TEMPORAL AND SPATIAL VARIATION IN SESTON AVAILABLE TO OYSTERS AND THE CONTRIBUTION OF BENTHIC DIATOMS TO THEIR DIET IN THE DUPLIN RIVER, GEORGIA

by

MERRILEE THORESEN

(Under the Direction of Merryl Alber)

ABSTRACT

This study examined the quantity and quality of seston available to oysters and the contribution of benthic diatoms to their diets in the Duplin River, Georgia, and how it varied over different temporal and spatial scales. Average suspended particulate material (SPM), particulate organic carbon (POC), and chlorophyll *a* concentrations were significantly higher at the mouth (327.6 mg L^{-1}, 5.0 mg L^{-1}, 19.9 µg L^{-1}) than at the headwaters (93.4 mg L^{-1}, 1.6 mg L^{-1}, 9.4 mg L^{-1}). The quality of the seston was lower at the mouth with significantly higher carbon to nitrogen and POC to chlorophyll *a* ratios, but the seston was detrital-dominated throughout the inlet. Significant differences in seston characteristics were observed over tidal cycles at the mouth only, but all sites exhibited differences over lunar (spring tides greater than neap) and seasonal (spring and summer maxima) cycles. These differences were most consistent for SPM but were observed at some stations for other characteristics as well. Seston variability was greatest at the mouth at any temporal scale, but when compared within each site, the two sites closest to the mouth exhibited variability on tidal and lunar scales that was comparable to or even greater than seasonal scales, whereas at the up-river sites seasonal variability was the greatest. A significantly higher proportion of the diatoms were classified as benthic (pennate) at the headwaters as compared to the mouth in both seston (37% vs. 17%) and oysters (33% vs. 21%), although there was no evidence of selection for benthic forms. Microscopic observations of diatoms in seston and oysters were used to calculate the ^{13}C and ^{34}S values of oysters, assuming a diet of strictly diatoms, and these agreed well with observed values. This suggests that diatoms are a major food resource of oysters in this system and that benthic diatoms contribute to this pool. Oyster performance was evaluated at the study sites using shell height, dry tissue weight and condition index values. Oysters were significantly larger at the three up-river sites, which could be related to less than optimal feeding conditions and the high-energy physical regime near the mouth.

INDEX WORDS: *Crassostrea virginica*, salt marsh, estuarine food web, seston, benthic diatoms, Sapelo Island, Georgia coast, suspended matter, particulate matter, tidal creek

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INTRODUCTION

The eastern oyster (*Crassostrea virginica*) is the dominant suspension-feeding organism in many estuaries. Although the estuarine waters they inhabit are highly productive, the sessile habit of oysters requires them to adapt to temporal changes in the seston and utilize what is available to them in their local environment. Oysters encounter food that includes upland- and salt-marsh derived detritus, phytoplankton, and benthic microalgae, and stable isotope evidence from the field suggests they derive their carbon from a mixture of sources (Peterson et al.1985; Langdon & Newell 1990; Deegan & Garritt 1998). Recently several authors have suggested that resuspended benthic microalgae are important to the diet of oysters in shallow coastal environments, and may in fact be their primary food source (De Jonge &Van Beusekom 1992; Zurburg et al. 1994; Miller et al.1996; Riera & Richard 1996). However, this has not been directly quantified. This study focused on the quantity and quality of seston available to oysters in the Duplin River, Georgia, and examined the availability and utilization of benthic diatoms through microscopic observations and stable isotope analysis (^{13}C and ^{34}S) of seston, oysters and benthic microalgae.

Both the quantity and quality of seston are important determinants of the food resources of bivalves and these factors are both highly variable in estuaries. Working in two adjacent sub-estuaries of the Choptank River, Maryland, Berg and Newell (1986) found that the estuary with the higher seston concentration had larger oysters, providing support for the notion that increases in the quantity of seston increases oyster growth.

However, quality is also important, and it is well established that oysters preferentially select food particles from non-nutritive ones (Newell & Jordan 1983). In both eastern and Pacific oysters (*C. gigas*) the ability to sort food items decreases with increasing seston concentration (Urban and Kirchman 1992; Barille et al. 1997). Therefore, high concentrations of suspended particulate material (SPM) decreases the efficiency of particle selection, is deleterious to the feeding process and can ultimately lead to decreased growth (Barille et al. 1997). Seston in estuaries can vary over tidal and seasonal time scales. Fegley et al. (1992) found that in Great Sound, New Jersey, the material available to suspension feeders increased significantly from ebb to flood as resuspended bottom material increased. There is also seasonal variation in the seston with a decrease in phytoplankton during the fall and winter while terrestrial detritus increases due to seasonal inputs from senescent upland- and salt-marsh plants (Pomeroy et al. 1981).

In environments with extensive intertidal regions, benthic microalgae can contribute significantly to primary production and their production may even exceed that of phytoplankton and macroalgae (MacIntyre et al. 1996). This material is potentially available to benthic suspension feeders when it is resuspended, and it has been demonstrated that resuspension can contribute substantial amounts of chlorophyll *a* to the water column during changes of tide (Baillie & Welsh 1980). Resuspended microphytobenthos made up ~60% of the total phytoplankton community in the upper reaches of the Dollard in the Ems estuary, The Netherlands (De Jonge & Van Beusekom 1992). In addition, Shaffer and Sullivan (1988) found that 74% of the diatom taxa in the water column of Barataria Bay, Louisiana, was comprised of benthic pennate forms and concluded that the primary productivity of well-mixed shallow estuaries is greatly augmented by displaced benthic algae.

The importance of resuspended microalgae varies over tidal cycles, as described above, but also over lunar and seasonal cycles. The contribution of benthic microalgae to water column chlorophyll *a* is most important during spring tides when current velocities are highest. In the Bay of Marennes-Oleron, France, samples taken during neap tide had lower seston concentrations and most of the water column chlorophyll *a* was derived from phytoplankton, while samples taken during spring tide had higher seston levels and contained both phytoplankton and benthic microalgae (Zurburg et al. 1994). In the same estuary it was also observed that while benthic forms comprised 50% of the diatoms in the water column during spring tide they accounted for only 10% during neap tide (Prou 1991). Lukatelich and McComb (1986) observed that in the Peel-Harvey estuary, Australia, benthic microalgae achieved maximum biomass when phytoplankton blooms declined with sediment chlorophyll *a* levels greatly exceeding (e.g. 40 times) that of water column. They also determined that resuspension was seasonally influenced and was most significant during the summer when this system is exposed to prolonged periods of high winds.

There is some evidence that resuspended benthic microalgae are important to suspension feeders. In the Ems-Dollard estuary, resuspended benthic microalgae were estimated to provide ~50% of the available food to suspension feeders living on tidal flats (De Jonge and Van Beusekom 1992). In the Bay of Marennes-Oleron, Zurburg et al. (1994) suggested that resuspended microphytobenthos made a large contribution to the diet of Pacific oysters and mussels (*Mytilus edulis*), especially during the winter. In a later study Riera and Richard (1996) showed that the isotope signatures of Pacific oysters living adjacent to mudflats resembled benthic diatoms and inferred they were important in their diet. In a review of the ecological role of microphytobenthos in foodwebs, Miller et al. (1996) suggested that resuspension could potentially be a significant food source for suspension feeders and pointed out that stable isotope studies confirm its importance to the diet of many organisms. However, they also emphasized that little is known about the consumption of microphytobenthos in quantitative terms, and most studies have been conducted under laboratory conditions.

The work described here was conducted in the Duplin River estuary, which is located within the Sapelo Island National Estuarine Research Reserve (SINERR). The Duplin River is a tidal inlet that was well suited for this work for several reasons. First, extensive oyster reefs line the banks of the main channel of the river (Harris 1980). Second, there are abundant benthic algal resources. Approximately 80% of the watershed is intertidal salt marsh and mudflat and this large intertidal area is known to support highly productive populations of benthic microalgae (Pomeroy 1959; Pomeroy et al. 1981). In an extensive study of benthic microalgae on Sapelo Island, Williams (1962) determined that pennate diatoms comprised 75 to 93% of the total benthic algal biomass, that 90% of these diatoms belonged to one of four genera (*Cylindrotheca, Gyrosigma, Navicula*, or *Nitzschia*), and that the number of cells increased ten-fold in the winter. Furthermore, Stevens (1983) made several interesting observations with regard to benthic diatoms in relation to oyster reefs in Flume Creek, a tidal tributary to the Duplin River: 1) reef associated sediment contained almost twice as many benthic diatom cells as non-reef sediment, 2) twice as many diatoms were found in suspension over reefs, and 3) a major component of the phytoplankton found over the reefs was *Navicula*, a benthic diatom. Third, the tidal range is approximately 2-3 m, so there is ample tidal energy and the physical conditions exist that could lead to resuspension during semi-diurnal changes of tide. It is worth noting that in this system, where tidal asymmetry results in greater ebb velocities over flood, oysters exhibit a slight statistical preference to orient with the ebb-current direction, which optimizes the delivery of resuspended food (Frey, Basan and Smith 1987).

The physical movement of water in the Duplin is well-documented. There are four tidal prisms along the 12.5 km length of the Duplin River, with the lower-most water mass moving from the river to Doboy Sound during the ebb tide and the uppermost prism moving completely from the river and flooding the adjacent salt marsh during flood tide (Ragotzkie & Bryson 1955). There is no permanent stratification of the water column, because there is no riverine input, so the tidal reaches are basically separate water masses with little exchange (Ragotzkie & Pomeroy 1957; Imberger et al. 1983). We previously sampled oysters in the area and our data showed a difference in oyster shell height in the three tidal reaches in the channel (the fourth is in small tidal creeks and on the salt marsh at high tide), with larger oysters at the upstream sites. The Duplin therefore gave us an opportunity to study the importance of resuspended benthic microalgae across a gradient of tidal energy.

In this dissertation we first evaluated the seston available to oysters, in terms of both quantity [suspended particulate material (SPM), particulate organic carbon (POC), chlorophyll *a* concentrations] and quality [carbon to nitrogen ratio (C:N), percent phaeopigment, POC to chlorophyll *a* ratio], and how it varied over spatial scales (i.e., at five sites along the length of the Duplin River) and different temporal scales (tidal, lunar, seasonal) over the course of two years (June 2000 through June 2002) (Chapter 1). In Chapter 2, we examined the contribution of benthic diatoms to the seston over oyster reefs and to the diets of the oysters at the mouth and the headwaters of the Duplin River. Analysis of these data focused on seasonal differences in chlorophyll *a* concentrations in both the seston and the sediment and direct observations of the diatoms in the seston and oysters to determine the proportion that were benthic. Stable isotopic signatures of seston and oysters were also used to further analyze what the oysters might be assimilating. Chapter 3 presents the shell heights, dry tissue weights and the condition of oysters at all of the study sites over the course of the study. These data were then related to our observations of the spatial and temporal differences in the seston available to the oysters in the different reaches of the Duplin River.

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CHAPTER 1

SESTON OVER OYSTER REEFS: OBSERVATIONS OVER DIFFERENT TEMPORAL AND SPATIAL SCALES IN THE DUPLIN RIVER, GEORGIA, USA[1]

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[1] Thoresen, M. and M. Alber. To be submitted to *Estuarine and Coastal Shelf Science*

Introduction

Bivalve molluscs, the dominant benthic suspension-feeders in many estuaries, derive their nutrition from suspended particulate food resources that vary greatly in both quantity and quality. Variation in the seston available to bivalves arises from the interaction of numerous biological and physical factors that occur over both space and time. Significant changes in the quantity and quality of the seston have been documented over short time scales (hours) (Fegley et al., 1992; Rheault & Rice, 1996; Smaal & Haas, 1997) and small distances (m) (Judge et al., 1993; Wilson-Ormond et al., 1997), as well as over longer time periods (annual) (Widdows et al., 1979; Berg & Newell, 1986; Cranford & Hill, 1999; Huang et al., 2003) and greater distances (km) (Peterson et al., 1985; Smaal et al., 1986; Ruckelshaus et al., 1993; Gardner, 2000). Given these types of observations, it is evident that a thorough examination of seston availability to bivalve consumers must encompass all of these different scales of variability.

Temporal variation in suspended particulate material can arise from both predictable cyclic events such as tidal cycles, lunar phases (spring vs. neap tides), and seasonal patterns, or from non-cyclic events such as wind-driven mixing or changing freshwater inflows due to climate change or human activities. A number of researchers have documented changes in the quantity and the composition of seston within a tidal cycle, although both the magnitude and the timing of these changes varies among estuaries. In an examination of seston over mussel (*Mytilus edulis*) and cockle beds (*Cerastoderma edule*) in the Oosterschelde estuary, The Netherlands, Smaal and Haas (1997) observed increases in all seston parameters (suspended particulate material (SPM), particulate organic carbon (POC), and chlorophyll *a*) both before and after low slack water, with significantly higher chlorophyll *a* concentrations during flood as compared to ebb water. In Canary Creek salt marsh, Delaware Bay, biological components of the seston (chlorophyll *a*, bacteria, heterotrophic nanoflagellates) available to ribbed mussels (*Geukensia demissa*) were significantly greater during high flood tide and high slack water as compared to ebb tide (Huang et al., 2003). In contrast, Roegner (1998) observed maximum chlorophyll *a* concentrations during ebb flows over dense assemblages of infaunal clams (*Mya arenaria*) in Eel River estuary, Nova Scotia. Although the details of their findings may differ, a number of researchers have found that the variation in seston observed in one tidal cycle can exceed that observed over an entire year (Fegley et al., 1992; Smaal & Haas, 1997; Wilson-Ormond et al., 1997). In terms of the lunar cycle, higher concentrations of seston are generally observed during spring tides as compared to neap tides (Ward, 1981; Zurbug et al., 1994; Hawkins et al., 1996; Urrutia et al., 1996; Barille et al., 1997; Grabemann & Krause, 2001)**.** In the Bay of Marennes-Oleron, France, Barille and co-workers (1997) observed significantly higher levels of suspended particulate material, particulate organic material and chlorophyll *a* during spring as compared to neap tides, although the overall quality (as indicated by carbon to nitrogen and carbon to chlorophyll *a* ratios) did not vary. The increase in seston during spring tides was attributed to increased current velocities and enhanced shear forces acting on the bottom material and causing resuspension. Seasonal differences in the seston are well documented: both the quantity and quality of seston generally increases during spring and summer months due to blooms of phytoplankton, which are accompanied by decreasing carbon to nitrogen and carbon to chlorophyll *a* ratios (Widdows et al., 1979; Cadee, 1982; Berg & Newell, 1986; Cranford & Hill, 1999; Toro et al., 1999; Gardner, 2000). Climatic events can also lead to changes in the seston. In a study of daily variability in seston available to clams (*Mercenaria mercenaria*) on an intertidal sandflat in Cape Henlopen, Delaware, Bock and Miller (1994) found that wind-induced resuspension led to an increase in the quantity of suspended particulate material and a decrease in percent organic matter due to the dilution of organic particles with inorganic particles. Rainfall regimes also have an effect, with periods of high flooding having overall higher concentrations of suspended particulate material than those observed during low-flushing periods (Bianchi & Argyrou, 1997). These changes affect quality as well: Richard et al. (1997) found that flooding periods brought increased amounts of "fresh" terrestrially-derived detrital material that was rich in bacterial biomass and had a lower carbon to nitrogen ratio than the aged, refractory detritus that was predominant during low-flow periods.

Spatial variation in the seston of estuaries can result from differences in local habitat, differences along salinity gradients, or differences among watersheds. In the shallow, well-mixed estuary of Padilla Bay in Puget Sound, Washington, significant differences in the quality and δ^{13}C signature of seston between adjacent neritic and eelgrass habitats were attributed to differences in the dominant autotrophs that were contributing to the pools of POC at each location (Ruckelshaus et al., 1993). Other researchers have used stable isotopes of carbon to examine how the sources of POC vary along the length of an estuary. In the Bay of Marennes Oleron estuary in France, seston from the upper reaches of the estuary had δ^{13}C signatures that resembled terrestrial detritus (-29.2 to –27.4 ‰), particularly during times of high freshwater inflows, whereas in the lower reaches of the estuary the carbon isotopic values were similar to marine phytoplankton (-21.8 to –19.5 ‰) (Riera & Richard, 1996). In Maine, Incze and co-workers (1982) looked at the carbon isotope values of seston from along the length of two estuaries and identified major differences that were attributable to hydrology. In the Sheepscott estuary there was a systematic landward decrease in the $\delta^{13}C$ signature of the POC due to increased inputs of terrestrially-derived detritus, whereas in the Damariscotta there was no evident trend and isotope values were indicative of marine sources of POC. They attributed these differences to the fact that, in contrast to the Sheepscott estuary, the Damariscotta lacked a significant riverine freshwater source. Differences in seston have also been attributed to patterns of land use surrounding estuaries. In New South Wales, Australia, Paterson and co-workers (2003) examined seston quality and quantity in two estuaries and compared drainages within each estuary that had different levels of development. The areas with more development had elevated levels of nutrients and chlorophyll *a* as well as higher concentrations of particulate material. The carbon to chlorophyll *a* ratios were significantly different among all the drainages, but the most industrialized area had the lowest ratio, suggesting a higher contribution of phytoplankton to the particulate organic matter.

There are numerous studies that have examined seston variability in relation to bivalves over different temporal and spatial scales. However, few studies have closely examined how the significance or relative importance of the different temporal scales (tidal, lunar, seasonal) can vary among different locations within an estuary. Berg and Newell (1986) examined seston variability over seasonal scales in two sub-estuaries of the Choptank River, Maryland, and related seasonal trends at both sites to fluctuations in riverine discharge and runoff as well as to changes in biological activity. Although the quality of the seston was similar between the two sites, one had consistently higher levels of seston and this was attributed to differences in the drainage patterns of the two basins. Roegner (1998) examined tidal variability at four different locations within the Eel River estuary, Nova Scotia and identified steep horizontal gradients in chlorophyll *a* due to tidally-driven circulation and local algal productivity. These findings were utilized to investigate the potential for seston depletion over dense beds of clams (*Mya arenaria*). Although both of these studies examined seston variability in relation to bivalve consumers on both temporal and spatial scales, each limited their focus to one temporal scale (seasonal or tidal) and did not compare the magnitude of the temporal variation in the seston among different locations within the estuaries they studied. The goal of the current work was to examine how the seston available to eastern oysters (*Crassostrea virginica*) varies over temporal (tidal, lunar, seasonal) scales and how the magnitude of variation at each of these time scales compares among different locations within an estuary.

This study was conducted in the Duplin River estuary, Georgia. The Duplin River is a 12.5 km tidal inlet on Sapelo Island, Georgia, that empties into Doboy Sound (Figure 1.1). The watershed of the Duplin River is approximately 80% intertidal salt marsh (dominated by *Spartina alterniflora*) and mudflat and 20% permanently subtidal (Chalmers, 1997). The Duplin River is primarily influenced by tidal energy and is considered to be a macrotidal system, with a tidal range of 2-3 m. The physical movement of the water in the river is well-documented. There are 4 tidal prisms along the length of the inlet, with the uppermost prism moving completely from the river and flooding the adjacent salt marsh during flood tide and the lower-most prism moving from the river to Doboy Sound during ebb tide (Ragotzkie & Bryson, 1955). There is no riverine input and the tidal reaches essentially behave as separate water masses with little exchange between them (Ragotzkie & Pomeroy, 1957; Imberger et al., 1983). There is no permanent stratification and the water column is generally well-mixed. At the headwaters of the Duplin River potential sources of particulate material include inputs from the marsh surface (e.g., *S. alterniflora* detritus, benthic microalgae, eroded surficial sediments), the water column (phytoplankton, bacteria, etc.) and the bottom (inorganic silt and sand particles, sediment-associated organic matter, benthic microalgae, detritus). In contrast, the mouth of the Duplin is adjacent to Doboy Sound, which receives numerous inputs of particulate material from nearshore water of the Atlantic Ocean and the Altamaha River, as well as the extensive salt marshes and tidal creeks that are found on the littoral fringes of the Sound. These separate sources of particulate material, taken together with the fact that the water masses remain separate, suggests that there could be spatial differences in the suspended particulate material along the length of the inlet from the headwaters to the mouth. We were therefore interested in determining whether variation that arises from differing temporal scales (tidal, lunar, and seasonal) might have a varying effect in the headwaters, middle-reaches, and mouth of the Duplin River.

Methods

Study sites and sampling regime

Seston was sampled from above oyster reefs at 5 sites along the length of the Duplin River, which is located in the Sapelo Island National Estuarine Research Reserve (SINERR) (Figure 1.1). At the two sites closest to the mouth, Marsh Landing (ML) and

Jack Hammock (JH), the oyster reefs, including both live and dead shell cover, extend from the edge of the *S. alterniflora* at the upper edge of the intertidal zone down to the edge of the permanently submerged sub-tidal region. The type of formation found at these two sites is typical of the oyster reefs that line the edge of the main channel of the Duplin River. At the next two sites, Kenan Field (KF) and Hunt Camp (HC), the oysters form patches or mounds that are interspersed across the intertidal mud and sandflats that extend from the edge of the *S. alterniflora* zone out into the main channel of the river. At the furthest up-river site, Flume Dock (FD), the oyster reef is similar to those observed at the mouth but it is located at the mouth of a tidal creek so that during flood tide some of the water that runs along the length of the main channel is diverted across the reef and into the tidal creek.

During the two-year study period (June 2000 through June 2002) sampling was conducted at approximately 5-week intervals to allow for alternating spring and neap tides (full or new and quarter lunar phases, respectively), for a total of 20 observations at each site. In a previous study, Stevens (1983) observed maximum and minimum seston concentrations during high-slack and mid-ebb water, respectively, in Flume Creek, a tidal tributary near the mouth of the Duplin River. During the first year of this study we therefore sampled water during both late flood/high-slack water and mid-ebb water. In the second year, seston was only sampled during mid-ebb water. The sampling regime outlined above allowed us to look at spatial variation along the length of the tidal inlet and temporal variation on tidal, lunar, and seasonal time scales at each site (Table 1.1).

Seston analyses

Water for seston analyses was pumped using a Cole Parmer MasterFlex® peristaltic pump (Vernon Hills, Illinois). Either end of the PharMed® latex tubing (Maple Plain, Minnesota) that ran through the pump apparatus was fitted to nalgene tubing (I.D. 0.8 cm) using brass adaptors. The intake tube was fed through an approximately 3 m long, 5-cm diameter PVC pipe and out through a hole drilled about 10 cm from the end. A dive weight (~2.27 kg) was attached to the end of the pipe so it could be deployed down through the water column and maintained in a stable and upright position while water was pumped from approximately 10 cm above the oyster reefs. At the outflow end an additional length of nalgene tubing was spliced to the PharMed® latex tubing and was used to fill replicate acid-washed 2-L nalgene bottles. Sample bottles were kept on ice and in the dark until they could be processed (within 2 h). In the laboratory a known volume (25-200 ml, depending on seston concentration) was filtered onto pre-combusted Whatman 25 mm GF/F filters (nominal pore size 0.7 µm) for determination of the concentration of suspended particulate material (SPM) (dry weight at 60°C), CN content (Carlo Erba Flash EA 1112 Series NC Soil Analyzer), and chlorophyll *a*/phaeopigments (fluorometric analysis of acetone-extracted samples, Parsons et al., 1984). Samples for POC/PON and chlorophyll *a*/phaeopigment analysis were frozen and transported at 0°C and stored at -70°C until they were processed. Samples for SPM analysis were transported dry and at room temperature prior to being placed in a drying oven. For each observation at each site two replicate water samples were taken, and for each parameter analytical replicates were taken from each bottle as follows: SPM (3 filters), POC/PON (2 filters), and chlorophyll *a*/phaeopigment (3 filters).

Data analyses

Statistical comparisons of seston data (measures for both quantity and quality) were made on all of the spatial and temporal scales that were examined in this study. To compare seston among sites (spatial comparison) we used the mid-ebb water data from all twenty sampling trips, including 11 spring, 8 neap tides and one intermediate tide (Table 1.1). For the temporal comparisons (tidal, lunar, seasonal) sample size varied because there were a different number of observations made for each of the different scales we examined. To compare tidal stage we used both high-slack water and mid-ebb water data from the first ten sampling trips. For the spring vs. neap tide comparison we used mid-ebb water data only from 11 spring tides and 8 neap tides (the one intermediate tide that was sampled in December 2000 was excluded from this analysis). For the seasonal comparison we used only mid-ebb water data but included all twenty sampling trips, encompassing both spring and neap tides for each season (Table 1.1).

Analysis of variances were performed to examine both differences among sites and seasonal variation within each site, and Duncan's least significant differences procedures were used for post hoc analyses. Independent Student T-Tests were used to compare seston characteristics during spring and neap tides within each site. Paired Sample Student T-Tests were used to compare seston characteristics during high-slack water and mid-ebb water for all of the data combined across the five sites. Once significant differences were detected in the combined data then this same analysis was repeated for each individual site.

General linear models were run to see if the different temporal scales were significant predictors of seston quantity and quality within each site. This method was used because the number of observations at each temporal scale was unequal (i.e., was not balanced) and the model controls for this inequality. The models were run for each site for each or the five seston parameters (SPM, POC, Chlorophyll *a*, C:N, percent phaeopigment). Each model provided: 1) an overall R-squared value that can be used to assess the strength of the predictive relationship between all three temporal scales and the seston parameters, 2) individual p-values for each of the temporal scales and for the interactions among them so that each could be individually evaluated in terms of their significance in the model, and 3) predicted standard deviations for each parameter at each temporal scale, which could be used to compare the amount of variability that could be attributed to each time scale. Due to the large variability in the suspended particulate material (SPM), these data were logarithmically transformed to meet the assumption of homogeneity of variance prior to performing statistical analyses. All statistical analyses were performed using SPSS for PC (SPSS Inst., Inc. 2000) except for the Paired Sample Student T-Tests and the General Linear Model Procedures, which were performed using SAS for PC (SAS Inst., Inc. 2000).

Results

Overall summary of seston quantity and quality

For the purpose of this study the concentration of SPM, particulate organic carbon (POC) and chlorophyll *a* were used to assess seston quantity whereas organic carbon to nitrogen ratio (C:N), and percent phaeopigment (percent of the total concentration of chlorophyll *a* and phaeopigment that is phaeopigment) were used to assess seston quality. In addition, POC to chlorophyll *a* ratios were used to examine the relative contribution of living vs.

non-living (i.e., detrital) material to the pool of POC. POC to chlorophyll *a* ratios that are less than 100 indicate a living phytoplankton-dominated POC pool whereas ratios over 100 indicate a detrital-dominated pool. (Zeitzschel, 1970).

To examine overall seston patterns in the Duplin River we combined our observations of seston at five-week intervals over two years and across the five sites. Overall, SPM concentration was high and variable, and averaged 194.8 ± 255.0 mg L^{-1} (mean ± s.d.) (Table 1.2). POC concentration averaged 3.0 ± 2.7 mg L^{-1} and the ratio of particulate organic carbon to particulate organic nitrogen was 9.1 ± 4.3. Overall, POC was a very small proportion of SPM suggesting that there is a large amount of inorganic material contributing to the total seston pool. Average chlorophyll *a* concentration was 12.6 ± 7.7 µg L^{-1} and percent phaeopigment was 29% ± 18. The POC to chlorophyll *a* ratio was high (204 ± 93). This high ratio indicates that the POC pool was clearly detrital-based and provides further evidence that the seston in the Duplin River is low quality.

Spatial variation in the quantity and quality of seston

There were clear differences in the quantity of seston (SPM, POC, chlorophyll *a*) among the 5 study sites, with a gradient from lower to higher concentration from the headwaters to the mouth of the Duplin River (Table 1.3; Figure 1.2). Overall, there was approximately a three-fold increase in SPM concentration (93.4 ± 85.2 mg L^{-1} to 327.6 ± 321.8 mg L^{-1}), a three-fold increase in POC concentration (1.57 ± 1.00 mg L^{-1} to 5.03 ± 2.94 mg L^{-1}) and a two-fold increase in chlorophyll *a* concentration (9.42 ± 5.59 µg L^{-1} to 19.90 ± 8.80 µg L^{-1}) from the headwaters to the mouth. The five stations fell into three groups in terms of SPM, with the two sites closest to the mouth having significantly higher SPM concentrations than those observed at the three up-river sites ($p < 0.001$) and the furthest up-river station having a significantly lower SPM concentration than the two middle-reach sites ($p = .011$) (Figure 1.2A). It should be noted that very high SPM concentrations (> 1200 mg L^{-1}) were observed at the two sites closest to the mouth, during a rain event in May 2002 however SPM concentrations were still significantly higher when these data were excluded from the analysis. The five stations also fell into three groups in terms of POC and chlorophyll *a* concentrations, but in this case the mouth had significantly higher concentrations as compared to the next up-river station, and both of these sites were significantly higher than the three up-river sites ($p < 0.001$) (Figure 1.2B&C). Given the similar patterns of POC and chlorophyll *a* concentration, we did a regression analysis to determine whether there was a difference in the relationship between POC and chlorophyll *a* between the two sites at the headwaters and the two sites at the mouth (Figure 1.3). Although the slopes were different (a given amount of POC was associated with a higher concentration of chlorophyll *a* at the headwaters), chlorophyll *a* was responsible for a similar amount of variation in POC at either end of the tidal inlet (R^2 mouth = 0.57 vs. R^2 headwaters = 0.59).

In terms of seston quality there was a consistent increase in C:N ratio from the headwaters (8.1) to the mouth (10.0) as well as in percent phaeopigment (from 27% to 40%) and POC to chlorophyll *a* ratios (from 157 to 248) (Table 1.3; Figure 1.4) all of which are consistent with a greater detrital contribution to the seston. Differences among sites were similar to those observed in terms of seston quantity, with the two sites closest to the mouth having significantly greater C:N ratios, higher percent phaeopigment and higher POC to chlorophyll a ratios than the three up-river sites ($p < 0.001$). In terms of phaeopigment, the middle station (KF) had a significantly higher percent phaeopigment as compared to the furthest up-river station (FD) ($p = 0.005$).

Tidal variation in the quantity and quality of seston

Seston quantity exhibited very little variation between late flood/high-slack and mid-ebb water at most of the sites (Table 1.4). The only significant differences were observed at the mouth of the tidal inlet (ML), where both SPM and POC concentration were significantly greater during late flood/high-slack water as compared to mid-ebb water, 390 ± 308.3 mg L^{-1} vs. 215.3 ± 152.9 mg L^{-1} ($p = 0.002$) and 7.00 ± 3.46 mg L^{-1}vs. 4.66 ± 2.38 mg L^{-1} ($p < 0.0001$), respectively (Figure 1.5). In terms of seston quality, there were no significant differences in either C:N ratio, percent phaeopigment, or POC to chlorophyll *a* ratios between late flood/high-slack and mid-ebb water (Table 1.4; Figure 1.6).

Lunar variation in the quantity and quality of seston.

Seston quantity was generally greater during spring tides as opposed to neap tides. SPM concentration was significantly higher during spring tides at all but the most up-river station (FD). POC and chlorophyll *a* concentrations were also significantly greater during spring tide at two sites (JH and KF) (Table 1.5, Figures 1.7-1.9; p-values are indicated on the figures). AT KF average POC concentration was 25% higher and chlorophyll *a* concentration was 37% higher during spring tide and at JH, POC and chlorophyll *a* were 39% and 47% higher, respectively.

There were some differences in the quality of the seston between spring and neap tides, however there was no consistent trend to suggest that the lunar strength of the tide had a clear and predictable influence on seston quality. The only significant difference in the C:N ratio of the seston was observed at the headwaters (FD), where C:N was significantly lower (7.66 ± 2.06) during spring tides as compared to neap tides (8.73 ± 1.62) ($p = 0.013$; Table 1.5; Figure 1.10E). There were no significant differences in the percent phaeopigment between spring and neap tides, however at all of the sites percent phaeopigment was 6-8% higher during spring tides (Table 1.5; Figure 1.11A-E). There were no consistent patterns in POC to chlorophyll *a* ratios when comparing spring and neap tides (Table 1.5).

Seasonal variation in the quantity and quality of seston.

There were significant seasonal differences in the quantity of seston at most sites but the patterns varied from one location to another (Table 1.6; Figures 1.12-1.14; post-hoc analyses p-values for the seasonal differences are provided in Appendix I, Tables I.1-I.6). At ML SPM concentration was significantly greater in the spring as compared to the summer (Figure 1.12A); at JH it was significantly greater in the winter as compared to the summer and fall (Figure 1.12B); at HC it was significantly greater in the summer and winter as compared to the fall and spring (Figure 1.12D); and at FD it was significantly greater during the spring and summer as compared to the fall (Figure 1.12E). For POC significant seasonal differences were observed at the four sites up-river from the mouth, where POC concentration in the summer was always significantly greater than in the winter (Figure 1.13B-E). These differences were also reflected in chlorophyll *a* values, where concentrations in the summer were significantly greater than all other seasons at the two most up-river sites (Figure 1.14D-E). Other seasonal changes were observed in terms of both POC and chlorophyll *a* but these varied from site to site.

The quality of the seston also exhibited seasonal differences at each of the sites, although again they were not consistent. Moreover, for any given site the patterns were not consistent from one parameter to another. The only sites where C:N was significantly different among seasons was at KF and HC. At KF it was higher in the fall and spring as compared to the other seasons (Table 1.6; Figure 1.15C) and at HC it was higher in the summer than the winter (Table 1.6; Figure 1.15D). At the mouth (ML) and the next two up-river sites (JH and KF), percent phaeopigment was significantly greater in the fall as compared to the other seasons; at HC it was significantly lower in the spring as compared to all other seasons; and at the most up-river site (FD) it was significantly lower in the spring than the fall and winter (Table 1.6; Figure 1.16). There were no significant seasonal differences in POC to chlorophyll *a* ratios, but in general at most of the sites the lowest ratios were observed during the spring and summer (Table 1.6; Figure 1.17).

Influence of the different temporal scales on seston parameters

General linear models (GLM) were used to examine the influence of the three different temporal scales on the measures of seston quantity and quality within each site. The R-squared values for the overall model and the individual p-values for each temporal scale and their interactions are provided in Table 1.7. Seasonal time scales were significant predictors of seston quantity and quality in almost every model, although tidal and lunar scales and their interactions with seasonal cycles were also important in many cases. The only cases where there were no significant relationships with any time scales were for C:N ratios at KF, JH, and ML. These results suggest that seston parameters can be predicted based on tidal, lunar and seasonal cycles, although there are clearly other sources of variability as well.

Comparison of the different scales of variability

Standard deviations were used to compare the variability among the 5 sites (that is, to determine which sites exhibited the greatest dispersion for any particulate parameter) (Table 1.3). When all observations were combined for the duration of the study the standard deviations of all measures of seston quantity (SPM concentration) were greater at the mouth than the headwaters: the standard deviations of SPM were three to four-fold greater at the mouth (JH & ML) than at the headwaters; those of POC were three-fold greater; and those of chlorophyll *a* were one and a half to two-fold greater. Moreover, these spatial differences in the standard deviation of seston quantity held for all temporal scales. That is, the standard deviation of SPM concentration are at least 2 and up to 12 times greater at the mouth as compared to the headwaters when stations are compared over different tidal scales (i.e., at late flood/high-slack or mid-ebb water, Table 1.4); lunar scales (i.e., at spring or neap, Table 1.5); or within any season (Table 1.6). For POC concentration the standard deviations were 2 to 3 times greater over lunar and tidal scales and from 11 to 29 times greater within the seasons at the mouth as compared to the headwaters, except during the summer when the standard deviations were the same at both locations. For chlorophyll *a* the standard deviations were actually larger at the headwaters as compared to the mouth over tidal scales and during the summer, but during the other three seasons they were greater at the mouth. There were no obvious differences in the standard deviation of chlorophyll *a* over lunar scales. The standard deviations of the measures of seston quality (C:N and percent phaeopigment) were generally comparable throughout the river, although at JH the standard deviation for the C:N ratio was two-fold greater than at any of the other sites. Given these observations, the picture that emerges is of wide variability in seston quantity at the mouth as compared to the headwaters, at all temporal scales, but no real spatial differences in terms of seston quality.

Next, we examined differences in the variability of the different temporal scales within each site. We did this by ranking the predicted standard deviations from the GLM procedures (Table 1.8). (We did not rank observed standard deviations because the number of observations varied for each temporal scale, but the general linear model takes this into account.) For the three up-river sites seasonal variability in all seston parameters (SPM, POC, chlorophyll *a*, C:N and percent phaeopigment) was the greater than lunar or tidal variability. At the two sites closer to the mouth the comparison was not as straightforward. At ML and JH, SPM variability was comparable on both lunar and seasonal time scales, whereas POC was most variable over lunar time scales at ML and tidal time scales at JH. At ML, all of the other parameters exhibited the greatest amount of variability over seasonal time scales. However, at JH chlorophyll *a* exhibited the greatest amount of variability over tidal cycles, C:N exhibited the most variability over lunar cycles and percent phaeopigment exhibited the most variability over seasonal cycles.

To summarize our findings on seston variability in the Duplin River, the most significant trend was observed over spatial scales. Regardless of temporal scale, we consistently observed larger standard deviations for SPM, POC, and chlorophyll *a* at the mouth as compared to the headwaters of the Duplin River (Table 1.3; Figure 1.2). However, there were no clear spatial trends in the variability of seston quality (C:N and percent phaeopigment). Within each site we observed the greatest amount of variability in terms of both seston quantity and quality over seasonal cycles at the three up-river sites. At the two sites closest to the mouth both lunar and tidal variability were either comparable or exceeded seasonal variability for several of the parameters (SPM & POC at both sites; chlorophyll *a* and C:N at JH), suggesting that these other temporal scales are also important sources of variation at these locations.

Discussion

General overview

The seston concentrations observed in this study are higher than other reported values for southeastern salt marsh estuaries. Seston concentrations in the Duplin River averaged 194.8 ± 255.0mg L^{-1} and ranged from 13.7 to 2260.0 mg L^{-1}. Working in a tidal creek tributary of the Duplin River, Odum and De La Cruz (1967) reported mean concentrations of suspended particulate "detritus" that were approximately 1/4th of this value (48.8 mg L^{-1}) when combined across tidal, lunar and seasonal observations. This is likely due to the fact that they were in a tidal creek and not in the main channel of the Duplin River. Other observations of SPM concentrations in the estuarine waters of Georgia are limited, but Oertel and Dunstan (1981) observed highly variable SPM in St. Catherines and Ossabaw Sounds and reported a range of 10 to over 400 mg L^{-1}. Galstoff and Luce (1930) observed SPM concentrations in coastal Georgia that ranged from 10.7 to 913.0 mg L^{-1} with an average of 93.7 ± 155.7 mg L^{-1}. In reference to their observations of SPM, these researchers noted that in coastal Georgia, "We cannot speak about normal conditions in a region where wide fluctuations are the rule rather than the exception." In a salt marsh tidal channel in Kiawah Island, South Carolina, Ward (1981) observed SPM concentrations ranging from 6 to 200 mg L^{-1} and in North Inlet, South Carolina, Hutchinson and co-workers (1995) observed an average concentration of 169.1 mg L^{-1}.

The POC concentrations observed in this study were much lower and less variable as compared to SPM. Our overall mean POC concentration of 3.0 ± 2.7 mg C L^{-1}agrees well with the 3.2 ± 1.4 mg C L^{-1} reported by Chalmers and co-workers (1985) (when combining their data across seasons and between the upper lower Duplin River water masses). In the North Inlet estuary, South Carolina, Williams and co-workers (1992) observed POC concentrations over the course of an annual cycle in a tidal creek that ranged from 0.63 to 5.3 mg C L^{-1} and our average POC concentration was within this range. In the Ogeechee River estuary in coastal Georgia, average POC concentration was 1.31 ± 0.46 mg C L^{-1} (Alber, 2000), which was approximately half the amount of POC we observed here. The lower POC concentrations in the Ogeechee River could be related to the fact that it is a riverine estuary as compared to the tidal creek systems considered here.

The chlorophyll *a* concentrations we observed were also comparable to those reported for other tidal inlets in southeastern salt marshes. Our observations averaged 12.6 ± 7.7 µg L^{-1}, whereas Ragotzkie (1959), also working in the Duplin River, reported average values of 12.9 ± 7.6 µg L^{-1}. It should be noted that our method of measuring chlorophyll *a* utilized fluorometrics and an acidified correction for interference from phytopigment degradation products, whereas Ragotzkie utilized spectrophotometrics without an acid correction, which may have overestimated chlorophyll *a* concentrations. Over two years in several creeks in North Inlet, South Carolina, Wetz and co-workers

(2002) observed chlorophyll *a* values that ranged from approximately 3 to 23 µg L^{-1} and our observations are consistent with the range reported in this study. Other studies that provide data on chlorophyll *a* concentrations in coastal Georgia have generally been conducted in fluvial inlets with significant freshwater inflows (Alber, 2000; Verity, 2002) or along transects across sounds and out onto the continental shelf with comparisons focused on inner vs. outer shelf water masses (Verity et al., 1993; Yoder et al., 1993). In the Skidaway River estuary, Georgia, Verity (2002) reported chlorophyll *a* concentrations that ranged from approximately 2.5 to 27.5 µg L^{-1} and in the Ogeechee River estuary, Georgia, Alber (2000) reported an average chlorophyll *a* concentration of 15.2 ± 5.1 µg L^{-1}.

Seston quality in the Duplin River was generally lower than what has been observed in other estuaries (Sutcliffe, 1972; Incze & Roman, 1983; Cifuentes et al., 1988; Dame et al., 1989; Zurburg et al., 1994; Cranford & Hill, 1999). POC made up a small proportion of the seston pool and POC:chlorophyll *a* ratios were high. In a similar study of seston over oyster reefs in Galveston Bay, Texas, high C:N ratios and POC to chlorophyll *a* ratios were attributed to the fact that phytoplankton comprised a small portion of the organic matter available to oysters (Wilson-Ormond et al., 1997). Our average observed C:N ratio (9.1 ± 4.3) was higher than the 6.4 to 6.6 reported by Verity (2002) in the Skidaway River estuary and comparable to the 8.8 ± 1.7 reported by Alber (2000) in the Ogeechee River estuary. The percent phaeopigment, which was the proportion of the total chlorophyll *a* and phaeopigment pool that was phaeopigment, was 29% ± 18, which again is comparable to that observed in the Ogeechee River estuary (32%) (Alber, 2000). In terms of carbon to chlorophyll *a* ratio, however, Alber (2000) reported an average of 107 ± 29 whereas in the Duplin River it was much higher averaging 204 ± 93. These higher ratios indicate that the POC pool in the Duplin River is dominated by detrital sources, which is consistent with the observations of Odum and De La Cruz (1967).

Spatial variation

We observed a clear spatial gradient in the quantity and quality of the seston in the Duplin River, with increasing concentrations of SPM, POC, and chlorophyll *a* at the mouth as compared to the headwaters, and decreasing quality (increasing C:N ratios, percent phaeopigment, and POC to chlorophyll *a* ratios) (Table 1.3; Figure 1.2 & 1.4). Spatial variation in seston within estuaries has been attributed to numerous factors including differences in the predominant local primary producers (Ruckelshaus et al., 1993), proximity to sources of marine and riverine particulate material (Incze et al., 1982; Riera & Richard, 1996; Murrell & Hollibaugh, 2000; Roegener & Shanks, 2001), and variations in physical factors that influence mixing (tidal and climatic regime, hydrology and geomorphology) (Berg & Newell, 1986; Powell et al., 1989; Smaal & Haas, 1997; Roegner, 1998).

The higher concentration of SPM and lower seston quality that we observed at the mouth of the Duplin River is probably related to the fact that the mouth is adjacent to Doboy Sound, where turbulent mixing is higher and where the Altamaha River and nearshore oceanic water can contribute particulate material from a number of sources. Oertel and Dunstan (1981) specifically refer to a highly dynamic turbidity maximum that is located at the inlet throat of Doboy Sound. These researchers noted that high and variable SPM concentrations are generally observed in riverine estuaries (i.e., “fluvial inlets") and can be attributed to the influence of increased freshwater inflows. Although the Duplin River is not a fluvial inlet, low salinity water from the Altamaha River can enter the Doboy Sound and the mouth of the Duplin River during periods of high discharge (Chalmers, 1997). The higher carbon to nitrogen ratios and POC to chlorophyll *a* ratios observed at the two sites closest to the mouth suggest that detritus, rather than living phytoplankton, was making a greater contribution to the POC pool at these sites (Table 1.3; Figure 1.4). In some estuaries higher seston concentrations are accompanied by a decrease in quality (Anderson & Meyer, 1986; Berg & Newell, 1986; Matson & Brinson, 1990; Urrutia et al., 1996; Bianchi & Argyrou, 1997; Richard et al., 1997; Murrell & Hollibaugh, 2000), which can be attributed to an increased influx of terrestrial detritus that occurs with increased freshwater inflows. Resuspension of inorganic material and detritus during wind-driven turbulent mixing events could also effect seston quality. The mouth of the Duplin River is an open-water environment where wind, tidal energy and freshwater inflows influence water movement and could contribute to turbulent mixing and resuspension events, which could be responsible for keeping dead organic material in suspension and may therefore be the cause of increased percent phaeopigment observed at the mouth. Other researchers have found that phaeopigment concentration is correlated with current velocities and the total amount of suspended particulate material (Vosjan & Tijsen, 1978; Cadee, 1982; Schuchardt & Schirmer, 1991). In sum, the differences in seston quality observed here reflect both of these Processes: the mouth is likely receiving detritus of terrigenous origin via the Altamaha River, but it is also subject to increased tidal mixing and wind-driven events as compared to the up-river sites.

In contrast to the mouth, sources of particulate material at the headwaters are limited to local inputs from the surrounding salt marsh, the sediments, and the water column of the Duplin River and the associated tidal creeks. In this system, where freshwater inputs are limited to rainfall and groundwater, the four tidal prisms found along the length of the main channel remain separate and there is no net advection from the tidal prism at the head of the river into Doboy Sound, so it is isolated from the influence of fluvially-derived material that would be present at the mouth (Ragotzkie & Bryson, 1955; Ragotzkie & Pomeroy, 1957; Imberger et al., 1983). In addition, this location is subject to decreased turbulent mixing as compared to the mouth which probably results in lower seston concentrations. Moreover, the lower C:N ratios suggest that at this location detrital inputs are less important than at the mouth. This is supported by decreased POC to chlorophyll *a* ratios as well, which averaged 157 ± 40 at the headwaters as compared to 248 ± 110 at the mouth. Although these values are still relatively high, they suggest that the contribution of living microalgae (both benthic and planktonic) to the seston pool is greater at the headwaters as compared to the mouth (Table 1.3; Figure 1.4).

Tidal variation

There were very few significant differences in either seston quantity or quality over the course of the tidal cycle observed at any of the stations studied here, although the concentrations of SPM and POC at the mouth of the Duplin River were both significantly greater during late flood/high-slack water as compared to mid-ebb water (Table 1.4; Figure 1.5 & 1.6). This is the opposite of what we expected to observe. Stevens (1983), working in a tidal tributary near the mouth of the Duplin River, observed minimum seston concentration during high-slack water and maximum seston concentration during mid-ebb water. Similar observations have been reported elsewhere (Cadee, 1982; Chrzanowski et al., 1982; Schuchardt & Schirmer, 1991; Alber 2000) and these have been attributed to the fact that the material tends to settle out of the water during slack tide and be resuspended during both flood and ebb-water when tidal energy is greater. The fact that our observations were not consistent with these other workers could be a consequence of the timing of our sampling which began during late flood-water as opposed to high slack (this sampling strategy was a consequence of the short duration of the high-slack water stage and the fact that we had to transit the entire inlet to sample all 5 stations before the tide began to ebb). In North Inlet, South Carolina, Dame et al. (1986) observed maximal chlorophyll *a* concentrations on either side of high-slack water, and we could have been observing the peak seston concentrations that can be associated with the late stage of flood tide.

A more likely explanation for the increased concentration of SPM and POC at the mouth during flood tide is that it is a consequence of the significant spatial gradient in seston concentrations in combination with the tidally-driven movement of material back and forth along the length of the tidal inlet. Changes in seston quantity (SPM, POC, chorophyll *a*) within a tidal cycle can be attributed to either intratidal deposition and resuspension (i.e., vertical exchange) or advective transport (i.e., horizontal exchange) (e.g., Cadee, 1982; Schuchardt & Schirmer, 1991). In a study of seston variability over tidal cycles in Great Sound, New Jersey, Fegley and co-workers (1992) emphasized that the source of water (i.e., the Atlantic Ocean) was the greatest determinant of seston quantity and quality and that local changes in physical factors such as current speeds were not important. Likewise Dunstan and Oertel (1981) described a dynamic and highly mobile turbidity maximum that forms in Doboy Sound during mid-ebb tide, progresses seaward through ebb-tide and low-slack water and then returns to the mouth of the inlet during mid-flood tide. This material would be pushed further up the river during flood tide as compared to ebb, resulting in higher concentrations during flood water at any given location. It is likely that the effect of the horizontal movement of water masses during the tidal cycle is more important than any decrease that might occur due to settling at slack-tide. In a study of the exchange of organic carbon exchange between a salt marsh and a tidal creek in North Inlet, South Carolina, Wolaver and Spurrier (1988) made observations similar to ours wherein mean ebb POC concentrations were generally lower than those observed on flood tide. These observations provide another example of how the horizontal movement of the water led to observations of higher POC concentrations on flood as compared to ebb tide.

Lunar variation

In general, spring tides have a greater amplitude and higher current velocities than neap tides and thus they are usually associated with increased turbulence, vertical mixing and the resuspension of bottom sediments along with associated organic material (phaeopigment, detritus, benthic microalgae etc.). Changes in SPM concentrations in a number of estuaries have been attributed to neap-spring differences in current speed and tidally-driven resuspension (Ward, 1981; Milliman *et al.*, 1984; Cloern *et al.*, 1989; Zurburg et al., 1994; Hawkins et al., 1996; Urrutia et al., 1996; Barille et al., 1997; Grabemann & Krause, 2001). In this study the concentration of SPM was significantly greater during spring as compared to neap tides at all of the study sites except the headwaters (Table 1.5; Figure 1.7). Additionally, the mid-reach sites (JH and KF) had a significantly greater amount of POC and chlorophyll *a* in the seston during spring tides as compared to neap tides (Table 1.5; Figures 1.8 & 1.9). These two sites are in close proximity to each other, and although the main channel in this region of the river is fairly deep (5-10 m), there is sediment deposition and shoaling on the eastern shore that has created an extensive intertidal mudflat that extends almost the entire distance between these two sites. Thus, the stronger currents associated with the spring tides is likely resuspending this material. Other researchers have documented instances where changes in the turbulent-mixing regime led to significant fluctuations in POC and chlorophyll *a* concentrations (Roman & Tenore, 1978; Incze & Roman, 1983; Demers et al., 1987; Garcia-Soto et al., 1990). In the Duplin River, Imberger et al. (1983) specifically noted that POC concentrations were almost completely determined by turbulence.

There were no clear differences in the quality of the seston between spring and neap tides, which suggests that even though overall seston concentration increased during spring tides the composition of the seston was not altered. This is consistent with the observations of Fegely et al. (1992) where an increase in seston concentration was not accompanied by a change in quality. The only significant difference in seston quality was observed at the headwaters (FD) where the C:N ratio was significantly lower during spring tides (Figure 1.10). One possible explanation for this observation could be due to the increased flooding of the marsh surface during high water at the headwaters. In lagoonal systems the tidal prisms are 3.3 times larger during spring tides than neap tides (Oertel & Dunstan, 1981). This leads to an increase in the amount of water that enters the small tidal creeks and rises up over the channel edges flooding a greater amount of salt marsh surface area. It has also been observed that as water leaves tidal creek channels after flooding the salt marsh surface, there is an increase in marsh-derived POC that has a large amount of associated bacteria and this increase in bacterial biomass during ebb water could be responsible for our observed decrease in C:N ratio (Erkenbrecher & Stevenson, 1975; Erkenbrecher & Stevenson, 1977). At the headwaters the decrease in C:N ratio was accompanied by an increase in the POC:chlorophyll a ratio which suggests that the lower C:N ratio was probably related to an increase in bacterial rather than microalgal biomass. The only consistent trend observed at all of the sites, although not statistically significant, was for a higher percent phaeopigment during spring tides (29% to 42%) as compared to neap tides (23% to 34%) (Table 1.5; Figure 1.11). Increased phaeopigment concentrations in the Bay of Marennes-Oleron were attributed to spring tide-induced resuspension, resulting from increased current velocities and higher bedshear (Zurburg *et al.,* 1994).

Seasonal variation

Seasonal variation in the quantity of seston is well documented, although the specific seasonal patterns vary among different estuaries and can even vary within one estuary. Within our study site we did not observe consistent seasonal differences in POC and chlorophyll *a* at the mouth, although there was a marked spring peak in SPM (Table 1.6; Figure 1.12). This suggests there was an increase in inorganic material during the spring, although it is not clear why this is the case at all of our study sites. Some of our highest SPM concentrations were made in spring 2002 and at least one of these observations (May 2002) was made immediately following a storm-event (Figure 1.7). The lack of a clear seasonal cycle may be because the mouth receives numerous inputs of POC from riverine, estuarine, and oceanic sources throughout the year so seasonal cycles would be difficult to detect unless they co-occurred. In North Inlet Estuary, South Carolina, Chrzanowski et al. (1982) did not observe seasonal variation in POC concentrations at two of their study sites (North Jones Creek and Town Creek), which were located in transitional zones where tidal inlets flowed into an open-water environment that was adjacent to the Atlantic Ocean. It should be noted that our study (June 2000 - June 2002) coincided with a period of persistent drought in the region with a cumulative rainfall deficit in coastal Georgia of 60 to 75 cm (NOAA Drought Information Center, NWS Southern Region). Under normal conditions peak rainfall would occur during the late summer and early-fall and this would lead to increased discharge in the Altamaha River, which could have resulted in higher levels of POC at the mouth of the Duplin River. Thus, the drought could be partly responsible for the lack of any distinct seasonal trends at this location. Other researchers have observed higher POC concentrations in estuaries as a result of increased river discharge (Garcia-Soto et al., 1990; Grange & Allanson, 1995; Bianchi & Argyrou, 1997).

At the headwaters, seasonal differences in seston concentration were more pronounced. The highest concentrations of SPM, POC and chlorophyll *a* were generally observed in the spring and summer (Figure 1.12-1.14). Sources of organic material in this area are limited to local production in the salt marsh, creeks, and main river channel, all of which exhibit seasonal cycles of productivity that are reflected in the summer peaks in POC and chlorophyll *a*. Seasonality in phytoplankton is well documented in many systems, with increases in POC coinciding with spring and summer blooms (Cadee, 1982; Berg & Newell, 1986; Smaal & Haas, 1997; Cranford & Hill, 1999; Toro et al., 1999). Working in the Duplin River during summer months, Imberger et al. (1983) noted that POC distribution in the headwaters was very patchy and was likely due to the phytoplankton blooms that were occurring during this time. These observations are also consistent with those in North Inlet, South Carolina where maximum SPM and POC concentrations were observed in the spring and summer (Wolaver and Spurrier, 1988; Gardner et al., 1989; Childers et al., 1993).

We also observed seasonal cycles in seston quality, which were most pronounced at the headwaters, that are consistent with our interpretations of seasonal changes in quantity. Seasonal changes in the quality of the seston are generally attributed to the annual cycles of primary producers in salt marsh environments. During the warm seasons increased algal and microbial biomass lead to decreased C:N ratios, lower percentages of phaeopigment and lower POC to chlorophyll *a* ratios. Conversely, all of these measures of seston quality increase during the cool seasons, when phytoplankton biomass decreases, salt marsh macrophytes become senescent, and detrital inputs increase (Happ et al., 1977; Widdows et al., 1979; Kranck, 1980; Roman et al., 1983; Bianchi & Argyrou, 1997; Wilson-Ormond et al., 1997; Canford & Hill, 1999; Burdloff et al., 2002; Huang et al., 2003). Although there were no significant seasonal differences in POC:chlorophyll *a* ratios at the mouth, they were generally lower during the spring and summer, which suggests that at these times phytoplankton makes a greater contribution to the organic matter pool. Moreover, at the three sites closest to the mouth percent phaeopigment was significantly higher in the fall as compared to other seasons suggesting that there was an increase in the senescence of phytoplankton at this time. At the headwaters, chlorophyll *a* comprised a greater proportion of the POC (Figure 1.3), which is consistent with the suggestion that phytoplankton dynamics are more important in driving the seasonality in this location. At the two sites closest to the headwaters, percent phaeopigment was significantly lower in the spring as compared to all of the other seasons, which is just prior to the maximal chlorophyll a concentrations during the summer bloom. There were no significant differences in POC: chlorophyll a ratios at this station although again the ratios were generally lower during the spring and summer months when phytoplankton biomass increased and made a slightly greater contribution to the POC pool.

Carbon to nitrogen ratios did not exhibit any significant seasonal differences except at HC where the seston C:N was slightly higher in the summer as compared to the winter. The lack of a significant seasonal trend in C:N ratios is generally observed in estuaries where autotrophs do not make a significant contribution to the organic matter pool so this observation was consistent with the fact that we have a detritus-dominated system (Ruckelshaus et al., 1993). In the Bay of Marennes-Oleron, France, which is a shallow turbid estuary where phytoplankton do not make a significant contribution to the POC pool, Zurburg et al. (1994) did not observe any seasonal change in carbon to nitrogen ratios.

Influence of the different temporal scales on seston parameters

The GLM procedures showed that tidal, lunar and seasonal scales, and their interactions were all important, but the greatest number of significant relationships were observed for seasonal time scales. This suggests that seasonal dynamics were probably driving a lot of the observed seston characteristics. The R-squared values indicate that 16-82% of the variability in the seston was explained by these time scales, so there are clearly other sources of variability in the data. In the work of Kranck (1980), where horizontal advection of water masses was the primary source of seston variability that was observed over tidal cycles, the short-term periodic variability in the particulate material was very difficult to interpret or predict. Fegley and co-workers (1992) determined that differences in the seston were related to the advection of water from the Atlantic Ocean during flood-water, however relationships between the seston characteristics and current speed only explained a moderate amount of the variability observed in their data (40-48%). Huang et al. (2003) noted that maximum current speeds were observed before and after high slack water but there was no appreciable effect on seston concentration and most of the time tidal currents could not explain seston variability at their study site. From these observations, as well as our own in the Duplin River, it is clear that seston is highly variable and that it can be difficult to relate observed variability to just one or even several factors, when numerous biological, chemical and physical processes influence its quantity and composition.

Scales of variability in the Duplin River.

In this study the greatest amount of overall variability in seston characteristics was observed at the two sites closest to the mouth of the Duplin River. Regardless of temporal scale, the standard deviations for all of the seston parameters, in terms of both quantity and quality, were the largest at the mouth and the next up-river station. The higher variability observed at these locations can probably be attributed to the close proximity of these sites to the open-water of Doboy Sound, where the physical influences of the nearshore Atlantic ocean, riverine discharges, winds and tidal energy all influence the dynamics of suspended particulate material.

At the three up-river sites seasonal variability was the greatest for all of the measures of seston quantity and quality (Table 1.7). In southeastern salt marshes, warm spring and summer water temperatures are accompanied by a high level of biological activity that can result in maximum annual seston concentrations (Ward, 1981; Berg & Newell, 1986; Gardner et al., 1989). At the up-river stations in the Duplin River the seston concentrations exhibited strong seasonal dynamics and the spring/summer peaks probably contribute to the increase in seasonal variability. At the mouth lunar and tidal effects were comparable or exceeded seasonal effects for many parameters. This difference in the relative importance of different scales of variability between the mouth and the headwaters could be related to the fact that the mouth is an open water environment where short term tidal and lunar effects have a more significant effect on the seston due to the influences of the adjacent Doboy Sound, the nearshore Atlantic ocean and the Altamaha River.

A number of researchers have observed that seston variability over short time scales such as tidal cycles can exceed that observed over an entire annual cycle (Gelfenbaum, 1983; Vale & Sundby, 1987; Fegley et al., 1992; Smaal & Haas, 1997; Huang et al., 2003). Many of the other studies of seston have been conducted in higher latitude estuaries, with considerably lower concentrations of material and lower overall variability. For example, Fegley et al. (1992) observed a minimum SPM concentration of 37.1 mg L^{-1} and a maximum of 78.1 mg L^{-1} over the course of a tidal cycle (a range of 41.0 mg L^{-1}). In this study we observed mid-ebb and late flood concentrations of SPM at the mouth of the Duplin River, that were 215.3 and 390.0 mg L-1 (a range of 174.7 mg L^{-1}). Tidal variability at this station was high and even greater than that observed by Fegley et al. (1992) but seasonal differences were similar to or greater than those observed over tidal cycles. For example, spring had the highest average SPM concentration as compared to the lowest average in summer (504.3 and 199.8 mg L^{-1}, respectively) with a range of 305.0 mg L^{-1}. Thus, the seasonal difference in SPM was greater than that observed over tidal cycles. In southeastern estuaries it thus appears that, depending on location, tidal variability can be as great as elsewhere, but other differences (i.e., lunar and seasonal) can be greater still.

Implications for oysters and their food resources.

The results of our study are consistent with other observations that the seston in the Duplin River is predominantly detrital. Overall, the C:N ratios were greater than eight and POC:chlorophyll *a* ratios always exceeded 100, confirming that the POC pool is predominantly detrital. Detritus is generally considered to be a poor quality food resource for estuarine bivalves as compared to phytoplankton. Crosby et al. (1989) determined that *S. alterniflora* detritus met less than 1% of the carbon requirement for oysters in the Choptank River, a sub-estuary of Chesapeake Bay. These researchers did suggest, however, that in the southeastern U.S.A. detrital carbon could provide as much as 20% of the carbon requirement of oysters, given the higher crude fiber content of the seston. Oysters can enrich the quality of the food resources that they ingest by selecting organic over inorganic particles (Newell & Jordan, 1983) and also by selecting more labile organic material (e.g., phytoplankton and benthic microalgae) over more refractory sources (e.g., detritus) (Ward et al., 1998). Although there is always detrital POC available to oysters in the Duplin River, when water column chlorophyll *a* concentrations are higher they probably select living microalgal material over detritus.

Oysters in the Duplin River have approximately three times as much POC and twice as much chlorophyll *a* available to them at the mouth as compared to the headwaters at all temporal scales but there are still differences within each site over tidal, lunar and seasonal scales. At the mouth there is generally more POC and chlorophyll *a* during late flood/high slack as compared to ebb tide, and during spring as compared to winter. At the stations closer to the headwaters there were no significant differences over the tidal cycle, but there was lunar variability (more POC and chlorophyll a during spring tide) as well as seasonal differences (more during summer as compared to winter). All of this suggests that oysters in the inlet will have different amounts of food depending on where they live, the stage of the tide, the stage of the moon and the time of the year. There is also greater variability in the food resources at the mouth than at the headwaters at any temporal scale. Oysters can adapt to dietary changes by adjusting ingestion rates, absorption efficiencies, digestive processes (Bayne et al. 1987, 1989), but an acclimation period of about two-weeks is needed for the oysters to derive the full benefits of these changes. These compensatory mechanisms are probably more useful in adapting to seasonal changes in food availability and quality than short-term changes (Newell & Langdon, 1996).

Although there were higher concentrations of particulate food resources at the mouth as compared to the headwaters, the seston at the mouth was lower quality (the C:N ratio was 19% higher at the mouth and the POC:chlorophyll *a* ratio was 57% higher) which would make it less nutritious for oysters. Additionally, the very high SPM concentrations observed at the mouth exceeded the threshold levels where the turbidity is so high that feeding activity decreases or stops altogether (Fig. 7) (Newell & Langdon, 1996). Jordan (1987) used feeding models to predict that eastern oyster feeding rates would decrease at a threshold SPM level of 25 mg L^{-1} and Barille and co-workers (1997) determined that feeding rates of Pacific oysters (*C. gigas*) would decrease at a level of 90 mg L^{-1}. Oysters living in coastal Georgia are undoubtedly well-adapted to feeding under turbid conditions and probably do not exhibit decreased feeding rates at the lower SPM concentrations reported by Jordan (1987), however in open-water environments such as the mouth of the Duplin River there are probably times when extremely high seston levels inhibit the feeding process. Given that the seston quality was lower, tubidity was higher, and variability was greater at the mouth as compared to the headwaters, one might expect that the oysters living at the headwaters experience more favorable conditions for feeding despite the lower concentrations of POC.

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TABLE 1.1. Sampling schedule for June 2000 through June 2002 showing tide (spring or neap) and season (summer, fall, winter, spring) for each of the twenty trips.

Trip	**Date**	**Tide (lunar phase)**	**Season**
Year One (high-slack & mid ebb-water sampling)			
1	15 June 2000	Spring	Summer
2	21 July 2000	Neap	Summer
3	29 August 2000	Spring	Summer
4	2 October 2000	Neap	Fall
5	14 November 2000	Spring	Fall
6	14 December 2000	Intermediate	Winter
7	24 January 2001	Spring	Winter
8	3 March 2001	Neap	Spring
9	8 April 2001	Spring	Spring
10	15 May 2001	Neap	Spring
Year Two (mid ebb-water sampling only)			
11	21 June 2001	Spring	Summer
12	27 July 2001	Neap	Summer
13	17 September 2001	Spring	Fall
14	10 October 2001	Neap	Fall
15	15 November 2001	Spring	Fall
16	13 January 2002	Spring	Winter
17	20 February 2002	Neap	Winter
18	28 March 2002	Spring	Spring
19	20 May 2002	Neap	Spring
20	24 June 2002	Spring	Summer

TABLE 1.2. Overall characteristics of seston (combined across the 5 sites) in the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (μg L^{-1}), % PHAE = % phaeopigment and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 100 observations).

Parameter	**Mean ± s.d.**
SPM	194.8 ± 255.0
POC	3.0 ± 2.7
C:N	9.1 ± 4.3
CHL *a*	12.6 ± 7.7
% PHAE	29% ± 18
POC:CHL *a*	204 ± 93

TABLE 1.3. Spatial characteristics of seston at 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002 (for site locations see Figure 1). SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (µg L^{-1}), % PHAE = % phaeopigment, and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 20 observations per site).

	Site				
Parameter	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
SPM	93.4 ± 85.2	136.7 ± 127.5	156.8 ± 178.5	324.1 ± 408.1	327.6 ± 321.8
POC	1.6 ± 1.0	1.9 ± 1.4	1.8 ± 0.8	4.5 ± 3.4	5.0 ± 2.9
C:N	8.1 ± 1.9	8.4 ± 1.9	8.7 ± 2.2	10.0 ± 5.1	9.6 ± 2.6
CHL *a*	9.4 ± 5.6	10.0 ± 6.0	10.8 ± 5.4	15.7 ± 10.8	19.9 ± 8.8
% PHAE	27% ± 15	30% ± 14	33% ± 14	40% ± 19	38% ± 14
POC:CHL *a*	157 ± 40	171 ± 56	172 ± 57	278 ± 116	248 ± 110

TABLE 1.4. Comparison of late flood/high-slack water vs. mid-ebb water characteristics of of seston at 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through May 2001. SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (µg L^{-1}), % PHAE = % phaeopigment, and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 10 observations for each tide at each site).

		Site				
Parameter	**Tide**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
SPM	High Slack	54.0 ± 40.0	85.7 ± 59.5	138.4 ± 144.4	177.5 ± 197.0	390.0 ± 308.3
	Mid Ebb	68.1 ± 68.5	77.8 ± 57.8	97.7 ± 111.7	156.8 ± 129.3	215.3 ± 152.9
POC	High Slack	1.3 ± 1.3	2.0 ± 1.3	2.0 ± 0.9	2.8 ± 1.4	7.0 ± 3.5
	Mid Ebb	1.7± 1.1	1.6 ± 1.1	1.6 ± 0.8	3.4 ± 2.5	4.7 ± 2.4
C:N	High Slack	9.5 ± 11.7	8.6 ± 3.5	9.1 ± 3.6	9.7 ± 3.3	10.1 ± 2.2
	Mid Ebb	7.9 ± 2.3	8.1± 2.2	8.5 ± 2.7	9.9 ± 6.8	9.6 ± 3.4
CHL *a*	High Slack	9.3 ± 6.0	7.9 ± 4.0	9.4 ± 2.8	10.8 ± 3.5	15.8± 5.1
	Mid Ebb	8.9 ± 6.0	9.1 ± 6.9	9.1 ± 3.5	10.1 ± 3.6	15.7± 3.9
% PHAE	High Slack	17% ± 12	24% ± 16	22% ± 14	28% ± 18	29% ± 19
	Mid Ebb	17% ± 12	20% ± 11	20% ± 10	27% ± 17	30% ± 13
POC:CHL *a*	High Slack	167 ± 80	253 ± 39	227 ± 100	280 ± 166	516 ± 388
	Mid Ebb	233 ± 39	176 ± 35	170 ± 33	308 ± 190	270 ± 124

TABLE 1.5. Comparison of lunar (spring vs. neap) characteristics of seston at 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (µg L^{-1}), % PHAE = % phaeopigment and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 11 observations for spring tide and n = 8 for neap tide).

		Site				
Parameter	**Lunar**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
SPM	Spring	92.7 ± 78.7	183.5 ± 143.5	195.4 ± 203.0	463.8 ± 495.2	331.1 ± 218.3
	Neap	102.8 ± 96.2	82.9 ± 70.2	116.3 ± 132.9	154.3 ± 115.0	336.9 ± 447.9
POC	Spring	1.6 ± 0.8	2.1 ± 1.5	2.0 ± 1.0	5.5 ± 4.0	5.2 ± 1.9
	Neap	1.7 ± 1.2	1.7 ± 1.3	1.5 ± 0.4	3.4 ± 1.9	4.3 ± 4.0
C:N	Spring	7.7 ± 2.1	8.7 ± 2.0	8.8 ± 2.3	9.4 ± 2.3	9.9 ± 3.1
	Neap	8.7 ± 1.6	8.3 ± 1.8	8.7 ± 2.1	11.0 ± 7.9	9.2 ± 1.8
CHL *a*	Spring	9.3 ± 4.9	10.4 ± 4.8	13.2 ± 5.8	19.9 ± 12.9	20.9 ± 7.5
	Neap	10.6 ± 6.3	10.2 ± 7.4	8.3 ± 3.4	11.1 ± 3.8	19.0 ± 10.8
% PHAE	Spring	29% ± 13	32% ± 13	33% ± 14	42% ± 17	41% ± 7
	Neap	23% ± 16	27% ± 16	34% ± 24	37% ± 23	34% ± 22
POC:CHL *a*	Spring	186 ± 91	169 ± 50	159 ± 53	320 ± 185	460 ± 640
	Neap	159 ± 38	172 ± 66	205 ± 127	241 ± 105	228 ± 81

TABLE 1.6. Seasonal characteristics of seston at 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (µg L^{-1}), % PHAE = % phaeopigment and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

		Site				
Parameter	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
SPM	Summer	89.6 ± 32.8	153.9 ± 104.5	102.4± 63.2	193.5 ± 102.1	199.8 ± 87.8
	Fall	48.4 ± 16.1	105.6 ± 132.4	129.8 ± 157.5	248.1 ± 312.4	256.8 ± 195.1
	Winter	99.6 ± 92.0	106.5 ± 161.0	189.1 ± 126.2	387.0 ± 246.5	357.2 ± 256.8
	Spring	140.0 ± 108.3	146.0 ± 132.5	217.1 ± 206.6	490.8 ± 740.1	504.3 ± 515.9
POC	Summer	2.8 ± 0.8	3.9 ± 2.0	2.1 ± 0.5	4.8 ± 3.3	5.0 ± 0.9
	Fall	1.1 ± 0.2	1.4 ± 0.3	1.8 ± 0.9	4.8 ± 3.2	4.8 ± 2.2
	Winter	0.7 ± 0.1	0.9 ± 0.1	1.4 ± 0.2	3.0 ± 0.3	4.3 ± 2.9
	Spring	1.3 ± 0.3	1.2 ± 0.4	1.9 ± 0.8	5.7 ± 5.4	6.0 ± 5.0
C:N	Summer	8.9 ± 2.1	9.2 ± 1.7	8.5 ± 1.4	8.6 ± 2.3	8.7 ± 1.6
	Fall	8.3 ± 0.7	9.0 ± 0.9	9.1 ± 1.0	10.4 ± 0.6	10.2 ± 0.6
	Winter	7.7 ± 0.9	8.0 ± 0.9	8.3 ± 1.1	9.8 ± 0.9	10.2 ± 1.7
	Spring	8.7 ± 0.8	8.3 ± 0.6	9.4 ± 0.8	10.6 ± 1.3	9.5 ± 0.9
CHL *a*	Summer	17.9 ± 3.8	17.3 ± 6.2	14.0 ± 3.1	15.7 ± 3.4	21.7 ± 2.8
	Fall	8.4 ± 4.5	8.4 ± 4.2	9.0 ± 5.8	15.8 ± 12.0	21.2 ± 8.9
	Winter	5.1 ± 2.4	6.2 ± 4.4	10.5 ± 5.4	12.4 ± 6.8	15.8 ± 7.3
	Spring	7.8 ± 2.4	8.8 ± 3.4	12.0 ± 6.7	19.1 ± 15.3	23.0 ± 11.8
% PHAE	Summer	20% ± 12	28% ± 15	24% ± 17	34% ± 20	27% ± 14
	Fall	32% ± 9	36% ± 9	44% ± 21	51% ± 12	46% ± 15
	Winter	29% ± 17	33% ± 19	31% ± 16	38% ± 16	34% ± 14
	Spring	20% ± 17	22% ± 17	23% ± 20	29% ± 23	26% ± 24
POC:CHL *a*	Summer	161 ± 42	164 ± 22	153 ± 44	295 ± 166	230 ± 36
	Fall	146 ± 42	188 ± 65	211 ± 73	318 ± 72	236 ± 98
	Winter	160 ± 62	189 ± 98	154 ± 67	278 ± 100	306 ± 210
	Spring	162 ± 7	147 ± 29	169 ± 38	199 ± 77	233 ± 95

TABLE 1.7. Summary of the R-squared and p-values from the general linear models examining the influence of the three temporal scales (tidal, lunar, seasonal) on seston within each of the 5 sites located along the length of the Duplin River. LN(SPM) = natural log transformed (suspended particulate material), POC = particulate organic carbon, C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* and % PHAE = % phaeopigment

			Main Effects			**Interactions**		
Site	**Parameter**	**R^2**	Tidal	Lunar	Seasonal	TidexLunar	TidexSeason	LunarxSeason
ML	LN(SPM)	0.28	**0.0240**	**< 0.0001**	**< 0.0001**	0.7824	0.0860	0.0507
	POC	0.42	**< 0.0001**	**< 0.0001**	**0.0081**	**< 0.0001**	**0.0289**	**0.0055**
	CHL-*a*	0.25	**0.0072**	**0.0368**	**0.0053**	0.8296	**0.0925**	**0.0014**
	C:N	0.09	0.2011	0.0819	0.1728	0.9585	0.8349	0.1828
	%PHAE	0.60	**< 0.0001**	0.6592	**< 0.0001**	**0.0217**	**< 0.0001**	**< 0.0001**
JH	LN(SPM)	0.51	**< 0.0001**	**< 0.0001**	**< 0.0001**	0.3546	**0.0064**	0.1544
	POC	0.29	**0.0017**	**0.0255**	0.2923	**0.0189**	**0.0470**	0.2148
	CHL-*a*	0.34	**0.0004**	**0.0013**	**0.0171**	**0.0002**	0.0868	0.0548
	C:N	0.10	0.4005	0.1042	0.6711	0.8101	0.4576	0.0577
	%PHAE	0.57	**< 0.0001**	0.6096	**< 0.0001**	0.7805	**0.0655**	**< 0.0001**
KF	LN(SPM)	0.34	0.6840	**0.0002**	**< 0.0001**	0.3028	**0.0002**	**0.00031**
	POC	0.50	**0.0002**	0.7286	**< 0.0001**	**< 0.0001**	**< 0.0001**	**0.0002**
	CHL-*a*	0.49	0.0547	**0.0010**	**< 0.0001**	**< 0.0001**	**0.0138**	**< 0.0001**
	C:N	0.10	0.2875	0.3703	0.1134	0.6812	0.6077	0.3596
	%PHAE	0.48	**< 0.0001**	**0.0205**	**< 0.0001**	0.0809	0.1960	**< 0.0001**
HC	LN(SPM)	0.37	0.1294	**0.0008**	**0.0011**	**0.0782**	**0.0665**	**< 0.0001**
	POC	0.46	0.1039	0.0620	**< 0.0001**	0.1541	**0.0467**	0.5617
	CHL-*a*	0.72	**< 0.0001**	**0.0387**	**< 0.0001**	0.9629	**0.0009**	**< 0.0001**
	C:N	0.26	0.2116	0.5165	0.0706	0.0844	**< 0.0001**	0.4466
	%PHAE	0.60	0.1054	**0.0406**	**< 0.0001**	0.6819	**< 0.0001**	**< 0.0001**
FD	LN(SPM)	0.21	**0.0004**	0.5267	**0.0007**	0.6739	0.1507	0.1977
	POC	0.42	0.6357	0.6406	**< 0.0001**	0.6600	0.2269	**< 0.0001**
	CHL-*a*	0.82	**0.0007**	**< 0.0001**	**< 0.0001**	0.1893	0.2178	**< 0.0001**
	C:N	0.16	0.1850	0.1469	**0.0082**	**0.0512**	0.0807	0.0833
	%PHAE	0.53	**< 0.0001**	0.9660	**< 0.0001**	**0.0088**	0.1378	**< 0.0001**

TABLE 1.8. Summary of the predicted standard deviations (σ) from the general linear models examining the influence of the three temporal scales (tidal, lunar, seasonal) on seston within each of the 5 sites located along the length of the Duplin River. LN(SPM) = natural log transformed (suspended particulate material), POC = particulate organic carbon, C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* and % PHAE = % phaeopigment

		Predicted Standard Deviations		
Site	**Parameter**	**Tidal**	**Lunar**	**Seasonal**
ML	**LN(SPM)**	0.14	0.33	0.33
	POC	1.07	1.43	0.86
	CHL *a*	1.60	1.24	2.27
	C:N	0.29	0.41	0.54
	% PHAE	4.80	0.42	9.32
JH	**LN(SPM)**	0.24	0.49	0.46
	POC	0.76	0.56	0.48
	CHL *a*	2.30	2.03	2.05
	C:N	0.35	0.69	0.51
	% PHAE	5.64	0.57	9.60
KF	**LN(SPM)**	0.03	0.25	0.46
	POC	0.22	0.02	0.36
	CHL *a*	0.57	0.97	2.42
	C:N	0.27	0.23	0.64
	% PHAE	5.82	2.54	7.99
HC	**LN(SPM)**	0.09	0.21	0.25
	POC	0.16	0.19	0.71
	CHL *a*	1.50	0.53	4.64
	C:N	0.26	0.14	0.61
	% PHAE	1.41	1.77	8.65
FD	**LN(SPM)**	0.22	0.04	0.26
	POC	0.04	0.04	0.57
	CHL *a*	0.76	1.20	5.43
	C:N	0.83	0.94	2.29
	% PHAE	4.91	0.04	5.96

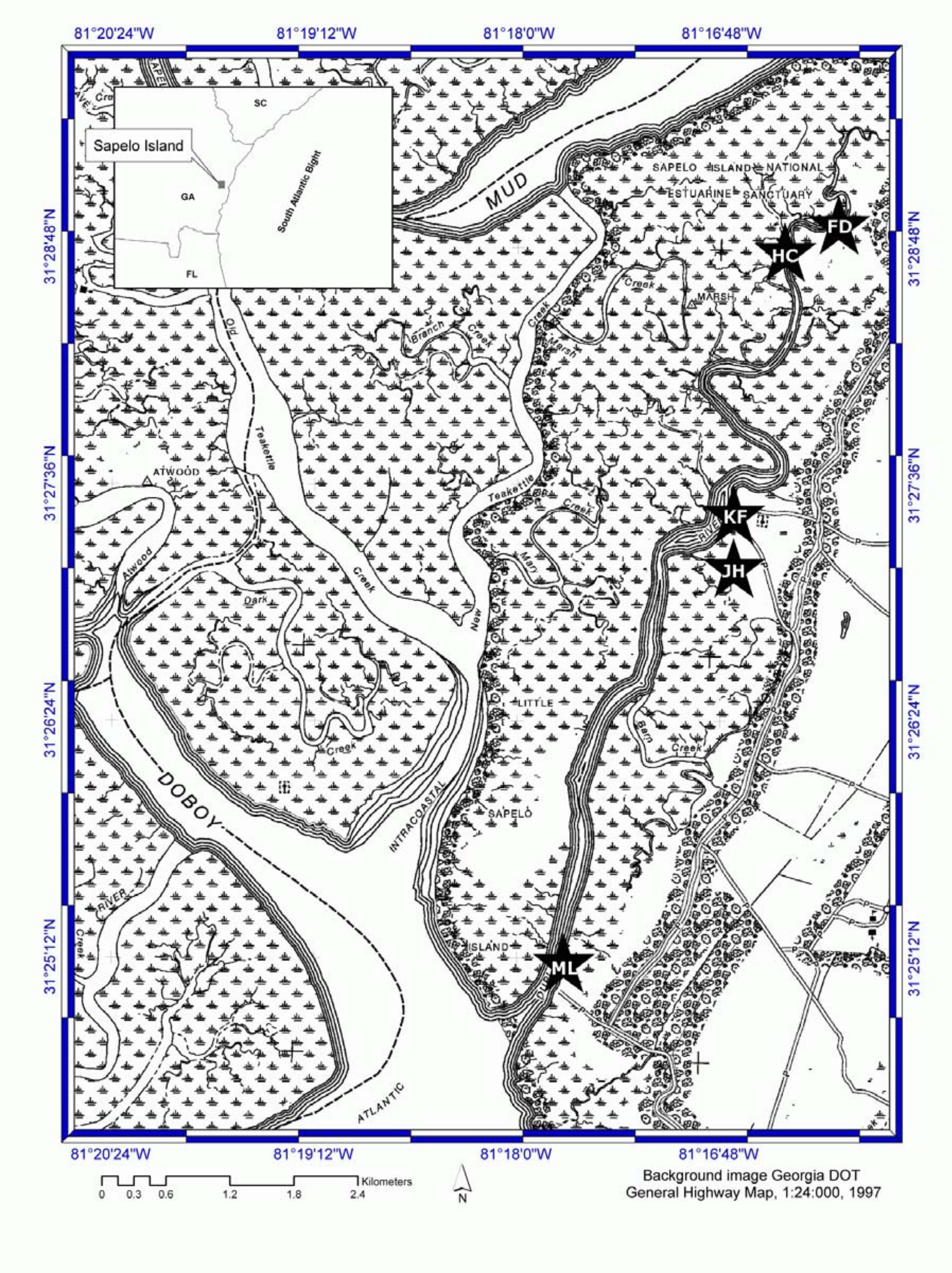


FIGURE 1.1. Map of the Duplin River showing the location of the five study sites (Marsh Landing = ML, Jack Hammock = JH, Kenan Field = KF, Hunt Camp = HC and Flume Dock = FD) where seston over oyster reefs was sampled at five-week intervals over two years (June 2000-June 2002).

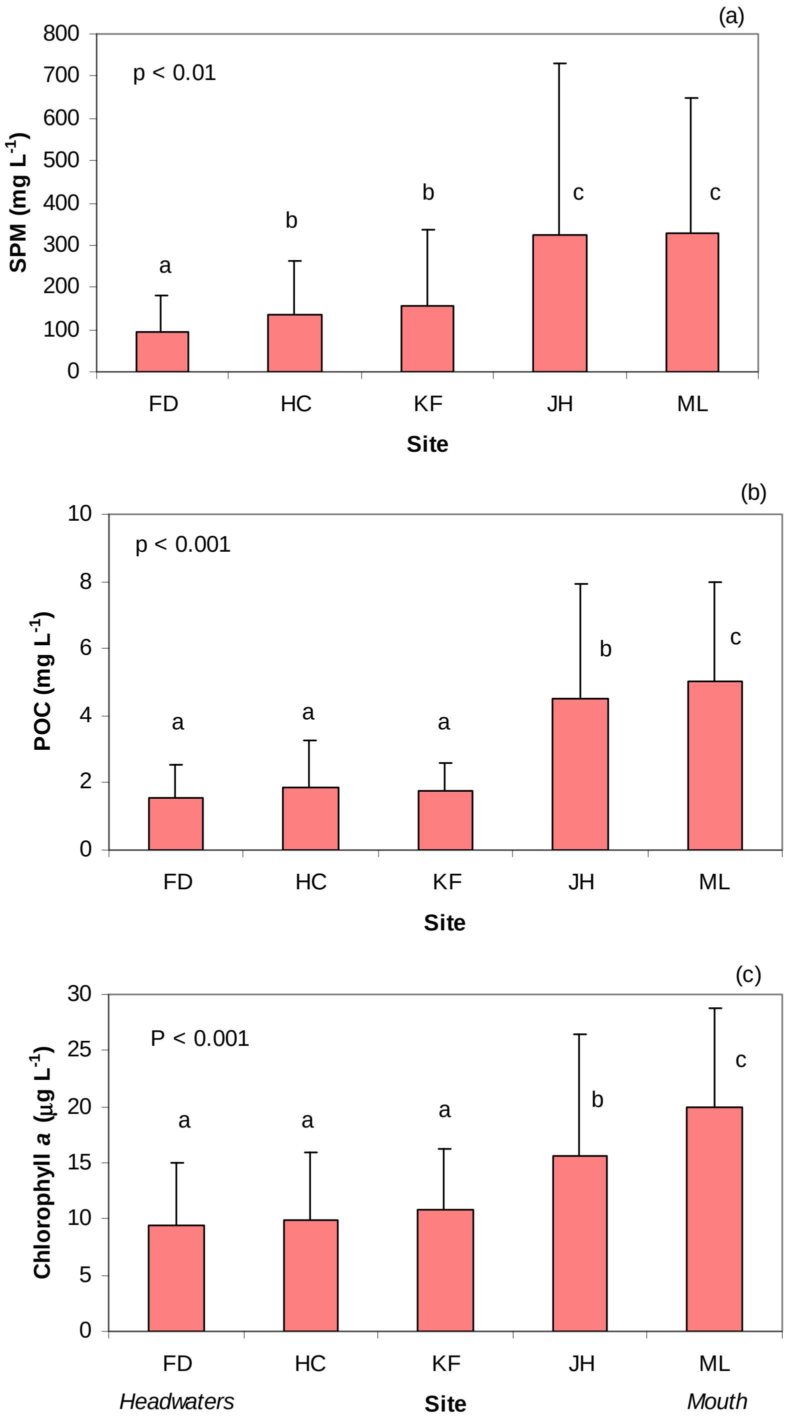


FIGURE 1.2. Two-year average concentrations (± s.d.) June 2000 through June 2002 for (a) suspended particulate material (SPM), (b) particulate organic carbon (POC) and (c) chlorophyll *a* over oyster reefs during mid-ebb water at five sites (Figure 1) along the length of the Duplin River (Analysis of variance; Duncan's least significant difference post-hoc tests; site differences denoted by letters.)

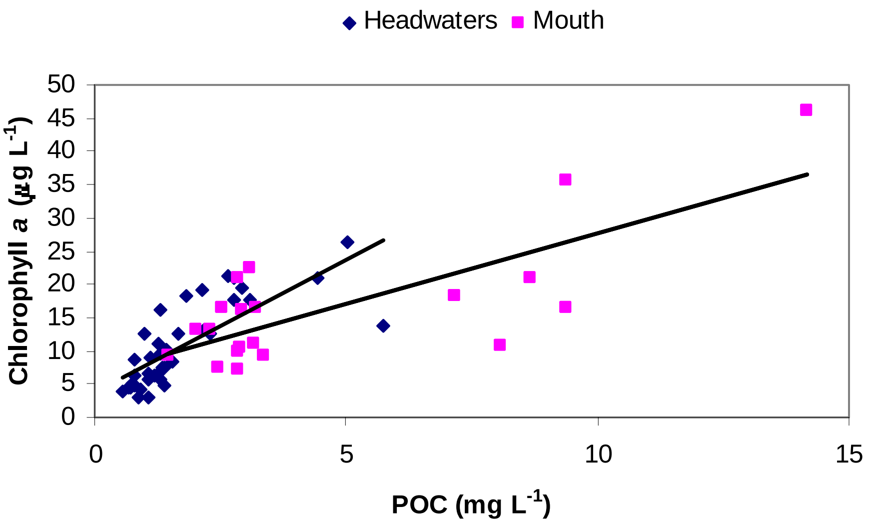


FIGURE 1.3. POC vs. chlorophyll *a* in seston over oyster reefs during mid-ebb water June 2000 through June 2002, combining the two sites closest to the headwaters (FD & HC) and the two sites closest to the mouth (JH & ML) (Figure 1.1).

Linear equations are as follows:

Mouth: $Y = 2.10X + 6.6$ ($R^2 = 0.57$)

Headwaters: $Y = 4.01X + 3.8$ ($R^2 = 0.59$)

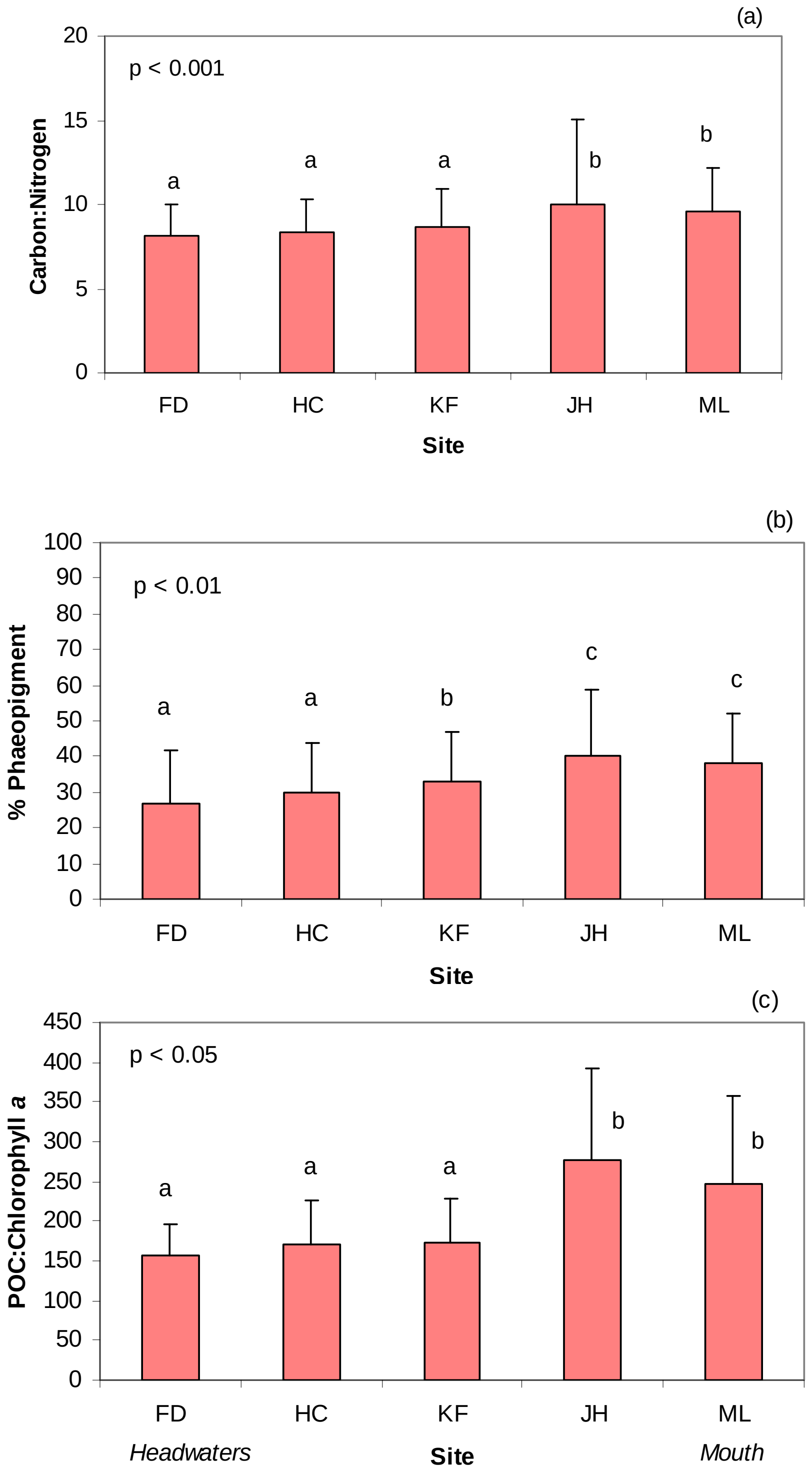


FIGURE 1.4. Two-year averages (± s.d.) June 2000 through June 2002 for (a) carbon to nitrogen ratio and (b) percent phaeopigement and (c) particulate organic carbon to chlorophyll *a* ratioover oyster reefs during mid-ebb water at five sites (Figure 1) along the length of the Duplin River. (Analysis of variance; Duncan's least significant difference post-hoc tests; site differences denoted by letters.)

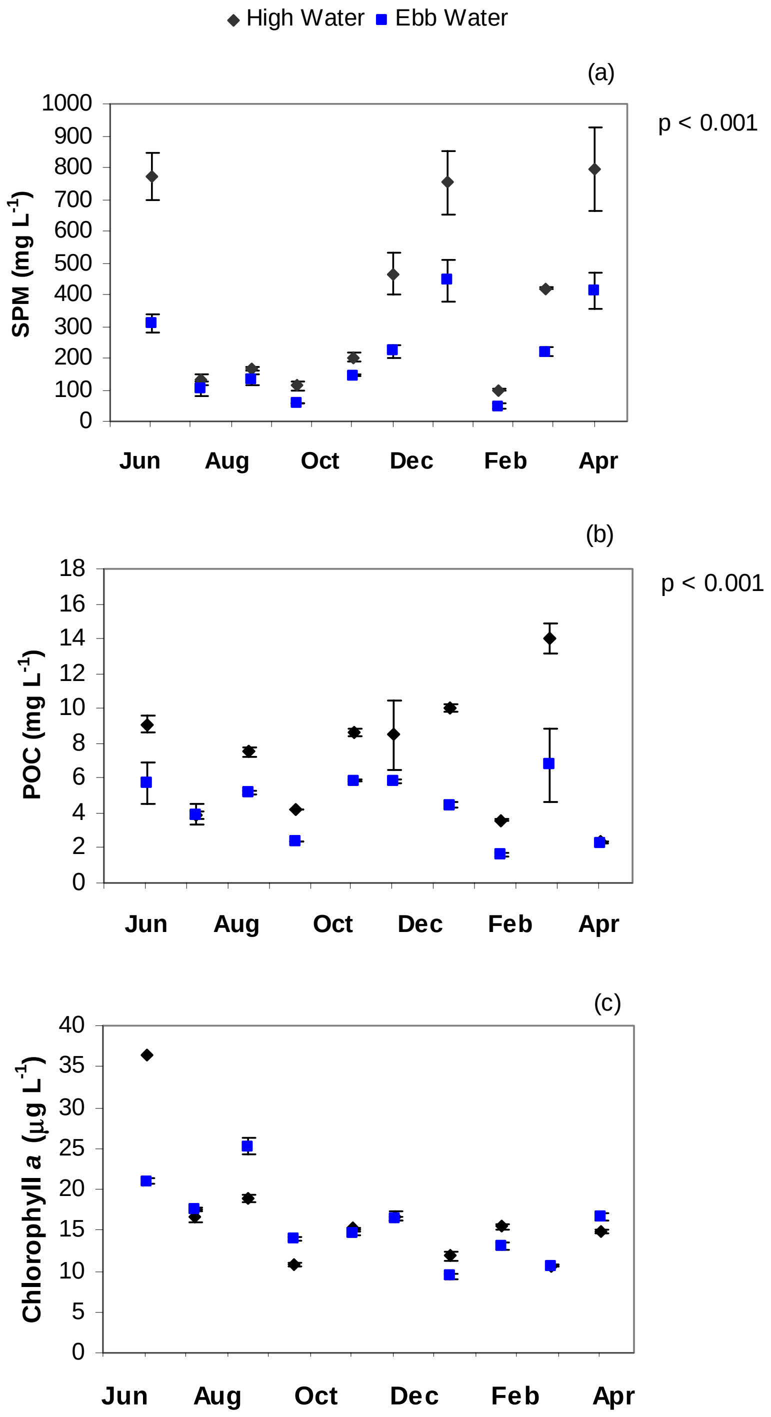


FIGURE 1.5. Late flood/high-slack vs. mid-ebb water concentrations (± s.e.) from June 2000 through May 2001 of (a) suspended particulate material (SPM), (b) particulate organic carbon (POC), and (c) chlorophyll *a* over oyster reefs at the mouth (ML; Figure 1.1) of the Duplin River. (◆ = high-slack water; ■ = mid-ebb water) (Paired samples student's t-test; p-values indicated where significant differences between tidal stages were observed.)

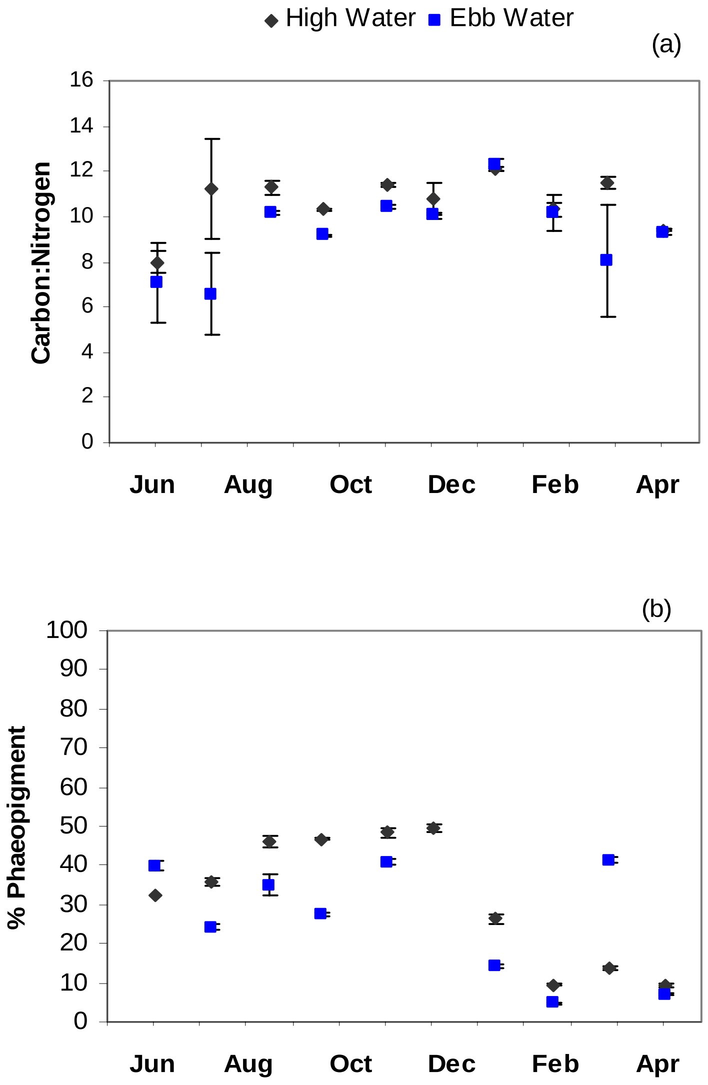
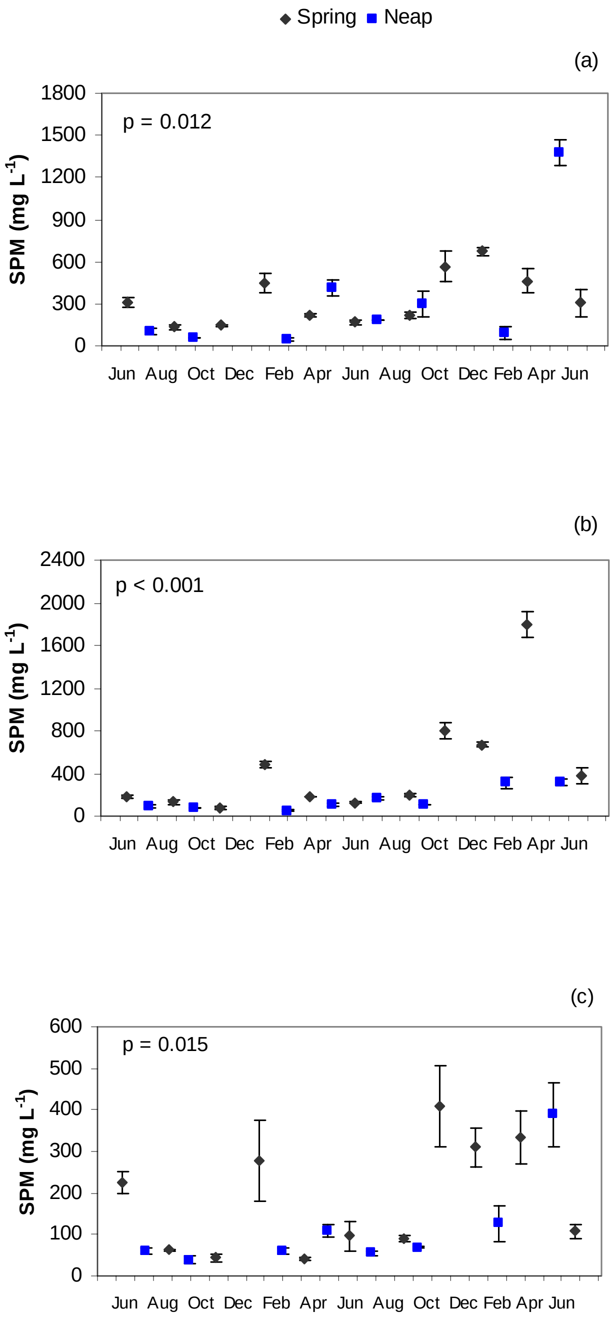
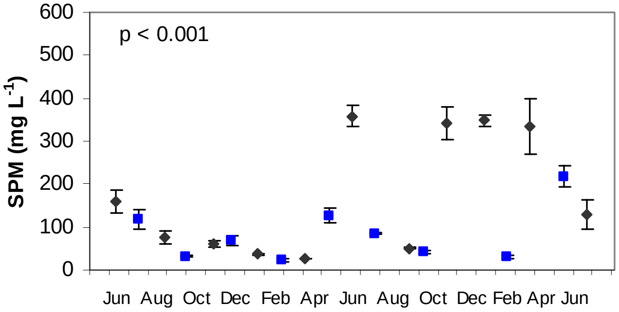


FIGURE 1.6. High-slack vs. mid-ebb water averages (± s.e.) from June 2000 through May 2001 for (a) carbon to nitrogen ratio, and (b) percent phaeopigment over oyster reefs at the mouth (ML; Figure 1.1) of the Duplin River. (◆ = high-slack water; ■ = mid-ebb water) (Paired samples student's t-test; p-values indicated where significant differences between tidal stages were observed.)

FIGURE 1.7. Suspended particulate material (SPM) concentration (± s.e.) over oyster reefs at mid-ebb water during spring and neap tides from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (◆ = spring tide; ■ = neap tide) (Independent samples student's t-test; p-values indicated where significant differences between tides were observed.)

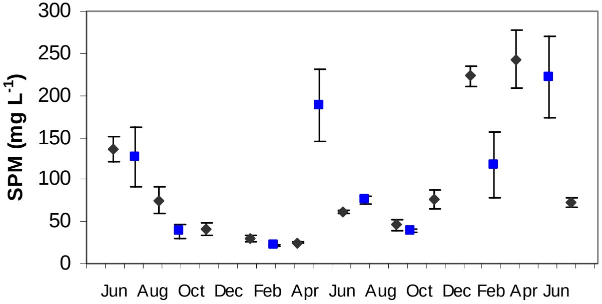

◆ Spring ■ Neap
(a)
p = 0.012
SPM (mg L^{-1})
0
300
600
900
1200
1500
1800
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(b)
p < 0.001
SPM (mg L^{-1})
0
400
800
1200
1600
2000
2400
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(c)
p = 0.015
SPM (mg L^{-1})
0
100
200
300
400
500
600
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun

(d)



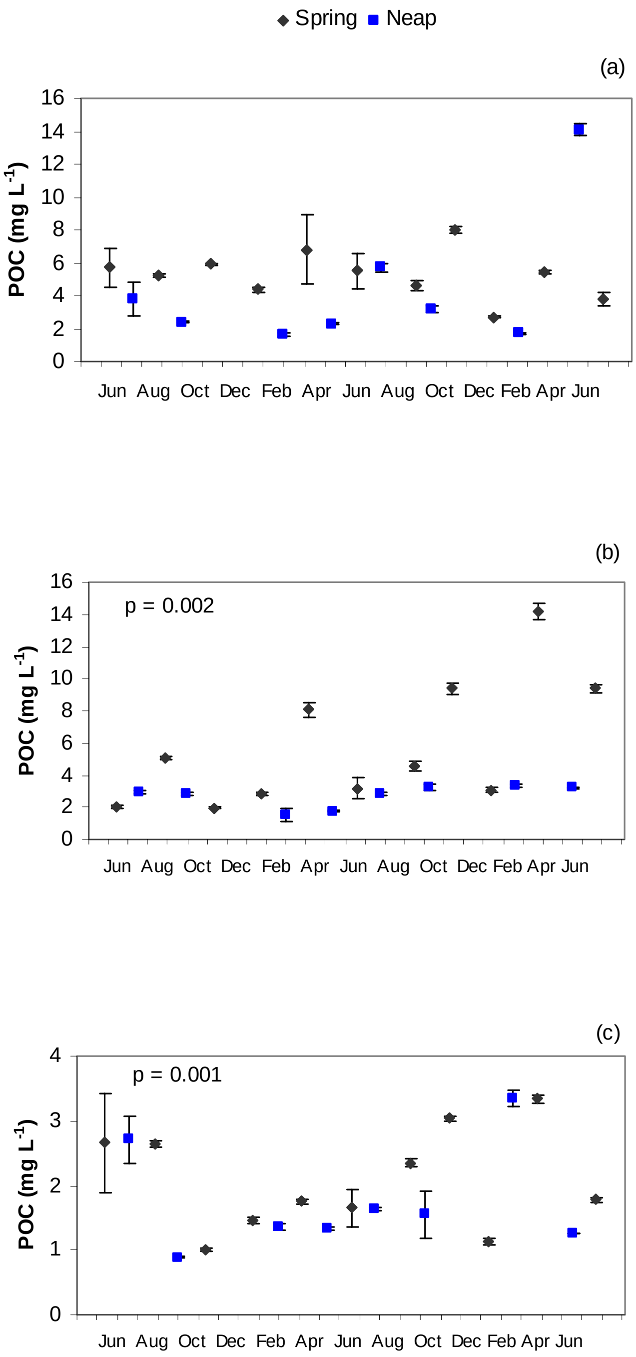
p < 0.001
SPM (mg L-1)
600
500
400
300
200
100
0
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun

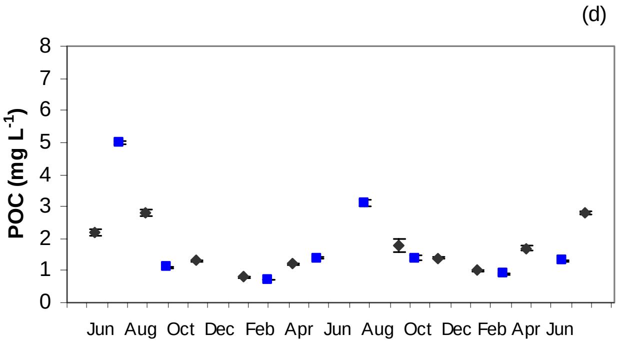
(e)



SPM (mg L-1)
300
250
200
150
100
50
0
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun

FIGURE 1.8. Particulate organic carbon (POC) concentration (± s.e.) over oyster reefs at mid-ebb water during spring and neap tides from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (◆ = spring tide; ■ = neap tide) (Independent samples student's t-test; p-values indicated where significant differences between tides were observed.)


◆ Spring ■ Neap
(a)
POC (mg L^{-1})
0 2 4 6 8 10 12 14 16
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(b)
p = 0.002
POC (mg L^{-1})
0 2 4 6 8 10 12 14 16
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(c)
p = 0.001
POC (mg L^{-1})
0 1 2 3 4
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(d)
POC (mg L^{-1})
0
1
2
3
4
5
6
7
8
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

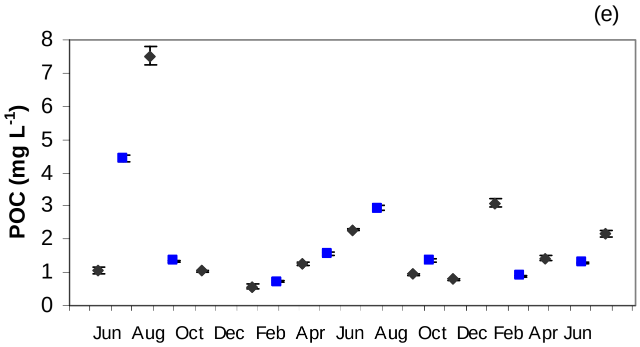
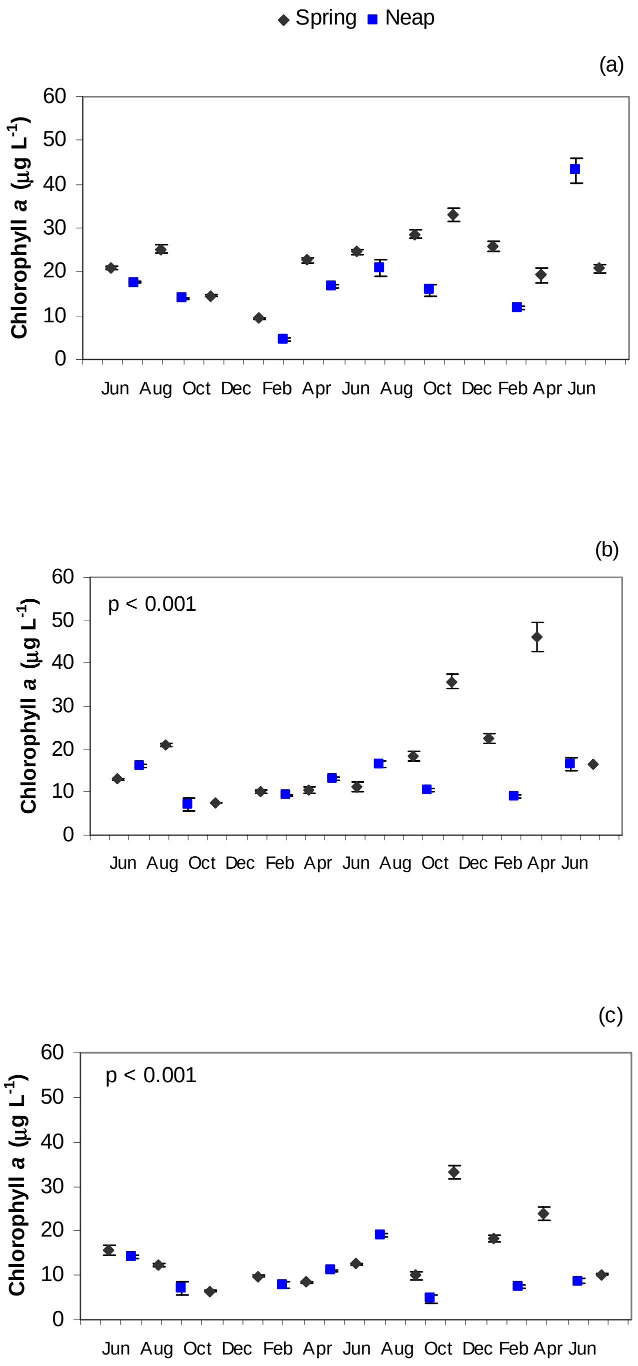
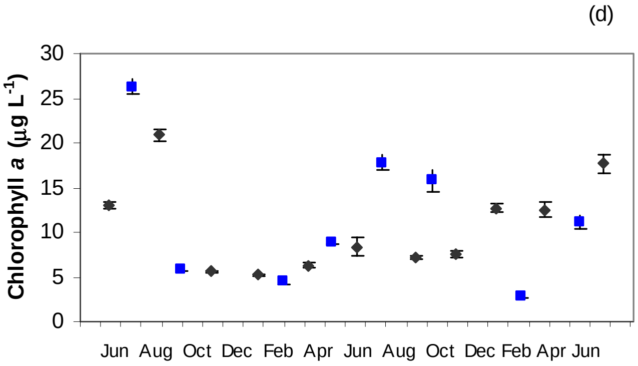

(e)
POC (mg L^{-1})
0
1
2
3
4
5
6
7
8
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

FIGURE 1.9. Chlorophyll *a* concentration (± s.e.) over oyster reefs at mid-ebb water during spring and neap tides from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (◆ = spring tide; ■ = neap tide) (Independent samples student's t-test; p-values indicated where significant differences between tides were observed.)


◆ Spring ■ Neap
(a)
Chlorophyll a ($\mu g\ L^{-1}$)
0
10
20
30
40
50
60
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(b)
p < 0.001
Chlorophyll a ($\mu g\ L^{-1}$)
0
10
20
30
40
50
60
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(c)
p < 0.001
Chlorophyll a ($\mu g\ L^{-1}$)
0
10
20
30
40
50
60
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(d)
Chlorophyll a (μg L-1)
30
25
20
15
10
5
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

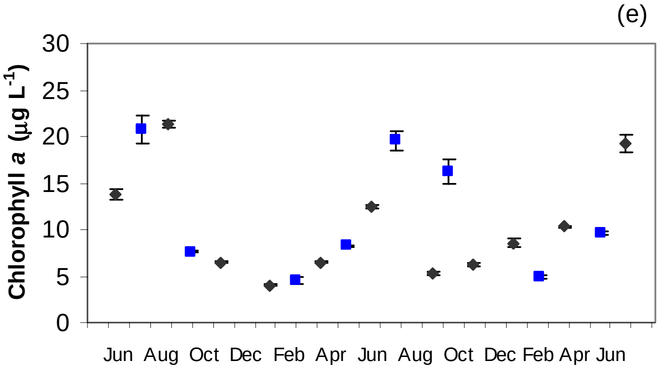
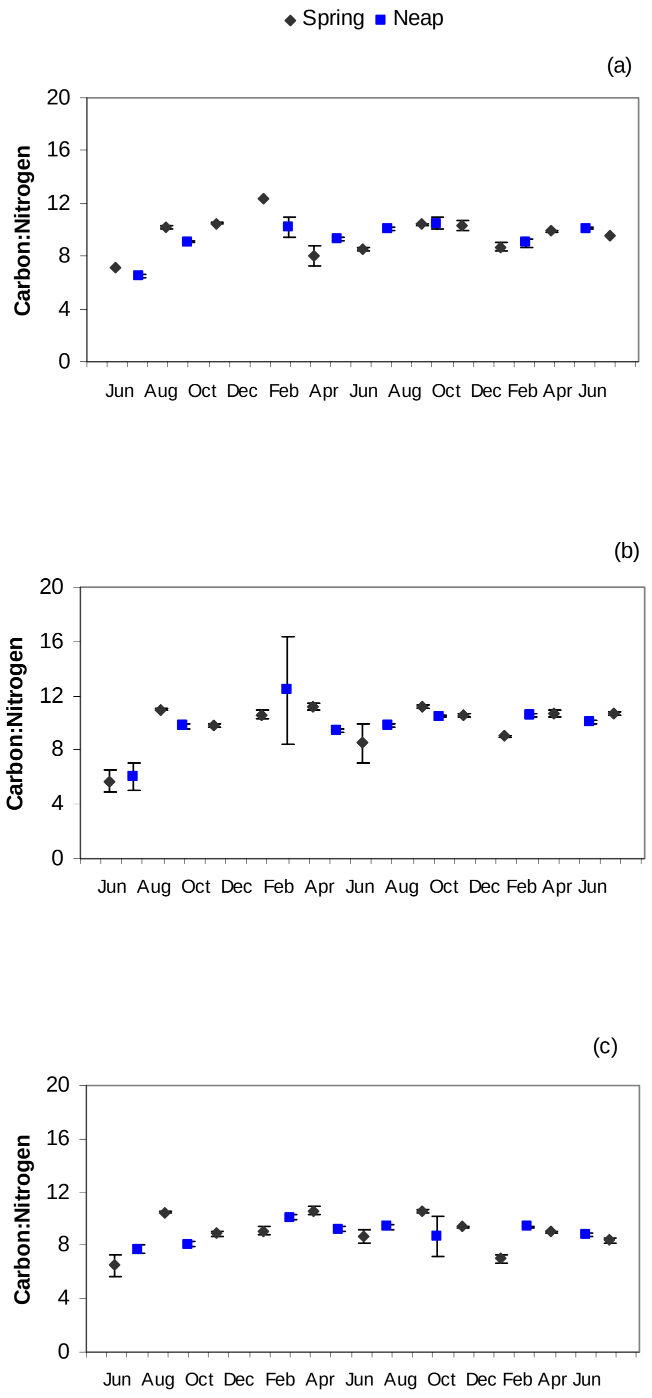
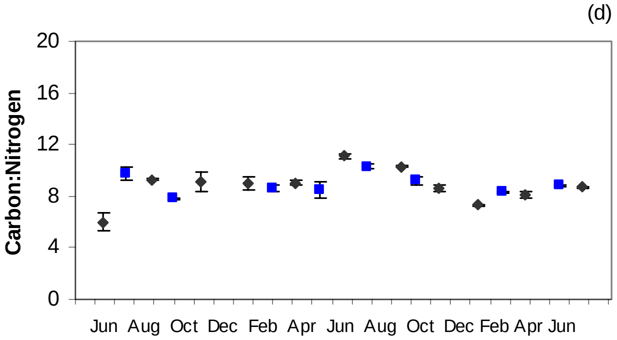

(e)
Chlorophyll a (μg L-1)
30
25
20
15
10
5
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

FIGURE 1.10. Carbon to nitrogen ratio (± s.e.) of seston over oyster reefs at mid-ebb water during spring and neap tides from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (◆ = spring tide; ■ = neap tide) (Independent samples student's t-test; p-values indicated where significant differences between tides were observed.)


◆ Spring ■ Neap
(a)
Carbon:Nitrogen
20
16
12
8
4
0
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(b)
Carbon:Nitrogen
20
16
12
8
4
0
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun
(c)
Carbon:Nitrogen
20
16
12
8
4
0
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(d)
Carbon:Nitrogen
20
16
12
8
4
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

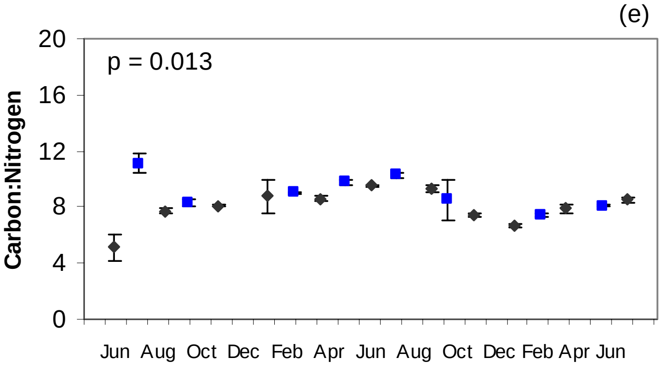
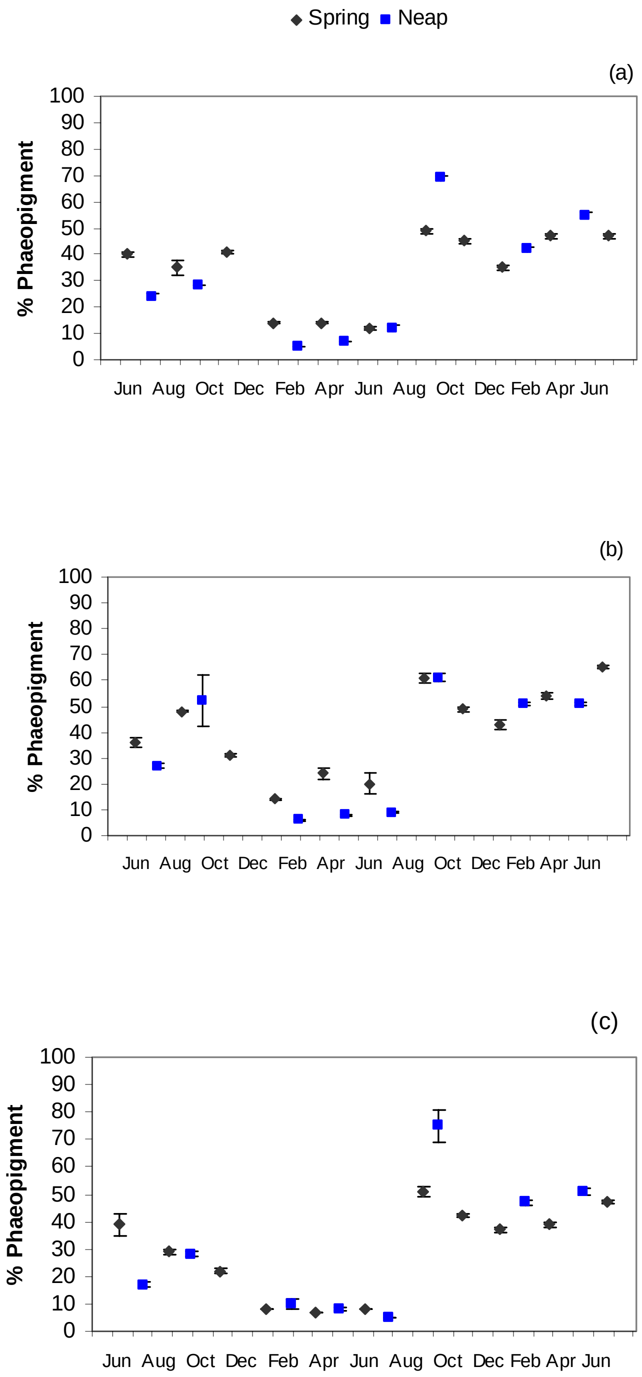
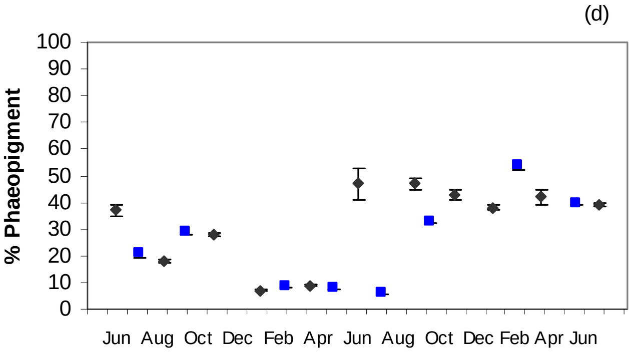
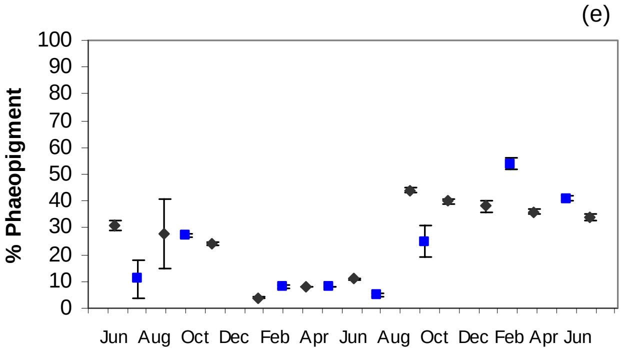

(e)
p = 0.013
Carbon:Nitrogen
20
16
12
8
4
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

FIGURE 1.11. Percent phaeopigment (± s.e.) of seston over oyster reefs at mid-ebb water during spring and neap tides from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (◆ = spring tide; ■ = neap tide) (Independent samples student's t-test; p-values indicated where significant differences between tides were observed.)


◆ Spring ■ Neap
(a)
(b)
(c)
% Phaeopigment
100
90
80
70
60
50
40
30
20
10
0
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(d)
% Phaeopigment
100
90
80
70
60
50
40
30
20
10
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun


(e)
% Phaeopigment
100
90
80
70
60
50
40
30
20
10
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

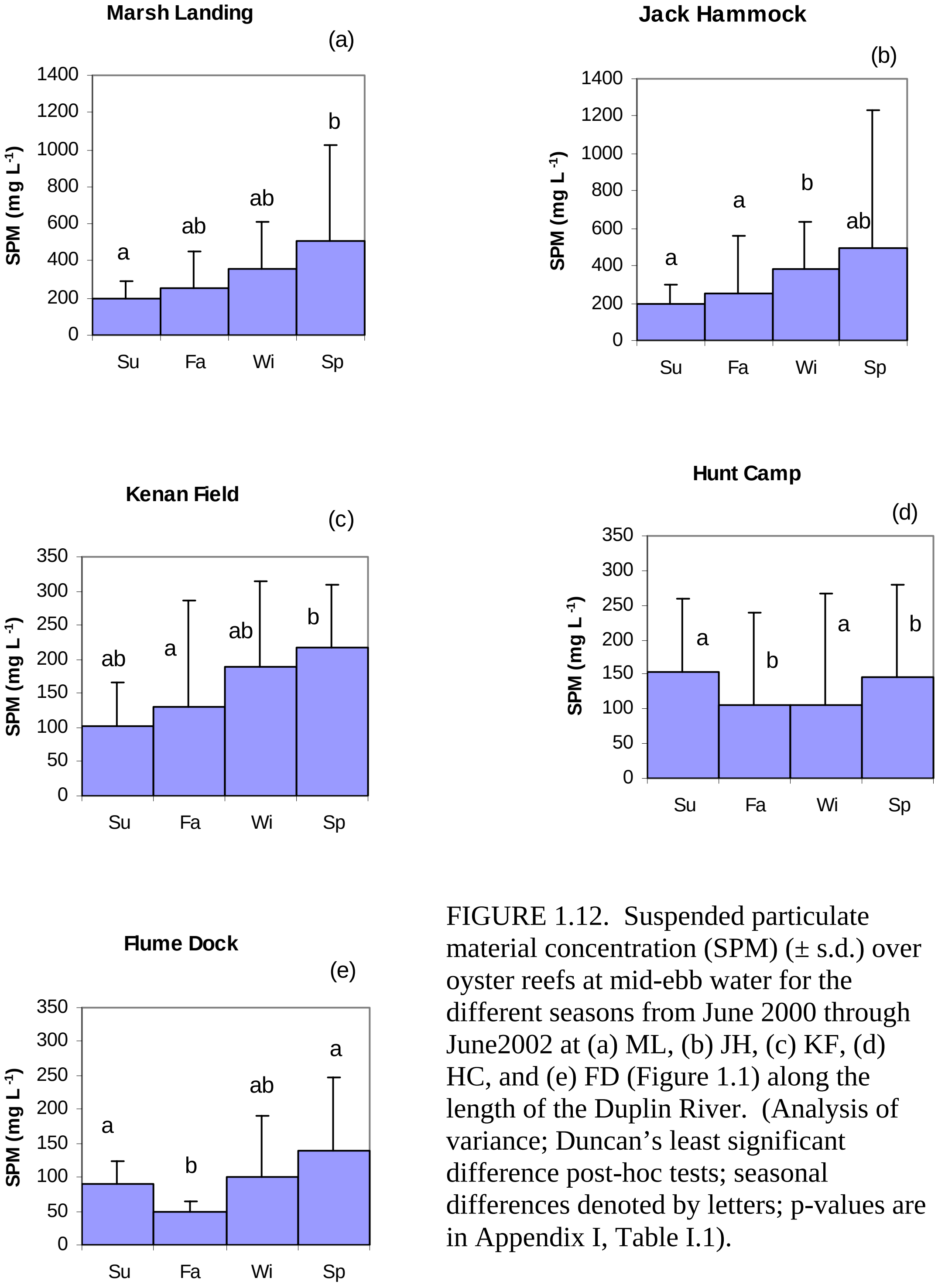
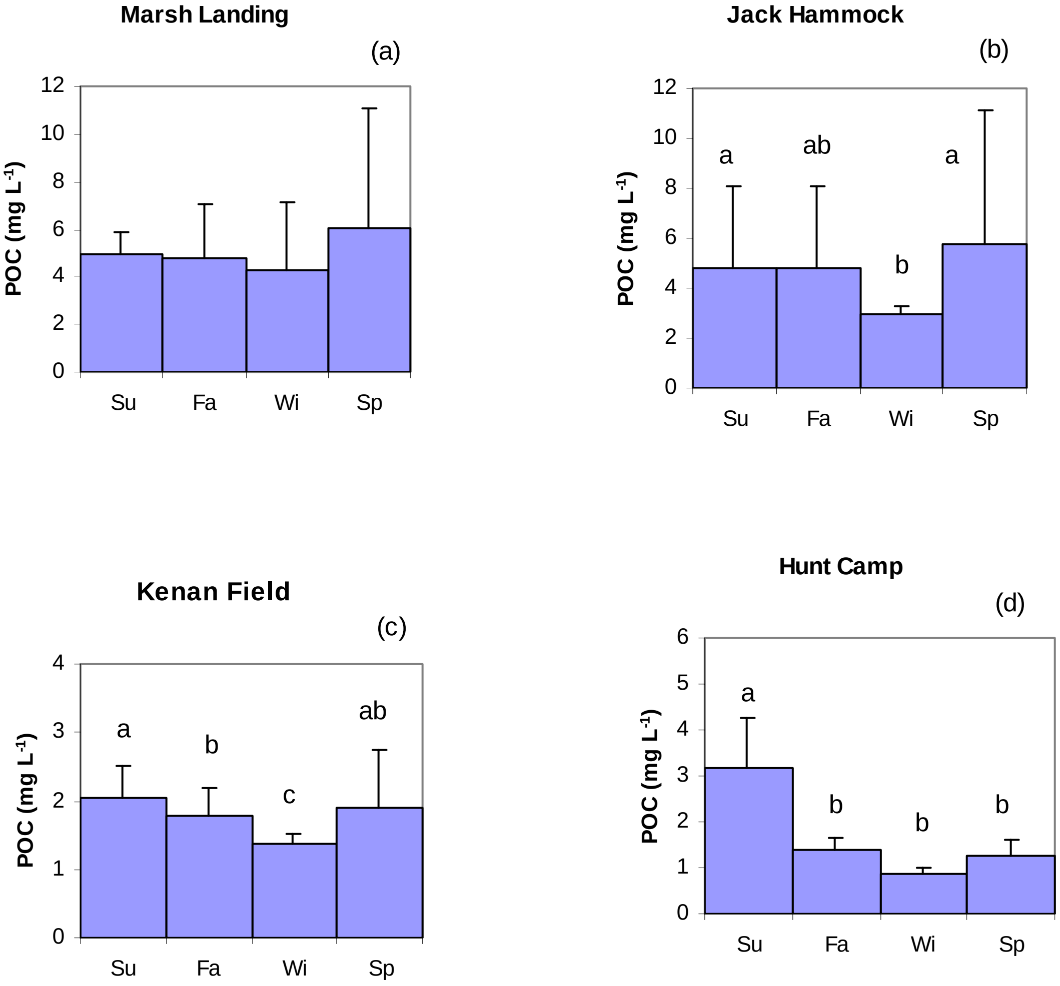


FIGURE 1.12. Suspended particulate material concentration (SPM) (± s.d.) over oyster reefs at mid-ebb water for the different seasons from June 2000 through June2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (Analysis of variance; Duncan’s least significant difference post-hoc tests; seasonal differences denoted by letters; p-values are in Appendix I, Table I.1).



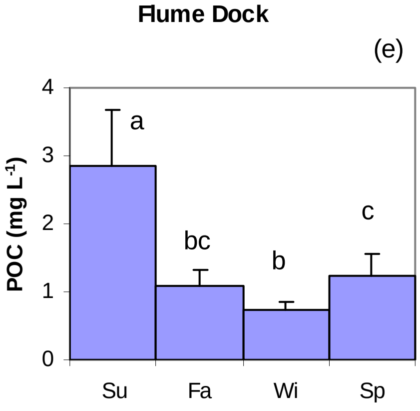
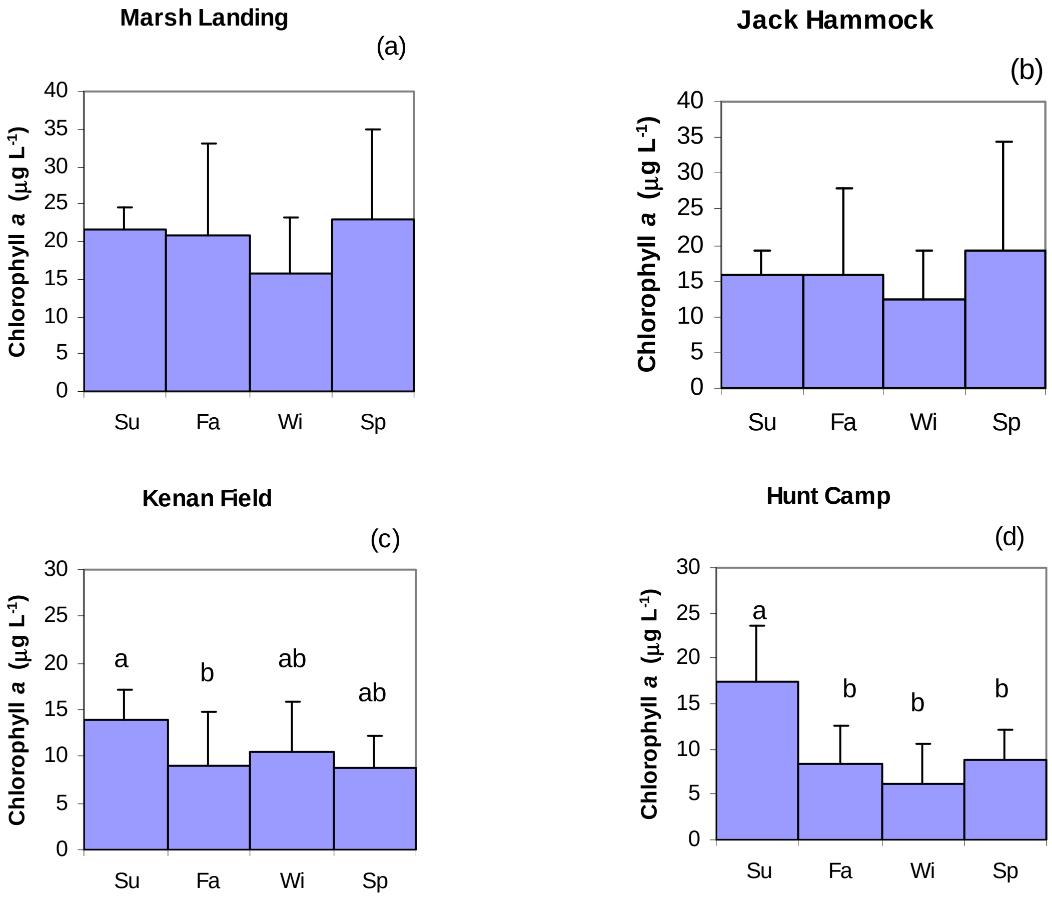


FIGURE 1.13. Particulate organic carbon (POC) concentration (± s.d.) over oyster reefs at mid-ebb water for the different seasons from June 2000 through June2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (Analysis of variance; Duncan's least significant difference post-hoc tests; seasonal differences denoted by letters; p-values are in Appendix I, Table I.2).



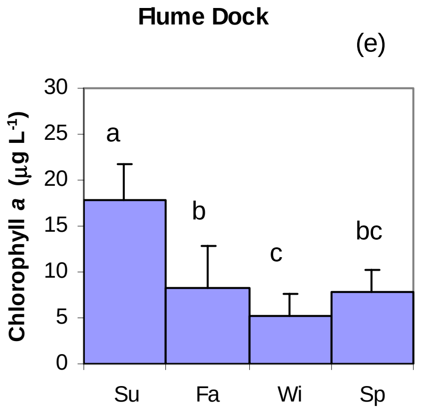


FIGURE 1.14. Chlorophyll *a* concentration (± s.d.) over oyster reefs at mid-ebb water for the different seasons from June 2000 through June2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (Analysis of variance; Duncan's least significant difference post-hoc tests; seasonal differences denoted by letters; p-values are

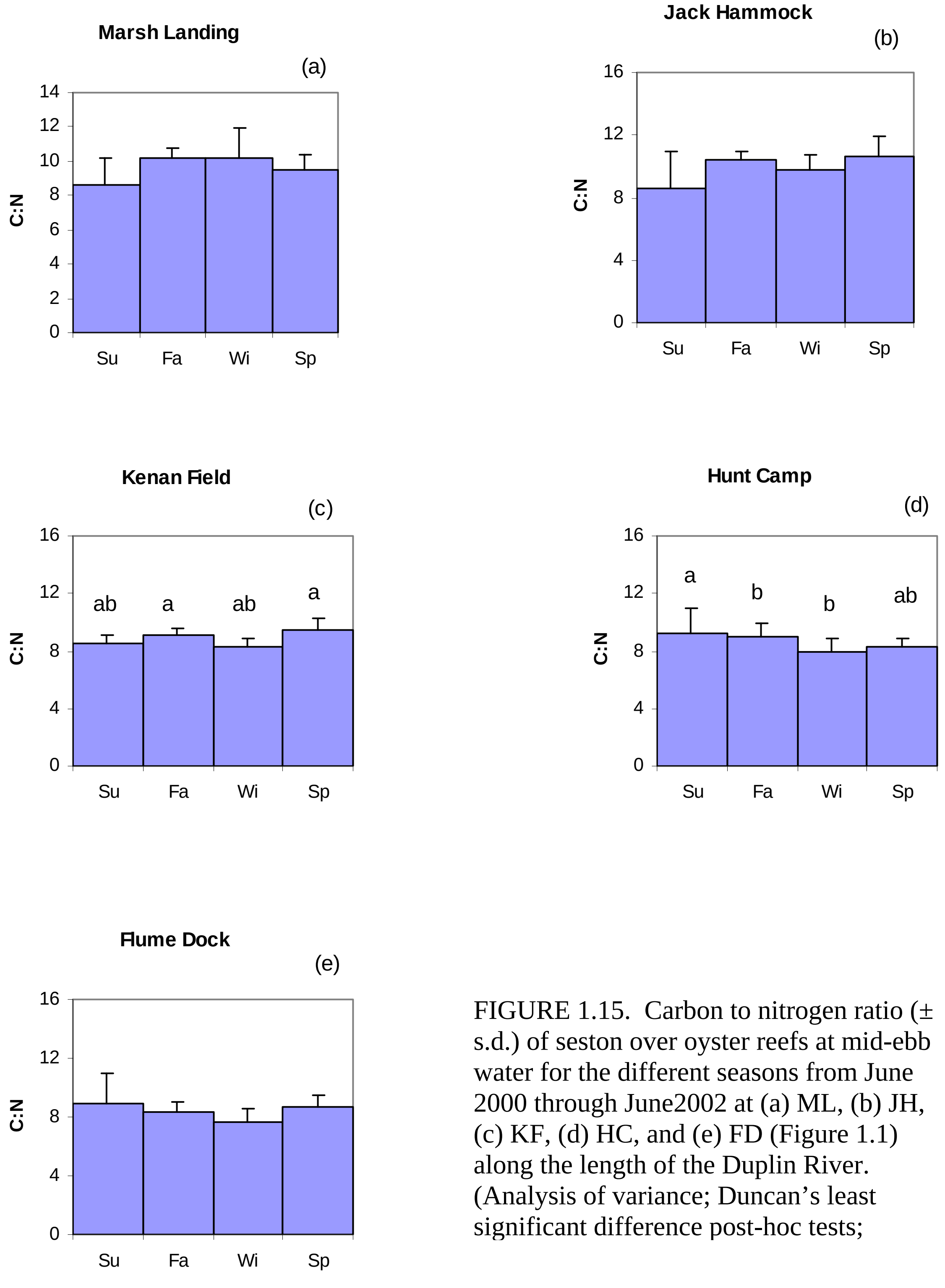


FIGURE 1.15. Carbon to nitrogen ratio (± s.d.) of seston over oyster reefs at mid-ebb water for the different seasons from June 2000 through June2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (Analysis of variance; Duncan's least significant difference post-hoc tests;

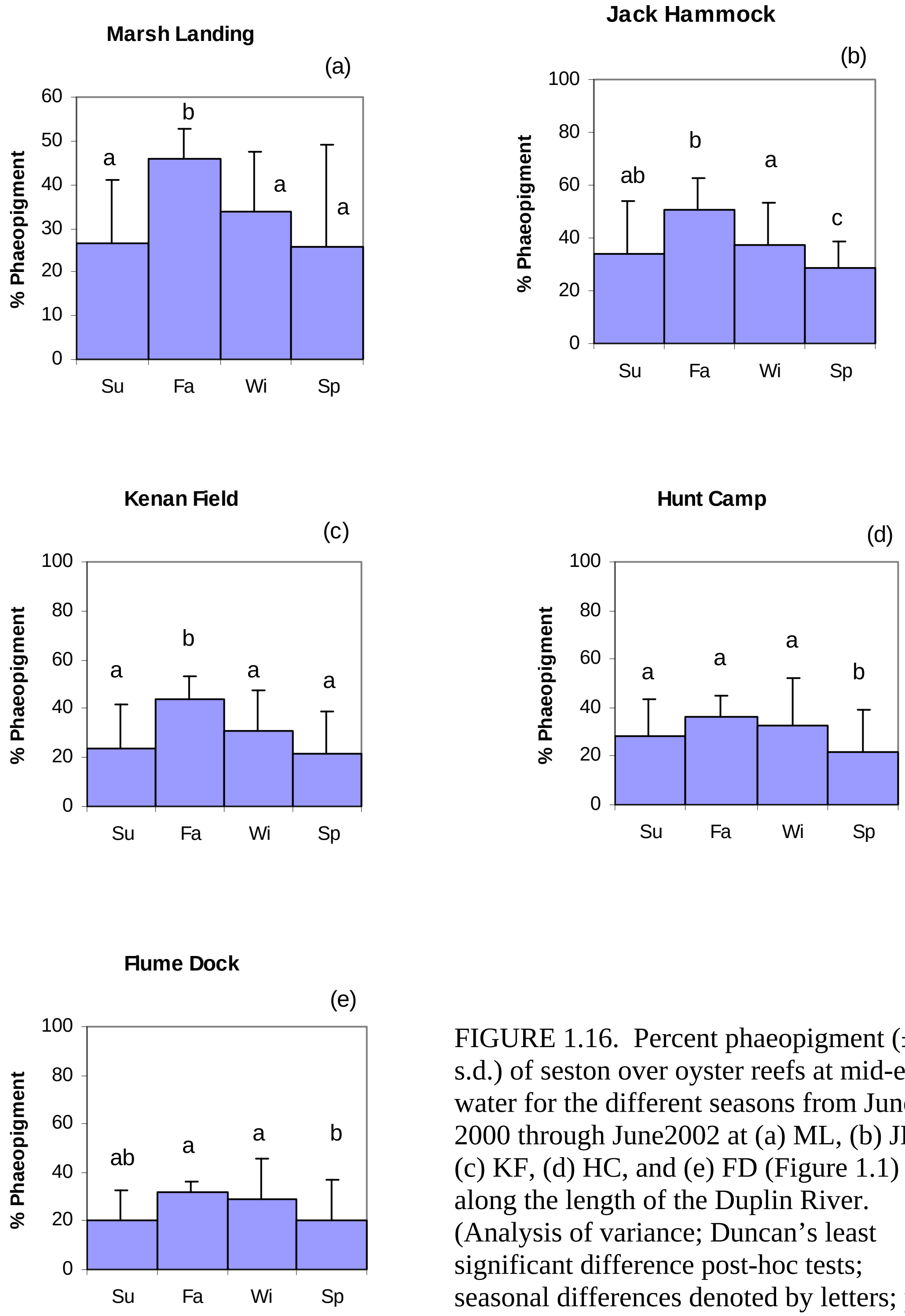


FIGURE 1.16. Percent phaeopigment (± s.d.) of seston over oyster reefs at mid-ebb water for the different seasons from June 2000 through June2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (Analysis of variance; Duncan's least significant difference post-hoc tests; seasonal differences denoted by letters; p-values are in Appendix I, Table I.5).

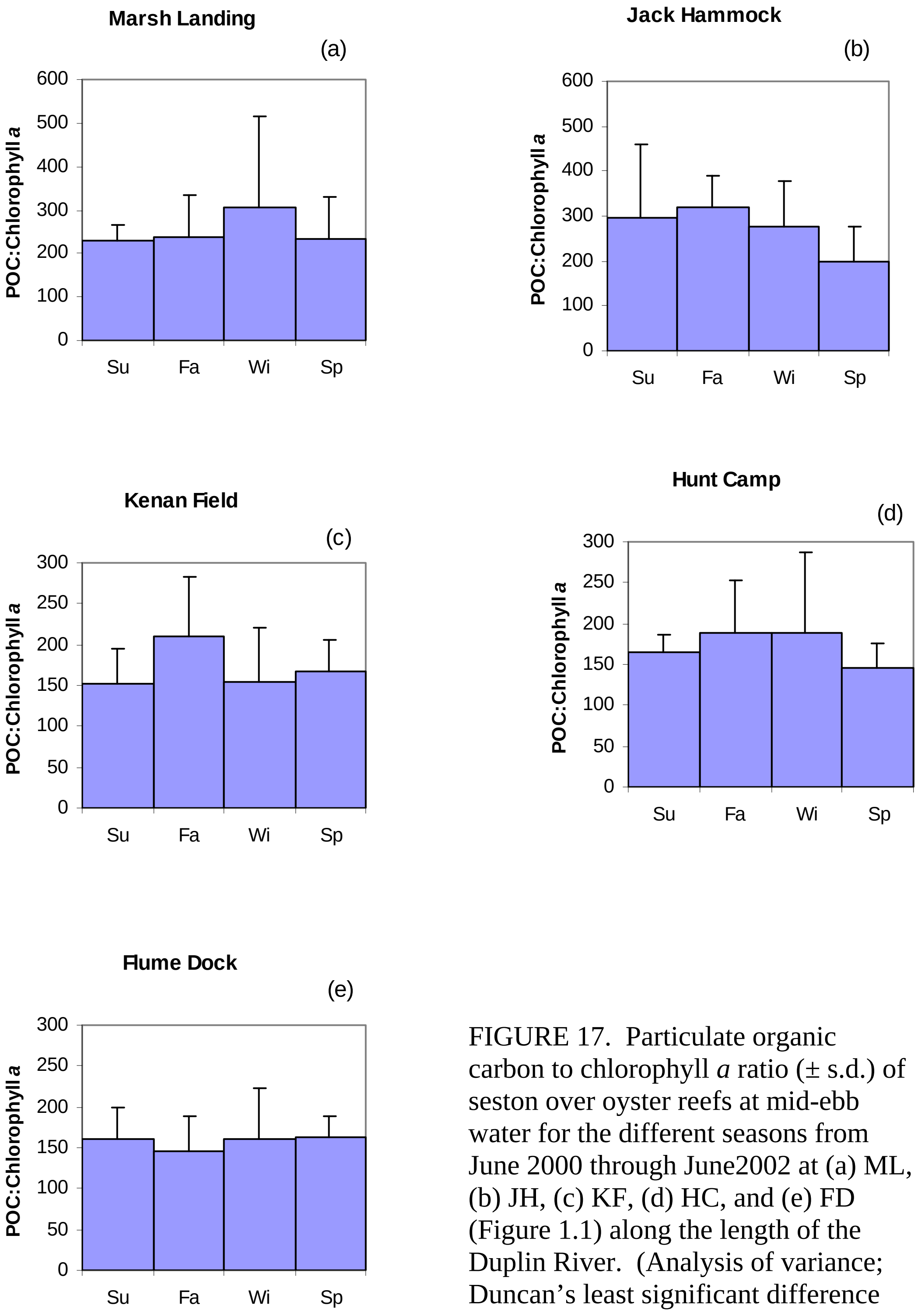


FIGURE 17. Particulate organic carbon to chlorophyll *a* ratio (± s.d.) of seston over oyster reefs at mid-ebb water for the different seasons from June 2000 through June2002 at (a) ML, (b) JH, (c) KF, (d) HC, and (e) FD (Figure 1.1) along the length of the Duplin River. (Analysis of variance; Duncan's least significant difference post-hoc tests; p-values are in

CHAPTER 2

BENTHIC DIATOMS IN SESTON AND EASTERN OYSTERS: PATTERNS OF SPATIAL AND SEASONAL ABUNDANCE[1]

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[1] Thoresen, M. and M. Alber. To be submitted to *Marine Ecology Progress Series*

Introduction

Bivalves are often the dominant suspension-feeder in estuaries and numerous investigators have focused on the feeding and nutrition of this significant group of consumers (Dame 1996). Although feeding studies in laboratory environments typically provide diets of phytoplankton and sometimes a varying proportion of inorganic silt, in natural estuarine environments these organisms utilize a diverse array of suspended particulate material or seston (Palmer 1980; Kiorboe & Mohlenberg 1981; Shumway et al. 1985; Bayne et al. 1987; Cranford and Grant 1990; Barille et al. 1994; Ward et al. 1994). The organic portion of the seston can originate from local sources such as phytoplankton, resuspended benthic microalgae, and detritus from salt marsh plants, macroalgae and seagrasses, or can be imported from terrestrial or nearshore oceanic sources.

Numerous studies that utilized the stable isotope composition of bivalve consumers as an indication of their food resources have found that bivalves can assimilate organic material from multiple sources although the relative contribution of each component varies. In riverine estuaries several isotopic studies have identified a trophic gradient from the head of the estuary to the open ocean, wherein the $\delta^{13}C$ signature of the particulate organic carbon (POC) in both the seston and bivalve consumers become progressively enriched, from values that reflect riverine detritus of terrigenous origin at the head of the estuary to values that reflect marine phytoplankton closer to the mouth (Incze et al. 1982; Riera & Richard 1996). In the Duplin River, a tidally-dominated salt marsh estuary on Sapelo Island, Georgia, where freshwater inputs are primarily limited to rainfall and groundwater, Haines (1976) and Haines and Montague (1979) found that oysters, (*Crassostrea virginica*), marsh mussels (*Geukensia demissa*), and the POC available to them reflected the $\delta^{13}C$ signatures of benthic and pelagic microalgae. In the Great Sippewissett Salt Marsh in Massachusetts, Peterson et al. (1985) examined the stable isotope signatures of carbon, nitrogen and sulfur in bivalves and found that both oysters and marsh mussels incorporated a combination of *Spartina*-derived detritus and phytoplankton, but that the further into the marsh the bivalves lived (i.e., further from the influence of oceanic sources of phytoplankton) the more heavily they relied upon detritus as a food resource. Based on these types of observations, it is evident that the food resources available in estuaries can vary on spatial scales and that sessile suspension-feeding bivalves utilize what is available to them locally.

One potentially important food for suspension-feeders is benthic microalgae. Benthic microalgae are significant primary producers in estuaries that can contribute to the diets of suspension feeders when they are displaced from the sediments and become suspended in the water column (MacIntyre et al. 1996). In the Ems-Dollard estuary resuspended benthic microalgae were estimated to provide ~50% of the available food to filter feeders living on mudflats (e.g., *Macoma balthica* L., *Cerastoderma edule* L., and *Mytilus edulis* L.) (De Jonge & Van Beusekom 1992). Riera and Richard (1996) found that Pacific oysters (*Crassostrea gigas*) living adjacent to extensive mudflats in the Bay of Marennes-Oleron, France, had isotopic signatures that were similar to benthic diatoms and inferred that they were important to their diet. Newell et al. (1989) found that over two-thirds of the algal species identified in gut contents of mussels (*Mytilus edulis*) were of benthic origin. In a follow-up to this study, Muschenheim and Newell (1992) found that the mussels were selectively feeding on large resuspended benthic diatoms (*Gyrosigma* *balticum* and *Navicula* spp.) that were only prevalent in the seston within 5 cm of the bottom and were rapidly depleted as they were advected over the mussel beds. Working in Carpinteria Salt Marsh in California, Page (1997) found that the isotopic signatures of suspension feeding bivalves were intermediate between benthic microalgae and phytoplankton, suggesting that both were contributing to their diet.

Patterns of benthic microalgal availability and their potential contribution to the diets of bivalves will vary on both temporal and spatial scales in estuaries. On short-term time scales, changes of tide or wind-events can resuspend benthic microalgae and contribute significant amounts of chlorophyll *a* to the water column (Roman & Tenore 1978; Baillie & Welsh 1980; Roman et al. 1983; Shaffer & Sullivan 1988; Demers et al. 1987; De Jonge & Van Beusekom 1992; Schreiber & Pennock 1995). Over lunar cycles the contribution of benthic microalgae to water column chlorophyll *a* will also vary. Zurburg et al. (1994) found that spring tides were typified by higher seston levels and an increased contribution of benthic chlorophyll *a* to the water column and Prou (1991) reported that benthic diatoms accounted for 50% of the total diatom forms during spring tides as opposed to only 10% during neap tides. Over seasonal cycles in the Peel-Harvey estuary, Australia, benthic microalgae achieved maximum biomass when phytoplankton blooms declined. At those times, chlorophyll *a* concentrations in the sediment greatly exceeded (e.g., a factor of 40) those in the water column. In this same study they also found that resuspension is seasonally influenced and is most important in the summer when this system is exposed to prolonged periods of high winds (Lukatelich & McComb 1986). Seasonal patterns of availability were also identified by Zurburg et al. (1994), who suggested that resuspended microphytobenthos made a large contribution to the diet of Pacific oysters and mussels in the Bay of Marennes-Oleron, especially during the winter. In North American salt marshes the seasonal cycle of microalgal production is different from higher plants, in that and much of the benthic algal production occurs during the winter months when macrophytes are dormant. Thus, the potential contribution of the benthic algae to total energy flow is greater at these times (Gallagher & Daiber 1974; Van Raalte et al., 1976).

In a review of the ecological role of microphytobenthos in food webs, Miller et al. (1996) pointed out that stable isotope studies confirm its importance to the diet of many organisms and suggested that resuspension could potentially provide estuarine filter feeders with a significant food resource. However, they also emphasized that little is known about the consumption of microphytobenthos in quantitative terms, and that most studies had been conducted under laboratory conditions. The goal of the current research was to investigate the potential contribution of benthic diatoms to the diets of eastern oysters (*Crassostrea virgincia*), the dominant suspension feeder in the Duplin River estuary, Georgia (Harris 1980).

The Duplin River is a 12.5 km tidal inlet within the Sapelo Island National Estuarine Research Reserve (SINERR) in coastal Georgia. It is approximately 80% intertidal salt marsh and mudflat and supports extensive intertidal oyster reefs (Harris 1980) which might utilize benthic microalgae. In an extensive study of the benthic microalgae on Sapelo Island, Williams (1962) determined that pennate diatoms comprised 75-93% of the total microalgal biomass. Also working on Sapelo Island, Pomeroy (1959) found that annual gross benthic algal production was approximately 200 g C m^{-2} or about nearly 25% of aerial *Spartina alterniflora* productivity and accounted for 10% of the productivity of the entire salt marsh estuary (Pomeroy et al. 1981). Stevens (1983) made several interesting observations with regard to benthic diatoms in relation to oyster reefs in Flume Creek, a tidal tributary at the mouth of the Duplin River: 1) reef associated sediment contained almost twice as many benthic diatom cells as non-reef sediment, 2) twice as many diatoms were found in suspension over reefs, and 3) a major component of the phytoplankton found over reefs was *Navicula*, a benthic diatom. Given that the tidal range is 2-3 m in this system, there is ample physical energy for resuspension during the semi-diurnal changes of tide. Gallagher (1975) observed that benthic pennate diatoms were lifted from the marsh sediments as a surface film during the flooding tide and found that over one-third of the net photosynthesis of the water column occurred in this film. It is also interesting to note that in this system, where tidal asymmetery results in greater ebb velocities than flood, oysters exhibit a slight statistical preference to orient with ebb-current direction, which would optimize the delivery of resuspended food (Frey et al. 1987). Given these types of observations we expect that benthic microalgae could make a significant contribution to the diets of oysters living in this salt marsh estuary.

In the previous chapter we examined the spatial and temporal variation in the seston over oyster reefs in the Duplin River. The system is generally very turbid (SPM concentrations average 100-300 mg L^{-1}) and is predominantly detrital: POC to chlorophyll *a* ratios are in excess of 100, averaging 217 ± 127 (mean ± s.d.) throughout the inlet, which is indicative of a POC pool that is mostly non-living detrital material (Zeitzschel 1970). We found greater concentrations of material at the mouth (almost three times the concentration of suspended particulate material (SPM) and particulate organic carbon (POC) and almost twice the concentration of chlorophyll *a*) as compared to the headwaters. There were also differences on temporal scales, particularly over tidal scales at the mouth (higher concentrations during late flood/high slack as compared to ebb-water), lunar scales at most sites (higher concentrations during spring as compared to neap tides) and seasonal cycles at all of the sites (higher concentrations during spring and summer). We therefore expected to see both spatial (headwaters vs. mouth) and temporal (seasonal) differences in the contribution of benthic diatoms to the seston and the diets of oysters in the Duplin River.

Materials and Methods

Sampling regime

To allow us to look at both spatial and temporal variation in the availability of benthic diatoms and their utilization by oysters, sampling was done at 2 oyster reefs (one located at the headwaters an one located at the mouth of the Duplin River; see Fig. 2.1) over a period of two years. At the headwaters, the oysters form mounds or clumps that are interspersed across an intertidal mudflat and the main channel of the river is narrow and dendritic, splitting off into numerous tidal creeks that bisect the surface of the surrounding salt marsh. At this location, tidal energy is responsible for a majority of the water movement. At the mouth of the Duplin River the main channel widens as it opens into Doboy Sound and the mixing regime is influenced by the nearshore Atlantic Ocean and the Altamaha River in addition to the strong tidal currents. At the mouth, the oyster reefs located in this open-water environment form channel-edge reefs of living oysters and dead shell that expand from the edge of the *S. alterniflora* down to the mean low water mark. Over the two-year study period (June 2000 through June 2002) sampling was conducted at 5-week intervals for a total of twenty sampling trips. During each sampling event seston and suspended diatoms were sampled from above oyster reefs during mid-ebb water and oysters and sediments were sampled during low water.

Water sample collection and pre-processing

Water was pumped using a Cole Parmer MasterFlex® peristaltic pump (Vernon Hills, Illinois). Either end of the PharMed® tubing (Maple Plain, Minnesota), that ran through the pump apparatus was fitted to nalgene tubing (I.D. 0.8 cm) using brass adaptors. The intake end was then passed through an approximately 3 m long, 5 cm diameter PVC pipe and out through a hole that was drilled about 10 cm from the end of the pipe. A dive weight (~2.27 kg) was attached to the end of the pipe so it could be deployed down through the water column and maintained in a stable and upright position while water was pumped from approximately 10 cm above the oyster reefs. At the outflow end an additional length of nalgene tubing was spliced to the Master flex tubing and was used to fill replicate two liter nalgene bottles that were kept on ice and in the dark until they could be processed (within 2 h). In addition, approximately 10 L was filtered through a 10 µm mesh phytoplankton net and the concentrated plankton sample was transferred to a 125-ml nalgene bottle and preserved with 37% formalin at a final concentration of 2%. This was done twice for a total of two replicate phytoplankton samples and these samples were transported on ice to the laboratory where they were stored in a refrigerator prior to processing.

HPLC analysis of seston.

At quarterly intervals over the course of the two-year study seston samples that were collected from above the oyster reefs were analyzed for phytopigment composition by

HPLC. In addition to the headwaters and the mouth three additional sites along the length of the river were also sampled. To prepare these samples, a known volume of water (25-200 ml depending on seston concentration) was filtered onto pre-combusted 25 mm Whatman GF/F filters (nominal pore size 0.7 μm) and placed immediately into liquid nitrogen for transport to the laboratory where they were stored at -70ºC prior to processing. Due to the fact that much of the particulate material was in these samples consisted of inorganic silt and sediment as well as detritus, it was difficult to collect enough algal material for pigment extraction and we had to pool our replicate filters (3) from each bottle. HPLC analysis of pigments (chlorophylls, phaeopigments, carotenoids, and xanthophylls) was performed as described by Nelson (1993) using a binary gradient system and Shimadzu components.

Sediment chlorophyll analysis.

Sediments for benthic chlorophyll *a* and phaeopigment determination were collected at approximately five-week intervals during the second year of the study (June 2001 through June 2002). However, rain events prevented us from sampling in June 2001 and May 2002 when sediments were visibly scoured so we have a total of 8 observations of sediment chlorophyll *a*. (Numerous researchers working at Sapelo have observed significant scouring and erosion of intertidal sediments when there is rainfall during low water, and Williams (1962) found that this led to a drastic reduction of benthic diatom standing stocks.) During each sampling event two sediment cores were taken from each site during low water. Cores were taken using 14 cm diameter, 12 cm high PVC tubes that were pushed 6 cm into the sediment. A rubber-flushing cap was placed over the top of the tube to create suction and ensure that the sample remained intact when it was pulled from the substrate. The capped PVC tube was then placed in a plastic container and put on ice in a cooler for transport. Three portions of approximately 1 cm^2 area of surficial sediment (upper 2-3 mm) was then sub-sampled from each core and each one was placed in an individual pre-weighed 15 ml centrifuge tube and kept frozen at 0º C for transport to the laboratory where they were stored at -70º C prior to analysis. Samples were ground and extracted in 90% acetone and the concentration of chlorophyll *a* and phaeopiments in the extract was determined fluorometrically (Parsons et al. 1984). To be able to quantify chlorophyll *a* and phaeopigment concentration per gram dry sediment the acetone was discarded after analysis and the extracted material was dried at 50º C for approximately 72 h and then weighed.

Percent benthic and planktonic diatoms

Seston was analyzed to determine the relative proportion of benthic and planktonic diatoms in the phytoplankton samples that were pumped from over the oyster reefs. In the laboratory each of the formalin-preserved phytoplankton samples was concentrated via a series of centrifuge cycles at 3600 rpm so that all the particulate material was contained in one 10 ml volume. The samples were then transferred to a glass test tube and 10 ml of a 2:1 (69.0-70.0%) nitric and (minimum of 51.0%) sulfuric acid mixture was added. The tubes were then placed in a hot water bath and maintained at a low boil until obvious signs of oxidation concluded. Final oxidation was achieved by adding several drops of 30% hydrogen peroxide (as adapted from Hasle & Fryxell 1970). The solution was then centrifuged again, the supernatant was decanted, 10 ml of deionized water was added as a rinse and the sample was centrifuged again. This rinse/centrifugation step was repeated two more times and the final 10 ml was used for slide preparation. A range of 100 to 400 μl, depending on the visible concentration of particulates, was then pipetted onto a clean dry coverslip and allowed to dry overnight. Once the sample was completely dried the coverslip was turned over onto a clean, dry glass slide and the procedures for permanent slide mounting using Meltmount 1.704 (Cargille Laboratories Inc., Cedar Grove, New Jersey) were followed. For each slide a total of 600 diatom frustules were counted at 100-200X (300 cells) and were identified as either pennate or centric. The proportion of pennate frustules was taken to be the percent of benthic diatoms in the sample (Hasle & Fryxell, 1970). An example of a diatom preparation for a seston sample is provided in Fig. 2.2A.

Oysters were also analyzed to determine the proportion of benthic and planktonic diatoms in their guts. The oysters were collected from each site during low water and kept cold until they could be processed (within 2-3 h). Three oysters from each site were randomly selected for this analysis. In each case, shell length from umbo to outer shell margin was measured to the nearest 0.1 mm with Vernier calipers, oysters were opened and their digestive glands were removed. Samples were preserved in 2% formalin and filtered seawater and refrigerated until processing. Samples were analyzed as described above for the seston samples except that 5 mls of the acid mixture was added to the samples instead of 10 mls, and when the rinse/centrifugation series was completed all except approximately 100 μl of supernatant was removed from the tube and the remaining volume (which contained the concentrated sample material) was pipetted onto a clean, dry, coverslip. An example of a diatom preparation for an oyster sample is provided in Fig. 2.2B.

Stable isotopes analysis.

At quarterly intervals over the course of the two-year study both seston and oysters were also sampled for stable isotope analysis. For the water samples a known volume (25-200 ml depending on seston concentration) was filtered onto 25 and 47 mm pre-combusted Whatman GF/F filters (nominal pore size 0.7 µm) and placed immediately into liquid nitrogen for transport to the laboratory where they were stored at -70ºC prior to processing. Filters were then dried at 50º C for approximately 72 h, excess filter around the edges was trimmed off and the filters were placed in pre-combusted 7 ml glass scintillation vials. Oysters were sampled from each site at low water and kept cold until they were processed. Ten oysters were randomly selected from each site and shell length from umbo to ventral shell margin was measured to the nearest 0.1 mm with Vernier calipers. Each oyster was opened, and the adductor muscle was removed, rinsed with deionized water and wrapped in pre-combusted aluminum foil and frozen at 0ºC for transport and then stored at -70ºC. To prepare them for stable isotope analysis, tissues were then dried at 50ºC, finely ground with a Wig-L Bug® (Crescent Dental, Lyons, Illinois) and then placed in pre-combusted 7 ml glass scintillation vials. Both the seston and tissue samples were submitted to Coastal Sciences Laboratory, Austin, Texas, for determination of stable isotopes of carbon and sulfur using a VG (Micromass© Unlimited UK) mass spectrometer with reference standards of NBS 22 for carbon and IAEA S1 and S2 for sulfur.

We initially examined stable isotopes of carbon and sulfur for oyster and seston samples collected at each site in January, April, July and October 2001 to see if there were any differences in δ^{13}C isotopic composition at these different times of year. There were no apparent temporal trends in the seston or the oysters in these preliminary results so we pooled the samples across these dates but kept the sites separate. Combining filters across sample dates allowed us to get enough material to obtain a ^{34}S signature for the seston. Oyster tissue from each site was pooled across all of the quarterly trips (the four listed above plus June and October 2000 and January and May 2002).

In November 2003, we collected additional samples of oysters and benthic microalgae from our study sites in order to conduct additional stable isotope analysis. The oysters were sampled utilizing the methods outlined above to obtain adductor tissues for analysis. Benthic microalgae were collected during low water from intertidal sediments around the oyster reefs at each site utilizing the net technique, which takes advantage of the vertical migration of benthic diatoms at low water (Darley et al. 1979). Immediately after the water receded enough to expose the sediments, 10 “plots” were laid out at each site and sprayed with twice-filtered (0.7 µm) seawater. Each “plot” consisted of one layer of a 12 x 18 cm sheet of 150 µm mesh Nitex® that was placed on the surface of the sediment, with a smaller (10 x 15 cm) piece of 75 µm mesh Nitex® placed on top of it. The plots remained in place until maximum low water and then they were carefully retrieved, the two layers of mesh were separated and the upper sheet (where most of the cells were) was rinsed with twice-filtered (0.7 µm) seawater into a 250 ml glass filter apparatus fitted with a pre-combusted, 47 mm, GF/F filter to collect the benthic microalgae. The filters were dried at 50 º C for approximately 72 h and were submitted to Coastal Sciences Laboratory for stable isotope analysis.

Data analyses

Statistical analyses of sediment chlorophyll *a* concentrations and the percentage of benthic diatoms in seston and oysters were used to identify significant differences between the two sites and among the seasons within each site. For the seston HPLC data, a linear regression was used to examine the amount of variability in chlorophyll *a* concentration that could be explained by fucoaxanthin concentration. Concentrations of sediment chlorophyll *a* were compared among the sites using Independent Samples Student T-Tests and analysis of variance (ANOVA) was used to examine seasonal differences within each site with post-hoc analysis using Duncan's least significant difference procedure to identify the specific differences among the seasons. General linear model (GLM) procedures were used to compare the sites in terms of percentage of benthic diatoms in seston and oysters, and ANOVA was used to identify differences among the four seasons within each site with post-hoc analysis using Duncan's least significant difference procedure to identify the specific differences among the seasons. A linear regression was used to examine the relationship between the percentage of benthic diatoms in the seston vs. the percentage of benthic diatoms in the oysters. The Student T-Tests, ANOVA and post hoc analyses were performed using SPSS for PC (SPSS Inst., Inc. 2000) and the GLM analyses were performed using SAS for PC (SAS Inst., Inc. 2000). The number of sampling efforts used to compile the seasonal sediment chlorophyll *a* data for year two (Table 2.1; Figure 2.4) are as follows: summer (2), fall (3), winter (2) and spring (1). The number of sampling efforts per season reported as "n" in Table 2.2 and Figures 2.8 and 2.9 are as follows: summer (6), fall (5), winter (4), and spring (5). No statistical analyses of the stable isotope data were performed due to the small sample size.

Results

Chlorophyll a *Concentration in Sediments*

Sediment chlorophyll *a* concentrations (mean ± s.d.) were comparable between the mouth (69.0 ± 24.0 µg g^{-1} dry wt.) and the headwaters (74.9 ± 48.1 µg g^{-1} dry wt.) of the Duplin River (Table 2.1). Our observed values are also generally high compared to observations made in estuaries in the southern U.S. In seagrass beds in Mississippi Sound, Daehnick et al. (1992) observed a range of chlorophyll *a* concentrations from 26 to 86 mg m^{-2} with an average value of 44 ± 19 mg m^{-2}. (These data and the following were reported in units that are scaled up to mg m^{-2} thus, our reported values have to be multiplied by 10 to be in equivalent units for comparison and scaling up to 1 m^2 probably over estimates sediment chlorophyll *a* concentrations.) In North Inlet, South Carolina sediment chlorophyll *a* concentrations ranged from 24 to 93 mg m^{-2} (Pinckney & Zingmark 1991). A large range of sediment chlorophyll *a* concentrations (~50 to 400 mg m^{-2}) were observed in a microbial mat community on an intertidal sand flat in North Carolina (Pinckney et al. 1995). Our values greatly exceeded even the high range of these observations, which likely is the result of the fact that we sampled close to oyster reefs. Other researchers have observed increased sediment chlorophyll *a* concentrations in oyster reef-associated sediments (Stevens 1983).

Sediment chlorophyll *a* concentration at both stations exhibited a similar peak in February, but there was a large peak in September at the headwaters that was not observed at the mouth (Fig. 2.3). When analyzed on a seasonal basis the mouth had significantly higher concentrations of chlorophyll *a* in the winter as compared to the other seasons ($p < 0.001$) (Fig. 2.4B), whereas the headwaters had significantly higher concentrations in the fall as compared to the summer ($p = 0.004$) (Fig. 2.4A). Many factors influence primary production rates over the course of the year but high water and air temperatures during early September probably contributed to the increase in microalgal biomass that we observed at the headwaters (Pomeroy 1959). It is unclear why a similar increase was not observed at the mouth, but it may be due to the fact that the sampling location at this site was close to the *S. alterniflora* at the edge of the channel, which may have shaded the microalgae. Other researchers have observed an increase in benthic microalgal biomass during the late fall and winter months when vascular plants dieback and more sunlight can reach the sediments (Gallagher & Daiber 1974; Sullivan & Daiber 1975; Van Raalte et al. 1976). The peak concentrations of microalgae observed during the winter at both sites coincides with a time of year when benthic microalgae can be highly productive. When microalgae are fully exposed at low water the lower light intensities during this time of year leads to decreased photo-inhibition, whereas when they are submerged, decreased water column turbidity allows for more light to reach the bottom (Pomeroy 1959). From our observations of the seston in chapter one we know that except for during storm events, turbidity tends to be low during the winter months.

Seston Pigment analysis

Phytopigment analysis of the seston confirmed the importance of diatoms to the microalgal community in the water column of the Duplin River. Fucoxanthin, an accessory pigment of diatoms, was present in all samples collected quarterly along the length of the river. Ratios of fucoxanthin to chlorophyll *a* in pure cultures of diatoms range from approximately 0.6 to 0.8 (Jeffrey et al. 1997) and the ratios in our samples ranged from 0.2 to 0.5, providing evidence that diatoms are a significant component of the microalgal community in this system. When chlorophyll *a* is plotted against fucoxanthin it is clear that much of the observed chlorophyll *a* dynamics can be explained by changes in fucoxanthin ($R^2 = 0.97$) (Fig. 2.5). The only exceptions occurred during the July sampling at the two headwaters sites, where there were high concentrations of peridinin due to a dinoflagellate bloom (outliers noted on Fig. 2.5). Dinoflagellate blooms during summer months have been reported previously in the headwaters of the Duplin River (Ragotzkie & Pomeroy 1957). (These points were excluded from the regression analysis.)

Although these observations provide evidence that diatoms are responsible for much of the variation in chlorophyll *a* concentration in the Duplin River, it does not distinguish between planktonic forms and benthic diatoms that are resuspended due to tidal or wind energy or are scoured from the marsh surface and channel edges during rain events (Williams 1962; Roman & Tenore 1978; Baillie & Welsh 1980; Roman et al. 1983; Demers et al. 1987; Shaffer & Sullivan 1988). Additionally, some caution needs to be used in the interpretation of pigment information because it is influenced by a large number of factors including light, temperature, nutrient regime and growth status (Cariou-LeGall & Blanchard 1995; Barranguet et al. 1997; Bianchi & Argyrou 1997; Lucas & Holligan 1999; Lucas et al. 2000; Cahoon & Safi 2002).

Proportions of Benthic and Planktonic Diatoms

The proportion of benthic diatoms in seston ranged from 9 to 50% over the course of the study with consistently higher proportions in the headwaters (36.6 % ± 7.3) (mean ± s.d.) as compared to the mouth (16.9% ± 5.7) (GLM $p < 0.001$) (Table 2.2; Fig. 2.6A). There were no clear temporal patterns, but peak concentrations did occur at similar times during both years of the study: at the mouth we saw peaks in January 2001, March 2001 and January 2002 whereas at the headwaters the percentage of benthic diatoms in the seston remained high July through December 2000 and again from August through December 2001. When these data were analyzed in terms of seasonal categories we observed significant seasonal trends in the contribution of benthic diatoms to the seston at both locations, with significantly higher proportions of benthic diatoms in the winter as compared to the spring (ANOVA mouth $p = 0.047$; headwaters $p = 0.017$) (Fig. 2.8). From our examination of seston in the previous chapter we know that water column chlorophyll *a* concentration begins to increase in April throughout the Duplin River and the increased contribution of planktonic diatoms to the seston is probably responsible for the spring decrease in the proportional contribution of benthic diatoms.

As in the seston, we consistently saw a greater percentage of benthic diatoms in the oysters at the headwaters (33.3% ± 13.2) as compared to those at the mouth (21.0% ± 9.8) (GLM $p < 0.001$) (Table 2.2; Fig. 2.6B). The percent benthic diatoms in oysters at the headwaters was significantly higher in the fall as compared to the summer and spring (ANOVA $p < 0.01$) and in the winter as compared to the spring ($p = 0.035$) (Fig. 2.9). These fall and winter peak at the headwaters coincided with times when chlorophyll *a* concentration in the sediments was the highest and, based on our findings in the previous chapter, water column chlorophyll *a* concentrations were the lowest. This observation illustrates the potential importance of benthic microalgae as a food resource during periods (i.e., winter) when the contribution of other salt marsh producers is at a seasonal minimum (Gallagher & Daiber 1974; Van Raalte et al. 1976).

At both stations the peaks in the percentage of benthic diatoms in the oysters generally coincided with those that were observed in the seston. Indeed, there was a fairly good relationship between the percentage of benthic diatoms in the seston versus those in the oysters ($R^2 = 0.64$) (Fig. 2.7). This suggests that, overall, oysters consume benthic diatoms in proportion to their availability in the seston.

Stable Isotopes

The $\delta^{13}C$ signature of seston samples pooled over the course of the study was –20.0‰ at the mouth of the Duplin River and –21.7‰ at the headwaters (Table 2.3). These values are slightly enriched as compared to reported values of $\delta^{13}C$ of the seston in phytoplankton-dominated systems (Peterson et al. 1986; Currin et al. 1995; Deegan & Garritt 1997; Wainright et al. 2000) but they are comparable to previous observations in the Duplin River (Haines 1976; Haines & Montague 1979; Peterson & Howarth 1987). Estuarine phytoplankton have $\delta^{13}C$ signatures that range between –22 and -30‰ (Deegan & Garritt 1997), whereas the average $\delta^{13}C$ signature of detrital *S. alterniflora* is –15.0‰ and that of benthic microalgae is –16.6‰ (Currin et al. 1995), so the enrichment of the seston in the Duplin River could reflect contributions from either of these sources. Based on our seston observations in the previous chapter, we know that our particulate material has high carbon to chlorophyll *a* ratios (> 100) and that our POC pool is primarily detrital rather than living phytoplankton and we also have observed benthic diatoms in the seston. Therefore, we can probably attribute our slightly enriched $\delta^{13}C$ values, relative to phytoplankton, to the contribution of detritus and benthic microalgae to the seston at our study sites.

The $\delta^{34}S$ signature of the seston samples analyzed in this study was +3.9 ‰ at the mouth and +8.5 ‰ ± 0.1 at the headwaters (Table 2.3). If our samples were predominantly phytoplankton we would expect to see a value closer to seawater sulfate (+20.0‰) (Peterson et al. 1986) whereas both *S. alterniflora* and benthic microalgae utilize reduced sulfur and have lower values [–5.1 to +9.0‰ for detrital *S. alterniflora* (Deegan & Garritt 1997) and +4 to +14‰ for benthic microalgae (Sullivan & Moncrieff 1990)], so again the values we observed suggest that one or both of these sources may be important. There are not many observations of $\delta^{34}S$ of seston in the literature but Peterson et al. (1986) reported a value of +18.6‰ for a mixture of diatoms and copepods (153 µm size fraction) and Wainright et al. (2000) reported a range of +0. 5 to +3‰ for total particulate material in Delaware Bay (0.7 µm and larger). Wainright et al. (2000) offered several possible explanations for their depleted ^{34}S values, including the presence of resuspended benthic microalgae, contamination with reduced inorganic sulfur, or reduced availability of seawater sulfate at lower salinity study sites

The oysters collected over the course of the two-year study had a $\delta^{13}C$ signature of –18.6 ‰ ± 0.1 at the mouth as compared to –21.3 ‰ ± 0.1 at the headwaters. Our preliminary review of the isotopic data did not indicated a seasonal shift in the diet of the oysters in the Duplin River and the data we report are from tissue samples that were pooled across our sample dates. Note that these values are slightly lower than the signatures of oysters collected in November 2003 (19.8‰ ± 0.1 at the mouth and -22.1‰

± 0.1 at the headwaters) (Table 2.3 & 2.4). All of these observations are in keeping with previous observations on Sapelo Island [Haines (1976) reported $\delta^{13}C$ signatures for oysters that were –21.0‰ and Peterson & Howarth (1987) reported values of –18.8‰ and –19.1‰]. These values suggest that the oysters are relying heavily on phytoplankton, but since they are slightly enriched it is again likely that *S. alterniflora* detritus and/or benthic microalgae contribute to their diets.

The $\delta^{34}S$ signature of the oysters collected over the 2-year study period averaged +16.8‰ ± 0.2 at the mouth and +15.5‰ at the headwaters. These values are slightly higher than the signatures of the oysters collected in November 2003 (+15.5‰ at the mouth and +13.5‰ ± 0.1 at the headwaters) (Table 2.3 & 2.4). Peterson and Howarth (1987) reported $\delta^{34}S$ signatures for oysters on Sapelo Island of +13.4‰ and +14.1‰. When they examined both the carbon and sulfur isotope data of the oysters in their study they noted that these consumers had a lower $\delta^{34}S$ value than one would expect for an organism that had a $\delta^{13}C$ value that was so similar to phytoplankton, and that either the food resources of the oysters were poorly classified or *S. alterniflora* detritus, benthic microalgae and/or sulfur bacteria were contributing to their diets.

The benthic microalgae at our study sites had $\delta^{13}C$ signatures of –19.1‰ at the mouth and –17.7‰ ± 0.1 at the headwaters and $\delta^{34}S$ signatures of 7.1‰ and 9.7 ‰ ± 0.1, respectively (Table 2.4). Currin et al. (1995) reported an average $\delta^{13}C$ value of –16.6‰ for microalgae that was based on values compiled from the literature, and is close to the –17.4‰ they observed in a North Carolina salt marsh and the –16.7‰ Peterson and Howarth (1987) observed on Sapelo Island. Our values at the headwaters are comparable to these other observations but our values at the mouth are slightly depleted although they compare well with the –20.6‰ reported by Sullivan and Moncrieff (1990) in a Mississippi salt marsh. There are very few published values for $\delta^{34}S$ given the technical difficulty of getting enough microalgal biomass that is free of detritus and sediment for the sulfur analysis. Our ^{34}S values for benthic microalgae were in the middle of the range of +2 to +13‰ reported by Wainright et al. (2000) for benthic microalgae in Delaware Bay and the +4 to +14‰ reported by Sullivan and Moncrieff (1990) for edaphic algae in the Graveline Salt Marsh, Mississippi.

Given our goal of understanding the potential contribution of benthic diatoms to the diets of oysters, we coupled the stable isotope values of phytoplankton and benthic microalgae with our observations of the percentage of benthic diatoms in the oysters (21% at the mouth and 33% at the headwaters, Table 2.2) to predict what the isotope composition of oysters would be if diatoms were their predominant food source (i.e., if we do not consider detritus or other types of phytoplankton). We used our observed $\delta^{13}C$ and $\delta^{34}S$ values for the benthic microalgae at each location and published ^{13}C and ^{34}S values of –21.3‰ and 18.8‰, respectively for planktonic producers from Sapelo Island (Kaplan et al. 1963; Kaplan & Rittenberg 1964; Hartman & Nielsen 1969; Gearing et al. 1984) as reported by Peterson and Howarth, (1987). When we do this calculation the predicted the $\delta^{13}C$ and $\delta^{34}S$ of oysters at the mouth is –19.1‰ and +16.4‰ and at the headwaters is –20.1‰ and +15.8‰, respectively. These values compare fairly well with the observed isotopic composition of the oysters (Table 2.5). If the oysters consumed diatoms in proportion to their availability, as suggested by the regression of percent diatoms in seston versus oysters (Fig. 2.7) then these calculations can also be done using the percentage of benthic diatoms observed in the seston. When we do this, the predicted

$\delta^{13}C$ and $\delta^{34}S$ values for the oysters are even closer to what was observed (Table 2.5). Thus, the stable isotopic signatures provide independent confirmation of our direct observations of benthic diatoms in oysters and suggest that diatoms (both planktonic and benthic) are the primary food source of oysters in the Duplin River Estuary.

Discussion

The role of benthic diatoms as a significant resource for deposit feeders in salt marshes is well established, however more recently they have also been identified as a potentially significant food resource for suspension feeders (Miller et al. 1996). Benthic diatoms are made available to estuarine suspension-feeders when they are resuspended from the sediments due to wind-driven mixing or tidal currents (Roman & Tenore, 1978; Baillie & Welsh 1980; Roman et al. 1983; Demers et al. 1987; Shaffer & Sullivan 1988; De Jonge & Van Beusekom 1992; Schreiber & Pennock 1995). In shallow coastal waters both surface winds and tidal currents regulate mixing and on the inner shelf at the Georgia/South Carolina border 75-90% of the total energy of inner shelf waters is due to tidal energy (Redfield 1958; Pietrafesa et al. 1985). With a tidal amplitude of 2-3 m and a tidal excursion of 5-8 km, there is strong tidal mixing and a number of researchers have examined its influence on the temporal and spatial distributions of chlorophyll *a* in this region (Oertel & Dunstan 1981; Verity et al. 1993; Yoder et al. 1993; Verity et al. 1998). Working in the North Edisto estuary, South Carolina Verity et al. (1998) observed that pennate diatoms and centrics attached to detrital material or mineral grains accounted for 75% of all the diatoms observed in suspension at periods of maximum current velocities during flood and ebb tides. Across both of our sites in the Duplin River, benthic diatoms accounted for up to half of all the diatoms in suspension over oyster reefs. In North Inlet, South Carolina, Dame et al. (1986) observed that during ebb-water, 35% of the diatoms in the water column of tidal creeks were benthic. In the Gulf of Mexico wind-events rather than tides provide the energy for resuspension and in Barataria estuary, Louisiana, Shaffer and Sullivan (1988) observed that 74% of all the diatom taxa in the water column were benthic.

The contribution of benthic diatoms to the seston can vary spatially. In the Duplin River we observed a significantly higher percentage of benthic diatoms in the seston over oyster reefs at the headwaters as compared to the mouth even though sediment chlorophyll *a* concentrations were similar (Table 2.2; Fig. 2.3 & 2.6A). This may be because the upper water mass at the headwaters has increased exchange with the marsh surface at high water as compared to the mouth (Ragotzkie & Bryson 1955), resulting in a greater supply of benthic microalgae at this location. Spatial differences in the availability of benthic microalgae to consumers has been described in other estuaries. In Padilla Bay estuary, Washington, Ruckelshaus et al. (1993) observed that the percent of benthic algal species in the seston was higher in eelgrass beds (*Zostera marina*) and over mudflats as compared to neritic, open-water environments. In Perdido Pass, Alabama, Judge et al. (1993) found that 90% of the near-bottom microalgae were pennate diatoms over seagrass beds (*Halodule wrightii*) and that this represented a locally concentrated food resource for *Mercenaria mercenaria* living in seagrass as opposed to bare sand habitat. In the Hudson River estuary, Bianchi et al. (1993) observed high concentrations of chlorophyll *a* and fucoxanthin in sandy as opposed to silty habitats, and attributed their observations to the presence of benthic diatoms also noting that they provided a high quality (low C:N ratio) diet as compared to the detritus associated with the muddy areas.

There were no highly significant seasonal trends in the proportion of benthic diatoms in the seston, although the highest percentages were observed during the winter months at both the headwaters and the mouth (Fig. 2.8). Sediment chlorophyll *a* concentrations also peak in winter (Fig. 2.4) and this period of time is when we observed lower chlorophyll *a* concentrations in the water column (Chapter 1). It is therefore not surprising that benthic diatoms make a greater contribution to the pool of chlorophyll *a* over oyster reefs during winter. This supports the ideas of earlier workers, where benthic microalgae could provide greater food web support during the fall and winter when other marsh producers have decreased biomass and lower rates of productivity (Gallagher & Daiber 1974; Van Raalte et al. 1976). Benthic diatoms dominate the production in Barataria and Caminada Bays in Louisiana during the fall but increased dissolved organic carbon concentrations during winter storms were attributed to the release of soluble organic matter by benthic diatoms (Happ et al. 1977). In Biscayne Bay, Florida, Roman et al. (1983) found that submerged macrophytes and benthic diatoms were responsible for 90% of the Bay's productivity throughout the year but that both summer squalls and winter cold fronts greatly increased the relative importance of benthic diatoms in the water column.

Based on our findings and those of other researchers, it is clear that benthic diatoms are not only an available food resource to bivalves in estuaries but are also ingested by these estuarine suspension-feeders. In this study our direct observations of the diatoms in oysters indicated that anywhere from 6 to 60% were benthic depending on the location and the time of year (Table 2.2; Fig. 2.6B). In Frenchman's Bay, Maine, Muschenheim and Newell (1992) determined from chlorophyll, carbon, and direct cell counts of seston that mussels (*M. edulis*) preferentially fed on high concentrations of resuspended benthic diatoms. Newell et al. (1989) also examined the gut contents of *M. edulis* and determined that over two-thirds of the algal species were of benthic origin. Ruckelshaus et al. (1993) observed increased growth mussel growth (*M. edulis*) in Padilla Bay Estuary, in areas where benthic microalgae made a greater contribution to local seston composition.

Direct observations show that our oysters were ingesting benthic diatoms, but stable isotope evidence is useful for showing incorporation. Both the δ^{13}C and δ^{34}S values of oysters suggest that they are relying primarily on phytoplankton, but that either benthic microalgae or *S. alternifora* detritus likely make a contribution to their diet. Although previous investigators have found that oysters can use *Spartina*-derived lignocellulose, this is usually a small (< 1%) contribution to their diet (Crosby et al. 1989). In this study, when we used direct observations of availability of benthic and planktonic diatoms in the seston to oysters, the calculated isotopic values for both carbon and sulfur closely match the observed signatures of the oysters (Table 2.5). Although detritus or other microalgae probably do contribute to the diets of oysters as well, these results support the notion that diatoms are the primary food resource of the oysters in this system. Diatoms have been identified as an excellent food resource for bivalves (Enright et al. 1986; Volkman et al. 1989) and Beukema and Cadee (1991) observed that in the Wadden Sea, The Netherlands, *Macoma balthica* responded to higher diatom abundances with faster growth and increased condition.

In contrast to the oysters the isotope values of the seston indicate a contribution of ^{34}S-depleted material such as *S. alterniflora* detritus. This is in keeping with our observations in chapter one that the particulate material in the Duplin River is detritus-dominated by POC to chlorophyll *a* ratios that always exceeded 100. The oyster $\delta^{34}S$ signatures indicate that oysters are not ingesting bulk seston, but rather are selecting microalgae. Oysters can select organic particles over inorganic ones (Newell & Jordan 1983) and can even differentiate between lower quality detritus and higher quality microalgae (Ward et al. 1998). Thus, we have a large pool of organic matter that is predominantly detrital but the oysters can preferentially select diatoms over *S. alterniflora* detritus. Note however, that our results suggest that oysters are not necessarily selecting for benthic diatoms over planktonic ones, but are rather ingesting them in proportion to their availability, as evidenced by the strong relationship between them (Fig. 2.7).

In this study we found that benthic diatoms are available to and ingested by oysters in the Duplin River. Microscopic observations of benthic diatoms in oysters were supported by both the calculated and observed isotopic signatures of the oysters. We also identified a spatial gradient in the utilization of benthic diatoms between the headwaters and the mouth. The significantly higher proportion of benthic diatoms in both the seston and oysters at the headwaters reflects a greater contribution of benthic microalgae to the water column chlorophyll *a* pool at this location. This could be attributed to greater exchange between the water in the Duplin River and the surface of the salt marsh at the headwaters or to higher water column chlorophyll *a* concentrations at the mouth, which would lower the relative contribution of benthic chlorophyll *a* at this location. Utilization of benthic diatoms by oysters was greatest in the fall at the headwaters when benthic chlorophyll *a* increased. Our results also illustrated the ability of oysters to select among different food resources. In the Duplin River the oysters are enriching the quality of their diet and select for living microalgae over *S. alterniflora* detritus. Thus, while the results of our seston analysis (in terms of both our quality data in chapter one and the ^{34}S isotopic signature of the seston in the current chapter) indicate a large contribution of detritus to the particulate organic matter pool, the oysters actually ingest a high quality diet that appears to consist primarily of diatoms. In conclusion, both our microscopic observations and the stable isotope data support the idea that benthic diatoms are available to and ingested by oysters in the Duplin River, and that spatial and temporal patterns of availability will influence the relative contribution that they make to the diets of bivalves within a salt marsh estuary.

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TABLE 2.1. Chlorophyll *a* (μg g^{-1} dry wt.) concentration in surface sediments around oyster reefs at the headwaters and the mouth of the Duplin River sampled at 5-week intervals from July 2001 through June 2002 averaged for the entire year (mean ± s.d.) (n = 8) and categorized by season (n = 2 observations for summer; n = 3 for fall; n = 2 for winter; n = 1 for spring).

		Site	
		Headwaters	**Mouth**
Overall :	1-year average	75.0 ± 48.1	69.0 ± 24.0
Seasonal:	Summer	44.7 ± 3.2	63.9 ± 18.4
	Fall	96.0 ± 45.9	59.5 ± 12.0
	Winter	75.0 ± 39.6	95.9 ± 29.0
	Spring	71.7	53.6

TABLE 2.2. Percent benthic diatoms in seston and oysters at the headwaters and the mouth of the Duplin River sampled at 5-week intervals from June 2000 through June 2002 averaged over the entire two year study (mean ± s.d.) (n = 20) and categorized by season (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

		Site			
		Headwaters		**Mouth**	
Percent Benthic Diatoms:		**seston**	**oyster**	**seston**	**oyster**
Overall	2-yr average	36.6% ± 7.3	33.3% ± 13.2	16.9% ± 5.7	21.0% ± 9.8
Season:	Summer	37.0% ± 3.2	32.5% ± 9.4	18.2% ± 8.6	22.1% ± 14.1
	Fall	37.8%± 7.0	42.7% ± 10.7	14.6% ± 3.9	22.1% ± 6.5
	Winter	40.1% ± 4.9	34.2% ± 12.0	20.3% ± 8.4	21.4% ± 11.1
	Spring	31.8% ± 6.2	24.3% ± 9.3	14.9% ± 6.0	18.1% ± 12.1

TABLE 2.3. Stable isotopes of carbon ($\delta^{13}C$) and sulfur ($\delta^{34}S$) for seston and oyster tissue from the headwaters and the mouth of the Duplin River sampled quarterly over the course of the two-year study from June 2000 through June 2002. (mean ± s.e.; no s.e. is provided when the results of analytical replicates were exactly the same.)

Sample Type & Location	$\delta^{13}C$	$\delta^{34}S$
Seston: (n = 4 pooled)		
Headwaters	-21.7‰	+8.5‰ ± 0.1
Mouth	-20.0‰	+3.9‰
Oyster: (n = 8 pooled)		
Headwaters	-21.3‰ ± 0.1	+15.5‰
Mouth	-18.6‰ ± 0.1	+16.8‰ ± 0.2

TABLE 2.4. Stable isotopes of carbon ($\delta^{13}C$) and sulfur ($\delta^{34}S$) for oyster tissue, surface and benthic microalgae from the headwaters and the mouth of the Duplin River sampled in November 2003. (mean ± s.e.; no s.e. is provided when the results of analytical replicates were exactly the same.)

Sample Type & Location	$\delta^{13}C$	$\delta^{34}S$
Oyster: (n = 3 pooled)		
Headwaters	-22.1‰ ± 0.1	+13.5‰ ± 0.1
Mouth	-19.8‰ ± 0.1	+15.5‰
Benthic Microalgae:		
Headwaters	-17.7‰ ± 0.1	+9.7‰ ± 0.1
Mouth	-19.1‰	+7.1‰

TABLE 2.5. Calculated carbon ($\delta^{13}C$) and sulfur ($\delta^{34}S$) values compared to observed values for the stable isotopic signatures of oysters based on the different mixtures of benthic and planktonic diatoms in seston and oysters from the headwaters and the mouth of the Duplin River from June 2000 through June 2002. (Isotopic values for phytoplankton were taken from the literature ($\delta^{13}C$ -21.3‰ and $\delta^{34}S$ +18.8‰) as reported in Peterson and Howarth (1987); isotopic values for the benthic microalgae were based on our observations from each location in November 2003 (Table 2.4).)

		$\delta^{13}C$		**$\delta^{34}S$**	
		calculated	**observed**	**calculated**	**observed**
Headwaters	BDs in oysters[1]	-20.1‰	-21.3‰	+15.8‰	+15.5‰
	BDs in seston[2]	-20.0‰		+15.4‰	
Mouth	BDs in oysters[3]	-20.9‰	-18.6‰	+16.4‰	+16.8‰
	BDs in seston[4]	-19.1‰		+16.8‰	

Headwaters: [1] Based on a diet of 33% benthic diatoms and 67% planktonic diatoms.
[2] Based on a diet of 37% benthic diatoms and 63% planktonic diatoms.
Mouth: [3] Based on a diet of 21% benthic diatoms and 79% planktonic diatoms.
[4] Based on a diet of 17% benthic diatoms and 83% planktonic diatoms.

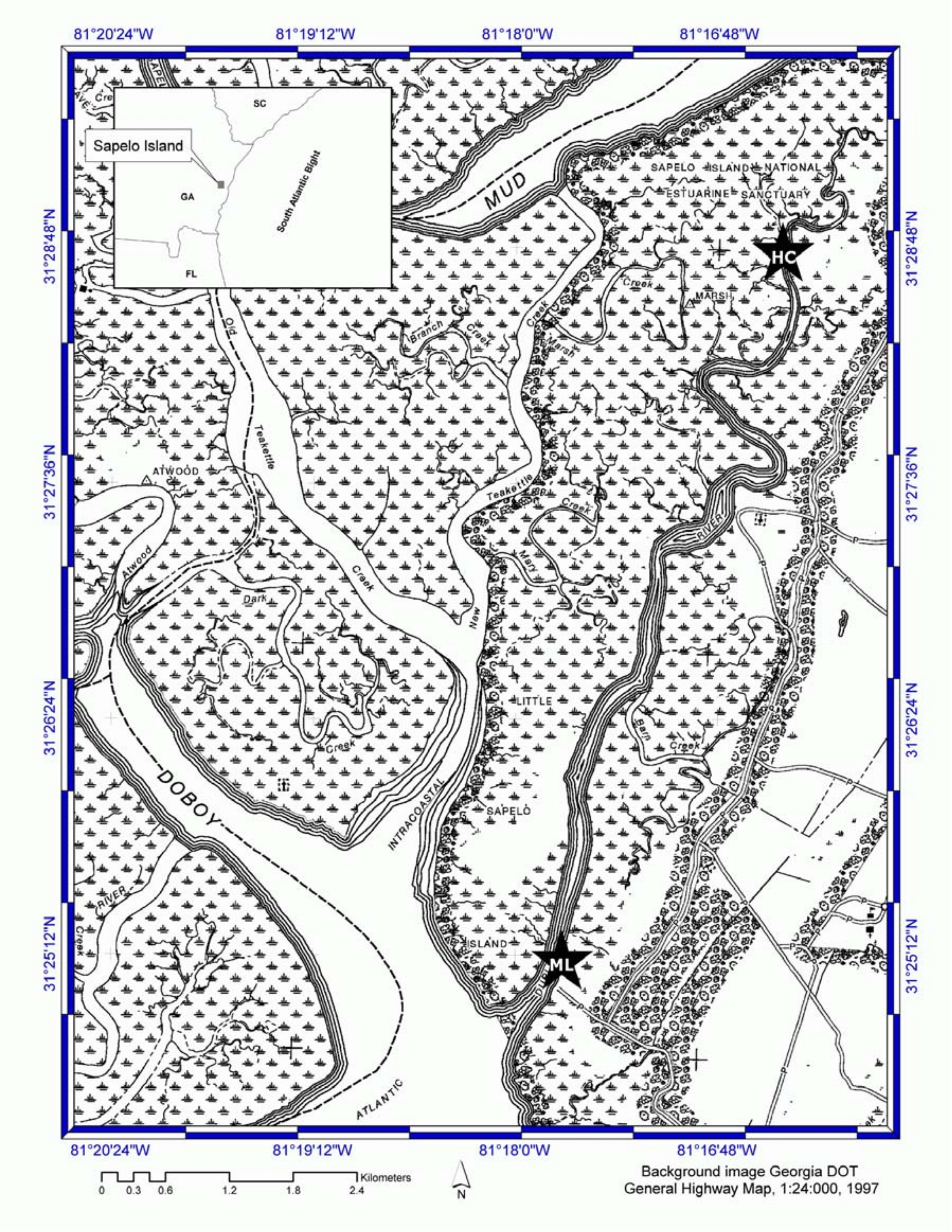

Fig. 2. 1. Map of the Duplin River showing the location of the headwaters and the mouth where seston, oysters and sediments were sampled at five-week intervals from June 2000 through June 2002.

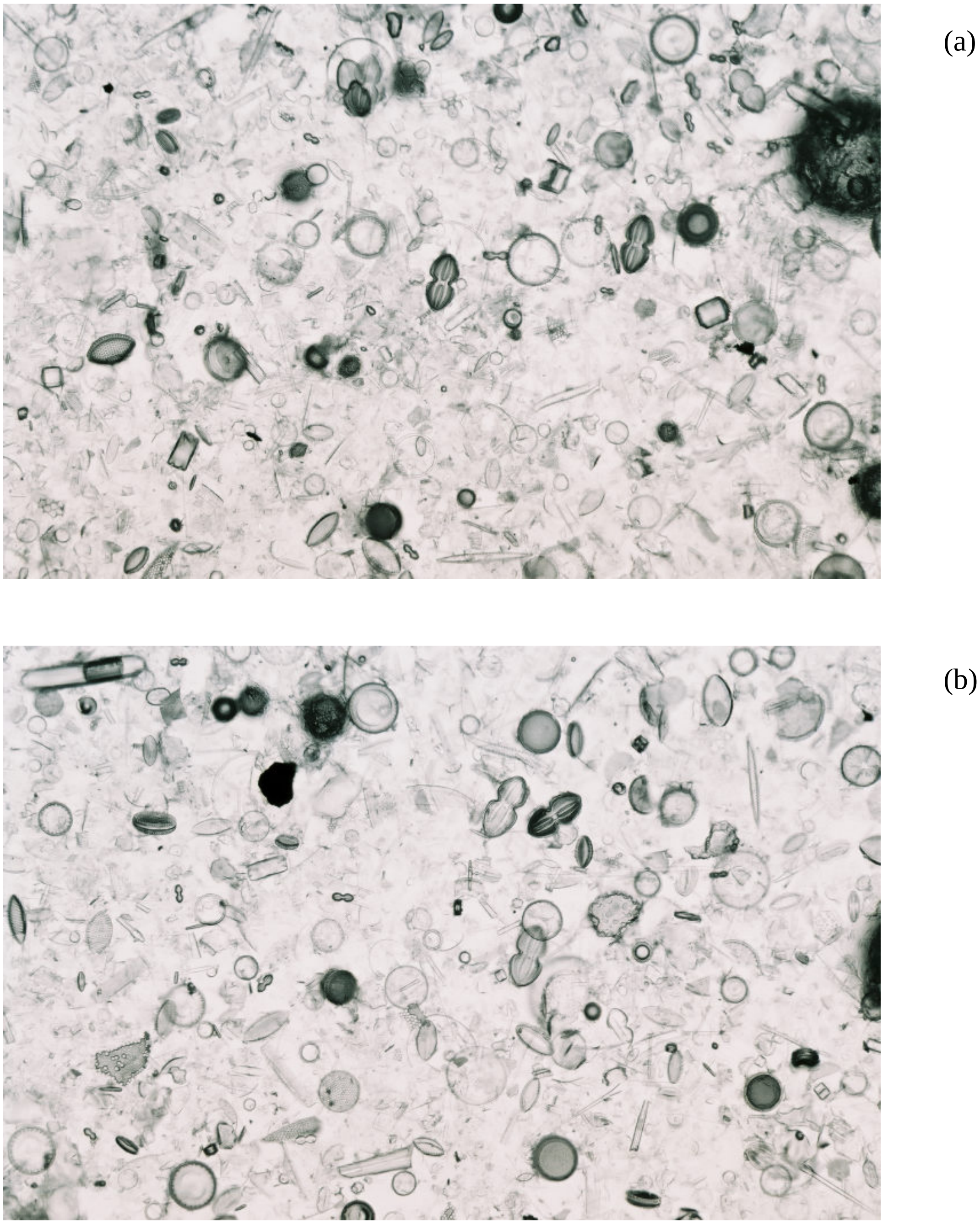

Fig. 2.2. Photographs of diatom preparations observed at 200X (total magnification) from (a) seston and (b) oyster samples collected at the mouth of the Duplin River on 15 May 2001.

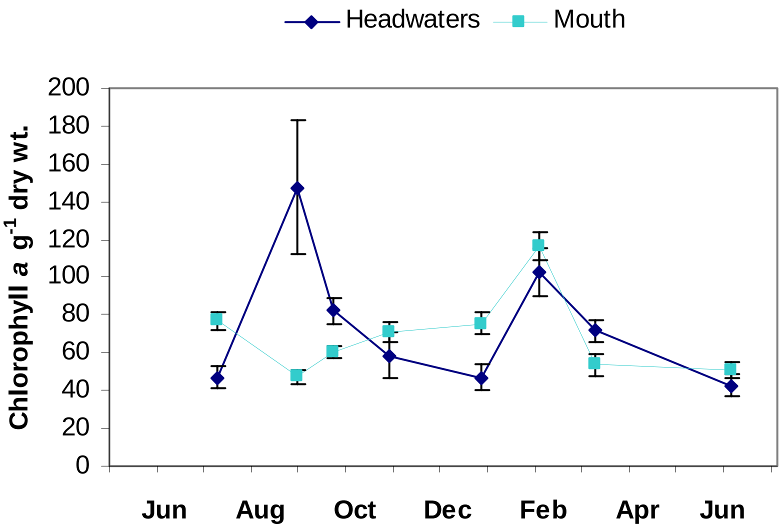

Fig. 2.3. Chlorophyll a concentration (± s.e.) in sediments around oyster reefs at the headwaters and the mouth of the Duplin River from July 2001 through June 2002 (May 2002 excluded due to heavy rainfall on the sampling date). (No significant difference was found between the two sites based on the results of Independent samples student's t-test).

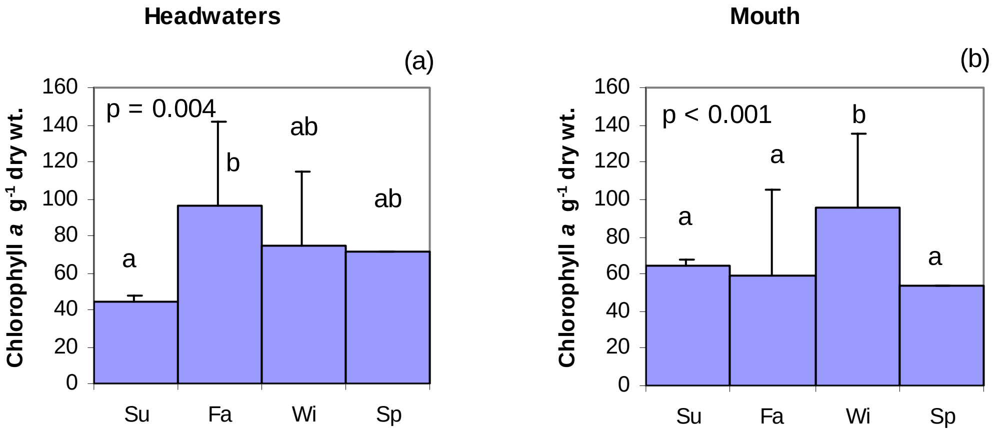

Fig. 2.4. Chlorophyll a concentration (± s.d.) in sediments around oyster reefs at the (a) headwaters and (b) mouth of the Duplin River for the different seasons from July 2001 through June 2002. (Analysis of variance; Duncan's least significant difference post-hoc tests; seasonal differences denoted by letters).

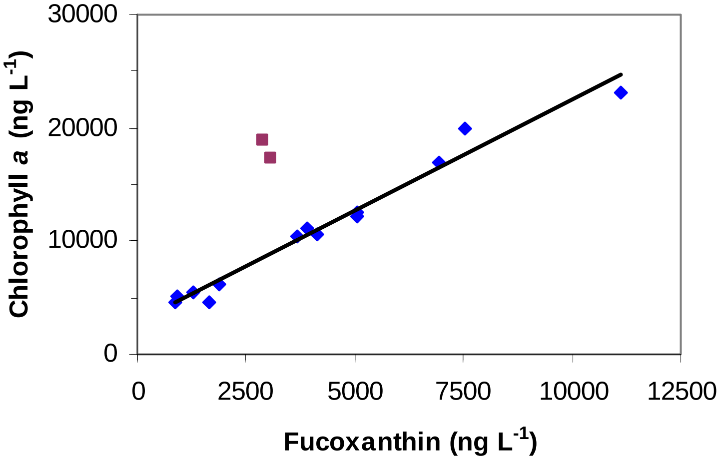

Figure 2.5. Fucoxanthin vs. chlorophyll *a* concentration for seston over oyster reefs sampled at 5 sites (including the headwaters and the mouth) along the length of the Duplin River sampled in January, April and July 2001. Two excluded outliers are from the headwaters in July where there was a large increase in peridinin due to a dinoflagellate bloom. Linear Equation: Y = 1.96X + 2852.2 9 (R^2 = 0.97)

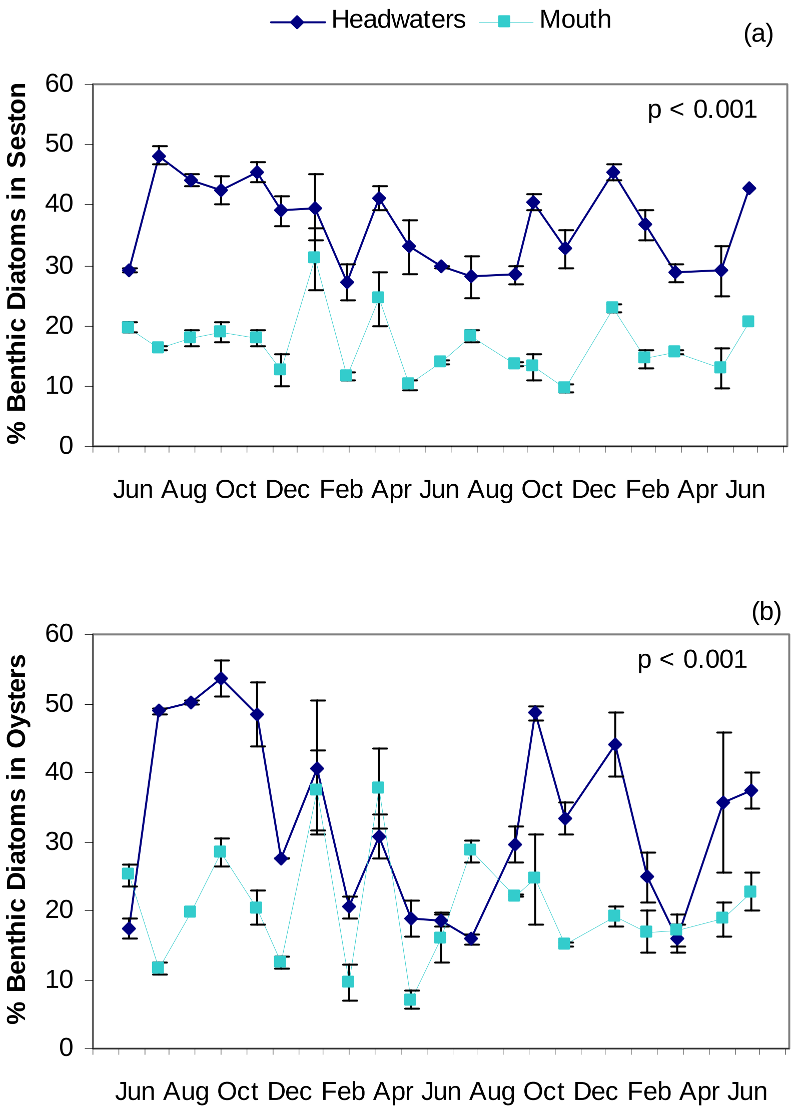

Fig. 2.6. Percent benthic diatoms (mean ± s.e.) in (a) seston over oyster reefs and (b) oysters at the headwaters and the mouth of the Duplin River from June 2000 through June 2002. (Significant differences between the two sites as determined by general linear model procedure denoted by p-values.)

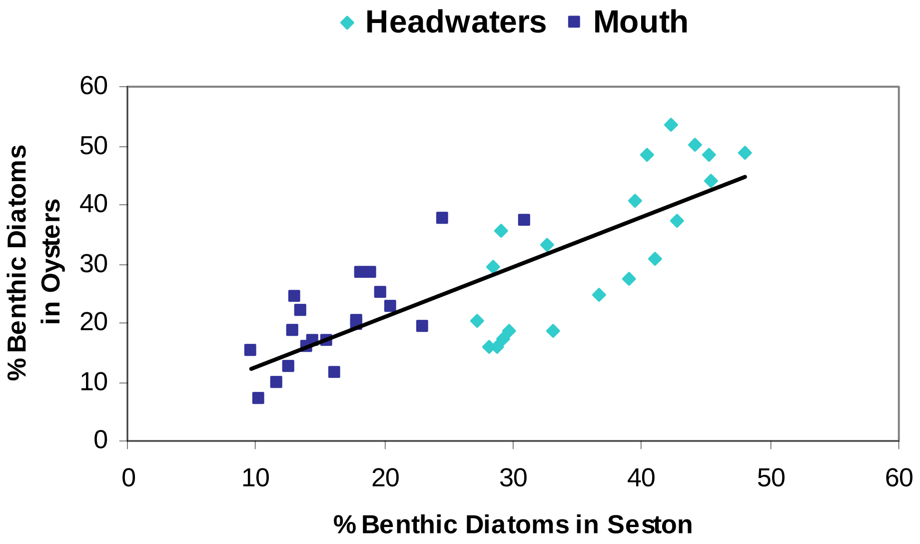

Fig. 2.7. Percent benthic diatoms in seston vs. oysters at the headwaters and the mouth of the Duplin River from June 2000 through June 2002.
Linear Equation: Y = 0.84X + 4.27 (R^2 = 0.64)

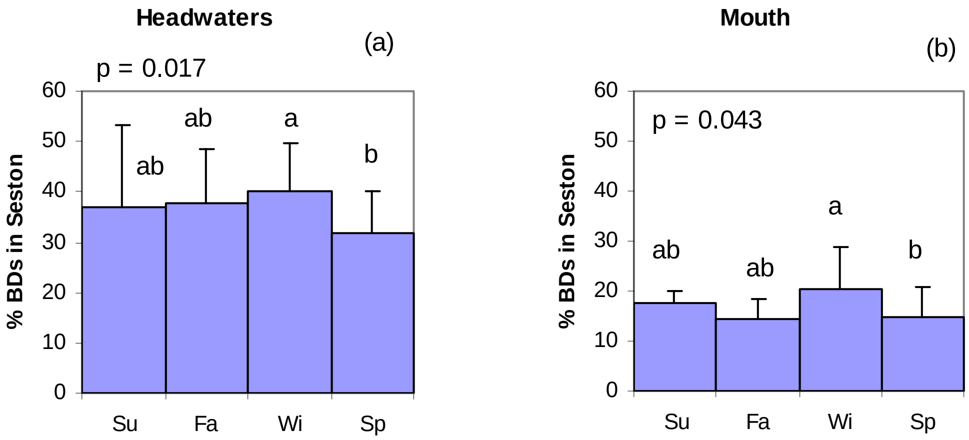

Fig. 2.8. Percent benthic diatoms (BDs) (± s.d.) in seston over oyster reefs at the (a) headwaters and (b) mouth of the Duplin River for the different seasons from June 2000 through June 2002. (Analysis of variance; Duncan's least significant difference post-hoc tests; seasonal differences denoted by letters).

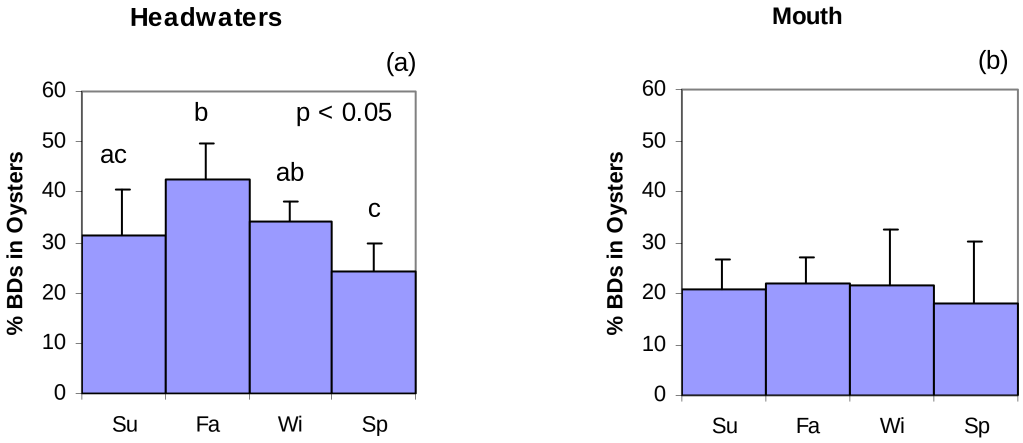

Fig. 2.9. Percent benthic diatoms (BDs) (± s.d.) in oysters at the (a) headwaters and (b) mouth of the Duplin River for the different seasons from June 2000 through June 2002. (Analysis of variance; Duncan's least significant difference post-hoc tests; seasonal differences denoted by letters; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

CHAPTER 3

OYSTER SIZE AND CONDITION IN A TIDAL INLET: DOES LOCATION MATTER TO OYSTERS IN THE DUPLIN RIVER ESTUARY, GEORGIA, USA?[1]

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[1] Thoresen, M. and M. Alber. To be submitted to *Aquaculture*

Introduction

The distribution of oysters and other bivalves in salt marsh estuaries is a function of the complex interaction of chemical, biological, physical, and geological factors (Galstoff, 1964; Bahr and Lanier, 1981; Frey et al., 1987). In coastal Georgia, U.S.A. eastern oysters (*Crassostrea virginica*) are found in intertidal areas where they occur as either small clusters of several individuals, larger mounds on tidal flats, or in more extensive beds along the margins of tidal creeks and estuaries (Bahr, 1976; Frey and Basan, 1985). In an early assessment of the oyster resources on the Georgia coast Galstoff and Luce (1930) classified the estuarine habitats into three categories: 1) open sounds, 2) rivers, and 3) small creeks and marshes. These three basic categories were then evaluated in terms of their suitability for the culture of oysters with an emphasis on local salinity, pH, the concentration of suspended particulate material, and bottom substrate characteristics. Based on these criteria they determined that the small creeks and salt marshes were preferred to the mouths of large rivers and open sounds. The rivers were determined to be deleterious to oyster growth and survival due to periods of high freshwater inflows and siltation, whereas the sounds were undesirable due to exposure to heavy northeast seas from the ocean and heavy predation pressure under an oceanic salinity regime. More recent studies that assess habitats for oyster reef restoration efforts or their suitability for bivalve culture focus on water temperature and salinity, food quantity and quality, and flow regime in relation to optimal food delivery (Grant, 1996; Coen and Luckenbach, 2002). These environmental variables are generally examined in relation to the growth and condition of the organisms, which is measured in terms of shell height, shell weight, internal shell volume, dry tissue weight, or as a combination of some of these variables which is used to calculate a condition index (Walne and Mann, 1975; Rainer and Mann, 1992).

Both water temperature and salinity affect nearly every aspect of oyster biology. In a review of natural environmental factors, Shumway (1996, and the references cited therein) identified these two variables as the most important abiotic factors influencing oysters. Seasonal patterns of reproduction, development and growth are directly linked to changes in temperature and are also indirectly related to temperature through food web effects. In a modeling study focused on the population dynamics of oysters in the Gulf of Mexico and Chesapeake Bay, Hofmann et al. (1992) emphasized the critical role water temperature plays in the timing and duration of spawning and in the establishment of spring and fall phytoplankton blooms, both of which influence the reproductive effort of oysters over a spawning season. According to this study, the period of time when temperature and food availability coincide to produce a good reproductive effort decreases at higher latitudes, which limits the likelihood of spawning success in these areas. Salinity also affects the distribution of oysters. Oysters can survive in a wide range of salinities, but populations that live in areas where salinities range from 0 to 10 psu generally exhibit low recruitment and growth and experience high annual mortality, so densities tend to be low. At salinities from 10-20 psu oysters occur in high densities due to high reproductive output and the lack of predators. At 25 psu and greater growth and reproduction are also high, but densities tend to decrease in comparison to intermediate salinity sites because predation and competition pressure is greatest (Butler, 1954).

The effects of temperature and salinity on oysters are consistent with observations made in Georgia. In coastal Georgia and other lower latitude locations, water temperatures remain high enough to support spawning from April to October (Heffernan et al., 1989) and recruitment levels remain high and are generally sustained throughout the entire 6 month period (O'Beirn et al., 1995). In terms of salinity, Galstoff and Luce (1930) observed that periods of increased freshwater inflows or "freshets" were deleterious to oysters living in riverine estuaries, whereas open sounds have stable and high salinities that are favorable for oyster growth, but they are places with high predation pressure from drills (*Urosalpinx cinerea*, *Thais haemostoma, Eupleura caudata*) and starfish (*Asterias forbesi*), all of which have been observed in association with oyster reefs along the Georgia coast (Durant, 1968). In more recent years, as diseases such as Dermo and MSX have taken their toll on oysters on the eastern U.S. coast and in the Gulf of Mexico, many researchers have observed that high and stable salinity regimes favor the establishment, proliferation and persistence of the protistan parasites that cause these diseases [*Perknisus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX)] (Ford and Tripp, 1996, and the references cited therein).

Food quantity and quality are also important considerations for the growth and survival of oysters and other estuarine bivalves. Wilson (1987) found that differences in growth of oysters (*Ostrea edulis*) and scallops (*Pecten maximus*) among locations could be explained by differences in POC concentrations in the seston as well as temperature and current speeds. In two sub-estuaries of Chesapeake Bay, Berg and Newell (1986) observed higher oyster growth in one of the study sites and attributed it to differences in the quantity of the seston but no differences in seston quality were observed. In Padilla

Bay, Washington, Ruckelshaus et al. (1993) examined seston quantity and quality in relation to mussel (*Mytilus edulis*) growth in different habitats (neritic, mudflat, eelgrass, slough). Slower growth was observed in the slough habitats and these researchers suggested that this could be related to lower quality seston, i.e., high C:N, that consisted primarily of refractory detritus.

Oysters can adjust their feeding activity in response to both food concentration and quality. At concentrations lower than 1 mg L^{-1} oysters remain closed, from 1 to 5 mg L^{-1} they open their shells and clearance rates rapidly approach their size-dependent maximum, from 5 to 10 mg L^{-1} clearance rates are maximal and particle capture begins to exceed ingestion rates (Higgins, 1980). Once maximum ingestion rates are attained further increases in seston concentration result in increasing amounts of material being rejected as pseudofeces (Haven and Morales-Alamo, 1966). Clearance rates do not begin to decline until concentrations exceed 25 mg L^{-1} and do not cease altogether until they exceed 75 mg L^{-1} (Newell and Langdon, 1996). Oysters can also select organic over inorganic particles (Newell and Jordan, 1983) and can even discriminate among organic particles of differing quality, selectively ingesting more nutritive particles (Ward et al., 1998). Thus, oysters can greatly enrich their diets relative to what is available in the bulk seston, although a number of studies have observed better growth and condition when chlorophyll *a* and particulate organic matter concentrations were high (Toro et al., 1995; Rheault and Rice, 1996; Sara and Mazzola, 1997). However, at high seston loads there is a sharp reduction in particle selection (Urban and Kirchman, 1992). In studies of the Pacific oyster (*Crassostrea gigas*) Barille et al. (1997) observed a decrease in the scope for growth at high seston concentrations (> 160 mg L^{-1}), which they attributed to decreased selectivity due to an overloading of the ctenidia and/or the labial palps.

Natural and cultured assemblages of bivalves rely on particulate food resources that can vary greatly in terms of both concentration and nutritive quality on both spatial and temporal scales. Spatially, the complete absence of bivalve populations (Gardner, 2000) or differences in growth rates, condition or densities (Berg and Newell, 1986; Smaal et al., 1986; Wilson 1987; Brown 1988; Smaal and van Stralen, 1990; Toro et al., 1995; Paterson et al., 2003) have been attributed to differences in the quantity and quality of available seston among different locations. Temporally, differences in bivalve growth have been documented over both short and long term temporal scales. In Cape Henlopen, Delaware Bock and Miller (1994) found that the shell growth of quahogs (*Mercenaria mercenaria*) responded to daily changes in the organic composition of the seston, which was a function of wind-induced resuspension on intertidal sand flats. On the west coast of South Africa, Stenton-Dozey and Brown (1994) found that short-term increases in clam (*Venerupis corrugatus*) production were correlated with cyclic patterns of food supply over tidal cycles. Over longer time scales, a number of researchers have observed differences in the growth of bivalves that were related to seasonal cycles in primary producers (i.e., phytoplankton) (Vahl, 1980; Toro et al., 1995; Sara and Mazzola, 1997; Sara et al., 1998; Toro et al., 1999). Differences in bivalve growth have also been attributed to human influences on food resources. Working in several estuaries on Cape Cod, Massachusetts, Weiss et al. (2002) found that quahogs (*M. mercenaria*) and soft-shell clams (*Mya arenaria*) grew fastest in estuaries where phytoplankton abundance was highest due to increased anthropogenic nitrogen loads. In two estuaries in NSW

Australia, Paterson et al. (2003) observed higher growth rates in Sydney rock oysters (*Saccostrea glomerata*) that were grown in developed versus undeveloped locations.

The supply of food to benthic suspension feeders is controlled not only by the concentration of particulate organic matter in the water column but also by the rate of delivery to the organisms, which is a function of the flow regime and the growth formation of the oysters (Frechette and Bourget, 1985; Muschenheim, 1987; Grizzle and Lutz, 1989; Grizzle and Morin, 1989; Newell, 1990; Rheault and Rice, 1996; Wilson-Ormond et al., 1997; Roegner, 1998; Roegner and Shanks, 2001). Bivalves generally occur as dense assemblages, forming patches or reefs, and a number of studies have documented local seston depletion both immediately above and downstream of them, emphasizing the importance of flow regimes that renew food resources and minimize depletion (Smaal et al., 1986; Frechette and Bourget , 1985; Frechette and Bourget, 1987; Frechette et al., 1989; Muschenheim and Newell 1992; Butman et al., 1994; Rheault and Rice, 1996; Wilson-Ormond et al., 1997). Based on experiments with fluctuating seston loads and mussels (*M. edulis*), Frechette and Bourget (1987) suggested that growth rates could be depressed by small-scale heterogeneity in phytoplankton availability. In a study of dense aggregations of mussels in Maine, Newell (1990) examined growth in relation to patch size, location within a patch, current speeds and flow direction in relation to the tide. Mussels located on the edges of large (10 m diameter) patches grew significantly larger than those on the inside of patches, presumably due to increased food availability. However, this edge effect was not observed in smaller patches (2-5 m) unless the flow regime was slow. In addition, faster growth on the edges of some patches depended on the flow direction, because of differences in food concentration associated with currents from different sources. Lenihan (1999) evaluated differences in oyster growth and mortality in the Neuse River estuary, North Carolina, in relation to their location on a reef. In this study oysters located on the crests of tall (2 m) and short (1 m) reefs had higher shell growth and condition as compared to oysters on dredged (0.6 m) and low (0.1 m) reefs. He found that 81% of the variability in oyster growth and mortality could be explained by differences in flow and food concentrations. This work highlights the interaction between heterogeneity, food concentration and the local flow regime. Human activities can also alter flow regimes in estuaries, with consequences for bivalve food resources. In the Oosterschelde estuary, The Netherlands, the construction of a storm surge barrier reduced the mixing energy of the estuary and decreased the exchange of water between the estuary and the North Sea. The horizontal advection of phytoplankton-rich water was reduced, food resources were depleted around dense beds of cultured mussels (*M. edulis*) and both mussel condition and annual landings decreased (Smaal and van Stralen, 1990; van Stralen and Dijkema, 1994).

The aim of this current work was to evaluate oyster size and condition in response to differences in food availability along the length of the Duplin River Estuary, Georgia. The Duplin River is a 12.5 km tidal inlet located within the Sapelo Island National Estuarine Research Reserve (SINERR) in coastal Georgia. The Duplin River is an excellent location for this work because the oysters that live in this system are exposed to marked differences in food resources. In a previous study, we described the variation in both food quantity [suspended particulate material (SPM), particulate organic carbon (POC), chlorophyll *a*] and food quality [carbon to nitrogen ratio (C:N), percent phaeopigment, and POC to chlorophyll *a* ratio] measured over 5 oyster reefs, and these results are summarized in Table 3.1. We found that overall SPM and POC concentrations were approximately three times higher and chlorophyll *a* concentrations were approximately two times high at the mouth as compared to the headwaters of the tidal inlet. Additionally, there was a gradient of increasing quality from the mouth to the headwaters with lower carbon to nitrogen ratios and percent phaeopigment at the headwaters. The pool of POC was generally considered to be detrital as indicated by carbon to chlorophyll *a* ratios in excess of 100 throughout the tidal inlet, although these also decreased at the headwaters.

In this paper we describe the size and condition of oysters sampled simultaneously with the seston study described above. We expected to see better growth and condition in oysters at the up-river sites, despite the fact that there were significantly higher concentrations of POC and chlorophyll *a* at the mouth. This was because SPM concentrations were much higher at the mouth and often exceeded the threshold where filtration rates are observed to decline or even cease and lead to decreased efficiency of particle selection in eastern oysters (Newell & Langdon 1996 and sources cited therein; Barille et al., 1997). In addition, food quality was decreased at the mouth with higher C:N ratios, percent phaeopigment and POC to chlorophyll *a* ratios. Some of these differences can be attributed to the fact that the mouth is a high-energy open water environment that, consistent with the predictions of Galstoff and Luce (1930), should provide a less favorable location for oysters as compared to the more protected environment found in the upper reaches of the Duplin River and the associated tidal tributaries.

Methods

Study site

The Duplin River watershed is approximately 80% intertidal *Spartina alterniflora* salt marsh and mudflats and exhibits a 2-3 m tidal range. There are abundant intertidal oyster reefs in the Duplin River (Harris, 1980; Walker and Cotton, 2001). Their formations range from typical channel-edge reefs that extend from the edge of the *S. alterniflora* to the mean low water mark to mounding, round patch reefs that range from small (2-3 m diameter) to large (10 m) and are interspersed across mud and sand flats that extend form the *S. alterniflora* zone out into the main channel of the river. At the headwaters the main-channel of the river is narrow and dendritic splitting off into numerous tidal creeks that bisect the surface of the surrounding salt marsh (Frey and Basan, 1985). At this location, tidal energy is responsible for a majority of the water movement. In contrast, at the mouth of the Duplin River the main channel widens as it opens into Doboy Sound and the mixing-regime is influenced not only by tidal currents, but also by the nearshore Atlantic Ocean and the Altamaha River. There are no significant freshwater inflows so the salinity regime is fairly stable, and the water is vertically well mixed. Freshwater inputs at the headwaters are limited to rainfall and ground water, whereas at the mouth low salinity water can be introduced to Doboy Sound by the Altamaha River during periods of high discharge via North and Back Rivers or the Atlantic Ocean, and can enter the mouth of the Duplin River during flood tide (Chalmers, 1997).

We sampled oysters at five-week intervals from five sites along the length of the tidal inlet (Fig. 3.1). At the two sites closest to the mouth, Marsh Landing (ML) and Jack Hammock (JH), the oyster reefs, including both live and dead shell cover, occur as channel-edge reefs. At the next two sites, Kenan Field (KF) and Hunt Camp (HC), the oysters form patches (~1 m diameter) or mounds (~2-3 m diameter) on intertidal flats. At the furthest up-river site, Flume Dock (FD), the oyster reef is similar to those observed at the mouth but it is located at the mouth of a tidal creek so that during flood tide some of the water that runs along the length of the main channel is diverted across the reef and into the creek.

Oyster sampling

Oysters were sampled at five-week intervals over two years (June 2000 – June 2002) for a total of twenty sampling trips. On each sampling effort clumps of oysters were randomly selected from each study site and placed on ice for transport back to the laboratory where they were refrigerated prior to processing. Ten oysters were then removed from the clumps and scrubbed to remove loose mud and debris from their shells. Shell height of each individual was measured (outer shell umbo to ventral shell margin) (Galstoff, 1964) to the nearest 0.1 mm using Vernier calipers. The oysters were then opened, the wet tissues were placed in clean, labeled, plastic weight boats, and wet weight was determined gravimetrically. The wet tissues and the shells were then placed in a drying oven at 50˚C where they were allowed to completely dry (at least 72 h). Upon removal from the oven encrusting barnacles and other fouling organisms were removed from the shells and the shells and the dry tissues were weighed.

We used the relationship from Walne and Mann (1975) to determine condition index (CI) where CI = dry meat weight x 100/dry shell weight. Although we recorded both shell height and dry tissue weight over time, we could not estimate instantaneous growth rates of the populations (Ricker, 1975) because in coastal Georgia we experience almost continual recruitment over a 6-month period from April to October (O'Beirn et al., 1995) so we end up sampling multiple cohorts. As a result, it is possible observed a decrease in mean shell height over time which results in a negative growth rate.

Statistical analyses

All of the oyster parameters (shell height, dry tissue weight, and condition index) were compared among the sites and within each site among the different seasons. Due to the large amount of variability in the measurements of shell height and dry tissue weight, these data were natural log transformed prior to performing statistical analyses. Analysis of variance and Duncan's least significant difference post hoc tests were used to compare these parameters among the sites and within each site among the seasons. Additionally, correlation analysis was used to examine the relationship between shell height and dry tissue weight. Linear regressions were used determine whether the different measures of seston quality and quantity had a measurable effect on the oysters in terms of shell height, dry tissue weight or condition index. All of the statistical analyses were performed using SPSS for PC (SPSS Inc., 2000).

Results

Physical variables

We obtained information on salinity (psu) and water temperature (˚C), which were measured at 30 minute intervals over the course of the study with permanent YSI Hydrolab Sonde (Yellow Springs, Ohio) monitoring stations maintained by the SINERR site at the mouth (ML) and the headwaters (HC) of the Duplin River (Fig. 3.1). Water temperature and salinity were comparable at the two locations (Fig. 3.2). Average water temperature was 21.4 ± 6.3˚C at the mouth as compared to 22.2 ± 6.5˚C at the headwaters and average salinity was 35.7 ± 3.2 psu as compared to 35.7 ± 3.9 psu. Temperature followed a predictable seasonal cycle over the duration of our study (June 2000 through June 2002) with a winter minimum and summer maximum. Salinities remained stable and high (~30 psu or higher) throughout much of the two-year study. Although the average salinities observed here were similar to other reports in the Duplin River, the range during this study was narrower: between approximately 20 and 35 psu in this study as compared to 10 or 15 to 30 psu in previous reports (Chalmers, 1997; O'Beirn et al., 1997). This difference in the salinity regime can probably be attributed to the drought that was affecting coastal Georgia during this time of our study. The Duplin River is a tidal inlet so we do not expect to see large inputs of freshwater but it is influenced by both rainfall and ground-water, and, during periods of high discharge from the Altamaha River, reduced salinities can be observed at the mouth (Chalmers, 1997). During the course of this study the cumulative rainfall deficit in coastal Georgia was 60 to 75 cm (NOAA Drought Information Center, NWS Southern Region) and the Altamaha River median daily flow was 246 m^3s^{-1}**,** which was almost half the "normal" flow rate of 406 m^3s^{-1}.

The fact that all of the oysters were under similar temperature and salinity regimes suggests that pressure from parasites and predators was probably similar throughout the tidal inlet. The high and stable salinity regime (> 25 psu) ensures that salinity stress was not a factor during the study (Medcof and Needler, 1941), although parasitism by the causative agent of Dermo (*Perkinsus marinus*) and predation pressure were both probably severe due to these persistently high salinities. Indeed, based on our own *P. marinus* monitoring efforts in the Duplin River in 1999-2000 (Thoresen and Alber, 2004) and those of O'Beirn and co-workers (1996) in 1993-1994, we know that disease prevalence is high (70-100%) and almost all of the oysters are infected by this parasite.

Oyster size, weight and condition

Over the course of this study shell height averaged 70.0 mm, dry weight averaged 580.4 mg and condition index averaged 3.3 (Table 3.2). Shell height was significantly correlated with dry tissue weight ($n = 998$; $r = 0.813$; $p < 0.001$; Fig. 3.3). Our average shell height was shorter than that reported in a previous study of oysters in the Duplin River (77.0 mm; O'Beirn, 1997), which may reflect inter-annual variability. We do not have other information on dry tissue weight or condition of oysters in the Duplin River with which to compare our observations.

Spatial trends in oyster size and condition

There were some significant spatial differences in oyster size and condition among the five sites along the length of the Duplin River, wherein oysters at the headwaters (particularly HC) generally did better than those at the mouth (i.e., ML) (Table 3.3; Fig. 3.4). Oysters at headwaters (HC) and mid-reach (KF) had significantly taller shell heights as compared to the other three sites ($P < 0.01$) (Fig. 3.4A); the two headwaters sites (FD & HC) had significantly greater dry tissue weights as compared to the sites further downstream (KF, JH & ML) ($p < 0.01$) (Fig. 3.4B); and oyster condition at the headwaters (HC) was significantly higher than that observed at any of the other sites ($p < 0.01$) (Fig. 3.4C). Taken together, these results indicate that the headwaters provide a better environment for oyster growth than the mouth.

Temporal trends in oyster size and condition

Temporal patterns in average shell height, dry tissue weight and condition index were examined in terms of annual and seasonal cycles. There was a lot of month to month variability, which makes it difficult to make any general statements about annual cycles (Fig. 3.5-3.7). This is probably because Georgia has such a long settlement period that we were sampling many different size classes of individuals on any given sample date, which obscured the growth characteristics of any particular cohort (Fig. 3.5). When these data on oysters are categorized on a seasonal basis, however, some consistent trends emerged, which were most apparent in terms of CI. At three of the sites (ML, KF, and HC) CI was significantly higher in the winter and spring than in the summer and fall. At the 4th site (JH) CI was also higher in the winter and spring, although not significantly. At the final site (FD) CI in the spring was significantly higher than during any of the other seasons and was again lower in the summer and fall (Table 3.4; Fig. 3.10). These seasonal differences were less apparent in either dry tissue weight or shell height, although some summer/spring differences were significant at ML and at HC the dry tissue weight in in winter was significantly different from summer (Fig. 3.9). The decreased variability in condition index as compared to just dry tissue weight probably can be attributed to the fact that in the calculation for condition, dry tissue weight is a sensitive numerator against the relatively stable denominator of shell weight (Rainer and Mann, 1992).

Discussion

Over the course of this two-year study we surveyed the size and condition of oysters throughout the Duplin River estuary. Galstoff and Luce (1930) observed the growth of oysters that settled onto planted brush in the Duplin River, and referred to one year old oysters as those ranging from 24 to 69 mm and two year olds as those ranging from 55 to 110 mm. Our average shell heights ranged from 62.8 mm at ML to 78.1 mm at HC but within each site the minimum and maximum observations were from 32.1 to 117.9 mm at ML and from 37.2 to 143.7 mm at HC (Table 3.3). Thus, the individuals in this study were probably one to two years old.

Absolute values for oyster condition cannot be compared among studies.. There are a number of different methods for determining condition in oysters, all of which utilize dry tissue weight in relation to either shell cavity volume or shell weight. The accuracy of the different methods has been the subject of debate (Crosby and Gale, 1990; Rainer and Mann, 1992), however none of the measures of condition are comparable among different investigators working at different times and in different locations (Galstoff, 1964).

Condition indices can be used within a study however, to assess temporal or spatial trends. In terms of temporal trends, major changes in oyster condition generally are associated with gametogenic cycles (Shumway, 1996), which are controlled by both endogenous (e.g., stored nutrients) and exogenous (e.g., salinity, temperature) factors (Thompson et al., 1996 and the references cited therein). In coastal Georgia, water temperature and food availability remain high enough that oysters continue to actively feed and grow through the winter (Heffernan and Walker, 1988). In our study site the continual build up of energy reserves or “fattening” resulted in oyster condition indices that were the highest during the winter and spring prior to the start of spawning (Fig. 3.10). Similar observations of seasonal cycles of condition have been made in other salt marsh estuaries in the southeastern U.S. (Lawrence and Scott, 1982; Van Dolah et al., 1992) and in Chesapeake Bay (Engle, 1958).

We also observed spatial differences among the sites with significantly greater shell height and dry tissue weight at the three up-river sites as compared to the mouth and significantly higher CI at one of the headwaters sites (HC) (Table 3.3; Fig. 3.3). Water temperature and salinity regimes were almost identical at the headwaters and the mouth, which indicates that they were not responsible for the observed differences in the oysters. We therefore evaluated the differences in food quantity and quality, flow regime, and reef formation among the sites, since all these factors can influence oyster growth.

The results of chapter one identified significant differences among the sites in terms of the quantity and quality of the seston available to the oysters (i.e., higher concentration, lower quality, greater overall variability at the mouth as compared to the headwaters). We therefore ran a series of linear regressions to look for predictive relationships between either food quantity (SPM, POC, chlorophyll *a*) or quality (carbon to nitrogen ratio, POC to chlorophyll *a* ratio, percent phaeopigment as a proportion of the total chlorophyll *a* and phaeopigment pool) and oyster performance (shell height, dry tissue weight, condition index). These regressions were run both within each site and for all of the sites combined. However, these analyses did not indicate any significant relationships between the seston and the oysters. Thus, measures of seston availability or quality were not good predictors of oyster performance in the Duplin River although the oysters did do better in sites where food quality was better. In the Wadden Sea, The

Netherlands, mussel condition was strongly correlated with annual primary production but not with chlorophyll *a* concentrations (Smaal and van Stralen, 1990). In contrast, Brown and Hartwick (1988) identified that significant site differences in the growth of Pacific oysters (*C. gigas*) could be attributed to differences in chlorophyll *a* concentration and salinity. In Padilla Bay, Washington, Ruckelshaus et al. (1993) observed lower growth in slough habitats where mussels had lower quality seston available to them, but measures of seston quality were not significantly related to mussel growth.

Flow regime is important in terms of the delivery of food resources and the renewal of seston when it becomes depleted over dense assemblages of bivalves (Newell, 1990; Lenihan, 1999). In the Duplin River tidal energy is significant and fast current speeds have been observed in the main channel (maximum speed ~ 1 m sec^{-1}) (Pomeroy and Imberger, 1981). Thus, given high food availability and high current speeds, oysters in the Duplin River probably do not exhibit differences in growth that are related to food delivery or low flow conditions. It should be noted, however, that at the mouth the oysters are living in an open water environment with an overall higher turbulent mixing regime and higher turbidity. During our study we observed overall high average SPM concentrations (327.6 mg L^{-1}; Table 3.1), which got even higher (> 1200 mg L^{-1}) in conjunction with storm events. It is likely that oysters living at the mouth experience such high turbidity that the feeding process is less efficient in general, and, under certain extreme circumstances, could cease altogether. Increased turbulence at the mouth could indirectly affect the oysters through increased SPM concentrations and could also have a direct effect through wave shock. Decreased growth in oysters in Beaufort, North

Carolina, was attributed to the physical disturbance from turbulence related to waves (Ortega, 1981).

Another potential difference in growth of the oysters in the Duplin River could be related to the height of the oyster reefs and the different formations they exhibited. At both HC and KF, where shell height was significantly higher than at any of the other sites, the oysters occurred as large mounds interspersed across tidal flats. The oysters at HC were also the only ones that exhibited significantly higher condition indices. The oysters living on these reefs could be benefiting from habitat differences similar to those observed by Lenihan (1999) where oysters attained larger sizes and better condition on reefs that were 1-2 m tall as compared to reefs that were only 0.1-0.6 m tall. The reefs at the other sites (FD, JH, ML) were all channel-edge reefs where clusters of oysters were interspersed across loose dead shell and there is little to no vertical growth.

In the early oyster investigations of Galstoff and Luce (1930) in coastal Georgia, they concluded that the optimal habitat for oyster growth would be in tidal creeks associated with salt marshes. Open water habitats of the sounds were considered less favorable because they were high-energy environments with a lot of turbulent water movement and disturbance as compared to the salt marsh creeks. In our study oysters were smaller at the mouth of the Duplin River as compared to the three up-river sites. We were unable to specifically identify why oysters at the up-river sites were larger, but possible explanations for lower growth at the mouth include: lower quality seston, higher than optimal SPM concentrations, a high-energy physical regime and shorter reef formations that exhibit little vertical growth. Our assessment of the oyster habitats of coastal Georgia agree with those of Galstoff and Luce (1930), with locations up in the headwaters of the Duplin River providing a more favorable growth environment for oysters as compared to the mouth.

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TABLE 3.1. Spatial characteristics of seston at 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002 (for site locations see Figure 3.1). SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (µg L^{-1}), % PHAE = % phaeopigment, and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 20 observations per site).

	Site				
Parameter	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
SPM	93.4 ± 85.2	136.7 ± 127.5	156.8 ± 178.5	324.1 ± 408.1	327.6 ± 321.8
POC	1.6 ± 1.0	1.9 ± 1.4	1.8 ± 0.8	4.5 ± 3.4	5.0 ± 2.9
C:N	8.1 ± 1.9	8.4 ± 1.9	8.7 ± 2.2	10.0 ± 5.1	9.6 ± 2.6
CHL *a*	9.4 ± 5.6	10.0 ± 6.0	10.8 ± 5.4	15.7 ± 10.8	19.9 ± 8.8
% PHAE	27% ± 15	30% ± 14	33% ± 14	40% ± 19	38% ± 14
POC:CHL *a*	157 ± 40	171 ± 56	172 ± 57	278 ± 116	248 ± 110

TABLE 3.2. Overall average shell height (mm), dry tissue weight (mg), and condition index of oysters (combined across the 5 sites) in the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002 (n = 998).

Parameter	**Minimum**	**Maximum**	**Mean ± s.d.**
Shell Height (mm)	26.1	143.7	70.0 ± 19.3
Dry Tissue Weight (mg)	60.0	2840.0	580.4 ± 415.7
Condition Index[1]	0.80	12.9	3.3 ± 1.1

[1] Based on the calculation of Walne and Mann (1975) dry meat x 100/ shell weight

TABLE 3.3. Spatial characteristics of oysters at 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002 (for site locations see Figure 3.1). (Shell height (mm), dry tissue weight (mg), and condition index[1])

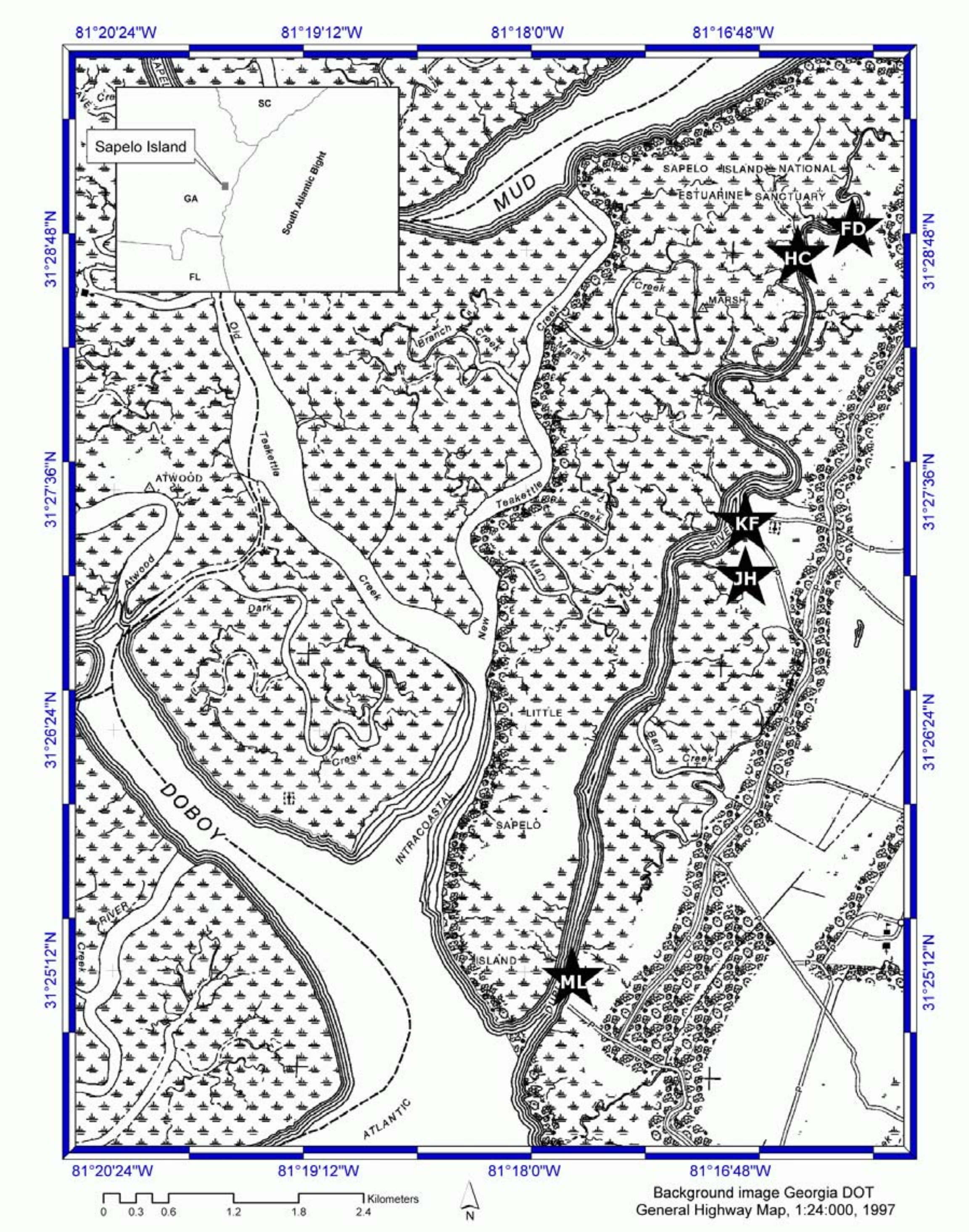
	Shell Height		**Dry Tissue Weight**		**Condition Index**	
Site	Min., Max.	Mean ± s.d.	Min., Max.	Mean ± s.d.	Min., Max.	Mean ± s.d.
FD	26.1, 116.0	68.2 ± 17.8	90, 2410	642 ± 430	0.8, 12.9	3.1 ± 1.1
HC	37.2, 143.7	78.1 ± 22.8	60, 2840	765 ± 556	1.0, 9.6	3.6 ± 1.2
KF	39.0, 133.5	73.2 ± 17.8	120, 2110	552 ± 333	1.1, 7.6	3.3 ± 1.1
JH	29.7, 124.3	67.9 ± 20.2	60, 2280	473 ± 334	0.8, 6.0	3.0 ± 0.9
ML	32.1, 117.9	62.8 ± 15.7	60, 1660	466 ± 295	0.9, 8.1	3.2 ± 1.0

[1] Based on the calculation of Walne and Mann (1975) (dry meat x 100/ shell weight)

TABLE 3.4. Seasonal characteristics of oysters at 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (Shell height (mm), dry tissue weight = dry weight (mg), and condition index = CI[1])

		Site				
Parameter	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Shell Height	Summer	69.4 ± 20.1	74.5 ± 20.8	72.3 ± 17.3	68.1 ± 19.0	56.5 ± 12.9
	Fall	62.9 ± 15.5	80.7 ± 22.8	74.3 ± 15.8	69.4 ± 19.4	67.4 ±15.9
	Winter	72.2 ± 18.6	83.4 ± 20.7	74.6 ± 19.4	66.9 ± 24.1	62.1 ± 15.5
	Spring	69.0 ± 15.8	75.4 ± 25.8	71.8 ± 19.4	67.2 ± 19.7	66.3 ± 16.6
Dry Weight	Summer	592.3 ± 385.0	538.7 ± 341.7	498.2 ± 306.4	422.5 ± 247.3	339.0 ± 199.3
	Fall	497.4 ± 358.8	735.0 ± 481.7	467.0 ± 252.4	471.4 ± 311.9	404.4 ± 220.7
	Winter	670.8 ± 403.3	1042.8 ± 589.4	699.8 ± 440.1	443.8 ± 290.1	533.5 ± 273.3
	Spring	821.8 ± 504.6	845.2 ± 689.3	581.8 ± 298.8	558.2 ± 452.8	624.6 ± 378.5
CI[1]	Summer	2.6 ± 0.8	3.2 ± 1.2	3.0 ± 1.0	2.7 ± 0.8	2.7 ± 0.8
	Fall	2.9 ± 0.8	3.2 ± 1.0	2.7 ± 0.8	2.6 ± 0.7	3.0 ± 1.1
	Winter	3.1 ± 0.8	3.7 ± 1.1	3.8 ± 1.1	3.4 ± 0.9	3.7 ± 0.8
	Spring	3.9 ± 1.6	4.2 ± 1.3	3.7 ± 1.0	3.5 ± 1.0	3.6 ± 1.1

[1] Based on the calculation of Walne and Mann (1975) (dry meat x 100/ shell weight)



Background image Georgia DOT
General Highway Map, 1:24:000, 1997

FIGURE 3.1. Map of the Duplin River showing the location of the five study sites (Marsh Landing = ML, Jack Hammock = JH, Kenan Field + KF, Hunt Camp = HC, and flume Dock = FD) where oysters were sampled at five-week intervals over two years (June 2000 through June 2002).

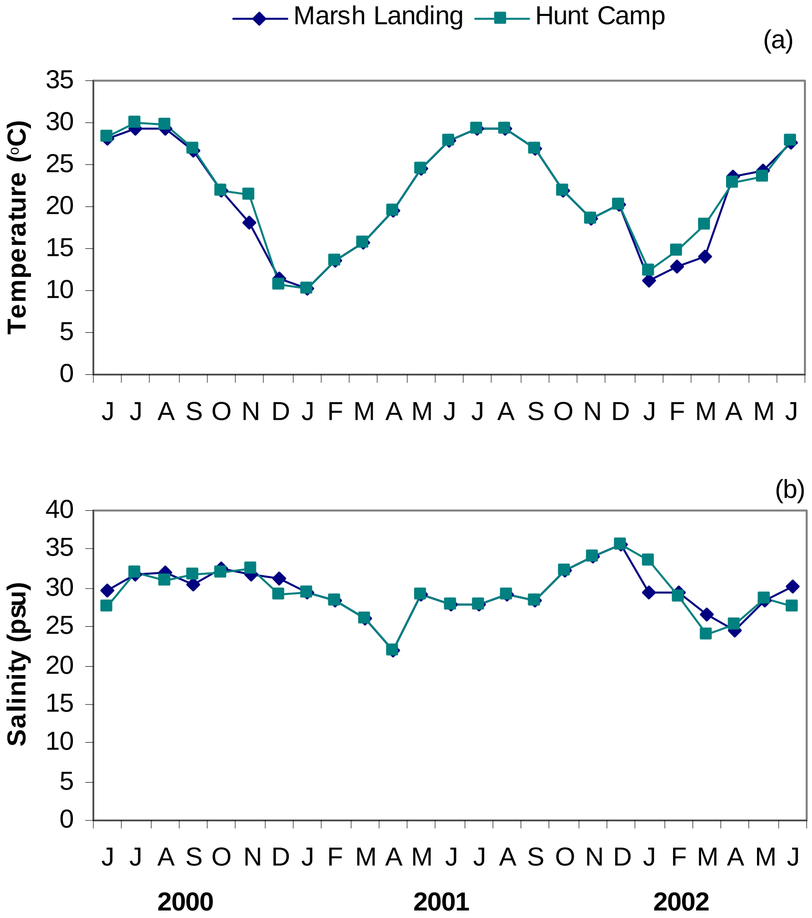


FIGURE 3.2. Average monthly water temperature (ºC) and salinity (psu) at Marsh Landing (mouth) and Hunt Camp (headwaters) of the Duplin River over the two year study period (June 2000 – June 2002).

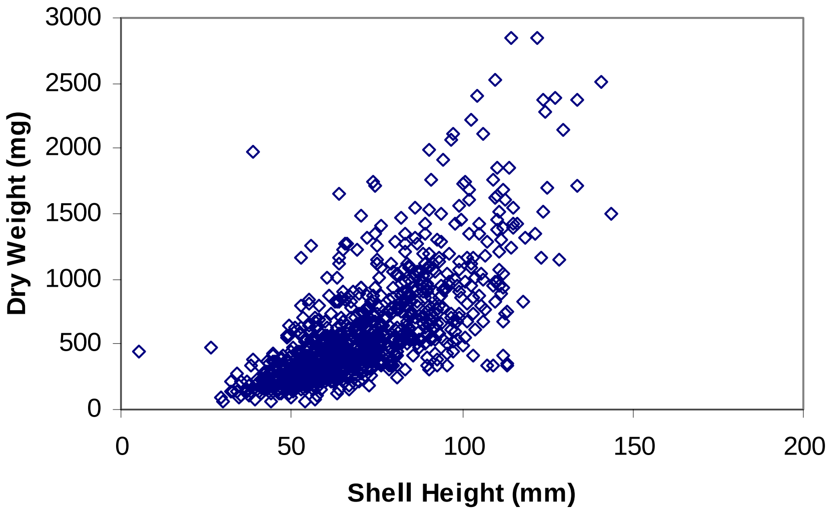


FIGURE 3.3. Individual shell height (mm) vs. dry tissue weight (mg) measurements for oysters (n = 998) sampled at five-week intervals from each of the five sites (Figure 3.1) along the length of the Duplin River over the course of the study (June 2000 – June 2002). (Significant correlation for natural log transformed values ($p < 0.001$); Pearson's correlation coefficient = 0.813.)

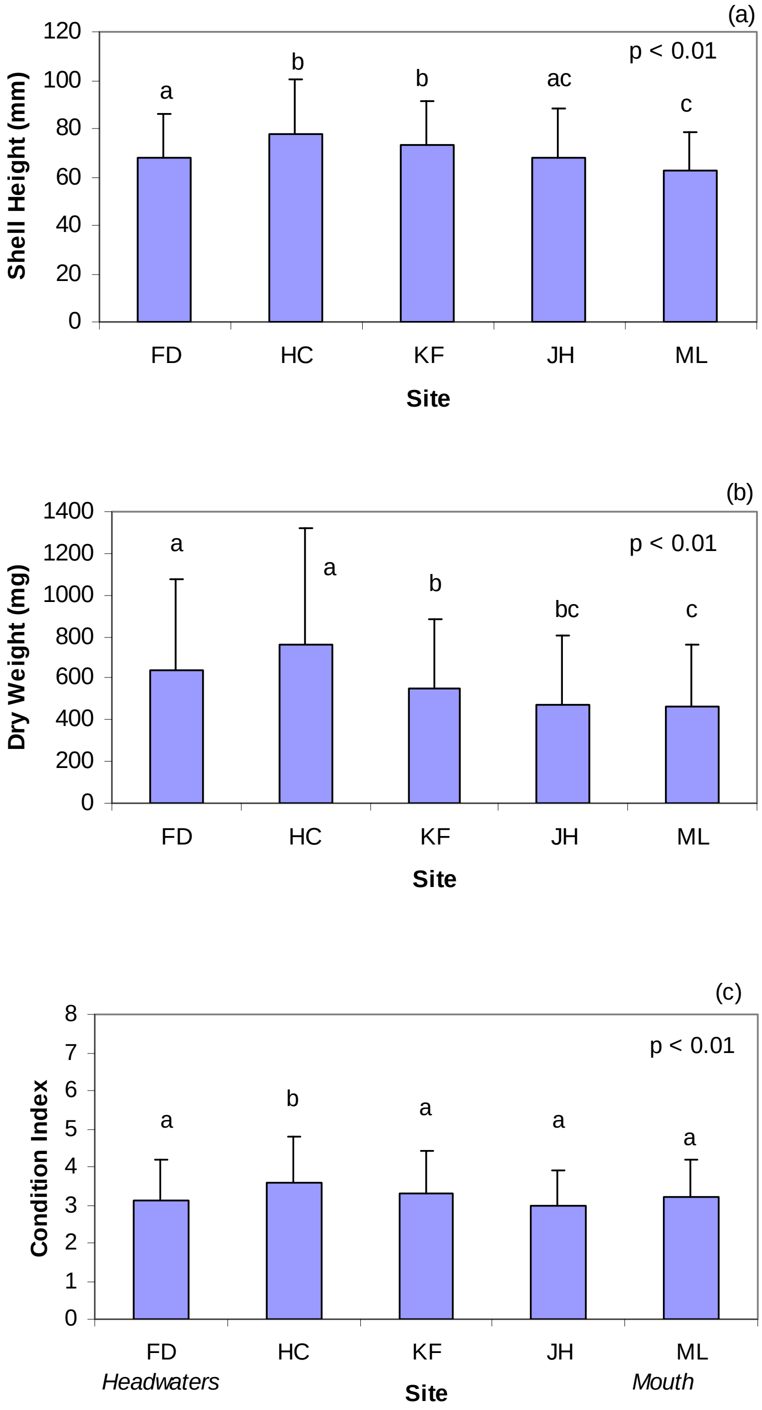
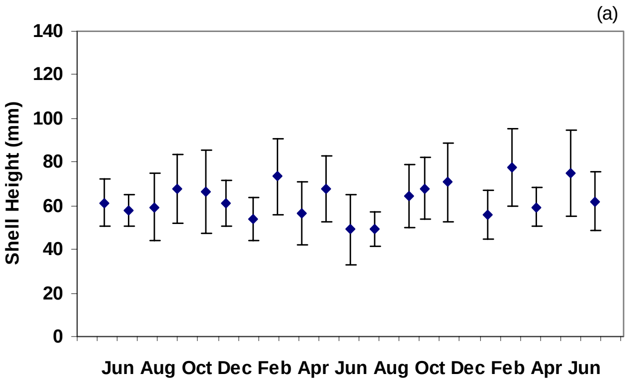
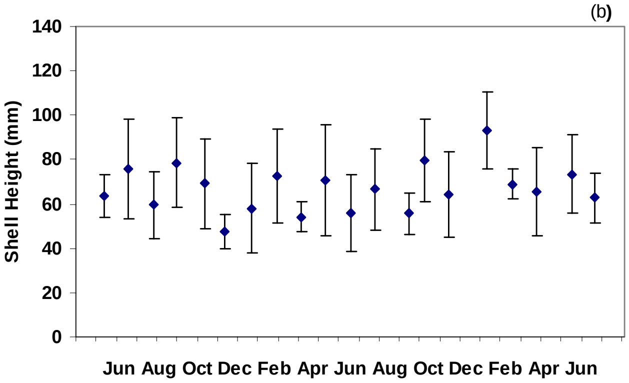
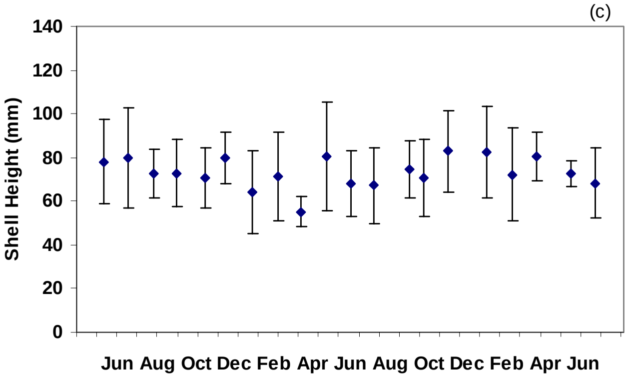


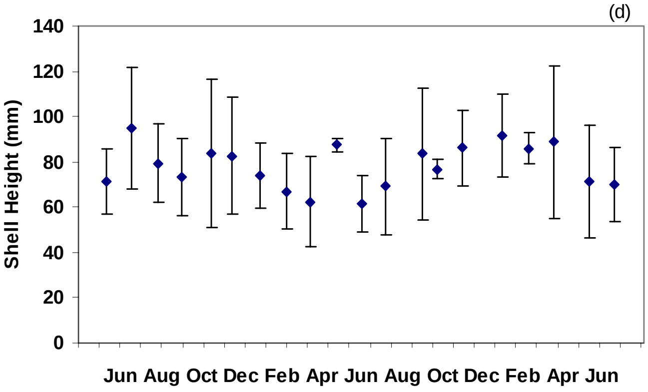
FIGURE 3.4. Two-year average (± s.d.) June 2000 – June 20002 for (a) shell height (mm), (b) dry tissue weight (mg), and (c) condition index for oysters from each of the five sites (Figure 3.1) along the length of the Duplin River. (Analysis of variance; Duncan's least significant different post-hoc tests; site differences denoted by letters.)

FIGURE 3.5. Average shell height (mm) (± s.d.) for oysters (n = 10) sampled at five-week intervals from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC and (e) FD.


(a)
Shell Height (mm)
0
20
40
60
80
100
120
140
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(b)
Shell Height (mm)
0
20
40
60
80
100
120
140
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(c)
Shell Height (mm)
0
20
40
60
80
100
120
140
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(d)
Shell Height (mm)
0
20
40
60
80
100
120
140
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun

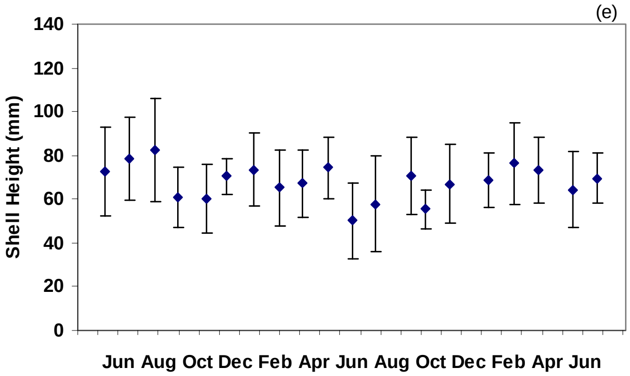
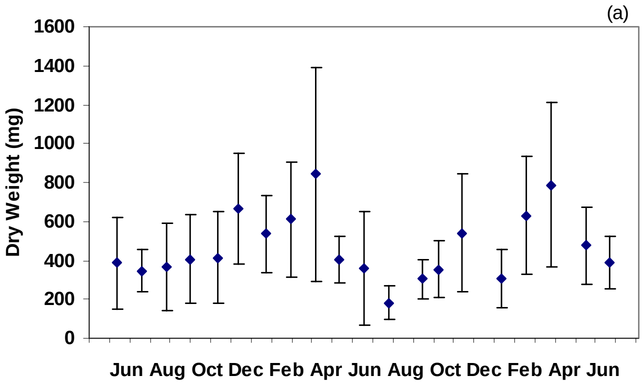
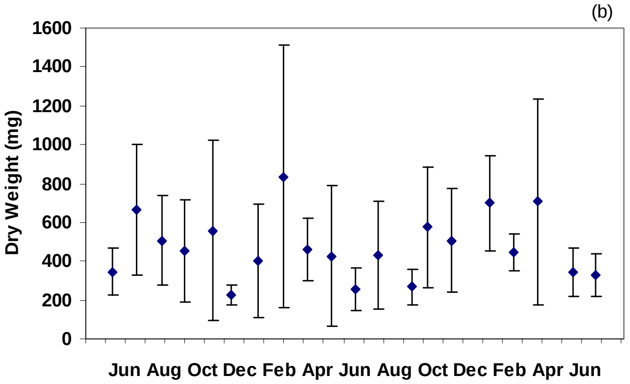
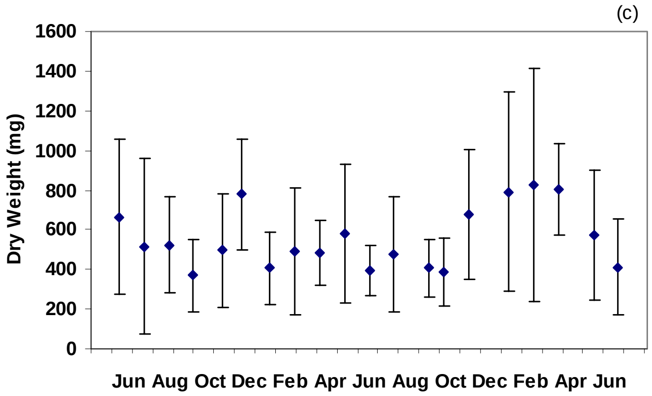
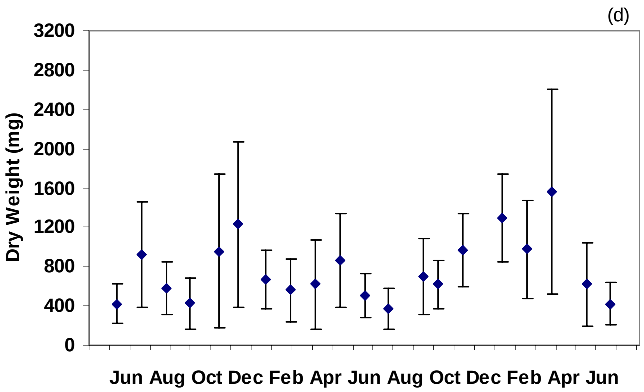

(e)
Shell Height (mm)
140
120
100
80
60
40
20
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

FIGURE 3.6. Average dry tissue weight (mg) (± s.d.) for oysters (n = 10) sampled at five-week intervals from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC and (e) FD.


(a)
1600
1400
1200
1000
800
600
400
200
0
Dry Weight (mg)
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(b)
1600
1400
1200
1000
800
600
400
200
0
Dry Weight (mg)
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(c)
1600
1400
1200
1000
800
600
400
200
0
Dry Weight (mg)
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(d)
3200
2800
2400
2000
1600
1200
800
400
0
Dry Weight (mg)
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun

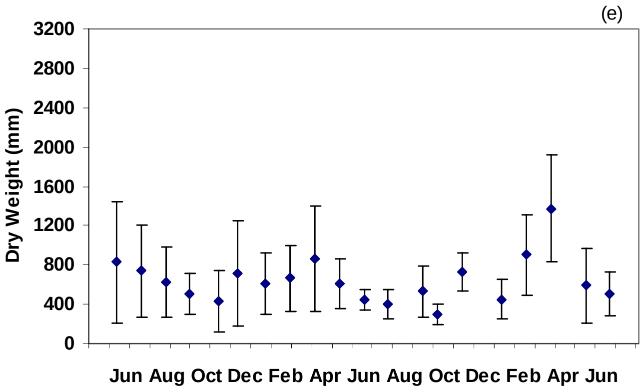
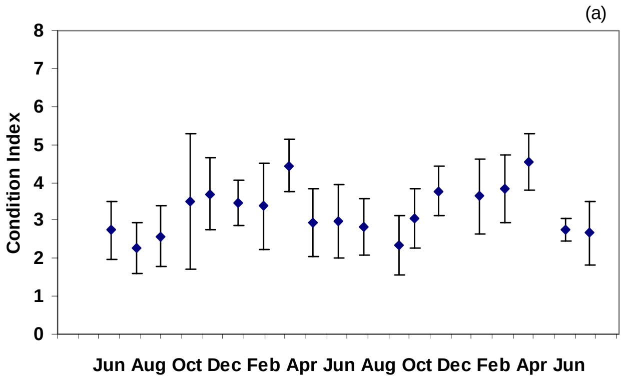
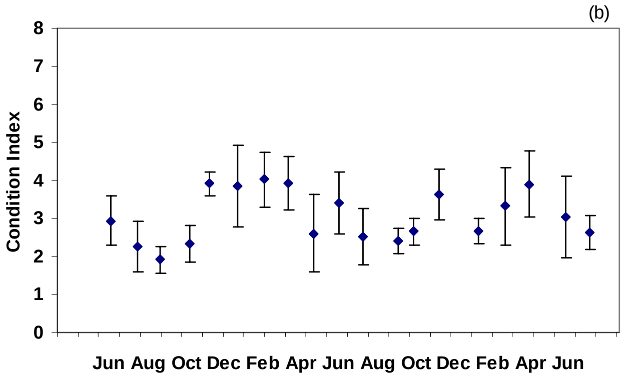
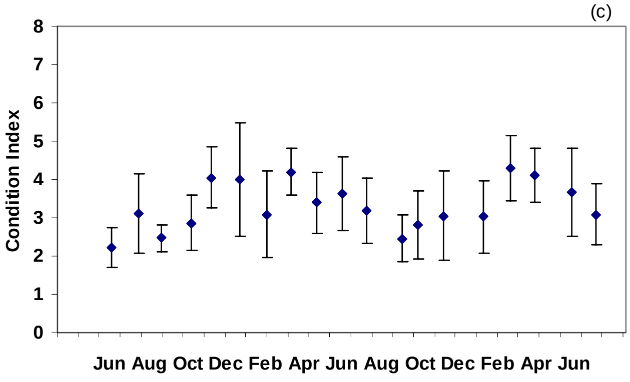
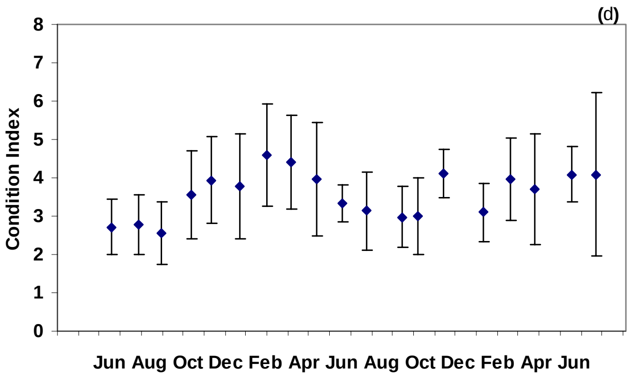

(e)
Dry Weight (mm)
3200
2800
2400
2000
1600
1200
800
400
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun

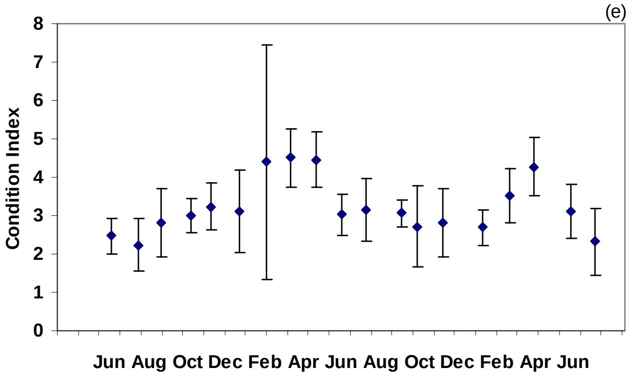
FIGURE 3.7. Average condition index value (± s.d.) for oysters (n = 10) sampled at five-week intervals from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC and (e) FD.

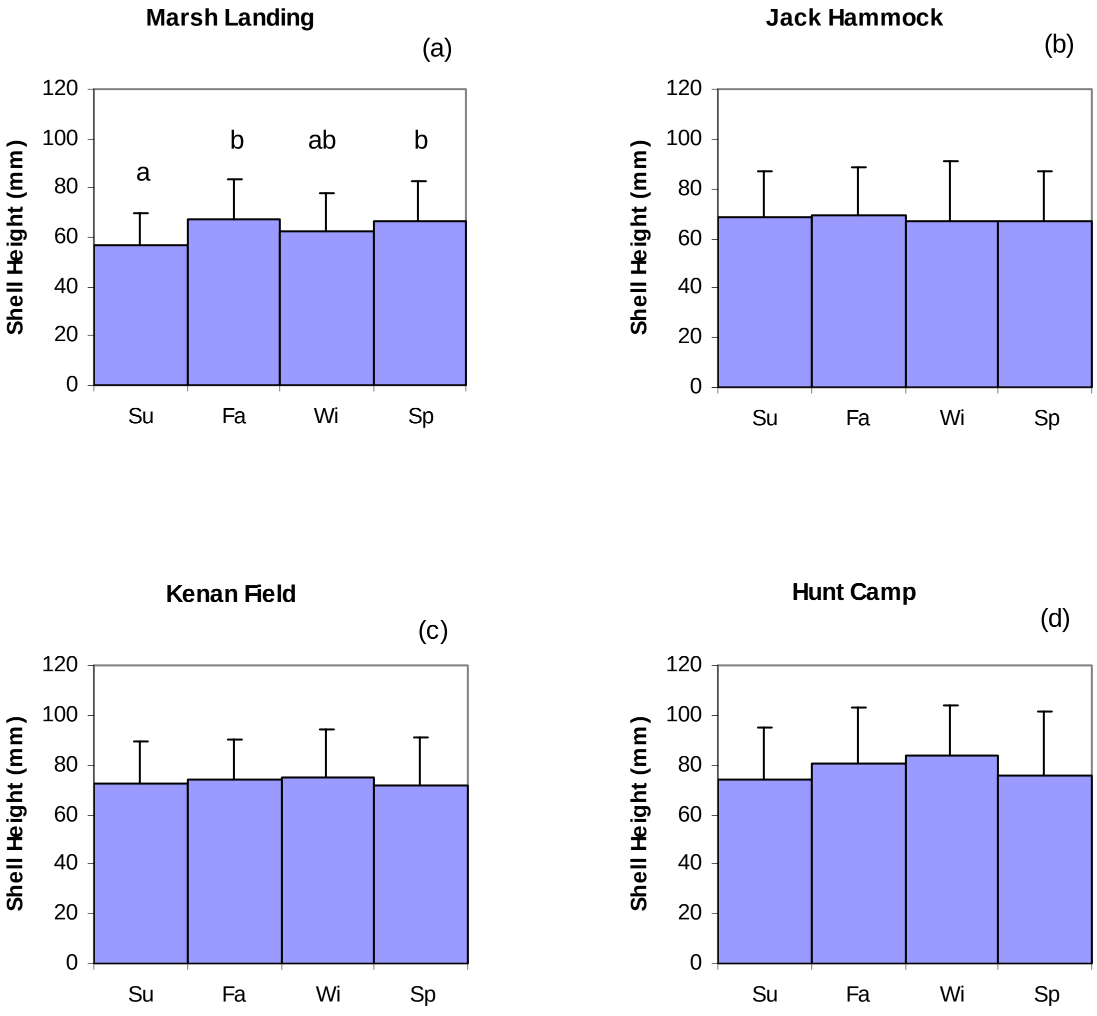

(a)
8
7
6
5
4
3
2
1
0
Condition Index
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(b)
8
7
6
5
4
3
2
1
0
Condition Index
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(c)
8
7
6
5
4
3
2
1
0
Condition Index
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(d)
8
7
6
5
4
3
2
1
0
Condition Index
Jun Aug Oct Dec Feb Apr Jun Aug Oct Dec Feb Apr Jun


(e)
Condition Index
8
7
6
5
4
3
2
1
0
Jun
Aug
Oct
Dec
Feb
Apr
Jun
Aug
Oct
Dec
Feb
Apr
Jun



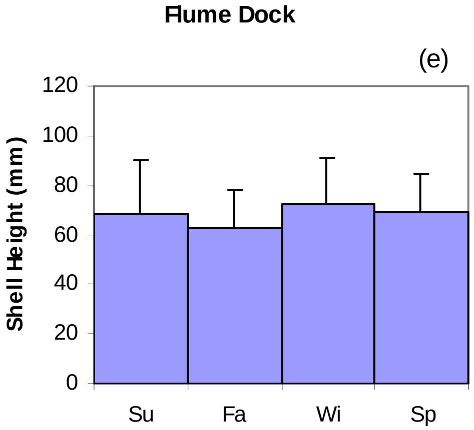
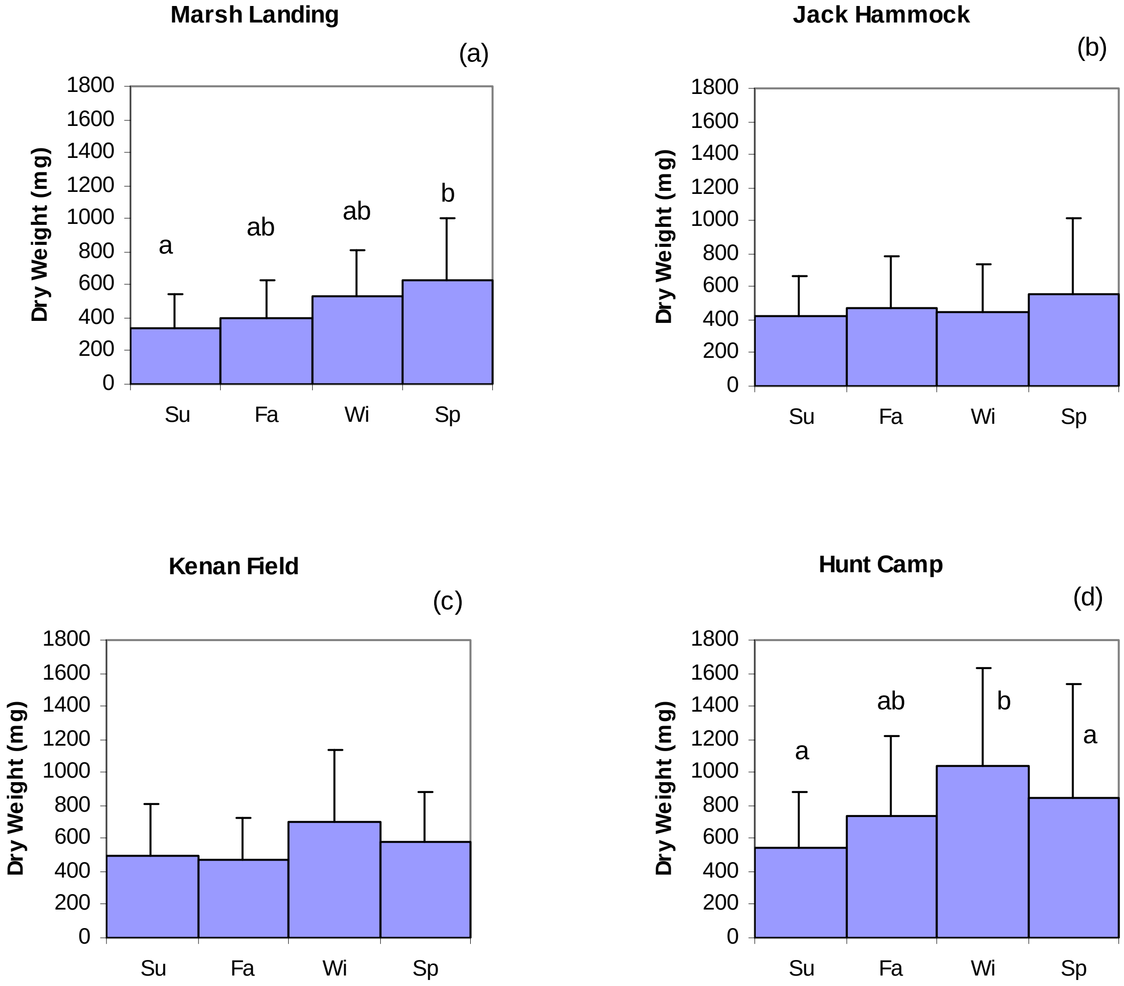


FIGURE 3.8. Average shell height (mm) (± s.d.) for oysters compared among the different seasons from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC and (e) FD. (Analysis of variance; Duncan's least significant difference post hoc tests; significant differences denoted by letters; p-values are in Appendix II; Table II.1.)



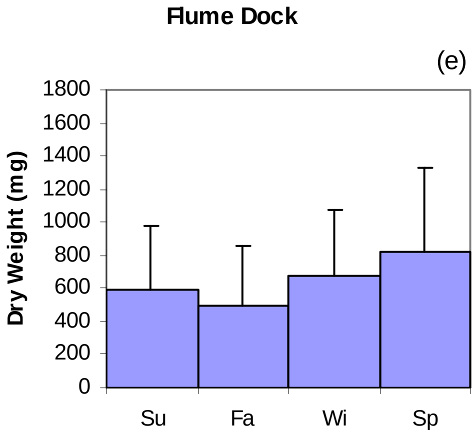


FIGURE 3.9. Average dry tissue weight (mg) (± s.d.) for oysters compared among the different seasons from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC and (e) FD. (Analysis of variance; Duncan's least significant difference post hoc tests; significant differences denoted by letters; p-values are in Appendix II; Table II.2.)

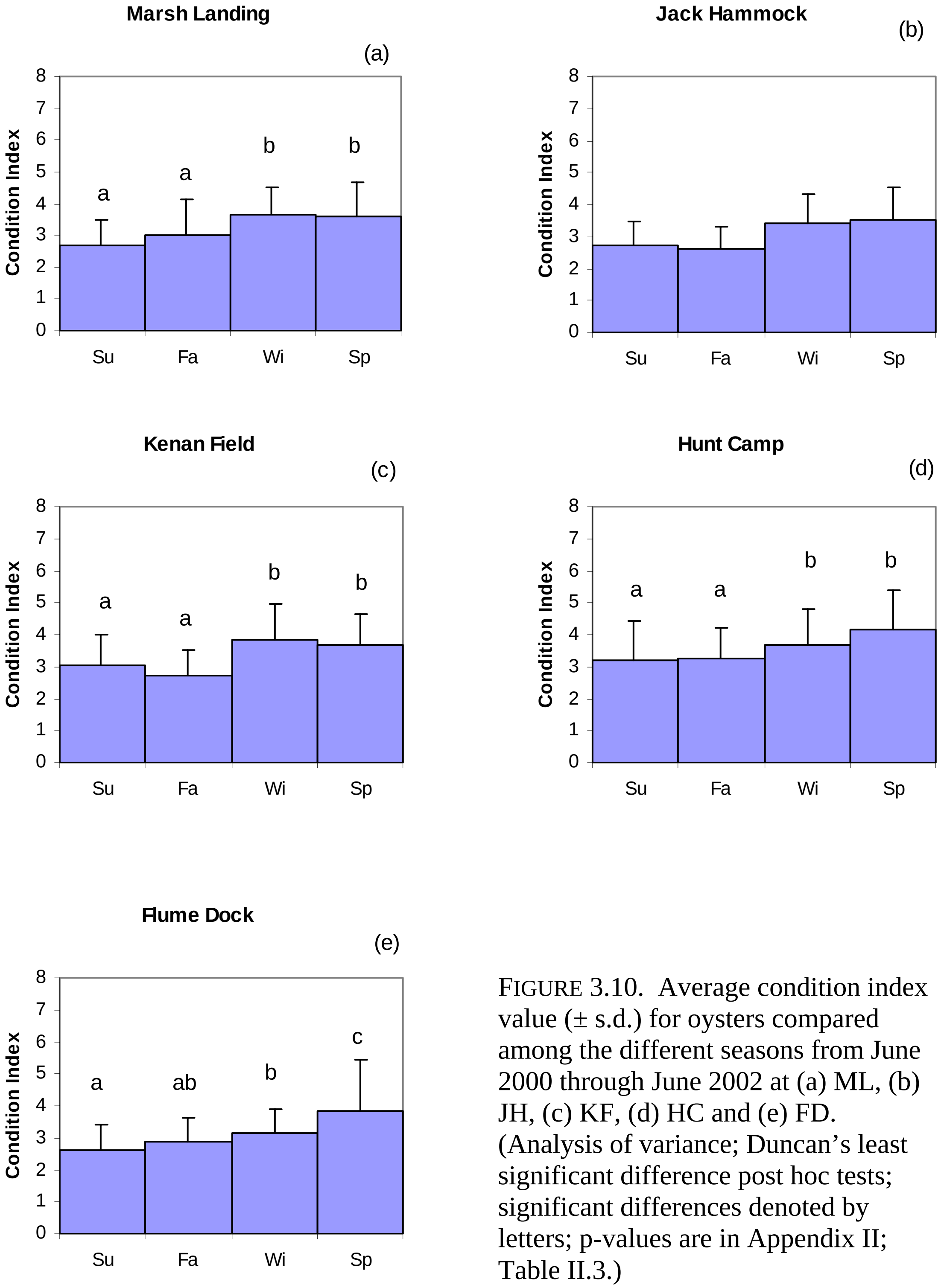


FIGURE 3.10. Average condition index value (± s.d.) for oysters compared among the different seasons from June 2000 through June 2002 at (a) ML, (b) JH, (c) KF, (d) HC and (e) FD. (Analysis of variance; Duncan's least significant difference post hoc tests; significant differences denoted by letters; p-values are in Appendix II; Table II.3.)

CONCLUSIONS

This study examined both temporal (tidal, lunar, seasonal) and spatial variation (5 sites along the length of a tidal inlet) in seston over oyster reefs in the Duplin River estuary, Georgia, from June 2000 through June 2002. It also examined spatial and seasonal differences in the contribution of benthic diatoms to the seston over oyster reefs and to the diets of oysters, utilizing both microscopic observations and stable isotopic analysis. Finally, oyster shell height, dry tissue weight and condition index values were used to examine differences in oyster performance among the 5 sites.

The seston available to oysters in the Duplin River exhibited a pronounced spatial gradient in quantity and quality from the headwaters to the mouth. In chapter one we determined that overall suspended particulate matter (SPM) and particulate organic carbon (POC) concentrations were approximately three times higher and chlorophyll *a* concentrations were approximately twice as high at the mouth as compared to the headwaters. Average SPM, POC and chlorophyll *a* concentrations were 327.6 mg L^{-1}, 5.0 mg L^{-1} and 19.9 µg L^{-1} at the mouth, and 93.4 mg L^{-1}, 1.6 mg L^{-1} and 9.4 mg L^{-1} at the headwaters. There was also a gradient of increasing quality from the mouth to the headwaters, with lower carbon to nitrogen ratios (8.1 vs. 9.6), lower carbon to chlorophyll *a* ratios (157 vs. 248) and lower percent phaeopigment (37% vs. 38%) at the headwaters. Overall, however, the pool of POC was generally considered to be detrital, as indicated by carbon to chlorophyll *a* ratios in excess of 100 throughout the tidal inlet.

Tidal, lunar and seasonal patterns were not always consistent among the different study sites. Differences in seston characteristics over a tidal cycle were only observed at the mouth, where both SPM and POC concentrations were significantly higher during late flood/high-slack water as compared to ebb water. This increase was attributed to horizontal advection of highly turbid water from Doboy Sound into the mouth of the river during flood tide. Lunar differences in the seston were observed for SPM concentration, which was higher at all of the sites during spring as compared to neap tides. This was consistent with the fact that spring tides are associated with larger tidal prisms, larger tidal amplitudes and higher current velocities than neap tides. Thus, the physical regime during spring tides favors resuspension of bottom material and can result in an overall increase in SPM concentrations. At the two mid-reach sites we also observed significantly higher POC and chlorophyll *a* concentrations during spring tides. We attributed this difference to the fact that there is an extensive intertidal mudflat that extends between these two sites along the eastern shore of the Duplin River. Therefore, spring tides could be responsible for resuspending sediment associated organic material (e.g., detritus, benthic microalgae) from this extensive intertidal mudflat, resulting in the higher concentrations of POC and chlorophyll *a* observed at these sites. A consistent seasonal pattern with higher SPM concentrations in the spring was observed at all of the study sites. However, only the three up-river sites exhibited a clear seasonal trend in POC and chlorophyll *a* concentrations, with a distinct summer maximum and winter minimum. The lack of a clear seasonal trend at the mouth could be attributed to the fact that there were numerous sources of organic material from the Atlantic Ocean and Altamaha River with consistently high concentrations of SPM, POC and chlorophyll *a* throughout the year. At the headwaters sources of particulate material were limited to local production in the marsh and the main channel of the river, which exhibited a distinct seasonality that can probably be attributed to annual cycles of microalgal productivity.

The three temporal scales we examined were good predictors of seston characteristics (both quantity and quality) at all of the sites, and explained anywhere from 16 to 82% of the variability in the seston. All three temporal scales and their interactions were significant, but the greatest number of significant observations were for seasonal time scales. The stronger relationships (where 50 to 82% of the variability was explained) were observed for POC and chlorophyll *a* concentrations at the three up-river sites where there was a strong seasonal cycle.

One of our objectives was to compare the different scales of variability to determine which scale was responsible for the greatest amount of seston variability in this system. We found that differences across spatial scales were more important than temporal differences. For any given temporal scale, the greatest amount of variability among the sites was observed at the mouth of the Duplin River as compared to the up-river sites. To compare temporal variability within each site, we used predicted standard deviations for the different temporal scales (tidal, lunar, seasonal). We found that SPM concentration exhibited the greatest variability over seasonal scales at all of the sites, although lunar variability was of a similar magnitude at the two sites closest to the mouth. For POC and chlorophyll *a* measurements, tidal and lunar variability was actually greater than seasonal variability at the two sites closest to the mouth, but at the up-river sites seasonal variability was still the greatest. At the mouth, short-term variability in the seston was comparable to or even greater than that observed over longer time scales, which contrasted with the strong seasonal cycles observed at the up-river sites.

In chapter two we examined the potential contribution of benthic diatoms to the oysters living in the Duplin River and we also identified a gradient in their availability and utilization. Water column chlorophyll *a* concentrations were significantly higher at the mouth than at the headwaters, but only exhibited a seasonal cycle at the headwaters (a summer maximum and a winter minimum). Sediment chlorophyll *a* concentrations were similar at both sites, but they were highest in the winter at the mouth and in the fall at the headwaters. Based on HPLC examination of seston pigments (carotenoids, chlorophylls, and xanthophylls), we found that diatoms were the predominant microalgal group in the water column of the Duplin River. Potential sources of diatoms to the seston include both planktonic forms living in the water column and benthic forms that are resuspended during tidal cycles.

Microscopic counts of benthic (i.e., pennate) and planktonic (i.e., centric) diatoms in both seston and oysters were used to examine the contribution of benthic forms to the diatom pool available to and ingested by oysters. A significantly higher proportion of benthic diatoms were observed in the seston (37% vs. 17%) and oysters (33% vs. 21%) at the headwaters as compared to the mouth. We determined that there was a significant relationship between the proportion of benthic diatoms in the seston and the oysters, indicating that oysters were ingesting benthic diatoms based on their availability. The fact that benthic diatoms were proportionately more important at the headwaters is consistent with the fact that sediment chlorophyll *a* concentrations were comparable to the mouth but overall water column chlorophyll *a* concentrations were lower.

Seasonally, the greatest percentage of benthic diatoms was observed in the seston at both locations during the winter and in the oysters at the headwaters during the fall. (There was no seasonal increase in the percentage of benthic diatoms in oysters at the mouth.) This is in keeping with the timing of peak sediment chlorophyll *a* concentrations.

We examined the stable isotopic signatures of seston, oysters and benthic microalgae to further investigate the utilization of benthic diatoms by oysters. These results supported our microscopic observations. We predicted values for the $\delta^{13}C$ and the $\delta^{34}S$ signatures of oysters based on our microscopic observations of the percentages of benthic and planktonic diatoms in the seston and oysters at either the mouth or the headwaters. This calculation assumes a diet of only diatoms (i.e., no detritus and no other phytoplankton). Whether we used the percent diatoms in the seston or the oysters the predicted values closely matched the observed signatures of the oysters at each location. This provided strong evidence that oysters in the Duplin River rely heavily on diatoms for their nutrition and that benthic diatoms are a part of this pool.

Overall, the availability and utilization of benthic diatoms by oysters exhibited spatial and seasonal differences in this salt marsh estuary, with a greater contribution at the headwaters. These observations support the concept of "benthic-pelagic-benthic coupling," wherein benthic diatoms have to be suspended into the water column in order to provide food web support for benthic suspension feeders such as the oysters. Moreover, oyster tissues were enriched in ^{34}S as compared to the available seston, which suggests selection for food resources such as benthic and planktonic diatoms over *Spartina alterniflora* detritus.

In chapter three we compared oyster performance (shell height, dry tissue weight, and condition index) among the five study sites. Overall, oysters at the three up-river sites had greater shell heights and dry tissue weights as compared to the down-river sites, but only the oysters close to the headwaters had significantly higher condition indices. None of the measures of seston quantity and quality exhibited significant relationships with the measures of oyster performance. We identified several factors that could help explain why the up-river sites might provide a more favorable environment for oyster growth. Very high average SPM levels (327.6 mg L^{-1}) and high seston variability over short time scales at the mouth of the Duplin River could have negatively impacted the feeding of the oysters at this location because: 1) the efficiency of particle selection by oysters decreases at high SPM concentrations, 2) at very high SPM levels oyster feeding can cease altogether, and 3) mechanisms to cope with changes in the quantity and composition of the seston are more effective at dealing with longer term rather than short term changes. In comparison, at the headwaters average SPM concentrations were lower (93.4 mg L^{-1}) and significant temporal variability was only observed over seasonal scales. These differences could have resulted in a more favorable environment for food acquisition at the headwaters as compared to the mouth.

Additionally, several physical factors were identified that could have contributed to larger sized oysters up-river. The mouth of the Duplin River is essentially an open-water environment and the oysters living adjacent to Doboy Sound are exposed to high-energy, turbulent conditions that have been observed to significantly reduce oyster growth and mortality due to "wave shock." The oysters at the mouth also occurred as clumps of living oysters interspersed with dead shell and exhibited little vertical growth. At the mid-reach site and the next up-river location the oysters grew as mounds that were approximately 0.5 to 1 m above the substrate. Both oyster growth and survival has been observed to be significantly greater when oysters grow on reefs that are elevated at least 0.5 m above the substrate.

In the future it would be useful to better quantify the dietary contribution of benthic diatoms to oysters, which are the dominant suspension feeders in the Duplin River. Information on cell volume and carbon content of benthic diatoms could be used to estimate how much of the nutritional needs of oysters were being met by benthic diatoms. Additionally, it would be interesting to quantify both benthic algal biomass and productivity in this system. With this information we could construct an overall budget to determine what proportion of the microalgal biomass and productivity in the Duplin River is utilized by the intertidal oysters, and how it varies over space and time.

APPENDIX I

SUMMARY OF DUNCAN'S LEAST SIGNIFICANT DIFFERENCE POST-HOC ANALYSES OF THE SEASONAL SESTON DATA

TABLE I.1. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for the natural log of suspended particulate material (SPM) concentrations among the seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

LN(SPM)		**Site**				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	0.003**	0.006**	0.648	0.331	0.714
	Winter	0.199	0.466	0.215	0.032*	0.153
	Spring	0.861	0.006**	0.106	0.395	0.026*
Fall	Summer	0.003**	0.006**	0.648	0.331	0.714
	Winter	0.136	0.048*	0.105	0.006**	0.295
	Spring	0.002**	0.839	0.045*	0.097	0.073
Winter	Summer	0.199	0.466	0.215	0.032*	0.153
	Fall	0.136	0.048*	0.105	0.006**	0.295
	Spring	0.159	0.039*	0.782	0.197	0.512
Spring	Summer	0.861	0.006**	0.106	0.395	0.026*
	Fall	0.002**	0.839	0.045*	0.097	0.073
	Winter	0.159	0.039*	0.782	0.197	0.0512

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE I.2. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for particulate organic carbon (POC) concentration among the different seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

POC		**Site**				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	< 0.001***	< 0.001***	0.006**	0.339	0.790
	Winter	< 0.001***	< 0.001***	0.001**	0.037*	0.875
	Spring	< 0.001***	< 0.001***	0.429	0.376	0.113
Fall	Summer	< 0.001***	< 0.001***	0.006**	0.339	0.790
	Winter	0.156	0.397	0.630	0.348	0.711
	Spring	0.565	0.936	0.061	0.111	0.269
Winter	Summer	< 0.001***	< 0.001***	0.001**	0.037*	0.875
	Fall	0.156	0.397	0.630	0.348	0.711
	Spring	0.039*	0.328	0.015*	0.009**	0.127
Spring	Summer	< 0.001***	< 0.001***	0.429	0.376	0.113
	Fall	0.565	0.936	0.061	0.111	0.269
	Winter	0.039	0.328	0.015*	0.009**	0.127

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE I.3. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for chlorophyll *a* (CHL a) concentrations among the different seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

CHL *a*		Site				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	< 0.001***	< 0.001***	0.013*	0.979	0.973
	Winter	< 0.001***	< 0.001***	0.169	0.318	0.090
	Spring	< 0.001***	< 0.001***	0.337	0.531	0.861
Fall	Summer	< 0.001***	< 0.001***	0.013*	0.979	0.973
	Winter	0.003**	0.100	0.253	0.260	0.050
	Spring	0.327	0.873	0.079	0.443	0.810
Winter	Summer	< 0.001***	< 0.001***	0.169	0.318	0.090
	Fall	0.003*	0.100	0.253	0.260	0.050
	Spring	0.036*	0.073	0.604	0.066	0.081
Spring	Summer	< 0.001***	< 0.001***	0.337	0.531	0.861
	Fall	0.327	0.873	0.079	0.443	0.810
	Winter	0.036*	0.073	0.604	0.066	0.081

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE I.4. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for the atomic carbon to nitrogen ratio (C:N) among the different seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

C:N		**Site**				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	0.355	0.011*	0.097	0.072	0.598
	Winter	0.339	0.006**	0.415	0.493	0.382
	Spring	0.411	0.069	0.504	0.200	0.832
Fall	Summer	0.355	0.011*	0.097	0.072	0.598
	Winter	0.906	0.727	0.478	0.336	0.700
	Spring	0.102	0.512	0.030*	0.661	0.773
Winter	Summer	0.339	0.006**	0.415	0.493	0.382
	Fall	0.906	0.727	0.478	0.336	0.700
	Spring	0.107	0.340	0.172	0.602	0.524
Spring	Summer	0.411	0.069	0.504	0.200	0.832
	Fall	0.102	0.512	0.030*	0.661	0.773
	Winter	0.107	0.340	0.172	0.602	0.524

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE I.5. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for % phaeopigment (% Phae) among the different seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

% PHAE		**Site**				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	0.112	0.133	0.030*	0.323	0.038*
	Winter	0.346	0.281	0.820	0.132	0.938
	Spring	0.156	0.027*	0.082	0.001**	0.253
Fall	Summer	0.112	0.133	0.030*	0.323	0.038*
	Winter	0.516	0.678	0.010*	0.005*	0.020*
	Spring	0.112	< 0.001***	< 0.001***	< 0.001***	< 0.001***
Winter	Summer	0.346	0.281	0.820	0.132	0.938
	Fall	0.516	0.678	0.010*	0.005**	0.020*
	Spring	0.013*	< 0.001***	0.108	0.051	0.247
Spring	Summer	0.156	0.027*	0.082	0.001**	0.253
	Fall	0.001**	< 0.001***	< 0.001***	< 0.001***	< 0.001***
	Winter	0.013*	< 0.001***	0.108	0.51	0.247

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE I.6. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for the particulate organic carbon to chlorophyll *a* ratio (POC:CHL *a*) among the seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

POC:CHL *a*		**Site**				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	0.555	0.526	0.104	0.758	0.936
	Winter	0.983	0.544	0.960	0.825	0.323
	Spring	0.969	0.636	0.631	0.223	0.965
Fall	Summer	0.555	0.526	0.104	0.758	0.936
	Winter	0.609	0.994	0.152	0.625	0.377
	Spring	0.547	0.275	0.255	0.153	0.972
Winter	Summer	0.983	0.544	0.960	0.825	0.323
	Fall	0.609	0.994	0.152	0.625	0.377
	Spring	0.955	0.299	0.700	0.355	0.360
Spring	Summer	0.969	0.636	0.631	0.223	0.965
	Fall	0.547	0.275	0.255	0.153	0.972
	Winter	0.955	0.299	0.700	0.355	0.360

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

APPENDIX II

SUMMARY OF DUNCAN'S LEAST SIGNIFICANT DIFFERENCE POST-HOC ANALYSES OF THE SEASONAL OYSTER DATA

TABLE II.1. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for the natural log of oyster shell height (mm) among the seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

LN(shell height)		**Site**				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	0.424	0.163	0.535	0.742	< 0.001***
	Winter	0.206	0.043*	0.670	0.484	0.065
	Spring	0.432	0.859	0.708	0.829	0.001***
Fall	Summer	0.424	0.163	0.535	0.742	< 0.001***
	Winter	0.053	0.490	0.881	0.332	0.100
	Spring	0.130	0.132	0.343	0.603	0.694
Winter	Summer	0.206	0.043*	0.670	0.484	0.065
	Fall	0.053	0.490	0.881	0.332	0.100
	Spring	0.610	0.036*	0.455	0.635	0.202
Spring	Summer	0.432	0.859	0.708	0.829	0.001***
	Fall	0.130	0.132	0.343	0.603	0.694
	Winter	0.610	0.036*	0.455	0.635	0.202

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE II.2. Summary of p-values from Duncan’s least significant difference post hoc procedures from the analysis of variance of the natural log of oyster dry tissue weight (mg) among the different seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

LN (dry weight)		**Site**				
		FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Season	**Season**					
Summer	Fall	0.051	0.136	0.346	0.450	0.367
	Winter	0.516	0.002**	0.278	0.072	0.195
	Spring	0.920	0.985	0.847	0.739	0.008**
Fall	Summer	0.051	0.136	0.346	0.450	0.367
	Winter	0.231	0.078	0.844	0.012*	0.655
	Spring	0.064	0.131	0.457	0.279	0.077
Winter	Summer	0.516	0.002**	0.278	0.072	0.195
	Fall	0.231	0.078	0.844	0.012*	0.655
	Spring	0.578	0.002**	0.369	0.138	0.221
Spring	Summer	0.920	0.985	0.847	0.739	0.008**
	Fall	0.064	0.131	0.457	0.279	0.077
	Winter	0.578	0.002**	0.369	0.138	0.221

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE II.3. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for oyster condition index among the different seasons at the 5 sites along the length of the Duplin River, GA sampled at 5-week intervals from June 2000 through June 2002. (n = 6 observations for summer; n = 5 for fall; n = 4 for winter; n = 5 for spring).

Condition Index		**Site**				
Season	**Season**	FD *(Headwaters)*	HC	KF	JH	ML *(Mouth)*
Summer	Fall	0.259	0.919	0.103	0.445	0.092
	Winter	0.025*	0.054	< 0.001***	< 0.001***	< 0.001***
	Spring	< 0.001***	< 0.001***	0.001***	< 0.001***	< 0.001***
Fall	Summer	0.259	0.919	0.103	0.445	0.092
	Winter	0.238	0.066	< 0.001***	< 0.001***	0.003**
	Spring	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.004**
Winter	Summer	0.025*	0.054	< 0.001***	< 0.001***	< 0.001***
	Fall	0.238	0.066	< 0.001***	< 0.001***	0.003**
	Spring	0.001***	0.058	0.430	0.695	0.823
Spring	Summer	< 0.001***	< 0.001***	0.001***	< 0.001***	< 0.001***
	Fall	< 0.001***	< 0.001***	< 0.001***	< 0.001***	0.004**
	Winter	0.001***	0.058	0.430	0.695	0.823

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

APPENDIX III

OYSTER DAM CREEK SAMPLING

Two additional sites were sampled in conjunction with our regular sampling 9described in chapter one) form June 2001 through June 2002. Both of these sites were located at the mouths of small tidal creeks that had oyster dams at their entrances. One of the creeks was located near the headwaters of the Duplin River (designated TC for tidal inlet creek) and the other was located near the mouth of Folly River on the littoral fringe of Doboy Sound (designated SC for sound creek) (Figure III.1). These dams prevent all of the water in the creek from leaving during ebb water as a pool of water remains trapped behind the oysters. Given the large amount of nutrients in the sediments surrounding the oyster reefs these pools are sites of potentially high algal productivity. Thus, it was thought that these pools might provide additional food resources to the oysters when they filled during flood water, and that there could also be an increased contribution of benthic diatoms to oyster diets at these two locations.

Both sites were sampled at five-week intervals during the second year of the study for a total of 10 field-sampling efforts (June 2001 through June 2002). The method of sample collection and processing was identical to that described in the methods sections of chapters one, two and three, with water for seston and diatom analysis sampled during mid-ebb water and oysters and sediments sampled during low water. Samples for diatom and isotopic analyses were collected quarterly in July and October 2001, and in January and May 2002. Seston analyses included determination of suspended particulate material (SPM), particulate organic carbon (POC), particulate organic nitrogen (PON), chlorophyll *a* and phaeopigment concentrations. Diatom analysis of seston and oysters involved determining the proportion of benthic diatoms available to and ingested by oysters. Chlorophyll *a* concentrations were also determined for surficial sediment samples. Oysters were measured for shell height, dry tissue weight and shell weight and both shell and dry tissue weights were used to calculate condition index. Finally, seston samples and oyster adductor muscles were submitted to Coastal Sciences Laboratory (Austin, Texas) for determination of ^{13}C and ^{34}S stable isotopic signatures.

The creek sites generally resembled the adjacent system for all measured parameters, i.e., the data from TC were similar to the headwaters of the Duplin River (HC and FD) whereas the data from SC were similar to the mouth of the Duplin River or Doboy sound (ML). This was true for: 1) seston quantity (SPM, POC, chlorophyll *a*) and quality [carbon to nitrogen ratios (C:N), percent phaeopigment (as the proportion of total chlorophyll *a* and phaeopigment that was phaeopigment), POC to chlorophyll *a* ratios], 2) benthic microalgae (sediment chlorophyll *a*, percent benthic diatoms in seston, oysters), 3) stable isotope signatures (seston, oysters) and 4) oyster performance (shell height, dry tissue weight, condition index). Thus, the creek sites did not represent a unique habitat for oysters, and our conclusions from these data are similar to the comparisons that were made throughout this dissertation in terms of differences between the mouth and the headwaters. The data are summarized below.

The seston data for the two creek sites are summarized in Table III.1 and plotted in Figures III.2 through III.6. SPM, POC and chlorophyll *a* concentrations were all significantly higher (student t-tests, $p = 0.004$ for SPM; $p = 0.001$ for POC and chlorophyll *a*) at SC where the creek was adjacent to Doboy Sound as compared to TC, where the creek was a tidal tributary near the headwaters of the Duplin River. For seston quality, the average C:N ratio, POC to chlorophyll *a* ratio and percent phaeopigment were all significantly greater (e.g., lower quality) at SC as compared to TC (student t-tests, $p < 0.001$ for percent phaeopigment; $p = 0.004$ for C:N and POC to chlorophyll *a* ratios). The concentrations of all parameters measured were similar to those observed at the nearby channel sites. Seasonal comparisons within each site are plotted in Figures III.7 & III.8 (p-values for the significant differences are provided in Tables III.3 and III.4). At both sites SPM exhibited significantly higher concentrations in the spring than the other seasons, which was consistent with the nearby channel sites. POC and chlorophyll a concentrations exhibited a summer maximum at TC, which was consistent with the other sites near the headwaters of the Duplin River. At SC, POC concentration exhibited at fall peak and chlorophyll *a* concentration exhibited a spring peak, this contrasted with the mouth of the Duplin River where there were no significant seasonal differences in either of these parameters. Seasonal patterns of seston quality were not clear or consistent among the two sites, although at SC seston quality was lower in the summer and fall with higher C:N ratios, percent phaeopigment and POC to chlorophyll *a* ratios during these times of year. At the nearby reference sites seston quality did not exhibit significant seasonal trends.

Sediment chlorophyll *a* concentrations were not significantly different between the two sites, which was consistent with what we observed for the nearby channel sites. Average sediment chlorophyll *a* concentrations were 52.0 ± 37.4 $\mu g\ g^{-1}$ dry wt. at SC and

42.8 ± 35.4 μg g^{-1} dry wt. at TC (Table III.5). Seasonally, the patterns of differences were consistent between both sites, with maximum concentrations in the spring, intermediate values in summer and winter, and minimum concentrations in the fall (Table III.5; Figure III.9). This was different than the seasonal pattern exhibited in the channel sites, where maximum sediment chlorophyll *a* values were observed in the fall and winter.

We only have quarterly observations of diatoms in seston and oysters from each of the creek sites (Table III.6; Figure III.10). Overall, the proportion of benthic diatoms was significantly higher at TC than at SC, with 34.2 ± 9.0% in the seston at TC (vs. 20.12 ± 3.2% at SC) and 39.3 ± 14.5% in the oysters at TC (vs. 29.1 ± 6.2% at SC). Again, similar to patterns in percent benthic diatoms in nearby channel sites. On a seasonal basis, there was a significantly lower percentage of benthic diatoms in the seston at TC in the summer and spring as compared to the other seasons ($p < 0.01$) and in the oysters in the summer ($p < 0.01$). There were no significant seasonal differences at SC. Thus, there was no obvious relationship in these observations to sediment chlorophyll *a* concentration.

The stable isotope signatures of oysters and seston at each of the creek sites are summarized in Table III.7. The $\delta^{13}C$ signatures of the oysters closely matched the available seston, which was similar to what we observed at the non-creek sites at the mouth and the headwaters of the Duplin River and indicate a diet that was predominantly microalgal material. However, this includes both phytoplankton and benthic microalgae, which cannot generally be differentiated from each other based on ^{13}C signatures. The $\delta^{34}S$ values of the oysters were again enriched relative to what was available in the seston. The depleted sulfur values for the seston probably reflect the contribution of detrital material to the pool of organic material and the enriched oyster signatures suggest that the oysters are selecting living microalgae over detrital particles. When we calculated the isotopic signatures of the oysters based on the proportions of diatoms observed microscopically in the seston and the oysters, they closely matched the observed signatures of the oysters (Table III.8). These observations were also consistent with what we observed for the non-creek sites that we studied in this system as well.

Overall measures of oyster performance (shell height, dry tissue weight, condition index) are summarized in Table III.9 and are categorized by season in Table III.10. Based on independent samples student t-tests, both dry tissue weight and oyster condition were significantly higher at TC as compared to SC ($p = 0.007$ and $p = 0.028$, respectively). This was also consistent with our observations in nearby channel sites where oyster living closer to the headwaters of the Duplin River, in areas that were more sheltered than the mouth, were significantly larger and had higher condition index values. When plotted over the course of one year there is a lot of variability in these data but the trends are similar to what was observed at the other study sites (Figure III.11). Increases during the winter in dry tissue weight and condition reflect the annual reproductive cycle with fattening and the storage of energy reserves and a decline in dry tissue weight and condition during the summer reflect the mobilization of these reserves (Figure III.11). This pattern is more evident when the data are examined seasonally and was similar to what we observed at the other study sites (Figure III.12). Significant seasonal differences, determined by analysis of variance, are indicated by letters in Figure III.12 and p-values from the post-hoc tests are provided in Table III.11.

TABLE III.1. Characteristics of seston at two creek sites sampled at 5-week intervals from June 2001 through June 2002 (SC and TC; Figure III.1). SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (µg L^{-1}), % PHAE = % phaeopigment, and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 10 observations per site).

	Site	
Parameter	**TC** *(tidal inlet creek)*	**SC** *(sound creek)*
SPM	171.1 ± 169.2	201.4 ± 26.0
POC	1.5 ± 0.5	4.5 ± 3.7
C:N	8.3 ± 1.2	10.3 ± 4.5
CHL *a*	13.0 ± 6.0	17.3 ± 7.5
% PHAE	40 % ± 7	51% ± 11
POC:CHL *a*	132 ± 31	242 ± 102

TABLE III.2. Seasonal characteristics of seston at two creek sites sampled at 5-week intervals from June 2001 through June 2002 (SC and TC; Figure III.1). SPM = suspended particulate material (mg L^{-1}), POC = particulate organic carbon (mg L^{-1}), C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a* (µg L^{-1}), % PHAE = % phaeopigment, and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (mean ± sd) (n = 3 observations for summer; n = 3 for fall; n = 2 for winter; n = 2 for spring).

		Site	
Parameter	**Season**	**TC** *(tidal inlet creek)*	**SC** *(sound creek)*
SPM	Summer	116.5 ± 42.4	158.3 ± 82.3
	Fall	120.2 ± 127.8	186.0 ± 89.5
	Winter	229.1 ± 169.1	270.6 ± 318.6
	Spring	271.1 ± 171.6	419.3 ± 65.7
POC	Summer	2.2 ± 0.5	4.1 ± 1.4
	Fall	1.3 ± 0.2	5.8 ± 3.5
	Winter	0.9 ± 0.2	1.9 ± 1.1
	Spring	1.9 ± 0.7	4.0 ± 2.6
C:N	Summer	8.7 ± 0.4	10.2 ± 0.1
	Fall	9.2 ± 0.2	12.0 ± 2.6
	Winter	8.2 ± 1.6	8.6 ± 0.6
	Spring	8.2 ± 0.5	9.3 ± 0.9
CHL *a*	Summer	13.8 ± 3.1	17.8 ± 7.9
	Fall	9.8 ± 2.5	18.1 ± 9.0
	Winter	9.9 ± 7.4	15.3 ± 9.8
	Spring	13.7 ± 4.5	23.0 ± 10.3
PHAE	Summer	41% ± 11	22% ± 12
	Fall	40% ± 3	55% ± 9
	Winter	38% ± 7	43% ± 1
	Spring	40% ± 2.7	40% ± 4
POC:CHL *a*	Summer	134 ± 27	303 ± 112
	Fall	135 ± 27	308 ± 45
	Winter	122 ± 72	129 ± 14
	Spring	135 ± 8	165 ± 41

TABLE III.3. Summary of p-values from Duncan’s least significant difference post hoc procedures from the analysis of variance for seasonal differences in seston from the sound creek (SC) sampled at 5-week intervals from June 2000 through June 2002. LN(SPM)= natural log of suspended particulate material, POC = particulate organic carbon, C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a*, % PHAE = % phaeopigment, and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (n = 3 observations for summer; n = 3 for fall; n = 2 for winter; n = 2 for spring).

Season	**Season**	**LN(SPM)**	**POC**	**C:N**	**CHL a**	**PHAE**	**POC:CHL *a***
Summer	Fall	0.392	0.103	0.160	0.058	0.157	0.933
	Winter	0.807	0.081	0.239	0.656	< 0.001***	0.038*
	Spring	0.001**	0.981	0.485	0.001**	< 0.001***	0.080
Fall	Summer	.392	0.103	0.160	0.058	0.157	0.933
	Winter	0.595	0.002**	0.018*	0.240	< 0.001***	0.0348
	Spring	0.011*	.137	0.054	0.066	< 0.001***	0.072
Winter	Summer	0.807	0.081	0.239	0.656	< 0.001***	0.038*
	Fall	0.595	0.002**	0.018*	0.240	< 0.001***	0.034*
	Spring	0.005**	0.114	0.656	0.009**	0.814	0.628
Spring	Summer	0.001**	0.981	0.485	0.001**	< 0.001***	0.080
	Fall	0.011*	0.137	0.054	0.066	< 0.001***	0.072
	Winter	0.005**	0.114	0.656	0.009**	0.814	0.628

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE III.4. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for seasonal differences in seston from the tidal inlet creek (TC) sampled at 5-week intervals from June 2000 through June 2002. LN(SPM) = natural log of suspended particulate material, POC = particulate organic carbon, C:N = atomic carbon to nitrogen ratio, CHL *a* = chlorophyll *a*, % PHAE = % phaeopigment, and POC:CHL *a* = particulate organic carbon to chlorophyll *a* ratio. (n = 3 observations for summer; n = 3 for fall; n = 2 for winter; n = 2 for spring).

Season	**Season**	**LN(SPM)**	**POC**	**C:N**	**CHL a**	**PHAE**	**POC:CHL *a***
Summer	Fall	0.332	< 0.001***	0.193	< 0.001***	0.682	0.959
	Winter	0.286	< 0.001***	0.280	< 0.001***	0.235	0.738
	Spring	0.071	0.032*	0.306	0.028*	0.695	0.979
Fall	Summer	0.332	< 0.001***	0.193	< 0.001	0.682	0.959
	Winter	0.056	0.045*	0.028*	0.969	0.235	0.704
	Spring	0.009**	0.002**	0.032*	0.044*	0.695	0.984
Winter	Summer	0.286	< 0.001***	0.280	< 0.001***	0.235	0.738
	Fall	0.056	0.045*	0.028*	0.969	0.408	0.704
	Spring	0.489	< 0.001	0.958	0.070	0.464	0.742
Spring	Summer	0.071	0.032*	0.306	0.028*	0.695	0.979
	Fall	0.009**	0.002**	0.032*	0.044*	0.979	0.984
	Winter	0.489	< 0.001	0.958	0.070	0.464	0.742

* = significant at the 0.05 level
** = significant at the 0.01 level
*** = significant at the 0.001 level

TABLE III.5. Chlorophyll *a* (µg g^{-1} dry wt.) concentration in surface sediments around oyster reefs at SC (sound creek) and TC (tidal inlet creek) sampled at 5-week intervals from July 2001 through June 2002 averaged for the entire year (mean ± s.d.) (n = 8) and categorized by season (n = 2 observations for summer; n = 3 for fall; n = 2 for winter; n = 1 for spring).

		Site	
		TC *(tidal inlet creek)*	**SC** *(sound creek)*
Overall :	1-year average	42.8 ± 35.4	52.0 ± 37.5
Seasonal:	Summer	29.3 ± 8.9	62.8 ± 30.5
	Fall	12.6 ± 6.1	13.8 ± 4.9
	Winter	64.5 ± 26.6	75.6 ± 25.6
	Spring	109.5 ± 16.1	97.9 ± 14.1

TABLE III.6. Percent benthic diatoms (%BDs) in seston and oysters from sound creek (SC) and tidal inlet creek (TC) sampled quarterly from June 2001 through June 2002. (mean ± s.e.)

	TC (tidal inlet creek)		**SC (sound creek)**	
	% BDs seston	**% BDs oysters**	**% BDs seston**	**% BDS oysters**
Overall	34.2 ± 3.2	39.3 ± 4.2	20.1 ± 1.1	29.1 ± 1.8
Summer	21.9 ± 0.6	18.9 ± 0.5	23.4 ± 0.7	25.4 ± 0.6
Fall	40.1 ± 2.6	51.8 ± 6.7	20.4 ± 0.1	36.0 ± 4.8
Winter	43.3 ± 1.2	38.7 ± 2.0	18.7 ± 1.7	27.3 ± 1.6
Spring	31.5 ± 0.7	47.8 5 ± 3.5	18.0 ± 4.0	27.8 ± 3.6

TABLE III.7. Stable isotopes of carbon ($\delta^{13}C$) and sulfur ($\delta^{34}S$) for seston and oyster tissue from SC (sound creek) and TC (tidal inlet creek) of the Duplin River sampled quarterly over the course of the two-year study from June 2000 through June 2002. (mean ± s.e.; no s.e. is provided when the results of analytical replicates were exactly the same.)

Sample Type & Location	**$\delta^{13}C$**	**$\delta^{34}S$**
Seston: (n = 4 pooled)		
TC *(tidal inlet creek)*	-21.1‰	+9.0‰ ± 0.1
SC *(sound creek)*	-19.4‰ ± 0.4	+6.4‰ ± 0.1
Oyster: (n = 4 pooled)		
TC *(tidal inlet creek)*	-20.8‰	+15.2‰ ± 0.1
SC *(sound creek)*	-18.9‰ ± 0.1	+15.7‰ ± 0.1

TABLE III.8. Calculated carbon ($\delta^{13}C$) and sulfur ($\delta^{34}S$) values compared to observed values for the stable isotopic signatures of oysters based on the different mixtures of benthic and planktonic diatoms in seston and oysters from TC and SC from June 2001 through June 2002. (Isotopic values for phytoplankton were taken from the literature ($\delta^{13}C$ -21.3‰ and $\delta^{34}S$ +18.8‰) as reported in Peterson and Howarth (1987); isotopic values for the benthic microalgae were based on our observations from the headwaters and the mouth of the Duplin River in November 2003 (Chapter 2).

		$\delta^{13}C$		**$\delta^{34}S$**	
		calculated	**observed**	**calculated**	**observed**
TC	BDs in oysters[1]	-19.7‰	-20.8‰	+15.2‰	+15.2‰
	BDs in seston[2]	-18.2‰		+15.7‰	
SC	BDs in oysters[3]	-20.6‰	-18.9‰	+15.4‰	+15.7‰
	BDs in seston[4]	-17.2‰		+16.4‰	

TC: [1] Based on a diet of 39% benthic diatoms and 61% planktonic diatoms.
[2] Based on a diet of 34% benthic diatoms and 66% planktonic diatoms.
SC: [3] Based on a diet of 29% benthic diatoms and 71% planktonic diatoms.
[4] Based on a diet of 20% benthic diatoms and 80% planktonic diatoms.

TABLE III.9. Spatial characteristics of oysters at TC (tidal inlet creek) and SC (sound creek), GA sampled at 5-week intervals from June 2001 through June 2002 (for site locations see Figure III.1). (Shell height (mm), dry tissue weight (mg), and condition index[1])

	Shell Height		Dry Tissue Weight		Condition Index	
Site	Min., Max.	Mean ± s.d.	Min., Max.	Mean ± s.d.	Min., Max.	Mean ± s.d.
TC	34.2,115.5	69.1 ± 16.3	150,3390	717 ± 497	0.9,5.7	3.1 ± 1.0
SC	28.0,123.8	73.8 ± 18.1	130,1940	546 ± 372	0.8,5.1	2.8 ± 0.9

[1] Based on the calculation of Walne and Mann (1975) (dry meat x 100/ shell weight)

TABLE III.10. Seasonal characteristics of oysters at TC (tidal inlet creek) and SC (sound creek) sampled at 5-week intervals from June 2001 through June 2002. (Shell height (mm), dry tissue weight = dry weight (mg), and condition index = CI[1]

		Site	
Parameter	**Season**	**TC** *(tidal inlet creek)*	**SC** *(sound creek)*
Shell Height	Summer	64.1 ± 14.0	65.4 ± 11.5
	Fall	72.1 ± 16.3	72.7 ± 15.8
	Winter	66.8 ± 15.4	83.7 ± 21.4
	Spring	74.2 ± 19.0	77.9 ± 21.0
Dry Weight	Summer	476 ± 239	319 ± 159
	Fall	579 ± 275	519 ± 237
	Winter	864 ± 519	782 ± 494
	Spring	1143 ± 693	694 ± 436
CI[1]	Summer	2.6 ± 0.7	2.6 ± 0.8
	Fall	2.8 ± 0.7	2.9 ± 0.8
	Winter	3.7 ± 1.0	2.9 ± 0.2
	Spring	3.7± 1.3	2.7 ± 1.1

[1] Based on the calculation of Walne and Mann (1975) (dry meat x 100/ shell weight)

TABLE III.11. Summary of p-values from Duncan's least significant difference post hoc procedures from the analysis of variance for seasonal differences in oysters from the tidal inlet creek (TC) and sound creek (SC) sampled at 5-week intervals from June 2000 through June 2002. Shell Height = shell. Ht. (mm), Dry Tissue Weight = Dry Wt. (mg); Condition Index = CI[1] (n = 3 observations for summer; n = 3 for fall; n = 2 for winter; n = 2 for spring).

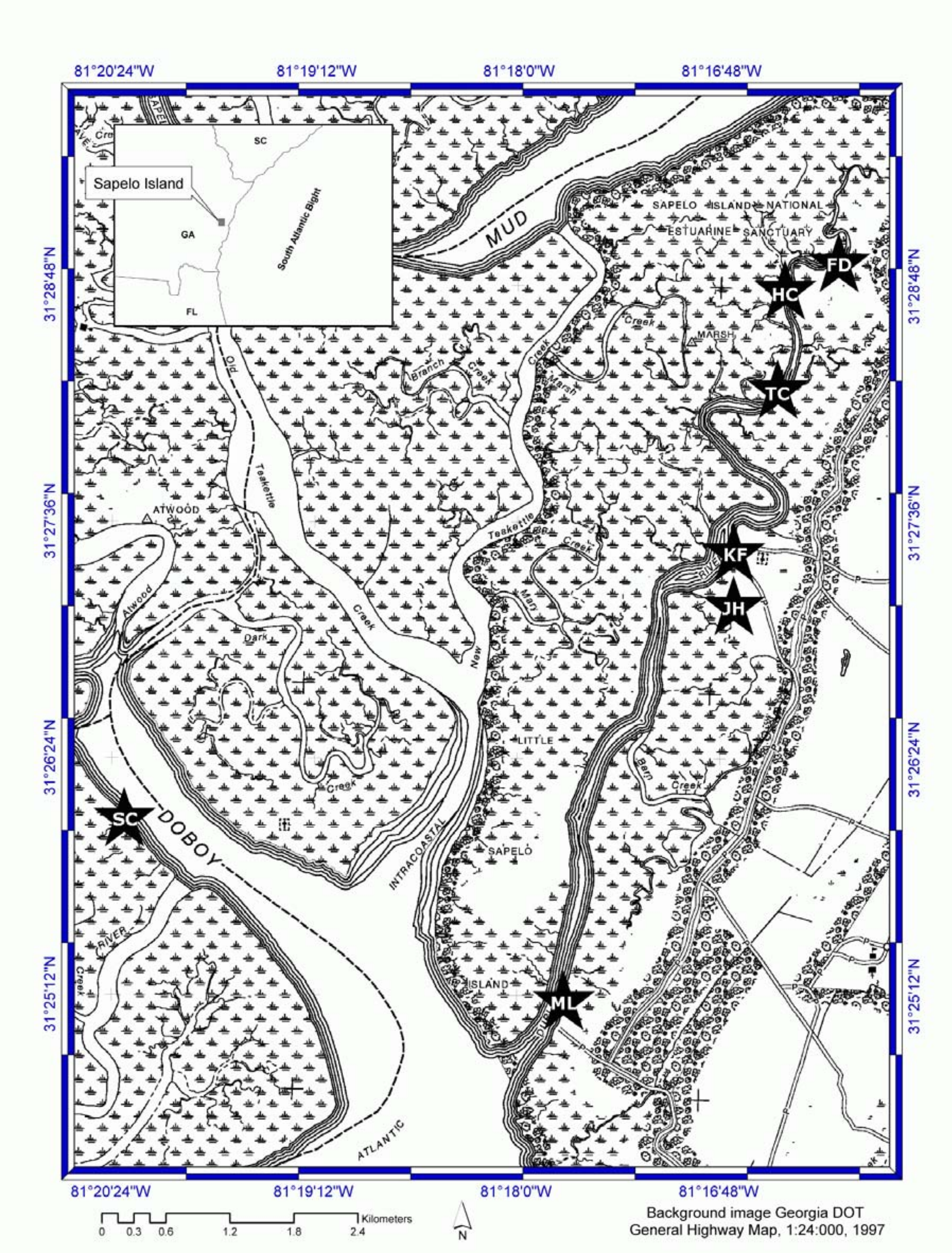
		TC *(tidal inlet creek)*			**SC** *(sound creek)*		
Season	**Season**	**Shell Ht.**	**Dry Wt.**	**CI**	**Shell Ht.**	**Dry Wt.**	**CI**
Summer	Fall	0.057	0.362	0.471	0.100	0.022*	0.147
	Winter	0.568	0.003**	< 0.001***	< 0.001***	< 0.001***	0.246
	Spring	0.033*	< 0.001***	< 0.001***	0.013*	< 0.001***	0.715
Fall	Summer	0.057	0.362	0.471	0.100	0.022*	0.147
	Winter	0.263	0.027*	0.002**	0.029*	0.007	0.888
	Spring	0.662	< 0.001***	0.001***	0.298	0.071	0.348
Winter	Summer	0.568	0.003**	< 0.001***	< 0.001***	< 0.001***	0.246
	Fall	0.263	0.027*	0.002**	0.029*	0.007**	0.888
	Spring	0.157	0.047*	0.819	0.291	0.407	0.466
Spring	Summer	0.033*	< 00.001***	< 0.001	0.013*	< 0.001***	0.715
	Fall	0.662	< 0.001***	0.001	0.298	0.071	0.348
	Winter	0.157	0.047*	0.819	0.291	0.407	0.466

[1] Based on the calculation of Walne and Mann (1975) (dry meat x 100/ shell weight)

* = significant at the 0.05 level

** = significant at the 0.01 level

*** = significant at the 0.001 level



Background image Georgia DOT General Highway Map, 1:24:000, 1997

Figure III.1. Map of the study site indicating the five main sampling locations in the Duplin River, GA (ML, JH, KF, HC, FD; chapters 1-3) in relation to the two creek sites which were sampled during the second year of the study June 2001 through June 2002).

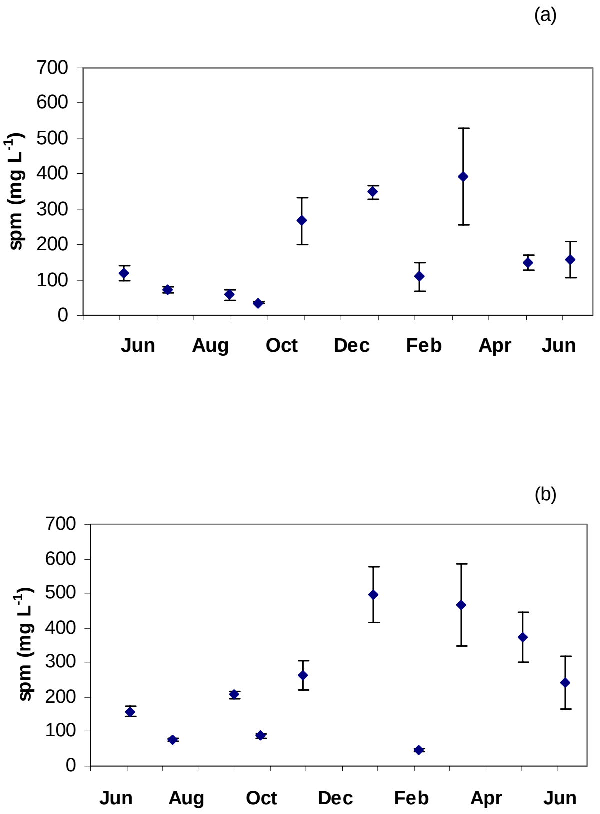


Figure III.2. Suspended particulate material (SPM) (mg L^{-1}) concentration (± s.e.) over oyster reefs at (a) TC and (b) SC from June 2001 through June 2002, see Figure III.1 for site locations. (Independent samples student's t-test comparing the two sites $p = 0.004$)

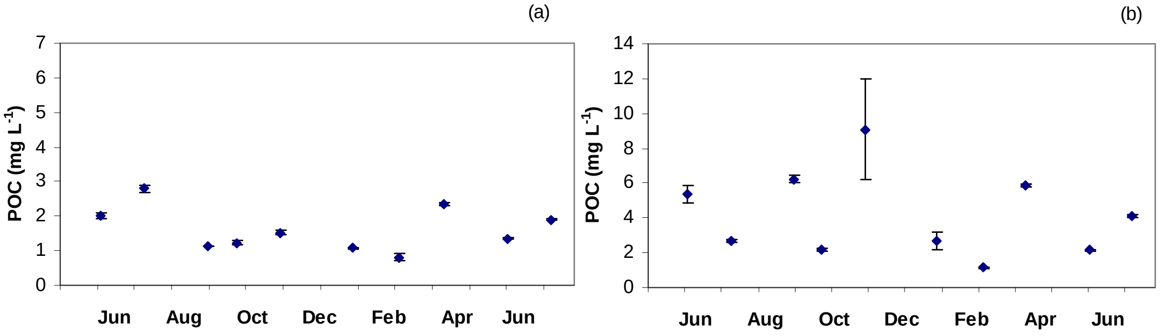


Figure III.3. Particulate organic carbon (POC) (mg L^{-1}) concentration (± s.e.) in seston over oyster reefs at (a) TC and (b) SC from June 2001 through June 2002. (Independent samples student's t-test comparing the two sites $p = 0.001$)

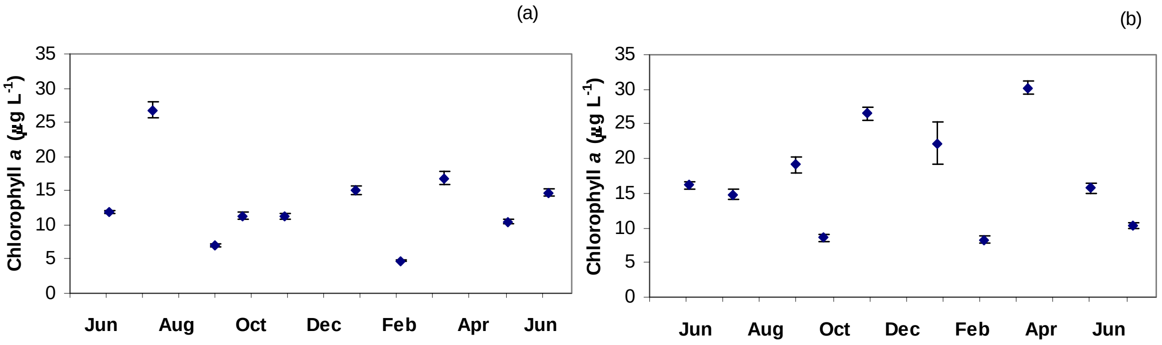


Figure III.4. Chlorophyll *a* concentration (μg L^{-1}) (± s.e.) in seston over oyster reefs at (a) TC and (b) SC from June 2001 through June 2002. (Independent samples student's t-test comparing the two sites $p = 0.001$)

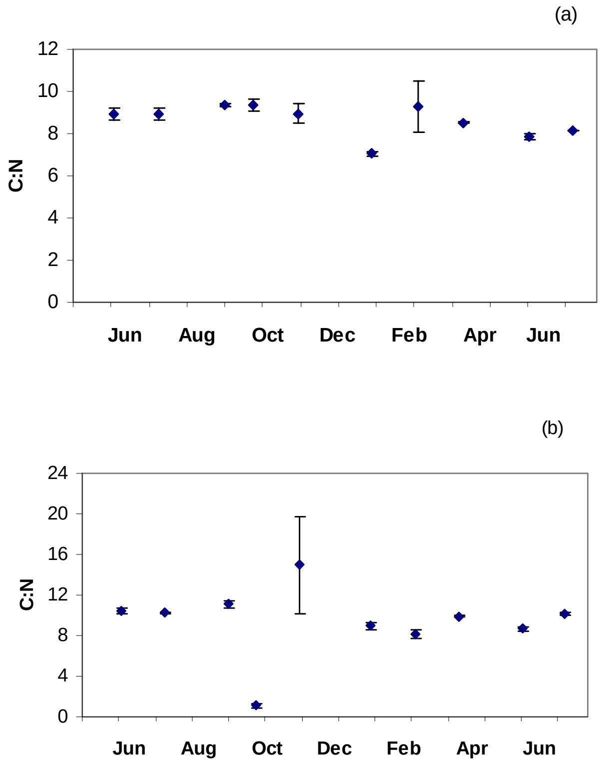


Figure III.5. Carbon to nitrogen ratio (C:N) (± s.e.) of seston over oyster reefs at (a) TC and (b) SC from June 2001 through June 2002. (Independent samples student's t-test comparing the two sites $p = 0.004$)

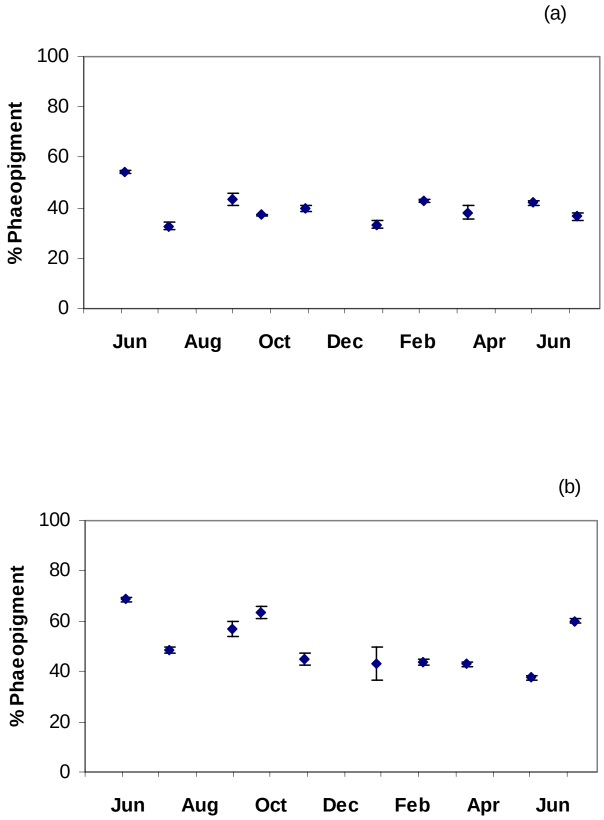


Figure III.6. Percent phaeopigment (± s.e.) of seston over oyster reefs at (a) TC and (b) SC from June 2001 through June 2002. (Independent samples student's t-test comparing the two sites $p < 0.001$)

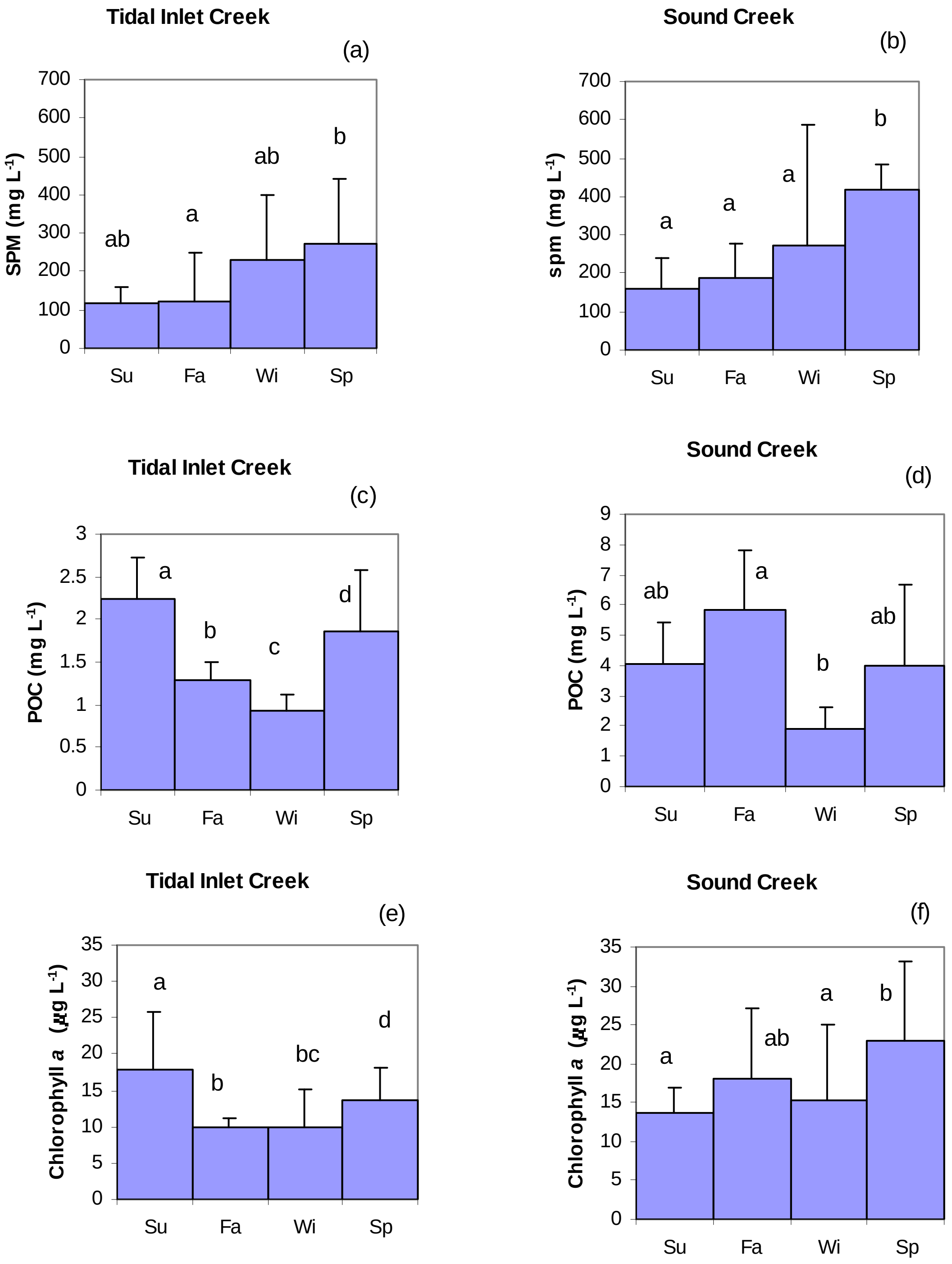


Figure III.7. Seasonal seston characteristics at tidal inlet creek (TC) and sound creek (SC) from June 2001 through June 2002; (a-b), suspended particulate material (SPM) (mg L^{-1}); (c-d), particulate organic carbon (POC) (mg L^{-1}); (e-f), chlorophyll *a* (μg L^{-1}) (± s.d.). (Analysis of variance was used to identify significant seasonal differences; post-hoc test p-values in Tables III.3 & III.4.)

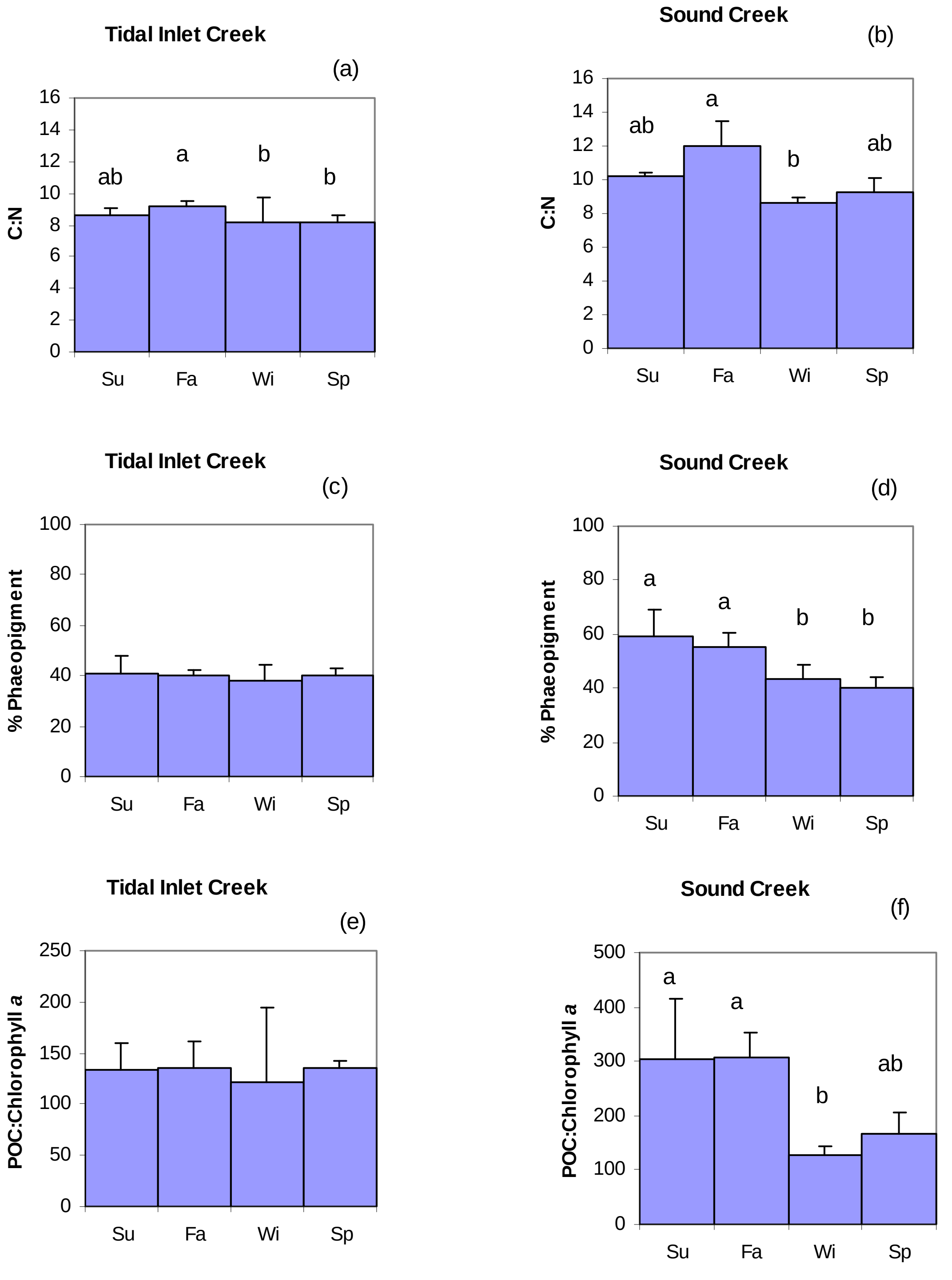


Figure III.8. Seasonal seston characteristics at tidal inlet creek (TC) and sound creek (SC) from June 2001 through June 2002; (a-b), carbon to nitrogen ratio (C:N); (c-d), percent phaeopigment; (e-f), particulate organic carbon (POC) to chlorophyll *a* ratio (± s.d.). (Analysis of variance was used to identify significant seasonal differences; post-hoc test p-values in Tables III.3 & III.4.)

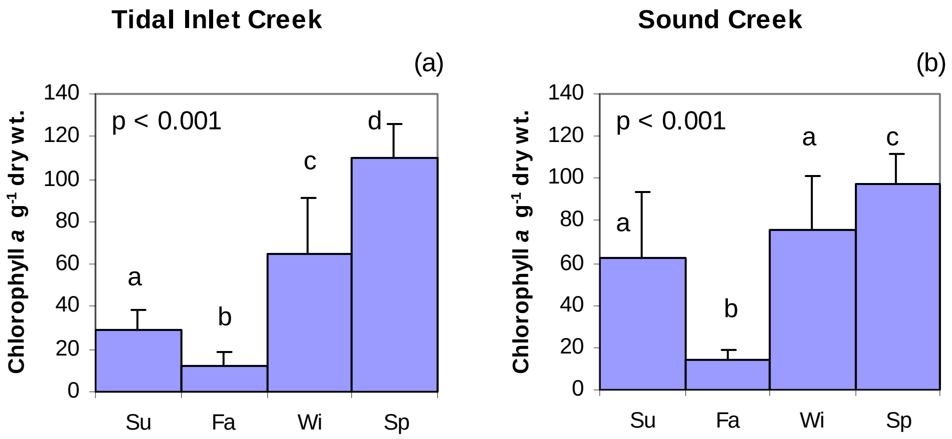


Figure III.9. Seasonal sediment chlorophyll *a* concentrations (μg g^{-1} dry wt.) (± s.d.) at (a) tidal inlet creek (TC) and (b) sound creek (SC) from July 2001 through June 2002. (Analysis of variance was used to determine significant seasonal diffe

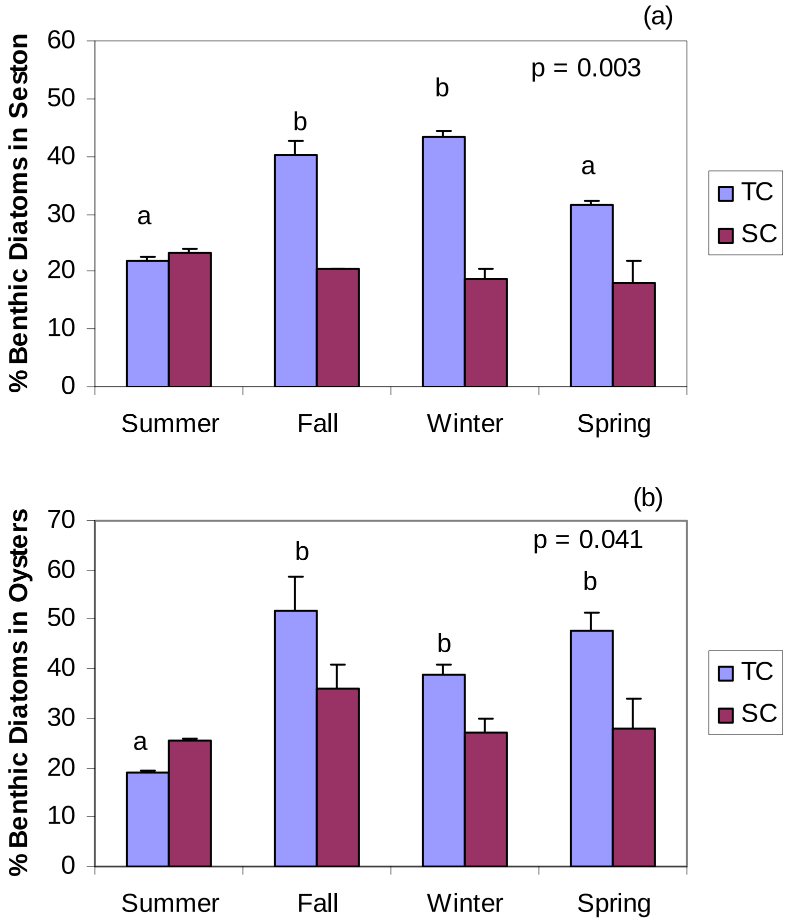


Figure III.10. Percent benthic diatoms at tidal inlet creek (TC) and sound creek (SC) in (a) seston and (b) oysters sampled quarterly from June 2001 to June 2002. (p-values from independent samples student's tests comparing the two sites indicated on charts; significant seasonal differences determined by analysis of variance and post-hoc tests for TC indicated by letters.)

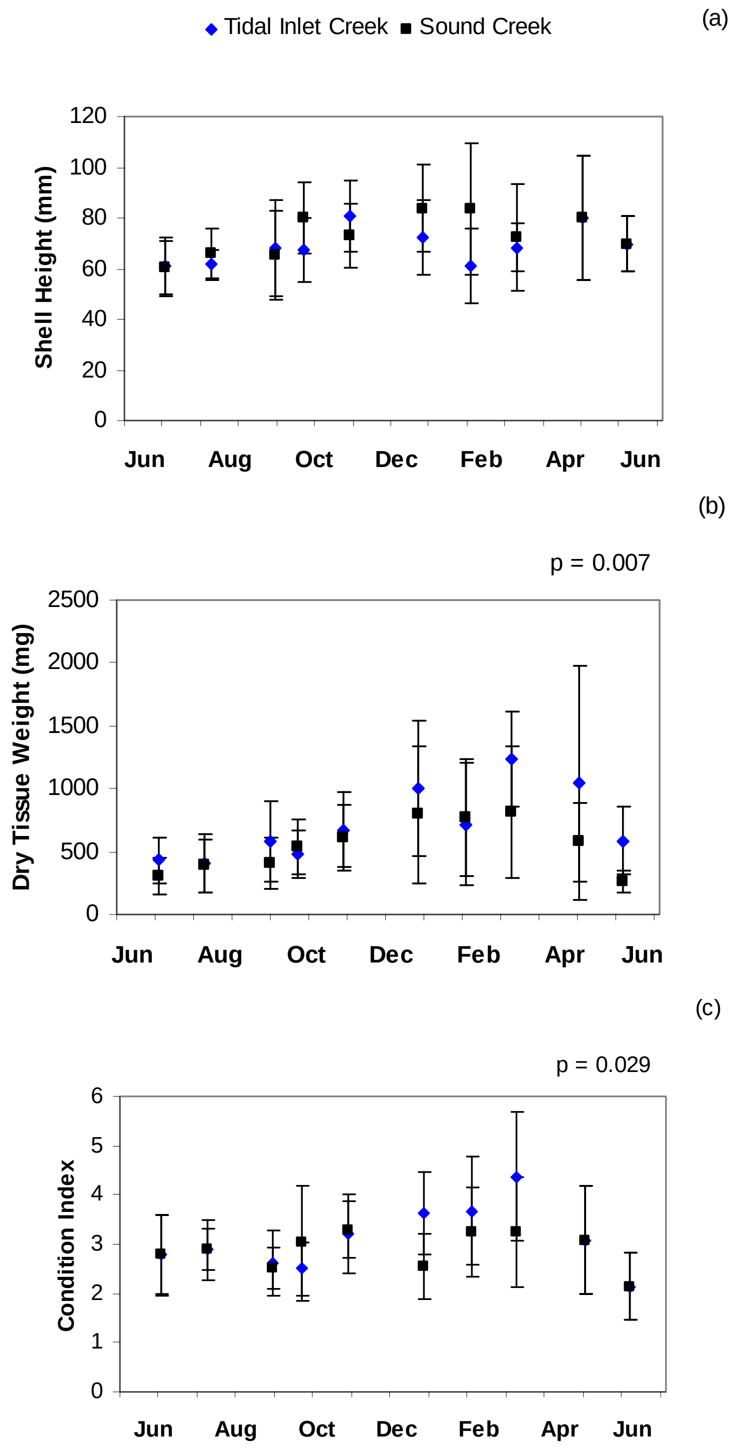


Figure III.11. Average oyster (a) shell height (mm), (b) dry tissue weight (mg) and (c) condition index (± s.d.) at tidal inlet creek (TC) and sound creek (SC) from June 2001 through June 2002. (P-values from independent samples student's t-test comparing the two sites indicated on charts.)

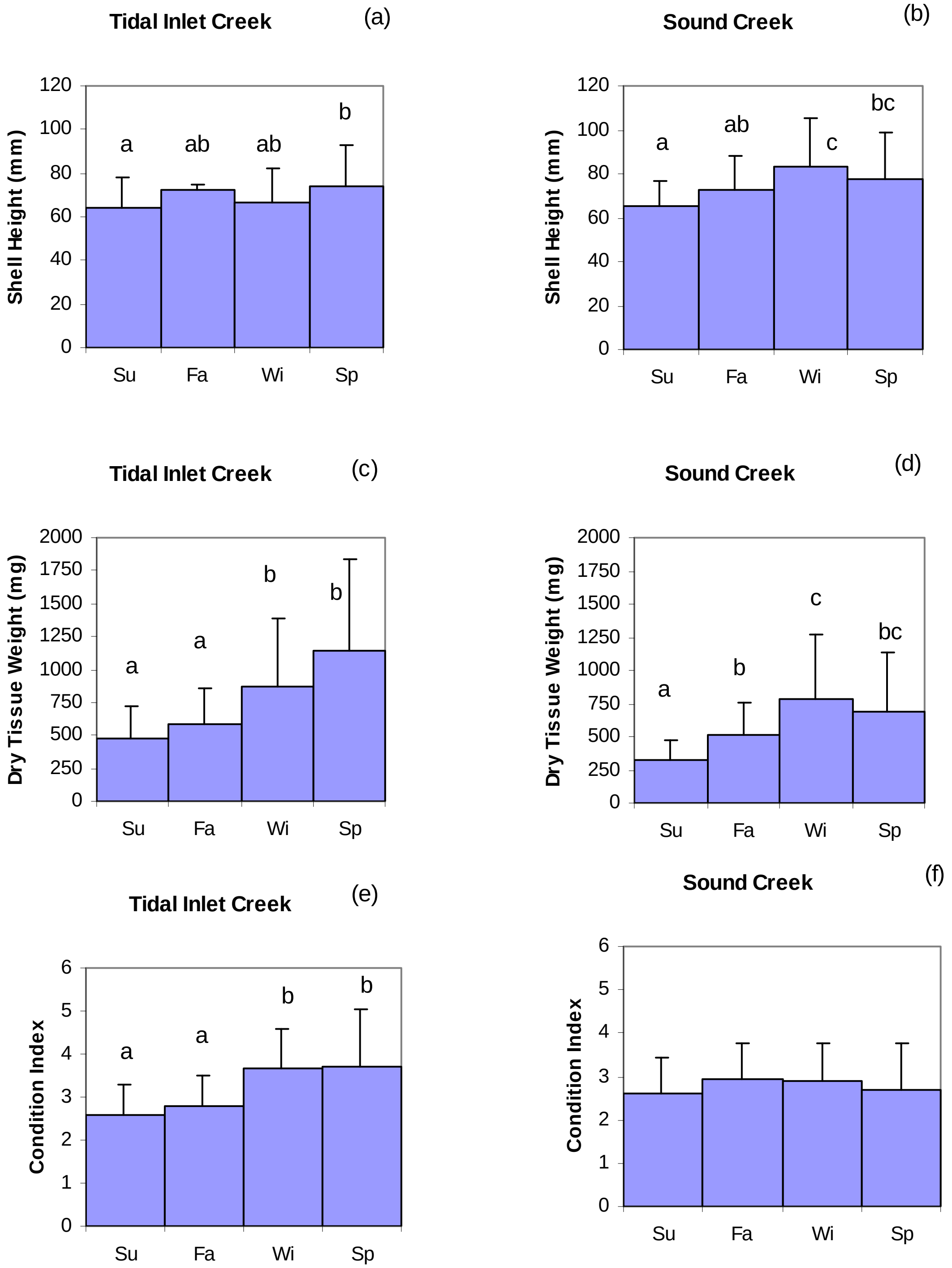


Figure III.12. Average seasonal oyster (a-b) shell height (mm), (c-d) dry tissue weight (mg), and (e-f) condition index (± s.d.) at SC (sound creek) and TC (tidal inlet creek) from June 2001 through June 2002. (Significant seasonal differences determined using analysis of variance; post-hoc test p-values are in Table III.11.)