to increase salinity.

Where necessary in order to solve the equations, it is assumed that the relative magnitudes of net flows between sub-regions follow the relative magnitudes of the exchange flows including the freshwater supply. For example, in a month when the net freshwater supply to the north-central sub-region is the net flows from the north-central sub-region into each of the other sub-regions are given by

$$\begin{aligned} Q_j^{3,1} &= \frac{Q_{NET}\,X1}{X1 + X3 + X5} \\ Q_j^{3,2} &= \frac{Q_{NET}\,X3}{X1 + X3 + X5} \\ Q_j^{3,4} &= \frac{Q_{NET}\,X5}{X1 + X3 + X5} \end{aligned} \qquad (2.3)$$

Thus, the net exchange between basins is derived from the exchange between all connected basins, as well as precipitation, runoff, and evaporation. The net exchange then influences the salinity based on the salinity of the water being exchanged and the amount of net exchange relative to the sub-regions volume.

Results

Time Series

The mean Bay-wide salinity of Florida Bay for each cruise is depicted in Fig. 2.3. The most noticeable feature in this time series is the annual oscillation between high salinity in the early summer and low salinity in the early winter. The annual cycle in salinity computed from monthly averages lags the annual cycle of precipitation in south Florida depicted in Fig. 2.4a by approximately 4 months, with salinity values steadily dropping after the wet season commences (from May to November) and rising after the dry season commences (from December to April). The mean Florida Bay salinity varied from a minimum of 24.2 in November of 1999 to a maximum of 41.8 in July of 2001 and 2004 (Fig. 2.4b). The single most dramatic decrease in mean Bay-wide salinity for Florida Bay was 6.1 between two surveys taken on October 5-6, 1999 and October 18-19, 1999, representing a mean decline of nearly 0.5 per day. Increases in mean salinity were significantly more gradual than decreases ($F_{1,72}$=4.63, p=0.035, F-test of the mean daily change in salinity between surveys for which salinity increased versus those that decreased) and the most rapid salinity escalation was an increase of just 4.6 over the 35 day period from April 2, 2002 to May 7, 2002, representing a mean increase of about 0.1 per day.

The monthly means for salinity, precipitation, runoff, and evaporation were calculated and plotted to depict the typical annual cycle observed during the study period (Fig. 2.4a). The lowest monthly mean salinities occurred from October to January at the end of the rainy season or shortly thereafter, as precipitation and subsequent runoff dilute the salinity of Florida Bay (Figs. 2.3 and 2.4). The highest salinities were recorded in the beginning of the summer, May through July, just after the beginning of the rainy season which corresponds to the highest rate of evaporation (Figs. 2.3 and 2.4).

Fig. 2.4b depicts monthly means of runoff, precipitation, and evaporation for each month during the study period, together with average Bay-wide salinity values. The variability in evaporation was moderate, displaying a mean range slightly greater than a factor of two, with a maximum rate of approximately 15 cm per month during the summer and a minimum rate of approximately 6 cm per month during the winter. Precipitation was more variable; however, a wet season from May to November and a dry season from December to April were typically observed. Runoff displayed some interannual variation, but typically peaked during the last six months of each year (July to December) and fell to near zero sometime during the first six months of each year (January to June).

Contour maps of the mean seasonal salinity of Florida Bay reveal great differences in the spatial salinity pattern throughout the year (Fig. 2.5). In fact, the one constant is that the lowest salinity water was always observed in the northeast corner of the Bay. This is not surprising since direct freshwater runoff is concentrated in this sub-region, and this sub-region also is largely isolated from the Atlantic Ocean by the upper Florida Keys. During the freshest months, November to January (Fig. 2.5a), the highest salinity, although still below oceanic values, was in the southern Bay where there is no direct runoff and where there is greater exchange with the coastal Atlantic Ocean through the tidal passages of the Florida Keys (Lee and Smith 2002). The minimum salinity value of 18 is located in the northeast sub-region near the mouth of Taylor Slough, with rapidly increasing salinity (up to approximately 26) away from the northeast region towards the boundaries with the north-central and south sub-regions. Outside of the northeast sub-region, there is a general trend of gradually increasing salinity along the northeast to southwest axis of the Bay.

The mean seasonal salinity contour maps from February to April (Fig. 2.5b) and May to July (Fig. 2.5c), together with the data shown in Fig. 2.4b, indicate that there are steady salinity increases in Florida Bay from January to June. In the mean contour map for February to April the northeast corner, again, had the lowest salinity, but it has risen to approximately 23 from the previous season due to decreased precipitation and freshwater runoff (Fig. 2.4b). The maximum salinities of 36 are in the north-central and south sub-regions of Florida Bay as a result of the beginning stages of evaporative salinization. Further west, salinity decreases due to interactions along the open boundary with the southwest Florida shelf where freshwater runoff has lowered the near-shore salinity of the shelf waters, which in turn via exchange lowers the salinity along the western boundary of Florida Bay.

The highest salinities in Florida Bay occurred annually in the early summer from May through July. The mean salinity distribution during this time period is shown in Fig. 2.5c. As in the preceding months, the salinity maximum is located in the central Bay with values now reaching over 40, and gradually decreasing in a roughly radial pattern away from the maximum. Again, Florida Bay's northeast corner had the lowest mean salinity at about 26. Similar to the previous map, the west sub-region had a slightly lower salinity than the central Bay as a result of exchange with the southwest Florida shelf waters. However, the salinities in west Florida Bay were still greater than those found in the adjacent coastal ocean, due to their proximity to the salinity maximum in the north-central Bay.

In the middle of the wet season, from August through October (Fig. 2.5d), salinity throughout Florida Bay shows an overall decrease. The highest salinities, approximately 38, are located in the south-central Bay. The north-central Bay shows a dramatic drop in salinity from greater than 40 down to 32, while in the northeast Bay salinities were reduced to 24 and in the west salinity values show a slight decrease from those in the nearby north-central sub-region.

Regional Partitioning

All of the seasonal plots of Florida Bay salinity display a high degree of spatial heterogeneity among the four sub-regions of Fig. 2.1, indicating differing degrees of influence by the various forcing factors (exchange with the Atlantic Ocean, exchange with the southwest Florida shelf, runoff, precipitation, evaporation, etc.) on salinity (Fig. 2.5). This spatial heterogeneity is likely due to the topographical separation between the basins created by the shallow mud-banks characteristic of Florida Bay (Fig. 2.1). Many other parameters previously measured in Florida Bay exhibited a similar spatial heterogeneity, including light attenuation (Kelble et al. 2005), water quality (Boyer et al. 1997), sediments (Wanless & Tagett 1989), seagrass (Zieman et al. 1989), fisheries (Tilmant 1989), and benthic mollusks (Turney & Perkins 1972). Previous work evaluating the freshwater influence in Florida Bay determined that the effect of freshwater input varied greatly among sub-regions in a similar manner as was observed in this study (Nuttle et al. 2000). Thus, it was decided to partition the Bay into four sub-regions (Fig. 2.1) roughly following the boundaries used by Nuttle et al. (2000).

Figure 2.6a shows that the time series of mean salinity for each of the four sub-regions differ markedly. The northeast sub-region, as can be inferred by the seasonal contour plots (Fig. 2.5), was nearly always the freshest sub-region of Florida Bay. However, there were several occasions when the mean salinity of the north-central Bay was slightly lower for a single survey conducted at the peak of the wet seasons of 1999, 2001, and 2003. Furthermore, the north-central sub-region exhibited the most extreme salinity variations. The most dramatic salinity reduction in north-central Florida Bay for the period of record was a drop of over 14 in the 26 days from September 22-23, 1999 to October 18-19, 1999, equivalent to a reduction of greater than 0.5 per day. The greatest rate of increase in salinity was less dramatic, with an increase in salinity of over 6 in the 29 days from May 18-19, 2004 to June 16-17, 2004 representing a mean increase of about 0.2 per day. These rates of decrease and increase in salinity in the north-central sub-region surpass those for any of the other sub-regions. The south and west sub-regions of Florida Bay displayed more moderate salinity fluctuations than the north-central sub-region and tended to have more oceanic salinities than the northeast sub-region (Fig. 2.6a). The south and west sub-regions also tended to be more similar than any other sub-region pair.

Mean monthly salinities for each sub-region are depicted in Fig. 2.6b. The northeast sub-region exhibited the lowest mean salinity every month, with the greatest contrast from the other sub-regions (greater than 5) observed during the period of increasing salinity from January to May. The difference was not as significant during the wet season, with the mean salinity for the northeast sub-region only 1.5 less than the north-central sub-region. Furthermore, the largest range in mean monthly salinity (23.3-

34.7) was observed in the northeast sub-region, although the range for the north-central sub-region was only slightly less (28.2-39.0). The north-central sub-region exhibited its lowest mean salinity in November, whereas all the other sub-regions had their lowest salinities in January. Also, the north-central sub-region featured the largest single month change in salinity for both increasing and decreasing salinity, with an increase of 3.7 from March to April and a decrease of 5.8 from September to October. The west and south sub-regions had similar mean monthly salinities, with a much smaller range than either the north-central or northeast sub-regions. The south sub-region showed the highest mean monthly salinity (39.3 in July), although it was only slightly higher than the mean monthly salinity of the north-central sub-region (39.0 in July). The slightly lower mean monthly salinity for the north-central region was largely influenced by the 2002-2003 anomalous salinity distributions attributed to El Nino, because in both years the north-central salinity was much less than the south sub-region (Fig. 2.6a). The major difference between the west and south mean monthly salinity time series shown in Fig. 2.6b is that the west sub-region maintains a lower salinity during and just after the wet season.

Mass Balance Model

Calibration of the mass balance model identifies a set of values for the model parameters that minimizes the sum of squared errors. The model parameters comprise the set of seven exchange fluxes (Fig. 2.2) and three parameters that define the variation in evaporation within a year. The errors are calculated as the difference between the salinity calculated by the model and the mean salinity values estimated from the survey data in each sub-region. The calibrated model estimates salinity quite accurately with a root mean square error (RMSE) of 2.1 for the Bay as a whole. Furthermore, the model performed reasonably well in each of the sub-regions (Fig. 2.7). The errors were slightly larger in the north-central and northeast sub-regions (RMSE 2.4 and 2.2, respectively), which also displayed larger ranges of variation in salinity (Fig. 2.6). Evaporation, estimated by model calibration, has an annual average of 134 cm per year, and the highest evaporation is estimated to occur just before the onset of the summer wet season. This is about 10 percent higher than the evaporation estimated by Nuttle et al. (2000), which was based on a steady state salinity mass balance model, but both are within the range of all previous evaporation estimates. The model estimated mean evaporation value was nearly identical to the mean annual evaporation calculated from the C-MAN station for this seven-year study period (136 cm).

The Nash-Sutcliffe model efficiency statistic provides a better measure of the model's accuracy at predicting mean salinity both Bay-wide and for each of the four sub-regions (Nash & Sutcliffe 1970). Model efficiency, *Eff,* is calculated from the mean square error normalized to the variance of the observed salinity and is similar to the coefficient of determination statistic in regression models.

$$Eff = 100 * (1 - \mathrm{MSE} / \mathrm{Var(observed)}) \qquad (2.4)$$

where MSE is the mean of the squared residual errors and Var(observed) is the variance of the observed salinity data. The calibrated mass balance model achieves a model efficiency of 86 for all four sub-regions taken together; model efficiency values for each of the sub-regions taken separately are 85, 85, 79 and 64 for the north-central, northeast, south and west sub-regions, respectively. Model efficiency for the whole Bay is higher than the average of sub-region results because the variance of the observed salinity for the entire Bay includes the effect of spatial variation between sub-regions that is not present in the variance within sub-regions.

Correlation Analyses

To attempt to understand exactly how precipitation and runoff into Florida Bay affect Bay-wide, as well as sub-regional, mean salinities we examined the Pearson correlation coefficients between precipitation, runoff, evaporation, and salinity. The correlation between monthly mean precipitation and salinity Bay-wide and for each of the four sub-regions is given in Table 2.1, with lags from zero to six months. Correlation coefficients were highest at a lag of four months for all analyses except the north-central. The four-month lag for Bay-wide salinity is clear in Fig. 2.4b, in that maximum mean monthly precipitation occurs in September and the minimum salinity is in January. The minimum mean monthly salinities were also observed in January for the northeast, south, and west sub-regions, further evidencing their four-month lag. The lone exception, the north-central sub-region, had the highest correlation coefficient for a two month lag and its minimum mean monthly salinity was observed in November, two months after the peak precipitation.

To investigate the relationship between precipitation and runoff, correlation analysis was performed between runoff into Florida Bay and precipitation over the Florida peninsula south of Lake Okeechobee (Divisions 5 and 6 from NCDC CLIMVIS) and indicated a lag time of 1 month (Table 2.2). The lag between precipitation and runoff can also be seen in Fig. 2.4b, where peak precipitation is observed in September and peak runoff one month later in October. The correlation and lag between runoff and salinity (Table 2.1) are intermediate in character with a lag between runoff and mean Bay-wide salinity of two months. All of the sub-regions displayed slightly different lagged correlations between runoff and salinity. A one-month lag was observed in the north-central sub-region, a two-month lag occurred in the northeast, in the west the lag was two to three months and in the south it was three months. These lags are partially a reflection of the mixing time it takes for runoff to decrease salinities throughout a large portion of Florida Bay, but they also may be the cumulative effect of runoff on salinity. Furthermore, the relationship between runoff and salinity is complicated by upstream water management decisions taken to avoid flooding and manage the water supply. The correlation between evaporation and salinity was similar throughout Florida Bay (Table 2.1), with no lag in any of sub-regions. Therefore, differences in evaporation rates between sub-regions, although not calculated herein, are unlikely to contribute to temporal salinity variability among sub-regions.

Net Freshwater Supply

The typical annual cycle of net freshwater supply for Florida Bay is shown in Fig. 2.8 based upon monthly means of precipitation, runoff, and evaporation. Net freshwater supply was positive toward the peak of the wet season (August to October) and significantly negative toward the end of the dry season (March to May). During the rest of the year the net freshwater supply was near zero. It is important to realize that the net freshwater supply calculated here is an underestimate, because runoff into Florida Bay has been assumed to be limited exclusively to the nine creeks quantified in this study. These nine creeks cannot be expected to contain all of the freshwater discharged into Florida Bay from the Everglades, especially during significant rain events where runoff through the Buttonwood Embankment can be significant. Moreover, fresh groundwater flux is assumed to be zero, primarily because groundwater entering Florida Bay is typically saline to hypersaline (Corbett et al. 1999).

The lag between the net freshwater supply and the wet season/dry season cycle of two to three months is the result of several factors. First, at the commencement of the rainy season in May or June, much of the potential runoff has not yet reached Florida Bay (Fig. 2.4); therefore, only direct precipitation is lowering salinity. The first rains are required to saturate the Everglades and initiate sheet-flow; accordingly, little early runoff reaches Florida Bay. Evaporation exceeds precipitation over Florida Bay while runoff is still negligible, resulting in negative net freshwater until June (Fig. 2.8). The same relationships are seen in the three month lagged correlation between gross freshwater supply (runoff plus precipitation) to Florida Bay and mean Bay-wide salinity (Table 2.1).

The dominant feature in the mean Bay-wide salinity time series (Fig. 2.3) is an annual oscillation. In general, negative net freshwater supply from March through May increases salinity while net positive freshwater supply from August to October decreases salinity (Fig. 2.4). The lowest Bay-wide salinities often occur in January (Fig. 2.4), several months after the net freshwater supply decreases to near zero. There are several underlying reasons for this lag. First, the cumulative effect of net freshwater supply only requires net freshwater supply ($Q_j^{i,k}$ in Equation 2) to be greater than zero to decrease salinity. Second, the west sub-region of Florida Bay is affected by indirect runoff which has an inherent delay, as the rivers along the southwest Florida shelf decrease near-shore salinities, which over time exchange with the western sub-region of Florida Bay, ultimately lowering its salinity. Lastly, this could result from runoff into Florida Bay being somewhat underestimated by the nine creeks we quantified, resulting in an underestimate of net freshwater supply in this study.

To examine interannual variability in net freshwater supply we calculated the budget for each year of the study period (Table 2.3, Fig. 2.9). This highlighted the large degree of variability that was measured in each of the components on an annual basis. Annual runoff varied by greater than a factor of two (10.4 cm to 25.7 cm), precipitation had slightly lower variation, and evaporation was much more stable varying over a range that was less than 17% of the mean. These variations combined to produce variations in the net freshwater supply of over 92 cm from the peak in 1999 to the minimum in 2004; however, the mean salinity remained significantly more stable varying from 31.2 to 36.3 (less than 16% of the mean). The stability in annual average Bay-wide salinity is likely due to the fact that historical conditions affect the salinity and thus a unidirectional long term trend is required to significantly alter the mean salinity value.

The observed rates of precipitation, runoff, and net freshwater supply to Florida Bay for this detailed seven-year period of study are similar to those calculated in a study summarizing freshwater influence on Florida Bay (Nuttle et al. 2000), despite the fact that the two studies employed very different methods for calculating runoff and precipitation. The precipitation values in the present study were obtained from the Climvis program at NCDC for Division 7 of Florida, which corresponds to the Florida Keys and Flamingo, whereas Nuttle et al. (2000) used longer records of precipitation from land stations calibrated against shorter records for stations in the Bay to produce estimates of precipitation directly over Florida Bay. There was a difference in mean annual precipitation of 13 cm between the two studies, from 98 cm in the prior study to

111 cm in the present study, which is within one standard deviation of the mean annual precipitation (σ =18.5). Methodologies for estimating runoff were also very different. Nuttle et al. (2000) defined runoff as the upstream monthly discharges into Taylor Slough and the C111 canal. The present study used runoff measurements made directly at the mouth of six major discharge sites into northern Florida Bay and estimated discharge at three other sites. Runoff in the present study was more than double that of the previous study, 20 cm vs. 9 cm; however, as the magnitude of overall runoff is small compared to precipitation, the effect of this difference on the overall freshwater supply to Florida Bay is relatively minor. Our study found a slightly negative mean annual net freshwater supply of -5.3 cm, though there were significant interannual differences ranging from -59.2 in 2004 to 33.1 cm in 1999 (Table 2.3). The annual net freshwater supply for this study (-5.3 cm) is similar to that calculated by Nuttle et al. 2000 (-3.0 cm) and both values are well within one standard deviation (σ=28.9) of the large interannual variation in net freshwater supply we observed. If the lower evaporation estimate calculated from the mass balance model, -134 cm per year, were used in calculating net freshwater supply, the mean net annual freshwater supply for the present study would increase to -3.5.

Discussion

<u>Spatial Salinity Distribution</u>

Salinity differences for each of the four sub-regions arise from differing influences in direct and indirect runoff and advection. The northeast had the lowest salinity throughout the study with only a few exceptions (Fig. 2.6a). This sub-region receives the vast majority of the direct freshwater runoff from the Everglades. Five of the six major runoff points into Florida Bay measured in this study were located along the northern boundary of the northeast sub-region, and these five accounted for over 94% of estimated runoff. In the beginning of the dry season, from January to May, the salinity in the northeast remained much lower then the other three sub-regions (Fig. 2.6), due to continued runoff from January through March, while very little direct precipitation occurred over Florida Bay (Fig. 2.4).

The large range in salinity observed in the northeast is the combined result of the seasonally variable direct freshwater supply with shallow bathymetry. The northeast sub-region is the second shallowest in the Bay (after the north-central sub-region). In fact, when freshwater input is minimal, evaporation can become the dominant factor, elevating the salinity dramatically due to the sub-region's shallow depth. Thus, hypersaline conditions are often observed in this sub-region during drought periods such as the summer of 2004 (Fig. 2.6a).

Salinity in the north-central sub-region varies primarily as a result of local precipitation and evaporation. The shallow depth of this sub-region enhances salinity sensitivity to the effects of these two forcing factors by simple dilution and evaporative concentration (c.f. Equation 2.2). There is minimal direct freshwater runoff into this sub-region (less than 6% of the measured total) and exchange with other sub-regions is also minimal with an approximate residence time of over 6.6 months, due to the large expanse of shallow mud-banks which surround and are contained within this sub-region (Fig. 2.1) (Lee et al. 2006). The quick responses in this sub-region's salinity time series forced primarily by local precipitation and evaporation are shown in the relatively short lagged correlations between precipitation and runoff to salinity (Table 2.1). The lag between precipitation and salinity in the north-central sub-region is only two months, roughly half the lag period observed in the other three sub-regions where salinity is more affected by direct and/or indirect runoff.

The relatively quick response of salinity in the north-central sub-region to direct precipitation was evidenced by salinity in this sub-region being as low as or lower than that observed in the northeast following large precipitation events (during three years 1999, 2001, and 2003). Additionally, for all years except 2002 and 2003, the highest annual salinities were also located in the north-central sub-region (Fig. 2.6a). The north-central sub-region exhibited the greatest rates of both salinity increase and decrease. A reduction of over 14 in 26 days coincided with the passing of Tropical Storm Harvey and Hurricane Irene near Florida Bay in September and October 1999. In contrast, a salinity increase of over 6 in 28 days was observed between May and June of 2004, due to anomalously low precipitation (only 2 cm, about 20% of the monthly mean precipitation for this period) during a period of high evaporation (Fig. 2.4).

The salinities in the south and west sub-regions of Florida Bay were typically similar to one another (Fig. 2.6) indicating that these sub-regions are subject to similar forcing and are more closely coupled by advection than the other sub-regions. Both the south and west sub-regions are affected by the nearshore waters of the southwest Florida shelf, though exchange in the south is somewhat limited by mud-banks in this region (Wang et al. 1994). These shelf waters are seasonally less saline than waters found further offshore in the Gulf of Mexico or Florida Straits due to freshwater runoff along the coast of southwest Florida. In addition to these nearshore shelf waters, the south sub-region is also influenced by exchange with the coastal waters of the Florida Keys through tidal passages (Lee & Smith 2002). The exchange with the Keys waters, which do not display the same seasonal salinity patterns as the southwest Florida shelf and are typically stable at about 36.3 (Johns et al. 2005), takes place on both tidal and long-term time scales as a result of regional wind forcing and horizontal pressure gradients. In both cases, exchange with adjacent coastal waters has a stabilizing effect upon interior Bay salinity. Therefore, both the south and west sub-regions display much smaller salinity fluctuations than observed in the northeast and north-central sub-regions. Nonetheless, the west and south sub-regions still exhibit the annual salinity oscillation typical for Florida Bay (Fig. 2.6) indicating that the annual cycle in net freshwater supply is the dominant force driving the temporal salinity distributions of both regions.

There were significant differences between the salinity of the west and south sub-regions. Most notably, the south typically had higher salinities in summer months than the west. Several factors contributed to this difference. First, as depicted in Fig. 2.1, a significant area of the south sub-region is covered by mud-banks and is on average shallower than the west sub-region, resulting in greater salinity sensitivity to evaporation. Second, exchange between the west sub-region and the southwest Florida shelf is less restricted than exchange between the south sub-region and either the southwest Florida shelf or Atlantic Ocean (Wang et al. 1994), thus salinity remains more stable in the west sub-region. Third, there is some direct connection between the north-central and south sub-regions, which allows the hypersaline waters of the north-central sub-region to exchange into the south sub-region (Lee et al. 2006). Moreover, Atlantic coastal waters off the Keys are on average more saline than southwest Florida shelf waters, because there is a large amount of freshwater runoff from rivers along the southwest Florida coast. This lower salinity water on the southwest Florida shelf then exchanges with west Florida Bay and decreases its salinity. Whereas, in the south the indirect runoff, which can come from two sources (northeast Florida Bay and the southwest Florida shelf), must first mix throughout the northeast or west sub-region and decrease its salinity before exchanging with and decreasing the salinity in the south. This is evidenced by the lagged correlation from runoff to mean salinity in the south being the longest (three months), while in the west the correlation was slightly less (two to three months) (Table 2.1). However, this last explanation assumes that runoff from rivers on the southwest Florida shelf has a similar temporal distribution to runoff directly into Florida Bay.

Salinity anomalies

There were several cases where the observed salinity values seemed anomalous, but upon closer examination were found to be in concert with meteorological events. For example, the lowest mean Bay-wide salinity observed, 24.2, was measured on November 16, 1999. Furthermore, October, November, and December of 1999 were the only months for the entire 7-year record that mean Bay-wide salinity was less than 26. The likely proximate cause of these anomalously low salinities was the passing of Hurricane Irene just to the west and north of Florida Bay on October 15, 1999 (Fig. 2.10). Precipitation was intense during this event, with a recording station in Tavernier on the eastern edge of Florida Bay reporting precipitation of 20.8 cm in one day.

This amount of precipitation had a large and immediate impact on the salinity of Florida Bay due to the Bays shallow depth. Assuming the precipitation value at Tavernier is representative of the entire Bay, and using the estimate mean water depth of 1.4 m in the Bay derived from the recent bathymetric survey (Hansen & Dewitt 2000), the quantity of direct precipitation associated with Irene equaled an astonishing 15.3% of Florida Bay's total volume. There was a regularly scheduled survey run on October 5-6, 1999, approximately 10 days before Hurricane Irene, and an additional survey was conducted on October 18-19, just a few days after Hurricane Irene, specifically to measure any hurricane related changes. The pre-Irene survey had a mean Bay-wide salinity of 30.5. Three days after Irene, the mean salinity had dropped 20% to 24.4 (Fig. 2.11). This was the most rapid Bay-wide decrease in salinity observed during our 7 yr record (nearly 0.5 per day).

Furthermore, the survey conducted just after Hurricane Irene revealed a unique spatial salinity distribution (Fig. 2.11). It was the only survey that showed direct freshwater outflow from the Everglades along the northern boundary of central and western Florida Bay. Sheetflow runoff into these areas of Florida Bay has been hypothesized to have occurred frequently prior to the drainage of the Everglades and the dramatic reduction in freshwater runoff to Florida Bay (Hunt & Nuttle 2007). It is hypothesized that only when water levels in the Shark River Slough are sufficiently high, can runoff enter central Florida Bay from the north through the Buttonwood Embankment and out of McCormick Creek. Thus, if such historical water levels were restored by CERP, runoff through these areas might occur more frequently, and perhaps not just in response to major events such as tropical cyclones, possibly reducing the frequency and magnitude of hypersalinity events in north-central Florida Bay.

Salinity values calculated with the mass balance model failed to adequately capture the response of salinity in the north-central sub-region to the freshwater delivered by Hurricane Irene (Fig. 2.7). Similarly, the mass balance model failed to capture the low-salinity extremes in 2002 and 2004. Two aspects of the model might account for these deficiencies. First is the assumption that precipitation is uniform over the Bay and is equal to the Climvis Division 7 values. Hurricane Irene passed to the west of Florida Bay (Fig. 2.9) which may have subjected the north-central and west sub-regions to greater precipitation than the Florida Keys where the precipitation stations included in the Division 7 data set are located. Second, as noted above, direct freshwater runoff into the north-central sub-region was anomalously high immediately following Irene's passage. This anomaly is not reflected in the flow data estimated from the discrete estuarine creeks. Therefore, model estimates of net freshwater supply into the north-central sub-region likely underestimate the supply of freshwater into this region under these unusual conditions.

The highest mean Bay-wide salinities were measured in July of 2001 (41.8) and 2004 (41.7). They were the result of precipitation deficiencies in the preceding years, 2000 and 2003, followed by a delayed onset of the subsequent rainy season. In 2000, precipitation was far below normal resulting in an annual net freshwater supply of -20 cm (Table 2.3). In 2003, annual net freshwater supply was higher at 1 cm, but precipitation and runoff were temporally more uniform than usual, resulting in higher than typical salinities at the end of 2003. Subsequently, in both 2001 and 2004, precipitation was unimodal and did not peak until late summer, whereas typically precipitation is bi-modal, peaking in early summer (May or June) and again in late summer (August or September). The delayed onset of the rainy season during 2001 and 2004 resulted in anomalous negative freshwater supply numbers in the summer when evaporation is at its highest (but is typically offset by precipitation), and led to the maximum salinities observed in July of both 2001 and 2004.

We examined the hypersalinity distribution sequence for 2004 to describe the typical development and evolution of hypersaline events in north-central Florida Bay (Fig. 2.12). High salinities were first observed in the western half of the north-central sub-region (Fig. 2.12a), an area with the largest concentration of shallow mud-banks (Fig. 2.1). This hypersaline water then moved to the east and intensified (Fig. 2.12b), due to increased temperatures in mid-summer, which resulted in increased evaporation (Fig. 2.4). Eventually, the hypersaline water decreased in magnitude and its center shifted to the southeast as precipitation and runoff began to increase and western Florida Bay freshened via exchange from the southwest Florida Shelf (Fig. 2.12c). In contrast to the model's performance during periods of anomalously low salinity values, the mass balance model matched observed salinity behavior during these periods of anomalously high salinity values quite well (Fig. 2.7). Presumably, the effects of underestimates in net freshwater supply are minimized when runoff is so markedly decreased.

The maximum rate of salinity increase Bay-wide (over 0.1 per day) was observed from April 2-3, 2002 to May 7-8, 2002 (Fig. 2.13a). However, the second and third highest increases, both slightly greater than 0.1 per day, were observed from April 20-21, 2004 to May 18-19, 2004 and May 18-19, 2004 to June 16-17, 2004, several months before the second highest mean Bay-wide salinity of 41.7 was recorded on July 21, 2004. Note that the maximum rate of salinity decrease (nearly 0.5 per day) was more than four-fold greater than the maximum rate of salinity increase. Accordingly, it can be concluded that Florida Bay requires a significantly prolonged drought to produce the historically documented extreme hypersaline conditions.

Another anomalous salinity pattern was observed in the last six months of 2004, with the usually estuarine northeast sub-region having much higher salinity than typical and in fact displaying the highest salinity of all four sub-regions during August and September 2004 (Fig. 2.6a). The cause of this anomalous salinity pattern is likely the unusual distribution of regional precipitation during the 2004 wet season. Precipitation was dramatically lower than any other year during this study, which resulted in by far the lowest observed direct runoff to northeast Florida Bay, Table 2.3. Moreover, Hurricanes Charlie, Frances, and Jean all passed just to the north of Lake Okeechobee in the late summer to early fall of 2004. Although these hurricanes had minimal direct effects upon Florida Bay in either precipitation or runoff, nevertheless they indirectly affected the salinity patterns in the Bay by markedly reducing the salinity along the southwest Florida shelf, and these waters subsequently advected into the western Bay (Johns et al. 2005). This exchange was sufficient to reverse the typical difference observed between salinity in the northeast sub-region and the other three sub-regions, resulting in the northeast sub-region displaying the highest salinity for several months during the wet season of 2004.

Interannual Variation

To examine the variation between years and attempt to uncover any long term and/or anomalous trends, annual values of mean salinity, precipitation, runoff, and net freshwater supply were calculated (Table 2.3 and Fig. 2.9). Annual runoff was significantly less than annual precipitation, ranging from 13.3% to 21.1% of precipitation with a mean annual runoff value that was 17.9% of the mean annual precipitation. While

17.9% is significantly higher than the less than 10% calculated if runoff values were assumed to be equal to upstream values at C-111 and Taylor Slough (Nuttle et al. 2000), the true percentage may be even higher as our runoff measurements do not include all of the direct freshwater runoff pathways into Florida Bay, and must therefore be assumed to be a conservative estimate of total runoff.

Although both the maximum and minimum annual salinity coincided with the minimum and maximum precipitation and runoff, respectively, annual salinity was not consistently correlated with annual precipitation and runoff. In 2001, the second highest mean annual salinity observed coincided with the second highest annual precipitation and runoff values. To examine such apparent incongruities, the annual temporal distribution of salinity and precipitation plus runoff was plotted for each year (Fig. 2.13). In 2000, the preceding year, precipitation and runoff were the second lowest during the survey period (Table 2.3 and Fig. 2.13). Thus, at the beginning of the ensuing year the salinity remained high. The onset of the rainy season in 2001 was delayed until July, resulting in the high salinities during the first six months of the year. Subsequently, August and September 2001 were the wettest in the seven-year data set, and July and October were the second wettest (Fig. 2.13b). As a result, 2001 was a year of unusual salinity extremes, varying from the highest value measured, 41.8 in July, to the second freshest values for October, November, and December (Fig. 2.13a).

To examine the interannual variation in precipitation and salinity, these values were separated by year and plotted for each individual annual cycle (Fig. 2.13b). This revealed another salinity anomaly in 2002, in that July had the lowest salinity for the year, rather than December or January. In 2002, precipitation and runoff peaked much earlier than usual (Fig. 2.13b), from May through July, causing decreased salinity earlier in the summer and subsequent increases in salinity through the end of the year. Overall, in 1998, as well as in 2002 and 2003, the annual oscillation in salinity as well as runoff and precipitation was dampened (Fig. 2.13). Precipitation patterns of 1998, 2002, and 2003, were more evenly distributed throughout the seasons (Figs. 2.4b and 2.13b). As a result, salinities became more uniformly distributed temporally, remaining between 28 and 36, and lacked the typical seasonal patterns (Figs. 2.4a and 2.13a). The cause of the anomalous precipitation pattern is thought to be ENSO which was observed in Pacific Ocean sea surface temperature anomalies during 1997-1998 and again in 2002-2003 (Wang & Fiedler 2006). ENSO has been shown to affect precipitation throughout the Florida peninsula by increasing the amount of precipitation during the dry season (Sun & Furbish 1997). The 1997-1998 ENSO caused a reversal of the typical dry and wet seasons of south Florida with a dry summer/fall in 97 and a wet winter/spring in 98 (Johns and Wilson 1999; Lee et al., 2002). Others have hypothesized that ENSO has a strong effect on salinity in Florida Bay based upon carbon isotopic analysis of coral skeletons (Swart et al. 1996, Swart et al. 1999).

Conclusions

Florida Bay is a seasonally hypersaline estuary with a slightly negative mean annual net freshwater supply of between -3.5 and -25.1 cm. On average, direct runoff into Florida Bay accounts for greater than 15% of all freshwater entering the Bay, indicating that although the freshwater supply is dominated by precipitation, runoff cannot be neglected especially in the northeast sub-region. Salinity patterns in Florida Bay are directly related to the seasonal climate of south Florida. The net freshwater supply during the peak of the wet season is generally positive, decreasing salinity through a minimum in January. From March to June the net freshwater supply is typically negative, causing salinity values to increase until hypersaline conditions prevail throughout a large portion of Florida Bay.

The salinity of Florida Bay is also affected by extreme meteorological and climatic variability. Lowest overall mean salinities in Florida Bay were measured after the passing of Hurricane Irene, the only tropical storm or hurricane to have a significant direct effect upon Florida Bay during this study. The ENSO events of 1997-1998 and 2002-2003 resulted in a significant dampening of the wet season/dry season annual precipitation cycle, reducing temporal salinity variability during these periods.

Comparisons of direct observations and a mass balance model demonstrate that it is possible to reasonably estimate mean salinity for Florida Bay and each of the four sub-regions from runoff and precipitation alone ($Eff > 63$ in all regions), except after major precipitation events. Because net freshwater supply in Florida Bay is near zero, on average, significant reductions or increases in runoff can cause significant changes in the salinity patterns. For example, a significant change in the salinity pattern of Florida Bay could occur by shifting to the west sources of runoff along the northern boundary of Florida Bay, causing more frequent and a greater amount of runoff to discharge directly into the north-central or western sub-regions during the wet season. This runoff pattern was only observed once during our 7-year study period, just after the passing of Hurricane Irene, but has been hypothesized to have been a typical occurrence in the past when water levels in the southern Everglades were higher.

Table 2.1 Lagged Pearson correlation coefficients for mean Bay-wide salinity and in each of the four sub-regions with precipitation, runoff, evaporation, and gross freshwater supply (precipitation plus runoff), from top to bottom respectively. The p-value is the probability of a type I error with the statistically significant values highlighted in bold.

			no lag	1 month	2 month	3 month	4 month	5 month	6 month
Precipitation Vs. Salinity	Entire Bay	Pearson r	-0.07	**-0.31**	**-0.45**	**-0.49**	**-0.52**	**-0.46**	-0.17
		p-value	0.57	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.17
	North-central	Pearson r	-0.17	**-0.41**	**-0.53**	**-0.49**	**-0.46**	**-0.33**	-0.08
		p-value	0.16	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**0.01**	0.50
	Northeast	Pearson r	0.00	-0.24	**-0.40**	**-0.44**	**-0.50**	**-0.48**	-0.23
		p-value	0.98	0.05	**<0.01**	**<0.001**	**<0.001**	**<0.001**	0.05
	South	Pearson r	-0.03	-0.28	**-0.36**	**-0.46**	**-0.53**	**-0.50**	-0.20
		p-value	0.83	0.02	**<0.01**	**<0.001**	**<0.001**	**<0.001**	0.10
	West	Pearson r	-0.08	-0.28	**-0.40**	**-0.46**	**-0.49**	**-0.44**	-0.11
		p-value	0.53	0.02	**<0.01**	**<0.001**	**<0.001**	**<0.001**	0.36
Runoff Vs. Salinity	Entire Bay	Pearson r	**-0.39**	**-0.58**	**-0.62**	**-0.58**	**-0.46**	-0.22	
		p-value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.08	
	North-central	Pearson r	**-0.52**	**-0.66**	**-0.65**	**-0.52**	**-0.35**	-0.08	
		p-value	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.01**	0.50	
	Northeast	Pearson r	-0.30	**-0.53**	**-0.59**	**-0.55**	**-0.44**	-0.27	
		p-value	0.02	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.03	
	South	Pearson r	-0.30	**-0.51**	**-0.56**	**-0.59**	**-0.50**	-0.27	
		p-value	0.02	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.03	
	West	Pearson r	**-0.35**	**-0.49**	**-0.54**	**-0.55**	**-0.43**	-0.20	
		p-value	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.01**	0.11	
Evaporation Vs. Salinity	Entire Bay	Pearson r	**0.63**	**0.49**	0.21				
		p-value	**<0.001**	**<0.001**	0.08				
	North-central	Pearson r	**0.50**	**0.35**	0.09				
		p-value	**<0.001**	**<0.001**	0.49				
	Northeast	Pearson r	**0.59**	**0.53**	0.28				
		p-value	**<0.001**	**<0.001**	0.020				
	South	Pearson r	**0.67**	**0.54**	0.27				
		p-value	**<0.001**	**<0.001**	0.03				
	West	Pearson r	**0.65**	**0.44**	0.16				
		p-value	**<0.001**	**<0.001**	0.20				
Gross Freshwater Supply Vs. Salinity	Entire Bay	Pearson r	-0.14	**-0.38**	**-0.51**	**-0.53**	**-0.52**	**-0.42**	-0.12
		p-value	0.26	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.34
	North-central	Pearson r	-0.25	**-0.48**	**-0.59**	**-0.52**	**-0.45**	-0.28	-0.03
		p-value	0.04	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.02	0.80
	Northeast	Pearson r	-0.06	**-0.31**	**-0.46**	**-0.49**	**-0.51**	**-0.44**	-0.19
		p-value	0.62	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.12
	South	Pearson r	-0.09	**-0.34**	**-0.42**	**-0.51**	**-0.53**	**-0.46**	-0.15
		p-value	0.48	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.22
	West	Pearson r	-0.14	**-0.33**	**-0.45**	**-0.50**	**-0.49**	**-0.40**	-0.06
		p-value	0.25	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.64

Table 2.2 Pearson correlation between precipitation over the Florida Peninsula south of Lake Okeechobee (NCDC Climvis divisions 5 and 6) and runoff into northeast Florida Bay. The time value corresponds to the lag from precipitation to runoff and bold values represent statistically significant correlations.

	no lag	1 month	2 month	3 month	4 month
Pearson r	**0.52**	**0.68**	**0.51**	**0.37**	0.19
p-value	**<0.001**	**<0.001**	**<0.001**	**<0.01**	0.10

Table 2.3 Annual mean Bay-wide salinity, precipitation, runoff, evaporation, and net freshwater supply.

Year	Salinity	Precipitation (cm)	Runoff (cm)	Evaporation (cm)	Net
1998	32.4	109	19.1	135	-6.6
1999	31.2	133	25.7	126	33.1
2000	33.7	101	16.1	137	-20.3
2001	35.5	130	24.4	142	12.5
2002	31.8	112	23.6	133	2.5
2003	32.4	113	19.4	131	1.0
2004	36.3	78	10.4	148	-59.2
MEAN	33	111	19.8	136	-5.3

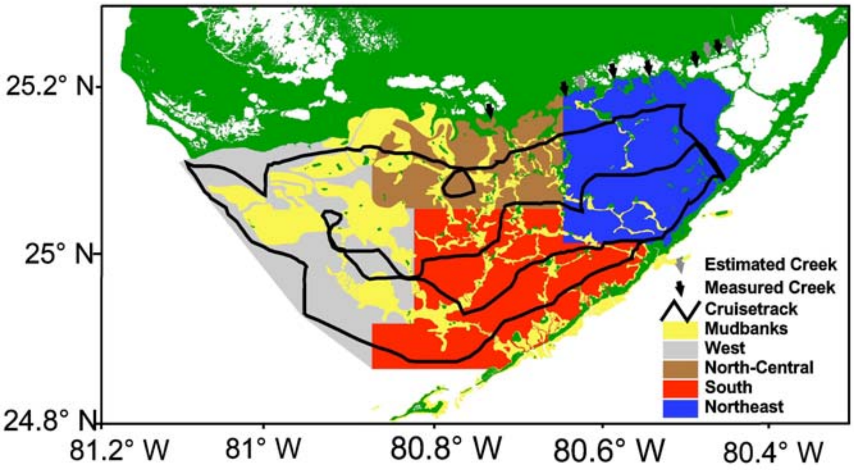

Figure 2.1 Map of Florida Bay depicting the vast system of mangrove islands and shallow mud-banks (shown in gray), as well as the sub-regional delineations.

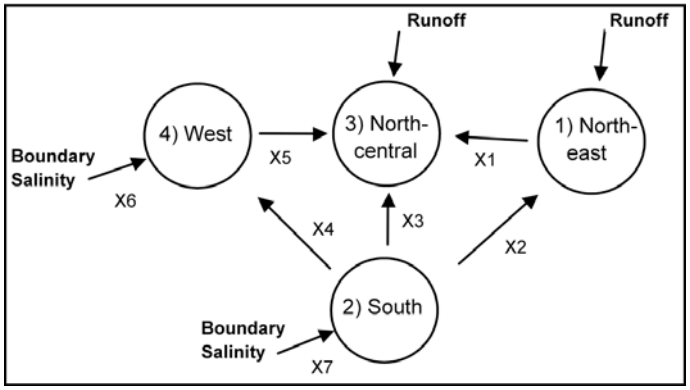

Figure 2.2. Structure of the monthly time-step model showing the location of inflows from the Everglades and defining the exchange parameters. The arrows that represent the fluxes connecting the sub-regions establish the direction of "positive" values of the average discharge and exchange fluxes.

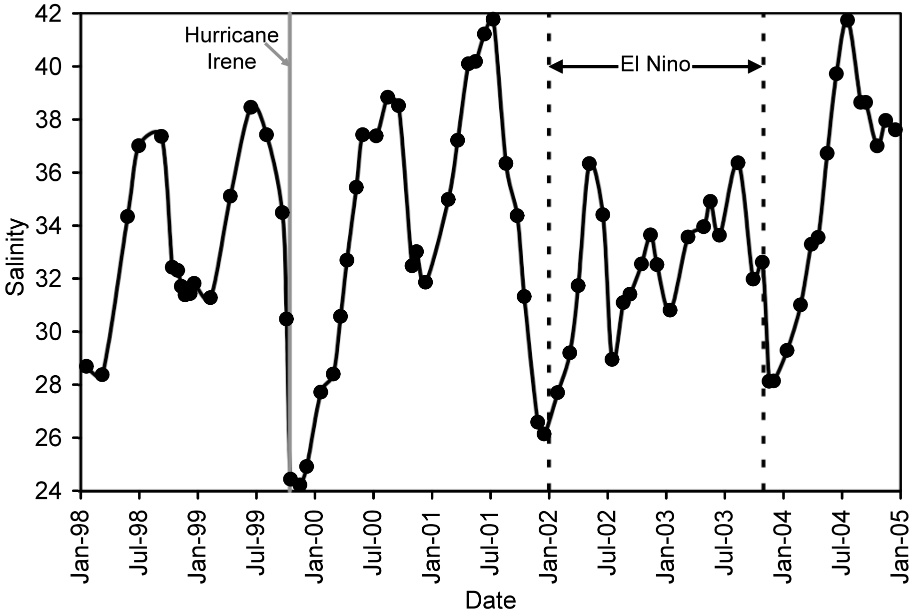

Figure 2.3 Time series of mean salinity throughout Florida Bay for the seven year study period.

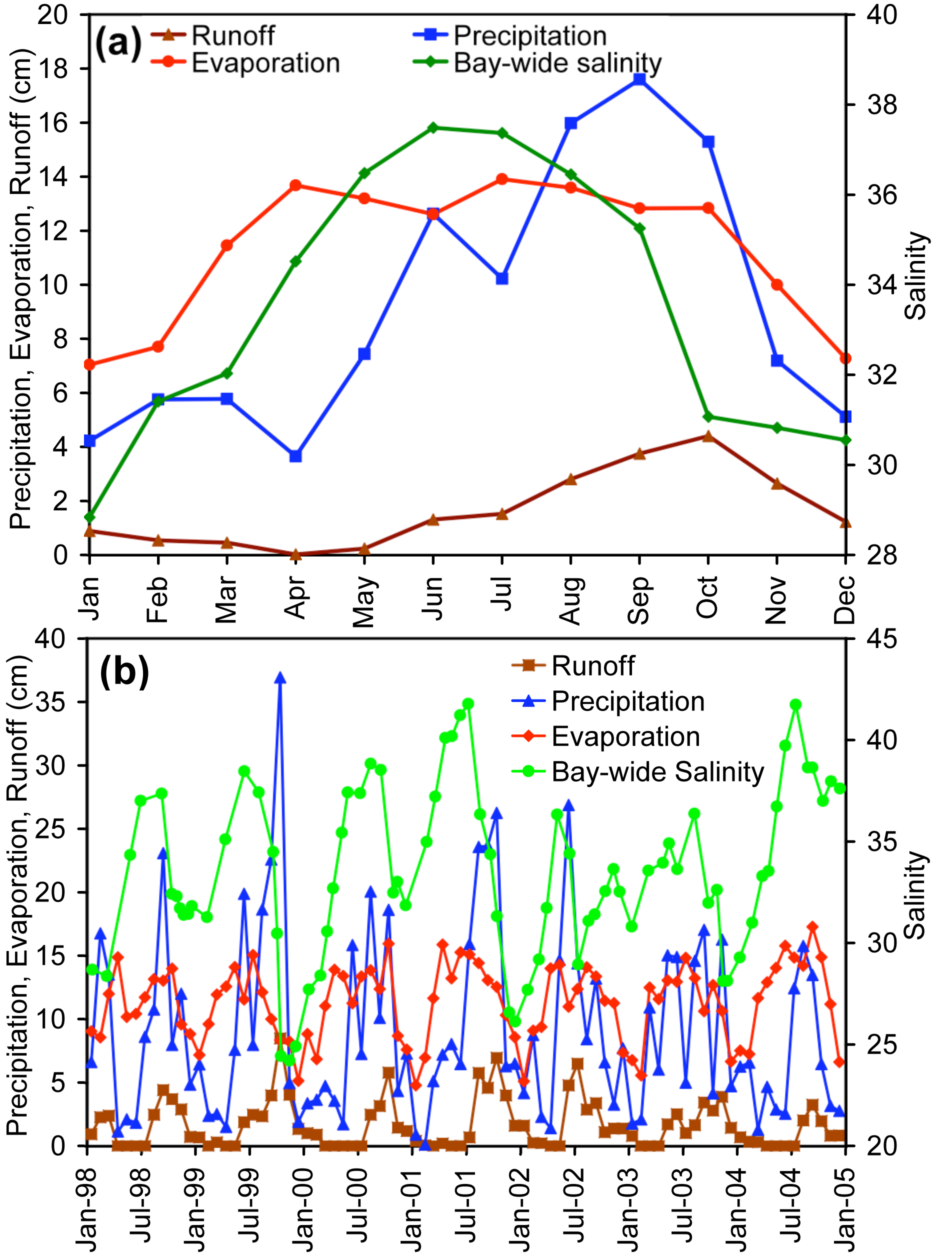

Figure 2.4 (a) Monthly means for runoff, precipitation, evaporation, and mean Bay-wide salinity. (b) Time series of runoff, precipitation, evaporation and mean Bay-wide salinity from 1998 through 2004.

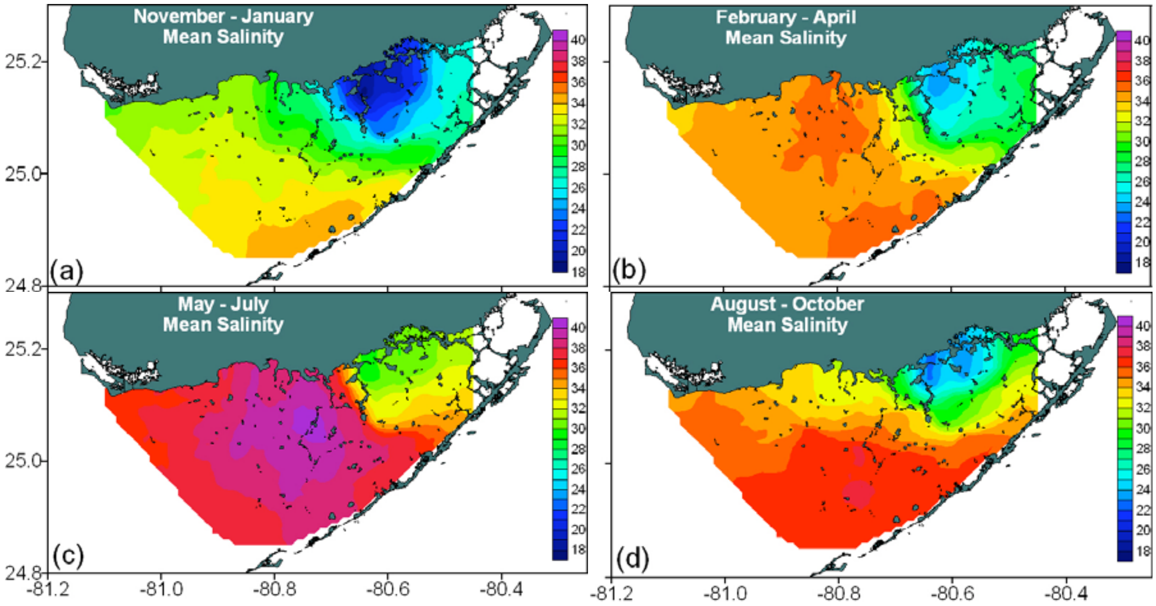

Figure 2.5 Seasonal contour maps of salinity in Florida Bay.

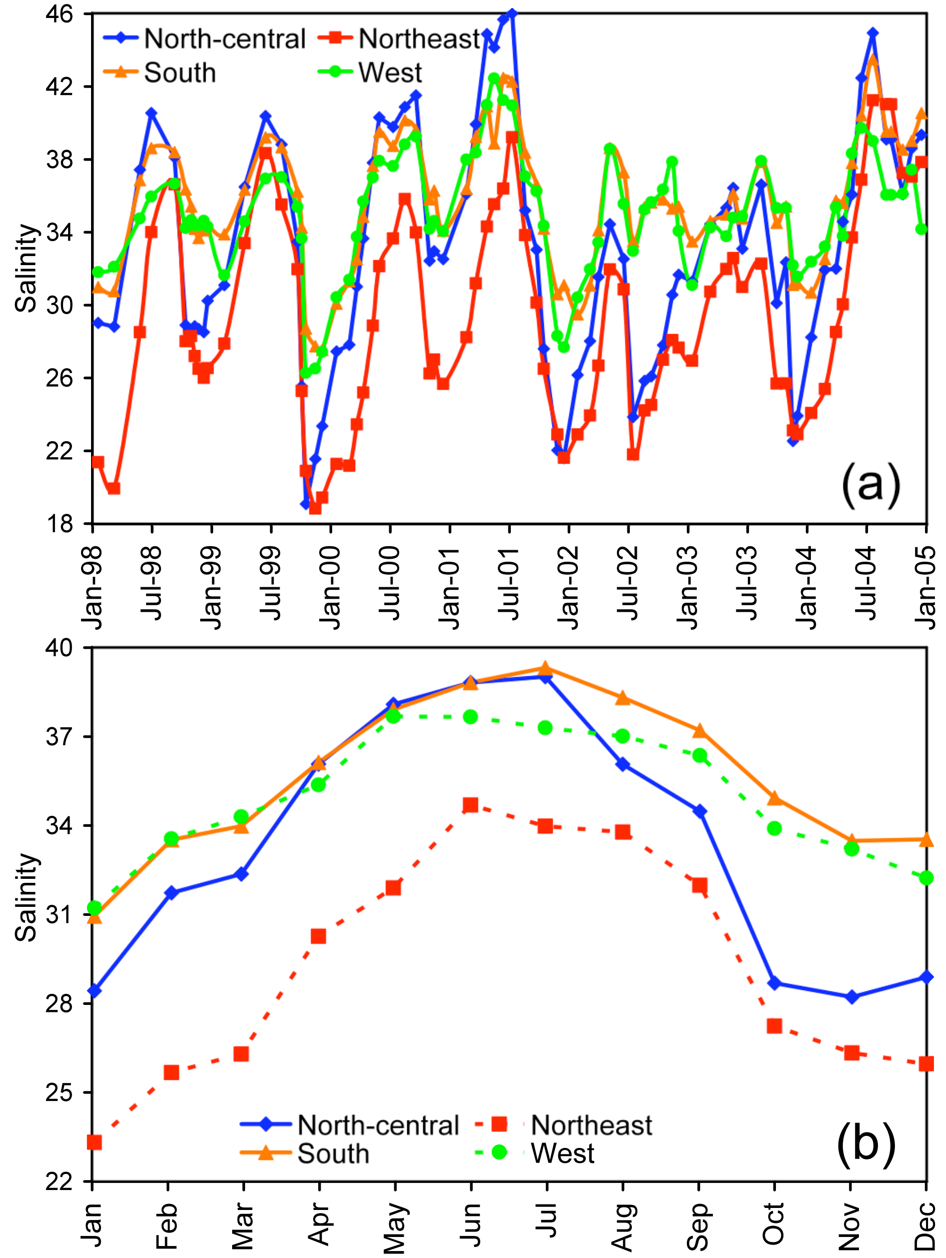

Figure 2.6 (a)Time series of mean salinity for each of the four sub-regions in Florida Bay. (b) Mean monthly salinity for each of the four sub-regions.

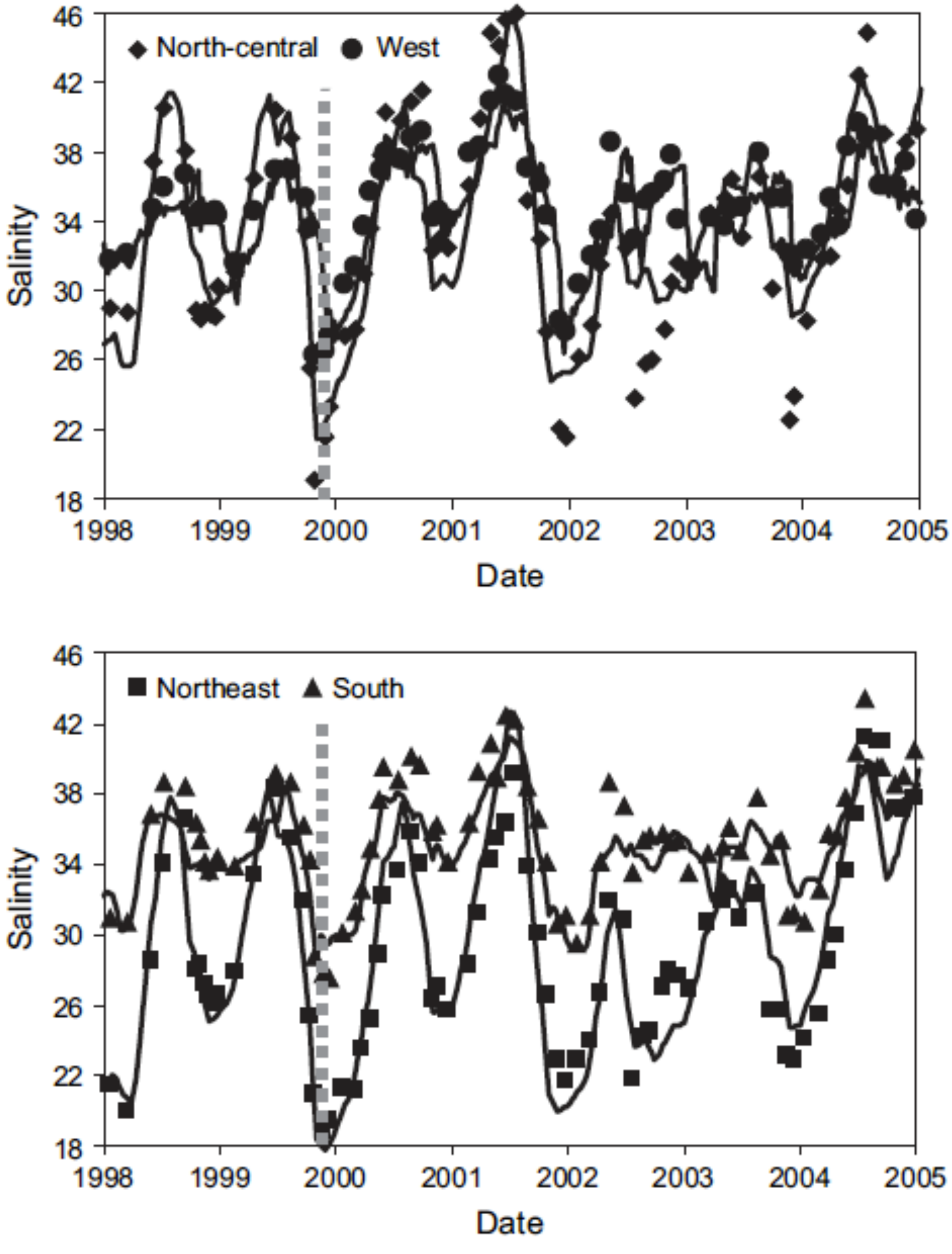

Figure 2.7 Times series of mean salinity from observations (circles, triangles, squares, diamonds) and salinity calculated by the mass balance model (solid lines) for each of four sub-regions in Florida Bay. The vertical dashed line indicates the occurrence of tropical storm Irene, which delivered over 20 cm of freshwater to the Bay.

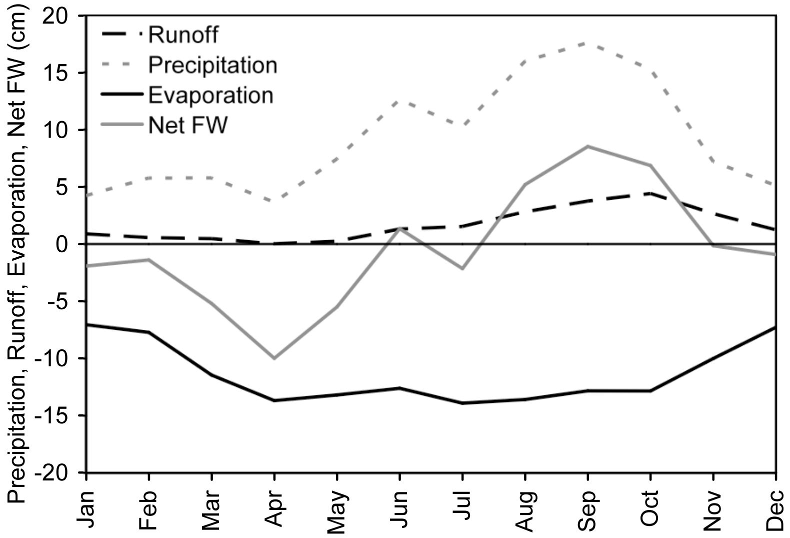

Figure 2.8 The mean annual freshwater budget for Florida Bay from 1998-2004.

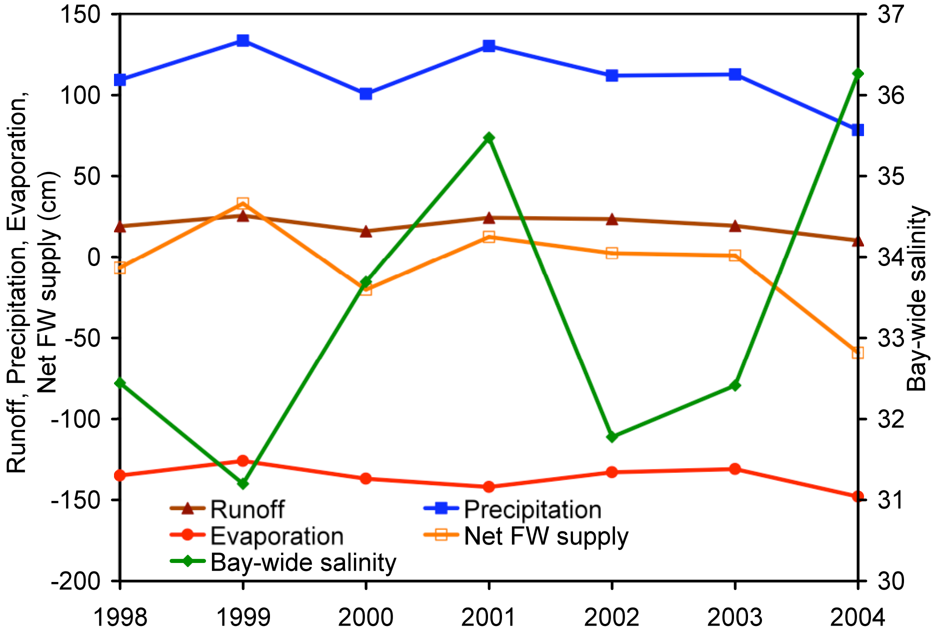

Figure 2.9 Plot of the mean annual values for runoff, precipitation, evaporation, net freshwater supply, and Bay-wide salinity.

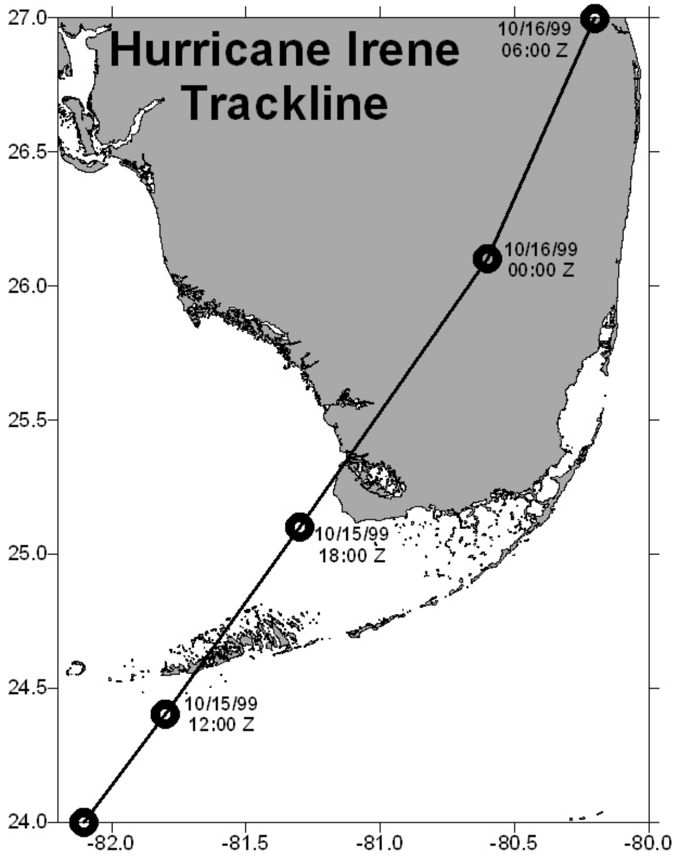

Figure 2.10 The track of the center of Hurricane Irene as it passed just to the west of Florida Bay in October 1999.

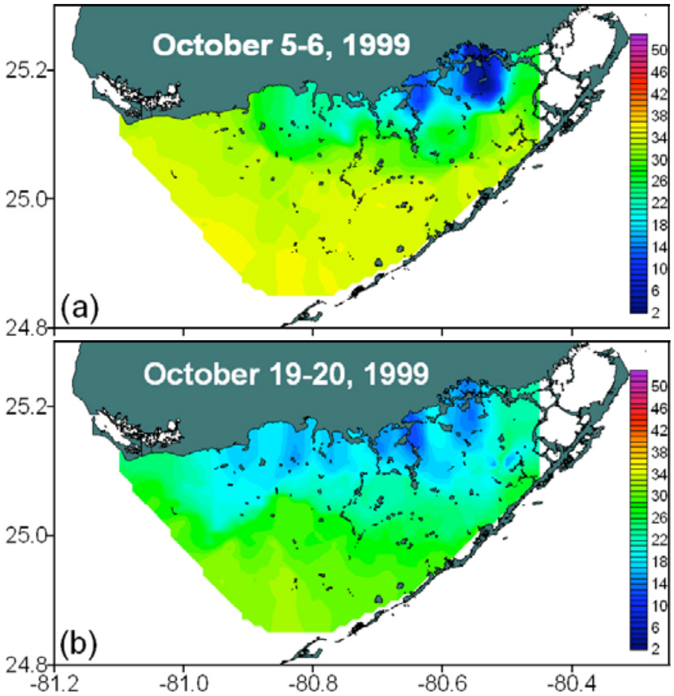

Figure 2.11 Salinity contour maps for surveys conducted (a) 10 days prior to Hurricane Irene and (b) 4 days after Hurricane Irene.

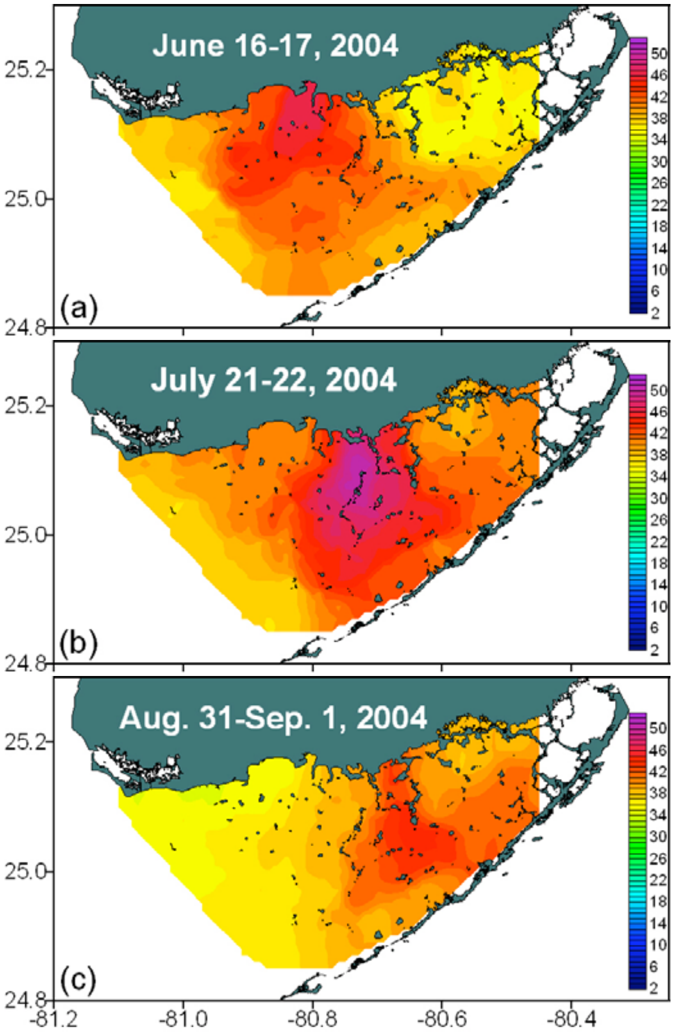

Figure 2.12 Series of salinity contour maps showing the formation and movement of a typical hypersalinity event from (a) June 2004, (b) July 2004, and (c) August 2004.

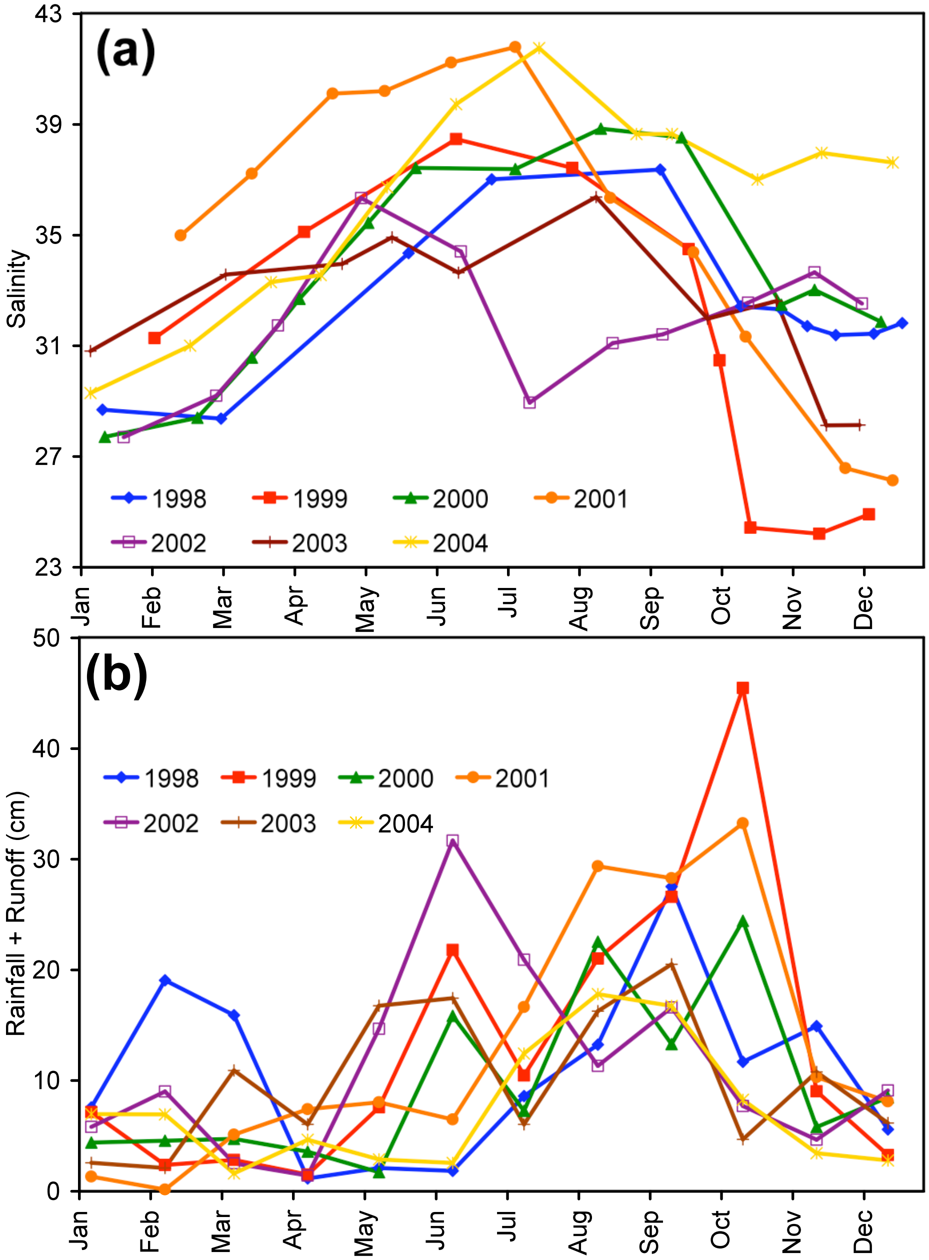

Figure 2.13 Annual time series of (a) salinity and (b) precipitation plus runoff for each of the seven years during the study.

CHAPTER 3

TEMPORAL AND SPATIAL VARIABILITY OF MESOZOOPLANKTON IN A SHALLOW SUB-TROPICAL BAY: INFLUENCE OF TOP-DOWN CONTROL

Summary

Quantifying the relationship between mesozooplankton and water quality parameters identifies the factors that structure the mesozooplankton community and can be used to generate hypotheses regarding the mechanisms that control the mesozooplankton population and potentially the trophic network. To investigate this relationship, mesozooplankton and water quality data were collected in Florida Bay from 1994-2004. Three key characteristics were found in the mesozooplankton community structure: 1) There are significant differences between the four sub-regions of Florida Bay; 2) There is a break in May of 1997 with significant differences before and after this date; 3) There is a positive correlation between mesozooplankton abundance and salinity. The latter two characteristics are closely correlated with predator abundance, indicating the importance of top-down control. Hypersaline periods appear to provide a refuge from predators, allowing mesozooplankton to increase in abundance despite the increased physiological stress.

Background

Mesozooplankton provide a vital connection in marine trophic webs, transferring energy from autotrophic organisms or microzooplankton to higher trophic levels (Wiebe et al. 2000). It is therefore critical to understand what factors may influence mesozooplankton populations. The dominant historical theory was that prey-limitation controlled mesozooplankton biomass (Roelke et al. 1999, Murrell & Lores 2004). More recently, it has been proposed that populations may be controlled by predation (Purcell 1997, Mowitt et al. 2006). Other researchers have stressed mesozooplankton population regulation by environmental factors including temperature, salinity, and climatic cycles such as El Niño Southern Oscillation (ENSO) (Keister & Peterson 2003, Kimmel & Roman 2004). The effect of environmental factors on zooplankton populations can be either direct (i.e. physiological) or indirect (e.g. environmental factors affect the predator or prey abundance and thus the mesozooplankton community).

To investigate relationships between environmental parameters and mesozooplankton community structure it is necessary to analyze a long-term database. Without long-term data it is impossible to examine the effect of cyclical events such as ENSO (Fernandez-Alamo & Farber-Lorda 2006) or wet/dry periods (Kimmel & Roman 2004, Kimmel et al. 2006a) and episodic events such as tropical cyclones(Greening et al. 2006). There are relatively few long-term studies of mesozooplankton assemblages in coastal regions with simultaneous synoptic measurements of environmental parameters. However, long-term oceanic studies have documented significant fluctuations in zooplankton assemblages on interannual time scales that are related to climate-scale phenomena (Beaugrand & Reid 2003, Piontkovski et al. 2006). Most studies in coastal embayments tend to focus directly on the effects of water quality variables or water source on zooplankton community composition, with few examining the role of larger scale climatic phenomena (Kimmel & Roman 2004, David et al. 2005, Kimmel et al. 2006a). There are even fewer long-term mesozooplankton studies from subtropical coastal embayments such as Florida Bay and only one prior study in the southeastern

United States examined the relationship between ENSO and mesozooplankton (Allen et al. 2008).

Florida Bay is ideally suited to examine the relationship between environmental parameters and mesozooplankton assemblages because it has a high degree of internal spatial heterogeneity. The salinity regime of Florida Bay is estuarine in the northeast, highly variable and seasonally hypersaline in the north-central, and fairly stable with near marine salinities in the south and west (Fig. 3.1) (Kelble et al. 2007). This level of heterogeneity between sub-regions has also been observed in other environmental variables likely to influence mesozooplankton, including water quality (Boyer et al. 1997), phytoplankton species composition (Phlips & Badylak 1996), sponge biomass (Peterson et al. 2006), and Chromophoric Dissolved Organic Matter (CDOM) (Kelble et al. 2005). Florida Bay also shows a bay-wide response to larger scale forcing including climatic cycles, specifically ENSO which dampens the seasonal salinity oscillation, and tropical cyclones (Kelble et al. 2007).

This study will analyze a 10-year mesozooplankton assemblage data set collected in conjunction with a suite of synoptically measured environmental variables. These data were collected over time and space scales sufficient to investigate the effects of salinity, water quality and climatic phenomena on the mesozooplankton assemblage. The aims of this study are to: (1) determine if there are significant spatiotemporal differences in the mesozooplankton communities; (2) identify the environmental parameters that are significantly correlated with the observed mesozooplankton community structure; (3) examine the potential mechanisms responsible for structuring the mesozooplankton community; and (4) draw inferences regarding the potential effect of Everglades Restoration upon the mesozooplankton assemblage in Florida Bay.

Materials and Methods

Study Site

Florida Bay is a triangular coastal embayment located between the base of the Florida peninsula and the Florida Keys (Fig. 3.1). Florida Bay provides a vital link in south Florida's hydrology and ecosystem connectivity by receiving freshwater runoff from the Everglades and exchanging water with the coastal Atlantic Ocean through tidal passages in the Florida Keys. The Greater Everglades ecosystem including Florida Bay has been significantly altered over the past century as the human population in adjacent areas has markedly increased. To accommodate this population increase much of the historic Everglades ecosystem was drained and numerous fill islands were built in the Florida Keys to accommodate a railway. This resulted in decreased runoff and circulation in Florida Bay that likely induced a cascade of negative environmental events (Fourqurean & Robblee 1999). The first such event to garner significant public attention in Florida Bay was the mass seagrass die-off that began in 1987 (Zieman et al. 1988). The seagrass die-off was succeeded by several other indicators of a degrading coastal ecosystem, including a persistent cyanobacterial bloom and sponge die-off (Butler et al. 1995). Ecological degradation was not limited to Florida Bay, and was observed throughout the altered Everglades ecosystem (Ogden & Davis 1994) prompting state and federal agencies to begin undertaking Everglades Restoration. The centerpiece of this restoration is the Comprehensive Everglades Restoration Plan (CERP) (FFA 2000, WRDA 2000). CERP aims to restore the quality, quantity, timing, and distribution of freshwater flow through the Everglades with the goal of creating a sustainable ecosystem while at the same time permitting continued human development in the presently inhabited areas.

The concerns raised by detrimental ecological events resulted in the initiation of extensive monitoring programs and ecological studies within Florida Bay. These have enabled quantification of the dynamics and distribution of many individual components of the ecosystem, including nutrients (Boyer et al. 1999), phytoplankton (Phlips & Badylak 1996), sea grass (Zieman et al. 1999), shrimp (Browder et al. 2002), sponges (Peterson et al. 2006), and juvenile fish (Thayer et al. 1999). Despite these monitoring studies, a significant gap remains in understanding mesozooplankton dynamics in Florida Bay. Not only do mesozooplankton form a vital trophic link that transfers energy from pelagic primary producers or microzooplankton to higher trophic levels, but there is also a potential for zooplankton to significantly affect the extent and duration of phytoplankton blooms (Dagg 1995, Dagg & Govoni 1996).

Many ecological studies in Florida Bay have examined how the distribution and dynamics of different ecosystem components change throughout the year as a function of salinity (Thayer et al. 1999, Browder et al. 2002, Jurado et al. 2007). Salinity is selected as the primary independent abiotic variable since fluctuations in salinity are greater than temperature and it is the variable that will be most directly affected by Everglades Restoration projects. Hyper- and hyposalinity conditions can often be observed simultaneously in different sub-regions of the Bay and within the same sub-region at different times of the year (Kelble et al. 2007). The Bay receives freshwater runoff from two distinct sources having different water quality characteristics (direct, oligotrophic runoff into northeast Florida Bay, and indirect runoff from the southwest Florida shelf with higher nutrient concentrations) further complicating relationships between ecological variables and salinity. These characteristics make Florida Bay an ideal study site to assess the impact of water quality on mesozooplankton assemblages in sub-tropical embayments.

Mesozooplankton Sample Collection and Identification

As part of the joint South Florida Ecosystem Restoration Program mesozooplankton samples were collected at approximately 60-day intervals at 10 stations in Florida Bay (Fig. 3.1) from September 1994 until September 2004, with a gap from November 1998 until November 1999. These 10 stations vary in depth from 1 to 2 meters. The samples were collected aboard the *R/V Miller* and the *R/V Virginia K* with a 64um mesh, 0.5m diameter ring-net from Sea-Gear Corporation equipped with a General Oceanics Model 2030 flowmeter. The net was towed for five minutes at a speed of 1 knot off a davit to ensure the net remained outside the ship's wake. The net was towed just below the water's surface, because the shallow station depth did not allow for a deeper tow. The samples were preserved in 10% formaldehyde upon retrieval.

In the laboratory the preserved samples were split using a Folsom Plankton Splitter. Mesozooplankton were identified to the lowest taxonomic category distinguishable with a dissecting, stereoscope (magnification 32x). This varied from genera in Copepoda to class in Mollusca. Progressively more concentrated splits were counted until at least 50 individuals of the major taxonomic categories had been counted. In most cases, this was slightly greater than 0.1% of the total sample. All of the samples were counted through 1998; thereafter, a subset of four stations, one from each sub-region, were counted at 4-month intervals. A one-year subset of these samples was selected to measure lengths and widths of the mesozooplankton taxa and identify the copepods to species.

Water Quality Sample Collection

Before each mesozooplankton net tow, samples were taken for dissolved inorganic nutrients, chlorophyll *a*, temperature and salinity. Temperature and salinity were measured *in situ* with a Seabird Model 21 thermosalinograph. For chlorophyll *a*, duplicate samples were filtered onto Whatman GF/F 25 mm filters that effectively retain particles greater than 0.7 um. These filters were then placed in liquid nitrogen and stored at -80°C at the laboratory until analyzed. Chlorophyll *a* concentration was determined via extraction in a 60:40 mixture of 90% acetone and dimethyl sulfoxide (Shoaf & Lium 1976). The fluorescence of each duplicate was measured on a Turner Designs model TD-700 before and after acidification to correct for phaeophytin. The fluorescence values were calibrated against concentrations of chlorophyll *a* determined spectrophotometrically from *Anacystis andulans* standards.

The dissolved inorganic nutrients measured included nitrate plus nitrite, ammonium, silica, and Soluble Reactive Phosphate (SRP). Samples were collected by filtering sample water through a 0.25um nylon filter into two test tubes. The test tube for ammonium analysis was immediately fixed with a drop of chloroform and then both test tubes were placed on ice. Once back at the lab, the ammonium sample was placed in a refrigerator and run within five days. The test tube for nitrate, nitrite, silica and SRP was stored at -20°C. The dissolved inorganic nutrient samples were analyzed on an Alpkem gas-segmented continuous flow auto-analyzer and their concentrations were determined colorimetrically utilizing methodologies described in detail elsewhere (Zhang & Berberian 1997, Zhang et al. 1997a, Zhang et al. 1997b, Zhang & Chi 2002).

Supplemental water quality data (total phosphate (TP), total organic carbon (TOC) and turbidity) that were not collected as part of this study, but were nonetheless utilized in the statistical analysis, were provided by the SERC-FIU Water Quality Monitoring Network supported by SFWMD/SERC Cooperative Agreement #4600000352 as well as EPA Agreement #X7-96410603-3. These data were always collected within two weeks of the mesozooplankton sample. The data were from the closest station to the mesozooplankton sample and were always within the same basin. Sampling and analysis methodologies for these variables are described in detail elsewhere (Boyer & Briceno 2008).

While the inclusion of this data inherently includes a temporal disparity between mesozooplankton and water quality data, it was included for several reasons. TP, TOC and turbidity measure important ecological aspects of Florida Bay that may not be captured by the concurrently collected water quality data. TP is a limiting nutrient for phytoplankton growth throughout much of Florida Bay, thus providing an important measure of key ecosystem processes (Fourqurean et al. 1993). TOC is a potential proxy for microbial activity, which has been documented to provide significant inputs into Florida Bay's trophic network (Richardson et al. 2003). Turbidity is an important proxy for TSS and thus for light attenuation because tripton is the dominant factor controlling the light regime of Florida Bay (Phlips et al. 1995, Kelble et al. 2005). Prior analyses of these variables has shown that the short-term variability on the order of the temporal mismatch between the mesozooplankton and water quality data is not as great as seasonal or interannual trends that are being examined in this study (Boyer et al. 1999).

Statistical analysis

The majority of the multivariate exploratory statistical methodologies were conducted with the Primer-6® software package (Clarke & Gorley 2006). Prior to conducting the multivariate analyses the abundance data were log transformed as $\log(N_i+1)$ of the raw data, where N_i is the abundance of the i^{th} taxonomic category in each sample. A Bray-Curtis similarity matrix was then produced from the log transformed data. Non-metric multi-dimensional scaling ordination (n-MDS) was applied to the Bray-Curtis similarity matrix to recreate the higher dimensional correlations of the mesozooplankton assemblage in two dimensions. In the n-MDS plot the distance between samples is equivalent to the similarity between samples. The BEST routine was applied to identify the combinations of water quality parameters most closely correlated with the observed mesozooplankton communities by analyzing the highest correlation between the species assemblage Bray-Curtis similarity matrix for the mesozooplankton and a subset of the normalized Euclidean distance similarity matrix from the environmental variables. It calculates a test statistic rho that is the rank correlation calculated by matching element to element from the mesozooplankton assemblage matrix to the subset of environmental parameters. The statistical significance of rho is calculated by comparison against 999 permutations of rho from a random and thus uncorrelated set of values for these similarity matrices to test the null hypothesis of no correlation (Clarke & Gorley 2006). A CLUSTER analysis was conducted incorporating a similarity profile (SIMPROF) test with 999 permutations to define statistically significant clusters within the mesozooplankton samples. The similarity percentages (SIMPER) routine quantified the relative contribution of each mesozooplankton taxonomic category to within cluster similarities for statistically significant clusters. The mathematical background and basis for all of these routine has been described in detail elsewhere (Clarke & Warwick 2001). The lone multivariate technique not conducted in PRIMER® was the principal components analysis (PCA) which was undertaken with Statistica®. A single PCA was calculated from the water quality variables and the mesozooplankton taxa were plotted as supplementary variables. These supplementary variables were not used to calculate the PCA eigenvalues or eigenvectors and the row and column values for the supplementary values were calculated utilizing the equations from the water quality PCA to plot their relative location on the same factor plane (Legendre & Legendre 1998). PCA analysis with supplementary variables has been effectively employed to examine the correlation between the mesozooplankton community and environmental parameters (Beaugrand & Ibanez 2004, David et al. 2005). All univariate statistical methodologies were conducted with Statistica®. The α-value for the Spearman rho correlations between water quality and mesozooplankton taxa were adjusted via Bonferroni correction by dividing $\alpha = 0.05$ by the number of tests in each sub-region (n=49)

Results

Spatial and Temporal Distribution

A total of 283 samples were enumerated to zooplankton taxonomic categories. The seven taxonomic groupings that dominated these samples were the classes Bivalvia and Gastropoda, as well as Harpacticoida, *Acartia*, *Oithona*, Paracalanidae and copepod nauplii. Harpacticoida, *Acartia*, *Oithona* and Paracalanidae are members of the sub-class Copepoda and consist of both the adult and copepodid stages; nauplii in this analysis are treated as a separate taxonomic group. For the one-year subset where copepods were identified to species *Acartia* was dominated by *Acartia tonsa*, which accounted for at least 96% of *Acartia* in each sample and corresponds well with findings in nearby estuaries (Woodmansee 1958, Putland & Iverson 2007). *Oithona* was dominated by *Oithona nana*, which accounted for at least 64% of *Oithona* in each sample. Paracalanidae was dominated by *Parvocalanus crassirostris*, which accounted for at least 62% of Paracalanidae in each sample. The seven broad taxonomic groupings accounted for over 92% of all mesozooplankton per sample on average and in only two samples (i.e. less than 1% of the samples) did they not constitute the majority of mesozooplankton. The time series of mesozooplankton community assemblage divided by sub-regions displays both spatial heterogeneity and commonality across sub-regions (Fig. 3.2).

The most pronounced commonality among sub-regions was low abundance of mesozooplankton from the beginning of sampling in September 1994 until May 1997. All four sub-regions had significantly lower abundances for all seven taxonomic groups from the projects inception until May 1997 (Mann-Whitney U-test, $p < 0.003$). After May 1997, mesozooplankton abundance increased throughout Florida Bay.

Beyond the general long-term temporal commonality, there was a large degree of spatial heterogeneity between sub-regions and temporal heterogeneity on shorter time scales within sub-regions in both total mesozooplankton abundance and community composition. The north-central sub-region typically had the highest abundance of mesozooplankton with a median of 125,830 individuals m^{-3}, followed by the west (median = 79,889 ind. m^{-3}), and then less abundant were the south (median = 35,670 ind. m^{-3}) and northeast (median = 26,736 ind. m^{-3}). In both the west and north-central sub-regions nauplii were most abundant and more than double *Oithona*, which was the second most abundant taxa (Fig. 3.3). *Acartia,* Paracalanidae and Gastropoda all accounted for the same percentage of the mesozooplankton community in the west and north-central; whereas, Bivalvia was the third most abundant taxa in the North-central, but dropped to sixth most abundant in the west. In the northeast and south, nauplii and *Oithona* were tied for the most abundant, but in the northeast Gastropoda had the same relative abundance as these two taxa and in the south Gastropoda was less than half the relative abundance of nauplii and *Oithona*.

The seven most common mesozooplankton taxa were compared between sub-regions utilizing the non-parametric Mann-Whitney U-test (Table 3.1). *Acartia* had significantly higher abundance in the north-central sub-region than the other three sub-regions and there was no difference in *Acartia* abundance between these three sub-regions. The north-central and west had significantly higher abundance of *Oithona* than the northeast sub-region and the north-central was significantly higher than the south, but there was no difference between the north-central and west. Paracalanidae had a fairly uniform distribution throughout Florida Bay with the only significant difference between the south and northeast sub-regions. The west had a significantly higher abundance of Harpacticoida than the other three sub-region and the northeast had a significantly lower abundance of Harpacticoida than the other thee sub-regions with no difference between the north-central and south. Gastropoda was also relatively uniform throughout the Bay with the only difference between the north-central and the south sub-region. The north-central had significantly higher abundances of Bivalvia from all three other sub-regions with no other significant differences. The west and north-central sub-regions had significantly higher abundances of nauplii than the northeast and south with no difference between the south and northeast or west and north-central.

Mesozooplankton community structure

To analyze the structure within the mesozooplankton community a two-dimensional n-MDS plot was produced with a stress of 0.13. This stress was calculated from a scale of 0 to 1, where a value of zero equates to the 2-dimensionl nMDS perfectly representing the 32-dimensional space of the similarity matrix. This plot corroborates the interannual differences observed in the time series. Specifically, the majority of samples from 1994, 1995, 1996 and early 1997 are plotted away from the tight cluster that is formed by the samples from 1998-2004 (Fig. 3.4). Thus, this interannual difference between mesozooplankton populations contributed the most to the structure of the mesozooplankton community in Florida Bay during the study period.

The BEST technique was then applied to identify water quality variables that are significantly correlated with the mesozooplankton community. The combination of the 9 [DIN was not included in this analysis, because of its tight correlation with ammonium] environmental parameters with the highest correlation to the mesozooplankton community was salinity, temperature, turbidity, and ammonium (Table 3.2). The ten combinations with the highest correlation to the mesozooplankton community all had a level of significance less than or equal to 0.001 and they all included salinity, but none included SRP or chlorophyll *a*, indicating that salinity is closely correlated with the mesozooplankton community.

A cluster analysis on the individual mesozooplankton samples was undertaken to identify significant differences between mesozooplankton samples and determine what if any parameters accounted for these differences. The cluster analysis found 29 statistically significant clusters ($\alpha = 0.05$). Of these 29 significant clusters, 7 contained a single sample. Within these clusters, a relationship with salinity was clearly evident. 18 of the 22 significant multi-sample clusters had over 50% of their samples from a single salinity class when salinity was divided into the following bins: <20, 20-28, 28-33, 33-38, >38. An interannual effect was also apparent in the clustering with 18 of the 22 clusters having over 50% of their samples from a single year. Moreover, only two of the 22 clusters contained samples from both pre- and post-May 1997. A sub-regional effect was observed with 16 of the 22 multi-sample clusters containing samples from a single sub-region.

Principal components analysis verified the relationships identified by the other multivariate techniques. Seven of the water quality parameters were reduced to two principal factors that accounted for greater than 50% of the variability. The location of these parameters was then plotted on the two-dimensional factor plane. Overlaid on this factor plane are the locations of the 7 most common mesozooplankton taxa as supplementary variables that were not utilized to calculate the eigenvalues or eigenvectors in the principal components analysis (Fig. 3.5). Five (*Acartia*, *Oithona*, nauplii, Gastropoda and Harpacticoida) of the seven mesozooplankton taxa had trajectories similar to temperature and salinity which were tightly coupled in the PCA. The tight coupling of temperature and salinity in the PCA is reflective of the tight coupling observed between temperature and salinity in Florida Bay (Kelble et al. 2007).

The trajectory for Paracalanidae was similar to that of chlorophyll *a* and TP, although no relationship between overall mesozooplankton and chlorophyll *a* was observed in any other multivariate analysis. The tight coupling of TP and chlorophyll *a* was observed in a similar analysis of water quality parameters in Florida Bay (Boyer et al. 1997).

Correlation between mesozooplankton and water quality

A SIMPER analysis was employed to determine the mesozooplankton taxa that played a key role in structuring the community and thus identify the taxa that should be examined with univariate techniques. The SIMPER analysis found that the top 3 taxa contributing to within cluster similarities were always from the top 7 most abundant mesozooplankton taxa (*Oithona, Acartia,* Paracalanidae, Harpacticoida, Gastropoda, Bivalvia and nauplii). This SIMPER analysis justifies the closer examination of the seven most common mesozooplankton taxa and their correlation with water quality variables. The water quality variables selected for the correlation analysis included all of the variables that were identified in the top ten correlations from the multivariate BEST analysis and chlorophyll *a* which did not appear in any of these combinations, but is a proxy for phytoplankton biomass and thus often correlated with prey availability for mesozooplankton. Also, ammonium and nitrate plus nitrite were combined into a single DIN water quality variable for the correlation analysis.

Throughout Florida Bay, chlorophyll *a* and salinity were both significantly correlated with 4 of 7 mesozooplankton taxa. The 5 other water quality variables were correlated with two or less mesozooplankton taxa (Table 3.3). Salinity was the only water quality parameter with at least one significant correlation in 3 of the 4 sub-regions and

Paracalanidae and *Acartia* were the only two taxa not correlated with salinity in any of the sub-regions of Florida Bay.

There were differences between sub-regions with respect to the correlation between mesozooplankton and water quality. In the northeast, TOC was correlated with 5 mesozooplankton taxa, TP was correlated with 2 taxa and salinity was correlated with 1 taxa. In the north-central, DIN was correlated with 2 of 7 taxa and no other water quality parameters had significant correlations. In the south, salinity was correlated with 2 of 7 taxa and turbidity was correlated with a single taxa. The west showed a variety of relationships with 5 of the 7 water quality parameters displaying significant correlations with at least one mesozooplankton taxonomic category; although salinity was the only water quality parameter correlated with more than half of the taxa. The differing influences among sub-regions indicate that there is a large degree of heterogeneity in the relationship between mesozooplankton and water quality parameters other than salinity.

Discussion

Correlation with Water Quality

The large quantity of significant correlations between mesozooplankton and water quality was not surprising given that relationships between various water quality parameters and mesozooplankton are often observed (Park & Marshall 2000, David et al. 2005, Reese et al. 2005, Roman et al. 2005). Despite the number of significant relationships, there is clear evidence that several factors are of greater importance in structuring the mesozooplankton community. These include: 1) spatial differences in the mesozooplankton community between sub-regions (Table 3.1 and Fig. 3.3); 2) an interannual effect with a break in May 1997 (Figures 3.2 and 3.4); and 3) a strong positive correlation with salinity (Tables 3.2 and 3.3; Figure 3.5).

Sub-regional distinctions in mesozooplankton communities were expected, given the spatial heterogeneity that has previously been observed within Florida Bay and the relative isolation of the sub-regions with residence times on the order of several months (Boyer et al. 1997, Lee et al. 2006, Lee et al. 2008). The north-central sub-region had the largest median biomass of mesozooplankton and was dominated by nauplii followed by copepodites and adult copepods. Although this sub-region receives little freshwater run-off, it is highly productive with occasional intense seasonal algal blooms and high seagrass biomass (Kelble et al. 2005, Hunt & Nuttle 2007). This available organic matter supports a large amount of microbial activity in this sub-region, which may in turn support the higher mesozooplankton biomass. It has been suggested by inverse network analysis that heterotrophic bacteria associated with increased microbial activity may be grazed upon by microzooplankton that are then grazed by mesozooplankton (Richardson et al. 2003). The west sub-region had the next highest abundance of mesozooplankton and again was dominated by adult copepods, copepodites and nauplii. This sub-region receives indirect freshwater runoff from the Shark River and undergoes seasonal diatom blooms when runoff is elevated in the fall (Jurado et al. 2007). These diatom blooms are potentially able to support substantial copepod populations that directly consume the diatoms. However, chlorophyll *a* was uncorrelated with mesozooplankton in the west (Table 3.3). Interestingly, the two sub-regions with the highest abundances of mesozooplankton (west and north-central) are also the sub-regions with the highest percent nauplii composition that may indicate that copepod populations in these sub-regions are more productive. Both the south and the northeast had lower mesozooplankton abundance and were dominated by Copepoda, primarily *Oithona*. The northeast sub-region is oligotrophic with the lowest seagrass biomass and likely can only support a low abundance of mesozooplankton (Richardson et al. 2003). The south sub-region is also oligotrophic, in part because of exchange with the coastal waters of the Florida Keys through tidal channels (Lee et al. 2002).

Interannual differences showed a specific break in mesozooplankton community structure in May of 1997 (Fig. 3.2 and 3.4). This break did not correspond with any of the climatic cycles, such as ENSO and the North Atlantic Oscillation (NAO), known to affect Florida Bay's physical environment or mesozooplankton communities elsewhere (Kelble et al. 2007, Allen et al. 2008). However, this early period does correspond to a period of heightened bay anchovy, *Anchoa mitchilli*, abundance (Thayer et al. 1999, Ortner et al. 2001). *A. mitchilli* is the dominant zooplanktivorous fish in Florida Bay (Powell et al. 2007) and can play a key role in structuring mesozooplankton communities (Mowitt et al. 2006). Interestingly, this time period also corresponds to an inflection point in south Florida's hydrology when a severe drought ended with several wet years (Briceno & Boyer 2008). This appears to have reduced the maximum salinities in Florida Bay to such a degree that hypersalinity was not prevalent even during the summer months (Fig. 3.2). This lack of hypersalinity may have caused the increased abundance of *A. mitchilli*, which prefer lower salinities (Lewis et al. 2007, Putland & Iverson 2007).

The correlation between mesozooplankton and salinity (Tables 3.2 and 3.3; Figure 3.5) was both expected and fortuitous, because salinity is the abiotic factor that will be most directly altered by CERP projects. However, the nature of the relationship between salinity and mesozooplankton in Florida Bay is unique. In the majority of estuaries including an adjacent embayment, low salinities are associated with high productivity because of high nutrient loads from runoff and mesozooplankton abundance is inversely related to salinity with peak abundance at salinities significantly below the adjacent coastal ocean (Woodmansee 1958, Greenwald & Hurlbert 1993, Kimmel et al. 2006b, Zhang et al. 2006, Putland & Iverson 2007). Contrarily, in Florida Bay mesozooplankton abundance is positively correlated with salinity (Spearman rho = 0.354, $p < 0.01$) and all seven of the major taxa have their highest median abundance during hypersaline conditions (Fig. 3.6).

The effect of salinity is not just upon mesozooplankton abundance, but also upon the number of mesozooplankton functional groups observed (Fig. 3.7). However, an important caveat to this observation is that this study only delineated taxa down to functional groups and not species. In any case, the relationship between functional groups and salinity was also contrary to the majority of other estuaries with the number of functional groups increasing linearly with salinity ($F_{1, 281} = 109$, $R^2 = 0.28$, $p<0.001$), and this increase continued into periods of hypersalinity (Fig. 3.7). This positive correlation is surprising given that a negative correlation between zooplankton diversity and salinity has been found in similar systems to Florida Bay (Brucet et al. 2009).

Evidence of Top-Down Effect

There are three potential explanations for the increased abundance (and possibly diversity) of mesozooplankton during hypersaline periods in Florida Bay: 1) increased prey available at higher salinities; 2) a physiological advantage at higher salinities; and/or 3) decreased predation at higher salinities. These hypotheses are not mutually exclusive and it is likely that different controlling mechanisms may be structuring the mesozooplankton community at different temporal and spatial scales. The goal herein is to determine which of these mechanisms best explains the positive correlation between mesozooplankton and salinity in Florida Bay.

The possibility of increased phytoplankton prey at high salinities was examined by correlation analysis of parameters related to pelagic primary productivity and salinity in Florida Bay (Table 3.4). This analysis found significant negative correlations with salinity and at least one parameter associated with pelagic primary productivity in each sub-region of Florida Bay and no positive correlations with salinity. The overall data displayed a significant correlation with salinity and every water quality parameter associated with pelagic primary productivity, except SRP. However, these correlations were both positive and negative indicating that there is not a clear correlation between salinity and pelagic primary productivity. Thus, it is unlikely that pelagic primary productivity systematically increases with salinity.

However, most copepods and many other mesozooplankton are omnivorous and their prey field may be dominated by bacterioplankton and/or microzooplankton that are unrelated to pelagic primary productivity. Unfortunately, data on microzooplankton in Florida Bay is too sparse to investigate its potential effect on mesozooplankton. Bacterial productivity and abundance data was available from May 2001 through January 2003 (Boyer unpublished data). No correlation was found between salinity and bacterial productivity or bacterial abundance throughout Florida Bay (Spearman rho = -0.070, $p > 0.1$ and rho = 0.024, $p > 0.1$, respectively). When delineated by sub-regions, there were significant inverse correlations ($p < 0.05$) between bacterial productivity and abundance with salinity in the northeast (Spearman rho = -0.488 and -0.488) and bacterial productivity with salinity in the north-central (Spearman rho = -0.417). However, no significant correlations were observed in the west or south. The lack of a systematic positive correlation to salinity with bacterial productivity, bacterial abundance, chlorophyll *a* or nutrients likely indicates that there is not increased bacterioplankton or phytoplankton prey available at high salinities; however, no comment can be made with regards to microzooplankton, because of the scarcity of data.

Furthermore, the BEST analyses always included salinity, but rarely included any parameters correlated with primary productivity. The analyses never included chlorophyll *a* or SRP, only once included TOC and only twice included TP (Table 3.2) indicating that many of the parameters correlated with primary productivity in Florida Bay were not as strongly correlated as salinity with mesozooplankton structure. This does not mean bottom-up controls are unimportant. In fact, they are well correlated with the sub-regional differences between mesozooplankton communities and chlorophyll *a* was significantly correlated with 4 of the 7 mesozooplankton taxa as discussed previously.

Physiological effects are another possible limiting factor and not easily dismissed. The dominant functional groups all have individual salinity optimums, but often the rate of change in salinity can cause greater physiological stress than the median salinity (Cervetto et al. 1999). This is likely to be of importance in Florida Bay which can undergo dramatic salinity decreases, while increases are more gradual (Kelble et al. 2007). Thus, lower salinity periods sometimes occur after rapid decreases, whereas hypersalinity periods always occur during very stable gradual increases. While numerous laboratory studies have been conducted to establish several *Acartia* species as euryhaline

(Cervetto et al. 1999, Calliari et al. 2008), similar laboratory studies are not available for *Oithona* or Paracalanidae. Microcosm experiments using organisms from San Dieguito Lagoon, which has a similar salinity range to Florida Bay, found an inverse relationship between salinity and total mesozooplankton abundance for salinities greater than 17 that was independent of predation and food limitation. Overall, copepods were scarce in the hypersaline microcosm that had a salinity of 51. Furthermore, that study found *Acartia* abundance to peak at a salinity of 34 and *Oithona* and Harpacticoida abundance both peaked between 17-34 (Greenwald & Hurlbert 1993). A study in adjacent Biscayne Bay found a negative correlation with total zooplankton abundance and salinity, exactly the opposite of what was observed in this study (Woodmansee 1958). Based on these studies, it is unlikely that improved physiological performance in hypersaline waters is the primary cause of increased abundance of Copepoda or its nauplii during hypersaline conditions.

The other possible explanation for higher mesozooplankton abundance in the hypersaline periods is decreased predation. The primary planktivorous fish in Florida Bay, *A. mitchilli*, is found throughout many estuaries and can play a key role in structuring zooplankton communities (Baird & Ulanowicz 1989, Luo & Brandt 1993, Mowitt et al. 2006). In a nearby sub-tropical embayment the relationship between *Acartia tonsa* viable egg production per female and salinity peaks at a salinity of less than 10 and decreases significantly at salinities greater than 14, yet abundance was observed to peak at a salinity of 20. This was hypothesized to be a result of increased abundance of *A. mitchilli* at salinities less than 20 (Putland & Iverson 2007). *A. mitchilli* are known to inhabit estuaries with salinities significantly less than oceanic and was the dominant species during the summer in low salinity areas throughout the Gulf of Mexico (Lewis et al. 2007). Within Florida Bay its population increased dramatically during a period from 1994-1996 when hypersalinity did not occur (Thayer et al. 1999).

An examination of zooplanktivorous fish data collected in Florida Bay from 1984 to 1985 and 1994 to 2001 was undertaken to quantify relationships to salinity and interannual variability. This data was collected as part of a separate study in Florida Bay and detailed methods and results are presented elsewhere (Thayer et al. 1999, Powell et al. 2007).The frequency of occurrence of planktivorous fish had an inverse linear relationship with salinity throughout Florida Bay (Fig. 3.8, $F_{1,4} = 80.8$, $p<0.001$, $R^2 = 0.95$). Moreover the mean abundance peaked at a salinity of 25-30 (0.077 fish m^{-2}) and decreased by an order of magnitude in hypersaline conditions (0.008 fish m^{-2}). Throughout all salinity bins, *Anchoa* was the dominant genus of the zooplanktivorous fish community accounting for greater than 81% of the community by number in any individual bin. This indicates that predation pressure on mesozooplankton was significantly greater during lower salinities consistent with mesozooplankton abundance peaking during hypersalinity.

Unfortunately, the sample collection of fish ended in 2001 and did not completely overlap with the mesozooplankton data. Despite this, strong interannual differences are apparent in the zooplanktivorous fish community that indicate top-down predation may also be the primary factor responsible for the interannual differences (Fig. 3.4). Specifically, the frequency of occurrence in 1994, 1995 and 1996 was more than double other years and the abundance was more than 6-fold greater than other years (Fig. 3.9).

This higher abundance of zooplanktivorous fish from 1994 to 1996 may explain the lower abundances of mesozooplankton observed during this time period.

However, these insights are purely correlative and it is necessary to determine if consumption of mesozooplankton by zooplanktivorous fish could possibly account for the observed differences. The productivity of mesozooplankton and consumption of planktivorous fish in Florida Bay were calculated utilizing equations with a number of underlying assumptions and thus were compared only to ensure that they were roughly equivalent and did not rule out the importance of top-down control. Mesozooplankton productivity in g m^{-3} d^{-1} was calculated from the median abundance observed during hypersaline periods. This period was selected due to the presumed minimal loss to predation. The abundances of each mesozooplankton taxa were converted to biovolumes based on the length and width measurements quantified for a one-year subset of these samples. The summed biovolumes were then converted to biomass assuming that 1 mm^3 of biovolume is equal to 1.05 mg biomass (Patoine et al. 2006). The biomass in g m^{-3} was then converted to productivity assuming a 2-week generation time (Paffenhofer 1993, Schipp et al. 1999). This yielded an estimated mesozooplankton productivity of 0.0337 g m^{-3} d^{-1}. To calculate zooplanktivorous fish consumption the mean abundance at salinities less than 30 was calculated from the data in Powell et al. 2007 (0.0676 fish m^{-2}). The entire zooplanktivorous fish community was assumed to be *A. mitchilli* since they accounted for greater than 97% of the zooplanktivorous fish abundance. Abundance was converted to density assuming the trawl sampled the lower 0.5m of the water column which is on average 1.5m deep in Florida Bay (Kelble et al. 2007). Density was converted to biomass assuming a biomass of 0.35 g $fish^{-1}$, which was the mean weight of

A. mitchilli collected in Florida Bay (Powell et al. 2007). This biomass was converted to consumption based upon a consumption rate of 20% of the fish biomass per day that was estimated from a bioenergetics model for *A. mitchilli* (Luo & Brandt 1993). The result was a consumption rate of 0.0203 g m^{-3} d^{-1} in Florida Bay, which is reasonably close to the mesozooplankton production rate of 0.0337 g m^{-3} d^{-1}.

These findings support the hypothesis that top-down control is an important regulator of mesozooplankton abundance in Florida Bay. Increased predation at low salinities significantly contributes to decreased mesozooplankton abundance and diversity, while hypersalinity provides a refuge from predation allowing mesozooplankton to increase in abundance and diversity. This refuge may exist in part because anthropogenic manipulations to this system over the past century have increased the severity of hypersalinity (Swart et al. 1996, Swart et al. 1999). At low salinities, increased predation may result in a more efficient trophic transfer that increases the amount of energy available to upper trophic levels including commercial and recreational fishery species.

Potential Impact of Everglades Restoration

Given these significant relationships with salinity, it is probable that Everglades Restoration will alter the mesozooplankton community. The goal of the restoration with respect to Florida Bay is to minimize hypersalinity and return to a more temporally and spatially diffuse runoff pattern. A successful restoration will reduce hypersaline intervals during which mesozooplankton appear to have a refuge from predators and increase in abundance. This is likely to mimic the salinity patterns observed from 1994 to 1996 and is likely to decrease mesozooplankton abundance. The decrease is potentially a positive with respect to overall ecosystem health, because it is not necessarily reflective of decreased mesozooplankton production, but of increased predator abundance. In fact, some mesozooplankton such as *Acartia tonsa* are more productive at lower salinities (Putland & Iverson 2007). Thus, the decrease in abundance may indicate a more efficient trophic transfer with more mesozooplankton being consumed by planktivorous fish.

Conclusions

Mesozooplankton in Florida Bay are significantly correlated with water quality parameters, specifically salinity. This strong correlation with salinity is a common finding in coastal and estuarine mesozooplankton communities; however, in previous investigations the correlation was negative or mesozooplankton abundance peaked far below the adjacent oceanic salinities (Greenwald & Hurlbert 1993, Park & Marshall 2000, Mouny & Dauvin 2002, Putland & Iverson 2007, Brucet et al. 2009), whereas in this study peak mesozooplankton abundances were observed during hypersaline periods. Three characteristics had a dominant role in structuring the mesozooplankton community of Florida Bay: 1) sub-regional differences in the mesozooplankton community, 2) a break in May of 1997 with a distinct mesozooplankton structure before and after this date throughout the Bay and 3) a positive correlation between mesozooplankton abundance and salinity.

The difference between sub-regions was expected and is almost certainly a function of sub-regional differences in freshwater sources, nutrient sources, and trophic structure (Phlips & Badylak 1996, Boyer et al. 1997, Richardson et al. 2003, Kelble et al. 2007). The difference in mesozooplankton before and after May of 1997 was not expected. If interannual differences were observed, it was expected that they would be correlated with climatic cycles, such as ENSO. Instead this disjunction seems to be correlated with changes in predator abundance. The positive correlation with mesozooplankton and salinity is likely also a reflection of predation pressure, with the dominant zooplanktivorous fish favoring lower salinities. The hypersalinity time periods could provide a refuge from predation, thus allowing the mesozooplankton to increase in abundance and diversity although not occupying their physiologically preferred environment.

One of the goals of Everglades Restoration is to reduce the magnitude, duration and spatial extent of hypersalinity in Florida Bay. Our data suggests this may result in reduced mesozooplankton abundance, but not as a result of decreased secondary productivity, rather as a result of increased predation. Therefore, restoration could result in a more efficient trophic network translating to increased upper trophic level productivity.

Table 3.1 Mann-Whitney U-test p-values comparing the abundance of the seven most common mesozooplankton taxa between sub-regions in Florida Bay. The significant values (∝=0.05) are in bold and the arrow indicates the direction of significant differences with respect to the sub-region given in the row (i.e. *Acartia* is significantly more abundant in the north-central sub-region than all three other sub-regions).

Acartia

	NE	NC	S	W
NE	---	**<0.001↓**	0.310	0.573
NC	**<0.001↑**	---	**<0.001↑**	**<0.001↑**
S	0.310	**<0.001↓**	---	0.603
W	0.573	**<0.001↓**	0.603	---

Oithona

	NE	NC	S	W
NE	---	**<0.001↓**	0.086	**0.003↓**
NC	**<0.001↑**	---	**0.024↑**	0.186
S	0.086	**0.024↓**	---	0.256
W	**0.003↑**	0.186	0.256	---

Paracalanidae

	NE	NC	S	W
NE	---	0.128	**0.017↓**	0.208
NC	0.128	---	0.629	0.653
S	**0.017↑**	0.629	---	0.306
W	0.208	0.653	0.306	---

Harpacticoida

	NE	NC	S	W
NE	---	**<0.001↓**	**<0.001↓**	**<0.001↓**
NC	**<0.001↑**	---	0.117	**0.004↓**
S	**<0.001↑**	0.117	---	**<0.001↓**
W	**<0.001↑**	**0.004↑**	**<0.001↑**	---

Gastropoda

	NE	NC	S	W
NE	---	0.073	0.589	0.747
NC	0.073	---	**0.036↑**	0.178
S	0.589	**0.036↓**	---	0.410
W	0.747	0.178	0.410	---

Bivalvia

	NE	NC	S	W
NE	---	**0.009↓**	0.653	0.343
NC	**0.009↑**	---	**0.015↑**	**0.003↑**
S	0.653	**0.015↓**	---	0.833
W	0.343	**0.003↓**	0.833	---

Nauplii

	NE	NC	S	W
NE	---	**<0.001↓**	0.053	**<0.001↓**
NC	**<0.001↑**	---	**<0.001↑**	0.164
S	0.053	**<0.001↓**	---	**0.001↓**
W	**<0.001↑**	0.164	**0.001↑**	---

Table 3.2 Results from the BEST routine in PRIMER® display the 10 combinations of water quality parameters with the highest correlation to mesozooplankton community structure.

Variables Included	**ρ (Rho)**	**p-level**
Salinity, Temperature, Turbidity, NH_4	0.232	0.001
Salinity, Temperature, NH_4	0.217	0.001
Salinity, Temperature, Turbidity	0.216	0.001
Salinity, Turbidity, NH_4	0.215	0.001
Salinity, Temperature, Turbidity, NO_X, NH_4	0.212	0.001
Salinity, Temperature	0.211	0.001
Salinity, Temperature, TOC, Turbidity, NH_4	0.206	0.001
Salinity, Temperature, TP, Turbidity, NH_4	0.206	0.001
Salinity, Temperature, NO_X, NH_4	0.199	0.001
Salinity, Temperature, TP, NH_4	0.198	0.001

Table 3.3 Spearman rho correlation coefficients between the 7 most common mesozooplankton taxa and water quality parameters throughout Florida Bay (n=283) and within each of the four sub-regions (northeast n=89, north-central n=52, south n=63 and west n=79). The significant values at α = 0.05 after Bonferroni correction are bold, italicized, and underlined.

		Nauplii	Bivalvia	Gastropoda	*Oithona*	*Acartia*	Paracalanidae	Harpacticoida
All	Salinity	***0.382***	0.192	***0.251***	***0.330***	0.047	-0.029	***0.483***
	TP	0.081	-0.068	-0.175	-0.005	0.012	0.037	***0.238***
	Chl *a*	***0.272***	0.166	-0.001	***0.222***	0.149	***0.208***	***0.369***
	DIN	***-0.198***	0.057	-0.088	-0.147	-0.013	-0.041	***-0.311***
	TOC	***-0.240***	0.076	-0.138	-0.091	0.032	-0.085	***-0.419***
	Temp.	0.102	***0.234***	0.158	***0.202***	0.020	-0.077	0.015
	Turbidity	-0.034	-0.028	-0.142	-0.131	0.022	-0.007	0.069
Northeast	Salinity	0.256	0.195	0.159	0.202	-0.098	-0.115	***0.373***
	TP	***-0.352***	-0.296	-0.318	***-0.354***	-0.234	0.051	-0.222
	Chl *a*	-0.176	-0.081	-0.199	-0.083	-0.217	0.075	-0.097
	DIN	-0.028	0.112	0.071	0.070	-0.048	0.282	-0.099
	TOC	***-0.598***	-0.330	***-0.352***	***-0.544***	***-0.493***	-0.311	***-0.533***
	Temp.	0.019	0.112	0.020	-0.049	-0.006	0.063	-0.084
	Turbidity	-0.203	-0.084	-0.095	-0.074	-0.097	0.132	-0.067
North-central	Salinity	0.317	0.166	0.342	0.122	0.317	-0.328	0.321
	TP	0.007	0.133	-0.215	-0.066	0.095	-0.014	-0.094
	Chl *a*	-0.177	0.227	-0.322	0.171	0.014	0.326	-0.164
	DIN	***-0.475***	-0.311	-0.377	-0.430	***-0.443***	0.022	-0.332
	TOC	-0.162	0.152	-0.238	0.268	0.044	0.323	-0.218
	Temp.	0.062	0.329	0.224	0.313	0.266	-0.071	-0.114
	Turbidity	0.037	0.232	-0.226	0.021	0.123	-0.025	0.065
South	Salinity	0.385	0.342	***0.477***	***0.434***	0.196	-0.001	0.242
	TP	-0.248	-0.165	-0.282	-0.173	-0.053	0.045	-0.109
	Chl *a*	0.194	0.252	-0.002	0.234	0.334	0.332	0.244
	DIN	-0.215	-0.009	-0.227	-0.061	-0.143	-0.217	-0.128
	TOC	-0.018	0.140	-0.059	0.182	0.009	-0.041	-0.053
	Temp.	0.054	0.213	0.135	0.273	0.014	-0.167	-0.030
	Turbidity	-0.337	-0.211	-0.300	***-0.439***	-0.19	0.046	-0.211
West	Salinity	***0.469***	***0.431***	***0.393***	***0.411***	-0.063	-0.085	***0.394***
	TP	***-0.421***	-0.191	***-0.460***	-0.313	0.002	-0.069	-0.286
	Chl *a*	-0.105	-0.045	0.197	-0.048	0.252	0.249	-0.106
	DIN	-0.136	-0.041	-0.201	-0.204	-0.125	-0.256	-0.033
	TOC	***-0.367***	-0.072	-0.303	-0.260	-0.064	***-0.373***	-0.285
	Temp.	0.180	***0.372***	0.278	0.305	-0.080	-0.226	0.057
	Turbidity	***-0.380***	-0.264	***-0.477***	***-0.538***	-0.047	-0.086	-0.213

Table 3.4 Spearman rho correlation coefficients between salinity and water quality parameters related to pelagic primary production throughout Florida Bay (n=283) and within each of the four sub-regions (northeast n=89, north-central n=52, south n=63 and west n=79). The significant values at α = 0.05 are bold, italicized, and underlined.

	Overall	Northeast	North-central	South	West
Chlorophyll *a*	***0.225***	0.032	***-0.331***	-0.092	***-0.228***
DIN	***-0.313***	-0.020	***-0.313***	-0.201	0.063
TP	***0.149***	***-0.236***	-0.182	***-0.278***	***-0.367***
TOC	***-0.235***	0.031	-0.149	-0.030	***-0.230***
SRP	-0.033	-0.131	-0.193	0.050	0.110

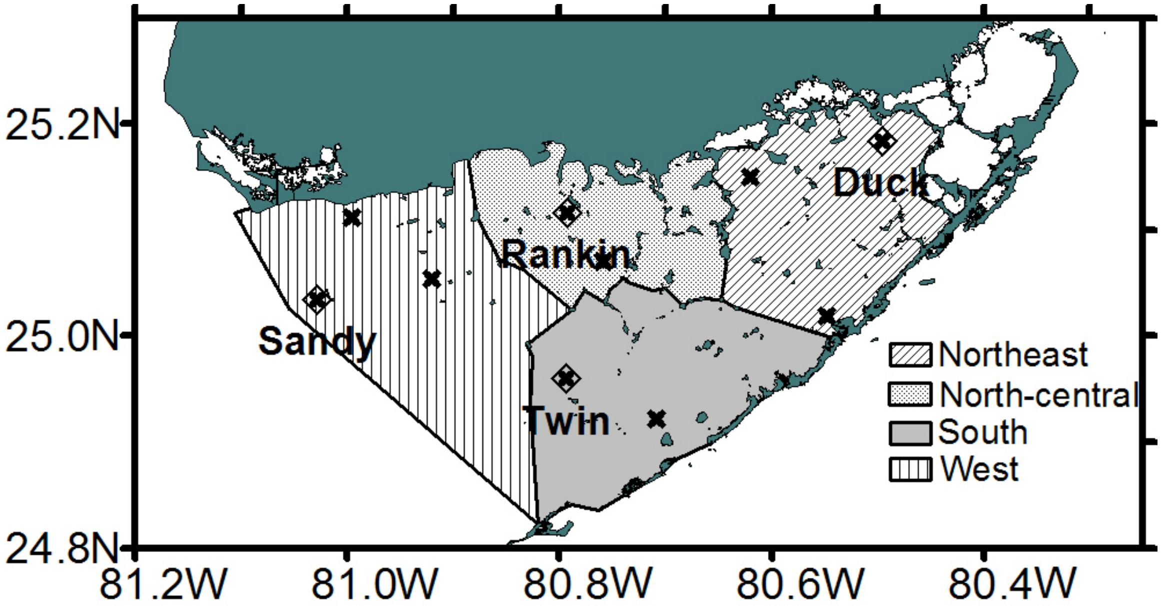

Figure 3.1 Map of Florida Bay depicting the sub-regional delineations within the Bay. The ten stations sampled are indicated with an **X** and the four core stations are labeled with their names.

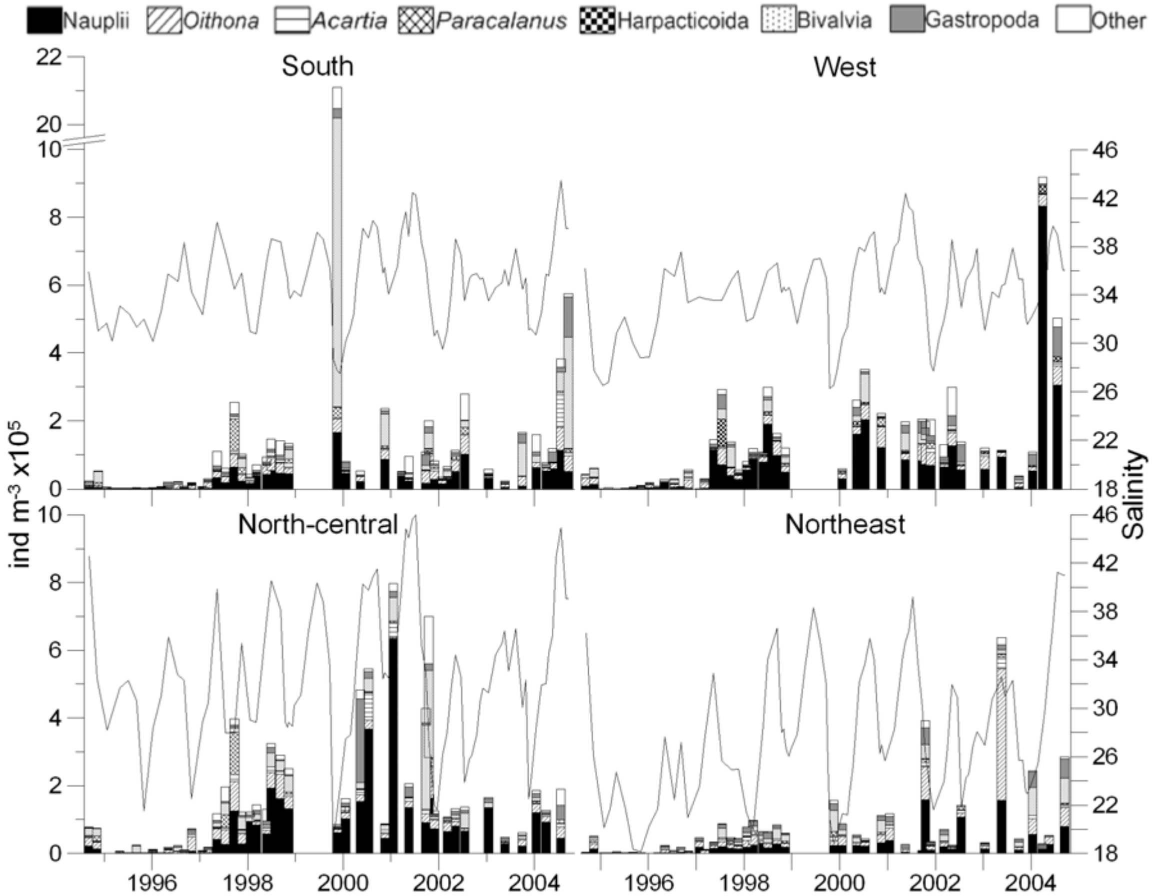

Figure 3.2 Time series of mesozooplankton abundance (delineated by broad taxonomic categories) and mean salinity within each sub-region.

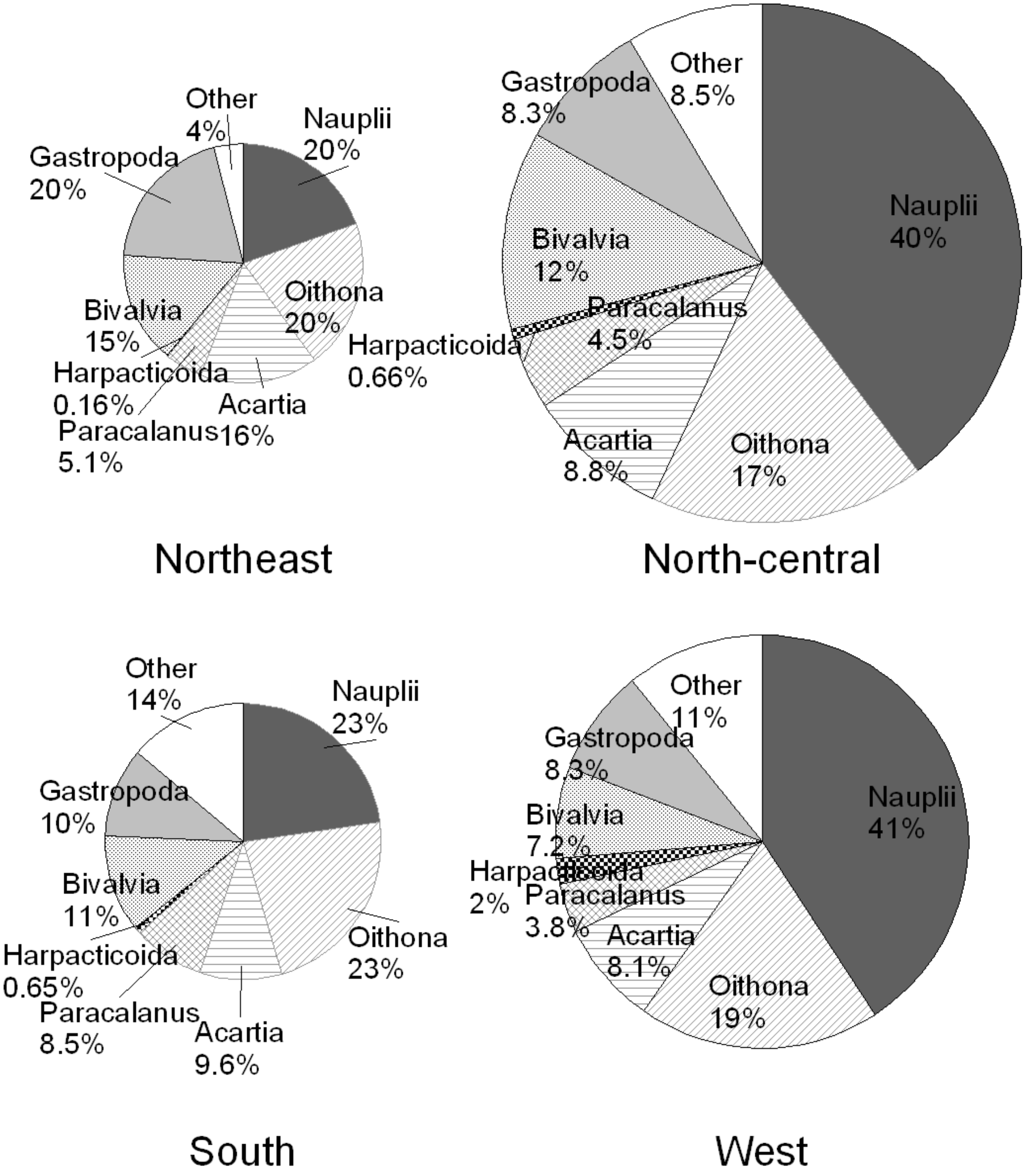

Figure 3.3 Pie charts depicting the mean percent contribution of the seven mesozooplankton taxa in each sub-region, scaled by the median mesozooplankton abundance for that sub-region.

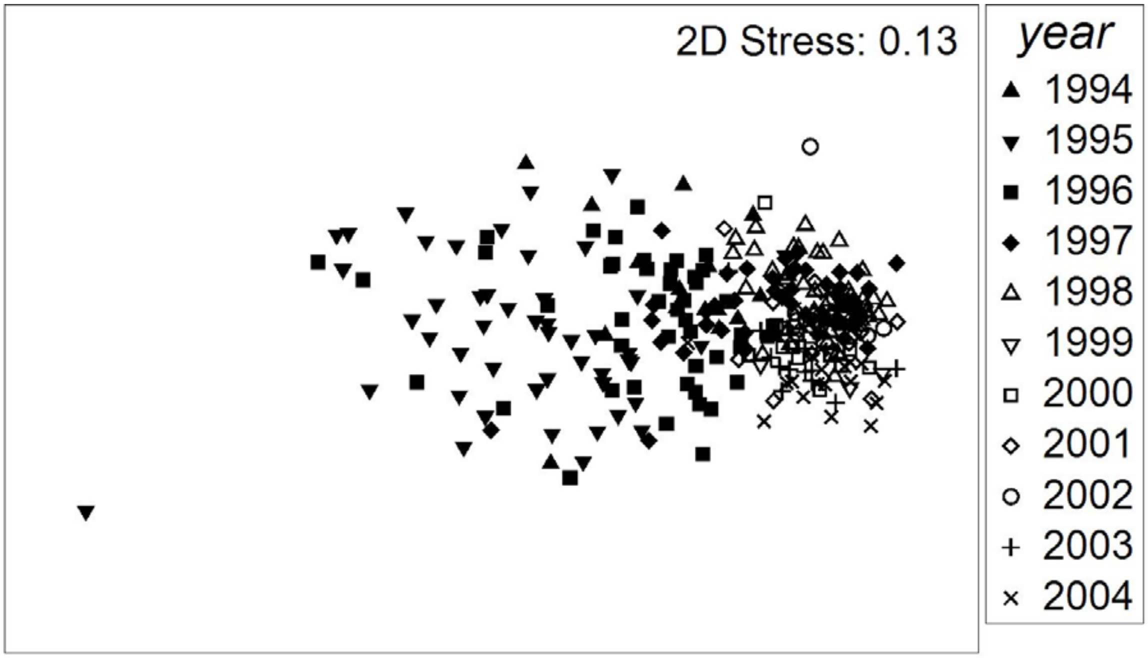

Figure 3.4 Plot of the two-dimensional n-MDS of mesozooplankton assemblages grouped by year.

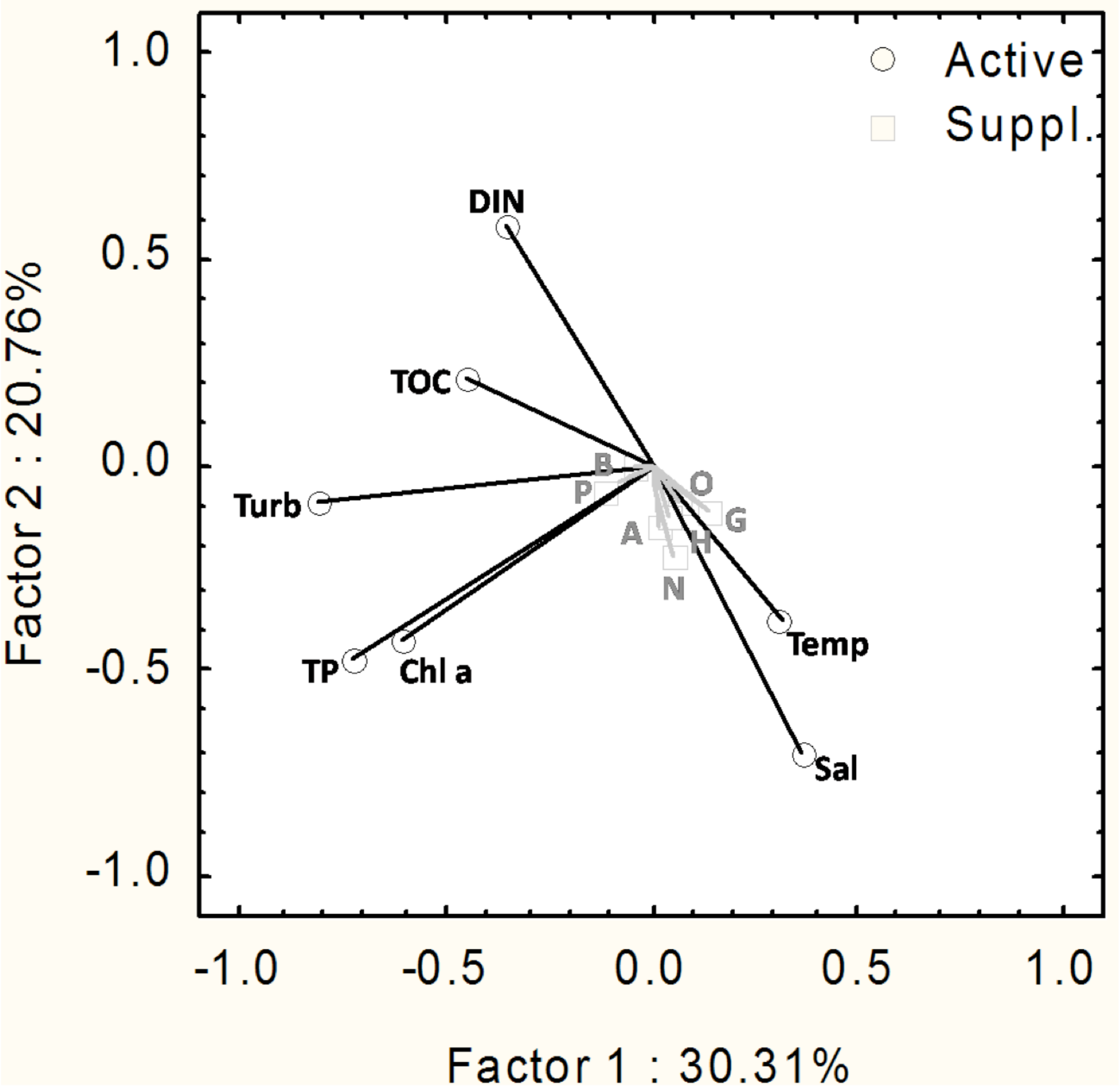

Figure 3.5 Plot depicting the location and trajectory of the seven water quality parameters on the two-dimensional factor-plane from principal components analysis (PCA). Overlaid in grey on this plot is the location and trajectory of the seven most common mesozooplankton taxa as supplemental variables, because they were not utilized to calculate the eigenvalues and eigenvectors in the PCA (A=*Acartia*, O=*Oithoina*, P=Paracalanidae, H=Harpacticoida, N=nauplii, G=Gastropoda and B=Bivalvia).

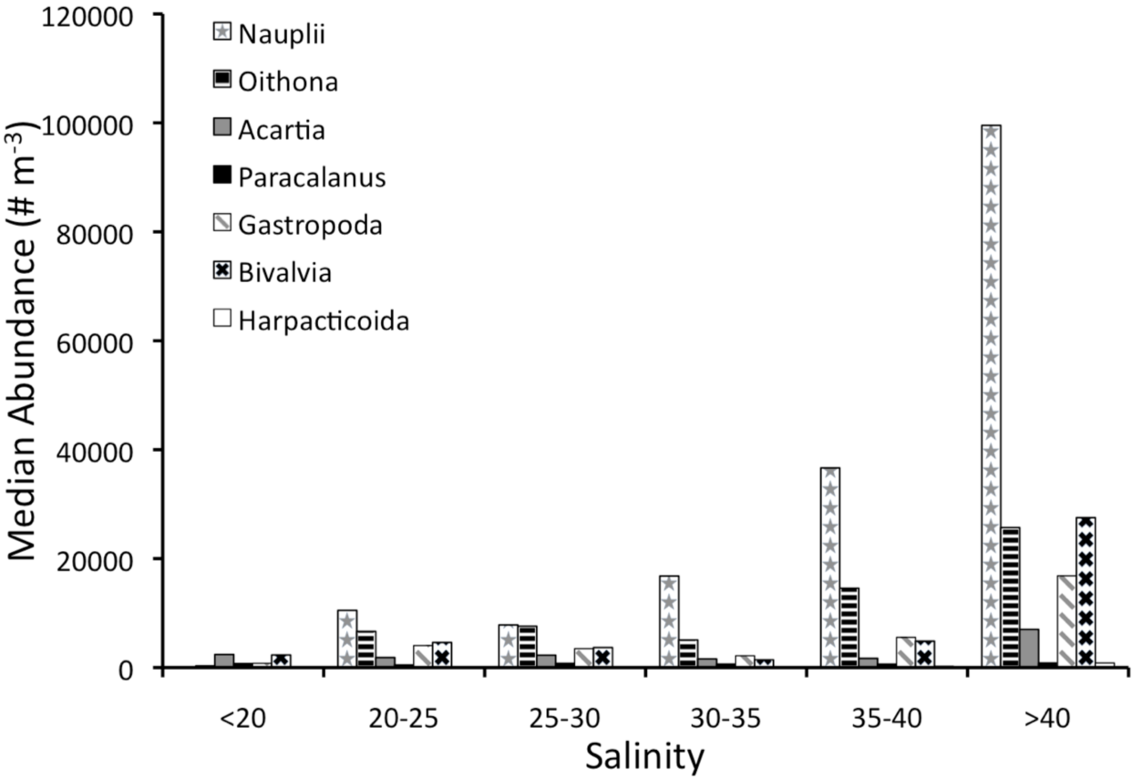

Figure 3.6 The median abundance is depicted for the seven most common mesozooplankton taxa in each of the salinity bins delineated.

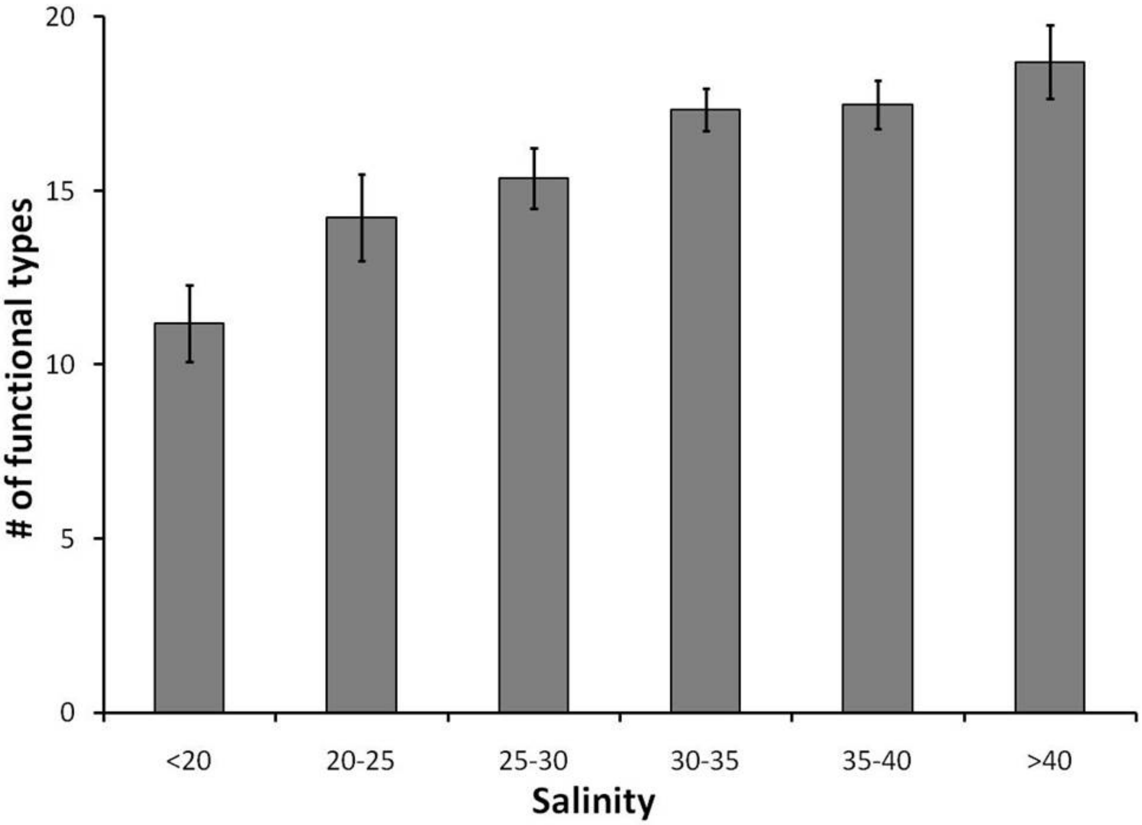

Figure 3.7 The mean number of functional groups for each salinity bin with error bars depicting the 95% confidence interval.

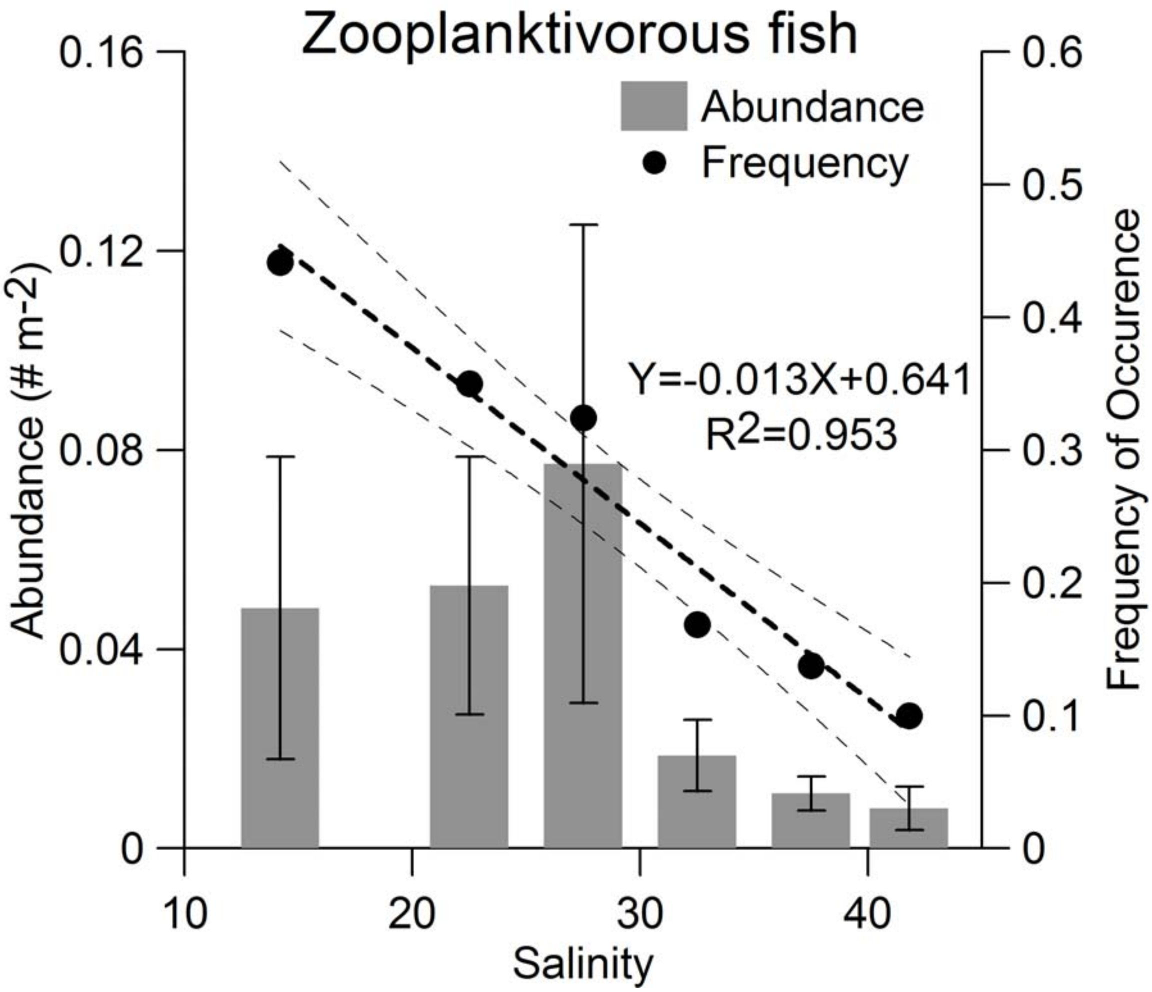

Figure 3.8 Abundance and frequency of occurrence of planktivorous fish in Florida Bay plotted versus salinity. Data are from Powell et al. 2007.

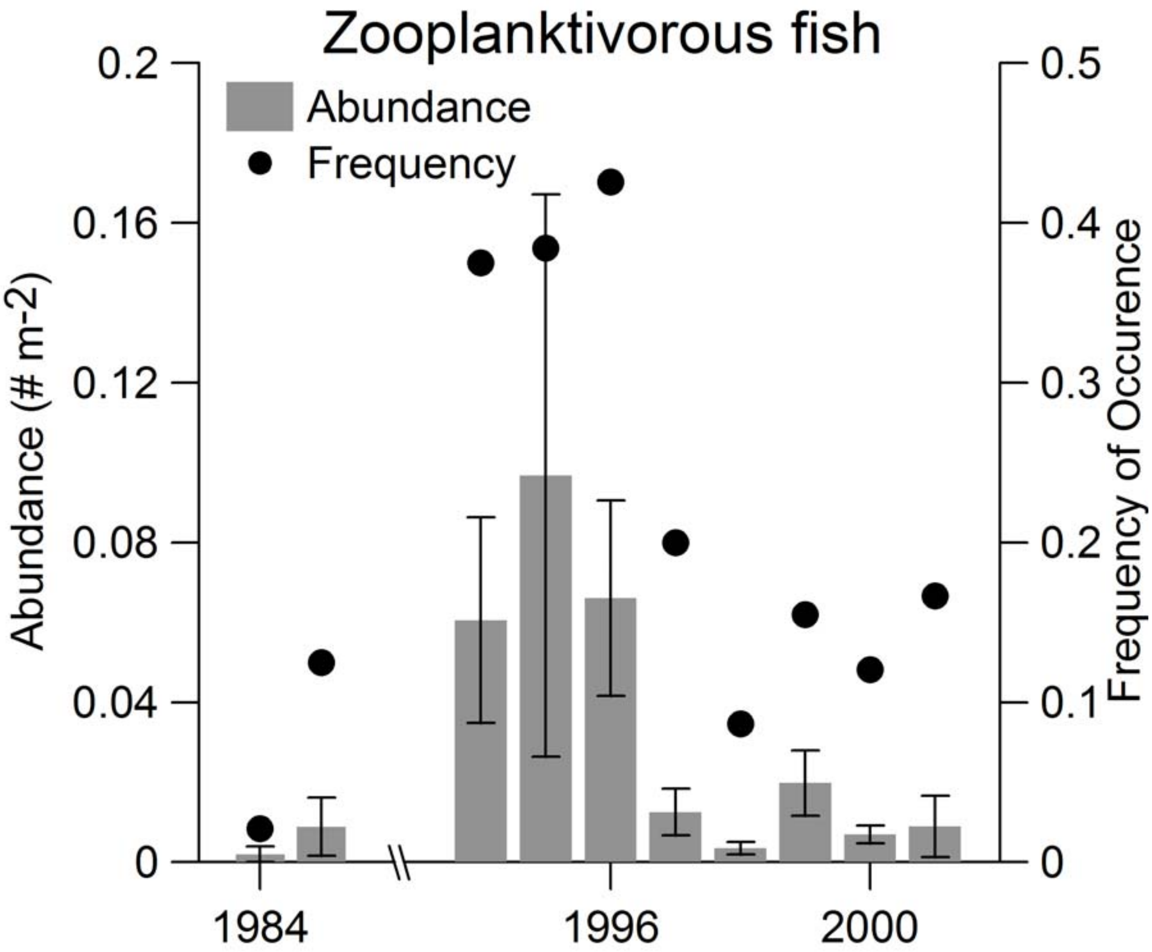

Figure 3.9 Abundance and frequency of occurrence of planktivorous fish by year in Florida Bay. Data are from Powell et al. 2007.

CHAPTER 4
MODELING BAY ANCHOVY, *ANCHOA MITCHILLI*, PREDATION ON MESOZOOPLANKTON COMMUNITIES IN A SUB-TROPICAL EMBAYMENT

Summary

The interaction between *Anchoa mitchilli* and mesozooplankton is closely correlated to salinity in sub-tropical bays. Variability in this relationship can propagate both up and down the trophic-network. This key trophic interaction was investigated in Florida Bay, USA with a mechanistic model to simulate mesozooplankton and *A. mitchilli*, populations from 1994 through 2001. From 1994 through May 1997, salinities were lower, *A. mitchilli* were significantly more abundant, and mesozooplankton were significantly less abundant than after May 1997 accurately reflecting observed population patterns. During this period, the model suggests predation was the dominant control on mesozooplankton. After May 1997, *A. mitchilli* abundance decreased, mesozooplankton abundance increased, and the model suggested resources primarily limited mesozooplankton during this period. The model output suggests the presence of a trophic cascade initiated by high *A. mitchilli* abundance during the early part of the simulation. This is supported by observations of higher phytoplankton biomass during this period that may in part be due to decreased grazing by mesozooplankton. However, omnivory by mesozooplankton confounds the impact of the trophic cascade on phytoplankton abundance by altering the microzooplankton population and thus their grazing pressure. Results from the model indicate that changing salinity patterns associated with climactic cycles or anthropogenic activities could have significant impacts on the abundance of mesozooplankton and *A. mitchilli*, and thereby influence the larger trophic network.

Background

The relationship between *Anchoa mitchilli* and mesozooplankton can have a major influence in structuring the pelagic trophic web of coastal ecosystems (Mowitt et al. 2006, Ludsin et al. 2009). Mesozooplankton occupy a key trophic niche that transfers energy from pelagic primary producers and microzooplankton to fish (Wiebe et al. 2000). Several studies have highlighted the importance of predators in structuring the mesozooplankton community in coastal embayments (Purcell 1997, Mowitt et al. 2006, Putland & Iverson 2007, Kelble et al. 2010). Other studies have alternatively hinted that bottom-up controls are dominant, specifically phytoplankton community dynamics (Murrell & Lores 2004). *A. mitchilli* is the primary prey for several commercial and recreational fish species (Baird & Ulanowicz 1989). Other species from the same sub-family, Engraulinae, occupy a wasp-waist niche in other coastal ecosystems (Shannon et al. 2008) meaning they are the only species or one of a few species that dominate intermediate trophic levels. Thus, changes in their population can propagate both up and down the trophic web creating significant changes throughout the ecosystem (Bakun 1996).

Investigations in a variety of coastal ecosystems have shown a correlation between mesozooplankton abundance and salinity (Woodmansee 1958, Greenwald & Hurlbert 1993, Kimmel & Roman 2004, Kimmel et al. 2006b, Kelble et al. 2010). These correlations are typically positive, and reflect either physiological preferences, or increased prey availability, at lower salinities that are often associated with increased nutrient loading from runoff (Kimmel & Roman 2004). However, in some sub-tropical ecosystems the peak abundance of mesozooplankton is shifted farther up the salinity spectrum than could be expected from sheer physiology (Putland & Iverson 2007, Kelble et al. 2010). In both such studies, the shift was correlated with an increased abundance of *A. mitchilli* at lower salinities. Increased abundance of *A. mitchilli* at lower salinities can be explained by a salinity response in juvenile recruitment (Peebles et al. 2007).

The role salinity might play in mediating the interaction between mesozooplankton and *A. mitchilli* is important, given that there will be changes in coastal ocean salinity patterns due to both local and regional forcing events. Cyclical climactic phenomena are correlated with significant changes in regional rainfall patterns (Sun & Furbish 1997) that can, in turn, influence the salinity of ecosystems further downstream (Kelble et al. 2007). Moreover, recent studies have suggested that freshwater runoff is decreasing globally at temperate and tropical latitudes (Dai et al. 2009).

Florida Bay provides an ideal study site to examine the interaction among salinity, mesozooplankton, and *A. mitchilli*. The time-series for mesozooplankton and *A. mitchilli* are synoptic, overlap for 8-years from 1994 to 2001, and encompass a period of significant change in these populations and a large degree of salinity variability. From 1994 through May 1997, mesozooplankton were approximately an order of magnitude less abundant and *A. mitchilli* were approximately two-fold more abundant then from May 1997 through the end of 2001 (Kelble et al. 2010). This period of heightened *A. mitchilli* abundance coincided with the occurrence of persistent wide-spread phytoplankton blooms (Butler et al. 1995, Hitchcock et al. 2007) and lower salinities (Thayer et al. 1999). These observations led to a hypothesis that Florida Bay had undergone a regime shift from benthic dominance of primary productivity to pelagic and thus altered the trophic structure (Thayer et al. 1999). However, a subsequent study found benthic productivity to still dominate Florida Bay (Chasar et al. 2005).

Another potential hypothesis is that this increase in *A. mitchilli* abundance may have induced a trophic cascade that reduced grazing pressure on phytoplankton and may have contributed to the persistence and/or spatial dispersion of the phytoplankton blooms. In whole lake experiments that increased nutrient concentrations, a significantly greater increase in chlorophyll was observed in lakes dominated by planktivorous fish than in lakes dominated by piscivorous fish (Carpenter et al. 2001). This is based on the theory that increasing planktivore biomass will decrease the biomass of large herbivorous zooplankton (Carpenter et al. 1985). This theory has been supported by experimental manipulations of ecosystems and mesocosms (Elliott et al. 1983, Elser & Carpenter 1988). Similar observations were documented in marine ecosystems where overfishing reduced the population of piscivorous fish increasing planktivorous fish biomass and decreasing zooplankton (Shackell et al. 2010). Thus, the large increase in *A. mitchilli*, the dominant planktivorous fish in Florida Bay, from 1994 to May 1997 could potentially have induced a trophic cascade.

However, control by predation alone is not sufficient to explain population regulation across all trophic levels in a system (Hairston et al. 1960). Given the large temporal variability in mesozooplankton, *A. mitchilli* and chlorophyll *a* from 1994-1997 (Briceno & Boyer 2010, Kelble et al. 2010), it is reasonable assume that each trophic level may have experienced population regulation by predation and resource-limitation at different points during this time period. The possibility that resource-limitation may have limited the mesozooplankton population is further supported by the oligotrophic nature of

Florida Bay and the dominance of benthic over pelagic primary production (Herbert & Fourqurean 2008).

To investigate these dynamics, we developed a coupled bay anchovy-mesozooplankton mechanistic model to simulate mesozooplankton and *A. mitchilli* populations in Florida Bay from 1994 to 2001 (Fig. 4-1). The goals of our study are 1) to quantify the role of predation and resource-limitation in controlling mesozooplankton populations, 2) to investigate the manner in which salinity mediates the interaction between *A. mitchilli* and mesozooplankton, 3) to determine if predation by *A. mitchilli* shifts peak abundances of mesozooplankton to higher salinities than would be expected based upon physiology alone, 4) to investigate the potential for highly variable *A. mitchilli* populations to initiate trophic cascades that may alter the abundance of phytoplankton and 5) to investigate the relationship between biomass, productivity and relative loss of mesozooplankton to predation for a key trophic interaction in sub-tropical embayments.

Methods

BAMZO Model

The coupled Bay Anchovy/MesoZOoplankton model (BAMZO) was developed with the Stella® software package. The model description follows the overview, design, details (ODD) protocol (Grimm et al. 2006).

1) Purpose

This model was developed to test the following primary hypotheses:

H_0) Predation alone controls mesozooplankton abundance in Florida Bay

H_1) Resource-limitation alone controls mesozooplankton abundance in Florida Bay

H_2) Resource-limitation and predation are both controlling mechanisms for mesozooplankton in Florida Bay

The model was also designed to examine the manner in which salinity affects the interaction between mesozooplankton and *A. mitchilli*. Specifically, the model will help determine if the correlations between *A. mitchilli* and mesozooplankton with salinity are direct and develop a mechanistic understanding of the relationship between these populations and salinity. Furthermore, this model was designed to examine the potential effect of different salinity regimes on the Florida Bay ecosystem through trophic interactions involving *A. mitchilli* or mesozooplankton.

2) Entities, state variables, and scales

The model simulated bay-wide populations of *A. mitchilli*, the six most common mesozooplankton functional types (*Acartia*, *Oithona*, Paracalanidae, Harpacticoida, Bivalvia larvae and Gastropoda larvae), and mesozooplankton prey with a daily time-step (Fig. 4.1). The model was run for 10-years. The first 2-years initialize the model and the remaining 8-years simulate populations in Florida Bay from 1994 to 2001. The environmental state variables utilized to calculate recruitment are bay-wide mean temperature and salinity. *A. mitchilli* are modeled from juvenile recruitment at 15mm to their maximum length at 90mm. The state variables of *A. mitchilli* cohorts are length, mortality, growth and consumption. Mesozooplankton are modeled from nauplii recruitment through their maximum adult longevity. The state variables of mesozooplankton are daily-size classes, fecundity, stage duration, mortality, sex ratio, respiratory carbon demand, and longevity. Mesozooplankton prey is simulated as the carbon content of a single population with a logistic growth equation utilizing the state variables r, growth, and K, carrying capacity. The use of a single mesozooplankton prey population results in the lumping of microzooplankton with phytoplankton as both are potential prey items (Kleppel et al. 1998).

3) Process overview and scheduling

The model simulates time as a daily time-step. The model moves each mesozooplankton and *A. mitchilli* cohort within each population to the next daily class after removing the portion of the cohort lost to mortality, including predation. The mesozooplankton prey population does not have distinct cohorts and the model first removes the portion of this population lost to mortality, including predation, and then calculates the quantity of carbon biomass to be input to the mesozooplankton prey population. The model then updates environmental parameters and calculates the abundance of the new recruit cohort and places them in the first daily class for each population. After updating the populations, the model calculates predation by *A. mitchilli* upon mesozooplankton and mesozooplankton grazing upon their prey population to be removed in the mortality term the next day.

4) Design Concepts

Emergence: The response of both *A. mitchilli* and mesozooplankton populations to salinity was quantified from the model and based not just upon salinity, but also upon the size of the adult populations and temperature.

Adaptation: *A. mitchilli* first prey upon adult and copepodites and the unfulfilled consumption is then removed from the mollusks and nauplii to follow feeding preferences suggested by an individual based model of *A. mitchilli* (Rose et al. 1999).

Mesozooplankton first graze upon their prey population. If this is insufficient to satisfy their respiratory carbon demand, they then graze upon their nauplii and eggs; a behavior that has been documented for similar taxa in another coastal environment (Uye & Liang 1998). If this is still not sufficient, mesozooplankton mortality is increased and fecundity decreased in proportion to the percent of the respiratory carbon demand that is unfulfilled. Mesozooplankton also decrease fecundity in lower temperatures and with higher salinity to reflect documented responses (Kleppel 1992, Chen et al. 2006, Putland & Iverson 2007, Berasategui et al. 2009).

Objectives: The adaptive traits described above are merely undertaken in response to current conditions and not to improve future fitness. Thus, the only objective is to minimize mortality during that time-step.

Interaction: The *A. mitchilli* population consumes mesozooplankton. However, *A. mitchilli* do not experience resource-limitation if the mesozooplankton population is too small to fulfill their requirements, because *A. mitchilli* are known to prey on other organisms that are not simulated in the model, such as Myscids (Peebles et al. 2007). The mesozooplankton population consumes the mesozooplankton prey and if the mesozooplankton prey population is not large enough, the mesozooplankton population is subject to resource-limitation.

Stochasticity: Stochasticity is built into the model at several steps. The number of *A. mitchilli* juvenile recruits is determined by taking a random sample each day from a log-normal distribution with the mean equal to the calculated number of recruits that day from the environmental state variables and the 30-40mm standard length *A. mitchilli* population. Stochasticity is incorporated into mesozooplankton recruitment each day by randomly sampling the nauplii productivity rate, NPR, from a log-normal distribution with a mean and standard deviation estimated from literature values. The mortality rates also incorporated stochasticity by randomly selecting a mortality rate from a normal distribution each day.

Observation: The population outputs, including abundances and number of recruits, for *A. mitchilli* and the 6 mesozooplankton functional groups are captured to compare with observations from Florida Bay.

5) Initialization

The model was initialized with the median population density of each taxa. The abundance was distributed amongst length/day classes assuming the mean mortality. The model is also run for two years before outputs are captured to aid in the initialization of the model. This is done utilizing the environmental data from 1994 and 1995 and then the data capture process begins by re-utilizing the data from 1994.

6) Input Data

In situ temperature and salinity are input into the model from measurements taken by the marine monitoring network of Everglades National Park. These measurements were collected at 15-minute intervals at 10 stations in Florida Bay, but are input to the model as the bay-wide daily mean temperature and salinity.

7) Submodels

a) Anchoa mitchilli module

The *A. mitchilli* module is parameterized primarily from literature values (Table 4.1). Only mortality rate and juvenile recruitment were, in part, parameterized with observations from Florida Bay. The model calculates the number of recruits each day, and then places them in a cohort with the initial juvenile length. After initial recruitment, a percent of the cohort is removed each day with a mortality rate, and the remaining individuals then progress to the next length class (Fig. 4.2). This continues until the cohort reaches a maximum length of 90mm based upon literature values of (Newberger & Houde 1995, Ayala-Perez et al. 1997, Acosta 2000) when the entire cohort is terminated.

The instantaneous mortality for juveniles and adults up to 40mm was calculated directly from the length frequency curve (Beverton & Holt 1957) of samples collected in Florida Bay between 1994 and 2001. The instantaneous mortality for individuals greater than 40mm had to be parameterized using literature values (Houde 1987, Leak & Houde 1987, Wang 1992, Rose et al. 1999), because the otter trawl utilized in Florida Bay did not effectively catch *A. mitchilli* above this length. The growth in length per day, G, is given in Table 4.1 and was derived from literature values. Greater weight was given to values from nearby embayments (Leak & Houde 1987, Zastrow et al. 1991, Newberger & Houde 1995, Wang & Houde 1995, Ayala-Perez et al. 1997, Rose et al. 1999, Acosta 2000, Mowitt et al. 2006).

BAMZO estimates the daily recruits of *A. mitchilli* from a regression of recruits per day with temperature, salinity and the population size of adults between 30mm and 40mm. This multiple regression included the quadratic terms for the variables and the interactive terms between them. The regression was conducted exclusively on data from the north-central and west sub-regions of Florida Bay, since length-frequency histograms show these are the sole sub-regions with active *A. mitchilli* recruitment (Fig. 5.1). The multiple regression was significant ($F_{6,68} = 52.743$, $p<0.001$) and explained over 80% of the observed variance (Fig. 4.3). The output of this regression was multiplied by the fractional area of Florida Bay encompassed by the west and north-central sub-regions (0.51) to calculate recruits per day for the entire Bay.

$$\begin{aligned} R = (&0.137*tmp - 0.037*sal + 3.95*Ad - 0.009*Ad^2 \\ &- 0.025*tmp*Ad - 0.089*sal*Ad - 2.02)*0.51 \end{aligned} \tag{4.1}$$

where tmp is temperature (°C), sal is salinity, and Ad is the abundance of adult *A. mitchilli* (30mm to 40mm). BAMZO sets R to zero if the temperature 30 days prior was less than 20°C, because *A. mitchilli* do not spawn at these temperatures, and 15mm recruits are approximately 30 days old (Leak & Houde 1987).

b) A. mitchilli consumption

A bioenergetics methodology was applied to calculate consumption of mesozooplankton by *A. mitchilli*. Each length class was converted to weight via an equation calculated from the observational data:

$$W(g) = 0.00000617 * \ell(mm)^{3.16} \tag{4.2}$$

The consumption of each *A. mitchilli* in each length class was calculated according to the following equation (Luo & Brandt 1993):

$$C = a_c W^{b_c} f(t) \tag{4.3}$$

where C is consumption in g, a_c is the max consumption of a 1g *A. mitchilli*, b_c is the dimensionless exponent for the weight-dependence of consumption, and $f(t)$ is a proportional adjustment of consumption that is a function of temperature and varies from 0 to 1 (Kitchell et al. 1977):

$$f(t) = V^X * e^{x(1-v)} \tag{4.4}$$

where $V = (t_m - t)/(t_m - t_o)$, t_m and t_o are the maximum and optimal temperature for consumption, respectively, t is the daily temperature and X is given by the following equation (Kitchell et al. 1977).

$$X = \frac{W^2(1+(1+40/Y)^{1/2})^2}{400} \tag{4.5}$$

Here $W = ln(Q)*(t_m\text{-}t_o)$, $Y = ln(Q)*(t_m\text{-}t_o+2)$ and Q is the slope of temperature-dependent consumption. The values for a_c, b_c, Q, t_m and t_o used in BAMZO are given in Table 4.1. The consumption for each fish, *C*, in each length class is multiplied by the population of that length class to yield total length class consumption. Consumptions by all length classes are summed to compute total *A. mitchilli* consumption.

Adult and copepodites were preferentially preyed upon by *A. mitchilli*. In order to convert abundance to biomass, the abundance of mesozooplankton in each taxa was multiplied by the average biovolume of each taxa as measured over a one-year period (Kelble et al. 2010). This biovolume was converted to biomass in g m^{-3}, assuming that 1 mm^3 of biovolume is equal to 1.05 mg wet weight biomass (Patoine et al. 2006). The remaining A. *mitchilli* consumption was subsequently applied to the nauplii, Bivalvia, and Gastropoda compartments, since *A. mitchilli* stomach contents from Florida Bay showed they prey upon all 7 mesozooplankton taxa (P. Ortner personal communication). An index that increased linearly from 0 at a population density of 0 to 0.5 at two times the median observed population density for each mesozooplankton taxa was applied to predation. This resulted in at most 50% of the individuals in each taxa being consumed each day and rare taxa being minimally consumed. This prevented a population collapse in response to unrealistically high predation rates. Moreover, it is known that *A. mitchilli* in sub-tropical embayments also consume hyperbenthic invertebrates, specifically mysid shrimp (Peebles et al. 2007); these organisms are not modeled in BAMZO and were not effectively captured by the mesozooplankton sampling methodology (Kelble et al. 2010). Thus, we assume *A. mitchilli* would not prey upon increasingly rare mesozooplankton taxa when other, more abundant food sources may be available.

c) Copepoda module

The mesozooplankton module simulates the population dynamics of four Copepoda taxa (*Acartia*, Paracalanidae, *Oithona* and Harpacticoida) and two Mollusca taxa (Gastropoda and Bivalvia). These are the six most abundant mesozooplankton taxa in Florida Bay (Kelble et al. 2010). The Copepoda taxa are modeled through naupliar, copepodite, and adult stages (Fig. 4.4). Copepoda are not modeled by stage groupings, but rather by age groupings in days, because copepod stage duration in sub-tropical environments is often less than the 1-day time step of the model (Hopcroft & Roff 1998b, Hirst & Kiorboe 2002, McKinnon et al. 2003). Only adult females are modeled since there is little literature data on longevity of adult males. To accomplish this, 50% of the individuals exiting the last copepodite stage are removed with the assumption that the sex ratio at this stage is 1:1. The modeled adult female abundance is then multiplied by the inverse of the sex ratio from literature values to calculate the total adult population (Digby 1950, Lee & McAlice 1979, Londsdale 1981, Norrbin 1994, Liang & Uye 1996, Hirst et al. 1999, Hirst & Kiorboe 2002, Drillet et al. 2008).

The duration of nauplii and copepodite stages is highly temperature-dependent (Drillet et al. 2008). Therefore, literature values were selected from observations with water temperatures consistent with sub-tropical embayments, roughly 15°C to 30°C. Under these conditions, *Acartia* and Harpacticoida both had 4-day nauplii development times (Carlotti & Sciandra 1989, Williams & Jones 1994, Hopcroft & Roff 1998b, Matias-Peralta et al. 2005, Drillet et al. 2008). On the other hand, Paracalanidae and *Oithona* had 3-day nauplii development times (Chisholm & Roff 1990, Webber & Roff 1995b, McKinnon 1996, Hopcroft & Roff 1998b, Hirst & Kiorboe 2002, McKinnon et al. 2003). The copepodite duration in all Copepoda taxa was four days (Johnson 1974, Newbury & Bartholomew 1976, Carlotti & Sciandra 1989, Chisholm & Roff 1990, Webber & Roff 1995a, Liang & Uye 1996, McKinnon 1996, Schipp et al. 1999, Williams & Jones 1999, Hirst & Kiorboe 2002, Matias-Peralta et al. 2005).

Adult female copepods in each taxa were removed the day after they achieved the longevity listed in Table 4.2. The longevity of Harpacticoida and *Oithona* were defined as 34 days in BAMZO (Hoppenheit 1976, Londsdale 1981, Paffenhofer 1993, Sabatini & Kiorboe 1994, Matias-Peralta et al. 2005). The longevity of *Acartia* in BAMZO was 24 days, which was the shortest longevity in the literature values; but the only observation at water temperatures greater than 20°C (Parrish & Wilson 1978, Londsdale 1981). Paracalanidae longevity is 16 days and thus reflects the shorter life cycle compared to *Acartia* and *Oithona* (Londsdale 1981, Paffenhofer 1993).

The natural mortality of copepods in BAMZO was derived from laboratory experiments conducted in the absence of predators and with adequate food supply. The natural mortality value used was highest for *Acartia* at 13% per day (Lincoln et al. 2001, Drillet et al. 2008). The next highest mortality was 9% per day for Harpacticoida (Londsdale 1981, Carlotti & Sciandra 1989). Paracalanidae had 5% mortality in BAMZO (McGurk 1987, Paffenhofer 1993). *Oithona* had the lowest natural mortality of 4% per day (Londsdale 1981, Paffenhofer 1993).

An equation for summer viable egg production rate in Apalachicola Bay, Florida USA was modified to calculate *Acartia* fecundity (Putland & Iverson 2007).

$$\textit{Acartia}\text{ recruits female}^{-1}\text{ d}^{-1} = 51 \times e^{-0.5(\ln(sal/6)/7)^2} \times T_i \tag{4.6}$$

where sal is salinity. We adjusted this equation for year-round use by incorporating a temperature index, T_i, which ranged from 0.46 at the coldest temperature observed to 1.0 at all temperatures greater than 21°C. This was done because winter egg production was observed to be, on average, 46% of summer egg production for *Acartia tonsa* in a sub-tropical embayment (Putland & Iverson 2007), and because *Acartia* reproduction has been shown to be temperature-independent above 21°C (Kleppel 1992, Kleppel et al. 1998). The fecundity of the other copepod taxa was calculated using the equation:

$$\text{Nauplii Recruits female}^{-1}\text{ d}^{-1} = \text{NPR} * S_i * T_i \tag{4.7}$$

where NPR is given in Table 4.2 (Londsdale 1981, Uye & Shibuno 1992, Paffenhofer 1993, Liang & Uye 1996, McKinnon 1996, Saito & Taguchi 1996, Hopcroft & Roff 1998a). However, no literature values for Paracalanidae NPR were found in the literature. Thus, Paracalanidae NPR values in equation 4.7 were calculated by multiplying egg production rates with hatching success to yield nauplii production, assuming no egg predation (Uye & Shibuno 1992, Liang & Uye 1996, McKinnon 1996, Saito & Taguchi 1996, Hopcroft & Roff 1998a). S_i is a salinity index designed to incorporate the inverse relationship between daily female productivity and salinity that has been observed in some coastal systems for several copepod species (Chen et al. 2006, Berasategui et al. 2009). S_i ranged from 0 at the highest salinity to 1 at the lowest salinity.

d) Mollusca module

The Mollusca taxa were modeled assuming a seasonal reproductive cycle governed the number of new larval recruits. These larvae were part of the mesozooplankton community until they reached the end of their pelagic larval stage (Fig. 4.5). The seasonal distribution of new Mollusca larval recruits was based on the seasonal spawning dynamics of the dominant Gastropoda and Bivalvia taxa in sub-tropical embayments, and the maximum number of larvae observed in Florida Bay net tows (Kelble et al. 2010).

Brachidontes exustus is the most numerically abundant bivalve species in Florida Bay and accounts for >86% of benthic bivalve species (Brewster-Wingard et al. 2001, Nizinski 2007). *Brachidontes exustus* displays seasonal spawning with peaks in both the spring and fall in a similar sub-tropical embayment, Tampa Bay (Barber et al. 2005). BAMZO utilizes a Bivalvia pelagic larval duration of 20 days (Table 4.2). This is based upon *Brachidontes* spp., which has a pelagic larval duration of approximately three weeks (Campos & Ramorino 1980, Fields & Moore 1983). Additionally, the hard clam, *Mercenaria*, another prominent Bivalvia in sub-tropical embayments, has only an 8-day pelagic larval duration (Arnold et al. 2005). The seasonal distribution of bivalve larval recruits per day was estimated from the seasonal cycle in *Brachidontes exustus* reproduction and the maximum number of Bivalvia larvae observed in Florida Bay, normalized to a Bivalvia pelagic larval duration of 20 days (Fig. 4.6). Natural mortality during the larval stage in mussels is high and ranges from 0.1 d^{-1} to 0.2 d^{-1} in aquaculture studies; thus, we assumed an instantaneous Bivalvia mortality of 0.15 d^{-1} (Widdows 1991).

The Gastropoda community within Florida Bay is dominated by several species. The most common are *Bittiolum varium*, *Nassarius albus*, *Crepidula* spp., *Cerithium eburneum* and *Conus jaspideus* (Nizinski 1998, Brewster-Wingard et al. 2001). *Bittiolum varium* is among the four most abundant Mollusca species throughout Florida Bay. *B. varium* larvae are present in large numbers from spring through fall in Indian River Lagoon, a nearby embayment (Qurban 2000). However, *Cerithium eburneum* was observed to have peak spawning from January through March in nearby Biscayne Bay (Houbrick 1973). Based upon these observations, we assigned peak Gastropoda spawning to March, kept spawning at approximately one-half the magnitude of the March peak through September, and assumed minimal values from October through December. While there is a large range in the pelagic larval duration, the model includes a constant 27-day pelagic larval duration, which is the mean of literature values (Qurban 2000, Chan & Morton 2005, Schmidt et al. 2006, Couceiro et al. 2007). The mortality rate for Gastropoda (0.074 d^{-1}) is based upon aquaculture experiments under similar environmental conditions (Pechenik & Levine 2007, Genio et al. 2008).

Consumption by *A. mitchilli* was imported into the mesozooplankton module from the *A. mitchilli* module. Adult and copepodites were preferentially preyed upon by *A. mitchilli*. This reflects the findings of (Rose et al. 1999). In order to convert abundance to biomass, the abundance of mesozooplankton in each taxa was multiplied by the average biovolume of each taxa as measured over a one-year period (Kelble et al. 2010). This biovolume was converted to biomass in g m^{-3}, assuming that 1 mm^3 of biovolume is equal to 1.05 mg biomass (Patoine et al. 2006). The remaining A. *mitchilli* consumption was subsequently applied to the nauplii, Bivalvia, and Gastropoda compartments, since

A. mitchilli stomach contents from Florida Bay showed they prey upon all 7 mesozooplankton taxa (P. Ortner personal communication). A density-dependent index that increased linearly from 0 at a population density of 0 to 0.5 at two times the median observed population density for each mesozooplankton taxa was applied to predation. This resulted in at most 50% of the individuals in each taxa being consumed each day and rare taxa being minimally consumed. This procedure prevented a population collapse in response to unrealistically high predation rates. Moreover, it is known that *A. mitchilli* in sub-tropical embayments also consume hyperbenthic invertebrates, specifically mysid shrimp (Peebles et al. 2007); these organisms are not modeled in BAMZO and were not effectively captured by the mesozooplankton sampling methodology (Kelble et al. 2010). Thus, we assume *A. mitchilli* would not prey upon increasingly-rare mesozooplankton taxa when other, more abundant food sources are available.

e) Mesozooplankton prey

Mesozooplankton prey was modeled with a logistic equation to incorporate density-dependence and resource-limitation. The daily input to the prey population followed the equation:

$$P_{input} = rP\left(1 - \frac{P}{K}\right) \tag{4.8}$$

where r is the intrinsic rate of increase, P is the prey population in g C m^{-3}, and K is the carrying capacity for the prey population. The prey in this case includes both phytoplankton and microzooplankton, since mesozooplankton efficiently graze both prey items in sub-tropical embayments (Raby et al. 1997, Kleppel & Hazzard 2000, Richardson et al. 2003). The intrinsic rate of increase was randomly selected from a normal distribution with a mean of 0.5 and a standard deviation of 0.1 based upon growth rates from the literature (Strom et al. 2003, Lawrence et al. 2004). A carrying capacity, K, of 0.16 g C m^{-3} was calculated from the biomass reported in a one-year study of plankton in Florida Bay (Lavrentyev et al. 1998).

Mesozooplankton respiratory carbon demand was calculated with the biomass of each mesozooplankton taxon. Biomass was converted to carbon biomass based upon previous studies (Peters 1983, Moloney & Field 1991).

$$\text{Biomass (mg C ind}^{-1}) = 0.07 \text{ x Biomass (mg ind}^{-1}) \qquad (4.9)$$

The respiration rate, as oxygen consumption, was computed for each taxa according to the regression analysis of carbon biomass and *in situ* temperature (Ikeda 1985).

$$R\ (\mu\text{l } O_2 \text{ ind}^{-1}\text{ h}^{-1}) = e^{(0.5254 + 0.8354*\ln(\text{Biomass}) + 0.0601*\ln(\text{tmp}))} \qquad (4.10)$$

where R is the respiration rate. The respiration rate was converted to carbon demand (C.D.) as ug C ind^{-1} h^{-1} from a respiratory quotient (RQ), and the weight of carbon in carbon dioxide (Omori & Ikeda 1984).

$$C.D. = R * RQ * \frac{C_w}{CO_2} \qquad (4.11)$$

The RQ value of 0.97 was selected since it corresponds to a protein substrate with ammonia as the excretory product, and the carbon to carbon dioxide ratio was 0.5357 (with 12 grams of carbon per each mole (22.4 l) of carbon dioxide). Carbon demand was calculated per individual per hour and multiplied by 24 and the density of individuals in a taxon to estimate the carbon demand for the entire taxon per cubic meter per day.

This carbon demand for mesozooplankton is calculated in each time step and subtracted from the prey biomass, P, unless the volume filtered by mesozooplankton was insufficient to allow filtering of the entire water column. In that case, the lesser of the mesozooplankton carbon demand or the total volume filtered was removed from the prey population. The volume filtered was calculated from average clearance rates per individual (Dagg 1983). Mesozooplankton are never permitted to consume more than 80% of the prey or nauplii population in order to prevent an artificial collapse. This is because there is no immigration in the model.

Results

A. mitchilli

To compare the BAMZO model results with observations, the model was run 10 times for each formulation, and the mean of all ten iterations was calculated for each day. This step is necessary to incorporate the stochasticity within BAMZO. Under these conditions, BAMZO accurately simulated the recruitment patterns observed for the *A. mitchilli* population of Florida Bay (Fig. 4.6A). There was no difference between the frequency distributions of recruits in the observations and in the BAMZO output (x^2_{50} =0.219, p=1.00). However, a chi-square test of the modeled number of recruits and the observed recruits present on specific sampling days did find significant differences between the two values (x^2_{1210}=28,550, p<0.001).

The otter trawl that sampled *A. mitchilli* in Florida Bay was most effective at capturing individuals between 20mm and 40mm standard lengths. Thus, the comparisons between BAMZO and observations are limited to this size range. The relative frequency distributions between BAMZO and observations contain some differences (Fig. 4.6B); however, a chi-square test found no significant difference between the two distributions (x^2_{19}=0.3349, p=1.00). The chi-square test of observed and modeled *A. mitchilli* densities throughout the time-series found significant differences (x^2_{37}=93,030, p<0.001). This difference is likely due in part to the low number of observations of *A. mitchilli* during this time period (n=38) and the fact that observations contain zero values, with only a small percentage of the Bay sampled on each survey (<0.01%).

Observational data of *A. mitchilli* in Florida Bay shows significantly higher abundances before May, 1997 (Kelble et al. 2010). This interannual difference was captured by BAMZO with significantly higher densities of both recruits and 20-40mm standard length *A. mitchilli* before May 1997 (Fig. 4.7, Mann-Whitney U-test, Z=15.73, p<0.001 and Z=23.58, p<0.001 for recruits and 20-40mm standard lengths respectively). However, there were significant differences for annual medians between BAMZO and observed *A. mitchilli* populations (x_7^2=23.07, p=0.002 and x_7^2=1144, p<0.001 for recruits and 20-40mm, respectively). In particular, BAMZO underestimated *A. mitchilli* recruits in 1994, and overestimated recruits in 1995 and 1997 (Fig. 4.7A). BAMZO also overestimated the population of 20-40mm standard length *A. mitchilli* in 1995, 1997, 1998 and 2000 (Fig. 4.7B). For all other years, the BAMZO values were within the confidence interval defined for the observations. While BAMZO did reproduce the largest interannual patterns in the observations, it tended to overestimate the 20-40mm population after May 1997.

A major feature of *A. mitchilli* distributions in sub-tropical embayments is maximum abundances at lower salinities (Peebles et al. 2007, Putland & Iverson 2007). Both BAMZO and the observations contain significant differences between salinity bins. This was the case in both recruits (Fig. 4.8A; Kruskal-Wallis $H_{4,2922}$=1105, p<0.001 and $H_{4,1211}$=101.2, p<0.001 for the model and observations, respectively) and 20-40mm standard length *A. mitchilli* (Fig. 4.8B, $H_{4,2922}$=1471, p<0.001 and $H_{4,38}$=13.95, p=0.008

for the model and observations, respectively). The greatest change in abundance for both the model output and observations occurred at a salinity of 30. Mann-Whitney U-test results distinguish significantly higher densities of recruits and 20-40 mm standard length *A. mitchilli* at salinities less than 30 (α=0.01). Although BAMZO accurately captures the major pattern of salinity variability in the observations, it did significantly overestimate recruits in 3 of the 5 salinity bins, and the 20-40mm standard length population in 4 of the 5 salinity bins (α=0.05).

Mesozooplankton

Copepod populations in BAMZO all displayed exponential growth when density-dependent factors were absent (c.f. Fig. 4.9). The mesozooplankton population reached unrealistic densities before 2001. The Mollusca taxa did not exhibit exponential growth because the larvae released were independent of the adult population and restricted to a constant annual cycle throughout the model years. This suggests that density-dependent processes must also be incorporated into BAMZO to accurately simulate the observational data. Although significant differences remain between BAMZO output and observations after density-dependence is included, the BAMZO output was significantly and positively correlated with the observations for all mesozooplankton taxa except Gastropoda (Table 4.3). Moreover, BAMZO accurately simulated the major observed patterns of interannual variability and salinity association.

All 7 mesozooplankton taxa in BAMZO had significantly lower densities before May 1997 than after (Mann-Whitney U-tests, $p<0.001$). This trend accurately reflects one of the key observed patterns in Florida Bay (Kelble et al. 2010). Moreover, both the observations and BAMZO output showed significant differences between years based upon a Kruskal-Wallis analysis (α=0.05). The annual median output from BAMZO was positively correlated with observed annual median data for all copepod taxa, excluding nauplii (Table 4.3). However, there were significant differences between the annual median of the BAMZO output and the observations for all seven mesozooplankton taxa (Fig. 4.10, x_7^2, p<0.001). Annual differences between modeled and observed values were calculated with a Mann-Whitney U-test (α=0.05). Nauplii, *Oithona*, and Paracalanidae were significantly overestimated in BAMZO in all years (Fig. 4.10A, 4.10C and 4.10D). The simulation for *Acartia* was better. BAMZO significantly underestimated the population in 1996, 1998 and 1999, with no significant difference between the modeled and observed *Acartia* population in the other years (Fig. 4.10B). Harpacticoida was significantly overestimated in BAMZO during 1995, 1999 and 2001, but significantly underestimated in 1996 (Fig. 4.10E). Bivalvia was significantly overestimated in BAMZO during 1995, 1996 and 1999 (Fig. 4.10F). Gastropoda was significantly overestimated in 1994, 1995, 1996 and 1997 (Fig. 4.10G).

The major pattern between salinity and mesozooplankton was accurately reproduced. Significant differences in abundance were found within each taxa, except *Acartia* and Paracalanidae among bins delineated by salinities less than 25, 25 to 30, and greater than 30 based upon a Kruskal-Wallis test (α=0.05, Fig. 4.11). The *Acartia* p-value was 0.066, which suggests there might be differences among salinity bins within *Acartia*, but the statistical power of the test was likely insufficient due to the low sample size (n=3, 14, 20) to detect these differences. The BAMZO output reproduced the observations with all taxa having significant differences among these salinity groupings. All mesozooplankton populations, except Paracalanidae, had significantly lower populations in the 25 to 30 salinity bin than the greater than 30 salinity bin (Mann-Whitney U-tests, α=0.05). The same pattern was evident in the BAMZO output for all mesozooplankton taxa, except Harpacticoida. Although BAMZO captured these broad salinity effects, the median model output in each salinity bin was not well correlated with observations (Table 4.3). The lack of a correlation with observations could, in part, be due to the small sample size (n=5).

Daily copepod biomass (g m^{-3}), NPR (N f^{-1} d^{-1}), and the ratio of copepod biomass losses attributed to *A. mitchilli* predation compared to all copepod losses were calculated from the BAMZO output. Copepod biomass had a weak, but significant inverse correlation with NPR (Kendall-Tau = -0.038, $p<0.01$) and a strong, significant inverse correlation with relative loss to predation (Kendall-Tau = -0.672, $p<0.01$). The period from 1994 to 1996 had the three highest annual median values for relative loss to predation and NPR, but the lowest three annual median values of copepod biomass (Fig. 4.12B). The correlations involving salinity were not as clear (Fig. 4.12A). NPR had an inverse linear relationship with salinity. Relative loss to predation also had an inverse linear relationship with salinity with the exception of the lowest salinity bin where the relative loss to predation was nearly equal to that in the highest salinity bin. Copepod biomass had a peak at lowest salinities, with a dramatic decrease in the 25 to 30 salinity bin, and a slight increase in biomass for salinities greater than 30.

Influence of predation and salinity

BAMZO was modified to examine the effect of predation and salinity on the mesozooplankton community. BAMZO was run with no *A. mitchilli* predation upon mesozooplankton. This did not impact the *A. mitchilli* population, because BAMZO assumes mesozooplankton prey does not limit *A. mitchilli*. However, the lack of predation drastically altered the mesozooplankton community. There were still significant differences in abundance of all mesozooplankton taxa, except Bivalvia, before and after May 1997. However, contrary to the observations and base BAMZO output (the model runs with predation, salinity variability, and density-dependence) the mesozooplankton abundances were significantly higher before May 1997 with no predation (Mann-Whitney U-tests, α=0.05). The output from BAMZO without predation was uncorrelated with the overall observations, contained 4 significant inverse correlations with observed interannual median data and had two significant correlations with the salinity bins (Table 4.3). BAMZO with no predation produced an inverse linear relationship with salinity for all copepod taxa (Fig. 4.11). This resulted in the significant differences between the salinity classes as described above; however, without predation the population in the 25 to 30 salinity bin is significantly higher than in the greater than 30 salinity populations for all taxa (Mann-Whitney U-tests, α=0.05). This is the opposite of both observations and base BAMZO output.

To examine the impact of salinity on these relationships, salinity was held constant for all model compartments at the median salinity of 31.77. This changed the *A. mitchilli* and mesozooplankton populations. Modeled *A. mitchilli* recruitment is a function of salinity (Eq. 4.1), thus when salinity is constant it minimizes the variability in juvenile recruitment. This resulted in a decrease in the interannual variability. There were still significant interannual differences with a shift in May 1997; however, without salinity variability the population of *A. mitchilli* was smaller before May 1997 (Fig. 4.7B, Mann-Whitney U-test, Z=-2.256, p=0.024 and Z=-6.266, p<0.001 for recruits and 20-

40mm standard lengths respectively). This is contrary to observations and base BAMZO output. The correlation between *A. mitchilli* and salinity was also altered. The highest population abundances were still evident at the lowest salinity; however, there were minimal differences in density between salinity of 25 to 40 and a decrease in densities above 40 (Fig. 4.8). There was still a significant difference between salinity bins when salinity was constant, but the difference was not as great ($H_{4,2922}$=103.1, p<0.001 and $H_{4,2922}$=290.0, p<0.001 for recruits and 20-40mm standard length individuals, respectively). Moreover, there was no significant difference in recruit density below and above a salinity of 30 (α=0.01).

Holding the salinity constant significantly affected the mesozooplankton community. The BAMZO model with constant salinity differed from the observations and the base model runs. There were still significant differences between the populations of nauplii, Gastropoda, Harpacticoida and *Oithona* before and after May 1997. However, contrary to the observations and base BAMZO output these populations were significantly higher before May 1997 with constant salinity (Mann-Whitney U-test, α=0.05; Fig. 4.10). The BAMZO output with constant salinity was not correlated with the overall and observed interannual median data, and only contained one significant correlation with respect to observed salinity bin medians (Table 4.3). The 20-25 salinity bin had a median values more than two-fold higher than the 25-30 bin for all observed taxa and the base BAMZO outputs. This pattern did not occur when salinity was held constant.

The S_i index was removed from BAMZO to investigate the relative strength of correlations with salinity to *A. mitchilli* and mesozooplankton. This run also allowed us to examine the model's sensitivity to the S_i index. This index was based on an inverse correlation between copepod productivity and salinity that has not been reported for all copepod taxa in the model (Chen et al. 2006, Berasategui et al. 2009). Moreover, there were no numerical relationships for this correlation in the literature and a suitability index from 0 to 1 was adopted. Thus, it was necessary to test the model's sensitivity to this parameter given the low degree of confidence in its accuracy.

The output when S_i is removed is significantly correlated with the observations for all taxa, except Gastropoda (Table 4.3). This level correlation is identical to the base BAMZO output. The interannual median data were also similar in the base model and the runs with S_i removed (Fig. 4.10). The salinity bin medians did show a significant difference from the base model output within all four taxa that incorporated the S_i term (nauplii, *Oithona*, Paracalanidae and Harpacticoida; Fig. 4.11A, C, D and E). All four taxa showed a linear increase with salinity at salinities of 25 to > 40 when S_i is removed (Fig. 4.11). This pattern was not evident in the observational data. These results indicate that the value of the S_i term does not significantly alter the model output. The similarity in the base BAMZO runs and those with S_i removed suggest that the relationship between mesozooplankton and salinity is largely an indirect effect of the salinity response in *A. mitchilli*, and not a direct effect of S_i on mesozooplankton.

Discussion

The model output suggests neither density-dependence through resource-limitation or predation alone limited mesozooplankton populations in Florida Bay from 1994 through 2001. This is not surprising since the relative effect of these two factors can vary both spatially and temporally within an estuary (Kimmel et al. 2006b). Both density-dependence and predator limitations are required to properly simulate the major trends in the mesozooplankton community of Florida Bay (Fig. 4.9, 4.10 and 4.11). Density-dependence is necessary to restrict mesozooplankton population densities within reasonable values (Fig. 4.9) and predator-induced mortality is necessary to replicate the observed interannual variability in mesozooplankton (Fig. 4.10). It is also essential to reproduce the correlation with salinity (Fig. 4.11). Prior to May 1997, model output calculates that mesozooplankton respiratory carbon demand was met over 93% of the time; however, after May 1997 it was met less than 31% of the time. This suggests that predation was the dominant control of mesozooplankton populations prior to May 1997 and resource-limitation was the dominant population control after May 1997.

This period where top-down trophic controls were dominant may have initiated a trophic cascade. The occurrence of intense algal blooms in both the western and central sub-regions of Florida Bay in the early to mid 1990s (Hitchcock et al. 2007) suggests this trophic cascade may have potentially propagated down to affect primary producers. The observed chlorophyll *a* concentrations from two monitoring programs in Florida Bay (Kelble et al. 2005, Boyer & Briceno 2008) had significantly higher chlorophyll *a* biomass during this period of high *A. mitchilli* abundance (Mann-Whitney U-test, $Z=3.89$, $p<0.001$). In fact, the median biomass was 1.5-fold higher from 1994 through May 1997 than from June 1997 through 2001. The modeled mesozooplankton prey population was over three-fold greater from 1994 until May 1997 (0.146 g C m^{-3}) than from May 1997 through 2001 (0.045 g C m^{-3}) further suggesting the existence of trophic cascades.

However, the modeled prey component theoretically consists of both phytoplankton and microzooplankton which reflects the omnivorous diet of mesozooplankton in Florida Bay (Kleppel et al. 1998). This is a confounding factor that likely weakens the impact of the trophic cascade on phytoplankton especially in the north-central sub-region of Florida Bay where cyanobacteria dominate the phytoplankton community (Phlips & Badylak 1996). Smaller mesozooplankton such as Bivalvia larvae are know to graze upon cyanobacteria (Raby et al. 1997); however, copepods are ineffective at grazing these small phytoplankton and thus likely graze primarily upon microzooplankton (Kleppel et al. 1998). Their grazing upon microzooplankton can in turn reduce microzooplankton grazing on small phytoplankton (Richardson et al. 2003). In 1994 to May 1997 when mesozooplankton were less abundant, there may have been reduced direct grazing upon phytoplankton by mesozooplankton, but increased grazing by microzooplankton causing the trophic cascade to both positively and negatively affect phytoplankton abundance.

It is necessary to consider the relationship between salinity and mesozooplankton in sub-tropical bays since salinity is typically the abiotic factor that accounts for the greatest variability (Kelble et al. 2010). Peak abundances of mesozooplankton are often observed at salinities far below those of the adjacent coastal ocean. However, in some sub-tropical embayments, peak mesozooplankton abundances are observed at salinities greater than the physiologically defined optimal range. In these environments, it has been hypothesized that the observed peak at higher salinities was the result of increased *A. mitchilli* predation at low salinities (Putland & Iverson 2007). In the absence of predation, the BAMZO model suggests that mesozooplankton abundance linearly decreases with increasing salinity (Fig. 4.11). With predation, the modeled mesozooplankton still have a maximum abundance at the lowest salinity, but abundance at salinities between 25 and 30 is significantly lower than at salinities >30; this trend reproduces *in situ* observations (Fig. 4.11). The results from this simulation support the hypothesis that *A. mitchilli* predation can shift copepod abundance distributions to higher salinities than that expected solely on physiology.

BAMZO had to incorporate the effect of salinity as a factor in the interaction between *A. mitchilli* and mesozooplankton in order to accurately reproduce the observed patterns in populations (Fig. 4.10 and 4.11). When salinity was held constant, the model did not reproduce observations accurately (Table 4.3). The removal of S_i removed the direct salinity effect on Copepoda (except *Acartia*). The model output with *Si* removed was similar to the base runs in BAMZO and observational data suggesting little direct effect of salinity on copepod populations in Florida Bay (Table 4.3; Fig. 4.10 and 4.11). These results suggest the correlation between mesozooplankton and salinity is largely an indirect effect of the relationship between *A. mitchilli* and salinity (Fig. 4.7, 4.8, 4.10 and 4.11). This is supported by studies in nearby sub-tropical embayments that have reported a salinity response in *A. mitchilli* juvenile recruitment (Peebles et al. 2007).

The influence of salinity on the Florida Bay ecosystem is complex and there is a high degree of spatial heterogeneity in salinity distributions (Kelble et al. 2007). Moreover, Florida Bay is not a positive gradient estuary with increasing salinity shoreward of a river-mouth, but instead is a seasonally hypersaline lagoon with localized runoff and isolated sub-regions with high residence times (Nuttle et al. 2000, Kelble et al. 2005, Lee et al. 2006, Lee et al. 2008). This physical heterogeneity results in a large degree of biological heterogeneity in Florida Bay, including mesozooplankton and *A. mitchilli* distributions (Powell et al. 2007, Kelble et al. 2010). However, BAMZO is a bay-wide model that replicates the mean salinity of Florida Bay and despite this simplification still reproduces the major patterns of bay-wide mean *A. mitchilli* and mesozooplankton populations.

The relationship between mesozooplankton abundance and salinity in Florida Bay was improved when samples were considered from sub-regions instead of bay-wide surveys (Kelble et al. 2010). This suggests further insight could be gained if the model is modified to incorporate spatial dynamics and if it can examine the contribution of the different sub-regions on mesozooplankton and *A. mitchilli* community dynamics. However, this refinement would require more observations to calibrate the model within each sub-region of Florida Bay.

Climactic cycles, climate change and anthropogenic activities can all significantly influence salinity distributions (Kelble et al. 2007, Dai et al. 2009). Based upon our analysis, these changes in salinity will likely affect *A. mitchilli* and mesozooplankton populations in Florida Bay (Fig. 4.9 and 4.11). Potentially this could occur in other sub-tropical ecosystems where *A. mitchilli* has a similar juvenile recruitment response to salinity. These changes could alter the entire ecosystem through changes in the trophic structure. Input of a predicted future salinity regime from a hydrological model could yield insights and predictions as to the future state of this key trophic interaction. In this manner, BAMZO could be used to conduct management scenario evaluations for different proposed freshwater management alternatives within the South Florida coastal ecosystem.

In recent years there has been increasing emphasis on quantifying fluxes and rates within an ecosystem in order to determine ecosystem functionality (Ulanowicz 1986, 1997). Our analysis provides further evidence that is consistent with this emphasis. The reduced abundance of mesozooplankton before May 1997 suggests there may be less prey available to the pelagic food. However, during this period there was significantly higher *A. mitchilli* abundances. In BAMZO, years with low copepod biomass correspond to higher productivity on a nauplii per female basis and higher relative loss rates to predation (Fig. 4.12). Prior to May 1997, the copepod loss attributed to *A. mitchilli* predation was 69.0% of all biomass losses in the model. After May 1997 only 24% of the copepod biomass losses were attributed to predation. These are unrealistically high trophic efficiencies (Ulanowicz 2004), in part, because BAMZO does not incorporate losses due to respiration. Moreover, copepod biomass in BAMZO had a significant inverse correlation with the relative loss to predation. This suggests these time-periods of low copepod biomass are not detrimental to pelagic trophic webs.

In summary, in order to accurately reproduce the observed patterns in mesozooplankton populations in a sub-tropical bay it was necessary to incorporate density-dependence, predation, and relationships with salinity. The density-dependent terms restrict the populations within possible population levels, while predation and the predator-salinity relationship account for the observed patterns of interannual variability. Increased predation at low salinities skews mesozooplankton distributions to higher salinities than would be observed in the absence of predation. The effect of salinity on *A. mitchilli* and mesozooplankton is largely mediated by the variability in *A. mitchilli* juvenile recruitment attributed salinity variations. Thus, alterations in salinity pattern forced by climactic cycles, climate change, or anthropogenic activities are all likely to significantly affect this key trophic interaction.

Table 4.1 Model values for population and consumption parameters used in the *A. mitchilli* module of BAMZO along with the range of literature values and references. Standard deviations, where applicable are given in parentheses.

Parameter	**Model Value**	**Literature Range**	**Source(s)**
Growth (Juvenile)	0.6 mm d^{-1}	0.4-0.7 mm d^{-1}	Zastrow et al. 1991, Leak and Houde 1987, Jordan et al. 2000, Rose et al. 1999
Growth (30-40mm)	0.3 mm d^{-1}	0.2-0.46 mm d^{-1}	Mowitt et al. 2006, Zastrow et al. 1991, Newberger & Houde 1995
Growth (40-50mm)	0.2 mm d^{-1}	0.05-0.46 mm d^{-1}	Mowitt et al. 2006, Zastrow et al. 1991, Newberger & Houde 1995, Rose et al. 1999, Ayala-Perez et al. 1997, Wang & Houde 1995
Growth (50-60mm)	0.1 mm d^{-1}	0.03-0.1 mm d^{-1}	Newberger & Houde 1995, Rose et al. 1999, Ayala-Perez et al. 1997, Wang & Houde 1995, Acosta et al. 2000
Growth (60-90mm)	0.05 mm d^{-1}	0.03-0.09 mm d^{-1}	Newberger & Houde 1995, Rose et al. 1999, Ayala-Perez et al. 1997, Wang & Houde 1995, Acosta et al. 2000
Maximum length	90 mm	85mm - 110mm	Newberger & Houde 1995, Ayala-Perez et al. 1997, Acosta et al. 2000
a_c	0.41 g d^{-1}	0.41 g d^{-1}	Luo & Brandt 1993
b_c	-0.33	-0.33	Luo & Brandt 1993
Z (Juvenile)	0.063 d^{-1} (0.01d^{-1})	0.01 - 0.45	Rose et al. 1999, Houde 1987, Leak and Houde 1987
Z (30-50mm)	0.025 d^{-1} (0.01d^{-1})	0.004-0.032 d^{-1}	Rose et al. 1999, Houde 1987,Wang 1992
Z (50-60mm)	0.01 d^{-1} (0.005 d^{-1})	0.004-0.01 d^{-1}	Rose et al. 1999, Wang 1992
Z (60-70mm)	0.009 -> 0.005 d^{-1} (0.004 d^{-1})	0.004-0.01 d^{-1}	Rose et al. 1999, Wang 1992
Z (70-90mm)	0.005 d^{-1} (0.004 d^{-1})	0.004-0.01 d^{-1}	Rose et al. 1999, Wang 1992
$f(t)$	$(V^x))(e^{x(1-V)})$	$(V^x))(e^{x(1-V)})$	Kitchell et al. 1977
t_m	33	33-37	Luo & Brandt 1993, Rose et al. 1999
t_o	27	27-28	Luo & Brandt 1993, Rose et al. 1999
Q	2.22	2.22	Luo & Brandt 1993

Table 4.2 Model values for population parameters used in the mesozooplankton module of the BAMZO model along with corresponding range of literature values for each parameter.

Taxa	Parameter	Model Value	Lit. Range	Source(s)
Acartia	Copepodite Duration	4 days	2-6 days	Johnson 1974, Schipp et al. 1999
Acartia	Longevity	24 days	24-44 days	Lonsdale 1981, Parrish & Wilson 1978
Acartia	Mortality	13% d^{-1}	0-20% d^{-1}	Drillet et al. 2008, Lincoln et al. 2001
Acartia	Naupliar Duration	4 days	4-5 days	Hopcroft & Roff 1998
Acartia	Sex Ratio	0.7	0.57-0.85	Drillet et al. 2008, Hirst et al. 1999, Lee & McAlice 1979, Norrbin 1994
Bivalvia	Mortality	0.15 d^{-1}	0.1-0.2 d^{-1}	Widdows 1991
Bivalvia	Pelagic Larval Duration	20 days	8-40 days	Campos & Ramorino 1980, Fields & Moore 1983, Arnold et al. 2005
Gastropoda	Mortality	0.074 d^{-1}	0.05-0.23 d^{-1}	Genio et al. 2008, Pechenik & Levine 2007
Gastropoda	Pelagic Larval Duration	27 days	15-60 days	Chan & Morton 2005, Couceiro et al. 2007, Schmidt et al. 2006, Qurban 2000
Harpacticoida	Copepodite Duration	4 days	3-5 days	Carlotti & Sciandra 1989, Matias Peralta et al. 2005, Williams & Jones 1994
Harpacticoida	Longevity	34 days	34-62 days	Lonsdale 1981, Matias-Peralta et al. 2005
Harpacticoida	Mortality	9% d^{-1}	0-30% d^{-1}	Carlotti & Sciandra 1989, Lonsdale 1981
Harpacticoida	Naupliar Duration	4 days	3-6 days	Carlotti & Sciandra 1989, Matias Peralta et al. 2005, Williams & Jones 1994
Harpacticoida	Nauplii Pod. Rate (NPR)	6 N f^{-1} d^{-1}	3.8-10 N f^{-1} d^{-1}	Hopcroft & Roff 1998, Lonsdale 1981
Harpacticoida	Sex Ratio	0.5	0.5	Lonsdale 1981
Oithona	Copepodite Duration	4 days	3-10 days	Hirst & Kiorboe 2002, Webber & Roff 1995
Oithona	Longevity	34 days	15-71 days	Lonsdale 1981, Paffenhofer 1993, Sabatini & Kiorboe 1994
Oithona	Mortality	4% d^{-1}	3-5% d^{-1}	Lonsdale 1981, Paffenhofer 1993
Oithona	Naupliar Duration	3 days	2-4 days	Hirst & Kiorboe 2002, Hopcroft & Roff 1998, Webber & Roff 1995
Oithona	Nauplii Pod. Rate (NPR)	7.6 N f^{-1} d^{-1}	3.8-13.6 N f^{-1} d^{-1}	Lonsdale 1981, Paffenhofer 1993
Oithona	Sex Ratio	0.85	0.79-0.94	Digby 1950, Hirst & Kiorboe 2002, Lonsdale 1981
Paracalanidae	Copepodite Duration	4 days	3-9 days	Chisholm & Roff 1990, Liang & Uye 1996, McKinnon 1996, Newbury & Bartholomew 1976
Paracalanidae	Longevity	16 days	10-25 days	Lonsdale 1981, Paffenhofer 1993
Paracalanidae	Mortality	5% d^{-1}	5% d^{-1}	McGurk 1987, Paffenhofer 1993
Paracalanidae	Naupliar Duration	3 days	2-4 days	Chisholm & Roff 1990, Hopcroft & Roff 1998, McKinnon 1996, McKinnon et al. 2003
Paracalanidae	Nauplii Pod. Rate (NPR)	16 N f^{-1} d^{-1}	2-40 N f^{-1} d^{-1}	Hopcroft & Roff 1998, Liang & Uye 1996, McKinnon 1996, Saito & Taguchi 2003, Uye & Shibuno 1992
Paracalanidae	Sex Ratio	0.7	0.69-0.85	Hirst & Kiorboe 2002, Liang & Uye 1996

Table 4.3 Kendall-Tau correlation values for the observed mesozooplankton taxa to base model output (BAMZO), the model output without predation (No Predation), the model output with salinity held constant (No Salinity) and the model output with S_i removed (No S_i). Significant values are bold, underlined and italicized.

OVERALL

	Acartia	*Oithona*	Paracalanidae	Harpacticoida	Nauplii	Bivalvia	Gastropoda
BAMZO	***0.453***	***0.390***	***0.375***	***0.309***	***0.234***	***0.291***	0.120
No Predation	-0.057	-0.096	-0.057	-0.210	-0.168	0.207	-0.078
Constant Salinity	0.021	0.114	-0.108	0.012	-0.009	0.207	-0.066
No S_i	***0.477***	***0.538***	***0.228***	***0.441***	***0.465***	***0.309***	0.123

INTERANNUAL

	Acartia	*Oithona*	Paracalanidae	Harpacticoida	Nauplii	Bivalvia	Gastropoda
BAMZO	***0.571***	***0.571***	***0.643***	***0.643***	0.500	0.500	0.357
No Predation	***-0.643***	***-0.643***	-0.500	-0.429	***-0.786***	0.143	0.286
Constant Salinity	-0.143	0.286	-0.071	-0.429	0.143	0.143	0.214
No S_i	0.429	***0.643***	0.500	***0.571***	***0.714***	***0.643***	0.357

SALINITY

	Acartia	*Oithona*	Paracalanidae	Harpacticoida	Nauplii	Bivalvia	Gastropoda
BAMZO	-0.200	0.200	***0.800***	0.000	-0.200	-0.200	0.600
No Predation	-0.200	-0.200	***0.800***	-0.200	-0.400	-0.400	***0.800***
Constant Salinity	0.400	0.600	-0.600	0.400	***0.800***	-0.200	0.600
No S_i	-0.200	0.200	-0.400	0.400	0.400	-0.200	0.600

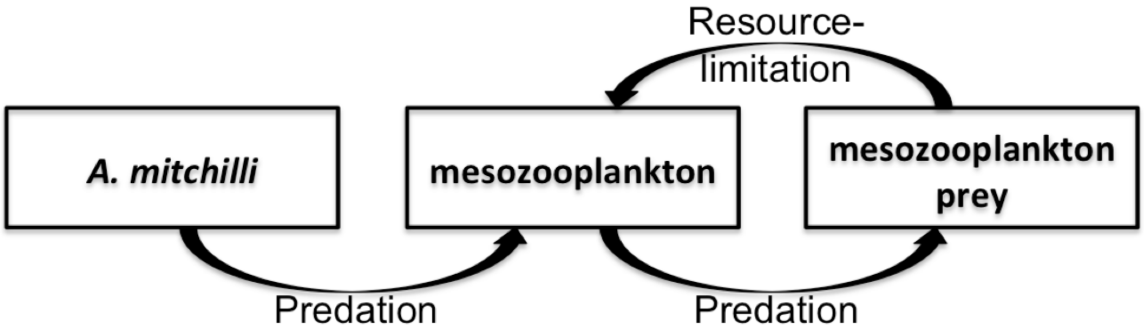

Figure 4.1 Depiction of model entities and their interactions.

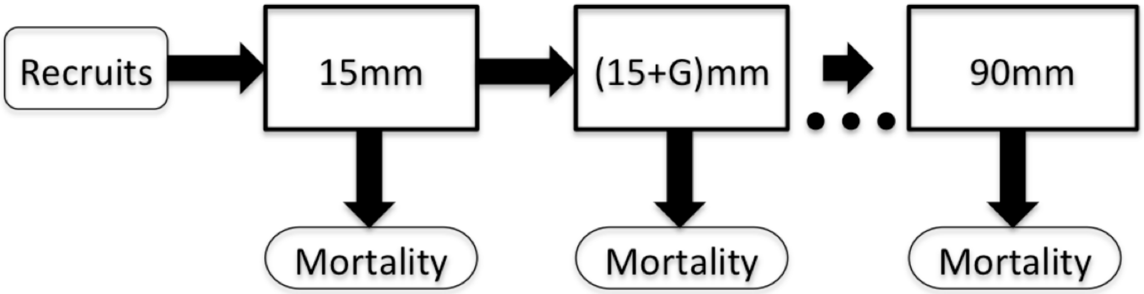

Figure 4.2 Depiction of the *Anchoa mitchilli* module of the BAMZO model. At each daily time step, a percentage of the population succumb to mortality and the remainder progress to the next length increment for the next day until the maximum length of 90mm is achieved. At which point they senesce the next day. Also, new recruits are added with each daily time step according to equation X that is a function of temperature, salinity and the population size for adults between 30mm and 40mm.

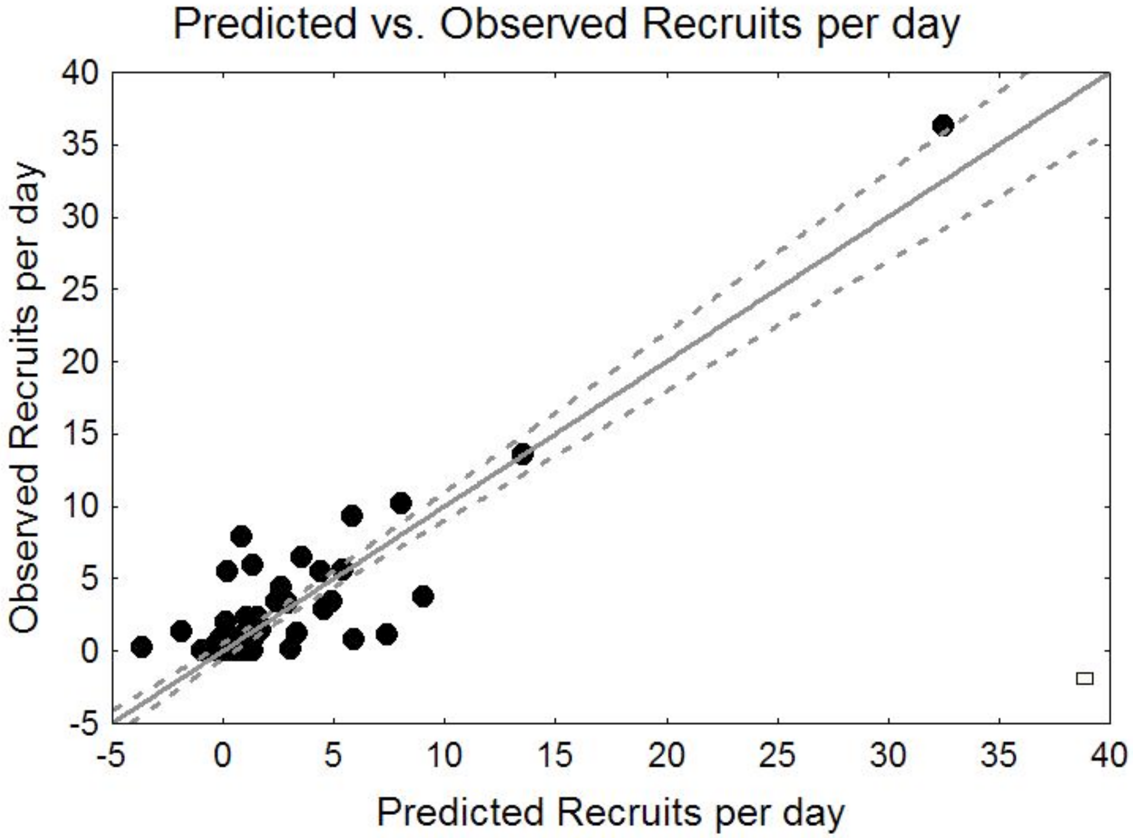

Figure 4.3 Multiple regression to estimate the number of recruits to west and north-central Florida Bay per day.

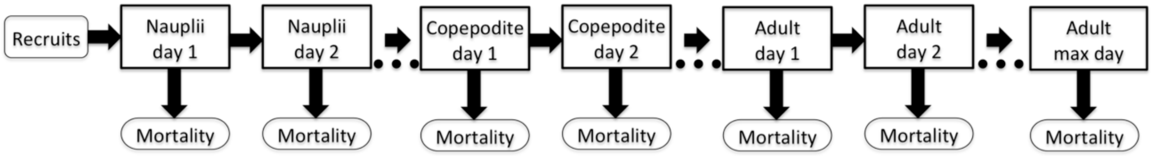

Figure 4.4 Depiction of the structure of Copepoda taxa component models in the mesozooplankton module of BAMZO. Viable eggs recruit to nauplii each daily time step and at each time step a percentage of each daily age class succumb to mortality and the remainder progress to the next stage class. Progression from nauplii to copepodites and from copepodites to adults occurs at the daily age class equivalent to the end of the nauplii or copepodite development time at which point they pass onto the next stage.

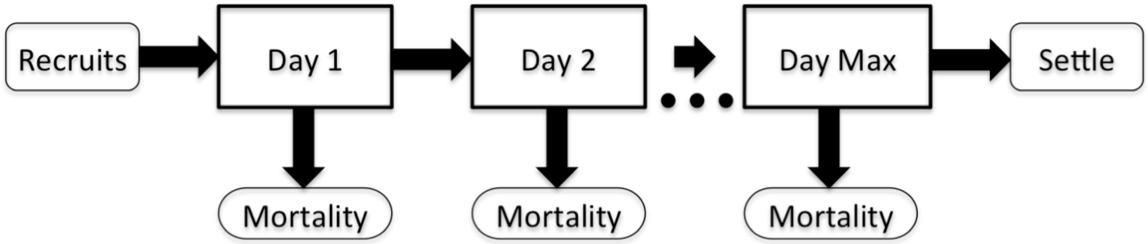

Figure 4.5 Depiction of the structure of the Bivalvia and Gastropoda components within the mesozooplankton module.

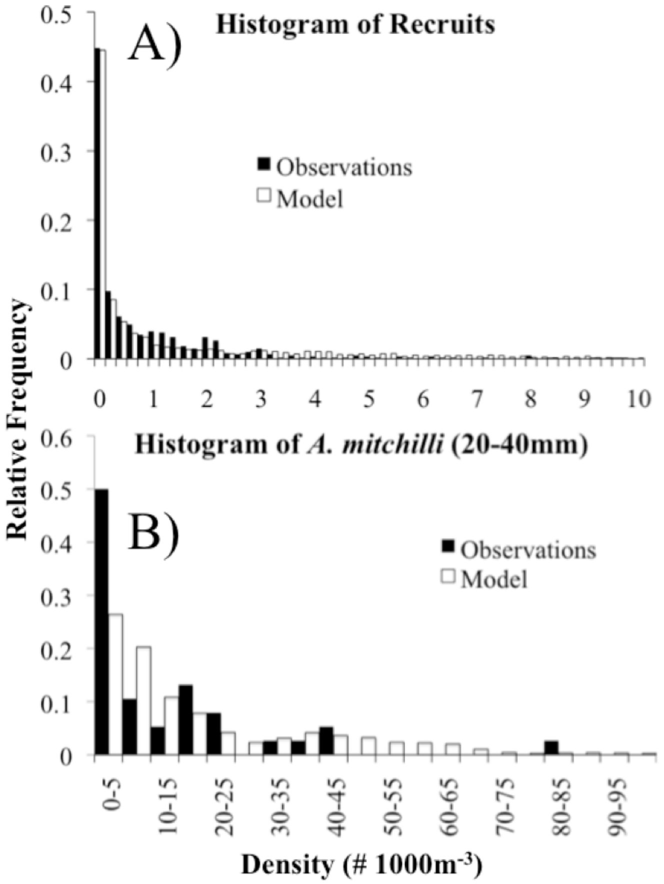

Figure 4.6 Histogram of the relative frequency of the density of *A. mitchilli* recruits (top panel) and 20-40mm standard length *A. mitchilli* (bottom panel) for both observations and model output. It represents the proportion of observations and model outputs that are within the range of densities delineated on the x-axis. Adjacent black and white columns denote the relative frequency of observations and model output, respectively, that were within the same density range.

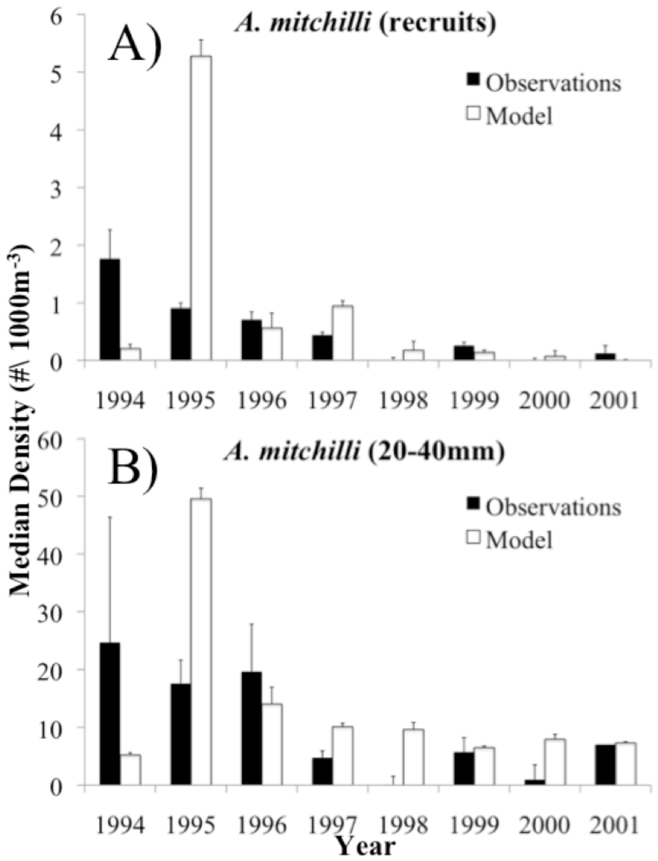

Figure 4.7 Median density of recruits (top panel) and 20-40mm standard length *A. mitchilli* for each year from observations, the BAMZO model and the BAMZO model with salinity held constant (Constant Salinity). The error bars reflect the standard error.

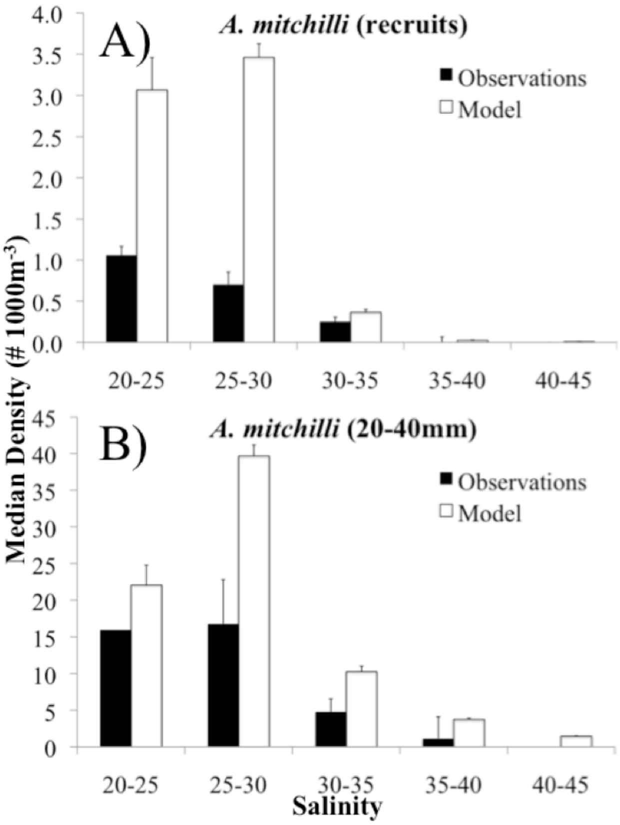

Figure 4.8 Median density of recruits (top panel) and 20-40mm standard length *A. mitchilli* for each salinity bin from observations, the BAMZO model and the BAMZO model with salinity held constant (Constant Salinity). The error bars reflect the standard error.

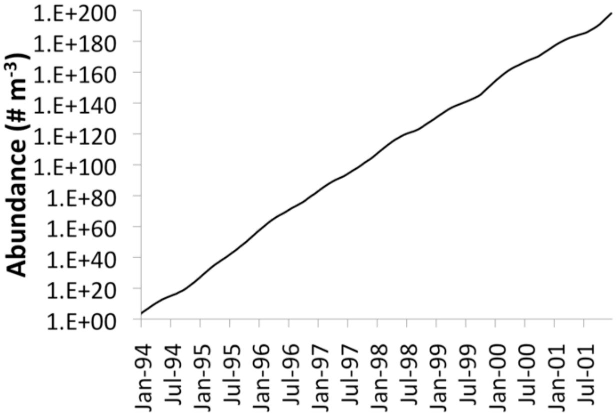

Figure 4.9 Time-series of *Acartia* density from BAMZO with no density-dependence (Note: The y-axis is logarithmic).

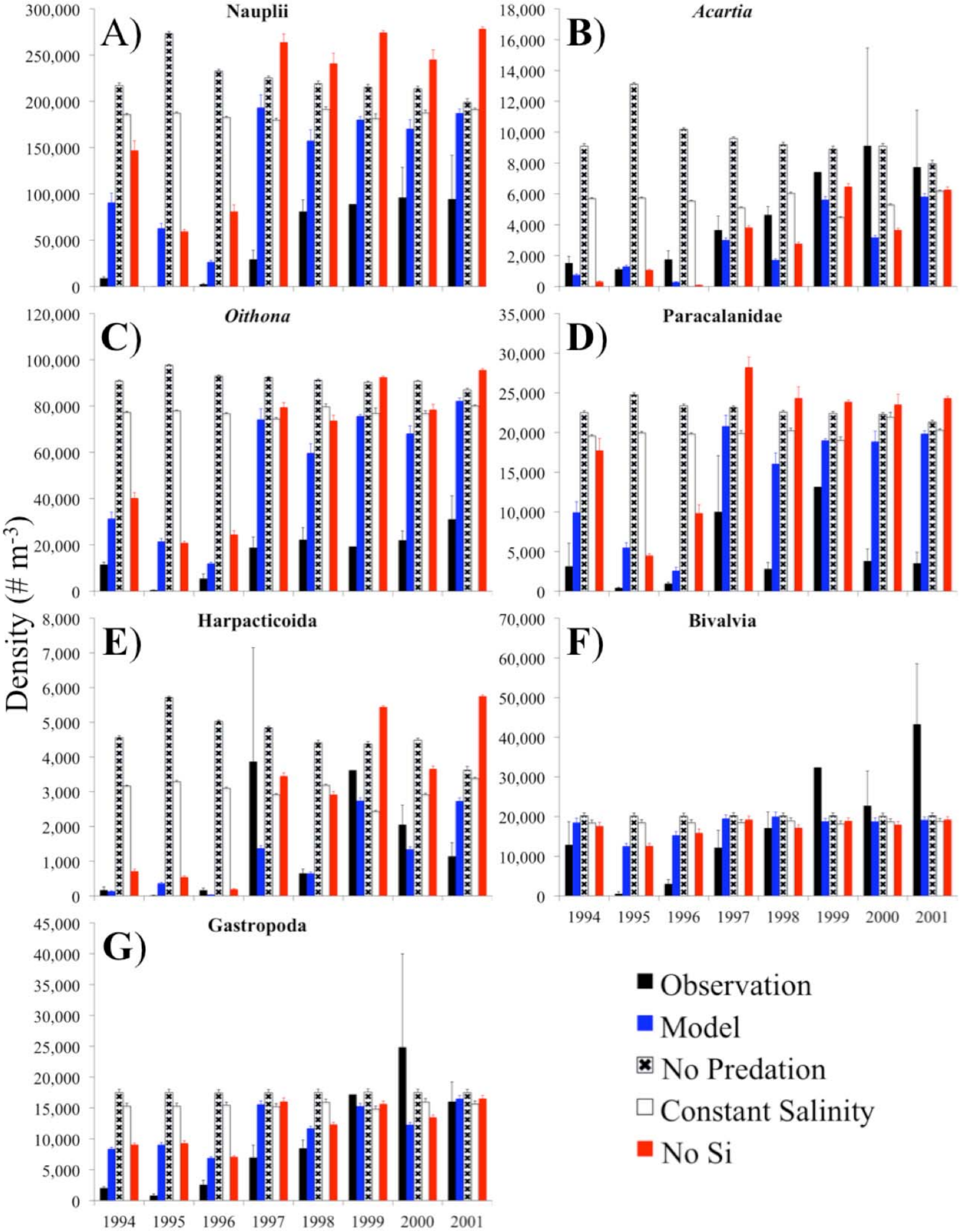

Figure 4.10 Annual median density for each mesozooplankton taxa from observations (observations), BAMZO base output (model), BAMZO output with no predation (No Predation) by *A. mitchilli*, BAMZO output with salinity held constant (Constant Salinity) and BAMZO output with S_i removed (No Si). The error bars reflect the standard error.

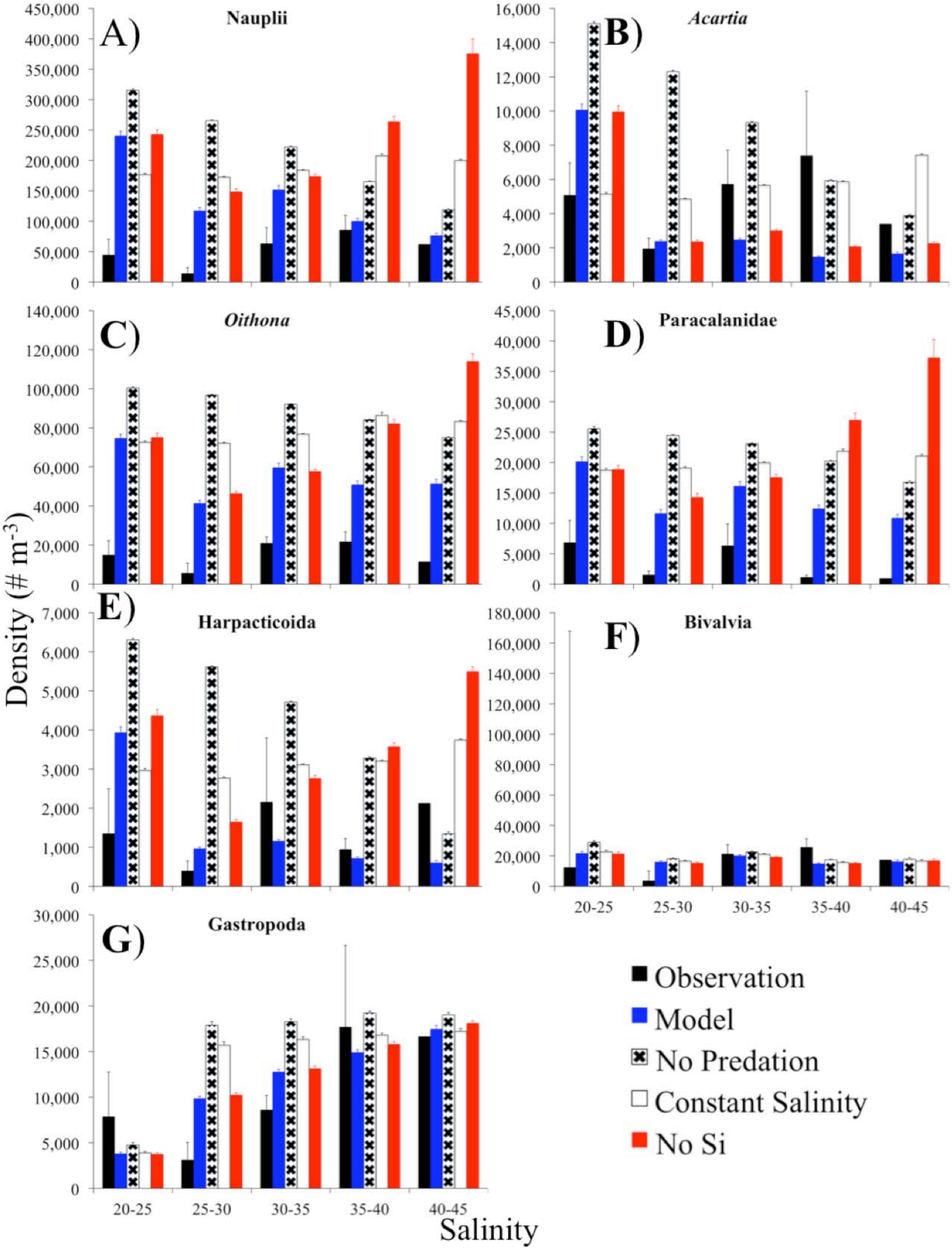

Figure 4.11 Median density within each salinity bin for each mesozooplankton taxa from observations (observations), BAMZO base output (model), BAMZO output with no predation (No Predation) by *A. mitchilli*, BAMZO output with salinity held constant (Constant Salinity) and BAMZO output with S_i removed (No Si). The error bars reflect the standard error.

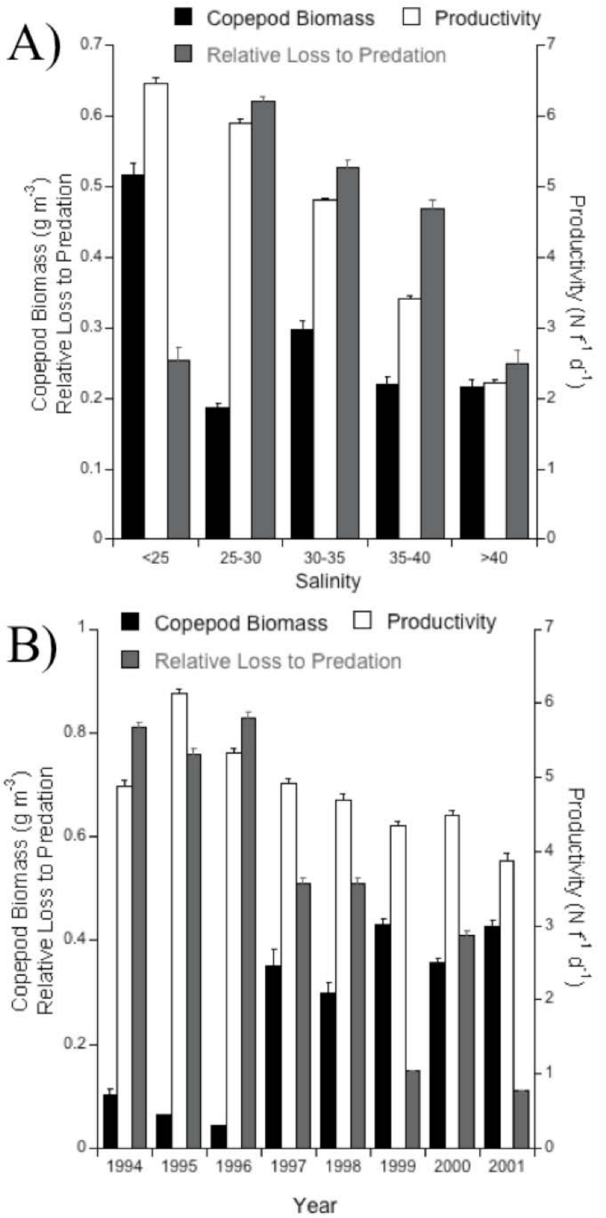

Figure 4.12 Median copepod biomass (g m^{-3}), nauplii productivity per female per day and the ratio of losses in BAMZO that are the result of *A. mitchilli* predation for A) each salinity bin (top panel) and B) year (bottom panel).

CHAPTER 5

SYNTHESIS, IMPLICATIONS AND FUTURE RESEARCH

Summary of Findings

This dissertation suggests that if CERP is capable of altering salinity regimes within Florida Bay, it could potentially produce significant ecological consequences. However, the effect of CERP on the Florida Bay ecosystem will occur against a backdrop of climactic variability. Discriminating management effects from natural variability is critical to determine the success of CERP. At present, the most effective tool to accomplish this is by combining observations with models that will simulate conditions without management influences (Trexler & Goss 2009). Specifically, hydrologic and salinity models are needed to simulate the salinity distribution with and without management effects. Subsequently, ecological models can be run under the observed salinity regime and a modeled salinity regime that would not incorporate the effects of CERP. The development of models to simulate key ecosystem parameters is also essential to conduct scenario evaluations and institute effective ecosystem based management (Levin et al. 2009).

Salinity variability in Florida Bay is driven by the annual cycle of freshwater supply for south Florida (Fig 2.4). Under current conditions only 15% of the freshwater received in Florida Bay is direct runoff from gauged streams and the vast majority is rainfall (Fig. 2.8). The complex geomorphology of Florida Bay results in a large degree of compartmentalization among the sub-regions with respect to salinity (Fig. 2.5 and 2.6). These different salinity environments and the isolation between sub-regions (Lee et al. 2006, Lee et al. 2008) result in a large degree of spatial heterogeneity within Florida Bay for water quality, phytoplankton and other variables (Phlips & Badylak 1996, Boyer et al. 1997, Kelble et al. 2005).

Given this, it was hypothesized that mesozooplankton would also have significant sub-regional differences. In fact, mesozooplankton did have significant differences between sub-regions with higher abundances in the west and north-central sub-regions (Fig. 3.3). These are also the most productive sub-regions. However, the most striking feature of the time series was a common interannual variability in all sub-regions (Fig. 3.4). All sub-regions had significantly lower mesozooplankton populations before May 1997 (Fig. 3.2). A significant positive correlation was observed between mesozooplankton and salinity, with the highest median abundance for all mesozooplankton taxa occurring during hypersaline periods (Fig. 3.6). Both the positive correlation with salinity and the pattern in interannual variability were correlated with the abundance of the primary planktivorous fish in Florida Bay, *A. mitchilli*, suggesting the importance of top-down controls in Florida Bay (Fig. 3.8 and 3.9).

Further investigation of this interaction was undertaken with a mechanistic model that simulated *A. mitchilli* and mesozooplankton populations within Florida Bay. Top-down control alone was insufficient to simulate mesozooplankton populations (Fig. 4.9). Thus, density-dependence was incorporated based on a simple logistic mesozooplankton prey population. Once both mechanisms were incorporated, the model reasonably reproduced the observed interannual variability in both mesozooplankton and *A. mitchilli* (Fig. 4.7 and 4.10). Although the observational data showed a strong correlation between mesozooplankton and salinity, the model results suggest this interaction is largely an indirect effect. Salinity variability caused changes in *A. mitchilli* recruitment that, through predation, reduced the mesozooplankton population (Fig. 4.10 and 4.11). This suggests that future changes in salinity could potentially alter this key trophic interaction.

Implications

If CERP is successful at increasing freshwater runoff sufficiently to alter salinity in Florida Bay, this dissertation suggests that it is likely to alter *A. mitchilli* recruitment, which subsequently could alter mesozooplankton populations (Fig. 2.4A, 3.6, 4.10, 4.11). These changes will coincide with climactic variability that could also alter the salinity regime and environment of Florida Bay (Fig. 2.3; (Briceno & Boyer 2010). This backdrop confounds the impact of freshwater management actions on the Florida Bay ecosystem and requires models to partition management effects upon salinity from natural variability (RECOVER 2007, Trexler & Goss 2009). The box model developed in chapter 2 and the ecological model developed in chapter 4 could be coupled with a hydrological model to evaluate the effect of different freshwater management scenarios on the populations of *A. mitchilli* and mesozooplankton. The US Army Corps of Engineers programmatic regulations require alternative water management scenarios to be evaluated with respect to their ecological consequences using tools such as the ecological model developed in chapter 4 (USACoE 1999).

One of CERP's interim goals is to minimize the intensity, frequency, duration and spatial extent of hypersalinity in Florida Bay (RECOVER 2005). Hypersalinity develops in north-central Florida Bay and it was present during every non-El Niño summer from 1998 to 2004 (Fig. 2.5C and Fig. 2.6). The findings from chapter 2 in conjunction with investigations of sub-region circulation and transport (Lee et al. 2006, Lee et al. 2008) imply a portion of the freshwater runoff during the dry season could be diverted from the northeast to the north-central sub-region to mitigate hypersalinity (Lee et al. 2008).

Interestingly, not only is north-central Florida Bay the epicenter of hypersaline conditions, but it also had the highest recruitment of juvenile *A. mitchilli* (Fig. 5.1). *A. mitchilli* recruitment is known to occur preferentially at lower salinities within sub-tropical embayments (Peebles et al. 2007). The data in Florida Bay are consistent with these prior findings, and show an inverse correlation between juvenile *A. mitchilli* recruitment and salinity. In fact, no recruitment was observed at salinities greater than 40 (Fig. 4.8A). Management actions that either mitigate hypersalinity or reduce all salinities throughout the year might significantly increase the population of *A. mitchilli* in Florida Bay (Fig. 3.8 and 4.8). The strength of this response would be dependent upon a supply of juvenile *A. mitchilli*, most likely from nearby coastal waters (Jung & Houde 2004).

It has been suggested that pelagic trophic webs are strongly influenced by variation in a few key species, or trophic levels, and that changes to these key populations can affect a large portion of the pelagic trophic web (Verity & Smetacek 1996). Moreover, species from the same sub-family, Engraulinae as *A. mitchilli*, have been documented to occupy wasp-waist niches in other coastal ecosystems (Shannon et al. 2008). In this dissertation it was shown that *A. mitchilli* predation and density-dependence are both controlling processes for mesozooplankton populations in Florida Bay. Variability in the *A. mitchilli* population caused a significant shift in the mesozooplankton population with an order of magnitude lower mesozooplankton abundance during the period of high *A. mitchilli* abundance before May 1997 (Fig. 3.2 and 3.9).

Management Scenario Evaluations

Two different scenarios were tested with respect to the effect of altered salinity regimes upon *A. mitchilli* and mesozooplankton populations. The alternatives tested were 1) a targeted approach to minimize hypersalinity and 2) a general approach that lowered salinities throughout the year.

The targeted scenario was designed to evaluate the ecological effect of achieving CERP's interim goal of mitigating hypersalinity. Options were limited in that BAMZO is a bay-wide model. This scenario was tested by lowering salinity values input to BAMZO by 10% whenever the mean bay-wide salinity was greater than 37. This assumes an increase of freshwater runoff to the Bay during the dry season, rather than a diversion of runoff from the northeast to north-central sub-region. A 10% reduction in salinity was essentially an arbitrary choice for illustrative purposes. To actually test the impact of a diversion of freshwater runoff to mitigate a hypersalinity in north-central Florida Bay would require a spatially explicit model, with at least one sub-module parameterized for the four-sub-regions.

The second alternative lowered all salinities by 5%. This would replicate a partial restoration of the reduced freshwater flow to Florida Bay that has been present for the past 50-years (Smith et al. 1989, Light & Dineen 1994).

The targeted reduction of hypersalinity resulted in little impact on either *A. mitchilli* abundance or copepod biomass (Fig. 5.2). Mann-Whitney U-tests did show significantly higher *A. mitchilli* abundance with the reduction of hypersalinity, but no change in copepod biomass (α=0.10). Furthermore, the median abundance of *A. mitchilli* increased from 32.7 to 33.7 1000m^{-3}. Both the model and our prior observations indicate that recruitment was near zero at salinities greater than 30; however, both observed and modeled recruitment more than tripled within the 25-30 salinity bin and increased even more in the 20-25 salinity bin (Fig. 4.8A). Since reducing hypersalinity by 10% has little impact on the duration of low salinity conditions, it did not dramatically increase *A. mitchilli* recruitment in the model and likely would not do so in Florida Bay. The effect on copepods was also negligible.

In contrast, reducing salinity by 5% throughout the year led to significant changes in the model output for both *A. mitchilli* abundance and copepod biomass (Fig. 5.2). Mann-Whitney U-tests showed a significant increase in *A. mitchilli* abundance and a significant decrease in copepod biomass (α=0.10). In fact, BAMZO predicted a 5% reduction of salinity would result in a nearly two-fold increase in the median *A. mitchilli* abundance (32.7 to 62.2 1000m^{-3}) and a 6-fold decrease in the median copepod abundance (0.182 to 0.030 g m^{-3}). The annual medians for *A. mitchilli* in BAMZO increased systematically from 69% to 122% over the initial output (Fig. 5.3A). Changes in the annual medians for copepod biomass were more variable (Fig. 5.3B). In fact, 1994-1996 showed minimal reductions in copepod biomass, whereas 1997, 1998 and 2000 all had greater than a five-fold decrease in copepod biomass. It is possible that the modeled copepod biomass from 1994-1996 was already near its theoretical minimum. This is potentially due to the fact that *A. mitchilli* never consumed more than 50% of the copepods in any taxa in a single day; thus, the increased predation did not greatly alter the modeled copepod biomass during these years. Reducing salinities during the wet season, when salinities are near or less than 30, can result in large changes in *A. mitchilli* recruitment (Fig. 4.8A). The large increases in *A. mitchilli* abundance and decreases in mesozooplankton that accompany a 5% decrease in salinity reflect non-linear responses in BAMZO (Eq. 4-1) and are likely also present in Florida Bay (Fig. 4.8A).

The results from BAMZO suggest CERP must consider the ecological consequences of a proposed management approach rather than simply target the removal of an unnatural physical situation. This preliminary evaluation suggests that significant changes could occur in the pelagic trophic web if management attempted to restore historic salinity lows rather than minimize the higher-than-historic hypersalinity periods. That said, it is of course important to decide whether a condition of high *A. mitchilli* and low mesozooplankton abundance is desired in Florida Bay. Moreover, the ecological consequences of water management alternatives on other key ecosystem components, such as algal blooms, seagrass and fish must also be evaluated.

Direct freshwater runoff from gauged streams and canals accounted for 15% of the freshwater supply to Florida Bay (Table 2.3). However, this does not include indirect freshwater runoff from rivers along the southwest Florida shelf (Fig. 2.12) and direct runoff from unmeasured sheet-flow and streams (Fig. 2.11B). Both of these were obvious influences that affect the salinity patterns of Florida Bay (Fig. 2.5, 2.11 and 2.12). Moreover, the box-model was unable to replicate the lowest salinity values when these unmeasured sources were not included (Fig. 2.7). Therefore, it is reasonable to assume that freshwater runoff from the Everglades accounts for at least 20% of the total freshwater input to the Bay. The box-model developed in chapter 2 suggests overall freshwater supply would need to increase by 16.5% to affect a 5% mean salinity reduction. Assuming current runoff is 20% of freshwater supply, this equates to an 82% increase in runoff. Although this is a large increase, it does not represent a restoration to historic conditions. Paleoecologic studies suggest that salinity in some parts of Florida Bay were 34% lower and runoff to the Bay was 2.5 to 4-times higher before anthropogenic alteration of hydrology (Marshall et al. 2009).

Potential Effects on Florida Bay Ecosystem

The changes to a key trophic interaction with altered salinity could result in changes throughout the Florida Bay ecosystem that propagate up and down the trophic-web (Bakun 1996). Altered mesozooplankton populations would result in significant changes to the grazing pressure on phytoplankton and microzooplankton in Florida Bay (Richardson et al. 2003). Minimizing phytoplankton blooms in Florida Bay is one other CERP interim goal (RECOVER 2005), because previous blooms have resulted in a cascade of negative ecosystem impacts (Butler et al. 1995). However, the emphasis in controlling phytoplankton blooms has focused exclusively on the impact of nutrients or bottom-up control with little attention to the potential impact of top-down control (RECOVER 2007). Model results suggest that altering freshwater delivery, and thus the salinity distribution in Florida Bay, could significantly alter the grazing pressure on phytoplankton. If lower salinities do result in enhanced *A. mitchilli* recruitment, with lower mesozooplankton biomass, it could significantly decrease the grazing pressure on phytoplankton, (Fig. 5.2B and 5.3B). Alternatively, mesozooplankton grazing on microzooplankton could mediate this effect by decreasing grazing by microzooplankton on phytoplankton (Richardson et al. 2003, Lawrence et al. 2004).

The mesozooplankton carbon demand output from BAMZO, 0.001 to 0.020 g C m^{-3} d^{-1}, is in reasonable agreement with values calculated from observational data, 0.0005 to 0.012 g C m^{-3} (Dagg and Brenner personal communication). This output was compared to observed phytoplankton chlorophyll *a* data from both Florida International University and NOAA as described in (Kelble et al. 2005, Boyer & Briceno 2008). The chlorophyll *a* concentration was multiplied by the average carbon to chlorophyll *a* ratio observed in Florida Bay to yield phytoplankton carbon concentration (Lavrentyev et al. 1998). Both the time series and monthly means suggest that mesozooplankton carbon demand per day is slightly less than 10% of phytoplankton carbon biomass (Fig. 5.4).

However, the grazing impact upon prey can often be two to three times higher than the calculated mesozooplankton respiratory carbon demand. This calculated carbon demand per day equals the carbon consumed each day to fulfill respiratory requirements, and therefore does not account for inefficient carbon transfer, egestion, sloppy feeding and reproduction (Omori & Ikeda 1984). Thus, the grazing loss may be 20%-30% of the phytoplankton standing stock and as such represents an important loss term for phytoplankton in Florida Bay. In fact, the model output showed an increase in mesozooplankton carbon demand throughout Florida Bay in 1997, which corresponded with a decrease in observed phytoplankton biomass after 1997 (Fig. 5.4A).

Changes in mesozooplankton and *A. mitchilli* could propagate up the trophic web as well. The relative loss of mesozooplankton to *A. mitchilli* predation was calculated from BAMZO. This ratio increased when relatively more mesozooplankton were consumed by *A. mitchilli* than were lost to natural mortality and cannibalism. Again, there was minimal change in the relative loss to predation between the initial scenario and that with a 10% decrease in hypersalinity, but relatively large change associated with the 5% decrease in overall salinity (Fig. 5.6A). In fact, the annual median for the relative loss to *A. mitchilli* predation was three-fold higher for a 5% salinity reduction (Fig. 5.6B). The potential for an increase in *A. mitchilli* biomass to influence upper trophic levels has been observed in other embayments in which *A. mitchilli* is an important prey species for several commercial fishery species (Baird & Ulanowicz 1989).

Within Florida Bay, *A. mitchilli* is a significant dietary component of numerous fish species, including tarpon, spotted seatrout and mackerel. All of these have significant fisheries within or around Florida Bay (Hettler 1989, Rutherford et al. 1989, FDEP 1997). The otter trawls utilized for the *A. mitchilli* observations in this dissertation were ineffective at capturing potential *A. mitchilli* predators (Powell et al. 2007). However, there was a significant increase in juvenile spotted seatrout in 1994 and 1995 that coincided with the large population of *A. mitchilli* (Thayer et al. 1999). While this may suggest a trophic effect, there are a number of complicating factors that govern the abundance of juvenile fish species. Therefore, it is not possible to conclude that this was the result of a healthier adult population due to increased *A. mitchilli* abundance.

Future Research

Topic 1: Zooplankton effects upon phytoplankton bloom dynamics

Understanding trophic interactions within phytoplankton blooms, in particular *Synechococcus* blooms, is important because they have significant ecological consequences (Butler et al. 1995, Phlips et al. 1999) and little is known about the role that top-down controls may have in limiting or terminating blooms. The model runs suggest a 5% reduction in Florida Bay salinity could result in a large decrease in mesozooplankton biomass, and thereby alter grazing pressure upon phytoplankton (Fig. 5.2B, 5.3B, 5.4 and 5.5). The annual median mesozooplankton carbon demand decreased up to 88% when salinity was reduced by 5% (Fig. 5.5B). This change in carbon demand could result in large changes in phytoplankton standing stock. However, the mesozooplankton-phytoplankton interaction is complicated in Florida Bay, since mesozooplankton also feed upon microzooplankton (Kleppel et al. 1998). Moreover, zooplankton are not the only phytoplankton grazers in Florida Bay. Grazing by benthic organisms, such as sponges can be significant (Peterson et al. 2006) and the relative importance of pelagic and benthic grazing has not been quantitatively determined. Another major unknown is the prey preference of Bay mesozooplankton species. The only study of mesozooplankton diet in Florida Bay suggested *Acartia tonsa* grazed both phytoplankton and microzooplankton, with diet differing spatially (Kleppel et al. 1998). However, little is known about the prey preference for other species that are more abundant in Florida Bay.

<u>Specific future research needs:</u>

- Quantify the prey preferences of all six of the most common mesozooplankton taxa
- Identify the primary pelagic and benthic grazers of *Synechococcus* during Florida Bay blooms and estimate the losses to grazing
- Investigate microzooplankton population dynamics and the degree to which they are coupled to mesozooplankton population dynamics
- Determine if there is a numeric response by mesozooplankton and/or microzooplankton to phytoplankton blooms of different types, compositions, intensities and durations
- Identify the underlying mechanism(s) governing mesozooplankton density-dependence that is required to keep their populations within realistic bounds

Topic 2: Upper trophic level effects of A. mitchilli population variability

Understanding the linkages between adult fish abundance and the population of *A. mitchilli* is important, because a CERP performance measure is to "increase fish diversity and density, and in particular increase the abundance of Florida Bay seatrout and mangrove fish assemblages" (RECOVER 2008). Future research should examine the factors that influence fish diversity and abundance in Florida Bay and investigate correlations between other fish and *A. mitchilli* populations.

Specific future research needs:

- Examine creel survey data from Everglades National Park and other sources of fisheries dependent data to determine if there is a relationship between *A. mitchilli* abundance and the landings of its major predators
- Examine the data from the current Florida Fish and Wildlife Commission study of fish populations in northeast and north-central Florida Bay to determine if other species are correlated with *A. mitchilli*
- Conduct limited fisheries independent surveys to determine the degree to which available landings data may be used to estimate population abundances

Topic 3: Ecological modeling

Modeling activities form a cornerstone of effective ecosystem management. Predictive models are required within CERP to evaluate freshwater management alternatives. The ecological benefit of any CERP project must be quantified and a cost-benefit analysis undertaken before the project reaches the implementation phase (USACoE 1999). Moreover, significant knowledge of ecosystem processes can be gained through heuristic models.

Specific future research needs:

- Develop a spatially explicit BAMZO model to incorporate sub-regional populations of mesozooplankton (Fig. 3.3) and *A. mitchilli* (Fig. 5.1) and differences in salinity dynamics (Fig. 2.5). This would permit proper evaluation of water management alternatives that may not require a large increase in freshwater runoff, such as diverting a portion of runoff from the northeast to the north-central sub-regions during the dry season.
- Significant knowledge may be gained by coupling BAMZO with water quality and phytoplankton models already under development within Florida Bay (Madden & MacDonald 2008) to examine the impact of freshwater management on phytoplankton grazing and blooms
- Although there are relatively few observations for verification and validation, a mechanistic, predictive microzooplankton model for Florida Bay could be coupled with BAMZO and the phytoplankton model yielding a more comprehensive planktonic ecosystem model. This model should be spatially explicit with at least one formulation for each of the sub-regions.
- These models should be coupled to hydrological and salinity models to evaluate water management alternatives within CERP, and determine the ecological benefit of diverting water towards Florida Bay during the restoration, a requirement of CERP's programmatic regulations (USACoE 1999).
- Other modeling approaches, such as ecosystem network analysis, should be undertaken to investigate the trophic impact of variations in mesozooplankton of *A. mitchilli* populations in the Florida Bay ecosystem. Such an approach could

assist in identifying key species to monitor that will indicate ecosystem functionality and resiliency within Florida Bay (Ulanowicz 2004).

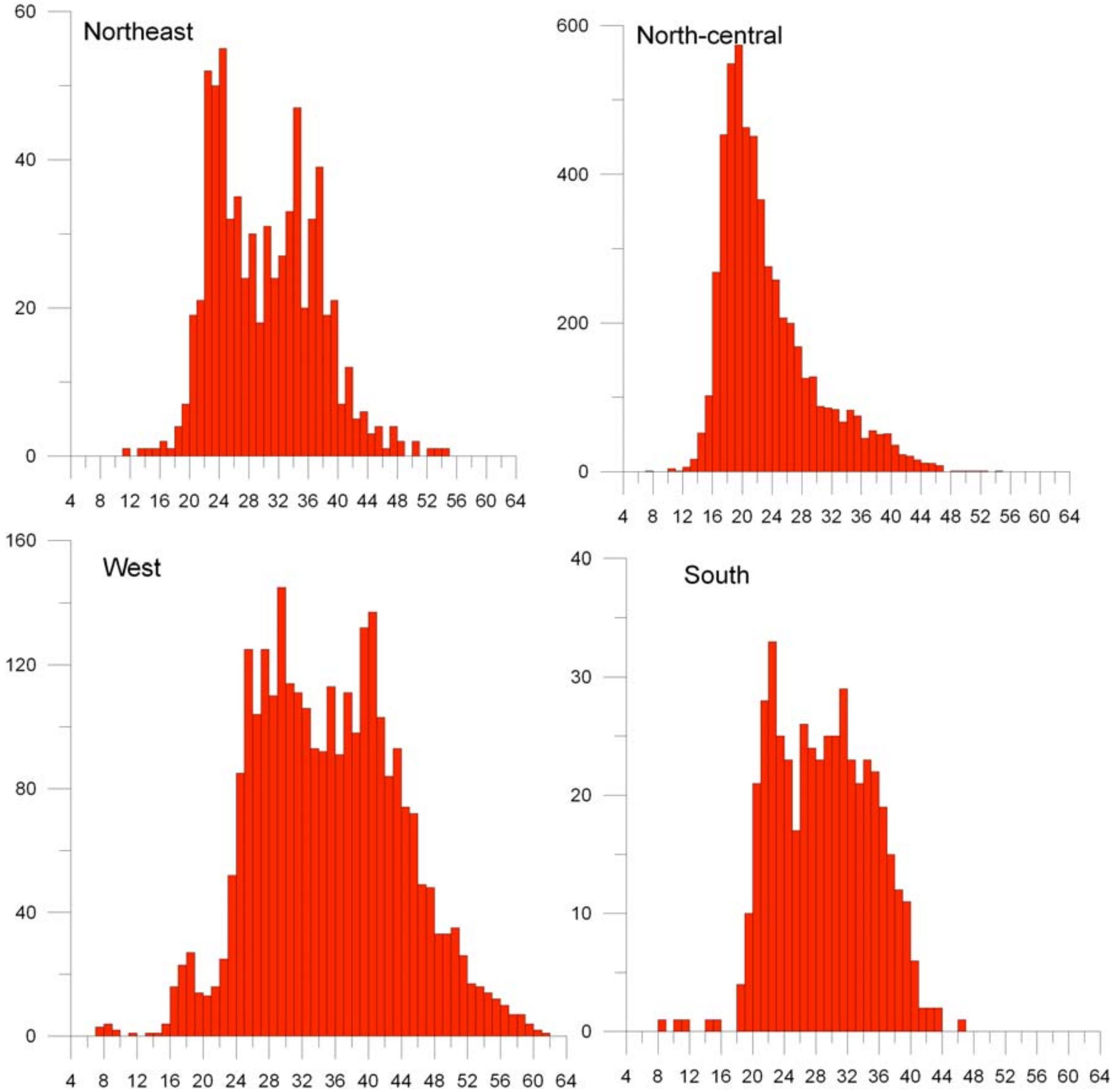

Figure 5.1 Length-frequency histograms of *A. mitchilli* in each sub-region of Florida Bay. The length on the x-axis is standard length in mm and each bin is 1mm wide. On the y-axis is the number of observations for that standard length fish in each sub-region.

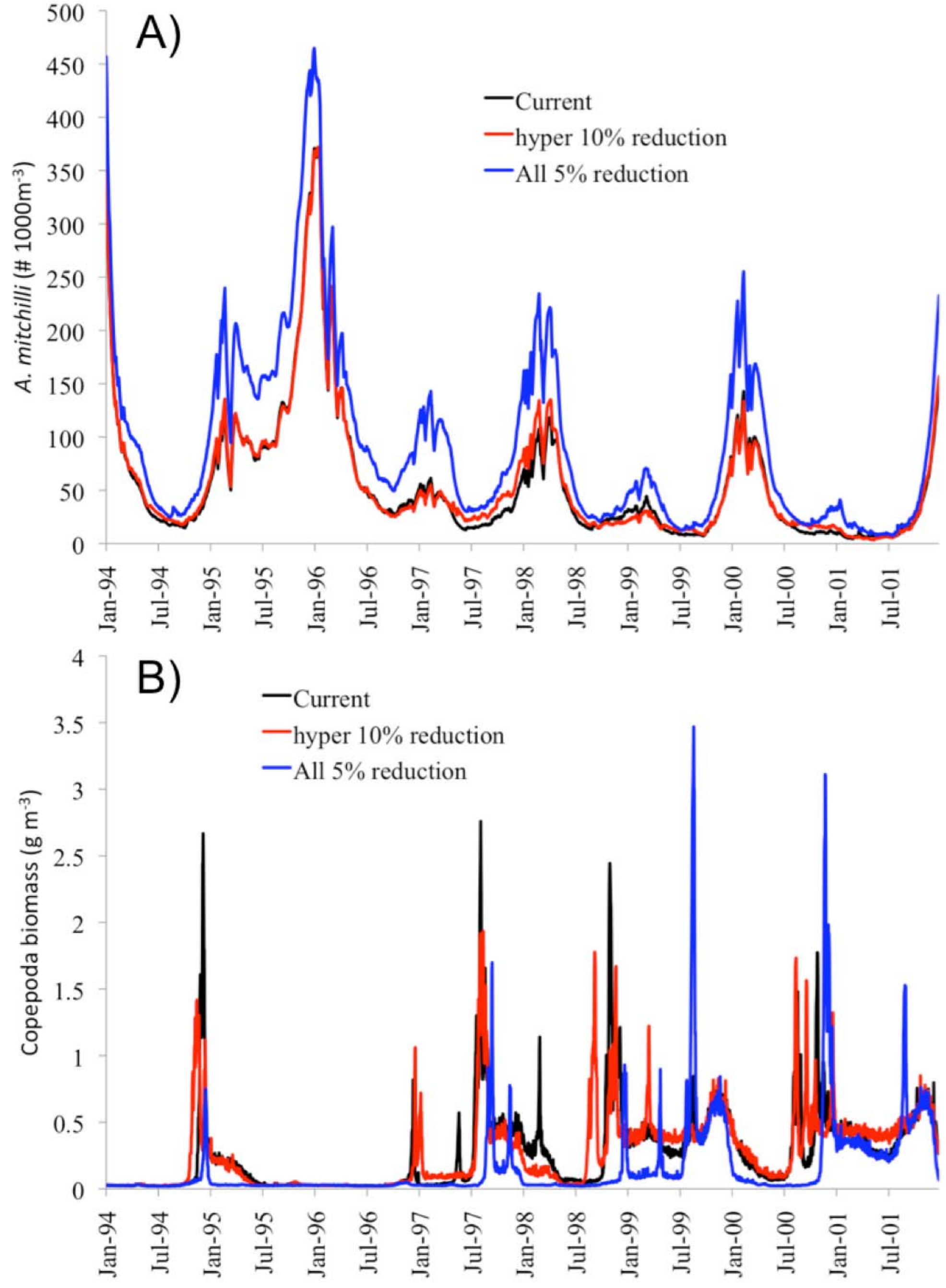

Figure 5.2 Time series of BAMZO output of A) *A. mitchilli* abundance and B) copepod biomass for the period of record under current conditions (Current), a 10% reduction of hypersaline events (hyper 10% reduction) and a 5% reduction of salinity throughout the year (All 5% reduction).

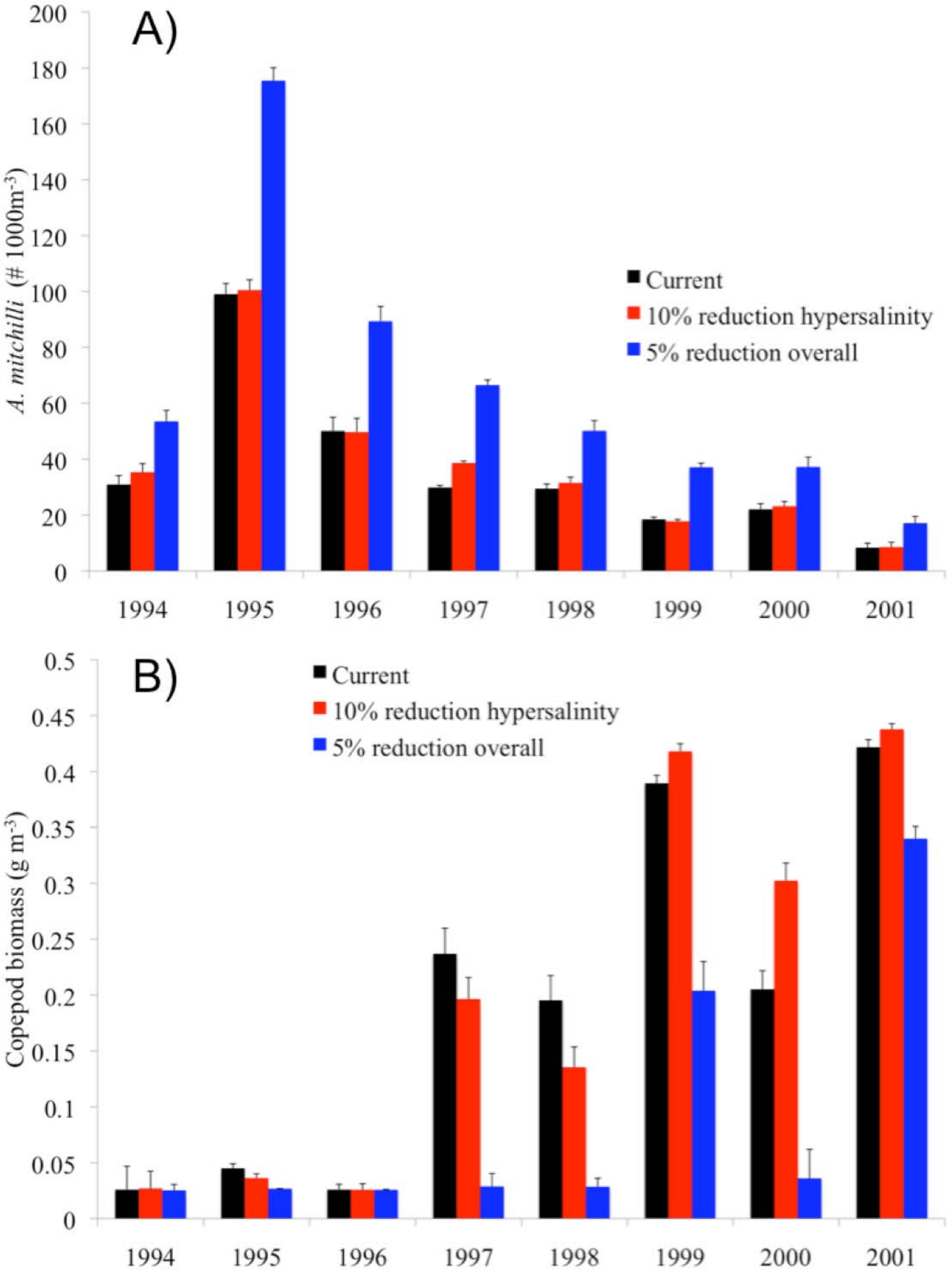

Figure 5-3 Annual medians of daily BAMZO output for A) *A. mitchilli* abundance and B) copepod biomass under current conditions (Current), a 10% reduction of hypersaline events (10% reduction hypersalinity) and a 5% reduction of salinity throughout the year (5% reduction overall). The error bars represent the standard error in each year.

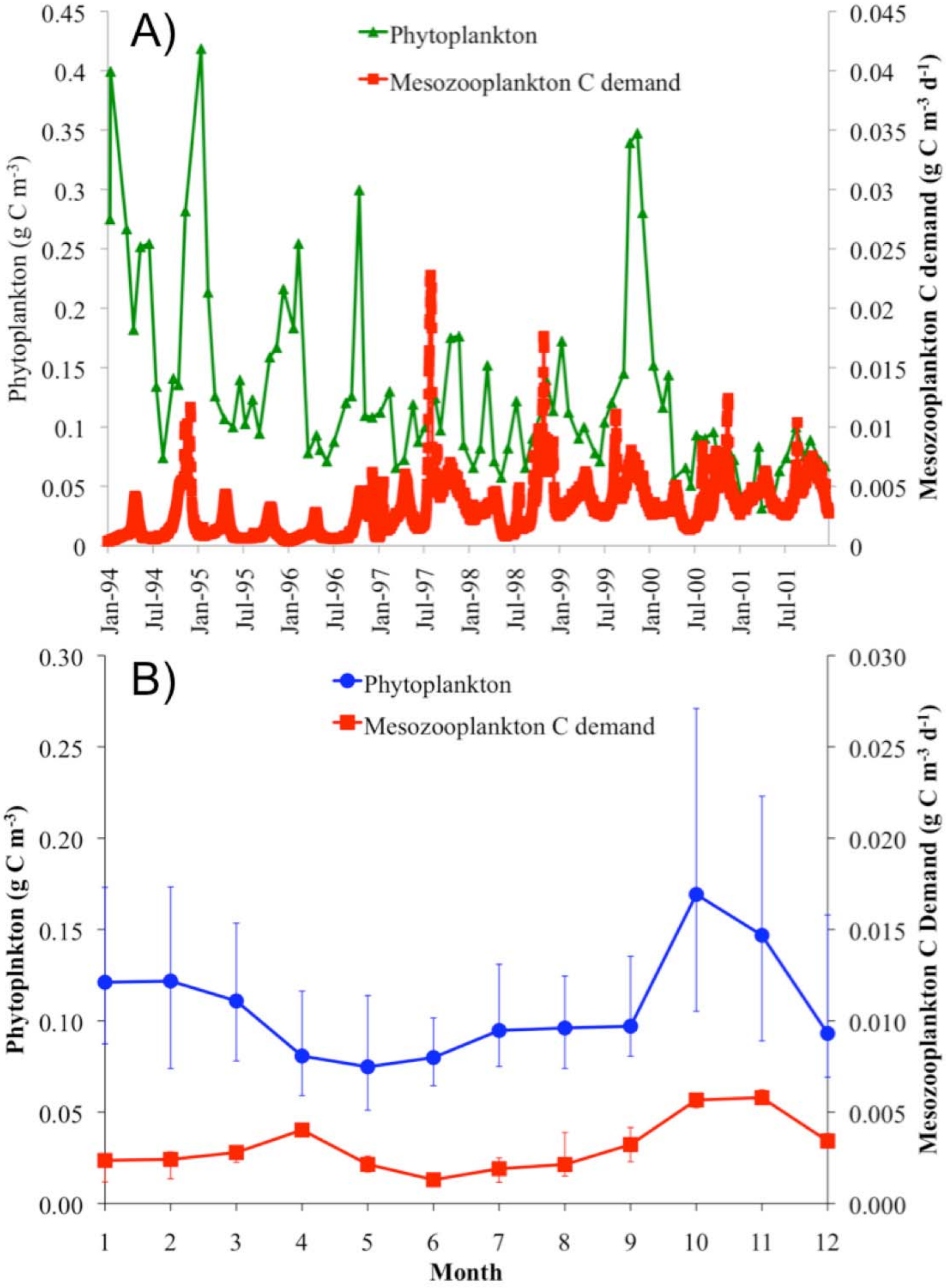

Figure 5.4 Mesozooplankton carbon demand calculated from the BAMZO model and phytoplankton carbon biomass from observations for A) the entire time series and B) monthly medians with the 95% confidence interval for the median represented by error bars.

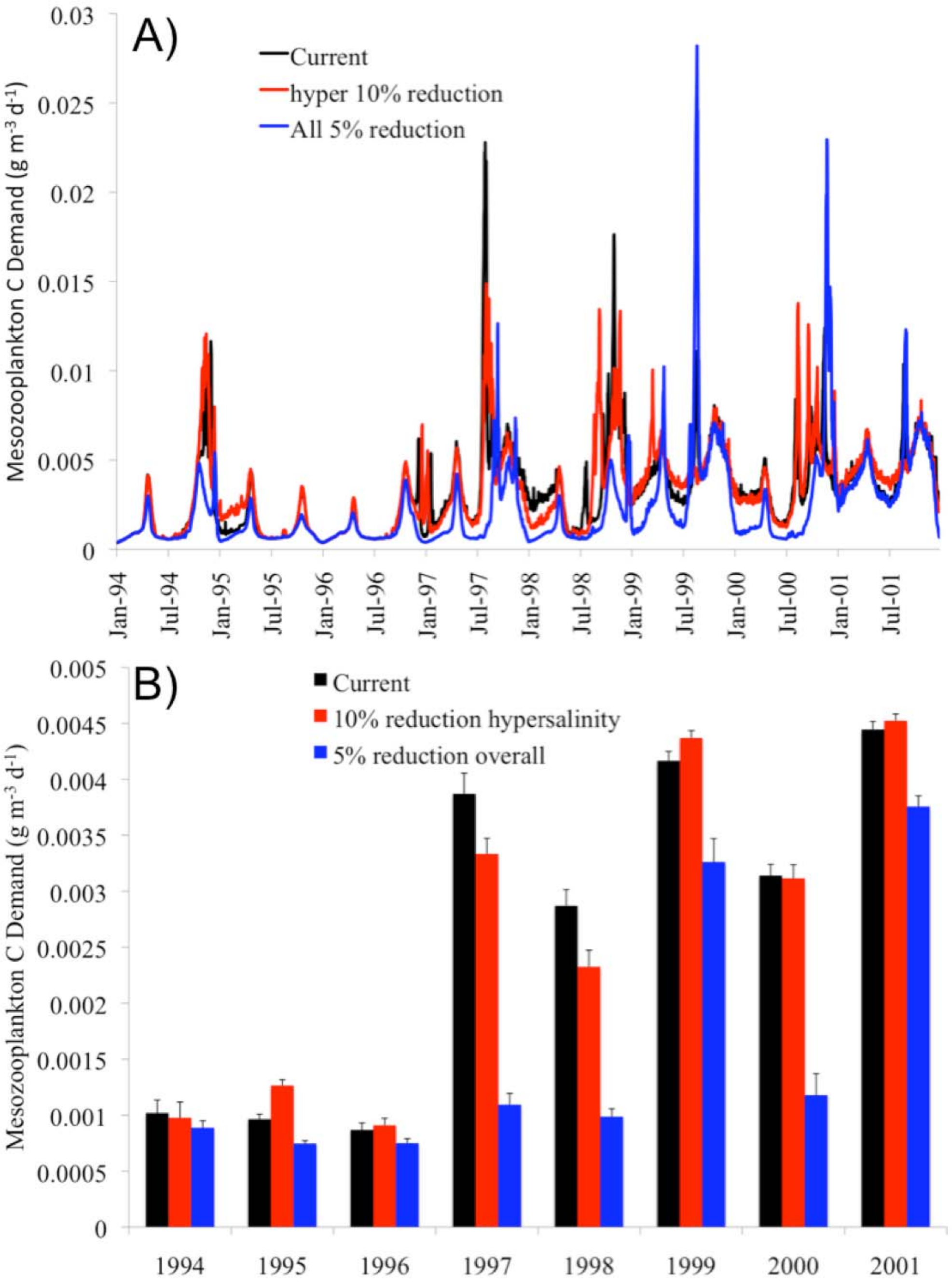

Figure 5.5 A) Time-series output of mesozooplankton carbon demand from BAMZO for the Base scenario, a 10% reduction in hypersalinity and a 5% reduction of all salinities and B) the annual medians in mesozooplankton carbon demand from BAMZO for each of these scenarios. The error bars reflect the standard error in the annual median.

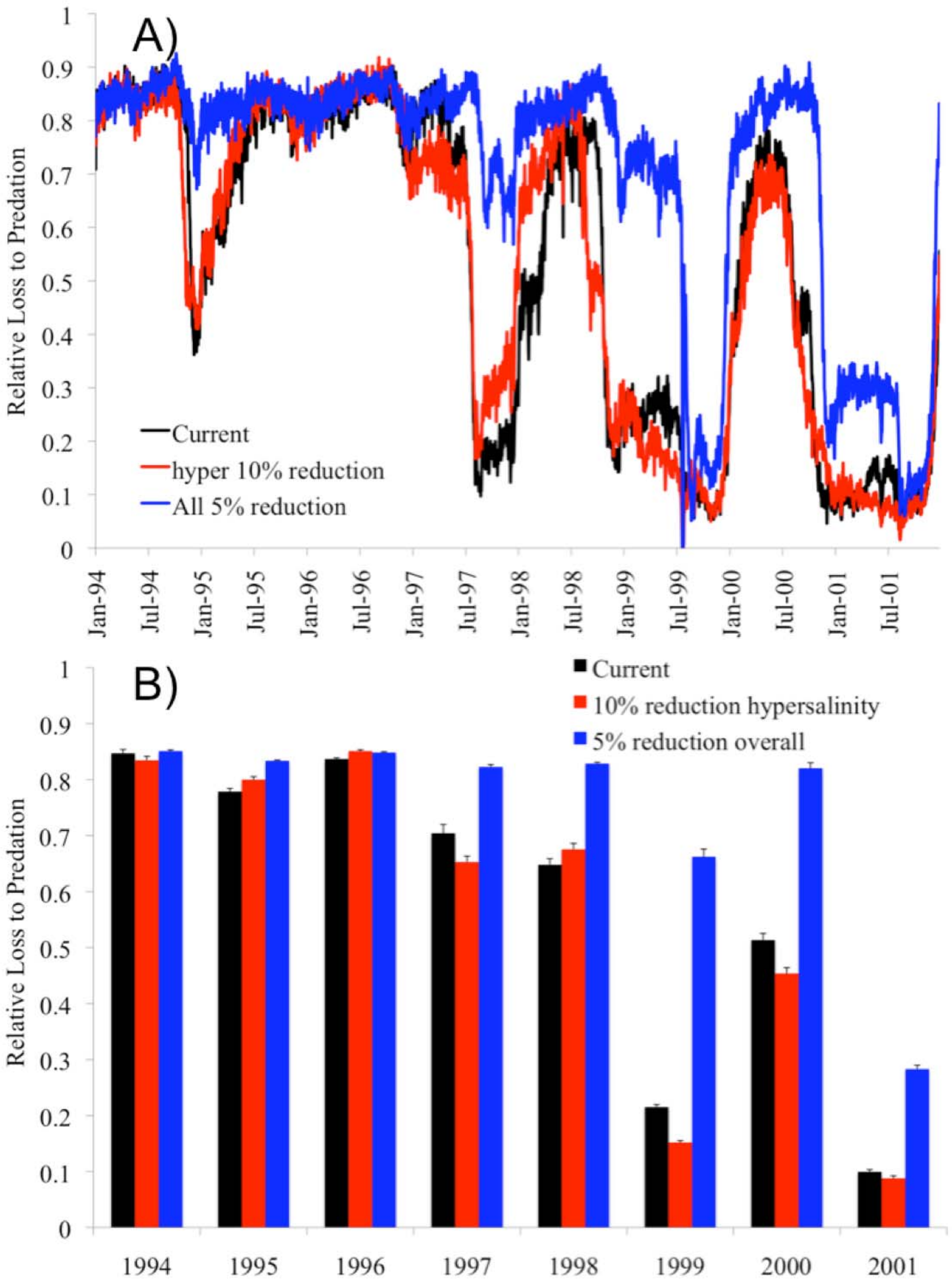

Figure 5.6 A) Time-series output of mesozooplankton relative loss to *A. mitchilli* predation from BAMZO for the Base scenario, a 10% reduction in hypersalinity and a 5% reduction of all salinities and B) the annual medians in mesozooplankton relative loss to *A. mitchilli* predation from BAMZO for each of these scenarios. The error bars reflect the standard error in the annual median.

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