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Abstract

Predator effects on *Zostera marina* L. seed abundance were studied in the York River, VA, USA, using enclosure and exclosure caging experiments. Seeds were placed in cages in two concurrent experiments. The first experiment was a predator exclosure experiment to test the effects of excluding predators, using a full predator exclosure cage, a partial exclosure top-only cage, a partial exclosure side-only cage and uncaged plots. The second experiment was a predator enclosure experiment, using two highly abundant macro-benthic predators in the Chesapeake Bay: the decapod crustacean *Callinectes sapidus* Rathbun and the sciaenid fish *Micropogonias undulatus* L. Additionally, two-week long trials of sequentially protected and exposed seeds were also performed. Replicate treatment plots were sampled by removing the top 5–10 cm of the sediment surface with a suction sampler and still viable seeds in each plot were counted. Full exclosure cages contained significantly higher numbers of seeds than the uncaged or partial caged treatments. Seed abundances in the *C. sapidus* enclosure cages were significantly less than the full exclusion cage, but not significantly different than the uncaged treatments. Seed abundances in the *M. undulatus* cages were not significantly different than the full exclusion cage. The least number of seeds were found in the uncaged and partial cage treatments. Results of the sequentially protected and exposed trials were similar to results from the one-week uncaged treatments. These experiments suggest that seed predation can affect the abundance of *Z. marina* seeds, possibly causing up to 65% of the seed losses observed in these experiments. Results suggest that seed predation has the potential to be an important force governing the sexual reproductive success and propagation of eelgrass beds and that the degree of seed loss via predation may be related to predator and primary food abundances.

Keywords: Callinectes sapidus; Eelgrass; *Micropogonias undulatus*; Predation; Seeds; *Zostera marina*

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1. Introduction

Seagrasses, marine angiosperms adapted to survival in subaqueous environments, reproduce asexually through rhizomatous growth or sexually through seed production. The relative contributions of each reproductive mode to the maintenance of existing beds or the colonization of new areas is poorly understood. Seagrasses can produce large numbers of seeds (Table 1); e.g., *Halophila tricosta* can produce more than 70 000 seeds/m^2 (Kuo et al., 1993). However, similar to observations in the terrestrial environment (Kershaw and Looney, 1985; Packham et al., 1992; Leck and Simpson, 1994), recorded seedling abundances are considerably lower than the number of seeds produced (Keddy and Patriquin, 1978; Churchill, 1983; Gates, 1984; Bodnar, 1985; Orth and Moore, 1986; Hootsmans et al., 1987; Kuo and Kirkman, 1992; Harrison, 1993; Orth et al., 1994; van Lent and Verschuure, 1994). The causes for this low seedling abundance in seagrasses are not well known.

Zostera marina L. (eelgrass) is a common seagrass in the North Temperate Zone along the coasts of North America, Europe, and Japan (Den Hartog, 1970). The timing of anthesis and seed production generally increases with increasing latitude, occurring between April/May in North Carolina, and July/August in Nova Scotia (Phillips et al., 1983b; Silberhorn et al., 1983). Seed production is highly variable for this species, ranging from 200 to over 78 000 seeds/m^2 while seedling abundance is significantly less, ranging from 0–40% of the seed yield (Table 1).

Several processes may decrease *Z. marina* seed abundances and thus cause the discrepancy between seed production numbers and seedling abundances. Seeds may be transported from existing beds while still attached to floating reproductive shoots in a process called "rafting" (Setchell, 1929; Taylor, 1957a,b; McRoy, 1968; De Cock, 1980; McMillan, 1983; Phillips and Backman, 1983; Thayer et al., 1985; Bodnar, 1985; Bodnar, personal observation). Gates (1984) estimated that 36% of the potential seed yield may be lost from a bed due to rafting. However, some rafted seeds may be transported to areas where the seeds can successfully establish (Nienhuis, 1983). Similarly, short distance transport may occur via gas bubbles that can adhere to seeds as they are released from the plant, allowing the seed to float away from the bed (De Cock, 1980). Churchill et al. (1985) estimated 5–13% of the seed yield could be exported up to 200 m in this way.

Inherent non-viability, damage, disease, and eventual rot can account for some seed loss (Harrison, 1993; Keddy and Patriquin, 1978). Seeds may also be lost through vertical transport into the sediment to depths at which the germinated seedling can not reach the sediment/water interface. The mechanism of the transport has not been well studied, but hydrodynamics and bioturbation are each potentially responsible for this burial. Although Moore et al. (1992) and Bigley (1969) found *Z. marina* seeds to germinate as deep as 25 mm and 15 mm in the sediment, respectively, these depths may be the lower burial limits at which a germinating seedling can reach the sediment surface (Churchill, 1992).

Finally, predator activities such as direct consumption or damage to the seeds from indirect activity (i.e., foraging activities) may partially account for seagrass seed loss. The role of predation in terrestrial seed loss has been extensively studied and is a

Table 1
Summary of studies on seagrass seed yields and seedling success

Species	Location	Potential Seed Yield	Number of Seedlings	Reference
Cymodocea nodosa	French Mediterranean	80–220 found in sediment	2 individuals	Caye and Meinesz (1986)
Halophila ovalis	Austalind Indian Estuary, Australia	480 in sediment	0% survival in lab	Kuo and Kirkman (1992)
H. tricosta	Queensland, Australia	70 000	0% survival in lab	Kuo et al. (1993)
H. engalmannii	Redfish Bay	74 in sediment		McMillan (1988a)
H. decipiens	Toro Point, Panama	13 500 in sediment		McMillan (1988b)
Zostera noltii	Netherlands	9000	32% of seed yield in lab. In field. ≤5% of all plants were seedlings	Hootsmans et al. (1987)
Zostera marina L. (annual)	Sea of Cortez, Mexico	19,783–37 286		Phillips and Backman (1983)
Z. marina L. (annual)	Nova Scotia, Canada	78 224		Keddy (1987)
Z. marina L. (annual)	Nova Scotia, Canada		1.3–6.4% seedling survival in lab	Keddy and Patriquin (1978)
Z. marina L.	Netherlands	200	40% of seed yield	Hootsmans et al. (1987)
Z. marina L.	Netherlands	3571	1.3% of seed yield	Harrison (1993)
Z. marina L.	Puget Sound and North American West Coast	36 936		Phillips et al. (1983a)
Z. marina L.	South Oyster Bay, NY, USA; Smith Point, NY, USA	2776 (ovules) 5818 (ovules)	8–104 seedlings/m^2 5–136 seedling/m^2	Gates (1984)
Z. marina L.	Great South Bay, NY, USA	1802	0% seedling survival	Churchill and Riner, 1978
Z. marina L.	Northwest Creek, NY, USA		7–32 seedlings/m^2	Churchill, 1983
Z. marina L.	Northwest Creek, NY, USA	2125 (ovules)	112 seeds/m^2 recovered = 5% of potential yield	Bodnar, 1985
Z. marina L.	Chesapeake Bay, NY, USA	8127		Silberhorn et al., 1983

Potential seed yield in seeds/m^2 determined by number of reproductive shoots/m^2 × number of seeds/shoot unless otherwise noted

significant factor affecting the distribution and abundance of seeds (Janzen, 1971; van der Pijl, 1972; Howe and Smallwood, 1982; Willson, 1983; Howe, 1986; Hendrix, 1988; Christensen and Whitham, 1993). However, the role of predators on seagrass seed loss is poorly understood. Up to 18% and 23% of the diets of juvenile and adult pinfish, respectively, can consist of undigested eelgrass, eelgrass seeds and algae (Adams, 1976). Wassenberg and Hill (1987) reported over 90% of the collected juvenile brown tiger prawn *Penaeus esculentus* had *Zostera capricorni* seeds in their stomachs when seeds were available, accounting for up to 13% of the shrimp's ash-free dry weight. Larger juvenile *P. esculentus* have been found to consume more *Z. capricorni* than smaller prawns and that seeds contributed a large part of the animal's diet (O'Brien, 1994). Wigand and Churchill (1988) found *Z. marina* seed predation by several crustaceans and snails under laboratory conditions when their primary food was unavailable. However, the fate of seagrass seeds (mortality or survival) depends on whether seeds can survive passage through the guts of a particular species and thus be dispersed. For example, 30% of the freshwater species *Najas marina* seeds that Mallard ducks (*Anas platyrhynchos*) ingest can remain viable and be transported an estimated 100–200 km during flight (Agami and Waisel, 1986).

In the Chesapeake Bay, a variety of crustacean and fish species utilize *Z. marina* beds in the Chesapeake Bay (Heck and Orth, 1980; Orth and Heck, 1980; Heck and Thoman, 1981), including *Callinectes sapidus* (blue crab), *Palaeomonetes* spp. (grass shrimp), *Crangon septemspinosa* (sand shrimp), *Leiostomus xanthurus* (spot) and *Micropogonias undulatus* (Atlantic croaker). Although the foraging activities of these species have the potential to affect seed viability and abundance, the role they have in directly causing seed loss has been poorly studied.

In this study, we conducted predator enclosure/exclosure experiments to determine if predation could play an important role in *Z. marina* seed loss. We selected two numerically abundant species from this region for these experiments: *C. sapidus*, a keystone invertebrate predator on benthic communities (Virnstein, 1977), and *M. undulatus*, a vertebrate benthic feeder. Both species are considered omnivores in their feeding habits.

2. Methods

2.1. Seed and animal collection

Mature seeds were collected by harvesting reproductive shoots in *Z. marina* beds in the lower York River, Chesapeake Bay, VA, in late May and early June 1993. Shoots with seeds were placed in nylon mesh bags and returned 9 km upstream to the laboratory at Gloucester Point, where the shoots were placed in 3.8 m^3 circular tanks. These tanks were aerated and supplied with running seawater from the York River at Gloucester Point. After seeds matured and were released from the shoots, they were separated from the decaying shoot material by sieving with a nested series of sieves and then placed in a single aerated, running seawater holding tank.

Micropogonias undulatus L. (Atlantic croaker) and *Callinectes sapidus* Rathbun (Blue

crab) were collected in the lower York River with an otter trawl. Animals were brought back to the lab and held in separate large holding tanks until used in the experiments. Intermolt *C. sapidus* males of 6–9 cm carapace width were used to insure they would feed in the experiment while 15±1 cm long *M. undulatus* were used. These size classes were abundant in grassbeds during the study period (pers. obs.). Animals were fed every other day if necessary and animals were starved for 24 h prior to the beginning of the experiment.

2.2. Seed predation experiments

Two seed predation caging experiments were designed to test potential effects of predators on seed abundances. These were conducted in the York River, VA, USA (37° 15.0′ N, 76° 30.3′ W) in September and October 1993 at Gloucester Point (Fig. 1), an unvegetated site that once supported *Z. marina* beds prior to 1972 (Orth and Moore,
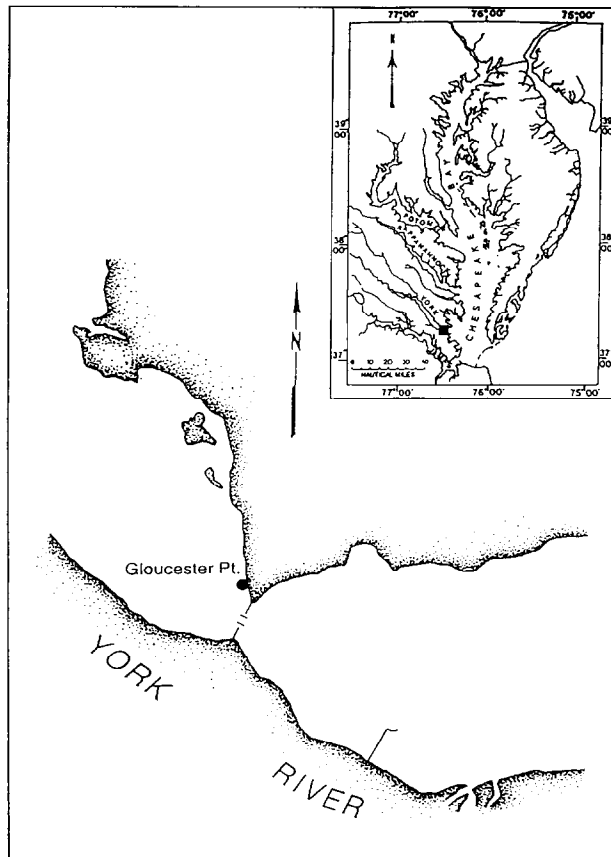

Fig. 1. Location of the study site at Gloucester Point in the lower York River, VA, USA.

1984; Orth et al., 1994). This site has been used extensively since 1972 for both whole plant transplants and seed dispersal experiments (Orth et al., 1994; Orth, unpublished data). Since 1972, very few seedlings have been observed to recruit naturally at the site, and no eelgrass patches have survived for more than five years. Cores taken a few days prior to these experiments did not contain any seeds already in the sediments. Sediments at the site consisted of sand with less than 5% silt/clay.

Predator exclosure or enclosure cages were constructed with 2.54 cm polyvinyl chloride (PVC) piping, 6 mm rat wire mesh, and aluminum flashing. Cages were cylindrical, measuring 100 cm in diameter and 50 cm high (area = 0.785 m^2). A 15 cm aluminum apron was riveted to the bottom of the cage. The apron was pushed 10 cm into the sediment to prevent burrowing of animals under the cage.

The first experiment ("Predator Exclosure Experiment") tested the effect of excluding all predators larger than the 6 mm mesh size and examined caging effects. Three replicates of four treatments were used in the design: "whole", a cage with sides and top designed to exclude large predators; "top", a cage with a top but no sides, allowing predator access from the sides and testing cage effects; "side", a cage with sides but no top, allowing predator access from above and testing cage effects; and a "no cage" treatment which was an uncaged plot.

Concurrently, a second experiment ("Predator Enclosure Experiment") tested the effects of including predators inside cages. Three replicates of three treatments were used in this design: "whole", the same cage described in the Exclosure experiment; "crab", a cage which included a single male C. sapidus of 6–9 cm carapace width; and a "croaker" cage which included a single M. undulatus of approximately 15 cm total length.

Three 1-week trials for both experiments were initiated on 13, 23 and 30 September 1993. Each of the replicates for all treatments was randomly assigned locations in a 12 × 20 m gridded area approximately 50 m from shore at Gloucester Point in 0.5 m MLW depth. Each cage plot was approximately 3 m distant from the adjacent plots.

Since sedimentation inside the cages appeared to bury the seeds, a third experiment was conducted that addressed the question of the vulnerability of these buried seeds to predation once the cages were removed and predators were allowed access to the plots. Two 2-week long "Protected/Exposed" trials were initiated by placing three predator-exclusion cages in the area described above. After seeds were placed in the cages and left for 1 week, the cages were removed and the plot carefully marked with small stakes. This exposed the plots to predators. After a week of uncaged conditions, all plots were sampled and processed as described below. Protected/Exposed trial dates were 13–30 September and 30 September–14 October 1993, with 3000 seeds and 1000 seeds per plot used in these trials, respectively, with three replicate plots per trial. The results of the Protected/Exposed experiment were qualitatively compared to the whole and no cage treatments from the Predator Exclosure experiment.

Seed counts required for each treatment were estimated volumetrically less than 24 h prior to the beginning of each experiment. Replicate 5 ml samples containing viable seeds, non-viable seeds and detritus were taken from the seed tank and examined to count the number of viable seeds. A viable seed was considered to be one with a dark brown or black color, hard seed coat and no damage to the seed husk. The mean number

of viable seeds per 5 ml sample was then used to calculate the volume of material from the seed holding tank required to attain the needed number of viable seeds for each treatment. Appropriate volumes of seeds were placed in jars of seawater until released into the treatments.

Numbers of viable seeds in each cage used during each of the three Predator Exclosure and Enclosure trials varied: 3000 seeds in the 13–20 September trial, 1000 seeds in the 23–30 September trial and 2000 seeds in the 30 September–8 October trial.

Before the cages were set into the sediment, the sediment surface of each plot was carefully examined for the presence of C. sapidus and if present, crabs were chased out of the cage by moving a ruler across the sediment surface. After the cage was placed into the sediment, a known number of viable seeds was gently released into the center 0.1 m^2 of the plots immediately above the sediment surface during calm, low, slack tide. Once seeds were released, the C. sapidus and M. undulatus were added into the appropriate treatments and the tops secured on all appropriate cages.

Cages were visually inspected daily for undercutting by waves, currents, or crab or fish excavating activity. Any areas around the cages where undercutting was evident were filled in with surrounding sediment. Predator enclosure cages were closely monitored at this time and at time of sampling to ensure that the animals were still in the cages.

At the end of each trial, the entire caged area of each treatment was sampled to a depth of 5–10 cm with a suction sampling device (Orth and van Montfrans, 1987). All sediment was passed through a 0.5 mm mesh nylon bag, which retained seeds (seed dimensions are slightly larger than 1 mm by 3 mm). Bag contents were then sieved a second time through a 1 mm mesh sieve and retained material was placed in a plastic bag and frozen until processed.

In each sample, the number of viable seeds (undamaged seeds with a hard seed coat, or those seeds in the process of germinating) was counted. Presence of seed husks or damaged seeds was also recorded.

To evaluate effects of other potential seed predators or potential alternate food sources, all C. sapidus other than the original animal were counted and identified by size (crabs less than 25 mm carapace width were grouped into a single size class). During the trials, infaunal abundances in areas adjacent to the plots were sampled with an 8.89 cm inside-diameter acrylic core to depths of 20 cm. Cores were sieved with a 1 mm sieve, and frozen until animals could be enumerated and identified. Stomach contents of animals were not examined for presence of seeds because it was assumed gut clearance rates were less than 24 h for all macrofauna.

To test the efficiency of the sampling technique, three replicate trials were conducted in which 200 seeds were placed on the sediment surface in a whole cage and immediately suctioned. This method was thus determined to be 87% ($\pm$1.69% S.E.) effective in recovering seeds.

2.3. Statistical analysis

Seed count data were corrected for the 87% recovery efficiency and converted to percent recovered relative to number of seeds initially released in each plot. Data were

then arcsin square root transformed for statistical analysis. Treatments were compared using parametric (Scheffé test), or if necessary, non-parametric (Kruskal–Wallis) multiple comparisons.

3. Results

Since there was no significant difference between trials ($F = 0.991$, df = 2, $P = 0.378$), data from the three trials were pooled into a single data set. The data from the predator exclosure experiment did not meet the homogeneity of variance test (Bartlett's test $P = 0.0006$); therefore, a Kruskal–Wallis multiple comparisons test was used to determine treatment level effects (Hollander and Wolfe, 1973). The data from the predator enclosure experiment met the basic assumptions of ANOVA (Bartlett's test $P = 0.590$) so a one-way ANOVA, followed by a Sheffé multiple comparisons test was used at an experiment-wise error rate of 0.05 to test for treatment effects (Sokal and Rohlf, 1981).

In the predator exclosure experiment, seed abundances varied between treatments with significantly higher abundances ($P \geq 0.05$) in the whole and side cage treatments compared to the top and no cage treatments (Fig. 2A). The side cage treatment was not significantly different from either the whole or the top cage treatments. Mean recoveries for the whole and side cages were 56.58% ($\pm 7.18\%$ S.E.) and $35.97 \pm 8.61\%$, respectively, while mean recoveries in the top and no cage treatments were $6.30 \pm 1.36\%$ and $4.53 \pm 0.93\%$, respectively.

Seed abundances varied significantly in the predator enclosure experiment ($F = 7.769$, df = 2, $P = 0.003$, Fig. 2B). *Micropogonias undulatus* seed abundances (mean $44.65 \pm 5.88\%$) was not significantly different from the whole exclosure treatment ($P = 0.510$)). However, there were significant differences between the *C. sapidus* enclosure treatment (mean seed abundance $20.42 \pm 7.67\%$) and both the whole and croaker treatments ($P = 0.003$ and $P = 0.044$, respectively).

Initial protection and burial of seeds had little effect over a one week period, as seed recoveries in the protected/exposed trials (mean of $4.57 \pm 1.44\%$ recovery) were qualitatively similar to those in the no cage treatments in the predator exclosure experiment (Fig. 2c). Statistical analysis was not performed due to the absence of a 2-week-long whole cage control treatment.

Seed husks were observed in all treatments, but were qualitatively more apparent in the crab, top, side and no cage treatments. In addition, seeds that were cut in half were more abundant in the crab treatment.

Infaunal abundances varied between 494–602 individuals/m^2. Major infaunal species included the polychaetes *Spiochaetopterus oculatus, Clymenella torquata, Nereis* sp. (rare), capitellids, oligochaetes, the bivalve *Tagelus* sp. (rare), phoronids and nemerteans.

Uncontrolled crab abundances in the plots varied between 0–10 *C. sapidus* of less than 25 mm carapace-width per cage, and 0–2 *C. sapidus* 25–34 mm carapace-width per cage (Table 2).
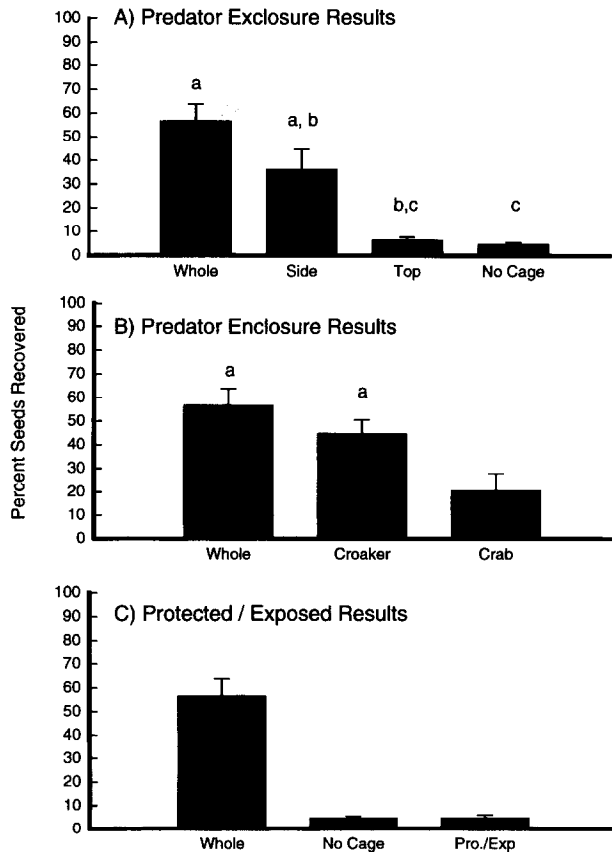
Fig. 2. Results of the (A) Predator Exclosure experiment; (B) Predator Enclosure experiment; and (C) Protected/Exposed treatments. Values are mean % of seeds recovered ($\pm$S.E) relative to amount of seeds initially released. Non-significant differences are indicated by similar letters, using Kruskal–Wallis multiple comparisons test at $\partial = 0.05$ for the predator exclosure experiment and the Scheffé test at $P = 0.05$ for the predator enclosure experiment.

4. Discussion

Seed abundances in the predator exclosure and enclosure experiments suggest that predation may play an important role in *Z. marina* seed loss, and may explain some of the variation between potential seed yield and seedling abundances often reported for this species (Table 1) (Keddy and Patriquin, 1978; Gates, 1984; Bodnar, 1985; Harrison, 1993) and possibly for other seagrass species (Caye and Meinesz, 1986; Hootsmans et al., 1987; Kuo and Kirkman, 1992). Seed predation is important in terrestrial systems (Janzen, 1971; van der Pijl, 1972; Howe and Smallwood, 1982; Willson, 1983; Fenner, 1985; Howe, 1986; Hendrix, 1988; Travis, 1992; Christensen and Whitham, 1993) and may be more common in seagrass species than previously suspected. In at least one

Table 2
Abundances of juvenile *Callinectes sapidus* found in each treatment replicate of the Predator Exclosure and Predator Enclosure experiments

Experiment	Treatment	Carapace width ≤ 25 mm	Carapace width 25–34 mm
Predator Exclosure			
	Whole	11.67	1.50
	No Cage	0	0
	Top	3	1.33
	Side	8.50	2.17
Predator Enclosure			
	Crab	7.50	0.50
	Croaker	2.50	0.67

Numbers are means of three replicates per trial, for three trials.

seagrass species, *Zostera capricorni*, seeds are an important dietary component of shrimp *Penaeus esculentus* during times of peak seed production (Wassenberg, 1990).

Seed loss in the experiments were high (up to 96% in the no cage treatments) and occurred rapidly (1 week), suggesting either intense predation or transport from the plots via hydrodynamics. We discount hydrodynamics as a major factor for the following reasons: A seed's high specific gravity (≥ 1) and high settling velocity (about 6 cm/s) precludes distant suspended load transport (Orth et al., 1994). Furthermore, the topography of the sediment at the study site is complex, with sand ridges, feeding pits, burrows and worm tubes. All of these structures can increase particle deposition (Howard and Dörjes, 1972; Yager et al., 1993) and reduce seed transport via bed or suspended-load transport. Ridges and pits on the sediment surface have also been observed to trap seeds and impede transport (Fishman, 1994, VIMS, unpublished data).

Furthermore, caging effects can also minimize hydrodynamics as a potential mechanism of the seed loss in this study. Currents are usually reduced in a cage as evidenced by distinct sedimentary differences, such as a higher silt-clay content, in many studies using cages (Orth, 1977; Virnstein, 1977; Hall et al., 1990). Although sediment data were not collected in this study, qualitative visual examination inside the cages revealed a fine flocculent layer that was different than the surrounding sediments. Furthermore, the 5 cm of aluminum skirt protruding from the sediment in each cage probably impeded bed load transport.

Additional evidence for minimal seed movement was from observations of the positions of seedlings in the experimental plots several months after the experiments. Although the patches were not dense, which was expected given the high efficiency of the sampling technique, most seedlings were within the 1 m diameter of the plots, including the no cage plots. The scarcity of seedlings outside of this 1 m diameter does not support the explanation that hydrodynamics was a major factor in removing seeds from the plots. Therefore the cage skirt, bottom roughness, and a seed's settling characteristics appear to have prevented hydrodynamic-mediated seed loss from the plots. This conclusion is supported by seed dispersal experiments previously conducted at the site (Orth et al., 1994) and observations of seed burial over short distances under current flows up to 21 cm/s (Fishman, 1994).

Another possible explanation for seed losses in these experiments is that uncontrolled predation by organisms smaller than the 6 mm cage mesh size may have been responsible for seed loss, as some seeds were lost even in the whole cage. These experiments were conducted at the peak period of *C. sapidus* post-larval settlement and highest abundance of juveniles in the lower Chesapeake Bay (Orth and van Montfrans, 1987; van Montfrans et al., 1990). Small crabs could enter the cage and molt to a size too large to exit the cage. These crabs could then prey on seeds. This hypothesis is supported by the presence of several small crabs less than 25 mm carapace-width (Table 2) and of the presence of seed husks in the whole cage. However, compared to the other treatments in the predator exclosure experiment, the cage was effective in protecting a large proportion of seeds from transport or predation.

The enclosure experiments suggest that *C. sapidus* can significantly reduce seed abundance and that predation may be a function of individual predator foraging strategies. The high abundance of seed husks in the *C. sapidus* treatments suggests that the crabs were actively handling the seeds, further evidenced by the presence of seeds that were cut in half. The type of activity (i.e., direct consumption or food handling) these crabs exert on seeds is unclear from these results; however, *C. sapidus* apparently have a destructive effect, causing up to a 65% loss of seeds relative to number of seeds recovered in the whole cage exclosure. Seed husks have been found in *C. sapidus* stomachs caught in grassbeds during the time of seed release (personal observation). This is not unexpected, since *C. sapidus* are omnivores (Laughlin, 1982). Wigand and Churchill (1988) found *Pagurus longicarpus* to consume seeds or handle them with maxillipeds which caused damage to the seeds. *Callinectes sapidus* (both the ones used in the enclosure experiment and the smaller crabs trapped in other cages) may be acting in a similar manner, destroying seeds by direct consumption or inflicting damage that results in the presence of seed husks and broken seeds.

Micropogonias undulatus did not significantly affect seed abundances. However, it is not clear if the cages may have interfered with the feeding of *M. undulatus*. Croaker feed by diving into the sediment at 30–45°, backing out and swimming away as sand drops from their mouths (Roelofs, 1954). Many studies have found that the *M. undulatus* diet consists of mostly invertebrates (polychaetes, mollusks, copepods, amphipods, decapods), however detritus comprises up to 40% of the diet (Roelofs, 1954; Stickney et al., 1975; Chao and Musick, 1977; Kobylinski and Sheridan, 1979). Since stomachs were not examined at the end of the experiments, it is possible that the fish did not feed during the experiments; or if they fed, either did not ingest seeds or excreted whole, viable seeds. The low number of small *C. sapidus* found in the croaker cages (Table 2) suggests that *M. undulatus* may have been eating small *C. sapidus* instead of seeds. The potential does exist, however, that *M. undulatus* can ingest seeds. *Micropogonias undulatus* have been found in grassbeds and stomachs from those fish contained large quantities of plant material (personal observation).

The low seed abundances in the protected/exposed treatments after cages were removed (Fig. 2c) suggest that seeds remain vulnerable even when shallowly covered with sediment. Although we did not measure the depth of seeds in the sediment when cages were removed, we suggest burial depth was shallow (probably less than 5 mm) and that seeds were subject to predation. *Callinectes sapidus* forages for infauna by

either thrusting the chelae into the sediment or by digging pits, both methods potentially exposing seeds previously buried at shallow depths.

The results of this study provide evidence that crab predation is an important factor in *Z. marina* seed loss. However, although not directly examined as part of this study, many possible factors may have affected the degree of seed predation during these experiments. For example, during this study, infaunal abundances (or primary food abundances) at the study site were extremely low (mean abundance of 584 individuals/ m^2) relative to other years when 2000–8000 individuals/m^2 have been recorded at unvegetated shoals in the York River (Virnstein, 1977; Zobrist, 1988). *Callinectes sapidus*, like many other crustaceans, are opportunists and will prey on whatever food is locally abundant at the time (Laughlin, 1982; Haefner, 1990; Wassenberg, 1990). The primary food sources for *C. sapidus* are polychaete worms, bivalves, crustaceans, fish and other infauna (Laughlin, 1982). Low primary food abundances (infauna) may have created a threshold encounter rate to exist between *C. sapidus* and primary food, below which the crabs will turn to seeds as alternative food. *Zostera marina* seeds are of intermediate nutrition, with a protein content of 13.2% and carbohydrate content of 50.9% (Felger and Moser, 1973), and although not as nutritious as infauna, they may be relatively more important sources of alternative food when preferred prey are less abundant. Wigand and Churchill (1988) found that the hermit crab *P. longicarpus* will eat *Z. marina* seeds when a primary alternative food is in low supply. Additionally, during this study, juvenile *C. sapidus* (carapace-width 15–50 mm) abundances were relatively higher than previous years (VIMS, unpublished data). Low infaunal abundances and high crab abundances may have contributed to relatively higher encounter rates between crabs and seeds. Seed loss due to predation may thus be a function of abundances of both predators and their preferred prey.

These experiments were performed in unvegetated areas; however, seed loss in vegetated areas may be more difficult to predict. Although vegetated areas, where seeds are produced, would be expected to contain large numbers of seeds, there are also higher abundances of primary food (infauna) and increased abundances of predators such as *C. sapidus* or finfish inside a bed (Orth, 1973; Virnstein, 1977; Heck and Thoman, 1981; Orth et al., 1984; Heck et al., 1989; Orth, 1992), the relative densities of which could exert varying predation pressures on seeds. Furthermore, shoot bases and root-rhizome mats in beds increase habitat complexity, offering some protection from predation (Orth et al., 1984).

The results of this study provide potential explanations for seed losses in other studies. Predation may have accounted for some of the seed losses observed by Churchill (1983) where *Z. marina* seeds in Northwest creek, New York were lost during the winter and spring with no survivors by May. Predation may also account for some of the *Z. marina* seed losses noted by Harrison (1993). The 60–97% loss of viable seeds in the study by Orth et al. (1994) which was conducted in the same area and time period as the experiments in this study, may have been caused by predation.

Our study suggests that predation must be considered as a factor of seed loss in the seagrass *Z. marina* . These losses have implications in the maintenance of *Z. marina* beds and colonization of new habitats, especially those distant from existing beds. This study suggests that successful seedling establishment may require the input of far more

seeds than can be preyed upon. To colonize denuded areas, enough seeds must be produced so that of the few that are transported into unvegetated areas, enough seeds will survive predation and other losses to establish. Even slight burial may not provide significant refuge from predation. This study has illustrated the potential role of predators in determining the survival of seeds, and suggests seed survival to be a function of predator type. Studies focusing on the importance of predator density, seed abundance and availability of different food resources on the degree of seed predation are necessary to further examine the ecological ramifications on sexual reproductive success and colonization of seagrasses.

Acknowledgments

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