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Spatial and temporal patterns of predation on seeds of the surfgrass *Phyllospadix torreyi*

Received: 8 June 1999 / Accepted: 2 February 2000

Abstract Spatial and temporal patterns of predation on seeds of the seagrass *Phyllospadix torreyi* S. Watson were quantified at four sites near Santa Barbara, California, USA. Over a period of four flowering seasons during 1995 to 1998, monthly patterns of seed fall and intensity of seed predation were similar among sites, but were temporally quite variable. Abundance of dispersed seeds varied greatly both among seasons and years. Within any one year, seeds were present in the environment every month, but they peaked in abundance during the fall months following the annual flowering period. Seeds were more abundant during the earlier years of the study. The intensity of predation steadily increased throughout the study period, from a low of $\leq 10\%$ seeds consumed during 1995 to $\sim 50\%$ consumption by 1997, and it was not correlated with abundance of seeds in the environment. Pre-dispersal seed loss also was estimated in two flowering seasons by counting the numbers of seeds consumed prior to release from the plant, and was relatively low ($< 15\%$). No differences were detected among the four study sites in patterns of pre-dispersal loss. Field surveys were done at two sites to identify potential seed predators. Three of the most abundant species identified in these surveys were tested in the laboratory to determine size-specific patterns of feeding activity and to assess which early life stages of *P. torreyi* (fruits within spadices, dehisced fruits, seedlings) were most vulnerable to predation. All three of the

early life stages were consumed. The crabs *Pugettia producta* (Randall) and *Pachygrapsus crassipes* Randall were much more voracious predators than the isopod *Idotea resicata* Stimpson.

Introduction

Seagrasses are the primary group of seed-producing plants in marine environments. They can produce copious amounts of seeds, but similar to terrestrial plants, seedling abundance is usually low relative to seed production (Turner 1985; Fishman and Orth 1996; authors' unpublished data). Reasons for the relatively low rates of seedling establishment are poorly understood, as the processes that affect seeds during maturation, dehiscence, and germination have been little investigated. The few studies conducted to date have identified two factors that contribute to loss of mature seeds within seagrass beds: rafting of seeds still attached to reproductive shoots was estimated to account for loss of over one-third of the seeds from a bed of *Zostera marina* L. (Gates 1984), whereas predation accounted for up to 65% of the losses of seeds of *Z. marina* observed during 2wk-long experiments (Fishman and Orth 1996). The relative importance of these and other mechanisms that contribute to seed loss in seagrasses undoubtedly will vary both spatially and temporally as well as among species. However, so little is known about the patterns and causes of seed loss that it is not yet possible to make interspecific comparisons or predictions about the consequences to population dynamics, particularly regarding the potential for population recovery via seedling recruitment following large disturbances.

A variety of birds, fishes and invertebrates (including crustaceans and molluscs) has been identified as predators of seagrass seeds (Adams 1976; O'Brien 1984; Agami and Waisel 1986; Wassenberg and Hill 1987; Wigand and Churchill 1988; Wassenberg 1990; Williams 1995; Fishman and Orth 1996). However, relatively few

Communicated by M. H. Horn, Fullerton

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attempts have been made to quantify and compare losses of seeds among different sites, relate losses to the action of specific predators, or explore whether variation in predation intensity is related to variation in abundance of seeds. Here, we explore effects of predation on seed loss in the surfgrass *Phyllospadix torreyi* S. Watson. This species occurs in rocky intertidal and shallow subtidal zones and, unlike most other seagrasses, its distribution is limited to rocky reefs in areas of high wave-action (Phillips 1979; Phillips and Menez 1988). Plants are dioecious, and both sexes produce spikes of flowers called spadices. The non-fleshy fruit of *P. torreyi* contains a single seed (Dudley 1893) whose endocarp forms two arms with stiff bristles that attach it to a host plant (Gibbs 1902; Turner 1983; Blanchette et al. 1999). After release from the spadix, the negatively buoyant fruit (commonly referred to as a seed) drifts along the bottom until it entangles on a host alga (or sometimes a conspecific plant), where the seed germinates. After many months, development of the rhizome of the seedling is sufficient to anchor it firmly to the rocky substrate, and the host plant is no longer needed. Like other seagrasses, *P. torreyi* can produce large numbers of seeds (up to 10 000 per m² during its annual flowering season: Williams 1995; Reed and Holbrook unpublished data), but typically very few seedlings become established (Stewart 1989; Williams 1995; authors' unpublished data).

The goals of this study were to examine spatial and temporal patterns of predation in natural populations of *Phyllospadix torreyi* as well as conduct feeding trails in the laboratory to establish which early life stages of surfgrass were consumed by several species of predators. Over a period of four flowering seasons from 1995 to 1998, we quantified patterns of seed fall and estimated the strength of predation on post-dispersal seeds at four sites. Pre-dispersal loss also was estimated during two flowering seasons by counting the number of fruits consumed prior to release from the spadix. These measurements enabled us to establish spatial and temporal patterns of seed predation and to explore the relationship between abundance of seeds and intensity of predation. We did field surveys and laboratory experiments to ascertain which species of invertebrates were potential predators. We conducted tests on three species (the crabs *Pugettia producta* (Randall) and *Pachygrapsus crassipes* Randall and the isopod *Idotea resicata* Stimpson) to determine size-specific patterns of feeding activity and to assess which early life stages of *Phyllospadix torreyi* (ripe seeds within spadices, dehiscid fruits, seedlings) were vulnerable to predation.

Materials and methods

Study sites

Field work was conducted in *Phyllospadix torreyi* S. Watson beds at four moderately wave-exposed intertidal sites (Alegria, Shore-

line, Devereux, Hendry's) located in Santa Barbara County, California, USA. In these areas, *P. torreyi* forms extensive beds on rocky benches and boulders from the low intertidal zone into the subtidal to depths of ~4 m. An ecologically-similar congener, *P. scouleri* W. Hooker, which can co-occur with *P. torreyi*, was not present at these sites. The four study sites were located along a 58 km stretch of shoreline. Shoreline and Hendry's were separated by a distance of ~3 km, and were the southernmost of the sites. Alegria and Devereux were ~55 and 15 km to the north, respectively. There were no obvious differences among the sites as to wave exposure, seawater temperature or other environmental conditions.

Patterns of pre-dispersal seed predation

Flowering in *Phyllospadix torreyi* is seasonal (Williams 1995). At our study sites, flowers first appear in early summer (June/July), reaching peak densities in late summer (usually September: Reed and Holbrook unpublished data). Fruits ripen and are released from the spadix in the late summer and fall. On average, there are 10 to 13 flowers per female spadix on plants growing in the intertidal zone.

The intensity of predation on fruits prior to maturation and release from the spadix was assessed at each site at the peak of the flowering season (September) in 1997 and in 1998. At each site, 10 to 30 rhipidia (reproductive shoots containing one or more spadices) containing a total of 36 to 162 spadices were haphazardly collected on each sampling date and returned to the laboratory for examination. Each spadix was categorized as immature (spadix not open and no flowers are exposed) or opened (at least one flower exposed). Flowers and fruits in opened spadices were classified into the following groups: (1) receptive (flowers open and stigmas exerted); (2) immature (green ripening fruits with developing seeds); (3) mature (dark-brown seed coat visible); (4) dehiscid (fruit missing, no sign of damage to spadix); (5) aborted (small abnormal fruit showing signs of atrophy); (6) eaten (seed absent, fruit or spadix cleanly ripped or torn). We explored patterns of pre-dispersal predation in two ways. First, the proportion of spadices from a site that was damaged by predators during each sampling period was calculated by dividing the number of spadices with at least one eaten fruit by the total number of spadices examined. Differences among sites and between years in the proportion of spadices damaged by predators were evaluated with a two-factor ANOVA (without replication) with site and year as fixed factors. Although this analysis does not allow tests of interactions between factors, it does provide a test of main effects. Second, the proportion of fruits eaten per spadix was determined by dividing the number of eaten fruits in a spadix by the total number of fruits in that spadix. The effects of site and year on the mean proportion of eaten fruits per spadix were evaluated by two-way ANOVA, with site and year as fixed factors. Data were transformed to arcsine square-root prior to analysis to meet the assumptions of normality and homoscedasticity.

Patterns of post-dispersal seed predation

Seed traps were deployed in the surfgrass zone at the four sites from August 1995 until December 1998 to assess patterns of abundance of dehiscid fruits (containing seeds) and intensity of predation. Each trap consisted of two pieces of 30 × 30 cm polyester mesh tied together at their centers, where they were bolted to the substrate along permanent transects within the surfgrass zone ($N = 10$ traps per site). The two pieces of fabric had different mesh sizes to accommodate the slight variability in fruit size: 1.7 mm-diam polyester stretch mesh with round openings (polyester netting #9622, Research Nets, Inc., Redmond, Washington) and 1.0 mm-diam mesh with square openings (nylon netting Delta 1004A, Memphis Net and Twine). The fabric diameter of the mesh was similar to that of branched algae known to facilitate fruit attachment, and laboratory tests in an oscillating flow tank revealed that fruits attached to the fabric of the collectors at rates similar to that on many common host algae (Blanchette et al. 1999). Traps were put

out at the sites and retrieved a month later, at which time empty traps were re-deployed in the same positions. Upon return to the laboratory, traps were placed in seawater where they were held until seeds were counted (up to 48 h). The entire trap was searched for fruits, which were carefully removed and categorized as whole (intact with a viable seed present), germinated (intact seed with emergent shoot), eaten (seed visibly eaten out of fruit) or partial (only one arm present) (Fig. 1). The condition of the exocarp of eaten fruit was variable. In some cases the exocarp was intact, and in others it was partially missing. It was unlikely that fruits found in the traps and categorized as "eaten" were actually damaged by predators prior to their release from the spadix (and thus actually represented pre-dispersal seed predation). The reason for this is that predators that consumed fruits from spadices damaged them extensively, leaving little or no intact exocarp and greatly damaging the bristled arms that are necessary for attachment to a host alga or the mesh of the traps.

The effects of site on the abundance of fruits caught in traps was evaluated by an analysis of covariance with site as a fixed factor and sample date (month and year) as a covariate. Spatial (among site) and temporal patterns of seed predation were investigated by calculating the proportion of total fruits whose seeds had been eaten (E) for each site during each monthly period as

$$E = \frac{e}{w + g + e + 0.5p}, \quad (1)$$

where e = number of eaten fruit, w = number of whole fruit, g = number of germinated fruit and p = number of partial fruit. The value of p was divided by two to insure that the number of total fruit was not overestimated by counting two detached arms from the same fruit as two different fruits. The effect of site on the proportion of total fruits with eaten seeds was evaluated by analysis of covariance, whereby site was considered a fixed factor and sample date the covariate. Data were transformed to arcsine square-root prior to analysis. We also examined the relationship between intensity of predation (mean proportion of eaten seeds in each monthly sample) and abundance of seeds (mean number of seeds caught per trap) in a linear regression analysis.

Patterns of abundance of predators in the field

We conducted surveys in the surfgrass zones at two of the study sites, Devereux and Hendry's during fall 1997, spring 1998 and fall 1998 to estimate abundance of potential macro-invertebrate seed predators. Sites were visited a total of 5 (Devereux) or 6 (Hendry's) times in order to obtain time-averaged estimates of abundance.

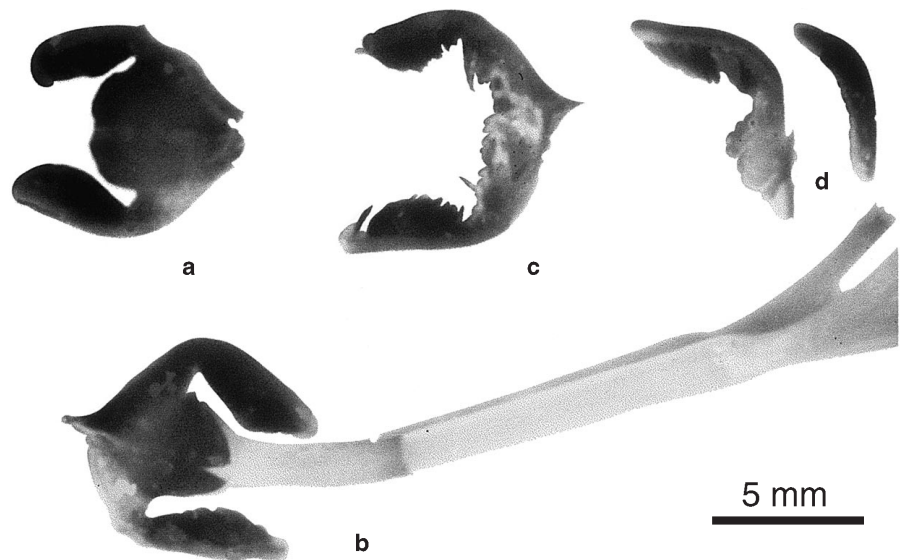
During each visit, 23 to 50 $1 \times 1 \text{ m}^2$ quadrats were randomly placed in the low intertidal zone and searched for potential predators of surfgrass seeds. Only four species [the hermit crab *Pagurus hirsuti-sculus* (Dana), the cancer crab *Cancer productus* Randall, the kelp crab *Pugettia producta* (Randall) and the shore crab *Pachy-grapsus crassipes* Randall] of potential seed predators were sufficiently abundant. They were counted and measured (carapace width). The isopod *Idotea resicata* (Stimpson) was commonly observed on the leaves of surfgrass, but was not counted. Half the quadrats were placed within the surfgrass bed, the other half in adjacent rocky areas lacking surfgrass. We sampled both areas because the potential predators are mobile and can forage in both areas, and because surfgrass seeds disperse into both the surfgrass bed and surrounding habitat. The density of each species (number m^{-2}) at each site was calculated using quadrats as replicates.

Laboratory tests of predation on early life stages of *Phyllospadix torreyi*

Laboratory experiments were conducted to assess level of predatory activity of four species of invertebrates on three early life stages of *Phyllospadix torreyi* – seeds within spadices, dehiscid fruits, and 2 to 3 wk-old seedlings with fruits still attached. The species screened for evidence of predatory activity were *Pagurus hirsuti-sculus*, *Pugettia producta*, *Pachygrapsus crassipes*, and *Idotea resicata*. In these tests individuals of each species were placed in running seawater in separate flow-through containers with spadices, fruits or seedlings, and evidence of consumption was assessed after 48 h. Based on their predatory activity, *Pugettia producta*, *Pachygrapsus crassipes* and *I. resicata* were chosen for more detailed study. Although *Pagurus hirsuti-sculus* was very abundant in our field surveys, it did not consume early life stages of surfgrass in the preliminary trials, so it was not considered further.

In the laboratory trials, individual predators were offered one of three early life stages of *Phyllospadix torreyi* – spadices containing fruits, dehiscid fruits, or seedlings (<5 cm shoot length) for a period of 4 d. Fruits were obtained from female plants of *P. torreyi* growing in the shallow subtidal zone (<4 m water depth) adjacent to the University of California, Santa Barbara (34°25'N; 119°57'W). Mature reproductive shoots (rhipidia) were collected and immediately transported to the laboratory, where they were maintained in seawater for use in experiments. Fruits were dehiscid by gently running a finger along the length of a female spadix. Mature fruits dislodged easily with one pass of the finger. Seedlings were obtained by culturing seeds in the laboratory (for details see Reed et al. 1998).

Fig. 1 *Phyllospadix torreyi*. Photograph of fruits collected in seed traps placed in surfgrass beds. Fruits were categorized for analysis as (a) whole, (b) germinated, (c) eaten and (d) partial (only one arm present)



Once experiments had been initiated, daily observations were made to assess consumption of the food items, but no additional food was added. In addition, the type of damage inflicted was noted for comparison with fruits caught in the seed traps. Controls in each experiment consisted of containers ($N = 2$ to 4) with food items but without predators. Predators of a range of body sizes were collected from the field just prior to initiation of the experiments, and housed individually in the laboratory in running seawater. *Idotea ressecata* used ranged from 2.5 to 12.8 mm in total length (excluding antennae). *Pugettia producta* were 7.0 to 76.0 mm in carapace length, and *Pachygrapsus crassipes* were 8.0 to 31.7 mm in carapace length. All predators were maintained in the laboratory on *Macrocystis pyrifera* (L.) (giant kelp). Prior to each experiment, predators were starved for 24 h to standardize their hunger level. Experiments began when predators were placed in running seawater with spadices, fruits, or seedlings in separate flow-through containers ($N = 24$ to 28 individuals for each species of predator). Two spadices were placed with each predator, and their numbers of fruits and total weight were determined at the beginning and end of the 4 d experiment. A total of eight fruits or eight seedlings were given to each predator. The body size of each predator was determined at the beginning of each experiment by measuring the width and length of the carapace for crabs and total length (excluding antennae) for *I. ressecata*. The relationship between body size and degree of consumption of seeds, seedlings and spadices was explored for each species of predator.

Results

Patterns of pre-dispersal seed predation

Surveys revealed that predation damage to *Phyllospadix torreyi* seeds prior to their release from the spadix was relatively low. The proportion of spadices at each site that was damaged by predators ranged from 7 to 24% overall (Fig. 2A). These values did not differ among sites ($F_{3,3} = 4.52$, $P = 0.12$); in contrast, damage to spadices did differ between years (two-factor ANOVA without replication, $F_{1,3} = 12.0$, $P = 0.04$), with a greater proportion of spadices having eaten fruits in 1997. Even though predators attacked a relatively low proportion of spadices overall, they frequently did extensive damage. Considering all damaged spadices from both years combined, in more than half the cases every one of the fruits in the spadix was consumed (54 out of 105 spadices).

Overall, the proportion of fruits in a spadix that was consumed prior to dehiscence was ~15% in 1997 and less than half that amount in 1998 (Fig. 2B). Two-way ANOVA revealed no significant differences among the four sites ($F_{3,592} = 0.59$, $P = 0.61$), but a significant difference between years ($F_{1,592} = 5.25$, $P < 0.025$). This difference between years was observed at all four sites, and there was no significant site \times year interaction ($F_{3,592} = 0.03$, $P = 0.99$ for site \times year interaction).

Patterns of post-dispersal seed predation

Availability of dehisced seeds in the environment was temporally highly variable. The number of fruits caught in traps peaked during the fall months (September to

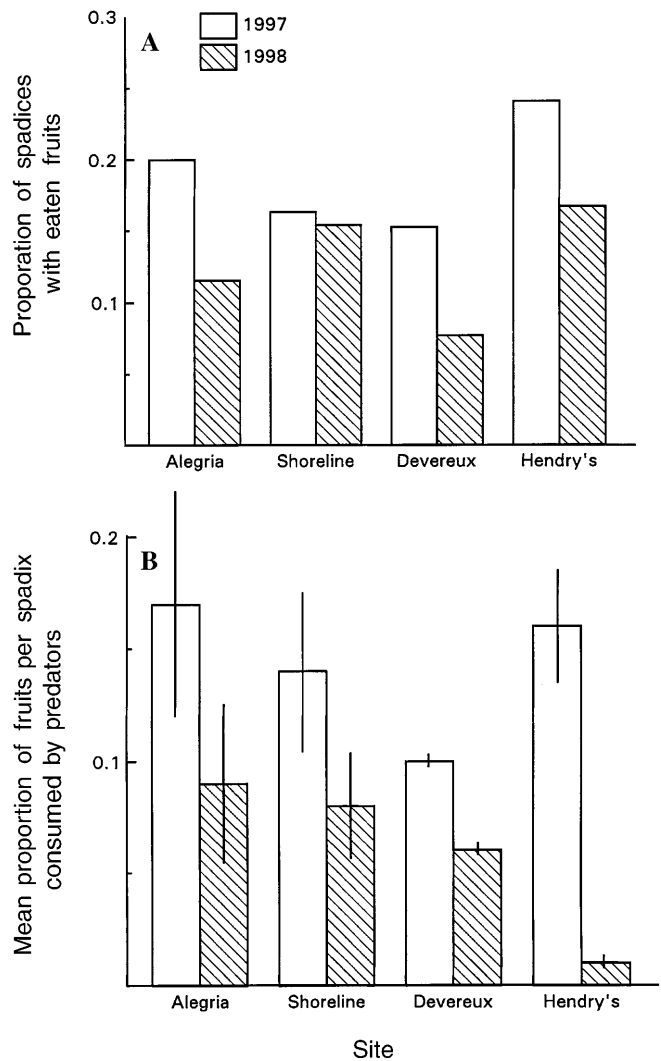


Fig. 2 *Phyllospadix torreyi*. Proportion of spadices with at least one eaten fruit (A) and mean proportion of fruits eaten per spadix (± 1 SE) (B) at four intertidal sites during peak flowering season (September) in 1997 and 1998. ($N = 39$ to 162 spadices per site per year)

November), following the annual fruiting period (Fig. 3). Inter-annual variation in abundance of fruits was also marked, with very low numbers observed during 1998 compared to the other three years (Fig. 3). Results of an analysis of covariance revealed that the effects of site on mean number of fruits caught in traps did not vary over time ($F_{3,149} = 2.43$, $P = 0.07$ for site \times date interaction). The mean number of fruit caught per trap was similar among sites but varied greatly over time [$F_{3,152} = 0.76$, $P = 0.52$ for site and $F_{1,152} = 10.17$, $P = 0.002$ for date in the reduced ANCOVA model, where the interaction term was dropped (as per Neter et al. 1996)]. Similarly, the proportion of fruits caught in traps that were missing seeds due to predation did not differ among the sites, but differed significantly over time [$F_{3,131} = 0.6$, $P = 0.62$ for site and $F_{1,131} = 86.06$, $P < 0.0001$ for date in the reduced ANCOVA model in which the non-significant inter-

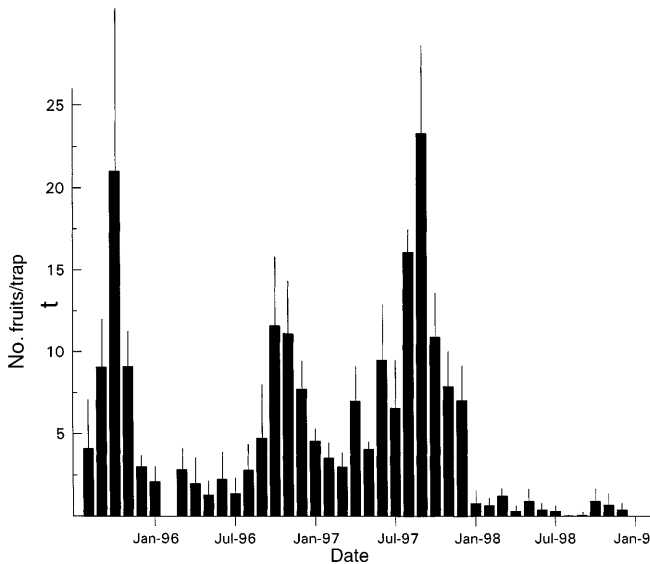


Fig. 3 *Phyllospadix torreyi*. Temporal pattern of abundance of dehiscenced fruits in the environment. Data are mean (+1 SE) number of fruits caught per trap per site per month. ($N = 4$ sites)

action term site \times date ($F_{3,128} = 1.84$, $P = 0.14$) was dropped]. We observed a steady increase over time in the proportion of fruit caught each month whose seeds had been eaten by predators during the first three years of the study (Fig. 4). At the beginning of the study in 1995, fewer than 10% of fruits caught had lost their seeds to predation, but this amount had risen to ~50% by the end of 1997, at which time predation leveled off. High variability in the proportion of seeds eaten in 1998 reflected the low numbers of seeds caught during that time. Linear regression revealed no significant relationship between the intensity of seed predation (proportion of fruit with eaten seeds) and seed abundance (mean number of fruit in the trap; $F_{1,134} = 0.06$, $P = 0.80$).

Patterns of abundance of potential seed predators

Several species of crabs occurred in and adjacent to *Phyllospadix torreyi* beds at the study sites. *Pagurus hirsutiusculus* was by far the most numerous, occurring

Table 1 *Phyllospadix torreyi*. Patterns of abundance of potential seed predators of this plant at two intertidal sites, Devereux and Hendry's. Data are means (SE) of individuals counted per 1 m² quadrat during three surveys. For *Pagurus hirsutiusculus*, $N = 59$

Site	<i>Pagurus hirsutiusculus</i>	<i>Cancer productus</i>	<i>Pugettia producta</i>	<i>Pachygrapsus crassipes</i>
Devereux				
Mean	5.7	0.06	0.89	1.53
(SE)	(0.73)	(0.20)	(0.18)	(0.22)
Hendry's				
Mean	16.21	0.55	0.29	0.15
(SE)	(2.77)	(0.03)	(0.06)	(0.04)

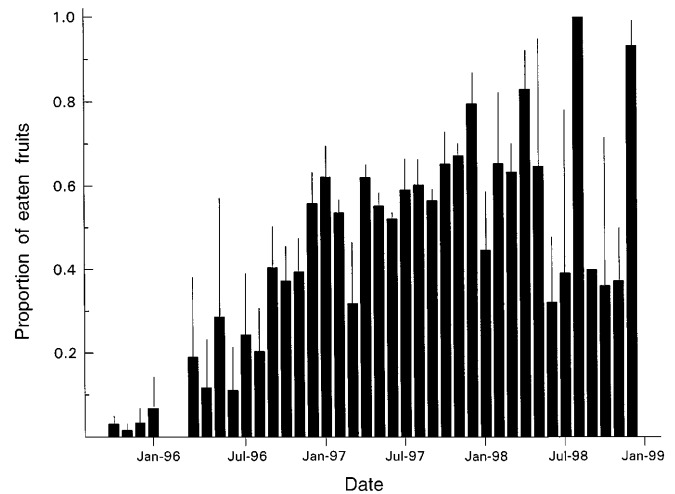


Fig. 4 *Phyllospadix torreyi*. Temporal pattern of predation on surfgrass seeds. Data are mean (+1 SE) proportion of fruits caught in seed traps each month whose seeds had been eaten by predators [E: Eq. (1) in "Materials and methods"] ($N = 4$ sites)

in almost every quadrat sampled at the sites, and *Cancer productus* Randall was the rarest (Table 1).

Laboratory tests of predation on early life stages of *Phyllospadix torreyi*

In laboratory feeding trials, the species of predators varied greatly in the life stages of *Phyllospadix torreyi* that they consumed, as well as in the intensity of consumption. The degree to which each predator consumed life stages of *P. torreyi* depended on both the proportion of individual animals that fed during a feeding trial as well as on how much was consumed by each individual that did feed. The proportions of predators that fed actively, and the proportion of food items that only these active feeders consumed during experiments are presented in Table 2. Figure 5 shows the overall proportion of food items consumed by all individuals (those that fed and those that did not feed) of each species tested during a feeding trial.

All three species of predators consumed seeds from the spadix, but *Pugettia producta* was by far the most

quadrats for Devereux and $N = 40$ quadrats for Hendry's; for all other species, $N = 204$ quadrats for Devereux and $N = 163$ quadrats for Hendry's

Table 2 *Phyllospadix torreyi*. Summary of feeding activity on three early life stages of this plant by three species of predators (*Idotea ressecata*, *Pugettia producta*, and *Pachygrapsus crassipes*; arranged in increasing order of importance) during 4 d-long laboratory experiments. Data are proportion of individuals of each predator that consumed a life stage, total number of predators tested, and mean (± 1 SD) proportion of each life stage eaten by those predator individuals that actively fed. Life stages offered to each predator were spadices ($N = 2$) containing mature fruits, dehisced fruits ($N = 8$) and seedlings ($N = 8$)

Life stage	Proportion of predators	No. of predators	Mean proportion consumed
Spadices			
<i>Idotea ressecata</i>	0.21	28	0.06 (0.05)
<i>Pugettia producta</i>	0.94	18	0.90 (0.23)
<i>Pachygrapsus crassipes</i>	0.38	24	0.10 (0.05)
Dehisced Fruits			
<i>Idotea ressecata</i>	0	28	0
<i>Pugettia producta</i>	0.50	26	0.96 (0.24)
<i>Pachygrapsus crassipes</i>	0.36	25	0.69 (0.40)
Seedlings			
<i>Idotea ressecata</i>	0	25	0
<i>Pugettia producta</i>	0.83	24	0.96 (0.16)
<i>Pachygrapsus crassipes</i>	0.89	27	0.96 (0.18)

voracious. All but one *P. producta* individual ate seeds from spadices during the experiment, whereas fewer than half the individuals of the other two species consumed seeds from spadices (Table 2). Overall, *P. producta* consumed 85% of the seeds offered to them during the spadix experiment while *Pachygrapsus crassipes* and *Idotea ressecata* consumed $< 5\%$ (Fig. 5A). When a particular spadix was attacked by *P. producta* during an experiment, its seeds tended to be almost entirely consumed (Table 2). In contrast, *P. crassipes* and *I. ressecata* attacked relatively few of the spadices offered during the experiment and, when an individual predator attacked a spadix, it consumed $< 10\%$ of its seeds (Table 2).

Idotea ressecata did not consume dehisced seeds, regardless of whether they were germinated or not. In contrast, both species of crabs readily consumed dehisced seeds. Overall, during the 4 d experiment, about half the seeds were eaten by *Pugettia producta* and about one-fourth by *Pachygrapsus crassipes* (Fig. 5B). The type of damage done by crabs during the laboratory experiment was similar to that sustained by fruits caught in the seed traps (Figs. 1c and 6). Feeding behavior varied substantially among individual crabs of both species. A large fraction (up to 64%) of the individuals tested in each experiment consumed no seeds at all, but the individuals that did eat during the trial consumed on average most of the seeds offered them (Table 2).

None of the *Idotea ressecata* ate seeds attached to seedlings (Fig. 5C, Table 2); they did graze a small amount of leaf tissue from the seedlings (authors' personal observations). In contrast, both species of crabs consumed the seeds from $\sim 80\%$ of the total seedlings offered them during the course of the experiment (Fig. 5C). The majority of individual crabs fed, and

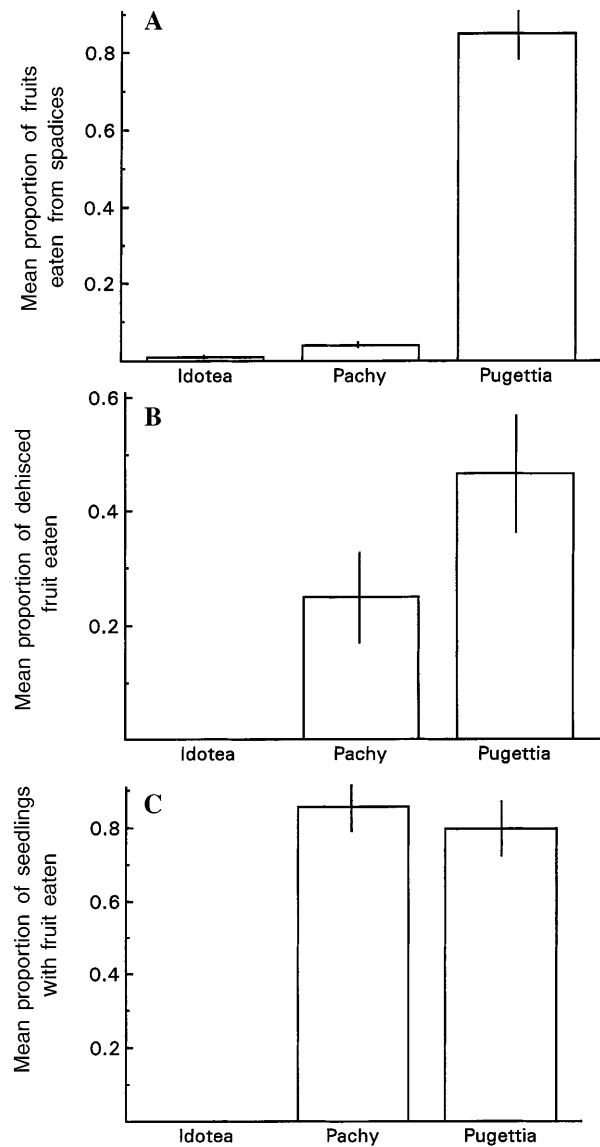


Fig. 5 *Phyllospadix torreyi*. Damage to spadices, dehisced fruits and seedlings by three predators during 4 d-long laboratory feeding experiments. Data are mean proportions (± 1 SE) of eaten fruits from spadices (A), groups of dehisced fruits (B), and seedlings (C). Number of replicate predators in each trial was 18 to 28; predators arranged in increasing order of importance (*Idotea* = *Idotea ressecata*; *Pachy* = *Pachygrapsus crassipes*; *Pugettia* = *Pugettia producta*)

those that did consumed virtually all the seeds from the available seedlings (Table 2).

Predator size had only minor effects on foraging efficiency in our experiments. *Pugettia producta* and *Pachygrapsus crassipes* < 10 mm carapace width did not consume any fruits or seeds. Other than this threshold in body size, there was no relationship between predator size and amount of spadices, seeds, or seedlings consumed by these two species. Very few *Idotea ressecata* ate fruits or seeds in our experiments, despite testing individuals that spanned the natural range of sizes for this species.

Fig. 6 *Phyllospadix torreyi*. Photograph of fruits whose seeds were consumed by *Pugettia producta* during laboratory trials. All seeds have been removed from the fruits, and extent of damage is variable



Discussion

Several previous studies have indicated that in short-term experiments, predation rates on seagrass seeds can be extremely high. For example, losses of outplanted *Zostera marina* seeds during brief (1 wk) field experiments ranged up to 96%, and predator enclosure-experiments identified blue crabs (*Callinectes sapidus* Rathbun) as the major predator (Fishman and Orth 1996). In their experiments, predators were argued to account for up to 65% of the overall loss of seeds (Fishman and Orth 1996). Our studies on the surfgrass *Phyllospadix torreyi* at four intertidal sites over several years suggest that the high rates of predation observed in short-term experiments can occur on a sustained basis in the field. After an initial period in 1995 of relatively low seed predation, losses of seeds at our study sites rose steadily and have remained high. During the last 2 yr of our study, 7 to 15% of seeds were eaten prior to dehiscence, and half or more of the dehisced seeds caught in traps each month were consumed by predators. All four sites examined showed similar temporal patterns in the intensity of seed predation.

Of the species tested in our laboratory experiments, the crabs *Pugettia producta* and *Pachygrapsus crassipes* were the most active predators on early life stages of *Phyllospadix torreyi*. *Pugettia producta* was particularly voracious, consuming most of the seeds from spadices, as well as virtually all seeds and seedlings offered to it in laboratory experiments. Comparisons of seeds and seedlings exposed to crab predators in the laboratory to those obtained in seed traps showed similar patterns of damage, in that the seed and much of the exocarp were removed, leaving one or both of the bristled arms behind. These patterns are not consistent with mechanical

damage that could arise in the high-energy surfgrass habitat. Early life stages of *Phyllospadix torreyi* can also be vulnerable to additional predators that we did not consider in our feeding trials. For example, Williams (1995) found the herbivorous fish *Girella nigricans* (Ayres) caused characteristic damage in a small proportion of male, but not female, spadices of *P. torreyi* at Santa Catalina Island, California. *G. nigricans* is not common at our study sites, and we did not observe its characteristic pattern of damage to spadices during our study; thus we attribute most of the predation observed in our study to crabs.

The results of our laboratory experiments are largely consistent with previous laboratory investigations of the behavior of predators on seeds of other seagrasses, particularly *Zostera marina*. All but the smallest individuals (<10 mm carapace length) of both crabs (*Pugettia producta* and *Pachygrapsus crassipes*) used in the experiments could easily consume seeds and seedlings, and once this threshold size was reached there was no relationship between predator size and amounts of spadices, seeds, or seedlings consumed. Similarly, Wiggand and Churchill (1988) argued for a threshold body size (of between 7 and 9 mm carapace length) in the ability of hermit crabs (*Pagurus longicarpus* Say) to feed on eelgrass (*Z. marina*) seeds in laboratory experiments. We found that all sizes of *Idotea ressecata* tested were capable of some degree of consumption of seeds from the spadix, but they did not attack dehisced seeds or seedlings. This may result from a need for *I. ressecata* to grasp the spadix in order to break open the seed. The behavior of *I. ressecata* appears similar to that observed for juvenile prawns (*Penaeus esculentus* Haswell), who search for and eat mature seeds of *Z. capricorni* Aschers when they are still attached to the plant (Wassenberg 1990).

Our field studies revealed strong seasonal and inter-annual variation in the abundance of seeds as estimated by captures in seed traps. However, we did not detect a relationship between intensity of predation and abundance of seeds, which might be expected if predators became satiated when seeds were abundant. Reasons for the steady increase in the proportion of seeds eaten during our 4 yr study are unknown. There was no indication that weather conditions were the underlying cause. The observed pattern could result from a temporal decline in the availability of more preferred, alternate food, which increased the tendency of crab predators to feed on surfgrass seeds. This phenomenon has been observed in a laboratory feeding study: Wigand and Churchill (1988) found that several species of crustaceans and molluscs displayed a reduced tendency to consume seagrass seeds when alternate foods (particularly animal tissue such as pieces of clam or scallop) were present. Similarly, McGuinness (1997) argued that spatial variation in consumption rates of seeds of various species of mangroves by red mangrove crabs [*Sesarma (Neosarmatium) meinerti* de Man] resulted from variation in availability of more highly preferred foods. Thus, it is possible that the increasing rates of seed predation during the course of this study resulted from a per capita decrease in availability of more preferred alternate foods for surfgrass seed predators. This lowered supply could be the result of higher populations of predators, lower amounts of the alternate foods, or both.

Surfgrass is a long-lived clonal plant that reproduces by vegetative spreading as well as through periodic episodes of seedling recruitment. Clearly, the amount of predation loss of seeds of surfgrass is of a magnitude that potentially could contribute to the low numbers of seedlings typically observed in the populations we study. However, even when the amount of seed predation is so great that a majority of seeds that are produced by a population are consumed (Price and Jenkins 1986; McGuinness 1997; Wurm 1998), there is no consensus regarding the potential for an impact on population dynamics or spatial distribution. Some studies have revealed that seed predation can have substantial effects on local populations. For instance, removal of rodent seed-predators greatly affected both the distribution and abundance of grassland species in the Chihuahuan Desert (Brown and Heske 1990). In contrast, in some cases even very high rates of losses of seeds to predators did not affect population abundance due to density-dependence in processes operating at other life stages (Borchert and Jain 1978). Thus, for surfgrass, a high rate of seed predation could potentially influence population abundance if it occurred during times when conditions are favorable for seedling recruitment, and if density-dependent losses from other sources did not offset variation arising from differences in losses to predators. Clearly, resolving the importance of seed losses to population dynamics of surfgrass will require much additional information. This includes a fuller understanding of patterns of spatial and temporal variation in the intensity of seed predation as

well as their underlying causes, so that the importance of seed predation relative to other processes that affect distribution and abundance can be assessed.

Acknowledgements We thank the many individuals that assisted us in the field and in the laboratory, especially M. Anghera, S. Bull, C. Cowan, J. Diener, M. Harriet, M. Lee, G. Snyder and S. Worcester. This research was supported by the County of Santa Barbara and by the Minerals Management Service, U.S. Department of the Interior, under MMS Agreement No. 14-35-00011-30758. Funding for interns was provided by a Research Training Grant (BIR 94-13141) from the National Science Foundation. The views and conclusions contained in this document are those of the authors and should not be interpreted as necessarily representing the official policies, either express or implied, of the U.S. Government. All experiments using live animals were conducted according to laws of the U.S. Government.

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