Predation on seeds of the seagrass *Posidonia australis* in Western Australia

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ABSTRACT: Despite much evidence that predation governs seed abundance, and ultimately seedling and adult plant distribution and abundance in terrestrial ecosystems, there is a dearth of information from seagrass dominated ecosystems. We report here on the first study to examine predation rates from seeds of *Posidonia australis* measured during field tethering experiments at 5 locations in Western Australia. Seeds that were recently dehisced from ripe fruits and at a similar stage of development were tethered in seagrass and adjacent unvegetated sand for 24 h and then assessed for damage. Seed predation was noted at all sites and ranged from partially to completely eaten seeds. Higher daily proportional damage was observed in seagrass (34 to 53%) than on unvegetated sand (3 to 20%), but was significantly greater at only 3 of the 5 sites. There was no significant difference in proportional mortality for seeds among seagrass meadows, whereas in sand, there was a significant site effect. While we were unable to identify specific seed predators, the type of damage we observed on the seeds suggest small fish or invertebrates are the primary causative agents. Our results add to the growing body of evidence that seagrass seed predation does occur, that it has the potential to affect recruitment, and has implications for understanding the dynamics of *P. australis* meadows. Finally, our data present an interesting contrast to the paradigm for seagrass faunal studies, which almost invariably have shown higher proportional mortality in bare sand than in seagrass.

KEY WORDS: Seeds · Seagrass · Predation · *Posidonia australis* · Western Australia · Tether

INTRODUCTION

Predation is important in influencing a large variety of plant and animal populations (Jansen 1971, Sih 1985, 1987). In marine systems where structured habitats such as marshes, seagrass meadows or mangrove forests are prevalent, predation has long been known to be important in determining faunal abundances (see reviews by Orth et al. 1984, Bell & Pollard 1989, Bell et al. 1991, Heck & Crowder 1991). However, the impor-tance of seed predation, in particular for seagrasses, is incompletely understood.

Predation does appear to be an important factor in the few existing studies on the fate of seagrass seeds. For example, Wassenberg & Hill (1987), Wassenberg (1990) and O'Brien (1994) found seeds of *Zostera capri-corni* to be an important part of the diet of the juvenile brown tiger prawn *Penaeus esculentus* during periods of seed production. Wigand & Churchill (1988) found that a variety of crustaceans fed on *Z. marina* seeds in the laboratory when alternative foods were not available. Fishman & Orth (1996) found the blue crab *Calli-nectes sapidus* to be an important seed predator of *Z.*

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marina in field experiments, and Holbrook et al. (2000) found seeds of *Phyllospadix torreyi* eaten both in the predispersal, i.e. still on the parent plant, as well as the dispersal phase. Nakaoka (2002) reported seed producing spathes of *Z. marina* and *Z. caulescens* with seeds that were bored by a tanaid crustacean, *Zeuxo* sp., which resides within the spathe. Given the importance of seed predation in terrestrial systems (Jansen 1971) and the similar, but limited, evidence that exists for marine angiosperms, predation might generally be expected to be an important process influencing the abundance of seagrass seeds, and subsequent seedling establishment.

Species in the genus *Posidonia* dominate seagrass beds in temperate regions of Australia, with 7 species presently known in Western Australia (Cambridge & Kuo 1979, Kirkman 1985, Kirkman & Walker 1989, Kirkman & Kuo 1990, Campey et al. 2000). One species, *P. australis* Hook. f., occurs in sheltered water (less than 10 m) in embayments on coasts of the southern half of Australia, and in Shark Bay forms extensive meadows of 100s of km^2 (Kirkman & Walker 1989, Walker 1989).

Flowering and fruit development of *Posidonia australis* occur from late winter (July to August) to early summer (November to December). Numbers of fruits produced range from 8 to 20 per pedicel, with 1 seed per fruit (Kuo & Kirkman 1996). *P. australis* generally produces abundant fruits every year (Kirkman & Kuo 1990) with recorded densities of up to 678 m^2 (Cambridge & Hocking 1997). Fruits are buoyant and float to the surface when broken off from the pedicel. Seeds of *P. australis*, which have no dormancy period (Inglis 2000, Orth et al. 2000), are negatively buoyant and sink to the bottom when released from the floating fruit, where they become buried and develop into seedlings. Seeds are large (up to 20 mm long) and consist of an enlarged storage organ or hypocotyl, an embryo in the distal portion of the hypocotyl, an epicotyl, a plumule with leaf primordia and a pair of root primordia (Cambridge & Kuo 1979, Kuo & Kirkman 1996), which may begin growth in the fruit before dehiscence. *P. australis* seeds, when first released from the fruit, have significant nutritional value for seed eating predators (Hocking et al. 1980, Kuo & Kirkman 1996). The distal portion of the seed, which contains the plumule with growing leaves along with root primordial, is rich with protein but contains little starch. The hypocotyl has starch but little protein.

Recently released seeds have been observed on bare sediments and in *Posidonia australis* meadows (pers. obs.), although newly established seedlings have only been observed in unvegetated areas or areas vegetated with *Halophila ovalis* (Orth 1999). The fate of *P. australis* seeds within *P. australis* beds remains unknown.

We hypothesized that seed predation is a major cause of the lack of seedlings in *Posidonia australis* beds. To test this hypothesis, we conducted experiments at a number of locations along the Western Australian coast. We report here on the results of the first study to experimentally examine predation rates on seeds of *P. australis*.

MATERIALS AND METHODS

Study sites. Seed predation experiments were conducted in *Posidonia australis* beds at 5 locations in Western Australia. Two were at Rottnest Island (Stark Bay, Parker Point), 1 was at Woodman Point south of Perth and 2 were in Shark Bay (Denham and Eagle Bluff), the most northern limit of this species (Fig. 1).

Seed collection. Mature fruits of *Posidonia australis* were collected by hand from beds at either Woodman
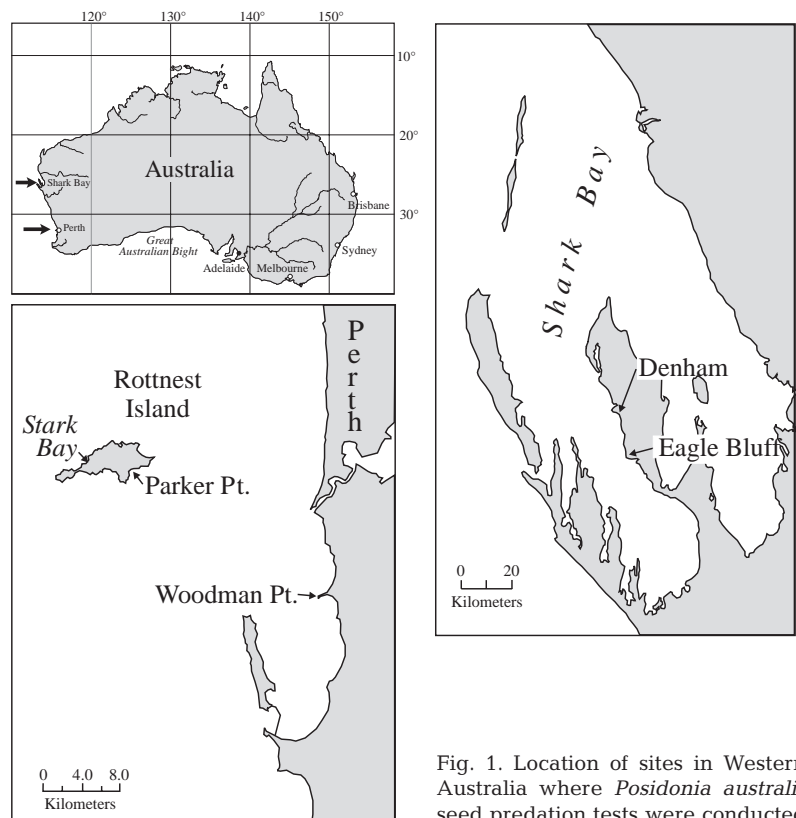

Fig. 1. Location of sites in Western Australia where *Posidonia australis* seed predation tests were conducted

Point or Rottnest Island (Fig. 1). Fruits were gently removed from reproductive stalks, placed in cloth mesh bags and returned to the laboratory where they were placed in 20 l buckets until seeds dehisced from the fruit. Because seeds have no dormancy and can begin growing even within the fruit, we only used seeds that were at a similar stage of development. Seeds with either developing roots or an emerging leaf were not used in experiments. Water was exchanged every 24 to 48 h. Seed experiments in Shark Bay were conducted just after the period of seed shedding and local seeds were unavailable. Instead, seeds from the Woodman Point location were used at the 2 Shark Bay sites. Fruits were transported in seawater to Shark Bay and we only used recently dehisced seeds at the same stage of development as in the southern locations.

Field experiments. Experiments were conducted by anchoring tethered seeds in either seagrass stands or in adjacent bare sand and checking them for damage at 24 h intervals. Tethering has been used successfully in animal studies to examine predation potential (Pile et al. 1996). Concerns have been expressed in using tethering techniques with highly mobile species such as some decapod crustaceans (Peterson & Black 1994, Aronson & Heck 1995, Kneib & Scheele 2000, Aronson et al. 2001). Mobility of seeds can only occur via biotic, e.g. by animals ingesting seeds or bioturbation that could bury seeds, or abiotic (water current) mechanisms (Chambers & MacMahon 1996) and thus, should not be subject to the types of artifacts noted in mobile prey. We therefore believe that the tethering technique is an appropriate tool to determine proportional mortality of seeds.

The tethering process entailed threading a 3.6 kg test monofilament line through the center of the hypocotyl and attaching approximately 0.4 m of line. The line with the tethered seed was attached to a steel anchor, which was then inserted into bottom sediments. The hypocotyl of *Posidonia australis* is extremely fibrous, and once threaded, could only be removed from the tether by breaking the seed in half.

At each of the 5 sites, 2 arrays of 5 tethered seeds were placed in vegetation and 2 arrays in unvegetated sand. Approximately 25 m separated each array. Thus, each site had a total of 20 seeds. Tethered seeds in each array were placed haphazardly in either seagrass or sand approximately 1 to 2 m from the edge of the bed, with each seed located 1 to 2 m from the next seed. After 24 h, seeds were examined and scored for predation effects. Any missing seeds, and seeds that had been partially eaten, were noted and replaced for the subsequent 24 h period. If any part of the seed including the epicotyl was gone, it was recorded as partially eaten. If a seed was missing from the tether, we assumed that it was lost to predation because of the difficulty we encountered in physically removing seeds from the tether.

Experiments were conducted in November and December 2001. Trials were run for 8 d at Parker Point (November 21 to 28), 4 d at Stark Bay (November 26 to 29), 7 d at Woodman Point (December 2 to 8), 4 d at Denham (December 6 to 9) and 3 d at Eagle Bluff (December 6 to 8). At each site, we measured water depth, canopy height and shoot density. Water depth was estimated for each site. Five shoots were randomly harvested from each experimental site and the longest leaf from each shoot was measured for the determination of the canopy height. Shoot density was determined by counting the number of shoots from within 3 randomly tossed 10×10 cm quadrats at each experimental site. We did not directly measure tidal height but used data available from the Government of Western Australia's Department for Planning and Infrastructure.

We attempted to identify potential seed predators within the Parker Point seagrass bed by observing seeds *in situ* that were suspended above the canopy. Ten seeds (5 at each of the 2 sites) were tethered and tied to a line placed above the canopy, so that each seed was suspended approximately 20 cm above the canopy. The lines were placed within 5 m of the locations where the seed predation experiments were being conducted. Divers could easily observe these seeds at a distance of approximately 10 m. Seeds remained tethered to the line for a 48 h period. Direct observations were made for approximately 30 min at the initiation of the test period and a second 30 min period 24 h later. At the end of the test period, all seeds were removed and carefully examined for signs of predation.

Although we assumed that artifacts of the tethering process were minimal (see above), we made observations of untethered seeds at each location to gain a better understanding of seed movement once a seed settled on the sediment surface after dehiscing from the fruit. We were particularly interested in the seed's lateral movement on the sediment surface that could possibly be compromised by restraining seeds with the tether. At the initiation of each daily predation experiment, we placed 5 or 6 untethered neutral red stained seeds in the sand area next to one of the arrays, and located them 24 h later. The staining facilitated distinguishing seeds used in the experiment from any seeds that might have washed into the site. While the stain could have played some role in compromising biotic interactions, the goal here was simply to better understand the behavior of a seed and how far it could move over a 24 h period.

Statistical methods. Proportional mortality was calculated for each seed array as the proportion of initial seeds that was missing or partially eaten. These data were then arc-sign square-root transformed for analysis. Variance in proportional mortality across sites did not meet the assumptions of homogeneity of variance required by ANOVA, so effects of habitat type (grass or sand) were tested at each site individually with a Mann-Whitney *U*-test (Zar 1996). A 1-factor ANOVA tested for differences in mortality between days of the experiment at each site. A Kruskal-Wallis test was used for each vegetation type to identify differences in mortality among sites (Siegel 1956, StatSoft 2000).
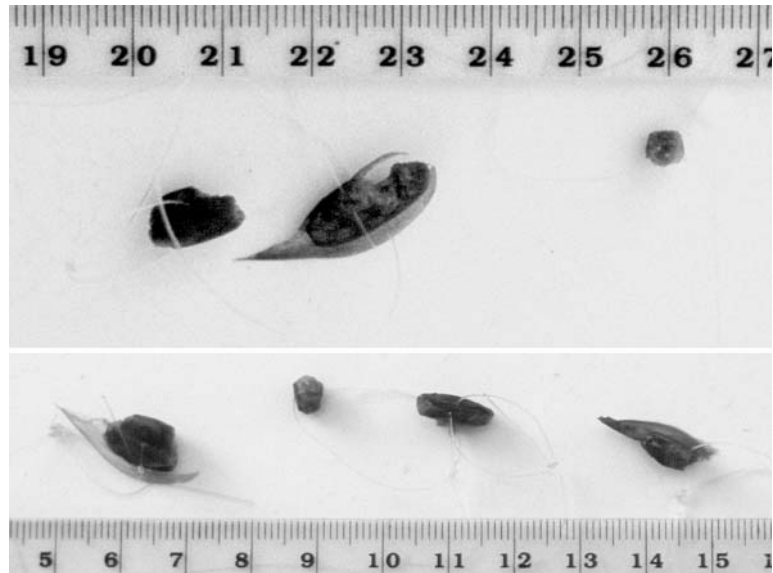

Fig. 2. *Posidonia australis.* Some tethered seeds that were partially eaten during seed predation experiments

RESULTS

Predation on *Posidonia australis* seeds was evident at all sites as noted by either a partially eaten seed or seeds completely missing from the tether. Seeds that were partially eaten (Fig. 2) ranged from those showing removal of the distal ends of the seed including the epicotyl, to those with a few bite marks on the hypocotyl and finally, to the complete removal of the seed. Because of this pattern, we were confident that seeds absent from a tether were likely to have been eaten. Interestingly, while not quantified, we noted that many of the seeds were eaten only at the distal end.

Mann-Whitney *U*-tests showed significantly higher proportional mortality in the seagrass than in sand at Woodman Point, Parker Point and Stark Bay, but no significant differences at Denham or Eagle Bluff (Table 1, Fig. 3). Mortality did not differ significantly between days in 9 of 10 cases (Table 2). Kruskal-Wallis tests showed no significant site differences in mortality within seagrass; however, mortality in sand differed significantly between sites (Table 3). At each site, of the total seeds that were damaged or lost entirely, the percentage that was partially eaten (as opposed to missing) (Fig. 3)

was 32, 18, 71, 41 and 75% in Woodman Point, Parker Point, Stark Bay, Denham or Eagle Bluff seagrass beds, respectively, while in the sand, 54, 0, 0, 38, and 100% were partially eaten at Woodman Point, Parker Point, Stark Bay, Denham or Eagle Bluff, respectively (Fig. 3).

Direct observations for approximately 30 min d^{-1} showed no animal approaching the seeds tethered from the line and suspended above the canopy. We observed no signs of predation on any of the seeds over the 48 h test period.

During the trials, only 3 tethered seeds in sand were found buried, 1 at Parker Point and 2 at Stark Bay. In Stark Bay, a large hole had been excavated in the sand near the experimental seeds, probably by a large ray, and disturbed sediment covered 2 seeds.

Table 1. *Posidonia australis.* Results of Mann-Whitney *U*-tests comparing proportional mortality between habitat types (grass vs sand) at each site

Site	U	n grass	n sand	p
Woodman Pt.	10	14	14	0.00001
Parker Pt.	4	16	16	0.00000
Stark Bay	13.5	8	8	0.04988
Denham	20.5	8	8	0.23450
Eagle Bluff	11	6	6	0.30952

Table 2. *Posidonia australis.* Results of 1-way ANOVA testing for differences in proportional mortality among days for each site and habitat type

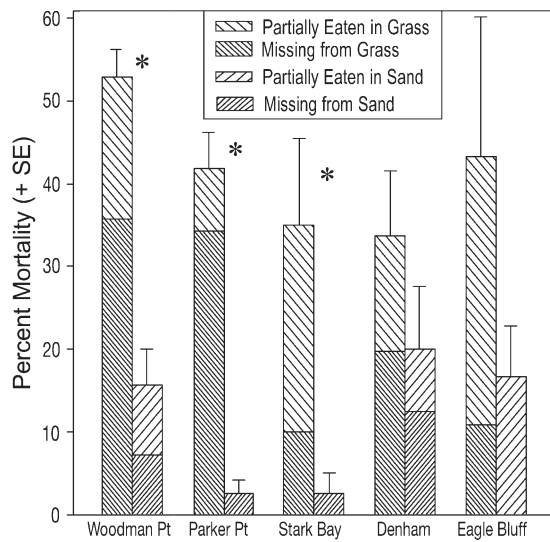| Site	Habitat type	df effect	df error	F	p
Woodman Pt.	Grass	6	7	0.5814	0.7371
	Sand	6	7	0.5199	0.7783
Parker Pt.	Grass	7	8	0.3254	0.9216
	Sand	7	8	0.8571	0.5741
Stark Bay	Grass	3	4	3.1035	0.1513
	Sand	3	4	1.0000	0.4789
Denham	Grass	3	4	0.6368	0.6297
	Sand	3	4	1.2323	0.4076
Eagle Bluff	Grass	2	3	0.0584	0.9443
	Sand	2	3	22.7877	0.0153

Fig. 3. *Posidonia australis.* Proportional mortality of seeds in seagrass beds vs bare sand at the 5 sites (mean + SE). Average mortality is divided into 2 components representing the overall proportion of partially eaten seeds and completely removed seeds for each site and each substrate. *Significant differences between the 2 habitat types (see Table 1 for significance levels)

At Parker Point and Stark Bay, 83% of the untethered stained seeds remained close to or within 1 m of the release point. Careful examination of the sediment surface for the missing seeds did not reveal any buried seeds. During 1 trial at Parker Point, no untethered seeds were found. We attributed this to boat propeller disturbance, as a small area near the release point showed characteristic sediment disturbance by propellers. At Woodman Point, only 26% of the untethered seeds were recovered, while at the Denham and

Table 3. *Posidonia australis.* Kruskal Wallis tests of site differences in proportional mortality in each habitat type

Grass	$H(4, n = 52) = 7.151963$		
	n	Rank sum	
Woodman Pt.	14	398	
Parker Pt.	16	321	$p = 0.1281$
Stark Bay	8	246.5	
Denham	8	197	
Eagle Bluff	6	215.5	
Sand	$H(4, n = 52) = 15.62039$		
	n	Rank sum	
Woodman Pt.	14	418	
Parker Pt.	16	328	$p = 0.0036$
Stark Bay	8	164	
Denham	8	239	
Eagle Bluff	6	229	

Eagle Bluff sites, only 5% of the untethered seeds were recovered. Seagrass beds at Parker Point and Stark Bay were protected from waves by a nearby sandstone reef system, while the other sites had fetches of 10 or more km, which probably contributed to the varying retention rates of the untethered seeds.

Eagle Bluff was the shallowest location where experiments were conducted, while water depths were greatest at Parker Point and Stark Bay (Table 4). Mean tidal range for Parker Point, Stark Bay and Woodman Point was 0.64 to 0.95 m (maximum range, 1.3 to 1.5 m), while at Denham and Eagle Bluff, mean tidal range was 0.83 to 1.10 m (maximum range, 1.61 to 1.94 m) (Table 4). Shoot densities were lowest at Eagle Bluff and similar at the other 4 sites. Canopy height was shortest at Eagle Bluff and greatest at Woodman Point.

DISCUSSION

Seed predation has figured prominently in numerous studies of terrestrial ecosystems across broad latitudinal gradients (Jansen 1971, Harper 1977). In many areas, 100% of seed production is lost to predation (Jansen 1971). The relatively few studies to date suggest that predation on seagrass seeds may be an important process governing seed survival and ultimately, seedling establishment (Wassenberg & Hill 1987, Wigand & Churchill 1988, Wassenberg 1990, Fishman & Orth 1996, Holbrook et al. 2000). In particular, one of the more comprehensive studies on seed predation to date on surfgrass, *Phyllospadix torreyi*, (Holbrook et al. 2000) found predation occurring in both the predispersal (7 to 15%) and dispersal (>50%) phases, and to be temporally variable (10 to 50%). Our study, the first to tether seeds in different habitats, adds to the growing body of evidence that significant seagrass seed predation does occur. *Posidonia australis* seeds, which are some of the largest seeds produced by any seagrass species (Inglis 2000) and visible on the sediment surface, suffered higher proportional mortality in all vegetated areas than in unvegetated areas.

Invertebrates, principally decapod crustaceans, have been identified as key predators on seeds (Wassenberg & Hill 1987, Wigand & Churchill 1988, Wassenberg 1990, Fishman & Orth 1996, Holbrook et al. 2000, Nakaoka 2002), although fish and waterfowl have also been reported to ingest seeds of seagrass (Adams 1976, Baldwin & Lovvorn 1994) and of freshwater submersed macrophytes (Agami & Waisal 1986). Seagrass beds in Western Australia, in the locations where we conducted our experiments, have a diverse assemblage of vertebrates and invertebrates (Black et al. 1990, Ayvazian & Hyndes 1995). While we were unable to

Table 4. Environmental and seagrass characteristics at the 5 sites where the seed predation experiments were conducted

Site	Latitude, longitude	Water depth (m)	Mean tidal range (m)	Shoot density No. per 100 cm^2 (±SD)	Canopy height (cm ± SD)
Parker Pt.	32.02240° S, 115.52870° E	2	0.64–0.95	6.1 ± 1.7	28.2 ± 5.0
Stark Bay	32.00654° S, 115.48691° E	2	0.64–0.95	4.4 ± 1.7	36.0 ± 6.1
Woodman Pt.	32.13660° S, 115.74508° E	2	0.64–0.95	4.9 ± 1.2	45.2 ± 5.2
Denham	25.92697° S, 113.53041° E	1	0.83–1.1	6.5 ± 1.1	35.9 ± 5.9
Eagle Bluff	26.09463° S, 113.58468° E	0.5	0.83–1.1	2.7 ± 1.1	16.2 ± 4.7

observe any direct seed predation, we did note numerous fish species both in and above the seagrass canopy as well as in the adjacent unvegetated sand. As many of the bite marks that we observed on the seeds were generally small, we suggest that potential predators are small fish, such as juvenile leatherjackets *Monacanthus* spp., zebra fish *Girella zebra* and buff bream *Khyphosus* spp., and possibly decapods. However, we saw no evidence of mobile decapods during qualitative visual surveys at both Parker Point and Stark Bay. One large potential decapod predator, the blue swimmer crab *Portunus pelagicus*, present in the Woodman Point area, has not been observed around the Rottnest Island area (D. Walker pers. comm.). The blue swimmer crab has been observed with whole seeds in its chela (M. Cambridge pers. comm.) and it is possible that the higher number of seeds preyed upon at Woodman Point in the unvegetated sand compared to Stark Bay and Parker Point may be due to their foraging activities.

Because seeds were preyed upon preferentially in seagrass, we expected to observe predation on the seeds that were suspended immediately above the canopy at the Parker Point site. Quite surprisingly, we did not observe a single seed preyed upon during the 48 h test period, even though seeds were being preyed upon within the canopy at the experimental sites during this same period. The lack of any predation on these suspended seeds suggests that seed predators at this site were grassbed residents that remained within the canopy.

We found no significant difference among sites in proportional mortality for seeds in seagrass, whereas in sand there was a significant site effect. The differences in predation rates in sand might be a function of different predator guilds and the foraging strategy of these species in sand. The predation results from the Rottnest Island area may explain, in part, observations made earlier from a number of locations around Rottnest Island that seedlings from seeds produced early in the season were found only in unvegetated sand or in *Halophila* spp. beds, and not in dense *Posidonia* spp. (Orth 1999). Because recently released seeds of *Posidonia australis* are present in *P. australis* beds as well

as bare sand (pers. obs.) during the period of maximum seed release, seeds in *P. australis* beds are more likely to incur higher proportional mortality than in bare sand. *Halophila* spp. has low structural relief (i.e. short, oval leaves with maximum canopy height of approximately 5 to 10 cm) and it may be that the seed predator guild present in *Posidonia* spp. is absent in *Halophila* spp. Whether this pattern of seedling distribution across the distributional gradient of *Posidonia* spp. is atypical will require additional studies.

We are uncertain whether or not partially eaten seeds could continue developing into viable seedlings. If the distal end, which contains the embryo, is consumed, it is likely the seed ceases to exist. This section contains higher amounts of protein than the hypocotyl (Kuo & Kirkman 1996) and can be a significant food source during seed production. Wassenberg (1990) suggested that the high energy content of *Zostera capricorni* seeds could be a valuable food source for juvenile brown tiger prawns (*Penaeus esculentus*). If only a portion of the hypocotyl is consumed, the seed may be able to continue to develop. We did observe a number of tethered seeds where only the distal ends were eaten suggesting that predators may be selecting the higher nutritional portions of the seed. Future work could examine how much of a seed could be eaten to prevent successful seedling development.

These data have implications for understanding the dynamics of seagrass meadows dominated by *Posidonia australis. P. australis* seeds, which are produced annually, may be more important in the initial establishment of a patch, and play less of a role in a bed's subsequent development (sensu 'Initial seedling recruitment', Eriksson 1989). Seed dispersal into developing patches would more likely incur higher proportional mortality depending on how rapidly patches develop their associated faunal community, including seed predators. Seeds deposited on unvegetated sand, even in close proximity to seagrass bed margins, are more likely not to be eaten, allowing the seed to develop into a seedling and contribute to the expansion of the meadow. Given the dynamic nature of seagrass assemblages in Western Australia (Kendrick et al. 2000, 2002) where hydrodynamic processes can lead to

and maintain patches of seagrass, relatively higher survival in sand may be necessary to allow for rapid colonization of denuded areas following large-scale disturbances.

Our seed predation data present an interesting contrast to the predation refuge paradigm developed for seagrass fauna. Results from numerous faunal studies have generally shown higher proportional mortality in bare sand, with increasing structure leading to higher proportional survival of prey (see reviews by Heck & Crowder 1991, Heck et al. 1997). Processes influencing seed survival may therefore be quite different from what has been documented for fauna and may need to be considered in future seagrass ecosystem models.

This first study of seed predation in the genus *Posidonia* included only 1 of the 7 species found in Australian waters. Future studies should focus on relative predation rates of other *Posidonia* species as well as the fate of seeds settling within the canopy of co-occurring species or canopies of different genera (e.g. *Posidonia*, *Amphibolis*, *Halophila*). Also, the suite of potential seed predators within canopies of the different seagrass species in Western Australia must be identified as well as other sources of seed mortality, and their individual impacts studied in order to better understand the role of seed predation as it influences seagrass dynamics in these areas.

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