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Algal morphology, flow, and spatially variable recruitment of surfgrass *Phyllospadix torreyi*

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ABSTRACT: Causes of spatial variation in recruitment of the surfgrass *Phyllospadix torreyi* were explored. Recruitment of seedlings in this dominant, late successional seagrass is dependent on the presence of host plants (mainly branched algae), which serve as substrates for seed attachment and anchor the seedling during its early growth stages. Field observations indicated that attachment of seeds and seedlings to host plants was not always proportional to abundance of host plants. To explore mechanisms causing this pattern we measured seed attachment to 7 algal species and surfgrass in the laboratory under 3 water flow regimes. Laboratory experiments were conducted using a flow tank designed to produce oscillatory flow. The primary objectives of our laboratory experiments were to determine the relative seed catching ability of different host species, and the extent to which the seed catching efficiency of a host varied with flow velocity. The flow tank experiments revealed significant effects of both host species and flow regime, and no significant interaction between host species and flow. Seed attachment to all species was greatest at a moderate flow (max. velocity 85 cm s⁻¹) and was reduced significantly at both lower (max. velocity 45 cm s⁻¹) and higher (max. velocity 180 cm s⁻¹) flows. Seed attachment was highest on the intertidal red alga *Chondracanthus canaliculatus* (Harv.) Guiry and the subtidal coralline alga *Lithothrix aspergillum* Gray. Differences in seed attachment among the remaining 6 species were generally small; on average these plants collected about half as many seeds as *C. canaliculatus* and *L. aspergillum*. Data collected from field surveys were generally consistent with results obtained in the laboratory. The field abundance of host species having high seed-attachment potential in the laboratory explained a significant amount of spatial variation in seedling density at 3 of 4 intertidal sites (numbers of seedlings at 2 subtidal sites were very low and precluded similar analyses). Nonetheless, a substantial amount of variability in seedling recruitment remained unexplained by the abundance and species composition of host plants. Data obtained from standardized seed collectors placed in the field were consistent with this observation as the numbers of seeds attached were highly variable both within and among sites. This suggested that factors that influence seed production, dispersal and seedling survivorship also contribute to spatial variability in the density of seedlings in nature.

KEY WORDS: Seagrass · Seedling · Algal host · Recruitment · *Phyllospadix torreyi* · Marine ecology · Oscillatory water flow

INTRODUCTION

Understanding the dynamics of recruitment (i.e. the addition of new individuals to populations) is a central issue in ecology (Cook 1979, Roughgarden et al. 1985, 1988, Goldberg 1987, Eriksson 1989, 1993, Underwood & Fairweather 1989, Santelices 1990, Menge 1991,

Willson 1992, Menge et al. 1993, Booth & Brosnan 1995, Caley et al. 1996). Processes that affect the scale or magnitude of recruitment may have important consequences at the population and community levels (see reviews by Booth & Brosnan 1995, Caley et al. 1996). The few relatively long-term studies of recruitment in marine systems indicate that recruitment typically varies in both space and time (Caffey 1985, Connell 1985, Raimondi 1990).

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While it is generally understood that variation in recruitment can have important consequences for populations and communities, the causes underlying this variation are not always known. Patchiness in recruitment may result from non-uniformity in delivery, settlement, or survival of propagules. In marine systems, characteristics of propagules (e.g. behavior; Raimondi 1988a, 1991, Wellington 1992, Jones 1997, Schmitt & Holbrook 1999) and physical processes that affect them (Gaines et al. 1985, Butman et al. 1988, Raimondi 1988b, Kingsford 1990, Mullineaux & Butman 1990, Pawlik et al. 1991, Caselle & Warner 1996, Jones 1997) can produce non-uniform settlement. Spatially patchy settlement appears to be the case for the surfgrass *Phyllospadix torreyi* S. Watson, an abundant marine angiosperm that occurs along the west coast of North America (authors' pers. obs.). Unlike other seagrasses that grow in soft sediments of protected bays and coasts, *P. torreyi* lives in rocky, wave-swept habitats. Although seeds of surfgrass are incapable of the behavior exhibited by larvae and algal spores, their settlement is spatially patchy (Turner 1983, authors' pers. obs.), due in part to the fact that surfgrass seeds are not 'sticky' and cannot immediately attach to rock. Seeds attach instead to a host plant during the early growth period until the roots and rhizomes grow and attach securely to the rock (Turner 1983). Surfgrass seeds are well adapted for attachment to bushy algae as they possess 2 arm-like appendages lined with stiff, inwardly pointing bristles (Gibbs 1902) (Fig. 1). Seeds are negatively buoyant and drift along the bottom in the surf zone until they become entangled in a host plant. Once a seed attaches, it can germinate and produce grass-like leaves. Turner (1983) found that seeds

of a related species (*P. scouleri* Hooker) are uniquely adapted for attachment onto branched algae with a central axis of approximately 1 mm in diameter, because the space between the seed 'arm' and the body of the fruit is approximately 1 mm (Fig. 1). Seeds of *P. torreyi* are similar in shape and morphology to those of *P. scouleri*, although seeds of *P. torreyi* are slightly smaller (~20%, authors' unpubl. data). Spatial variation in the availability of suitable host plants may provide one potential explanation for spatially variable recruitment in surfgrass.

Several species of branched algae act as host plants for the early life stages of surfgrass (Turner 1983, authors' unpubl. data). The degree to which these species vary in their ability to facilitate seed attachment has not been investigated, nor have the specific morphological features that cause one host species to entangle more seeds than another. Further, the efficiency of attachment may vary with environmental conditions. Water motion in the intertidal and shallow subtidal habitats where *Phyllospadix torreyi* is found can vary between gentle oscillatory flows and extremely turbulent, high velocity breaking waves, depending on tide, depth and swell conditions. It seems likely that the efficiency of seed attachment to any particular host species would be influenced by these differing flow conditions. Of particular interest here is how flow velocity may influence the degree to which certain host species facilitate seed attachment.

Here we investigate the degree to which spatial variability in the recruitment of surfgrass seedlings is explained by the abundance and species composition of host plants. In the laboratory we measured seed attachment to several common host species under 3 conditions of oscillatory flow. Encounter rates of seeds with algal hosts were kept constant among all flow regimes and host species tested in the tank experiment in order to isolate the main and interactive effects of host species and flow on seed capture rates. Additionally, we measured the relative abundances of different host species in the field and the number of seedlings attached to those hosts. We calculated a seed attachment index which took into account both the quantity (proportional abundance) and quality (strength of seed attachment facilitation) of host species and used linear regression analysis to determine the amount of variability in density of surfgrass seedlings explained by the quality and quantity of host plants. Finally, standardized seed col-

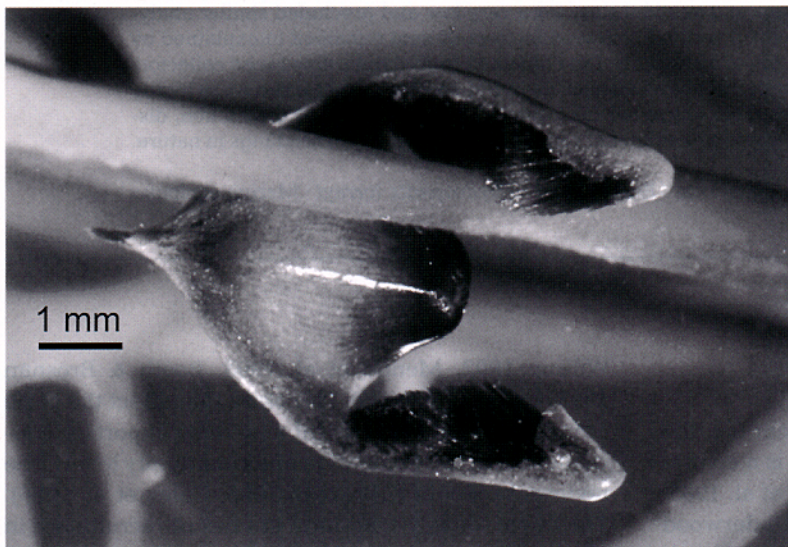


Fig. 1. *Phyllospadix torreyi* and *Chondracanthus canaliculatus*. Close-up photo of a seed of *P. torreyi* attached to a branch of *C. canaliculatus*

lectors in the field shed light on patterns of within-site variation in seed attachment that were not explained by the abundance and species composition of host species.

METHODS

Laboratory measurement of seed attachment. We measured seed attachment to several common host plant species in the laboratory using an oscillating flow tank. The flow tank measured 4.9 m long, 0.3 m wide and 0.6 m deep (Fig. 2) and was constructed out of 6 mm thick clear acrylic. The acrylic tank was mounted on a wooden frame for stability, and the frame was attached to an adjustable fulcrum so that the tilt angle could be varied. Oscillatory flow was accomplished manually by alternately raising and lowering the ends of the tank at a constant rate to predetermined heights.

The host species tested in the flow tank were *Bossiella orbigniana* (Dec) Silva, *Chondracanthus canaliculatus* (Harv.) Guiry, *Corallina chilensis* Dec., *Corallina vancouveriensis* L., *Gelidium purpurascens* Gardn., *Gracilariopsis lemaneiformis* (Bory) Dawson, Acleto & Foldvik, and *Lithothrix aspergillum* (Gray). All of these species have a branching morphology with an axis diameter suitable for the attachment of surfgrass seeds (see Abbott & Hollenberg 1976 for line drawings of these species). In addition, these species were relatively abundant at our study sites and were the species to which most seeds and seedlings were commonly attached in the field. We also tested *Phyllospadix torreyi* in the flow tank because we observed seeds and

seedlings attached to remaining portions of senescent leaves in the field. Accordingly, the *P. torreyi* specimens tested in the tank consisted of leaves less than 25 cm in length, many of which were senescent. Specimens of plants were obtained from the field by chiseling out the rock beneath the algal holdfast (or rhizome in the case of surfgrass), and then gluing the rock (with the attached algal clump or surfgrass) to an acrylic plate using marine epoxy putty (Koppers Splash Zone compound, Koppers Co., Los Angeles, CA). Plates with test specimens were fastened onto a slotted area in the center of the tank so that the plate was flush with the tank bottom.

Surf zone organisms such as those examined in this study routinely experience extreme fluctuations in flow velocities ranging from zero to more than 1400 cm s⁻¹ as surge oscillates back and forth with the passing of waves (Denny 1988). To account for potential interactions between host morphology and flow velocity, we tested all host species at 3 different flow regimes chosen to represent a range of flow environments typically experienced by these plants in nature. Our choice of flow speeds was based on our qualitative field observations of water motion, published values recorded in similar habitats (Denny 1988), and the ease of reproducing these speeds in the laboratory. The low flow regime was designed to mimic the surge-like, oscillatory flow typical of relatively calm days in the shallow subtidal where surfgrass is found. In the low flow regime test specimens were continually submerged and the maximal velocity was 45 cm s⁻¹. The medium and high flow regimes were designed to mimic more turbulent flows typical of shallower depths. In both the medium and high flow regimes, test specimens were alternately submerged and exposed with each oscillation. Maximal velocities in the medium and high flow regimes were 85 and 180 cm s⁻¹ respectively. Velocities were measured over repeated oscillations by placing a Marsh McBirney flow probe at the center of the tank 2 to 3 cm from the bottom. We used fresh filtered seawater in all tank trials.

Fifteen specimens of each host species were tested in each of the 3 flow regimes. A trial for a specimen at a given flow consisted of 25 oscillations of the tank. Prior to each trial (when the tank was level and the water was still), 80 mature surfgrass seeds were introduced into the tank (40 on each side of the centrally mounted test specimen). Although seeds as well as newly germinated seedlings are capable of attaching to host plants, we used ungerminated seeds in all trials. Surfgrass seeds are negatively buoyant and tended to tumble along near the bottom of the tank in all but the most turbulent flows. Because all seeds in every trial (with the exception of those attached to the host) passed through the middle of the tank in every oscilla-

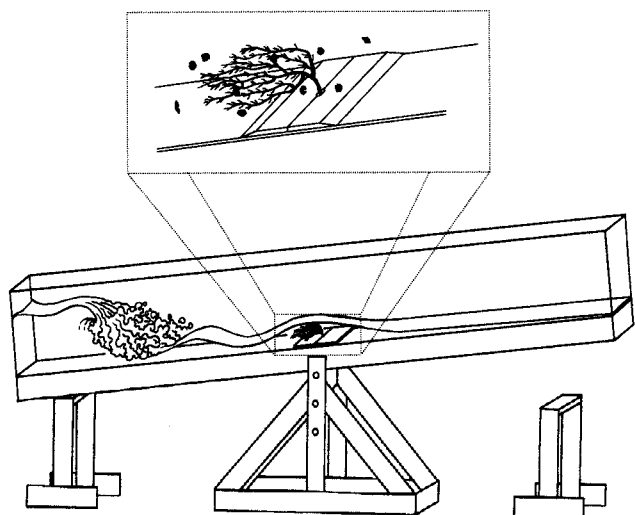


Fig. 2. Schematic representation of the oscillating-flow tank. The box at the top of the figure illustrates a close-up view of the algal test specimen and surfgrass seeds

tion, the rates that seeds encountered hosts (defined as the number of times that a seed passed the plane of the test specimen in each trial of 25 oscillations) were standardized among all trials and flow regimes. Following the final oscillation the specimen was removed from the tank and all seeds attached to it were counted. Since seeds attached to algae are often cryptic and difficult to see, we also counted all the seeds remaining in the tank to insure that the total number of seeds attached to the test specimen and in the tank equaled 80.

We standardized measures of seed attachment for each host species in 3 ways: (1) the number of attached seeds divided by the planform area of the specimen, (2) the number of attached seeds divided by the basal area of the specimen, and (3) the number of attached seeds divided by the volume of the specimen. Planform area is the frontal area of the plant when viewed in 2 dimensions, and basal area refers to the area of the plant attached to the substratum. Both area measurements were calculated from photos of the specimens using NIH Image 1.51 image analysis software. Plant volume was estimated by measuring water displacement in a graduated cylinder. We chose to standardize seed attachment by volume as opposed to biomass, because the calcium carbonate composition of the coralline algae complicates interspecific comparisons of size based on biomass (see Table 1 for host sizes). These 3 different ways of standardizing seed attachment each provided different information about the ability of a plant to facilitate the attachment of surfgrass seeds. Planform area is a relevant measure because it is the 2-dimensional area that a seed would need to intercept in order to become attached. Basal area provided information on the number of seeds collected by a species occupying a defined area of

the bottom. Standardizing to plant volume provided a more general estimate of the numbers of attached seeds based on overall plant size.

The effects of species and flow regime on seed attachment were investigated using a repeated measures analyses of variance (ANOVA) mixed model design where specimens nested within species was specified as a random effect and flow was considered a fixed factor. Separate analyses were done for the 3 standardized estimates of seed attachment described above. All data were transformed $[\ln(x+1)]$ to meet the assumption of homoscedasticity (Sokal & Rohlf 1981). Multiple comparisons among species and among flow regimes were made using the Ryan-Einot-Gabriel-Welsch multiple range test (SAS Institute 1990). All statistical analyses were performed using SAS statistical software (SAS Institute 1990).

Field surveys of seedling density and abundance of hosts. Field surveys were done in the winter months (January–February; the time when seedlings are most abundant; authors' unpubl. data) to measure the density of surfgrass seedlings and host plants at 4 intertidal and 2 subtidal sites in Santa Barbara County, CA. Data were collected in haphazardly placed quadrats ($N = 11$ to 39 quadrats site⁻¹, quadrat size was 1×1 m in 1996; due to time constraints in the field quadrat size was reduced to 30×30 cm in 1997). We sampled 2 intertidal sites (Corral Beach and Hendry's) and 1 subtidal site (Mohawk) in winter 1996 and 2 intertidal sites (Corral Canyon and Miramar) and 1 subtidal site (Forney's) in winter 1997. In each quadrat the primary percent cover of each species of algae and surfgrass was estimated visually, the number of seedlings was counted and the species of host plant of each seedling was determined. Seed and seedling data were standardized to number per m² for analysis.

To investigate the amount of variability in seedling density explained by abundance of host species we calculated a 'Seed Attachment Index' for each quadrat using data on seed attachment obtained in the flow tank and host plant abundance obtained in the field. To calculate this index, species were ranked according to their seed-collecting ability as determined by their performance in the oscillating-flow tank. Relative performance (P) was estimated as:

$$P = X_i/Y$$

where X_i = mean number of seeds collected by host species i in a flow tank trial, and Y = mean number of seeds collected during a trial averaged over all host species tested in the flow tank. The Seed Attachment Index (S) of a quadrat was calculated as:

$$S = \sum_{i=1}^n Pa_i$$

Table 1. Mean sizes (± 1 standard error) of host species tested in the flow tank. Host species abbreviations: Co = *Corallina chilensis*, Bo = *Bossiella orbigniana*, La = *Lithothrix aspergillum*, Pt = *Phyllospadix torreyi*, Gl = *Gracilariopsis lemaneiformis*, Cv = *Corallina vancouveriensis*, Gp = *Gelidium purpurascens*, Cc = *Chondracanthus canaliculatus*, Collector = artificial seed collector

Species	Planform area (m ² × 10 ⁻²)	Basal area (m ² × 10 ⁻³)	Volume (m ³ × 10 ⁻⁵)
Co	9.84 ± 0.30	5.98 ± 0.19	1.50 ± 0.08
Bo	8.61 ± 0.25	4.19 ± 0.20	2.00 ± 0.10
La	5.92 ± 0.19	4.04 ± 0.18	1.50 ± 0.07
Pt	12.30 ± 0.55	1.09 ± 0.17	1.80 ± 0.07
Gl	7.26 ± 0.24	3.26 ± 0.08	1.60 ± 0.06
Cv	4.36 ± 0.12	6.23 ± 0.20	1.80 ± 0.07
Gp	8.79 ± 0.25	5.18 ± 0.17	2.20 ± 0.10
Cc	6.93 ± 0.31	5.52 ± 0.12	1.60 ± 0.10
Collector	27.00 ± 0.00	6.00 ± 0.00	1.70 ± 0.00

where a_i = proportional abundance of host species i , and n = total number of host species in the quadrat. Seed Attachment Indices were calculated for each quadrat using values of P from data obtained for each of the 3 flow regimes as well as for data averaged over the 3 flow regimes.

Linear regression analysis was used to determine the amount of variability in the density of surfgrass seedlings at each site explained by the quantity and quality of host plants capable of facilitating seed attachment (i.e. S). Regressions were done for values of S calculated from data obtained from each of the 3 flow regimes as well as from data averaged over all flow regimes.

Estimates of spatial variation in seeds. Artificial seed collectors were deployed at our study sites to evaluate the degree to which spatial variability in seedling density varied independently of host plant abundance and seed-catching ability. Ten collectors were fastened to permanently fixed bolts in the surfgrass zone at 3 intertidal sites (Alegria, Hendry's and Shoreline) and 1 subtidal site (Mohawk). Collectors were placed and retrieved monthly from July 1997 through January 1998, the time of year when the vast majority of seed attachment occurs (authors' unpubl. data). Each collector consisted of 2 pieces of 30.5×30.5 cm fabric mesh which were fastened to the bolts by a nylon cable tie. The cable tie was cinched around the centers of the square mesh allowing the majority of mesh material to move freely in the surge. Two types of mesh were used to accommodate variability in seed size: 1.7 mm diameter polyester stretch mesh with round openings (polyester netting #9622, Research Nets Inc.) and 1.0 mm diameter mesh with square openings (nylon netting Delta 1004A, Memphis Net and Twine). The fabric diameter of the mesh was similar to that of algae known to facilitate seed attachment and seeds attached to the fabric of the collectors much like they attached to branches of algae. Each collector was attached to 1 of 10 permanently fixed bolts in the surfgrass zone at each site. We disassembled the collectors (the cable ties were cut and the mesh squares were laid out flat) upon retrieval and counted all seeds attached to the mesh. The seed-catching ability of the seed collectors was tested in the oscillating-flow tank using the same protocol described for host species (see above) to verify their efficacy as seed collectors.

RESULTS

Laboratory measurement of seed attachment

Host species differed significantly in their ability to facilitate attachment of surfgrass seeds in oscillating

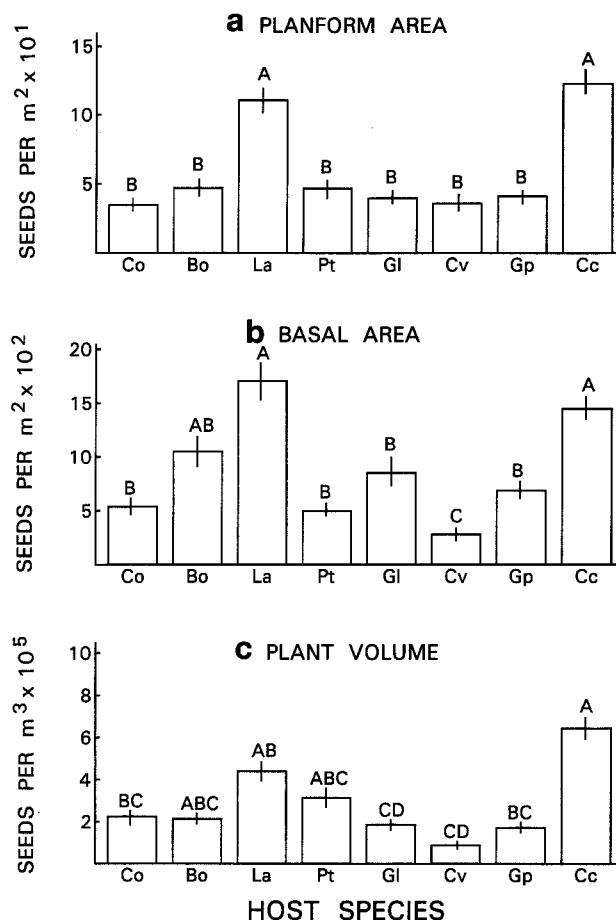


Fig. 3. The number of seeds collected by each species in the flow tank standardized to (a) planform area (m^2), (b) basal area (m^2), and (c) volume (m^3). Data are means (± 1 SE) averaged over all 3 flows. $N = 45$ trials per species (3 flow regimes \times 15 trials / flow regime). Means with different letters are significantly different from one another at $\alpha = 0.05$ (Ryan-Einot-Gabriel-Welsch multiple range test). Host species abbreviations: Co = *Corallina chilensis*, Bo = *Bossella orbigniana*, La = *Lithothrix aspergillum*, Pt = *Phyllospadix torreyi*, Gl = *Gracilariopsis lemaneiformis*, Cv = *Corallina vancouveriensis*, Gp = *Gelidium purpurascens*, Cc = *Chondracanthus canaliculatus*

flow (Fig. 3; $F_{7,112} = 13.99$, $p < 0.0001$, $F_{7,112} = 11.13$, $p < 0.0001$, and $F_{7,112} = 8.14$, $p < 0.0001$ for seed attachment based on planform area, basal area and plant volume respectively). The subtidal alga *Lithothrix aspergillum* and the intertidal alga *Chondracanthus canaliculatus* collected significantly more seeds than the other 6 species when specimen size was standardized to planform area, and significantly more than all but 1 species (*Bossella orbigniana*) when size was standardized to basal area (Fig. 3). There were no significant differences in seed-catching ability among the other species (including *Phyllospadix torreyi*) with the exception that *Corallina vancouveriensis* caught significantly fewer

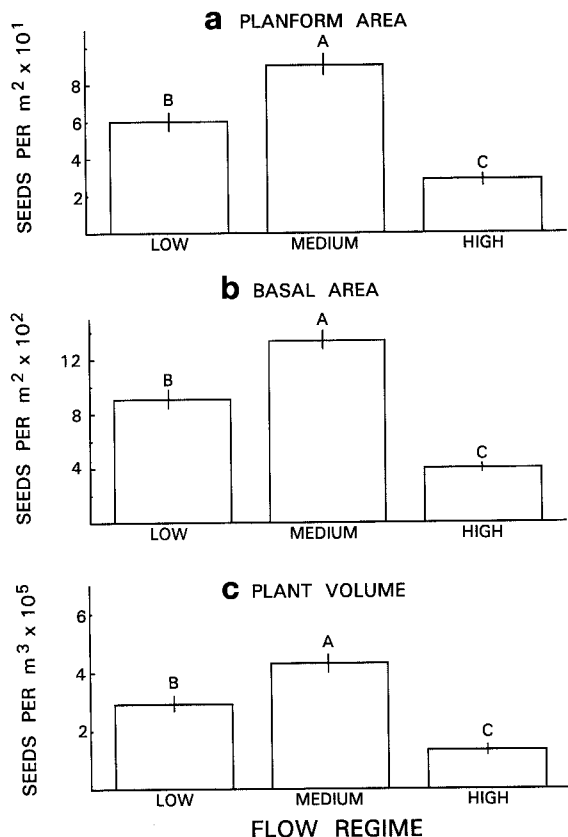


Fig. 4. (a) The number of seeds collected per planform area (m^2) of all species for each flow regime, (b) the number of seeds collected per basal area (m^2) of all species for each flow regime; and (c) the number of seeds collected per volume (m^3) of all species for each flow regime. Data are means (± 1 SE) averaged over all species. $N = 120$ trials per flow regime (8 species \times 15 trials / species). Means with different letters are significantly different from one another at $\alpha = 0.05$ (Ryan-Einot-Gabriel-Welsch multiple range test)

seeds than all other species when size was standardized to basal area. The general pattern of seed attachment was similar when standardized to volume; however, differences among species were generally smaller (Fig. 3).

The number of seeds collected by a test specimen was also significantly influenced by flow (Fig. 4; $F_{2,224} = 68.19$, $p < 0.0001$, $F_{2,224} = 43.22$, $p < 0.0001$, and $F_{2,224} = 26.06$, $p < 0.0001$ for seed attachment based on planform area, basal area and plant volume respectively). Seed attachment in all cases was greatest under moderate flow conditions, indicating that an optimal seed capturing velocity exists for all species tested. Plants exposed to the low flow regime caught significantly fewer seeds than when exposed to intermediate flows and significantly more seeds than when exposed to high flows, and no significant interactions between host species and flow regime were observed

for any of the standardized seed attachment measures (Fig. 4). The effects of flow speed on seed attachment were similar for all species ($F_{14,224} = 1.40$, $p = 0.15$, $F_{14,224} = 1.33$, $p = 0.19$, and $F_{14,224} = 1.34$, $p = 0.19$ for species \times flow interaction based on planform area, basal area and plant volume respectively).

Field surveys of seedling density and abundance of hosts

Chondracanthus canaliculatus, the intertidal species that had the highest seed-collecting ability in the flow tank experiments, was also the most abundant algal host species sampled at all 4 intertidal sites (Fig. 5). Consistent with the flow tank results, more seedlings were found attached to *C. canaliculatus* than any other host species sampled in the field.

Regression analyses revealed that the quality and quantity of host plants (as defined by the Seed Attachment Index) explained a significant amount of variation in seedling density at 3 of the 4 intertidal sites (Fig. 6; Corral Beach, $F_{1,9} = 6.65$, $p = 0.03$) Corral Canyon, $F_{1,19} = 5.24$, $p = 0.03$; Hendry's, $F_{1,23} = 7.12$, $p = 0.01$). Seed Attachment Indices for quadrats sampled at Miramar were not significant ($F_{1,37} = 2.72$, $p = 0.11$) and fell into 2 groups. The relationship between seedling number and S was not significant for either group when regressed separately. (Because there was no significant interaction between host species and flow regime in the flow tank study, we present only data from the Seed Attachment Index averaged over all flows. Regression results were extremely similar for

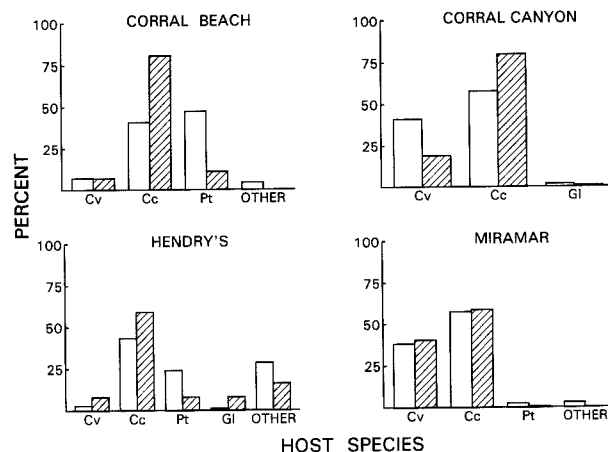


Fig. 5. The relative abundance (percent cover) of each host plant species (open bars) and the percentage of seedlings attached to each host plant species (hatched bars) at 4 intertidal sites. Host species abbreviations as in Fig. 2; OTHER = all other algal species not tested in the flow tank. $N =$ number of seedlings per site: Corral Beach $N = 54$, Corral Canyon $N = 110$, Hendry's $N = 126$ and Miramar $N = 37$

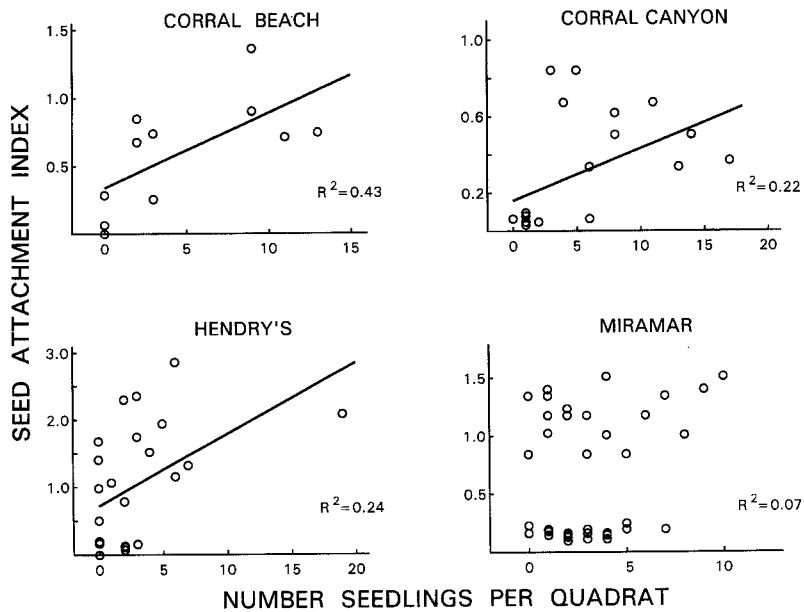


Fig. 6. The relationship between Seed Attachment Index (as described in text) and number of seedlings per quadrat at 4 sites. Each linear regression analysis used a Seed Attachment Index calculated from the relative seed-collecting performance of each host species averaged over all flow tank regimes. Number of quadrats per site: Corral Beach N = 11, Corral Canyon N = 21, Hendry's N = 25 and Miramar N = 39

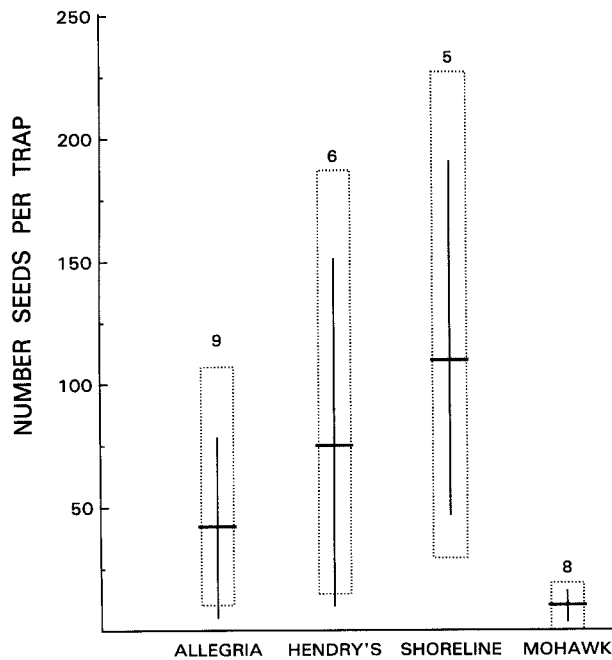


Fig. 7. Number of seeds caught by collectors at 3 intertidal sites (Allegria, Hendry's and Shoreline) and 1 subtidal site (Mohawk) from July 1997 to January 1998. Horizontal lines indicate the mean number of seeds collected at a site. Vertical lines indicate ± 1 SD and the dashed box indicates the range. The number above each dashed box is the number of collectors sampled at each site

Seed Attachment Indices calculated from data collected at each of the 3 flow regimes.)

Very few seedlings were observed in the surveys of the 2 subtidal sites despite relatively large sampling efforts (46 and 64 quadrats were sampled at Mohawk and Forney's, respectively). The low numbers of seedlings observed at these sites precluded analyses like those performed for the intertidal sites. Despite the low numbers, the patterns of occurrence of seedlings on subtidal hosts were notable. Of the 4 seedlings found at Mohawk, 2 were attached to *Lithothrix aspergillum* (the subtidal species that displayed the greatest seed-catching ability in the flow tank) despite its rarity (2% of the host plants sampled).

Interestingly, the other 2 seedlings found at Mohawk occurred on *Coralina officinalis* (a species of only moderate seed-catching ability), which accounted for 59% of the host algae sampled. By contrast, the data from

Forney's were not consistent with the findings of the flow tank experiments. Only 2 of 8 seeds were found on *L. aspergillum*, which had a relative abundance of 28%, while 3 of 8 seeds were attached to *Bossiella orbigniana* (a species that displayed moderate seed-catching ability), which had a relative abundance of only 6%.

Estimates of spatial variation in seeds

The average number of seeds attached to seed collectors in the oscillating-flow tank was 2.12×10^1 (SE = 0.23×10^1) seeds m^{-2} , 9.52×10^2 (SE = 1.04×10^2) seeds m^{-2} , and 3.35×10^5 (SE = 0.36×10^5) seeds m^{-3} (averaged over all flows) based on planform area, basal area and volume respectively. This is within the range observed for the average host specimen, indicating that the artificial collectors caught seeds at rates similar to host plants occupying a similar amount of space. At our field sites, the number of seeds trapped by the collectors varied tremendously both within and among sites (Fig. 7). On average, substantially more seeds were collected at the 3 intertidal sites compared to the subtidal site. However, within-site variation in numbers of seeds collected was also very high, with at least an order of magnitude difference among collectors in the number of seeds caught.

DISCUSSION

Turner (1983) showed that seed attachment in *Phyllospadix scouleri* was facilitated by algae with a central axis approximately 1 mm in diameter. The results of our laboratory studies extended Turner's findings to *P. torreyi* and revealed that the effectiveness of seed attachment varied even among branched algae with a morphology capable of entangling seeds (i.e. having branches with a central axis of approximately 1 mm diameter). More importantly, the species-specific differences in seed-collecting ability detected in the laboratory usually explained a significant amount of variability in the distribution of surfgrass seeds and seedlings observed in the field. Abundance of surfgrass seedlings at 3 of 4 intertidal sites was positively correlated with the abundance of algae with high seed-collecting abilities (as determined by laboratory experiments using the oscillating-flow tank).

The results of our laboratory experiments on seed attachment were largely similar for the 3 size-standardization measures, indicating that the differences in seed attachment observed among species resulted more from differences in species architecture or morphology (i.e. branching patterns, axis diameter) than from absolute differences in plant size. *Chondracanthus canaliculatus* showed significantly greater seed attachment than all other species regardless of which size parameter was used in the standardization. Thus, there appeared to be some size-independent aspect of the morphology of *C. canaliculatus* that facilitated seed attachment. The relative performance of the other 6 species appeared to be more sensitive to plant size. The number of seeds collected by these species when standardized to planform area were extremely similar, but differed somewhat when standardized to basal area, and volume (Fig. 3). One notable difference was observed in *Corallina vancouveriensis*, a short calcified alga that collected significantly fewer seeds than all other species when standardized to basal area. This difference is ecologically important because seed counts standardized to basal area provide one way to estimate the seed attachment potential for algae in field surveys based on percent cover estimates.

Phyllospadix torreyi appeared as proficient at entangling its own seeds as several of the algae known to facilitate seed attachment (*Lithothrix aspergillum* and *Chondracanthus canaliculatus* being notable exceptions). Although we routinely found seeds and seedlings attached to surfgrass in the field, the numbers were generally lower than might be expected based on the high abundance of surfgrass and its seed-collecting ability. This discrepancy may have resulted from the difficulty in finding seeds on adult surfgrass relative to

algae. Not only were seeds and the senescent leaves to which they attached similar in color, they were frequently inundated by sand, making it very difficult to sample them in the field. For similar reasons it was often difficult to distinguish seedlings from new shoots arising from existing rhizomes. Consequently, our field data probably underestimated the actual number of seeds and seedlings that became attached to adult surfgrass.

Our laboratory findings and field observations contrasted with Turner's (1983) conclusion that seeds of *Phyllospadix scouleri* cannot attach to adult surfgrass. Differences between *P. scouleri* and *P. torreyi* in seed and leaf size may account for this discrepancy; *P. torreyi* has slightly smaller seeds and more slender leaves than *P. scouleri*. However, we found both *P. torreyi* and *P. scouleri* seeds attached to *P. scouleri* adults at sites north of Point Conception, CA, and at Santa Cruz Island, CA, where *P. scouleri* was more common. The differences between the 2 studies likely stem from the difficulty in finding seeds and seedlings within established stands of surfgrass.

Water motion significantly influenced a host plant's ability to facilitate seed attachment in laboratory flows. Seed attachment was significantly greatest at intermediate flows for all species tested. The consistent effect of water motion observed among species was evidence for the generality of this result. At the low flows tested, the negatively buoyant seeds tended to tumble along the bottom of the tank where encounter rates with upright branches were low. Many of the seeds that encountered branches failed to become entangled, possibly because they lacked the momentum needed to securely attach to the host plant. By contrast, in the high flow regime seeds generally were suspended slightly higher in the water column where encounter rates with branches were higher. However, under conditions of high flow flexible organisms such as algae reconfigure to minimize drag (Koehl 1986, Gaylord et al. 1994, Hurd & Stevens 1997). Consequently, the branches of host plants became compressed in the high flow regime (author's pers. obs.), thereby reducing the area available for seed attachment relative to intermediate flows. Moreover, the high velocities caused many seeds to skim over the compressed branches of the host plant, as has been seen in other plants (Worcester 1995). It should be noted that seed encounter rates in our experiments were purposely held constant so that we could isolate the effects of flow velocity on the seed capture efficiency of different host species. In nature, however, plants living in high flow environments will encounter more seeds than plants exposed to lower flows (assuming the concentration of seeds in the water column at the 2 environments is the same). The extent to which

seed capture efficiency and seed encounter rates are influenced by flow to affect patterns of seedling recruitment in surfgrass is unknown.

Although host plant abundance and morphology generally explained a significant amount of variability in seedling abundance in the field, much variability remained unexplained. Data obtained from identically constructed seed collectors verified that a substantial amount of variability in seed and seedling abundance was caused by factors other than the abundance of hosts having a high capacity to entangle seeds. The high variability observed among collectors may have resulted from: (1) spatial variability in seed production that influenced the number of seeds available for dispersal, (2) variability in flow that influenced both the delivery of seeds and the efficiency of collectors to entangle them, and (3) variability in the retention of seeds.

The relative importance of different sources of variability likely varies with the spatial scale. For example, spatial variability in seed production is more likely to produce differences in seedling abundance among sites than it is within sites. Support for this reasoning comes in part from our observations that many seeds became entangled in collectors long after the disappearance of fruit on female plants. These observations suggest that the dispersal time for many seeds may be relatively long (i.e. weeks to months). Consequently, any patchiness in the distribution of seeds arising from within-site patchiness in seed production is likely to be homogenized during dispersal by the extensive mixing that occurs in the surf zone. Additionally, we saw no relationship between the number of seeds trapped by a collector and its proximity to seed-producing plants.

Evidence that variability in seed production influenced patterns of seedling abundance at larger spatial scales (i.e. among sites) came from field observations of seed/seedling abundance on natural host algae and artificial seed collectors. In both cases there was at least an order of magnitude fewer seeds/seedlings at subtidal sites relative to intertidal sites. Interestingly, seed production in *Phyllospadix torreyi* is known to decline with depth (Williams 1995) and we found seed production to be an order of magnitude lower at our subtidal site (Mohawk) compared to intertidal sites (authors' unpubl. data).

Spatially variable flow may have contributed to some of the unexplained variability in seedling abundance and the high within-site variability observed among artificial seed collectors. Gaylord (1997) showed that flow velocities in the surf zone can vary tremendously over very small spatial scales and our flow tank data indicate that flow velocity can significantly influence the seed-collecting ability of host plants and artificial collectors. Not to be overlooked is the potential for

large within-site variability in seed and seedling survival. Predation on seeds and seedlings by fish, crabs and other invertebrates can be severe (Williams 1995, authors' unpubl. data), and spatial variability in the distribution of predators has the potential to greatly influence patterns of abundance of seeds and seedlings. In addition, different species of algae may differ in their ability to retain seeds once they catch them. Such differences in seed retention could have contributed to the unexplained variation observed in seedling abundance.

In conclusion, our laboratory results demonstrated that algal morphology can influence seed attachment in *Phyllospadix torreyi*, and flow velocity can directly affect the strength of this facilitation. Although a significant amount of variability in seedling abundance can be explained by the abundance and morphology of host plants at most sites, the causes of the remaining variation are unknown. Additional studies will provide much needed information on the degree to which flow velocity interacts with seed production and supply, and seedling retention and survival to influence patterns of surfgrass recruitment in nature.

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