INTERACTIONS AMONG PHYTOPLANKTON, MICROZOOPLANKTON, AND MESOZOOPLANKTON IN RIVERINE COASTAL SYSTEMS ALONG THE WEST COAST OF PENINSULAR FLORIDA

By

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For my Dad.

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Rivers represent major conduits transporting nutrients to coastal oceans from natural and anthropogenic sources. The fates of these nutrients and their impacts on coastal systems are controlled not only by physical and chemical processes in nearshore and coastal environments but also by co-occurring biological interactions. One conceptual model predicts that discharges from large rivers create buoyant, freshwater plumes in which physical, chemical, and "top-down" and "bottom-up" biological controls combine to yield i) lower phytoplankton growth rates and biomasses in low light environments near river mouths; ii) higher phytoplankton growth rates and biomasses in zones where light climates improve and nutrients remain available; and iii) decreasing phytoplankton growth rates and biomasses in zones where grazing and depletion or dilution of nutrients become important. Grazing rates and abundances of microzooplankton and mesozooplankton are predicted to respond to this spatial pattern according to their grazing abilities and rates of reproduction. Microzooplankton grazers feed on smaller phytoplankton and reproduce more rapidly, so their abundances and the rates at which they remove phytoplankton standing crops more closely track increases in phytoplankton growth rates and biomasses. Mesozooplankton eventually respond, and their abundances and grazing rates become more

important further offshore. The applicability of this conceptual model was tested in four salinity zones that delineated the influences of the Suwannee, Withlacoochee and Weeki Wachee Rivers along the west coast of peninsular Florida. Results from four sets of field sampling and 24-hour grazing experiments were not consistent with the model. In the Suwannee system, phytoplankton biomasses and growth rates were highest near the river mouth rather than peaking in the zone characterized by intermediate salinities. In the Withlacoochee and Weeki Wachee systems, phytoplankton biomasses and growth rates remained fairly uniform across the range of salinities. Microzooplankton grazing rates and abundances and mesozooplankton abundances were similar across the salinity gradients in the three systems. Microzooplankton grazing represented an important pressure on phytoplankton standing crops, because it removed an average (± standard deviation) of 99.5 ± 46.8%, 81.3 ± 31.6%, and 87.1 ± 12.6% of primary production per day in the Suwannee, Withlacoochee, and Weeki Wachee systems. In comparison, mesozooplankton grazing impact was negligible, with ≤ 0.05% of phytoplankton production consumed per day. Interactions among phytoplankton, microzooplankton, and mesozooplankton were not consistent with the model; therefore, we hypothesized that river discharge was below the threshold required to induce the physical processes that establish the predicted gradients. For example, the light environment supported phytoplankton growth closer to shore than expected in all systems, and nutrients were quickly depleted in nearshore, coastal waters. The relatively large impact of grazing by microzooplankton suggests that the microbial loop plays a primary role in the transformation of nutrients delivered to coastal waters by the Suwannee, Withlacoochee, and Weeki Wachee Rivers, with consequences for cycling of elements, structure and function of food webs, and production of fisheries resources.

CHAPTER 1
INTRODUCTION

Estuaries and adjacent coastal waters are highly productive systems, driven in large part by the infusion of nutrient-rich waters from rivers. Excessive nutrient inputs increase the likelihood of eutrophication or production of excess organic matter (Cloern 2001). In turn, over-production of organic matter in coastal waters can cause patches of hypoxia via settling and microbial decomposition of phytoplankton (Cloern 2001), changes in the biogeochemistry of sediments as hypoxic conditions alter chemical flux at the sediment-water interface (Jørgensen (1996), declines in the abundance of submerged macrophytes if high concentrations of phytoplankton decrease light availability at depth (Duarte 1995), shifts in zooplankton community structure in response to changes in algal communities (Paerl 1988), and mortalities of fish and shellfish from algal toxins (Rosenberg & Loo 1988). The negative ecological consequences of nutrient over-enrichment often have broad and far-reaching socio-economic implications. For this reason, it is essential to more fully understand the factors and processes controlling phytoplankton and zooplankton production in river-impacted coastal waters.

Due to the complex nature of coastal systems, the influence of river discharge on interactions between nutrients, light, phytoplankton, and zooplankton is likely to vary markedly among systems and times. Phytoplankton dynamics are dependent on complex interactions between the availability of light, nutrients, and other factors that promote growth and factors like sinking aggregation and grazing that result in loss. Empirical studies and modeling indicate that in coastal systems dominated by river input, the spatial and temporal availability of nutrients and light can be directly affected by mixing and the density fronts created by wind stress, tidal cycles, and river discharge (Liu & Dagg 2003, Chen et al. 1997, Yin et al. 1997). These physical forces and the gradients they create are highly variable in both space and time; therefore,

phytoplankton growth rates and production vary as well (Bowman et al. 1986). Variation in phytoplankton production interacts with zooplankton production because of the tight coupling between the zooplankton and phytoplankton communities (Cloern 2001, Kiørboe 1993). In riverine coastal systems along the Gulf of Mexico, zooplankton grazers are known to be an important factor regulating phytoplankton biomass (Juhl & Murrell 2005, Liu & Dagg 2003, Bledsoe 2003, Strom & Strom 1996, Fahnenstiel et al. 1995).

In coastal systems where large rivers dominate, phytoplankton production and zooplankton grazing and abundance have been described with a conceptual model based on processes occurring along gradients of nutrients and light (Dagg & Breed 2003). In the model, as water moves offshore from the river mouth, phytoplankton biomass and production and zooplankton abundance and grazing rates are low in or near the river, rise to maximum in the mid-field as characterized by salinities between fresh and oceanic water, and decline again in the far field characterized by oceanic salinities. Near the river mouth, algal growth rates are low, primarily attributed to an unfavorable light regime caused by high concentrations of suspended particulate matter. Algal growth rates are greater in the near field as a consequence of sedimentation of lithogenic particles, which leads to a more favorable light environment. In the mid-field, where nutrient concentrations remain sufficiently high and the light environment is more favorable, algal growth rates are the highest. In the far field, as nutrients are diluted and depleted via uptake, growth rates decline. The predicted grazing response of microzooplankton and mesozooplankton to this distribution of algal biomass is thought to be dependent on their respective rates of production. Because of the closer coupling between microzooplankton and phytoplankton production (Azam et al. 1983, Thingstad et al .1999), microzooplankton grazers are expected to respond more rapidly than mesozooplankton grazers to an increase in

phytoplankton biomass and remove a larger percentage of the phytoplankton production in the mid-field. In the far field marked by oceanic salinities, mesozooplankton will have had enough time to respond to phytoplankton production, and they will peak in abundance and remove a greater percentage of phytoplankton than microzooplankton (Kiørboe & Johansen 1986, Kahru et al. 1984).

To date, the conceptual model has only been tested explicitly in the plume of the 6260 km long Mississippi River (Liu & Dagg 2003). The drainage basin of this river encompasses greater than 40% of the continental United States or an area of approximately 354,000 km^2 (Berner & Berner 1987). This drainage basin generates high annual riverine discharge (15,000 m^3 s^{-1}), which results in a large region of interaction between the plume and the receiving waters of the Gulf of Mexico (Dagg & Breed 2003). Light attenuation is attributed to high concentrations of lithogenic particles (Dagg & Breed 2003). River nutrient concentrations are also high at 2.8 x 10^8 to 2.8 x 10^9 μg TN L^{-1} and 9.29 x 10^6 to 1.55 x 10^8μg PO4 L^{-1} (Lohrenz et al.1999). The findings reported by Liu & Dagg (2003) were generally consistent with the model. Phytoplankton growth and microzooplankton grazing rates were low in the near field, highest in the mid-field, and decreasing in the far field. Mesozooplankton grazing impact was low at the near and mid-field, and highest in the far field.

This study tested the generality of the conceptual model developed for riverine coastal systems by describing interactions among phytoplankton growth and biomass and microzooplankton and mesozooplankton grazing across salinity gradients in river-influenced systems along the west coast of peninsular Florida. These river systems are ideal for examining key interactions in the model because discharge rates, nutrient concentrations, and light environments vary among the systems. If the interactions described by the model are observed in

these systems under a variety of flow regimes, then the model may apply to a wide range of riverine coastal systems world wide.

CHAPTER 2
MATERIALS AND METHODS

To test the model's generality, biomass and growth of phytoplankton and abundance and grazing rates of microzooplankton and mesozooplankton were estimated in riverine coastal waters off the Suwannee, Withlacoochee, and Weeki Wachee rivers along the west coast of peninsular Florida (Figure 2-1). The three rivers differ in the areal extent of their watersheds, historical annual discharge rates, light attenuation coefficients, and nutrient concentrations (Frazer et al. 1998). Intra-annual variability in discharge also was expected to yield high and low discharge regimes for each river. Therefore, natural differences among the systems were anticipated to provide a range of scenarios in which the model could be tested. Phytoplankton biomasses were estimated by using chlorophyll concentrations as proxy measures. Phytoplankton growth and microzooplankton grazing rates were estimated using the microzooplankton dilution technique (Landry & Hassett 1982), and mesozooplankton grazing impact was estimated using the mesozooplankton addition technique (Calbet & Landry 1999). Microzooplankton and mesozooplankton abundances were determined with standard identification and enumeration techniques (Omoi & Ikeda 1984).

Study Sites

The Suwannee River originates in the Okeefenokee Swamp, Georgia, and it drains approximately 28,600 km^2 of southern Georgia and north central Florida (Wolfe & Wolfe 1985) before discharging into the Gulf of Mexico (Figure 2-1). Surface water and groundwater contribute to flow in this system (Bledsoe & Phlips 2000). Mean annual discharge is 280 $m^3 s^{-1}$, with maximum and minimum rates typically occurring in the spring and fall months, respectively (USGS Water Resources 2007). Light availability at depth is normally the lowest of the three systems. Concentrations of lithogenic particles are low, with light attenuation attributed to

colored dissolved organic matter (particularly during high discharge), tripton, and algal particles (Bledsoe & Phlips 2000). Nutrient concentrations are normally highest of the three systems, with 10-year (1996-2006) means (± SD) for total nitrogen (TN) and total phosphorus (TP) equal to 503.2 ± 287.7 μg L^{-1} and 48.7 ± 33.0 μg L^{-1}, respectively (T. Frazer, University of Florida, unpublished data).

The Withlacoochee River originates in the Green Swamp (Figure 2-1), and its drainage basin covers 5,232 km^2 (Yobbi 1989). As in the Suwannee River, flows are generated by surface water and groundwater, with a mean annual discharge of 23 m^3 s^{-1} (USGS Water Resources 2007). Discharge rates vary intra-annually. Light availability at depth is typically intermediate among the three systems; however, water clarity improves during periods of low rainfall because spring waters comprise the bulk of the discharge. Among the three systems, Concentrations of TN are the lowest and TP concentrations are intermediate among the three systems, with 10-year means (± SD) of 420.8 ± 188.9 μg L^{-1}, and 39.4 ± 26.8 μg L^{-1}, respectively (T. Frazer, University of Florida, unpublished data).

The Weeki Wachee River originates at a first magnitude spring and meanders 13 km before discharging into the Gulf of Mexico (Figure 2-1). The river has a drainage basin of less than 26 km^2 (Medard et al. 1968). The annual mean discharge of the Weeki Wachee River is 4.5 m^3 s^{-1} (USGS Water Resources 2007). High and low flows normally occur in the fall and spring, respectively. Light availability at depth is the greatest for the three systems, with high water clarity due to low suspended particle loads as is typical of spring-fed systems (Frazer et al. 2001). Concentrations of TN are intermediate among the three systems with a 10-year mean (± SD) of 469.1 ± 203.8 μg L^{-1}, while TP concentrations are the lowest, with a 10-year mean (± SD) of 8.8 ± 4.4 μg L^{-1} (T. Frazer, University of Florida, unpublished data).

Sample Collection

Environmental data, water for dilution and addition experiments, and mesozooplankton samples were collected from each of the systems four times in 2006, with effort made to sample twice during the low and high discharge periods for each river. Whole water for microzooplankton enumeration was collected and preserved twice from each system in the fall months. Distinct salinity ranges were used to select the four separate fields of interaction or zones within each river plume, i.e. the river mouth (10-15 psu), near field (19-22 psu), mid-field (28-30 psu), and far field (>30 psu). Samples of water from the three stations within each zone were combined to yield physical means.

Environmental data were collected at each station during each sampling period. Water temperature (°C), salinity (psu), dissolved oxygen (mg L^{-1}), and pH were measured 0.5 m below the surface with a Yellow Springs, Inc. sonde coupled to an electronic datalogger (Models: 600R & 650 MDS). Secchi depths (m) were determined. Photosynthetic ally active radiation was measured with Li-Cor. Instruments, Inc. cosine-corrected submersible light sensors connected to a Li-Cor (LI 1400) datalogger that simultaneously recorded surface and downwelling radiation. At each station, underwater light levels were measured just below the water's surface, approximately at the mid-point of the water column, and 0.3 m above the bottom in water less than 5.0 m deep. The attenuation coefficient (K_d) was calculated using Lambert-Beer's Law (Equation 2-1), where I_0 is surface irradiance (μmol photons m^2 s^{-1}) and I_z is light intensity at depth (z):

$$K_d = \frac{\ln\left(\frac{I_0}{I_z}\right)}{z} \qquad (2\text{-}1)$$

In each of the target salinity zones, approximately 70 L of seawater was collected for experiments and microzooplankton samples between the surface and 0.1 m off the bottom using an integrated sampling tube (Bledsoe & Phlips 2000). The submerged end of the tube was covered with 1.0-mm mesh to filter out large zooplankton. When water depths exceeded the length of the tube, only the top three meters of the water column were sampled. Pulled water was filtered through 190-µm Nitex mesh prior to filling a 20-L plastic carboy at each station; this water was used for the dilution and addition experiments. An additional 8 L of water was pulled and filtered to serve as rinse water for the filtration system. Microzooplankton samples were collected by filtering water through 190-µm mesh to fill one-third of a 5-L carboy and then preserving the sample with Lugol's solution. Five hundred to 2000 ml of water from each station was filtered through Whatman GF/F filters for subsequent analysis of chlorophyll concentration. Filters were stored in a container with desiccant that was placed on ice.

Mesozooplankton were collected at two stations within each zone using a 202-µm mesh, 0.5-m diameter plankton net with a filtering cod-end. Whenever possible, net tows undulated between the surface and a depth of 3.0 m. At stations where the water depth was less than 3.0 m, tows sampled the middle of the water column. Tows lasted for approximately 5 min, with volumes determined from a General Oceanics mechanical flowmeter set off-center inside the net. Each mesozooplankton sample was carefully poured into a 3.4-L plastic insulated container with a 2000-µm mesh screen placed approximately 5.0 cm above the bottom. An OTAB® was added to supplement the oxygen supply in the water during transport to the laboratory.

Upon returning to the laboratory, water for the experiments and mesozooplankton samples were stored for 16 to 22 hrs in a climate controlled environment prior to the start of the experiments. Water temperatures during storage did not deviate more than 3.0°C from the

temperature measured in situ, except in November when water temperatures in samples from the Withlacoochee became 5.0-10.0°C warmer. Air stones attached to aquarium air pumps were inserted in each mesozooplankton container to reduce the potential for low dissolved oxygen concentrations. The preserved microzooplankton samples were stored in a climate controlled dark room prior to identification and enumeration.

Laboratory Procedures

Using water collected during each sampling period, phytoplankton growth rates and microzooplankton grazing rates were estimated for each zone using the dilution technique first developed by Landry & Hassett (1982). Seawater collected from a given zone and discharge period was filtered through 190-µm Nitex mesh to exclude mesozooplankton from the experimental medium (Bledsoe 2003). This water was designated as whole seawater, and it included microzooplankton that is zooplankton smaller than 200 µm. Fifteen liters of whole seawater were filtered through a step filtration system comprised of 10-µm, 5-µm, and 1-µm sediment filters, as well as a 0.2-µm Gelman Microcapsule filter to create the dilution medium that lacked particles larger than 0.2 µm. In order to maintain the appropriate salinity in each batch of dilution medium, the filtration system was flushed by filtering approximately 5 L of whole seawater prior to preparing the dilution medium. Duplicate 100, 75, 50, 25, and 10 percent whole water treatments were created by combining whole seawater with dilution medium in 2.8-L glass flasks with an experimental volume of 2.5 L.

Mesozooplankton grazing rates were estimated using the addition method (Calbet & Landry 1999). Aliquots of 100, 200, and 400 mL were removed from each mesozooplankton sample using a 10-mL Hensen-Stimpel pipette. The mesozooplankton aliquots were added to 2.8-L glass flasks to create duplicate 100 percent whole seawater treatments with an experimental volume of 2.5 L. Separate, but equal, aliquots of mesozooplankton were removed

and filtered through pre-weighed 20.0-µm polycarbonate filters that subsequently were dried at 60°C for 48 hrs and weighed to obtain total mesozooplankton dry weights (mg). Only organisms healthy enough to swim upward through a 2000-µm mesh screen set inside each insulated container were added to treatment flasks or used to determine dry weights. Immediately following the removal of aliquots for experiments and determination of dry weights, two additional subsamples (50 to 100 mL) were taken and preserved in Lugol's solution for subsequent identification and enumeration. Subsamples were taken from above and below the 2000-µm mesh in the sample container to determine if the mesozooplankton assemblage added to treatments was representative of the mesozooplankton assemblage collected in situ.

Changes in chlorophyll concentrations were used as a proxy measure for changes in phytoplankton density in the dilution and addition experiments. Initial and final chlorophyll concentrations ($\mu g\ L^{-1}$) were determined from three subsamples of whole water taken at the start of each experiment and two subsamples taken from each experimental flask at the end of each experiment. Subsamples of 500, 1000, 1500, or 2000 mL were filtered onto Whatman GF/F glass-fiber filters that were frozen until processing. Each filter was placed into a test tube with 8.0 mL of 90 percent ethanol and heated in a 78°C water bath for 5 min. After 24 to 72 hrs of passive extraction, filters were removed, and the sample was centrifuged to separate particulate debris. Chlorophyll concentrations in the supernatant were determined using a Hitachi U200 dual beam spectrophotometer, and the acidification method was used to correct for phaeophytin (APHA 1998).

Experimental flasks were incubated for approximately 24 hrs in a climate controlled laboratory with a 12/12 light/dark cycle in March, April, November, and December and a 14/10 light/dark cycle in May, June, July and September. Light was provided by cool white fluorescent

lights with an average intensity of 50 μE m^{-2} s^{-1}. Every six hours, flasks were gently swirled to resuspend any settled material.

Mesozooplankton and microzooplankton in the preserved samples were identified and enumerated. For mesozooplankton, three separate aliquots were taken from each preserved subsample with a 1-mL Hensen-Stempel pipette, placed into a counting wheel, and then processed using a dissecting microscope. Microzooplankton subsamples (minimum three) were identified and enumerated using a Leica inverted-contrast microscope after being added to settling chambers at least 30 min prior to processing. Both mesozooplankton and microzooplankton counts were terminated after 100 individuals of any taxon were counted (Utermohl 1958).

River discharge for each sampling event in the Suwannee, Withlacoochee, and Weeki Wachee systems was taken as the daily mean calculated from hourly records at United States Geological Survey gauging stations located at Wilcox (FL), Holder (FL), and Brooksville (FL), respectively (USGS Water Resources 2007). Data used to calculate historical mean monthly discharges were also taken from these gauging stations.

Controls

Assumptions underpin the microzooplankton dilution and mesozooplankton addition techniques (Landry & Hassett 1982, Calbet & Landry 1999). The techniques are founded on four assumptions: (1) phytoplankton growth is not density dependent, (2) phytoplankton growth is exponential, (3) phytoplankton growth is not nutrient limited, and (4) the probability of a phytoplankton cell being consumed is directly related to encounter rate of consumers. The mesozooplankton addition technique also assumes that mesozooplankton added to treatments are representative of the in situ assemblages.

To prevent nutrient limitation of phytoplankton growth, excess nutrients (KNO_3, KPO_4, $NaSiO_4$) were added to each microzooplankton and mesozooplankton treatment flask (10 mL of 400 μg N L^{-1}, 40 μg P L^{-1} and 400 μg Si L^{-1}). To verify that excess nutrients were available for phytoplankton uptake during the dilution and addition experiments, two sets of controls were used. Firstly, two additional 100 percent whole seawater treatment flasks that were not spiked with nutrients provided estimates of phytoplankton growth rates in situations where limitation was possible during the incubation period (Jett 2004). These flasks and nutrient amended flasks containing 100 percent whole seawater without mesozooplankton served as controls for the mesozooplankton addition experiment. Secondly, soluble reactive phosphorus (SRP) was measured in one 60 to 100 mL subsample from each 100 percent whole seawater treatment before and after the incubation periods. These subsamples allowed the availability of phosphorus to be compared between treatments with and without excess nutrients, and they provided estimates of phosphorus availability within each flask at the beginning and end of experiments. The latter information provided a means to evaluate if the nutrient-replete assumption of the dilution and addition techniques was being met throughout the incubation period. All subsamples were refrigerated prior to being analyzed within 72 hrs. Subsamples were filtered through Millipore glass fiber pre-filters, a color reagent was added, and the solution was analyzed on a Hitachi U2000 dual beam spectrophotometer after ten minutes of color development.

The representativeness of mesozooplankton added to treatment flasks was determined by comparing the taxa and numbers found in subsamples taken from above and below the 2000-μm mesh inserted in holding containers. If taxonomic compositions and abundances differed substantially between the two subsamples, then estimates of in situ grazing rates could be adjusted.

Calculations

Phytoplankton Growth and Microzooplankton Grazing Rates

Phytoplankton growth and mortality due to microzooplankton grazing was estimated according to the methods of Landry & Hassett (1982). The relationship between the dilution fraction (*D*) of unfiltered seawater and the net change in phytoplankton concentration over time (i.e. apparent growth rate or AGR) was calculated using least squares regression based the linear equation:

$$\left(\frac{1}{t}\right)\ln\left(\frac{P_t}{P_0}\right) = k - gD \qquad (2\text{-}2)$$

where P_0 is the concentration of phytoplankton at the start of the experiment, P_t is the final concentration of phytoplankton after time t, the y-intercept, *k*, is the instantaneous maximum specific phytoplankton growth rate, and the negative slope, *g*, is the instantaneous microzooplankton grazing rate. Values of P_0 measured in whole seawater were corrected for dilution by multiplying by the appropriate dilution factor (i.e. 1.00, 0.75, 0.50, 0.25, and 0.10).

If the relationship of apparent growth rate to dilution fraction was found to be non-linear for less dilute treatments, then grazing was assumed to be saturated and a piecewise linear grazing model was fit to the data (Redden et al. 2002). The phytoplankton concentration at which grazing becomes saturated, P_s, was calculated using Equation 2-3, and the variables *k* and *g* were obtained from a least squares linear regression to data from treatments diluted below P_s where equation 2-2 applied.

$$P_s = \frac{k\left[P_t - P_0\exp(kt)\right]}{gD\left[1 - \exp(kt)\right]} \qquad (2\text{-}3)$$

Microzooplankton impacts on phytoplankton were estimated in two ways (Landry & Hassett 1982). The percent of phytoplankton biomass removed per day due to grazing (S) was

calculated using grazing coefficients, *g*, and Equation 2-4; and the percent of phytoplankton production lost per day due to grazing (%PP) was calculated using grazing coefficients, *g*, instantaneous maximum specific phytoplankton growth rates, k, and Equation 2-5.

$$S = \left(1 - e^{-g}\right) * 100 \tag{2-4}$$

$$\%\mathrm{PP} = \left[\frac{1 - \left(\mathrm{e}^{(k-g)} - 1\right)}{\left(\mathrm{e}^{k} - 1\right)}\right] * 100 \tag{2-5}$$

Mesozooplankton Grazing Rates

Mesozooplankton grazing rates were estimated according to the methods of Calbet & Landry (1999). The initial concentration of phytoplankton (P_0), the final concentration of phytoplankton (P_t), the duration of the experiment (t), the appropriate instantaneous maximum specific phytoplankton growth rate (*k*), and the biomass of mesozooplankton added to the treatment were used in a least squares linear regression based on Equation 2-6 to calculate an instantaneous experimental grazing rate (*z*) that was scaled to in situ biomass of mesozooplankton (Equation 2-7) to yield z_0, an instantaneous grazing rate, if the regression was significant.

$$\left(\frac{1}{\mathrm{t}}\right)\ln\left(\frac{\mathrm{P_t}}{\mathrm{P_0}}\right) = k - z * \text{mg dry wt added } \mathrm{L^{-1}} \tag{2-6}$$

$$\mathrm{z_0} = z * \text{mg dry wt } \mathrm{m^{-3}} \tag{2-7}$$

Instantaneous in situ grazing rates, z_0, were used to estimate the impact of mesozooplankton on phytoplankton. In situ phytoplankton growth (k_0) was estimated with equation 2-8 (Moigis & Gocke 2003), where μ_0 is the apparent growth rate of phytoplankton from experimental controls and *g* is the appropriate instantaneous microzooplankton grazing rate,

and this value was combined with the appropriate instantaneous in situ mesozooplankton grazing rate (z_0) to estimate the percent of phytoplankton growth consumed daily (Equation 2-9).

$$k_0 = \mu_0 + g \tag{2-8}$$

$$\text{Percent phytoplankton growth consumed} = \left(\frac{z_0}{k_0}\right) * 100 \tag{2-9}$$

Data Analyses

Regressions and analyses of variance (ANOVAs) were performed with the JMP software package (v5.1, SAS). ANOVAs were used to test for differences in environmental parameters and coefficients from dilution experiments among systems, zones, and discharge periods. Tukey's HSD ($\alpha = 0.05$) was employed as a follow-up test. Environmental data and coefficients were tested for normality using Shapiro-Wilk goodness-of-fit tests and homoscedasticity using Cochran's tests. Data were $\log_{10}$, square root, or fourth-root transformed to improve normality and homoscedasticity. Non-normal and heteroscedastic data were analyzed, and the results were interpreted cautiously.

Multivariate analyses of microzooplankton and mesozooplankton abundances were performed using the Plymouth Routines In Multivariate Ecological Research (v6.1.6; PRIMER-E Ltd, Plymouth) software package. Only taxa contributing at least 3% to any given sample were included in analyses and counts were $\log_{10}(x+1)$ transformed. Similarity indices were calculated using the Bray-Curtis coefficient (Bray & Curtis 1975). Non-metric multi-dimensional scaling (MDS) and analysis of similarity (ANOSIM) were used to discriminate differences in microzooplankton and mesozooplankton assemblages among systems, sampling events, and zones. Ordinations with the lowest dimensionality that yielded stress values below 0.20 were considered acceptable. The test-specific, R-value permutation distribution was used to determine significance for ANOSIM ($p < 0.001$). The degree of dissimilarity between groups (pair-wise

comparisons) was assessed by examining the R-values for each pair, where large values are indicative of complete separation and low values suggest little or no segregation (Clarke & Warkwick 2001). The similarity percentages (SIMPER) routine was conducted when significant dissimilarities were found to determine which taxa contributed to groupings.

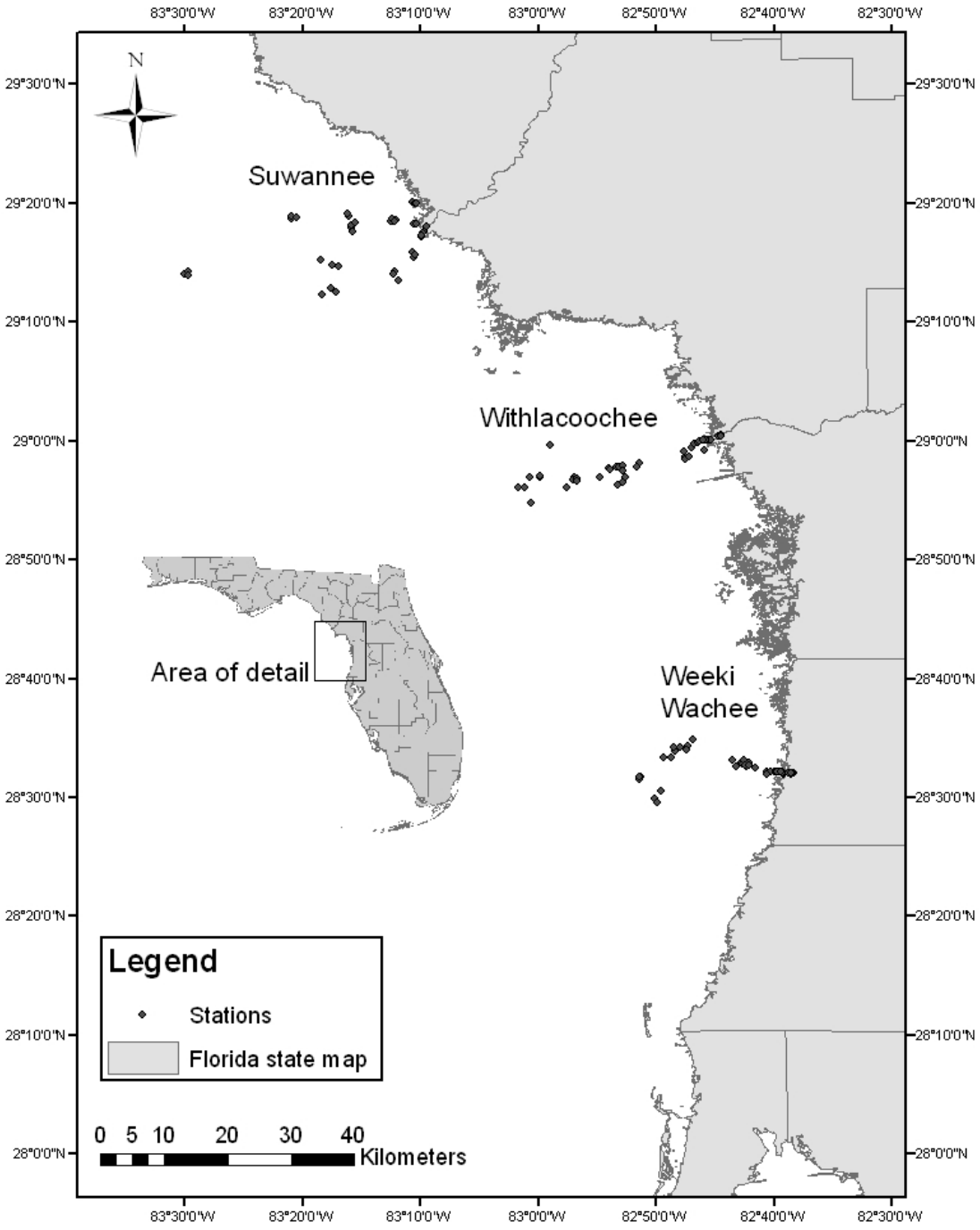

Figure 2-1. Location of study systems along the west coast of Florida. Filled circles denote stations sampled.

CHAPTER 3
RESULTS

Field Parameters

Mid-range to extremely dry conditions in the southeastern United States (standardized precipitation index values -1.0 to below -2.0) and the second driest November-December experienced in Florida over the 111-year record resulted in lower than expected discharge from both the Suwannee and Withlacoochee Rivers (Guttman & Lawrimore 2007, Table 3-1). Nevertheless, river discharge varied significantly among the systems (Table 3-2), with discharge from the Suwannee River greater than discharge from the Withlacoochee and Weeki Wachee rivers (Tukey's HSD; $q = 2.79$, $p < 0.05$). No significant differences in discharge were found between the Withlacoochee and Weeki Wachee rivers.

Water temperatures, salinities, and dissolved oxygen concentrations measured in each of three study systems were typical for those systems (T. Frazer, University of Florida, unpublished data). Surface water temperatures ranged from 13.7 to 32.7°C, with both the minimum and maximum values recorded at Withlacoochee in December and July, respectively. Fourth-root transformed water temperatures varied significantly among systems (Table 3-2), but the variation was unlikely to be biologically significant. Salinities were normally within the targeted range for a particular zone. However, deviations greater than 2.0 psu below the desired range occurred in the river mouth of the Suwannee during November (Table 3-1). Log_{10} transformed dissolved oxygen concentrations (mg L^{-1}) varied significantly among systems (Table 3-2), with concentrations in the Withlacoochee higher than those in the Weeki Wachee (Tukey's HSD; $q = 2.79$; $p < 0.05$). Nonetheless, water in all systems was normoxic whenever it was measured (Table 3-1).

Light attenuation coefficients (K_d) measured in the three study systems were lower than values normally observed in those systems. (T. Frazer, University of Florida, unpublished data). Log_{10} transformed K_d values did not differ significantly among systems (Table 3-2). However, light attenuation did vary significantly among zones within systems (Table 3-2), with light attenuation in the Suwannee system near the river mouth and in the near field being greater than light attenuation in the far field (Figure 3-1; Tukey's HSD; $q = 3.97$; $p < 0.05$). In the Withlacoochee and Weeki Wachee systems, light attenuation did not vary significantly among zones. Attenuation coefficients also varied significantly among discharge periods within systems and zones (Table 3-2), with light attenuation being higher in the river mouth and near field in the Suwannee system during the high discharge period (Table 3-2; Tukey's; $q = 3.73$; $p < 0.05$).

Log_{10} transformed chlorophyll concentrations ($\mu g\ L^{-1}$) differed significantly among systems, among zones, and among discharge periods (Table 3-2). Chlorophyll concentrations in the Suwannee system were greater than those in the Weeki Wachee system (Tukey's HSD; $q = 2.79$; $p < 0.05$). In each system, chlorophyll concentrations were typically highest near the river mouth, declining in the near and mid-fields, and lowest in the far field (Figure 3-2). This spatial pattern was statistically significant in the Suwannee system (Table 3-2), with concentrations being higher near the river mouth than in the far field (Tukey's HSD; $q = 3.97$; $p < 0.05$). Chlorophyll concentrations also differed significantly between discharge periods (Table 3-2). During the high discharge period, chlorophyll concentrations in the river mouth, near field, and mid-field were greater than chlorophyll concentrations in the far field in the Suwannee system (Tukey's HSD; $q = 7.15$; $p < 0.0001$). A gradient in chlorophyll concentrations also was found in the Withlacoochee system during high discharge, with concentrations near the river mouth being significantly higher than in the mid-field and far field (Tukey's HSD; $q = 4.85$; $p < 0.001$).

During high discharge in the Weeki Wachee system, chlorophyll concentrations near the river mouth were greater than those in the mid-field (Tukey's HSD; $q = 3.72$; $p < 0.05$). Similar patterns in chlorophyll concentrations were observed during low discharge periods for the Suwannee and Weeki Wachee systems (Tukey's HSD; $q = 3.72$; $p < 0.05$). There was no significant variation in chlorophyll concentrations among the zones for the Withlacoochee system during the low discharge period.

Phytoplankton Growth Rates

Twenty-eight of the 48 dilution experiments produced valid estimates of instantaneous maximum specific phytoplankton growth rates (Tables 3-3 to 3-5). Phytoplankton growth rates (k) ranged from -0.40 to 2.50 (mean ± SD 0.99 ± 0.68), 1.00 to 2.37 (mean ± SD 1.55 ± 0.58), and 0.55 to 1.31 (mean ± SD 0.89 ± 0.27) in the Suwannee, Withlacoochee, and Weeki Wachee systems, respectively. Square-root transformed growth rates did not vary significantly among systems or among discharge periods (Table 3-6). Significant variability in k across salinity zones was found only in the Suwannee system (Table 3-6), where growth rates near the river mouth were higher than those in the far field (Tukey's HSD; $q = 4.01$; $p < 0.05$). In the Withlacoochee and Weeki Wachee systems, k values were fairly uniform across zones.

Microzooplankton Grazing Rates and Assemblages

Microzooplankton grazing was determined to be a substantial loss factor for phytoplankton communities in each of the three systems (Tables 3-3 to 3-5). Estimates of instantaneous grazing rates (g) ranged from 0.38 to 2.04 (mean ± SD = 0.92 ± 0.53) in the Suwannee system, 0.39 to 1.67 (mean ± SD 1.03 ± 0.54) in the Withlacoochee system, and 0.34 to 1.17 (mean ± SD = 0.72 ± 0.25) in the Weeki Wachee system. These rates correspond to grazers removing an average of approximately 50% of the phytoplankton standing crops on a daily basis (Tables 3-3 to 3-5). Estimates of percent phytoplankton production lost daily were high in each system (Tables 3-3 to

3-5). Microzooplankton grazers accounted for, on average (± SD), 99.45 ± 46.76%, 81.25 ± 31.59%, and 87.10 ± 12.63% of primary production lost per day in the Suwannee, Withlacoochee, and Weeki Wachee systems, respectively. Square-root transformed microzooplankton grazing rates did not vary significantly among systems, salinity zones, or discharge periods (Table 3-6).

Retrospective power analyses based on least square effect means of square-root transformed *g*-values were conducted. For the system effect, a power analysis based on an estimated weighted standard deviation (σ_{wt}) of 0.27, 2 extra parameters in the model (Table 3-2), a type I error rate (α) of 0.05, and power of 0.80 indicated that a minimum of 199 samples were required to detect a difference of the magnitude observed. Thus, approximately 66 estimates of *g* per system were needed. If $\sigma_{wt} = 0.27$ and n = 15, the minimum detectable difference among systems was 0.43, a value markedly larger than the observed maximum difference of 0.14 between Withlacoochee (0.98) and Weeki Wachee (0.84). Among zones in the Suwannee system, with n = 13 and $\sigma^2_{wt} = 0.16$, 15 estimates of *g* (~ 4 per zone) are required to attain power of 0.80. This value suggests the intended sample size (n = 16) would have been sufficient for ANOVA to detect a significant difference if one existed. However, given the variability (σ_{wt} = 0.16) and actual sample size (n = 6), the minimum detectable difference was 0.80, a value greater than the observed difference of 0.44. In the Withlacoochee system, where n = 4 and $\sigma^2_{wt} = 0.16$, 10 estimates of *g* were needed to attain power = 0.80. Given n = 3 and $\sigma_{wt} = 0.16$, the minimum detectable difference was 2.36, a value considerably greater than the observed maximum difference of 0.50. In the Weeki Wachee system, the minimum sample size was 189 at n =11 and $\sigma_{wt} = 0.16$. This large sample size (~ 50 estimates of *g* per zone) is likely a reflection of the similarity observed for means of *g* among zones. The minimum detectable difference was 2.35 (n

= 3; σ_{wt} = 0.16), a value greater than the observed maximum difference of 0.11. Overall, the power analyses indicate that significant differences in microzooplankton grazing rates among systems or zones would only be detected if they were considerably larger or if considerably more samples were taken.

Total microzooplankton abundance ($\log_{10}$ individuals L^{-1}) varied significantly among systems in the September-December sampling events (Table 3-6), with total abundances in the Suwannee and Withlacoochee systems greater than total abundance in the Weeki Wachee system (Tukey's HSD; q = 3.84, p <0.01). Microzooplankton abundance did not vary significantly among zones within any of the three systems (Table 3-6).

The microzooplankton taxa that occurred most frequently within the three systems were copepod nauplii (100% occurrence in samples), tintinnids (100%), rotifers (92%), ciliated protozoans (88%), *Prorocentrum* spp. (83%), and *Protoperdinium* spp. (83%). Ordination indicated some dissimilarity among assemblages (Figure. 3-3); however, ANOSIM indicated that assemblages were similar among salinity zones.

Mesozooplankton Grazing Rates and Assemblages

Six of the 48 addition experiments produced valid estimates of instantaneous rates of in situ mesozooplankton grazing (z_0). These estimates (range = 0.0003 to 0.0008) indicate that mesozooplankton grazers had a negligible impact on phytoplankton biomass relative to microzooplankton grazers in the Suwannee, Withlacoochee, and Weeki Wachee systems. Daily phytoplankton growth consumed by mesozooplankton was ≤0.05% in all cases.

Total mesozooplankton abundance ($\log_{10}$ individuals m^{-3}) did not vary significantly among systems or among zones within a system (Table 3-6). There was, however, significant variation in total abundance among discharge periods (Table 3-6). During the low discharge period in the Suwannee system, total mesozooplankton abundance in the near field and mid-field was greater

than abundance near the river mouth (Tukey's HSD; $q = 3.78$; $p < 0.05$). No significant differences in abundance were detected among zones in the Withlacoochee and Weeki Wachee systems during either discharge period or among zones in the Suwannee during the high discharge period.

When samples from all three systems were considered together, the five most frequently occurring taxa were the calanoid copepods *Acartia tonsa* (occurrence in 98% of samples), *Paracalanus* sp. (76%), *Parvocalanus* sp. (74%), brachyuran crab zoea (72%), and the harpacticoid copepod *Euterpina acutifrons* (69%). *Acartia tonsa* was numerically dominant in each system and often in each zone (Tables 3-10 to 3-12). Fifty percent of the zones at Suwannee, 63% at Withlacoochee, and 81% at Weeki Wachee were dominated by *A. tonsa*. Despite the dominance of *A. tonsa* across systems, ordination suggested dissimilarity among assemblages in the three systems (Figure 3-4). This finding was supported by ANOSIM results (global R = 0.82). Pair-wise comparisons indicated strong dissimilarity between mesozooplankton assemblages in the Suwannee and Weeki Wachee systems (R = 0.92) and in the Withlacoochee and Weeki Wachee systems (R = 0.95). SIMPER identified the higher abundances of *Balanus* nauplii and *Parvocalanus* sp. and lower abundances of gastropod larvae in the Suwannee as the primary causes of dissimilarity between the Suwannee and Weeki Wachee systems. Dissimilarity between the Withlacoochee and Weeki Wachee systems was driven by greater abundances of *Parvocalanus* sp. and *E. acutifrons* and lower abundances of gastropod larvae in the Withlacoochee system.

Ordination and ANOSIM for each system suggested potential dissimilarities in mesozooplankton assemblages across time and space in the Suwannee system (Figure 3-5; global R = 0.30). Pair-wise comparisons indicated that the assemblages in March (R = 0.50) and May

(R = 0.59) differed significantly from those present in November. This difference was driven by large numbers of *E. acutifrons* and the cladoceran, *Penilia* sp., in November. Significant spatial variation also was found (global R = 0.35), with the river mouth (R = 0.61) and near field (R = 0.57) differing significantly from the far field (Figure 3-6). This gradient was due to the presence of the copepods *Temora* sp. and *Corycaeus* sp. and absence of *Balanus* nauplii in the far field.

In the Withlacoochee and Weeki Wachee systems, ordinations and ANOSIM indicated dissimilarity in assemblages within each system in space but not time (Withlacoochee 3D stress = 0.11, global R = 0.88; Weeki Wachee 3D stress = 0.14, global R = 0.75). Within both systems, the river mouth assemblage differed significantly from the assemblages in the mid- and far fields (pair-wise R-values: Withlacoochee RM, MD = 0.33, RM, FF = 0.56; Weeki Wachee RM, MD = 0.49, RM, FF = 0.77). Greater abundances of shrimp zoea, the copepods *Labidocera* sp. and *Parvocalanus* sp., gastropod larvae, and isopods in the higher salinity zones drove groups at Weeki Wachee. At Withlacoochee, differences in assemblages were due to the greater abundance of *Corycaeus* sp., brachyuran crab zoea, *Temora* sp., *Parvocalanus* sp., *E. acutifrons*, and *Oithona* spp. in the mid-field and far field relative to the two lower salinity zones.

Controls

Initial concentrations of soluble reactive phosphorus (SRP) in the nutrient amended treatments were significantly greater than concentrations in the controls for each system (t-test, $p < 0.05$). This result was also observed for the final SRP concentrations in experiments using water taken from the Withlacoochee and Weeki Wachee systems, but not for experiments using water from the Suwannee system (t-test, $p > 0.05$). The lack of a significant difference suggests the nutrient amended treatments may have become phosphorus limited during the incubation period. However, an analysis of nutrient-enrichment experiments found experiments lasting ≤1 day exhibited time lags in the numerical response of phytoplankton to nutrient addition

(Downing et al. 1999). Therefore, the decline in SRP concentrations during the 24-hr incubation likely had a negligible impact on phytoplankton growth rates.

Final SRP concentrations ($\mu g\ L^{-1}$) from the mesozooplankton treatments were significantly greater than concentrations in treatments without mesozooplankton (t-test, $p < 0.0001$). In addition, final SRP concentrations for each system often exhibited a positive linear relationship with mesozooplankton biomass (mg dry wt added L^{-1}). Linear regressions were significant for the Suwannee ($r^2 = 0.31$, $p < 0.0001$), Withlacoochee ($r^2 = 0.34$, $p < 0.0001$), and Weeki Wachee ($r^2 = 0.23$, $p < 0.0001$) systems, but they had low coefficients of determination.

To determine if the mesozooplankton added to treatments was a true reflection of the in situ assemblage and not biased by taxon-specific mortality rates, the frequency that the dominant taxon in the surface subsample was also the dominant or secondary dominant in the corresponding bottom subsample was calculated. These frequencies are as follows: 93% of the samples from Suwannee, 71% of Withlacoochee samples, and 84% of Weeki Wachee samples. The high degree of agreement between subsamples from each system indicates that the mesozooplankton added to treatments was normally dominated by same taxa that dominated the in situ assemblage.

Table 3-1. Mean values for the physical, chemical, and biological parameters measured in the Suwannee, Withlacoochee, and Weeki Wachee systems. Means are based on measurements from three stations within each zone. Historical river discharge rates are the calculated monthly means (± SD) for the 1994-2004 period of record at the same gauging stations used to estimate daily mean river discharge rates. Notation "nd" indicates no data.

	Suwannee					Withlacoochee					Weeki Wachee			
		RM	NF	MF	FF		RM	NF	MF	FF		RM	NF	MF	FF
Sampling Date	3/27					6/27					4/3				
Daily Discharge $m^3 s^{-1}$	244.1					9.7					4.6				
Historical Discharge $m^3 s^{-1}$	392.8 ± 296.3					10.7 ± 9.1					4.1± 1.0				
Depth m		1.17	2.67	4.63	11.73		3.37	2.70	>5.00	>5.00		1.60	1.77	2.43	3.43
Temperature°C		18.15	17.98	17.16	17.73		29.97	29.36	29.34	29.27		24.06	23.73	22.45	21.77
Salinity psu		13.41	21.67	31.57	33.63		13.35	21.61	28.35	30.87		13.00	18.95	27.21	30.85
DO mg L^{-1}		7.84	9.22	6.08	4.30		7.18	6.69	5.73	5.73		9.08	8.58	7.76	8.00
K_d m^{-1}		3.34	1.53	0.80	0.57		0.72	0.67	0.99	0.65		1.18	0.93	0.81	0.65
Chl µg L^{-1}		3.69	3.98	1.82	0.35		10.87	6.74	3.69	2.18		1.36	0.54	0.24	0.73
Tow Volume m^3		27.63	29.59	32.71	22.65		29.77	19.33	29.81	35.86		27.65	29.74	29.74	29.74
Sampling Date	5/23					7/4					6/6				
Daily Discharge $m^3 s^{-1}$	125.2					8.1					4.1				
Historical Discharge $m^3 s^{-1}$	196.1 ± 101.7					16.6 ± 20.7					3.8 ± 0.9				
Depth m		2.70	2.50	1.83	>5.00		2.20	3.60	>4.00	>5.00		1.63	1.67	2.77	3.73
Temperature°C		26.01	25.77	25.61	25.19		31.74	30.88	30.32	30.04		29.04	28.89	28.39	28.49
Salinity psu		8.05	21.67	29.67	33.63		13.90	20.99	28.56	31.68		12.04	20.92	29.43	32.73
DO mg L^{-1}		9.93	5.16	6.41	6.90		8.22	6.74	6.38	6.39		8.41	7.59	8.61	8.32
K_d m^{-1}		2.09	1.81	1.94	0.70		1.81	0.76	0.85	1.28		0.72	0.82	0.76	0.94
Chl µg L^{-1}		24.13	11.69	9.38	0.53		10.59	3.84	1.42	0.87		1.10	0.68	0.70	0.47
Tow Volume m^3		36.96	27.04	25.05	33.29		20.74	19.27	36.10	36.90		34.82	34.32	30.04	24.94
Sampling Date	9/25					11/28					9/18				
Daily Discharge $m^3 s^{-1}$	91.5					4.4					4.4				
Historical Discharge $m^3 s^{-1}$	191.9 ± 107.2					27.6 ± 21.6					4.7 ± 1.0				
Depth m		1.33	3.03	3.70	>6.00		3.43	3.23	4.30	>7.00		2.03	3.50	3.97	>5.00
Temperature°C		19.40	17.66	18.97	18.02		17.94	18.27	16.35	16.62		29.47	29.26	29.12	28.93
Salinity psu		6.06	22.39	29.64	32.72		10.91	22.18	28.64	31.64		14.09	20.56	29.32	32.64
DO mg L^{-1}		8.06	6.60	5.75	6.31		8.41	7.59	8.61	8.32		nd	nd	nd	nd
K_d m^{-1}		1.39	1.48	0.62	0.49		nd	nd	nd	nd		0.95	0.45	0.51	0.46
Chl µg L^{-1}		3.61	1.56	1.79	0.91		1.75	2.09	2.50	1.79		1.64	0.86	0.48	0.59
Tow Volume m^3		31.25	34.14	21.63	19.30		33.40	30.37	12.53	32.71		43.01	38.92	43.27	38.31

Table 3-1. Continued

	Suwannee					Withlacoochee					Weeki Wachee			
		RM	NF	MF	FF		RM	NF	MF	FF		RM	NF	MF	FF
Sampling Date	11/13					12/11					11/1				
Daily Discharge $m^3 s^{-1}$	58.9					4.5					4.4				
Historical Discharge $m^3 s^{-1}$	212.5 ±124.5					20.7 ± 12.3					4.8 ± 0.9				
Depth m		1.33	3.03	3.70	>6.00		4.53	3.57	4.23	>7.00		2.03	3.50	3.97	>5.00
Temperature°C		19.40	17.66	18.97	18.02		14.74	14.48	13.77	14.57		29.47	29.26	29.12	28.93
Salinity psu		6.06	22.39	29.64	32.72		11.82	20.32	29.52	32.39		14.09	20.56	29.32	32.64
DO mg L^{-1}		6.49	5.40	4.35	7.58		8.81	8.51	7.38	6.67		6.74	7.19	5.75	7.51
K_d m^{-1}		1.23	1.48	0.62	0.49		1.03	1.03	0.69	0.49		1.61	1.09	0.76	0.71
Chl µg L^{-1}		3.61	1.56	1.79	0.91		1.75	1.75	1.60	1.40		1.64	0.86	0.48	0.59
Tow Volume m^3		31.25	34.14	21.63	19.30		36.08	33.38	32.40	32.78		43.01	38.92	43.27	38.31

Table 3-2. Analyses of variance for transformed river discharge ($m^3 s^{-1}$), light attenuation ($K_d m^{-1}$), in situ total chlorophyll concentrations ($\mu g L^{-1}$), water temperature (°C), and dissolved oxygen concentrations (DO, $mg L^{-1}$).

Variable	Source	df	MS	F	p
Discharge Rate m^3s^{-1}	System	2	20635.5000	9.4748	0.0061
	Error	9	2177.9000		
	Total	11			
$\sqrt[4]{\text{Temp.°C}}$	Model	23	0.0743	10.105	< 0.0001
	System	2	0.0957	43.0250	< 0.0001
	Zone(System)	9	0.0022	0.0178	1.0000
	Discharge Period(System, Zone)	12	0.1248	16.9699	< 0.0001
	Error	120	0.0074		
	Total	143			
Log_{10}DO $mg L^{-1}$	Model	23	0.0519	4.1882	< 0.0001
	System	2	0.1312	4.3698	0.0472
	Zone(System)	9	0.0300	0.5453	0.8158
	Discharge Period(System, Zone)	12	0.0551	4.4446	< 0.0001
	Error	120			
	Total	143			
$Log_{10}K_d$ m^{-1}	Model	23	0.1776	6.8752	< 0.0001
	System	2	0.4851	1.7165	0.2335
	Zone(System)	9	0.2866	5.5776	0.0037
	Discharge Period(System, Zone)	12	0.0514	1.9894	0.0320
	Error	107	0.0258		
	Total	130			
Log_{10}Chl $\mu g L^{-1}$	Model	23	1.1647	23.8733	< 0.0001
	System	2	6.4836	5.6779	0.0254
	Zone(System)	9	1.1419	3.8665	0.0163
	Discharge Period(System, Zone)	12	0.2953	6.0535	< 0.0001
	Error	120	0.0488		
	Total	143			

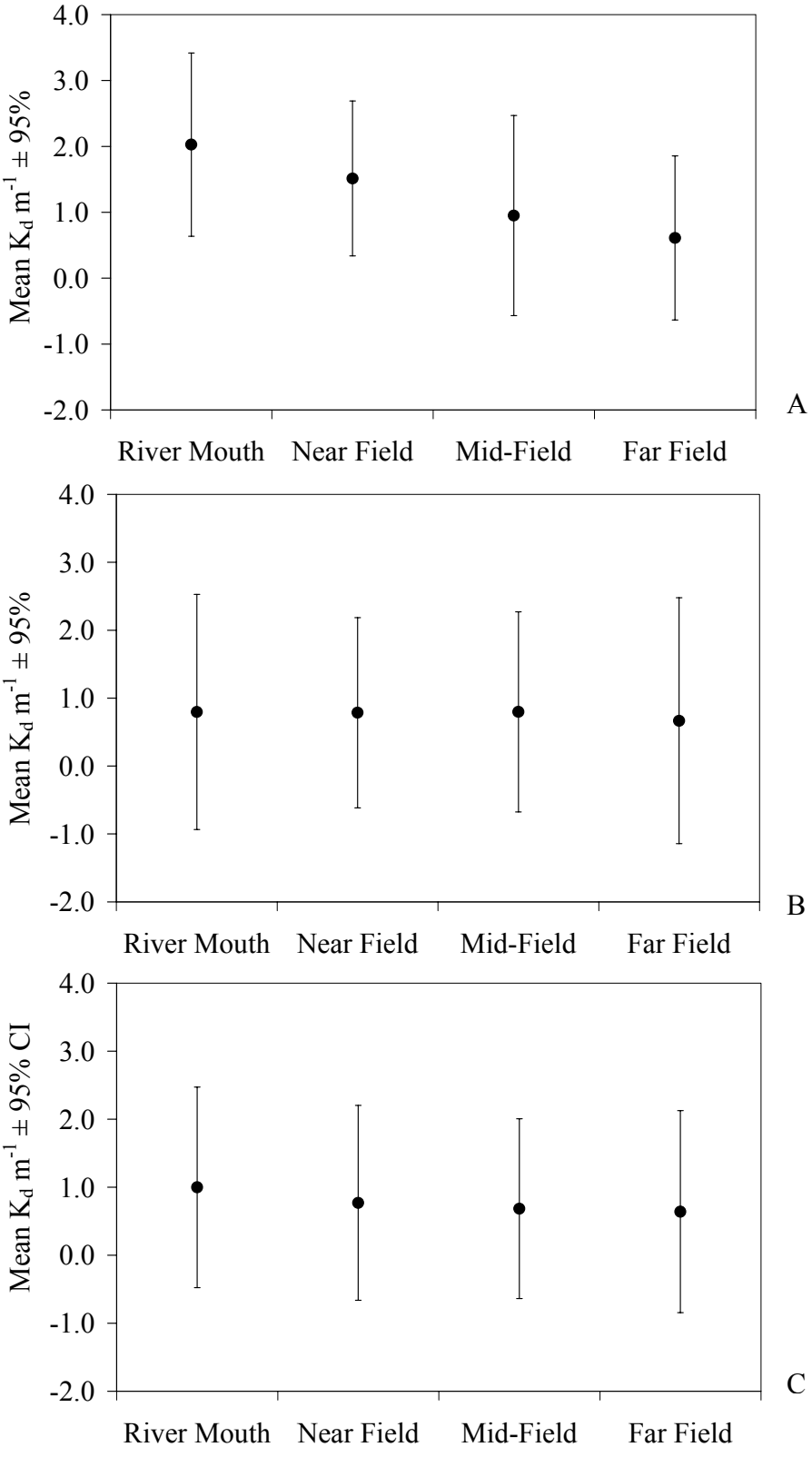

Figure 3-1. Back transformed mean light attenuation (K_d m^{-1}) ± 95% confidence intervals (CI) for zones. A) Suwannee system. B) Withlacoochee system. C) Weeki Wachee system.

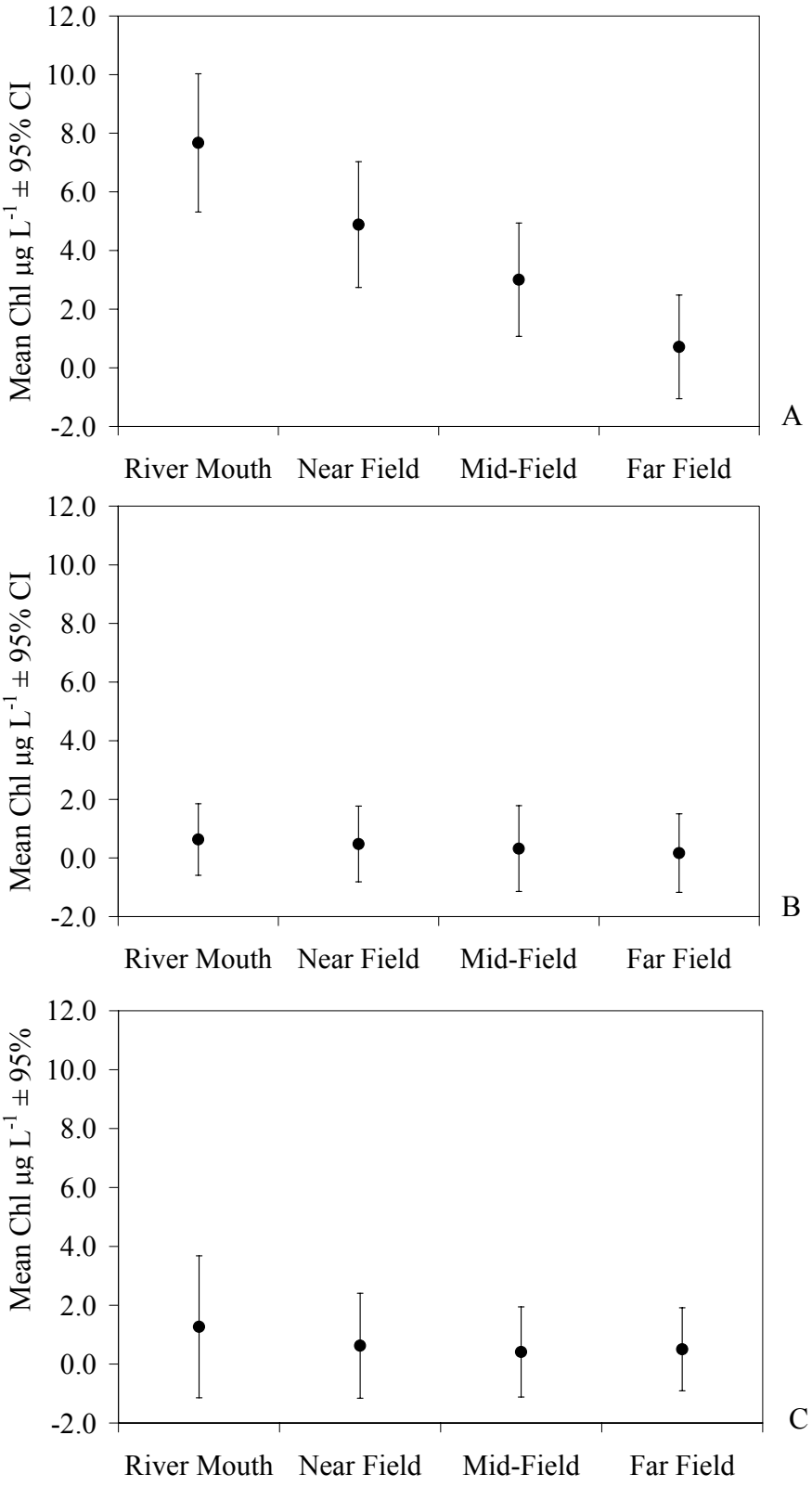

Figure 3-2. Back transformed mean chlorophyll concentrations (µg L^{-1}) ± 95% confidence intervals (CI) for zones. A) Suwannee system. B) Withlacoochee system. C) Weeki Wachee system.

Table 3-3. Suwannee system: estimates of apparent growth rate (AGR) in controls (μ_0), instantaneous maximum specific phytoplankton growth rates (k ± SE), instantaneous microzooplankton grazing rates (g ± SE), percent of phytoplankton standing crop removed daily (%PSC d^{-1}), and percent of phytoplankton production lost daily (%PP d^{-1}) during March, May, September, and November. Upper (U) and lower (L) 95% confidence limits (CL) were calculated using the corresponding confidence limits of k and g coefficients.

Sampling Date	Zone	u_0	k ± SE	L95%	U95%	g ± SE	L95%	U95%	r^2	p	%PSC Removed d^{-1}	%PSC Removed d^{-1} L95%	%PSC Removed d^{-1} U95%	%PP Lost d^{-1}	%PP Lost d^{-1} L95%	%PP Lost d^{-1} U95%
3/27	RM	0.37	1.12 ± 0.10	0.89	1.35	0.85 ± 0.17	0.47	1.23	0.77	< 0.001	57.17	37.34	70.73	84.82	63.45	95.35
	NF	0.43	1.16 ± 0.13	0.85	1.46	0.82 ± 0.21	0.33	1.31	0.65	< 0.01	55.91	27.78	73.08	81.59	48.38	95.25
	MD	0.12	0.59 ± 0.04	0.51	0.67	0.38 ± 0.06	0.24	0.51	0.84	< 0.001	31.27	21.62	39.74	69.82	53.84	80.98
	FF	-1.57	-0.40 ± 0.18	-0.80	0.00	0.92 ± 0.00	0.92	0.93	0.62	< 0.05	60.26	60.01	60.52	-122.23	-48.58	22036.89
5/23	RM	0.70	2.50 ± 0.22	2.00	3.00	2.05 ± 0.35	1.23	2.86	0.81	< 0.001	87.10	70.89	94.28	94.86	81.94	99.20
	NF	0.40	1.32 ± 0.18	0.90	1.73	0.81 ± 0.29	0.14	1.49	0.49	< 0.05	55.60	12.75	77.41	75.98	21.46	94.07
	MD	0.20	1.49 ± 0.07	1.33	1.65	1.68 ± 0.11	1.42	1.94	0.96	< 0.0001	81.31	75.74	85.59	104.93	102.91	105.94
	FF	-0.59	0.33 ± 0.13	0.03	0.62	0.92 ± 0.21	0.43	1.40	0.71	< 0.01	59.95	35.15	75.27	215.49	1157.61	162.67
9/25	RM†	0.62	1.49 ± 0.17	1.09	1.90	1.63 ± 0.53	0.17	3.10	0.70	< 0.05	80.49	15.49	95.49	103.78	23.30	112.38
	NF*	-0.15	1.20 ± 0.11	0.94	1.45	0.38 ± 0.18	-0.04	0.80	0.34	ns	.	.	.	.	.	.
	MD*	0.24	0.32 ± 0.16	-0.05	0.68	0.06 ± 0.24	-0.50	0.62	0.01	ns	.	.	.	.	.	.
	FF	0.24	0.66 ± 0.08	0.48	0.85	0.53 ± 0.13	0.23	0.83	0.67	< 0.01	41.08	20.30	56.44	84.76	53.38	98.76
11/13	RM*	-0.42	0.55 ± 0.09	0.33	0.76	0.29 ± 0.15	-0.05	0.64	0.32	ns	.	.	.	.	.	.
	NF	0.35	0.76 ± 0.08	0.58	0.94	1.00 ± 0.13	0.15	0.75	0.60	< 0.01	35.98	13.60	52.56	67.53	30.96	86.08
	MD	0.34	0.98 ± 0.04	0.89	1.06	0.47 ± 0.06	0.33	0.62	0.87	< 0.0001	37.75	28.02	46.17	60.61	47.70	70.46
	FF	0.33	0.93 ± 0.04	0.83	1.03	0.51 ± 0.07	0.34	0.68	0.86	< 0.001	40.07	29.08	49.36	66.23	51.67	76.74

†k and g calculated using a piecewise linear model.

*k and g from non-significant regressions not used in analyses.

Table 3-4. Withlacoochee system: estimates of apparent growth rate (AGR) in controls (μ_0), instantaneous maximum specific phytoplankton growth rates ($k \pm$ SE), instantaneous microzooplankton grazing rates ($g \pm$ SE), percent of phytoplankton standing crop removed daily (%PSC d^{-1}), and percent of phytoplankton production lost daily (%PP d^{-1}) during June and July. No estimates of k and g from experiments conducted in November and December were used in analyses because the regressions did not meet the assumptions of the dilution technique. Upper (U) and lower (L) 95% confidence limits (CL) were calculated using the corresponding confidence limits of k and g coefficients.

Sampling Date	Zone	u_0	$k \pm$ SE	L95%	U95%	$g \pm$ SE	L95%	U95%	r^2	p	%PSC Removed d^{-1}	%PSC Removed d^{-1} L95%	%PSC Removed d^{-1} U95%	%PP Lost d^{-1}	%PP Lost d^{-1} L95%	%PP Lost d^{-1} U95%
6/27	RM	0.28	1.42 ± 0.32	0.69	2.15	1.20 ± 0.52	0.01	2.39	0.41	< 0.05	69.64	1.43	90.83	92.24	2.87	102.83
	NF	0.05	1.00 ± 0.16	0.63	1.36	0.85 ± 0.26	0.25	1.44	0.57	< 0.05	57.09	22.02	76.38	90.52	47.15	102.66
	MD*	0.13	1.45 ± 0.13	1.16	1.74	0.23 ± 0.20	-0.24	0.70	0.14	ns	.	.	.	.	.	.
	FF	1.72	2.37 ± 0.10	2.15	2.60	0.39 ± 0.16	0.02	0.75	0.43	< 0.05	31.95	2.04	52.73	35.24	2.31	56.98
7/4	RM*	0.35	1.13 ± 0.14	0.82	1.45	0.37 ± 0.22	-0.14	0.88	0.26	ns	.	.	.	.	.	.
	NF	0.05	1.42 ± 0.15	1.09	1.76	1.68 ± 0.24	1.13	2.23	0.86	< 0.001	81.34	67.70	89.22	107.14	102.13	107.75
	MD*	1.53	1.76 ± 0.11	1.51	2.01	0.29 ± 0.18	-0.11	0.70	0.26	ns	.	.	.	.	.	.
	FF*	1.49	1.36 ± 0.21	0.88	1.83	0.26 ± 0.34	-0.52	1.04	0.06	ns	.	.	.	.	.	.

*k and g from non-significant regressions not used in analyses.

Table 3-5. Weeki Wachee system: estimates of apparent growth rate (AGR) in controls (μ_0), instantaneous maximum specific phytoplankton growth rates ($k \pm$ SE), instantaneous microzooplankton grazing rates ($g \pm$ SE), percent of phytoplankton standing crop removed daily (%PSC d^{-1}), and percent of phytoplankton production lost daily (%PP d^{-1}) during March, May, September, and November. Upper (U) and lower (L) 95% confidence limits (CL) were calculated using the corresponding confidence limits of k and g coefficients.

Sampling Date	Zone	u_0	$k \pm$ SE	L95%	U95%	$g \pm$ SE	L95%	U95%	r^2	p	%PSC Removed d^{-1}	%PSC Removed d^{-1} L95%	%PSC Removed d^{-1} U95%	%PP Lost d^{-1}	%PP Lost d^{-1} L95%	%PP Lost d^{-1} U95%
4/3	RM	-0.07	0.56 ± 0.10	0.33	0.80	0.59 ± 0.17	0.20	0.98	0.61	< 0.01	44.51	18.26	62.33	103.26	65.55	113.06
	NF	-0.01	0.71 ± 0.11	0.46	0.96	0.58 ± 0.18	0.18	0.99	0.58	< 0.05	44.12	16.15	62.76	87.05	43.96	101.96
	MD	0.39	0.83 ± 0.01	0.81	0.86	0.48 ± 0.16	0.10	0.85	0.52	< 0.05	37.81	9.65	57.20	66.88	17.37	99.42
	FF*	0.61	1.01 ± 0.08	0.82	1.20	0.21 ± 0.14	-0.10	0.53	0.23	ns	.	.	.	.	.	.
6/6	RM	0.45	1.31 ± 0.21	0.84	1.78	0.87 ± 0.33	0.10	1.64	0.46	< 0.05	58.02	9.32	80.57	79.49	16.44	96.88
	NF*	0.05	0.37 ± 0.22	-0.15	0.89	0.31 ± 0.36	-0.53	1.15	0.08	ns	.	.	.	.	.	.
	MD	0.49	1.27 ± 0.19	0.84	1.70	1.17 ± 0.30	0.47	1.87	0.65	< 0.01	68.90	37.45	84.54	95.92	66.00	103.53
	FF	0.39	1.08 ± 0.09	0.88	1.29	0.79 ± 0.15	0.45	1.13	0.78	< 0.001	54.66	36.37	67.70	82.60	62.30	93.35
9/18	RM†	0.64	0.87 ± 0.08	0.69	1.06	0.83 ± 0.24	0.16	1.51	0.74	< 0.05	56.53	14.65	77.86	96.97	29.33	119.34
	NF*	0.15	0.62 ± 0.13	0.32	0.92	0.27 ± 0.21	-0.22	0.76	0.17	ns	.	.	.	.	.	.
	MD	0.17	0.55 ± 0.09	0.35	0.74	0.35 ± 0.14	0.03	0.67	0.44	< 0.05	29.39	2.93	48.64	69.85	9.93	92.84
	FF*	0.00	0.55 ± 0.17	0.15	0.94	0.51 ± 0.28	-0.14	1.16	0.28	ns	.	.	.	.	.	.
11/1	RM	0.37	0.85 ± 0.14	0.52	1.19	0.59 ± 0.23	0.05	1.13	0.44	< 0.05	44.73	5.20	67.78	77.95	12.81	97.63
	NF	0.08	0.63 ± 0.10	0.40	0.85	0.64 ± 0.16	0.28	1.00	0.67	< 0.01	47.06	24.14	63.05	101.26	72.68	110.42
	MD	0.09	1.15 ± 0.19	0.71	1.59	1.08 ± 0.31	0.37	1.80	0.60	< 0.01	66.07	30.66	83.40	96.69	60.20	104.82
	FF*	-0.03	0.51 ± 0.09	0.31	0.72	0.25 ± 0.15	-0.08	0.59	0.27	ns	.	.	.	.	.	.

†k and g calculated using a piecewise linear model.
*k and g from non-significant regressions not used in analyses.

Table 3-6. Analyses of variance for transformed phytoplankton growth rates (k), microzooplankton grazing rates (g), microzooplankton total abundance, and mesozooplankton total abundance.

Variable	Source	df	MS	F	p
$\sqrt{k}$	Model	17	0.0558	1.1756	0.4172
	System	2	0.1469	2.3175	0.1507
	Zone(System)	8	0.0710	3.4385	0.0333
	Discharge Period(System, Zone)	7	0.0181	0.3807	0.8918
	Error	9	0.0474		
	Total	26			
$\sqrt{g}$	Model	17	0.0428	0.6750	0.7713
	System	2	0.0189	0.3067	0.7422
	Zone(System)	8	0.0666	2.5352	0.0725
	Discharge Period(System, Zone)	7	0.0218	0.3436	0.9153
	Error	10	0.0635		
	Total	27			
Microzooplankton Total Abundance (Log_{10} Individuals L^{-1})	Model	11	0.1203	0.8622	0.5936
	System	2	0.4969	13.5590	0.0019
	Zone(System)	9	0.0400	0.2626	0.9737
	Error	12	0.1396		
	Total	23			
Mesozooplankton Total Abundance (Log_{10} Individuals m^{-3})	Model	23	0.5452	2.6010	0.0011
	System	2	0.1105	0.1938	0.8272
	Zone(System)	9	0.5701	0.9519	0.5187
	Discharge Period(System, Zone)	12	0.5989	2.8574	0.0029
	Error	72	0.2096		

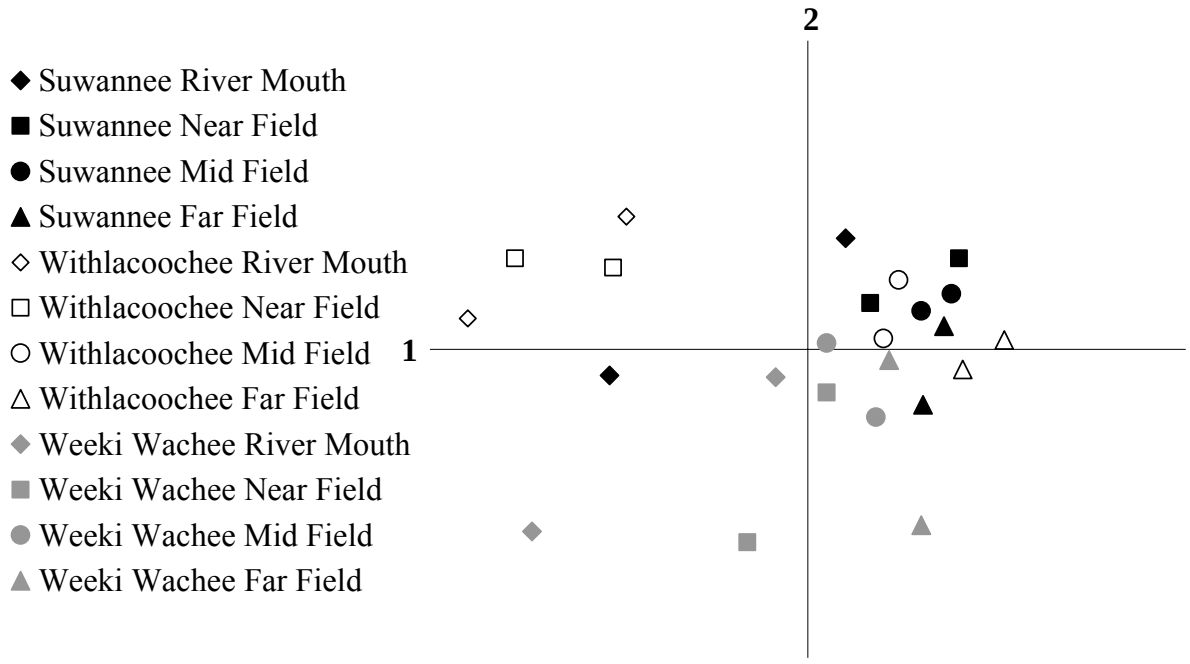

Figure 3-3. Two-dimensional ordination (stress value = 0.11) based on microzooplankton abundances in the Suwannee, Withlacoochee, and Weeki Wachee systems. Distance between points is indicative of similarity where points further apart are less similar than those closer together.

Table 3-7. Suwannee system: microzooplankton total abundance (individuals L^{-1}) and common taxa during September and November.

September				November			
River Mouth	1502	Copepod nauplii	49.0%	River Mouth	274	Copepod nauplii	50.4%
		Tintinnids	24.1%			Tintinnids	15.1%
		Rotifers	11.9%			Protozoa	7.3%
		Tintinniopsis sp.	3.8%			*Prorocentrum* spp.	6.9%
						Rotifer	3.9%
Near Field	2939	*Prorocentrum* spp.	37.8%				
		Copepod nauplii	18.0%	Near Field	774	Copepod nauplii	27.3%
		Protoperidinium sp.	7.2%			Tintinnids	10.7%
		Pryophacus spp.	6.9%			Rotifers	7.0%
		Tintinniopsis sp.	4.9%			Larvacean	4.1%
		Rotifer	3.9%			Nematode	3.7%
		Tintinnids	3.7%			*Ceratium* spp.	3.1%
Mid-Field	1476	Copepod nauplii	29.8%	Mid-Field	597	Copepod nauplii	31.2%
		Prorocentrum spp.	12.3%			Larvacean	15.6%
		Protoperidinium sp.	10.9%			*Pryophacus* spp.	9.1%
		Ceratium sp.	8.3%			*Ceratium* sp.	7.3%
		Larvacean	3.3%			Protozoa	7.3%
		Parvocalanus sp.	3.2%			*Prorocentrum* sp.	6.2%
						Nematode	3.4%
Far Field	607	Copepod nauplii	43.0%				
		Pryophacus spp.	20.4%	Far Field	431	Copepod nauplii	53.3%
		Ceratium spp.	7.8%			Tintinnids	7.7%
		Protoperidinium sp.	4.8%			*Parvocalanus* sp.	6.4%
						Prorocentrum spp.	5.3%
						Protozoa	3.1%

Table 3-8. Withlacoochee system: microzooplankton total abundance (individuals L^{-1}) and common taxa during November and December.

November				December			
River Mouth	2277	Protozoa	43.9%	River Mouth	396	Protozoa	78.6%
		Tintinnids	35.6%			Copepod nauplii	9.5%
		Copepod nauplii	14.8%			Rotifers	4.5%
						Tintinnids	3.8%
Near Field	852	Tintinnids	41.2%				
		Copepod nauplii	41.0%	Near Field	369	Protozoa	76.2%
		Tintinnopsis spp.	5.2%			Rotifers	13.3%
		Protozoa	4.3%			Copepod nauplii	4.7%
						Tintinnids	3.8%
Mid-Field	1485	Tintinnids	22.6%				
		Copepod nauplii	15.8%	Mid-Field	294	Copepod nauplii	27.7%
		Prorocentrum sp.	11.6%			Tintinnids	18.7%
		Rotifers	8.8%			*Ceratium* spp.	10.4%
		Protoperidinium sp.	6.4%			*Protoperidinium* sp.	6.5%
		Pryophacus spp.	6.2%			Rotifers	6.5%
		Ceratium sp.	4.3%			*Prorocentrum* sp.	5.5%
						Pryophacus spp.	4.6%
Far Field	877	Copepod nauplii	24.0%				
		Protoperidinium sp.	21.4%	Far Field	801	Copepod nauplii	34.5%
		Pryophacus spp.	18.6%			*Ceratium* sp.	11.1%
		Ceratium sp.	5.8%			*Protoperidinium* sp.	9.5%
		Ceratium hircus	5.5%			*Pryophacus* spp.	9.3%
						Protozoa	3.1%

Table 3-9. Weeki Wachee system: total abundance (individuals L^{-1}) and common taxa during September and November.

September				November			
River Mouth	731	Copepod nauplii	37.7%	River Mouth	94	Copepod nauplii	55.4%
		Prorocentrum sp.	16.9%			Tintinnids	21.5%
		Gastropod larvae	9.5%			Nematode	4.1%
		Protozoa	5.8%			*Prorocentrum lima*	3.1%
		Bivalve veliger	5.5%				
		Rotifers	3.4%				
		Tintinnids	3.1%	Near Field	241		
						Copepod nauplii	42.5%
Near Field	347	Copepod nauplii	30.9%			*Prorocentrum* sp.	19.9%
		Gymnodinium sp.	9.2%			Tintinnids	9.0%
		Protozoa	8.8%			Nematode	6.0%
		Bivalve veliger	7.4%				
		Prorocentrum sp.	4.7%	Mid-Field	313	*Ceratium hircus*	30.9%
		Nematode	4.1%			Copepod nauplii	20.2%
		Gastropod larvae	3.9%			Tintinnids	11.2%
		Rotifers	3.7%			*Prorocentrum lima*	6.2%
		Pryophacus spp.	3.5%			*Tintinniopsis* sp.	3.7%
Mid-Field	235	Copepod nauplii	16.2%	Far Field	197	Copepod nauplii	47.2%
		Protozoa	9.1%			*Ceratium hircus*	8.3%
		Tintinnids	9.0%			*Prorocentrum lima*	3.6%
		Ceratium hircus	8.5%			*Gymnodinium* sp.	3.6%
		Bivalve veliger	7.1%				
		Pryophacus spp.	4.1%				
Far Field	607	Copepod nauplii	22.6%				
		Bivalve veliger	15.6%				
		Ceratium hircus	11.9%				
		Pryophacus spp.	7.2%				
		Protoperidinium sp.	6.5%				
		Tintinnids	4.7%				
		Tintinnopsis sp.	4.3%				
		Polychaete larvae	4.2%				

Table 3-10. Suwannee system: mesozooplankton total abundance (individuals m^{-3}) and common taxa during March, May, September, and November.

March				May cont.				November			
River Mouth				Far Field				River Mouth			
Stn 1	2925	*Acartia tonsa*	97.2%	Stn 1	535	*Acartia tonsa*	25.9%	Stn 1	1341	*Acartia tonsa*	41.1%
						Paracalanus spp.	25.8%			*Parvocalanus* spp.	21.2%
Stn 2	18715	*Acartia tonsa*	99.8%			*Corycaeus* spp.	16.0%			*Balanus* nauplii	18.0%
Near Field						*Centropages* spp.	5.1%			*Euterpina acutifrons*	5.4%
Stn 1	6409	*Acartia tonsa*	96.7%			*Oithona* spp.	4.9%			*Penilia* spp.	4.4%
						Parvocalanus spp.	3.4%			*Daphnia* spp.	4.2%
Stn 2	4589	*Acartia tonsa*	73.0%								
		Bivalve veliger	15.2%	Stn 2	625	*Acartia tonsa*	23.9%	Stn 2	408	*Balanus* nauplii	47.0%
		Larvacean	5.1%			*Paracalanus* spp.	21.5%			*Acartia tonsa*	20.8%
Mid-Field						*Corycaeus* spp.	14.5%			*Penilia* spp.	12.8%
Stn 1	21695	*Acartia tonsa*	69.3%			*Oithona* spp.	4.6%			*Euterpina acutifrons*	6.9%
		Gastropod larvae	13.8%			Bivalve veliger	4.6%			*Parvocalanus* spp.	6.7%
		Bivalve veliger	4.9%			Gastropod larvae	4.3%	Near Field			
		Balanus nauplii	4.2%			*Parvocalanus* spp.	3.9%	Stn 1	12544	*Acartia tonsa*	91.6%
						Euterpina acutifrons	3.9%				
Stn 2	6248	*Acartia tonsa*	83.6%			*Centropages* spp.	3.7%	Stn 2	10205	*Acartia tonsa*	72.1%
		Balanus nauplii	5.7%	September						*Penilia* spp.	11.2%
Far Field				River Mouth						*Parvocalanus* spp.	9.1%
Stn 1	1959	*Paracalanus* spp.	53.7%	Stn 1	918	*Balanus* nauplii	59.5%			*Euterpina acutifrons*	4.4%
		Corycaeus spp.	12.4%			*Parvocalanus* spp.	36.0%	Mid-Field			
		Oithona spp.	7.1%			Copepod nauplii	9.1%	Stn 1	10595	*Acartia tonsa*	34.4%
		Pseudocalanus spp.	5.8%			*Paracalanus* spp.	6.2%			*Parvocalanus* spp.	25.0%
		Parvocalanus spp.	4.4%			Barnacle cyprid	5.9%			*Euterpina acutifrons*	11.0%
		Acartia tonsa	4.2%			*Acartia tonsa*	5.4%			Radiolarian	10.2%
		Sagitta spp.	3.6%			*Chthalamus* nauplii	3.1%			*Penilia* spp.	6.4%
										Temora spp.	4.9%
Stn 2	3374	*Paracalanus* spp.	43.1%	Stn 2	174	*Parvocalanus* spp.	13.0%			*Balanus* nauplii	4.1%
		Corycaeus spp.	17.3%			Copepod nauplii	9.1%				
		Oithona spp.	12.8%			*Balanus* nauplii	9.1%	Stn 2	17587	*Penilia* spp.	43.0%
		Acartia tonsa	12.1%			*Acartia tonsa*	6.8%			*Parvocalanus* spp.	21.8%
		Centropages spp.	5.1%	Near Field						*Acartia tonsa*	18.0%
		Parvocalanus spp.	3.7%	Stn 1	29670	*Acartia tonsa*	60.5%			*Euterpina acutifrons*	8.9%
May						*Paracalanus* spp.	12.6%			*Balanus* nauplii	3.1%
River Mouth						*Balanus* nauplii	9.1%	Far Field			
Stn 1	359	Brachyuran crab zoea	97.8%			*Euterpina acutifrons*	5.3%	Stn 1	21585	*Penilia* spp.	58.9%
						Pseudocalanus spp.	4.3%			*Parvocalanus* spp.	10.7%
Stn 2	396	Brachyuran crab zoea	90.1%			*Parvocalanus* spp.	3.4%			*Euterpina acutifrons*	7.8%
		Balanus nauplii	6.3%							*Oithona* spp.	6.7%
Near Field				Stn 2	9763	*Acartia tonsa*	77.3%			*Corycaeus* spp.	6.7%
Stn 1	1021	Brachyuran crab zoea	35.0%			*Parvocalanus* spp.	8.9%			*Temora* spp.	4.8%
		Parvocalanus spp.	16.5%			*Euterpina acutifrons*	5.1%				
		Acartia tonsa	15.0%			*Balanus* nauplii	4.3%	Stn 2	1925	*Parvocalanus* spp.	44.0%
		Balanus nauplii	12.9%	Mid-Field						*Acartia tonsa*	15.6%
		Gastropod larvae	6.7%	Stn 1	6718	*Acartia tonsa*	77.3%			*Euterpina acutifrons*	12.8%
		Marine mite	5.7%			*Euterpina acutifrons*	20.7%			*Oithona* spp.	10.0%
						Parvocalanus spp.	5.7%			*Temora* spp.	6.2%
Stn 2	261	Brachyuran crab zoea	76.2%			*Temora* spp.	4.7%			*Corycaeus* spp.	4.1%
		Marine mite	8.9%			*Balanus* nauplii	3.8%				
		Acartia tonsa	3.9%								
		Parvocalanus spp.	3.3%	Stn 2	29227	*Acartia tonsa*	63.6%				
		Balanus nauplii	3.3%			*Euterpina acutifrons*	27.8%				
Mid-Field						*Parvocalanus* spp.	4.2%				
Stn 1	5749	*Acartia tonsa*	30.9%			Brachyuran crab zoea	3.2%				
		Brachyuran crab zoea	24.9%	Far Field							
		Parvocalanus spp.	11.2%	Stn 1	3804	*Temora* spp.	76.7%				
		Paracalanus spp.	10.2%			*Euterpina acutifrons*	8.6%				
		Gastropod larvae	9.6%			*Paracalanus* spp.	4.0%				
						Brachyuran crab zoea	3.3%				
Stn 2	1103	*Acartia tonsa*	27.2%								
		Brachyuran crab zoea	23.5%	Stn 2	19910	*Temora* spp.	66.0%				
		Balanus nauplii	11.6%			*Euterpina acutifrons*	14.8%				
		Gastropod larvae	9.6%			*Acartia tonsa*	3.9%				
		Parvocalanus spp.	8.9%			*Paracalanus* spp.	3.5%				
		Paracalanus spp.	3.9%			*Corycaeus* spp.	3.3%				

Table 3-11. Withlacoochee system: mesozooplankton total abundance (individuals m^{-3}) and common taxa during June, July, November, and December.

June				July cont.				November cont.			
River Mouth				Near Field cont.				Far Field			
Stn 1	9454	*Acartia tonsa*	78.1%	Stn 2	6769	*Acartia tonsa*	58.4%	Stn 1	3545	*Parvocalanus* spp.	30.0%
		Parvocalanus spp.	3.9%			Bivalve veliger	21.7%			*Temora* spp.	26.7%
		Bivalve veliger	9.9%			*Parvocalanus* spp.	7.0%			*Acartia tonsa*	11.4%
						Brachyuran crab zoea	5.0%			*Oithona* spp.	10.1%
Stn 2	12136	Bivalve veliger	45.4%							*Euterpina acutifrons*	9.5%
		Acartia tonsa	44.7%	Mid-Field						*Penilia* spp.	7.1%
		Calanoid copepod	4.2%	Stn 1	1358	*Acartia tonsa*	46.0%				
Near Field						*Parvocalanus* spp.	24.0%	Stn 2	10085	*Parvocalanus* spp.	32.1%
Stn 1	7529	Bivalve veliger	69.1%			Brachyuran crab zoea	8.7%			*Euterpina acutifrons*	31.1%
		Acartia tonsa	7.5%			*Euterpina acutifrons*	5.9%			*Oithona* spp.	12.6%
		Parvocalanus spp.	7.4%			*Oithona* spp.	3.6%			*Temora* spp.	9.3%
		Brachyuran crab zoea	6.1%							*Penilia* spp.	7.4%
		Euterpina acutifrons	3.2%	Stn 2	2364	*Acartia tonsa*	28.4%				
						Parvocalanus spp.	23.4%	December			
Stn 2	2159	Bivalve veliger	42.4%			Brachyuran crab zoea	22.6%	River Mouth			
		Gastropod larvae	21.1%			*Euterpina acutifrons*	5.4%	Stn 1	863	*Acartia tonsa*	91.6%
		Brachyuran crab zoea	13.8%			Shrimp zoea	4.0%			*Balanus* nauplii	4.1%
		Acartia tonsa	7.8%			*Labidocera* spp.	3.2%				
		Euterpina acutifrons	3.8%	Far Field				Stn 2	378	*Acartia tonsa*	83.8%
Mid-Field				Stn 1	1933	*Acartia tonsa*	45.7%			*Paracalanus* spp.	4.6%
Stn 1	3167	*Acartia tonsa*	45.6%			Brachyuran crab zoea	25.6%			Ostracod	3.7%
		Parvocalanus spp.	18.0%			*Parvocalanus* spp.	9.5%	Near Field			
		Euterpina acutifrons	12.3%			*Paracalanus* spp.	5.7%	Stn 1	1318	*Acartia tonsa*	90.2%
		Brachyuran crab zoea	6.1%			*Centropages* spp.	3.3%			Calanoid copepod	4.3%
		Pseudodiaptomus spp.	5.7%								
				Stn 2	1649	Fish larvae	48.5%	Stn 2	2420	*Acartia tonsa*	96.9%
Stn 2	3363	*Acartia tonsa*	40.3%			Brachyuran crab zoea	25.2%	Mid-Field			
		Euterpina acutifrons	20.8%			*Acartia tonsa*	11.4%	Stn 1	2431	*Acartia tonsa*	36.4%
		Parvocalanus spp.	12.2%			*Paracalanus* spp.	4.4%			*Parvocalanus* spp.	34.3%
		Pseudodiaptomus spp.	5.2%	November						*Euterpina acutifrons*	11.4%
		Paracalanus spp.	4.4%	River Mouth						*Oithona* spp.	5.9%
		Brachyuran crab zoea	3.5%	Stn 1	1530	*Acartia tonsa*	92.3%			Barnacle cyprid	3.7%
		Pseudocalanus spp.	3.2%			Calanoid copepod	3.1%				
Far Field								Stn 2	3298	*Parvocalanus* spp.	62.3%
Stn 1	1707	*Acartia tonsa*	40.9%	Stn 2	1118	*Acartia tonsa*	88.9%			*Euterpina acutifrons*	15.7%
		Brachyuran crab zoea	27.9%			Calanoid copepod	5.0%			*Acartia tonsa*	7.8%
		Shrimp zoea	6.8%	Near Field						*Oithona* spp.	6.6%
		Centropages spp.	6.2%	Stn 1	933	*Acartia tonsa*	91.4%	Far Field			
		Euterpina acutifrons	3.9%					Stn 1	1488	*Euterpina acutifrons*	29.6%
		Paracalanus spp.	3.2%	Stn 2	1150	*Acartia tonsa*	89.8%			*Parvocalanus* spp.	21.7%
				Mid-Field						*Acartia tonsa*	20.6%
Stn 2	3188	*Acartia tonsa*	40.9%	Stn 1	2836	*Acartia tonsa*	34.0%			*Temora* spp.	15.2%
		Brachyuran crab zoea	28.0%			Copepod nauplii	12.5%			*Oithona* spp.	8.4%
		Centropages spp.	9.1%			*Oithona* spp.	9.3%				
		Euterpina acutifrons	4.4%			*Parvocalanus* spp.	8.6%	Stn 2	2070	*Parvocalanus* spp.	30.7%
		Parvocalanus spp.	3.2%			Polychaete larvae	7.8%			*Euterpina acutifrons*	19.6%
July						*Paracalanus* spp.	6.8%			*Acartia tonsa*	18.5%
River Mouth						*Balanus* nauplii	4.3%			*Temora* spp.	16.6%
Stn 1	3041	*Acartia tonsa*	82.5%							*Oithona* spp.	5.1%
				Stn 2	3681	*Acartia tonsa*	44.7%				
Stn 2	4070	*Acartia tonsa*	46.7%			*Parvocalanus* spp.	21.9%				
		Bivalve veliger	14.2%			*Euterpina acutifrons*	6.7%				
		Brachyuran crab zoea	12.2%			*Temora* spp.	5.6%				
		Balanus nauplii	4.8%			*Oithona* spp.	5.2%				
		Parvocalanus spp.	4.7%			Ostracod	5.1%				
		Gastropod larvae	3.9%			*Balanus* nauplii	4.2%				
Near Field						*Paracalanus* spp.	3.6%				
Stn 1	5673	*Acartia tonsa*	56.1%			Calanoid copepod	3.3%				
		Bivalve veliger	18.6%								
		Parvocalanus spp.	6.5%								
		Gastropod larvae	4.9%								
		Oithona spp.	4.2%								

Table 3-12. Weeki Wachee system: mesozooplankton total abundance (individuals m^{-3}) and common during April, June, September, and November.

April				June cont.				November cont.			
River Mouth				Far Field				Mid-Field			
Stn 1	6453	*Acartia tonsa*	98.3%	Stn 1	917	Gastropod larvae	57.6%	Stn 1	1308	*Acartia tonsa*	41.6%
						Acartia tonsa	13.0%			Gastropod larvae	18.9%
Stn 2	5536	*Acartia tonsa*	93.7%			*Labidocera* spp.	8.8%			*Parvocalanus* spp.	16.6%
		Calanoid copepod	4.6%			Shrimp larvae	5.1%			Isopod larvae	5.8%
Near Field						Brachyuran crab zoea	4.1%			Brachyuran crab zoea	5.0%
Stn 1	38467	*Acartia tonsa*	87.0%			Pagurus crab zoea	4.0%				
		Isopod larvae	6.8%			Isopod larvae	3.2%	Stn 2	2072	*Acartia tonsa*	62.5%
		Brachyuran crab zoea	5.1%							*Parvocalanus* spp.	11.3%
				Stn 2	1190	Gastropod larvae	61.5%			*Oithona* spp.	8.3%
Stn 2	28648	*Acartia tonsa*	87.3%			*Acartia tonsa*	19.9%			Gastropod larvae	5.3%
		Isopod larvae	5.8%			Shrimp larvae	8.1%			Isopod larvae	4.8%
		Brachyuran crab zoea	4.6%			*Labidocera* spp.	3.9%				
Mid-Field				September				Far Field			
Stn 1	8662	*Acartia tonsa*	79.7%	River Mouth				Stn 1	1840	*Acartia tonsa*	53.3%
		Isopod larvae	3.9%	Stn 1	5499	Gastropod larvae	48.5%			*Parvocalanus* spp.	17.0%
		Brachyuran crab zoea	3.5%			*Acartia tonsa*	39.6%			Gastropod larvae	8.3%
						Pseudioaptomus spp.	3.4%			Brachyuran crab zoea	4.5%
Stn 2	9474	*Acartia tonsa*	73.4%							Shrimp larvae	4.1%
		Labidocera spp.	7.5%	Stn 2	1168	*Acartia tonsa*	68.0%			Isopod larvae	3.0%
		Brachyuran crab zoea	3.7%			Gastropod larvae	26.9%				
		Sagitta spp.	3.3%	Near Field				Stn 2	1872	*Acartia tonsa*	58.5%
Far Field				Stn 1	2551	*Acartia tonsa*	81.9%			*Parvocalanus* spp.	18.4%
Stn 1	61385	*Acartia tonsa*	72.3%			Gastropod larvae	4.3%			*Oithona* spp.	5.7%
		Brachyuran crab zoea	6.3%							Shrimp larvae	4.4%
		Isopod	4.2%	Stn 2	2207	*Acartia tonsa*	56.7%				
		Labidocera spp.	3.7%			Gastropod larvae	29.0%				
		Pagurus crab zoea	3.2%			Brachyuran crab zoea	6.1%				
				Mid-Field							
Stn 2	29370	*Acartia tonsa*	68.5%	Stn 1	2198	*Acartia tonsa*	91.4%				
		Gastropod larvae	8.6%			Brachyuran crab zoea	4.1%				
		Shrimp larvae	5.6%								
		Brachyuran crab zoea	3.7%	Stn 2	2241	*Acartia tonsa*	89.1%				
June						Isopod larvae	3.3%				
River Mouth				Far Field							
Stn 1	878	*Acartia tonsa*	93.7%	Stn 1	2215	*Acartia tonsa*	56.2%				
						Shrimp larvae	7.6%				
Stn 2	480	*Acartia tonsa*	88.1%			*Parvocalanus* spp.	6.2%				
		Euterpina acutifrons	4.5%			*Paracalanus* spp.	4.3%				
		Calanoid copepod	3.1%			Gastropod larvae	3.3%				
Near Field											
Stn 1	987	Gastropod larvae	26.0%	Stn 2	2671	*Acartia tonsa*	65.3%				
		Acartia tonsa	17.6%			*Parvocalanus* spp.	6.4%				
		Brachyuran crab zoea	6.7%			*Paracalanus* spp.	3.7%				
		Labidocera spp.	5.7%			*Euterpina acutifrons*	3.2%				
		Pagurus crab zoea	3.1%			Shrimp larvae	3.2%				
						Barnacle cyprid	3.2%				
Stn 2	2983	*Acartia tonsa*	64.1%	November							
		Gastropod larvae	59.7%	River Mouth							
		Brachyuran crab zoea	23.1%	Stn 1	835	*Acartia tonsa*	84.3%				
Mid-Field						Calanoid copepod	4.5%				
Stn 1	3219	*Acartia tonsa*	75.0%								
		Brachyuran crab zoea	8.7%	Stn 2	183	*Acartia tonsa*	84.4%				
		Gastropod larvae	5.1%			*Euterpina acutifrons*	4.7%				
						Harpacticoid copepod	3.5%				
Stn 2	509	*Acartia tonsa*	48.8%	Near Field							
		Gastropod larvae	26.0%	Stn 1	2266	*Acartia tonsa*	88.0%				
		Pagurus crab zoea	8.5%								
		Labidocera spp.	8.1%	Stn 2	2998	*Acartia tonsa*	93.2%				

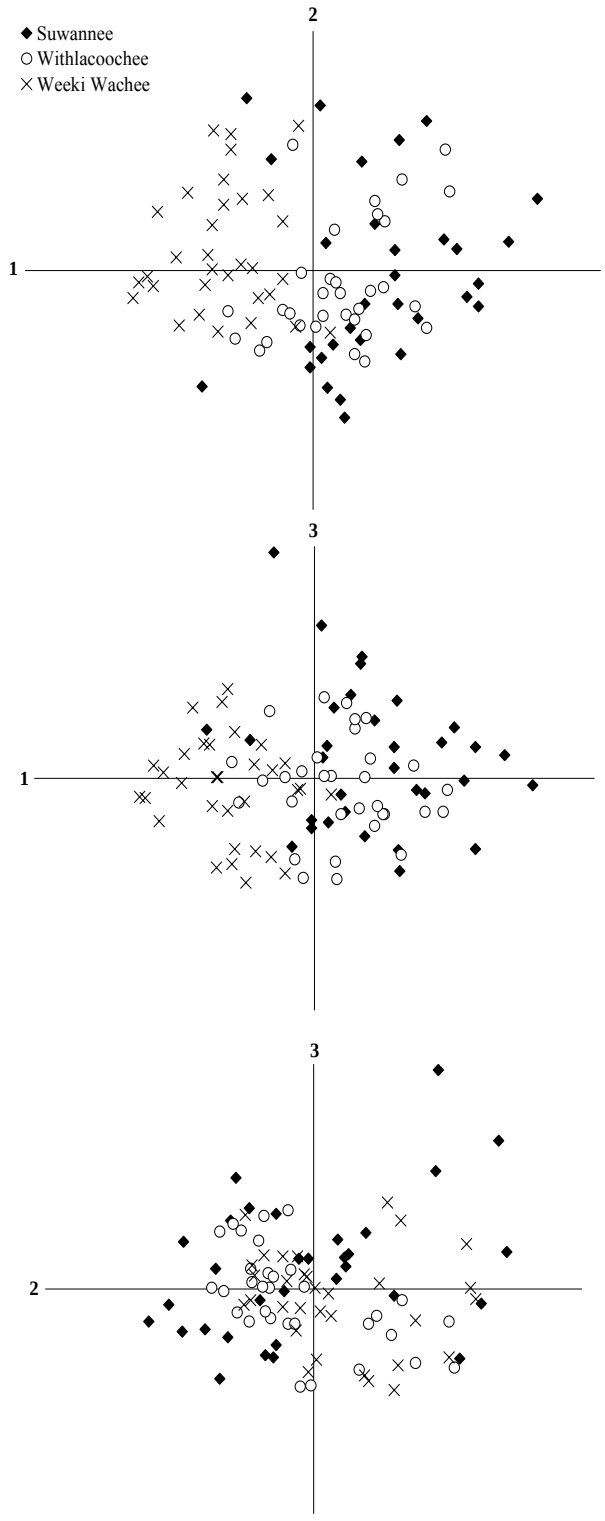

Figure 3-4. Three-dimensional ordination (stress = 0.16) based on mesozooplankton abundances in the Suwannee, Withlacoochee, and Weeki Wachee systems. Distance between points is indicative of similarity where points further apart are less similar than those closer together.

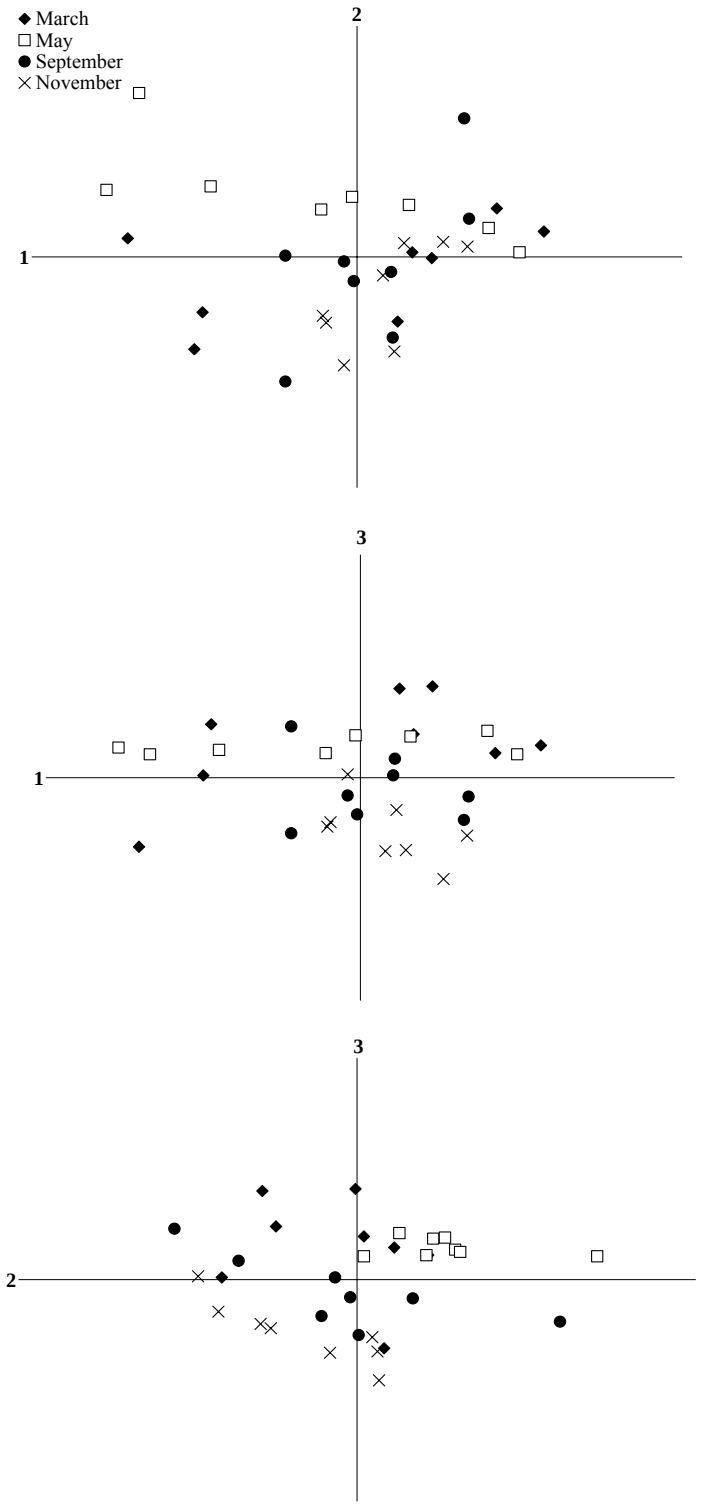

Figure 3-5. Three-dimensional ordination (stress = 0.12) based on mesozooplankton abundances in the Suwannee River plume during March, May, September, and November. Distance between points is indicative of similarity where points further apart are less similar than those closer together.

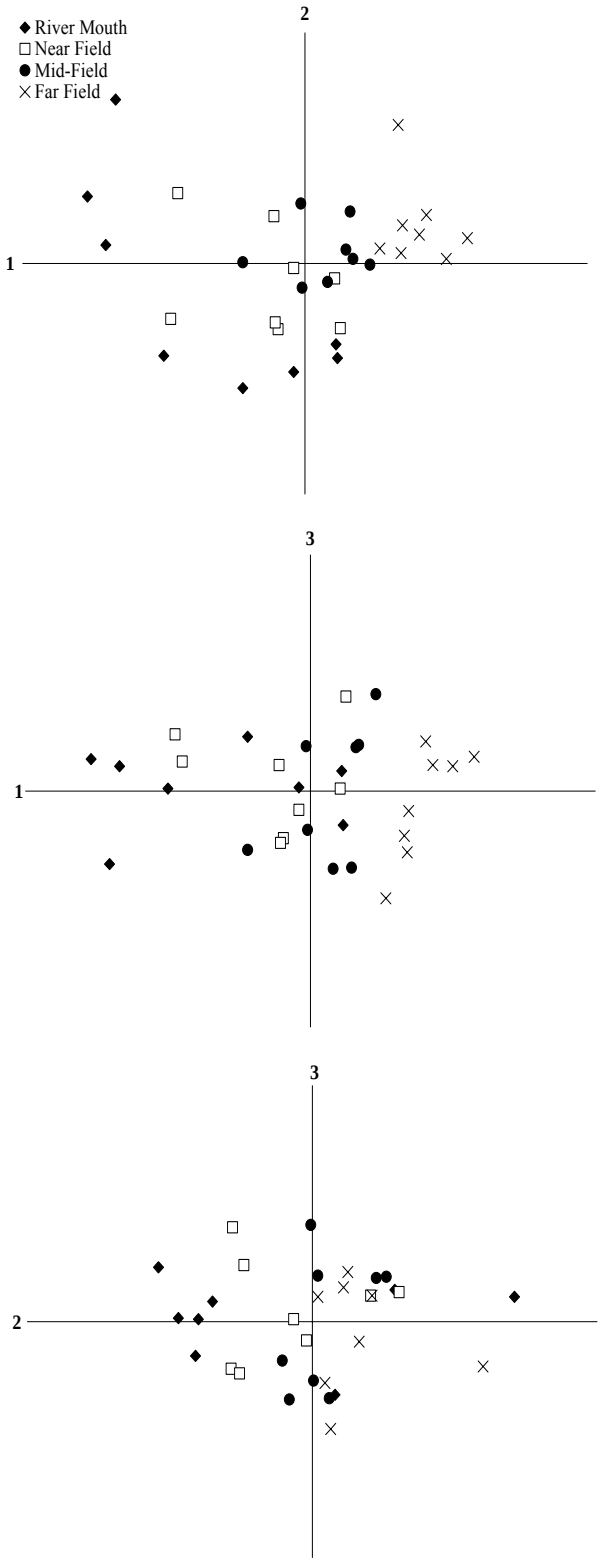

Figure 3-6. Three-dimensional ordination (stress = 0.12) based on mesozooplankton abundances in the Suwannee River plume. Distance between points is indicative of similarity where points further apart are less similar than those closer together.

CHAPTER 4
DISCUSSION

Overall, these results indicate the model proposed by Liu & Dagg (2003) and Dagg & Breed (2003) to describe interactions between phytoplankton and zooplankton along nutrient and light gradients in large, river-dominated, coastal systems cannot be generalized to these smaller, river-influenced, coastal waters. Spatial patterns of phytoplankton biomass and growth rates, microzooplankton grazing rates and abundance, and mesozooplankton grazing rates and abundance in each of the three systems were not consistent with the conceptual model. In the Suwannee system, where nutrient and light have been shown to vary inversely with salinity (Frazer et al. 1998), phytoplankton crops and phytoplankton growth rates were normally the highest at the river mouth, declining in the near field and mid-field, and lowest in the far field. Furthermore, microzooplankton grazing rates and abundance and mesozooplankton grazing rates and abundance did not peak in the two higher salinity zones as predicted. In the Withlacoochee and Weeki Wachee systems, where nutrients inversely varied with salinity (Frazer et al. 1998) and light availability was relatively consistent among zones (Figure 3-1), phytoplankton biomass tended to peak in the lower salinity zones and phytoplankton growth and microzooplankton grazing rates were similar among zones. Microzooplankton and mesozooplankton abundances varied among zones, but they were not particularly high in the mid field and far fields. Although spatial variability deviated from the model, estimates of phytoplankton biomass, phytoplankton growth rates, microzooplankton grazing rates and mesozooplankton assemblage composition were comparable to results of previous work in the three study systems and to studies of other coastal waters in the northern Gulf of Mexico. To explain the deviations from the model's predictions, we examined the hypothesis that river discharge rates were below the threshold

required to induce the physical processes that affect light availability on scales in time and space at which phytoplankton could respond.

Phytoplankton biomass estimates (chl μg L^{-1}) in the Suwannee, Withlacoochee, and Weeki Wachee systems were within the range of previously reported values for those systems (Quinlan & Phlips 2007, Frazer et al. 2007, Bledsoe 2003), and comparable to estimates from other coastal areas in the northern Gulf of Mexico (Mississippi River plume: Wysocki et al. 2006, Liu & Dagg 2003; Mobile Bay: Lehrter et al. 1999; Pensacola Bay: Murrell et al. 2002). The spatial distribution of phytoplankton biomass observed in this study, where biomass is highest near the river mouth and lowest in the far field, corroborates findings of Quinlan & Phlips (2007), Murrell et al. (2002), and Lehrter et al. (1999) indicating that mean chlorophyll concentrations normally declined along salinity gradients in systems with freshwater flows lower than the Mississippi River. Such a pattern is in stark contrast to that predicted by the model; chlorophyll maxima are expected to occur at the mid-field.

Phytoplankton growth and microzooplankton grazing rates in the Suwannee, Withlacoochee, and Weeki Wachee systems were typical of many coastal systems in the Gulf of Mexico and other locations around the globe (Table 4-1). Prior estimates of phytoplankton growth (range = -0.15 to 3.20) and grazing rates (range = 0.00 to 2.04) from the Suwannee River estuary are similar to those reported here (Table 4-1), despite differences in river discharge and the scale of sampling effort among studies. This similarity suggests rates of phytoplankton growth and mortality due to microzooplankton grazing are remarkably constant in space and time in the Suwannee system. Phytoplankton growth and microzooplankton grazing rates for the Withlacoochee and Weeki Wachee systems have not been reported previously. The rates for these systems were within the range of those reported from the Suwannee, indicating that

phytoplankton growth rates and microzooplankton grazing rates are likely to be uniform in waters along the west coast of peninsular Florida. This finding is noteworthy as microzooplankton grazing rates are generally assumed to be a function of prey concentration (Landry & Hassett 1982). In this study, chlorophyll concentrations in the coastal waters adjacent to the Suwannee were markedly higher than those in waters adjacent to the Weeki Wachee, and one might have expected corresponding differences in microzooplankton grazing rates. The similarity in grazing rates between these two systems suggests the need to consider other effects on microzooplankton, such as predation by mesozooplankton and/or the physical environment.

The relative consistency in microzooplankton grazing rates among systems as compared to the variability among results of dilution experiments was borne out by power analyses. These analyses indicated that considerably larger sample sizes or differences among grazing rates were needed to yield statistical significance. For example, power analyses indicated minimal detectable differences among square-root transformed g-values of approximately 2.3, which is greater than the square-root transformation of the largest g-value we found, i.e. $\sqrt{2.5} = 1.6$ (James & Hall 1998). In general, power analyses indicated that detecting statistical differences in microzooplankton grazing rates may require considerable effort.

Here, we report the first estimates of mesozooplankton total abundance and grazing impact along salinity gradients in the Suwannee, Withlacoochee, and Weeki Wachee systems. Individual estimates of total abundance among systems and zones varied widely, sometimes by an order of magnitude (Tables 3-10 to 3-11). A potential response in mesozooplankton production related to changes in phytoplankton biomass was found only in the Suwannee system during the low discharge period, where higher total abundances in the near field and mid-field were coincident with maximum chlorophyll concentrations near the river mouth. This pattern of spatial

variability supports the observation of Dagg (1995) that mesozooplankton exhibit a lag in responding to accumulation of phytoplankton biomass accumulation.

In cases where mesozooplankton grazing rates could be calculated, the corresponding percentages of phytoplankton consumed on a daily basis were quite low (≤0.05%), suggesting that mesozooplankton grazing impact is negligible in comparison to the impact of microzooplankton grazing. The limited success of the mesozooplankton addition experiments is indicative of the difficulties associated with collecting zooplankton and transferring them to a land-based laboratory. The mesozooplankton addition method has been successfully implemented on ships (Liu & Dagg 2003, Calbet & Landry 1999); however, its use may be inappropriate for land-based experiments when the time between collection and incubation exceeds a few hours. Qualitative observations during this study suggest that mesozooplankton mortality rates remained low during the first 6 to 8 hrs after collection and increased greatly thereafter. The few, low, estimates of mesozooplankton grazing rates may be due to moribund zooplankton being used in the addition experiments. This issue may be resolved by simply restricting the amount of time zooplankton are immersed in containers before being added to treatments.

Mesozooplankton assemblages have seldom been characterized in the shallow coastal waters along the central west coast of peninsular Florida. In fact, this is the first characterization of mesozooplankton from the coastal waters adjacent to the Suwannee, Withlacoochee, and Weeki Wachee rivers. The predominance of *Acartia tonsa* and *Paracalanus* spp. in each of the three study systems is consistent with findings from other coastal waters indicating the dominance of these copepods in mesozooplankton assemblages in the northern Gulf of Mexico (Apalachicola River estuary: Putland 2005; Mississippi River plume: Liu & Dagg 2003, Dagg

1995; Turkey Point, FL: Stalder & Marcus 1997). However, despite the overall dominance by *A. tonsa* and *Paracalanus* sp., mesozooplankton assemblages exhibited spatial heterogeneity along salinity gradients in each of the three study systems. Brachyuran crab zoea, barnacle nauplii, and euryhaline copepods like *A. tonsa* were abundant in nearshore assemblages while polyhaline copepods like *Temora* sp. and *Corycaeus* sp. primarily comprised assemblages offshore (Tables 3-10 to 3-12). Relative abundances of *A. tonsa* and *Paracalanus* spp. also varied with salinity, where *A. tonsa* was the numerical dominant nearshore, but became secondary to *Paracalanus* spp. offshore. Lower abundance of *A. tonsa* and higher numbers of *Paracalanus* spp. in the far fields of each system may reflect the ability of *Paracalanus* spp. to out-compete *A. tonsa* when phytoplankton concentrations are low (Paffenhöffer & Stearns 1988). In environments with low prey availability where it may be out-competed for food, A*cartia tonsa* likely exhibits facultative omnivory (Gifford & Dagg 1991), switching between feeding on phytoplankton and microzooplankton in response to their relative availability (Johnson & Allen 2005, Halvorsen et al. 2001, Kiørboe et al. 1996, Kleppel et al. 1992). Large numbers of adult *A. tonsa* and its juvenile stages in nearshore coastal waters could restrict microzooplankton production where the quantity of phytoplankton prey is relatively low (Batten et al. 2001). Furthermore, prey switching by *A. tonsa* assemblages along the west coast of Florida is a distinct possibility given the marked difference in chlorophyll concentrations between the Suwannee and Weeki Wachee systems. Because the relative availability of autotrophic (chl μg L^{-1}) to microzooplankton prey (individuals L^{-1}) is greater in the Suwannee system than it is in the Weeki Wachee system, *A. tonsa* would be expected to ingest proportionately more phytoplankton in coastal waters adjacent to the Suwannee River, and, conversely, more microzooplankton in waters adjacent to the Weeki Wachee River. *Acartia tonsa* exhibiting shifts in prey selectivity and feeding behavior (Kiørboe

et al. 1996) between the two systems would be especially likely during seasonal blooms of large phytoplankton taxa in the Suwannee system (Quinlan & Phlips 2007) because *A. tonsa* selectively feeds on particles larger than15μm (Rollwagen Bollens & Penry 2003).

In river-impacted, coastal systems, freshwater discharge, wind stress, and tide are the primary forces affecting the physical structure of plume waters (Chen et al. 1997, Yin et al. 1997). In large river systems, discharge is a dominating physical force. For example, during a period of high discharge, the Amazon's plume extended 162 km offshore (Smith & Demaster 1996). In contrast, low salinity water masses from rivers with low discharge rates persist at small temporal (hours) and spatial scales (2 – 11 km), and have horizontal and vertical structure that is proportionately more affected by wind stress and tidal forces (Gaston et al. 2006). The degree of mixing that occurs between fresh and marine waters in nearshore areas of coastal system likely depends on the momentum of river discharge. If the momentum of river discharge approximately equals the force of tidal currents, then the water column is vertically mixed by the interaction between riverine water and tidal forces. If the momentum of river discharge is less than the force generated by tidal currents, then the spatial extent of low salinity riverine waters in nearshore areas oscillates with the tide and turbulent mixing occurs. Furthermore, in shallow coastal systems like the Suwannee, Withlacoochee, and Weeki Wachee, wind-driven vertical mixing is also an important force to consider. Models of plume dispersion from the Ebro River (Spain) indicate that a discharge rate of 400 $m^3 s^{-1}$ is the threshold at which the river's momentum overcomes the effect of wind on the hydrodynamics at the river mouth to allow the evolution of a plume (Mestres et al. 2003). River discharge rates observed during this study were below this threshold, likely resulting in a highly turbulent environment. This lack of vertical structure would result in light conditions varying on spatial and temporal scales too finite to elicit a physiological

response from phytoplankton. Instead of light-shade acclimation, which occurs in stable light conditions (Tillmann et al. 2000), phytoplankton in well-mixed estuaries adapt to a mean light environment (MacIntyre & Cullen 1996). Phytoplankton growth rates would be similar in along salinity gradients, except when the interaction of wind and tide entrain algal stocks in areas with relatively higher nutrient availability (see Bledsoe 2003). Variability in the spatial distribution of algal biomass in coastal waters would be driven primarily by physical processes like conservative mixing rather than losses from grazing. Microzooplankton would not be able to adapt to changes in prey availability on the time scale they occur and so grazing rates would be relatively constant and reflect mean prey concentrations. Furthermore, a turbulent environment would also affect the feeding ecology of mesozooplankton assemblages dominated by *Acartia tonsa* because selection of ciliates increases with turbulence (Kiørboe et al. 1996). This preference would likely lead to greater regulation of microzooplankton production by *A. tonsa* in riverine coastal systems where water column vertical structure persists at small spatial and temporal scales.

Interactions between phytoplankton, microzooplankton and mesozooplankton in the Suwannee, Withlacoochee, and Weeki Wachee coastal systems may be best described by the Low Nutrient Model proposed by Putland (2005) for well-mixed or partially mixed river-dominated estuaries. This model suggests that in coastal areas impacted by rivers with low nutrient inputs, nutrient concentrations are low in the mid to high salinities and limiting phytoplankton growth. The phytoplankton community in smaller, riverine, coastal systems is dominated by picophytoplankton or nanophytoplankton due to the ability of small taxa to grow faster than large taxa in a low nutrient environment (Kiørboe 1993, Chisholm 1992). Phytoplankton growth rates and biomass are expected to peak in the river mouth to mid-field,

where light and nutrient availability are intermediate. Application of this conceptual framework to systems along the north central Gulf coast of peninsular Florida is likely appropriate because: (1) riverine nutrient inputs into systems are much lower (10 to 620 TN μg L^{-1}, 10 to 70 TP μg L^{-1}: Frazer et al. 1998, Frazer et al. 2007) than those from the Mississippi River (2.8 x 10^8 to 2.8 x 10^9 μg TN L^{-1}, 9.29 x 10^6 to 1.55 x 10^8 μg $P0_4$ L^{-1}: Lohrenz et al.1999) and (2) spatial variability in phytoplankton parameters observed in this study supports the predictions of high growth rates and accumulation of phytoplankton biomass in the river mouth and near field.

The major ecological implication of this model for Big Bend coastal systems is the expected dominance of the phytoplankton community by the picophytoplankton and nanophytoplankton. Cyanobacteria, chlorophytes, cryptophytes, and small dinoflagellates (e.g. *Katodinium*) are common and seasonally dominant in the river and nearshore regions of the Suwannee during periods of low river discharge (Quinlan & Phlips 2007, Bledsoe 2003). While the phytoplankton communities in the Withlacoochee and Weeki Wachee systems have yet to be characterized, the relatively lower nutrient concentrations in these coastal waters would likely lead to small taxa dominating the assemblage (Cloern & Dufford 2005). Because many mesozooplankton cannot effectively feed on phytoplankton cells smaller than 20 μm, carbon fixed by these primary producers must be first consumed by bacteria, heterotrophic nanoflagellates, and microzooplankton (i.e. the microbial food web) before it is made available to metazoan consumers (Azam et al.1983). Estimates of microzooplankton grazing impact in the three study systems support the hypothesis that the microbial food web plays a critical and major role, as microzooplankton grazers removed at least 51% of phytoplankton standing crops and 87% of primary production on a daily basis (Table 3-3 to 3-5). The few estimates of mesozooplankton grazing rates were very low, suggesting mesozooplankton grazing on

phytoplankton stocks was negligible in comparison to microzooplankton grazing. The importance of the microbial food web in the Suwannee, Withlacoochee, and Weeki Wachee systems has implications for carbon cycling, trophic ecology, and fisheries. Production by bacteria and small phytoplankton is likely to be a major source of energy transferred to higher trophic levels (Sherr & Sherr 1988). The apparent decoupling between grazing rates on primary producers and the abundance of mesozooplankton could be explained by feeding on microzooplankton (Olson et al. 2006, Batten et al. 2001, Kleppel et al. 1988). However, elongation of trophic pathways via the microbial food web and a link to mesozooplankton reduces the efficiency of carbon transport to higher consumers like juvenile fish (Ryther 1969). Therefore, in systems with low phytoplankton concentrations and/or those periodically dominated by small phytoplankton taxa, overall productivity is likely to be lower in comparison to coastal systems with higher riverine nutrient inputs.

The management implications of this study are three-fold. Firstly, conceptual models for large, river-dominated, coastal systems like the Mississippi River plume should not be generalized for management purposes to river-impacted coastal waters along the Big Bend Region without empirical validation. Secondly, because microzooplankton are major consumers of phytoplankton standing stocks in the Suwannee, Withlacoochee, and Weeki Wachee systems, managers need to incorporate microbial food web processes into models that predict how carbon cycles in these systems. Thirdly, increases in riverine nutrient loads will lead to higher concentrations of phytoplankton biomass at the river mouths. This has particular implications for systems with extensive seagrass beds because increases in phytoplankton abundance can reduce water clarity, shade seagrasses and result in their loss (Hale et al. 2004).

In conclusion, interactions between phytoplankton, microzooplankton and mesozooplankton in the Suwannee, Withlacoochee, and Weeki Wachee systems were not consistent with the conceptual model developed for coastal waters where large rivers dominate. Instead of peaking at the intermediate salinities, phytoplankton biomass and phytoplankton growth rates were highest near the river mouth in the Suwannee system. In the Withlacoochee and Weeki Wachee systems, the presence of turbulent water columns across salinity zones likely led to uniform phytoplankton growth rates across gradients of nutrients and light. Furthermore, microzooplankton grazing rates and abundance, and mesozooplankton total abundance were similar across the plumes in each of three systems. Although microzooplankton grazing rates did not vary significantly in space, grazing was an important loss factor for phytoplankton in each system. Nutrient over-enrichment of these coastal systems may disrupt the balance between algal production and its consumption by zooplankton grazers. This sort of perturbation will likely lead to increases in the concentration of particulate organic matter in the water column, with the potential to change food web dynamics (Cloern 2001) and cause the accumulation of phytoplankton biomass in the nearshore areas of the Suwannee, Withlacoochee, and Weeki Wachee systems.

Table 4-1. Published values of instantaneous maximum specific phytoplankton growth rates ($k \pm$ SE) and instantaneous microzooplankton grazing rates ($g \pm$ SE).

Environment	$k \pm$ SE	Range	$g \pm$ SE	Range	Issues	Reference
Suwannee River Plume, FL	0.99 ± 0.19	-0.40 – 2.50	0.92 ± 0.14	0.38 – 2.05		This Study
	1.56 ± 0.26	0.41 – 2.70	0.74 ± 0.14	0.11 – 1.41		Bledsoe 2003
	1.63 ± 0.11	-0.15 – 3.20	0.68 ± 0.07	0.00 – 2.04		Jett 2004
Withlacoochee River Plume, FL	1.55 ± 0.29	0.99 – 2.37	1.03 ± 0.27	0.39 – 1.67		This Study
Weeki Wachee River Plume, FL	0.89 ± 0.08	0.54 – 1.30	0.72 ± 0.07	0.34 – 1.16		This Study
Apalachicola River, FL	0.76 ± 0.07	0.08 – 1.92	0.71 ± 0.08	0.00 – 1.95		Putland 2005
Mobile Bay, AL						Lehrter et al. 1999
Bay	0.70 ± 0.14	-0.09 – 2.06	0.57 ± 0.07	0.05 – 0.96		
Bay Mouth	1.27 ± 0.19	0.25 – 2.87	0.97 ± 0.18	-0.03 – 2.44		
Offshore	1.62 ± 0.23	0.01 – 1.27	1.10 ± 0.20	-0.09 – 2.93		
Mississippi River Plume	1.13 ± 0.23	0.46 – 1.76	0.70 ± 0.19	0.28 – 1.39	a	Liu & Dagg 2003
Mississippi River Plume	1.11 ± 0.13	0.53 – 2.22	0.29 ± 0.05	-0.10 – 0.67		Strom & Strom 1996
Pensacola Bay, FL						Murrell et al. 2002
Upper Bay	1.02 ± 0.07	0.68 – 1.46	0.54 ± 0.05	0.26 – 0.81		
Lower Bay	1.00 ± 0.12	0.33 – 1.66	0.51 ± 0.10	0.08 – 1.25		
Santa Rosa Sound, FL	1.50 ± 0.16	0.50 – 2.10	0.80 ± 0.19	0.00 – 1.50		Juhl & Murrell 2005
Rhode River Estuary, MD	-	<0.1 – 1.80	-	0.00 – 1.50		Gallegos & Jordan 1997
Chesapeake Bay - Mid Bay	0.23 ± 0.06	0.03 – 0.41	0.24 ± 0.04	0.00 – 1.60		McManus & Ederington-Cantrell 1992
Estuarine	0.97 ± 0.07	-	0.53 ± 0.04	-		Calbet & Landry 2004
Coastal	0.67 ± 0.05	-	0.40 ± 0.04	-		
Oceanic	0.59 ± 0.02	-	0.39 ± 0.01	-		

a = mean (± SE) calculated by averaging across size fractions for a station and then finding the study's grand mean.

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BIOGRAPHICAL SKETCH

Kelly Lynn Robinson was born in 1982 in Tacoma, Washington to Harold and Adele Robinson. She and her younger sister, Katie, grew up in Washington and Colorado. Kelly attended Sweet Briar College, Virginia for her undergraduate education, and studied abroad for a semester at James Cook University, Townsville, Queensland (Australia). She graduated from Sweet Briar with a Bachelor of Science in biology (cum laude), and was the recipient of the Judith Elkins Prize for a senior graduating with a degree in the sciences. After graduating, she joined the research apprentice program at Friday Harbor Laboratories, University of Washington, where she was introduced by Dr. Jan Newton to the fields of biological oceanography and zooplankton ecology. While at Friday Harbor, Kelly was accepted into the Master of Science program at the Department of Fisheries and Aquatic Sciences, University of Florida (UF) under the advisement of Dr. Tom K. Frazer. During her tenure at UF, Kelly served on the executive committee of the department's graduate student organization, and was awarded "Outstanding Graduate Student of Year" for 2006. She graduated from UF with her MS degree in summer 2007. In her final year, Kelly was accepted into the PhD program in the Marine Sciences Department, University of South Alabama, and was awarded a Dauphin Island Sea Lab Fellowship. She plans to conduct her doctoral research at the Dauphin Island Sea Laboratory under the advisement of Dr. William M. Graham.