



Seasonal patterns of disturbance influence recruitment of the sea palm, *Postelsia palmaeformis*

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Abstract

Physical disturbance can have important effects on the distribution and abundance of sessile organisms, and temporal variation in the disturbance regime may strongly influence recruitment of species which reproduce seasonally. The sea palm *Postelsia palmaeformis* is a kelp with an annual, heteromorphic life history that inhabits the mid-tidal zones of some of the most wave-exposed rocky intertidal areas on the Pacific coast. *Postelsia* is thought to thrive in wave beaten areas, since winter storms remove patches of the mussel *Mytilus californianus*, the dominant competitor, thereby freeing bare space on the rock. To evaluate the effects of temporal variation in the physical disturbance regime and the effects of mussels on *Postelsia* recruitment, small plots in a mussel bed surrounded by existing *Postelsia* were seasonally cleared of mussels. Sea palm recruitment occurred in all plots, but was greatest in the most recent winter mussel removal treatment, suggesting survival of microscopic or young stages of *Postelsia* may be enhanced beneath mussel beds during fall/winter. *Postelsia*'s annual life history seems ideally suited to wave-exposed sites, where predictable winter disturbances remove mussels. This study shows that *Mytilus* can also have positive effects on *Postelsia* recruitment.

Keywords: Disturbance; *Postelsia palmaeformis*; Wave exposure; Seaweed; Sea palm; Recruitment; Mussel; *Mytilus californianus*

1. Introduction

Few ecological studies of physical disturbance have considered how temporal variation in disturbance may influence the abilities of species to persist or recruit at a site. Life cycles of many sessile organisms are strongly dependent on the occurrence of

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disturbance, since persistence of many sessile populations depends on dispersal to sites suitable for recruitment. The location and the proximity of a disturbed patch to sources of colonists are two factors that can greatly influence the mode and rate of colonization of a recently disturbed area, particularly for species that do not disperse their propagules very far (Dayton, 1973; Platt and Weis, 1977; Bormann and Likens, 1979; Paine, 1979; Horn, 1981; Sousa, 1984). The time at which a patch is created by disturbance will indirectly affect colonization if the availability of propagules varies over time (Kennelly, 1987a; Kennelly, 1987b; Reed et al., 1988; Reed, 1990; Sousa, 1979). In systems where disturbances occur seasonally and where there are colonist species with annual life histories, the timing of patch creation is especially important.

The relationship between the time at which a patch is created and patch recovery may be even more complicated in systems that contain plants with heteromorphic life histories (e.g., kelps, ferns). In these plants recruitment follows the successful completion of a separate, additional life history phase, the gametophyte. Following release from the adult sporophyte, mobile zoospores settle and germinate into either male or female gametophytes. Gametophytes are sessile, free-living, microscopic plants, which, when sexually mature, produce eggs or sperm. Following syngamy the sporophyte begins to develop. Thus sporophyte recruits are derived from an intermediate stage and are not the same individual as those that initially settled. In contrast to more advanced plants or sessile marine invertebrates, recruitment in primitive plants such as kelps may be influenced by post-settlement events which can occur in two very different life history stages: the sexual gametophyte or the asexual microscopic sporophyte. The biology of the gametophyte generation in kelps has been extensively studied (see Bold and Wynne, 1978; Kain, 1979); however, its ecology is poorly understood due to the small size of gametophytes and the difficulty of observing them in nature. Most studies of kelp recruitment have focused on the sporophyte stage (Sundene, 1962; Dayton, 1973; Paine, 1979; Paine, 1988; Chapman, 1984; Dayton et al., 1984; Harris et al., 1984; Reed and Foster, 1984; Reed et al., 1988; Dean et al., 1989; Reed, 1990). Kelp gametophytes constitute large but unseen populations which cannot readily be quantified or even, in some cases, identified (Santelices, 1990). By analogy with the seed bank of land plants (Harper, 1977), these microscopic algal populations have been referred to as the bank of microscopic stages of seaweeds (Chapman, 1986).

Theoretical studies of life history models support the idea that seasonal environments are crucial in the evolution of life histories which have more than one ecologically distinct phase (Istock, 1966). In support of this hypothesis, the orders of brown algae having heteromorphic life histories are poorly represented in tropical regions, and occur predominantly in temperate and polar latitudes that are characterized by pronounced seasonal changes in the physical environment (Clayton, 1988). Clayton (1988) suggests that seasonal factors such as winter disturbances have had an important selective effect on the evolution of heteromorphic life histories and that the different morphological phases have evolved in response to environmental change. Sporophytes of many algae in the orders Chordariales, Dictyosiphonales and annual species of Laminariales have relatively short life spans and commonly grow during the spring and summer. They shed their spores and degenerate before the onset of winter, while presumably the spores or gametophytes survive and/or grow in winter (Clayton, 1988). We can only speculate on

the adaptive significance of heteromorphic life histories in these orders, since there is very little experimental evidence to indicate which particular environmental factors have influenced natural selection.

This paper focuses on how the disturbance regime of the wave-exposed intertidal zones of the northeast Pacific may influence the recruitment and survival of the sea palm, *Postelsia palmaeformis*. *Postelsia* is a brown alga of the order Laminariales that lives in the middle and upper intertidal zones of wave-exposed shores. It ranges from central California to Vancouver Island, B.C. (Abbott and Hollenberg, 1976). The sea palm is a kelp with an annual, heteromorphic life history whose macroscopic sporophyte is a conspicuous member of wave-exposed, rocky shores where it often forms large aggregations in summer (Bold and Wynne, 1978). In Oregon, sporophytes begin to appear in January, grow rapidly through the spring and become reproductive in late spring/early summer. In summer the stipes of the sporophytes can reach lengths of 50–75 cm (Paine, 1988) and support a dense crown of blades which function both in photosynthesis and reproduction. The spores are produced in longitudinal groves on blades, drip onto the substrate at low tide and probably attach immediately and become microscopic gametophytes (Dayton, 1973; Paine, 1979; Paine, 1988). Following reproduction, the sporophytes are usually ripped from the rock by large waves in winter storms.

Wave-induced disturbances are important in allowing *Postelsia* to coexist with the mussel, *Mytilus californianus*, the competitive dominant in the mid-tidal zone (Paine, 1966; Dayton, 1971; Dayton, 1973). In fact, the ability of *Postelsia* to persist at a site is dependent on the occurrence of predictable disturbances above some threshold magnitude and at a sufficient rate for *Postelsia* to occupy sites continually (Paine, 1979; Paine, 1988). These disturbances remove clumps of *Mytilus*, the dominant competitor, and create patches of bare rock space, judged by Paine (1988) to be the most suitable substratum for *Postelsia* recruitment and survival. *Postelsia* is not found in wave protected areas and apparently cannot persist in sites with low disturbance rates, since *Mytilus* can eventually exclude *Postelsia* if undisturbed (Paine, 1979).

Postelsia can also assist in the creation of bare rock space by overgrowing and smothering competing organisms such as mussels, barnacles and other algae. Bare space is renewed when sporophyte *Postelsia* become so large that the drag forces on the *Postelsia* produced by large waves overcome the ability of the organisms to adhere to the rock. The sea palm, as well as the organisms it had overgrown, are then ripped from the rock. In the scenario proposed by Dayton (1973), more *Postelsia* zoospores from adjacent plants can then settle and germinate in the summer on the space made available. However, this scenario is questionable in the context of *Postelsia*'s annual life history in a seasonally disturbed environment. In summer, when sea palms are reproductive, bare space may be deluged with spores from neighboring *Postelsia*. However, since *Postelsia* is thought to be an annual, it seems improbable that these spores will go through the entire heteromorphic alternation of generations and appear on the rock as sporophytes in the same summer that they settle. Since most disturbances to the mussel bed occur during winter storms when spore-producing *Postelsia* are no longer present, recruitment of the next generation of sporophytes to these disturbed patches should not be apparent until the spring a minimum of 12 months following the time of patch creation. Thus, if

disturbance occurs most often in winter, but reproduction occurs in summer when many disturbed patches have already been colonized by sessile organisms or even closed by mussel encroachment, how do *Postelsia* come to dominate newly cleared patches?

This study experimentally evaluates the effects of temporal variation in the disturbance regime and of *Mytilus* on the recruitment of *Postelsia* under field conditions.

2. Methods

To test the effect of season of disturbance on recruitment density of *Postelsia*, experimental clearings were created in mussel beds at different times of the year and the clearings were allowed to be seeded naturally with sea palm recruits. This experiment was conducted at the South Point of Depoe Bay (SPDB; 44°49'N, 124°04'W) on the central Oregon coast. The site is a slightly sloping, rocky (basalt) headland fully exposed to oceanic waves. Experimental plots were located on a slightly sloping rock surface in the middle of the *Mytilus/Postelsia* zone. *Postelsia* are scattered patchily throughout the mussel bed in this area in clumps of 50–100 plants. Although occasional plants grow directly on mussels, most *Postelsia* are confined to these small clusters in the mussel bed.

The experimental clearings were 45 × 45 cm plots marked at the corners with stainless steel screws. Sixteen plots were established in the mussel bed, all within 0.5 m of existing *Postelsia* clusters and located in areas that were likely to be seeded with *Postelsia* spores during the summer reproductive season. One of four treatments was randomly assigned to each plot: 1) summer disturbance; 2) winter disturbance; 3) winter disturbance and sterilization; and 4) no disturbance (unmanipulated). For the summer disturbance treatment, mussels were removed from each plot in July 1991. In the winter disturbance and winter disturbance plus sterilization treatments, mussels were removed from each plot in December 1991 when there were very few remaining adult *Postelsia* at the site. Any remaining adult *Postelsia* that were within 25 m of the plots were also removed in winter. In the winter disturbance plus sterilization treatment, the rock in each plot was 'sterilized' following mussel removal in an effort to eliminate microscopic algal spores. Sterilization was accomplished by scraping each plot with a stiff wire brush and chiseling off 0.5–1.0 cm of rock from the top layer of each plot. The experiment was repeated the following year, 1992, using the same method for the new summer and winter disturbance plots. In addition to re-chiseling the winter disturbance plus sterilization plots, two coats of oven cleaner were applied to each of the plots in an attempt to kill microscopic algal forms hidden in cracks.

To avoid edge effects, only the inner 0.16 m² of each plot was sampled. The number of *Postelsia* in each plot was recorded each month in the year following the experiment. The number of *Postelsia* in each plot monthly in 1993 was also recorded from the winter and summer disturbance 1991 plots. Data analysis employed repeated measures analysis of variance. Residual and normal probability plots were visually examined and the density data were log transformed to achieve approximate normality. Seasonal effects of clearing and the effects of sterilizing rock on *Postelsia* densities were determined using multiple contrasts within the repeated measures analysis.

3. Results

3.1. First year (1992)

Postelsia first began to appear in the experimental plots in February and persisted through September (Fig. 1). No *Postelsia* appeared in the summer plots immediately following summer mussel clearings. There was large variation in *Postelsia* densities within treatments and the treatment effect in the repeated measures analysis of variance was not statistically significant (Table 1). There were also no significant differences between treatments over the course of the experiment. On average, plots in which mussels were removed in winter had the highest *Postelsia* densities. Plots that were cleared of mussels in winter and scraped and chiseled had lower *Postelsia* densities than plots that were cleared in winter and not scraped. Plots that were cleared of mussels in summer had densities similar to those that were cleared of mussels and scraped in winter. Plots that were not cleared of mussels had the lowest *Postelsia* densities.

3.2. Second year (1993)

In the second experimental year at SPDB, *Postelsia* first appeared in the plots in February and persisted through November (Fig. 2). Plots disturbed in winter had the highest densities of *Postelsia* in the following year. *Postelsia* recruitment was intermediate on plots cleared in the summer and lowest on sterilized and control plots. In addition, *Postelsia* densities varied significantly depending on both the experimental

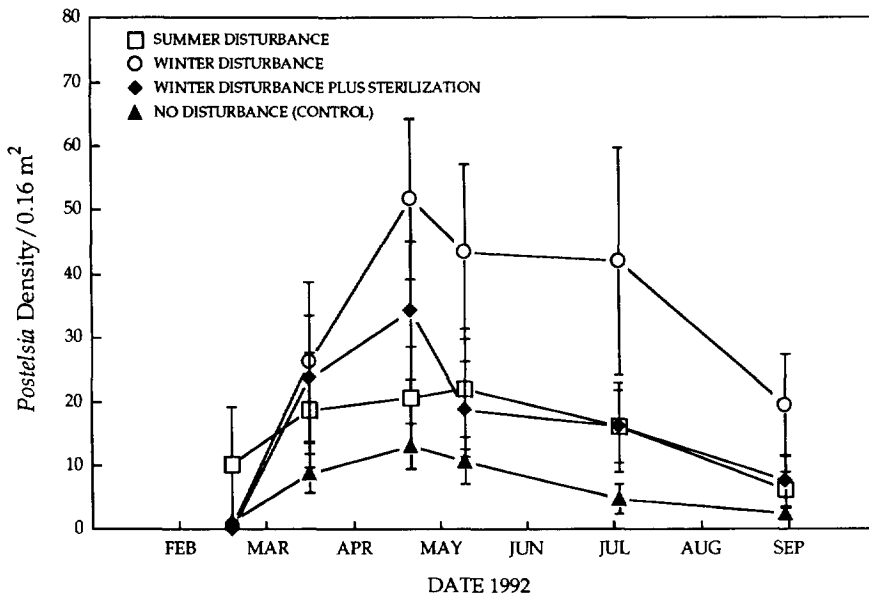


Fig. 1. Mean density of *Postelsia* ± 1 standard error of the mean (S.E.M.), in each of the treatment plots in the first year of the mussel removal experiment, 1992.

Table 1

Repeated measures ANOVA of the effect of disturbance regime (treatment) and sampling date on *Postelsia* density (log transformed) in the year following the experimental manipulations

1992				
	df	MS	F-Ratio	p
Between Subjects				
Treatment	3	3.915	0.844	0.496
Error	12	4.640		
Within Subjects				
Date	3	1.784	5.339	0.004
Treatment × Date	9	0.464	1.388	0.230
Error	36	0.334		
Multivariate repeated measures analysis				
	df	Wilks' Lambda	F-Ratio	p
Date	3, 10	0.380	5.443	0.018
Treatment × Date	9, 24	0.374	1.354	0.262
1993				
	df	MS	F-Ratio	p
Between Subjects				
Treatment	3	64.946	32.990	<0.001
Error	12	1.969		
Within Subjects				
Date	6	0.943	8.077	<0.001
Treatment × Date	18	0.234	2.005	0.020
Error	72	0.117		
Multivariate repeated measures analysis				
	df	Wilks' Lambda	F-Ratio	p
Date	6, 7	0.178	5.402	0.022
Treatment × Date	18, 20	0.072	1.725	0.118

treatment and census date (Table 1). The first and last dates (February, October and November) were not included in the analysis since *Postelsia* densities are very low both early and late in the season. The effect of sterilizing was highly significant and plots that were cleared of mussels in the winter and sterilized had far lower densities of *Postelsia* than those that were cleared and not sterilized. Unmanipulated plots, within which *Postelsia* recruits grew directly upon mussels, had slightly higher densities of *Postelsia* than sterilized plots.

Plots cleared in the most recent winter (1992) had significantly higher densities of *Postelsia* in 1993 than those cleared in the previous winter (1991) (Fig. 3, Table 2). *Postelsia* densities did not differ significantly between plots cleared in summer 1991 and summer 1992. Within a year, *Postelsia* densities were higher in plots cleared in winter than in summer, although these differences were only significant in 1993.

In summary, mussel bed areas that were disturbed in winter, when no sporophyte *Postelsia* were present, had significantly higher densities of *Postelsia* than areas disturbed in summer, which were surrounded with fertile plants at the time bare space was created. Areas most recently disturbed had greater sea palm densities than areas that had been free of mussels for several seasons. Scraping, chiseling and applying oven

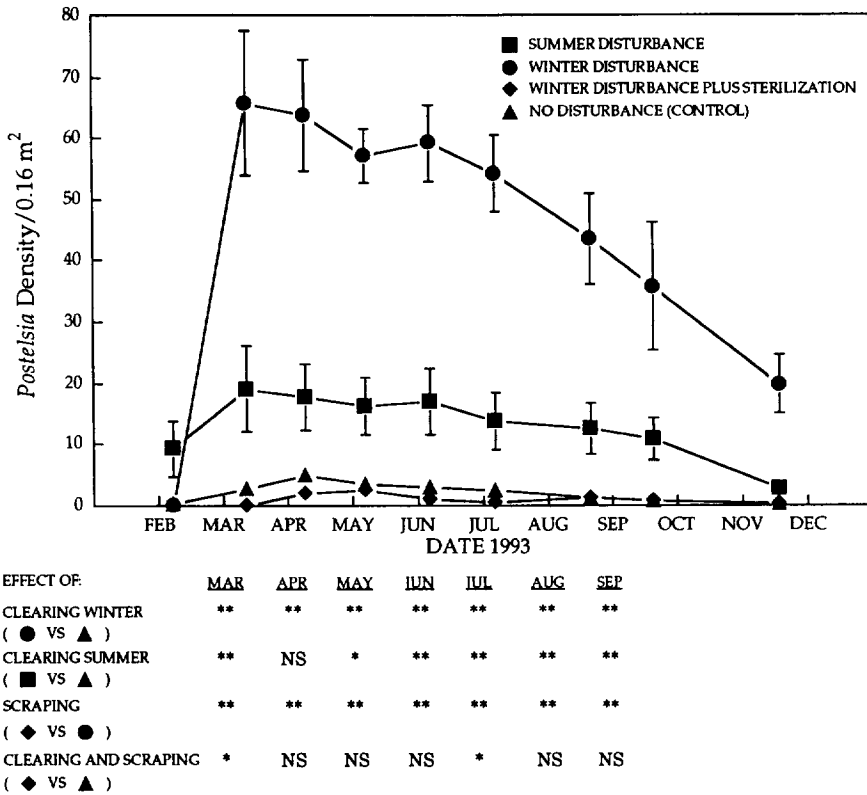
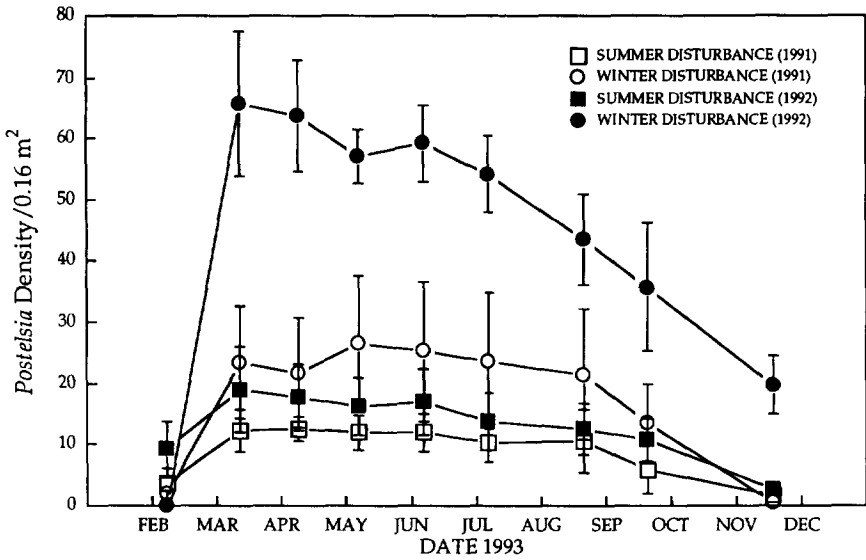


Fig. 2. Mean density of *Postelsia* (± 1 S.E.M.) in each of the treatment plots in the second year, 1993, of the mussel removal experiment. Multiple comparisons, based on a repeated measures analysis of variance, were done within each month from March to September when *Postelsia* were at peak densities. * = significance at $p < 0.05$, ** = significance at $p < 0.01$.

cleaner to the rock in winter greatly reduced, but did not eliminate *Postelsia* recruitment in spring.

4. Discussion

The wave-exposed rocky intertidal shores of the Pacific Northwest are characterized by intense competition for space (Connell, 1961; Paine, 1966; Paine, 1974; Dayton, 1971; Paine and Levin, 1981). Sea palms that live in wave-exposed areas where *Mytilus* is present rely on some degree of disturbance to remove mussels and renew bare space on the rock (Dayton, 1973; Paine, 1979; Paine, 1988). The results of the mussel clearing experiments presented in this study show that *Postelsia* can settle on and survive on mussels, but do so only at very low densities. Dayton (1973) proposed the following mechanisms for the lack of *Postelsia* recruitment on *Mytilus*: (1) filtration and ingestion



EFFECT OF:	MAR	APR	MAY	JUN	JUL	AUG	SEP
BETWEEN YEARS (WINTER) (○ VS ●)	NS	*	*	*	*	NS	NS
BETWEEN YEARS (SUMMER) (□ VS ■)	NS	NS	NS	NS	NS	NS	NS
SEASON WITHIN YEARS (1991) (○ VS □)	NS	NS	NS	NS	NS	NS	NS
SEASON WITHIN YEARS (1992) (● VS ■)	*	*	**	*	*	**	NS

Fig. 3. Mean densities of *Postelsia* (\pm S.E.M.) in 1993, in both the winter and summer mussel removal treatments, from disturbances initiated in the first year, 1991 (represented as open symbols), and the second year, 1992 (represented as closed symbols).

Table 2

Repeated measures ANOVA of the effect, in 1993, of the disturbance regime (treatment) and sampling date, on *Postelsia* density (log transformed), in both the 1991 and 1992 winter and summer disturbance plots

	df	MS	F-Ratio	p
Between Subjects				
Treatment	3	17.123	2.919	0.078
Error	12	5.866		
Within Subjects				
Date	6	1.403	9.166	<0.001
Treatment \times Date	18	0.096	0.626	0.868
Error	72	0.153		
Multivariate repeated measures analysis				
	df	Wilks' Lamba	F-Ratio	p
Date	6, 7	0.222	4.078	0.044
Treatment \times Date	18, 20	0.431	0.390	0.975

of algal spores by *Mytilus*; (2) mortality of spores and gametophytes due to siltation and grinding between the shells of adjacent mussels; (3) chemical antibiosis of *Mytilus* on *Postelsia*; (4) a grazing effect of the limpets occurring on the *Mytilus* valves. As in Dayton (1973), it is not convincing that any of these mechanisms alone can explain the observed patterns of low recruitment of *Postelsia* on *Mytilus*. The fourth mechanism (grazing effects of limpets residing on the *Mytilus* valves) probably holds the most merit. Two common Oregon limpet species, *Lottia digitalis* and *Lottia pelta*, both occur at high densities on the valves of *Mytilus*. *Lottia pelta* residing within *Postelsia* patches have been shown (through gut analysis) to consume large quantities of *Postelsia* relative to the amounts of other available algae (Craig, 1968). *Lottia pelta* are known to have significant negative effects on *Postelsia* densities, particularly at the gametophyte and young sporophyte stages, when these plants can be entirely consumed by limpets (Blanchette, 1994).

An additional mechanism could explain not only the low level of *Postelsia* recruitment to *Mytilus* valves, but also the intriguing results in Dayton's (Dayton, 1973) experiments where *Postelsia* sporophytes suddenly appeared at sites in mid summer, immediately following an early summer mussel removal. It is hypothesized that the majority of *Postelsia* spores released by adult sporophytes dribble down through the interstices between neighboring mussels and settle on the rock beneath the mussel bed. Only a minority of the spores adhere permanently to the valves of *Mytilus*. Of those spores that settle on *Mytilus* valves (and/or gametophytes and sporophytes that form from these spores), some are probably consumed by limpets, some are probably killed by desiccation and high temperatures on the black, quick heating valves of *Mytilus* and some survive and appear as young sporophytes in the following spring. On the other hand, spores that settle beneath the mussel bed and survive to the gametophyte stage may overwinter and reproduce more successfully in this dark, cool environment. Later, disturbances which remove areas of mussel beds in winter allow light penetration to the resting spores and/or gametophytes, perhaps triggering spore germination, gametogenesis or the growth of the young sporophytes. Rapid *Postelsia* growth in early spring would then occur before other algal or invertebrate species could become established and monopolize the newly created patches.

The idea that mussels and macroalgae may coexist in mid-intertidal habitats in a complex matrix of interactions has been explored by Santelices and Martinez (1988). They found that the Chilean mussel, *Perumytilus purpuratus* was an important consumer of algal spores, but that beds of this mussel could protect algal germlings from desiccation, affect their patterns of settlement and even fertilize the growing thalli.

Spore germination in many algal species is a seasonal phenomenon and several different ecological factors seem to be involved in germination (see Santelices, 1990 and Brawley and Johnson, 1992 for reviews). Several properties of light such as photoperiod, spectral quality and irradiance levels may affect gametogenesis in seaweeds, though elevated irradiance or direct exposure to sunlight may be generally damaging or lethal (Jones, 1959; Burns and Mathieson, 1972). Blue light is necessary for gametogenesis in some kelps (Luning and Dring, 1972) and irradiance levels must exceed certain thresholds in *Desmarestia* (Chapman and Burrows, 1970) and many laminarians (Luning and Neushul, 1978; Luning, 1980; Deysher and Dean, 1984; Deysher and Dean, 1986;

Novaczek, 1984). Nutrient levels may have some effect on gametogenesis and it is known that nitrogen is required for gametogenesis in *Laminaria* (Hsiao and Druehl, 1973). Gamete release also commonly occurs following a change in irradiance (Hollenberg, 1935; Smith, 1947; Muller et al., 1985). *Laminaria* release gametes within a few minutes of the beginning of the dark cycle when gametophytes are grown in the laboratory (Tseng et al., 1959; Luning, 1980). Most studies on the effect of illumination on gamete release have been done in the laboratory and little is known of the factors important to algal reproductive events in the field.

Although spore germination usually takes place soon after attachment in most macroalgae (Fletcher and Callow, 1992), dormancy may occur after initial settlement, as in the brown alga *Dictyota* (Richardson, 1979). The possibility of persistence as a microscopic form with suspended growth is generally recognized as an adaptation of the algae to survive conditions stressful for the macroscopic thallus (Santelices, 1990). This hypothesis has been tested in the young and microscopic stages of Laminariales. In the field, these large kelps frequently shade their own recruits. Measurements of light intensities in subtidal *Macrocystis* (Clendenning, 1961) and *Laminaria* (Kain, 1966, Smith, 1967) forests have found intensity values far below the optimum required for active growth of young sporophytes. Anderson and North (1969) concluded that bottom light intensities could be limiting for growth about 50% of the time, although these low light levels apparently did not prevent kelp establishment. Presumably, rapid growth of microscopic stages would quickly follow an increase in ambient light. In *Desmarestia aculeate* the development of microscopic gametophytes produced in winter is suspended until spring when the light irradiance increases (Chapman and Burrows, 1970). In other algae, the duration of suspended growth can vary from a few days to several months. Schonbeck and Norton (1980) reported finding viable microscopic *Pelvetia* germlings beneath adult stands of the same species 8 months after the end of the fertile season.

Dayton's (Dayton, 1973) removal experiment, conducted in late spring/early summer in areas close to existing *Postelsia* patches, resulted in the apparent recruitment of large densities of *Postelsia* in mid-summer. Since only some *Postelsia* have reached reproductive sizes by late spring, it seems unlikely that these few reproductive plants would be able to fully seed the experimental plots. In addition, the spores released in these plots would have to complete the entire heteromorphic life history (i.e., go from spores to gametophytes to sporophytes) in a matter of weeks. It seems more likely that gametophytes and young sporophytes already present beneath the mussel bed (derived from the previous summer's generation of reproductive sporophytes) grew quickly to visible sizes following the removal of the overlying mussel layer.

Results of the mussel clearing experiment at SPDB support this explanation. Young sporophytes appeared in plots in February, following the removal of mussels overlying these plots in winter, when there were no remaining reproductive sporophytes at the site to seed the recently disturbed areas. Plots cleared of mussels in winter (the time of year when most natural disturbances occur) had the highest densities of *Postelsia* in the following spring (Fig. 1 and Fig. 2). Plots cleared of mussels in mid/late summer made bare space available at a time when older *Postelsia* were reproductively mature. These plots had significantly higher densities of *Postelsia* in the following year than undisturbed plots, but had significantly lower *Postelsia* densities than plots disturbed in

winter (Fig. 1 and Fig. 2). Also, plots that were cleared of mussels in the most recent winter had higher *Postelsia* densities than plots cleared in previous summers and winters (Fig. 3). This result suggests that the overlying cover of mussels had a protective effect on young *Postelsia*. There are two possible mechanisms for this protective effect: (1) the environment under the mussel bed is dark and cool and the probability of desiccation during periods of daytime tidal exposure is low. Gametophytes or spores that are in open plots in late summer are exposed to the potentially adverse effects of the sun (heating, ultraviolet radiation, desiccation). (2) Limpets are relatively common on open surfaces in the *Postelsia/Mytilus* zone during most of the year, particularly in fall, and while limpets are common on shells of *Mytilus*, they are relatively uncommon on the rock beneath the mussel bed (personal observation). Thus, the layer of rock beneath the mussel bed may act as a refuge from physical stress, grazing or both. Santelices and Martinez (1988) submit that enhanced algal growth beneath mussels in their experiments in Chile may result not only from protection from desiccation, but also from the fertilization effects of the fecal materials ejected by mussels.

Contrary to the conclusions of Dayton (1973) that *Mytilus* exerts a strong negative influence on recruitment of *Postelsia*, *Mytilus* may actually enhance recruitment of *Postelsia* in areas that are subject to frequent disturbance, but negatively affect subsequent growth in the absence of disturbance. Therefore *Mytilus* can have a positive effect on *Postelsia*.

It is unclear why no *Postelsia* sporophytes were seen in the summer disturbance plots in the late summer/fall immediately following the clearing. The summer disturbances were purposely created when most of the adult plants surrounding these plots were reproductive. However, the timing of this manipulation may have been too late in the season to stimulate germination of plants beneath the mussel bed.

The presence of *Postelsia* in plots that were sterilized (by scraping, chiseling and oven cleaner application) suggests that the spores/gametophytes of *Postelsia*: (1) are extremely hardy, (2) can actually bore into the rock, (3) can disperse at the spore or gametophyte stage, or (4) are partly resistant to the sterilization technique. While it is convincing that the plants are extremely hardy at this stage, it is also convincing that there is some secondary dispersal at either the spore or gametophyte stage, or both. Spores of brown algae are mobile (spores of brown algae are also referred to as zoospores), and it is unknown how long they can persist before germination to the gametophyte stage. Reed et al. (1992) found that spores of both *Macrocystis pyrifera* and *Pterygophora californica* could not swim for longer than 120 h, but though they were no longer actively swimming, they retained their capacity to produce viable sporophyte recruits.

Syngamy (fertilization) requires that male gametophytes release sperm to fertilize female gametophytes and it is unknown how far the sperm of male gametophytes can travel. If the sterilization technique in this experiment was effective but the gametophytes can disperse, than both the male and female gametophytes must be capable of movement at this stage. In kelp, the female gametophyte is typically sessile and is fertilized by motile sperm (van der Meer and Todd, 1980). Dispersal at the spore, gamete, gametophyte and/or sporophyte may also occur via animal vectors. Algal spores have been observed on the legs and shells of amphipods and other invertebrates and

some invertebrates consume the reproductive tissue of algae, sometimes preferentially (Buschman and Bravo, 1990; Santelices, 1990). Spores can survive passage through the digestive tract of some invertebrates such as limpets and several species of algae have been successfully cultured from fecal pellets (Santelices and Paya, 1989). Thus, although sporophytic *Postelsia* are limited in their spore dispersal capabilities to only a few meters (Dayton, 1973) there may be some secondary dispersal at the gamete/gametophyte stage or via animal vectors, although this secondary dispersal is probably not ecologically significant in terms of *Postelsia*'s long term population persistence.

5. Conclusion

The annual life history of *Postelsia* seems ideally suited to life in a seasonally disturbed environment. Patches in mussel beds that are disturbed by wave action in the winter have the highest recruitment of *Postelsia* in the following spring, presumably because the sea palm propagules can survive beneath the mussel bed in fall and are somehow stimulated to germinate and grow following the occurrence of a winter disturbance. Although mussels are superior space competitors and preclude primary space, they can have positive effects on the survival of microscopic *Postelsia* and enhance subsequent *Postelsia* recruitment at sites subject to frequent winter disturbance.

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