

# Predation on *Posidonia australis* seeds in seagrass habitats of Rottnest Island, Western Australia: patterns and predators

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**ABSTRACT:** Seed predation is an important process governing the dynamics of many plant populations. We assessed seed mortality due to predation in the seagrass *Posidonia australis* by identifying predators and quantifying predation events using underwater video cameras, laboratory and field observations, and field tethering experiments in shallow-water habitats off Rottnest Island, Western Australia in 2003 (2 sites) and 2004 (5 sites). We assessed 4 dominant habitats: within seagrass meadows of (1) *P. australis*, (2) *Amphibolis antarctica* and (3) *Halophila ovalis*, and on (4) unvegetated sand. Video analysis and field and laboratory observations showed that at least 6 different crustacean taxa were seed predators—the portunid crabs *Nectocarcinus integrifrons* and an unidentified portunid similar to *Thalamita crenata*, the majid *Naxia aurita*, the isopod *Cymodoce* sp., and the hermit crabs *Paguristes purpureantennatus* and *Calcinus dapsiles*—with *N. integrifrons* and *Cymodoce* sp. being the principal seed predators. Various species of fishes were observed approaching (but never eating) seeds in the video analysis, and none appeared to be seed predators. In 2003, daily seed predation rates were dramatically higher in *A. antarctica* beds than in other habitats at Parker Point (mean 63% d<sup>-1</sup> compared to means of <20% d<sup>-1</sup> for the other habitats), but not at Nancy Cove, the only other site studied in 2003. In 2004, daily seed predation rates were higher in *Posidonia australis* (40 to 73% d<sup>-1</sup>) and *A. antarctica* (36 to 85% d<sup>-1</sup>) beds than in *H. ovalis* (9% d<sup>-1</sup>) beds and unvegetated sand (3 to 13% d<sup>-1</sup>) at all 5 sites studied. Logistic regression showed an approximately 20-fold increased chance of a predation event occurring within a 24 h period in *P. australis* and *A. antarctica* beds compared to unvegetated sand, but no increase in predation in the *H. ovalis* beds compared to sand. Although predation rates varied among sites and years, patterns among habitats were generally consistent. *P. australis* and *A. antarctica*, the 2 seagrass species with structurally complex canopies, had much higher rates of seed predation than the habitats with less structure, i.e. *H. ovalis* and bare sand, which may provide insufficient refuge for seed predators. These results may have important consequences for plant demographics and genetic structuring of local populations. Viewing seagrass seed dispersal strategies in the context of faunal-dependent predation processes, rather than simply in terms of plant–plant competitive interactions, may provide a better understanding of seagrass spatial distributions and successional dynamics.

**KEY WORDS:** *Posidonia australis* · Seagrass · Seed predation · Predators · Western Australia

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## INTRODUCTION

Seed predation is an important process regulating the dynamics of plant populations (Janzen 1971, Wenny 2000). For terrestrial plants, seed predation can

be significant, reaching almost 100% of seed production in some cases (Crawley 1992, Wenny 2000, Clarke & Kerrigan 2002). Predation has been suggested as a major mechanism underlying the 'Escape Hypothesis' explaining higher survival of seeds and seedlings at

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greater distances from adult plants (Janzen 1970, Connell 1971, Howe & Smallwood 1982, Harms et al. 2000, Howe & Miriti 2000). In marine vascular plants, for which seed dispersal is facilitated by buoyancy and water movement (Orth et al. 2006), losses due to predation in the habitats to which seeds disperse have been poorly documented (Orth et al. 2006).

Predation on seagrass seeds or dispersing propagules has been demonstrated for a few seagrass species, and has been attributed primarily to a variety of crustacean taxa, and secondarily to fishes (Wassenberg & Hill 1987, Wigand & Churchill 1988, Wassenberg 1990, Williams 1995, Fishman & Orth 1996, Holbrook et al. 2000, Nakaoka 2002, Orth et al. 2002). The results of several of these studies suggest that seed predation may be important in governing seed survival, and ultimately seedling establishment (Fishman & Orth 1996, Holbrook et al. 2000, Lacap et al. 2002, Orth et al. 2002). However, seed survival may be also influenced by such factors as seagrass structural complexity (e.g. shoot density, leaf morphology) and density of predators of crustaceans and fishes in different seagrass habitats. These factors have been shown to influence predation rates on fauna (Heck & Orth 2006), but little information is available for seeds.

*Posidonia australis* Hook. F., 1 of 8 seagrass species in this genus, is abundant in sheltered water (<10 m) embayments of temperate southern Australia (Larkum & den Hartog 1989). *P. australis* produces large (approx. 20 mm), fleshy fruits annually from mid-November through early December at fruit densities of up to 678 m<sup>-2</sup> (Kuo & McComb 1989, Cambridge & Hocking 1997). Each fruit contains a single embryo or seed, which grows continuously in the fruit while it remains on the plant, as well as in the dispersal phase after the buoyant fruit breaks off from the parent plant. There is no dormancy, and thus the plants could be considered viviparous (Kuo & Kirkman 1996). While an actively growing, mature seed can be released from the fruit while it remains on the parent plant, actively growing seeds generally dehisce from the fruit while this is floating on the water surface, and subsequently sink to the sediment surface. For the purpose of this paper, we use the term 'seed' to refer to the dispersing unit after it has dehisced from the fruit and settled on the sediment surface, but before it becomes established in the sediment. We reserve the term 'seedling' for an established plant growing in the sediment.

In western and southwestern Australia, it is not uncommon to find up to 8 sympatric species of seagrass (*Posidonia ostenfeldii* complex, *P. australis*, *P. sinuosa*, *P. angustifolia*, *Amphibolis antarctica*, *A. griffithii* and ephemeral species such as *Halophila* spp. and *Zostera tasmanica*) (Kendrick et al. 2000). While it is probable that *P. australis* seeds could settle in any of these struc-

tured habitats, depending on the timing of seed dehiscence and the spatial distribution of seagrasses and unvegetated sand, established seedlings have only been reported to date from either bare sand or in *H. ovalis* patches (Kuo & Kirkman 1996, Orth 1999, R. J. Orth pers. obs.). Settled *P. australis* seeds have been observed within canopies of other seagrass species, but their ultimate fate has not been determined (R. J. Orth pers. obs.). A recent study found higher daily mortality of *P. australis* seeds due to predation in beds of *P. australis* compared to bare sand (Orth et al. 2002), suggesting that seed predators may regulate seed survival in vegetated areas; however, only 2 habitats were compared, and no direct observations were made of any predation events (Orth et al. 2002).

The objective of this study was to assess *Posidonia australis* seed mortality due to predation in seagrass meadows of the species *P. australis*, *Amphibolis antarctica* and *Halophila ovalis*, as well as in unvegetated sand, by identifying predators and quantifying predation events using underwater video cameras, laboratory and field observations, and field tethering experiments. We compare our results to other seed predation studies.

## MATERIALS AND METHODS

**Study sites.** *Posidonia australis* seed predation observations and experiments were conducted in 2003 and 2004 in meadows of 3 seagrass species and in bare sand off Rottnest Island, Western Australia. In 2003, experiments were conducted between November 21 and 28 at 2 sites (Parker Point, 7 d; Nancy Cove, 3 d) in 4 habitat types (*P. australis*, *Amphibolis antarctica*, *Halophila ovalis* and bare sand) (Fig. 1). In 2004, experiments were conducted between November 22 and December 2 at 5 sites (Parker Point, Nancy Cove, and Stark, Armstrong and Parakeet bays, 7 d each) in the same habitats, except that *H. ovalis* was included only at Parakeet Bay and Nancy Cove (Fig. 1). Seagrass beds at all sites ranged from 1 to 3 m in water depth (tidal range 0.64 to 0.95 m). Within each site, all habitats were located within 25 to 100 m of each other. Only habitats that were monospecific and continuous for a minimum of 20 m were chosen for the experiments, in order to accommodate transects of 10 seeds at 2 m intervals. Mean *P. australis* shoot densities within 10 haphazardly tossed 20 × 20 cm quadrats at Parker Point, Nancy Cove, Stark Bay, Armstrong Bay and Parakeet Bay were 380, 460, 390, 510 and 600 shoots m<sup>-2</sup>, respectively. *A. antarctica* shoot densities (defined as the density of single stems each with a cluster of leaflets) were 500, 520, 640, 970 and 630 shoots m<sup>-2</sup>, respectively for the same sites. *H. ovalis* shoot

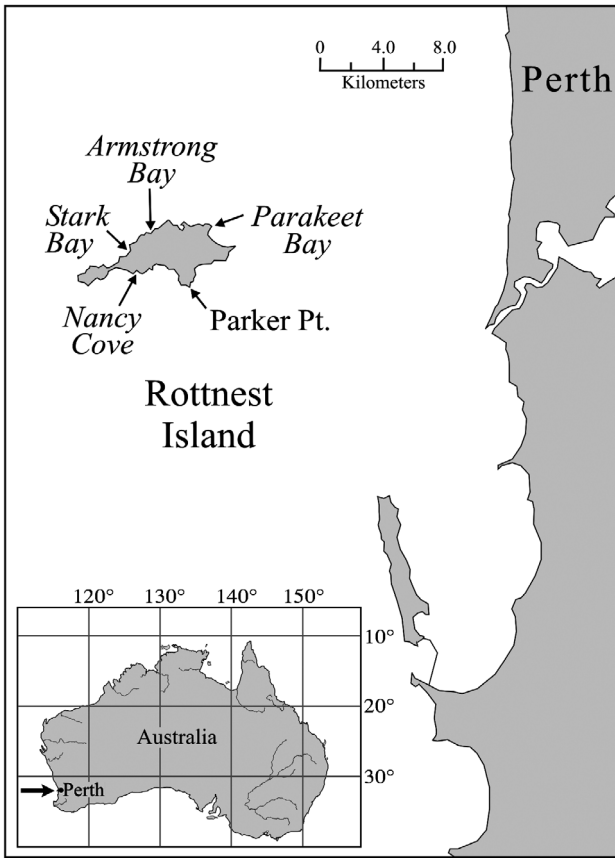


Fig. 1. Experimental sites on Rottneest Island, Western Australia

densities for Parker Point and Nancy Cove were 900 and 1040, shoots  $m^{-2}$ , respectively.

**Video assessments.** Video cameras were deployed in *Posidonia australis* and *Amphibolis antarctica* meadows at Parker Point between November 19 and 22, 2003 and November 23 and 29, 2004. In 2003, deployments were made at 2 to 3 m depth, 50 m from the beach; 6 Sony TRV15 digital video cameras in underwater housings were deployed for various periods during both daytime and nighttime. Cameras were run either with time lapse (2 s recordings at 30 s intervals) or continuously. Continuous recording gave the best results because the crabs observed eating seeds were highly mobile and moved in and out of the field of view within seconds. Untethered and tethered seeds were both used initially, but untethered seeds were carried away by animals rather than being consumed in front of the cameras, so tethered seeds were used after initial trials. Some canopy clearing was necessary, as some leaves and stems of the seagrasses obscured the seeds. The field of view was small, covering a  $20 \times 20$  cm area horizontally in front of the camera. The crabs observed consuming seeds moved quickly through the field of view of the video camera, and predation events lasted for  $<1$  min.

In November 2004, 6 Sony TRV15 digital and 4 Sony Handycam Hi8 analog cameras were deployed on 6 nights in *Posidonia australis* and *Amphibolis antarctica* meadows (2 to 3 m depth) at Parker Point after dusk (between 19:00 and 21:30 h). All seed predation activity in 2003 was observed during the period after dusk. Deployments occurred during peak fruiting of *P. australis* between November 23 and 29 2004. Far red lighting ( $>600$  nm wavelength) was deployed to illuminate the seeds; 3 seeds were tethered on the same line and placed 15 cm in front of the cameras. Tethered seeds were collected when cameras were recovered, and partially eaten and lost seeds were documented. The video was then viewed using either a TV or a laptop computer: 340 min continuously recorded analog video and 160 to 240 min digital video were captured for *P. australis* and *A. antarctica* meadows during each evening deployment. Observations of seed predation, responsible predator, and time and duration of predation were recorded. The activity of animals unrelated to seed predation and the activity of fishes and cephalopod predators of crabs were also recorded.

**Seed-predator collection.** In 2003, we hypothesized that hermit crabs could be important seed predators, based on their abundance in the different meadows, and a direct observation of a hermit crab taking a tethered seed into its shell. We collected several crabs of 2 species (*Paguristes purpureantennatus* and *Calcinus dapsiles*) and placed a single individual with a *Posidonia australis* seed in a plastic tray with ambient seawater under natural light, and observed them for feeding patterns over several 24 h periods. In addition, hermit crab abundance was measured in a  $1 \text{ m} \times 10 \text{ m}$  transect in each habitat at each site ( $n = 8$  transects).

In 2004, likely seed predators were collected at night by pushing a net ( $55 \times 75$  cm, 2 mm mesh) by hand through *Posidonia australis* beds at Parker Point. Samples were sorted in the field and returned immediately to the laboratory. Crabs, shrimp, and the isopod *Cymodoce* sp. were isolated with a single *P. australis* seed in plastic trays with ambient seawater and natural light conditions, and observed for 24 h. Partially eaten seeds were photographed and bite marks were compared with those on partially eaten seeds from field experiments.

**Seed-tethering experiments.** Mature fruit of *Posidonia australis* was collected by hand from beds adjacent to Rottneest Island. The fruit was removed from the reproductive stalks, placed in cloth mesh bags, returned to the laboratory, and stored in seawater. Ripe seeds were removed from the fruit immediately prior to an experiment.

Predation experiments were conducted by anchoring tethered seeds for 24 h test periods. Seeds were tethered by threading 15 cm of 3.6 kg test, monofila-

ment line through the center of the hypocotyl. The hypocotyl of *Posidonia australis* is fibrous and, once threaded, could only be removed from the tether by breaking the seed in half. The monofilament was tied to a metal anchor, which was then inserted into bottom sediments. Each anchor had a small piece of orange flagging tape to facilitate locating the seed inside dense canopies. Our previous effort with tethered seeds addressed potential tether artifacts, and found limited movement of untethered seeds (Orth et al. 2002). In 2003, untethered seeds were used as targets for video monitoring; the videos confirmed that tethers rarely reduced seed movement relative to untethered seeds, except when they were taken by a seed predator. In addition, in 2004 we assessed whether the flagging tape and/or tether entanglement influenced seed mortality in a *P. australis* canopy, by attaching seeds on 1 cm tethers to anchors without flagging tape on each of 3 days at Stark Bay.

To assess daily seed mortality in each habitat type, 10 tethered seeds were placed along the 20 m transect approximately 2 m apart. After 24 h, missing seeds and seeds that had been partially eaten were counted and replaced with new tethered seeds for the subsequent 24 h period. If any part of the seed including the epicotyl was missing, it was recorded as partially eaten. If a seed was missing from the tether we assumed that it had been lost to predation, since we found it difficult to physically remove seeds from the tether, and they were in a comparatively low-energy environment. This assumption was supported by observations of (1) many seeds that had been eaten away to within a few millimeters of the monofilament, suggesting that other, missing, seeds had been entirely eaten, (2) many seeds that had been cut in half, illustrating the ability of predators to remove entire seeds from the line, and (3) severed tethers. All partially eaten seeds were returned to the laboratory and examined under a dissecting microscope to compare their markings with those on seeds that had been partially eaten by a known predator in the laboratory.

**Statistical analyses.** Seed predation rates were compared among sites and habitats using logistic regression; for 3 reasons: (1) the response variable is binary; (2) the analysis accommodates unbalanced sampling and experimental designs that are not fully crossed (7 d at Parker Point vs. 3 d at Nancy Cove in 2003, incomplete representation of *Halophila ovalis* across sites in 2004); and (3) our primary interest was the relative likelihood of predation within different seagrass canopies vs. that on bare sand. Logistic regression

provides these probabilities in the form of odds ratios with confidence intervals. Data were analyzed separately for 2003 and 2004 as the proportion of the 10 seeds in each transect scored as partially eaten or missing. The 2003 data set incorporated 40 proportions representing 400 seeds (7 d × 4 habitats + 3 d × 4 habitats); the 2004 data set had 119 proportions representing 1190 seeds (7 d × 3 habitats × 5 sites, plus 7 d × 1 habitat [*H. ovalis*] × 2 sites). Analysis was conducted using SAS Version 9 Logistic procedure (SAS Institute).

## RESULTS

### Video analysis 2003

In 2003 at Parker Point, feeding was observed on 2 individual seeds; both seeds were grazed at night just after sunset. A small *Nectocarcinus integrifrons* (Fig. 2a) was observed taking the seeds in its claw and slicing off large pieces (Fig. 2b), which it subsequently ate in full view of the camera (Fig. 2c). On 5 separate occasions the video camera showed this crab species foraging, but it was only observed consuming seeds twice. Hermit crabs were observed by video foraging nearby, but these did not eat seeds. Camera deployments throughout the night, before and after dawn, and during the day did not record any grazing activity, but predators of crabs regularly swam into their field of view. The most common of these were the cobbler *Cnidoglanis macrocephalus* and the flatheads *Platycephalus laevigatus*, *Leviproa inops*; both of these fish predators are likely to have influenced the seed predation behavior of the crabs.

### Video analysis 2004

In 2004, *Nectocarcinus integrifrons* was recorded most frequently, accounting for 73% of seed consumption recorded by video (Table 1). Several other crab

Table 1. *Posidonia australis*. Total number of seed predation events recorded by video cameras, and number of cameras that recorded at least one predation event in *P. australis* and *Amphibolis antarctica* meadows at Parker Point, Western Australia, in 2004

	<i>P. australis</i>		<i>A. antarctica</i>		Total	
	Events	Cameras	Events	Cameras	Events	Cameras
<i>Nectocarcinus integrifrons</i>	11	9	5	3	16	12
Unidentified portunid (cf. <i>Thalamita crenata</i> )	0	0	1	1	1	1
Unidentified crab	3	3	0	0	3	3
Decorator crab (cf. <i>Naxia aurita</i> )	2	1	0	0	2	1

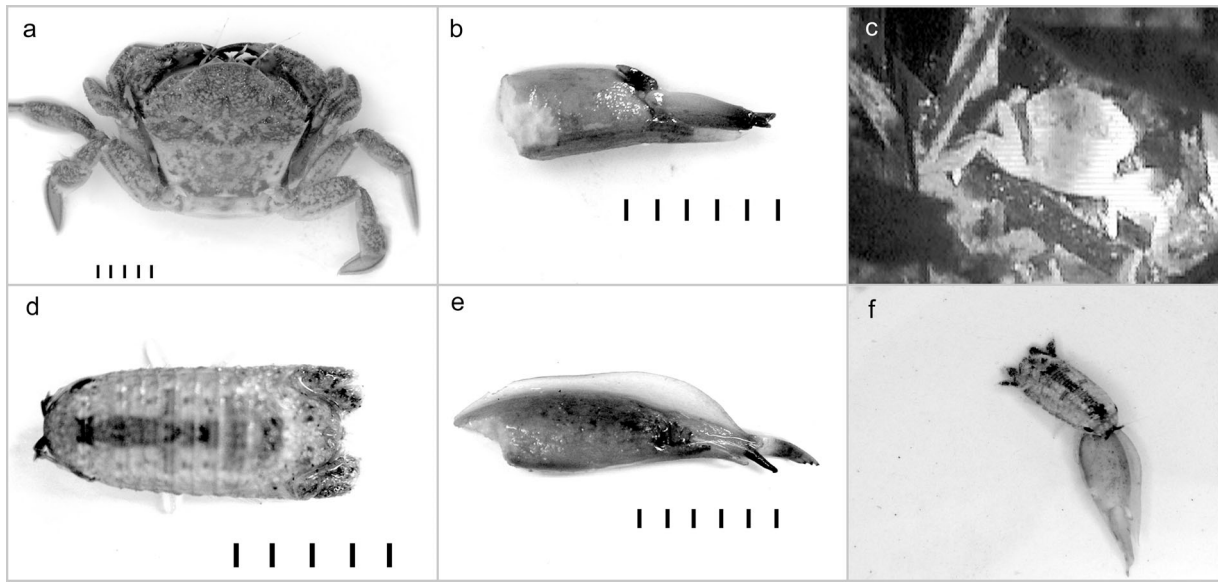


Fig. 2. Crab and isopod species identified as *Posidonia australis* seed predators, and patterns of seed damage. (a) *Nectocarcinus integrifrons*; (b) seed eaten by *N. integrifrons*; (c) image extracted from video of *N. integrifrons*; (d) *Cymodoce* sp.; (e) seed eaten by *Cymodoce* sp.; (f) *Cymodoce* sp. eating a seed in a laboratory experiment (Scale marks in mm)

species (tentatively identified as the decorator crab *Naxia aurita* and an unidentified portunid crab similar to *Thalamita crenata*) were observed eating seeds, accounting for 4.5 and 9% of seed consumption, respectively. The remaining recorded consumption (13.5%) was by species that could not be identified on the video recordings. Hermit crabs, velvet crabs, small spider crabs, and shrimp were observed, but did not interact with seeds. The isopod *Cymodoce* sp. (Fig. 2d), which was responsible for damage to seeds in the tethering experiment, was not observed in the video recordings, perhaps because of its small size and mobility.

Crab activity accounted for only a few minutes of each evening deployment. For *Amphibolis antarctica* and *Posidonia australis* beds, only 21 and 17 min of seed predation were observed on 3320 and 3480 min of continuously recorded video tape, respectively. Only a few of the deployed cameras recorded seed predation: 4 of the 28 cameras (14%) deployed in the *A. antarctica* meadow and 12 of the 30 cameras (40%) in the *P. australis* meadow. Predators of crabs were also observed, and when cobbler, flatheads, trumpeters (*Pelsartia humeralis*) and the cephalopod *Octopus* sp. cf. *maorum* appeared on the video tape, no further crab activity was observed on that particular video tape.

In the *Amphibolis antarctica* meadow, more bite marks were noted on target seeds collected after camera deployments than were filmed by the cameras (Fig. 3a). Between 0 and 2 seed predation events were recorded by video each night. The nature of the

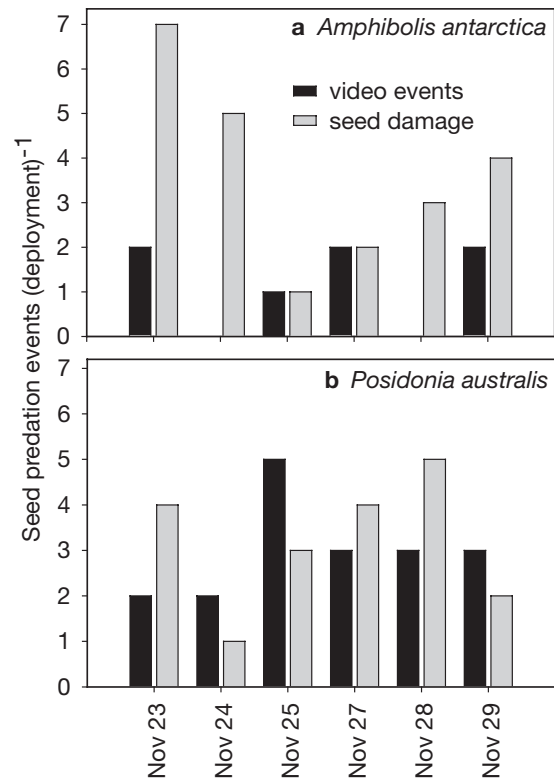


Fig. 3. *Posidonia australis*. Predation events observed on *P. australis* seeds in (a) *Amphibolis antarctica* and (b) *Posidonia australis* meadows on videotape versus events assessed by post-hoc examination of bite marks on video target seeds. Each date represents a camera deployment of 3 h, starting at dusk

canopy (consisting of flexible stems bearing many clusters of leaves, sometimes heavily epiphytized with macroalgae) and the oscillatory motion of living stems and detrital leaves through the field of view of the cameras made it difficult to keep a clear view of the tethered seeds. Also, small grazers of seeds, such as the isopod *Cymodoce* sp. (Fig. 2d), were easily hidden from view. In the *Posidonia australis* meadow, video-recorded seed predation was similar to that observed on tethered seeds, and at times was greater (Fig. 3b), with more than 1 predation event being observed on a single seed during camera deployment. Between 1 and 5 seed predation events were recorded each night.

### Field experiments

In 2003, daily seed predation rates were dramatically higher in *Amphibolis antarctica* meadows than in the other habitats at Parker Point (>60% d<sup>-1</sup> compared to a mean of <20% d<sup>-1</sup> for the other habitats,) but this was not the case at Nancy Cove (Fig. 4a). Logistic

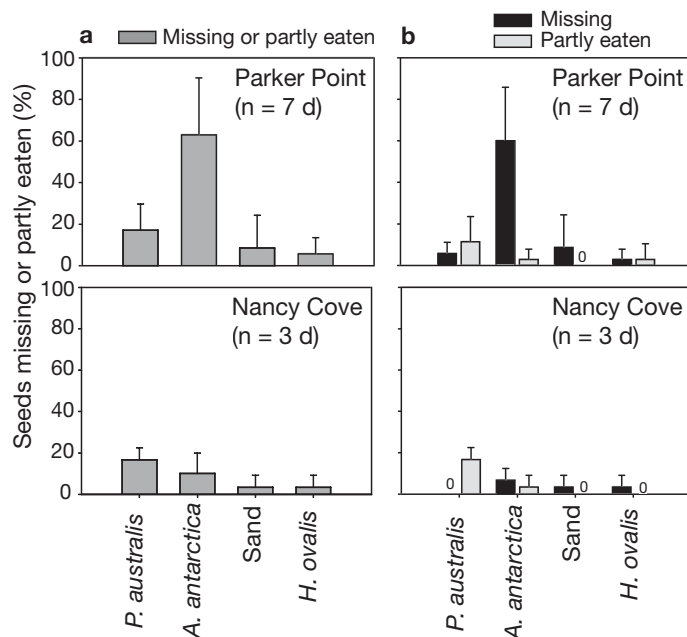


Fig. 4. *Posidonia australis*. Percentage (mean + SD, n = 7 d) of 10 seeds tethered in 4 habitats in 2003 that were either missing or partially eaten after 24 h. (a) Total percentage affected (either missing or partly eaten); (b) missing versus partly eaten

Table 2. *Posidonia australis*. Odds ratios (increase in predation risk relative to the site and habitat reference conditions, 'Parker' and 'sand', respectively) for probabilities of seed predation events at different sites and in various habitats. Odds generated by logistic regression independently for 2003 and 2004

Year	Comparison	Odds ratio	95% Wald confidence limits	
2003				
Site	Nancy vs. Parker	0.23	0.11	0.50
Habitat	<i>Amphibolis antarctica</i> vs. sand	13.38	5.53	32.37
Habitat	<i>Posidonia australis</i> vs. sand	2.80	1.09	7.14
Habitat	<i>Halophila ovalis</i> vs. sand	0.70	0.21	2.29
2004				
Site	Armstrong vs. Parker	0.21	0.13	0.34
Site	Nancy vs. Parker	0.41	0.26	0.65
Site	Parakeet vs. Parker	0.56	0.35	0.88
Site	Stark vs. Parker	0.33	0.21	0.52
Habitat	<i>Amphibolis antarctica</i> vs. sand	18.52	11.39	30.10
Habitat	<i>Posidonia australis</i> vs. sand	21.26	13.06	34.59
Habitat	<i>Halophila ovalis</i> vs. sand	1.34	0.63	2.85

regression revealed a 13-fold increased chance of a predation event within a 24 h period in *A. antarctica* compared to sand (Table 2) ( $\chi^2 = 58.58$ ,  $p < 0.0001$ ), but no significant difference between *Posidonia australis* meadows and sand ( $\chi^2 = 0.66$ ,  $p = 0.41$ ). Site and habitat both displayed significant effects (Wald chi-square: site df = 1,  $\chi^2 = 14.16$ ,  $p = 0.0002$ ; habitat df = 3,  $\chi^2 = 59.17$ ,  $p < 0.0001$ ). In the *A. antarctica* meadow at Parker Point, most seeds were missing, with many of the monofilament tethers severed, and relatively few partially eaten seeds remaining (Fig. 4b).

In 2004, daily seed predation rates were higher in *Posidonia australis* (average 40 to 73% d<sup>-1</sup>) and in *Amphibolis antarctica* (36 to 85% d<sup>-1</sup>) meadows than in *Halophila ovalis* (9% d<sup>-1</sup>) meadows and sand (3 to 13% d<sup>-1</sup>) (Fig. 5a). Logistic regression revealed significant effects of site and habitat in the overall model (Wald chi-square: site df = 4,  $\chi^2 = 46.26$ ,  $p < 0.0001$ ; habitat df = 3,  $\chi^2 = 214.98$ ,  $p < 0.0001$ ). There was an approximately 20-fold increase in the chance of a predation event occurring within 24 h in *P. australis* ( $\chi^2 = 130.15$ ,  $p < 0.0001$ ) and *A. antarctica* ( $\chi^2 = 107.67$ ,  $p < 0.0001$ ) meadows compared to unvegetated sand, but no increase in predation in *H. ovalis* meadows compared to sand (Table 2). The ratio of missing to damaged seeds varied among habitats: in *A. antarctica* meadows, most seeds were missing, while in *P. australis* meadows there were similar numbers of missing and damaged seeds (Fig. 5b). Statistically significant site differences were driven by differences in the total percent of seeds con-

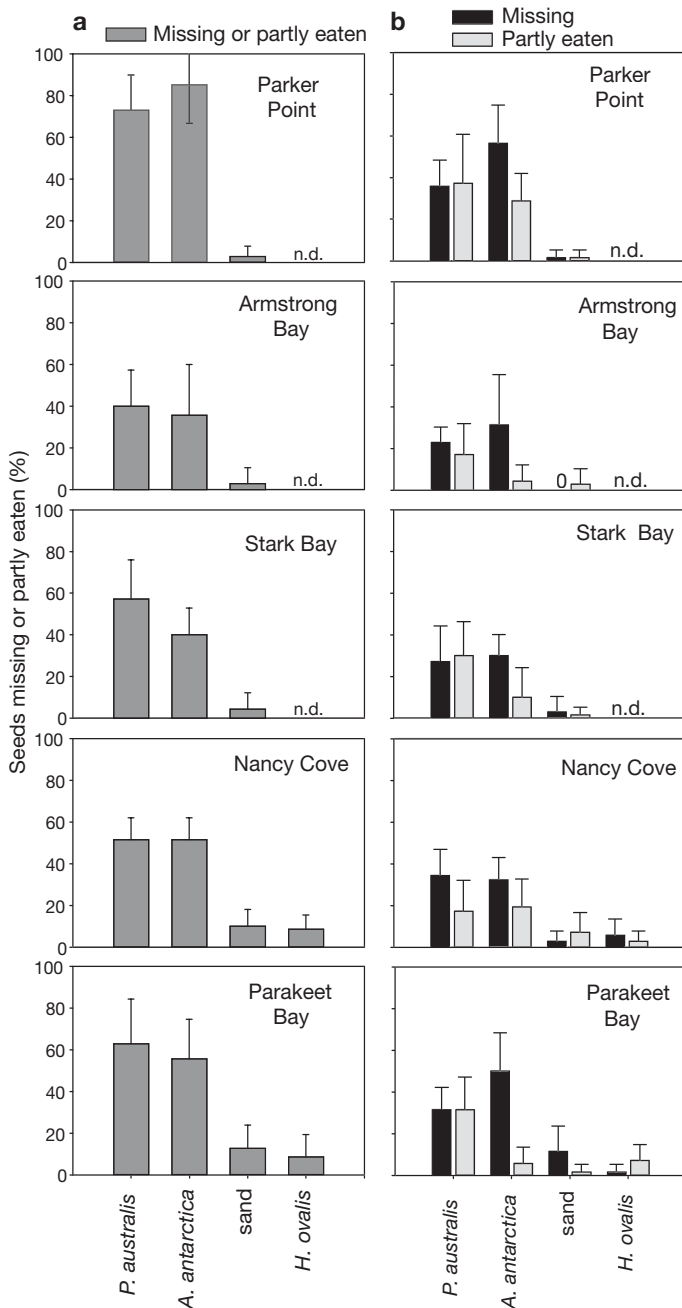


Fig. 5. *Posidonia australis*. Percentage (mean + SD,  $n = 7$  d) of 10 seeds tethered in 4 habitats in 2004 that were either missing or partially eaten after 24 h. (a) Total percentage affected (either missing or partly eaten); (b) missing vs. partly eaten. n.d.: no data

summed between sites (Fig. 5a); patterns in predation rates among habitats were similar among sites.

The experiment testing tethering artifacts in *Posidonia australis* meadows showed that our predation estimates were conservative. Mortality for seeds on 1 cm tethers with no flagging tape was significantly higher than for seeds on normal (~7 cm) tethers marked with

flagging tape (90, 77 and 60% seed mortality on 3 test days on 1 cm tethers compared with 60, 50 and 40%, respectively, on ~7 cm tethers; paired  $t$ -test  $df = 2$ ,  $t = 4.30$ ,  $p = 0.013$ ). Rather than increasing predation, either as a result of predator attraction to the colorful tape or through increased encounter rates resulting from entanglement with longer tethers, any tethering artifacts appear to diminish observed predation rates.

Post-hoc comparison of patterns of damage to tethered seeds with seeds partially eaten by known predators in 2004 suggested that the portunid crab *Nectocarcinus integrifrons* was responsible for most predation in *Posidonia australis* meadows, with most of the remaining seeds being damaged by the isopod *Cymodoce* sp. (Table 3). In *Amphibolis antarctica* meadows, damage was evenly attributed to the 2 predators.

### Laboratory observations

In 2003, we observed one of the tested hermit crab prey on a seed during the 24 h test period. In 2004, only *Nectocarcinus integrifrons* and *Cymodoce* sp. were observed to prey on a seed. Interestingly, within minutes of a seed being placed in a container, the isopod would climb onto it and begin eating it.

### Crab surveys

In 2003, the abundance of the hermit crabs *Paguristes purpureantennatus* and *Calcinus dapsiles* in 10 m<sup>2</sup> surveyed transects was not correlated with intensity of seed predation. At Parker Point, no hermit crabs were found in *Amphibolis antarctica* meadows, 7 in *Posidonia australis* meadows, 2 in *Halophila ovalis* meadows, and 0 in sand. However, at Nancy Cove, where predation was much lower, hermit crab abundances were 21, 10, 5 and 0, respectively. Frequent video observations of hermit crabs ignoring available seeds corroborate the conclusion that the distribution and behavior of hermit crabs are not consistent with their being significant *P. australis* seed predators.

### DISCUSSION

Predation appears to be a major source of mortality for *Posidonia australis* seeds settling in some seagrass meadows at Rottnest Island, Western Australia, and thus has the potential to be a significant obstacle to seedling establishment in these habitats. Seed predation was greater in meadows of the structurally com-

Table 3. *Posidonia australis*. Presumed cause of damage to partially eaten seeds in each habitat at 5 sites. Partially eaten seeds were stored for the duration of the experiment, then classified post-hoc by comparison with test seeds known to be grazed by either an isopod (*Cymodoce* sp.) or a crab (*Nectocarcinus integrifrons*) in laboratory experiments. –: no damaged seeds from this site

Site	<i>Amphibolis antarctica</i>		<i>Posidonia australis</i>		<i>Halophila ovalis</i>		Sand		Total	
	Crab	Isopod	Crab	Isopod	Crab	Isopod	Crab	Isopod	Crab	Isopod
Parker	5	9	10	5	–	–	1	0	16	14
Nancy	7	7	5	2	1	1	0	5	13	15
Stark	4	3	22	11	–	–	1	1	27	15
Armstrong	3	3	7	5	–	–	0	2	10	10
Parakeet	3	1	11	6	0	1	0	1	14	9
Total	22	23	55	29	1	2	2	9	80	63

plex seagrasses *P. australis* and *Amphibolis antarctica* than in structurally simpler *Halophila ovalis* meadows and unvegetated sand, supporting results of our earlier work showing higher predation rates in *P. australis* beds than in bare sand at other sites in Western Australia (Orth et al. 2002). This pattern of higher predation in these structured habitats parallels that reported for many terrestrial studies, showing high predation rates near the parent plant, where most seeds fall and where seed predators have easy access to an abundant food source (Harms et al. 2000, Wenny 2000, Clark et al. 2005). The major seed predators, identified through video analysis and laboratory observations, were the portunid crab *Nectocarcinus integrifrons* and the isopod *Cymodoce* sp. We also observed 4 other crabs consuming seeds (portunid cf. *Thalamita crenata*, the majid *Naxia aurita*, the hermit crabs *Paguristes purpureantennatus* and *Calcinus dapsiles*), but at comparatively inconsequential rates. While hermit crabs were abundant at our study sites, they were not considered an important seed predator based on the rarity of their approaching seeds during the video recordings and the lack of correlation between crab abundance and observed predation rates. Various species of fishes were observed approaching but never eating seeds in the video analysis, and none appeared to be seed predators.

Most previous studies documenting predation on seagrass seeds have found crustaceans to be the dominant predators (Wassenberg & Hill 1987, Wigand & Churchill 1988, Wassenberg 1990, Fishman & Orth 1996, Holbrook et al. 2000, Lacap et al. 2002, Nakaoka 2002). Williams (1995) reported herbivory on surfgrass (*Phyllospadix torreyi*) male spadixes by the fish *Girella nigricans*, but seed consumption may have been incidental to more generalized herbivory. Seed predation by crustaceans has also been shown to be important in structuring species distributions and densities in mangrove habitats as well as tropical coastal forests (Smith et al. 1989, Sousa & Mitchell 1999, Clarke & Kerrigan 2002, Lindquist & Carroll 2004). Crustaceans are abun-

dant in seagrass beds in western and southern Australia (Kirkman et al. 1989, Edgar 1996), and *Nectocarcinus integrifrons* is one of the dominant crustacean species in these seagrass beds (Kirkman et al. 1989). Klumpp & Nichols (1983) and Johnston & Freeman (2005) found high cellulase activity in both the hepatopancreas and gut of *N. integrifrons*, which eats primarily living leaves of *Posidonia australis* and is capable of assimilating 40 to 60% of seagrass carbon primarily from the leaves (Nichols et al. 1985). Their ability to digest cellulose is also likely to facilitate their consumption of seed coats, leaf plumules and the large amounts of starch found in the seed itself (Kuo & Kirkman 1996). Likewise, the majid *Naxia aurita* has previously been reported to consume living seagrass tissues (Edgar 1996); however, in the present study, although on the videos it was often visible moving among seagrass shoots, only once was it observed handling a seed.

The pattern of high seed predation rates in structurally complex canopies fits parsimoniously with the general principal that structurally complex habitats provide greater refuge from predation (Bell et al. 1991) than structurally simple habitats when viewed in terms of the mobile crustacean seed predators, rather than in terms of the seeds themselves. Our direct video observations of seed predation support the proposition that seed predators minimize exposure to their own predators. Crabs spent only short intervals consuming seeds before fleeing from the clearing where seeds were tethered; when predators of crabs (octopuses, flatheads, cobblers) were observed foraging past the cameras, crab activity ceased.

The low mortality rates of *Posidonia australis* seeds in *Halophila ovalis* meadows may be a consequence of this structurally simple plant providing insufficient refuge for crustaceans from their predators. Its small (2 to 4 cm high), widely-spaced leaves offer little protection. However, this has distinct benefits for *P. australis* seeds, which may be more likely to survive and become established, possibly explaining why seed-



lings occur in both *H. ovalis* beds and on bare sand but not in *P. australis* beds (Orth 1999). Further careful examination of beds of *P. australis* and *Amphibolis antarctica* has so far failed to yield any *P. australis* seedlings (R. J. Orth pers. obs.). This is consistent with the results of the present study and past work (Orth et al. 2002), indicating that seeds settling in these seagrass canopies are extremely vulnerable to predators.

The intensity of seed predation appears temporally and spatially variable, a pattern also documented by Holbrook et al. (2000) during a 3 yr study of predation on *Phyllospadix torreyi* seeds. In the present study, we recorded differences in proportional mortality between sites (Table 2) and between years (Table 4), and differences in dominant predators inferred from the proportion of partially eaten seeds in the 2 structured habitats (Table 3). These differences could be a function of seed predator densities, or densities of higher-level predators (flatheads, cobblers, octopuses) that influence either the abundance or behavior of the seed predators.

The results reported here have identified seed predators operating in seagrass beds in temperate Western Australia, and demonstrated high, but habitat-specific, predation rates. Additional (unpublished) preliminary work we have carried out suggests that predation rates may be relatively unpredictable at other sites and in other habitats. For example, predation rates observed in 2003 in Two Peoples Bay (SW Australia) were greater in *Posidonia sinuosa* than in *P. australis* beds, but the opposite pattern was seen on Rottneest Island in 2004 in a *P. sinuosa* bed at 1 site (R.J. Orth unpubl. data). Also, in Two Peoples Bay in 2003, we observed a distinct pattern of intense seed predation by amphipods in a localized area associated with a dense layer of seagrass leaf detritus in a *Halophila ovalis* bed, contrasting with the low mortality rates noted in *H. ovalis* beds on Rottneest Island that did not have this detrital layer (R. J. Orth unpubl. data). This observation demonstrates scale-dependent habitat complexity; since amphipods are able to find predation refuge in habitats that are less complex than those required by crabs, there may be little basis for *a priori* expectations of 'habitat complexity vs. pre-

dition intensity' relationships at sites that have seed predators of diverse sizes.

The magnitude of seed predators' impact on *Posidonia australis* recruitment, and ultimately on competitive dynamics among plant species in seagrass assemblages, is currently unknown. This study assessed 2 of the variables necessary for construction of a local-scale *P. australis* seed budget, including seed supply and daily probability of seed mortality. However, potentially substantial rates of seed import and export from local sites were not quantified, and may be important to regional demography. Our focus is the relative risk of seed predation among local habitats as an explanatory factor in the local distribution of *P. australis* seedlings. To expand the study to assess regional limitation of *P. australis* recruitment would require an understanding of seed export rates from source beds and delivery rates to nearby and distant habitats, both significant experimental challenges. Alternatively, seed consumption rates of experimentally manipulated seed densities could be assessed in order to estimate the consumptive capacity of seed predator populations relative to observed rates of seed supply.

These data add to the growing body of evidence that seed predation in seagrasses does occur, may be temporally and spatially variable, and is strongly influenced by canopy complexity. The high survival of seeds in a structurally simple habitat such as *Halophila ovalis* beds or bare sand may have important consequences for seagrass bed dynamics. In addition, our results raise the question as to whether the influence of seed dispersal on plant demographics and local genetic structure may be modified by local faunal dynamics. Viewing seagrass seedlings in the context of fauna-dependent predation processes, rather than simply in terms of plant-plant competitive interactions, may enable a better understanding of seagrass spatial distributions and successional dynamics.

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Table 4. Interannual variability in mean daily percentage seed mortality in 2 seagrass habitats at 3 sites (2001 data from Orth et al. 2002). nd: no data

Site	<i>Posidonia australis</i>			<i>Amphibolis antarctica</i>	
	2001	2003	2004	2003	2004
Parker Point	53	17	73	63	85
Stark Bay	37	nd	57	nd	40
Nancy Cove	nd	17	51	10	52

## LITERATURE CITED

- Bell SS, McCoy ED, Mushinsky HR (1991) Habitat structure: the physical arrangement of objects in space. Chapman & Hall, New York
- Cambridge ML, Hocking PJ (1997) Annual primary production and nutrient dynamics of the seagrasses *Posidonia sinuosa* and *Posidonia australis* in south-western Australia. *Aquat Bot* 59:277–295
- Clark, CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT (2005) Comparative seed shadows of bird-, monkey-, and wind dispersed trees. *Ecology* 86:2684–2694
- Clarke PJ, Kerrigan RA (2002) The effects of seed predators on the recruitment of mangroves. *J Ecol* 90:728–736
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine mammals and in rain forest trees. In: Boer PJ, Gradweel G (eds) Dynamics of populations. Pudoc, Wageningen, p. 298–310
- Crawley MJ (1992) Seed predators and plant population dynamics. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, p 157–191
- Edgar GJ (1996) The distribution and diet of crabs associated with seagrass and unvegetated habitats in Western Port, Victoria. In: Kuo J, Phillips R, Walker DI, Kirkman H (eds) Seagrass biology. Proceedings of an International Workshop. Rottneest Island, Western Australia. Faculty of Science, University of Western Australia. Perth, p 225–232
- Fishman JR, Orth RJ (1996) Effects of predation on *Zostera marina* L. seed abundance. *J Exp Mar Biol Ecol* 198:11–26
- Harms KE, Wright SJ, Calderon O, Hernandez A, Herre EA (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495
- Heck KL Jr, Orth RJ (2006) Predation in seagrass meadows. In: Larkum AWD, Orth RJ, Duarte C (eds) Seagrasses: Biology, ecology and conservation. Springer Verlag, Berlin, p 537–550
- Holbrook SJ, Reed DC, Hansen K, Blanchette CA (2000) Spatial and temporal patterns of predation on seeds of the surfgrass *Phyllospadix torreyi*. *Mar Biol* 136:739–747
- Howe HF, Miriti MN (2000) No question: seed dispersal matters. *Trends Ecol Evol* 15:434–436
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:210–228
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Janzen DH (1971) Seed predation by animals. *Annu Rev Ecol Syst* 2:465–492
- Johnston D, Freeman J (2005) Dietary preferences and digestive enzyme activities as indicators of trophic resource utilization by six species of crab. *Biol Bull (Woods Hole)* 208:36–46
- Kendrick GA, Hegge BJ, Wyllie A, Davidson A, Lord DA (2000) Changes in seagrass cover on Success and Parmelia Banks, Western Australia between 1965 and 1995. *Estuar Coast Shelf Sci* 50:341–353
- Kirkman H, Humphries P, Manning C (1989) The epibenthic fauna of seagrass beds and bare sand in Princess Royal Harbour and King George Sound, Albany, south-western Australia. In: Wells FE, Walker DI, Kirkman H, Lethbridge R (eds) The marine flora and fauna of Albany, Western Australia. Western Australia Museum, Perth, p 553–563
- Klumpp DW, Nichols PD (1983) Utilization of the seagrass *Posidonia australis* as food by the rock crab *Nectocarcinus integrifrons* (Latreille) (Crustacea: Decapoda: Portunidae). *Mar Biol Lett* 4:331–339
- Kuo J, Kirkman H (1996) Seedling development of selected *Posidonia* species from southwest Australia. In: Kuo J, Phillips R, Walker DI, Kirkman H (eds) Seagrass biology: Proceedings of an International Workshop. Rottneest Island, Western Australia. Faculty of Science, University of Western Australia, Perth, p 57–64
- Kuo J, McComb AJ (1989) Seagrass taxonomy, structure and development. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, p 6–73
- Lacap CDA, Vermaat JE, Rollon RN, Nacorda HM (2002) Propagule dispersal of the SE Asian seagrasses *Enhalus acoroides* and *Thalassia hemprichii*. *Mar Ecol Prog Ser* 235:75–80
- Larkum AWD, den Hartog C (1989) Evolution and biogeography of seagrasses. In: Larkum AWD, McComb AJ, Shepherd SA (eds) Biology of seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region. Elsevier, Amsterdam, p 112–156
- Lindquist ES, Carroll CR (2004) Differential seed and seedling predation by crabs: impacts on tropical coastal forest composition. *Oecologia* 141:661–671
- Nakaoka M (2002) Predation on seeds of seagrasses *Zostera marina* and *Zostera caulescens* by a tanaid crustacean *Zeuxo* sp. *Aquat Bot* 72:99–106
- Nichols PD, Klumpp DW, Johns RB (1985) A study of food chains in seagrass communities III. Stable carbon isotope ratios. *Aust J Mar Freshw Res* 36:683–690
- Orth RJ (1999) Settling rates of *Posidonia coriacea* seeds and *Posidonia* spp. seedling abundance off Rottneest Island, Perth, Western Australia. In: Walker DI, Wells FE (eds) The seagrass flora and fauna off Rottneest Island, Western Australia. Western Australia Museum, Perth, p 51–61
- Orth RJ, Heck KL Jr, Tunbridge DJ (2002) Predation on seeds of the seagrass *Posidonia australis* in Western Australia. *Mar Ecol Prog Ser* 244:81–88
- Orth RJ, Harwell MC, Inglis GJ (2006) Ecology of seagrass seeds and seagrass dispersal processes. In: Larkum AWD, Orth RJ, Duarte, C (eds) Seagrasses: Biology, ecology and conservation. Springer Verlag, Berlin, p 111–133
- Smith TJ III, Chan HT, McIvor CC, Robblee MB (1989) Comparisons of seed predation rates in tropical tidal forests in three continents. *Ecology* 70:146–151
- Sousa WP, Mitchell BJ (1999) The effect of seed predators on plant distributions: Is there a general pattern for mangroves? *Oikos* 86:55–66
- Wassenberg TJ (1990) Seasonal feeding on *Zostera capricorni* seeds by juvenile *Penaeus esculentus* (Crustacea: Decapoda) in Moreton Bay, Queensland. *Aust J Mar Freshw Res* 41:301–310
- Wassenberg TJ, Hill BJ (1987) Natural diet of tiger prawns *Penaeus esculentus* and *Penaeus semisulcatus*. *Aust J Mar Freshw Res* 13:85–92
- Wenny DG (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecol Monogr* 70:331–351
- Wigand C, Churchill AC (1988) Laboratory studies on eelgrass seed and seedling predation. *Estuaries* 11:180–183
- Williams SL (1995) Surfgrass (*Phyllospadix torreyi*) reproduction: reproductive phenology, resource allocation, and male rarity. *Ecology* 76:1953–1970