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Effects of edge/interior and patch structure on reproduction in *Zostera marina* L. in Chesapeake Bay, USA

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Abstract

We examined the effects of location (patch edge vs. interior) and shoot density (individual, patchy, continuous) on reproduction in three natural and two transplanted Chesapeake Bay (USA) stands of the submerged marine angiosperm *Zostera marina* L. (eelgrass; Zosteraceae). There were no edge effects on demographic-based reproductive effort or reproductive output (propagule production), and patch structure (individual, patchy, continuous) alone never accounted for the majority of variability in any metric. Transplant site was the most important predictor of eelgrass reproduction response, and relationships among metrics were predictable within sites. Our results suggest that, in Chesapeake Bay eelgrass, environmental factors acting at a regional scale (km) have a stronger impact on reproductive investment than those at a patch scale (1–10 m). Since tradeoffs between clonal and sexual production are mediated primarily by exogenous environmental factors, site selection may be more critical than transplant configuration for producing self sustaining stands, and achieving long-term restoration success.

Keywords: Edge effects; Patch structure; Reproductive effort; Reproductive output; *Zostera marina*

1. Introduction

Reproductive effort, the amount of energy invested in the formation of gametes and their associated structures, and reproductive output, propagule production, are the most direct measures of plant fitness (Bazzaz and Reekie, 1985; Bazzaz and Ackerly, 1992). Reproductive output of a single plant can be affected by intrinsic factors, and is often directly proportional to its biomass (Aarssen and Jordan, 2001). Interpopulation variation in reproductive effort and output is affected by extrinsic factors, and can be closely correlated with population size (Bazzaz and Ackerly, 1992), with evidence from several plant species showing individual reproductive effort increases as a function of population density (Bazzaz and Reekie, 1985). Larger population numbers often correlate with more potential pollen and ovule donors (e.g. Molano-Flores and Hendrix, 1999), while, in small populations, demographic constraints can reduce gamete encounter probabilities and genetic factors such as inbreeding depression can reduce fitness (e.g. McClanahan, 1986).

Processes at the landscape scale can also affect reproductive strategies. Studies have shown that reproductive effort and output can vary from the edge to the interior of plant stands (e.g. Lovejoy et al., 1986; Graham, 2003). As a result, differences in a population's reproduction response between edge and interior habitats may hypothetically influence the overall rate of population spread. Fragmentation also affects survivorship of juveniles, with poor recruiting success of plants at the edge of stands for populations under fragmentation stress when compared to continuous stands (Jules, 1998).

We studied the effects of landscape-scale processes on reproductive strategies in *Zostera marina* L. (eelgrass; Zosteraceae), the most common temperate marine angiosperm (Moore and Short, 2006). Eelgrass is both monoecious and protogynous (Setchell, 1929), and flowering is controlled by environmental factors, including temperature, salinity, and day length (McMillan, 1976). Although outcrossing is typical in some stands, and is maintained by asynchronous flowering of males and females (Ruckelshaus, 1995), self fertilization through geitonogamy (fertilization between separate flowers on

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the same plant), or gamete exchange among clonemates is possible in this species (Ruckelshaus, 1996; Rhode and Duffy, 2004b). Reproductive effort and output vary within stands, within regions, and over time (Churchill and Riner, 1978), with the percentage of total *Z. marina* biomass allocated to reproduction ranging from 1 to 34% for perennial forms (Sand-Jensen, 1975; Jacobs, 1979; Robertson and Mann, 1984; van Lent and Verschuure, 1994). In the annual form of *Z. marina*, up to 100% of vegetative shoots develop into reproductive shoots (Phillips et al., 1983). Demographic-based metrics of reproductive effort have been used in the seagrass literature in the past. In fact, Harrison (1979) argues that no realistic biomass-based estimates of reproductive effort can be made for *Z. marina* on an individual genet basis because of high fragmentation of the rhizome that connects shoots. Flowering shoot densities have been used as a measure of reproductive effort and output in *Posidonia australis*, and *P. sinuosa* (Inglis and Lincoln Smith, 1998; Marbà and Walker, 1999), *Z. marina*, *Z. noltii*, and *Z. capricorni* (Inglis and Lincoln Smith, 1998; Laugier et al., 1999; Marbà and Walker, 1999; Meling-Lopez and Ibarra-Obando, 1999), *Amphibolis antartica* and *A. griffithii* (Marbà and Walker, 1999), *Heterozostera tasmanica* (Marbà and Walker, 1999), and *Thalassodendron pachyrhizum* (Marbà and Walker, 1999).

Eelgrass stands are composed of overlapping heterogeneous patches (mosaics) of different-aged plants. This patchiness is, in part, the result of disturbance by hydrodynamic factors (e.g. Fonseca and Bell, 1998) and bioturbation (Townsend and Fonseca, 1998). Theoretically, patchiness could affect eelgrass reproductive strategies by limiting successful pollination (Williams, 1995; but see Inglis, 2000), or increasing susceptibility of reproductive shoots to uprooting (sensu Patterson et al., 2001) from potentially different hydrodynamic regimes at the edge *versus* the middle of a stand. Increased reproductive effort or output at a patch's edge may occur as a result increased stress (Silberhorn et al., 1983; Kautsky, 1987; Conacher et al., 1994; van Lent and Verschuure, 1994; Laugier et al., 1999), or wave exposure (Fonseca and Bell, 1998). In contrast, decreased reproductive effort or output may occur as a result exposure to increased water flow (Fonseca et al., 1982) and its potential to mechanically damage reproductive shoots (Patterson et al., 2001).

In this study, we used a combination of manipulative transplant experiments and observations on unmanipulated eelgrass stands to examine reproductive strategies for five eelgrass sites in lower Chesapeake Bay. Our objectives were to (i) determine whether eelgrass reproductive strategies vary from patch edge to interior at transplant sites, (ii) determine whether patch size or structure influences eelgrass reproduction metrics, and (iii) quantify relationships between reproduction metrics from transplanted and unmanipulated eelgrass sites.

2. Methods

2.1. Transplants and unmanipulated areas

Transplants were done in October 1998 following established protocols (Orth et al., 1999). Shoots were taken from a single donor (source) stand (Allens Island, York River, Virginia, USA; 37° 15.1′ N, 76° 25.7′ W), and were placed into two sites: James River (36° 58.2′ N, 76° 24.6′ W; approximately 44 km from the plant source) and York River (37° 13′ N, 76° 30′ W; approximately 7 km from the source). At each site, individual shoots were planted at a density of 19.25 shoots m^{-2}, lower than natural densities (1418–2576 shoots m^{-2}; Orth and Moore, 1986) but capable of reaching sustainable stand sizes within a single season of vegetative growth (Orth et al., 1999).

Shoots were planted to create three different shoot arrangement treatments: individual (one $2\ m \times 2\ m$ plot consisting of 14 shoots planted 15 cm apart in each of five rows spaced 0.5 m apart; Orth et al., 1999), patchy (five rows of five shoots: $2\ m \times 2\ m$ plot; plots 2 m apart), and continuous (five rows of five shoots - $2\ m \times 2\ m$ plots; plots adjacent). Three randomly arrayed replicates of each shoot arrangement treatment were planted at each site. Within a site, all treatments were at least 20 m from each other, a distance greater than that hypothesized for pollen dispersal in this species (Ruckelshaus, 1996), such that most or all reproductive activity happens within, rather than among, treatments.

To identify comparable treatment structures within natural stands, we utilized methods similar to those of Hovel and Lipcius (2001). A combination of GIS distribution maps (Orth et al., 1998) and ground truthing was used to identify naturally occurring individual, patchy, and continuous shoot arrangements in each of the two rivers (James River, approximately 8 km away from the James River transplant; 37° 0.9′ N, 76° 20.4′ W; York River, approximately 8 km away from the York River transplant; 37° 13.7′ N, 76° 25.6′ W), and at Allens Island, the source eelgrass site.

2.2. Reproduction response metrics

We hypothesized that there was no difference in reproduction metrics between interior and edge for the shoot arrangement treatments. Transplants in both the James and York rivers were sampled in mid-May 1999, just prior to seed release. Within each replicate (three shoot arrangements, three replicates per arrangement), we haphazardly sampled three edge (sampled from the outermost rows of a $2\ m \times 2\ m$ plot), and three interior (sampled from the interior three rows of a $2\ m \times 2\ m$ plot) subsamples using a 20 cm diameter ring ($0.032\ m^2$), counting all shoots, and harvesting all reproductive shoots from a $1.0\ m^2$ area. Reproductive shoot samples were stored in a temperature-controlled room (4 °C) until processing, which occurred within a week of harvesting. Sampling of individual, patchy, and continuous unmanipulated areas (natural and source) was conducted as described above using a 20 cm diameter ring ($0.032\ m^2$). As the patchy and continuous unmanipulated areas were generally located within larger eelgrass stands with no clear patch structure, no sampling was conducted to examine the edge and interior relationships measured in the transplants.

Vegetative shoot density and number of reproductive shoots, a demographic-based estimate of reproductive effort, were counted for all harvested samples. Total seed production, a