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Growth and Reproduction of *Ruppia maritima* in the Northern Gulf of Mexico

TAMARA M. MCGOVERN

Submerged aquatic vegetation (SAV) is an important component of many marine ecosystems, but SAV populations have been declining worldwide in recent years. These declines demonstrate the importance of understanding the basic population dynamics (e.g., patterns of growth, reproduction, and recruitment) of SAV species. In this study, I present baseline data on population dynamics for *Ruppia maritima* in the northern Gulf of Mexico. I documented patterns of growth and biomass allocation, allocation to reproduction, and seed density in the sediment at two depths within four sites near Mobile Bay. There was significant heterogeneity in patterns of biomass allocation, reproductive output, and the potential for recruitment across sites. The effects of depth on the biomass and reproductive variables varied according to site. Strong correlation between seed production and seeds present in the sediment suggests that populations may be relatively closed, which would have implications for management.

Submerged aquatic vegetation (SAV) is an important component of many marine ecosystems, but SAV species have been declining worldwide in recent years (reviewed in Short and Wyllie-Echeverria, 1996; Hemminga and Duarte, 2000). These declines have been accompanied by alteration and instability of the associated communities (Bachelet et al., 2000; Cardoso et al., 2004) as well as reduced sediment stability and increased turbidity (Louda et al., 2004).

In the face of declining SAV populations, it is critical to understand patterns of growth, reproduction, and recruitment of SAV species. Though clonal spread is common in many SAV species, sexual reproduction is the only mechanism for producing genetically diverse progeny that may be better capable of coping with diverse biotic or abiotic challenges (reviewed in Hurst and Peck, 1996). Additionally, though vegetative reproduction may be the predominant mode of colonization (or recolonization) of open substrate within and near existing SAV populations (Duarte and Sand-Jensen, 1990; Olesen et al., 2004; Rasheed, 2004), colonization of new or distant areas and the natural recolonization of extinct beds is accomplished primarily by sexual reproduction and seedling recruitment (Duarte and Sand-Jensen, 1990; Hemminga and Duarte, 2000; Olesen et al., 2004; Rasheed, 2004). The degree to which populations retain or export locally produced offspring is a critical consideration for management of threatened species (Harwell and Orth, 2002).

Ruppia maritima has a broad distribution (the Mediterranean: e.g., Bonis and Lepart, 1994; both sides of the Atlantic: e.g., Orth and Moore, 1988; Figuerola et al., 2002; the Pacific: e.g.,

Bigley and Harrison, 1986) and is common in the northern Gulf of Mexico (Eleuterius, 1987; Cho and Poirrier, 2005). Other species of SAV are also present in the northern Gulf of Mexico (e.g., *Thalassia testudinum* and *Halodule wrightii*; Eleuterius, 1987), but *R. maritima*'s broad salinity tolerance allows it to inhabit areas with heavy freshwater input such as Lake Pontchartrain (Cho and Poirrier, 2005) and the nearshore habitats around Mobile Bay (Johnson et al., 2006), making it a dominant species in many of these areas. Because *R. maritima* relies relatively more on sexual reproduction and recruitment from seed than on clonal growth and perennating structures (Verhoeven, 1979; Harrison, 1982; Dunton, 1990; Cho and Poirrier, 2005; Kahn and Durako, 2005), it is particularly important to understand the dynamics of sexual reproduction and recruitment in this species. Though Cho and Poirrier (2005) collected data on growth and reproduction of *R. maritima* from Lake Pontchartrain, the physical environment to which SAV is exposed there may be quite different to that in other SAV habitats of the northern Gulf of Mexico. For example, the average salinity in Lake Pontchartrain is 4 parts per thousand (ppt) (USGS, 2002) whereas the average salinity in Grand Bay, MS (just west of Mobile Bay and the area in which this study was conducted) is 24 ppt, (Nipper et al., 2010). This study was therefore designed to provide important information on *R. maritima* in a portion of its range and under environmental conditions where its reproductive ecology has previously not been examined.

The specific objectives of this study were to provide baseline data on patterns of growth and

Fig. 1. Map of study sites.

reproductive allocation of *R. maritima* at four sites near Mobile Bay. In addition to data on growth and reproduction, I simultaneously collected data on the presence of seeds in the sediment to determine the relationship between local production and the potential for sexual recruitment. I also present data on recruitment potential for 11 additional sites in the northern Gulf of Mexico based on single samples at the end of the reproductive season. This preliminary data will be useful in identifying important aspects of reproductive ecology and population dynamics that need to be further investigated as well as potential source populations that should be protected.

Study species.—*Ruppia maritima* is considered to be an opportunistic, weedy species (Dunton, 1990; reviewed in Kantrud, 1991; Cho and Poirrier, 2005) and is known to be able to tolerate a broad range of temperatures and salinities (reviewed in Kantrud, 1991; Lazar and Dawes, 1991; Cho and Poirrier, 2005). It has a shallow, weak root system (reviewed in Kantrud, 1991) and its primary nutrient repository is the aboveground leaves (Pulich, 1989; Dunton, 1990). It has been reported to flower vigorously (reviewed in Kantrud, 1991; Cho and Poirrier, 2005) from late spring until early fall (Cho and Poirrier, 2005). *Ruppia* is monoecious and is

capable of self-fertilization (reviewed in Kantrud, 1991). Seeds germinate from the winter through early spring and recruitment is frequently from seeds (Cho and Poirrier, 2005). Seeds can apparently remain dormant and viable in the sediments for several years and germinate when conditions are appropriate, though more deeply buried seeds (reviewed in Kantrud, 1991; Bonis and Lepart, 1994) and older seeds (Bonis and Lepart, 1994) are less likely to germinate. The species acts much like an annual plant in many years, although it can also regenerate in the spring from overwintering rhizomes (Dunton, 1990; Cho and Poirrier, 2005).

METHODS AND MATERIALS

Growth, reproduction and recruitment potential.—I monitored growth, reproduction, and the potential for recruitment in *R. maritima* at four sites in the Northern Gulf of Mexico (Fig. 1; GPS coordinates available upon request). Sites included Bayou le Batre, AL (BB); Pointe aux Pines, AL (PP); Bayou Heron, MS (HE); and the sheltered side of a small island near Bayou Heron (IS) (the latter two sites both located within the Grand Bay National Estuarine Research Reserve, MS). Sampling commenced in mid-March 2006 and was performed on a biweekly basis through mid-September 2006,

TABLE 1. Peak estimates for total biomass, root biomass, and aboveground or total shoot biomass in g/m² (mean estimates in parentheses) as well as peak and mean densities of seeds in the sediment (number/m²) in the four sampled populations.

Site ^a	Total biomass peak (mean)	Root biomass peak (mean)	Shoot biomass peak (mean)	Sediment seed density peak (mean)
PP	107.61 (29.05)	34.19 (11.98)	77.32 (17.07)	1,193 (324)
BB	87.64 (18.26)	24.38 (8.44)	63.27 (10.00)	2,187 (517)
HE	112.40 (24.64)	37.27 (8.53)	90.38 (16.77)	17,296 (3,480)
IS	327.31 (7.53)	35.11 (12.77)	304.56 (39.22)	31,809 (10,154)

^a Abbreviations: PP, Pointe aux Pines, AL; BB, Bayou le Batre, AL; HE, Bayou Heron, MS; IS, the sheltered side of a small island near Bayou Heron.

encompassing the growth and reproductive season documented by Cho and Poirrier (2005) in Lake Pontchartrain, LA.

Because light is an important determinant of SAV productivity (Short and Wyllie-Echeverria, 1996), I sampled in both shallow (30–60 cm) and deep (>100 cm) portions of each site on each date, collecting three paired SAV and sediment cores at each depth using methods similar to those in other studies on *R. maritima* in the Gulf of Mexico (see, e.g., Pulich, 1985; Dunton 1990; Cho and Poirrier, 2005). The SAV cores were collected with a 15-cm-diameter polyvinyl chloride (PVC) corer to a depth of approximately 15 cm. As much sediment as possible was removed in the field by wet-sieving through a 1-mm mesh screen. Plants were placed in water in resealable 1-gallon bags for transport back to the lab and samples were frozen until processing. Processing involved removing epiphytes and epifauna and separating the plant material into three major components: roots/rhizomes, nonreproductive shoots, and reproductive shoots. Because the reproductive shoots bear leaves as well as strictly reproductive structures, allocation to reproduction and photosynthetic capabilities could be confounded by simply measuring allocation to reproductive shoots. I therefore subdivided reproductive shoots into vegetative and strictly reproductive structures for samples from May through September (the period during which there was some investment in reproductive shoots at sites). Material that was considered strictly reproductive in function included inflorescences, seeds, and the pedicels bearing them. I counted the number of seeds before adding them to the strictly reproductive material for estimation of biomass (these seeds will hereafter be referred to as attached seeds). I dried all the plant components for a minimum of 2 d at 80°C in preweighed foil containers and obtained dry weights to determine the relative allocation to each component. For each sampling date, I calculated the average biomass of the various components and the average number of attached seeds from the three samples at each depth at each site.

Because much of the regrowth of *R. maritima* in the spring is likely to come from seed germination rather than vegetative growth (Verhoeven, 1979; Harrison, 1982; Dunton, 1990; Cho and Poirrier, 2005; Kahn and Durako, 2005), the number of seeds present in the sediment should be a major determinant of recruitment. I therefore used the density of seeds in the sediment as a proxy for the recruitment potential. Sediment seed densities were determined by examining sediment cores taken in conjunction with the SAV samples described above. Using a 7.5-cm-diameter PVC corer to a depth of approximately 15 cm (below which seeds are unlikely to germinate, Kantrud 1991), I collected a sediment sample within 1 m (and generally within 0.5 m) of the paired SAV sample. Samples were returned to the lab in resealable 1-quart bags and frozen until processing. Samples were divided lengthwise, and one-half of the sample was weighed and wet-sieved through a 0.5-mm mesh screen. (Initial trials using multiple mesh sizes determined that all seeds would be retained by use of 0.5-mm mesh.) I examined the material retained on the 0.5-mm mesh using a dissecting scope and counted the seeds. In addition to the four sites sampled from March through September, I sampled SAV and sediment seed densities at 11 additional sites in September in order to estimate the relationship between plant density and recruitment potential at a greater number of sites.

Effects of site and depth.—To compare patterns of biomass allocation and number of attached seeds between sites, I used two-way analyses of variance (ANOVAs) with site and depth as factors. Variables were averaged across samples at each depth and data were log transformed (except for attached seeds, which was square-root transformed) to meet the assumptions of the analyses. Because the interaction terms were significant for every dependent variable analyzed (see Table 1), I also conducted paired t-tests with sequential Bonferroni corrections (Rice, 1989) between shallow and deep regions of each site

Fig. 2. Biomass of various plant components (in g/m^2) and the number of attached seeds in shallow (S) and deep (D) regions of (A) Pointe aux Pines, AL; (B) Bayou le Batre, AL; (C) Bayou Heron, MS; and (D) the sheltered side of a small island near Bayou Heron. The solid portion of bar represents allocation to roots and rhizomes. The hatched portion of the bar represents allocation to nonreproductive shoots. The open portion of the bar represents the portion of the flowering shoots that is not strictly reproductive. The grey portion of the bar represents the strictly reproductive portion of the reproductive shoots. Because this last biomass component was typically small and is not visible in all weeks, asterisks designate the dates on which there was a nonzero allocation to strictly reproductive biomass. The secondary axis shows the number of attached seeds (indicated by the open circles). Solid lines and dashed show change in numbers of attached seeds at shallow and deep regions of the sites, respectively.

for each variable to determine if growth and reproduction declined in deeper water.

Relationship between reproductive allocation and recruitment potential.—To examine the relationship between reproduction and the potential for recruitment, I regressed sediment seed densities against total plant biomass, the biomass of reproductive shoots, the biomass of strictly reproductive material, and the number of attached seeds (all regressions on transformed data). Because there were significant site and site by depth effects (see below), variables were averaged within depth and within site across sampling periods, generating eight data points. To examine the potential for recruitment at other sites in the region, I plotted the sediment seed densities against total *R. maritima* biomass for 11 additional sites sampled only in September along with the eight points from the focal sites (on which regressions were based).

RESULTS

Growth, reproduction and recruitment potential.—Total biomass from all locations and both depths ranged from 0.95 to 327.31 g/m^2 (mean = 31.10 g/m^2). Root biomass ranged from 0.53 to 37.27 g/m^2 (mean = 10.54 g/m^2) and above-ground or total shoot biomass ranged from 0.41

to 304.56 g/m^2 (mean = 20.71 g/m^2). The peak and mean biomass values for total plant biomass, root biomass, and aboveground biomass are shown for each population in Table 1.

Seasonal trends in the biomass of all plant components as well as the numbers of attached seeds at each site are shown in Figure 2. At three of the four sites (BB, HE, IS), the biomass of nonreproductive components was low at the beginning of the sampling period, but began to increase in early spring. Biomass peaked in early summer, then decreased as plants senesced. Toward the late summer, plant health visibly decreased. Aboveground portions were heavily epiphytized, and the roots had darkened and were no longer anchoring the plants into the sediment.

The one exception to the pattern described above was at PP (Fig. 2A). At this site, biomass associated with nonreproductive plant components was relatively higher at the beginning of the sampling periods. In the shallow portion of this site, nonreproductive biomass eventually increased to a level similar to that observed for other sites, and followed the same pattern of senescence. In the deeper portion of the PP site, nonreproductive biomass never increased beyond its initial level.

The biomass of reproductive shoots at all four sites followed the seasonal patterns observed for

Fig. 3. Number of seeds per gram in the sediments in (A) shallow and (B) deep regions of Pointe aux Pines, AL (circles); Bayou le Batre, AL (triangles); Bayou Heron, MS (squares); and the sheltered side of a small island near Bayou Heron (diamonds).

nonreproductive biomass at the BB, HE, and IS sites: there was an increase in biomass beginning in midspring, a peak in early summer, and a decrease as plants senesced (note change in axis values between sites). The biomass of strictly reproductive material (inflorescences and seeds) was always small and peaked slightly earlier than the biomass of reproductive shoots (late spring at IS and HE, slightly later at PP; BB had virtually no biomass associated with strictly reproductive material). The biomass of strictly reproductive material declined to 0 by early to mid-July even though there continued to be biomass in residual flowering shoots. The number of attached seeds, like the biomass of strictly reproductive material, peaked in early summer then declined to 0 by late June (BB, HE, IS), though the peak and only observations of attached seeds were later at PP.

The number of seeds per gram of sediment ranged from 0 to 0.979 across all samples (mean = 0.088 seeds/g). The peak and mean number of seeds in the sediment (estimated seeds/m² for comparison with other studies) are shown for each population in Table 1. Unlike the patterns observed for the biomass components and the number of attached seeds, there was no significant seasonal peak in the density of seeds present in the sediment (Fig. 3).

Effects of site and depth.—In two-way ANOVAs on the biomass components and numbers of attached seeds, site differences were significant for allocation to reproductive shoots, strictly reproductive biomass, and the number of attached seeds, but nonsignificant for allocation to roots/rhizomes and nonreproductive shoots (Table 2). The effect of depth was nonsignificant for all variables but the interaction term was significant for every variable except attached seeds (Table 2), indicating that plants were not responding consistently across depth at all sites (Fig. 4). When paired t-tests were conducted on each variable from shallow and deep regions within each site, some differences emerged despite reduced sample sizes. At PP and BB, allocation to the various biomass components and the number of attached seeds tended to be greater in shallow water, whereas the reverse trend was observed at HE and IS (Table 3). At the sites with the largest number of paired samplings across depth (PP and HE, both with 11 dates with both shallow and deep samples), differences were either significant ($P < 0.05$) or marginal ($P < 0.1$) for many comparisons (see Table 3).

There were significant effects of site and a site by depth interaction in the two-way ANOVA on sediment seed densities (Table 2). Within-site t-tests also showed a significant effect of depth at

TABLE 2. Results of two-way ANOVAs with site, depth, and their interaction as factors. Shown are the F ratios and P values associated with each factor. All tests had 1 d.f. ANOVAs were run separately for four biomass components (roots/rhizomes, nonreproductive shoots, reproductive shoots [including vegetative and reproductive material], and strictly reproductive biomass, all shown in grams) as well as the number of attached seeds and the density of seeds in the sediments (number/g). Data on strictly reproductive biomass and the number of attached seeds are available for fewer sampling periods and analyses were therefore run on fewer data points.

Variable	Site (F/P)	Depth (F/P)	Site $\times$ depth (F/P)
Root/rhizome biomass	2.206/0.089	0.010/0.921	1.559/0.004
Nonreproductive shoot biomass	1.022/0.384	0.615/0.430	2.822/0.040
Reproductive shoot biomass	22.103/<0.001	0.458/0.500	6.317/<0.001
Strictly reproductive biomass	22.196/<0.001	0.015/0.902	9.836/0.003
Attached seed numbers	22.904/<0.001	0.067/0.796	1.892/0.134
Sediment seed densities	214.336/<0.001	0.679/0.411	7.963/<0.001

all but one site (Table 3), though the trend was different at HE and IS (where deep areas of the site had more seeds in the sediment) than at PP and BB (where shallow areas had more seeds in the sediment, Fig. 4)

Relationship between reproductive allocation and recruitment potential.—There were positive relationships between the density of seeds in the sediment and total plant biomass ($r^2 = 0.612$, $P = 0.022$), the biomass of reproductive shoots ($r^2 = 0.457$, $P = 0.066$), strictly reproductive

biomass ($r^2 = 0.766$, $P = 0.004$), and the number of attached seeds ($r^2 = 0.501$, $P = 0.049$; the last shown in Fig. 5).

Though I do not have data from the additional 11 sites from the peak reproductive season, samples gathered in September varied in the presence of *R. maritima* and sediment seed densities. There were six sites at which *R. maritima* was absent, three of which had no seeds present in the sediment, three of which had sediment seed densities similar to that seen at PP and BB throughout the season (Fig. 6). There

Fig. 4. Effects of site and depth on biomass components (in g/m²), seed production, and recruitment. Shown are averages (with standard errors) across sampling dates for (A) root biomass, (B) the biomass of nonreproductive shoots, (C) the number of attached seeds, and (D) the number of seeds per gram in the sediment. The biomass of flowering shoots and strictly reproductive material are not shown, but exhibited a similar pattern to that shown for attached seeds in panel C.

TABLE 3. Results of paired t-tests between shallow and deep regions with sites for roots/rhizomes, nonreproductive shoots, reproductive shoots (including vegetative and reproductive material), and strictly reproductive biomass as well as the number of attached seeds and the density of seeds in the sediments. Data on strictly reproductive biomass and the number of attached seeds were available for fewer sampling periods and analyses were therefore run on fewer data points. Comparisons that were significant at the 0.05 level following sequential Bonferroni corrections are shown in bold.^a

Variable	PP			BB			HE			IS		
	t	P	df	t	P	df	t	P	df	t	P	df
Root/rhizome biomass	S>D -2.228	0.050	10	S>D -2.388	0.049	7	D>S 2.345	0.043	10	S>D -0.966	0.387	8
Nonreproductive shoot biomass	S>D 1.405	0.193	10	S>D -3.272 0.015 7			D>S 3.143 0.011 10			S>D -1.120	0.320	
Reproductive shoot biomass	S>D -2.833 0.018 10			S>D -1.683	0.144	7	D>S 3.821 0.004 10			D>S -0.128	0.9	8
Strictly reproductive biomass	S>D -2.310	0.074	5	S>D -1.310	0.260	5	D>S 2.256	0.090	4	D>S 0.027	0.9	4
Attached seed numbers	S>D -2.200	0.083	5	S>D -1.540	0.188	5	D>S 2.543	0.068	4	D>S 0.243	0.828	4
Sediment seed densities	S>D -3.877 0.003 10			S>D 0.601	0.527	8	D>S 3.579 <0.001 10			D>S 3.351 0.010 8		

^a Abbreviations: PP, Pointe aux Pines, AL; BB, Bayou le Batre, AL; HE, Bayou Heron, MS; IS, the sheltered side of a small island near Bayou Heron; S, shallow; D, deep.

were five sites where *R. maritima* was present, and all of these had some seeds in the sediment. The number of seeds per gram at the additional sites where *R. maritima* was present was higher ($t = 2.262$, $P = 0.007$) than at the sites without *R. maritima*.

DISCUSSION

Total biomass, root biomass, and total shoot (aboveground) biomass estimates were variable across the four sites. All but one site (IS) had lower peak biomass estimates than that reported

Fig. 5. Relationship between the number of attached seeds and sediment seed densities. Points were generated using the averages (across sampling dates) for each variable at each depth within a site. Sites are labeled as follows: Pointe aux Pines, AL (circles); Bayou le Batre, AL (triangles); Bayou Heron, MS (squares); and the sheltered side of a small island near Bayou Heron (diamonds). Deep portions of sites are represented by closed symbols, shallow portions by open symbols.

Fig. 6. Relationship between total biomass and sediment seed densities. Sites are labeled as follows: Pointe aux Pines, AL (circles); Bayou le Batre, AL (triangles); Bayou Heron, MS (squares); and the sheltered side of a small island near Bayou Heron (diamonds). Deep portions of sites are represented by closed symbols, shallow portions by open symbols. The points for shallow and deep regions of the four focal sites represent averages across sampling dates. The same relationship for the four focal sites on the final sampling dates (indicated by hatched symbols), as well as for 11 additional sites sampled at the same time (indicated with 'X's) is also shown.

by Cho and Poirrier (2005) for Lake Pontchartrain (155–489 g/m²). The estimates from this study are comparable to estimates of total biomass and root biomass for *R. maritima* from southern Texas (Pulich, 1985) and exceed estimates of shoot biomass from Canada (Harrison, 1982). The differences between studies could reflect differences in factors such as light levels, salinity, temperature, and wave energy because all of these factors are known to affect growth in various SAV species (Thursby, 1984; Pulich, 1985, 1989; Orth and Moore, 1988; Dunton 1990; Lee and Dunton 1997). Salinity is higher in the area examined in this study relative to Lake Pontchartrain (the only other area in the northern Gulf of Mexico in which *R. maritima* has been studied), and though the sites in the current study were relatively protected, they are likely to experience greater wave energy than that experienced in Lake Pontchartrain. Comparisons between this and other studies must be made with caution, however, because the results of this study are based on only a single growing season that may or may not reflect average years. Water temperature, salinity, and dissolved oxygen were intermediate in 2006 relative to other years for which there are data from the region (2003–2009; Mymobilebay, 2009) and storm activity was low (National Hurricane Center, 2009); it is not known whether the other studies were conducted in average years.

Seasonal patterns of growth and reproduction of *R. maritima* in the region near Mobile Bay were similar to those observed in other parts of this species' range (Harrison, 1982; Pulich, 1985; Cho and Poirrier, 2005). Nonreproductive biomass began to increase in the spring and peaked in early summer. By late summer, biomass generally had decreased and plants were beginning to uproot and senesce. The exception to this pattern was the PP site. Particularly at the deep region of this site (and to a lesser extent at the shallow region) there was greater starting nonreproductive biomass relative to other sites. PP is the only site of the four included in this study where *R. maritima* co-occurs with *Halodule wrightii*, a species that produces an overwintering rhizome mat. Though *R. maritima* often has population dynamics resembling that of an annual plant, recolonizing from seed every spring (Harrison, 1982; Dunton, 1990; Kahn and Durako, 2005), it can overwinter in some populations (e.g. Dunton, 1990). It is possible that the plants sampled early in the year at PP had greater starting biomass because they had overwintered there, perhaps stabilized by the *H. wrightii* rhizome mat. In the deep portion of the PP site, nonreproductive biomass increased very little relative to the initial level. Competition with *H. wrightii*, which is more common in the deeper regions of the site, may have kept the biomass of *R. maritima* low at this site relative to the three other sites. Decreased growth in seagrasses due

to interspecific competition has been reported for other species (Bando, 2006).

The density of seeds in the sediment showed no seasonal trend, perhaps reflecting a persistent seed bank and therefore a relatively stable supply of seeds for germination and recruitment. The sediment seed densities in this study, when converted to seeds/m², are generally similar to or higher than those observed for *R. maritima* in other studies (McMillan, 1985; Bonis et al., 1995; Acosta et al., 1999; Rodríguez-Pérez and Green, 2006; Porter et al., 2007), though only the study by Acosta et al. used the same sampling methodology, so direct comparisons should be made with caution.

Although the effect of site and depth in nonreproductive biomass components (root/rhizomes and nonreproductive shoots) were relatively minor and inconsistent (Fig. 4A,B; Table 2), there were strong site effects on all reproductive variables and sediment seed densities. Although depth had nonsignificant effects across site, the interactions between site and depth were significant for all but one of the measured variables (attached seeds). A comparison of shallow and deep regions within each site demonstrates the reason for these significant interactions. At PP and BB, though many comparisons were nonsignificant, there was typically greater biomass (total, root, and shoot) and more seeds, both attached to the plants and in the sediment, in shallow samples. The pattern was reversed for most variables at HE and IS, with greater biomass (reproductive and otherwise), more attached seeds, and more seeds in the sediment in deeper samples. The pattern observed for seeds in the sediments in this study is consistent with the findings of other studies that demonstrated variation between microsites (McMillan, 1985; Bonis et al., 1995). Such variation (which probably underestimates true intersite variability given the temporal and geographical sampling limitations of this study) could have important implications for the management of this species and definitely deserves further investigation.

Ruppia maritima seeds have numerous potential ways to disperse away from the site where they are produced. Seeds could potentially disperse as sediment gets redistributed during major storm events (Bell et al., 2008). Seeds may also disperse while still attached to the plant (Harwell and Orth, 2002; Bell et al., 2008). Toward late summer, whole plants uprooted and began to drift along the substrate (T. M. McGovern, pers. obs.), so the dispersal of dying vegetation bearing seeds seems particularly likely for *R. maritima* in the study area. Finally, the

common name for this species—widgeongrass—denotes the potential for dispersal by waterfowl that feed on the seeds (e.g., Figuerola et al., 2002).

The high correlations between the density of seeds in the sediment and the number of attached seeds suggests that, despite numerous avenues for transport away from the site of production, recruitment—and future *R. maritima* density—could be dependent on local reproductive output. Reed et al. (2009) demonstrated a similar correlation between reproductive structures and seed numbers in *Phyllospadix torreyi*. Seagrass canopies increase particle retention (Hendriks et al., 2010), so the presence of mature plants is likely to increase the retention of seeds as well as the sediment that may retain them even after the mature plants die back. These observations suggest that *R. maritima* populations may be relatively closed. In a genetic survey of *H. wrightii* in Galveston Bay, Travis and Sheridan (2006) also found evidence of localized recruitment, and such genetic studies are clearly warranted for *R. maritima* in the northern Gulf of Mexico to determine the extent to which seeds are dispersed vs retained.

Coupling between local reproduction and recruitment has implications for both the regional dynamics and the management of this important species. If *R. maritima* populations are relatively closed, establishment of new beds or recolonization of extinct beds would depend on proximity to existing populations and may become increasingly unlikely as populations are lost or decline in health and interpopulation distances increase. Localized recruitment would also have the effect of increasing genetic structuring of *R. maritima* populations. Lacking recruitment from other populations, effective population sizes would be smaller, increasing genetic drift and the probability of mating between related individuals. This would lead to reduced genetic variability and a potentially decreased ability to respond to environmental challenges (Micheli et al., 2005). Relatively closed population dynamics in *R. maritima* would also suggest that the protection of existing beds or establishment of new beds should be concentrated in areas conducive to flowering. Quantification of the differences in biotic and abiotic environments of the four sites discussed here was outside the scope of the current study, but studies identifying the various factors (both biotic and abiotic) that promote vigorous growth and reproduction in this species would be of great importance given the observed variability.

If we are to slow or reverse the decline of SAV species, it is critical to understand their popula-

tion dynamics and the factors influencing these dynamics. This study provides baseline information on seasonal patterns of growth and reproduction in one of the important SAV species in the northern Gulf of Mexico. Data from multiple years and additional sites are necessary to confirm the patterns reported here. However, this study suggests that sites differ in their ability to support *R. maritima* reproduction and that populations could be relatively closed. This study should therefore serve as a baseline for understanding the various factors that determine the health and maintenance of natural *R. maritima* populations.

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