

Spatial and Temporal Dynamics of Epiphytic Microalgae on the Cordgrass *Spartina alterniflora* in North Inlet Estuary, South Carolina

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ABSTRACT: Epiphytic microbial biomass (as chlorophyll *a*) was measured monthly in North Inlet Estuary, South Carolina, for 16 months on spatially distinct stem sections (bottom and middle) of dead and living *Spartina alterniflora* growth forms (tall, medium, and short) exposed at low tide. The highest biomass was located on the bottom section of tall plants, presumably due to their relatively longer contact with creek water and associated phytoplankton, and their closer proximity to marsh sediments with associated benthic microalgae, both recruitment sources for epiphytes. Dead plants left standing from the previous year's growth cycle had higher epiphytic biomass than living plants, which occurred mostly in late spring through fall. Epiphytic biomass was highest in the winter (mean of 1.77 mg chl *a* (m² marsh)⁻¹) and lowest in the summer (mean of 0.34 mg chl *a* (m² marsh)⁻¹). Because phytoplankton and *Spartina* production are lowest in the winter, the results emphasize the relative importance of epiphytes to growth of herbivores in this season.

Introduction

Edaphic algae (e.g., epiphytes, microphytobenthos) can contribute significantly to overall primary production in salt marsh estuaries (e.g., Stowe and Gosselink 1985; Pinckney and Zingmark 1991, 1993). Epiphytes in salt marshes are found primarily attached to *Spartina alterniflora* and are comprised of eukaryotic microalgae and macroalgae, diatoms, cyanobacteria, and heterotrophic bacteria (Stowe 1972, 1982; Alexander 1973; Gleason 1986; Currin and Paerl 1998a). This epiphytic community has been less studied than other primary producers in these systems (e.g., *S. alterniflora*, phytoplankton, microphytobenthos, macroalgae) but is recognized as an important structural and functional component of salt marsh ecosystems (e.g., Sullivan 1982). The epiphytic community presumably plays an important role in the trophodynamics of estuarine food webs. Epiphytes have been reported as an important source of primary production and food for some zooplankton, stem-

dwelling meiofauna, and small macrofauna during some seasons of the year (Jones 1980; Rutledge and Fleeger 1993; Gregg and Fleeger 1998; Quiñones-Rivera and Fleeger 2005).

Knowledge of the spatial and temporal variability of the structure and dynamics of epiphytes on *Spartina* communities is important to determine their role in estuarine carbon and energy fluxes, as carbon entering the food web originating from microalgae may be as important to salt marsh consumers as carbon originating from other estuarine producers (Page 1997; Moens et al. 2002). Carbon flux related to microalgal seasonal processes (e.g., phytoplankton spring bloom deposition) are particularly important to estuarine systems, as it affects benthic processes by increasing macrobenthic production (Graf et al. 1982; Marsh and Tenore 1990) and by enhancing summer microbial processes and nutrient regeneration (Jensen et al. 1990), and recruitment success of juvenile demersal fishes (Townsend and Cammen 1988).

This paper focuses on the variability in epiphytic biomass associated with different growth forms of *Spartina* in North Inlet Estuary, a high salinity salt marsh estuary near Georgetown, South Carolina. Because composition and biomass of phytoplankton and benthic microalgae, potential recruitment

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sources for the epiphytic community, vary seasonally (Pinckney and Zingmark 1993; Lewitus et al. 1998) and also with tidal stage (Chrzanowski and Zingmark 1986; Kulkarni et al. 2005), it is possible that similar temporal changes will be reflected in the epiphytic community on *Spartina*. We tested the hypothesis that epiphytic biomass varies spatially and temporally in NIE. Spatial variability was determined based on sections of *Spartina* stems (bottom, middle, top) and growth forms of *Spartina* (short, medium, tall). Temporal variability included comparisons between seasons and tidal stages. Epiphytic biomass on dead and living plants also was compared. Because NIE is part of the United States National Estuarine Research Reserve System and considered a model or reference estuary due to its relatively pristine condition, results from this study will help provide a picture of epiphytic communities that may be representative of similar salt marsh estuaries prior to anthropogenic impacts.

Study Area

North Inlet Estuary (NIE: 33°20'N, 79°20'W) is a high salinity (36–37.5‰), microtidal, subtropical, tidally-driven, pocket salt marsh, and a well-mixed estuarine system (Kjerfve 1978; Kjerfve et al. 1991; Monbet 1992; Lewitus et al. 2004; Voulgaris and Meyers 2004). Approximately 17% of its total area (41 km²) is below 1 m mean sea level (MSL), while the ubiquitous *S. alterniflora* and less abundant *Juncus roemerianus* populations occupy about 83% of the total estuarine area (Morris et al. 2005). Because of its relatively pristine condition, small size, and limited connections to surrounding aquatic environments, NIE is representative of a near-natural salt marsh estuarine ecosystem (White et al. 2004).

The shoreline along the creek banks throughout the estuary is characterized by tall forms of *Spartina* (Ornes and Kaplan 1989). Tall plants occur primarily within a 5–10 m wide band along the creek side; short and medium forms extend between the tall *Spartina* zone and the high tide line (Pinckney 1992). Moving inland, the ground elevation gradually rises, and the height of *Spartina* plants exhibits a gradient of tall (low marsh), medium (mid marsh), and short (high marsh) forms (Ornes and Kaplan 1989). Tall plants are ≥ 1.5 m, while short plants are ≤ 0.5 m (Dame and Kenny 1986). The height of medium *Spartina* ranges between 1.0 and 1.5 m. Both dead and live *Spartina* growth forms have similar height distributions (Jackson personal observation).

NIE water temperature ranges from 13°C to 32°C with an annual mean of 24.4°C (White et al. 2004). Mean particle size of sediments in the tidal creeks ranges from 25 to 75 μm and they form flocs during

neap tides. During spring tides, larger flocs and larger individual grain particles are also found (Voulgaris and Meyers 2004). Mean creek depths throughout NIE average only 3 m, which make tidal range a significant fraction of the total water depth. Most of the marsh lies < 1 m above MSL. As a consequence, the marsh is partially flooded at each high tide, and completely flooded at least a few times each year, especially during spring tides (Kjerfve et al. 1991).

Semidiurnal tides with an annual mean range of 1.6 m are dominant in NIE with an average spring tidal range of 2.5 m and a neap tidal range of ca. 1.0 m. Because ebb currents are measurably stronger than flood currents, an asymmetry between filling and emptying of the marsh occurs. The lack of freshwater inflows and gravitational (estuarine) inflows makes the tidal pumping mode the most important factor driving water circulation (Kjerfve et al. 1991).

Ammonium is the major inorganic nitrogen source in NIE (Lewitus et al. 1998; White et al. 2004) due to restricted freshwater input, oyster regeneration, subtidal drainage, and episodic runoff from forested wetlands (Wolaver et al. 1988; Dame et al. 1989; Whiting and Childers 1989; Childers et al. 1993). Nitrate concentrations are typically < 1 μM , but they can reach ca. 2 μM following stochastic rain events, which introduce new nitrogen into the system. Surrounding forested upland areas are sources of new dissolved organic nitrogen (DON), whose concentrations in NIE are > 10 μM (White et al. 2004). Major storm events may increase DON concentration through groundwater and surface creeks (Wolaver et al. 1986; Krest et al. 2000; Lewitus et al. 2000). Phosphate and silicate in NIE creeks result from inputs, internal processes in the water column and sediments, and biological uptake (White et al. 2004).

Materials and Methods

Initially, three locations in NIE—Clambank (CB, the main channel connecting the estuary to the open ocean), Bly Creek (BC, a shallow enclosed drainage basin), and Oyster Landing (OL, a small shallow tidal tributary bordering the maritime forest)—were chosen as sampling sites. Data analysis (Jackson 2004) showed that the epiphytic biomass found at CB and BC were not significantly different from that measured at OL, so the study was performed at OL, a site closer to the laboratory that allowed faster processing of samples.

Epiphytes on three distinct standing growth forms of *Spartina* (tall, medium, and short) were sampled to examine the effect of plant location on epiphytic biomass. Chlorophyll *a* (chl *a*) was used as a biomass indicator (De Junge and Colijn 1994). Standing

dead and living *Spartina* growth forms at about the same height were sampled, because epiphytic biomass might differ between these forms due to leachates released from dead plants (Stowe 1982). In this study, we consider standing dead stems as remnant culms that remained upright and attached following their death during the previous winter. Epiphytes on different stem sections (bottom, middle, and top) were also evaluated to test the spatial and temporal effects of irradiance and water exposure (tidal emersion and submersion). The bottom and middle sections of *Spartina* (defined here as the first $\frac{1}{3}$ and $\frac{2}{3}$ of the stem height above the sediment surface, respectively) are formed as culms (stems) by imbricate leaves, while at the top, these leaves separate from one another. *Spartina* plants were also sampled at low tide (LT1) followed by the immediate high tide (HT1) to investigate variation in epiphytic biomass at different tidal cycles. Changes in water velocity affects temporal and spatial variation of periphyton (Singer et al. 2005), so it was expected that different flow velocities at LT1 and HT1 may cause the epiphytic community to detach from plant stems, causing variation in epiphyte biomass. Initial results were inconsistent (Jackson 2004), so plants were collected during 5 consecutive days at sequential tidal stages in the winter (January): LT1, HT1, LT2 (immediate low tide following HT1), and HT2 (high tide immediately following LT2). On days 3 and 5, *Spartina* were not collected at HT2 because flood tide water levels were moderated and pushed seaward by strong winds and never reached the plants.

Initial calibration showed that only 0–5% of total epiphytic biomass was located in the upper section of the aboveground stems (separated leaves) of the plants. To manage the number of replicates used in routine analyses without losing a significant amount of biomass information, only the bottom and middle sections of the plants were evaluated in this study. Eight dead and eight living plants of the three growth forms of *Spartina* were collected approximately every 3 m along 24-m transects parallel to the creeks in OL. Each plant was located at least 3 m from the next replicate to minimize dependence effects on variability (Spurrier personal communication).

After harvesting, the bottom and middle parts of the plants were separated and placed in individually labeled plastic bags, transported to the laboratory on ice (in a dark cooler), and stored at an average temperature of 4°C until analysis. In the laboratory, 10-cm segments of the bottom-most part of each stem section (bottom and middle) were cut, and their diameter measured. Stems were then gently scraped three times using a rubber policeman to

remove epiphytes without damaging epidermal tissue.

The scraped material was placed in vials, and 1 ml of saturated MgCO_3 was added to prevent chl *a* phaeophytinization. Chl *a* was extracted using the freeze-thaw method of Mukerji and Morris (1976) with some modifications as follows. Vials were frozen at -20°C for 24 h to 15 d. Nine milliliters of 100% acetone were added to frozen epiphytes, making the extract solvent concentration 90%. Vials were kept in the dark at 4°C and shaken once a day. After 2 d, extracts of chl *a* were measured using a Turner Model 450 fluorometer. Final chl *a* concentrations (in μg) were normalized to the area scraped on each 10 cm stem segment (in cm^2), which was calculated by $10\pi d$, where d is the stem diameter in centimeters.

Epiphytic biomass on *Spartina* stems (in μg chl *a* cm^{-2}) is reported as mean \pm 1 standard error. Analysis of variance (ANOVA) tests using SAS (version 8.0 for Windows, SAS Institute, Inc., Cary, North Carolina) were performed to determine differences in epiphytic biomass among sites and on different plant categories. A level of significance ≤ 0.05 was considered acceptable in the analyses. Chl *a* data was transformed as $(\log_{10}[x + 1])$ prior to analysis to obtain normality (Zar 1999).

Biomass of epiphytes per m^2 of marsh was calculated as the product of the total biomass of epiphytes per stem of *Spartina* sampled, the surface area of *Spartina* stems per m^2 of marsh, and the number of dead and living stems per m^2 in areas of short, medium, and tall plants. The total biomass per stem was based on the sum of the epiphytic biomass found on the bottom and middle sections of each aboveground plant. Twelve, fifteen, and twenty quadrats (0.5 m^2) were used to assess the number of plants per m^2 in areas containing the various growth forms.

Results

LIVE VERSUS DEAD *SPARTINA*

Living plants were collected only from May 2002 to January 2003; during the rest of the year they were either senescent, dead (late winter), or too young (early to mid spring) to have accumulated epiphytes. Comparisons between live and dead plants were limited to 9 mo (Fig. 1). Results of ANOVA indicated that epiphytic biomass was significantly influenced by plant condition, i.e., dead versus living ($F = 59.29$; ANOVA; $p < 0.0001$). Biomass of epiphytes on tall and medium *Spartina*, was generally higher on dead plants than on living ones (Fig. 1). Differences between epiphytic biomass on dead and live stems of short plants were not as evident. The seasonal trends in

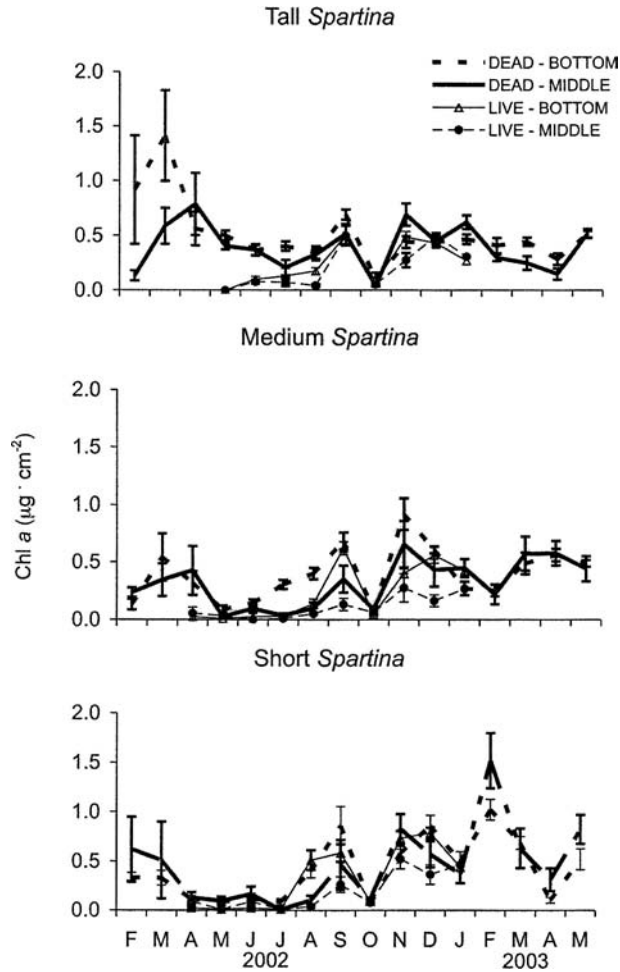


Fig. 1. Monthly epiphytic biomass ($\mu\text{g chl } a \text{ cm}^{-2}$; mean \pm 1 standard error, $n = 8$) on the bottom and middle sections of dead and living tall, medium, and short *Spartina alterniflora* at Oyster Landing, North Inlet estuary, South Carolina.

epiphytic biomass were similar between living and dead plants.

DIFFERENT SIZES OF *SPARTINA*

Epiphytic biomass on *Spartina* varied among different plant sizes (tall, medium, and short) over time (Fig. 1; $F = 11.73$; ANOVA, $p < 0.0001$). Tall *Spartina* contained more epiphytic biomass than the other sizes from February to June 2002, but relatively higher values were often measured in the other size classes throughout the remaining experimental period.

DIFFERENT PLANT SECTIONS

The bottom section of dead, tall plants contained substantially higher biomass in February and March 2002 (Fig. 1; $F = 18.00$; $p < 0.0001$), but overall showed similar values of epiphytic biomass as the

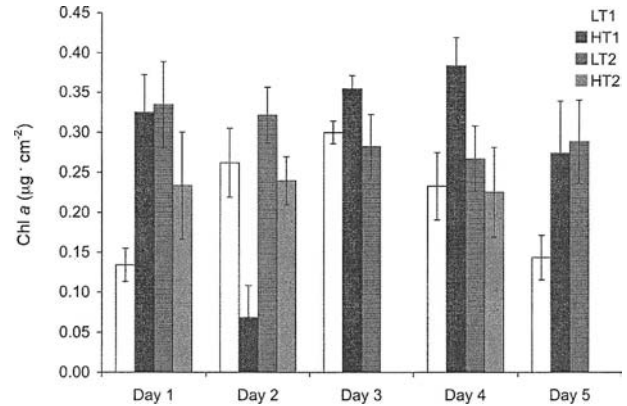


Fig. 2. Epiphytic biomass ($\mu\text{g chl } a \text{ cm}^{-2}$; mean \pm 1 standard error, $n = 8$) at 2 low tides and two high tides in Oyster Landing, North Inlet estuary, South Carolina. LT1 = first low tide, HT1 = immediate high tide following LT1, LT2 = immediate low tide following HT1, HT2 = high tide immediately following LT2. On days 3 and 5, *Spartina alterniflora* were not collected at HT2 because creek water levels did not reach the plants.

middle section. On medium and short plants (Fig. 1) bottom sections generally contained higher amounts of epiphytic biomass, particularly from July through September 2002 and in November and December 2002.

SEASONAL TRENDS

Seasonal variability was observed in epiphytic biomass on all *Spartina* forms (Fig. 1; $F = 20.63$; ANOVA, $p < 0.0001$). Less variability was found on medium plants compared to tall and short *Spartina*. The highest biomass values were associated with tall plants in spring 2002, and generally higher biomass was measured on short plants from the end of summer 2002 to the beginning of spring 2003 (August 2002 to March 2003). During the summer, biomass of epiphytes was lowest on almost all short forms and on all live, tall and medium plants ($< 0.5 \mu\text{g chl } a \text{ cm}^{-2}$). A precipitous drop occurred on all plant forms in October ($< 0.2 \mu\text{g chl } a \text{ cm}^{-2}$).

CONSECUTIVE TIDAL STAGES

A consistent pattern in epiphytic biomass was observed at LT1 and HT1 (except on day 2), when a decrease in those values from one tidal stage (LT1) to another (HT1) was registered (Fig. 2). No other pattern in epiphytic biomass over tidal stages was observed.

BIOMASS OF EPIPHYTES PER m^2 OF MARSH

Monthly average biomass of epiphytes per plant category per m^2 of marsh is shown in Fig. 3. Highest values were associated with dead plants, and a pronounced seasonal trend was observed with maxima in winter to early spring. The maximum epiphytic

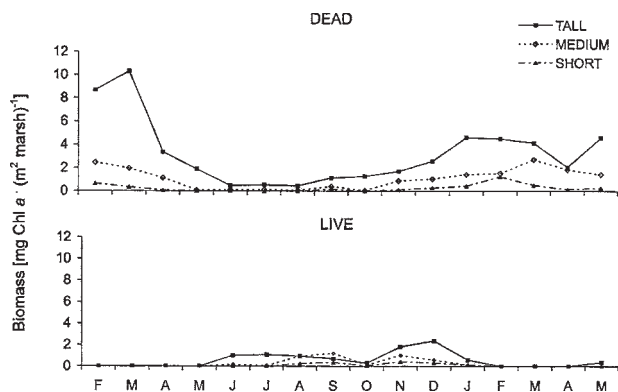


Fig. 3. Monthly average epiphytic biomass on dead (tall, medium, and short) and live (tall, medium, and short) *Spartina alterniflora* per m^2 marsh in North Inlet estuary, South Carolina. Standard errors were too small to be displayed.

biomass on live plants was $2.4 \text{ mg chl } a \text{ (m}^2 \text{ marsh)}^{-1}$ on tall forms in December 2002, and the highest biomass on dead plants was $10.3 \text{ mg chl } a \text{ (m}^2 \text{ marsh)}^{-1}$ on tall forms in March 2002.

Discussion

Spartina alterniflora, the dominant vascular plant in salt marshes on the eastern coast of the U.S., has the highest biomass among producers in this ecosystem (Dame and Kenny 1986), although the assimilation efficiency of invertebrates that consume live or recently dead plants is very low due to the refractory lignocellulosic structure of these plants (Kreeger et al. 1988; Langdon and Newell 1990; Charles and Newell 1997), improving as detritus ages due to the acquisition of detritivores (Haines and Montague 1979). Quantification of standing stock of other producers in the salt marshes is necessary to assess their importance as potential carbon sources. Although the importance of primary producers in salt marsh was thoroughly covered by Nixon (1980), his study did not include reference to the epiphytic community, a ubiquitous feature on *Spartina* stems. Therefore this study focused on the poorly studied epiphytic community on *Spartina*. The seasonal biomass of this community was investigated on dead and living plants of tall, medium and short growth forms of *Spartina* in NIE. Epiphytic microalgal biomass at consecutive tidal cycles was also investigated.

Variability of epiphytic biomass on NIE *Spartina* was generally high throughout the year in all plant categories. It was also variable at different tidal stages (with exception of LT1). This variability could be related to the natural patchiness of epiphytes on *Spartina* stems. Episodic tidal sloughing or scouring due to an increase in flow velocity also might have contributed to epiphytic biomass

variability. Current velocities higher than 0.6 m s^{-1} are capable of detaching microalgae from the biofilm at late stages of colonization (Blenkinsopp and Lock 1994). Biggs et al. (1998) reported a decrease in periphytic biomass when current velocities exceeded 0.4 m s^{-1} . Although the average current velocity in NIE is 0.2 m s^{-1} , ebb tidal velocities up to 2.3 m s^{-1} occasionally occur (Kjerfve personal communication). Top-down control (grazing) by the periwinkle snail *Littoraria irrorata* on *Spartina* epiphytes in NIE should also be considered. Although this snail feeds heavily on standing stems of *Spartina* (Silliman and Bertness 2002), there are reports of *L. irrorata* feeding on benthic algae (Kraeuter and Wolf 1974) and epiphytes (Kemp et al. 1990; Newell and Fallon 1989). An ongoing study developed by Zingmark (unpublished data) to determine trophic transfers between the epiphytic algae on *Spartina* and herbivore species that are linked with commercially important fish and shellfish species in NIE shows that *L. irrorata* feeds actively on *Spartina* epiphytes. Significant quantities of various species of epiphytic diatoms, green and red algae, and cyanobacteria were found in stomach and fecal contents of *L. irrorata*, as opposed to occasional pieces of *Spartina* epidermis and fungal hyphae. Grazing by *Palaemonetes pugio* should also be considered as a potential factor in decreasing epiphytic biomass, because this shrimp can use algal epiphytes as a source of food (Fleeger et al. 1999; Quiñones-Rivera and Fleeger 2005).

A significant interaction between most of the factors considered (plant condition, size, location, and time of the year) made it difficult to analyze their effects on the biomass of epiphytes separately. Epiphyte biomass was highest on tall *Spartina* in spring 2002 but not thereafter. A more consistent pattern was observed when comparing live versus dead plants. Biomass of epiphytes on dead, tall *Spartina* was generally higher than that measured on live, tall plants. The lack of a dense epiphytic community on live leaves compared to an extensive community on dead plants has also been reported by other authors (Stowe 1982; Fallon et al. 1985; Currin and Paerl 1998a,b; Quiñones-Rivera and Fleeger 2005). Higher epiphytic accumulation on dead stems might be related to their presence throughout the year, while accumulation of epiphytes on living plants was restricted to the timing of their seasonal appearance and growth of about 8 mo (April–November). Stowe (1982) suggested that higher biomass on dead plants could also be a result of leachates released from dying standing grasses during the winter. Dead plants also accumulated more mud and organic material, creating crevices for the settlement of microalgae as compared to live plants, whose surface was smoother, with obviously

less sediments (Jackson personal observation). Young (1945) reported that, compared to older stems, the surface of young ones was wax-like and slick, and did not favor the attachment of epiphytes. Stowe (1972) suggested that the seasonality of epiphytic algae was strongly related to this factor in addition to factors influencing seasonality of phytoplankton (e.g., water temperature and nutrients).

When comparing different sections of *Spartina* stems, higher epiphytic biomass was generally found on the bottom section of the plants (especially on tall forms). This result was similar to that reported by Day et al. (1973) and Stowe (1982). Close proximity to the sediments possibly resulted in the immigration and buildup of mud-inhabiting benthic microalgae on the bottom section of tall stems. This section also was constantly inundated by tidal waters, which provide a source of microalgae and nutrients at each tidal cycle. Nutrient uptake (bottom-up control) depends on several biological and physical parameters (Aksnes and Egge 1991), such as a combination of degree of turbulence, type of organism and its swimming ability (Karp-Boss et al. 1996; Peters and Marrase 2000), type and concentration of particles in the water (Goldman and Dennett 2001), light (Yin et al. 1998), density (Stevenson and Glover 1993), and position of the cell in the biofilm matrix (Burkholder et al. 1990). None of these factors were examined during this study.

Epiphytic biomass showed high seasonal variability, which was not surprising as epiphytic biomass is related to the *Spartina* culm emergence-senescence cycle (Stowe 1982; Quiñones-Rivera and Fleeger 2005). The most biomass (i.e., peak) was measured in the winter, as opposed to the summer, when the lowest epiphytic biomass was registered. In the winter, all plants were senescent or dead and had accumulated the highest epiphytic biomass. Assuming that some phytoplankton is passively filtered by mucus associated with the epiphytes on *Spartina* and becomes incorporated into this community, we suggest that a winter peak in epiphytic biomass may also be related to a decline in phytoplankton biomass from its summer high, which is very distinct during this season in NIE (Lewitus et al. 1998, 2000; Dame et al. 2002). A decrease in grazing pressure in the winter (due to reduced temperatures) may also contribute to the winter maximum. Zingmark (unpublished data) found a high number of algal cells in the digestive tract of *L. irrorata* in NIE during the winter, and Quiñones-Rivera and Fleeger (2005) reported a high percent of epiphytic biomass reduction by the grass shrimp *P. pugio* in the salt marsh of Louisiana also during the winter. The lowest epiphytic biomass values found on tall plants

during the summer might be associated with grazing by the zooplankton, which controls the phytoplankton population during this season (along with light limitation; Lewitus et al. 1998, 2000). Amphipods were often observed on the stems of tall *Spartina*, and according to Duffy and Harvilicz (2001) and Froneman (2001), they are capable of grazing epiphytes. Grant (1981) reported the occurrence of three species of sand-burrowing amphipods in NIE. The species that fed mostly on microphytobenthos lived on the top few centimeters of sediments and could be displaced from its substrate by currents (Bousfield 1970; Grant 1981). It is possible that these resuspended organisms settled on tall *Spartina* stems and subsequently contributed to a reduction in the epiphytic biomass. Although possibly responsible for reducing biomass, high grazing pressure stimulates growth (high production), due to nutrients liberated by grazers (Strickland 1972). A local release of nutrients as opposed to a patchy distribution of increased nutrients in the water column might enhance production of epiphytes.

During the summer months, epiphytic organisms are more exposed to high evaporation rates and desiccation due to higher temperatures, especially in the areas of short and medium plants, where they are not regularly inundated during tidal exchange as occurs in the tall *Spartina* zones. This factor could have contributed to lower the biomass of the epiphytic community on these plant forms. Stowe (1982) suggested that dense *Spartina* canopy (present in NIE especially during summer months) protects epiphytes from extremes of radiation and dehydration even though these areas are not frequently submerged. This might be true for the medium *Spartina* zone, which had a denser canopy when compared to short plants (Jackson personal observation).

Although consistently higher during the fall months in NIE, epiphytic biomass dropped significantly on all *Spartina* forms in October, when an F2 category tornado (Fujita scale) touched down in Georgetown (ca. 9 km from OL; National Oceanic and Atmospheric Administration [NOAA] National Weather Service, Tropical Prediction Center, National Hurricane Center). Sustained strong winds and strong wind stress (indirect meteorological forcing transferred by coastal ocean) caused an increase in the absolute sea surface elevation. Spring tides in NIE on that day were reported as high as ca. 2 m (NOAA National Water Level Observation Network), whereas they are on average ca. 1.8 m. As a consequence, these waters would have reached and covered the medium and short *Spartina* zones (located ca. 1.4 m above MSL) for ca. 6 h, possibly sloughing more epiphytes on those

plants. Stronger than usual currents during the touchdown of the tornado for the same phase of the tide and tidal range most likely occurred (Kjerfve personal communication) and might have caused epiphytes to detach from the stems. It has been reported that sudden increases in velocity raise instantaneous periphyton loss rates by an order of magnitude or more (Jacoby et al. 1990) due to a rapid intensification of frictional forces and shear stress on the particle surface (Cheng et al. 1997).

Among all *Spartina* growth forms, higher epiphytic biomass was generally found on tall plants. This might be related to lower grazing pressure by *L. irrorata*. Field observations suggested that *L. irrorata* was not frequently seen on tall *Spartina* but were more commonly observed on short plants. These observations were in accordance with the study by Lewis and Eby (2002), who suggested that snail density at the seaward edge of the *Spartina* zone was low due to high risks of predation. Krager (1992) reported that *L. irrorata* densities in NIE were positively correlated with marsh elevation, being lowest in areas of tall *Spartina*.

The tall *Spartina* zone also exhibited the highest biomass of epiphytes per m² of marsh in NIE. Pinckney (1992) also registered a high mean biomass of benthic diatoms in sediments surrounding tall plants, but those data were three orders of magnitude higher than the ones reported for epiphytes in this study. The highest mean epiphytic biomass on a square meter basis was registered in the winter due to a higher number of dead stems, suggesting that epiphytes on *Spartina* stems could be an important source of food for herbivores. During this season, phytoplankton and *Spartina* production are at their lowest (e.g., Sellner et al. 1976; Dame and Kenny 1986).

Although variable, the biomass of epiphytes on NIE *Spartina* was generally significantly lower when compared to values reported from other salt marshes in the southern U.S. For example, in the salt marsh of Beaufort, North Carolina, Piehler et al. (1997) reported values ranging from 30 to 36 µg chl *a* per 4 cm stem segment of standing dead plants. The lowest epiphytic biomass value reported by Quiñones-Rivera and Fleeger (2005) on the 10 cm bottom of standing dead culms in a Louisiana marsh was 28.4 µg chl *a*. In NIE, the highest values (found on dead, tall forms) were less than 2 µg chl *a* per 10 cm stem segment. The relatively lower biomass on NIE *Spartina* may be related to lower nutrients in NIE than in these other estuaries (Angelidaki and Leonard 1996; White et al. 2004). Another reason may relate to the fact that most of the epiphytic algae were comprised of diatoms and flagellates, as reported by Jackson (2004) using high performance liquid chromatography, chemical tax-

onomy (CHEMTAX; Mackey et al. 1996, as modified by Lewitus et al. 2005), and microscopy analyses. These populations are generally less dense than macrofilaments of cyanobacteria, the dominant epiphytes on *Spartina* in the Beaufort salt marsh (Currin and Paerl 1998a), and also less dense than an assemblage of diatoms and brown, green, and red algae or possibly cyanobacteria in Louisiana (Quiñones-Rivera and Fleeger 2005).

Epiphytes on *Spartina* stems at low concentrations may be significant in food webs. And being mostly diatoms and flagellates, their turnover rates would be expected to be higher than the larger filamentous and thalloid algal epiphytes. Epiphytes were reported to be grazed by *L. irrorata* (Currin et al. 1995; Zingmark unpublished data), and *P. pugio* (Quiñones-Rivera and Fleeger 2005), which in turn are prey for blue crabs (*Callinectes sapidus*; Silliman and Bertness 2002), penaeid shrimps (Kneib and Knowlton 1995), and bay anchovies (*Anchoa mitchilli*; Fulling and Peterson 1999; Dame et al. 2000). These animals are part of commercial fishery stocks in many southern states (Dame et al. 2000). If any disturbance in this food web occurs, these organisms might be affected. An example of a disturbance that frequently occurs in salt marshes is nutrient overload caused by pollution generated by activities related to rapid coastal development and urbanization near salt marsh areas. This overload can cause microorganisms to bloom. By releasing toxic compounds in the water or consuming high amounts of oxygen due to rapid reproduction, these microorganisms can kill many aquatic plants and animals, including consumer organisms, such as finfish (e.g., bay anchovy) and shellfish (shrimps, crabs, and clams; Lewitus et al. 1999; Boesch 2000), jeopardizing not only the food web equilibrium, but also the fishery in the area.

It is important to consider that although the epiphytic algal community may be at the basis of the salt marsh food web, knowledge of its composition is important to detect whether carbon from microalgae is transferred to higher trophic levels, as there are potentially higher (e.g., diatoms) or lesser edible taxa (e.g., dinoflagellates and cyanobacteria; Roelke et al. 1997). The paradigm in estuarine ecology that organic detritus (derived mostly from vascular plants) are the major energy source for salt marsh food webs may be changing as studies (e.g., Fleeger et al. 1999; Fejes et al. 2005; Quiñones-Rivera and Fleeger 2005) show that microalgae may be as or more important as other producers in carbon propagation up the food web. Access to basic information on the biology and ecology of epiphytic microorganisms is important to understand how food webs are organized in the marsh. They will also allow conservation and management

of sustainable fisheries in coastal zones, since salt marshes are nursery grounds for commercially important fishery species.

Conclusions

Biomass of the epiphytes on stems of *Spartina alterniflora* in NIE was extremely variable. Grazing and sloughing due to shear forces promulgated by tidal currents might have contributed to this variability. Epiphytic biomass was generally highest on tall plants when compared to the other growth forms (medium and short) and also highest at the bottom of the plant stems as opposed to the middle section. Inundation time and proximity to the creeks and sediments might have increased the amount of epiphytes on these plant categories. Dead *Spartina* stems usually accumulated more epiphytes than living ones, which occur in NIE for only the 8-mo growing season. Epiphytic biomass also varied throughout the year, but highest biomass values per marsh area occurred in the winter (due to an increasing number of seasonally dead plants). This represents an important contribution to the estuarine food web, as primary production from other sources is relatively low during this season.

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