Geographic Variability in Salt Marsh Flooding Patterns may Affect Nursery Value for Fishery Species

Thomas J. Minello · Lawrence P. Rozas · Ronald Baker

Abstract Flooding of salt marshes controls access to the marsh surface for aquatic organisms and likely regulates the value and use of this habitat for juvenile fishery species. We examined geographic variability in marsh access by measuring tidal flooding characteristics in 15 *Spartina alterniflora* marshes in the southeastern US between South Texas and lower Chesapeake Bay. Flooding duration and flooding frequency were correlated with the elevation of the marsh edge in relation to mean low water and with the tidal range. Mean annual flooding duration over the years 2006–2008 was highest in Texas (91.5% in Aransas Bay) and North Carolina (89.3% in Pamlico Sound) and lowest in Timbalier Bay, LA (54%) and the lower Carolinas and Georgia (55–57%). We used published data on densities of blue crabs and penaeid shrimps as a measure of habitat selection, and there was a positive relationship between marsh selection and flooding duration.

Keywords Blue crab · Nekton · Penaeid shrimp · *Spartina alterniflora* · Tidal hydrology

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Introduction

Coastal salt marshes are generally considered valuable nursery habitats for many fishery species, but the ecological processes involved in supporting fishery production are still being explored (Weinstein and Kreeger 2000; Beck et al. 2001). Marshes may function to supply food for transient nekton through outwelling of nutrients and detritus (Teal 1962; Nixon 1980; Childers et al. 2000), through trophic relays (Kneib 1997), or directly as foraging grounds when flooded (Zimmerman et al. 2000). Vegetative structure in marshes can also provide protection against predators (Minello et al. 1989; Kneib 1995). Because access to the marsh surface for aquatic organisms is controlled by marsh flooding, the importance of these different functional mechanisms is likely regulated by hydrology. Geographic and temporal variability in estuarine hydroperiod and marsh inundation patterns can be substantial; mean daily tidal ranges vary from approximately 0.3 m in estuaries of the Gulf of Mexico (GoM) to over 3 m along the southeastern Atlantic coast of the US. The relative importance of astronomical and meteorological forcing on water levels, the elevation of the marsh edge in relation to tidal datums, and the extent of time that the marsh surface is flooded all vary geographically (McKee and Patrick 1988; Rozas 1995). Whether marshes provide food or protection for transient nekton, tidal inundation patterns are fundamentally important in determining marsh use and value (McIvor and Rozas 1996; Rountree and Able 2007).

Marshes in Texas are flooded much of the time and are used extensively by many juvenile fishery species (Minello 1999). Research there has focused on the direct use of the vegetated marsh surface (Zimmerman et al. 1984), and high densities of penaeid shrimps, blue crabs, and some fishes have been reported in the first few meters of vegetation adjacent to open water (Minello et al. 2008). While similar

patterns of marsh use have been observed in Louisiana (Baltz et al. 1993; Rozas and Reed 1993; Peterson and Turner 1994), direct use of the marsh surface by shrimp and crabs does not appear to be as consistent there as in Texas (Fry 2008; Rozas and Minello 2010). Individual-based models developed to investigate factors affecting brown shrimp productivity in estuaries of the northwestern GoM support the importance of tidal inundation patterns and access to marsh vegetation (Haas et al. 2004; Roth et al. 2008).

Nekton distribution patterns in estuaries of Mississippi and Alabama (Howe et al. 1999; Howe and Wallace 2000; Heck et al. 2001; Shervette and Gelwick 2008) and the Florida panhandle (Rozas et al. 2011) indicate that use of the marsh surface by blue crabs and penaeid shrimps is variable and appears related to the presence of submerged aquatic vegetation (SAV). Along the eastern coast of the US, relatively few studies have compared nekton use of the marsh surface with open bay water and results are conflicting (Hettler 1989; Mense and Wenner 1989; Rozas 1993; Fitz and Wiegert 1991; Cicchetti 1998). Where the relationship has been examined, there appears to be a correlation between marsh use and the extent of tidal inundation (Kneib and Wagner 1994; Rozas 1995; Minello et al. 2003).

Despite the recognized importance of hydrology in coastal salt marshes, relatively few studies have examined geographic variability in flooding patterns (Rozas 1993,

1995). Our objective was to compare flooding characteristics of *Spartina alterniflora* Loisel marshes throughout the southeastern US. We measured elevations near the marsh edge in 15 tidal marshes located near NOAA tide gages in estuaries between southern Texas and lower Chesapeake Bay (Fig. 1). Tide gage records were used to calculate flooding metrics for each of these marshes and the adjacent open bay bottom. We also compared patterns of marsh use by juvenile fishery species (penaeid shrimps and blue crabs) with these flooding metrics.

Methods

Our selection criteria required that marshes were (1) near an active NOAA tide gage with a continuous tidal record for several years before and during our field study, (2) located in the lower estuary, and (3) open to free tidal exchange (not impounded) but protected from major erosional forces. Distances from the tide gages to the study marshes ranged from <1 km in Pamlico Sound and Galveston Bay to 8.5 km at Aransas Bay (Table 1).

At each marsh, sediment surface elevations were measured on seven randomly located transects along approximately 1 km of marsh shoreline. Data were collected from only five transects in Barataria Bay due to equipment malfunction. Elevations were measured from

Fig. 1 Locations of the 15 study marshes in the southeastern US

June 2 to June 18, 2008, except in Galveston Bay where similar measurements were made on March 1, 2006 and June 3, 2010. Transects ran perpendicular to the shoreline and extended 20 m into the marsh vegetation and 30 m into adjacent open water. We focused measurements on the marsh edge (identified as the location where the lowest growing culms of vegetation occurred) and measured elevations at 1-m intervals for 10 m on either side of the edge. Elevations were generally obtained by measuring water depth and comparing this depth to mean lower low water (MLLW) on the tide gage record at the time of measurement. If the marsh surface was not flooded, we used a laser level to record elevations in relation to the water's surface. The overall approach assumes no lag time and a flat water surface between the gage and the marsh,

and proximity of the marsh to the gage will likely affect the accuracy of our estimates (Table 1).

Shorelines of all study marshes were dominated by *S. alterniflora*, and monoculture stands of this vegetation extended along the 20 m of our marsh transects in most Atlantic coast marshes. In the GoM, vegetation away from the edge was generally dominated by *S. alterniflora* but often included *Juncus roemerianus* Scheele, *Distichlis spicata* (L.) Greene, *Salicornia virginica* L., and *Batis maritima* L.; black mangrove *Avicennia germinans* (L.) L. was abundant throughout the marshes in Timbalier Bay and Barataria Bay. Oysters were present within marsh vegetation and subtidally at Cedar Key, Wrightsville Beach, Newport River, Pamlico Sound, and Chesapeake Bay. Seagrass (mainly *Halodule wrightii* Asch.) occurred in

Table 1 Locations of study marshes and relationship to tide gages

Study marsh	Marsh location (lat, long DD)	Tide gage (NOAA ID)		Distance to gage (km)	Marsh edge elevation (cm)				Tide data availability (%)
					MLLW	MSL	NAVD88	(SE)	
Aransas Bay, TX	27.97° N, 96.97° W	Rockport	(8774770)	8.5	−17.3	−23.2	11.0	(3.88)	99.9
Galveston Bay, TX	29.26° N, 94.92° W	Pier 21[a]	(8771450)	<1	−0.7	−25.9	−5.0	(2.10)	99.9
Sabine Lake, TX/LA	29.72° N, 93.85° W	Sabine Pass N	(8770570)	2.1	24.1	−5.2		(3.16)	99.2
Timbalier Bay, LA	29.12° N, 90.22° W	Port Fourchon	(8762075)	2	19.3	−0.4		(1.61)	97.1
Barataria Bay, LA	29.28° N, 89.97° W	Grand Isle	(8761724)	3.4	9.2	−7.1		(1.39)	100.0
Bay St. Louis, MS	30.34° N, 89.36° W	Bay Waveland Yacht Club	(8747437)	4.2	23.4	−3.1	13.4	(4.05)	99.1
West Bay (Panama City, FL)	30.13° N, 85.66° W	Panama City	(8729108)	2.5	6.9	−13.4	−10.1	(2.44)	99.9
Cedar Key, FL	29.14° N, 83.05° W	Cedar Key	(8727520)	2.3	39.1	−23.0	−29.6	(3.43)	98.9
Chicopit Bay (Mayport, FL)	30.38° N, 81.47° W	Mayport Bar Pilots Dock	(8720218)	4.3	62.9	−13.0	−29.9	(3.43)	100.0
St. Simons Sound, GA	31.14° N, 81.45° W	St Simon's Island	(8677344)	5.5	95.9	−11.8	−31.8	(5.82)	95.3
Charleston Bay, SC	32.75° N, 79.95° W	Charleston	(8665530)	4.2	78.6	−10.4	−17.1	(6.73)	99.9
Wrightsville Beach, NC	34.20° N, 77.81° W	Wrightsville Beach	(8658163)	<1	50.4	−12.0	−26.1	(4.83)	99.2
Newport River (Beaufort, NC)	34.74° N, 76.69° W	Beaufort	(8656483)	3.2	28.4	−23.7		(3.37)	99.9
Pamlico Sound (Oregon Inlet, NC)	35.80° N, 75.55° W	Oregon Inlet Marina	(8652587)	1.9	−2.4	−20.0	−22.6	(2.51)	99.8
Lower Chesapeake Bay, VA	37.10° N, 75.96° W	Kiptopeke	(8632200)	8	35.0	−8.4	−23.0	(6.18)	99.8

Data availability is the percentage of hourly tide values available and used in calculations over the 3-year period from 2006 to 2008

SE 1 standard error in edge elevation from replicate transects

[a] Distance listed is to a temporary gage that was installed near the marshes at 29.255° N, 94.915° W. Marsh elevations in relation to MLLW on the Pier 21 gage were transferred using regression analysis as described in the "Methods" section

subtidal waters at Aransas Bay, West Bay, Pamlico Sound, and Chesapeake Bay.

Water level records were downloaded for the years of 2006, 2007, and 2008 from the National Ocean Service database at http://tidesandcurrents.noaa.gov. The percentage of the 26,304 hourly readings available and used in our calculations was high for most gages (Table 1). The NOAA Grand Isle gage (Barataria Bay) had the most missing records (15.4% in 2007 and 10.2% in 2008; mainly from winter months). We estimated these missing values using linear regression from a nearby gage (USGS 073802515 Barataria Bay Pass E of Grand Isle, LA) when both gages were operational in winter 2006 ($p<0.001$, $R^2=0.99$). In Galveston Bay, we used a temporary water level gage installed in 2005 at Gangs Bayou (29.255° N, 94.915° W) because we could not identify marshes that met our selection criteria near the NOAA Pier 21 gage. This Gangs Bayou gage was operational from 2006 through August of 2008. The remaining water level values for 2008 were estimated using a polynomial regression of hourly water levels with a 3-h lag between Pier 21 and the Gangs Bayou gage ($p<0.001$, $R^2=0.92$). This regression also was used to transfer the tidal datum of MLLW from the Pier 21 gage.

We calculated four tidal metrics that describe patterns of marsh flooding potentially important in determining marsh value for nekton. These included:

1. Flooding duration—Percentage of time that water was over 0 cm deep at the marsh edge. This basic metric provides information about the annual and seasonal availability of the marsh surface. The time that water was over 5 cm at the marsh edge was also calculated because this depth appears to be the minimal depth required for juvenile penaeid shrimps to use the marsh surface in Galveston Bay.
2. Flooding frequency—Number of times that water flooded the marsh edge, calculated as the frequency that water levels changed from zero to a positive value at the edge. Crossing the marsh/open water interface may be dangerous for prey, and this metric provides information on how frequently such crossings would be required if nekton attempted to continually inhabit marsh when available.
3. Flood area index—For any time period, this index (expressed as a percentage) is the sum of hourly observations at each distance from the edge (from 0 to 10 m) where flooding was >5 cm deep divided by the total number of these tidal observations. There is evidence from Texas marshes that the first 5–10 m of vegetation inland from the marsh edge are used more frequently by fishery species than marsh farther from the edge (Minello et al. 1994, 2008). This index combines time and area into a

percentage and represents a combination of flooding duration and flooding extent into the first 10 m of marsh vegetation. For example, if water is 5 cm deep over the entire first 10 m of marsh for the year, this metric would be 100%. The value will decline if water either floods only the first 5 m of marsh for the entire year (50%) or if it floods the entire 10 m for half of the year and the marsh is drained for the remainder of the year (50%). The metric takes the marsh slope into consideration, and values can be affected by many combinations of elevation and water level.

4. Access distance—Minimum distance that nekton must travel over open water to maintain marsh occupancy over some arbitrary time period (we calculated as a mean value in meters per day). Between consecutive floodings of the marsh edge, the metric equals double the maximum distance that the water's edge moved from the marsh edge, and hence, measures the minimum distance an animal must travel if it remained in the water and tried to maintain marsh residency whenever it was available. Measured over a fixed time period, the metric is influenced by the frequency of flooding and the slope of the open water bottom adjacent to the marsh. If the marsh is continually flooded, the value would be zero.

Relationships between tidal datums and our flooding metrics were explored using linear and nonlinear regressions (JMP, Version 9.0, SAS Institute Inc., Cary, NC, USA). Our goal in these analyses was to fit curves that maximized the R^2 value. These regressions should not be used to predict values outside of the range of the data presented.

We used data from an earlier review and meta-analysis by Minello et al. (2003) to assess whether juvenile fishery species such as blue crab *Callinectes sapidus*, brown shrimp *Farfantepenaeus aztecus*, and white shrimp *Litopenaeus setiferus* selected marsh habitat over adjacent open water when the marsh was flooded. That analysis yielded paired comparisons of mean densities in these habitats from Aransas Bay, Galveston Bay, Barataria Bay, Charleston Bay, and Chesapeake Bay, and we supplemented the comparisons with more recent data from Barataria Bay (Rozas and Minello 2010). Most of the data were from Galveston Bay, and only blue crab densities were available from single studies in Charleston Bay and Chesapeake Bay. Comparisons were restricted to polyhaline and mesohaline areas of these estuarine systems where *S. alterniflora* was present at the marsh edge. The index was calculated by subtracting the mean density in open water from the density in the marsh, and a positive value was considered a measure of selection for marsh vegetation.

Results

The elevation of the marsh edge was variable among the 15 sites examined. In relation to the tidal datum MLLW, mean edge elevations ranged from −17.3 cm at Aransas Bay to 95.9 cm at St. Simons Sound (Table 1). This difference was reduced, however, in relation to other datums such as mean sea level (MSL). Survey data were available for 11 of the tide gages, and the edge elevation in relation to the North American Vertical Datum (NAVD88) ranged from −31.8 cm at St. Simons Sound to 13.4 cm at the Bay St. Louis marsh.

Marsh elevation profiles in relation to the edge also varied over this geographic range. Most marshes in the GoM (with the exception of Cedar Key) had shallow slopes with the highest elevations on our transects <40 cm above the marsh edge (Fig. 2). The marshes in Florida, Georgia, and South Carolina had steeper slopes with internal elevations well above 40 cm higher than the marsh edge. The marshes we examined in North Carolina and Virginia had elevation profiles similar to those in the GoM. Elevation profiles (bathymetry) for the bay bottom adjacent to the marsh were highly variable as well, both among sites and within some sites. While most marshes were adjacent to shallow water, the bay bottom near Timbalier Bay, St. Simons Sound, and Charleston Bay marshes often sloped steeply away from the marsh edge, generally related to the presence of tidal channels.

Mean annual flooding duration for the 3 years (2006–2008) ranged from 91.5% at Aransas Bay to 54.0% at Timbalier Bay (Fig. 3). Flooding values were variable among GoM sites but consistently low for marshes along the Atlantic coast between Florida and Cape Hatteras. Marsh flooding in Pamlico Sound was similar to Texas. If we only considered the marsh edge to be flooded when water was >5 cm deep, the mean reduction in flooding duration was 5.4% (ranging from 1.8% in St. Simons Sound to 9.6% in Barataria Bay). Flooding durations for water >0 and >5 cm deep were highly correlated ($p<0.001$, $r=0.94$). Interannual variability in flooding was generally high at sites in the western GoM and low in Georgia and the Carolinas (Fig. 3). Seasonal patterns in flooding duration generally showed the same trend among all sites, with the lowest flooding during winter, increasing through spring and summer, to the longest flooding durations in the fall (Fig. 4). There was a distinct geographic split in temporal variability in flooding duration. Marshes in the northern GoM showed much greater variability among seasons and among years than marshes along the Atlantic coast (Fig. 4).

Marshes with the lowest flooding durations generally had the highest flooding frequencies. From Florida to Cape Hatteras, the marshes were predictably flooded by regular semidiurnal tides, and the edge was inundated approximately twice a day (Fig. 3). In contrast, most GoM marshes with high flooding durations had mean flooding frequencies less than once a day, confirming the dominance of meteorological and climatological forcing in these systems (Rozas 1995).

We calculated the flood area index for 2008 (Fig. 5), and the geographic pattern was generally similar to the flooding duration for that year. Mean values were highest in Aransas Bay, Cedar Key, and Pamlico Sound. Lowest values were in Georgia, the lower Carolinas, Louisiana, and Mississippi. There was a positive linear relationship between flooding duration in 2008 and the flood area index ($p<0.001$, $R^2=0.68$).

The mean daily access distance was calculated for 2008 and ranged from <1 m in Aransas Bay to 87 m in Chicopit Bay. The geographic pattern for access distance (Fig. 5) was generally related to flooding frequency, but the large access distance values at Chicopit Bay and Cedar Key (47 m) appeared to be outliers in this relationship. If these values were omitted, there was a significant positive and linear relationship between flooding frequency in 2008 and access distance ($p<0.001$, $R^2=0.79$).

We examined relationships among tidal datums, elevation of the marsh edge, and our flooding metrics. As reported previously by McKee and Patrick (1988), there was a strong positive linear relationship between the mean range of tide (MN, difference between mean high water and mean low water [MLW]) and the elevation of the marsh edge in relation to MLLW or MLW (Fig. 6). The relationship is particularly tight for sites with the edge above 0.4 m MLW and MN >1 m, and for these marshes, the flooding duration is similar among sites (between 55% and 60%; Figs. 7 and 8). Flooding frequency at these sites matches the predicted frequency of the semidiurnal high tides. The sites in regions with lower edge elevations and smaller tidal ranges showed strong relationships between these values and our flooding indices. Flooding duration declined and flooding frequency increased with increasing edge elevations and MN (Figs. 7 and 8).

We used the mean difference between nekton density (juvenile brown shrimp, white shrimp, and blue crab) in marsh and open water as an index of habitat selection, and this value was positive for all species and locations examined, except for blue crabs in Charleston Bay. This selection index for marsh was positively related to flooding duration (Fig. 9), and there also was a positive linear relationship between the selection index and our flood area index for 2008 ($p=0.010$, $R^2=0.54$). There was a negative linear relationship between flooding frequency and the selection index ($p=0.010$, $R^2=0.54$) and between access distance and the index ($p=0.019$, $R^2=0.47$).

Fig. 2 Elevation profiles for the 15 marshes included in this study. Relative elevations on the seven transects in each marsh were standardized to be zero at the marsh edge. *Error bars* (±1 standard error) represent variability in elevation among transects
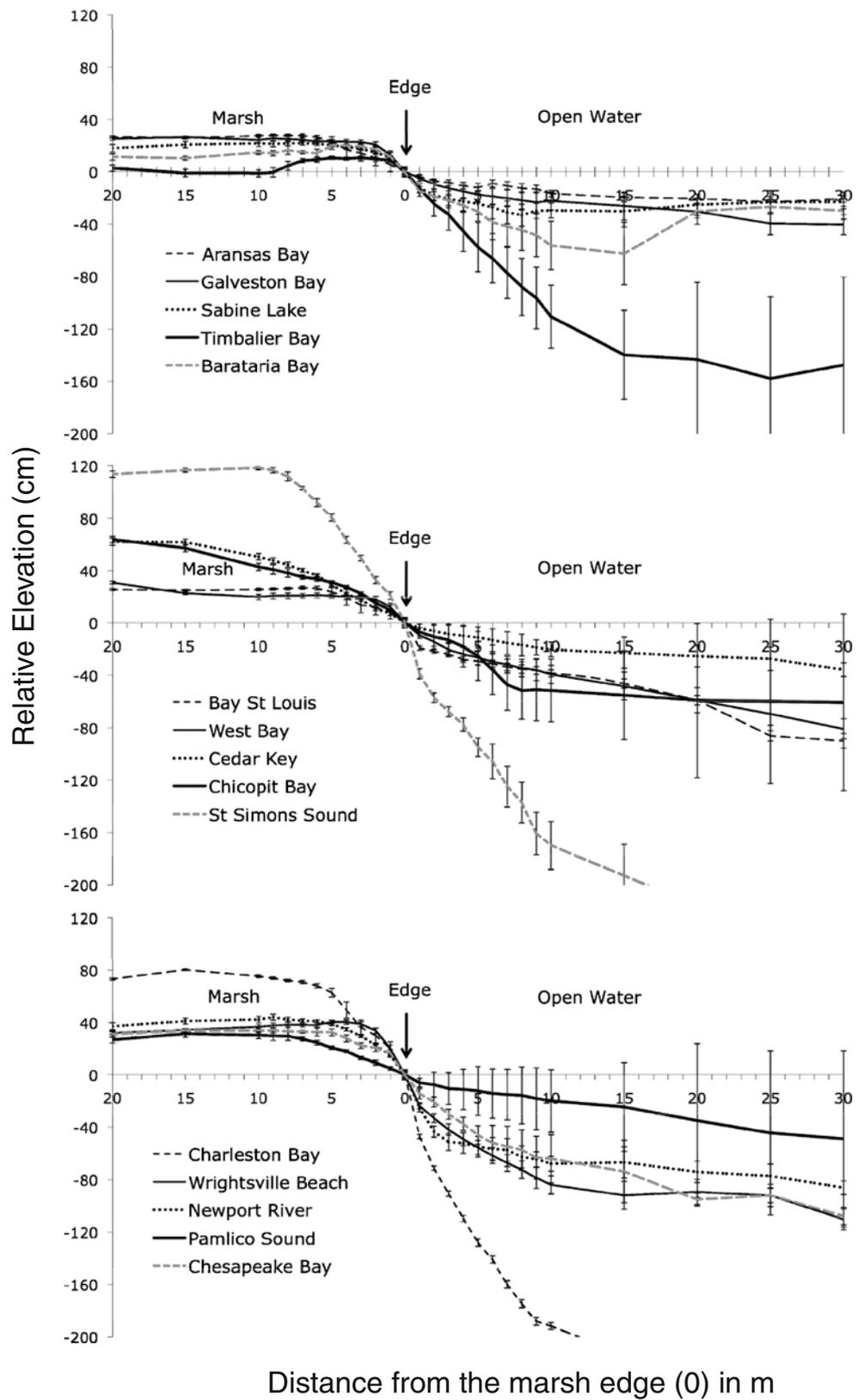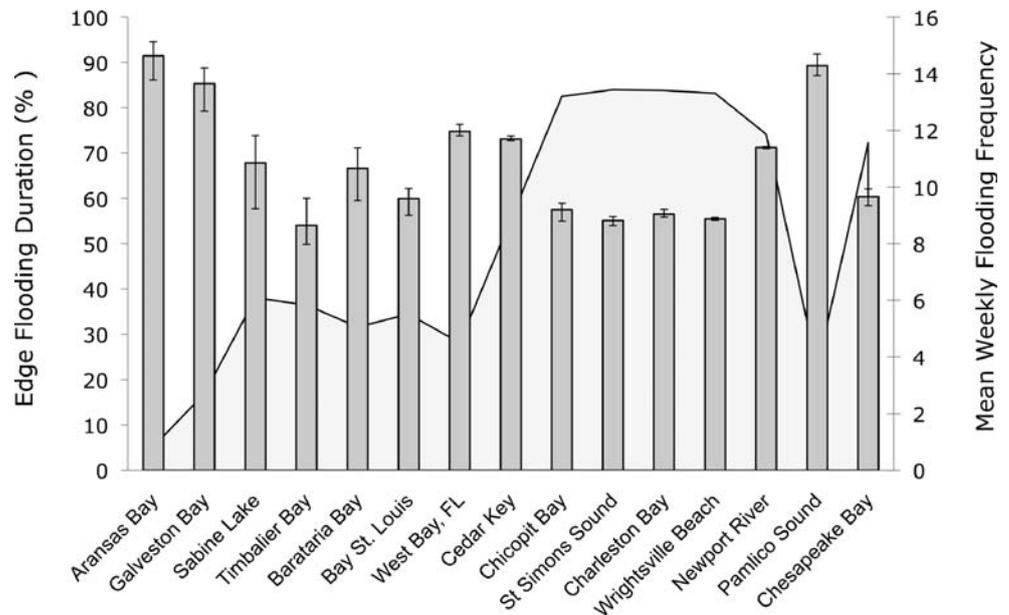
Fig. 3 Basic tidal metrics of flooding duration and frequency at the 15 marshes. *Bars* represent the mean flooding duration for the years 2006–2008 or the percentage of time that there was water over the marsh edge. *Error bars* show the range over the 3 years. The *line graph in the background* is the mean weekly frequency that the marsh edge was flooded

Discussion

The availability of the marsh surface for direct use by nekton is controlled by flooding patterns, and the metrics we measured show that access to the marsh edge in the US varies substantially across the geographic range from Texas to Virginia. Patterns of both marsh slope and elevation varied widely among the marshes we examined, even within the GoM. Flooding duration at the marsh edge was generally highest in the GoM compared with Atlantic coast marshes, but low flooding values were measured in Louisiana marshes and high values in Pamlico Sound. Both spatial and seasonal variability in flooding duration

appeared greater in the GoM compared with the Atlantic coast. Flooding frequency, measured as the number of times that tidal water flooded the marsh edge in a week, was negatively related to flooding duration. We also calculated a flood area index and an access distance, and while these additional metrics measure other characteristics of marshes and tidal flooding that may be related to nekton value, they were generally correlated with the more basic metrics of flooding duration and flooding frequency.

Spatial and seasonal patterns in marsh flooding highlight regional differences in the processes driving coastal water levels. In the GoM, meteorological and climatological events regularly override astronomical tides to regulate marsh flooding

Fig. 4 Seasonal and annual variability in marsh edge flooding duration (>0 cm deep at the marsh edge). Mean values are shown for spring (March–May), summer (June–August), fall (September–November), and winter (January–February, +December) in 2006–2008
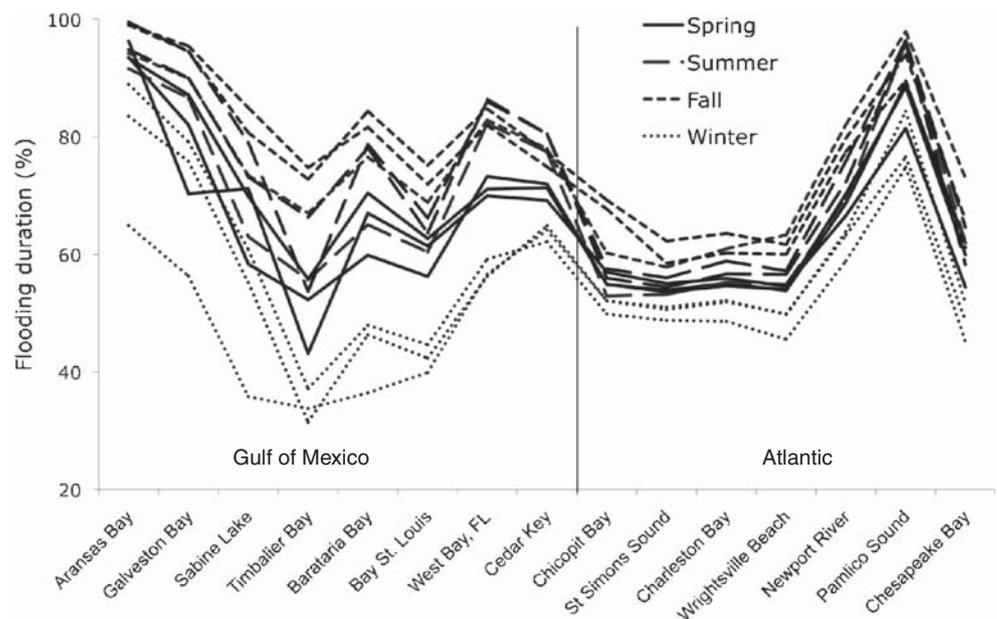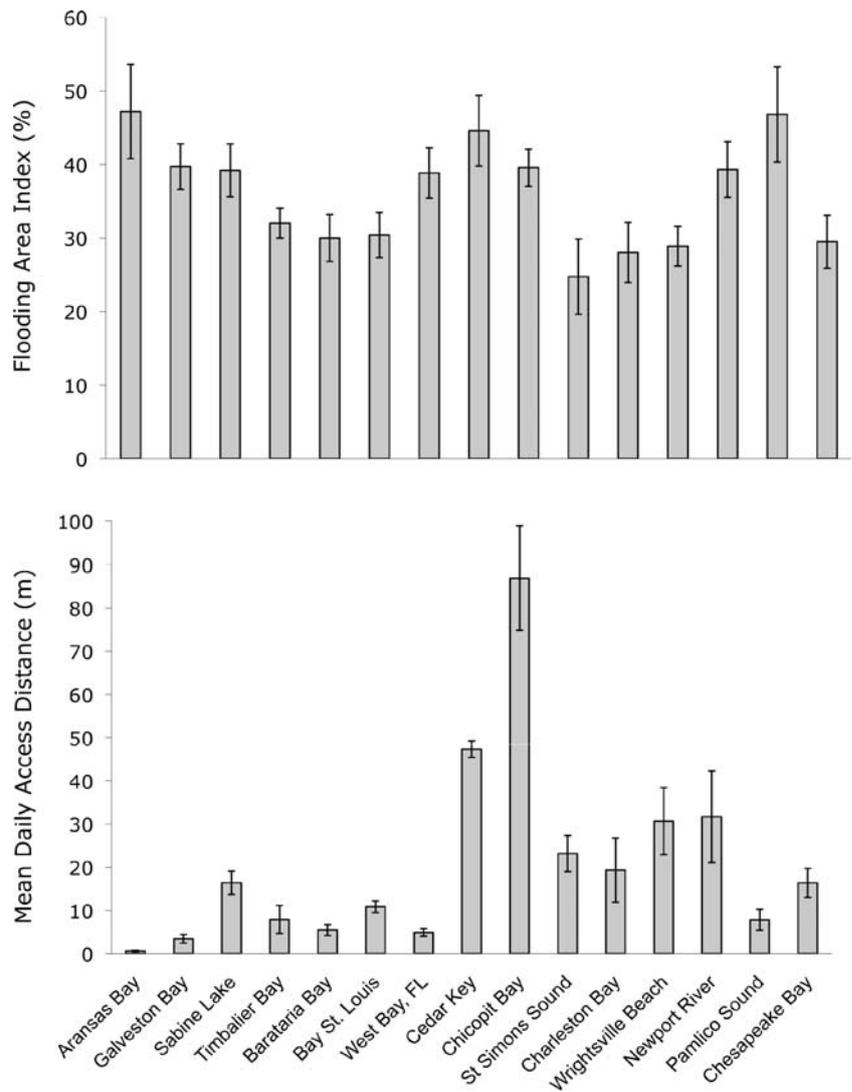
(Childers et al. 1990; Rozas 1995). As a consequence, there is considerable spatial and temporal variation in marsh flooding

at these sites, with the duration and frequency of flooding much more unpredictable over short time scales of days to
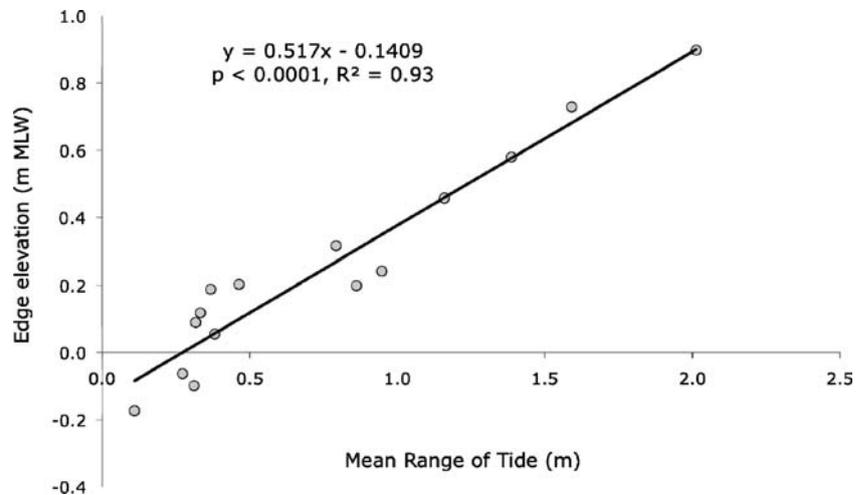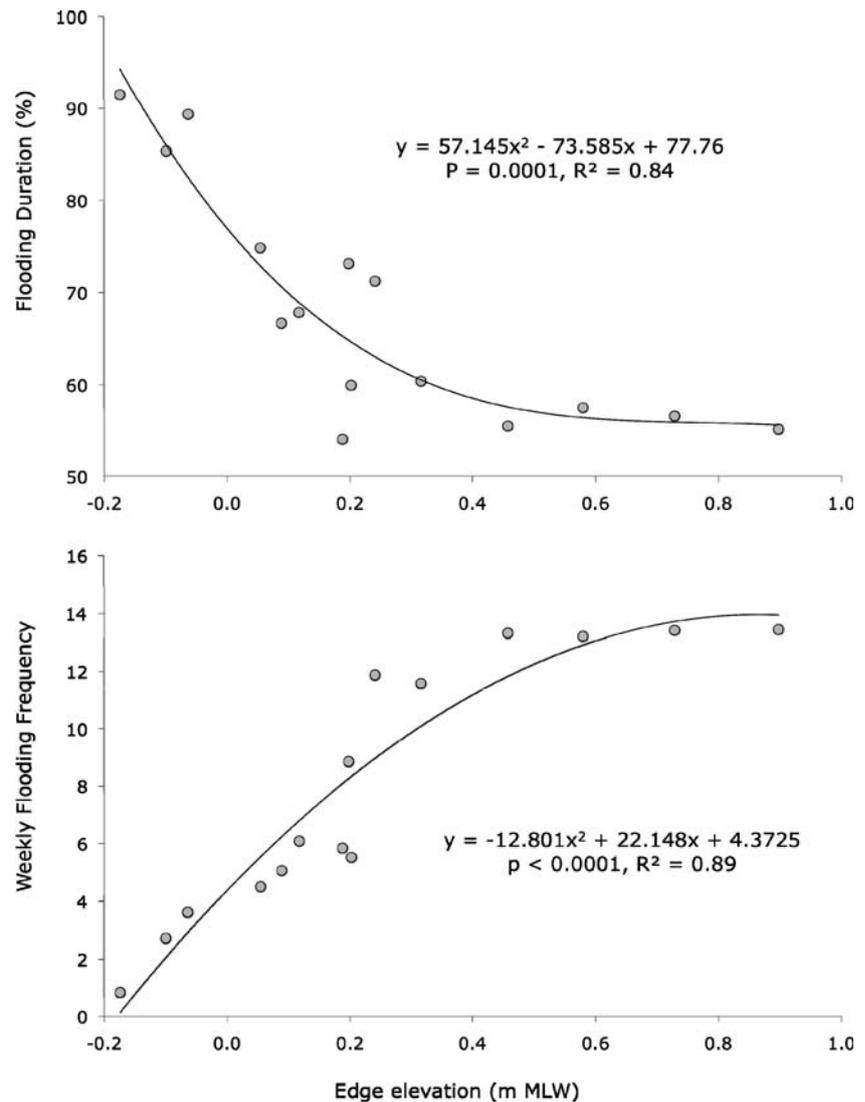
$$y = 0.517x - 0.1409$$
$$p < 0.0001, R^2 = 0.93$$

Fig. 7 The relationship between the elevation of the marsh edge in relation to MLW and the flooding duration (*top panel*) and flooding frequency (*bottom panel*) in 2006–2008. Flooding duration is the mean percentage of time that the marsh edge was flooded >0 cm. Flooding frequency is the mean number of times that water flooded the marsh edge >0 cm each week. Regressions developed to describe relationships should not be extrapolated out of this data range

$y = 57.145x^2 - 73.585x + 77.76$
$P = 0.0001, R^2 = 0.84$

$y = -12.801x^2 + 22.148x + 4.3725$
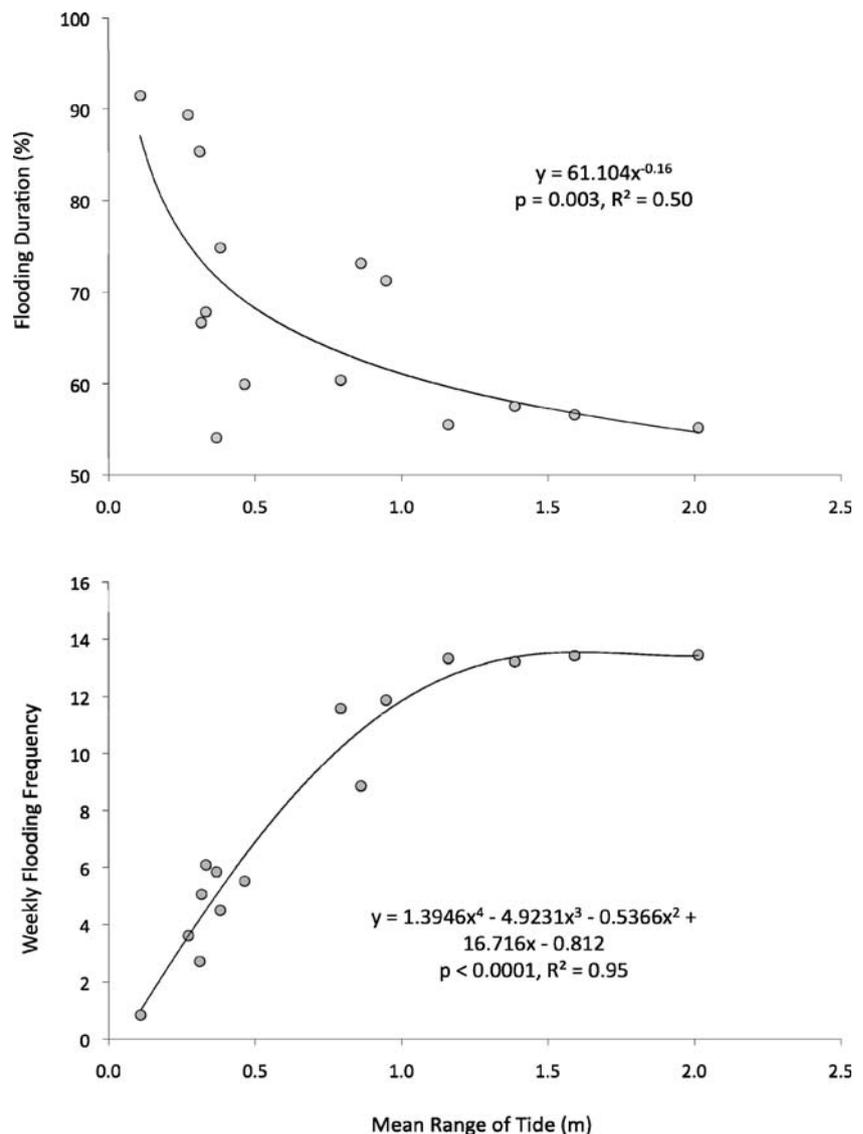$p < 0.0001, R^2 = 0.89$

Edge elevation (m MLW)

weeks. Along the Atlantic coast where the tide range is >1 m, marsh flooding appears to be primarily driven by astronomical tides, following predictable cyclical flooding patterns with minimal seasonal or annual variation. Edge elevations at these sites are such that flooding duration is similar among sites, and the marsh is flooded on most high tides.

While our study focused on comparing flooding dynamics in saline marshes across a broad geographical scale, variability of marsh edge flooding within bay/estuary systems also can be high (Rozas and Zimmerman 2000). Inferences about the flooding metrics reported here should be restricted to marshes in the lower bay because our marsh selection process was designed to provide comparable sites among regions and required proximity to active NOAA tide gages, which were located mainly in lower estuaries. While we measured some of the variability in marsh edge elevation and flooding by randomly locating transects along a 1-km shoreline, this variability is likely low in

comparison with the variability expected within the broader estuarine systems studied. Comparisons of our marsh flooding values with others in the literature can give us some indication of how well these values reflect overall marsh flooding in the system, but such comparisons are complicated by the location of measurements in relation to the marsh edge (based on our definition), the time period that observations were made (e.g., the year or season), the shoreline energy, the presence of restrictions to tidal exchange, and perhaps the marsh age. Flooding of the marsh edge reported in the literature may be underestimated if the defined location of the edge is inland and at a higher elevation than the edge defined in our study.

For Texas marshes, our flooding values generally agree with those from other studies. In Aransas Bay, Rozas and Minello (1998) reported that marsh edge habitat was flooded 87.3% of the time in 1993–1994. In Galveston Bay, Minello and Webb (1997) measured flooding of marsh edge habitat

in five marshes that ranged from 74% to 80%, and Whaley and Minello ([2002](#)) measured marsh edge flooding near our Galveston Bay marsh in 1995 to be around 75%. Rozas and Zimmerman ([2000](#)) reported that *S. alterniflora* marsh edge habitat in lower Galveston Bay was flooded around 66% of the time in 1993 and 1994; they also measured much lower flooding of a marsh in the upper bay (46%).

In coastal Louisiana, Sasser ([1977](#)) reported an average annual flooding percentage of 54% for *S. alterniflora*, but flooding of edge marsh was not specified. Rozas and Reed ([1993](#)) measured annual flooding of low-elevation hummocky *S. alterniflora* marsh in Terrebonne Bay, and flooding duration over the years 1987 to 1991 was around 52%. In Barataria Bay, Baumann ([1987](#)) reported annual flooding of saline marsh to be 50%, and the lowest marsh surface elevation examined by Reed and Cahoon ([1992](#)) was flooded 53% of the time in 1988.

We found few comparable measures of marsh edge flooding in the literature for Atlantic coast marshes. Kneib ([1993](#)) reported that the lowest elevation for *S. alterniflora* on Sapelo Island, GA was 98 cm MLW, similar to the 90 cm that we recorded at St. Simons Sound; he recorded flooding durations but at experimental marsh sites with elevations of 179 and 197 cm MLW. Annual flooding of a low marsh site in the Virginia Coastal Reserve, just north of our lower Chesapeake Bay marsh, was flooded 60% of the time (Christiansen et al. [2000](#)). Redfield ([1972](#)) concluded that *S. alterniflora* in Massachusetts could not survive if flooded more than 55% of the time. Chapman ([1960](#)) reported that the lower limit of *S. alterniflora* growth was at MSL in the GoM, and this elevation decreased with increasing latitude. Our data indicate that these generalities about the lower limit of growth are incorrect.
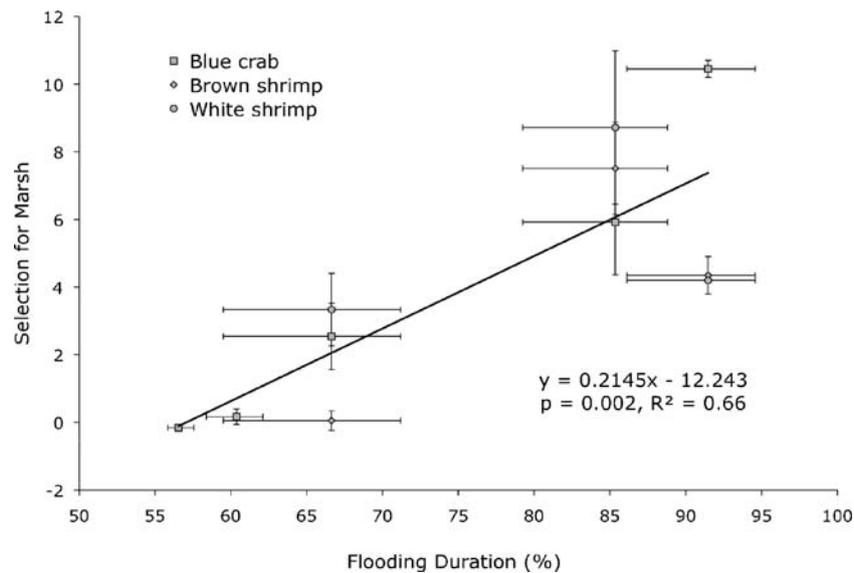
Fig. 9 The relationship between mean flooding duration and a mean index of selection for marsh edge vegetation by juvenile blue crab, brown shrimp, and white shrimp. Available data were from Aransas Bay, Galveston Bay, Barataria Bay, Charleston Bay, and Chesapeake Bay. The selection for marsh index is calculated by subtracting a mean density in open water from a mean density in flooded marsh, thus positive values indicate selection for marsh. *Vertical error bars* represent ±1 standard error from multiple measures of the index. *Horizontal error bars* show the range in flooding durations over the 3 years examined (2006–2008). The regression line is based on all 11 means shown

Despite the limited spatial extent of sampling used to represent a region in our current study, our edge elevations and flooding durations agree well with previously published values. In addition, we found the same strong relationship between edge elevation and tidal range reported by McKee and Patrick (1988). This close relationship with tidal range and the broader regional patterns of tidal range (Rozas 1995) support our conclusion that the flooding metrics we measured are regionally representative.

There is substantial evidence supporting the conclusion that access to salt marsh habitats affects productivity of decapod crustaceans such as blue crabs and penaeid shrimps. Turner (1977) identified a positive relationship between the amount of wetlands and shrimp production, and the mechanisms behind this relationship involve tidal flooding and the amount of marsh edge (Zimmerman et al. 2000; Minello et al. 2008; Roth et al. 2008). Annual and seasonal variability in flooding duration among our marsh sites was highest in the GoM and may be related to fishery production. Childers et al. (1990) showed that annual variability of marsh flooding and shrimp production in Barataria Bay was correlated with El Nino–Southern Oscillation events. Morris et al. (1990) also reported a weak relationship between annual water levels and shrimp landings.

In Texas, densities of juvenile nekton such as penaeid shrimps, blue crabs, spotted seatrout, and red drum are relatively high in marsh edge habitat (Minello 1999; Stunz et al. 2002; Neahr et al. 2010), and these high densities may be associated with the high flooding durations reported for these marshes. On a broader geographic scale, the data for blue crab, brown shrimp, and white shrimp suggest a positive relationship between selection for marsh habitat and flooding duration, but conclusions based on limited data from only five estuarine systems should be viewed with caution. Interactions with subtidal habitats such as seagrass may affect marsh value (Irlandi and Crawford 1997), and the presence of subtidal SAV or oysters may alter marsh selection patterns (Howe and Wallace 2000; Heck et al. 2001; Rozas and Minello 2010; Stunz et al. 2010) and complicate relationships with tidal flooding. Pink shrimp *Farfantepenaeus duorarum* in the Florida Panhandle do not appear to select for marsh when seagrass is present, even when marsh flooding durations are high (Rozas et al. 2011). The regularity of marsh flooding may also affect selection of marsh edge habitat. Because of different forcing mechanisms discussed earlier, flooding of the marsh surface in much of the GoM is variable, and this lack of dependability may increase the risk of stranding for nekton penetrating far into the marsh interior and limit marsh use to areas near the edge (Gibson 1988; Kneib and Wagner 1994). Data from the Carolinas where flooding metrics appear to vary greatly over a relatively short geographic range might especially be useful in examining these interactions. Interestingly, if the relationships reported here among flooding metrics, tidal range, and marsh use are consistent, information on the value of a marsh edge habitat for nekton might be estimated simply by examining the tidal datum sheet for a nearby tide gage.

Our data on flooding variability at the marsh edge may also be useful in assessing the relative importance of factors limiting the growth of *S. alterniflora*. Waterlogging of marsh soils is generally recognized as important in determining the lowest elevation where *S. alterniflora* can survive (Mendelssohn and Seneca 1980; Mendelssohn and McKee 1988), but details of the physiological processes involved are complex (Mendelssohn and Morris 2000; Pennings et al. 2005; Colmer and Flowers 2008). Our data show, however, that at some locations *S. alterniflora* can grow while continually submerged for entire seasons. *S. alterniflora* is a clonal organism linked through subsurface rhizomes, and the effects of stressful conditions at the marsh edge may be reduced if internal ramets are healthy (Xiao et al. 2010), but most of our highly flooded marshes also had relatively flat slopes, and internal ramets would have incurred high flooding durations as well. Additional factors such as sediment type, salinity, the presence of burrowing organisms, nutrient availability, and shoreline energy can interact to affect plant growth (Mendelssohn and Morris 2000; Colmer and Flowers 2008), but the relationship between marsh edge elevation and the mean range of tide suggests a functional relationship with tidal range. Flooding duration combined with water depth may affect photosynthesis through light attenuation or other mechanisms (Pezeshki 1994). The large tidal range at St. Simons Sound, for example, causes the annual mean depth of water over the marsh edge to be much higher than at marshes with higher flooding durations but lower tidal ranges. Our data do not support the concept of a tidal subsidy effect as proposed by Steever et al. (1976) for plant production because *S. alterniflora* extends its range of growth in areas of low tidal energy.

Information on geographic variability in marsh slopes and plant flooding tolerances may be useful in assessing potential impacts of sea level rise (SLR) on salt marshes and the nursery support they provide for fishery species. While factors that affect the ability of marshes to alter their elevation and compensate for SLR are being investigated (Reed 2002; Morris et al. 2002), compensation may not be possible at high rates of SLR and marsh survival might depend solely on the slope of the marsh surface and the amount of edge. For example, a rapid rise of 30 cm in sea level will flood all of the 20-m marsh transects at our western GoM sites. Combined with the large amount of edge in the region, marsh loss here is expected to be high unless migration inland is possible. Increased fragmentation and flooding likely provide short-term but unsustainable benefits for fishery species, but the long-term consequences of marsh loss will negatively affect fisheries dependent upon marsh systems (Zimmerman et al. 1991, 2000). In contrast to marshes in the western GoM, a similar rise in sea level of 30 cm in marshes with relatively steep slopes

(e.g., Cedar Key, Chicopit Bay, St. Simons Sound, or Charleston Bay) would only result in a few meters of lost marsh edge.

Our data also have implications for salt marsh restoration projects. When salt marshes are being created as habitat for nekton such as blue crabs and penaeid shrimps, estuarine systems where marshes can withstand high flooding durations should be targeted. These systems can be identified by tidal datums. In addition, our data can provide information about the proper elevation for planting of *S. alterniflora* in restoration projects. While planting elevations are generally transferred from a nearby marsh, this information is not always available. Under such conditions, the lowest planting elevation could be determined from the tidal datums of MLW and tidal range. Planting elevations based on NAVD88 do not appear dependable.

Information on variability in the nursery function of estuarine habitats and ecosystems is important for directing and prioritizing habitat protection and restoration efforts. While salt marshes are generally recognized as essential habitats for many juvenile fishery species, geographic differences in flooding patterns and in the use of the marsh surface indicate that marshes can be quite diverse in supplying this support function. We need to understand how adjacent habitats and changing environmental conditions affect the nursery value of salt marshes and how this function varies over broad geographic scales.

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