BRYOPHYTES AS INDICATORS OF WATER LEVEL AND SALINITY CHANGE ALONG THE NORTHEAST CAPE FEAR RIVER

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ABSTRACT

The focus of this study was to identify and describe bryophyte-environment relationships in wetland swamp forests of the Northeast Cape Fear River, southeastern North Carolina. A total of 44 genera consisting of 39 moss species and 21 liverwort species were identified. There was one new liverwort recorded not previously described from North Carolina, *Cololejeunea setiloba*. The diversity of bryophytes in the swamps of the Northeast Cape Fear River was higher than expected observations.

Bryophyte densities and species richness were compared to flood depth relative to the swamp surface, salinity, and elevation of the swamp surface for three sites each with six substations within a transect from riverbank to upland edge. There was a general trend of an increase in bryophyte density and species richness as flood depth and salinity decreased from river to upland.

Principal component analysis used 13 environmental variables, ranging from transect distance upriver, substation distance from river's edge to base of upland, hydrology, elevation, duration of flooding, and salinity. These environmental variables accounted for much of the variation in the abundance of bryophyte species. A principal component biplot showed clustering between species of bryophytes with correlation between certain species and their tolerance for specific stress-related environmental variables.

The majority of the bryophytes sampled were not common in the study system and have narrow habitat specificity. Although bryophytes may form a major part of several vegetation types and ecosystems, in this study, relatively few bryophyte species were ecologically abundant or dominant. *Isopterygium tenerum* is one occurring commonly and over a wide range of habitats.

Fontinalis sullivantii, a facultative aquatic bryophyte*,* in the Northeast Cape Fear River can clearly tolerate low salinity water. It occurs along exposed roots and bases of trees, such as bald cypress. It is submerged at rising and high tide and partially exposed at low tide therefore exposing it to varying salinity as well as desiccation. High salinity, in the range between 5 and 15 ppt, significantly reduced photosynthetic efficiency of the moss species, *Fontinalis sullivantii*, on the short time scale, followed by some recovery. Desiccation after approximately 3 hours also reduced photosynthetic efficiency. However, observed physical changes in the disappearance of *Fontinalis sullivantii* due to a major drought suggests a strong relationship between increasing salinity and disappearance of this species.

Long term implications of the current study are that bryophyte data will be used to assess future impacts due to current dredging projects in the Cape Fear River estuary.

ACKNOWLEDGMENTS

My thanks to my committee, especially Dr. Courtney Hackney for the hours of his time he spent helping me and Dr. Jon Shaw for the use of the Duke University Herbarium and to the Cape Fear River Harbor Deepening Project crew for the collection of hydrology and salinity data. Collections were identified at the Duke University Herbarium with the assistance and patience of Dr. Lewis Anderson and Charles Zartman. Thanks are also due to Mark Gay for additional technical support, Dr. Frierson for statistical support, Dr. Mike Durako and Jennifer Kunzelman for assistance with PAM fluorometry. Special thanks go to the undergraduate and graduate students that assisted in all aspects of fieldwork, especially Eddie Helton and Beth Cummins.

Personal thanks go to David Dumond, for whom without, this project would have never been born and to Bob York for being the light at the end of the tunnel.

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INTRODUCTION

There have been tremendous changes in wetland vegetation systems bordering the Cape Fear estuary since the first permanent European settlement in the 1720's, due to clearing and diking of swamps, deepening and widening of the main channel, and relative sea level rise (Hackney and Yelverton 1990). Hackney and Yelverton (1990) attributed a significant portion of a 67% increase in tidal amplitude at the upper reach of the estuary to the enlarged dimensions of the river channel. With the resulting rise in high-water and increased salinity in the estuary, swamps in the upper reaches are gradually disintegrating and being replaced by oligohaline tidal marshes (Rozas 1995).

Each tide that propagates up the Cape Fear River forces water from the main river channel into surrounding tidal wetlands. The degree and rate of water flow from the channel into adjacent wetlands depend on the height of the tide, elevation of the wetlands, natural friction in the surface of the wetlands, and availability of streams or rivulets within wetlands to move water (CZR Incorporated 2001). Biological impacts caused by an increase in sea level on wetlands could be significant in areas not currently experiencing saline water. Elevated salinity and frequent flooding during the growing season may stress many species currently inhabiting the system, including bryophytes. The effects of environmental variables including salinity and flooding may explain observed variation in species densities within the community (Gough and Grace 1999).

Despite a number of ecological studies of forested wetlands (see Conner and Day 1982, for a review), an understanding of vegetation dynamics, especially in response to flooding in wetland forests, is still only rudimentary (Conner and Brody 1989). The prediction of how communities will respond to changing environmental conditions is imperative (Gough and Grace 1999), often requiring inference of species-environment relationships from community composition data and associated habitat measurements (Ter Braak 1986). Although descriptive accounts of local or regional bryophyte communities are common in the literature, relatively few studies have correlated bryophyte vegetation and environmental factors. Nevertheless, bryophytes have more recently been used as ecological indicators, especially with respect to pollution (Burton 1990).

Evaluation of bryophyte diversity and community structure present several technical challenges including their small size, the often fragmentary nature of their colonies, the tendency of many species to grow on highly irregular surfaces, and their frequent presence as relatively low biomass components in communities dominated by other types of vegetation (Bates 1982). However, the absence of true roots and vascular systems in bryophytes creates a more direct and immediate relationship between the surface environment and the plant (Smith 1978) making them ideal indicators of habitat conditions. Changes in water, soil, and/or air quality due to pollution or other factors may quickly impact bryophyte growth, reproduction, establishment, and persistence.

According to Richardson (1981), light, temperature, and nutrient supply are factors which, in addition to water and salt, may cause stress and reduce the photosynthetic performance of mosses. To date there is no information on the extent to which increases in salinity can affect the physiology of bryophytes found in freshwater swamps. Although limited, physiological data on fresh to brackish water marsh vascular species suggest an adverse response to increased salinity (McKee and Mendelssohn 1989, Pezeshki *et al*. 1987a, Pezeshki *et al*. 1987b), but roots, rhizomes, and leaves buffer vascular plants from short-term exposures. Individual moss species have a physiology that responds more immediately to a combination of conditions that are best defined by the microclimate (Richardson 1981).

The genus *Fontinalis* Hedw. has been used frequently in physiological studies as a representative aquatic plant; including many pollution studies. It is widely distributed through the world's temperate regions (Glime 1984). Its large size and relative abundance further support its choice for detailed biological study. *Fontinalis sullivantii*, a species found in the Northeast Cape Fear River, is subjected to daily tides exposing it to dissolved sea salts as well as flooding and desiccation. Any change in either of these variables outside of what is experienced during a regular tidal cycle may cause immediate alterations in metabolism and physiology.

With photosynthetic plants, both the photochemical processes and the dark biochemistry of photosynthesis are sensitive to water stress (Schwab & Heber 1984, Lee & Stewart 1971). One method of measuring such changes is to monitor variation of photosynthetic efficiency of aquatic bryophytes in stressed habitats. The use of chlorophyll fluorescence techniques to investigate photosynthesis in vegetation, especially pulse-amplitude-modulated (PAM) fluorescence, has increased recently as a result of advances in technology and instrument availability (Murphy 2000). PAM fluorescence was found to be useful because it is non-invasive, quantitative (Kooten and Snel 1990), can be used in the field, and provides information about the photosynthetic efficiency of PSII (Ralph *et al*. 1998). PAM fluorescence has been used to measure light stress (Ralph and Burchett 1995; Dawson and Dennison 1996), salinity stress (Kamermans *et al*. 1999), and photosynthetic rates (Beer *et al*. 1998).

The focus of the current study was to determine species of bryophytes that occur along the Northeast Cape Fear River, N.C. and investigate distribution patterns as they relate to abiotic factors such as flooding and salinity. An additional objective of the study was to examine stress-response of bryophytes to variations in salinity with emphasis placed on the short-term response of an aquatic species, *Fontinalis sullivantii*.

MATERIALS AND METHODS

Study area

Study sites were located along the Northeast Cape Fear River (Figure 1) in North Carolina. The Northeast Cape Fear River is a blackwater river in North Carolina's Lower Coastal Plain at approximately 34° 16´ N and 77° 57´ W.

Belt transects (Figures 2, 3 and 4), 50 meters in width, were previously established at each of the three monitoring stations and extended from the river across a gradient of different wetland communities and aquatic regimes to the base of adjacent uplands (CZR Incorporated 2001). The three stations were located approximately 6.4, 12.8, and 25.6 km upstream from Wilmington, N.C. (Table 1) and all were tidal, although flooded to different depths and frequency. Approximate lengths of belt transects were; Rat Island = 300m, Fishing Creek = 348m, and Prince George Creek = 133m. (See Table 1 for other physical characteristics of stations).

Station characteristics

Each station contained an array of different wetland habitats and represented a gradient of diverse wetland types flooded by varying levels of water at a salinity range from 0-13 ppt.

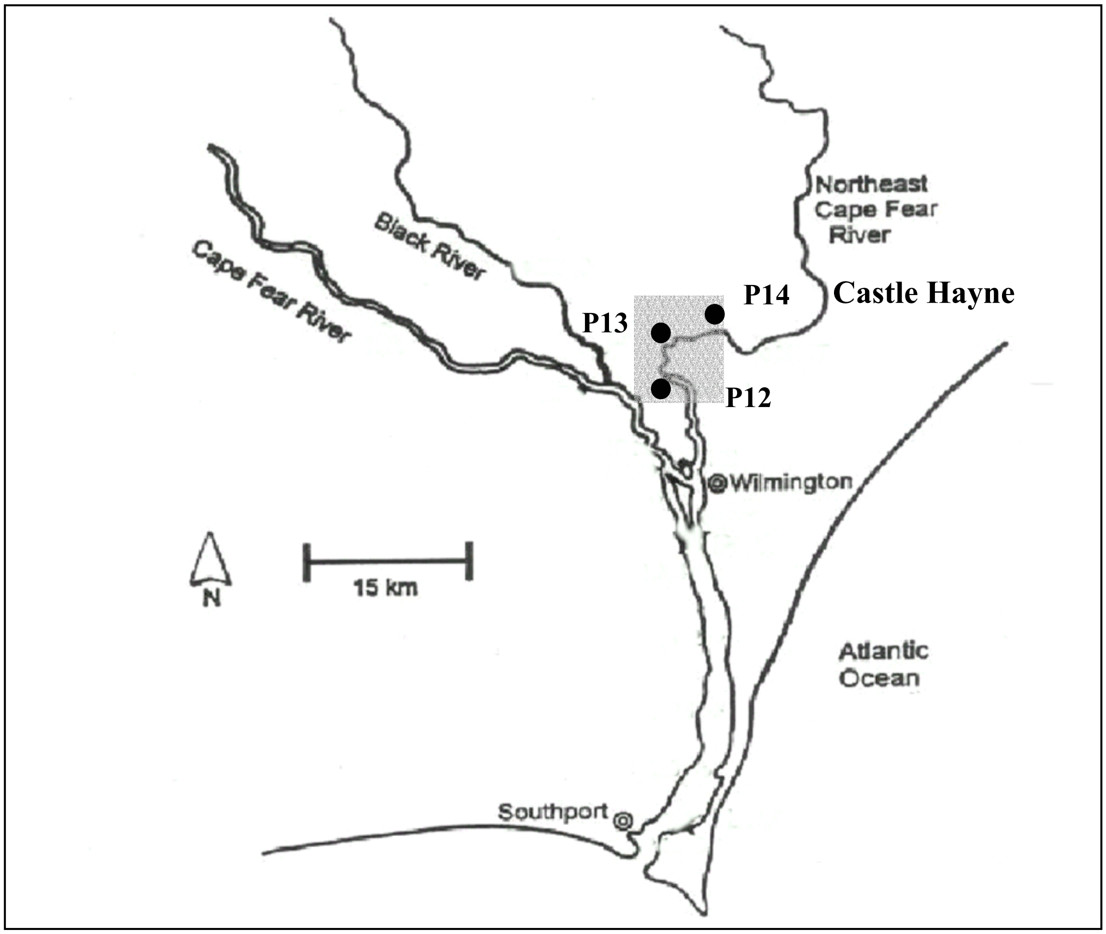

Figure 1. Map of study area indicating location of wetland transect stations; P12 (Rat Island), P13 (Fishing Creek) and P14 (Prince George) along the Northeast Cape Fear River in southeastern North Carolina

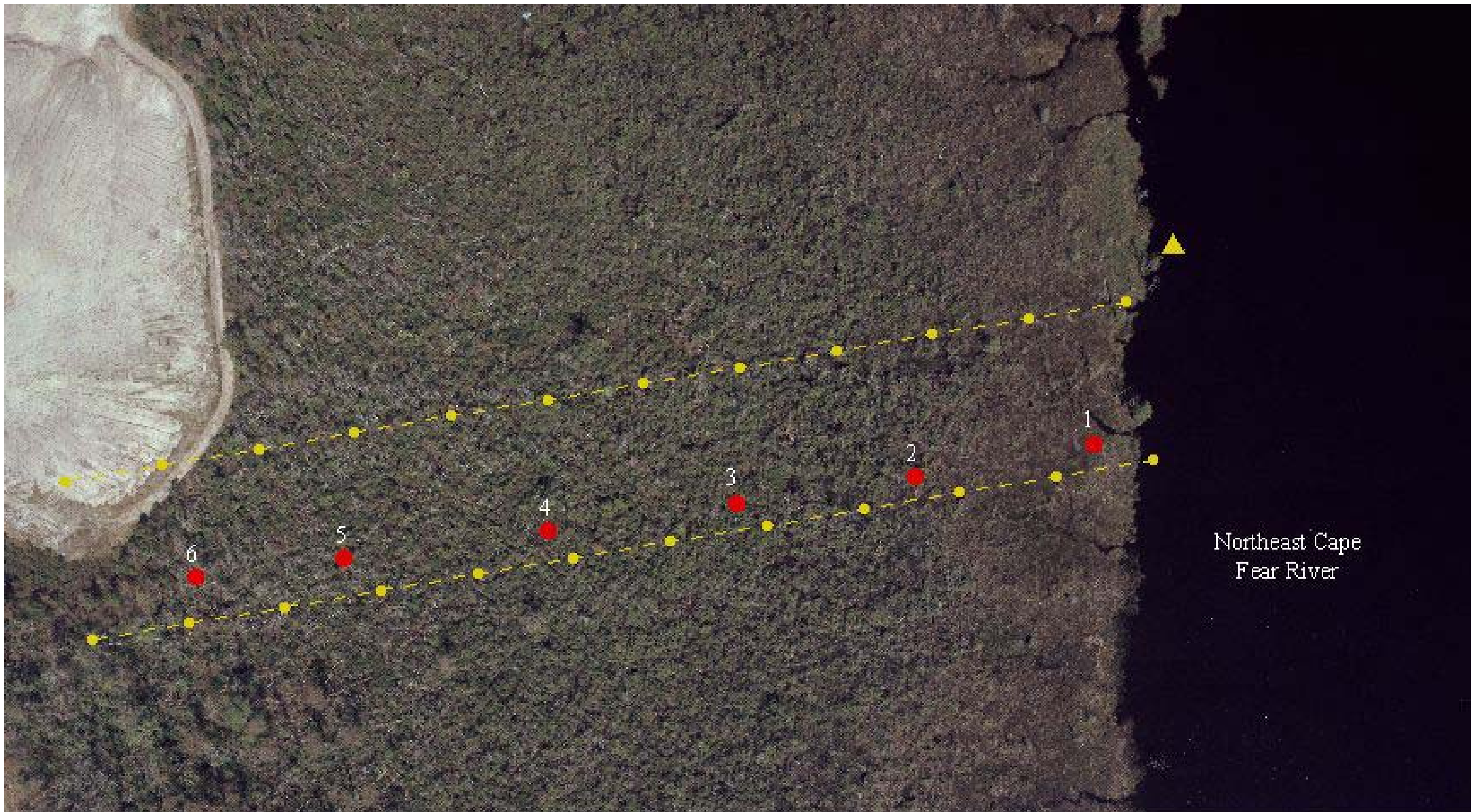

Figure 2. Locations of belt transect, substations 1-6 and data collection platform at Rat Island Station (P12), Wilmington Harbor monitoring project, Northeast Cape Fear River, North Carolina

Image and shape files used courtesy U. S. Army Corps of Engineers, Wilmington District

Prepared by David M. DuMond

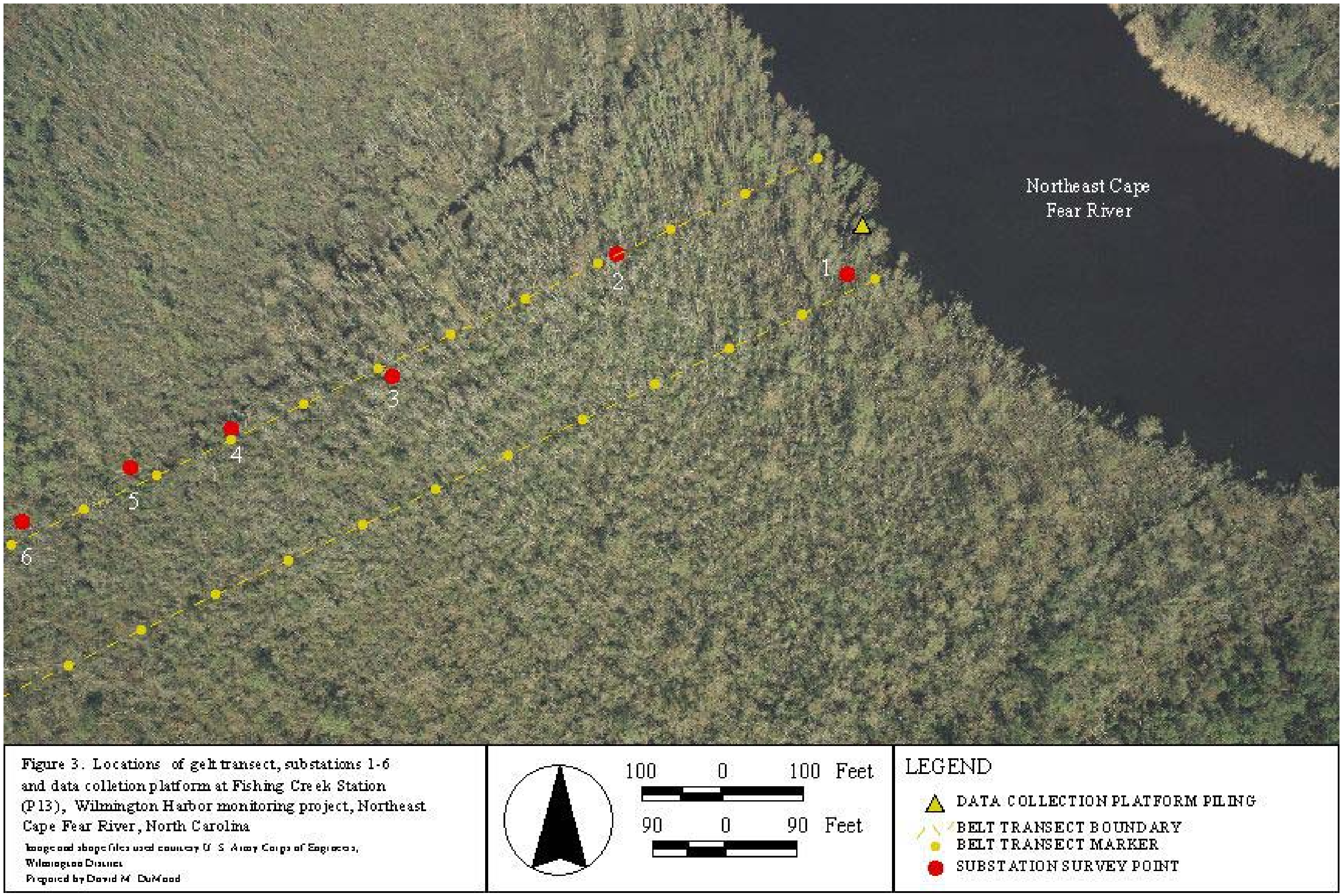

Figure 3. Locations of gelt transect, substations 1-6 and data colletion platform at Fishing Creek Station (P13), Wilmington Harbor monitoring project, Northeast Cape Fear River, North Carolina

Image and shape files used courtesy U. S. Army Corps of Engineers, Wilmington District

Prepared by David M. DuMond

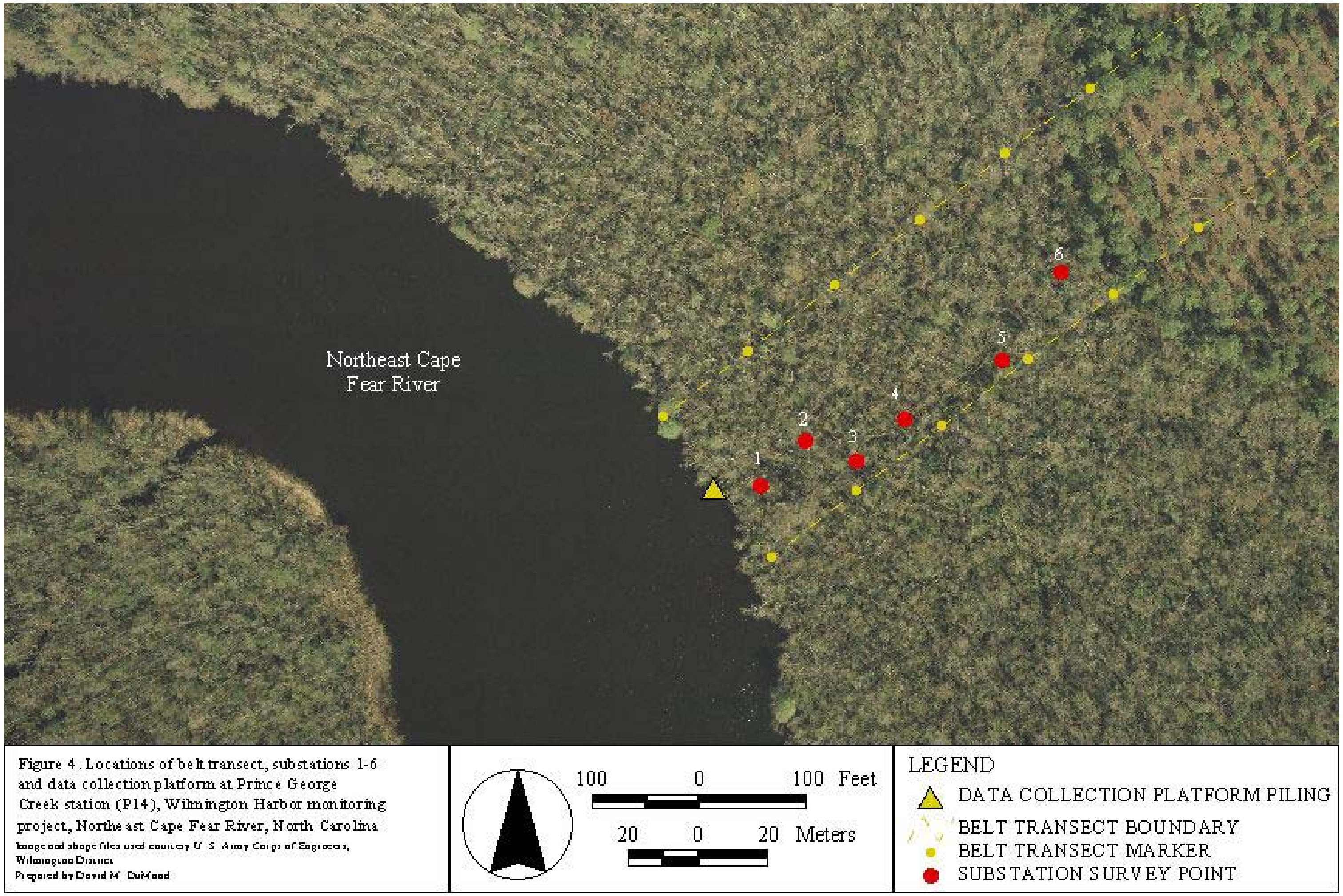

Figure 4. Locations of belt transect, substations 1-6 and data collection platform at Prince George Creek station (P14), Wilmington Harbor monitoring project, Northeast Cape Fear River, North Carolina

Image and shape files used courtesy U. S. Army Corps of Engineers, Wilmington District

Prepared by David M. DuMond

Table 1. Physical characteristics of each belt transect, including; transect distance upriver from Wilmington in km, latitude (LAT), longitude (LON), elevation of marsh surface in meters relative to NAVD88, approximate belt transect length in meters and substation distance in meters from the river. Shallow water wells and conductivity monitoring devices collected flooding and salinity data at each substation.

Station Name	Station Number	Distance upriver from Wilmington (km)	LAT	LON	Elevation (m)	Transect Length (m)	Substation Distance (m)
Rat Island	P12-1	6.4	34.1814	-77.574	0.27	300	15
	P12-2		34.1814	-77.5742	0.49		69
	P12-3		34.1814	-77.5744	0.60		125
	P12-4		34.1813	-77.5747	0.57		182
	P12-5		34.1813	-77.5749	0.62		245
	P12-6		34.1813	-77.5751	0.73		291
Fishing Creek	P13-1	12.8	34.2016	-77.594	0.43	348	15
	P13-2		34.2016	-77.5943	0.32		84
	P13-3		34.2014	-77.5946	0.23		174
	P13-4		34.2014	-77.5949	0.30		234
	P13-5		34.2013	-77.595	0.36		276
	P13-6		34.2013	-77.5952	0.49		324
Prince George	P14-1	25.6	34.221	-77.5619	0.21	133	10
	P14-2		34.2211	-77.5619	0.26		27
	P14-3		34.221	-77.5618	0.32		39
	P14-4		34.2211	-77.5618	0.37		56
	P14-5		34.2211	-77.5617	0.38		90
	P14-6		34.2212	-77.5616	0.45		113

Rat Island was a degrading tidal swamp/pocosin (Figure 2), altered by past intrusions of saline water (CZR Incorporated 2001). Salinity generally decreased from river to upland as elevation increased (Table 2). Habitats adjacent to the river consisted of a variety of grasses, sedges and forbs co-dominated by three-square (*Schoenoplectnu americanus*), sedge *(Carex hyalinolepis)*, and giant-cord grass *(Spartina cynosuroides*). Clumps of un-oxidized organic matter held within woody plant root mats supported relic stems of swamp rose (*Rosa palustra*) and southern bayberry (*Morella cerifera*) mixed with groundseltree (*Baccharis halimifolia*). Interior portions of the transect were less impacted by saline water and dominated by mixtures of red maple (*Acer rubrum)*, pond cypress (*Taxodium ascendens*), swamp bay (*Persea palustris*), sweet bay (*Magnolia virginiana)*, pond pine (*Pinus serotina*) and occasional loblolly pine (*Pinus taeda*).

The Fishing Creek station (Figure 3) was connected along its Northern boundary to a narrow canal. This canal was directly responsible for allowing movement of tidal brackish water into the swamp interior, 276 m into the transect (Table 2). The site was largely a swamp forest dominated by pond cypress and pumpkin ash (*Fraxinus profunda*). Swamp tupelo (*Nyssa aquatica*) and red maple were also scattered or locally dominant. Tree bases and root mats elevated above saturated substrate provided habitat for many species of vascular plants as well as bryophytes.

The Prince George Creek transect (Figure 4) was a fresh water site within a swamp forest until 2001 that followed the same hydrology and salinity patterns as the Rat Island station, with water level and salinity decreasing from river to upland (Table 2). Pumpkin ash, red maple and pond cypress were co-dominants at this station.

Table 2. Characterization of each station and substation includes habitat character, elevation of swamp/marsh surface (m), and percent frequency of flooding out of a two-week period. Range and mean of water level, duration of flooding on the marsh surface in hours, and salinity (ppt) are also shown. Data obtained from CZR Incorporated (2001).

Station	Substation	Habitat Character	Elevation	% Frequency of Flooding	Water Level		Duration		Salinity	
					Range	Mean	Range	Mean	Range	Mean
Rat Island	1	Marsh	0.27	91	0.2-0.9	0.5	6.0-7.3	6.5	<1-11	1.1
	2	Degraded swamp	0.49	72	0.4-0.9	0.6	4.4-5.5	5.0	<1-13	1.1
	3	Degraded swamp	0.60	35	0.5-0.9	0.6	3.8-5.9	4.9	<1-12	<1
	4	Mixed hardwood swamp	0.57	26	0.5-0.8	0.6	3.7-6.5	4.8	<1-11	<1
	5	Mixed hardwood swamp	0.62	14	0.5-0.8	0.7	5.2-6.9	6.2	<1-10	<1
	6	Pocosin	0.73	9	0.5-0.9	0.7	0-8.9	5.9	<1-2	<1
Fishing Creek	1	Mixed hardwood swamp	0.43	58	0.2-0.8	0.5	3.5-8.5	6.1	<1-9	<1
	2	Mixed hardwood swamp	0.32	78	0.2-0.8	0.4	4.2-7.0	5.6	<1-9	<1
	3	Mixed hardwood swamp	0.23	94	0.2-0.8	0.4	5.6-6.5	6.1	<1-9	<1
	4	Mixed hardwood swamp	0.30	92	0.1-0.8	0.4	6.7-9.7	7.6	<1-8	<1
	5	Mixed hardwood swamp	0.36	92	0.2-0.8	0.4	5.1-6.7	5.8	<1-7	<1
	6	Mixed hardwood swamp	0.49	34	0.2-0.8	0.5	2.6-5.4	3.9	<1-2	<1
Prince George	1	Mixed hardwood swamp	0.21	94	0.2-0.7	0.3	6.5-8.8	7.6	<1-2	<1
	2	Mixed hardwood swamp	0.26	93	0.2-0.7	0.4	5.1-8.3	6.9	<1-2	<1
	3	Mixed hardwood swamp	0.32	92	0.3-0.7	0.4	5.5-9.4	7.0	<1-2	<1
	4	Mixed hardwood swamp	0.37	86	0.3-0.7	0.4	5.6-7.4	6.5	<1-2	<1
	5	Mixed hardwood swamp	0.38	77	0.4-0.7	0.4	4.5-6.3	5.5	<1-2	<1
	6	Mixed hardwood swamp	0.45	48	0.3-0.7	0.5	4.3-8.3	6.3	<1-1	<1

More detailed descriptions of vegetation and station characteristics are available in CZR Incorporated (2001).

Bryophyte richness

A total of over 500 bryophyte specimens were collected along a 32 km length of the Northeast Cape Fear River and its adjacent swamps and marshes in 2001, extending from Castle Hayne to Wilmington, North Carolina (Figure 1). Collections were identified at the Duke University herbarium in spring 2001 using microscopic leaf and cell morphology characteristics. All bryophytes were identified to species, where possible. Scientific names for mosses followed Crum and Anderson (1981), and those for liverworts followed Hicks (1992). Collections are deposited in the herbarium at Duke University, Durham, North Carolina.

Bryophyte density sampling

A variation of the point - quarter or point - centered quarter method was utilized to determine the density (Bonham 1989), frequency, and cover of bryophyte species within belt transects (Figure 5). Six substations had previously been established haphazardly along each transect from river to upland (CZR Incorporated 2001). A PVC marker, driven to resistance, was surveyed (± 0.3cm) relative to NAVD88 datum. Point-centered quarter sampling was applied beginning at a distance of 5 m from the surveyed point to avoid areas that have been disturbed by humans. Four center points were established in an N, S, E, and W direction. At each center point, four 90° quadrants were established. In each quadrant, the distance from the center point to the center of the nearest patch of bryophytes was measured and elevation determined with a line level. A

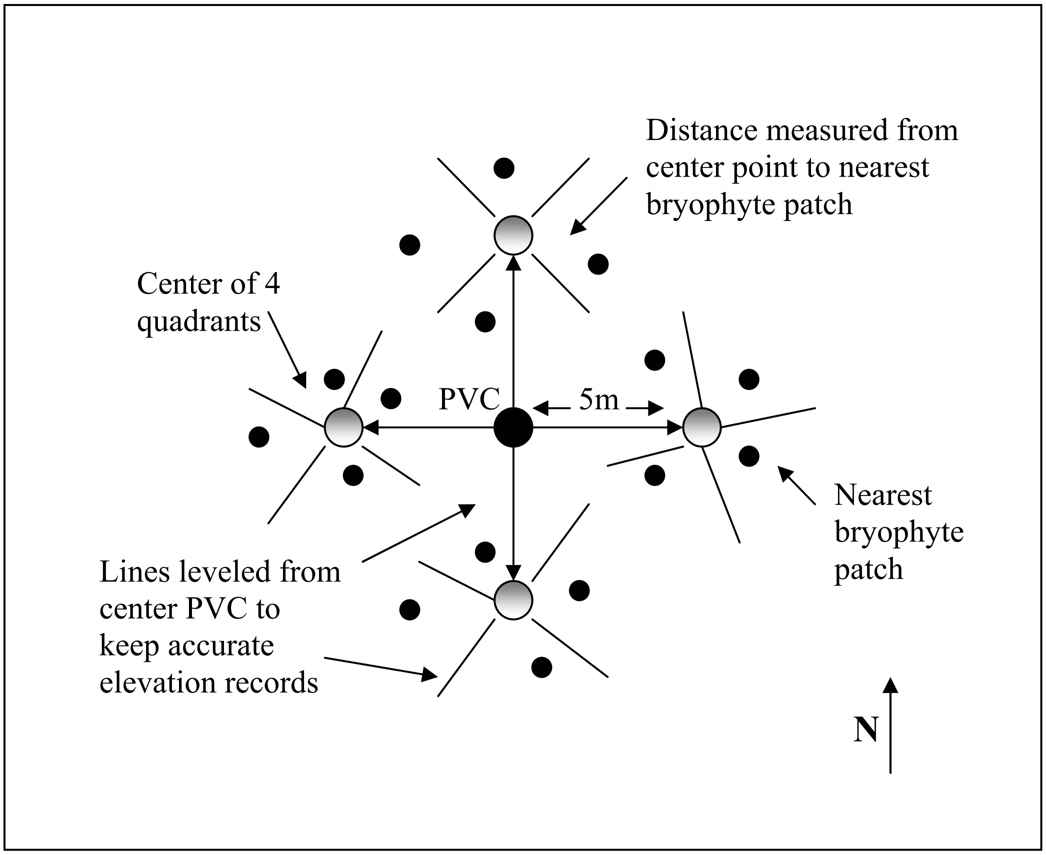

Figure 5. Schematic design of the point-quarter method utilized to assess the density, frequency and estimated percent coverage of sampled bryophyte species at each station and substation.

patch was defined as one or more species of bryophyte that contains living material. For more than one species to be included, they had to occur as a single patch in close proximity on a single substrate. A 1-dm^2 quadrat was placed on the center of the patch of bryophytes as a frame of reference for estimating percent cover contributed by each species in the quadrat. Substrate type was recorded and samples of bryophytic material were collected for later identification. A total of 288 quadrants were sampled.

Bryophyte density for point quarter sampling was determined by the formula D=1/A and $A=(\sum d_i/PQ)^2$, where D is the density in distance units squared, d_i is the distance from the center point to the nearest patch of bryophyte in the ith quadrant, P is the number of center points and Q is the number of quadrants taken for each center point. Frequency for a given species was determined by the formula $f_i=j_i/k$, where f_i is the frequency of species i, j_i is the number of sampling points at which species i was counted, and k is the total number of points sampled in a station.

Flooding and salinity data

Each belt transect had six substations, established in 1999, distributed haphazardly from the river's edge to the adjacent uplands. Substations were placed in a variety of different sub habitats. At each substation, a permanent well was installed spring 2000. Each permanent shallow well housing was made of slotted PVC above and below the soil surface. This allowed free movement of surface and porewater in and out of the well. Shallow water level wells recorded water levels above and below the marsh surface with Remote Data Systems (Model No. WL-40 or WL-20) monitoring devices. A Unidata Electrode Conductivity Micrologger (Model No. 6536B) recorded conductivity on the marsh surface.

At each substation, water level (± 9.0 cm) and salinity (± 0.7 ppt) were measured non-continuously, beginning in April 2000 to December 2001. Sampling was confined to a two-week period during winter/spring and summer/fall, as well as summer of 2000.

Flooding frequency, duration and depth were calculated and averaged using elevation relative to NAVD88. Conductivity data was converted to salinity and averaged using a transformation algorithm (Pond and Pickard, 1986).

Statistical analysis

Principal component analysis was performed using PRINCOMP procedure in SAS (SAS Institute 1989) to examine the relationships between quantitative environmental variables at 18 stations along the Northeast Cape Fear River and adjacent swamp forest. Average, minimum and maximum water level and salinity were used in the analysis, as well as, elevation, duration of floodwater, and percent of possible flood events in a two-week period. The first two principal components, containing the largest variance of the linear combinations of environmental variables and the presence/absence of bryophyte species were then plotted on a two-dimensional biplot to depict their joint relationship. Only bryophyte species that occurred more than 10 times in the distribution study were used in the analysis. The approximation used in the biplot is like that in principal components analysis; the biplot dimensions account for the greatest possible variance of the original data matrix. The biplot displays the environmental variables combined plotted as points. The configuration of points is essentially the same as scores on the first two principal components. Species data were plotted as vectors from the origin. Angles between vectors represent the correlation among variables. Angles between variable vectors reflect the correlation of the variables, so that variables with small angles are highly correlated, and variables at large angles are nearly uncorrelated.

Photosynthetic response to salinity-experimental design

One aquatic bryophyte species, *Fontinalis sullivantii*, closely associated with the river's edge was chosen for this study. According to CZR Incorporated (1998) there seems to be a strong relationship between increasing salinity and disappearance of this species. *Fontinalis* was exposed to salinity treatments of 0 ppt as control, 1, 2, 5, 10, and 15 ppt Instant Ocean saltwater diluted with 0 ppt river water. The salt solution was made fresh the day of each experiment and verified using an YSI, Model 30/10. Treatments were randomly assigned. *Fontinalis* response was evaluated at 0, 30, 90, 120, 180 minutes, 6 and 12 hours after exposure. Sub-samples of random populations of whole plants of *Fontinalis sullivantii* (Figure 6a.) were collected the day of each experiment in the freshwater portion of the Northeast Cape Fear River. A patch of *Fontinalis sullivantii* was placed entirely submerged in individual plastic containers (Figure 6b.). Leaf fluorescence measurements were made using a PAM fluorometer (Mini-PAM, Walz, Germany) (Figure 6c.). Photosynthetic efficiency (Fm, dark adapted) and effective quantum yield (Fo, light adapted) were measured on eleven replicates for each salinity treatment and time series. The effective quantum yield of photochemical energy conversion (Y, Yield) was calculated from the equation $Y=\Delta F/Fm$.

The photosynthetic efficiency response of *Fontinalis sullivantii* to a short-term desiccation treatment was also measured on eleven replicates over a 12-hour period. Fully hydrated shoots of *Fontinalis sullivantii* were allowed to dry in the laboratory in a)

b)

c)

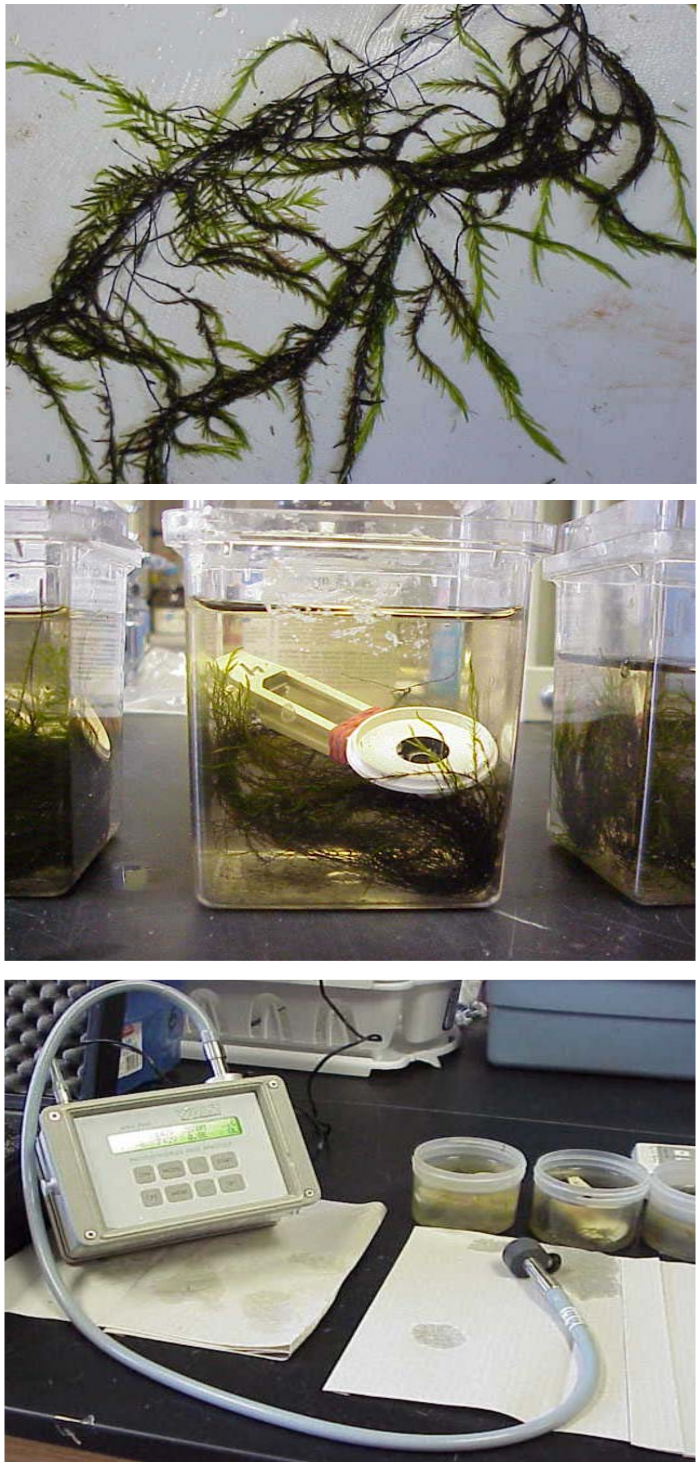

Figure 6. Photographs depicting a) close-up of the leaves and stems of *Fontinalis sullivantii*, b) replicate treatment containers with dark leaf clip, c) Mini-PAM fluorometer

individual plastic containers. Leaf fluorescence measurements were made using a PAM fluorometer (Murphy 2000). Photosynthetic efficiency (Fm, dark-adapted) and effective quantum yield (Fo, light adapted) were measured. The effective quantum yield of photochemical energy conversion (Y, Yield) was calculated from the equation $Y=\Delta F/Fm$.

RESULTS

Bryophyte richness

A total of 44 genera consisting of 39 moss species (Table 3) and 21 liverwort species (Table 4) were identified. There was one liverwort recorded not previously known from North Carolina, *Cololejeunea setiloba*. This species is usually found in swamps and floodplains of the mid-Gulf coastal plain (Breil 1970).

Bryophyte distribution

Bryophyte densities were averaged and compared to flood depth relative to the swamp surface (m), salinity (ppt), and elevation of the swamp surface (m) relative to NAVD88 datum for each station and substation (Figure 7a, b, and c). Prince George station (Figure 7a) followed a typical flood pattern for a tidal mixed hardwood swamp forest. Bryophyte density, ranging from <0.05 bryophytes/m^2 at the river's edge (substation 1) to almost 10 bryophytes/m^2 at the upland edge (substation 6), had a linear relationship with elevation of the swamp surface. However, flooding depth had an inverse relationship with bryophyte density as well as elevation, with water levels reaching <0.03 m at the river's edge and decreasing gradually to the upland. Prince George was a freshwater site with average salinity not exceeding 1ppt except for fall 2001 when the region experienced a severe drought. This resulted in a maximum salinity of 2ppt that reached substation 5 on a high tide (Table 2). Fishing Creek station

Table 3. List of moss species and author citation collected on the Northeast Cape Fear River and adjacent swamps and marshes. Names follow Crum and Anderson (1981).

Moss species and author citation
Amblystegium Schimp.sp.
Amblystegium serpens (Hedw.) Schimp
Amblystegium varium (Hedw.) Lindb.
Anomodon attenuatus (Hedw.) Huebener
Atrichum crispum (James) Sull.
Brachythecium acuminatum (Hedw.) Austin
Bryoandersonia illecebra (Hedw.) H. Rob.
Bryum Hedw. sp.
Clasmatodon parvulus (Hampe) Sull.
Climacium americanum Brid.
Climacium kindbergii (Ren. & Card.) Grout
Entodon seductrix (Hedw.) C.M.
Eurhynchium hians (Hedw.) Sande-Lac.
Eurhynchium pulchellum (Hedw.) Jenn.
Fontinalis sullivantii Lindb.
Fissidens fontanus (B.-Pyl.) Steud.
Haplocladium microphyllum (Hedw.)
Hypnum lindbergii Mitt.
Hypnum lindbergii var americanum (Ren. & Card.) Whiteh.
Isopterygium tenerum (Sw.) Mitt.
Leucobyrum albidum (Brid.) Lindb.
Leucodon bracypus Brid.
Leucodon julaceus (Hedw.) Sull.
Leptodictyum humile (P. Beauv.) Ochyra.
Leptodictyum riparium (Hedw.) Warnst.
Lindbergia brachyptera (Mitt.) Kindb.
Plagiomnium cuspidatum (Hedw.) T.J. Kop.
Racomitrium Brid. sp.
Schlotheimia rugifolia (Hook.) Schwagr
Sematophyllum adnatum (Mx.) E.G. Britt.
Sphagnum affine Renauld & Cardot
Sphagnum palustre L.
Sphagnum recurvum P. Beauv.
Steerecleus serrulatus (Hedw.) H. Rob.
Syrrhopodon texanus Sull.
Taxiphyllum deplanatum (Bruch & Schimp. *ex* Sull.) Fl.

(Cont.) Table 3. List of moss species and author citation collected on the Northeast Cape Fear River and adjacent swamps and marshes. Names follow Crum and Anderson (1981).

Moss species and author citation
Taxiphyllum taxirameum (Mitt.) Fl.
Thuidium allenii Aust.
Thuidium delicatulum (Hedw.) Schimp.

Table 4. List of liverwort species and author citation collected on the Northeast Cape Fear River and its adjacent swamps and marshes. Names follow Hicks (1992).

Liverwort species and author citation
Bazzania trilobata (L.) S. Gray
Calypogeia muelleriana (Schiffn.) K. Muell.
Cephalozia lunulifolia (Dum.) Dum
Chiloscyphus minor (Nees) Eng. & Schust.
Chiloscyphus polyanthos (L.) Corda
Chiloscyphus profundus (Nees)
Cololejeunea minutissima (Smith) Schiffn.
Cololejeunea setiloba A. Evans
Frullania kunzei Lehm. & Lindenb.
Jamesoniella autumnalis (DeCand.) Steph.
Lejeunea flava (Sw.) Nees
Lejeunea laetevirens Nees & Mont.
Leucolejeunea clypeata (Schwein.) Evans
Leucolejeunea conchifolia (Evans) Evans
Metzgeria Raddi sp.
Odontoschisma prostratum (Sw.) Trev.
Pallavicinia lyellii (Hook.) Gray
Porella pinnata L.
Radula complanata L. Dum.
Riccardia multifida (L.) S. Gray
Telaranea nematodes (Gott.) Howe

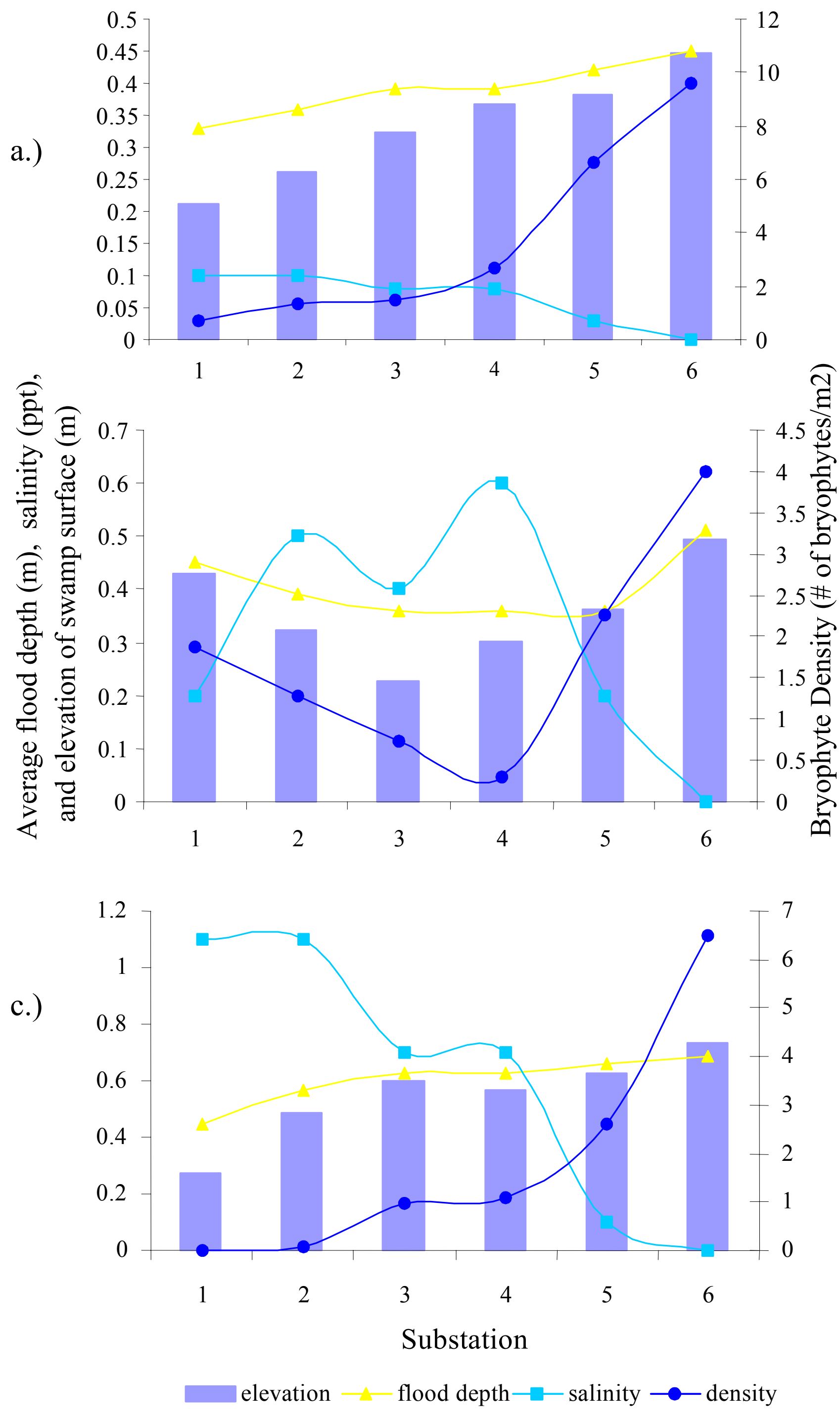

Figure 7. Bryophyte density in relation to flood depth, salinity and elevation of the swamp surface at each station and substation, a.) Prince George, b.) Fishing Creek and c.) Rat Island. Substation from river (1) to upland (6) is shown on the x-axis. Note different scales on y-axis with respect to all variables. Elevation and salinity are read on the same scale. Flooding depth is the difference between elevation and water level.

(Figure 7b) had fewer bryophytes near substations 3-5 on either side of a creek that ran through the center of the transect and connected directly to the river. Bryophyte density decreased gradually from substation 1 with approximately 2 bryophytes/m^2 to substation 4 with 0.3 bryophytes/m^2 and then a subsequent increase to 4 bryophytes/m^2 at substation 6. Flooding depth had an inverse relationship with bryophyte density as well as elevation, with water levels reaching <0.5m at substation 1 and increasing gradually to substation 3 with a subsequent decrease to the upland. Salinity followed the same pattern as flood depth with the maximum range occurring at substation 2 and 3 (Table 2), due to the effect of floodwaters via the creek. Bryophyte density at Rat Island station (Figure 7c) followed a pattern similar to Prince George station. As flood depth and salinity decreased from river to upland, bryophyte density increased from 0 bryophytes/m^2 at substation 1 to almost 7 bryophytes/m^2 at substation 6. Bryophyte density had a linear relationship with elevation of the swamp surface. Rat Island's elevation increased from almost 0.3m at the riverbank to approximately 0.8m at substation 6, 291 m away from the river edge.

Species richness, the number of species that occurred at each substation, was also calculated for each station and substation and compared to flood depth relative to the swamp surface (m) and salinity (ppt) (Figure 8a, b, and c). Prince George station (Figure 8a) showed a pattern of increasing species richness as flood depth and salinity decreased from river to upland. Fishing Creek (Figure 8b) showed a distinct pattern with species richness increasing progressively from river to upland, however, due to the effect of the creek, bryophyte species richness decreased at substation 3. Average salinity also decreased because of dilution from upland flow through the creek.

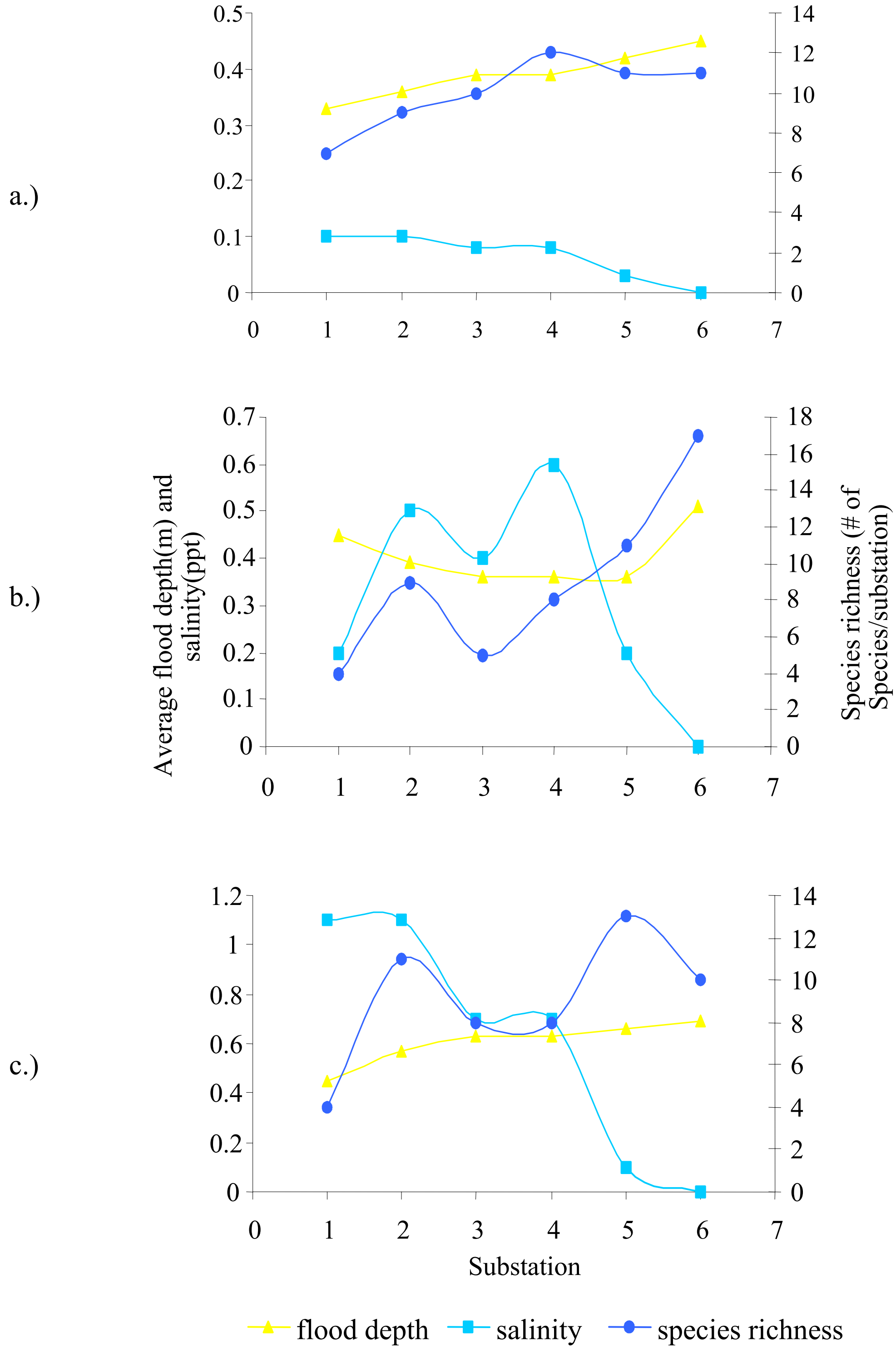

Figure 8. Bryophyte species richness in relation to flood depth and salinity at each station and substation, a.) Prince George, b.) Fishing Creek and c.) Rat Island. Substation from river (1) to upland (6) is shown on the x-axis. Note different scales on y-axis with respect to all variables.

Rat Island (Figure 8c) bryophyte species richness varied from river to upland with no obvious pattern.

Relationship of bryophyte species to environmental/physical variables

A principal component analysis identified two eigenvectors that accounted for 82% of variance with the first principal component (prin1) a linear combination of minimum and average water level, elevation of the marsh/swamp surface, and the occurrence of tidal flood events. The second principal component (prin2) was a linear combination of maximum and average salinity (Figure 9). Each transect contained substations clearly distributed over these two combinations of water level and salinity variables.

Figure 10, a biplot, depicts the relationship between 12 common bryophyte species and the 18 stations where each species was present with regard to the first 2 principal component scores. Only bryophyte species that occurred more than 10 times in the distribution study are included. Each of the 18 substations was also plotted. The configuration of each station was the same as scores on the first two principal components. The abundance or counts of bryophyte species at each station (Table 5) were plotted as vectors from the origin, and the angles between the vectors represent the correlation among species. Each vector points in the direction that is most like the environmental variable represented by the two axes. This is the direction which has the highest squared multiple correlation with the principal components. The length of the vector corresponds to the total abundance of each species found within study sites.

The 2nd quadrant of Figure 10 primarily consists of Rat Island substations 2 through 5, in which 3 liverwort species and 1 moss species were found most abundant;

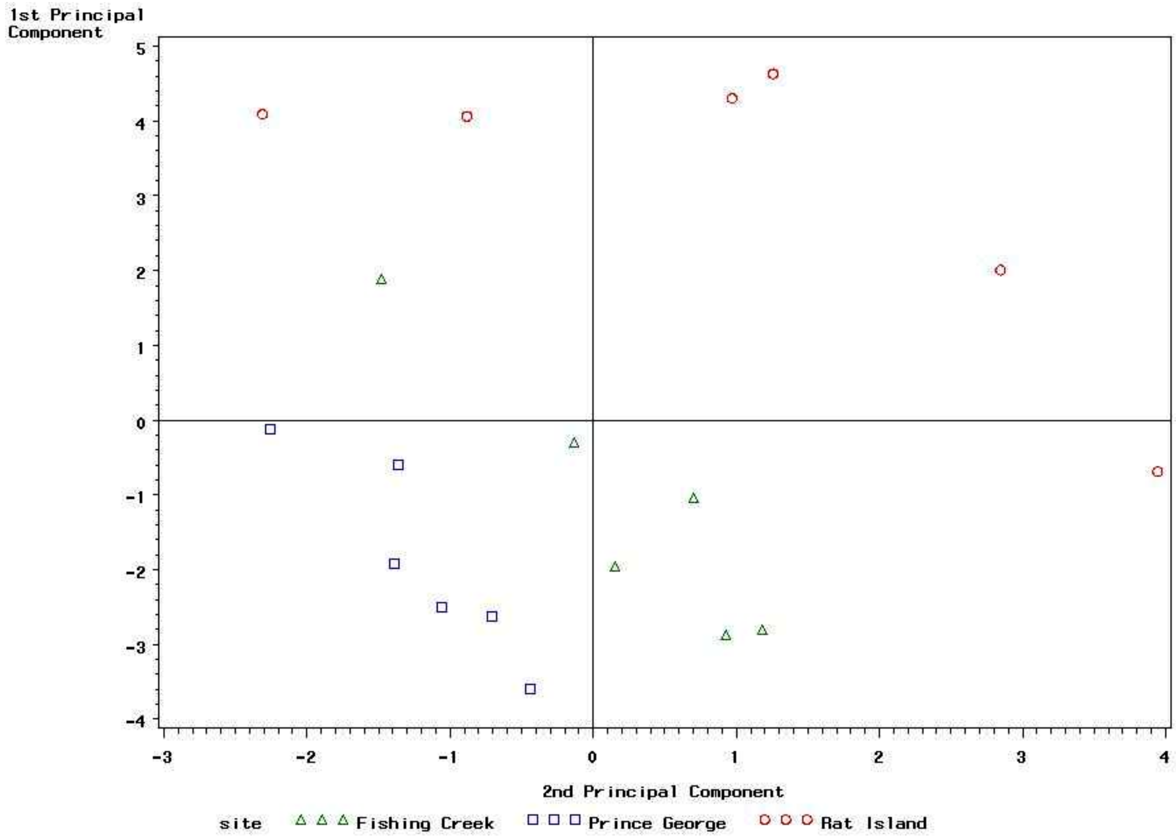

Figure 9. Substation score distribution along the first two principal components axes. Y-axis is Prin1, which accounted for 60% of the variation and the x-axis is Prin2, which accounted for 22% of the variation. Each station was plotted with regard to the environmental variable loading or eigenvector coefficient. Prince George, Fishing Creek, and Rat Island stations are represented by squares, triangles, and circles, respectively.

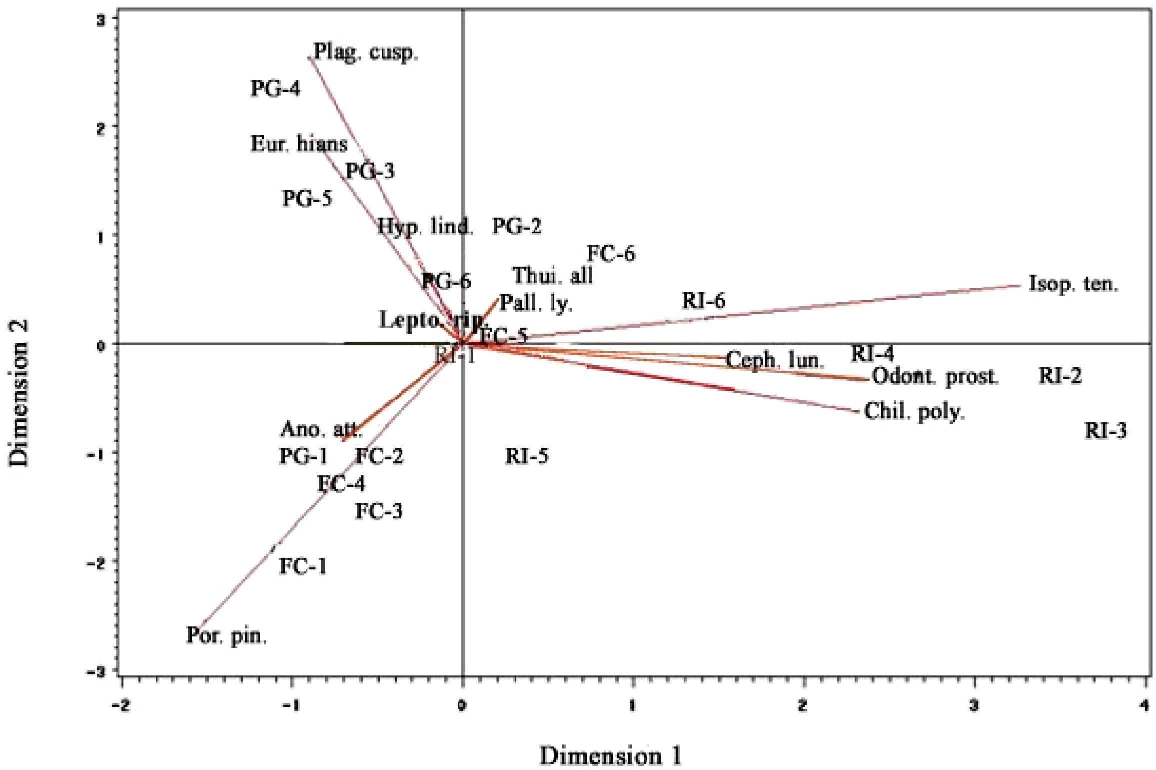

Figure 10. Principal component biplot of species abundance (vectors) of 12 bryophyte species and station locations (points). Each substation was associated with 16 quadrants at which bryophyte species were recorded. Dimension 1, the x-axis, represents the score of Prin 1 in Figure 9, and Dimension 2, the y-axis, represents the score of Prin 2 in Figure 9. Key to species: Ano. att. = *Anomodon attenuatus*; Eur. hians = *Eurhynchium hians*; Hyp. lind. = *Hypnum lindbergii*; Isop. ten. = *Isopterygium tenerum*; Lept. rip. = *Leptodictyum riparium*; Plag. cusp. = *Plagiomnium cuspidatum*; Thui. all. = *Thuidium allenii*; Ceph. lun. = *Cephalozia lunulifolia*; Chil. poly. = *Chiloscyphus polyanthos*; Odont. prost. = *Odontoschisma prostratum*; Pall. ly. = *Pallavicinia lyellii*; Por. pin. = *Porella pinnata.* Key to stations: Prince George Station, subsites 1 through 6 = PG-1, PG-2, …PG-6; Fishing Creek Station, subsites 1 through 6 = FC-1, FC-2, … FC-6; Rat Island Station, subsites 1 through 6 = RI-1, RI-2, … RI-6.

Table 5. Presence/absence data for bryophyte species occurring more than 10 times along river to upland transects. Each station (Rat Island, Fishing Creek, and Prince George) has 6 substations that run from river (1) to upland (6). These observational data were utilized in the principal component biplot. Each dash represents the absence of that species at that substation.

	Rat Island						Fishing Creek						Prince George					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
Species																		
Anomodon attenuatus	-	-	-	-	-	-	1	5	5	1	1	-	8	3	-	-	-	-
Eurhynchium hians	-	-	-	-	-	-	-	1	-	1	1	-	1	-	5	12	5	-
Hypnum lindbergii	-	1	-	-	-	-	-	-	-	3	2	4	-	1	-	2	5	-
Isoptyergium tenerum	1	13	13	6	4	14	1	-	-	-	5	8	-	8	3	1	-	3
Leptodictyium riparium	-	-	-	-	-	-	-	-	-	1	3	-	1	1	1	1	-	2
Plagiomnium cuspidatum	-	-	-	-	-	-	-	1	-	-	-	4	2	6	10	10	7	-
Syrrhopodon texanus	-	2	1	1	1	3	-	-	-	-	-	2	-	-	-	-	-	-
Thuidium allenii	-	-	2	3	1	-	-	-	-	1	1	3	-	1	1	1	2	7
Thuidium delicatulum	-	-	2	6	3	-	-	-	1	1	1	9	-	-	-	1	2	3
Cephalozia lunulifolia	-	4	10	6	-	-	-	-	-	-	-	1	-	-	-	-	-	-
Chiloscyphys polyanthos	-	11	9	8	6	-	-	1	1	-	-	2	-	-	-	-	-	-
Odontoschisma prostratum	-	9	12	5	1	1	-	-	-	-	-	1	-	-	-	-	-	-
Pallavicinia lyellii	-	-	-	-	1	4	-	-	-	-	-	3	-	-	-	-	1	3
Porella pinnata	-	1	1	-	6	1	14	7	8	10	1	1	7	1	1	3	-	-

Cephalozia lunulifolia, Odontoschisma prostratum, Chiloscyphus polyanthos and *Isopterygium tenerum*. The vector angle between *Chiloscyphus polyanthos* and *Odontoschisma prostratum* is very small due to a close association between the two liverwort species. The first substation of Rat Island is located at the centroid due to the absence of bryophyte species. The 3rd quadrant (Figure 10) includes 2 dominant species, *Anomodon attenuatus* and *Porella pinnata*, which occur at stations, PG-1 and FC-1 through FC-4, while the 4th quadrant depicts *Leptodictyum riparium* occurring most abundantly at FC-5, whereas *Hypnum lindbergii*, *Eurhynchium hians*, and *Plagiomnium cuspidatum* occur most often throughout Prince George station ranging from substation 2 to substation 5. The last two most abundant species, *Thuidium allenii* and *Pallavicinia lyellii* were found in close association within Fishing Creek station at substations 5 and 6.

Photosynthetic response to salinity

Dark-adapted plants in ambient 0-ppt river water as the control exhibited the highest photosynthetic efficiency over all 6 salinity treatments with an average quantum yield of 0.75 (Figure 11). A one – way ANOVA (p-value < 0.05) showed a significant reduction in photosynthetic efficiency for all other treatments; however, the 2 ppt treatment was not significantly different from the control in the first hour of the 12-hour time series. In the first hour of the 15-ppt treatment, there was a two-stage initial shock effect with a significant reduction in photosynthetic efficiency at 30 minutes and a subsequent sharp rise after an hour to level off with the other treatments.

The photosynthetic efficiency response of *Fontinalis sullivantii* to desiccation, (Figure 12), resulted in an initial increase in quantum yield from 0.65 in the first 3 hours and then gradually decreased to a quantum yield of 0.6.

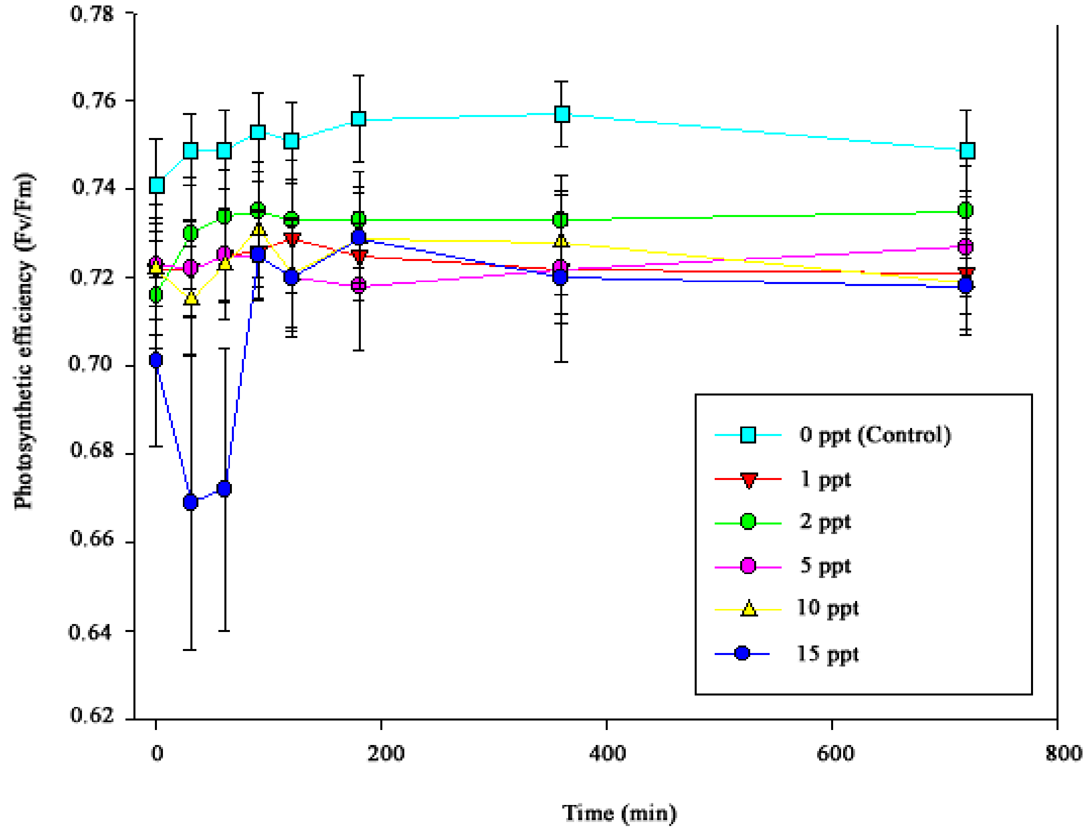

Figure 11. Photosynthetic efficiency response of dark-adapted leaves of *Fontinalis sullivantii* to varying salinity treatments (mean and standard error of eleven replicates per treatment and time series). N=11 for each mean.

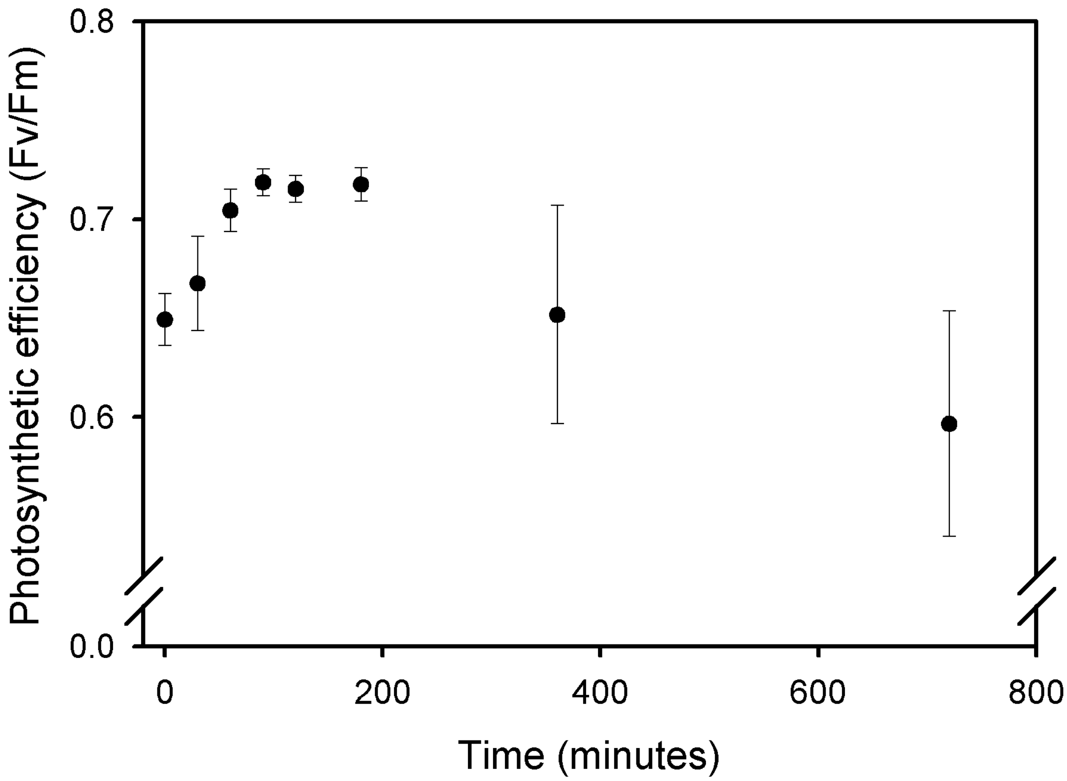

Figure 12. Photosynthetic efficiency response (Fv/Fm) of *Fontinalis sullivantii* to desiccation over a 720 minute time series (mean and standard error of eleven replicates).

DISCUSSION

Bryophyte richness

There is no known floristic list of bryophyte species for the swamp forests of the Southeastern United States. Tables 3 and 4 list moss and liverwort taxa representative of the swamp forests along the Northeast Cape Fear River in North Carolina. A larger than expected number of bryophyte species was identified. The present study identified only species collected within 3 feet of the soil surface. Additional species likely inhabit tree bark above this elevation within the swamp forests.

Cololejeunea setiloba with more subtropical affinities was found in North Carolina north of its usual distribution in swamps and floodplain forests of the mid-Gulf coastal plain (Briel 1970 and Schuster 1980).

Bryophyte distribution

Prince George station represents a typical tidal mixed hardwood swamp forest in southeastern North Carolina with flooding depth and salinity decreasing from river to upland. This creates an elevated response in the density and species richness of bryophytes from the riverbank to the upland (Figure 7 and 8). Fishing Creek station was unusual due to a berm at the river's edge which caused the riverbank to flood less than the interior and a canal that runs through the interior swamp. Bryophyte density and species richness were reduced in the interior substations. A dramatic rise in salinity at substation 4 occurred even though water levels were higher at substation 3, due to a dilution effect of the canal. Note that salinity and flooding are measured at substations for only two weeks each season so higher salinity may have occurred when instruments were not present. Saline water detected in soils at some substations during porewater sampling provides evidence that such events have occurred (Hackney *et. al* 2002). Several species of bryophytes (*Anomodon attenuatus, Eurhynchians hians, Hypnum lindbergii, Leptodictyum riparium, Plagiomnium cuspidatum and Porella pinnata*) were found both at Fishing Creek and Prince George because both stations have similar environmental gradients, *i.e.* substrate.

Bryophyte density and species richness at Rat Island station follows a pattern similar to Prince George with no bryophytes present along the river's edge, but increased gradually to 7 bryophytes/m^2 near the upland edge. Rat Island station is a degraded swamp, which was once pocosin habitat, but is now usually tidally flooded. Regular flooding by saline water has eliminated most of the trees once present near the river, eliminating potential substrate for bryophytes. The absence of substrate and the regular occurrence of salt intrusion is likely responsible for the absence of bryophyte species near the river at Rat Island.

There was one species, *Isopterygium tenerum,* that was present at all three stations with the highest frequency, cover and density occurring at all Rat Island substations. It appears that this species is highly adapted to the environmental gradients found along each transect due to it's variability in morphology. Most specimens can be identified without difficulty, but there is a very small widespread form with little distinction between stems and branch leaves that is difficult to identify (L. Anderson, Duke University Herbarium, Durham, NC – personal communication). The variation may be due to physiological response to salt intrusion.

Water level is an important environmental factor for bryophytes (Glime & Vitt, 1987 and Muotka & Virtanen, 1995). The number of truly aquatic species, such as

Fissidens fontanus and *Fontinalis sullivanti,* is much smaller than the number of species growing in habitats that are submerged only for shorter periods (Glime & Vitt 1987). Thus, the highest diversity of bryophytes was often found near average water level (Muotka & Virtanen 1995); a vertical ecotone. Some of the lowest absolute elevations in swamps and marshes along the Northeast Cape Fear River are farthest from the ocean, especially at Rat Island, Fishing Creek and Prince George stations. The long-term implication of this feature is that during low or no flow conditions there is the potential for a net flow of saline water upstream that can become incorporated in the porewater of the swamp. This was documented by the presence of saline water upstream of Point Peter at only one station (Eagle Island) in the Cape Fear River, while saline water was noted at Rat Island and Fishing Creek in the Northeast Cape Fear River (Hackney *et. al*. 2002). Upstream flow is limited in the Cape Fear River by higher flow rates in the river and a much larger drainage basin.

Relationship of bryophyte species to environmental/physical variables

Principal component analysis identified a distinct pattern of bryophyte community variation within each of the three transects (Figure 10). The importance of species loading in interpreting the site ordinations has already been stressed by Laurec et al. (1979). Environmental variables are often highly correlated (Ter Braak 1987) and so it can be impossible to separate their independent effects. Whenever the number of influential environmental variables is greater than two or three, there were 15 in the present study, principal component procedures often do not clearly relate species to environments of a specific type. However, bryophytes in a tidal swamp clustered well to specific combinations of environmental variables that represent differing degrees of tolerance to both flooding and saline water. *Isopterygium tenerum* and *Porella pinnata* have the longest vector length, which accounts for their highest abundance at all three sites. However, *Isopterygium tenerum* was more associated with Rat Island due to its high tolerance to varying salinity, which ranged from less than one ppt to over 6 ppt. A description of the species by Crum and Anderson (1981) provides evidence for its wide niche. *Isopterygium tenerum* is usually found on logs and stumps, bark at the base of trees, and soil (especially sand), typically in dry places in the Southeast. Sometimes it is found in swamps especially gum – cypress swamps. It is also found in the uplands of North Carolina. *Porella pinnata* was found at stations along the Fishing Creek and Prince George transects subjected to varying water levels as well as flooding by saline water. Average salinity for Fishing Creek ranged from 1- 6 ppt. Briel (1970) describes *Porella pinnata* as a liverwort usually submerged on logs or roots in flowing streams or, indiscriminately attached to trees, rarely exceeding the high-water mark of rivers; on floodplains, or swamps; rarely with other bryophytes. Observations of this species during the present study concur.

A high correlation between three liverwort species, *Cephalozia lunulifolia, Odontoschisma prostratum and Chilosyphus polyanthos* was near Rat Island substations 2 through 4. These species are described as occurring on moist sand, peaty soil, rotten logs or bases of trees above the water level in swamps and are often found in compact mats with other bryophytes (Briel 1970). The higher frequency of these liverworts occurring at Rat Island may be due to their higher tolerance to tidal flooding by saline water. *Anomodon attenuatus* was most highly correlated with the interior of Fishing Creek and adjacent to the river at Prince George. It was always found on the bark of trees approximately 0.3 m above the average water level. It was submerged on occasion during flooding tides with an average maximum salinity of at least 3.44 ppt.

Two species, *Thuidium allenii and Pallavicinia lyellii,* which are frequently found in swamps, were highly correlated and occur primarily in sites that were seldom flooded and rarely subjected to saline water. These species occur intertwined in the same mats implying similar environmental requirements. *Plagiomnium cuspidatum, Hypnum lindbergii* and *Eurhynchium hians* were present at the same subsites with similar water levels and salinities. These species have an average patch elevation approximately 0.3 m above the average water level of 0.3 m and do not exhibit any specific tolerance to flooding or saline water.

According to Soderstrom (1998) many bryophyte species are adapted to grow in habitat patches that are regularly disturbed. Disturbance, being defined here as salt intrusion and flooding tides, allows the establishment of early succession stages. Species adapted to early stages, known as shuttle species (Soderstrom 1998), often survive unfavorable situations by producing diaspores that will develop new gametophores when the situation becomes suitable again. This may be one reason why species described above can tolerate the varying conditions found in the swamps of the Northeast Cape Fear River.

Photosynthetic response to salinity

High salinity, in the range between 5 and 15 ppt, significantly reduced photosynthetic efficiency of the moss species, *Fontinalis sullivantii*, on the short time scale, followed by some recovery (Figure 11). However, observed physical changes in the decreased abundance of *Fontinalis sullivantii* in the fall of 2001 coincided with a major drought that eliminated most of the population at Prince George station suggesting a strong relationship between increasing salinity and disappearance of this species.

The acclimation of *Fontinalis sullivantii* to the 15 ppt treatment suggests that there are other physiological avenues by which this bryophyte can rid the salt ions from its cells, such as secondary metabolite production (M. Durako, University of North Carolina at Wilmington – Center of Marine Science, personal communication). Bates & Brown (1974, 1975) have shown that the coastal rock species *Grimmia maritima, Tortella flavovirens* and *Ulota phyllantha* have adapted to the effects of seawater on their metabolism better than the inland species they used for comparison. Plants growing along the saline – fresh water boundary must be somewhat tolerant to surges of salinity or have means to avoid it. Adam (1976) concluded that bryophytes in British salt marshes possess a very robust metabolic system that is able to withstand a range of external environmental conditions.

According to Vitt and Gime (1984), salt water aquatic mosses are rare. No species occurs submersed, while only a few tolerate intertidal situations, and these exist only at and above the high tide level. *Fontinalis sullivantii* in the Northeast Cape Fear River can clearly tolerate low salinity water. It occurs along exposed roots and bases of trees, such as bald cypress. It is submerged at rising and high tide and partially exposed at low tide therefore exposing it to varying salinity as well as exposure to air.

Fontinalis sullivantii is a facultative aquatic bryophyte and has the ability to tolerate considerable fluctuations in water level. It is often totally submersed at high tide or flooding condition, but during low tide, is able to tolerate short periods of desiccation. This is evident in Figure 12, which shows photosynthetic efficiency at a steady pace for the first 2 and ½ hours that gradually declines over the last 9 and ½ hours. There is a large body of literature describing the response of bryophytes to desiccation, of which many species show great tolerance (Penuelas 1984). *Fontinalis* sp. and *Fissidens* sp. clearly have ecophysiological adaptations to survive out of water when water levels are low during drought or extreme low tides.

CONCLUSION

The diversity of bryophytes in the swamps of the Northeast Cape Fear River was high. The majority of bryophytes were not common in this system and have narrow habitat specificity. Although bryophytes may form a major part of several vegetation types and ecosystems, relatively few bryophyte species in this study were ecologically abundant or dominant. *Isopterygium tenerum* is one species present in great abundance and that occurs in a wide range of habitats. *Fontinalis sullivantii* can clearly tolerate low saline water for short periods of time.

Long term implications of the current study are that bryophyte data will be used to assess future impacts due to current dredging projects in the Cape Fear River estuary.

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Appendix 1. Species that occur more than five times among all three transects. Data include station and substation occurrence, frequency (# of times occurring in a transect/# of total species collected), density (in 1m^2), average percent coverage (in a 1 dm2 quadrat), and coinciding environmental variables, including; average water level (m), average salinity (ppt), elevation of the swamp surface and average patch elevation (m) of the bryophyte species measured in each quadrat.
Abbreviations for stations are as follows: PG = Prince George Station; FC = Fishing Creek Station; RI = Rat Island Station, with each station containing 6 substations, substation 1 being next to the river and 6 at the upland.

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Anomodon attenuatus	PG	1	0.11	0.13	40	0.42	0.50	0.21	0.45
		2	0.11	0.17	70	0.36	0.50	0.26	0.73
	FC	1	0.14	0.00	1	0.24	6.00	0.43	0.71
		2	0.14	0.07	20	0.33	4.30	0.32	0.95
		3	0.14	0.13	60	0.42	3.90	0.23	0.59
		4	0.14	0.01	40	0.36	4.70	0.30	0.52
		5	0.14	0.02	15	0.30	4.20	0.36	0.58
Average			0.13	0.08	35	0.35	3.44	0.30	0.65
Standard deviation			0.01	0.07	25	0.06	2.12	0.08	0.17

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Eurhynchium hians	PG	1	0.20	0.01	20	0.42	0.50	0.21	0.46
		3	0.20	0.19	40	0.30	0.50	0.32	0.60
		4	0.20	0.42	20	0.24	0.50	0.37	0.66
		5	0.20	0.46	20	0.24	0.40	0.38	0.60
	FC	2	0.03	0.07	90	0.33	4.30	0.32	0.92
		4	0.03	0.00	5	0.36	4.70	0.30	0.57
		5	0.03	0.11	75	0.30	4.20	0.36	0.58
Average			0.13	0.18	39	0.31	2.16	0.32	0.63
Standard deviation			0.09	0.19	32	0.06	2.10	0.06	0.14

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Hypnum lindbergii	PG	2	0.08	0.06	75	0.36	0.50	0.26	0.74
		4	0.08	0.05	15	0.24	0.50	0.37	0.62
		5	0.08	0.67	30	0.24	0.40	0.38	0.59
	FC	4	0.09	0.01	10	0.36	4.70	0.30	0.54
		5	0.09	0.05	20	0.30	4.20	0.36	0.63
		6	0.09	0.20	20	0.21	1.20	0.49	0.60
	RI	2	0.01	0.00	10	0.33	6.30	0.49	0.70
Average			0.07	0.15	26	0.29	2.54	0.38	0.63
Standard deviation			0.03	0.24	23	0.06	2.46	0.09	0.07

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Isopterygium tenerum	PG	2	0.16	0.41	60	0.36	0.50	0.26	0.74
		3	0.16	0.04	15	0.30	0.50	0.32	0.58
		4	0.16	0.00	1	0.24	0.50	0.37	0.63
		6	0.16	0.21	10	0.15	0.40	0.45	0.61
	FC	1	0.14	0.00	1	0.24	6.00	0.43	0.71
		5	0.14	0.13	20	0.30	4.20	0.36	0.59
		6	0.14	0.53	30	0.21	1.20	0.49	0.61
	RI	1	0.50	0.00	1	0.54	6.40	0.27	0.70
		2	0.50	0.03	40	0.33	6.30	0.49	0.72
		3	0.50	0.34	40	0.21	5.30	0.60	0.69
		4	0.50	0.12	30	0.24	4.50	0.57	1.08
		5	0.50	0.07	10	0.18	3.30	0.62	0.77
		6	0.50	1.18	20	0.09	0.50	0.73	0.93
Average			0.31	0.24	21	0.26	3.05	0.46	0.72
Standard deviation			0.18	0.33	18	0.11	2.51	0.14	0.14

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Leucobryum albidum	PG	6	0.01	0.03	5	0.15	0.40	0.45	0.64
	FC	6	0.01	0.00	1	0.21	1.20	0.49	0.67
	RI	4	0.04	0.01	10	0.24	4.50	0.57	1.07
		5	0.04	0.02	15	0.18	3.30	0.62	0.80
		6	0.04	0.01	1	0.09	0.50	0.73	0.90
Average			0.03	0.01	6	0.17	1.98	0.57	0.81
Standard deviation			0.02	0.01	6	0.06	1.83	0.11	0.17

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Leptodictyum riparium	PG	1	0.06	0.01	20	0.42	0.50	0.21	0.44
		2	0.06	0.02	20	0.36	0.50	0.26	0.75
		3	0.06	0.01	5	0.30	0.50	0.32	0.59
		4	0.06	0.04	25	0.24	0.50	0.37	0.60
		6	0.06	0.04	1	0.15	0.40	0.45	0.59
	FC	4	0.04	0.00	20	0.30	4.20	0.30	0.54
		5	0.04	0.16	40	0.21	1.20	0.36	0.55
Average			0.05	0.04	19	0.28	1.11	0.32	0.58
Standard deviation			0.01	0.06	13	0.09	1.39	0.08	0.09

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Plagiomnium cuspidatum	PG	1	0.35	0.02	20	0.42	0.50	0.21	0.48
		2	0.35	0.14	30	0.36	0.50	0.26	0.74
		3	0.35	0.06	10	0.30	0.50	0.32	0.59
		4	0.35	0.31	20	0.24	0.50	0.37	0.67
		5	0.35	0.26	10	0.24	0.40	0.38	0.60
	FC	2	0.05	0.00	1	0.33	4.30	0.32	0.92
		6	0.05	0.05	5	0.21	1.20	0.49	0.61
Average			0.26	0.12	14	0.30	1.13	0.34	0.66
Standard deviation			0.15	0.12	10	0.08	1.42	0.09	0.14

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Sphagnum palustre	PG	6	0.03	1.26	70	0.15	0.40	0.45	0.62
	FC	6	0.02	0.50	100	0.21	1.20	0.49	0.59
	RI	5	0.03	0.07	20	0.18	3.30	0.62	0.68
		6	0.03	0.08	20	0.09	0.50	0.73	0.93
Average			0.03	0.48	53	0.16	1.35	0.57	0.71
Standard deviation			0.00	0.56	39	0.05	1.35	0.13	0.16

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Syrrhopodon texanus	FC	6	0.02	0.03	5	0.21	1.20	0.49	0.65
	RI	2	0.10	0.00	15	0.33	6.30	0.48	0.75
		3	0.10	0.01	10	0.21	5.30	0.60	0.73
		4	0.10	0.01	10	0.24	4.50	0.57	1.09
		5	0.10	0.00	1	0.18	3.30	0.62	0.80
		6	0.10	0.33	30	0.09	0.50	0.73	0.96
Average			0.09	0.06	12	0.21	3.52	0.58	0.83
Standard deviation			0.03	0.13	10	0.08	2.30	0.09	0.16

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Thuidium allenii	PG	2	0.13	0.02	20	0.36	0.50	0.26	0.75
		3	0.13	0.04	40	0.30	0.50	0.32	0.57
		4	0.13	0.02	10	0.24	0.50	0.37	1.00
		5	0.13	0.33	40	0.24	0.40	0.38	0.57
		6	0.13	0.60	10	0.15	0.40	0.45	0.58
	FC	4	0.05	0.00	5	0.36	4.70	0.30	0.57
		5	0.05	0.06	40	0.30	4.20	0.36	0.59
		6	0.05	0.02	5	0.21	1.20	0.49	0.63
	RI	3	0.10	0.03	25	0.21	5.30	0.60	0.69
		4	0.10	0.08	40	0.24	4.50	0.57	1.07
		5	0.10	0.00	1	0.18	3.30	0.62	0.76
Average			0.10	0.11	21	0.25	2.32	0.43	0.71
Standard deviation			0.03	0.19	16	0.07	2.06	0.13	0.18

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Thuidium delicatulum	PG	4	0.06	0.00	1	0.24	0.50	0.37	0.63
		5	0.06	0.23	30	0.24	0.40	0.38	0.60
		6	0.06	1.14	60	0.15	0.40	0.45	0.62
	FC	3	0.12	0.00	1	0.42	3.90	0.23	0.56
		4	0.12	0.00	5	0.36	4.70	0.30	0.76
		5	0.12	0.03	20	0.30	4.20	0.36	0.62
		6	0.12	0.70	30	0.21	1.20	0.49	0.64
	RI	3	0.50	0.02	10	0.21	5.30	0.60	0.69
		4	0.50	0.12	30	0.24	4.50	0.57	1.09
		5	0.50	0.30	60	0.18	3.30	0.62	0.77
Average			0.22	0.25	25	0.26	2.84	0.44	0.70
Standard deviation			0.20	0.38	22	0.08	1.99	0.13	0.15

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Cephalozia lunulifolia	FC	6	0.01	0.01	5	0.21	1.20	0.49	0.62
	RI	2	0.20	0.00	5	0.33	6.30	0.48	0.71
		3	0.20	0.03	5	0.21	5.30	0.60	0.70
		4	0.20	0.02	5	0.24	4.50	0.57	1.08
Average			0.15	0.02	5	0.25	4.33	0.54	0.78
Standard deviation			0.10	0.01	0	0.06	2.21	0.06	0.20

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Chiloscyphus polyanthos	FC	2	0.04	0.02	30	0.33	4.30	0.32	0.95
		3	0.04	0.01	10	0.42	3.90	0.23	0.66
		6	0.04	0.03	5	0.21	1.20	0.49	0.61
	RI	2	0.30	0.00	5	0.33	6.30	0.26	0.73
		3	0.30	0.05	10	0.21	5.30	0.32	0.69
		4	0.30	0.11	20	0.24	4.50	0.37	1.08
		5	0.30	0.08	10	0.18	3.30	0.38	0.74
Average			0.19	0.04	13	0.27	4.11	0.34	0.78
Standard deviation			0.14	0.04	9	0.09	1.61	0.09	0.17

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Odontoschisma prostratum	FC	6	0.01	0.00	1	0.21	1.20	0.49	0.61
	RI	2	0.30	0.00	5	0.33	6.30	0.48	0.73
		3	0.30	0.22	30	0.21	5.30	0.60	0.70
		4	0.30	0.09	30	0.24	4.50	0.57	1.09
		5	0.30	0.02	10	0.18	3.30	0.62	0.75
		6	0.30	0.00	1	0.09	0.50	0.73	0.89
Average			0.25	0.06	13	0.21	3.52	0.58	0.79
Standard deviation			0.12	0.09	14	0.08	2.30	0.09	0.17

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Pallavicinia lyellii	PG	5	0.04	0.25	60	0.24	0.40	0.38	0.59
		6	0.04	0.45	25	0.15	0.40	0.45	0.62
	FC	6	0.03	0.19	25	0.21	1.20	0.49	0.61
	RI	5	0.10	0.01	5	0.18	3.30	0.62	0.72
		6	0.10	0.43	20	0.09	0.50	0.73	0.92
Average			0.06	0.27	27	0.17	1.16	0.54	0.69
Standard deviation			0.03	0.18	20	0.06	1.24	0.14	0.14

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Porella pinnata	PG	1	0.13	0.10	30	0.42	0.50	0.21	0.44
		2	0.13	0.03	40	0.36	0.50	0.26	0.75
		3	0.13	0.03	30	0.30	0.50	0.32	0.54
		4	0.13	0.04	10	0.24	0.50	0.37	0.60
	FC	1	0.40	0.45	30	0.24	6.00	0.43	0.72
		2	0.40	0.12	20	0.33	4.30	0.32	0.93
		3	0.40	0.08	20	0.42	3.90	0.23	0.58
		4	0.40	0.06	30	0.36	4.70	0.30	0.51
		5	0.40	0.08	60	0.30	4.20	0.36	0.62
		6	0.40	0.01	5	0.21	1.20	0.49	0.61
	RI	3	0.30	0.01	10	0.21	4.50	0.60	0.69
Average			0.29	0.09	26	0.31	2.80	0.35	0.64
Standard deviation			0.13	0.12	16	0.08	2.14	0.12	0.13

Species Name	Belt Transect	Substation Number	Frequency	Density	Average Coverage	Average Water Level	Average Salinity	Elevation	Average Patch Elevation
Riccardia multifida	FC	5	0.04	0.01	5	0.30	4.20	0.36	0.59
		6	0.04	0.02	1	0.21	1.20	0.49	0.60
	RI	5	0.10	0.14	15	0.18	3.30	0.62	0.77
Average			0.19	0.06	11.08	0.21	2.76	0.43	0.57
Standard deviation			0.14	0.06	8.49	0.08	1.33	0.17	0.20