The Role of Predation on Zostera marina L (Eelgrass) Seed Abundance

James Fishman

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THE ROLE OF PREDATION ON
ZOSTERA MARINA L. (EELGRASS)
SEED ABUNDANCE

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

by
James R. Fishman
1994
THE ROLE OF PREDATION ON ZOSTERA MARINA L. (EELGRASS) SEED ABUNDANCE

This thesis is submitted in partial fulfillment of the requirements for the degree of Master of Arts

Approved, July 1994

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The following people also deserve recognition for their assistance in various aspects of my thesis: Dr. Robert Diaz for his statistical knowledge and direction; everyone who went seed collecting in May of 1993; Susan Bogardy and Renée Pardieck for field assistance; Karen Metcalf for crab abundance data; Curtis Harper for his field experience and assistance, good humor, and his "seeing the forest through the trees" attitude; and Jill Goodman, for her invaluable advice about computer programs and data management, putting up with me in the lab, and her advice on how to get through a master's degree.

Dedicated to my father.
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ABSTRACT

Predator effects on *Zostera marina* L. seed abundance were studied in the York River, Virginia using enclosure and exclosure caging experiments. Seeds were placed in cages in two experiments with the following treatments: Predator exclosure experiment with a full predator exclosure cage, partial exclosure top-only cage, partial exclosure side-only cage, and uncaged plots; and a predator enclosure experiment with a *Callinectes sapidus* enclosure cage and a *Micropogonias undulatus* enclosure cage. 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 sediment surface with a suction sampler and viable seeds in each plot were counted.

Resultant seed abundances in the *C. sapidus* cages were significantly less than the full exclusion cage, while 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 predation can affect the abundance of *Z. marina* L. seeds, possibly causing up to 65% of the seed losses observed in these experiments. Results suggest that predation is 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.
THE ROLE OF PREDATION ON
ZOSTERA MARINA L. (EELGRASS)
SEED ABUNDANCE
INTRODUCTION

Production of large numbers of offspring helps to insure that some offspring will survive to reproductive maturity. Despite several biological and physical mechanisms to disperse propagules and ensure reproductive success (Ridley, 1930; van der Pihl 1972; Harper, 1977; Howe and Smallwood, 1982), only a few offspring will survive to adulthood. For example, the emergent salt plant *Distichlis spicata* and the marsh plant *Ambrosia trifida* can lose up to 75% and 99% of their seeds, respectively (Bertness et al. 1987; Leek and Simpson 1994, respectively). High propagule losses also occur in the terrestrial environment; the herbaceous perennial *Amianthium muscaetoxicum* can produce up to 5000 seeds/m$^2$ but only a few percent survive (Travis 1992). Grasses such as *Vulpia ciliata* also can experience more than 90% seed mortality (Carey and Watkinson 1993) and many desert and grassland plants have seed losses exceeding 75% (Hendrix 1988).

Propagule loss can occur via several processes. Some may be dispersed into geographic areas or to sediment depths in which successful establishment and growth is unlikely. They may also be vulnerable to disease and rot, as well as to direct and indirect predation. The probability of successful establishment and growth of propagules to reproductive maturity may depend on the relative interactions of these processes, which may be particular to each species.

Seagrasses are marine angiosperms with about 55 species worldwide (Den Hartog, 1970) that reproduce both vegetatively through lateral growth and sexually through seeds. Although Oleson and Sand-Jensen (1994) show that beds of *Zostera marina* in Denmark are maintained mostly by vegetative growth
of lateral shoots while seeds are more important for colonization of new areas, there is still little information regarding the relative importance of these methods of reproduction in the maintenance of existing beds and in the colonization of unvegetated areas.

The potential number of seeds produced and the number of seedlings observed in the field can vary significantly in seagrasses (Table 1). Seedling abundances are usually far less than the number of seeds produced. Several seed experiments have shown that while germination rates are potentially high, seedling survival rates are usually low (Table 1). Therefore, seed mortality, potentially caused by a variety of mechanisms, is extremely important in determining sexual reproductive success.

In the Chesapeake Bay, Z. marina seed production occurs from early May to early June with production estimates as high as 8200 seeds/m² (Silberhorn et al 1983). Germination occurs between mid-October and mid-November and is correlated to temperature and low sediment oxygen concentrations (Orth and Moore, 1983, Moore et al. 1992). Despite this high seed production, seedling abundances within meadows can be as low as 66/m² (Orth and Moore 1986). Recent experiments by Orth et al. (in press) have shown that of thousands of Z. marina seeds released, only 3-40% of the viable seeds successfully establish as seedlings. The study also reports that seeds settle immediately to the sediment surface and once on the sediment, do not travel far from the site of deposition. The causes for this low seedling abundance and the fate of the remaining seeds are not well known.

Seagrass seed mortality (for Zostera marina seeds in particular) may occur via several processes. Seeds may be transported away from existing beds while still attached to floating reproductive shoots (personal observation, Setchell 1929, Taylor 1957(a and b), McRoy 1968, DeCock 1980, McMillan 1983, Phillips
Table 1: Summary of seagrass seed ecology studies.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Potential Seed Yield (seeds/m²)</th>
<th>Number of Seedlings</th>
<th>Maximum Germination Rate</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cymodocea nodosa</em></td>
<td>French Mediterranean</td>
<td>80-220 in sediment</td>
<td>few seedlings</td>
<td>90%</td>
<td>Caye and Meinesz, 1986</td>
</tr>
<tr>
<td><em>Phyllospadix iwatensis</em></td>
<td>Horay Jima, Japan</td>
<td></td>
<td></td>
<td>65%</td>
<td>Kuo et al 1990</td>
</tr>
<tr>
<td><em>Halophila ovalis</em></td>
<td>Austalind Indian Estuary, Australia</td>
<td>480 in sediment</td>
<td>little seedling survival</td>
<td>63%</td>
<td>Kuo and Kirkman, 1992</td>
</tr>
<tr>
<td><em>Halophila tricostata</em></td>
<td>Queensland, Australia</td>
<td>70,000</td>
<td>0% survival in lab</td>
<td>30% in lab</td>
<td>Kuo et al, 1993</td>
</tr>
<tr>
<td><em>Halophila engelmannii</em></td>
<td>Redfish Bay</td>
<td>74</td>
<td></td>
<td>32-94%</td>
<td>McMillan 1988 a</td>
</tr>
<tr>
<td><em>Halophila decipiens</em></td>
<td>Toro Point, Panama</td>
<td>13,500 in sediment</td>
<td></td>
<td>86-93%</td>
<td>McMillan 1988 b</td>
</tr>
<tr>
<td><em>Zostera noltii</em></td>
<td>Netherlands</td>
<td>9000</td>
<td>32% of seed yield in lab</td>
<td>up to 100% in lab</td>
<td>Hootsmans et al 1987</td>
</tr>
<tr>
<td><em>Zostera marina</em> L.</td>
<td>Sea of Cortez, Mexico</td>
<td></td>
<td></td>
<td>43% in lab</td>
<td>McMillan 1983</td>
</tr>
<tr>
<td><em>Z. marina</em> L. (annual)</td>
<td>Sea of Cortez, Mexico</td>
<td>19,763-37,286</td>
<td></td>
<td></td>
<td>Phillips and Backman, 1983</td>
</tr>
<tr>
<td><em>Z. marina</em> L. (annual)</td>
<td>Nova Scotia</td>
<td>Planted 300-450 seeds in lab</td>
<td>6.4%-1.3% seedling survival</td>
<td>34%-50% in lab</td>
<td>Keddy and Patriquin, 1978</td>
</tr>
<tr>
<td><em>Z. marina</em> L.</td>
<td>Netherlands</td>
<td>200</td>
<td>40% of seed yield</td>
<td>up to 100% in lab</td>
<td>Hootsmans et al 1987</td>
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<tr>
<td><em>Z. marina</em> L.</td>
<td>Netherlands</td>
<td>176 in sediment</td>
<td>1.3% of seed yield as seedlings</td>
<td>10% of seed yield</td>
<td>Harrison, 1993</td>
</tr>
<tr>
<td><em>Z. marina</em> L.</td>
<td>Puget Sound and North American West Coast</td>
<td>0-36,936</td>
<td></td>
<td>0-94%, mostly &lt;50%</td>
<td>Phillips et al, 1983</td>
</tr>
<tr>
<td>Species</td>
<td>Location</td>
<td>Potential Seed Yield (seeds/m²)</td>
<td>Number of Seedlings</td>
<td>Maximum Germination Rate</td>
<td>Reference</td>
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<tr>
<td><em>Z. marina</em></td>
<td>Great South Bay, New York</td>
<td>2776 (ovules)</td>
<td>8-104 seedlings/m²</td>
<td>44-50%</td>
<td>Gates, 1984</td>
</tr>
<tr>
<td></td>
<td>South Oyster Bay, Smith Point</td>
<td>5818 (ovules)</td>
<td>5-136 seedlings/m²</td>
<td>44-50%</td>
<td></td>
</tr>
<tr>
<td><em>Z. marina</em></td>
<td>Great South Bay, New York</td>
<td>1802</td>
<td></td>
<td>0% seedling survival</td>
<td>Churchill and Riner, 1978</td>
</tr>
<tr>
<td><em>Z. marina</em></td>
<td>Northwest Creek, New York</td>
<td></td>
<td>0% seedling survival</td>
<td>76-93%</td>
<td>Churchill, 1983</td>
</tr>
<tr>
<td><em>Z. marina</em></td>
<td>Northwest Creek, New York</td>
<td>1800 from seed bank,</td>
<td>7-32 seedlings/m²</td>
<td>45-100%</td>
<td>Bodnar, 1985</td>
</tr>
<tr>
<td></td>
<td>2125 (ovules)</td>
<td>112 seeds/m²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>potential yield</td>
<td>recovered= 5% of potential yield</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Z. marina</em></td>
<td>Chesapeake Bay</td>
<td>8127</td>
<td></td>
<td>38% in field</td>
<td>Orth and Moore, 1983</td>
</tr>
<tr>
<td><em>Z. marina</em></td>
<td>Chesapeake Bay</td>
<td></td>
<td></td>
<td></td>
<td>Silberhorn et al, 1983</td>
</tr>
</tbody>
</table>
and Backman 1983, Thayer et al. 1984, Bodnar 1985), which Gates (1984) estimates may be responsible for a loss of 36% of the potential seed yield. Not all of the seeds dispersed in this way may die, since this dispersal method may be responsible for the colonization of distant areas (Nienhuis 1983). Similarly, 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 as far as 200 m in this way.

Inherent non-viability, damage, disease, and eventual rot can account for some seed loss. Over half of the seed losses observed by Harrison (1993) were due solely to autonomous death. Because germination rates can be extremely low (Table 1), losses due only to seed nonviability can account for much of the seed loss. 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 (1981) 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).

Predation, either by direct consumption or by damage to the seeds from indirect activity (i.e. foraging activities) may partially account for seagrass seed loss. However, the role of this mechanism on seed loss is poorly understood. Previous studies have reported the presence of a freshwater submersed species' seeds in the guts of fish and waterfowl (Adams, 1976; Agami and Waisel, 1986). Up to 18% and 23% of the diets of juvenile and adult pinfish, respectively, consist of undigested eelgrass, eelgrass seeds, and algae (Adams, 1976). Wassenberg
and Hill (1987) reported over 90% of the juvenile penaeid *Penaeus esculentus* had *Zostera capricorni* seeds in their stomachs when seeds were available. Up to 13% of the shrimp's ash-free dry weight was accountable to the presence of seeds. Wigand and Churchill (1988) found *Z. marina* seed predation under laboratory conditions by several crustaceans and snails when primary food was unavailable. However, the fate of seagrass seeds (mortality or survival) depends on the species consuming that seed, as many seeds can survive passage through the guts and may thus be dispersed. For example, 30% of the *Najas marina* seeds Mallard ducks (*Anas platyrhynchos*) ingest can remain viable and be transported an estimated 100-200 km during flight (Agami and Waisel 1986).

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), each potentially able to prey on seeds. These include *Callinectes sapidus* (blue crab), *Palaeomonetes* spp. (grass shrimp), *Crangon septemspinosa* (sand shrimp), and local species of sciaenid fish, i.e. *Leiostomus xanthurus* (Spot) and *Micropogonias undulatus* (Atlantic Croaker). Because of the potential predatory impacts of these species on *Z. marina* seeds, they may significantly affect seed viability and abundance. However, the role these species have in reducing seed abundance has been poorly studied. Therefore, this study was performed to determine if predation by *C. sapidus* or *M. undulatus*, determined via predator enclosure/exclosure experiments, could have an important role in *Z. marina* seed loss.
METHODS

Mature seeds were collected by harvesting reproductive shoots in *Z. marina* beds in the lower York River, Chesapeake Bay, Virginia, in late May and early June 1993 (Figure 1). 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 m³ circular tanks. These tanks were aerated and supplied with running seawater from the York River at Gloucester Point. After seeds 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.

Seed counts required for each treatment were estimated volumetrically less than 24 hours prior to the beginning of each experiment. A sample of known displacement volume was taken from the seed tank and examined to determine 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. This number of viable seeds was used to calculate the volume of material from the seed holding tank required to attain the needed number of viable seeds. Appropriate volumes of seeds were placed in jars of seawater until released into the treatments.

*Micropogonias undulatus* (Atlantic Croaker) and *Callinectes sapidus* (Blue Crab) were collected in the lower York River by otter trawling at least 24 hours prior to each experiment. 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
Figure 1: Map of the lower York River, Virginia showing study sites at Mumfort Island, Gloucester Point, Allens Island, Guinea Marsh, and Goodwin Island.
experiment while 15 cm long *M. undulatus* were used. Animals were fed every other day if necessary. Animals were starved for 24 hours prior to the beginning of the experiment.

Predator exclosure/enclosure cages were constructed with 2.54 cm polyvinyl chloride (PVC) piping, 6 mm rat wire mesh, and aluminum flashing (Figure 2). Cages were cylindrical, measuring 100 cm in diameter and 50 cm high (area=0.785 m²). A 15 cm aluminum apron was riveted to the bottom of the cage, with 10 cm to be placed below the sediment surface to prevent burrowing of animals under the cage.

**Preliminary trials**

Preliminary seed predation experiments were conducted in unvegetated, shallow water areas at Gloucester Point and Mumfort Island (Figure 1). Both sites supported seagrasses prior to 1972 (Orth and Moore, 1984) and have been used previously in related seagrass research (Batiuk et al. 1992, Orth et al. in press). The objective of the preliminary tests was to determine if exposure to predators could reduce seed abundances.

A single cage was placed at both Gloucester Point and Mumfort Island along with an uncaged plot at Mumfort Island on August 4, 1993. Three uncaged plots were placed at Gloucester Point on August 23, 1993. Cages were placed on the plots so that the bottom of the PVC frame was buried. Cages were then secured with metal stakes inserted through the frame into the sediment.

Approximately 4000 seeds were released a few centimeters above the sediment surface in the center 0.1 m² of the Mumfort Island caged and uncaged plots and Gloucester Point caged plot during low, slack tide and under calm sea conditions. Approximately 3000 seeds were released at each Gloucester Point
Figure 2: Diagram of cage design. Cages were constructed out of 1 inch diameter PVC piping in a 50 cm high, 100 cm diameter cylinder frame, 6 mm mesh rat wire and aluminum sheet metal flashing. Cage area was 0.785 m².
uncaged plot.

Trials were conducted for one week. The Gloucester Point caged plot and Mumfort Island caged and uncaged plots were sampled on August 10 and 13, respectively while the Gloucester Point uncaged plot was sampled on August 30. Each plot was sampled by taking 8.89 cm (inside diameter) acrylic cores to sediment depths of 20 cm. Fourteen cores were taken in each caged plot; four in the center 0.10 m² of the plot where seeds were initially released, six along the inside edge of the plot, and four between the center and edge of the cage. Twelve cores were taken in the uncaged plot; four in the center 0.10 m², and eight along the edge of a 1 m² square. Approximately 11% and 9% of the caged and uncaged plots, respectively, were sampled with the cores. After processing through a 1.0 mm sieve, viable seeds were counted and major infaunal organisms enumerated and identified to species, if possible. Infaunal abundance data were corrected to individuals/m². Because of the non-random pattern of coring each plot, and of the fact that seeds were released in the center 0.10 m² of the plot and not dispersed over the entire plot, a high degree of error prevents the estimation of accurate seed abundances.

**Predator Exclosure and Enclosure Experiments**

The main experimental design tested the effects of seed predation by both excluding and including predators using the cages described above (Figure 3). The first experiment ("Predator Exclosure Experiment") tested the effect of excluding all predators larger than 6mm 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
Figure 3: Schematic of experimental designs of the Predator Enclosure experiment, Predator Exclosure experiment and two-week Protected/Exposed trials.
3 Trials, 3 Replicates per trial
Sept. 13-20, 1993  3000 Seeds
Sept. 23-30, 1993  1000 Seeds
Sept. 30-Oct. 8, 1993  2000 Seeds

2 Trials, 3 Replicates per trial
Sept. 13-30, 1993  3000 Seeds
Sept. 30-Oct. 14, 1993  1000 Seeds
effects; and a "no cage" treatment which was an uncaged plot.

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 one-week trials for both experiments were initiated on September 13, 23, and 30, 1993. Each of the replicates for all treatments was randomly assigned locations in a 12 m x 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.

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

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 allowed access to the plots. Two two-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 one week, the cages were removed and the plot carefully marked with small stakes. This exposed the plot to predators. After a week of uncaged conditions, all plots were sampled and processed as described below. Protected/Exposed trial dates were September 13-30 and September 30 - October 14, 1993, with 3000 seeds and 1000 seeds per plot used in these trials, respectively. The results of the Protected/Exposed
experiment were compared to the whole and no cage treatments from the Predator Exclosure experiment.

Before the cages were set into the sediment, the sediment surface of each plot was carefully examined for the presence of crabs and if present, crabs were gently 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 seeds was gently released onto the plots in the same manner and during the same sea conditions described above. 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 collected in a 0.5 mm mesh nylon bag, which retained seeds. Bag contents were then sieved through a 3 mm and 1 mm mesh sieve and retained material was placed in a plastic bag and frozen until processed.

In order 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% (+/- 1.69% standard error) effective in recovering seeds.

In each sample, the number of viable seeds (undamaged seeds with a hard seed coat, or those seeds in the process of germinating) were counted. Any
crabs were counted and identified by size (crabs less than 25 mm carapace width not recorded for length). Major fauna were identified and abundances recorded. Presence of seed husks was also recorded. Stomach contents of animals were not examined because it was assumed gut clearance rates were less than 24 hours.

Any seeds that escaped sampling or mortality during or after the trials grew as seedlings during the winter and spring of 1993-1994. The diameters of the resultant patches of seedlings in the September 13-20 trial were measured to determine if bed load transport had occurred.

**Statistical Analysis**

Seed count data was corrected for the 87% recovery efficiency and converted to percent recovered relative to number of seeds initially released in each plot. Data was then arcsin square root transformed for statistical analysis. Treatments were compared using parametric, or if necessary non-parametric multiple comparisons. Since there was no significant difference between trials, data from the three trials were pooled into a single data set (Table 2). The whole, crab and croaker cages (predator enclosure experiment) met the basic assumptions of ANOVA, so the Sheffé multiple comparisons test was used at p=0.05 (Sokal and Rohlf 1981). The whole, side, top, and no cage treatments (predator exclosure experiment) did not meet the homogeneity of variance test; therefore, the non-parametric Kruskal Wallis multiple comparisons test was performed on that data (Hollander and Wolfe, 1973).

**Seed Observations:**

The movement of seeds when placed at the sediment surface was observed in situ using SCUBA at not only the Gloucester Point site but also at
Table 2: ANOVA at $p=0.05$ and Bartlett's Chi-Square homogeneity of variance test of all data in the Predator Exclosure and Enclosure experiments, used to determine if data from three trials could be pooled into a single data set. Because $p > 0.05$, variance between trials was homogeneous and data was pooled for further analysis.

**ANOVA:**

<table>
<thead>
<tr>
<th>Sums of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>$F$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.200225</td>
<td>2</td>
<td>0.1001126</td>
<td>0.990603</td>
<td>0.3783838</td>
</tr>
</tbody>
</table>

**Test of Homogeneity of Variance Between Trials:**

<table>
<thead>
<tr>
<th>Bartlett Chi Square</th>
<th>df</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.037385</td>
<td>2</td>
<td>0.2190138</td>
</tr>
</tbody>
</table>
additional sites in the York River including Allens Island (5 km downriver) and Guinea Marsh (8km downriver) on the northern shore and Goodwin Island (8km downriver) on the southern shore. The purpose of these observations was to determine qualitatively the role of hydrodynamics on seed movement in order to help evaluate the possible role of hydrodynamics in causing seed loss in the predator exclosure and enclosure experiments. A 1 m² metal frame (with 10 cm fishing line grids) was placed 5 centimeters above the sediment surface, oriented perpendicular to current direction. Hydrodynamics were believed not to have been greatly affected by the fishing line and frame. Current speed was roughly estimated by timing a neutrally bouyant glass vial across 40 cm over the sediment surface. Four seeds were placed in the center of the frame and were carefully observed for up to 15 minutes with quantitative and qualitative observations recorded for each seed.
RESULTS

Total percents of seeds recovered from the Gloucester Point and Mumfort Island caged plots were 10.05 and 19.00%, respectively (Table 3). Seed recovery in the Mumfort Island uncaged plot was 0.35%. Seed recoveries in the three Gloucester Point uncaged plots were 1.03%, 0.27%, and 0.10% of the number of seeds released. Numerous seed fragments were found in the Mumfort Island uncaged treatment.

In the predator exclosure experiment, seed abundances were significantly higher in the whole and side cage treatments compared to the top and no cage treatments (Figure 4, Tables 4, 5). 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% (+/-7.18% standard error) and 35.97% (+/-8.61%) respectively while mean recoveries in the top and no cage treatments were 6.30% (+/-1.36%) and 4.53% (+/-0.93%), respectively.

No significant differences between the whole exclosure treatment and the croaker enclosure treatment were found in the predator enclosure experiment (Figure 5, Tables 4, 6) with a mean seed abundance in the croaker treatment of 44.65% (+/-5.88%). However, there was a significant difference at p=0.05 between the whole treatment and the crab enclosure treatment which had a mean seed abundance of 20.42% (+/-7.67%).

Seed recoveries in the protected/exposed trials (mean of 4.57% +/-1.44% recovery) were similar to those in the no cage treatments in the predator exclosure experiment (Figure 6).

Seed husks were observed in all treatments but were qualitatively more
Table 3: Summary of Preliminary trial results at Mumfort Island (August 4, 1993) and Gloucester Point (August 4 and August 23, 1993).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Total # seeds released</th>
<th>Total # seeds found in cores</th>
<th># Seeds in center 0.1 m²</th>
<th>Mean # seeds per core</th>
<th>Total % seeds recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gloucester Point Cage</td>
<td>4000</td>
<td>402</td>
<td>233</td>
<td>28.71</td>
<td>10.05</td>
</tr>
<tr>
<td>Mumfort Island Cage</td>
<td>4000</td>
<td>760</td>
<td>754</td>
<td>54.29</td>
<td>19.0</td>
</tr>
<tr>
<td>Gloucester Point No Cage</td>
<td>3000</td>
<td>31</td>
<td>20</td>
<td>1.67</td>
<td>1.03</td>
</tr>
<tr>
<td>1</td>
<td>3000</td>
<td>8</td>
<td>1</td>
<td>0.08</td>
<td>0.27</td>
</tr>
<tr>
<td>2</td>
<td>3000</td>
<td>3</td>
<td>3</td>
<td>0.25</td>
<td>0.10</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mumfort Island No Cage</td>
<td>4000</td>
<td>14</td>
<td>10</td>
<td>0.83</td>
<td>0.35</td>
</tr>
</tbody>
</table>
Table 4: Summary of results of the Predator Exclosure, Predator Enclosure, and Protected/Exposed trials. Values are mean percent of seed recovered (+/- standard error) relative to amount of seeds initially released. Similar superscripts denote non-significantly different means at p=0.05.

Predator Exclosure Experiment Results:

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean % Recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole</td>
<td>56.58 (7.18)a</td>
</tr>
<tr>
<td>Side</td>
<td>35.97 (8.61)a,b</td>
</tr>
<tr>
<td>Top</td>
<td>6.30 (1.36)b,c</td>
</tr>
<tr>
<td>No Cage</td>
<td>4.53 (0.92)c</td>
</tr>
</tbody>
</table>

Predator Enclosure Experiment Results:

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean % Recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole</td>
<td>56.58 (7.18)d</td>
</tr>
<tr>
<td>Croaker</td>
<td>44.65 (5.88)d</td>
</tr>
<tr>
<td>Crab</td>
<td>20.41 (7.64)</td>
</tr>
</tbody>
</table>

Two-week Protected/Exposed Results:

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean % Recovered</th>
</tr>
</thead>
<tbody>
<tr>
<td>One-Week Whole</td>
<td>56.58 (7.18)</td>
</tr>
<tr>
<td>One-Week No Cage</td>
<td>4.53 (0.92)</td>
</tr>
<tr>
<td>Two-Week Protected/Exposed</td>
<td>4.57 (1.44)</td>
</tr>
</tbody>
</table>
Table 5: Kruskal-Wallis Multiple Comparison Test at \( \alpha=0.05 \) of the Predator Exclosure experiment.

| Comparison         | \(|R_u - R_v| \geq q(3, k, \infty)(k(kn+1)/12)^{0.5}\) | Conclusions              |
|--------------------|--------------------------------------------------------|---------------------------|
| Whole: No Cage     | 20.11 12.76                                           | Significant Difference    |
| Whole: Top         | 17.44 12.76                                           | Significant Difference    |
| Whole: Side        | 5.77 12.76                                            | Not Significant           |
| No Cage: Top       | 2.62 12.76                                            | Not Significant           |
| No Cage: Side      | 14.34 12.76                                           | Significant Difference    |
| Top: Side          | 11.67 12.76                                           | Not Significant           |

where: \( R_u = \text{sum of ranks of data points in one treatment} \) \( n \)

\( R_v = \text{sum of ranks of data points in other treatment} \) \( n \)

\( n = \text{number of data points} \)

\( k = \text{number of treatments} \)

\( q(\alpha,k,\infty) = \text{critical q value (i.e. at p=0.05 and k=4)} \)

If \( (R_u - R_v) > q(\alpha,k,\infty) \), then there is a significant difference between the two treatments.
Figure 4: Results of the predator exclosure experiment. Error bars represent 1 standard error. Statistical significance calculated via the Kruskal Wallis multiple comparisons test and displayed as similarity bars.
Predator Exclosure Results

Percent Seeds Recovered

Whole  Side  Top  No Cage

- The graph shows the percent seeds recovered in different exclosure conditions: Whole, Side, Top, and No Cage.
- The Whole exclosure has the highest percent seeds recovered, with a value around 60%.
- The Side exclosure has a lower but still significant percent seeds recovered, around 40%.
- The Top and No Cage conditions have much lower percent seeds recovered, around 5% and 3% respectively.

The error bars indicate the variability or uncertainty in the measurements.
Table 6: ANOVA and Scheffé test of the Predator Enclosure Experiment. All comparisons except Whole:Croaker are significantly different at p=0.05.

ANOVA:

<table>
<thead>
<tr>
<th>Sum of Squares</th>
<th>df</th>
<th>Mean Square</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.866307</td>
<td>2</td>
<td>0.4331537</td>
<td>7.769314</td>
<td>0.0025019</td>
</tr>
</tbody>
</table>

Scheffé Test:

<table>
<thead>
<tr>
<th>Whole</th>
<th>Crab</th>
<th>Croaker</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole</td>
<td>XXXXXX</td>
<td>p=0.0031416</td>
</tr>
<tr>
<td>Crab</td>
<td>p=0.0031416</td>
<td>XXXXXX</td>
</tr>
<tr>
<td>Croaker</td>
<td>p=0.5101348</td>
<td>p=0.0441322</td>
</tr>
</tbody>
</table>
Figure 5: Results of the predator enclosure experiment. Error bars represent 1 standard error. Statistical significance calculated via the Scheffé test and displayed as similarity bars.
Predator Enclosure Results

Percent Seeds Recovered

Whole Crab Croaker Crab
Figure 6: Results of the two-week protected/exposed trials, relative to the one-week whole and no cage treatments. Error bars represent 1 standard error.
Protected/Exposed Trial Results

Percent Seeds Recovered

Whole
No Cage
Pro/Exp
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.

Most seedling patches measured in June 1994 were smaller than the diameters of the cages (100 cm). Mean patch diameter in the September 13-20 trial was 53.55 cm (Figure 7).

Seed movement on the topographically complex bottoms was dependent on current speed at the time of release at the different sites (Table 7). In current speeds of less than 7 cm/s, no movement of the seeds were seen. In current speeds of 11-15 cm/s, a few seeds oscillated back and forth in small depressions or sand ripple troughs. One of the four seeds was observed to travel from depression to depression, presumably under the influence of wave-current interactions, moving a few centimeters every few minutes. At the end of the 10 minute observation period, the seed had moved 94 cm from the point of release. Seeds tended to clump together in groups. At high current velocities (20-25 cm/s) sufficient to cause bed load transport, seeds rolled and settled in depressions or in the lee of sand ridges. Again wave-current interactions appear to be responsible. Two seeds settled behind a ridge only 2 or 3 mm high and were buried by sand moving over the ripple in 5 and 6 minutes time.

Infaunal abundances ranged from 494-602 individuals/m² at Gloucester Point and from 585-619 individuals/m² at Mumfort Island. Major infaunal species included the polychaetes *Spiochaetopteris oculatus*, *Clymenella torquata*, *Neries* sp. (rare), capitellids, oligochaetes, the bivalve *Tagelus* sp. (rare), phoronids and nemerteans.

Major fauna sampled via the suction sampler included 0-4 *Littorina* sp. per cage, 0-10 crabs of less than 25 mm carapace-width per cage, and 0-2 crabs 25-34 mm carapace-width per cage. The hermit crab (*Pagurus longicarpus*) was present in 3 plots.
Figure 7: Diameters of the patches of seedlings from seeds that remained after the September 13-20, 1993 trial of the Predator Exclosure and Enclosure experiments. Measurements were made in June, 1994.
Table 7: Summary of in situ seed observations under varying current speeds at Gloucester Point, Goodwin Island, Guinea Marsh, and Allens Island.

<table>
<thead>
<tr>
<th>Current speed (cm/s)</th>
<th>Location and Date</th>
<th>Max. Distance Travelled (cm)</th>
<th>Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-3</td>
<td>Gloucester Pt. 7/14</td>
<td>0</td>
<td>slight rocking movement from waves, in depressions</td>
</tr>
<tr>
<td>7</td>
<td>Goodwin Island 10/22</td>
<td>0</td>
<td>No movement</td>
</tr>
<tr>
<td>11-15</td>
<td>Guinea Marsh 8/27</td>
<td>3 seeds=0 cm 1 seed=54 cm</td>
<td>3 seeds=no movement 1 seed= into pits and depressions, sand ripples</td>
</tr>
<tr>
<td>20-25</td>
<td>Allens Island 8/19</td>
<td>20 cm</td>
<td>Rolled into depressions or sand ridges. 2 seeds=buried in 5 and 6 minutes</td>
</tr>
</tbody>
</table>
DISCUSSION

Seed abundances in the predator exclosure and enclosure experiments suggest that predation may have an important role in *Z. marina* seed loss. Compared to the whole cage, the abundance of seeds in the crab treatments represent a 65% loss. These results may explain some of the variation between potential seed yield and seedling abundances often reported for this species (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 has been reported to be important in terrestrial seed losses (Travis 1992, Hendrix 1988) and in at least one seagrass species, *Zostera capricorni* where seeds are an important dietary component of *Penaeus* shrimp during times of peak seed production (Wassenberg and Hill 1987). Seed predation may be common in more species than previously observed.

Based on previous studies, it was assumed that one week was adequate time for both seed burial and predation effects to have occurred. For example, Wigand and Churchill (1988) observed *Z. marina* seeds were consumed by *Pagurus longicarpus, Ovalipes ocellatus,* and *Panopeus herbstii* within a week during laboratory experiments. However, an unexpected result from these experiments was the extremely large degree of seed loss (up to 96%) in a relatively short time period (one week). Although the inclusion of predators coupled with the high concentrations of seeds in a small contained area would allow a predator access to a large food supply in a short time period, *Z. marina* seeds in the Chesapeake Bay are also released in a short period of time,
approximately 2-3 weeks. (Silberhorn et al. 1983). Seed predation could be expected to be higher during this brief time period.

Uncontrolled predation by blue crabs or shrimp smaller than the 6 mm cage mesh size may have been responsible for the 43% seed loss in the whole cage treatment. 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 25mm carapace-width (Table 8) and of the presence of seed husks in the whole cage. However, compared to the other treatments, the cage was effective in protecting a large proportion of seeds.

Seeds were not believed to have been buried deeper than the 5-10 cm sampled. Infaunal abundances, especially of highly active bioturbators, were extremely low. Therefore, burial of the seeds by bioturbation to those depths during the short time period of these experiments most likely did not occur.

An alternative hypothesis that may account for the seed losses may be hydrodynamic transport of the seeds out of the plots. Observations in this study (Table 7) and by Orth et al. (in press) suggest slight bed load transport is possible. The 4.5% recovery in the no cage plots are comparable to Orth et al. (in press) results in which only 3-40% of viable seeds released were seen as seedlings.

Although it is impossible to precisely estimate the loss from hydrodynamic transport, it is suggested that this loss is minimal, even in the no cage plots. Qualitative sampling from the perimeters of the preliminary cage and no cage plots showed that nearly all of the seeds remained in the center where they were released and fewer seeds were found along the perimeter. A seed's high
Table 8: Mean counts of juvenile *Callinectes sapidus* found in each treatment of the Predator Exclosure and Predator Enclosure experiments.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Carapace width &lt; 25 mm</th>
<th>Carapace width 25-34 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole</td>
<td>11.67</td>
<td>1.50</td>
</tr>
<tr>
<td>No Cage</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Top</td>
<td>3</td>
<td>1.33</td>
</tr>
<tr>
<td>Side</td>
<td>8.50</td>
<td>2.17</td>
</tr>
<tr>
<td>Crab</td>
<td>7.50</td>
<td>0.50</td>
</tr>
<tr>
<td>Croaker</td>
<td>2.50</td>
<td>0.67</td>
</tr>
</tbody>
</table>
specific gravity (>1) and high settling velocity (about 6 cm/s) precludes distant suspended load transport in current speeds up to 100 cm/s (Orth et al. in press). Furthermore, the topography of the sediment is complex, with sand ridges, feeding pits, burrows, and worm tubes. These structures can increase particle deposition (Howard and Dörjes 1972, Yager et al. 1993), thus reducing the probability of seed transport via bed or suspended-load transport. The bed load transport seen in this study and by Orth et al. (in press) was minimal even with wave/current interactions and required high current velocities. Ridges and pits on the sediment surface were observed to trap seeds and impede transport. Also, seeds were released at low, slack tide under calm sea conditions that remained so for several hours so that seeds would most likely remain in the plots.

Loss of seeds due to hydrodynamics was further discounted due to caging effects. 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 sedimentary characteristic data was not collected in this study, qualitative visual examination inside the cages revealed a fine flocculent layer, different than the surrounding sediments. Furthermore, the 5 cm of aluminum skirt protruding from the sediment in each cage probably impeded bed load transport. Therefore the skirt, rough topography, and a seed's high specific gravity may prevent hydrodynamics from removing most of the seeds from the plots.

Patch diameters support the hypothesis that hydrodynamics caused minimal seed loss. Although the patches were not dense, which was expected given the efficiency of the sampling technique, most seedling shoots were within the 1 m diameter of the plot (Figure 7). The lack of numerous seedlings outside of this 1 m diameter suggests that most surviving seeds that were not sampled or
preyed upon were not move far by currents. This further supports findings by Orth et al. (in press) that bed load dispersal is not a major dispersal mechanism.

Although not significantly different, the top and side cages were nearly significant at p=0.05. However, the nonparametric Kruskal Wallis test that was used is not extremely powerful and under a more powerful test, it is possible that significance may be found. If so, results from the partial cages would suggest that each of the cage types may influence predators with different foraging strategies. Although some crabs were observed on the sides of the side treatment, sides may have impeded the access of large predators along the bottom to a large enough degree to afford protection to seeds similar to that of the whole cage. Fish had access to the seeds from above, yet this did not appear to reduce the number of seeds in the cages, relative to the whole treatment. The fish may not have fed in the cage, or may not have entered the cage at all. The height of the cages kept the entire cage submerged for all but about 2 hours of the tidal cycle. The fact that no fish were ever observed caught in the side treatments as the tide ebbed supports the idea that fish predation was limited. In the top treatment, seed abundances were low. This cage allowed predators crawling along the bottom access to seeds, yet potentially impeded access for predators in the water column.

Results of the *C. sapidus* and *M. undulatus* enclosure treatments suggest that *C. sapidus* had a significantly greater effect on seed abundances. However, it is not clear if the cages may have interfered with the feeding of *M. undulatus* or *C. sapidus*. 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 found that the croaker diet consisted of mostly invertebrates (polychaetes, mollusks, copepods, amphipods, decapods), however detritus comprised up to 40% of the diet (Roelofs 1954, Stickney et al. 1975, Chao and Musick 1977,
Feeding activity can disturb sediments, as Palmer (1988) found that another sciaenid fish, *Leiostomus xanthurus* can kill 30-55% of meiofauna in the sediments from simply the disturbance caused during feeding. Since stomachs were not examined at the end of the experiments, it is possible that croaker 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 crabs found in the croaker cages (Table 8) suggests that croaker may have been eating small crabs instead of seeds. The potential does exist, however, that croaker can eat seeds. Croaker have been found in grassbeds (personal observation) and stomachs from those fish contained large quantities of plant material.

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 are exerting on seeds is unclear from these results; however, *C. sapidus* are apparently creating a destructive effect. Seed husks have been found in *C. sapidus* caught in grassbeds during the time of seed release (personal observation) This is not unexpected, since blue crabs are omnivores (Laughlin 1982). Wigand and Churchill (1988) found *Pagurus longicarpus* to consume seeds or handle them with maxillipeds which caused damage to the seed husks. *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.

Seed observations have shown that seeds may be buried faster in rapid currents (Table 7). Faster currents may be a short term advantage to a seed, in minimizing the amount of time a seed spends on the sediment surface exposed
to predators. If seed burial can act as a refuge from predation, the slower currents in an eelgrass bed (Fonseca et al. 1982) could leave seeds exposed on the surface for a longer period of time, resulting in a higher seed predation rate. However, this idea is not supported by the protected/exposed trials, in which despite shallow burial in the sediments, seed losses similar to the one-week no cage treatments were observed (Figure 6). Therefore, even when shallowly buried, seeds are still continuously subject to predation or other losses.

One factor that may influence the degree of crab predation on seeds is the relative abundance of infauna. The primary food sources for *C. sapidus* are polychaete worms, bivalves, crustaceans, fish, and other infauna (Laughlin 1982). *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). *Zostera marina* seeds are of intermediate nutrition, with a protein content of 13.2% and carbohydrate content of 50.9% (Felger and Moser 1973). 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. In this study, in the fall of 1993, infaunal abundances were extremely low (mean abundance of 584 individuals/m²) relative to other years. Virnstein (1977) found infaunal abundances of 4000-8000 individuals/m² in the fall of 1973 and 1974 in unvegetated shoal areas of the York River, close to the study site in this study. Zobrist (1988) found at Gloucester Point abundances of individual polychaete species (i.e. *Asabellides oculata*) in excess of 5000 individuals/m². Ranasinghe et al. (in preparation) estimate the optimal mean abundance of infauna in Chesapeake Bay to be approximately 2000 individuals/m².
While infaunal abundances were much lower than normal in 1993, juvenile *C. sapidus* (carapace-width 15-50 mm) abundances were relatively higher than previous years (Figure 8, Metcalf personal communication). Although that data was from a seagrass bed 10 km downriver, it was assumed that relative densities would be reflected in unvegetated areas. The low infaunal abundances in 1993 coupled with high juvenile *C. sapidus* densities may have caused alternative prey items, including *Z. marina* seeds, to be significantly more important in 1993. 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, vegetated areas may be more complex. Vegetated areas contain higher abundances of fauna, including crabs, finfish, and infauna. (Orth 1973, Virmstein 1977, Heck and Thoman 1981, Orth et al. 1984, Summerson and Peterson 1984, Heck et al. 1989, Orth 1992). Although *Z. marina* seed abundances would be expected to be higher in vegetated areas where they are produced, both predator densities and alternative prey abundances are also higher. Some protection is afforded to infaunal prey and seeds by the root-rhizome mat and complex habitat offered by the meadow (Orth et al. 1984). This could allow more seeds to survive in vegetated areas.

The results of these experiments suggest the possibility that a threshold encounter rate may exist between predators and primary food, below which predators will turn to seeds as alternative food. This threshold rate will change with varying predator and primary food abundances. Similarly large numbers of alternative food (i.e. seeds in these experiments) may increase predator/seed encounter rates making predation on seeds more energy efficient than predation on infauna.

The large discrepancy between seeds produced and those that survive
Figure 8: Mean abundances of *C. sapidus* of 15-50 mm carapace-width between August and October, 1983-1993. Abundances are from vegetated mesohaline shoals (Metcalf, unpublished data).
Callinectes sapidus  Abundances

(15-50 mm carapace width)

August- October

Density (Individuals / m²)

Year
(Table 1) is consistent with a predator-swamping reproductive strategy (Ims 1990) that ensures some seeds will escape predation by satiating predators with sheer numbers of seeds produced. However, as predation decreases the number of seeds, the lower abundance may decrease to a point at which the encounter rate between seeds and predators is lower than the encounter rate between predators and other foods, thereby releasing predation pressure from seeds. In these experiments and in the study by Orth et al. (in press), both situations may have occurred sequentially in the following manner: The large number of seeds released in the experiments made seeds an important prey for crabs. However, as predation continued, the decreasing abundances of seeds decreased the encounter rate between crabs and seeds low enough for crabs to turn to other foods, allowing a small percentage of seeds to survive.

Although not examined in this study, seed predation may act as a dispersal agent. Birds, fish and other animals have been well documented to ingest seeds of both terrestrial and aquatic plants where many of the seeds were still viable (Ridley 1930, Proctor 1959, De Vlaming and Proctor 1968, McRoy 1968, Jacobs et al. 1981) and often had higher germination rates after passage through the gut (Kretting and Roe 1949, De Vlaming and Proctor 1968, Owen 1980, Agami and Waisel 1986). Such passive dispersal (endozoic transport) can possibly transport seeds far distances. However, crab dispersal of seeds is unlikely because of the probable destruction of seeds from handling and mastication. Although croaker did not appear to feed on the seeds, the potential exists for those and other fishes to disperse eelgrass seeds if seeds are consumed and not damaged by digestion.

The results of this study provide partial 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 Great South Bay, 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 seen by Harrison (1993). The 60-97% loss of viable seeds in the study by Orth et al. (in press) may have been at least partially caused by varying degrees of predation and other losses. The results of this study show that predation loss must be considered as a factor of *Z. marina* seed loss.

Potential predation rates in this study of between 65% (the difference between the crab and whole cages) and up to 96% (observed in the no cage treatments, or higher since these are only one-week experiments), are comparable to seed losses from predation in the terrestrial environment. Hendrix (1988) observed that bruchid beetles can destroy up to 50% of the seed crop of many Central American legumes and that many desert ants and rodents can consume up to 75% of all desert plant seeds produced. Travis (1992) found that rodents heavily predate seeds of *Amianthium muscaetoxicum*.

These losses have implications in the maintenance of *Z. marina* beds or colonization of new habitats, especially those distant from existing beds. This study suggests that establishment of seedlings requires 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. The number of seeds surviving to become established as seedlings is a complex interaction of both biotic and abiotic elements. This study has illustrated the potential role of predators in determining the survival of seeds, which may be related to both predator foraging strategies, predator densities, and availability of primary food resources.
SUMMARY

This study has illustrated the potential role of predators in accounting for Zostera marina seed loss. Callinectes sapidus significantly reduced seed abundance in the predator enclosure experiment. Although Micropogonias undulatus did not significantly reduce seed abundances in the experiment, the potential still exists for seed predation by these animals to occur. Uncontrolled predation may have accounted for some of the losses seen in the predator exclosure experiment. Observations in this study and in the study by Orth et al. (in press) do not suggest that hydrodynamic transport into distant areas was a major factor in seed loss in the experiments. Also, seed losses of up to 96% occurred rapidly, within a week, and refuge from predation via shallow burial did not appear to hinder the degree of seed loss. Finally, it has been predicted that both infaunal and predator abundances may affect predation rate on seeds, due to changing encounter rates between predator, primary prey, and alternative food (Z. marina) seeds. This has significant implications on the sexual reproductive success of Z. marina and on the plant’s ability to recolonize denuded areas of the Chesapeake Bay.
Zostera marina L. (eelgrass), an aquatic angiosperm of the family Zosteraceae (Gleason and Cronquist, 1991), is one of the more common species of submersed aquatic vegetation (SAV) in the Chesapeake Bay (Orth and Moore 1984, Dennison et al. 1993). Z. marina meadows are of significant importance in that they are areas of high primary productivity. They are a source of detritus, which is a food source for some animals and bacteria, as well as a source of habitat for a variety of animals. Water quality has declined in recent decades, affecting the distribution and abundance of Z. marina (Orth and Moore 1983, Kemp et al. 1984) as well as other species of SAV.

Basic Ecology of Seagrasses and Zostera marina: L.

Seagrasses are important in the basic ecology of many shallow water areas. Vegetated areas are sites of high primary and secondary productivity, and also act to reduce current flow, stabilize the sediments, and provide habitat for organisms.

The amount of primary production by seagrasses rivals that of most terrestrial agricultural plants. Thalassia testudinum (turtle grass) has been found to produce standing stocks similar to Zea mays. (McRoy and McMillan 1977). Areas with seagrasses can have community production levels 2-5 times that of unvegetated areas (Kemp et al. 1984). Z. marina, although not as productive as Thalassia still has high amounts of biomass, varying from less than 100 g dry weight m⁻² to over 1000 g dry weight m⁻² (McRoy and McMillan 1977). Wetzel and Penhale (1983) report biomasses of Z. marina in the lower
Chesapeake Bay in the range of 150-225 g C dry weight/m². Rates of primary productivity are also high ranging from 0.2 g C/m²/day to 7.3 g C/m²/day. (McRoy and McMillan 1977).

Production in Z. marina is affected by many environmental factors. High salinities of about 30 ppt have been found to maximize photosynthesis (McRoy and McMillan 1977). Also temperature is one of the strongest factors controlling the production of Z. marina. Photosynthetic rates increase with temperature until about 28° C (Wetzel and Penhale 1983) when photosynthetic efficiency drops sharply. Z. marina can also survive well at very low temperatures around the freezing point. Temperature has been found to be important in many aspects of eelgrass' life cycle and will be discussed later.

The main environmental factor affecting Z. marina growth, distribution and abundance is light availability. Z. marina requires about 20% of incoming PAR (photosynthetically active radiation = 400-700 nm) to survive (Dennison et al. 1993) as compared to 0.5-2% PAR required for terrestrial plants and 0.5-1.0% PAR required for marine phytoplankton (Dennison et al. 1993). This high light requirement is needed to maintain a high root-rhizome biomass system in sediments which are anaerobic and contain high sulfide levels (Dennison et al. 1993). In the Chesapeake Bay, with its high light attenuation coefficient, Z. marina can only receive that 20% PAR light in water shallower than two meters (Orth and Moore 1988, Dennison et al. 1993). Under low light levels, Z. marina shoots (turions) are not very dense, thus minimizing leaf shading (Backman and Barlotti 1976). In addition, low light levels can inhibit flowering of the plant (Backman and Barlotti 1976).

Seagrasses have intermediate C:N ratios; therefore they are easier to decompose than marsh plants, yet they are not as valuable a food source as phytoplankton (Kemp et al. 1984). The only direct consumers besides bacteria
are waterfowl, manatees, and dugongs (Thayer et al. 1984) with herbivory on seeds by crustaceans and fish (Wigand and Churchill 1988, this study). However, high amounts of detritus are formed, which provide a food source for microbial decomposers and detritivores. The regular input of detritus is one reason why meadows have sediments with high organic contents (Kemp et al. 1984).

*Zostera marina* meadows affect currents in and around the meadows (Fonseca et al. 1982, Thayer et al. 1984, Short and Short 1984). In the canopy, water is slowed down due to friction with the shoots and leaves. The grass increases the thickness of the roughness height above the sediment (Fonseca et al. 1982), thereby deflecting the current and shielding the sediment from high current velocities which could possibly erode the sediment. For this reason, *Z. marina* meadows can tolerate currents as high as 120-150 cm/s (Fonseca et al. 1983). For every 1 cm/s current velocity, flow enters 1.25 cm into the bed (at shoot densities ranging from 400-1600 shoots/m$^2$) before current begins to slow (Fonseca et al. 1982). Similarly, the stiffness of the shoots can lessen wave energy within the bed (Fonseca et al. 1982).

Because of the reduced currents inside a seagrass meadow, finer sediments settle out of the water column, enriching the meadow with finer sediment particles and a poorer sorting of grains compared to bare sand outside the meadow (Orth 1977). Roots and rhizomes bind and maintain the sediment (Short and Short 1984). This in addition to reduced erosional ability by a reduced current causes an increase in the elevation of the bed from the surrounding unvegetated areas (Orth 1977, unpublished data).

Seagrasses can also act as nutrient pumps, absorbing phosphate and ammonia through the roots and leaves (McRoy and McMillan 1977). They can thus play an important role in the biogeochemical recycling of the nutrients.
Kemp et al. (1984) found that submersed aquatic vegetation quickly takes up high concentrations of inorganic N and P.

**Faunal ecology:**

Dense assemblages and high secondary production of invertebrates are characteristic of seagrass beds compared to adjacent unvegetated areas (Orth 1977, Orth et al. 1984, Fredette et al. 1990). Research by several investigators during the past few decades have attempted to elucidate the mechanisms resulting in the high diversity and density of both infauna and epifauna (Orth et al. 1984, Orth 1992). Those mechanisms mentioned most frequently are increased food supplies in a meadow (Peterson et al. 1984), increased habitat complexity and refuge from predation (Summerson and Peterson 1984, Gotceitas and Colgan 1989), increased larval supply due to hydrodynamic effects (Ekman 1983) and increased stability of substrate (Orth 1977).

Because of the reduced current flow and higher settlement of finer particles, seagrass meadows are enriched in organic matter (Orth 1977, Thayer et al. 1984, Fonseca et al. 1983). Peterson et al. (1984) found that the suspension feeding bivalve *Mercenaria mercenaria* had higher biomasses inside the meadow, even though current velocities are slower. The increased organic particles in the meadow allowed the bivalve to filter less water while obtaining more nutrition than the lower nutrient, faster current water outside the meadow.

Seagrasses offer increased habitat complexity which epibenthic, infaunal, and free-swimming organisms use to avoid predation (Nelson 1979, Heck and Thoman 1981, Orth et al. 1984, Summerson and Peterson 1984, Gotceitas and Colgan 1987, 1989). According to Orth et al. (1984), seagrasses offer refuge from predation by providing the following: 1) a root-rhizome mat, and 2) a dense plant canopy. The root rhizome mat hinders the ability of predators such as fish
and crabs to dig up buried organisms by creating a distinct barrier or by allowing prey time to escape (Orth et al. 1984). Increased seagrass canopy complexity (shoot density and blade surface area) also hinders predator foraging success; however, there is not a linear function between macrophyte density and predator success. Instead, there is a step-wise function, where certain levels of complexity must be obtained before significant changes in foraging success occurs (Nelson 1979, Heck and Thoman 1981, Goltceitas and Colgan 1989). This 'threshold hypothesis', first developed by Nelson (1979) has been demonstrated by Gotceitas and Colgan (1987, 1989) using *Lepomis macrochirus* (bluegills) and *Micropterus salmoides* (largemouth bass), where only at high shoot densities were bluegills able to successfully hide in the vegetation. The successful evasion of predators depends on shoot densities and predator size, since larger predators are less successful than smaller predators in areas of the same shoot density (Orth 1992). Some organisms take advantage of this refuge by foraging at night near the meadow, where food is still plentiful, but remaining close enough to the meadow to be able to avoid predators (Peterson et al. 1984, Orth et al. 1984).

Increased larval supply in a meadow is another mechanism explaining the high abundances and diversity of fauna inside a meadow. Most larvae have swimming rates significantly less than water currents and can be transported into the meadow by the current. Since currents are slower in the meadow (Fonseca et al. 1982), larvae settle out along with other passive particles and set on the sediment surface or on any structures (seagrass blades or tubes) (Ekman 1983). If the meadow is large enough and the larvae settle out of the water column, there may be a 'settlement shadow' at the center of the bed (Orth 1992).
Life Cycle of *Zostera marina* L:

The life cycle from seed to seed of *Z. marina* takes about two years to complete, although an annual form is known to occur, particularly in the Sea of Cortez, Mexico (McMillan 1983). Plants can live several years. In the Chesapeake Bay, seed production and seed release occurs from May through early June (Silberhorn et al. 1983) while seed germination occurs in late fall (October-November) (Moore et al. 1993).

*Zostera marina* seeds are cylindrical, and average 3.38 mm in length and 1.46 mm in width (Taylor 1957a) with 16-20 ribs on the seed coat (Setchell 1929). A seed germinates by first beginning cell elongation of the axial hypocotyl, which can grow in length up to 14 times its original size (Taylor 1957b). Also, the cotyledon expands by cell elongation, causing the plant to split the seed coat (testa) from end to end (Taylor 1957b). Churchill (1983) considers the first sign of germination as stage 1 and elongation of the axial hypocotyl and cotyledon as stage 2 of seedling development.

The caudicle then elongates and two adventitious roots begin to grow opposite the first node (Setchell 1929). Setchell describes a subsequent elongation of the internodes of the turion, with new turions appearing at the end of the elongating rhizome. At this time, there is considerable plumule growth and formation of root hairs (stage 3 according to Churchill 1983). After a period of quiescence (usually after the first growing season), the terminal turions grow quickly. Some begin to have an erect posture and form inflorescences (by the second year).

Non vegetative shoots are formed from rhizome segments; each shoot with a terminal turion, which may form the next year's reproductive shoot, and more lateral turions (Setchell 1929). Anthesis, pollination, and seed development occur in a spathe/spadix inflorescence (Setchell 1929) which
eventually sloughs off after seed release. There is usually one pistil (ovary, style, two stigmata) and one anther in each flower, (Jacobs and Pierson 1981). DeCock (1980) describes five stages in floral development. In stage 1, the female flower matures. The style bends upwards and in stage 2 bends backwards after pollination has occurred. The two stigmata will then abscise. In stage 3, the half anthers mature and release threadlike pollen. Stage 4 is seed maturation where the anthers disappear a week after pollination and the ovule fills the ovary. The average time for seed maturation is 32.9 days. Finally, in stage 5, the seeds are released when the ovary wall opens along the dorsal side and the seed is pushed out.

The abundances of reproductive shoots and number of seeds produced are highly variable. Silberhorn et al. (1983) reported densities of reproductive shoots between 303-424 /m² which was 11-19% of the total number of shoots. Churchill and Riner (1978) found the density of reproductive shoots to be 53 +/- 24/m² or 6-9% of total shoots. Setchell (1929) reported that there were probably 500-1000 seeds per shoot (Setchell probably was concerned with the entire plant and not individual shoot). The high variability in seeds produced is evident from Table 1.

The regulation and timing of anthesis and seed release appears to be related to water temperature as these two processes occur later with increasing latitude (Table 9) (Silberhorn et al. 1983, Phillips et al. 1983b).

Much of the early work on the reproductive ecology of Z. marina was done by Setchell (1929). He described the following growth aspects occurring at 5°C intervals: no vegetative growth below 10°C, vegetative growth and seed germination at 10°C, continued vegetative growth between 10 and 15°C, sexual reproduction between 15 and 20°C and no growth above 20°C. More recent studies suggest that there is considerable variation to Setchell's findings.
Table 9: Summary of reproductive ecology studies of eelgrass: timing of anthesis and seed release.

<table>
<thead>
<tr>
<th>Author</th>
<th>Location</th>
<th>Anthesis</th>
<th>Seed Release</th>
</tr>
</thead>
<tbody>
<tr>
<td>Silberhorn, et al, 1983</td>
<td>Chesapeake Bay</td>
<td>Feb-April</td>
<td>late May</td>
</tr>
<tr>
<td>Churchill and Riner, 1978</td>
<td>New York</td>
<td>May</td>
<td>mid June-July</td>
</tr>
<tr>
<td>Taylor, 1957</td>
<td>Prince Edward Island</td>
<td>mid July-August</td>
<td>early August-June</td>
</tr>
<tr>
<td>Setchell, 1929</td>
<td>Denmark Mediterranean</td>
<td>June-Feb-May</td>
<td>early August-June</td>
</tr>
<tr>
<td>Phillips and Backman, 1983</td>
<td>Sea of Cortez, Mexico</td>
<td>March-April</td>
<td>May</td>
</tr>
<tr>
<td>Jacobs and Pierson, 1981</td>
<td>Roscoff, France</td>
<td>High bed-May, Low bed-June</td>
<td></td>
</tr>
</tbody>
</table>
Silberhorn et al. (1983) found immature inflorescences were developing at 3°C and seed release occurring at 23-25°C. Churchill and Riner (1978) found anthesis to occur at 15°C (similar to Setchell) yet anthesis continued past 20°C. Jacobs and Pierson (1981) found flowering at 10-15°C. Also, Phillips et al. (1983a) discuss *Z. marina* anthesis in Puget Sound 8-9°C where temperatures rarely get above 15°C. Finally, Phillips and Backman (1983) found anthesis at temperatures over 20°C in the Sea of Cortez, Mexico. These data suggest regional adaptation to local temperature regimes. Within these regions, Silberhorn et al. (1983) also suggest that the longer a favorable water temperature exists and the slower the rise in temperature, the more flowers would be present (Churchill and Riner 1978 report 7.6 spathes per shoot in New York and Jacobs and Pierson (1981) report 20 spathes per shoot in Roscow France compared to Silberhorn et al. 1983 findings of 1-7.2 spathes per shoot in the Chesapeake Bay.

Irradiance levels can also affect flower induction. Backman and Barlotti (1976) found that flowering was inhibited by shading and that irradiance level directly affected reproductive shoot abundances. Jacobs and Pierson (1981) found that eelgrass beds in shallow water areas had more reproductive shoots (and more vegetative shoots) than deeper meadows, suggesting that irradiance affects flowering in addition to vegetative growth.

The timing of seed germination, as with other growth processes, is also highly variable. In the mid-Atlantic, most seedlings germinate in the fall between October and December when kept in sediment-filled containers (Churchill 1983, Moore et al. 1993). Yet germination has been observed throughout the winter and spring (Orth and Moore 1983).
Variation in the timing of seed germination may be related to temperature or salinity effects. Hootsmans et al. (1987) found that maximum germination occurred at 30°C and at 1.0 ppt salinity, decreasing with lower temperatures and higher salinities. However, Orth and Moore (1983) found that seeds held in oxygenated water germinated between 0-10°C and that the germination rate was not significantly affected by salinity. However, seeds held in sediment germinated at 15°C (Moore et al. 1993). McMillan (1983) also found that salinity had little effect on seeds from the Sea of Cortez, Mexico, and temperatures of 18-20°C had the highest germination rate. McMillan found that germination halted at temperatures around 28-30°C, suggesting that Hootsman's results may not apply to all Z. marina populations.

Results of seed germination work by Moore et al. (1993) suggest that conditions in sediment where seeds are deposited, notably oxygen availability, may influence the timing of seed germination. Previous seed germination work conducted without sediment may yield inaccurate conclusions about the timing of seed germination that occurs in the field.

Churchill (1992) found that seeds buried in the anoxic sediment can germinate, yet the seedlings display different growth patterns when grown under anoxic vs. oxic conditions. Under anaerobic conditions, the axial hypocotyl elongates and plumule and adventitious roots are not well developed. In aerobic conditions, the opposite occurs. This suggests that the seed can germinate in anoxic conditions, and then immediately begins to grow in such a way for it to reach oxic conditions needed to survive.

**Meadow growth:**

Maintenance or spread of an existing seagrass meadow by vegetative growth is a function of 1) the rate at which shoots are grown or lost, 2) the length
of time in the year eelgrass has to grow new shoots, and 3) initial density of shoots (Fonseca 1984).

The role of sexual reproduction (i.e. seed production) is a function of density of reproductive shoots (and the relationship of flowering and pollination to reproductive shoot density) and the fate of seeds once produced.

Both processes appeared to operate in the revegetation of a boat scar in the Chesapeake Bay by both *Ruppia maritima* and *Z. marina* (Moore and Orth 1982). They found that, although *R. maritima* recolonizes the area faster than *Z. marina*, *Z. marina* could recolonize the area in about three years. Lateral growth from the undamaged meadow shoots, relic turions, and seedlings were responsible for the recolonization. That study demonstrated the importance of seedlings and sexual reproduction in the colonization of denuded areas. However, this study was in a small area which was surrounded by vegetation. It does not account for introduction and growth of meadows in a previously unvegetated area.
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